



















7  
16

2

506.73  
W7W63

58740  
Smith

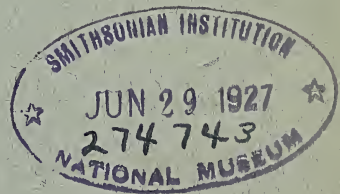
TRANSACTIONS  
 OF THE  
 WISCONSIN ACADEMY  
 OF  
 SCIENCES, ARTS AND LETTERS

35

VOL. XXI.



NATURAE SPECIES RATIOQUE



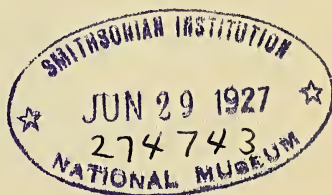
MADISON, WISCONSIN

1924

Volume XXI of the Transactions of the Wisconsin Academy of Sciences, Arts, and Letters is issued under the editorial supervision of the Secretary.

CHANCEY JUDAY,  
Secretary.

TRANSACTIONS  
OF THE  
WISCONSIN ACADEMY  
OF  
SCIENCES, ARTS AND LETTERS  
VOL. XXI.



MADISON, WISCONSIN  
1924



# CONTENTS

---

	Page
The Unification of South Africa: A Study in British Colonial Policy. PAUL KNAPLUND.....	1
The Removal of the Winnebago. LOUISE PHELPS KELLOGG...	23
Augustine of Hippo <i>qua</i> Patriot. ROBERT K. RICHARDSON...	31
Milton as a Writer on Education. OLIVER M. AINSWORTH...	41
Floundering in Modernity. GEORGE C. CLANCY.....	51
Bibliographical Evidence of the Vogue of Shaftesbury in the Eighteenth Century. WILLIAM E. ALDERMAN.....	57
Notes on New Names in Table of Formations and on Physical Evidence of Breaks between Paleozoic Systems in Wisconsin. (With two Figures) E. O. ULRICH.....	71
The Fauna of the Lake Winnebago Region. (With one Figure.) FRANK COLLINS BAKER.....	109
Observations on Parasitic Worms from Wisconsin Fishes. (With Plates I-III.) A. S. PEARSE.....	147
The Parasites of Lake Fishes. A. S. PEARSE.....	161
The Anatomy of <i>Troctes divinatorius</i> Muell. (With Plates IV-VI.) RUTH CHASE NOLAND.....	195
<i>Arrhenuri</i> from Washington and Alaska. (With Plates VII and VIII.) RUTH MARSHALL.....	213
New and Corrected Names of Certain Milk Bacteria. W. D. FROST and RUTH CHASE NOLAND.....	219
The Characteristics of Certain Fecal Bacteria as Shown by the Little Plate Method. (With Plate IX.) OLA E. JOHNSTON and WILLIAM D. FROST.....	223
On the Nature of Disease Resistance in Plants. J. C. WALKER	225
Some Ferns of Southwestern Wisconsin. SISTER M. ELLEN..	249
Notes on Parasitic Fungi in Wisconsin, IX. (With four Figures.) J. J. DAVIS.....	251
Notes on Parasitic Fungi in Wisconsin, X. (With two Figures.) J. J. DAVIS.....	271

	Page
Notes on Parasitic Fungi in Wisconsin, XI. (With two Figures.) J. J. DAVIS.....	287
The Cytology and Physiology of <i>Venturia inequalis</i> (Cooke) Winter. (With Plates X and XI.) CHARLES N. FREY..	303
Cytological Studies of <i>Taphrina coryli</i> Nishida on <i>Corylus americana</i> . (With Plates XII and XIII.) ELLA MAY MARTIN .....	345
The Structure and Behavior of the Nucleus in the Life History of <i>Phycomyces nitens</i> (Agardh) Kunze and <i>Rhizopus nigricans</i> Ehrbg. (With Plates XIV and XV.) E. A. BAIRD.....	357
A Quantitative Study of the Larger Aquatic Plants of Green Lake, Wisconsin. (With seven Figures.) H. W. RICKETT	381
The Rotifer Fauna of Wisconsin, II. A Revision of the Nottomatid Rotifers, Exclusive of the Dicranophorinae. (With Plates XVI-XLIII.) H. K. HARRING and F. J. MYERS .....	415
Proceedings of the Academy, 1921 to 1923.....	551

## THE UNIFICATION OF SOUTH AFRICA: A STUDY IN BRITISH COLONIAL POLICY

PAUL KNAPLUND

---

By a treaty with the Netherlands of August 13, 1814, Britain obtained permanent possession of the Cape of Good Hope.<sup>1</sup> At this time the white population of the new dependency consisted almost exclusively of descendants of the Dutch and of Huguenots brought there during the latter half of the seventeenth century by the Dutch East India Company. The settlements were small and centered largely around Table Bay. Little effort had been made to trace the northern boundary of the colony. Few realized then the agricultural possibilities of the great veld of the interior and none suspected the existence there of fabulous treasures in gold and precious stones. The Cape was valued as a convenient half-way station on the road to India. Isolated, the colony enjoyed almost complete immunity from foreign attacks. No European power had possessions within a wide radius from it; and the nearest, the neglected Portuguese colony of Mozambique, belonged to a friendly and allied state. Britain had no rival on the sub-continent.

During the last years of the Dutch occupation the Boers had been restive. Lessons of the American and of the French revolutions were not lost on a frontier community kept under the paternalistic management of a trading company. When Britain secured control, the political situation changed for the worse. The burghers lost whatever share they formerly had possessed in their own administration, and for more than a decade the English governor ruled with all the power of an autocrat.<sup>2</sup> Discontent with this regime soon manifested itself, and it grew in strength with the arrival of about 2,000 English settlers in the eastern provinces of the colony. The newcomers clamored for their rights as Englishmen and soon the imperial government, somewhat grudgingly,

<sup>1</sup> For the text of this treaty see G. W. Eybers, *Select Constitutional Documents Illustrating South African History 1795-1910* (London, 1918), pp. 19-23.

<sup>2</sup> G. E. Cory, *The Rise of South Africa* (4 Vols., London, 1910- . . . ), I, pp. 62, 63; II, pp. 240, 241.

conceded to the colonists a small share in the management of local affairs.<sup>3</sup>

Less salutary was, however, the cleavage which the coming of a new racial element created between the eastern portion and the older settlements in the west. Sectional strife looms large in the subsequent history of the Cape.<sup>4</sup> That the government seized upon the arrival of "very numerous British born subjects" as a pretext for attempts at suppressing the Dutch language must be considered even more disastrous. The Boers were to be denationalized by employing Britons, especially Scots, "in the parochial duties of the Reformed Religion"; and a decree of 1825 provided that after a given period "the English Language shall be exclusively used in all judicial and official Acts".<sup>5</sup> Although a later proclamation modified this decision,<sup>6</sup> the failure to place the two languages on an equal footing added fuel to the flame of discontent. And the subsequent abolition of slavery created, in the opinion of many Boers, an intolerable situation.<sup>7</sup>

Beginning in 1836 a large number of the most enterprising among the Dutch migrated or "trekked" in search for new homes. Actuated by one great desire, to be freed from British control, they pushed courageously into the wilderness. This object proved, however, difficult to obtain. No sooner did the Boers settle in Natal than Britain annexed the province. When they crossed the Orange and established themselves between this river and the Vaal, the Queen's sovereignty was proclaimed also over this territory.<sup>8</sup> But the more persistent among the malcontents crossed the Vaal and continued their quest for freedom. Faced with the possibility of having to extend their possessions to the equator in order to retain a handful of recalcitrant subjects, the British government finally decided to let them go.

<sup>3</sup> A proclamation of May 2, 1825, provided for the appointment of a council "to advise and assist in the administration" of the colony. This consisted, however, wholly of officials and not until 1852 was a representative government established. Eybers, *Constitutional Documents*, pp. 24, 45-55.

<sup>4</sup> In 1836 a separate district government was established in the eastern provinces; *ibid.*, pp. 39-41.

<sup>5</sup> *Ibid.*, pp. 23, 24. This proclamation was issued by the governor, Lord Somerset, and dated July 5, 1822.

<sup>6</sup> By ordinance of December 13, 1826; *ibid.*, p. 107. Not until 1882 did the Dutch secure equal language rights in the Cape parliament; *ibid.*, p. 66.

<sup>7</sup> A "Manifesto of the Emigrant Farmers" printed in the *Grahamstown Journal*, February 2, 1837, is given by Eybers, pp. 143-145. For additional declarations see *ibid.*, pp. 154, 155, 167-169.

<sup>8</sup> Several important documents dealing with these events are found in Eybers, *Constitutional Documents*, pp. 145-166; 260-275.



This step was in accordance with the views on colonial policy propounded by the leading economists of the period; but in taking it the colonial office seems to have been actuated more by a desire to solve pressing practical problems than by regards for abstract theories. With the growth of a sentiment favoring and the final adoption of free trade and with the repeal of the navigation acts many Englishmen considered the overseas dependencies a burden—a source of weakness and expense. Limitation rather than expansion of the boundaries of the empire became their slogan. Neither the governments nor the leading statesmen of the period formally accepted this doctrine, but it influenced the attitude of the public towards such questions as colonial defense. Since Waterloo a large portion of the British army had been kept in the colonies.<sup>10</sup> When, by the end of the forties, it was deemed necessary to strengthen the home defenses Parliament appeared unwilling to increase the army estimates; and the desired increase in the force stationed in the United Kingdom could be obtained only by withdrawing the outlying garrisons.

This was the opinion of Earl Grey, secretary of state for war and the colonies 1846–1852. He deplored the agitation of the “Little Englanders”, but he was deeply impressed with the views of the Duke of Wellington, and other eminent authorities, who warned England of the danger in neglecting to secure adequate protection for the British Isles. By recalling the scattered garrisons, already considered useless in case of war, a strong force could be created at the imperial base. Steam navigation which had increased the vulnerability of Britain also facilitated the sending of reinforcement to any dependency threatened by a foreign foe.<sup>11</sup>

In South Africa the presence of numerous warlike natives complicated the situation. Here the military expenditures were heavy and a further extension of British territory would necessitate an increase of the local force at a time when the troops were needed elsewhere. Therefore, quite apart from the problematic value of such new possessions, an expansionistic policy might tend to aid in

<sup>9</sup> A summary of these views is given by H. Duncan Hall, *The British Commonwealth of Nations* (London, 1920), pp. 39–53.

<sup>10</sup> For the opinions of leading British statesmen see debates in Parliament Jan. 16, 1838; April 13, May 29, June 12 and 30, 1840; February 8, April 19, and May 6, 1850. *Hansard*, 3rd series, XL, cols. 34–73; LIII, cols. 1063, 1064; LIV, cols. 731, 732, 1121, 1153; LV, cols. 239–245, 268, 269; OVIII, cols. 546–566, 606, 607, 1009; OX, cols. 565, 566, 578, 589, 1171, 1172. See also General Sir Robert Biddulph, *Lord Cardwell at the War Office* (London, 1904), pp. 38–41.

<sup>11</sup> Biddulph, *Lord Cardwell*, p. 39.

jeopardizing the safety of the whole empire. That Lord Grey had this under consideration appears certain, and it was he who decided to limit the empire's responsibilities on the sub-continent.<sup>12</sup> By the Sand River Convention of January 17, 1852, and the Bloemfontein Convention, two years later, the Boer settlements beyond the Vaal and those between the Orange and the Vaal respectively were cut adrift.<sup>13</sup> These agreements laid the foundations for the future republics. White South Africa became divided.

Hardly had this policy been adopted before protesting voices were heard.<sup>14</sup> The year of the latter of the two conventions witnessed the appearance of Sir George Grey as governor of the Cape and high commissioner for South Africa. Although still a young man, he had already served with distinction as governor of South Australia and of New Zealand.<sup>15</sup> In the latter colony he faced a native problem bearing some similarity to that of South Africa and had perceived serious danger in having foreign powers established in the neighborhood of a weak British colony.<sup>16</sup> Independent Boer republics might, indeed, likewise become potential rivals or enemies of Britain, while a union of all the white communities besides precluding this, would also enhance their safety.

Soon the able and energetic, but also proud and imperious, consul actively championed unification. In 1856 he inquired whether the government "might not be disposed to retrace the step which led to the abandonment of the Orange River Sovereignty"; and he advocated "a united South Africa under the British flag".<sup>17</sup> Although Henry Labouchere, then colonial secretary, declined to discuss the question Grey persisted in his efforts and received some encouragement both in South Africa and, later, from the home government. The Volksraad of the Orange Free State passed a

<sup>12</sup> *Hansard*, 3rd series, CXXXIII, cols. 72, 77.

<sup>13</sup> For the texts of these documents see "Reports on the Cape of Good Hope" in *British Parliamentary Papers*, hereafter cited P. P. 1853-54, Vol. III, Part I, pp. 36, 37; and Eybers, *Constitutional Documents*, pp. 281-285, 357-359.

<sup>14</sup> Inhabitants of the Orange River Sovereignty protested against the abandonment of the territory. Whether these protests represented the wishes of the majority is, of course, difficult to ascertain. See P.P. 1853-54, Vol. III, Pt. II, pp. 8-18, 21.

<sup>15</sup> No adequate biography of this remarkable man has yet been written. The two we have, G. C. Henderson, *Sir George Grey, Pioneer of Empire in Southern Lands* (London, 1907), and W. L. Rees and L. Rees, *The Life and Times of Sir George Grey* (2 vols., London, 1892), leave much to be desired.

<sup>16</sup> Grey urged in vain the annexation of various groups of islands in the South Pacific to forestall action of any other European power. Rees and Rees, *Sir George Grey*, I, pp. 128-132.

<sup>17</sup> Henderson, *Sir George Grey*, p. 168.

resolution favoring "a union or alliance with the Cape Colony",<sup>18</sup> and in September, 1858, Sir E. Bulwer Lytton invited Grey to give his opinion on the question of federating the South African colonies. Replying in a dispatch of November 19th, the high Commissioner urged consolidation of all the European communities and suggested that the government should take the initiative by securing the passage of an enabling act. In doing this Grey doubtless went further than Lytton had originally intended him to go. The considerations of imperial interests which had made the previous withdrawal desirable were opposed to the forward policy suggested by the zealous governor. In his eagerness to promote the cause of union Grey disobeyed orders and was recalled. While the colonial office later cancelled this recall, the attitude towards federation remained unchanged. Disappointed, the governor voiced his fear that "the opportunity of establishing such a federation as I had proposed has now been lost forever."<sup>19</sup>

Two events of the succeeding decade deeply influenced Britain's colonial relations and caused the imperial statesmen to modify their views regarding a South African union. The first of these, the withdrawing of the garrisons from the self-governing colonies, took place largely because it was deemed necessary to strengthen the home defenses without increasing the burden on the British taxpayers. The wishes of the colonies were completely disregarded.<sup>20</sup> On the other hand, the second, the establishment of the Dominion of Canada, was the result of a movement which originated in British North America and received the hearty support of the colonial office "on the ground, among others, that [federation] was eminently calculated to render easier and more effectual the provisions for the defence of the several Provinces."<sup>21</sup>

Once having accepted the principle of colonial federation the home government showed considerable zeal in attempting to secure a wide application for it. The Leeward Islands were federated according to a plan prepared by Governor Sir B. C. C. Pine. In this instance the impetus came from home. The Gladstone government seem to have entertained hopes that consolidation would ulti-

<sup>18</sup> G. McCall Theal, *The History of South Africa Since 1795* (5 Vols., London, 1908), III, p. 175.

<sup>19</sup> Despatch of July 31, 1859, P.P. 1860, Vol. XLV No. 357, p. 1. For the text of Sir George Grey's confederation despatch see Frank R. Cana, *South Africa from the Great Trek to the Union* (London, 1909), pp. 298-309.

<sup>20</sup> See Paul Knaplund "Intra-Imperial Aspects of Britain's Defence Question" in *The Canadian Historical Review*, III, pp. 120-125.

<sup>21</sup> Cardwell to Arthur Gordon, April 12, 1865, P.P. 1867, XLVIII, ed. 3769, p. 117.

mately lessen the charge upon the imperial exchequer. The islanders manifested little enthusiasm although they complied with the wishes of the colonial office and accepted the governor's scheme.<sup>22</sup>

A similar method of procedure was adopted in dealing with the South African situation. Frequent complaints had been made of the heavy military expenditures at the Cape, nor did the representative system of government, established in 1852, function properly. A change was deemed necessary, especially one which would enable or induce the colonies to assume greater responsibility for local defense.<sup>23</sup> In his instructions to the newly appointed governor and high commissioner, Sir Henry Barkly, Lord Kimberley discussed the various problems of the colony and called attention to the success of the Canadian federation.<sup>24</sup> This the former interpreted as clothing a desire to have a similar change effected in South Africa. Immediately upon assuming the duties of his offices Barkly, therefore, took steps toward the establishment of a federal state. Disregarding the protest of the Cape executive council he appointed a commission to consider the advisability of dividing the colony into three or more provinces and with these form a federation which might ultimately embrace all of white South Africa.<sup>25</sup>

Lord Kimberley approved. In a despatch of Nov. 16, 1871, he authorized Barkly "to sanction the convening of Delegates from [the Boer republics] and Natal for the purpose of considering the conditions of a Union". Hopes were also expressed that such a union, if established, would assume the responsibility for defense.<sup>26</sup> The policy was endorsed by the House of Commons,<sup>27</sup> but South Africa remained indifferent. Only the diamond diggers of Griqualand West supported federation.<sup>28</sup> A strong majority at the Cape

<sup>22</sup> P.P. 1871, XLVIII, cd. 353.

<sup>23</sup> Granville to Governor Sir P. E. Wodehouse, Dec. 9, 1869. P.P. 1871, XLVII, cd. 459, pp. 13-15. See also Kimberley to Sir Henry Barkly, Nov. 17, 1870; *ibid.*, p. 66.

<sup>24</sup> Kimberley to Barkly, Oct. 17, 1870; *ibid.*, p. 47.

<sup>25</sup> *Ibid.*, pp. 170, 171 "We . . . record our conviction that . . . the attempt to federate upon any satisfactory basis the eastern and western provinces of this Colony—the Basutos and adjacent native territories—including the Diamond-fields, the two Boer republics, and Natal, or indeed, any two or more of them, will present the very greatest, if not insuperable difficulties; and we fail to see the practical object or advantages of any such federation in the absence of that external pressure and rivalry of a powerful adjacent nation, which has had the chief share in effecting the consolidation of the Dominion of Canada." Minute of the colonial secretary, treasurer general, auditor general, and collector of customs, April 26, 1871; *ibid.*, p. 180. See also P.P. 1872, XLIII, cd. 508, p. 11.

<sup>26</sup> *Ibid.*, cd. 508, p. 14.

<sup>27</sup> *Hansard*, 3rd series, CCXI, cols. 806-815. Debate May 28, 1871.

<sup>28</sup> P.P., 1873, XLIX, cd. 732, p. 121. The address is dated August 28, 1872. It should be remembered, however, that Griqualand West was under the crown colony form of government which would naturally prove distasteful to the miners, the majority of whom were Englishmen.

resented the recognition afforded the separatist tendencies in the eastern provinces and especially a suggestion for moving the capital.<sup>29</sup> By annexing the diamond fields, claimed by the Orange Free State, Britain had antagonized the Boer republics.<sup>30</sup> Voluntarily these would not surrender their independence in exchange for a colonial status. Lacking the most essential elements for success, popular support, the Barkly-Kimberley attempts at federation accomplished nothing.

This failure might have taught British statesmen how to proceed if they desired to establish a South African union, but it did not. Lord Kimberley's Conservative successor, the Earl of Carnarvon, who had had the good fortune of steering the British North American Act through Parliament, erred even more egregiously. Deeply impressed with the success of the Canadian experiment, he was determined to confer the boon of federation upon South Africa even to the extent of imposing it upon the colonies. In dealing with this question the noble earl, who as a statesman possessed many admirable qualities, reminds one of the hero in Runeberg's poem "Sven Dufva", his heart was sound, but his head was rather weak.

At first Carnarvon seems to have recognized the necessity of securing public approval for his cherished plan. In 1875 he proposed to call a conference at some place in South Africa which should discuss native policy, the enforcement of criminal law, and federation. Probably fearful lest the frontiersmen should not know how to proceed, he also suggested how the delegates should be distributed and chosen and repeated the blunder of his predecessor in recognizing the sectional interests at the Cape.<sup>31</sup> When the colonists appeared lukewarm<sup>32</sup> Carnarvon sent James Anthony Froude, the historian, to South Africa as his personal representative. The choice proved singularly unfortunate. While touring

<sup>29</sup> *Ibid.*, pp. 43, 44.

<sup>30</sup> P. A. Molteno, *The Life and Times of Sir John Charles Molteno* (2 vols. London, 1900), I, pp. 185, 186. When the Cape Colony received responsible government President Burgers of the South African Republic, in a letter of December 27, 1872, congratulating the first prime minister, J. C. Molteno, on the occasion, said: "I am confident that it will direct the spirit of the nation in that proper channel which will ultimately lead to a closer union between the different colonies and states of South Africa." *Ibid.*, p. 202. A little more generosity on the part of the imperial government would have smoothed the way for the desired federation.

<sup>31</sup> See despatch, Carnarvon to Barkly, May 4, 1875. P.P., 1875, LII, cd. 1244, pp. 1-3.

<sup>32</sup> *Ibid.*, 1876, LII, cd. 1399, pp. 4, 5; *Life of Molteno*, I, pp. 335, 336, 346: Unqualified support was received from Natal and Griqualand West, P.P., 1876, LII, cd. 1399, pp. 19, 25, 55.

the Cape Colony, Froude, in the words of a competent observer, violated "publicly and preserveringly a constitutional obligation which the Colonists have a right to view as one of the essential safeguards of constitutional right."<sup>33</sup> This emissary of the colonial secretary virtually carried on a campaign against the ministry at the Cape.<sup>34</sup> By appealing to the particularism in the eastern provinces, he could truthfully report enthusiastic receptions; but these appeals also increased the suspicion with which the majority viewed his agitation and the cause he was supposed to further.<sup>35</sup>

Despite, or rather partly because of, Froude's activities, Lord Carnarvon finally realized that the desired conference would not meet in South Africa. He then decided to hold it in London. On August 3, 1876, representatives of South Africa met at the colonial office. Only those from Natal had been duly elected, the others were officials chosen by Carnarvon. J. C. Molteno, the prime minister at the Cape, was in London but refused to attend, deeming himself bound by the defeat of the federation project in the colonial legislature; and President Brand of the Orange Free State attended only after he had received definite assurances that there would be no serious "discussion of the merits of South African Confederation."<sup>36</sup> Under such conditions the conference could hardly be expected to achieve anything.

Carnarvon showed, however, a remarkable, although misplaced, perseverance. Encouraged by Messrs. Blaine and Paterson from the eastern provinces where the belief prevailed that confederation would bring them local anatomy, the colonial secretary announced, October 26, 1876, that in his opinion the time was now ripe for the drafting of a permissive bill.<sup>37</sup> Shortly afterwards a *Draft Bill*, which was in reality a complete constitution, was transmitted to

<sup>33</sup> Lord Blachford, "Native Policy in South Africa" in *The Edinburgh Review*, April, 1877, OXLV, pp. 232, 233. See also *Letters of Lord Blachford*, edited by G. E. Marindin (London, 1896), p. 364. Lord Blachford had served as permanent under-secretary of state for the colonies, 1860-1871.

<sup>34</sup> *Life of Molteno*, I, pp. 400, 401.

<sup>35</sup> On December 24, 1875, Froude declared hopefully, "The ministers of the Cape Colony have the appearance of victory, but we have the substance." John Skelton, *The Table-Talk of Shirley* (London, 1895), p. 153. He had run but not read.

<sup>36</sup> Present at the conference were Lord Carnarvon, Sir Garnet Wolseley, Sir Theophilus Shepstone and Messrs. Froude, Akerman, and Robinson. See P.P., 1876, LII, cd. 1631, pp. 51, 52. In a communication to Lord Carnarvon, dated October 2, 1876, Molteno expressed the opinion that a South African consolidation must assume the form of a legislative union. See *ibid.*, p. 11.

<sup>37</sup> *Ibid.*, 1877, LX, cd. 1732, pp. 13, 14. See also Herbert Paul, *The Life of Froude* (New York, 1905), p. 269.

Sir Henry Barkly to be presented before the people of South Africa.<sup>38</sup>

It met a fate similar to that of the proposal for a conference. The Cape saw in it another attempt to govern the colonies from Downing Street; Natal was dissatisfied; and even the high commissioner subjected the measure to severe criticism. In the republics the reception appeared decidedly hostile. The Orange Free State could not "accede to a union by which this State would sacrifice its independence"; and the Volksraad of the South African Republic rejected the bill.<sup>39</sup>

Suspecting Barkly of being too much under the influence of the Cape ministry Lord Carnarvon replaced him with Sir Bartle Frere, who received definite instructions to obtain a confederation of the various colonies and states.<sup>40</sup> To further this the Transvaal was annexed,<sup>41</sup> and the amended *Draft Bill* was introduced in Parliament, where it met with general approval, and upon receiving the Queen's assent it became the *South African Act, 1877*.<sup>42</sup>

All in vain. Natal favored the convening of a conference to discuss the question, but the Cape legislature remained obdurate. The annexation of the Transvaal had increased the hostility with which the Dutch, both in the English colonies and in the Orange Free State, regarded this purely English project.<sup>43</sup> With the uprising in and the retrocession of the Transvaal the cause of confederation became entirely hopeless. In August, 1882, the *South African Act* expired.

Lord Carnarvon's persistent attempt at federating the sub-continent throws interesting sidelights upon Britain's attitude towards the dependencies and upon the colonial policy of Disraeli's Ministry. One discerns a tendency to revive the paternalistic methods of "Mr. Mother Country" of the pre-Durham-Buller period and, in addition, a certain un-English faith in legal formulæ. Federation had triumphed in Germany and proved beneficial to Canada, therefore it ought to be adopted in South Africa.

<sup>38</sup> Carnarvon to Barkly, Dec. 14, 1876. P.P., 1877, LX, cd. 1732, pp. 20-29.

<sup>39</sup> *Ibid.*, pp. 32-36, 41-43; 1878, LV, cd. 1980, pp. 7-9, 18; Cana, *South Africa*, p. 80.

<sup>40</sup> Frere was in the opinion of Carnarvon, "The statesman . . . most capable of carrying my scheme of confederation into effect . . ." Carnarvon to Frere, Oct. 13, 1876. John Martineau, *The Life and Correspondence of the Right Honourable Sir Bartle Frere* (2 Vols., London, 1895), II, p. 162.

<sup>41</sup> J. A. Froude, *Oceana* (London, 1886), p. 53.

<sup>42</sup> P.P., 1877, VI, "House of Lords Bill. 271." For the changes in the original *Draft Bill* see *ibid.*, XLX, cd. 1732, pp. 43-52.

<sup>43</sup> *Life of Molteno*, II, pp. 364, 427, 428.

Few efforts were made to ascertain whether the conditions there were similar to those which had made the Canadian federation inevitable and, above all, whether the people concerned really desired consolidation in any form. The powerful social and economic factors which proved so potent thirty years later in creating a sentiment in favor of union were largely non-existent in the seventies. At this time even the most tactful of colonial secretaries would probably have failed in an endeavor to create a federation.

Several of those who had been responsible for these early attempts finally realized that a different method of procedure would be necessary in order to achieve success. Sir Bartle Frere, in writing to Sir George Colley, August 26, 1880, said: "One great mistake hitherto seems to me to have been trying to hasten and push on what can only result from natural growth, which must of necessity be tardy if it is to be enduring."<sup>44</sup> Lord Kimberley, upon resuming the duties of the colonial office, instructed Frere's successor, Sir Hercules Robinson, to work for federation but added, "It will be more convenient that any fresh movement for federation or union should be initiated spontaneously by the Colonies."<sup>45</sup> Froude, who had sinned grievously, also saw the light. Commenting on the South African confederation effort in his *Oceana*, he says: "If South Africa is to rule itself under a constitutional system, we must cease to impose English views of what is expedient on a people unwilling to act upon them."<sup>46</sup> And this became the established policy of the home government.

During the eighties and the nineties the Transvaal drifted politically farther and farther away from British connections. The London convention of 1884 increased the degree of independence enjoyed by the republic, but did not accomplish a complete reconciliation. Boers and Britons continued to regard each other with a suspicion which increased when the latter blocked all efforts on the part of the South African Republic to secure an outlet to the sea or to expand into the interior.

Powerful centripetal forces came into existence, however, with the discovery and opening up of the great Witwaters Rand gold mines. This region became the economic center of South Africa. It provided a market for the produce of the colonies and states,

<sup>44</sup> Martineau, *Life of Sir Bartle Frere*, II, p. 387.

<sup>45</sup> P.P., 1881, LXVI, cd. 2754, p. 4.

<sup>46</sup> J. A. Froude, *Oceana*, pp. 59, 60.



proved enormously important for the commercial and shipping interests of the coast towns, and stimulated the construction of railroads which converged on the Rand. Needs arose for adjusting railway rates and customs duties; and the Cape Colony, Natal, and the Orange Free State formed a customs union.<sup>47</sup> The Transvaal kept aloof, rather sullenly. With the construction of a railway to Delagoa Bay, in the Portugese territory, this republic became practically independent of the Cape and the Natal ports and showed little inclination to make sacrifices for the benefit of its neighbors. These, on the other hand, faced serious losses both among private concerns and especially for the state owned railways which had been built primarily for the purpose of securing the Rand traffic. A conflict of economic interest ensued which had a disturbing influence in South Africa and affected adversely the attitude of British imperialists to the Transvaal.

In the period between the collapse of Carnarvon's effort and the outbreak of the Boer war, several organizations kept the federation issue before the people of South Africa. Prominent among these was the Afrikander Bond which aimed at "the formation of a South African nationality."<sup>48</sup> Founded by Boers, the Bond at first gave a narrow interpretation of the term "nationality" and often opposed Boer as Boer to Englishman as Englishman. Later its vision broadened, and in 1896 it was described as "an organization which draws together and unites for common purposes a number of the early colonists and others holding certain views on social and political matters."<sup>49</sup> Other bodies, such as the South African Political Organization and the South African League, openly advocated union of all the whites.<sup>50</sup>

<sup>47</sup> *Cana South, Africa*, pp. 138, 139. *The Times* expressed the hope, Nov. 9, 1891, that practical necessity for concerted action would overcome the existing prejudices and bring about union. British officials also voiced the need of a common policy in despatches to the colonial office. P.P., 1890, XLVIII, cd. 5897, pp. 4, 5.

<sup>48</sup> Sir Lewis Mitchell, *The Life and Times of the Right Honourable Cecil John Rhodes* (2 vols., London, 1910), I, pp. 293, 294. See also Basil Williams, *Cecil Rhodes* (London, 1921), pp. 60, 61.

<sup>49</sup> Olive Schreiner and C. S. Cronwright Schreiner, *The Political Situation* (London 1896), p. 24; Williams, *Cecil Rhodes*, p. 67.

<sup>50</sup> *The Times*, Sept. 7, 1896. Nor had the imperial government given up all hopes for such a union. The colonial secretary, the Marquess of Ripon, said, Sept. 5, 1894: "What I look to is a sort of Federal Union of South Africa—British Territory, South African Republic, and Orange Free States—in which we, of course, should have the hegemony, but no more . . . and I should care little whether the Transvaal became a British Colony or remained the South African Republic *within such a Federation.*" Lucian Wolf, *Life of the First Marquess of Ripon* (2 vols., London, 1921), II, p. 222. On this point the views of Lord Ripon seem to have almost coincided with those of Cecil Rhodes; see Williams, *Cecil Rhodes*, p. 68.

The greatest single proponent of this idea was doubtless Cecil John Rhodes. A true empire-builder he combined the ability to dream dreams and see visions with a great capacity for practical affairs and an element of ruthlessness, often so necessary for success. Rhodes saw clearly the benefits which could be derived from union, presented its cause in several public addresses, and worked persistently to arouse popular interest in its favor. His private secretary testifies that the union of all the white communities in South Africa was Rhodes' "Lifelong dream."<sup>51</sup> Unfortunately his zeal for this proved at times stronger than his scruples and even than his discretion. It led him to plot the Jameson Raid—a crime and a blunder which discredited a great cause and precipitated a bloody and protracted war.<sup>52</sup>

Few wars fought by Britain in modern times have caused fiercer partisan controversies than that in South Africa, 1899-1902. Condemned by hostile critics as an unjust imperialistic attack upon two weak states at the behest of a small band of adventurers and capitalists, its defenders contended with equal vigor that it had been forced upon the empire by Kruger's violation of treaty obligations; his unfair treatment of the foreign born, the majority of whom were British; and necessitated by regards for the safety of the South African colonies. The Kruger government in the Transvaal was doubtless narrow in its conservatism, possibly corrupt and certainly galling to the Uitlanders. Germany's activities might also justify serious apprehensions.<sup>53</sup> But it appears probable that this war, like most conflicts of ancient and modern times, could have been avoided if a more conciliatory policy had been adopted by the British government. Chamberlain, Milner, Rhodes, and their lieutenants, were the proponents of great plans for the safeguarding and consolidation of the overseas possessions and favored aggressive methods in securing their aims. The republics lay close to the highway to the interior. Their annexation rounded off the South African Colonial empire, made it safer against for-

<sup>51</sup> P. Jourdan, *Cecil Rhodes, His Private Life by His Private Secretary* (New York, 1911), pp. 162, 163. Among the advocates of union were also found Mr. P. A. Molteno, the son of the first prime minister at the Cape. He favored a federation similar to that of the United States. See P. A. Molteno, *A Federal South Africa* (London, 1896).

<sup>52</sup> The best brief account of the Raid, revealing Cecil Rhodes' connections with it and the results, is found in Williams, *Cecil Rhodes*, pp. 242-275.

<sup>53</sup> Wolf, *Ripon*, II, pp. 231-233. German plans for an expedition to the Transvaal, 1896, seem to have been thwarted only by the common sense shown by the Portuguese foreign minister, the Marquis de Soveral. See Baron von Eckardstein, *Ten Years at the Court of St. James* (London, 1921), pp. 84, 85.

eign attacks, and benefitted important economic interests both there and at home.<sup>54</sup>

Upon the cessation of hostilities<sup>55</sup> enthusiasts for the cause of union believed that it could be obtained by quick and decisive action. Lord Milner shared this view. He therefore advocated the suspension of the Cape constitution, whereby all the British possessions would be placed more nearly on an equal footing and "the restoration of self-government in all the colonies [could be made to] coincide with the establishment of federation."<sup>56</sup> But Chamberlain, who favored strongly the desired consolidation, refused to sanction coercive measures. Mindful of past mistakes he abstained from dictating to South Africa; Lord Carnarvon's blunders were not without beneficial results.<sup>57</sup>

Although waiting watchfully, Downing Street was not inactive. Chamberlain himself called the attention of the South Africans to the benefits which might be derived from federation and appealed to them to think of their country 'as a whole.'<sup>58</sup> And the numerous young men sent to assist Lord Milner in reorganizing and rebuilding the new colonies, proved to be active and persistent advocates of union. Milner's "Kindergarten" combatted particularism in all its forms and attempted throughout to direct the thought and aspirations of the colonists so as to foster a spirit of unity.<sup>59</sup>

The work of reconstruction offered, indeed, favorable opportunities for this. A common police force, the South African Constabulary, was created and a joint loan of thirty-five million pounds secured for the Transvaal and the Orange River Colony.<sup>60</sup> During the war the railways of the two republics had been seized and organized as one system. This was continued, and an Inter-Colonial Council was established which assumed charge of the railways,

<sup>54</sup> Wolf, *Ripon*, II, pp. 253-257; Sir William Butler, *An Autobiography* (London, 1913), pp. 404-455.

<sup>55</sup> The Orange Free State and the Transvaal were annexed by proclamations of May 24 and Sept. 1, 1900. Peace was not concluded until May 31, 1902, by the Treaty of Vereeniging. For the texts of these documents see Eybers, *Constitutional Documents*, pp. 344-347, 514, 515. The territories of the two republics received the crown colony form of government.

<sup>56</sup> *The Times' History of the War in South Africa*, edited by L. S. Amery (7 vols., London, 1909), VI, pp. 66, 67. See also Mitchell, *Life of Rhodes*, II, p. 283.

<sup>57</sup> Harold Spender, *General Botha* (New York, 1916), p. 154.

<sup>58</sup> See speech at Cape Town, February 23, 1903. *Mr Chamberlain's Speeches*, ed. by Charles W. Boyd (2 vols., London, 1914), II, pp. 109-112.

<sup>59</sup> W. B. Worsfold, *The Union of South Africa* (Boston, 1913), p. 121. Called Milner's "Kindergarten" because of their youth.

<sup>60</sup> J. Buchan, *The African Colony Studies in Reconstruction* (London, 1903), p. 245.

the constabulary, and a number of minor services. The net earnings of the railways were used in defraying the expenses connected with the loan, the constabulary, and other charges.<sup>61</sup> Thus the two new colonies had a common administration of important departments and local barriers were broken down. The revived customs union included all the colonies and the conference in 1903, dealing with this question, expressed the hope that the time might not be far distant when a Commonwealth of South Africa would be created; and it also recommended the appointment of a commission to study the native problem, so important for all the colonies.<sup>62</sup>

Prominent among the factors which aroused the people of South Africa to a realization of the necessity for union were questions connected with the customs, railway administration, labor supply for the mines on the Rand, and native policy. The last came especially into prominence on account of the Natal rebellion of 1906 which revealed that the Kaffirs had not lost the martial spirit of their ancestors: In the report of the Native Affairs Commission of 1905, attention was called to a situation highly disquieting. Outnumbered more than five to one the whites faced a tremendous problem in dealing with native races noted for their fecundity and virility. While the old order among them disappeared rapidly no new restraining influence seemed ready to take the place formerly occupied by the chiefs. And the spread of a feeling of racial solidarity, as a result of the Ethiopian movement, gave further cause for alarm.<sup>63</sup>

All these elements were cleverly utilized by the young Englishmen employed in the crown colony administrations of the Transvaal and the Orange River Colony. Their well-written and well-documented arguments were finally published in book form entitled *The Government of South Africa*. And in another work, *The Framework of Union*, they showed the characteristics of some of the leading federated and unitary governments of the world.<sup>64</sup>

After the promulgation of self-governing institutions in the new colonies the advocates of union found powerful allies among the

---

<sup>61</sup> Lord Milner saw great possibilities in the Inter-Colonial Council "affecting much more than the two Colonies," Milner to Chamberlain, April 6, 1903. P.P., 1903, XLV, cd. 1641, p. 4.

<sup>62</sup> *Ibid.*, cd. 1640, p. 15.

<sup>63</sup> *Ibid.*, 1905, LV, cd. 2399; *The South African Natives: Their Progress and Present Condition*, edited by The South African Native Races Committee (London, 1908), pp. 192, 228.

<sup>64</sup> *The Government of South Africa* (Cape Town, 1908); *The Framework of Union* (Cape Town, 1908).

Boers. The Afrikaner Bond urged "the development of a feeling of national unity in South Africa and a federal union of the British South African Colonies, keeping in view the mutual interests of these Colonies and the supreme authority of the British Crown."<sup>65</sup> Mr. F. S. Malan, leader of the Bond forces in the Cape assembly, began in 1906 a series of vigorous articles favoring unification in *Ons Land*, the leading Dutch newspaper in South Africa.<sup>66</sup> Of even greater significance was the aid received from the leaders of the old republicans. Some of these had, indeed, agitated for a united South Africa in the years preceding the war, but by this they meant union under the republics. Now they advocated consolidation under the Union Jack.

M. F. Steyn, ex-president of the Orange Free State, related in language of pathetic simplicity how the view of a pool of blood from soldiers representing the Free State, the Transvaal, and the Cape had brought him to realize the folly of internecine strife.<sup>67</sup> His weighty influence was thrown in the scale favoring unification. General Smuts had already in 1895, as Mr. Advocate Smuts, urged cooperation among the whites.<sup>68</sup> With the war over he pleaded eloquently for reconciliation and union. Speaking at Potchefstroom in February, 1905, he refused to "hide the fact that the source of all our evils was disunion, disruption." "Our object of old," he continued, "was to found a United South Africa, stretching as far as *Zambesi* or farther, but because we were at sixes and sevens we did not succeed \* \* \*. Let us take the hand of brotherhood." At Klerksdorp "he advised his hearers to let 'The union of Boer and Briton resemble that of England and Scotland not that of England and Ireland. Let us cooperate in order to attain our old object: A United South Africa.'"<sup>69</sup>

Some of Smut's appeals for union thus antedated the grant of self-government to the Transvaal and the Orange Free State,

<sup>65</sup> "South African Union" in *The Edinburgh Review*, vol. CCX, p. 8 (July, 1909).

<sup>66</sup> *Ibid.*, p. 9.

<sup>67</sup> "De dag na de slag te Graspan nabij Reitz, waar generaals De Wet en De la Rey 'n vronwelager verlost, kwam ik op 't slagveld en wer mij de plaats getoond waar drie van onze mannen gesneueveld warn—'n Kolonialer 'n Vrijstater en 'n Transvaler, Ik zag hoe hun levensbloed in één grote plas tezamen gestroomd was. Ik stond als genageld bij die plas! Ik sprak met niemand. 't Was voor mij 'n heilig ogenblik. Nieuwe hoop en nieuwe moed vervulden mij. Ik Klom op mijn paard en reed weg overtuigd in mijn hart dat ik de ware vereniging van Zuid-Afrika gezeien had, want dat bloed kon geen mens meer scheiden!"—From a speech of March 19, 1908. N. J. van der Merwe, *Marthinus Theunis Steyn* (2 vols., Cape Town, 1921), II, p. 221.

<sup>68</sup> For quotations from this speech see N. Levi, *Jan Smuts* (London, 1917), pp. 25-27.

<sup>69</sup> *Ibid.*, p. 74.

but this timely concession increased his zeal and put the Boers in a receptive mood. Britain had proved generous and trusted them. Now their great commander in the weary years of a life and death struggle came forward with appeals for union. "The old Boers," said General Botha, "were pioneers of the Transvaal and as they were the pioneers in that matter so they should be on the question of Federation."<sup>70</sup> It held, indeed, promises of a great future for their race. They formed the majority of the total white population and in 1907 three out of the four governments were controlled by them. If united, the Boers had hopes of dominating a state which would rank with the great federations of Canada and Australia. Not all the Boers could appreciate these possibilities, but the majority of them were good "followers" and in Generals Botha and Smuts they possessed leaders and statesmen cast in a heroic mould.

When the conditions appeared favorable members of Milner's "Kindergarten" took prompt action. In 1906 a statement was drawn up which showed the urgent need for an administrative union.<sup>71</sup> Through the assistance of Dr., later Sir, Starr Jameson, then prime minister at the Cape, this was brought before the people of South Africa. In a minute of November 28, 1906, his government invited the high commissioner, Lord Selborne, "to review the general situation in South Africa in such a manner as may enable the people of this country to appreciate the difficulties of administration under the present system, and to consider whether (and if so by what means) it is advisable to establish a central national government embracing all the British Colonies and Protectorates."<sup>72</sup>

Lord Selborne forwarded the minute to the governments of Natal, the Orange River Colony, and the Transvaal and to the administrator of Southern Rhodesia.<sup>73</sup> When these concurred in the request he issued, January 7, 1907, his famous *Federation Memorandum*, which included the above mentioned statement.

The *Memorandum* presented in a clear, concise, and convincing manner the actual and unsatisfactory condition on the sub-continent as well as the dangers connected with a continued disunion.

<sup>70</sup> Quotation from a speech at Standerton, Jan., 1907. Spender, *General Botha*, p. 194.

<sup>71</sup> The authors of this statement were Messrs. Lionel Curtis, W. L. Hichens, Patrick Duncan, R. H. Brand, and Feetham. See Worsfold, *Union of South Africa*, pp. 122, 123; and Worsfold, *The Reconstruction in the New Colonies Under Lord Milner* (2 vols., London, 1913), II, 398-399.

<sup>72</sup> P.P., 1907, LVII, ed. 3564, p. 3.

<sup>73</sup> *Ibid.*, p. 9.

The many serious problems which confronted the various states could not possibly be solved by piecemeal measures. Three roads were open: "The make-shift regime of the High Commissioner, the jarring separatism of the States of South America, the noble union of the States of North America."<sup>75</sup> Although recommending union, Lord Selborne disclaimed any intention of attempting to force it upon the colonists. In his opinion "no healthy movement towards federation can emanate from any authority other than the people of South Africa themselves."<sup>76</sup> This official and temperate analysis of conditions which most thinking men admitted were serious had a marked effect upon public opinion and encouraged those who worked for union. An active educational propaganda was inaugurated and it continued till the goal had been reached.<sup>77</sup>

By 1907 it was generally felt that South Africa approached a crossroad. The existing customs union and railway agreements failed to satisfy the different colonies.<sup>78</sup> Since 1905 both the Cape Colony and Natal had experienced an economic depression which yearly grew more acute. Large deficits were accumulated and both colonies demanded higher tariff and railway rates. The finances of the Transvaal were, on the other hand, in a flourishing condition and here the people clamored for a lowering of the rates.<sup>79</sup>

As a result the government of the Transvaal served notice, May, 1907, to terminate the customs union and the railway agreement. A conference took place at Pretoria in the following year. Agreement could be reached only on a series of resolutions, to be submitted to the colonial parliaments, which declared that "an early union under the Crown of Great Britain" was desirable, and suggested that delegates should be appointed to consider and report on the most desirable form of such a union and prepare a draft constitution.<sup>80</sup>

<sup>74</sup> *Ibid.*, pp. 12-61. It was published as a pamphlet in July of the same year with the title, *A Review of the Mutual Relations of the British South African Colonies* (Cape Town, 1907).

<sup>75</sup> P. P., 1907, LVII, cd. 3564, p. 6.

<sup>76</sup> *Ibid.*, p. 5.

<sup>77</sup> R. H. Brand, *The Union of South Africa* (Oxford, 1909), p. 31.

<sup>78</sup> *Ibid.*, pp. 25-27; Paul Lederer, *Die Entwicklung der sudafricanische Union auf Verkehrspolitischer Grundlage* (Leipzig, 1910). J. Conacher, *Report upon the Distribution of Oversea Traffic Between the South African Railways* (Pretoria, 1908); H. E. S. Fremantle, *The New Nation* (London, 1909), p. 6; P.P., 1907, LVII, cd. 3564, pp. 35, 36; *The Government of South Africa*, I, pp. 195-229, 280-282.

<sup>79</sup> *The Times*, May 4 and 9, 1908; Fremantle, *The New Nation*, p. 154.

<sup>80</sup> *The Times*, May 6, 1908; Sir E. Walton, *The Inner History of the National Convention of South Africa* (New York, 1912), p. 26.

The Pretoria resolutions were, on the whole, well received by the colonies. Details were criticized, but there was general concurrence on the main issue. All of the party leaders supported the call for a National Convention; and the president of the Afrikaner Bond expressed the belief that the resolutions "would be a powerful factor in speedily establishing a united South Africa."<sup>81</sup> In England the reception was equally cordial. *The Times* declared that "The news was heartily welcomed here as a sign that the States of the sub-continent were entering the path which the best and highest interests of all of them dictate."<sup>82</sup> A resolution was passed unanimously by the House of Commons expressing the hope that the government would welcome the adoption of provisions calculated to render possible the ultimate inclusion of all of South Africa in a federal union. To this Mr. Winston Churchill and Colonel Seely, on behalf of the government, replied that, warned by precedent, they were determined not to attempt to lead, but to leave the matter for the decision of South Africa. The uncertainty of the situation prevented them from making any declaration as to what would happen in the event of federation. They would watch and wait,<sup>83</sup> a policy followed consistently while the convention was at work and the fate of South Africa hung in the balance.<sup>84</sup>

But the young imperialists in South Africa were furiously active. Mr. Lionel Curtis organized numerous "closer union societies," forming a network over all of South Africa. Their object was to familiarize the people with the problems connected with the union. When the convention was at work these societies published a magazine, *The State*, which discussed the questions then uppermost in the minds of the people. No particular form of union was advocated although Mr. Curtis and the majority of his followers had a strong leaning towards a legislative union.<sup>85</sup>

In a solemn message issued on the eve of the convention, General Botha appealed to the people of South Africa. "South Africa has its opportunity now," said he, now prime minister of the Transvaal, "and I expect South Africa to do its duty \* \* \* I expect the result of the Convention to include unity, and there-

<sup>81</sup> *The Times*, June 5, 1908.

<sup>82</sup> *Ibid.*, May 14, 1908.

<sup>83</sup> *Hansard*, 4th series, CLXXXVIII, cols. 1215-1295. Debate, May 13, 1908.

<sup>84</sup> See *ibid.*, CXCIII, col. 1268; CXCIV, cols. 1609, 1610.

<sup>85</sup> *Edinburgh Review*, CCX, p. 12.



from to arise and develop a happy, prosperous, strong and healthy nation.’’<sup>86</sup>

These appeals were apparently necessary in order to arouse the colonists, many of whom seemed quite apathetic. *The Times*’ correspondent feared lest disagreements among the unionists might “wreck the whole scheme in presence of the unenthusiastic many.’’<sup>87</sup>

Fortunately, the difficulties were overcome and the constitution for a united South Africa came into existence. This was affected by a series of compromises on important issues, but without them the attempt would surely have failed. Breadth of view and a willingness to sacrifice unessentials characterized the attitude of both Britons and Boers during the critical months in 1908 and 1909.<sup>88</sup> Most remarkable was perhaps the spirit of loyalty towards the empire manifested by such men as ex-president Steyn and Generals Smuts and Botha. Without the aid of these great Boer leaders the task could never have been accomplished.

The attitude of the high commissioner, Lord Selborne, remained studiously fair and correct. Loyal to his conviction that the problem was one for the people of South Africa to settle in their own way, he proved helpful and courteous without attempting to meddle or volunteer advice. The home government was likewise friendly and sympathetic, following strictly a policy of “hands off.”

The constitution as completed met with general approval in England.<sup>89</sup> *The Times* described it as “a political achievement of which the statesmen who modelled it and the people who endorsed it have every reason to be proud of.”<sup>90</sup> A delegation from South

---

<sup>86</sup> *The Times*, Oct. 12, 1908.

<sup>87</sup> *Ibid.*, Oct. 5, 1908.

<sup>88</sup> Prominent among the Boer representatives at the constitutional convention were, ex-President Steyn and generals Botha, Smuts, De Wet, de la Rey, and Herzog. These worked side by side with Sir Starr Jameson, Sir G. H. Farrar, and others who had taken a leading part in the controversies which preceded and to some extent caused the outbreak of the Boer War. A number of books have been written on the situation in South Africa during the unification period, but no authentic source of information exists for the actual work of the convention. The nearest approach to a contemporary account of what happened behind the closed doors when the future constitution was debated is Sir Edgar Walton’s *The Inner History of the National Convention*. The author was a prominent member of that body, but the book itself is written partly from memory and partly from rather incomplete notes; and it cannot be considered a full and complete account of what took place.

<sup>89</sup> For its reception in South Africa and the attitude of the separate states to it see Worsfold, *The Union of South Africa*, p. 128; Walton, *History of the Convention*, pp. 321–328.

<sup>90</sup> Leading Article, July 26, 1909.

Africa, headed by Mr. Schreiner, tried in vain to persuade Parliament to amend the clause in the constitution which barred the colored from seats in the Union parliament. A few friends of the natives, prominent among whom was Sir Charles W. Dilke, supported this plea.<sup>91</sup> It was clear, however, that the "colour-bar" represented the wishes of an overwhelming majority of the whites in South Africa, and the imperial government refused to accept amendments to the completed document. The leaders of the two great parties gave the constitution their whole-hearted support. Mr., now Earl, Balfour characterized the Union as unexampled in history; and the prime minister, Mr. Asquith, warned the House of Commons "not to wreck this great work \* \* \* of freedom and reconciliation."<sup>92</sup> It was finally passed without a division.

The union of South Africa was officially announced by royal proclamation of December 2, 1909; and May 31, 1910, the eighth anniversary of the peace of Vereeniging, was fixed as the day of union. General Louis Botha became the first prime minister and Lord Gladstone, a son of the great Liberal leader, was appointed as the first governor-general of the Union.

Thus was accomplished what Sir George Grey, Lord Carnarvon, Cecil Rhodes, and others had attempted to affect during the latter half of the nineteenth century. These early attempts were, no doubt, premature, but lessons were taught which proved valuable in the final effort. And it should also be remembered that without the Boer War South Africa could not have become united. Strong as were the economic and social forces favoring a union, an independent Transvaal was largely unaffected by them as long as its natural outlet to Delagoa Bay remained accessible, and labor for the mines could be recruited in Portuguese territory. Likewise, it appears certain that without the aid of the young Britons trained in the neo-imperialistic school of Chamberlain and Lord Milner the union could not have come into existence at this early date.

The views in regard to federation presented by the members of the "Kindergarten" were shared by their superiors, Conservatives as well as Liberals both in South Africa and in England. They labored for an end ardently desired by the imperial government while employed by it in the crown colony administration of the two new dependencies. While no evidence is available to show that

<sup>91</sup> Stephen Gwynn and Gertrude M. Tuckwell, *The Life of the Right Honourable Sir Charles W. Dike* (2 vols., London, 1917), II, pp. 375, 376.

<sup>92</sup> *The Parliamentary Debates*, 5th series, House of Commons, IX, cols. 1006, 1564.

Mr. Lionel Curtis and his friends worked under orders from Downing Street, their efforts must have been noticed and approved by the colonial office. Carnarvon's policy of dictation, slightly modified by crude attempts at persuasion, had failed; it was the part of wisdom to abandon the former and evolve more finesse in the use of the latter.<sup>93</sup> The presumption appears well-founded that the imperial government was at least indirectly an important factor in stimulating, during the period 1901-1909, that federation sentiment which more direct methods had failed to arouse thirty years earlier. But the sentiment itself could not have prevailed if great centripetal forces had not existed and the Boer leaders had not identified themselves with the cause of union.

---

<sup>93</sup> Of considerable interest, in this connection, is the following observation by Sir Wilfrid Laurier: "At each imperial conference," says Sir Wilfrid, "some colonial leader was put forward by the imperialists to champion their cause. In 1897 it was obvious that they looked to me to act the bell-wether, but I fear they were disappointed. In 1902 it was Seddon; in 1907, Deakin; in 1911, Ward." Oscar Douglas Skelton, *Life and Letters of Sir Wilfrid Laurier* (2 vols., New York, 1922), II, p. 342, note.



## THE REMOVAL OF THE WINNEBAGO

LOUISE PHELPS KELLOGG

---

The Black Hawk War sealed the fate of the Rock River band of Winnebago, and made their cession of that country inevitable. The whites had already looked with covetous eyes upon this rich and well watered region, especially on the western portion that abutted on the lead mines. After the Winnebago uprising of 1827 this tribe was summoned the ensuing summer to Green Bay to cede their portion of the lead mining region to the United States. Too few of the chiefs were present to form a treaty, so a provisional agreement was made for the cession of the territory west and south of the Blue Mounds and the Pecatonica River. This arrangement was confirmed by the treaty of Prairie du Chien in 1829, when the tribal lands were sold for an annuity of \$18,000 annually for thirty years. The Indians were also to be provided with three blacksmith establishments—one at Prairie du Chien, one at Fort Winnebago, and one on the waters of Rock River; they were also to have a cart and two yoke of oxen at the portage.

Meanwhile two sub-agencies were erected for this tribe—one at Fort Winnebago, whose incumbent was the well known John H. Kinzie. The other agent was Henry Gratiot, whose home at Gratiot's Grove was outside the Winnebago territory; he thereupon built an agency house on Sugar River, and there the blacksmith, Maurice Mata, of whom Mrs. Kinzie speaks so favorably, had his forge.<sup>1</sup>

Matters were in this condition until the Sauk uprising of 1832. There can be no doubt that many of the Winnebago sympathized with the hostiles, although the Rock River band was held to its allegiance with the United States by the efforts of Gratiot and Kinzie, ably seconded by Henry Dodge. In fact, White Crow, Little Priest, and other Rock River chiefs did the whites unrequited service not only as guides and scouts, but as the agents in the rescue of two captive white girls from Black Hawk's band.

<sup>1</sup> Juliette A. Kinzie, *Wau Bun* (Caxton Club edition, Chicago, 1901), 327.

Nevertheless, it was determined that the Winnebago must be removed from a territory so close to the settlements; so in September, 1832, their chiefs were summoned to Fort Armstrong, where General Winfield Scott and Governor John Reynolds, of Illinois, secured the cession of all their land south of the Fox-Wisconsin waterway. In return for this cession the Winnebago were granted the so-called neutral tract in Iowa ceded by the treaties of 1830 with the Sauk and Foxes on one hand and the Sioux on the other. This large tract was well watered and full of game. Its drawback was the fact that it lay close to the habitat of these fierce tribes still at enmity, and that its neutrality was far from being assured. In compensation for this exchange of lands the Winnebago were accorded an additional \$10,000 annually for twenty-seven years; they were to be served with a school and a band of white farmers to teach them agriculture, and the Rock River band was to be supplied annually with 1500 pounds of tobacco. In addition to the new cession in Iowa, the tribe still possessed a large tract of territory north of the Wisconsin River extending to the sources of Black River, sparsely settled by one or two small tribal bands. The treaty further stipulated that "In order to prevent misapprehensions that might disturb peace and friendship between the parties to this treaty, it is expressly understood that no band or party of Winnebagoes shall reside, plant, fish, or hunt after the first day of June next, on any portion of the country herein ceded to the United States."<sup>2</sup>

The winter following the Treaty of Rock Island was one of great hardship for the Winnebago. The Black Hawk War had prevented them from planting or harvesting any corn; game was not plentiful, and numbers of the tribe literally starved and froze to death. Mrs. Kinzie has given a graphic picture of this starving time, and told of the distress of her husband and herself at their inability to alleviate the condition of their poor Indian "children." "They would climb up on the outside [of the agency house], and tier upon tier of gaunt, wretched faces would peer in above, to watch us, and see if, indeed, we were as ill-provided as we represented ourselves." Corn had been purchased by the government to supply the Winnebago; but it had been detained at Green Bay during the winter, on account of the frozen waterways. Finally, in the spring the boats arrived and the famine was for the time being relieved.<sup>3</sup>

<sup>2</sup> Charles J. Kapler, *Indian Treaties* (Washington, 1904), 345-351.

<sup>3</sup> Kinzie, *Wau Bun*, 363-365, 380-383.

Now the time drew near when the major part of the tribe must abandon its ancestral home, and remove all its villages either north of the Wisconsin or to the new cession in Iowa. The government would not specify which region should be occupied. There was, however, rivalry among the government agents on this score. Agent Joseph M. Street, at Prairie du Chien, was strongly in favor of the Iowa location; he argued that it was merely a matter of time when the tribe must relinquish all its lands east of the Mississippi, and it would be best if it should be removed at once to the west bank. On the other hand, Kinzie and Gratiot, who best knew the Rock River band, urged a location just north of the Wisconsin. Street accused them of doing so in the interest of the American Fur Company and from self-interest for their sub-agencies. He was, however, intensely jealous of Kinzie, who was much more popular than himself both with the whites and the Indians. Street was a good man, with humane views, but not well adapted to the exigencies of the frontier, and somewhat impracticable in his plans for civilizing the red men.

Meanwhile the Fox River and Rock River bands were besieging their agents with importunities to be allowed to remain on their homelands until fall. If they might plant their accustomed fields once more and gather the harvest, then they promised that they would take their annuities and remove without making any difficulty. Both Kinzie and Gratiot favored this course, but were unable to secure the coveted permission from either the governors of Michigan or Illinois or from the commissioner of Indian affairs. The white settlers of the Illinois frontier were terrified by the recollections of the hostilities of 1832. John Dixon, of Rock River, informed the army officers of the frontier posts that he believed that the Winnebago were plotting with the Potawatomi for a new uprising. Gratiot was hurried to his Sugar River agency house; there he met an officer from Fort Winnebago who had been sent to test the temper of the tribesmen. The latter were terrified by what they thought was a threat of war. They could not be dissuaded from the belief that the whites were plotting to make war upon them. They admitted to Gratiot that the Potawatomi had sent them a message by their trader, Thibault, but insisted that it was a peaceful message. Gratiot himself saw the wampum and that it was tied with a green ribbon, signifying peace. The message was an invitation to hold a great council at Turtle village (on the site of Beloit). Here they were to have, wrote Gratiot,

a great "Medicine Feast," or a "Smoke to the Great Spirit." Then they hoped to secure permission to plant large fields of corn in that locality and to postpone their removal until the autumn.

In the meanwhile, Colonel Henry Dodge, who had been on the southwestern frontier organizing his regiment of dragoons, arrived at his home in Dodgeville. He had also been, during part of the winter, at Washington, where he was hailed as the victor over Black Hawk. He then proceeded to his Wisconsin home via Dixon's Ferry, where he heard the news of the Indian gathering. He wrote on April 13th, to General Alexander Macomb of the United States army, that he had seen Gratiot, who informed him that the Winnebago were peaceful, and that they requested until fall to make their removal. This, Dodge asserted, would by no means be tolerated by the frontier inhabitants. The tribesmen must go before June 1st. He ordered two companies of his newly-enlisted dragoons to march at once for the Illinois River and to be ready when ordered to advance into the Rock River region. Meanwhile Dodge met Kinzie, who assured him that the Winnebago were much frightened and would accede to any proposals from Dodge and their agents; that they were still in a state of semi-starvation and in great dread of the future.

Dodge decided to hold a conference with the principal chiefs at the Four Lakes, and sent them word to meet him at the old council ground on Fourth Lake, where he had talked with them the previous May, and restrained them from joining Black Hawk. April 28th was the day appointed. Dodge, Gratiot, and Kinzie arrived with their escorts; all the principal chiefs of the Rock River were there—Whirling Thunder, White Crow, Little Priest, Little Black, Spotted Arm, White Breast, and others. The Indians made their plea for time, which Dodge refused; they then asked for help to remove their families, for wagons and oxen to portage their canoes from the Rock River headwaters to the Wisconsin, and for provisions to enable them to live. These requests the white men granted. Dodge ordered his two companies of dragoons under Captains Browne and Beekes to bring wagons from Illinois; Gratiot ordered three wagons full of corn from Galena, and wrote to Governor Porter that he would be in person at Four Lakes by May 15th to superintend the distribution of rations.

Meanwhile the Winnebago of the lake of their name and of the upper Fox River had begun their removal to the Baraboo Valley. The Rock River Indians decided to settle on Sauk Prairie, where



there had previously been a large Indian village. By the latter part of May the dragoons reached Dodgeville, whence they proceeded at once to Fourth Lake, where they built a camp on the northwestern shore near a great spring which they named for the spring Camp Bellefontaine. They also built another on the Wisconsin River, naming it Camp Knox. Their instructions were to observe a mild but firm attitude towards the removing Indians, and to range up and down the streams to see that all the Indians crossed the Wisconsin. On the fifteenth of May thirty lodges of the tribesmen gathered at Four Lakes ready to cross to Sauk Prairie. They held a grand medicine dance somewhere near the present city of Madison, and performed ceremonies of removal. "On the eve of their departure they extinguished all their old fires, and kindled a new one procured by the friction of two sticks of wood, which they 'hoped would burn clear and make them happy,' " wrote their agent Gratiot. He then gave them some few presents, after which their canoes, wigwams, and effects, already brought up the chain of the Four Lakes, were loaded on to wagons and transported to the shore of Wisconsin River. Man Eater's village was left behind as the chief himself was at Fort Winnebago; Spotted Arm also was tardy in removing his band. June 10th Dodge himself visited the camp on Fourth Lake and went thence to Fort Winnebago, where he learned that sixty lodges of tribesmen were still left on the eastern branches of Rock River.

Kinzie had meanwhile sent out word that the annuities would be paid July 1st at the agency house at the portage. Unfortunately this payment was the occasion for a disgraceful orgy. Whisky dealers brought in a vast quantity of liquor, and opened it on private ground, where it could not be seized by the government. Several Indians were killed in drunken rows, and most of the silver paid them by the government passed into the hands of the liquor dealers and traders, so that the Indians were worse rather than better off for their annuities.

Dodge thought it necessary to keep the troops in the ceded territory, being certain that many of the Indians would return to Rock River waters after the annuity payment. Whirling Thunder and his band, encouraged by the traders John Dougherty, Oliver Armel, and Stephen Mack, returned to their old village. Lieutenant T. B. Wheelock, of the dragoons, followed them to Sugar River and arrested the white men and carried them and the Indian band to the Fourth Lake camp. Dodge being notified by

express, rode over from Dodgeville, released the traders, and sent a troop of fifty dragoons to escort Whirling Thunder and his party to Portage, and there set them across the river. This chief and some others of his tribesmen then decided to settle in the neutral ground. They went down the Wisconsin River to Prairie du Chien, and by mid-July Whirling Thunder with two hundred and fifty of the tribe, many of them from Lake Koshkonong and Turtle River, had crossed into Iowa. The dragoons' camp on Fourth Lake was kept up until October, when the troops had effectually cleared the region of Winnebago stragglers.

It would be too long a story to attempt to follow the tribesmen to their new homes. Those who went across to Iowa speedily returned because of an outbreak of hostilities between the Sauk and the Sioux, in which they feared to be involved. "After this, the tribe felt badly crowded in the territory north of the Wisconsin. "We are too many to live in so small a country," complained Chaetar to General Street at Prairie du Chien in 1834. Early in that year Whirling Thunder sought out his old friend and agent at Gratiot's Grove, who has preserved for us his pathetic speech: "Father—I have come to see you and get you to write a letter in my name and in the name of my Rock River band of Winnebagoes. We are tired of having no home—we are scattered all over the country like wild beasts, and wish to unite in the spring, and build a village and plant corn.

"Father Cass [Secretary of War]—I call on you particularly because you know us, you have traversed our country and know our habits, and our needs. . . .

"Father—you know better than we do that the land you gave us west of the Mississippi, is occupied by the Sac's and Foxes, the Sioux's and other tribes, and you know it [is] impossible for us to go and live there, because all these natives are jealous of us—it is useless for us to ramble about as we do. . . .

"Father—The Great Spirit has made the white and the read [sic] man, the white he made more numerous than the red, and gave them more sence they can read and they can write—it is for that reason the Great Spirit created a distinction between the two. The whites were made by the Great Spirit to take care of the red people who are ignorant." He then stated that the Prophet was intriguing against the whites and was at his old home on Rock River. Black Wolf, White Crow, and Little Priest

were also known to have visited their old homes during the winter of 1833-34.

So they came back—the dispossessed—year after year. White pioneers tell of the long trains of Indian visitors that used to come each summer to their old Rock River homes, to fish once more in the beloved waters, to stand once more beside the effigy mounds of their clans. The dispossessed make a sad picture, yet an inevitable one. The Great Spirit had willed that this valley of the Rock should be no longer a wilderness, haunted by barbarians, but the home of a great civilization. Let us, however, in our plenty and prosperity prove our humaneness by giving now and then a look into the past and a sigh of sympathy for the dispossessed red man, who loved the woods and streams and lakes of his ancestral home with a deep and abiding affection. “This,” said one of the Winnebago tribe to the writer, “is the home of my spirit.” From this home they were forced to go in the early summer of 1833, because of the unreasoning terror of the frontier settlers, and by the stern orders of the officers of the United States government.<sup>4</sup>

---

<sup>4</sup> This paper is based almost wholly upon the documents in the Indian office at Washington, copies of which are in the State Historical Library. Dodge's letters of this period are printed in *Iowa Historical Record*, v; 337-361; vi; 391-422, 445-467. See also a trooper's experience, in *Wis. Hist. Colls.*, x; 231-234. Mrs. Kinzie's valuable record in *Wau Bun* closes just before the removal and the payment of 1833. See incidents connected with the repeated return of the Winnebago, in *Wis. Hist. Colls.*, x; 258-259.



## AUGUSTINE OF HIPPO *qua* PATRIOT

ROBERT K. RICHARDSON

---

Historians differ widely as to St. Augustine's attitude toward his country and its misfortunes at the opening of the fifth century after Christ. Some consider him so devoted to the Heavenly City as to be indifferent to the sufferings of the Temporal City. Others discover in him a sorrowing patriot of the usual and accepted pattern. An intermediate view is that represented by Dr. Angus in his valuable work, *The Sources of the First Ten Books of Augustine's De Civitate Dei*. Dr. Angus holds that: "So far as the testimony of Augustine's writings is concerned, his attitude to the fall of Rome and the state of the Roman Empire of his day was neither of intense and deeply patriotic feeling, nor of heartless indifference, though nearer to the latter than to the former." "To say the least," continues Angus, "he appears surprisingly calm in the face of so terrible a calamity. Augustine's pride in Rome was centered in her achievements of the past, not in her present. He was more of a Christian than a Roman."<sup>1</sup>

A study of Augustine's letters and sermons, as well as of *The City of God*, directed to the relatively small point in question, but controlled by consideration of the broader matter of his general outlook on God and the World, suggests that an eclectic estimate of his position is closer to truth than any of the three views mentioned. This estimate may be subsumed in four propositions: (1) Augustine was fond, even proud, of the Empire; (2) he took a lively interest in the fortunes of the state; (3) not considering the situation hopeless, he bewailed this situation less than had he been endowed with insight more prophetic; and (4) the character of his Neo-Platonic Christianity lent moderation of grief alike to his thought and to his rhetoric.

*Augustine was fond, even proud, of the Empire.*

It is not unnatural to regard Augustine's attitude toward the Roman Empire as basically prejudiced by a theory that the state

<sup>1</sup> S. Angus, *The Sources of the First Ten Books of Augustine's De Civitate Dei*. 1906. 275. Cf. *ibid.*, 64-75 for quotations representative of one or the other of the types of view mentioned in the text.

originates in sin.<sup>2</sup> In reality he assigns no such origin to the state. The state, for Augustine, is an entity quite neutral in character, belonging to the sphere of things temporal to be sure, but practically adherent to the City of God or to the Earthly City as its rulers yield their conduct's allegiance to the one or to the other. Only when justice is disregarded do kingdoms become "great robberies."<sup>3</sup> The state *qua* state is the handiwork of Providence: *Prorsus divina providentia regna constituuntur humana.*<sup>4</sup> No political theory of the state, therefore, prejudices Augustine against his country.

Nor is his affection cooled by that country's idolatrous past. He finds in its pagan heroes models for the citizenry of the Kingdom of God and yearns for the eventual merging of the Commonwealth itself with the *Civitas Dei*. The great Romans of the past, he relates, "despised their own private affairs for the sake of the republic, and for its treasury resisted avarice, consulted for the good of their country with a spirit of freedom, addicted neither to what their laws pronounced to be crime nor to lust. By all these acts, as by the true way, they pressed forward to honors, power and glory; they were honored among almost all nations; . . . and at this day, both in literature and history, they are glorious among almost all nations."<sup>5</sup> Naturally Augustine does not forget that his country's ancient worthies were "overcome by love of fatherland and ardent desire for praise."

*Vincit amor patriae laudumque immensa cupido.*

*Haec sunt duo illa, libertas et cupiditas laudis humanae, quae ad facta compulsi miranda Romanos:*<sup>6</sup> and of course for the saint of Hippo at the opening of the Middle Ages *cupiditas laudis humanae* is a motive even more despicable than it was still felt to be at the close of the mediæval period by his vacillating fol-

<sup>2</sup> Cf. Harnack, *History of Dogma* (tr.), V, 153.

<sup>3</sup> *De Civitate Dei* (ed. B. Dombart, 1863), IV, 4.

<sup>4</sup> *Ibid.*, V, 1. In general. cf. Mausbach, *Die Ethik des Heiligen Augustinus*, 1909, I, 332-333: "Verkörperung des Weltreiches ist der heidnische, auf Vergötterung des Kreatürlichen ruhende Staat, nicht der Staat als solcher. Der letztere gehört wie die Güter der Menschennatur und der Familie zu einem Mittelbezirke zwischen den beiden Gegensätzen, dessen sich beide bedienen und bemächtigen müssen."

<sup>5</sup> *De Civ. Dei*, V, 15 (tr. Dods).

<sup>6</sup> *Ibid.*, V, 18. Cf. *ibid.*, Preface: ". . . iam . . . videamus, qua causa Deus, qui potest et illa bona dare, quae habere possunt etiam non boni ac per hoc etiam non felices, Romanum Imperium tam magnum tamque diuturnum esse voluerit." The utility of the temporal to the celestial peace is set forth in *De Civ. Dei*, XIX, 13, 14, 16, 17. It is worth noting that Augustine mentions a befitting synchronism between the founding of Rome and the beginning of Israelitish prophecy (*ibid.*, XVIII, 27).

lower, Petrarch. Notwithstanding, the seekers of the City of God may find spur and exemplar in these seekers of temporal welfare and human praise: "Let us consider," urges the saint, "how great things they despised, how great things they endured, what lusts they subdued for the sake of human glory, who merited that glory, as it were, in reward for such virtues; and let this be useful to us even in subduing pride, so that, as that city in which it has been promised to us to reign as far surpasses this one as heaven is distant from the earth . . . the citizens of so great a country may not seem to themselves to have done anything very great if, in order to obtain it, they have done some good works or endured some evils, when those men for this terrestrial country already obtained, did such great things, suffered such great things."<sup>7</sup>

How better, then, might Augustine express his patriotic good will toward his earthly country than by exhorting it to become a member of his celestial country? One of the most eloquent passages of the entire *Civitas Dei* is precisely such an invitation: *Nunc jam caelestem arripe, pro qua minimum laborabis, et in ea veraciter semperque regnabis. Illic enim tibi non Vestalis focus, non lapis Capitolinus, sed Deus unus et verus*

*nec metas rerum nec tempora ponit,  
Imperium sine fine dabit.*<sup>8</sup>

An identical thought is voiced in one of the sermons: *Manet civitas quae nos carnaliter genuit. Deo gratias. [No cold patriotism!] Utinam et spiritualiter generetur, et nobiscum transeat ad aeternitatem.*<sup>9</sup>

*Augustine took a lively interest in the fortunes of the state.*

The sermons and correspondence, alike, of St. Augustine, evince an anxious interest in contemporary political conditions, and, notably, in the Visigothic invasion. The letter to Italica, of about

<sup>7</sup> *Ibid.*, V, 17 (tr. Dods). At the end of the chapter Augustine finds a shadowy type of the Eternal Country in "asylum illud Romuleum, quo multitudinem, qua illa civitas conderetur, quorumlibet delictorum congregavit inpunitas." This is quite in the spirit of Dante's *De Monarchia*. Cf. also *Epistula CXXXVIII*, art. 17, in *Patrologia Latina*, XXXIII, 533, and Goldbacher, *Corpus Scriptorum Ecclesiasticorum Latinorum*, XLIV, 144-145.

<sup>8</sup> *De Civ. Dei*, II, 29. Cf. *ibid.*, II, 19, 21 and IV, 3, 4.

<sup>9</sup> *Sermo CV*, 7 in *Pat. Lat.*, XXXVIII. The next sentence is: "Si non manet civitas quae nos carnaliter genuit, manet quae nos spiritualiter genuit" and the chapter concludes with a discussion of the prophecy: "Exsurget gens super gentem, et regnum super regnum."

the time of the sack by Alaric, complains that the lady has not kept him informed of the Italian situation: "To this last letter, just now received, I lose no time in promptly replying, because your Excellency's agent has written me that he can send my letter without delay to Rome. By his letter we have been greatly distressed, because he has [not] taken pains to acquaint us with the things which are taking place in the city or around its walls, so as to give us reliable information concerning that which we were reluctant to believe on the authority of vague rumors. In the letters which were sent to us previously by our brethren, tidings were given to us of events, vexatious and grievous, it is true, but much less calamitous than those of which we now hear. I am surprised beyond expression that my brethren the holy bishops did not write to me when so favorable an opportunity of sending a letter by your messengers occurred, and that your own letter conveyed to us no information concerning such painful tribulation as has befallen you,—tribulation which, by reason of the tender sympathies of Christian charity, is ours as well as yours. I suppose, however, that you deemed it better not to mention these sorrows, because you considered that this could do no good, or because you did not wish to make us sad by your letter. But in my opinion, it does some good to acquaint us even with such events as these: in the first place, because it is not right to be ready to 'rejoice with them that rejoice,' but refuse to 'weep with them that weep;' and in the second place because 'tribulation worketh patience.' . . . Far be it, therefore, from us to refuse to hear even of the bitter and sorrowful things which befall those who are very dear to us!"<sup>10</sup>

If the just quoted letter imply a personal rather than a general sympathy, the sermons reveal Augustine's attitude toward the sufferings of the commonwealth as a whole. However redolent of other-worldliness, the sermons numbered CV and CCXCVI in Migne<sup>11</sup> are thus redolent only as are the passages therein borrowed from the Book of Job. As the ultimate clinging to God of the man of Uz is the expression and fruit of the deepest anguish of soul for the loss of sons and daughters, of wealth and neighborhood repute, so St. Augustine's recourse to God and to divine consolation suggests the agony of heart caused by the miseries of his country. "Be the world prosperous, be the world overturned: 'I

<sup>10</sup> Ep. XCIX, in Goldbacher, *op. cit.*, XXXIV and Pat. Lat., XXXIII. *Tr.* Cunningham.

<sup>11</sup> Pat. Lat. XXXVIII.



will bless the Lord,' who made the world. Utterly will I bless Him. Be it well according to the flesh, be it evil according to the flesh, 'I will bless the Lord at all times: His praise shall continually be in my mouth!' . . . 'The Lord gave and the Lord hath taken away: as the Lord pleases, so is it done: blessed be the name of the Lord.'''<sup>12</sup> And similarly with the other sermon: "The body of Peter, men are saying, lies in Rome; in Rome lies Paul's body, in Rome the body of Lawrence, in Rome lie the bodies of other holy martyrs—and Rome is wretched, Rome is devastated, afflicted, destroyed, burned. So numerous are death's slaughters, by famine, by pestilence, by sword: where are the shrines [*memoriae*, shrines, memories—an apparent play on words, quite Augustinian] of the Apostles? What sayest thou? Lo, this is what I said: Rome suffers so many evils, where are the shrines of the Apostles? They are there, but they are not in thee. Would they were in thee, whoever thou be who sayest such things, who art thus void of comprehension, who, called by the Spirit, art wise after the flesh! . . . Be patient, the Lord wills it. . . . Behold the Lord, thy God, behold thy Head, the example of thy life; harken to thy Redeemer, thy Shepherd: 'O my Father, if it be possible, let this cup pass from me.' Consider how He shows a human will and [yet] forthwith changes aversion to obedience—'Nevertheless not as I will but as Thou wilt, Father.'''<sup>13</sup> In such threnodies, at least, Augustine exhibits an emotion which is more than Neo-Platonic disinterestedness or monkish contempt!

On occasion, moreover, this quietistic and ascetic mystic exhibits the most earnest interest in practical measures for the suppression of danger to the integrity of the state and of society, even to the extent of according public security definite precedence over the claims of private renunciation. In evidence is a letter to Count Boniface upbraiding this official for inefficiency in office. The count is reminded that he had inclined to enter the monastic life but had been dissuaded by the joint advice of Alypius and Augustine, who, instead, had recommended adherence to continency in private life, but a continued connection with civic and military affairs. Boniface is now not only compromising his spiritual welfare by a second marriage—and that, too, with a lady who has been an Arian heretic—but is proving recusant to his military trust. "But what shall I say," complains Augustine, "of the

<sup>12</sup> Sermo CV.

<sup>13</sup> Sermo CCXCVI.

devastation of Africa at this hour by hordes of African barbarians, to whom no resistance is offered, while you are engrossed with such embarrassments in your own circumstances, and are taking no measures for averting this calamity? Who would ever have believed, who would have feared, after Boniface had become a Count of the Empire and of Africa, and had been placed in command in Africa with so large an army and so great authority, that the same man who formerly, as Tribune, kept all these barbarous tribes in peace, by storming their strongholds, and menacing them with his small band of brave confederates, should now have suffered the barbarians to be so bold, to encroach so far, to destroy and plunder so much, and to turn into deserts such vast regions once densely peopled? Where were any found who did not predict that, as soon as you obtained the authority of Count, the African hordes would be not only checked but made tributaries to the Roman Empire? . . . If these benefits, though earthly and transitory, are conferred on you by the Roman Empire,—for that Empire itself is earthly, not heavenly, and cannot bestow what it has not in its power,—if, I say, benefits are conferred on you, return not evil for good. . . .”<sup>14</sup> These, no doubt, are the words of a mediaeval transcendentalist, but they are hardly the language of a luke-warm patriot nor of an ill-balanced fanatic.

*Augustine misjudged the seriousness of the contemporary situation.*

As everyone knows, the rhetoric of the great church father is frequently characterized by a refrain of weariness and woe: *Concutitur mundus, excutitur vetus homo; premitur caro, liquescit spiritus.*<sup>15</sup> To translate is to lose the sob of it. *Perit mundus, senescit mundus . . . laborat anhelitu senectutis.*<sup>16</sup> Notwith-

<sup>14</sup> Ep. CCXX, in Goldbacher, *op. cit.*, LVII, and Pat. Lat., XXXIII. Tr. Cunningham. Cf. Ep. CCXXXVIII, to bishop Honoratus, advising the clergy to remain by their flocks in time of danger. The advice rests on distinctly religious grounds but illustrates, none the less, the active and practical side of Augustine's genius (Goldbacher and Pat. Lat., *ut sup.*) Cf., also, Joseph McCabe, *St. Augustine and His Age*, 1903, 487 *et seq.* Few first class biographies are less sympathetic in their treatment of their subjects.

<sup>15</sup> Sermo CCXCVI, *ut sup.*

<sup>16</sup> Sermo LXXXI, in Pat. Lat., XXXVIII. Cf. Sermo CCXCVI: “Audistis fratres, simul audivimus: *Erunt bella, erunt tumultus, erunt pressuræ, erunt fames.* Quare nobis ipsis contrarii sumus, ut quando leguntur credamus, quando implentur, murmuremus? Sermo CV: Virgil is made to say that he placed the famous lines: *His ego nec metæ rerum, nec tempora pono; imperium sine fine dedi*, into the mouth of Jove as not believing in their truth, and to affirm that his true views are to be found in the *Georgics*: *non res Romanæ perituraque regna.* Ep. XCIX (to *Italica*): *omnes autem nos dominus consolatur, qui et hæc temporalia mala prædixit et post hæc bona æterna promisit.* Ep. CXXVII, in Goldbacher, XLIV and Pat. Lat., XXXIII: *Labores et pericula et exitia huius transitoriae vitæ.* Sermo XI.

standing, the attentive auditor is again and again conscious of an iterated *non desperandum*. As will be explained directly, this is in part due to the Augustinian philosophy: in part, however, it is due to an inadequate estimate of the seriousness of contemporary conditions. As often before, so now, the state is being bettered, not destroyed, by its afflictions. “. . . the Roman Empire is afflicted rather than changed,—a thing which has befallen it in other times also, before the name of Christ was heard, and it has been restored after such affliction,—a thing which even in these times is not to be despaired of. For who knows the will of God concerning this matter?”<sup>17</sup> The sack of A. D. 410 is perhaps the worst of Rome’s misfortunes—Augustine is by no means sure of it<sup>18</sup>—but the chastisement is after all a merciful one.<sup>19</sup> “Behold,” he exclaims in one of his discourses, it is said “Rome is perishing in the times of the Christians: perchance Rome is not perishing: perchance it is being scourged, not cut off: chastized, not destroyed. Perchance Rome perishes not provided Romans do not perish. For they will not perish if they shall praise God: they will perish if they shall blaspheme. For what is Rome, if not Romans?”<sup>20</sup> The most remarkable example of this minimizing of the catastrophe of 410 is the *Sermo de Urbis Excidio*<sup>21</sup> which credulously cites the escape of Constantinople from a marvelous manifestation of divine wrath during the reign of Arcadius and maintains that the situation of 410 is analogous: “By the hand, therefore, of an amending God is that city receiving correction rather than destruction. Like a servant who, knowing the master’s will, does deeds worthy of stripes, it shall be beaten with many blows.”

Both in his apologetic, or quasi-apologetic, writing, as in the above sermon, and in his familiar correspondence, Augustine treats the disasters of the day as casual and not as final. Nor is it proper to ascribe this to apologetic requirements.<sup>22</sup> So thorough-going a

<sup>17</sup> De Civ. Dei, IV, 7 (tr. Dods). Cf. nn. 8, 9 *sup.* The passage cited is written 415: A. F. West, in Angus, *op cit.*, 60.

<sup>18</sup> Sermo CCXCVI, Pat. Lat. XXXVIII: Sed plus inquit, plus vastatur modo genus humanum. Interim considerata praeterita historia, salva quaestione, nescio utrum plus. Sed ecce sit plus: credo quia plus.

<sup>19</sup> De Civ. Dei, V, 23.

<sup>20</sup> Sermo LXXXI, Pat. Lat. XXXVIII. Cf. Sermo CCXCVI: after all, Rome has been burned twice before; Modo te quid delectat contra Deum stridere, pro ea quae consuevit ardere?

<sup>21</sup> Pat. Lat., XL.

<sup>22</sup> Cf. Dill, Roman Society in the Last Century of the Roman Empire, 2nd ed., 1905, 313–314, 70, n. 4. (On Orosius).

pagan as Rutilius Namatianus took even a rosier view: and, indeed, the sack by Alaric, in itself considered, appears to have been, in reality, a rather tame affair.<sup>23</sup> Surrounded by angry fugitives from the capital,<sup>24</sup> Augustine kept his head, appraised the situation as best he might,<sup>25</sup> avoided undue minimizing of the evil, and equally shunned its exaggeration.<sup>26</sup> That his estimate of conditions was too conservative is due, not to unpatriotic aloofness, but to the lack of perspective inherent in a contemporary position.

*Neo-Platonic Christianity lent moderation to Augustine's grief and to its expression.*

The reaction of the bishop of Hippo to the history of his time was doubtless largely, perhaps chiefly, the manifestation of his religious philosophy, a philosophy based, in its turn, as much on the harrowing experimentations of his soul as on a detached and placid Neo-Platonic metaphysic. His poise and self-possession are less apathy and insensibility than the behaviour of a prophet who sees God in the affairs of men and the affairs of men subsidiary to the eternal and loving purposes of God. Augustine is at once a pessimist and an optimist, and the firmness of his glance upon "the portentous events around him," to employ the phrase of Ozanam,<sup>27</sup> is due less to a balancing of the two tendencies than to a system which preserves each entire and manages harmoniously to blend the two apparent antitheses.

It is quite correct to describe St. Augustine as a thorough pessimist. The human will is, for him, since the Fall, congenitally diseased; the phenomenal world possesses but secondary existence; nature may better be discerned in the mind of God than by direct observation, and investigation of nature, in and for itself, is but soul-damning curiosity; our lives are dreary and arduous pilgrimages to a better land; imperfection is the necessary concomitant of all existence short of that of Deity itself. To be gripped in this view of the world is in advance to possess an antidote to the worst

<sup>23</sup> Dill, *op. cit.*, 309-311. H. F. Stewart, in Cambridge Medieval History, I (1911), 575-576.

<sup>24</sup> Dill, *op. cit.*, 62-63.

<sup>25</sup> Cf. Orosius's blind partizanship. Dill, *op. cit.*

<sup>26</sup> For emphasis on the darker aspects of contemporary life, *vid.*: Sermo CCXCVI in Pat. Lat., XXXVIII; Sermo XI, *ibid.*; Ep. XCIX and CXXVII, in Goldbacher, *op. cit.*, XXXIV; and Sermo LXXXI, in Pat. Lat., XXXVIII.

<sup>27</sup> A. Frédéric Ozanam, History of Civilization in the Fifth Century (*tr.* A. C. Glyn), I, 23.

of temporal misfortune. If Gregory the Great, strengthened by what he could grasp of this philosophy, might not be carried off his feet by the flood of evils of the latter portion of the sixth century, how much less might Augustine be moved by the lesser inundation of the early fifth!

On the other hand, from his very pessimism Augustine squeezes a cheerful and optimistic view of life. Positive though it be as an experience,<sup>28</sup> evil is, in its essence, negative. The only truly evil thing is evil will, and evil will, itself, as will, is good, for the good God could form it only like Himself. The creative Providence, foreseeing in its own eternity the necessary imperfections of temporal creatures made from nothing, plans the proper allowances and provides the appropriate compensations. The darker the background, the brighter the foreground: the sharper the condiment, the more piquant the sauce. The great and final Judgment will explicate and justify those lesser and daily judgments which perturb and perplex the human heart. The ills of life are incidents in the war of the two Cities. In His own time God will segregate the realm of Satan, and the City of God, centered ever in its Founder, be seised of repose unchanging and eternal peace.<sup>29</sup> Augustine, therefore, disciple of Plotinus and Neo-Platoniser of Christianity, is not unpatriotic when he comforts his contemporaries by an attempted valuation of temporal trials in terms of eternity.

In summary, then, it may be affirmed that one's appreciation and estimate of St. Augustine's attitude must necessarily be affected by one's own inmost and deeply private reaction to that "other-worldliness" and mysticism natural to historical Christianity. For the writer, the truth has best been expressed in two mutually supplementary statements of De Pressensé: "We feel that Christian as he is, he remains still a citizen," and "He mourns . . . but his tears do not conceal from him the destinies of the City of God."<sup>30</sup>

<sup>28</sup> Cf. Augustine's Confessions, Books VII, VIII. Paul Elmer More, *Shelburne Essays*, 6th. Series, Augustine, 88-89: "It [the *Tolle, lege; tolle, lege* scene] summoned him from the intellectual consideration of evil as a negation of good to the conviction of sin as something for which he was morally and terribly responsible. . . . Evil was the deliberate setting apart of the human will from the divine will, the voluntary separation of the soul from the source of life."

<sup>29</sup> For an excellent study of the Neo-Platonic character of Augustine's theology, *vid.* L. Grandgeorge, *Saint Augustin et le Néoplatonisme*, 1896.

<sup>30</sup> Quoted by Angus, *op. cit.*, 64-65.



## MILTON AS A WRITER ON EDUCATION

OLIVER M. AINSWORTH

---

Milton's contribution to educational theory, although neatly classified and apparently disposed of by several writers, still has possibilities for the investigator. Oscar Browning tells of a rude shock that his ideas on the subject once received, when he first thought of reprinting Milton's Tractate *Of Education*. "One of the senior masters at my school," says Browning, "set Milton as a subject for a Latin theme to his division, and told his boys that they were to prove that Milton, like Burke, went mad in his old age. I had never heard of this idea before, and I asked the master on what grounds it rested. He replied, 'Did he not write a crack-brained book about education, in his old age?' I concluded that my scheme was useless, and gave it up." Fortunately, however, Browning's discouragement was not final. Thanks to him and to others, Milton's ideas are to-day somewhat better known. And yet, if one may judge from the readiness with which some educators dispose of Milton, their interest does not seem to have penetrated much further than that of Browning's senior master, more than seventy years ago.

Milton's direct experience in teaching lasted only a few years; but the subject of education occupied his thoughts at frequent intervals throughout his whole life, as one may see from the many allusions to it in his writings. Even as an undergraduate at Cambridge, Milton was interested in educational theory. In one of his academic exercises,<sup>1</sup> an address delivered before his fellow-students and his instructors, he attacks the problem, vigorously condemning the barren subtleties of scholastic philosophy, which was then a prominent part of the curriculum, and contrasting it with the pleasures of history, literature, and natural science, in which he would have preferred to spend his time. His little treatise on education appeared some twelve or fifteen years later (1644) in the midst of his earlier writings on public reform. Another notable reference to education is to be found in the tract, *The*

---

<sup>1</sup> Masson, *Life of Milton*, 1:281.

*Likeliest Means to Remove Hirelings out of the Church* (1659). Here Milton desires better schools in different parts of England for the purpose of educating the clergy, without the necessity of their attending the University.<sup>2</sup> Again, in *The Ready and Easy Way to Establish a Free Commonwealth*, Milton's last direct effort in what he believed to be the cause of liberty, he has these remarkable words on the relation of education to representative government: "To make the people fittest to choose, and the chosen fittest to govern, will be to mend our corrupt and faulty education, to teach the people faith, not without virtue, temperance, modesty, sobriety, parsimony, justice; not to admire wealth or honor; to hate turbulence and ambition; to place every one his private welfare and happiness in the public peace, liberty, and safety."<sup>3</sup> Sound education, therefore, is the very basis of Milton's political structure. Even in *Paradise Lost*, as a friend of mine at a neighboring university has recently pointed out, Milton's thought was occupied with education as well as with theology and ethics.<sup>4</sup> These examples show that the idea of a better education was by no means a Utopian scheme of Milton's. He connected it with practical matters which he believed to be of the highest importance.

Moreover, the Tractate *Of Education*, Milton's principal expression of his views on the subject, is not a casual or isolated essay. In *The Second Defense of the People of England* there is a passage where Milton, in defending himself from the personal attacks of a foreign writer, gives rather an extended account of his own life and works. After mentioning his writings on the reform of church government and on marriage, he says: "I then discussed the principles of education in a summary manner, but sufficiently copious for those who attend seriously to the subject; than which nothing can be more necessary to principle the minds of men in virtue, the only genuine source of political and individual liberty, the only true safeguard of states, the bulwark of their prosperity and renown."<sup>5</sup> Thus Milton represents this work as merely incidental to his earlier writings in the cause of reform.

That Milton's opinions were valued, by at least one of his contemporaries, is evident, for the Tractate was written at the earnest solicitation of a friend—a man of some note in the London of

<sup>2</sup> *Prose Works*, ed. by St. John, 3:27.

<sup>3</sup> *Ibid.*, 2:126.

<sup>4</sup> Murray W. Bundy, "Milton's View of Education in *Paradise Lost*," *Journal of English and Germ. Philology*, 21:127.

<sup>5</sup> *Prose Works*, 1:259.



that day. This was Samuel Hartlib, who was well known and highly esteemed as a philanthropist and reformer. Of Prussian birth and Polish-English descent, Hartlib had important friends and correspondents on the Continent as well as in England. His interests ranged all the way from the promotion of mechanical inventions to a scheme of uniting the Protestant churches throughout Europe. Among them was the reform of schools. At the time of Milton's return to England in 1639, Hartlib was especially active in spreading abroad the ideas of Comenius, the great Moravian teacher. Milton expresses the highest regard for Hartlib's character and service; and it is significant of the esteem in which Milton was beginning to be held, that such a man as Hartlib should so earnestly desire his opinion on education.

Nevertheless, there are two points in the Tractate *Of Education* that may scarcely have been pleasing to Hartlib. In the first place, Milton expresses but little regard for Comenius. Milton's practical sense would naturally lead him to take the more skeptical view of the schemes of Pansophia or Universal Wisdom which at this time were bound up in Comenius' mind with the plan of educational reform. And it is likely that, after his years of application to study, and his experience as a teacher, Milton not unjustly believed himself quite as competent to theorize on the subject of education as the most of his contemporaries. At all events he expresses entire indifference to Comenius' writings.

Furthermore, one of the most prominent features of Milton's plan would be looked upon by Hartlib, and also by most modern educators, as a serious limitation. Milton's scheme, unlike that of Comenius, is not intended for the children of all classes; and nothing whatever is said about the education of girls. And yet, from Milton's words in *The Commonwealth* (quoted above) and from Sonnets 10 and 11 and the eulogy on Queen Christina of Sweden,<sup>6</sup> we know that Milton was by no means indifferent to these wider interests. In the Tractate he was particularly concerned with the training of leaders in Church and State, and he naturally looked for them among the young men of the best families.

Now, another of Hartlib's interests was the founding of an agricultural school; consequently, a glance at the reading-list in Milton's curriculum may have pleased him better. It includes many of the authoritative works of the day on natural science and its applications. That these books, as natural-scientific treatises,

<sup>6</sup> *Ibid.*, 1:249-250.

are now out of date, is no fault of Milton's. Natural science in the modern sense had then scarcely begun. The including of writers on agriculture, geography, medicine, and natural history must have appealed to Hartlib's "practical" inclinations. At any rate, it has given rise to a widely spread notion that Milton's academy was informational, rather than disciplinary, in method, and vocational, rather than cultural, in purpose.

It is significant in this connection that the oldest edition of Milton's treatise to be found in the library of Beloit College is bound in the same volume with Locke's *Thoughts Concerning Education*, a work which is a main source of utilitarian doctrine. The association of the two is not accidental. The editors give as the reason for it, that the subject of Milton's treatise "seemed more in harmony with the topics discussed by Mr. Locke than with the contents of any other volume in the intended series."<sup>7</sup>

Charles Lamb in his essay, *The Old and the New Schoolmaster*, clearly strikes the note of criticism. "The modern schoolmaster," says he, "is expected to know a little of everything, because his pupil is required not to be entirely ignorant of anything. He must be superficially, if I may say so, omniscient. . . . You may get a notion of some part of his expected duties by consulting the famous Tractate on Education addressed to Mr. Hartlib."<sup>8</sup>

Dr. Johnson, however, puts the case with greater emphasis, and I may be pardoned for quoting his remarks at more length. In discussing Milton's school he says:

The purpose of Milton, as it seems, was to teach something more solid than the common literature of the Schools, by reading those authors that treat of physical subjects; such as the Georgick, and astronomical treatises of the ancients. . . .

But the truth is, that the knowledge of external nature, and the sciences which that knowledge requires, or includes, are not the great or the frequent business of the human mind. Whether we provide for action or conversation, whether we wish to be useful or pleasing, the first requisite is the religious and moral knowledge of right and wrong; the next is an acquaintance with the history of mankind, and with those examples which may be said to embody truth, and prove by events the reasonableness of opinions. Prudence and Justice are virtues and excellences, of all times and of all places; we are perpetually moralists, but we are geometricians only by chance. Our intercourse with intellectual nature is necessary; our speculations upon matter are voluntary, and at leisure. Physiological learning is of such rare emergence, that one man may know another half his life, without being able to estimate

<sup>7</sup> *Library of Education*, 1:vii. Gray and Bowen, Boston, 1830.

<sup>8</sup> *The Work of Charles and Mary Lamb*, ed. by Thomas Hutchinson, 2 vols., Oxford, 1908, 1:536.

his skill in hydrostaticks or astronomy; but his moral and prudential character immediately appears.

Those authors, therefore, are to be read at schools that supply most axioms of prudence, most principles of moral truth, and most materials for conversation; and these purposes are best served by poets, orators, and historians.<sup>9</sup>

This is rather an uncompromising statement of the case for humanism; and yet for this very reason it is wide of the mark as a criticism of Milton. For Milton himself, above all things else, was a humanist. His life was dominated by intellectual and spiritual ideals. He devoted himself, for the good of humanity, to one of the noblest of human endeavors—the creation of beauty in art. And the art to which he dedicated his great powers of intellect and imagination was the art of poetry; poetry, too, not conceived of as amusement or pastime, but inspired by the most vital principle in human nature—the religious instinct.

One who has read Milton's works with attention and without prejudice can hardly doubt that he was in fundamental agreement with Johnson on the question of what studies are really the most "practical." The general substance of Johnson's remarks may be found in different passages of *Paradise Lost*,<sup>10</sup> and perhaps Milton himself, in deliberate prose, could not have stated his principles more faithfully than Johnson has done.

How, then, has the conception risen that Milton's scheme of education is materialistic? Simply through judging by the lists of reading alone, without sufficient attention to Milton's own explanation of his purpose and method.

Two definitions of education are an outstanding feature of the treatise. Near the beginning Milton says: "The end then of learning is to repair the ruins of our first parents by regaining to know God aright, and out of that knowledge to love him, to imitate him, to be like him, as we may the nearest by possessing our souls of true virtue, which, being united to the heavenly grace of faith, makes up the highest perfection."<sup>11</sup> After discussing the mistakes of the schools and universities, he says: "I call, therefore, a complete and generous education that which fits a man to perform justly, skilfully, and magnanimously, all the offices, both private and public, of peace and war."<sup>12</sup>

It is possible to see in these two definitions two distinct purposes, not wholly in accord with each other. The first is a religious

<sup>9</sup> *Lives of the Poets*, ed. by Waugh, 1:73-74.

<sup>10</sup> *Paradise Lost*, 7:111-130; 8:172-197; 12:553-587.

<sup>11</sup> *Prose Works*, 3:464.

<sup>12</sup> *Ibid.*, 3:467.

purpose, and may be humanistic; the second, considered by itself, is almost certainly utilitarian. And yet it seems strange, in so brief a work, that Milton should have had two purposes in mind at all; and stranger still, that they should have been in conflict, or even unrelated. Such is probably not the case. The true harmony of Milton's definitions may perhaps be most clearly shown by the analogy of faith and works. "These two divisions," says Milton in his *Christian Doctrine*, "though they are distinct in their own nature, and put asunder for the convenience of teaching, cannot be separated in practice."<sup>13</sup> Now, the basis of Milton's educational doctrine is character, both as an end in itself, and as the foundation of true service. These two values of character may be separately studied, but in practical life they are inseparable. Milton had no interest in a "fugitive and cloistered virtue" that never emerges in action. Furthermore, an education which does not produce character cannot, in Milton's estimation, prepare a man for service. For instance, one might suppose that the most important part of a statesman's education would be political science. But what does Milton say of the young men who leave college to enter politics? "Others," he says, "betake them to state affairs, with souls so unprincipled in virtue and true generous breeding, that flattery and court-shifts and tyrannous aphorisms appear to them the highest points of wisdom."<sup>14</sup> To be sure, Milton includes political science in his curriculum; but he sets no great value on science of any kind without right principles to guide and control it.

We may once for all set aside the notion that the school was to be vocational, for Milton expressly states that it is a place of "general studies"<sup>15</sup> in contrast to such special schools as those of law and medicine. The fact of its military organization is more important. Milton labored under no illusions on the subject of war; but he realized the ethical value of military training, as well as its practical necessity.

Let us now glance at one or two interesting features of Milton's curriculum.

The chief medium of instruction in that day was the Latin language; therefore the pupil's first task was to acquire it. The customary method of learning Latin in Milton's time was, first, the memorizing of many cumbrous rules of grammar, (often ar-

<sup>13</sup> *Ibid.*, 4:13.

<sup>14</sup> *Ibid.*, 3:466.

<sup>15</sup> *Ibid.*, 3:467.

ranged, for greater convenience, in rude verse); second, the practice of Latin composition in generous amounts, both in verse and in prose. Some Latin authors, of course, were read; but composition predominated. The pupil began the process about the age of ten, or even younger. If he survived it, he entered the university at the age, perhaps, of sixteen, with a fairly good command of Latin vocabulary, and the ability to understand lectures in the language, and to converse with his fellow-students in it.

The process, however, was not always successful, and never very agreeable. Roger Ascham's treatise, *The Scholemaster*, nearly seventy-five years earlier than Milton's, was the outcome of a conversation over the case of some boys who had run away from Eton School for fear of a beating.<sup>16</sup> One of Comenius' greatest achievements was in simplifying the method of teaching Latin. The problem was a close parallel to our modern one of how to teach the Freshman to write English. We are attacking it very much as Milton's contemporaries did—with unlimited quantities of theme-writing.

However, Milton's views on this subject were revolutionary. He insists on the principle that composition ought to be based on information of some kind, and not painfully spun out of the student's inner consciousness. He calls it a "preposterous exaction" to demand much writing of students until they have read widely in good authors, and acquired a moderate supply of information as well as a sense of style. Milton believed it possible to teach language chiefly through extensive reading—a belief shared by some good teachers to-day. Moreover, he regarded language, not as an end in itself, but merely as "the instrument conveying to us things useful to be known." Therefore, after teaching his students the elements of Latin grammar, he led them rapidly through a considerable amount of reading, and deferred the composition until a later part of the course. He followed the same method with Greek, which, of course, as a humanist, Milton felt to be indispensable.

Next to be considered is the subject-matter of the reading. It is chiefly to this that Dr. Johnson applies his criticism. The first authors to be studied are the Latin writers on agriculture; and between the ages, probably, of thirteen and sixteen, the pupils are to read treatises in Greek and Latin on such matters as architecture, astronomy, geography, medicine, and natural history,

<sup>16</sup> Roger Ascham, *English Works*, ed. by Wright, Cambridge, 1904, p. 175.

not forgetting to note the practical applications of these various arts and sciences, or omitting to call in the aid of practitioners for purposes of demonstration. Arithmetic and geometry had been studied in the earliest year of the course.<sup>17</sup>

All this looks somewhat as if Dr. Johnson were in the right. And yet, while Milton's curriculum incidentally imparts a great deal of information, both curious and useful, his ultimate purpose, even in the study of external nature, was to develop the mind through contemplation. This purpose he makes very clear at the outset, when he says that we cannot in any other way arrive so clearly at the knowledge of things invisible as we can by studying the visible creation.<sup>18</sup> In one passage of *Paradise Lost* Milton compares Nature, or the entire order of the Universe, to a "scale," or ladder,

"Whereon,

In contemplation of created things

By steps we may ascend to God."<sup>19</sup>

And in his essay on *The Reason of Church Government* Milton expressly states that the knowledge of God and of his true worship, and what is infallibly good and happy in the state of man's life, what in itself evil and miserable, is the only high valuable wisdom indeed.<sup>20</sup>

Furthermore, the very multitude of subjects covered in so short a time would make it impossible for the student to become very proficient in any one art or science. The course is distinctly a survey; but the reading of one or more unified treatises on each subject, though not expected to make the student even an amateur, would give him just what Milton desired to impart—an insight into the spirit and method of natural science. A final circumstance, of a kind to show that Milton looked upon natural science decidedly from the cultural point of view, is this: the study of external nature is to be rounded off by reading those poets who treat of it, and add to it what Wordsworth calls "the breath and finer spirit of all knowledge, the impassioned expression which is in the countenance of all science."<sup>21</sup>

<sup>17</sup> *Prose Works*, 3:469.

<sup>18</sup> *Ibid.*, 3:464.

<sup>19</sup> *Paradise Lost*, 5:507-512.

<sup>20</sup> *Prose Works*, 2:473.

<sup>21</sup> *Preface to the Lyrical Ballads*, 1800; *Poetical Works*, ed. by Hutchinson, Oxford, 1913, p. 938.

From the study of external nature the pupils proceed, in the next stage of the course, to the study of human ideals and institutions. Between the ages of sixteen and nineteen, they read the standard treatises on ethics, economics, politics, law, theology, and history both sacred and secular. These subjects are more in accord with what are commonly known as the humanities. They are intended, through the study of man and his works, to give the pupils a further insight into the purposes of the Creator, as well as to acquaint them with the nature of practical affairs. Toward the end of this stage, the greatest masterpieces of literature are read, and an attempt is made to impart something of their true spirit to the students.

In the last stage of all, the pupils are to learn the laws of construction that underlie every great type of writing; and now, but not before, are they to be formally trained in the art of composition, "when they shall be thus fraught with an universal insight into things."<sup>22</sup>

From Milton's use of natural science as a means of training the mind and building character, it may be inferred that he had no superstitious fear of its destroying religious faith. Indeed, in the matter of scientific truth as opposed to civil or ecclesiastical authority, Milton was on the side of scientific truth; for in visiting the aged Galileo, he defied the Inquisition. Milton, however, believed that true science and true theology both are ultimately rational; and he took no interest in the ingenious opposition between them, which has puzzled some minds since the time, probably, of Heraclitus.

At the same time, he realized that the functions of science and of religion are distinct, and that neither one can do the work of both. Science may lead us to a rational conviction of divine truth, but moral power is supplied by faith alone. Accordingly, since his chief object is the development of character, Milton takes care from the very outset of his course to instill religious faith into the minds of his pupils. "After evening repast, till bedtime," says he, "their thoughts would be best taken up in the easy grounds of religion, and the story of scripture."<sup>23</sup> He probably chose the evening as the time when the imagination is most active, and most open to feelings of reverence and affection. The severity of the master would be laid aside; and in after years the pupils would

<sup>22</sup> *Prose Works*, 3:474.

<sup>23</sup> *Ibid.*, 3:469.

cherish the impressions of these hours with a fondness and tenacity that formal precepts never could evoke.

The Tractate *Of Education* is so rich in suggestion that one is confined in a brief space to a few such outstanding features as I have discussed. Perhaps Milton's own words at the close of the treatise, since they show that he felt the work to be suggestive rather than final, may bring this paper to a fitting conclusion.

Thus, Mr. Hartlib, you have a general view in writing, as your desire was, of that which at several times I had discoursed with you concerning the best and noblest way of education; . . . many other circumstances also I could have mentioned, but this, to such as have the worth in them to make trial, for light and direction may be enough. Only I believe that this is not a bow for every man to shoot in, that counts himself a teacher; but will require sinews almost equal to those which Homer gave Ulysses; yet I am withal persuaded that it may prove much more easy in the assay, than it now seems at distance, and much more illustrious; howbeit, not more difficult than I imagine, and that imagination presents me with nothing but very happy and very possible according to best wishes; if God have so decreed, and this age have spirit and capacity enough to apprehend.<sup>24</sup>

---

<sup>24</sup> *Ibid.*, 3:478.



## FLOUNDERING IN MODERNITY

GEORGE C. CLANCY

---

It is surely unnecessary to remind our contemporaries that they are living in a modern age. Our times are reeking with "modernity," whatever that means. To be modern apparently implies escape from the dreary dullness of mid-Victorianism, the ennui of the *fin de siècle*, and the shackles of faith in anything whatsoever. Intellectually, it is a gay time to be on earth. For the generation latest born, life has particular zest. "Bliss is it in this dawn to be alive, but to be young is very heaven." Youth plays saucily with the gray-beards, and the older generation, for all its hoary wisdom, is hard put to it to preserve its dignity—alas, it has to defend its innermost shrines from sacrilege by its own children. If we were inclined to sentimental mooning we could shed a few tears in the grave-yard where lie buried sacred traditions of literature and art, ardent hopes for democracy, and some of the holy faiths of our fathers. Even our efforts at virtue and culture, into which we Americans have thrown what we think is a pardonable enthusiasm, are the object of the indulgent smiles of the intelligentsia. A recent article by a brilliant foreign critic refers to our orgies of prohibition and suppression as unbelievable to the civilized European, calls our reforms debauches of virtue, finds a malady of intellectual anæmia in the varied departments of American life, and scores the books of popular idealists as the namby-pamby product of moral soothsayers. Even the time-honored institution of marriage is under a hot cross-fire; the family, once a centre of intense loyalties, gives evidence of losing its unity; "Home," as Robert Frost says, "home is the place where, when you have to go there, they have to take you in." Our democracy as expressed in the House of Representatives at Washington, we are told is a mess of incompetence and imbecility. H. L. Mencken, writing on "Politics," says that our Congressmen are, in the overwhelming main, shallow fellows, ignorant of the grave matters they deal with and too stupid to learn, with the intelligence of the country newspaper editor, or the evangelical divine. As a

civilization we appear to be in a parlous state, at least if one's view is colored for him by the modern prophet of pessimism.

Yet these clever and incisive writers of our decade are more than masters of the telling phrase. There is ample evidence that things are not as they were with our fathers. Everywhere cables are slipping, moorings are lost; the thought of our age flounders amidst the tide-rips, the cross and shifting currents of an uncharted sea. Denial, rebellion, daring experimentation, are at the wheel, and the compass has evidently been thrown overboard. Thomas Hardy ventures the opinion that it would not be at all amiss if man should undertake the education of God as an effort toward the general improvement of things.

Modernity has entered the classic halls of learning—there is no doubt of that. Indeed, the once sacred precincts are proving particularly fertile soil for the growth of the new idea. In the better institutions, there is apparently little hostility on the part of administration and faculty towards the intellectual insurgency, wherever it is thoughtful and genuine. Unfortunately, college youth often assume an easy cynicism which in its sublime ignorance would be impertinent if it were not so absurd. It flaunts itself in the face of the instructor with such sophomoric assurance and condescending tolerance that the teacher may well be congratulated on his self-control in not wringing the necks of his protégés. But if the instructor has the grace of God in his heart to stand this arrant cockiness, he has reason to welcome the condition of which it is a symptom. It is the evidence nearly always of intellectual alertness, a thing vastly to be desired in the student, and all too frequently sought in vain. Cynicism and rebellion are not diseases of youth to be treated pathologically. They are growing pains, signs of healthy expansion in the body politic. "The most hopeful thing of intellectual promise in America today," says a daring modern writer, "is the contempt of the younger people for their elders; they are restless, uneasy, disaffected." However much our civilization may resent this contempt, it can seek within itself at least partial cause for its repudiation by the rising generation. Too often has it wrapped its faith about with the trappings of sanctity, and sacrificed logic to the promptings of mere sentiment. Striking as were the changes in the thinking of the nineteenth century, we and our fathers have been curiously helpless in our efforts to throw off the inhibitions of tradition. Again and again the cake of custom has not been broken up. The intrepid

spirit of the pioneer in things of the mind has found its freest expression in the realm of physical science. Professor James Harvey Robinson in his much-discussed book, "The Mind in the Making," says: "While we have permitted our free thought in the natural sciences to transform man's old world, we allow our schools and even our universities to continue to incalculable beliefs and ideals which may or may not have been appropriate to the past, but which are clearly anachronisms now. For, 'the social science' taught in our schools is, it would appear, an orderly presentation of the conventional proprieties, rather than a summons to grapple with the novel and disconcerting facts that surround us on every side."

Scholarship has apparently been at its best only where the processes of thought do not concern themselves with human motives or become intertwined with the heart-strings; if they are so involved, argument must make assurance doubly sure and take a bond of fate. Not that our scholarship is ever in the position of abject fear as it faces possible conclusions, but too often the wish is father of the thought, or the bias of heredity and temperament is an unconsciously determining influence. Who is there of us who would not surrender in a moment and without a pang Newton's law of gravitation or the solar system of Copernicus? In the laboratory of the true scientist there is never a fear for what lies at the bottom of the crucible when the test is over. Were the evidence to be found there to mean the denial of the hope of immortality, there would be no moment of hesitation, nor a quiver of the eye-lid. Is not truth in its purity, without compromise, goal sufficient for man or God? Yet we pursue with trepidation the paths that explore the fields of humanistic scholarship and cling with hazy-eyed and fond devotion to the formulæ of the past. More than that, most of us—unconsciously, to be sure—are special pleaders. We have a cause to promote, which is not truth but a particular brand of truth in which we have come to believe. The churchman today, for example, is far too likely to start with his conclusions and work back to his premises. Thus he is frequently driven to unconvincing and even specious argument to support positions rapidly becoming untenable. His cosmic philosophy will not tolerate the conception of a Godless universe or a denial of the immortality of the soul. And the radical thinker, on his part, is likely to be carried away by things in general—in art, literature, politics, and religion; he loses his mental balance, becomes a

shouter of empty slogans. Emma Goldman—of all people!—turns state's evidence on this point. "The average radical," she says, "is as hide-bound by mere terms as the man devoid of all ideas. 'Bloated plutocrats,' 'economic determinism,' 'class consciousness,' and similar expressions sum up for him the symbols of revolt. His hearing is dulled by the din of stereotyped phrases." The world is indeed rife with special pleadings by doctrinaires. We cannot with confidence seek our truth in the printed organ of the socialist party, the religious journal, or in the publications of the "wets." Such literature serves its purpose, which is essentially propagandist, but practically none of it is free from the taint of prejudice. To make the cause prevail—this is the primary purpose, and argument and data are selected and displayed to that end. It would be foolish to seek for an unbiased presentation of truth in any one of them.

In this intellectual chaos, it would not perhaps be unfair to say that scholarship, in its pure and detached form, is about the only agency engaged in a wholly disinterested search for truth—the scholarship of teacher and writer as we find them in their highest realization, the scholarship of the man working in the field of the pure sciences, the scholarship of the discriminating teacher of history, of the keen analyzer of our social unrest. In this statement no reference is made to things of purely spiritual content, except as they rest on scientific fact and so depend for their convincing power on the truth of a cosmic philosophy. If scholarship does occupy and can continue to maintain such a unique position in a world of flux, its power as a guiding and controlling force is inestimable. If it can draw to itself the best minds of the nation, men of intellect, poise, and devotion, men capable of mental perspective and detached judgment, it has a high destiny before it. It would be the supreme court in the world of the mind, judicial, wise, incorruptible. Such a court would command respect and win confidence wherever its qualities were recognized. The insurgency of college students has sometimes troubled good faculty members. They look askance at the welcome accorded at the universities to the preacher of heresies in religion and political economies, at the applause which a stirring apostle of radicalism wins in the college chapel. But if a college faculty is worthy of the great traditions and ideals of scholarship, and by its devotion to truth and untainted judgment has won the confidence of those it teaches, there will be little danger that

student opinion will be swept off its feet by the facile and intoxicating appeal of any superficial speaker. Judgments will be held in abeyance for leisurely review. But if there were to lurk in the mind of the undergraduate a suspicion of the integrity of the scholarship and free mental processes of his instructor, the student will take supreme—and, indeed, well-justified—joy in exploding bomb after bomb within the unprofaned precincts of his college. The student of today is quick as a flash to catch the note of insincerity and weak compromise; though often he himself is given to specious argument, he is scathing in his criticism when he finds such a defect in his instructor's reasoning. Fundamentally, the college student is the most stalwart of moralists, he is insistent on fair play, and his chronic radicalism is his attempt to set the world right. But unfortunately, he is also the most lax of thinking beings, his contempt for things in high places is not a disciplined contempt, he seldom seeks his data far, or subjects himself to the rigors of logical and painstaking analysis. He has the failings of the generation he represents, he is curious about the new, discards the old without compunction or regret, is hurried in his judgments and superficial in his culture; his ardor for things intellectual is unkindled. But his instincts are right and his capacity for devotion to what is fine is unlimited.

In the midst of the college and of the broader world of which the college is a part, the scholar may hold a position of eminence. In his make-up there can be no suggestion of the mere prettiness of culture; his mentality rather connotes wrought-iron; he teaches the Greek virtues of discipline, measure, and proportion; the very essence of his nature is a protest against the facile thinking of the man who would reform the world in thirty days. In the midst of an acquisitive society curiously obsessed by material values, he looks for things that are enduring, things tried by the fierce fires of human experience and suffering. He knows that civilization has been won by painful struggle, that its finest achievements are the product of disinterested searchers for truth. The continuation of the sublime traditions of his profession is not an easy task in these days when a thousand discordant voices are crying in the wilderness, "Prepare ye the way of the Lord." Vague and windy theorizing, glittering generalities, and sweeping denunciations must all be referred to the discriminating and wise scholarship which is the saving hope of our civilization.



## BIBLIOGRAPHICAL EVIDENCE OF THE VOGUE OF SHAFTESBURY IN THE EIGHTEENTH CENTURY

WILLIAM E. ALDERMAN

---

The importance of the contributions of Anthony Ashley Cooper, Third Earl of Shaftesbury, to the science of ethics has long been recognized and frequently elaborated, both in English and in German. Strangely enough, however, he has been notoriously neglected as a writer whose teachings entered largely into the consciousness of his century, and who, consequently, was a potent force in suggesting the content of a large body of English literature. So definitive a work as the *Cambridge History of English Literature* professes to be allows slightly less than two pages in its main entry<sup>1</sup> to an enumeration of his works and a partial cataloguing of his ideas. The utter disregard of certain writers is even more noticeable.<sup>2</sup> Only a very few authors of histories and handbooks give him the place of eminence which is indubitably his.<sup>3</sup>

It has long been the custom to trace a certain bent of the eighteenth century temper either immediately and wholly, in its beginnings, to certain poems of the preceding period, or largely, in its later developments, to certain foreign influences which, as time went on, became operative. To deny the partial truth of either of these points of view would be quite contrary to the spirit and method of this present study; but to suggest that certain poems of the seventeenth century have been credited with greater generative power than they, of themselves, possessed, and that certain foreign ideas found their counterparts already firmly entrenched in English thought and literature, is quite a different matter.

The present study, however, does not aim to suggest an elaborate philosophical background to the moods that mark the beginnings of romanticism, or to establish definitively the thesis that ideas identical with those to which Rousseau gave such brilliant state-

<sup>1</sup> Vol. IX, p. 334 ff.

<sup>2</sup> The index to *English Literature in the Eighteenth Century*, by T. S. Perry, contains not so much as a single reference to Shaftesbury.

<sup>3</sup> Gosse, *Eighteenth Century Literature* is perhaps the most complimentary.

ment, and which are variously branded as romantic, ultra romantic, sentimental, and naturalistic, were part and parcel of English speculations before the intellectual invasion from abroad; for this the reader must look elsewhere.<sup>4</sup> From what follows it is evident, however, that the ideas of Shaftesbury, whatever they were, were both popular and potent in the century to which they were given.

## I.

Forty years after the first collected publications of the essays of Shaftesbury under the title of *Characteristicks of Men, Manners, Opinions, Times* (1711), "Estimate" Brown, in reviewing their reception and influence, remarked: "It has been the fate of Shaftesbury's *Characteristics*, beyond that of most books, to be idolized by one party, and detested by another. While the first regard it as a work of perfect excellence, as containing everything that can render mankind wise and happy; the latter are disposed to rank it amongst the most pernicious of writings, and brand it as one continued heap of fustian, scurrility, and falsehood."<sup>5</sup>

So accurately does this represent the varying currents of approbation and disapprobation, that it deserves the place of prominence that it has been given in this study. For it must be kept in mind continually that the intellectual initiator is certain to have antagonists as well as vindicators, and that the volume of discussion that he provokes is likely to be in direct proportion to his significance. Mediocrity rarely begets either friends or enemies in great numbers. To greatness is reserved the honor of being both understood and misinterpreted.

With half a century more of retrospect than had Brown, Thomas Park, continuing and enlarging the *Royal and Noble Authors* of Walpole, gave attest to the same erratic popularity of Shaftesbury. "Few writings have attracted more attention, or excited more discussion, than the works of this noble author; who has been applauded and condemned with equal extravagance . . . . For a considerable time he stood in high repute as a polite writer, and was regarded by many as the standard of elegant composition; his imitators, as well as his admirers, were numerous, and he was

<sup>4</sup> See *The Significance of Shaftesbury in English Speculation*, by the present writer, P. M. L. A., Vol. XXXVIII, 175-195; *The Style of Shaftesbury*, also by the present writer, M. L. N., Vol. XXXVIII, 209-215; *Shaftesbury and the Ethical Poets*, by C. A. Moore, P. M. L. A., Vol. XXXI, 264-325.

<sup>5</sup> *Essays on the Characteristics*, p. 1.



esteemed the head of the school of sentimental philosophy. Of late years he has been as much depreciated as he was before extolled.”<sup>6</sup>

Although it is not at present the primary purpose to examine definitely that host of friendly and unfriendly essays of which the *Characteristics* was provocative, it must be borne in mind continually that they do attest eloquently to the fact that Shaftesbury had entered into the philosophical and theological consciousness of his own century, and that he was generally regarded as the most typical representative of a certain body of ideas, variously thought of as being wholesome or pernicious. It matters not, therefore, whether a writer champions, extenuates, or assails our author, his manner, or his doctrines; all attitudes substantiate the fact that Shaftesbury was to the people of his age a figure of no inconsiderable prominence.

Furthermore, it should be noted that, although many of the tenets of Shaftesbury are actually traceable to former sources, he is, for all practical purposes, generally regarded as their originator. It was he who gave them their most brilliant statement, and it was he, therefore, more than any one else, who was responsible for their vogue. It was with Shaftesbury himself, and not with his intellectual progenitors, that such prominent literary, philosophical, and theological writers as Mandeville, Butler, Berkeley, and Hutcheson were concerned. The frequency of his name in titles, and the direct and indirect references to him in poems, essays, novels, and controversial literature show how intimately and inseparably he was connected in the general consciousness with the inception and propagation of the ideas that stand to his credit or discredit.

This close association of the name of Shaftesbury with a large body of sentimental and optimistic ideas, and his indubitable prominence in several of the important intellectual wars of the century, lead one inevitably to question the validity of that form of criticism that has been all too religious in its attempt to trace to foreign sources all that is bad and much that is good in English thought and literature. Such a critic as Professor Babbitt sees immediately that “Considered purely as an initiator Shaftesbury is probably more important than Rousseau.”<sup>7</sup> But even a superficial examination of the writings of the century enforces the fact that he was more than initiator; he was a sincere and vigorous

<sup>6</sup> Walpole's *Royal and Noble Authors*, 5 vols., London, 1806, IV, 55.

<sup>7</sup> *Rousseau and Romanticism*, p. 44.

propagandist, whose writings, by reason of their manner and matter, became immediately popular and affected deeply the speculations of the time.

Elsewhere instances of a nature different from those cited below have been multiplied to show how Shaftesbury insinuated himself upon the thought of the age.<sup>8</sup> In many cases the borrowings have been immediate; in others, they are apparently secondhand. But this by no means lessens the importance of our figure. Whether the idea of a subsequent writer came from Shaftesbury, or Pope, or Akenside, or Hutcheson, or any one of a dozen others, matters little. The fact remains that Shaftesbury was a brilliant initiator, whose disciples helped to spread his doctrines broadcast. Socrates taught Plato, Plato taught Aristotle, and Aristotle taught Alexander the Great; but this does not lessen the greatness of the first of this illustrious quartette,—quite the contrary. Shaftesbury taught Hutcheson, Pope, and Thomson, and they, in turn, taught an increasingly large number of writers; but Shaftesbury remains the source whence the streams of optimism and sentimentalism of a certain hue flow.

## II.

Anthony Ashley Cooper, the son of Dryden's "shapeless lump" and the grandson of his "Achitophel," had the good fortune to be ushered into this world with Locke as the attending physician. By the grandfather, to this already famous philosopher was entrusted the health and mental development of the child. Applying his own theories of education, Locke had young Ashley instructed in Latin and Greek by the conversational method. The success of the method and the precocity of the youngster both find support in the fact that at the age of seven the coming Earl could read both languages readily—a fact that needs to be kept in mind when dealing with his indebtedness to the ancients. His travels on the continent after leaving school in 1686, his year in Holland after his enforced retirement from Parliament in 1698, his year in Holland in 1703–1704 when his health was "mightily impaired by fatigue in public affairs," and his withdrawal to Italy in 1711, all helped to make him the cosmopolitan that he was. His political positions gave him prestige and wide associations at home; and his affability and mental vigor made him the acceptable com-

<sup>8</sup> See note 4 *supra*; *The Influence of Shaftesbury on English Literature in the Eighteenth Century*, by the present writer, in MS in the library of the University of Wisconsin.

panion of such luminaries as Bayle and Le Clere abroad. Were not the purpose of this study other than biographical, much of interest could be said relative to his ardent Whiggism, his constant devotion to principle, the simplicity and sincerity of his private life, and his benevolence toward literary men, struggling students, and the poor of his own neighborhood. For these the reader must look elsewhere.<sup>9</sup> Suffice it to say here that such was his general culture that he has without exaggeration been called "the Matthew Arnold of Queen Anne's reign."<sup>10</sup> Gosse has characterized him as "the most accomplished Englishman of his day, the man with the widest taste and the most complete culture, while the purity of his personal character matched well with the charm of his intellect."<sup>11</sup> Generous both in theory and in practice; prodigal with advice, yet consistent and temperate in habits; devoted to a certain set of principles, but catholic in his point of view; this statesman, philosopher, and litterateur died before he had yet completed his forty-second year.<sup>12</sup> He was never vigorous physically, but lived actively and well; and his works stand as his best memorial.

Shaftesbury's first venture into print was in the year 1698 when a preface by him was prefixed to a volume of *Selected Sermons* by Dr. Benjamin Whichcote, the distinguished Cambridge Platonist or Latitudinarian.<sup>13</sup> A glance at their contents reveals the cause of Shaftesbury's warm feeling for them, for already at this early age he was committed to the "Benevolent Theory of Morals." The sermons became very rare, but were reprinted in Edinburgh in 1742, this time with a preface by Dr. Wishart.<sup>14</sup> Shaftesbury's *Preface* was reprinted in connection with a volume of his letters, which counted as the fourth volume of his *Characteristics*, in 1758.<sup>15</sup>

In 1698 Shaftesbury was compelled by poor health to leave Parliament and to seek strength in Holland. It was during this sojourn abroad that Toland surreptitiously published the *Inquiry*

<sup>9</sup> See Stephen's article in D. N. B.; Rand, *Life, Letters and Philosophical Regimen*; Fourth Earl of Shaftesbury, *Life of the Third Earl*; Bayle, *Life of Shaftesbury*, in General Dictionary.

<sup>10</sup> Leslie Stephen, *Freethinking and Plainspeaking*, p. 242.

<sup>11</sup> *Eighteenth Century Literature*, p. 171.

<sup>12</sup> Stephen, *English Thought in the Eighteenth Century*, II, 20, note, says that the *Characteristics* first appeared in 1711, the year of his death. This is an error. The *Characteristics* did first appear in 1711, but Shaftesbury did not die until 1713.

<sup>13</sup> For a full statement of the relationship that existed between Shaftesbury and Whichcote see P. M. L. A., XXXVIII, 183-189.

<sup>14</sup> See also *The Works of Benjamin Whichcote*, Aberdeen, 1751; Ernest P. Cambrague, *The Cambridge Platonists*, 1901.

<sup>15</sup> Fowler, *Shaftesbury and Hutcheson*, New York, 1883, p. 48.

concerning *Virtue* (1699).<sup>16</sup> Robertson's remark "that Shaftesbury should at the age of eighteen have produced from his own meditations a finished and formal treatise, of which the theses were capable of influencing European thought for a century, would be an extravagant assumption,"<sup>17</sup> is misleading, if not absolutely wrong as to date. Evidently he is thinking of the years 1698 and 1699, for he goes on to say that Shaftesbury could have learned his Spinoza in Holland at this time. This would make Shaftesbury twenty-eight rather than eighteen—a considerable difference, indeed! He can hardly be thinking of what Fowler<sup>18</sup> styles a "rough draft" sketched when the Third Earl was twenty. Nor did Shaftesbury regard this premature publication as "finished and formal," for in the First Edition of the *Characteristicks* (1711) the statement is made that the essay was "formerly printed from an imperfect copy; now corrected and publish'd intire." However complete the revision may have been,<sup>19</sup> it is certain that long before the publication of the *Preface* to Whichcote's *Sermons*, Shaftesbury was thinking deeply on questions that were to lead him to his system of ethics. The contradiction between zeal and lack of humanity in religion gave him occasion to inquire "what honesty or virtue is, considered by itself, and in what manner it is influenced by religion; how far religion necessarily implies virtue; and whether it be a true saying that it is impossible for an atheist to be virtuous, or share any real degree of honesty or merit."<sup>20</sup>

The so-called French Prophets, or poor Cevenol Protestants, by their extravagant enthusiasm and insane practices drew forth the opinion of Shaftesbury in *A Letter Concerning Enthusiasm* (1708) addressed to Lord Somers. Various methods of dealing with them had been proposed, but Shaftesbury contended that "raillery" and "good humor" were most potent against false enthusiasm, that "Ridicule and not Punishment, is the most effective weapon of Fanaticism." The *Letter* stirred up three replies in 1708 and 1709, and Shaftesbury returned to his general

<sup>16</sup> Stephen, *English Thought in the Eighteenth Century*, II, 20, note, remarks that the "Essay on 'Virtue' had been published in an imperfect state by Toland in 1698." Shaftesbury did go to Holland in 1698, but did not return to England until November 10, 1699. Evidently the publication took place in this latter year, for the essay is described in the first edition of the *Characteristics*, 1711, as "first published in 1699."

<sup>17</sup> *Characteristics*, Vol. I, p. XXXII.

<sup>18</sup> P. 15.

<sup>19</sup> Shaftesbury bought up the whole impression of Toland when but a few copies had been sold; consequently it is almost impossible to get hold of the earlier version for purposes of comparison.

<sup>20</sup> *Inquiry concerning Virtue*, Bk. I, Pt. I, section 1.

thesis in *Sensus Communis: An Essay on the Freedom of Wit and Humor*, (May, 1709).

*The Moralists, a Philosophical Rhapsody* (1709) is in imitation of the *Dialogues* of Plato. Bishop Hurd speaks of it as one of the three dialogues in the English language fit to be mentioned;<sup>21</sup> and this is no small praise, for some had preceded it and many others were to follow before Hurd passed his judgment. As Theocles, Shaftesbury unfolds his optimistic theories and theology, and sings his Nature hymns.

His next treatise, *Soliloquy: or Advice to an Author* (1710), is a mine of comment and reflection on various topics.<sup>22</sup> Of it he says in his *Miscellaneous Reflections* that "His pretense has been to advise Authors and Polish Styles; but his aim has been to correct Manners, and regulate Lives."<sup>23</sup>

*Miscellaneous Reflections* (1711) was first published in the First Edition of the *Characteristics*. Later it was described as "first printed in 1714", an error due, perhaps, to "Printed in the year M.DCC.XIV" which appears on the title page to the treatise in the collected works of that date. These *Reflections*, varied and illuminating, were intended to bolster and supplement the other treatises.

In Naples, whither he had gone for his health in 1711, he wrote *A Notion of the Historical Draught or Tablature of the Judgment of Hercules* and the *Letter Concerning Design*. The former was first printed in France, in the *Journal des Sçavans* for November, 1712, and appeared in English, separately, in 1713, and in the *Characteristics* of 1714; the latter, although it occurs in a large paper copy of the Second Edition in the British Museum, seems not to have been included generally until 1732.

That Shaftesbury was an assiduous writer of letters can be seen both from the total number that he wrote and the painstaking with which each was written. *Several Letters written by a Noble Lord to a Young Man at the University*, addressed to Michael Ainsworth, appeared first in 1716 and again in 1732. In 1721, Toland, forgetful of his first surreptitious venture of 1699 that had been so generously followed by an annual stipend from Lord Ashley, again

<sup>21</sup> *Works*, London, 1811, Vol. III, pp. 24-25. He says, "The Dialogues I mean are, *The Moralists* by Lord Shaftesbury; Mr. Addison's *Treatise on Medals*; and the *Minute Philosopher* of Bishop Berkeley." Also quoted by Warton, *Essay on Pope*, London, 1806, Vol. II, p. 198.

<sup>22</sup> For an excellent summary of it see Fowler, p. 54.

<sup>23</sup> Cited by Fowler, p. 54.

broke faith, this time with Shaftesbury's relatives and friends, by bringing out an unauthorized edition of certain private letters to Robert Molesworth. The epistles, according to Toland's "large introduction" are "upon two of the nicest Subjects possible, and the most important to Mankind; the one private, the other publick; the first being *the Choice of a Wife*, and the second *the Service to one's Country*."<sup>24</sup> Subsequent volumes of letters appeared in 1746, 1750 and 1758.

All of the works intended by Shaftesbury for publication, with the exception of the *Preface* to Dr. Whichcote's *Sermons*, are to be found in editions of the *Characteristics* beginning with 1732. His letters, the so-called *Philosophical Regimen*,<sup>25</sup> and treatises III and IV of *Second Characters*<sup>26</sup> did not appear until after his death.

Little more than a mere catalogue of his works has been attempted. The chronological tabulation of them given below<sup>27</sup> is illuminating, in that it shows that they were in great demand, and that his popularity did not die out at any point in the century.

<sup>24</sup> Letters to Molesworth, p. 1.

<sup>25</sup> Published 1900, Benjamin Rand, editor, Macmillan Co., N. Y.

<sup>26</sup> Rand, Cambridge University Press, 1914.

<sup>27</sup> 1698 *Preface* by Shaftesbury to *Selected Sermons* of Benjamin Whichcote.

1699 *Inquiry concerning Virtue*, surreptitiously published by Toland.

1708 *Letter concerning Enthusiasm*.

1709 *The Moralists, a Philosophical Rhapsody*.

1709 *Sensus Communis: An Essay on the Freedom of Wit and Humor*.

1710 *Soliloquy: or Advice to an Author*.

1711 *Miscellaneous Reflections* (published in the *Characteristics*).

1711 *Characteristicks of Men, Manners, Opinions, Times*, First Edition, 3 vols.

1712 *The Judgment of Hercules* (in French).

1713 *The Judgment of Hercules* (in English).

1714 *Letter concerning Design* (appears for the first time in a large paper copy of the Second Edition of the *Characteristics* in the British Museum.)

1714 *Characteristics*, Second Edition, 3 vols.

1716 *Several Letters written by a Noble Lord to a Young Man at the University*, addressed to Michael Ainsworth.

1721 *Letters from the Late Earl of Shaftesbury to Robert Molesworth, Esq.* Introduction by Toland.

1723 *Characteristics*, Third Edition. 3 vols., 8vo., London.

1727 *Characteristics*, Fourth Edition, 3 vols., 8vo., London.

1732 *Characteristics*, Fifth Edition, 3 vols., 8vo., London

1732 *Several Letters written by a Noble Lord to a Young Man at the University*.

1733 *Characteristics*, Another Edition, 3 vols., 12mo., London.

1737 *Characteristics*, Sixth Edition, 3 vols., 8vo., London.

1744 *Characteristics*, Another Edition, 3 vols., 12 mo.

1746 *Letters of the Earl of Shaftesbury*, collected in one volume.

1749 *Characteristics*, Another Edition, 3 vols., 12mo., London.

1750 *Letters of the Earl of Shaftesbury*, collected in one volume.

1758 *Letters of the Earl of Shaftesbury*, including the *Preface* to Dr. Whichcote's *Sermons*.

1773 *Characteristics*, Fifth Edition, printed by Baskerville, Birmingham.

1790 *Characteristics*, with a collection of letters, 8vo., Basil.

Long before Shaftesbury had established himself as a writer, the appearances of his unsigned treatises excited wide comment and speculation. Swift, writing from London to Robert Hunter in Paris, January 12th, 1708–09, remarks, “I cannot forbare telling you of your méchanceté to impute the *Letter on Enthusiasm* to me; when I have some good reasons to think the author is now in Paris.”<sup>28</sup> And again in writing to Ambrose Philips, September 14, 1708, he says, “There has been an essay on *Enthusiasm* lately published, that has run mightily, and is very well writ. All my friends will have me to be the author, *sed ego non credulus illis*. By the free Whiggish thinking I should rather take it to be yours, but mine it is not. . . .”<sup>29</sup>

The appearance, during the period 1698–1790, of twenty-five publications and republications of the works of this “noble author” was not without its cause. The books were popular and sold rapidly. The editor of the 1733 pocket edition triumphantly asserts that “all the best Judges are agreed that we have never had any work in the English language, so beautiful, so delightful, and so instructive as these *Characteristicks*.”<sup>30</sup> Nor can this be considered a commercial exaggeration, for he goes on to state what obviously was a fact: “And five large Editions being sold off, give a very sensible proof of their being generally liked.” Eleven editions of the *Characteristics*, each of three volumes, appeared between 1711 and 1790. “The reception these writings have met with from all persons of good taste and judgment, has been such as might have given great satisfaction to that truly noble and ingenious Author, if he had lived longer to enjoy it.”<sup>31</sup>

### III.

Nor are these numerous appearances of his works the only proofs of his vitality. Scarcely had his unsigned *Letter concerning Enthusiasm* (1708) appeared, when speculation began as to its authorship. Swift generally was thought to be its originator, but he in turn passed the implication on to Philips and Hunter. There were forthcoming almost immediately three replies—*Remarks on a Letter by a Lord concerning Enthusiasm, not written in raillery but in good humor*, published anonymously; *Bart’lemy Fair*, or

<sup>28</sup> *Correspondence of Jonathan Swift*, edited by F. E. Ball, London, 1910, p. 136.

<sup>29</sup> *Correspondence*, London, 1910, p. 111.

<sup>30</sup> *Preface to 1733 edition*.

<sup>31</sup> Gosse, *Eighteenth Century Literature*, p. 387.

*an Enquiry after Wit*, by Dr. Wotton; and *Reflections upon a Letter concerning Enthusiasm*, now generally credited to Dr. Edward Fowler, Bishop of Gloucester. All were alert to the possibility of the author's implied reflection upon the English clergy as well as his open attack on the Cevenol peasants. Shaftesbury was swift to come to the defense of his cherished doctrine with *Sensus Communis: An Essay on the Freedom of Wit and Humor* (1709). What, apparently, is another attack is that attributed to M. Astell entitled "*An Enquiry after Wit: wherein the trifling argument and impious raillery of the late Earl of Shaftesbury in his Letter concerning Enthusiasm . . . are fully answered.*"<sup>22</sup>

Doubtless the most formidable opponent of Shaftesbury was the arch cynic Bernard de Mandeville (1670-1733) whose *A Search into the Nature of Society* (1723), added to the second edition of the *Fable of the Bees*, launched his attack. As the eighteenth century representative of Hobbes he sees in man a "Compound of Evil Passions", makes a benefit of luxury, a vice of natural passions, and a necessity of crime. "Two systems", he says, "cannot be more opposite than his Lordship's and mine." By continuing his attacks in the *Dialogues*, published as a second part of the *Fable of the Bees* in 1728, Mandeville, as Cleomenes, represents Shaftesbury as an enemy of revealed religion.

But Mandeville's attack was too coarse to be tolerated by self-respecting and nation-loving subjects, and again Shaftesbury had his defenders in rapid succession. John Dennis's *Vice and Luxury Public Mischiefs* (1724), William Law's *Remarks on the Fable of the Bees* (1724), Richard Fiddes's *A General Treatise on Morality* (1724), Francis Hutcheson's *An Inquiry into the Original of our Ideas of Beauty and Virtue* (1725) and his *Observations upon the Fable of the Bees* (1725-27), Archibald Campbell's *Aretologia* (1728), and parts of Berkeley's *Alciphron* (1732), and John Brown's *Essays on the Characteristics* (1751) and *An Estimate* (1757) are at times as much *pro* Shaftesbury as they are *anti* Mandeville.

One of the most effective replies of the whole controversy was that of John Bulgay, a follower of Clarke, in *A Letter to a Deist concerning the Beauty and Excellency of Moral Virtue, and the support and improvement which it receives from the Christian Revelation* (1726). The burden of this rational work is well summarized in its own words: "In short, the question is not, which

<sup>22</sup> See British Museum Catalogue under Shaftesbury.



motives are the purest and most sublime; but which are most useful, and most effectual, to prevail with degenerate man and accomplish his regeneration." The answer is clearly implied in the title.

Joseph Butler (1692–1752) was both a friend and foe of Shaftesbury. In his *Preface* to the 1729 edition of the *Fifteen Sermons* he gives not a little space to the discussion of Shaftesbury's teachings. In fact the Third Earl is the only one to whom he does give elaborate or explicit attention. Although he readily admits him to be authoritative in the main, and says that "he has shown beyond all contradiction that virtue is naturally the interest or happiness, and vice the misery, of such a creature as man, placed in the circumstances which we are in this world," he cannot accept as adequate his "moral sense" as a guide to correct action.

Bishop Berkeley (1685–1753) in the third Dialogue of *Alciphron, or the Minute Philosopher* (1732), adopts a kind of Theological Utilitarianism not unlike that of Locke. "Alciphron, adapting Shaftesbury, reduces conscience to a taste, enlarges upon the beauty of virtue, and disparages faith in a future life as a selfish and cowardly appeal to hope and fear. Against this Euphranor maintains that a sense of the beauty of goodness is inadequate for making us good, as man needs for this a stronger and more awe-inspiring motive than taste: the springs of action must be sustained by faith in the destiny of man under God."<sup>33</sup> A strange answer to Berkeley appeared two years after the *Minute Philosopher* under the title *A Vindication of the Reverend D——B——Y from the scandalous imputation of being the author of the late book entitled Alciphron, or the Minute Philosopher*. Affecting to believe Berkeley's attack a forgery, the author refutes it with passages from Shaftesbury, and with statements none too friendly toward orthodoxy.

A country clergyman by the name of Elisha Smith came forward in 1736 with *The Cure of Deism*. In the title he charges Tindal and Shaftesbury with having given a "very imperfect account of the religion of Nature, and of Christianity," and proposes "the Mediatorial scheme of Jesus Christ" as "the only true Religion." The work proved to be of great interest and was reprinted in octavo form in 1737, 1739, and 1740. This is especially interesting in that it shows the constant tendency of the time to regard Shaftesbury as an open enemy to all those things sacred to orthodoxy. Dr. Warburton, who in his Dedication of the *Divine Legation* to

<sup>33</sup> Fraser in Preface to *Alciphron* in *Works*, Oxford, 1901. Vol. II, p. 10.

the Free-Thinkers (1738) has a scattered attack on Shaftesbury, wrote to Dr. Hurd, January 30, 1749-50, "Mr. Pope told me, that, to his knowledge, the *Characteristics* had done more harm to Revealed Religion in England than all the works of Infidelity put together."<sup>34</sup> Skelton, in *Deism Revealed*<sup>35</sup> asserts that Shaftesbury "labours to strike out and establish a new system of morality, unhappily founded on a notorious falsehood."<sup>36</sup> His teachings as to rewards and punishments he brands as "nothing else in effect but downright practical Atheism."<sup>37</sup>

But the attacks and defenses were not yet at an end. John Brown, realizing the seriousness of Shaftesbury's vogue, brought out his popular *Essays on the Characteristics* in 1751.<sup>38</sup> Taste is again thought to be too vague a criterion for the morality of the generality of mankind; only the orthodox belief in rewards and punishments can deter man from vice. Despite the general fairness of Brown, his book only served to fan the fire of admiration that had never died in the hearts of the friends of Shaftesbury. Almost immediately Charles Bulkley, a dissenting minister, came to the fore with *A Vindication of Lord Shaftesbury on the Subjects of Morality and Religion*; and an anonymous writer produced the well-written *Animadversions on Mr. Brown's Three Essays on the Characteristics*.

That curious respect that even the enemies of Shaftesbury had for his person and his works is typically stated by Leland in *View of the Principal Deistical Writers* (1754). "It gives me real concern, that among the writers who have appeared against revealed religion, I am obliged to take notice of the noble author of the *Characteristics*."<sup>39</sup> And yet these books "are so generally read, and by many so much admired, that it is necessary to take notice of those things in them which seem to have a bad aspect on religion, and to be of dangerous influence and tendency."<sup>40</sup> Having spoken of his style, his opposition to Hobbes, and his refined sentiments on virtue, Leland admits with regret that these "have very much prejudiced many persons in his favor, and prepared them for re-

<sup>34</sup> See Nichols' *Literary Anecdotes*, II, 212; or Chalmers' *Biographical Dictionary*, article on John Brown.

<sup>35</sup> Published in 1749 and 1751.

<sup>36</sup> Vol. I, p. 134.

<sup>37</sup> *Ibid.*

<sup>38</sup> Republished in 1752, 1764.

<sup>39</sup> 1757 edition, I, p. 48.

<sup>40</sup> I, p. 49.

ceiving, almost implicitly, whatever he hath advanced.”<sup>41</sup> Despite the dangers that Leland thought himself called upon to battle against, Shaftesbury remained popular, and the most sumptuous edition of his works was soon to appear—the famous Baskerville edition of 1773. Again the complaints and warnings of the orthodox were voiced, this time by John Ogilvie in *An Inquiry into the Causes of the Infidelity and Skepticism of the Times* (1783), in which Shaftesbury came in for his share of the blame. But the most significant reply was another edition of his treatises and letters seven years later.

Any writer, philosophical or other, who has it within him to create such a controversial furor as Shaftesbury precipitated, and who can, despite opposition, maintain his popularity and retain his defenders, is a man of no mean vigor. Thomas Gray in a letter to Richard Stonehewer, (August 18, 1758), accounting for his vogue as a philosopher, said: “First, he was a Lord; 2dly, he was as vain as any of his readers; 3dly, men are very prone to believe what they do not understand; 4thly, they will believe anything at all, provided they are under no obligation to believe it; 5thly, they love to take a new road, even when that road leads nowhere; 6thly, he was a fine writer, and seemed always to mean more than he said.”<sup>42</sup> But these reasons are puerile when we trace the constant republication of his works, and recall the challenge that he gave to the best intellects of the century. Men are not likely to continue to read the subtle speculations of a dead Earl simply because they cannot understand them, or for the sheer pleasure of being led they know not whither. A leader, no matter how suave or vain, will hardly make intellectual friends or enemies if there is no “obligation to believe” that which he says in all seriousness.

But Shaftesbury weighed heavily upon the conscience of the age. As John Armstrong remarked,<sup>43</sup>

“Ashley has turn’d more solid heads than one.”

No, Gray was all too nonchalant and facetious in accounting for the vogue of Shaftesbury.

Montesquieu in his *Penseés Diverses* ranks him with Plato, Malebranche, and Montaigne as one of the four great poets.<sup>44</sup> Voltaire

<sup>41</sup> I, p. 49.

<sup>42</sup> Gray, Gosse edition, p. 375.

<sup>43</sup> *Taste*, 1755, found in Chalmers XVI, p. 538.

<sup>44</sup> *Œuv. Comp.*, Paris, 1838, p. 626.

mentions him repeatedly in his *Lettres sur les Anglais* or *Lettres Philosophiques*. Diderot reproduced his *Inquiry concerning Virtue* in *Essai sur le Mérite et la Vertue* (1745 and 1751); and in 1769 a French translation of the whole of Shaftesbury's works, the letters included, together with a French introduction of twenty-six pages, appeared in Geneva. Herder in 1794 said that this "virtuoso of humanity" had signally influenced the best heads of the eighteenth century.<sup>45</sup> Leibnitz, Mendelssohn, and Wieland drank of his waters. He began to be turned into German in 1738, and in 1768 and 1776-1779 translations of his *Characteristics* appeared.

Here then we have an international as well as a national character. In order to determine wherein lay his peculiar power and originality, it would be necessary first to look into the ethical and theological dogmas of his predecessors. When their thoughts had been compared with his thoughts, and their ways with his ways, we could move with some certainty into the literature of the century in an attempt to see to what extent it took color from his style and his ideas. But this, which has been done elsewhere,<sup>46</sup> gains force in the light of the bibliographical facts just rehearsed. Shaftesbury becomes at once an originator and a propagandist, whose ideas, regarded both as toxic and as therapeutic, were widely disseminated and increasingly accepted in the century of "prose and reason".

Beloit College.

<sup>45</sup> See *Briefe zur Beförderung der Humanität*, Briefe 32, 33.

<sup>46</sup> See notes 4 and 8 *supra*.

NOTES ON NEW NAMES IN TABLE OF FORMATIONS AND  
ON PHYSICAL EVIDENCE OF BREAKS BETWEEN  
PALEOZOIC SYSTEMS IN WISCONSIN

E. O. ULRICH

---

*Introductory note by W. O. Hotchkiss.* The Geological and Natural History Survey of Wisconsin is deeply indebted to the writer of this paper, and to the United States Geological Survey for the cooperation which has made possible the important results set forth. The field work on which Dr. Ulrich's work is based began in 1913 and has been carried on during short periods of a few days or weeks each summer since, as the pressure of his other duties permitted. The work has added greatly to our knowledge of the Paleozoic formations, and while this is more than ample justification, it is satisfying to record that the results have been immediately applicable to economic uses as well. The successful search for local supplies of shale for road surfacing in western Wisconsin would have been impossible without Dr. Ulrich's work as a basis. The guidance of drillers of deep wells and the close identification of the strata in these wells which has made possible the finding of desirable water supplies also rests largely on the results of his work.

Dr. Ulrich's work has resulted in very much more detailed knowledge of the strata and has shown the need for giving names to the new units recognized. It has also been deemed advisable in his paper to discuss somewhat fully the physical evidence on which the limits of the various formations are determined.

THE BURROUGHS DOLOMITE

Near the top of Burrough's Bluff, at the northern end of Savannah, Ill., and also in and above Charles Miles' quarry near the southeastern edge of the same city the easily recognized Brainard shale at the top of the Maquoketa facies of the Richmond group is succeeded unconformably by a variable succession of bluish to

---

\*Published by permission of the Director of the U. S. Geol. Survey.

grayish yellow irregularly bedded magnesian mudstones and brownish dolomite aggregating some 50 to 60 feet in thickness. On weathering the upper half or more of these beds shows more or less of earthy chert in nodules and uneven plates. The bluish gray lower third contains few fossils, those found being of a diplograptid (? *Mesograptus* sp.) *Dictyonema* sp. and broadly branching carbonaceous films supposed to belong to some marine plant. The latter two seem indistinguishable from specimens found in the lower part of the Cataract formation in Ontario. The cherty upper beds contain a more varied though not abundant fauna. Among them I have provisionally identified the following: *Streptelasma* aff. *divaricans* and *radicans*, *Streptelasma* aff. *rustica*, *Lindstromia* sp., *Halysites* sp., *Favosites* sp., *Anaphragma* aff. *mirabile*, *Phaenopora ensiformis*, *Phaenopora* cf. *fimbriata*, *Nematopora* aff. *delicatula*, *Helopora* cf. *fragilis*, *Rhinopora* sp., *Lingula* sp., *Pholidops* sp., *Leptaena* cf. *rugosa*, *Plectorthis* cf. *whitfieldi*, *Dalmanella* cf. *edgewoodensis*, *Strophonella* cf. *patenta*, *Atrypa praemarginalis*, *Zygospira putilla*, *Tentaculites* cf. *oswegoensis*, *Orthoceras* cf. *sociale*, *Proetus* sp., *Calymene* sp. Obviously this fauna is decidedly post-Richmond; and it is as clearly older than Clinton. Evidently then it falls into some part of the intermediate Upper Medina stage in which the Edgewood formation of Missouri is probably a nearer contemporary than the Cataract of Ontario.

Lithologically the formation is so different from the Edgewood that it is thought unwise to employ that term for the beds under consideration, especially as there is some doubt as to their strict equivalence. According I propose the name Burroughs dolomite. The same beds are indicated, though mainly by debris, in the mounds in southwestern Wisconsin. Hitherto they have been classed with the Niagaran dolomite that caps these and similar mounds in northwestern Illinois and northeastern Iowa.

#### THE NAMES TREMPEALEAU FORMATION, ST. LAWRENCE LIMESTONE OR FORMATION, AND JORDAN SANDSTONE

Three facts have been mainly responsible for the proposal to substitute the new name Trempealeau formation for the series of beds to which I have previously applied the term St. Lawrence. First, the outcrops in St. Lawrence township, Minnesota, for which N. H. Winchell originally proposed the name St. Lawrence limestone is so limited and its relations to overlying and underlying

Cambrian beds so imperfectly indicated that the locality constitutes a most unsatisfactory type for the composite formation I had in mind when I adopted Winchell's term for it in 1914. Second, the name was originally applied only to the magnesian limestone that lies in the lower part of the formation. The subsequent expansion of the application of the name to everything between the top of the Dresbach sandstone and the base of the Jordan sandstone was unwise and unwarranted by rules governing in such cases. Third, the name St. Lawrence, as applied to a stratigraphic unit, ever since its proposal in 1874 has had an uncertain status and meaning. At times it was referred to the Lower Magnesian series and then to the St. Croixan; and only very recently Keyes<sup>1</sup> committed the now almost unpardonable error of correlating it with the Oneota dolomite of Iowa. Besides, prior to 1914, all who had occasion to refer to the St. Lawrence limestone made it the same as the really much younger Mendota limestone of Wisconsin; and even today a few of the more conservative geologists adhere to this old opinion. As an additional and final reason I may say that employed strictly in its original sense there is still a desirable and valid use for the term St. Lawrence limestone or dolomite. It is almost needless to say that the St. Lawrence in the type locality is not, as recently thought by Keyes, the Oneota dolomite but a much older and thinner bed that is widely distributed, especially in southern Wisconsin, where it lies either at or a few feet above the base of the Trempealeau formation. At St. Lawrence, as very generally too in Wisconsin, the bed is marked by a definitely Cambrian fauna that is entirely different from the Upper Ozarkian fauna which is found in the Oneota dolomite.

Judging from the varied and usually critical comments made by geologists who have kindly read the original draft of this paper it seems desirable and perhaps necessary to give a fairly full account of the nomenclatural history of the term St. Lawrence limestone and of the very different meanings in which the name has been used by authors since it was first proposed by Winchell. This account will at the same time serve in determining the relations of the real Jordan sandstone to other sandstones with which it has been confused and of the Franconia formation to the St. Lawrence, the "Sparta Shale," and other formations that have been named in the past ten years.

<sup>1</sup>Keyes, Charles, Terranal differentiation of Iowa Cambrian succession, *The Pan-American Geologist*, vol. 38, No. 4, p. 323, 1922.

The term St. Lawrence limestone was first proposed by N. H. Winchell in his 2nd Annual Report, Minnesota Geological Survey, page 152, 1874, the name being derived from exposures at St. Lawrence, Scott County, Minnesota. Here the bed so named consists of hard magnesian limestone layers speckled with green (glaucosite) with a total exposed thickness of 14.5 feet. According to well records given by Upham in his report on Scott County (Minn. Geol. Sur. Final Rept. 2, p. 120-121, 1888) this bed may reach 25 or possibly 30 feet. In 1874 Winchell regarded this outcrop as representing the lower division of the Lower Magnesian limestone of Owen (subsequently named Oneota, limestone by McGee) and as underlying the Jordan sandstone which he viewed as separating the two divisions of the "Lower Magnesian." The name Shakopee limestone was given at the same time to the dolomitic formation which overlies the Jordan in the valley of Minnesota River. So far as the sequence of these three formations is concerned Winchell's original view has been proved correct. But he was in error in correlating the Jordan and St. Lawrence with respectively middle and lower divisions of the Lower Magnesian. Both of these formations are pre-Oneota deposits. The Oneota belongs between the Jordan and the Shakopee, but in this part of the Minnesota Valley the lower and more important part of the "Lower Magnesian" limestone is thin and in places seems to be absent entirely.

In the 2nd, 4th, and 5th Annual Reports of the Minnesota Survey the Shakopee is confused at times with the Oneota, and in other places it is the St. Lawrence that is regarded as the equivalent of what we now distinguish as the Oneota. In the 2nd Annual Report, as said, the Jordan is regarded as a middle member of the Lower Magnesian series, the Shakopee as the upper, and the St. Lawrence as the lower division. In the 3rd Annual Report the name St. Lawrence is in places applied to the whole of the Lower Magnesian, the locally developed sandstone (that was later named New Richmond sandstone and which Winchell first suggested and later claimed to be the same as his Jordan sandstone) being absent in such places. "It (the St. Lawrence limestone) constitutes the principal portion of the Lower Magnesian" (4th Annual Rept., p. 33, 1876). That the "St. Lawrence" as used in the 4th Annual Report includes Shakopee is evident not only from the thicknesses given ("not far from 200 feet") but is indicated also by the mentioned presence in the upper part of the massive algal remains



which he later described as *Cryptozoon minnesotense* and which occur only in the Shakopee.

On page 34 of the 4th Annual Report the railroad cut section at Clear Grit is described as showing 16 feet of sandstone at the top which is called Jordan, and beneath this 30 feet of dolomitic limestone called St. Lawrence. In the first place the sandstone is not the Jordan but may be the New Richmond. It is a *red* sandstone which, as proved by experience, is of itself sufficient evidence to establish its age as post-Jordan, the latter being everywhere a grayish white though often iron-stained, case-hardened, interiorly friable sandstone, the weathered surface of which commonly is studded with highly characteristic rounded, often botryoidal concretions. Otherwise the true Jordan is closely similar to the St. Peter sandstone. The dolomite which underlies the red sandstone at Clear Grit belongs to the Lower Magnesian and most probably is the upper part of the Oneota dolomite.

At other places noted in the 3rd Annual Report the Jordan is properly recognized, but the overlying rock is not the Shakopee as then supposed by Winchell but the Oneota.

Winchell's discussion of the St. Lawrence, Jordan and Shakopee formations in the 5th Annual Report, 1877, is essentially as in his 4th Annual Report. However, in this year he introduces his subsequently more definitely stated belief that Irving's Mendota dolomite and Madison sandstone of south central Wisconsin correspond to the St. Lawrence and Jordan formations of Minnesota. That Winchell still correlated the St. Lawrence with what we now know to be the whole of the "Lower Magnesian," that is in places where the locally developed reddish weathering sandstone (the New Richmond) is absent, is clearly indicated by his statement on page 29, regarding the thickness (250 feet) of the formation at La Crosse.

In 1888 (Final Report, Vol. 2, pp. XXI and XXII) Winchell had changed his mind very greatly regarding the relations of the early Paleozoic beds in the Minnesota Valley to those exposed to the southeast in the bluffs along Root River and to the east along the Mississippi. He now recognized that both the Jordan sandstone and the St. Lawrence limestone are older than the lower main mass of the "Lower Magnesian limestone," that is than the Oneota dolomite as now known, and that the sandstone for which

he now adopts Woosters<sup>2</sup> designation New Richmond beds or sandstone and which occurs locally at the contact of the Shakopee and Oneota dolomites is a higher bed than the Jordan sandstone with which he had previously confused it. Moreover, he now placed the Jordan at the top of the St. Croix and referred the underlying St. Lawrence to a correspondingly lower position in the same formation or series. In this work also Winchell definitely correlated the Jordan and the St. Lawrence respectively with the Madison sandstone and the Mendota dolomite of the section at Madison, Wis.

In reading Winchell's comments on the several parts of the section one notes the suggested desire to expand the limits of the St. Lawrence so as to include "shaly beds with which it is associated and into which it seems to graduate." These shaly beds lie both above and beneath the typical St. Lawrence limestone but mainly beneath, and if these were included the expanded formation "will include beds to the amount of nearly 200 feet." However, in his designation and description of the cut and table showing the sequence of the lower Paleozoic formations in Minnesota this suggestion is not carried out, the St. Lawrence being described as 0-30 feet in thickness and the beds between the St. Lawrence limestone and the underlying Dresbach sandstone are separately given as "7. Sands and sandy shales . . . at least 200 feet" in the first table and as "Shales" in the second.

From 1888 on to 1895 the term St. Lawrence was used in the restricted original sense by all who had any occasion to refer to the formation. On two occasions during this time Hall<sup>3</sup>, and Hall and Sardeson<sup>4</sup> so used it. Also Keyes<sup>5</sup> and Calvin.<sup>6</sup> At the close of this period Hall and Sardeson<sup>7</sup> published an excellent paper in which they discuss the "St. Lawrence dolomites and shales" at considerable length and give the thickness of these beds as 213 feet. With such a thickness it would be impossible to exclude the Franconia part of the section. That the "shales" must refer mainly to the Franconia is clearly indicated by the fact that in the table of formations the item "St. Lawrence dolomite and sandy shale, 213 feet" immediately follows the "Faunal break" at the

<sup>2</sup> Geology of Wisconsin, vol. 4, pp. 106 and 127, 1882.

<sup>3</sup> Minn. Acad. Nat. Sciences Bull., vol. 3, No. 1, p. 134, 1889.

<sup>4</sup> Geol. Soc. America, vol. 3, p. 341, 1892.

<sup>5</sup> Iowa Geol. Survey, vol. 1, p. 23, 1893.

<sup>6</sup> *Ibidem*, vol. 4, p. 62, 1895.

<sup>7</sup> The Magnesian Series of the Northwestern States. Geol. Soc. America Bull., vol. 6, pp. 167-198, 1895.

top of the Dresbach sandstone. Besides, the succeeding Jordan sandstone is given a thickness of 200 feet and this of course drops the base of the Jordan far down toward the top of the Franconia. In fact it leaves between the Jordan and the Franconia only what would be required by the 30 feet or so of limy beds that constitute the typical St. Lawrence limestone. Moreover, knowing most of the localities mentioned by them I am certain that not only the greater part of the shales but also some of the magnesian limestones which they correlate with the typical St. Lawrence are really in the Franconia. But all this is difficult to reconcile with their definite statement (p. 172) that the beds exposed at the type locality represent "the lower half of the formation." Evidently limy beds of the Franconia were confused with those at St. Lawrence.

However erroneous some of the correlations of beds in the "St. Lawrence" of Hall and Sardeson's 1895 paper may be the fact of greatest importance in this connection is the implied and partly carried out intention to expand the stratigraphic meaning of the term St. Lawrence.

The first definite and unqualified change was made about 1910 when the U. S. Geological Survey Committee on Geologic Names decided how the Cambrian and Lower Ordovician rocks in the Upper Mississippi Valley were to be divided and what names they should bear. These decisions appear in two Water Supply Papers, No. 256, by Hall, Meinzer, and Fuller, and No. 293 by Norton and others, published in 1911 and 1912 respectively. Now for the first time since 1888—if we disregard the work of Hall and Sardeson mentioned in the preceding paragraph—the St. Lawrence limestone becomes a formation and is increased in thickness from the preceding maximum of 30 feet to over 200 feet. This expansion was brought about mainly by incorporating the underlying Franconia sandstone which had been named in the meantime. No reason is given anywhere in these two papers for this unwarranted and really quite inexcusable proceeding. Even though it was not yet known that still another formation—since described under the name Mazomanie sandstone—wedges in from the east between the base of the St. Lawrence limestone and the top of the Franconia, anyone well acquainted with the field relations of the concerned stratigraphic, faunal, and lithologic units could hardly have failed to recognize the thorough distinctness of the Franconia on the one hand and the beds above it on the other. The top also of this expanded St. Lawrence is an unnatural and often indefinite bound-

ary. Evidently it was drawn somewhere about the transition from the limy Lodi shale member to the Norwalk sandstone member of the Trempealeau formation, this position being indicated by the thickness (160 feet) assigned to the overlying "Jordan" sandstone and the fact that in the columnar sections the St. Lawrence is extended only to the top of the limy beds.

Even if the St. Lawrence formation as defined in these Water Supply Papers were a naturally bounded and permanently desirable stratigraphic unit I see no warrant for this expansion of the St. Lawrence except the suggestion by Winchell in 1888 and the paper by Hall and Sardeson, both of which are referred to above. But Winchell himself failed to carry out his suggestion, and Hall and Sardeson did so under obvious misconceptions as to the correlation of the concerned beds. Besides, the lower part of the expanded St. Lawrence had in the meantime been named by Berkey; and after the term Franconia sandstone had been proposed all possible excuse for extending the application of the name of the superposed smaller and in every respect less important stratigraphic unit so as to cover and completely eliminate Berkey's Franconia had been forfeited. Moreover, experience in the field has proved conclusively that the lower two-thirds or more of Hall and Norton's St. Lawrence formation—in other words, the Franconia—is as useful and as clearly defined a formation as any of the subdivisions of the Upper Cambria series in the Upper Mississippi Valley now recognized.

In 1914, two years after the appearance of Norton's paper, Walcott<sup>8</sup> published the sequence and preliminary classification of the Upper Cambrian formations in Wisconsin and adjoining States to the west that had been worked out the preceding field season by E. O. Ulrich. In this classification the Franconia is recognized and the St. Lawrence formation of Hall and Norton was not only restricted to beds above the Franconia, but its definition was again modified by extending its upper boundary so as to include a sandstone—here distinguished as the Norwalk sandstone member—that had been improperly referred to the lower part of the Jordan sandstone by the Minnesota and Iowa geologists. The Norwalk sandstone member is not present in the section at Jordan, Minn., but where both are found, as is generally the case in western Wisconsin, the two are usually separated by a well-defined boundary.

<sup>8</sup> Smithsonian Mis. Coll., vol. 57, p. 354, 1914.

Although this classification was regarded from the beginning as a merely preliminary effort to bring order out of the confusion that had previously prevailed in the published accounts of the Cambrian sequence in the Upper Mississippi Valley it has in the main proved a serviceable and reliable guide in the work during the past nine years. With unimportant modifications, except in the matter of much added detail that had accumulated in the meantime, the same classification was used in 1919 by Twenhofel and Thwaites.<sup>9</sup> Also in 1920 and 1922<sup>10</sup> by the writer, who on these occasions introduced a new formation—the Mazomanie sandstone—that had previously been regarded as the eastern representative of the Franconia but is now known to be a distinct formation that wedges in from the east in Wisconsin between the top of the Franconia and the base of the St. Lawrence limestone.

Knowledge of the lower Paleozoic section in Wisconsin and neighboring states having reached the stage where I feel warranted in presenting my final opinions concerning the formations and their classification, it seems desirable and important to subject the names of the formations to critical scrutiny as well as the strata themselves. The only nomenclatural change of importance that has been suggested by these inquiries is the proposed substitution of the new name Trempealeau formation for the beds that I had previously called St. Lawrence. The need for this change was first indicated when I sought an appropriate geographic name for the member to which Twenhofel and Thwaites had applied the designation "Calcareous beds" and found that the concerned member is actually the bed to which Winchell had originally applied the name St. Lawrence limestone. Under the circumstance I felt unwilling to propose a new name for this member; and this unwillingness persisted even when it became obvious that my refusal necessitated the proposal of a new name for the formation of which the St. Lawrence limestone is a member. On the other hand, however, the proposal of a new name for the broader unit clears up most of the confusion that at present attends the term St. Lawrence. That this confusion is very real is most clearly indicated in tabular form.

<sup>9</sup> Twenhofel, W. H., and Thwaites, F. T., The Paleozoic section of the Tomah and Sparta quadrangles, *Jour. Geol.*, vol. 27, p. 616, 1919.

<sup>10</sup> Ulrich, E. O., Major causes of land and sea oscillations. *Washington Acad. Sci. Jour.*, vol. 10, pp. 74-76, 1920, and reprint of same in *Ann. Rept. Smith. Instit.*, pp. 333-335, 1922.

TABLE SHOWING VARYING USE OF THE TERM ST. LAWRENCE FROM 1874 TO 1922.

Sequence of beds as now recognized	1914-1919, Walcott, Ulrich, Twenhofel and Thwaites	Hall, 1911 and Norton, 1912	Calvin, 1893	Winchell, Final Rept., 2, 1888	Winchell 2, 4, 5, Ann. Rept., 1874-7	Keyes, 1922
Canadian	{Shakopee dol. . . . .	Shakopee . . . . .	Shakopee . . . . .	Shakopee . . . . .	Shakopee . . . . .	Shakopee dol.
	{New Richmond ss. . . . .	Prairie du Chien group	Oneota . . . . .	New Richmond . . . . .	Jordan . . . . .	Jordan ss.
Ozarkian	{Oneota dol. . . . .	Oneota . . . . .	Oneota . . . . .	Main body of limestone . . . . .	St. Lawrence	Oneota dol. (St. Lawrence)
	{Madison ss. . . . .	Madison . . . . .	Corr. with Jordan . . . . .	Regarded as synonym of Jordan . . . . .	St. Lawrence	
	{Mendota dol. . . . .	Mendota* . . . . .	Corr. with St. Lawrence . . . . .	Regarded as synonym of St. Lawrence . . . . .	St. Lawrence	
	{Devils Lake ss. . . . .	Jordan . . . . .	Jordan . . . . .	Jordan . . . . .	Jordan . . . . .	Waukon ss.
Cambrian	{Jordan ss. . . . .	Jordan . . . . .	Jordan . . . . .	Jordan . . . . .	Jordan . . . . .	Waukon ss.
	{Norwalk ss. mem. . . . .					
	{Lodi sh. mem. . . . .					
	{St. Lawrence ls. mem. . . . .					
	{Tempealean	{St. Lawrence form . . . . .	{St. Lawrence form . . . . .	{St. Lawrence . . . . .	{St. Lawrence . . . . .	{St. Lawrence . . . . .
Eau Claire sh.	{Mazonian ss. . . . .					
	{Franconia ss. . . . .	Franconia . . . . .				Interval Albin shales
	{Dresbach ss. . . . .	Dresbach . . . . .				Interval Dresbach ss.
	{Eau Claire shale . . . . .	Eau Claire . . . . .				Eau Claire sh.
{Mt. Simon ss. . . . .	Mt. Simon . . . . .					Mt. Simon ss.

\*In the area covered by Twenhofel and Thwaites the Mendota is lacking.

The foregoing table shows that in 1874-7 Winchell mistakenly applied the terms St. Lawrence and Jordan to three distinct pairs of formations belonging to three systems. Only the Cambrian pair—originally described in 1874—is correctly named, the other usages of the terms by him being based on misapprehended correlations. The table indicates further that Winchell, and also Calvin, never included any other Cambrian beds in the St. Lawrence limestone than the calcareous 15-30 foot lower member of the Trempealeau formation ("St. Lawrence formation" of Ulrich, Walcott, Twenhofel and Thwaites, not Hall, Norton, or Winchell) to which I now propose to confine the term. The third fact shown by the table is that the St. Lawrence formation of Hall and Norton differs widely from the St. Lawrence of Walcott, Ulrich, Twenhofel and Thwaites (1914-1919) in that it is extended downwards to the top of the Dresbach sandstone and upward only to the base of the Norwalk sandstone member of the Trempealeau formation (St. Lawrence of Ulrich et al.).

In view of the consistent use of the term St. Lawrence by Winchell in 1874 and 1888 and by Calvin in 1895 I maintain that it was both unwise and contrary to the rules of stratigraphic nomenclature to introduce the great expansions of its meaning that were given it by Hall in 1911, Norton in 1912, and Ulrich in 1914. It would have been better to disregard Winchell's term entirely as a formation name and give a new name to the broader unit of which the original St. Lawrence is a part. The main reasons why I did not do so in 1914 were (1) the fact that the United States Geological Survey had previously adopted the term in the wide significance given it in the two publications by Hall, 1911, and Norton, 1912, and (2) the obvious need of further field studies before a final classification and nomenclature might be warranted. But the Franconia, proposed by Berkey in 1897, had proven too good a formation to be ignored, so I defined its boundaries as well as I could in that early stage of my investigations of the Cambrian in Wisconsin and Minnesota and restricted the St. Lawrence to beds above the Franconia.

In 1916 or 1917 another complication of the St. Lawrence question was introduced by Shipton,<sup>11</sup> who proposed the new, though preoccupied term Sparta shale for the same beds to which Hall, Norton, and others had applied the name St. Lawrence. And the

<sup>11</sup> Shipton, W. D., Proc. Iowa Acad. Sci., vol. 23, p. 142.

# GEOLOGIC COLUMN FOR WISCONSIN

WITH CORRELATION TABLE FOR THE PALEOZOIC ERA

GENERAL TIME SCALE

CENOZOIC	QUATERNARY	Pleistocene (Recent)	Marl, peat, and alluvium.
	TERTIARY		Till, sand, clay, gravel, and boulders of glacial, fluvial, and lacustrine origin (maximum thickness about 600 ft.); and loess of aeolian origin.
			Absent

		WEST WISCONSIN	EAST WISCONSIN
MESOZOIC	CRETACEOUS	Windrow formation (?)	(Absent)
	JURASSIC & TRIASSIC	(Absent)	(Absent)
DEVONIAN	PENNSYLVANIAN (Pa. 15,000 ft. ss. sh. & coal.)	(Absent)	(Absent)
	MISSISSIPPIAN (App. 3000 ft. ls. ss. & sh.)	(Absent)	(Absent)
	Neodevonian (N.Y. 7000 ft. sh. & ss.)	(Absent)	(Absent)
	Mesodevonian (N.Y. 1400 ft. ls. & sh.)	(Absent)	Milwaukee (0-170 ft.)
	Eodevonian (N.Y. 450 ft. sh. & ss.)	(Absent)	(Absent)
	Cayuga (N.Y. & Pa. 1400 ft. ls. sh. & ss.)	(Absent)	Waubesa dol. (0-50 ft.)
	Guelph (Ont.)	(Absent)	Guelph dol. (?)
	Racine (Wis.)	(Absent)	Racine dol. (?) 200 ft.
	Waukesha (Wis.)	(Absent)	Waukesha dol. to 250-300 ft. 550 ft.
	Byron (Wis.)	(Absent)	Byron dol. (100 ft.)
NEOPALEOZOIC	Upper Clinton (App. 500 ft. ss. sh. & ls.)	(Absent)	(Absent)
	Middle Clinton (App. 500 ft. ss. & sh.)	Hopkinton dol. (?) (Iowa 50 ft.; age doubtful.)	Mayville dol. (100 ft.)
	Lower Clinton (App. 600 ft. sh. ss. & ls.)	(Absent)	(Absent)
	Upper Medina (App. 350 ft. ss. sh. & ls.)	Burroughs dol. (60 ft.)	(Absent)
	(?)	(Absent)	Neda form (0-55 ft.)
	Elkhorn (Ind. 75 ft. ls. & sh.)	Brainard sh. (Iowa 30-90 ft.)	Richmond formation, the Brainard shale of the top and the Whitewater suggested beneath this. (50 to 340 ft.) (= Cincinnati shale of older reports.)
	Whitewater (Ind. 75 ft. ls. & sh.)	Probably absent	
	Fort Atkinson (Iowa 60 ft. ls.)	Fort Atkinson ls.	
	Liberty-Waynesville (Ohio 125 ft. sh. & ls.)	Probably absent	
	"Elgin" (Iowa 75 ft. sh. ls.)	"Elgin" sh. ls.	
Fennvale (Tenn 30 ft. sh. & ls.)	(Absent)		
Arnheim (Ohio 75 ft. sh. & ls.)	Probably absent		
Dubuque (Iowa 40 ft. ls. & sh.)	Dubuque ls.	(Absent?)	



PALEOZOIC		GENERAL TIME SCALE		WEST WISCONSIN	EAST WISCONSIN
		MONROVIAN (ULRICH)	MONROVIAN (CONWAY)		
ORDOVICIAN	BIG BUFFALO (ULRICH)	Maysville (Ohio 250 ft. ls. & sh.)	(Absent)	(Absent?)	
		Eden (Ohio 300 ft. sh. & ls.)	(Absent)	(Absent?)	
		Trenton (N.Y. & Pa. 400-600 ft. ls.)	Galena dol. (250 ft. inc. Prosser ls.)	Galena dol. (100-200 ft.)	
		Kimmswick (Mo. 100 ft. ls.)	(Absent)	(Absent)	
		Decorah (Iowa 60 ft. sh. & ls.)	Decorah (30+ ft. sh. & ls.)	Upper Blue dol. 15 ft.	
		Watertown (N.Y. & Tenn. 8-200 ft. ls.)	Platteville ls. (75 ft.)	Upper Buff dol. 52 ft.	
		Lowville (N.Y. & App. 600 ft. ls.)		Lower Blue dol. 25 ft.	
		Chazy (N.Y. & App. 7000 ft.)	(Absent)	Lower Buff dol. 28 ft.	
		Jochim (Mo. 100 ft. ls.)	St. Peter ss. & sh. (0-332 ft.)	St. Peter ss. & sh. (0-300)	
		St. Peter (Minn. 100 ft.)			
EVERTON	EVERTON	Everton (Ark. 120 ft. ls. & ss.)	(Absent)	(Absent)	
		with Kings River ss. and Sneed's ls. members.			
EOPALEOZOIC	CANADIAN	Upper Canadian (App. 2000 ft. ls.)	Shakopee dol. (70 ft.)	Shakopee dol. (0-100 ft.)	
		Middle Canadian (App. & Okla. 2500 ft.)	(Absent)	(Absent)	
		Lower Canadian (Pa. 700 ft. ls.)	(Absent)	(Absent)	
		Upper Ozarkian (App. 1800 ft. dol.)	Oneota dol. (0-200 ft.)	Oneota dol. (0-100 ft.)	
		Middle Ozarkian (App. 2000 ft. dol.)	(Absent)	(Absent)	
		Lower Ozarkian (Pa. & Ala. 2500 ft. dol.)	Madison ss. (40 ft.)	Madison ss. (30 ft.)	
			(Absent)	Mendota dol. (20 ft.)	
				Devils Lake ss. (100? ft.)	
CAMBRIAN	UPPER ST. CROIXIAN	Jordan (Minn. 80 ft. ss.)	Jordan ss. (75 ft.)	Jordan ss. (Generally Absent)	
		Trempealeau (Wis. 125 ft. sh. & ls.)	Norwalk ss. member (50 ft.)	(Absent)	
		(= St. Lawrence of Ulrich, 1914)	Lodi Shale (50 ft.)	Lodi Shale (0-25 ft.)	
			St. Lawrence ls. (25 ft.)	St. Lawrence (0-20 ft.)	
			Shale (local 20 ft.)	Shale (local)	
		Mazomanie (Wis. 150 ft. dol. ss.)	(Absent)	Mazomanie ss. (100-165)	
		Franconia (Minn. 125+ ft. gr. ss. sh. & ls.)	Upper Greensand (5+ 70)	Usually Absent	
			Yellow ss. (40-50)		
			Lower Greensand (40)		
			Micaceous sh. (15)		
Dresbach (Minn.)	Ironton ss. member (15)				
Eau Claire (Wis.)	Dresbach ss. (40-250 ft.)	Dresbach ss. (40-180 ft.)			
Mt. Simon (Wis.)	Eau Claire sh. (200-300 ft.)	Eau Claire sh. (350 ft.)			
Middle & Lower Cambrian (Rocky Mts. 12,000 ft. ss. sh. & ls.)	Mt. Simon ss. (100-200 ft.)	Mt. Simon ss. (700+ ft.)			
	(Absent)	(Absent)			
PRE-CAMBRIAN	ALGONKIAN	KEWEENAWAN	UPPER MIDDLE	DUNDON (BAYFIELD)	Chequamegon ss. 1000 ft.
					Devils Island ss. 300 ft.
					Oriente ss. 3000 ft.
					Amnicon Shale and Arkose 5000 ft.
					Eileen Sandstone 2000 ft.
					Freda Sandstone 12,000 ft.
					Nonesuch Shale 120-350 ft.
					Outer Conglomerate 800-1200 ft.
					Basalts; diabase, rhyolite, gabbro, felsites, conglomerates, etc. (17,000 to 30,000 ft.)
					Conglomerates and Quartzites (225-300 ft.)
Tyler formation, mica and clay slates, and graywackes (7,000-11,000 ft.)					
Ironwood formation, ferruginous cherts and cherty iron carbonates (600-1000 ft.)					
Palms formation (clay slate and quartzite 400-800 ft.)					
Bad River dolomite (200-300 ft.)					
Laurentian - granites, syenites, gabbros, and gneissoid equivalents.					
Keewatin - greenstones (schistose basalts), and green schists.					

case became even worse confounded when Keyes<sup>12</sup> a few months ago made the St. Lawrence in its typical exposure in Minnesota the same as the Oneota and the Jordan sandstone the same as the New Richmond sandstone, renamed the Franconia (Albin shale), also the typical St. Lawrence (Allamakee dol.), and proposed the name Waukon sandstone for what Hall, Sardeson and Norton had called Jordan.

Considering all this confusion—nomenclatural and stratigraphic—and wishing at the same time to preserve the credit really due to N. H. Winchell for naming two Cambrian horizons that are well marked both lithologically and faunally not only in Minnesota but also in the adjoining states of Wisconsin and Iowa, some radical changes in names and in the definition and correlation of the concerned stratigraphic units seem necessary. After thorough investigation of the facts and much thought the best and only just solution of the various difficulties and issues seems to be the one here followed and in part newly proposed: namely

(1) The restriction of the name Jordan sandstone to the wholly unfossiliferous, probably continental deposit of usually light grayish sandstone which occurs at Jordan, Minn., and is elsewhere in the Mississippi Valley easily recognized by its lithologic character and its position in the section between the top of the fossiliferous marine Norwalk sandstone member of the underlying formation and the more or less unconformable base of the often similarly sandy initial deposit of the succeeding Lower or Upper Ozarkian formation.

(2) The restriction of the term St. Lawrence, in the original form of St. Lawrence limestone and not St. Lawrence formation, to the well-characterized and widely recognizable calcareous zone to which this term was originally applied by Winchell and to which it was again confined by him in 1888.

(3) The proposal of a new name, the one chosen being Trempealeau formation, for the formation to which Ulrich in 1914 applied the term St. Lawrence formation and of which the typical St. Lawrence limestone usually constitutes the basal member. The Trempealeau thus embraces the beds between the top of the Franconia formation and the base of the true Jordan sandstone.

<sup>12</sup> Keyes, Charles, Terranal differentiation of Iowa Cambrian succession. *Pan-American Geologist*, vol. 38, 1922, pp. 313-326.

## THE TREMPEALEAU FORMATION AND ITS SUBDIVISIONS.

The Trempealeau formation is well displayed and in fairly typical composition in Trempealeau Bluff on Mississippi River. Other good sections may be seen (1) at Norwalk, (2) in and below Beans quarry, 2 miles northwest of Tunnel City, (3) in the bluff southeast of Mazomanie, (4) at Hillside just south of Wisconsin River from Spring Green, (5) in the bluffs on both sides of St. Croix River at Osceola, and many other places in Wisconsin. Most of the beds are exposed also at Lansing, in Iowa, and at Winona, Redwing, and Stillwater, in Minnesota.

There is considerable variation in the character and sequence of the component beds of the formation from place to place. Thus in eastern Wisconsin the upper (Norwalk) member is commonly and perhaps always absent. But the yellow calcareous shaly Lodi member is generally present and may also be called the most characteristic part of the formation. The same might be said of the next underlying St. Lawrence limestone or dolomite member, but in the middle and northern parts of the State this member is entirely wanting in many places, or it is so much altered by addition of relatively coarse quartz sand that the recognition of its zone is rendered difficult and uncertain.

In calling the Lodi member a shale it is to be understood that as defined by me the word shale applies generically to a rock of very fine grain, thinly laminated construction and containing some clay but not necessarily in preponderant quantity. All of these Cambrian shales consist mainly of finely divided siliceous matter.

## SUBDIVISIONS OF THE TREMPEALEAU FORMATION.

In its fullest development the Trempealeau formation is divisible into four lithologically and faunally distinct members. Locally one or two of these subdivisions might be mapped separately, but as a rule the topographic conditions are such that only the lower magnesian limestone member lends itself readily to such separate treatment. Names for at least three of these members are desirable if only for purposes of discussion. They differ notably in geographic distribution, and such facts are neither easily nor clearly to be brought out in descriptions of local stratigraphy without definite names for each of the several members.

*Norwalk sandstone member.*—The thickest and therefore perhaps the most important of these members is the one at the top for which the term Norwalk sandstone member is proposed. As a rule it consists of fine-grained grayish sandstone, sometimes nearly white and often with a yellowish or brownish tinge, commonly rather massive in its upper two-thirds and more or less thin bedded and in even plates 1 to 6 inches thick in its lower third. In thickness this member varies from 0 to over 40 feet. At Norwalk, where as usual it is in contact above with the Jordan sandstone, it is about 35 feet. In Beans quarry, near Tunnel City, it is 43 feet thick, at Osceola, Alma, and in the lower Beef Valley about 50 feet. From these maximum developments the member diminishes southeastwardly to 25 feet at Ironton and less than 7 feet in the vicinity of Mazomanie. It has not been observed to the east of Cross Plains, in which region the Trempealeau formation is terminated above by the Lodi shale member.

A large and varied fauna has been collected from the Norwalk sandstone member; and most of the species are strictly confined to its zone. Locally the sandstone is quite bare of fossil remains, but recognizable specimens of some of its characteristic species have been found in many places. At most of these localities the fossils occur mainly or solely in the thin-bedded lower part, but the reverse is the case at Norwalk where many were found in the upper third and very few in the beds beneath. *Osceolia osceola*, *Saukia pyrene*, *S. leucosia*, *Iliaenurus quadratus*, *Eurekia eos*, and *Sinuopea sweeti* are the species most commonly found.

*Lodi shale member.*—This term is proposed for the usually yellow calcareous shale-like sandstone that lies between the Norwalk sandstone and the St. Lawrence limestone. This shale member is widely distributed, the outcrops being everywhere recognizable from Stillwater, Minn., and Osceola, Wis., on the north to Spring Green on the south and the vicinity of Madison on the east. Locally the characteristically yellow shale is interbedded with purple shale, as in the vicinity of Mazomanie, or with layers of sandstone and in other places with dolomitic limestone, but even without considering the fossils there is seldom any difficulty in recognizing the Lodi shale. The thickness of the member rarely falls under 15 feet, with approximately 25 feet as the average and 50 feet as the maximum.

In view of the frequent miscorrelation of the underlying St. Lawrence limestone with the Mendota dolomite it is important to

note that in the 4 or 5 miles distance between Farwells Point on the north side of Lake Mendota and Pheasant Branch at the west extremity of the lake certain beds enter the section that are not present at Farwells Point or near-by in Maple Bluff. Namely, at Farwells Point only two feet of St. Lawrence limestone separate the Mendota dolomite from the underlying top of the Mazomanie sandstone. In the quarry at Pheasant Branch, on the contrary, the Mazomanie which outcrops on the lake shore is succeeded, first, by an undetermined but small thickness (less than 10 feet) of soft shaly and glauconitic sandstone beds, second, by 12 feet of St. Lawrence limestone, and, third, by at least 5 feet of yellow and purple calcareous sandy shale that not only has the lithological characters of the Lodi shale but also some of its characteristic fossils. Above this shale the section is not exposed for about 35 feet, when a three-foot ledge of coarse white and brownish sandstone that resembles the Jordan but more probably belongs at the base of the Oneota dolomite comes to the surface. The covered interval may be occupied by either the Madison sandstone or the Mendota dolomite or by thin representatives of both, or, as seems the more probable, by Jordan sandstone only. In the near-by Leith well only one limestone (evidently the St. Lawrence) is found beneath the Oneota.

The Lodi shale member usually is fossiliferous, and its fauna, so far as known, is almost entirely confined to this member. As the commonest and most characteristic of its species we may cite *Dikelocephalus minnesotensis*, *Saukia crassimarginata*, *S. lodensis*, and *Aglaspis barrandei*. With these, and usually more abundantly than anything else, occur species of brachiopods provisionally identified with *Westonia stoneana* and *W. aurora*.

*St. Lawrence limestone or dolomite* (as originally defined).—As stated on a preceding page, some distinctive name is desirable for the bed of highly magnesian limestone that commonly underlies the Lodi shale member in Wisconsin, Minnesota, and probably also in northeastern Iowa. Further, as the name St. Lawrence limestone proved on visiting the type locality to have been based by Winchell on the very bed for which a name would now be a useful aid in describing the several divisions of the Trempealeau formation it has seemed eminently proper to adopt Winchell's term in the restricted sense in which it was originally used. There is no doubt whatever in my mind that the "St. Lawrence limestone" described by N. H. Winchell in 1874<sup>13</sup> is the bed here referred to as

underlying the Lodi shale member of the Trempealeau formation. As described by Winchell the St. Lawrence limestone member at the type locality consists of grayish magnesian limestones, mottled with red and yellowish brown blotches and more or less profusely speckled with the green grains of glauconite, in layers 2 to 18 inches thick and aggregating a total thickness of between 14 and 15 feet. Under it is a shaly bed, 18 feet of which was observed by W. O. Hotchkiss and the writer in 1915 in a ravine north of the quarry. The latter exposure did not extend down to the top of the Franconia which probably underlies the Trempealeau in the valley of Minnesota River as elsewhere. Whether the Franconia is present here or not the observed shale bed is lithologically at least like the bed that is found at many places in Wisconsin at the base of the Trempealeau and usually beneath the calcareo-magnesian zone that is correlated with the typical St. Lawrence limestone or dolomite.

Regarding the propriety of the latter correlation it would be amply warranted by the similarity of lithologic characters alone—especially the likeness in the sequence and thickness of the lithologic units concerned. But we have corroborating fossil evidence that with the lithologic evidence of the rocks themselves settles the question beyond all reasonable doubt. Fossils are seldom plentiful in the St. Lawrence limestone and only rarely are they in a good state of preservation. Despite these disadvantages a considerable fauna from this zone has finally accumulated. More important is the fact that this fauna includes a number of characteristic species that are sufficiently distinctive to be recognized even in poor condition. Nearly always this zone affords some brachiopods, particularly a form of *Billingsella* that we have not yet succeeded in distinguishing from *B. coloradoensis*—a common lower Franconia shell. Also a variety of *Dicellomus politus*, a species otherwise not found above the basal layers of the Franconia. With these usually is the *Finkelburgia osceola corrugata* which so far seems confined to this zone. Perhaps a surer but rarer guide fossil is a large trilobite that may be the species described by Walcott under the name *Dikelocephalus vanhornei*. Specimens of all of these four species rewarded a half hour's search in the quarry at St. Lawrence, Minn.

In Dane and Iowa counties, Wisconsin, the St. Lawrence dolomite is notable for certain interesting additions to its more usual

<sup>13</sup> Second Ann. Rept. Geol. and Nat. Hist. Sur. Minnesota, p. 152.

fauna, referred to and discussed by Ulrich in 1916.<sup>14</sup> These additions—in all 10 species, most of them obviously primitive gastropods—make up what may be called a distinguishable but undeniable preoccurrence of species typically developed in the much younger Lower Ozarkian Mendota dolomite. Many even more striking instances of recurring faunas are now known, so that no particular importance is to be attached to this at first perplexing case.

In southern and western Wisconsin the zone of the St. Lawrence limestone is seldom absent. Where present it is always more limy than the superjacent and inferjacent beds; and as a rule it is unquestionably indicated by thick, often quarried layers of characteristically colored crystalline magnesian limestone. No other bed that resembles it at all closely occurs in the prevailing sandy Upper Cambrian series in the Upper Mississippi Valley. However, it varies greatly in thickness from place to place. In the vicinity of Sparta it usually is only about 2 feet thick, between Mazomanie and Black Earth 3 or 4 feet, at Spring Green about 6 or 7 feet, at Pheasant Branch (west end of Lake Mendota) 12 feet, at Farwells Point, on north shore of Lake Mendota, only 2 feet. Apparently it is entirely absent to the north and east of the Baraboo Range. In the bluffs along the Mississippi its development is variable. It was not observed in the section at La Crosse, but to the north of that place, as far at least as Stillwater, Minn., its zone is generally recognizable.

*Basal shale.*—The base of the Trempealeau is often a shale or shaly sandstone with considerable greensand and occasionally thin layers of dolomitized sandstone. At the bottom usually there is a thin layer of sandstone conglomerate. In thickness it varies from 0 to 15 or even 20 feet, the latter maximum being found on the east side of Blue River Valley about 4 miles southwest of Muscoda. This place also is the only one at which satisfactory fossils were procured from this shaly bed. The fauna as indicated by this collection of seven or eight species comprises three or four seen nowhere else and two small species of *Saukia* that can be compared only with *S. pyrene* and *S. leucosia*, two species known elsewhere only in the Norwalk member of the formation.

It is not at all certain that the shaly bed at the base of the Trempealeau is always of the same age as the one found in this

<sup>14</sup> Correlation by displacements of the strandline. Geol. Soc. America, Bull., vol. 27, p. 477, 1916.

position in the valley of Blue River. Indeed, this correlation is decidedly doubtful in the case of the basal Trempealeau shale in sections where, as at Norwalk and below Beans quarry near Tunnel City, the St. Lawrence dolomite member is either absent or unrecognizable. In such places the basal shale may well be of the age of the St. Lawrence dolomite. Until this question can be further investigated and determined it is thought advisable to defer proposing a special name for the basal shale.

#### THE FRANCONIA FORMATION AND ITS SUBDIVISIONS

The Franconia formation is divisible everywhere in the western half of the State into four, five, or six members, but these differ regionally so much in character and sequence that it is difficult and as yet impossible to correlate exactly those prevailing in the northwestern quarter with those found in the southwestern quarter or in either of these with those seen in the middle part of the State.

In the area lying to the south of Trempealeau we can usually distinguish two main greensand zones, one—50 feet to 70 feet thick—at the top of the formation; the other—30 feet to 45 feet thick—in the lower half. The upper of these greensand zones is characterized faunally by several species of *Ptychaspis*, among which the most notable is *P. miniscaensis*. The lower greensand contains few fossils.

Between the greensand members is another usually well defined zone—10 feet to 40 feet thick—that differs from the adjoining beds in consisting mainly of yellowish platy sandstones of which occasional layers often are filled with highly characteristic remains of trilobites. These include *Ellipsocephalus curtus*, *Chariocephalus whitfieldi*, various species of *Ptychaspis*, and species of the new genus *Wilburnia*, Walcott ms., including the typical form of *W. diademata* (Hall).

Under the lower greensand is a fourth member that is distinguished from the others by its shaly and thin-bedded micaceous sandstone and sandy limestone. The latter occurs in the lower third of this member and usually is marked by an abundance of valves of articulate brachiopods. These belong to two or three species of *Eoorthis*, of which *E. remnicha* probably is the most characteristic. Many small trilobites occur with these and in the shaly sandstones above.



Finally at the base of the formation is a 2 to 15-foot bed of reworked Dresbach sand. Usually this forms a single massive ledge and bench at the top of the Dresbach bluffs, commonly holding this position because its top is more or less silicified and therefore more resistant than the relatively incoherent mass of sandstone beneath it. It contains some highly characteristic fossils which distinguish this initial deposit of the Franconia from all preceding and succeeding beds in this region. Some of the more useful of these fossils are mentioned on a following page.

Of these five members only the lowest and possibly the shaly micaceous bed above it are clearly recognizable by their respective lithologic and faunal characters in the Franconia as developed in the tops of the mounds in Adams County. In these mounds the soft greensand members are represented, as is clearly established by their fossil contents, by much harder red and gray sandstones; but the intervening yellowish sandstone member is not easily distinguished from the beds on either side of it. However, the sandstones that are believed to correspond to the upper part of the intermediate member form unusually massive, coarsely grained and but sparingly fossiliferous ledges.

In the northwestern quarter of the State, speaking particularly of the area between Mondovi and Alma on the south and St. Croix Falls on the north, no two of the many Franconia sections are strictly alike. And yet a general similarity in both the character and the sequence of the beds is manifestly maintained. Compared with the Franconia in the southwestern quarter only one of the members usually determinable there is clearly identifiable in the northwest. The zone referred to is the yellow sandstone member. In places, particularly in the area between Hudson and Menomonie, this member maintains in fair approximation the color and character of bedding that distinguish it in the region between Sparta and Lavalley. However, followed from Hudson both to the north, as at Franconia, Minn., and to the southeast, as in Beef River valley between Alma and Mondovi and also at Durand, nearly the whole of this member becomes so strongly charged with glauconite that were it not for its abundant and highly characteristic fossil contents it would hardly be distinguished from the associated greensand beds.

In the northwestern quarter of the State there also is a fairly persistent "Lower Greensand" zone. At its top is a bed of variable

thickness (2 to 15 feet) that contains some magnesian limestone layers with dismembered plates of crinoids or cystids and other fossils that is recognized as far south as La Crosse. At this latter place, however, it rests on the initial Franconia deposit of reworked Dresbach sand containing *Camaraspis convexus* (Whitf.). At Hudson, on the contrary, it is underlain by about 27 feet of soft sandstone more or less profusely charged with greensand; and this ought to correspond to the "Lower Green sand" of the Sparta region. Granting this decidedly questionable conclusion it would follow that the "Micaceous shale" of the Sparta region is unrepresented in the sections at Hudson and elsewhere in the area to the north of La Crosse. It would follow also that the lower half of the Franconia contains two distinct limy zones, the one in the north containing crinoidal fragments and lying above the "Lower Greensand," the one in the south without crinoidal remains and occurring beneath or at the base of the "Micaceous shale." But these doubtful correlations can as yet be viewed only as provisional suggestions to be entertained until proved or disproved by the results of detailed comparisons of sections and fossils now being carried on. At present it seems more probable that the limy zones are the same and that the "Lower Greensand" of the south, rather than the "Micaceous bed," thins out or becomes unrecognizable to the north.

As in southwestern Wisconsin, so also in the sections at Franconia, Minn., Hudson, Durand, west of Mondovi and as far south as Trempealeau in Wisconsin, the base of the Franconia is made by a fossiliferous bed that consists mainly of reworked Dresbach sand. But in the mentioned latter places the initial Franconia deposit contains more glauconite. Its fossils also are quite different from those found in the basal Ironston sandstone member of the formation in the southwestern quarter of the State. In the latter region the fossils in the basal sandstone consist almost entirely of trilobites, most of which have been found only in this bed. On the other hand, the fauna of the basal sandstone in the mentioned northern localities consists entirely of a few species of inarticulate brachiopods. Of these brachiopods a species of *Dicelolomus*, usually referred to *D. politus*—a common fossil in the Eau Claire shale—is most abundant. A small elongate and very narrow species of *Lingulella* is more characteristic of the zone.

These regional variations in the composition of the lower third or half of the Franconia, when all is considered, can be interpreted only as indicating differential oscillation of surface and conse-

quent varying local migrations of the strandline during the early stages of the Franconia age. Abundant data indicating the character and order of occurrence of these oscillations and the areas affected by them are available, but their citation and discussion would require more time and space than the present opportunity warrants.

*The Ironton sandstone member.*—Of the various members of the Franconia formation above briefly discussed only one is named on this occasion. The member so distinguished is the basal sandstone of the formation in the southwestern quarter of the State. The Ironton sandstone member, as it is proposed to call it, has been recognized and studied at many places in Sauk, Richland, Vernon, La Crosse, Monroe, Jackson, Adams and Juneau counties. So far as observed in these counties the bed varies in thickness from about 2 feet to 12 or possibly 15 feet. At Ironton, the type locality, it varies from 5 to 10 feet. The top of the bed is even, the rapid inequalities in thickness being due to unevenness of its base. As a rule it forms the slightly hardened top of Dresbach sandstone bluffs and for this reason has usually been regarded as the terminal bed of that formation.<sup>15</sup> However, it is now quite clear and commonly accepted that it is of later date and, in fact, the initial deposit of the Franconia.

The Ironton member is composed mainly of reworked washed and relatively coarse residual grains of Dresbach sandstone, the surface of which had previously been subjected to subaërial leaching and wear. The line of the break between the two formations—Dresbach and Franconia—lies at the undulating plane where washing and sorting of the loose quartz grains of the underlying formation is first indicated. In other words, the Ironton sandstone member extends downward to the lowest plane indicating reworking and redeposition of the weather-loosened top sands of the underlying Dresbach formation. Commonly the new deposit includes a few grains of glauconite and other material that is not present in the undisturbed underlying beds of Dresbach sandstone.

But to make sure of the identification of the Ironton member it is advisable to search for its characteristic fossils. In the Dresbach proper no organic remains—except perhaps worm bur-

<sup>15</sup> Twenhofel and Thwaites in their paper on the Paleozoic section in the Tomah and Sparta quadrangles, Jour. Geo., vol. 27, p. 616, 1919, apply the term "Wormstones" to relatively firm sandstone at the top of the Dresbach that may be a part of the Ironton sandstone member.

rows—have so far been observed. The overlying basal sandstone of the Franconia, however, only rarely fails to reward a few minutes' use of the hammer with indubitable evidence of the presence of such remains. The most abundant and characteristic of these are the nearly hemispheric cephalic shields of several species of a new genus of trilobites, one of which was long ago described by Whitfield under the name *Arionellus convexus*. As this trilobite does not belong to either *Arionellus* or any other previously established genus it is proposed to change its designation to *Camaraspis convexus* (Whitfield) Ulrich and Resser.

#### PHYSICAL EVIDENCE OF THE BREAKS BETWEEN THE PALEOZOIC SYSTEMS IN WISCONSIN

*General discussion.*—In Wisconsin, as indeed is the rule elsewhere on our own and other continents, the physical evidence indicating long interruptions of the process of marine sedimentation consists mainly of phenomena of stratigraphic overlap. By careful comparison of the fossil contents of the successive beds and the identification of the fossiliferous zones in other regions we finally arrive at a fairly reliable conception of which stages of the composite geological time scale are represented by marine deposits in a given area and which are not. The most striking and important of the conclusions thus arrived at is that within the always relatively flat interior areas of the continents submergence by marine waters and the consequent marine depositional record is greatly inferior in volume of deposits and ages represented by these deposits than in the submarginal Appalachian, Ouachita and Cordilleran geosynclines. The structure of the latter regions with their long troughs and broader surface depressions naturally permitted more frequent and longer-enduring submergences than could have obtained within the more extensive, relatively stable and hence much less folded interior areas. But we must not overlook the fact that even in these submarginal troughs the stratigraphic record of geologic events is far from complete. In these also the record is broken at the usual horizons. Indeed, and despite the fact that the record in these troughs is more complete—or rather less interrupted, the stratigraphic planes at which conclusive evidence of retreat of the seas and emergence of the troughs is found are only much more numerous and each no less clearly indicated than in the geologic sections of the flatter interior areas. Consequently

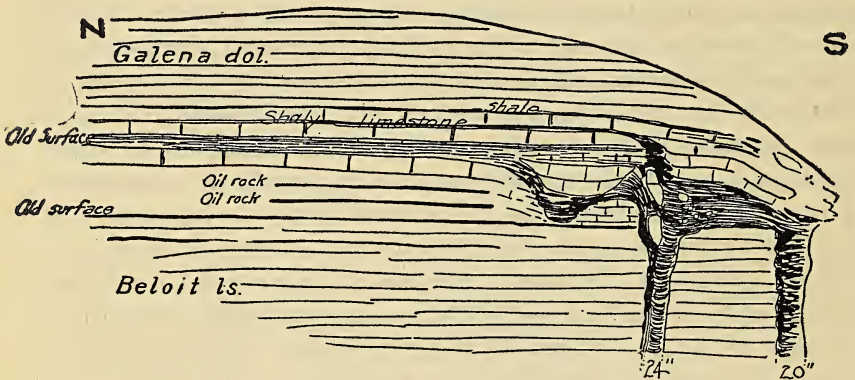
we can not escape the conviction that complete emergence of the area embraced in the present continent occurred at many times during the almost unbelievably long course of geologic history.

Though, as said, the evidence on which we base our conclusions respecting the frequency and relative duration of periods when the sea was withdrawn and land prevailed consists mainly of phenomena indicating alternating retreat and advance of the strandline and consequent absence of deposits found elsewhere and overlapping structure of those present, it is yet true that even in Wisconsin the sedimentary record is not wholly devoid of such more convincing criteria of preceding land conditions as basal conglomerates. These conglomerates vary greatly in composition of material and character of the enclosed pebbles. Naturally the character of both depends entirely upon the material available and relative nearness to the shore. Obviously, under usual conditions pebbles of large size can be distributed over the bottom of the new sea only for a mile or less out from the shore. Here and there a river may transport them for longer distances. The latter condition is suggested in some instances in Wisconsin; and in every one of these instances the pebbles consist of rolled quartz or quartzite derived from distant exposures of pre-Cambrian rocks. Moreover, their distribution is decidedly local.

Under more usual conditions the basal conglomerate consists of material washed out of the subaërially decomposed top of the underlying formation. If the latter consists of sand then the average size of the grains of quartz is larger than in the undisturbed part of the contributing formation. If the residual mantle of the re-submerged area comprises plates, blocks or concretionary masses of respectively limy sandstone, limestone or dolomite, or chert, then the character of the basal conglomerate, or perhaps more properly the initial deposit, of the succeeding formation is modified accordingly. Nearly always the initial deposit includes laminae or may be quite unstratified fine material transported by temporary suspension in the invading waters.

However, in many places the initial deposit contains nothing having any connection with the weathered residual mantle of a preceding land age. An excellent illustration of this condition is found in the large limestone quarry at Darlington. Here there is unquestionable evidence of a land stage that broke the continuity of Black River limestone deposition. The break was long enough

to permit subterranean solution and excavation of a cavern at least 25 feet wide and 20 feet deep in the limestone previously laid down here. Then the cavern was filled with fossiliferous shale and limestone. Not a trace of this filling or of its fossils is notable in the quarry face 30 feet to either side of the cavern. Beyond that



*Erosion channels in basal Galena and top of Platteville or Beloit limestone, Darlington, Wisconsin*

distance the layers of limestone seem so perfectly conformable to each other that none would suspect that one of the bedding planes—indeed it is one of the least evident—marks a time when this area was land and subject to surficial and subterranean erosion. Cases like this should make one pause before declaring in error another who thinks he sees a stratigraphic hiatus between two apparently conformable layers of rock.

Nor is the relative conspicuousness of the break any reliable indication of the time represented by the hiatus. The time may be immeasurably greater than in the case just described, and yet it may require very close scrutiny of the purely physical evidence to determine precisely where the break occurs or, indeed, whether any at all occurred. Of course, with the aid of the fossil evidence not only the actual presence and precise location of the break often is quickly established, but the fossils also give the best measure of the time represented by it.

*The Devono-Silurian break.*—So far as known this contact is everywhere unconformable, meaning by that only that the sea was

withdrawn at the close of the last of the Silurian deposits and that resubmergence of parts of the continent at the beginning of Devonian time left a bounding break of undetermined time value between the youngest of the Silurian deposits and the oldest of the succeeding Devonian sediments. The plane of separation between these is sharp and slightly undulating even when cementation has taken place so as to make it appear as passing through a single layer of rock—in such cases usually a limestone. In many places, among them east Wisconsin, the Devonian overlap was delayed to Middle Devonian time. Beds of the latter age there rest on some late or middle Silurian formation. At Louisville, Ky., the adjacent rocks of both systems are of limestone and the line of contact between the two is sometimes so obscure that it is scarcely determinable in a weathered slab two inches in thickness. However, the lower side of this slab contains Niagaran species of corals, the upper side Middle Devonian species. And yet nearly 2,000 feet of mainly limestone deposits were laid down in the northern Appalachian Valley during the time of the hiatus indicated by the fossils in the upper inch of this slab and those imbedded in its lower inch.

In Wisconsin the Middle Devonian Milwaukee formation follows the Waubakee dolomite, which is regarded as of late Silurian age. No outcrop showing the contact of the two formations in which the lower bed was positively identified as belonging to the Waubakee has been observed. But it is quite probable that this contact is exposed in a small quarry three-quarters of a mile northwest of Port Washington. Whatever age may finally be assigned to the lower formation at this place it is certain that the contact between it and the uneven, clearly overlapping base of the overlying Milwaukee dolomite is unconformable, with at least 1,000 feet of beds missing that were laid down elsewhere.

*The Siluro-Ordovician break.*—That the contact of the Silurian and Ordovician formations in Wisconsin and adjoining States marks a stratigraphic hiatus of considerable magnitude and introduced great changes in the geography of the time is also shown mainly by absence of certain elsewhere important late Ordovician formations and by early Silurian sea transgressions of extraordinary extent and correspondingly great overlaps of deposits left by them. These earliest Silurian transgressions occurred during the Richmond or Lower Medina stage. In the Upper Mississippi Valley the first of the Richmond formations lies on the Galena dolomite

which is of Trenton age. Accordingly the section here lacks the important Eden and Maysville groups of the Cincinnati series. Farther south in this great valley, as in southeastern Missouri and northern Arkansas, the hiatus beneath the Richmond is increased by elimination of the Galena so that the former lies on a limestone of either early Trenton or late Black River age. In the western half of the continent it is still further increased, the first of the Richmond deposits there being in contact with beds ranging in age from Middle or Lower Ordovician to Canadian, Ozarkian, or even Upper Cambrian.

In the Appalachian Valley region the hiatus between the Ordovician and the Silurian is of lesser time value than in the Mississippi Valley. But here, locally, as in the vicinity of Lewistown, Pa., the red Juniata sandstone, which is of Richmond or Lower Medina age and there rests on a thick mass of the latest Ordovician gray Oswego sandstone, is not only much thicker than usual but contains in its lower 400 feet many often thick beds filled with rounded quartz pebbles. In size the pebbles vary from very small to three inches in diameter. In central Pennsylvania, therefore, we find all the physical evidence that even the most critical observer could demand on which we may confidently base the conviction that the boundary between the base of the Richmond (or of formations corresponding in age to it) and the deposits beneath its base is of systematic value: (1) great thickness of red muddy sandstone indicating preceding, long enduring land-surface decay, (2) thick beds of quartz conglomerate, and (3) extensive transgressions of new seas over previously long emerged areas of much older rocks. It is important further to note that in Pennsylvania where the first and second of these conditions are more clearly indicated than usual the boundary between the Juniata and the overlying Tuscarora sandstone (Upper Medina with which Schuchert, Grabau, and other paleontologists propose to begin the Silurian) is practically indeterminable. And yet the part of the section in which it must lie is perfectly exposed in the section between Lewistown and Reedsville. Aside from the Oswego-Juniata contact above discussed the only other reasonably possible plane at which the boundary between the two systems might be drawn is at the locally clearly defined contact between the base of the Oswego sandstone and the top of the Reedsville shale (=Eden plus Lower



Maysville) where Butts,<sup>16</sup> following the long-continued practice of the State geologists of New York, recently drew it. But it is impossible to locate this plane in New York. There, as in Pennsylvania, the boundary must be placed above the Oswego.<sup>17</sup>

*The Ordovician-Canadian break.*—The Ordovician system as defined and restricted by Ulrich and given in the preceding table begins in the Upper Mississippi Valley with the St. Peter sandstone. That the surface upon which this sandstone was laid down is decidedly uneven because of preceding weathering and erosion has been long recognized in the geological reports of the State. The evidence in hand 40 years ago was already sufficient to establish much of the importance of the break between the St. Peter and the underlying formation which then was supposed to be always some part of the "Magnesian limestone." However, in more recent years much information bearing on this break has been acquired. We now know, especially from the evidence of deep wells, reported by Thwaites, that the St. Peter may rest on any formation between the top of the Shakopee and the eroded top of the Eau Claire formation. We have learned further that the St. Peter represents merely a late and perhaps the latest stage of an alternating series of limestones and sandstones that so far as known is best developed in northern Arkansas. There, moreover, it is clearly shown<sup>18</sup> that the deposition of this series was interrupted at least once by emergence and deep erosional wear of the Everton limestone. At the bottom of the series in Arkansas there is often a chert conglomerate which sometimes reaches a thickness of 8 or 10 feet. Under this lies the Powell limestone, which corresponds approximately in age to the Shakopee dolomite of Wisconsin and adjoining States to the west and south. Both of these formations are assigned to the upper division of the Canadian system.

But we have learned something more, too, about the occurrence of thick deposits of clastic material at the base of the St. Peter in southern Wisconsin and northern Illinois. This information has been acquired in limited amount from study of outcrops by the writer and his associates and in greater amount and details through the study of well records by Thwaites. This clastic material or conglomerate consists of great accumulations of chert boulders

<sup>16</sup> Geologic section of Blair and Huntingdon counties, central Pennsylvania. Amer. Jour. Sci., vol. 46, p. 536, 1918.

<sup>17</sup> This systemic break is discussed at length by E. O. Ulrich, Ordovician-Silurian Boundary, Int. Geol. Cong., XII, Canada, 1913, C. R., pp. 593-667, 1914.

<sup>18</sup> Geol. Atlas U. S., Eureka Springs-Harrison Folio, 202, 1916, p. 7.

and siliceous rock meal interbedded or irregularly mixed with quartz sand and fine siliceous clay-like deposits, locally attaining an aggregate thickness of nearly 200 feet and all derived from the surface wear of older formations to the north. The distribution of this basal St. Peter conglomerate suggests long continued work of streams of considerable size. In short, the physical data now in hand clearly establish the propriety of Ulrich's proposal to draw a systematic boundary between the top of the Shakopee and the base of the St. Peter in the Upper Mississippi Valley and at the corresponding everywhere easily identified plane elsewhere in America. Out of the hundreds of species of fossils found on the two sides of this stratigraphic break not a single one passes across the line; and of the Canadian genera many less than half their number are recognized in the succeeding Ordovician faunas. Besides, this restriction of the Ordovician system still leaves it with an aggregate thickness of deposits exceeding the average for most of the systems now recognized.

*The Canadian-Ozarkian break.*—In the Upper Mississippi Valley this break commonly lies within the mass of dolomitic limestone that up to ten or fifteen years ago was generally known as the Lower Magnesian limestone. More recently the locality term Prairie du Chien limestone or formation was ill-advisedly proposed to replace the lithologic name. Before that McGee<sup>19</sup> working in northeastern Iowa proposed the name Oneota for the lower part of the mass and Winchell<sup>20</sup> gave the name Shakopee to what we now know as its upper part. A sandstone believed to lie between the two was called New Richmond sandstone by Wooster.<sup>21</sup> Because of the formerly prevailing belief that these three divisions are coextensive much confusion has attended their identification from place to place in Iowa and Minnesota. In Wisconsin, following publication of Wooster's work in 1882, practically no published attempt has been made to distinguish the divisions.

The field work of the writer in Wisconsin and adjoining States, particularly during the past ten years, has demonstrated that the Shakopee is unquestionably distinguishable from the Oneota dolomite throughout their extent in the Upper Mississippi Valley. The evidence respecting the New Richmond sandstone is much less satisfactory. It is evident not only that this dolomitic series embraces

<sup>19</sup> U. S. Geol. Surv., 11th Ann. Rept., pt. i, p. 331, 1891.

<sup>20</sup> Minn. Geol. and Nat. Hist. Surv., 2d Ann. Rept., p. 138, 1874.

<sup>21</sup> Geology of Wisconsin, vol. IV, pp. 106 and 127, 1882.

more than one sandstone but also that the two dolomite formations are not by any means always separated by a sandstone. Moreover, it seems that the sandstone beds are in the form of geographically limited lenses lying at varying horizons within either of the dolomitic formations and passing laterally into sand-free dolomites. It has been established also that even the Shakopee and the Oneota are not coextensive. In some places the Oneota is absent, as at Jordan, Minn., and probably also at Ripon and Butte des Morts, in eastern Wisconsin. At many other places in Wisconsin the Shakopee is absent. In the former cases the absence of the Oneota is most probably due mainly to nondeposition. In the latter instances we can not be sure that the absence of the Shakopee is not caused entirely by the unusual activity of surface eroding agencies during and preceding deposition of the St. Peter sandstone.

Where both of the dolomitic formations are present and clearly exposed it has usually been found possible to point out precisely the plane of contact. But the contact zone is a very likely one to be affected and correspondingly obscured by secondary dolomitization. In such unfavorable places the boundary was located only approximately though with more time at our disposal than was available better results might well be expected. In yet other places the boundary proved to be quite irregular and was further emphasized by mineralization where the hollows contained original carbonaceous mud deposits and rather large pebbles of chert.

Good exposures of the contact were observed in the bluffs and quarries at Stillwater, Minn. Here it lies about 60 feet above the base of the Oneota which rests unconformably on the Jordan sandstone. Above the top of the Oneota the Stillwater section shows about 50 feet of Shakopee with usual characters. There is no sandstone worth mentioning between the two formations.

That the surface of the Oneota was eroded here before the Shakopee was laid on it is indicated clearly enough by (1) the relatively slight thickness of the lower formation, (2) the absence of the fossiliferous cherty zone that is commonly present in the upper part of Oneota sections at and to the south of Trempealeau, (3) the unevenness of the contact plane which shows irregularities of contour of a foot or more and corresponding dissection across sedimentary planes in distances of less than 10 feet; and (4) the presence of one to three inches of conglomerate with limestone and chert pebbles in a matrix of coarse quartz sand and grains of glauconite.

In the section at Prairie du Chien the Oneota is at least 150 feet thick, and the first of the fossiliferous cherts comes in about 65 feet above the bottom. The formation therefore comprises at least 90 feet of more or less cherty beds at the top that are wanting at Stillwater. At Dresbach, Minn., which lies about midway between Prairie du Chien and Stillwater, the Oneota is approximately 100 feet thick. The fossiliferous cherty zone referred to in this and the preceding paragraph occupies the upper 30 feet. The thinning of the Oneota to the northward, apparently by erosion of the upper beds, is suggested in similar manner by other sections in the valley north of Prairie du Chien.

A sandstone, which may or may not correlate with the lower of the two beds of sandstone at New Richmond, Wis., is locally present at the base of the Shakopee. A four to five-foot bed of sandstone occupies this position at Prairie du Chien. Five miles to the north of this city the same bed has thickened to about 10 feet. As remarked in a preceding paragraph a bed of sandstone may occur at the Shakopee-Oneota contact, but it is very unsafe to rely on its presence.

It has been shown that good physical evidence of the break between the Shakopee and the Oneota dolomites—in other words, between the representatives respectively of the Canadian and Ozarkian systems—is generally procurable in the numerous and often excellent exposures of the “Lower Magnesian limestone” in the Upper Mississippi Valley. But we must go elsewhere for the data required to appreciate the true significance of the break. By study of the sections in Wisconsin and Minnesota alone it would be impossible to reach the absolutely established conclusion that the Shakopee represents only the concluding stage of a great series of limestones and dolomites having an aggregate thickness of over 5,000 feet. In northern Arkansas the Powell limestone carries the same peculiar gastropod fauna that is found to the north in the Shakopee dolomite. In Arkansas and Missouri the Powell is underlain by three Canadian formations (Cotter, Jefferson City, and Roubidoux) each with its own characteristic fauna of which not a trace has been observed north of Illinois. On the other hand, all three of these faunal zones are clearly recognized in the Canadian limestones in the Appalachian Valley, particularly in northeastern Tennessee and western Virginia and also in central Pennsylvania. In Virginia the Roubidoux fauna occurs at the base of over 2,000 feet of dolomitic limestone; and the younger Canadian faunas

occur at appropriate horizons above it. In one of the best of the sections in Pennsylvania (at Bellefonte) the Roubidoux fauna lies over 3,000 feet beneath the base of the overlying Ordovician formations. Moreover, this section shows more than 1,000 feet of yet older Canadian limestones before reaching the top of the underlying Ozarkian system.

Without facts like these one could scarcely believe that the break between the Shakopee and Oneota in Wisconsin represents time so long that it sufficed for the slow marine deposition elsewhere of not less than 4,500 feet of limestone and dolomite. Nor is this all, for even in the thickest of the Appalachian sections the physical evidence of the break between the Canadian and Ozarkian systems appears quite as distinct and impressive as it is in Minnesota and Wisconsin between the Shakopee and Oneota dolomites.

Striking and conclusive evidence of subaërial erosion of the surface of the Ozarkian system during the interval between that and the succeeding Canadian period was procured recently in southeastern Missouri. Namely, in traveling northward through this state from Van Buren to Potosi and thence westward toward Meramec River the Gasconade dolomite, which in Missouri lies at the top of the Ozarkian and is always easily recognized by its peculiar chert and highly characteristic fossils, was found to be generally rather thin and in places entirely absent. Indeed the areas in which the Gasconade cherts and fossils were not observed must aggregate at least 50 square miles. At first this local absence of the Gasconade seemed most probably due to nondeposition but further investigation, which showed an altogether unusual amount of quartz sand and chert pebbles in the overlying Roubidoux formation, soon tended to change the first suggestion to the belief and finally to the conviction that the Gasconade after having been laid down over the entire region was then locally removed by erosion during the emergent interval between the two periods. The most convincing evidence favoring the latter view was the discovery of a ring or funnel of steeply inclined and highly fossiliferous Gasconade chert in the midst of horizontal beds of an older Ozarkian formation. As this older formation extended nearly to the tops of the surrounding hills and was succeeded in the section by conglomeratic Roubidoux sandstone and chert without intervention of the Gasconade, no other explanation of the mentioned funnel-shaped outcrop of Gasconade chert than that it is a remnant of the original

sheet of its formation which owes its preservation to collapse of the roof of an Eopaleozoic cavern seemed to fit the case.

The Oneota is of Upper Ozarkian age. The sea of its epoch lasted a long time in the southern Appalachian region but finally spread very widely over southeastern North America. Its rocks and characteristic fossils are recognized also in Missouri (Gasconade formation), in Alabama and east Tennessee (Chepultepec formation), in Pennsylvania, and in eastern New York. At the close of its stage this great inland sea was withdrawn perhaps entirely. The next succeeding invasion laid down the limestone and graptolitic shale deposits with which the accessible record of the history of the Canadian period begins. Whereas the preceding Oneota-Gasconade-Chepultepec stage spread northeastwardly from the south and west, the succeeding Lower Canadian stage had its development in North America mainly or entirely in Pennsylvania and New York. Judging from the distribution of its deposits this new sea must have differed from the preceding also in the location of its inlet and the direction of its invasion. It came in from the Atlantic side of the continent, whereas the preceding late Ozarkian sea invaded from the south. Evidently then the physical changes that occurred in passing from the Ozarkian to the Canadian period involved very considerable local warping and also more generally effective differential vertical movements of the lithosphere. The geographic changes at this time—meaning particularly changes in arrangement and outlining of water and land areas—also the faunal modifications, were greater and more important than at any other time between the close of the Cambrian and the beginning of the Ordovician period.

*The Ozarkian-Cambrian break.*—To get a true conception of the diastrophic changes that occurred in America during the passage from the Cambrian to the Ozarkian period we must study the stratigraphic records preserved in the great Appalachian and Cordilleran geosynclines. However, as we found in discussing the younger Paleozoic breaks, the record in Wisconsin and adjoining States regarding the Ozarkian-Cambrian break also is far from blank. In fact, the Devils Lake sandstone, which is the oldest of the Ozarkian formations in Wisconsin, affords a more impressive development and display of conglomerate than has been observed at this horizon anywhere else in America. This sandstone attains a thickness of at least 100 feet and at many places includes—as in Parfrey Glen, east of Baraboo, and at the northern end of the

gorge at Ableman—at its base and at various higher positions in the formation beds of almost perfectly rounded quartzite pebbles. These range in size from less than an inch in diameter to masses three or four feet across. The typical outcrop of the Devils Lake sandstone occurring, as they do, on the flanks of old quartzite ridges, were deposited under conditions admirably adapted to the production of such coarse clastic material.

Conglomerate of similar kind and probably derived from the same or similar sources occurs in southern Wisconsin somewhat rarely at the bases of preceding Cambrian formations. But the volume of such material in these older occurrences is far inferior to that found in the Devils Lake sandstone. This disparity in quantity suggests not only intervening diastrophic movements that made more of such material available but also the lapse of considerable time during which such large quantities might be produced. Really, in view of the demonstrable fact that the Devils Lake sandstone is of quite early Ozarkian age and the deposits beneath it very late Cambrian, the abundance and character of the conglomerates in the former prove to be the best objective evidence we have in establishing the verity of the break between the Cambrian and the Ozarkian.

That warping of the surface did occur in the Upper Mississippi Valley during the otherwise unrecorded interval between the Cambrian and Ozarkian is further clearly proven by the altogether different distribution of the Cambrian and early Ozarkian marine sediments. Thus, whereas the Cambrian formations are for the most part common to both the east and west sides of Wisconsin the first two of the Lower Ozarkian formations are confined to small areas in the eastern half of the State. The succeeding Madison sandstone seems to extend from the most southern of these areas across the State to the Mississippi, but even this appears to be confined to much narrower limits in north and south directions than were the Cambrian formations.

Another interesting and in this connection important fact is that whereas the organic remains in the Cambrian formations, excepting perhaps those of the Mazomanie, become fewer and finally disappear entirely when the formations are traced toward the east and especially the northeast angle of the State, the Lower Ozarkian formations, on the contrary, become barren in a westerly direction. This fact suggests at once that the seas in which the more important of the Cambrian formations were deposited terminated on the

northeast side against the beaches and low coastal plains of land areas then prevailing over and beyond the area of Michigan. The Lower Ozarkian seas, on the other hand, shallowed to beaches on the west side where seas with abundant life had prevailed in the preceding period. These suggestions are raised to the status of practically demonstrated facts when the distribution and origin of their respective faunas is carefully taken into account. Unpublished studies of Cambrian faunas have reached the point where we can say definitely that direct marine connections existed repeatedly and perhaps continuously between the Cambrian seas of the Upper Mississippi Valley and those of Wyoming and Montana and Oklahoma and central Texas. Indeed, there is no reason to doubt that the most characteristic genera and species of the Cambrian faunas found in the Upper Mississippi region migrated here from the west and southwest. But the case with respect to the Lower Ozarkian faunas of Wisconsin is totally different. These are like and must have been in communication with the Potsdam and Hoyt faunas of New York and, by extension of colonies southwardly, with Missouri. Moreover, the Lower Ozarkian faunas in the Mississippi Valley and New York are almost totally different from those of similar age in the Cordilleran province. The latter evidently invaded from the Arctic side of the continent.

The facts here presented in brief outline in support of the reputed high taxonomic importance of the break between the Cambrian and Ozarkian systems might by themselves be accepted as sufficient proof of the author's contention regarding the actual distinctness of the two systems. But it is unnecessary to be satisfied with the data supplied by Wisconsin localities alone. Other and many of them much more convincing data have been procured from other parts of North America. In fact, the Ozarkian is very incompletely represented in Wisconsin. A fuller sequence of its deposits is found in the Ozark Uplift of Missouri and Arkansas. But very much thicker deposits of this period have been observed and carefully studied in the Appalachian Valley region. There, particularly in central Pennsylvania and central Alabama, Upper Cambrian deposits consisting largely of limestone and aggregating thousands of feet in thickness are succeeded unconformably by Lower Ozarkian dolomites and relatively pure limestones that measure as much as 2,000 feet or more in a single completely exposed section. On these, then, rest thousands of feet of Middle and Upper Ozarkian limestones and dolomites giving a total volume of



limy deposits that must, on the basis of thickness alone, rank the Ozarkian among the most important of the Paleozoic systems.

In North America the Ozarkian system has as good or a better foundation in its diastrophic history, volume and character of deposits, and in its distinctive faunas than have the Silurian, Devonian, Permian, Triassic, and Jurassic systems, most of which are generally accepted by stratigraphers.

In the matter of areal distribution also, especially when we consider the fact that as one of the oldest of the Paleozoic systems its rocks are likely to be largely buried beneath younger sediments, the Ozarkian compares favorably with other Paleozoic systems. Rocks of its age are now definitely recognized as outcropping in New York, Vermont, New Jersey, Pennsylvania, Maryland, Virginia, Tennessee, Georgia, Alabama, Missouri, Iowa, Wisconsin, Minnesota, Oklahoma, central and western Texas, Colorado, Idaho, Nevada, and, through the explorations of Walcott, in British Columbia. By means of deep wells this already very widely demonstrated areal distribution doubtless will be extended to other States. Moreover, there are good reasons for believing that the system is represented also in Quebec and Newfoundland and on the other side of the Atlantic by the Tremadoc in Great Britain and perhaps in other European countries. For the present, however, certain very real difficulties, which always are encountered in the endeavor to correlate fossil shore and bottom faunas of widely separated provinces, forbid more definite statements regarding the possible and probable representatives of the Ozarkian on other than the North American continent.



# THE FAUNA OF THE LAKE WINNEBAGO REGION\*

---

## A QUANTITATIVE AND QUALITATIVE SURVEY WITH SPECIAL REFERENCE TO THE MOLLUSCA

FRANK COLLINS BAKER

During the summer of 1920 (July and August) a somewhat detailed survey was made of the Lake Winnebago region, including Lake Winnebago, Lake Butte des Morts, the Fox River at Omro, and the small swales and pools bordering the shores of these places. The work was carried on under the auspices of the Wisconsin Geological and Natural History Survey, by which the writer was commissioned to make a survey of the molluscan fauna of the State preparatory to the completion of a monograph of the Mollusca. The absence of any literature, excepting scattered records, concerning the mollusk fauna of the Winnebago region led to its selection as a profitable area for statistical study for comparison with other lakes which have been similarly treated.

Headquarters were established at the Wisconsin State Fish Hatchery at Oshkosh, where motor and row boats were placed at the writer's disposal, as well as suitable laboratory facilities for sorting and otherwise caring for the collections. Collections were made at definite stations along the west shore of Winnebago Lake from Asylum Bay to Long Point Island, a distance of about 12 miles. Shore material was also gathered at other places on the lake shore. In Lake Butte des Morts, collections were made at places covering the greater part of this body of water. Over 450 dredgings were made and, in addition, mollusks were collected from many places along the shore and in inland habitats. The dredgings were made with an Ekman bottom sampler. The results shown in the tables indicate the number of individuals per square meter of bottom.

The material upon which the study is based is preserved in the Zoological Museum of the University of Wisconsin (Mollusca) and

---

\*Contribution from the Museum of Natural History, University of Illinois, No. 32.

in the Museum of Natural History of the University of Illinois (Mollusca and associated animals).

My thanks are due a large number of people for assistance in the field work or in the subsequent study of the material. Chief among these are Professor Chancey Juday of the Wisconsin Geological and Natural History Survey, who made the study possible; and the Conservation Commissioners of the State, through Mr. I. H. Bloomer, in charge of the Fish Hatchery, who gave every possible facility for advancing the work. Mr. Hall and Mr. Apel, hatchery assistants, also granted many courtesies which greatly assisted in the success of the undertaking. To Mr. Clyde B. Terrell, of Oshkosh, the owner of the interesting aquatic farms on Lake Butte des Morts, the writer is greatly indebted for assistance in studying the fauna of that lake.

The sincere gratitude of the writer is especially due those specialists who cheerfully gave of their time for the identification of groups of animals in which they are experts. The large amount of material sent could not but have been somewhat of a burden to classify, and I am sure that the feelings of other workers in ecological subjects are expressed in the statement that the value of their assistance cannot be overestimated. The following persons assisted in this work of identification: Dr. Bryant Walker, Detroit, Mich., various mollusks; Dr. V. Sterki, New Philadelphia, Ohio, Sphaeriidae; Mr. Calvin Goodrich, Detroit, Pleurocera; Dr. Ruth Marshall, Rockford College, Rockford, Ill., Acarina; Dr. J. Percy Moore, University of Pennsylvania, leeches; Dr. J. G. Needham, Cornell University, aquatic insects; Dr. Cornelius Betten, Cornell University, Trichoptera; Dr. Paul S. Welch, University of Michigan, aquatic Lepidoptera; Professor Frank Smith, University of Illinois, Oligochaete worms and sponges; Dr. C. P. Alexander, University of Illinois, aquatic insects; Dr. Wm. Trelease, University of Illinois, certain plants; Miss Ada L. Weckel, Oak Park, Ill., Amphipoda; Mr. Waldo L. Schmitt, U. S. Nat. Mus., Washington, D. C., Isopoda; Prof. Chancey Juday, University of Wisconsin, Cladocera.

## PHYSIOGRAPHY AND GEOLOGY

### A. DESCRIPTION OF THE LAKE

Lake Winnebago lies in the eastern part of the State of Wisconsin in latitude 44° N. and between longitude 88° and 89° W. It is 33 miles west of Lake Michigan and 30 miles southwest of Green Bay. The lake is oriented north and south, which is its greatest length, and is about 28 miles (45 km.) in length by 10.4 miles (16.6 km.) in greatest width. The greatest depth is 20¾ feet (6.38 m). It lies at an elevation of 745 feet above the sea and 165 feet above Lake Michigan. The lake has a present area of about 215 square miles, which is about 5.5 per cent greater than its original area, the increase being due to the dams in the outlet channels which have raised the level of the lake several feet.

The eastern and western shores of Lake Winnebago differ greatly in character. The eastern shore presents an almost continuous margin broken by no bays or points of notable size. The western shore, on the contrary, is made up of a succession of bays and points with many shoals extending well into the lake. On the eastern side, the land rises rather abruptly forming cliffs or bluffs of a more or less bold character. In most places the rise is gradual (50 feet) for a quarter of a mile and then abrupt (100-150 feet) in a distance of a quarter or half a mile. Elevations of 1,000 feet, or 255 feet above the lake, occur at a distance of less than two miles from the lake margin.

The western margin of the lake is very low and lacks entirely the bold character of the eastern shore. Elevations of more than sixteen feet above the lake are not encountered within a distance of a mile west of the lake. Marsh areas occur at the south end near the City of Fond du Lac. West of the City of Oshkosh, low, marshy areas extend westward for a distance of nearly twenty miles, where smaller lakes, Butte des Morts, Poygon, and Winneconne, occupy wide areas.

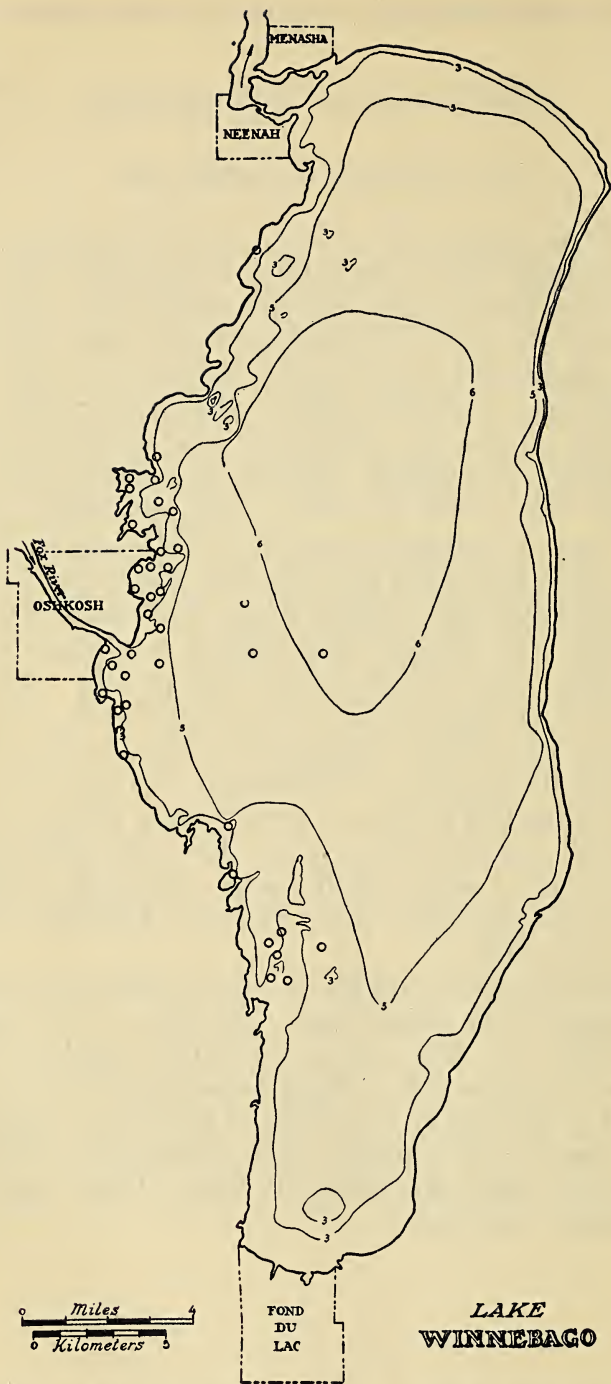


FIG. 1. Map of Lake Winnebago showing 3, 5, and 6 meter contour lines. The circles indicate the stations where collections were made.

Lake Winnebago is fed by a number of large streams. Fox River enters the northwest end of Lake Butte des Morts and forms a channel which extends through this lake, emptying into Lake Winnebago at Oshkosh. In fact, these lakes are really widened-out portions of the Fox River. Pine Creek and Willow Creek enter the western end of Lake Poygon and Wolf River enters the same lake from the north. Fond du Lac River, a small stream, enters Lake Winnebago at the southern end. The water shed of Lake Winnebago covers a wide area in east-central Wisconsin, approximating 6,200 square miles (see Whitbeck, 1915, pl. iv). The outlet of Lake Winnebago is by way of the Lower Fox River into Green Bay. Just below the dams the river widens to form Little Lake Butte des Morts.

The basin of Lake Winnebago is somewhat platter-shaped, the bottom descending more or less abruptly to a depth of three meters and then more gradually to five and six meters. The greater part of the lake bottom forms a subaqueous plain which varies but slightly in contour (see Juday, 1914, pl. 26, and Lake Survey map). Subaqueous terraces are rare on the eastern shore but common on the western shore, where there are many shallow bays, at the points of which bars and shoals extend into deeper water. In some places the slopes of these terraces are very steep. The bottom of the lake is of glacial drift of great thickness.

## B. ORIGIN OF LAKE WINNEBAGO

Lake Winnebago is the result of changes which occurred during the last glacial period—the Late Wisconsin. When the Green Bay lobe of the glacier receded it left a morainic dam in the Fox River Valley at the present site of the City of Menasha. The lake was at first much larger than at present and extended westward and southward in the valley now occupied by lakes Butte des Morts, Poygon, Winneconne, and a part of the Fox River Valley. Fond du Lac was also submerged. Due to readvances of the ice, the lake fluctuated in size before reaching its present level. The red till, so conspicuous in the wave-cut cliffs near South Asylum Bay, and elsewhere, was laid down during one of these advances of the Green Bay lobe.

The glacial outlet was at the present site of Menasha, at the northwest corner of the lake, where the bed rock comes to the surface and forms a rock-sill which held the water at different heights

as it was gradually cut down. The present level of the lake is controlled by the government dam at Menasha. The preglacial channel of the Fox River lies to the east of the present outlet, toward Clifton, but it was filled with glacial material, thus blocking the old outlet; this compelled the lake to find the lowest available col or notch which chanced to be at the present sites of Neenah and Menasha (see Whitbeck, 1915; Martin, 1916; Goldthwait, 1907; Alden, 1918).

### C. LAKE PHYSIOLOGY

Many agents, which may be called physiological, affect the habitats in Lake Winnebago. Among these, winds and waves are potent factors in shaping the physiography of the shores and consequently the character of the animal inhabitants. The great surface area of Lake Winnebago provides a fertile field for the action of winds, which disturb the surface of the lake and often descend to considerable depths. A severe gale from the northeast causes waves of great length and height and provides an undertow which disturbs the bottom to a depth of two meters or more. These heavy waves have made the peculiar rocky shores seen on Doemel Point, Asylum Point, Stony Point, and other places. Sand, gravel, and cobbles are constantly being carried from one point to another, profoundly affecting these habitats. In many places the waves and undertow have formed off-shore bars or shoals composed mostly of sand, the water being a third of a meter in depth on the bars and a meter or more between the bars. Gravel and cobble bars have also been formed off every point, in several places in water as deep as three meters. Plant zones are profoundly affected by wave action, being absent or scanty where this action is heaviest and most abundant where it is lightest.

*Temperature.* The temperature of a shallow lake like Winnebago is high in summer and low in winter; ice is formed in Lake Winnebago much earlier than in deeper lakes, which do not lose their heat as quickly. On account of its shallowness, there is no thermal stratification of the water in summer.

*Transparency.* The degree of transparency of the water of Lake Winnebago varies with the season and with the climatic conditions. During July and August, 1920, the turbidity of the water was great and transparency was reduced to a minimum. A



white disc could be seen only to a depth of a few inches in the open lake. This was due largely to the presence of vast quantities of phytoplankton which was universally distributed and unusually abundant during these months. The wind moved this mass from shore to shore. Occasionally some of the bays were free of the plankton and the water became fairly clear so that the bottom could be plainly seen at a depth of a meter. Almost everywhere the water was filled with fine sediment held in suspension. Compared with some other lakes the degree of transparency in Lake Winnebago is very low. Ekman (1915) gives 18 meters for Lake Vaettern in Sweden; Muttkowski gives three meters for Lake Mendota; and Baker found between four and five meters in Oneida Lake, N. Y.

#### D. POLLUTION

Lake Winnebago is suffering from some degree of sewage pollution. Sewage from the City of Oshkosh enters the Fox River and is discharged into the lake south of the city. Dredgings made about half a mile to a mile and a half south and east of Oshkosh showed a bottom of black mud at a depth of 4.6 meters, in which there was a large quantity of oil that came to the surface of the water in the pail containing the dredgings, forming a thick film. No animal life of any kind was found in these dredgings, but near by, outside of the channel of the Fox River, bottom life was fairly abundant at similar depths. The same conditions that compelled Chicago to divert its sewage from the source of water supply is now confronting Oshkosh and epidemics of typhoid or other water-borne diseases are liable to occur as the sewage increases in volume and becomes mixed with the water supply, which is drawn from the lake east of the city, about half a mile from shore, in water less than four meters in depth. It is probable that some manufacturing wastes also enter the lake. The sewage of Fond du Lac also contaminates the waters of this lake.

#### THE MACROFAUNA OF THE LAKE WINNEBAGO REGION

The region in which lie lakes Winnebago, Butte des Morts, and the Fox River provides unusual opportunities for the study of ecological variation. The Fox and Wolf rivers, flowing for many miles as typical rivers, expand to form large lakes west of Oshkosh. Lake Butte des Morts outflows through a wide river at Oshkosh,

which, after flowing for a distance of about two miles, enters Lake Winnebago. The waters of this lake find outflow by way of the lower Fox River which empties into Green Bay of Lake Michigan. The change in the physical environment from the comparatively quiet waters of a river to the rough and turbulent waters of a lake, has been strikingly reflected in at least one group of animals, the mollusks, the lake species being mostly different from the river species. As would be expected, Lake Butte des Morts, which is but the widening out of the lower part of the Fox River, shows on the whole less change from the river type than does Lake Winnebago, which is larger, with all the features of a true lake.

As has been shown elsewhere (Baker, 1916, 1918) the larger part of the macrofauna of a lake is found within the two meter contour (about six feet) and consists of animals in intimate contact with the substratum of the lake—the bottom and the plants growing on the bottom—where are found the optimum conditions for successful continuance of life—food and oxygen. This is the littoral (or eulittoral) area comparable to the great areas of the sea shore which teem with life.

The shallowness of Lake Winnebago, with a maximum depth of 6.38 meters, makes an ecological division of the lake into depth zones impossible; there is no deep area, or even a true aphytal area, as in the deeper lakes, such as Lake Mendota and Green Lake. An area possibly comparable to the aphytal region of the deeper lakes, where large aquatic plants are absent, may be represented in Lake Winnebago by the central area of maximum depth, although this may equally well be placed in the sublittoral region. The littoral (eulittoral) area extends from the shoreline to a depth of three meters, forming a narrow shelf bordering the shores of the lake; life is most abundant in this region. The sublittoral (or aphytal) area includes the remainder of the lake bottom. In this region the bottom consists of soft, black mud with a considerable amount of organic material.

Nearly all of the bottom of the lake is covered with a detritus which is made up of small fragments of plants, minute pieces of wood, crustacean skeletons, caddis-worm cases, and fragments of molluscan shells. This material is absent only where the waves are strong enough to wash it away. The plant fragments probably constitute an important source of food for the bottom-feeding forms.

Quantitative studies of the composition of the bottom fauna of the sea have been carried on for a number of years (see Petersen, 1911, 1915, etc.) but similar studies on the biota of inland lakes are of comparatively recent date (Baker, 1916, 1918; Ekman, 1915; Muttkowski, 1918). Petersen (1911, p. 71) has said that we must know the main points concerning the productibility of a body of water before that body can be exploited for fishery purposes. This statement applies even more forcefully to the inland waters because here the problems are in a measure simpler and fish culture is more easily controlled. Studies of this kind have been carried on by both counts of the number of animals found in a measured unit area and by weighing the dry animal matter of a unit area. Both methods are useful and should be used wherever practicable. In the Lake Winnebago work, which was conducted primarily to ascertain the number and kind of mollusks in Lake Winnebago and surrounding waters, only the counts of unit areas were made.

Table 1 shows the numerical results for the Mollusca, together with the associated animals, in the different physiographic regions. The depth of the water is given in meters and the character of the bottom is indicated. The figures indicate the number of individuals per square meter of bottom. In the mollusks, the identification has been carried to all varieties; in the associated animals, only the larger groups are recorded.

#### LAKE WINNEBAGO

*The Littoral Region.* This is the most profoundly affected of any part of the lake area, including in its territory the shore with its breaker line where the physical forces are constantly at work. The littoral area may be divided into three quite characteristic subdivisions; 1, the general shore line; 2, the breaker line; and 3, the plant areas. The first two divisions often overlap, and in the present paper will be considered under the several headings of boulders, sand, etc. The shore line is subject to great physiographic changes owing to the molar activity which causes the bottom to constantly shift more or less. Ecological conditions are here severe, the shifting bottom, the exposure to wide changes in temperature, and the pounding of the waves compelling the biota to make frequent readjustments to the environment. It is here that the greatest diversity of molluscan life occurs and the species

differ more or less markedly from the same type living in the quiet parts of the Fox River.

*Life on Boulder Shores.* All of the points facing the lake and all unprotected shores are covered with boulders, which form a typical breaker line; gravel, followed by sand, being distributed above the boulders (shoreward) and the same material occurring downward (lakeward). Typical rocky shores composed of large boulders seldom descend below two meters in depth. On long, exposed shores, as at Doemel Point, Far Rockaway Point, Asylum Point, and near Stony Beach, the boulders are frequently of large size, indicating that wave action has removed all of the finer particles, leaving the heavier material as a breaker line. The typical boulder shore (racion) is usually not over three meters wide on steep shores and descends to a depth of about a meter. Beyond this depth the bottom changes to coarse gravel, then to sand, and finally to mud.

The plant life of this region is scanty, as would be expected, consisting chiefly of filamentous algae (principally *Cladophora*) the plume-like fronds of which hang from the upper surface or sides of the rocks. A few emergent and submergent plants brave this inhospitable habitat, *Scirpus occidentalis* being found in one place, two species of *Potamogeton* in two places, and *Vallisneria* in another place. The last two plants occur in some abundance in several habitats, but *Scirpus* is rare. The gravel in these habitats made growth for these plants possible.

Animal life is not abundant in species although certain species may be abundant in individuals. Among the Mollusca eleven species of Unionidae occur, all of them modified in form to meet the rigorous conditions of this unstable environment. The shells are smaller and thicker, on the average, than those of their river representatives. They are not numerous in individuals, occurring scattered among the boulders, between which they burrow. The gastropods include such species as cling to rocks and feed upon algae. *Pleurocera*, *Physa*, and *Lymnaea* are typical rock inhabitants and occur in some abundance. *Planorbis parvus* and *Somatogyrus* are stragglers from other shores where they live among the algæ. All of the gastropods found on rocks (*Pleurocera*, *Physa*, *Lymnaea*) have a large, wide, ventral surface (the foot) which enables them to cling to the support and so prevents them from being dislodged by the waves. Species in this kind of

a habitat often have the foot unusually developed for this purpose. Three species make up 73 per cent of the total population of the boulder habitat: *Pleurocera acuta* 19 per cent; *Physa sayii* 43 per cent; and *Lymnaea winnebagoensis* 11 per cent. *Physa* is here the dominant species.

Associated animals are about six times as numerous in individuals as the Mollusca (Mollusca 17 per cent, associated animals 83 per cent). Fifteen higher groups of aquatic animals are represented. The conspicuous forms on the rocks are the caddie-flies (Trichoptera) the elongated or flattened tubes of which are fastened to the rocks by filmy anchors. The snail-like case of *Helicopsyche* and the flattened tubes of *Leptocella* are the most conspicuous. Hydroptilidae and *Agraylea* are also represented. Polycentropid larvae, with their funnel-shaped tubes attached to the rocks by broad bands of a fine cementing substance, are common. Chironomid larvae and pupae are abundant, their tubes being attached to the under side of the rocks. The Ephemeroidea, represented by the nymphs of *Heptagenia*, are occasionally seen on the under side of rocks, but these are not as numerous as was observed in Oneida Lake. *Caenis* occurred at one station. An *Enallagma* nymph was caught at another station. Coleoptera, represented principally by the flat larva of *Psephenus lecontei*, also included *Stenelmus bicarinatus*, *Gyrinus ventralis*, and an unknown larva of Dasyllidae.

In some places the smaller cobbles mixed with the larger rocks are covered with life, especially associated animals. Thus at station 12, 1,225 individuals, representing twelve higher groups, were picked from 24 rocks with a maximum surface area of 1,350 square centimeters.

Cladophora harbors certain species which cannot be strictly called petrophilous. Small Nematodes, Planaria, Cladocera, Ostracoda, the mites *Limnesiopsis*, *Hygrobates*, and *Lebertia*; two Hemiptera, *Belostoma* and a Corixid, occurred at two stations, including both adults and nymphs. The Amphipod, *Hyalella knickerbockeri*, was abundant where the alga was most plentiful. A few Chironomid larvae as well as Trichopterid larvae also live among the algae.

Burrowers, including small leeches and *Cambarus propinquus*, were observed beneath the boulders, but they were not abundant in the purely boulder habitats. The disparity in numbers between the Mollusca and the associated animals in the boulder habitats is

probably due to the better clinging powers of the latter, many of which are especially modified to meet these conditions, as for example the flattened bodies of *Psephenus* and *Heptagenia*. Three groups of associated animals make up 85 per cent of the entire population of this kind of habitat, Amphipoda with 23 per cent, Trichoptera with 38 per cent, and Diptera with 24 per cent.

Ecological conditions in the boulder habitats are usually rather rigorous. Feeding can only be done during periods of comparative calm. The snails are all phytophagous, eating the algae. The clams may secure their sustenance from the microorganisms that are brought to them by the waves and currents. The difference in shape and size between the clams of the river and lake may be due in part to the greater difficulty of obtaining a sufficient quantity of food in this rougher environment. The same laws govern many of the associated animals as regards their food supply.

*Life on Gravel Shores* (Table 1). Gravel habitats occupy a large part of the shore line around Lake Winnebago. Gravel is often found in association with boulders but is more usually found occupying the place of the boulders on some exposed shore. It varies in character from cobble stones to fine gravel, with which there is usually more or less sand, often in spots. The gravel or cobble is generally smooth and polished by the continuous wave action. This kind of habitat is such that the inhabitants must be good clingers or burrowers to escape being destroyed by the shifting character of the environment. Gravel beds may occur from shore to a depth of nearly two meters. In one place it was found at a depth of 3.4 meters, and subaqueous bars of gravel extend lakeward from the points for a long distance. Vegetation consists of the same species noted in the boulder habitats, with the addition of *Potamogeton lucens* and *Castalia odorata*.

Among the Mollusca the same kind of naiades occur but the number of species is reduced to six. *Sphaerium* appears sparingly and *Pisidium* increases in both species and individuals. A number of new gastropods appear and several of the boulder species (*Pleurocera*, *Physa*) are less numerous, while *Lymnaea* has disappeared. *Amnicola* and *Valvata* occur in some abundance owing probably to the presence of filamentous algae which is attached to the larger stones. Three species of gastropods are common and abundant on gravel bottom; *Amnicola limosa porata*, *Amnicola emarginata*, and *Valvata tricarinata* and its varieties. Habitat number 40 was the

most prolific; the bottom was mixed with sand and the depth of water and the distance from shore provided a habitat unusually favorable to the development of an abundant molluscan fauna. The associated animals were equally numerous. This station might equally well, perhaps, be included among the sand shore stations. Valvata makes up 46 per cent of the molluscan life of the gravel habitats. The number of species of Mollusca has increased from 22 on the boulder shore to 35 on the gravel shore, an increase of 63 per cent.

Among the associated animals some of the rock-loving species have disappeared or become less numerous. Heptagenia and Psephenus are absent; Leptocella and Polycentropidae are reduced in numbers. Agraylea, Oecetis, and Molanna are scarce. Hemiptera is represented by a few *Plea striola*, adult, and *Belostoma* nymphs. Among Coleoptera the larvae of an unknown Dascyllid, common on the boulder bottom, is rare, but *Gyrinus ventralis*, adult, is common. Of Hirudinea, *Glossiphonia complanata*, *nepheloidea* and *stagnalis*, *Expobdella punctata* and *Nephelopsis obscura* are common. The filamentous algae harbor a number of species, which occur sparingly in individuals, except in the Amphipods. Planaria, a few oligochaete worms, and a number of Chironomid larvae occupy this algal habitat.

The groups of associated animals most numerous on the gravel shores of Winnebago Lake are Amphipods, forming 31 per cent, and Chironomid larvae, forming 41 per cent. Compared with the boulder shores the gravel shores have about the same average population but there is less disparity between the mollusks and associated animals in the gravel habitats (Mollusca about 40 per cent).

*Animal Life on Sand Shores* (Table 1). Sand occurs on many parts of the shore of the lake, either in connection with gravel or boulders, or as large sand flats and shallows in more or less protected bays. Such areas are found in Miller Bay, Asylum Bay, and particularly along the shore south of the mouth of Fox River near Oshkosh, where sand borders the rocky shore for a distance of several miles. Fahney Bay and the bays north of Moreley and Black Wolf points, have sand beaches and shallows that are especially well developed. South of Long Point Island sand bottom occurs for upwards of a mile. The shore from Fox River to Stony Beach is perhaps characteristic of many parts of Winnebago Lake. This shore is bordered by boulders with some gravel. Sand begins

within a meter of the shore. At a distance of 50 or 60 meters from shore there is a succession of sand bars representing present and former breaker lines, which run parallel with the shore.

The transition from gravel to sand shore is in some places well marked and in others is almost imperceptible. Usually, pebbles and large stones gradually become less in number until they finally disappear. In the coves and bays, especially in the area between Fox River and Long Point Island, there is little fine gravel and no coarse gravel, all is fine sand of even texture. Sand bottom areas are usually shallow near shore (out to 150 meters) the depth seldom exceeding one meter. In the protected bays, and even on the more exposed shores, vegetation is abundant and varied, including both submerged and emergent species. In two habitats the sand was mixed with marly clay and *Chara* was abundant. Filamentous algae (*Cladophora*, etc.) are usually abundant. A sand bottom unbound by vegetation is generally a poor faunal habitat, the shifting character of the substratum burying the biota and smothering it. Some Naiades, however, prefer this kind of a habitat and are found abundantly in such places.

Mollusca are abundant in many of the habitats. Curiously enough, the Naiades, which are fairly common on gravel and boulder bottoms, occur sparingly on the sand bottom area. *Sphaerium* is rare and *Pisidium* not as abundant as on the gravel bottom. Of gastropods, *Somatogyrus* forms 22 per cent, *Amnicola limosa porata* 18 per cent, and *Planorbis parvus* and *Valvata tricarinata* each 8 per cent. *Pisidium* constitutes 12 per cent. As a whole, the molluscan fauna of the sand bottom is richer in species than the gravel bottom, increasing from 35 to 40. The presence of filamentous algae on the higher plants accounts in large measure for the abundance of some of the mollusks, as the Amnicolidae and *Valvata*.

The associated animals outnumber the mollusks about two to one. The most abundant being *Hyalella* (about 18 per cent) and Chironomid larvae (25 per cent). Oligochaete worms (mostly *Stylaria*) make up about 14 per cent. Trichoptera comprise six groups, *Agraylea*, *Molanna*, *Oecetis*, *Helicopsyche*, *Polycentropidae*, and a few *Leptocerids*. *Ephemeridae* includes nymphs of *Caenis*, *Ephemera*, and *Ephemerella*. *Acarina* is represented by five genera, *Limnesia*, *Limnesiopsis*, *Piona*, *Unionicola*, and *Hydrachna*, *Piona* being the most numerous. *Hemiptera* includes nymphs of *Belostoma*, adults of *Plea striola*, and a *Corixid* nymph which was



very abundant at station 28 in filamentous algae. Tubes of Chironomid larvae are very numerous in the sand habitats. Leeches are rare, *Glossiphonia fusca*, *stagnalis*, and *nepheloidea* and *Dina fervida* occurring as single individuals.

*Animal Life on Mud Bottom* (Table 1).

Mud bottom areas in shallow water near shore are not common in Lake Winnebago, occurring in protected bays and behind bars or points. This kind of bottom is found in Miller Bay, behind Asylum Point, in marsh portions of Fahney Bay, and in other small protected bays south of the mouth of the Fox River, as well as in several small beach pools behind the shore line. In parts of Miller Bay a marl or marly-clay bottom occurs on which no life was found. About the same species of plants are found here as on the sand bottom.

Among mollusks the Naiades are entirely absent from mud bottom in shallow water and but one specimen occurred on this kind of bottom in deeper water (5.2 meters). Pisidium is common in places. Of the gastropods, which form 78 per cent of the mullusks, Valvata includes 17 per cent, *Physa sayii* 11 per cent, and *Planorbis parvus* 17 per cent. The mollusks are fewer in number of species on a mud bottom than on any other kind of substratum except boulder. Habitat number 32, a stagnant pool behind the beach south of Roe Point, contained the largest number of individuals. Habitat number 42, a small bay on the south side of Long Point Island, contained the next largest number per unit area, due principally to the presence of filamentous algae. Taken as a whole, the mud bottom habitats in shallow water are poor in molluscan inhabitants.

Associated animals are 52 per cent more numerous in individuals than the mollusks. Three groups make up 68 per cent of the associated animal life; *Hyalella knickerbockeri* 28 per cent, *Asellus intermedius* 19 per cent, and Chironomid larvae 39 per cent. The other eleven groups are poorly represented. Among Ephemeroidea, Caenis, Heptagenia, and Ephemerella occur rarely. Of Odonata, nymphs of Enallagma, *Anax junius*, and *Tetragoneuria semiaequa* are represented by a few individuals; *Sialis infumata* was found only in habitat number 36, in a small bay south of Fahney Bay. Of Hemiptera, the large *Ranatra fusca* and a Belostoma occurred in one habitat, the mouth of a small creek near Eweco Park, south

of Oshkosh; Coleoptera is represented by adults of *Hydrovatus pustulatus*, *Haliplus ruficollis*, *Stenelmis bicarinatus*, and *Bidessus flavicollis*. Acarina includes *Limnesiopsis*, *Piona*, *Limnesia*, and *Arrhenurus*, all rare and occurring mostly at station 36, the small pool behind the beach at Roe Point. Leptocerids among Trichoptera are uncommon; and a single larva of the Lepidopterid Nymphula was found at station 23, the marsh behind Asylum Point. Leeches occur at five stations and include *Glossiphonia stagnalis*, *G. nepheloides*, *G. fusca*, *Erpobdella punctata*, and *Dina parva*.

*The Vegetation Areas.* Plants, owing to the shallowness of the water, are very abundant in Lake Winnebago, and occur commonly to a depth of two meters. Beyond this depth they decrease very rapidly. No plants (excepting algae and microscopic forms) were found below 2.5 meters and no filamentous algae below 3 meters. The great plant areas are in shallow water, 0.3 to 1.5 meters in depth, in bays and along the margins of shores. Plant zones of greater or less size extend entirely around the lake, bordering the shore. All of the bays contain an extensive flora which supports a large and varied fauna. Many individuals collected from the bottom are migrants, either by intention or accident, from these plant areas. All kinds of bottom, except boulder, support an extensive flora, and some plants occur on this inhospitable substratum, as at habitat 43 where two species of *Potamogeton* and a *Vallisneria* occurred.

Plants serve three very useful purposes for the bottom fauna. First, they form a binding medium which prevents the bottom from shifting; second, they form a means of attachment and support for the crawling and clinging members of the fauna; and third, they provide a foraging ground, either directly by their own material, or indirectly by harboring many small animals used as food by other members of the fauna or by providing support for filamentous algae, the principal food supply of many forms of animal life. The statement so often made by biologists—that an abundant fauna is dependent upon an abundant flora—is strikingly emphasized in Lake Winnebago, for the animal population is very large per unit area and the flora is equally luxuriant. The lake's large and varied fauna is due to the shallow depth which enables a rich flora to become established.

The aquatic flora may be divided broadly into two groups, emergent and submerged. These may be differentiated as follows:

Emergent	Submerged
<i>Zizania aquatica</i>	<i>Vallisneria spiralis</i>
<i>Scirpus validus</i>	<i>Elodea canadensis</i>
<i>Scirpus occidentalis</i>	<i>Ceratophyllum demersum</i>
<i>Castalia odorata</i>	<i>Myriophyllum verticillatum</i>
<i>Nymphaea advena</i>	<i>Potamogeton pectinatus</i>
<i>Lemna trisulca</i>	<i>Potamogeton richardsoni</i>
<i>Potamogeton natans</i>	<i>Potamogeton zosterifolius</i>
	<i>Potamogeton lucens</i>
	Chara
	Cladophora

No attempt was made to obtain a list of all the species of aquatic plants, only the common and conspicuous ones being included. The lake offers a wide field for botanists and a complete list of the flora would be quite extensive.

Animal life was four times as abundant in vegetation as on the sand bottom areas, which was the richest region of the bottom areas. The number of species represented, however, was not as great (sand 40, vegetation 25). Among mollusks, four species make up 91 per cent of the total population, *Amnicola limosa porata* 21 per cent, *Valvata tricarinata* 48 per cent, *Physa sayii* 13 per cent, and *Planorbis parvus* 9 per cent. Among associated animals, which are more than four times as abundant in individuals as the mollusks, three groups make up 87 per cent of the entire population; *Hyaella knickerbockeri* 41 per cent, Chironomid larvae 31 per cent and Oligochaete worms 15 per cent.

Several animals prefer certain species of plants as a habitat. Thus the broad leaves of *Nymphaea* and *Castalia*, principally on the under side, are tenanted by *Physa sayii*, *Planorbis parvus*, *Planorbis antrosus*, *Planorbis campanulatus*, *Amnicola limosa porata*, *Amnicola walkeri*, *Valvata tricarinata*, young *Bythinia tentaculata*, and *Lymnaea winnebagoensis*. Among associated animals such species as *Donacia proxima*, *Planaria maculata*, the larvae of *Nymphula*, and the eggs of *Donacia* and *Gyrinus* are common. Some *Hyaella* are always found on these leaves. *Scirpus* is the natural home of *Ferrissia parallela* and *Bythinia tentaculata*,

as well as the bryozoan *Plumatella polymorpha*. Elodea is used by *Physa sayii*, *Bythinia tentaculata* and *Planorbis parvus* among snails, and by *Anax junius*, *Enallagma*, and other insects. The Potamogeton leaves serve as a resting place or foraging ground for many mollusks and associated animals. Vallisneria, with its long, narrow leaves, is a favorite resort of *Amnicola* and young *Lymnaea* and *Planorbis*.

But over and above all the filamentous algae are the great foraging grounds of both mollusks and associated animals. Algae, in many places, cover all upright plants like a huge blanket (hence often called blanket algae) and among them many animals occur in great abundance. No less than 19 higher groups of animals have representatives that live among the tangled masses of Cladophora. *Planaria maculata*, leaches of several species, *Glossiphonia fusca*, *stagnalis*, *complanata*, *nepheloidea*, *Dina fervida*, and Oligochaete worms, *Stylaria*, are at times very abundant; minute Cladocera of several species are common; the Amphipod, *Hyaella knickerbockeri*, is the most abundant animal and with this is associated the Isopod, *Asellus intermedius*; among Ephemeroidea, *Caenis* is common; the nymphs of *Corixa*, *Belostoma*, *Notonecta*, and *Pleastria striola* are more or less abundant, with adults of *Pleastria* and *Ranatra fusca*; Trichoptera larvae, including *Agraylea*, *Hydropsyche*, *Oecetis*, *Leptocella*, *Phryganea*, *Polycentropidae*, and a few *Helicopsyche*, are common or abundant; Chironomids, next to *Hyaella*, are the most abundant, their larvae and pupae occurring in countless numbers in the mass of algae; Coleoptera include *Bidessus affinis* and *B. flavicollis*, as well as the larvae of Dytiscids and Dasytyphidae; the mites (Acarina) are the best represented as regards genera, of which eleven have been identified, including *Limnesia*, *Hydrachna* (common), *Tayas*, *Piona* (not common), *Hygrobatas*, *Lebertia porosa*, *Torrenticola*, *Limnesiopsis*, *Eylais*, *Unionicola*, and *Arrhenurus* (rare).

Nearly all aquatic mollusks frequent algal communities. *Bythinia*, young *Amnicola*, *Valvata*, and *Planorbis*, especially the smaller species, browse among the stringy filaments. As already noted in Oneida Lake (Baker 1918, p. 158) some species live in a plant habitat when young and later migrate to a different kind of a habitat. *Pleurocera acuta* when young is found in algae but later migrates to the boulder or gravel shores, where algal food may be gleaned from rocks. *Lymnaea winnebagoensis* also lives in algae when young and later occupies a sand, gravel or boulder

habitat. As observed in Oneida Lake (Baker, 1918, p. 151) many of the animals were of a peculiar green color due to the algae they had eaten. Even the shells of mollusks appeared green when containing the living animal.

*Habitats in Water Deeper than Two Meters* (Table 1.) Beyond the two meter contour both plant and animal life becomes greatly reduced in both number and kind. Upright plants were not found in Lake Winnebago below three meters. The fauna correspondingly decreases. Among Naiades only one species was found deeper than 3.4 meters, *Lampsilis luteola rosacea* at station 69 in water 5.2 meters deep on a mud bottom. *Sphaerium* descends to four meters, and *Pisidium* alone among Pelecypods frequents the deepest parts of the lake, about six meters, where it is abundant. Most of the gastropods disappear between three and four meters. *Amnicola limosa porata* descends to 5.5 meters and is abundant; *Valvata tricarinata* is rare at 6.1 meters.

There is a rapid decrease in number of species as the depth of the water increases. Thus, between 2 and 3 meters, 63 species occur; between 3 and 4 meters, 32 species; 4 to 5 meters, 29 species; and 5 to 6 meters, 13 species. This decrease is greater for Lake Winnebago than for Oneida Lake, the percentages being as follows:

Lake Winnebago	Oneida Lake
2 meters, 85 per cent.	86 per cent.
3 meters, 43 per cent.	60 per cent.
4 meters, 39 per cent.	44 per cent.
5 meters, 17 per cent.	40 per cent.

The depth areas seem divisible into three subregions: Littoral to a depth of three meters where rooted plants cease to grow; sublittoral to a depth of four meters where *Cladophora* and other algae cease to grow; and aphytal from four to six meters where plant life (except plankton algae) ceases to grow. The decrease in plant and in animal life with depth thus appears to be coincident.

The associated animals show about the same decrease with depth as the mollusks, although a greater variety inhabit deeper water. Chironomid larvae descend to a depth of over six meters and appear to bear the same relation to the associated animals that *Pisidium* does to the Mollusca. Leeches (*Glossiphonia* and *Dina*)

and Oligochaete worms also descend to six meters or more. This fauna is not large. *Hydra oligactis* occurred at two habitats on a gravel bottom and *Planaria maculata* was found in the same places; *Hyalella* was rare in the deeper habitats; *Ephemera* occurred at 2.5 meters, *Caenis* at 4 meters, and *Hexagenia* at 5.5 meters; *Sialis infumata* was rare; *Corixa* and *Plea striola*, nymphs, were rare; Trichoptera (*Molanna*, *Agraylea*, *Leptocella*, *Hydropsyche* and *Helicopsyche*) disappeared at 3.1 meters. A single larva of *Nymphula* was dredged at a depth of 4 meters on a mud bottom. Coleoptera included *Psephenus lecontei* at 2.8 meters, *Hydrovatus pustulatus* at 4 meters, and Dasyllid larvae down to 3.4 meters, none common. *Hygrobates* was found at 2.5 meters, and *Limnesiopsis* at 3.1 meters.

#### LAKE BUTTE DES MORTS (Table 1).

Lake Butte des Morts is about five miles long and two and a half miles wide with a maximum depth of 4.6 meters. It is but a widened-out lower portion of the Fox River, though carrying also the waters of Wolf River and several creeks. Most of the ecological conditions of a lake environment are present. Boulder shores are rare, occurring on such places as Plummers Point and Sunset Point, where, however, sand and gravel are quite as common and are usually closely associated with boulders. The shores in the bays are usually marshy with an abundant growth of sedge, cat-tails, and other aquatic plants. In many places this kind of shore is fully a quarter of a mile in width. The bottom of the bays is usually of mud, clay, or fine sand covered with a thick layer of plant debris. Sand occurs along some shores, as west of Plummers Point, as well as on the bottom of the marsh areas at the west end near the Fox River channel. The same vegetation occurs as in Lake Winnebago.

About the same kind of mollusks occur in this lake as in Lake Winnebago. A few species, as *Nephronaias carinata*, *Amblema costata*, and *Amnicola limosa*, indicate the influence of the Fox River fauna. As in Lake Winnebago, the number of species decreases with increased depth, 51 species being found between shore and 2 meters, 12 species between 2 and 3 meters, and but 3 species below 3 meters. Three species make up 53 per cent of the total molluscan population, *Amnicola limosa* 22 per cent, *Bythinia* 24 per cent and *Valvata* 7 per cent.

Associated animals a little more than equal the mollusks in abundance. They include a number of genera divided among fourteen higher groups. Two groups make up 65 per cent of the total, Hyalella, 43 per cent and Chironomid larvae 22 per cent. Caenis occurred at 2 and 3.4 meters and Hexagenia was found on a mud bottom in 1 to 3.4 meters. Enallagma and *Anax junius* were included among Odonata, both rare. Nymphula was rare at all but one station. *Plea striola*, adult and nymph, was not uncommon. Trichoptera included Agraylea, Leptocella, Helicopsyche, Molanna, and Polycentropidae, which were not found deeper than 1.5 meters. Among Coleoptera, *Bidessus flavicollis*, *Stenelmus bicarinatus*, *Donacia proxima*, and a Dasyllid larva occurred uncommonly in shallow water (1 meter) excepting *Donacia* which was found at 3 meters. The mites were very rare and included Hydrachna, Limnesiopsis, and Unionicola, mostly inhabitants of shallow water. Four species of leeches occurred in the deepest water on mud and sand bottom, *Glossiphonia stagnalis*, *nepheloidea*, *fusca*, *Erpobdella punctata*.

The vegetation population of this lake is large but not particularly varied. Only thirteen species of mollusks, of which *Bythinia*, *Amnicola limosa*, and *Ferrissia parallela* form about 79 per cent, were collected from plants as compared with 25 species in Lake Winnebago.

Among associated animals, Hyalella and Chironomid larvae make up 56 and 36 per cent respectively, but are otherwise poorly represented. At one station (93) the filamentous algae were fairly alive with Hyalella and Chironomid larvae. The genera represented in the vegetation include *Plea striola* and *Belostoma* nymphs; *Hexagenia* nymphs; *Enallagma* nymph; *Agraylea*, *Helicopsyche*, *Leptoceridae* larvae; *Nymphula* larva; *Donacia proxima*, *Bidessus flavicollis*, *B. affinis*, Dytiscid larva; *Hydraena*, *Limnesia*; *Asellus intermedius*; *Plumatella polymorpha*; *Hydra oligactis*, and *Glossiphonia* and *Erpobdella*.

#### FOX RIVER (Table 1).

Dredgings were made near Omro, the maximum depth found being 2.9 meters. The bottom is of mud, sand, clay, or gravel, mud occurring in all protected places. Gravel occurred near Omro in water 2.9 meters deep in which three species of Naiades were found. The shores of the river are swampy for the most part, low,

and bordered by marsh vegetation. Aquatic plants grow in the shallower parts of the river. Mollusks were most numerous near the shore on a sand or mud bottom in water 0.5 to 1 meter in depth. The Naiades are mostly different from the lake species as noted under Lake Winnebago species. The gastropods are mostly of species living in quiet habitats and there is not the variety found in the lakes, the latter being 50 per cent richer in species. Of the population of the river habitats *Sphaerium striatinum* makes up 67 per cent, forming great beds bordering the shore in many places.

#### QUANTITATIVE ANALYSES OF THE FAUNA

On rocky shores, a number of boulders were measured, the total animal life removed, and the area computed to the square meter unit. In the vegetation stations the total area covered by the plants was computed to the same unit. In several cases, as in *Scirpus* habitats, the unit included a column from surface to bottom.

The population of Lake Winnebago compares favorably with that of any lake studied, being exceeded only by Oneida Lake among American inland lakes. The average number of animals per unit area on the different kinds of bottom in the two lakes mentioned is shown in table 2.

It will be seen that among the Mollusca, Oneida Lake is 59 per cent richer, while among associated animals, Lake Winnebago is 9 per cent richer in individual population. The small population of the vegetation habitats in Oneida Lake is due to the fact that much of the population is included in the bottom areas which had an algal covering.

Table 3 shows that Oneida Lake has a greater population per unit of area in the shallower water, but that Lake Winnebago has a greater population in the deeper water. Lake Mendota has a very small population in the shallow water as compared with the other lakes. Lake Butte des Morts has the largest population in the deeper water as well as the largest total population per unit area.

The molluscan fauna of the Winnebago region is one of the most extensive and varied of any similar area yet studied. A total of 114 species and varieties of fluviatile and lacustrine forms were found, including three forms believed to be new to science. Table 4 shows the relative abundance of the molluscan fauna in the different parts of this region.



Table 5 shows the relation of the number of species of Mollusca to the depth of the water. The greatest variety is found at depths not exceeding two meters.

Table 6 shows the relation of the number of species of Mollusca to the character of the bottom in Lake Winnebago. The maximum number was found on sand bottom.

Table 7 shows the variety of the molluscan faunas of three lakes, namely, Oneida Lake, New York; Maxinkuckee Lake, Indiana; and Lake Winnebago, Wisconsin.

One of the interesting features brought out by the study of the molluscan fauna of the Lake Winnebago region is the difference in size and shape between the Unionidae of the Fox River and those of the lakes, a difference which appears to be comparable to that noted by Grier (1919) between the Naiads of Lake Erie and the upper drainage of the Ohio River. Grier states that "if we put a shell in the lake environment we may expect it will change its morphological features, not at random, but in a distinct, determinate, or orthogenetic direction." This change in the morphology of shells that have migrated from a river to a lake is strikingly shown in the Lake Winnebago fauna, and a study of the two areas by the methods of Grier would produce the same results as attained by the study of the Lake Erie shells. It is a significant fact that the same varietal forms inhabit both Lake Winnebago and Lake Erie, indicating that the law holds good under similar conditions in widely separated areas. Dr. Sterki notes that almost all of the Pisidium of the lake are small and slight, some even depauperate, and Sphaerium and Musculium are similarly affected. The gastropods of the lake are in the main different from those of the river. Thus the entire molluscan fauna is affected by the same law of variation produced by river and lake environment, clearly indicating that ecological station plays a large part in the evolution of species. A study of the tables and of the systematic list which follows will bring out additional features of this ecological characteristic. Just what factors have been potent in producing these changes does not seem to be definitely known. It is probable that variation in food supply, in the chemical character of the fluid medium in which they live, as well as in the general physical environment, plays a large part in these changes of form.

## LIST OF MOLLUSCA

## UNIONIDAE

*Dysnomia triquetra* Raf. A single small individual was dredged from the Fox River at Omro. This is the first record for Wisconsin, and the northernmost record for any locality. It occurs in southern Michigan.

*Lampsilis ventricosa* (Barnes). Common in the Fox River at Omro and other places.

*Lampsilis ventricosa canadensis* (Lea). Lakes Winnebago and Butte des Morts, abundant. Not before reported from Wisconsin.

*Lampsilis siliquoides* (Barnes). Common in the Fox River at Omro and other places.

*Lampsilis siliquoides rosacea* (DeKay). Lakes Butte des Morts and Winnebago, abundant. First authentic records from Wisconsin.

*Ligumia recta* (Lamarck). Lake Winnebago, common. The typical form from Lake Erie seems to be represented in the lake, where the individuals are smaller and more brightly colored and rayed than the large, black specimens from the rivers.

*Ligumia recta latissima* (Raf.). Fox River at Omro and other places. The large river form. Abundant.

*Proptera alata* (Say). Common in Lake Butte des Morts and Lake Winnebago. As noted by Ortman (1920) and others the Lake Erie form of *alata* is smaller and more swollen than the river forms and the epidermis is usually browner. The Winnebago Lake shells are of this form.

*Proptera alata megaptera* (Raf.). Fox River and other places, common. A much larger shell with more compressed valves.

*Leptodea fragilis* (Raf.). Omro and other places on the Fox River, abundant.

*Leptodea fragilis lacustris* (Baker). Lakes Winnebago and Butte des Morts, common. The lake shells differ markedly from the river shells in color and form. (Baker, 1922, p. 131.)

*Truncilla truncata* (Raf.). Omro, Fox River, common. Lake Butte des Morts, rare.

*Truncilla truncata* (Raf.) variety. A form of *truncata* occurs in Lake Winnebago which is somewhat smaller than the river type of this species. The umbones are less elevated, the valves are rounder and more compressed and the posterior ridge is much less developed. Not enough material is at hand to differentiate this from the typical species.

*Actinonaias carinata* (Barnes). Omro, Fox River, common; Lake Butte des Morts, rare.

*Strophitus rugosus* (Swainson). Omro, Fox River, rare.

*Strophitus rugosus* (Swainson). Var. Lakes Winnebago and Butte des Morts, not common.

*Anodonta imbecillis* Say. Omro, Fox River, common.

*Anodonta grandis gigantea* Lea. Omro, Fox River, common.

*Anodonta grandis footiana* Lea. Lakes Winnebago and Butte des Morts, abundant. This is the type locality for *footiana*.

*Lasmigona complanata* (Barnes). Omro, Fox River. The type locality is the Fox River.

*Lasmigona costata* (Raf.). Omro, common and typical.

*Elliptio dilatatus* (Raf.). Omro, not common.

*Elliptio dilatatus delicatus* (Simpson). Omro, not common.

*Elliptio dililatus sterkii* Grier. Lakes Winnebago and Butte des Morts, common. The lake forms are all smaller and seem in every way like the Lake Erie forms described by Grier (1918).

*Pleurobema coccineum* (Conrad). Omro, not common.

*Quadrula quadrula* (Raf.). Omro, not common.

*Quadrula verrucosa* (Raf.). Omro, not common.

*Amblema costata* (Raf.). Omro, Fox River, Lake Butte des Morts, rare.

*Fusconaia flava* (Raf.). Omro, not common.

*Fusconaia flava parvula* Grier. Lake Winnebago, not common. There is great variation in the diameter of the shells of this form.

#### SPHAERIIDAE

*Sphaerium sulcatum* Lam. Common in Winnebago and Butte des Morts.

*Sphaerium sulcatum planatum* St. Found only in Lake Winnebago.

*Sphaerium lineatum* St. In debris on Doemel Point, Lake Winnebago. Only one specimen found of this species, which seems rare in the lake.

*Sphaerium striatinum* Lam. Lakes Winnebago, Butte des Morts and Fox River. The species shows great variation and there may be a variety that can ultimately be separated when additional material is available.

*Sphaerium lilycashense* Baker. Fox River, rare.

*Sphaerium ohioense* St. Lake Winnebago, not common.

*Sphaerium flavum* Prime. Lake Butte des Morts, rare.

*Sphaerium solidulum* Prime. Lakes Winnebago and Butte des Morts, not common.

*Sphaerium stamineum* Conrad. Lake Winnebago and Fox River, not common.

*Sphaerium occidentale amphibium* St. Swale in woods on Plummers Point, Lake Butte des Morts. Abundant.

*Musculium transversum* Say. Lakes Winnebago and Butte des Morts, not common.

*Musculium truncatum* Linsley. Lake Buttes des Morts, not common.

*Musculium jayense* Prime. Lakes Winnebago and Butte des Morts, not common.

*Psidium virginicum* Gmelin. Lake Butte des Morts, one specimen, juv.

*Psidium compressum* Prime.

*Psidium compressum pellucidum* St. Lakes Winnebago and Butte des Morts, common, the variety *pellucidum* rarer.

*Psidium fallax* St. Lake Winnebago, not common.

*Psidium punctatum simplex* St. Lake Winnebago, rare.

*Psidium variabile* Prime. Lakes Winnebago and Butte des Morts, common.

*Psidium pauperculum* St. Same as above, not common.

*Psidium glabellum* St. Lake Butte des Morts, very rare.

*Pisidium minusculum* St. Lake Butte des Morts, rare. Types of this species were from the Fox River.

*Pisidium sargenti* St. Lakes Winnebago and Butte des Morts, not common.

*Pisidium adamsi affine* St. Lakes Winnebago and Butte des Morts, rare.

*Pisidium strengi* St. Same localities as above, not common. Pond in Terrel's gravel pit.

*Pisidium decorum* St. Lake Butte des Morts, rare.

*Pisidium griseolum* St. MS. Lake Winnebago, very rare.

*Pisidium milium* Held. Lake Winnebago, rare.

*Pisidium walkeri* St. Lake Winnebago, not common.

*Pisidium tenuissimum* St. Lakes Winnebago and Butte des Morts, common.

*Pisidium scutellatum cristatum* St. Lake Winnebago, not common.

*Pisidium vesiculare* St. Lake Winnebago, not common.

*Pisidium medianum* St. Lake Winnebago, common.

*Pisidium clavatum* St. MS. Lake Winnebago, not common.

*Pisidium splendidulum* Sterki. Lake Winnebago, rare.

#### PLEURO CERIDAE

*Pleurocera acuta* Raf. Very abundant in Lake Winnebago.

#### AMNICOLIDAE

*Somatogyrus subglobosus* (Say). Omro, Fox River, rare. Lakes Winnebago and Butte des Morts, common.

*Amnicola limosa* (Say). Omro, Fox River, common. Lake Butte des Morts, common.

*Amnicola limosa porata* (Say). Lake Winnebago, very abundant and the dominant form.

*Amnicola judayi* Baker. Lakes Winnebago and Butte des Morts. Not common.

*Amnicola walkeri* Pilsbry. Lakes Winnebago and Butte des Morts. Common.

*Amnicola lustrica* Pilsbry. Lake Winnebago, rare.

*Amnicola emarginata* Küster. Common in Lakes Butte des Morts and Winnebago.

*Bythinia tenaculata* (Lin.) Lakes Winnebago and Butte des Morts, very common, especially in vegetation.

#### VALVATIDAE

*Valvata tricarinata* (Say). Lakes Winnebago and Butte des Morts. One of the most abundant mollusks in these lakes. Five varieties have been noted in the lake material; their relative abundance is shown in table 1.

*V. tricarinata simplex* Gould

*V. tricarinata supracarinata* Baker

*V. tricarinata basalis* Vanatta

*V. tricarinata perconfusa* Walker

*V. tricarinata unicarinata* DeKay

VIVAPARIDAE

*Liliplax subcarinata* (Say). Lakes Winnebago and Butte des Morts, and Omro, Fox River, common.

*Campeloma rufum* (Haldeman). Same localities as above.

PHYSIDAE

*Physa sayii* Tappan. Lake Winnebago and Butte des Morts, common. These Physas are smaller than *sayii* from other localities, especially river habitats, and may be the result of a lake environment, as has been the case with so many other lake forms herein listed.

*Physa integra* Haldeman. Terrell's gravel pit, near Lake Butte des Morts, in small stream flowing from artificial pond. Rare.

*Physa integra billingsi* Heron. The Lake Winnebago and Butte des Morts specimens of *integra* seem referable to *billingsi*. Common.

*Physa gyrina hildrethiana* Say. Swale half mile north of Oshkosh.

*Physa gyrina oleacea* Tryon. Summer-dry pond in woods on Plummers Point, near Lake Butte des Morts. Abundant.

*Aplexa hypnorum* (Linn.). Swale half mile north of Oshkosh.

PLANORBIDAE

*Planorbis trivolvis* Say. Omro, Fox River, among vegetation, common. Lakes Butte des Morts and Winnebago in protected situations.

*Planorbis trivolvis fallax* Haldeman. Lakes Winnebago and Butte des Morts. In more exposed situations than typical *trivolvis*.

*Planorbis trivolvis pseudotrivolvis* Baker. Lake Winnebago and Butte des Morts in marshy places. Listed as *Planorbis glabratus* by Andrews (1915, p. 200).

*Planorbis truncatus* Miles. Lakes Winnebago and Butte des Morts. The most abundant *Planorbis* in the lake.

*Planorbis campanulatus* Say. Lakes Winnebago and Butte des Morts, common.

*Planorbis antrosus* Conrad. Same localities as above. Abundant only in places.

*Planorbis antrosus striatus* Baker. Same localities. The majority of the *antrosus* are referable to the striate form.

*Planorbis deflectus* Say. Lakes Butte des Morts and Winnebago, common.

*Planorbis exacuus* Say. Same localities as above, not common.

*Planorbis parvus* Say. Common in the two lakes. Rare at Omro, Fox River.

*Planorbis umbilicatellus* Kll. Shallow pool under railroad bridge on shore of Lake Butte des Morts, north of Oshkosh, rare; swale north of Oshkosh, rare; pool on Plummers point, in woods, Lake Butte des Morts, common. The first record for Wisconsin.

*Segmentina armigera* (Say). Small pool beneath railroad tracks north of Oshkosh on shore of Lake Butte des Morts, not common.

## LYMNAEIDAE

*Lymnaea stagnalis appressa* Say. Fox River, Omro, abundant. Lakes Winnebago and Butte des Morts in protected places, common.

*Lymnaea winnebagoensis* Baker. Common in the two lakes. (Baker, 1922, p. 22.)

*Lymnaea elodes* Say. Omro, Fox River. On vegetation in quiet, pond-like stretches of the river, associated with *stagnalis*. Common. Recorded by Andrews from Lake Butte des Morts (1915, p. 200).

*Lymnaea palustris* (Müller). Hatchery Bay among algae; Doemel Point in cat-tail pond behind point. Recorded by Andrews from marsh bordering Lake Butte des Morts (1915, p. 200).

*Lymnaea reflexa* Say. Swale north of Oshkosh; swale in woods on Plummers Point, Lake Butte des Morts; artificial pond in Terrell's gravel pit, Lake Butte des Morts.

*Lymnaea obrussa* Say. Small stream flowing from sand machine near Terrell's gravel pit, emptying into Lake Butte des Morts.

*Lymnaea obrussa exigua* Lea. Pond in Terrell's gravel pit.

*Lymnaea humilis modicella* Say. Hatchery Bay, Oshkosh, on leaves of water lily (*Castalia*). Rare.

*Lymnaea parva* Lea. Marshy border of Lake Butte des Morts, north of Oshkosh. Rare.

*Lymnaea caperata* Say. Shallow pool beneath railroad track north of Oshkosh; small stream flowing into Miller Bay, Lake Winnebago; pool in woods on Plummers Point, Lake Butte des Morts.

## ANCYLIDAE

*Ferrissia parallela* (Haldeman). Lake Butte des Morts, near Plummers Point on leaves of *Scirpus* and *Nymphaea*; Lake Winnebago, near Long Point Island, on *Scirpus* leaves.

## TERRESTRIAL PULMONATA

## HELICIDAE

*Polygyra multilineata algonquinensis* Nason. Long Point Island, Lake Winnebago, and Plummers Point, Lake Butte des Morts, common.

*Polygyra profunda* (Say). Long Point Island, Asylum Point, and Dormel Point, Lake Winnebago, not common.

*Polygyra monodon* (Rackett). Doemel Point, Lake Winnebago; Plummers Point, Lake Butte des Morts, not common.

*Polygyra fraterna* (Say). Doemel Point, Lake Winnebago, rare.

## ZONITIDAE

*Vitrea rhoadsi* Pilsbry. Doemel Point, Lake Winnebago; woods on Plummers Point, Lake Butte des Morts, rare.

*Zonitoides arborea* (Say). Woods on Plummers Point, Lake Butte des Morts, abundant.

*Zonitoides nitida* (Müller). Doemel Point, Roe Point, lake shore near Oshkosh, Lake Winnebago, common.

#### ENDODONTIDAE

*Pyramidula alternata* (Say). Doemel Point, Lake Winnebago; woods on Plummers Point, Lake Butte des Morts, abundant.

*Pyramidula cronkhitei anthonyi* Pilsbry. Woods on Plummers Point, common.

*Helicodiscus lineatus* (Say). Woods on Plummers Point, common.

#### SUCCINEIDAE

*Succinea ovalis* Say. Woods on Plummers Point, common.

*Succinea retusa* Lea. Swale north of Oshkosh; Far Rockaway Point, shore near fish hatchery, Oshkosh; shore of Lake Butte des Morts, north of Oshkosh, abundant.

*Succinea avara* Say. Common near shores of both lakes.

*Succinea avar major* W. G. Binney. Far Rockaway Point, Lake Winnebago, specimens 12 mm. in length.

#### PUPILLIDAE

*Strotilops virgo* (Pilsbry). Woods on Plummers Point, Lake Butte des Morts.

*Strotilope affinis* (Pilsbry). Common, associated with above.

*Gastrocopta contracta* (Say). Doemel Point, Lake Winnebago; woods on Plummers Point.

*Vertigo ovata* Say. Doemel Point, Lake Winnebago.

#### AURICULIDAE

*Carychium exiguum canadense* Clapp. Common in woods on Plummers Point.

### ANIMALS ASSOCIATED WITH THE MOLLUSCA

The following list includes the species or genera of the invertebrate animals found associated with the Mollusca. The list does not include all species that inhabit the territory under consideration, only those taken in dredgings. The names of those specialists who determined the groups are given in the introduction. All material is from the lakes.

#### HYDROZOA

*Hydra oligactis* Pallas

#### PORIFERA

*Spongilla fragilis* Leidy

TURBELLARIA

*Planaria maculata* Leidy

NEMATODA

Genera et species undetermined. Very small worms.

*Stylaria lacustris* (Linn).

*Naias* sp?

*Dero* sp? (Winnebago only)

*Sparganophilus eiseni* Smith (Lake Butte des Morts only).

*Limnodrilus* species, possibly *hoffmeisteri* Claparède.

*Lumbriculus* probably *inconstans* Smith.

HIRUDINEA

*Glossiphonia complanata* (Linn).

*Glossiphonia nepheloidea* (Graf).

*Glossiphonia stagnalis* (Linn).

*Glossiphonia fusca* Castle.

Variety *lineata*,

Variety *papillata*.

*Dina fervida* (Verrill).

*Dina parva* Moore.

*Dina macrostoma* Moore.

*Erpobdella punctata* Leidy.

*Nephelopsis obscura* Verrill.

*Placobdella phalera* (Graf).

CLADOCERA

*Eurycerus lamellatus* Müller.

*Simocephalus serrulatus* Koch.

*Simocephalus vetulus* Müller.

*Daphnia retrocurva* Forbes.

*Sida crystallina* Müller.

*Diaphanosoma brachyurum* (Liéven).

BRYOZOA

*Plumatella polymorpha* Kraepelin.

OSTRACODA

*Cypria* species.

*Cypridopsis* species.

AMPHIPODA

*Hyaella knickerbockeri* Bate.

*Gammarus fasciatus* Say.

ISOPODA

*Asellus intermedius* Forbes.

DECAPODA

*Cambarus propinquus* Girard.



ACARINA (Hydracarina)

Eylais.	Limnesiopsis sp. nov.
Hydrachna.	<i>Limnesia histrionica wolcotti</i> Piersig.
<i>Thyas cataphracta</i> Koenike.	<i>Limnesia paucispina</i> Wolcott.
<i>Arrhenurus americanus</i> Marshall.	<i>Unionicola crassipes</i> (Müll.) ♀
Torrenticola.	<i>Piona reighardi</i> Wolcott.
Lebertia.	<i>Piona turgidus</i> (Wolcott).
<i>Lebertia porosa</i> Thor.	Hygrobates.

EPHEMERIDA (Nymphs)

Ephemera	Callibaetis	Hexagenia
Ephemerella	Caenis	Heptagenia

ODANATA (Nymphs)

Gomphus	<i>Tetragoneuria semiaqua</i> Burm.
Tramea	Plathemis
<i>Anax junius</i> Drury.	Enallagma

HEMIPTERA (Adults and nymphs)

Coriza, adults and nymphs.	<i>Plea striola</i> Fieber.
Belostoma, adults and nymphs.	<i>Notonecta undulata</i> Say.
<i>Gerris marginatus</i> Say.	<i>Ranatra fusca</i> Beauv.

NEUROPTERA (Larvae)

*Sialis infumata* Newman.

TRICHOPTERA (Larvae)

Hydroptila	Agraylea	Hydropsyche
Molanna	Phryganea	Polycentropus
Leptocella	Leptocerus	Oecetis
	<i>Helicopsyche borealis</i> Hagen.	

LEPIDOPTERA (Larvae)

Calaclysta	Nymphula
------------	----------

COLEOPTERA (Mostly adult)

<i>Gyrinus ventralis</i> Kirby.	<i>Agabus gagates</i> Aube.
<i>Cnemidotus edentulus</i> Lec.	<i>Berosus peregrinus</i> Herbst.
<i>Haliplus ruficollis</i> DeGeer.	<i>Psephenus lecontei</i> Hald. Larva.
<i>Bidessus flavicollis</i> Lec.	<i>Stenelmis bicarinatus</i> Lec.
<i>Bidessus affinis</i> Say.	<i>Donacia proxima</i> Kirby.
<i>Hydrovatus pustulatus</i> Melsh.	Dasyllidae. Larva of unknown species.
<i>Comptosomus interrogatus</i> Fabr.	
<i>Laccophilus maculosus</i> Germar.	

DIPTERA (Larvae)

Chironomus	Palpomyia	Tanypus
	Psychodid pupa	

## LITERATURE CITED

- Alden, W. C.** 1918. The quaternary geology of southeastern Wisconsin. Professional Paper No. 106, U. S. Geol. Survey.
- Andrews, Olive V.** 1915. An ecological survey of the Lake Butte des Morts bog, Oshkosh, Wisconsin. *Bul. Wis. Nat. Hist. Soc.* 13: 196-211.
- Baker, Frank C.** 1916. The relation of mollusks to fish in Oneida Lake. *N. Y. State Coll. For. Syracuse Univ. Tech. Pub.* 4: 15-366.
- . 1918. The productivity of invertebrate fish food on the bottom of Oneida Lake, with special reference to mollusks. *N. Y. State Coll. For. Syracuse Univ. Tech. Pub.* 9: 11-233.
- . 1920. The effect of sewage and other pollution on animal life of rivers and streams. *Trans. Ill. Acad. Sci.* 13: 271-279.
- . 1922. a. New species and varieties of Mollusca from Lake Winnebago, Wisconsin, with new records from this state. *Nautilus* 36: 19-21.
- . 1922. b. New Lymnaeas from Wisconsin and Minnesota, with notes on shells from the latter state. *Nautilus* 36: 22-25.
- Chadwick, G. H.** 1902. Notes on Wisconsin Mollusca. *Bul. Wis. Nat. Hist. Soc.* 4: 67-99.
- Ekman, Sven.** 1915. Die Bodenfauna des Vättern. *Internat. Rev.* 7: 146-204, 275-425.
- Evermann, B. W. and Clark, H. W.** 1920. Lake Maxinkuckee. A physical and biological survey. Department of Conservation, State of Indiana. Pub. No. 7, 2 vols. Indianapolis.
- Grier, N. M.** 1918. New varieties of Naiades from Lake Erie. *Nautilus* 32: 9-15.
- . 1919. Morphological features of certain mussel-shells found in Lake Erie. *Ann. Carnegie Mus.* 13: 145-182.
- Goldthwait, J. W.** 1907. The abandoned shore lines of eastern Wisconsin. *Bul. 17, Wis. Geol. and Nat. Hist. Survey.* 134 pp. Madison.
- Juday, Chancey.** 1914. The inland lakes of Wisconsin.—Hydrography and morphometry. *Bul. 27, Wis. Geol. and Nat. Hist. Survey.* 137 pp. Madison.
- Martin, Lawrence.** 1916. The physical geography of Wisconsin. *Bul. 36, Wis. Geol. and Nat. Hist. Survey.* 549 pp. Madison.
- Muttkowski, R. A.** 1918. The fauna of Lake Mendota. *Trans. Wis. Acad. Sci., Arts, and Let.* 19: 374-482.
- Ortmann, A. E.** 1919. A monograph of the Naiades of Pennsylvania. Part III. *Mem. Carnegie Mus.* 8: No. 1.
- Ortmann, A. E. and Walker, Bryant.** 1922. On the nomenclature of certain North American Naiades. *Occ. Pa. Mus. Zool. Univ. Mich.* No. 112.
- Pearse, A. S. and Terrell, Clyde B.** 1920. Aquatic preserves. *Nat. Hist.* 20: 103-106.
- Petersen, C. G. J. and Jensen, P. B.** 1911. Valuation of the sea. Animal life of the sea bottom, its food and quantity. *Rept. Danish Biol. Sta.* 20: 1-76.
- Whitbeck, R. W.** 1915. The geography of the Fox-Winnebago valley. *Bul. 42, Wis. Geol. and Nat. Hist. Survey.* 105 pp. Madison.

TABLE 1. This table shows the average number of individuals per square meter in the bottom fauna of Lake Winnebago, Lake Butte des Morts and the Fox River at Omro in the summer of 1920. The bottom has been divided into areas according to depth and character as indicated in the headings of the different columns.

Organism	Lake Winnebago						Lake Butte des Morts		Fox River, Omro
	Boulder, 0.5-1.5 m.	Gravel, 0.3-1.5 m.	Sand, 0.3-0.9 m.	Mud, 0.3-1.5 m.	Vegetation, 0.3-1.5 m.	Sand, Gravel, Mud, 0.6-0.6 m.	Sand, Mud	Vegetation	0.5-0.3 m.
<i>Mollusca</i>									
<i>L. siliquioidea</i> .....									4.93
<i>L. s. rosacea</i> .....	7.51	2.57	1.92			1.33	1.24		
<i>L. v. canadensis</i> .....	4.75	1.28	1.92				1.24		
<i>L. recta</i> .....	2.71		.93						
<i>P. alta</i> .....	3.42	1.28	.93				.62		
<i>P. a. megaptera</i> .....									3.28
<i>P. gracilis</i> .....									1.64
<i>P. g. lacustris</i> .....	6.13		2.88			1.33	1.24		
<i>A. ligamentina</i> .....							.62		1.64
<i>A. elegans</i> .....									1.64
<i>A. elegans, var.</i> .....	1.33						.62		
<i>F. flava</i> .....									1.64
<i>F. f. parvula</i> .....	2.71	1.28				.66			
<i>A. costata</i> .....							.62		1.64
<i>E. dilatatus</i> .....									3.28
<i>E. d. sterkii</i> .....	3.42	1.28				1.99	.62		
<i>L. costata, var.</i> .....	.66								
<i>S. rugosus</i> .....									3.28
<i>S. rugosus, var.</i> .....	3.42						1.24		
<i>A. g. gigantea</i> .....									1.64
<i>A. g. footiana</i> .....	5.46	2.57	.93				.62		
<i>A. imbecillis</i> .....									1.64
<i>D. triquetra</i> .....									1.64
<i>S. sulcatum</i> .....	.66					8.91	6.22		
<i>S. s. planatum</i> .....			4.83			.66			
<i>S. solidulum</i> .....	.66	6.53	1.92			1.33	3.73		
<i>S. stamienum</i> .....			.93						3.28
<i>S. straitinum</i> .....			10.61			.66	26.88		485.28
<i>S. lilycashense</i> .....									1.64
<i>S. ohioense</i> .....				12.30					

TABLE 1.—Continued.

Organism	Lake Winnebago					Lake Butte des Morts		Fox River, Omro	
	Boulder, 0.5-1.5 m.	Gravel, 0.3-1.5 m.	Sand, 0.3-0.9 m.	Mud, 0.3-1.5 m.	Vegetation, 0.3-1.5 m.	Sand, Gravel, Mud, 0.6-0.6 m.	Sand, Mud	Vegetation	0.5-0.3 m.
<i>S. flavum</i> .....							6.22		
<i>S. species</i> .....						3.33	1.86		
<i>M. transversum</i> .....		3.91			.47	1.99	13.73		23.01
<i>M. jayense</i> .....			.93	4.93			4.97		
<i>M. truncatum</i> .....							2.48		
<i>M. species</i> .....							.62		
<i>P. variable</i> .....	.66	9.15	1.92			74.63	19.37		
<i>P. compressum</i> .....		35.28	13.52	29.59	.47	68.39	19.99		
<i>P. c. pellucidum</i> .....			.93				6.84		
<i>P. scutellatum</i> .....	1.33	11.86	28.97		.47	17.36	58.17		
<i>P. s. cristatum</i> .....		1.28	.93			3.33			
<i>P. medianum</i> .....	.66	1.28	.93			8.71			
<i>P. vesiculare</i> .....		1.28				7.37			
<i>P. clavatum</i> .....		1.28	1.92			3.33			
<i>P. punctatum simplex</i> .....		1.28							
<i>P. sargentii</i> .....		1.28		4.93		1.99	.62		
<i>P. pauperculum</i> .....		28.75			.93	1.33	4.37		
<i>P. tenuissimum</i> .....			8.69	4.93		54.52	1.24		
<i>P. adamsi affine</i> .....						.66	3.73		
<i>P. fallax</i> .....			.93						
<i>P. strengi</i> .....			1.92				.62		
<i>P. griseolum</i> .....						1.33			
<i>P. walkeri</i> .....						1.33			
<i>P. milium</i> .....						.66			
<i>P. splendidulum</i> .....						4.03			
<i>P. glabellum</i> .....							1.86		
<i>P. decorum</i> .....							1.24		
<i>P. virginicum</i> .....							.62		
<i>P. minusculum</i> .....							2.48		
<i>P. species</i> .....		6.35	5.79	4.93		26.21	4.97		
<i>Pl. acuta</i> .....	38.26	5.19	.93		4.26	2.66			
<i>L. subcarinata</i> .....			.93			1.99	3.73		102.03
<i>C. rufum</i> .....							3.73		31.24
<i>B. tentaculata</i> .....		31.37	1.92	7.37	25.77	13.46	161.45	53.59	

TABLE 1.—Continued.

Organism	Lake Winnebago						Lake Butte des Morts		Fox River, Omro
	Boulder, 0.3-1.5 m.	Gravel, 0.3-1.5 m.	Sand, 0.3-0.9 m.	Mud, 0.3-1.5 m.	Vegetation, 0.3-1.5 m.	Sand, Gravel, Mud, 0.3-0.6 m.	Sand, Mud	Vegetation	0.5-0.3 m.
<i>S. subglobosus</i> .....	2.71	1.28	88.88			4.03	1.86		1.64
<i>A. limosa</i> .....							155.84	100.61	24.66
<i>A. l. porata</i> .....		33.95	73.41	34.52	184.42	47.77			
<i>A. walkeri</i> .....		2.57	.93		.93	7.37	3.11	1.30	
<i>A. lustrica</i> .....		2.57	1.92			3.33	.62		
<i>A. emarginata</i> .....		5.19			2.84	10.08	1.24		
<i>A. judayi</i> .....		2.57				13.46	11.24		
<i>V. tricarinata</i> .....		118.91	34.75	66.66	373.20	120.52	50.66	9.15	
<i>V. t. basalis</i> .....		58.79		9.86	20.53	28.93	1.24		
<i>V. t. simplex</i> .....		7.82		2.44	7.15	10.08			
<i>V. t. uniearinata</i> .....		18.22	.93	4.93	3.68	.66			
<i>V. t. infracarinata</i> .....		3.91	.93	2.44					
<i>V. t. supracarinata</i> .....				2.44	1.42	6.04	1.24		
<i>P. trivoltis</i> .....				12.30	1.91		4.35		1.64
<i>P. t. fallax</i> .....			.93						
<i>P. truncatus</i> .....			.93	7.37	2.35	.66	2.48	3.91	
<i>P. pseudotrivoltis</i> .....				2.44					
<i>P. campanulatus</i> .....					.47		2.48		
<i>P. antrosus</i> .....		6.53			.47	2.66	2.48	1.30	
<i>P. parvus</i> .....	4.08		34.75	88.88	80.25	1.33	39.04	2.61	
<i>P. deflectus</i> .....		6.53	.93			.66	7.51	6.53	
<i>P. ezacuouus</i> .....		5.19	1.92	4.93	7.55	.66	3.73	1.30	
<i>S. armigera</i> .....			.93						
<i>P. umbilicatellus</i> .....								1.30	
<i>P. sayii</i> .....	86.12	2.57	27.99	56.74	107.98	6.04	29.37	26.13	
<i>P. i. billingsi</i> .....	2.04		25.11				1.24		
<i>F. parallela</i> .....				2.44	2.84		2.48	50.97	
<i>L. winnebagoensis</i> .....	20.53		3.86	121.58	2.84	3.33			
<i>L. S. appressa</i> .....				2.44	3.82		1.24	1.30	13.15
<i>L. elodes</i> .....									8.22
<i>L. h. modicella</i> .....					.47				

TABLE 1.—Continued.

Organism	Lake Winnebago					Lake Butte des Morts		Fox River, Omro	
	Boulder, 0.5-1.5 m.	Gravel, 0.3-1.5 m.	Sand, 0.3-0.9 m.	Mud, 0.3-1.5 m.	Vegetation, 0.3-1.5 m.	Sand, Gravel, Mud, 0.6-0.6 m.	Sand, Mud	Vegetation	0.5-0.3 m.
Associated animals									
<i>Hydrozoa</i> .....						10.75	7.51		
<i>Turbellaria</i> .....	4.08	39.19			33.90	2.66			
<i>Hirudinea</i> .....	54.66	37.86	3.86	19.74	46.79	50.39	28.75	16.97	
<i>Oligochaeta</i> .....	37.59	66.66	137.18	7.37	546.65	39.68	49.41	78.39	
<i>Nematoda</i> .....	1.33	10.45	7.73		1.91	2.66			
<i>Cladocera</i> .....	.66	5.19	15.42	2.44	60.53				
<i>Decapoda</i> .....	10.93	7.82							
<i>Ostracoda</i> .....	16.39	1.28				1.33	3.73		
<i>Amphipoda</i> .....	280.99	351.56	214.46	264.15	1,468.87	32.30	303.72	1,717.47	1.64
<i>Isopoda</i> .....		2.57	.93	182.59	4.44	1.33	90.12	1.30	
<i>Ephemera</i> .....	3.42		23.15	7.37	31.01	8.04	15.64	1.30	3.28
<i>Odonata (nymphs)</i> .....	.66			17.24	5.24		1.24	1.30	
<i>Neuroptera (lar.)</i> .....				4.93		1.33			
<i>Hemiptera</i> .....	19.10	6.53	163.27	7.37	61.99	2.66	10.62	32.66	
<i>Trichoptera (lar.)</i> .....	53.95	99.32	41.50	29.59	107.50	41.06	22.53	50.97	1.64
<i>Lepidoptera (lar.)</i> .....		1.28		2.44	8.08	.66	8.13	11.73	
<i>Diptera (lar.)</i> .....	287.12	466.62	306.23	375.25	1,100.95	222.86	155.09	1,105.75	1.64
<i>Coleoptera</i> .....	18.44	32.66	.93	14.79	40.61	5.37	5.59	43.10	
<i>Acarina</i> .....	4.08	1.28	14.58	17.24	25.28	1.33	3.73	2.61	

TABLE 2. Average number of individuals per square meter on bottoms of Lake Winnebago and Oneida Lake.

	Winnebago		Oneida	
	Mollusca	Associated Animals	Mollusca	Associated Animals
Boulder.....	201.75	119.36	344.85	1,150.10
Gravel.....	449.28	1,129.22	899.91	1,043.89
Sand.....	397.73	927.90	1,650.50	1,770.93
Mud (and clay).....	495.95	953.79	2,657.51	3,208.11
Vegetation.....	833.69	3,566.31	213.75	49.77
Average.....	472.84	1,553.62	1,153.21	1,464.29

TABLE 3. Relation of Mollusca to the depth of the water.

	Winnebago	Butte des Morts	Oneida	Mendota
2 meters.....	472.84	429.29	1,153.21	81.76
2-6 meters.....	584.38	1,860.72	395.07	222.64
Total population.....	529.72	1,144.77	774.14	157.76

TABLE 4. Distribution of the Mollusca by families in the Winnebago region.

	Fox R.	Butte des Morts	Winnebago	Swales, etc.	Total
<i>Unionidae</i> .....	20	9	11	.....	30
<i>Sphaeriidae</i> .....	4	19	28	1	37
<i>Pleuroceridae</i> .....	.....	.....	1	.....	1
<i>Amnicolidae</i> .....	2	7	7	.....	8
<i>Valvatidae</i> .....	.....	6	6	.....	6
<i>Viviparidae</i> .....	2	2	2	.....	2
<i>Physidae</i> .....	.....	2	2	4	6
<i>Planorbidae</i> .....	2	10	10	2	12
<i>Lymnaeidae</i> .....	2	5	4	4	10
<i>Ancylidae</i> .....	.....	1	1	.....	1
Total.....	32	61	72	11	113
Terrestrial species.....	.....	.....	.....	.....	19
Total mollusks.....	.....	.....	.....	.....	132

TABLE 5. Relation of the number of species of Mollusca to the depth of the water.

	2 Meters	3 Meters	4 Meters	5 Meters	6 Meters	7 Meters
Winnebago.....	63	32	29	11	13	8
Butte des Morts.....	51	12	3	.....	.....	.....
Oneida Lake, N. Y.....	56	39	29	26	11	.....

TABLE 6. *Relation of the number of species of Mollusca to the character of the bottom in Lake Winnebago.*

Boulder	Gravel	Sand	Mud	Vegetation
22	35	40	23	25

TABLE 7. *Comparison of the molluscan faunas of three different lakes.*

	Oneida, N. Y.*	Maxinkuckee, Ind.†	Winnebago, Wis.
<i>Unionidae</i> .....	14	14	12
<i>Sphaeriidae</i> .....	27	41	35
<i>Pleuroceridae</i> .....	1	10	1
<i>Amnicolidae</i> .....	11	4	9
<i>Valvatidae</i> .....	3	2	6
<i>Viviparidae</i> .....	3	3	2
<i>Physidae</i> .....	4	2	6
<i>Planorbidae</i> .....	10	7	12
<i>Lymnaeidae</i> .....	9	6	10
<i>Ancylidae</i> .....	3	4	1
Total.....	85	93	94

\*Baker, 1918.

†Everman and Clark, 1920.



OBSERVATIONS ON PARASITIC WORMS  
FROM WISCONSIN FISHES

---

A. S. PEARSE

The following descriptions of trematodes and nematodes from Wisconsin fishes relate partly to new species and partly to those that have been inadequately described or confused by previous writers.

TREMATODA

**ACETODEXTRA**, new genus

Flattened Distomata having the acetabulum on the right of the median line. Genital aperture between the acetabulum and the junction of the intestinal rami; situated somewhat toward the right side. Cirrus sac very small. Two more or less linear testes lie on either side at the posterior end of the body, between the intestinal rami and the median excretory duct. Ovary, somewhat lobate, elongated, near the center of the body. Uterus with many coils; extending across the body from the acetabulum nearly to the posterior end. Intestinal rami reaching nearly to the posterior end of the body.

Type species: *Acetodextra amiuri* (Stafford).

*Acetodextra amiuri* (Stafford)

(Fig. 6)

Stafford (1900) assigned this species to the genus *Monostomum*, believing that no acetabulum was present, though his figure plainly shows one. He was doubtless deceived by the fact that the acetabulum always lies to the right of the median line. The following description supplements his:

Length: 3.6 mm.; width: 1.8 mm.; pharynx, .14 by .10 mm.; length of esophagus: 25. mm.; diameter of oral sucker: .185 mm.; diameter of acetabulum: .277; egg: .035 by .026 mm.

The oral sucker is small; the pharynx is almost  $1\frac{1}{2}$  times as long as wide; esophagus, very slender, about three times as long as pharynx; intestinal rami, thick, extending to posterior end of the body.

Vitelline glands are in contact with the lateral surfaces of the intestinal rami, extending from the acetabulum to the tips of the rami; a duct from each group of glands extends directly across the body to the middle where it unites with that from the opposite side and enters a rounded yolk reservoir.

The testes are somewhat lobate and elongated antero-posteriorly. They lie between the intestinal rami and the posterior, median excretory duct. Cirrus sac: very small and ovate. The ovary lies just anterior to the vitelline ducts. It is lobate and elongated. The uterus is filled with eggs and occupies the space between the intestinal rami, from the acetabulum to the posterior end of the body.

The bullheads in Lake Pepin were often infected with this trematode. Figure 6 was drawn from a specimen taken from the swim bladder of *Ameiurus melas*, July 12, 1920 (U. S. Nat. Mus., Cat. No. 7618). Other specimens were found in the swim bladders of *A. natalis* and *A. nebulosus*. Young specimens were found encysted in the liver peritoneum of a *Schilbeodes gyrinus*, June 23, 1920.

### MACRODEROIDES, new genus

Elongated *Plagiorchiidae* with the two suckers of nearly equal size. The genital opening is at the anterior margin of the acetabulum. A slender prepharynx and a longer esophagus are present. The intestinal rami arise from the esophagus some distance anterior to the acetabulum. The body is covered with sharp spines which decrease in size posteriorly. The vitelline glands extend from a short distance behind the acetabulum to the posterior testis. The genus shows resemblances to *Macrodera* Loos, *Haplometra* Loos, and *Glypthelmins* Stafford.

Type species: *Macroderoides spiniferus*, Pearse.

*Macroderoides spiniferus*, new species

(Fig. 9)

Type: Cat. No. 7619, U. S. National Museum; Lake Pepin, Wisconsin; July 11, 1920; collector, A. S. Pearse.

Host: the short-nosed gar, *Lepisosteus platostomus* Rafinesque.

Description: Body slender; length 2.4 mm.; width, .25 mm.; covered with sharp spines, which decrease in size posteriorly. In the region of the pharynx there are about fifty spines on the circumference of a cross section of the body. The diameter of the acetabulum is slightly greater than that of the oral sucker, which measures .08 mm. The acetabulum is at the posterior end of the anterior seventh of the body.

A slender prepharynx is present. The pharynx measures .012 mm. in length and .088 in diameter. The slender esophagus is about twice as long as the pharynx. The intestinal rami are slender, join the esophagus more than the length of the esophagus anterior to the acetabulum, and extend nearly to the posterior end of the body.

The genital pore lies on the median line, just anterior to the acetabulum. The testes are ellipsoidal, their longest axis being in the same direction as that of the body. They are about equal in size, measuring .18 mm. in length. The anterior one is situated on the left side at the beginning of the posterior third of the body. The posterior one is slightly toward the right side, just in front of the posterior sixth of the body. The cirrus sac is long, thick, and somewhat sinuous, extending from some distance posterior to the acetabulum to the genital pore.

The ovary is ellipsoidal and about half as long as a testis. It is situated near the middle of the body, somewhat toward the left side. The vitelline glands are small, irregular in form but generally spherical; and distributed along each side of the body from a little posterior to the acetabulum to the posterior testis. The uterus is coiled from the genital pore to the posterior end of the body. It usually contains a couple of hundred eggs which are elliptical, without a distinct cap, and measure .04 mm. in length.

Eleven specimens, including the type, were taken from the intestine of a short-nosed gar on July 11, 1920. Four other specimens were found in bullheads caught in the slews at the outlet of Lake Pepin: three in an *Ameiurus natalis* on July 6, 1920; one in an *Ameiurus nebulosus*, July 7, 1920.

*Crepidostomum illinoiense* Faust

(Fig. 7)

Specimens studied: Cat. No. 7626, U. S. National Museum; June 25, 1920; Lake Pepin, Wisconsin; Collector, A. S. Pearse.

Sixteen specimens of this trematode were taken from the intestine of a mooneye caught in Lake Pepin, June 25, 1920. Two other mooneyes were captured at the same time. One contained twenty-one of the parasites; the other, none.

*Allocreadium armatum* MacCallum

(Fig. 8)

Length of a large contracted specimen, 3.2 mm. (U. S. Nat. Mus., Cat. No. 7620); width, 1.08 mm.; diameter of oral sucker, .35 mm.; diameter of acetabulum, .6 mm.; egg, .11 by .07 mm. Length of a smaller expanded specimen, 2.8 mm.; width, .53 mm. Cuticle minutely denticulate, especially toward the anterior end.

The diameter of the oral sucker is nearly two-thirds that of the acetabulum, which is situated at the posterior end of the anterior third of the body. A short prepharynx is present. The pharynx is about half the diameter of the oral sucker in length, and it is about as wide as long. The intestinal rami are slender and reach nearly to the posterior end of the body.

The ovary is about half as long as the anterior testis and oval, with the long axis extending across the body. It lies on the right side of the body just behind the acetabulum. The uterus is coiled between the acetabulum and the anterior testis, lying mostly on the left side. It may contain as many as eleven eggs. The genital pore is on the median line anterior to the acetabulum. The vitelline glands surround the intestinal rami in the posterior third of the body and extend forward outside the rami nearly to the middle of the acetabulum.

The two testes are somewhat lobate and are slightly elongated; their long axes lying across the body. They lie close together immediately posterior to the ovary between the intestinal rami, one being directly behind the other. The posterior testis is slightly larger than the anterior. The cirrus pouch is oval, about a third as wide as long, and is about as long as the diameter of the acetabulum.

Sixty-five specimens were taken from a sheephead, *Aplodinotus grunniens* Rafinesque, caught in Lake Pepin, Wisconsin, July 9, 1920. Other specimens were taken from the same locality and species on July 10, 13; from sunfishes *Eupomotis gibbosus* (Linnaeus) at Sturgeon Bay, Wisconsin, July 19, 23.

**Allocreadium ictaluri**, new species

(Fig. 5)

Type: Cat. No. 7621, U. S. National Museum; Lake Pepin, Wisconsin; July 3, 1920; collector, A. S. Pearse. Other specimens were found in the same host at the same locality July 8, 10.

Host: *Ictalurus punctatus* (Rafinesque), the channel catfish.

Length of body, 5.9 mm.; width, 1.85 mm. Diameter of acetabulum, .63 mm.; oral sucker, .5 mm.; pharynx, .3 mm. Cirrus sac, .45 by .25 mm. Egg, .08 by .045 mm.

Cuticula smooth except on the suckers, where it is rough. The acetabulum is slightly larger than the oral sucker. The latter is situated on the ventral surface close to the anterior end. The acetabulum is in the anterior end of the middle third of the body.

A very short and wide prepharynx connects the oral sucker and the pharynx, which is nearly spherical in form. There is apparently no esophagus. The intestinal rami are about .37 mm. in diameter and reach nearly to the posterior end of the body.

The genital aperture is on the median line at a point nearly half the distance from the acetabulum to the pharynx. The cirrus sac is broad, ovate, and reaches to the anterior margin of the acetabulum. The two testes lie in the anterior portion of the posterior third of the body. They lie on the median line. The posterior one is somewhat lobate and the anterior one is elongated with its axis across the body.

The vitelline glands extend from the pharynx to the posterior end of the body. They are absent for a space of about .25 mm. on either side of the acetabulum. They stain most heavily near the lateral margins of the body but a few occur throughout the middle portion also. The uterus is coiled between the posterior border of the acetabulum and the anterior testis. It contains about six hundred eggs. The ovary is spherical and lies about .1 mm. posterior to the acetabulum.

**Allocreadium boleosomi**, new species

(Fig. 4)

Type. Cat. No. 7622, U. S. National Museum; Lake Pepin, Wisconsin; July 9, 1920; collector, A. S. Pearse.

Host: the Johnny darter; *Boleosoma nigrum*; intestine.

Length of body, 1.33 mm.; width, .37 mm.; diameter of oral sucker, .14 mm.; diameter of acetabulum, .22. Eggs, .04 by .16 mm. Cuticula minutely denticulate.

Diameter of oral sucker slightly more than half that of acetabulum. No prepharynx. Pharynx, a little more than half the diameter of the oral sucker in length, spindle-shaped, about two-thirds as wide as long. Esophagus very slender, about two-thirds as long as the pharynx. Intestinal rami, slender, extending nearly to posterior end of body.

Genital pore, median, a short distance anterior to the acetabulum. Ovary, elliptical with the long axis across the body; .09 by .175 mm. Uterus between the ovary and the acetabulum, more on the right than the left side, containing as many as fourteen eggs. Vitelline glands forming large rounded follicles, about .05 mm. in diameter, which are distributed along margins of the body behind the acetabulum and across the posterior end.

The testes are elongated, median, and immediately behind the ovary. The anterior one measures .09 by .17 mm. and its long axis extends across the body. The posterior testis measures .13 by .21 mm. and its long axis is nearly longitudinal. The cirrus pouch is pyriform; length, .15 mm. It extends back to a little beyond the center of the acetabulum.

The type was one of seven specimens taken from the intestines of four Johnny darters collected at the lower end of Lake Pepin, July 9, 1920. Three other specimens were found in the intestine of a log perch, *Percina caprodes* (Rafinesque), collected at the same place July 5, 1920.

### *Phyllodistomum superbum* Stafford

(Fig. 2)

The writer is convinced that Stafford (1904) confused two species of the genus *Phyllodistomum*. Stafford's name is therefore retained for the species which most nearly fits his description and a new name, *P. staffordi*, is given to the other.

Length of body, 2.57 mm.; width, 1.5 mm. Diameter of acetabulum, .29 mm.; of oral sucker, .24 mm. Length of anterior testis, .38 mm.; of posterior testis, .52 mm.; of ovary, .22 mm. Size of egg, .022 by .033 mm. (Cat. No. 7623, U. S. Nat. Museum.)

Anterior end of body narrow (.33 mm. wide) as far back as acetabulum, which is about 1.2 mm. from the anterior end. Ex-

panded posterior portion is crinkled on margins. Posterior end, notched.

The esophagus is slender, and about .35 mm. in length; the intestinal rami are slightly lobate and reach to or a little beyond the posterior end of the posterior testis; diameter, about .15 mm.

The genital pore is about midway between the anterior margin of the acetabulum and the junction of the intestinal rami. The testes are lobate. They are of about the same width but the posterior one is longer than the anterior. Though the testes lie in about the same relative positions as in *P. fausti*, they are never in contact, but are separated by a distance of about .1 mm. The space between them is occupied by about two loops of the uterus.

The ovary is elongated and irregularly lobate. It lies on the right side, about .1 mm. posterior to the vitelline gland. The two vitelline glands, though elongated and pyriform, are rather irregular in outline. The uterus is filled with eggs and clearly arranged in coils. It is coiled throughout the posterior portion of the body posterior to the acetabulum. A few loops extend forward between the vitelline glands to about the middle of the acetabulum.

This trematode is not uncommon in the urinary bladder of the yellow perch, *Perca flavescens* Mitchill, from two Wisconsin lakes—Green Lake and Lake Michigan. Stafford (1904) apparently found this species at Montreal, Canada. The specimens from which the writer's description was made were collected at Sturgeon Bay, July 30, 1921.

#### *Phyllodistomum fausti*, new species

(Fig. 1)

Type: Cat. No. 7625, U. S. National Museum; Lake Pepin, Wisconsin; June 26, 1920; collector, A. S. Pearse. Fifteen specimens were taken from a single sheepshead.

Host: *Aplodinotus grunniens* Rafinesque; urinary bladder.

Length, 4.77 mm.; width, 2 mm.; diameter of oral sucker, .45 mm.; diameter of acetabulum, .7 mm.; egg, .037 by .028 mm. Body very flat, widest at junction of middle and posterior thirds; anterior third narrow, tapering toward anterior end. Middle portions of lateral margins crinkled.

Esophagus, .7 mm. in length; about .05 mm. in diameter. Intestinal rami about .1 mm. in diameter; reaching to the posterior fifth of the body.

Ovary .42 by .32 mm., lobate, on left side of body. Vitelline glands, ovate, slightly lobate, .25 by .13 mm. Uterus, slender, coiled throughout the body posterior to the acetabulum and on each side of the acetabulum through about half its length; filled with eggs; the coiled terminal duct passes dorsal to the acetabulum to the genital pore, which lies about midway between the anterior margin of the acetabulum and the junction of the intestinal rami.

The two testes lie between the intestinal rami, posterior to the vitelline glands, usually in contact with each other; the anterior one is on the right side, the posterior one is in the middle of the body; both have deeply incised lobes; the right one measures .35 by .65 mm., the median one .45 by .8 mm. Seminal vesicle about .3 mm. long and .17 wide.

#### ***Phyllodistomum staffordi*, new species**

(Fig. 3)

Type: Cat. No. 7624, U. S. National Museum; Lake Michigan, Sturgeon Bay, Wisconsin; July 21, 1920. Other specimens were found in *Ameiurus melas* (Rafinesque).

Host: the speckled bullhead, *Ameiurus nebulosus* (Le Seur); urinary bladder.

Length of body, 4.1 mm.; width, 2.98 mm. Diameter of oral sucker, .38 mm.; acetabulum, .52 mm. Egg, .027 by .021 mm. Anterior quarter of body narrow, flattened, sharply set off from the posterior portion by a groove. Behind the middle of the acetabulum the body is discoidal, being nearly circular in outline; the margins are thin, but not crinkled, and are covered with minute papillae. The esophagus is short—a little less than the diameter of the oral sucker in length. The intestinal rami are quite wide (about .3 mm.) and extend to the posterior eighth of the body.

The genital pore is nearer the anterior margin of the acetabulum than the junction of the intestinal rami, and is median. The testes are nearly equal in size, the left being a little larger, irregularly lobate, and lie on either side of the body; latero-posterior to the vitelline glands. The left testis is a little more posterior than the right, and the ovary lies between it and the nearest vitelline gland. The testes are small, measuring about .42 mm. in diameter. There is a seminal vesicle, about .5 by .7 mm.

The ovary is elongated, lobate, and measures about .25 mm. in length. The two vitelline glands are each composed of about eight



oval lobules. They are .15 mm. apart and about the same distance from the posterior margin of the acetabulum. The uterus is coiled between and posterior to the testes, largely between the intestinal rami. It does not come close to the lateral or posterior margins; its coils do not lie very close together and do not contain a continuous series of eggs, but discontinuous groups.

In writing descriptions of the three species of Phyllodistomum, the writer has examined specimens as follows: the first figure indicating the number of phyllodistomes and the second the number of fishes from which they came: *P. fausti*, 14-1; *P. superbum*, 11-7; *P. staffordi*, 18-5. The following key separates the three species:

Key to Species of Phyllodistomum in United States Fishes

- 1 (2) Anterior, narrow, portion of body separated from discoidal portion by a distinct groove; testes not extending into posterior quarter of body; esophagus not longer than oral sucker; uterus containing scattered groups of eggs, not reaching near margins of body; vitelline glands lobate.....*P. staffordi*
- 2 (1) Anterior, narrow, portion not separated from the posterior portion by a groove; posterior portion not discoidal, crinkled more or less along margins; esophagus longer than oral sucker; eggs close together in uterus; vitelline glands pyriform..... 3
- 3 (4) Post-acetabular portion of body widest just behind the acetabulum; testes somewhat separated; posterior margin of body with a distinct median notch.....*P. superbum*
- 4 (3) Post-acetabular portion of body widest in middle; testes close together; posterior margin of body without a distinct notch.....*P. fausti*

NEMATODA

**Ascaris lucii**, new species

(Fig. 12)

Type: Cat. No. 7613, U. S. National Museum; Lake Michigan, Sturgeon Bay, Wisconsin; July 23, 1920. Other specimens were collected from the same host at the same place on July 20, 21, 1920.

Host: the pickerel, *Esox lucius* Linnaeus; intestine.

No males of this species were obtained, but eleven females were examined.

Length of body, 36 mm.; diameter, 1.1 mm. Lip lobes: length, .1 mm.; width, .1 mm.; with thin, auriculate, proximal angles; interlabia absent. The cuticula bears about 48 annulations per millimeter. The anus is about 1.8 mm. from the posterior end of the body.

***Ascaris scaphirhynchi*, new species**

(Fig 11)

Type: Cat. No. 7611, 7612, U. S. National Museum; Lake Pepin, Wisconsin; June 20, 1920; collector, A. S. Pearse. Another specimen was taken from the stomach of another sturgeon on the same date. On June 23 six specimens were taken from the stomach of a sand sturgeon.

Host: the sand sturgeon, *Scaphirhynchus platorhynchus* (Rafinesque); intestine.

Length of females, 41 mm.; width, 1 mm.; length of male, 33; width, .9 mm. Cuticula with about 105 annulations per millimeter. Anus of female .4 mm. from posterior end; of male, .2 mm.

Lips, .17 mm. long and .15 mm. wide; rounded at tip; base recurved toward tip so that lateral angles are auriculate; two small papillae on either side of inner surface near distal end. Interlabia conical, rounded at tip, .05 mm. in length.

Posterior end of female, conical, rounded at tip; at .08 mm. from the end it tapers at a more acute angle and beyond this point is somewhat bent ventrally. Spicules of male .025 in diameter and .3 mm. long; somewhat curved, obliquely truncate at tip.

*Cystidicola serrata* (Wright)

(Fig. 13)

Sixteen specimens of this species were taken from the intestine of a sheepshead, *Aplodinotus grunniens* Rafinesque, caught in Lake Pepin, Wisconsin; July 13, 1920.

The largest female (Cat. No. 7609, U.S.Nat.Museum) is 12.25 mm. long, and .098 mm. wide; male, 7.53 mm.; .051 mm. In the female the anterior portion of pharynx is .4 mm. long; posterior portion, 2 mm. Ulva, 6.1 mm. from anterior end; anus, .2 mm. from posterior end. There are ten conical teeth surrounding the

mouth, and inside it. The posterior end of the male is coiled about three times. There is one short conical spicule, .025 by .015 mm., and one long signate spicule, .3 by .02 mm.

***Capillaria catostomi*, new species**

(Fig. 10)

Type: Cat. No. 7627, U. S. National Museum; Lake Michigan; Sturgeon Bay, Wisconsin; August 2, 1920; collector, A. S. Pearse. One female was examined and males are unknown.

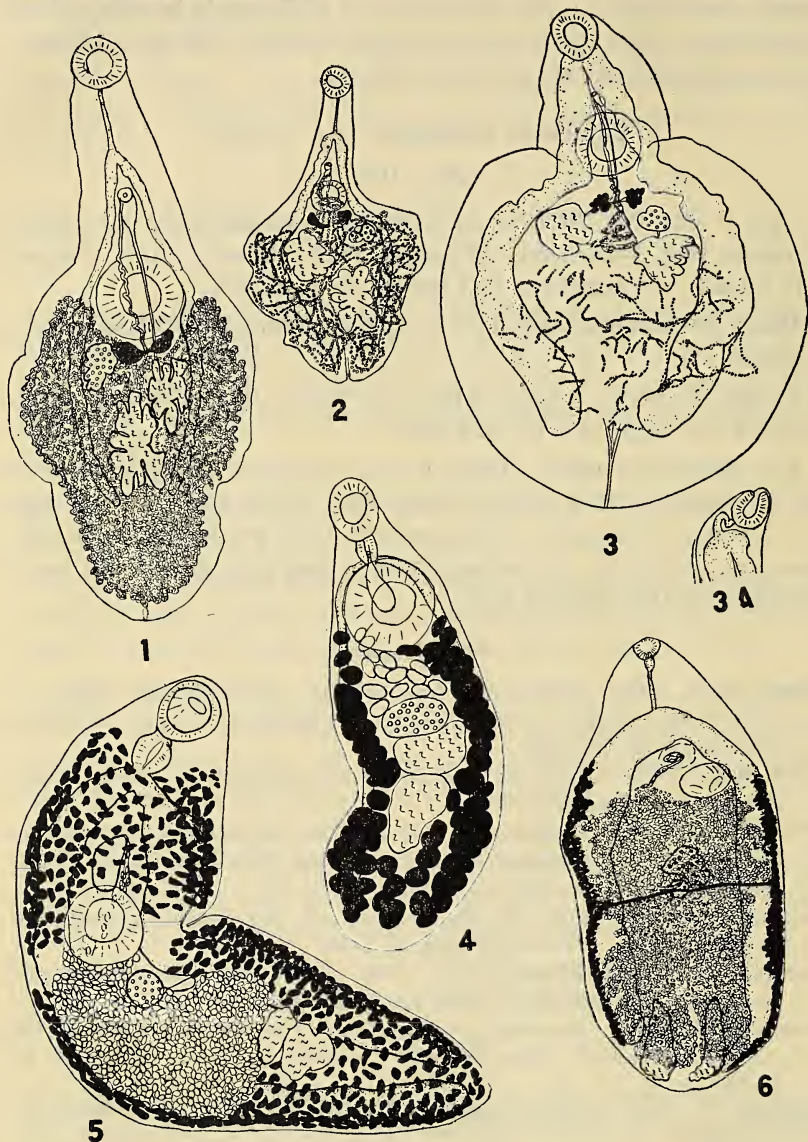
Host: the common sucker, *Catostomus commersonii* (Lacepede); intestine.

Length of body, 8 mm.; width, .06 mm.; ulva, 2.55 mm. from anterior end; eggs .055 by .025 mm.

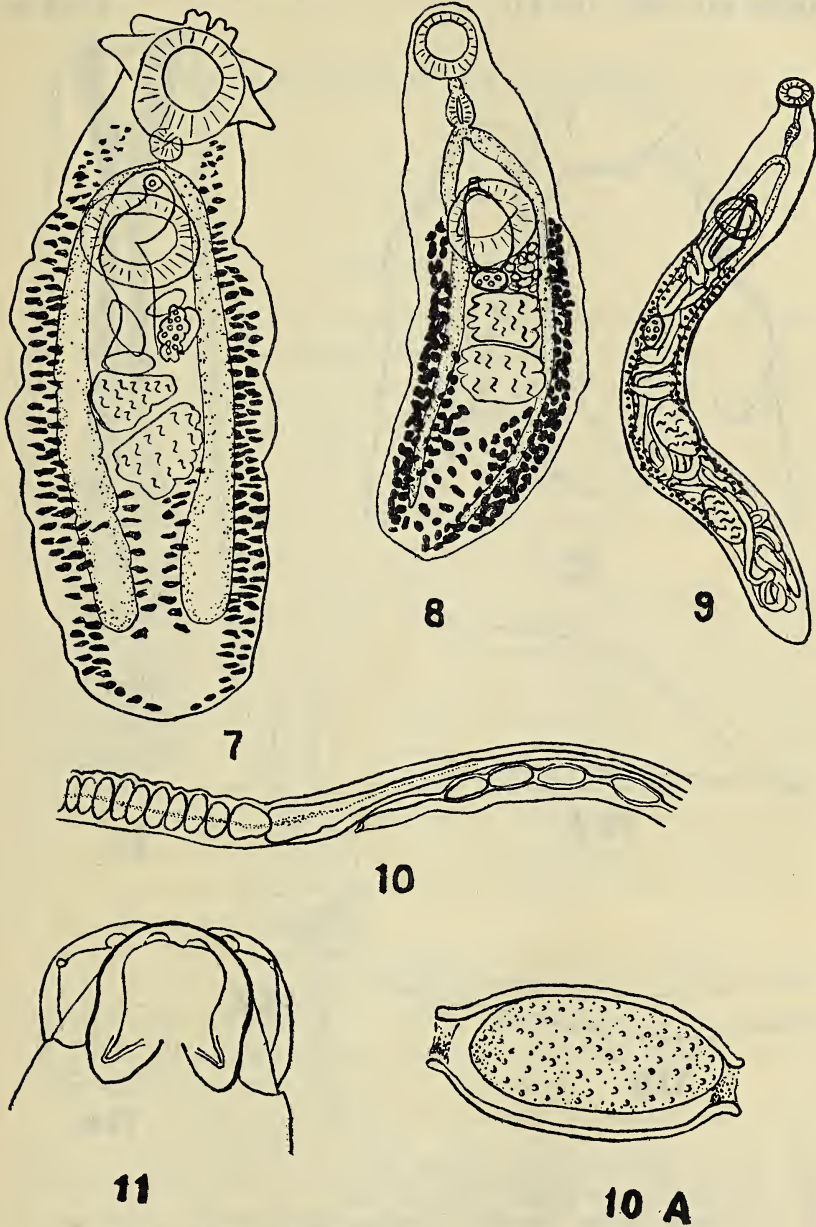
The cuticle is smooth. There are one hundred eighty-seven cells in the esophagus and about seventy eggs in the uterus. The eggs are typically trichurid; lemon-shaped, with a plug at each end. Near the ulva they are arranged in a single row, but are more crowded together further back.

BIBLIOGRAPHY

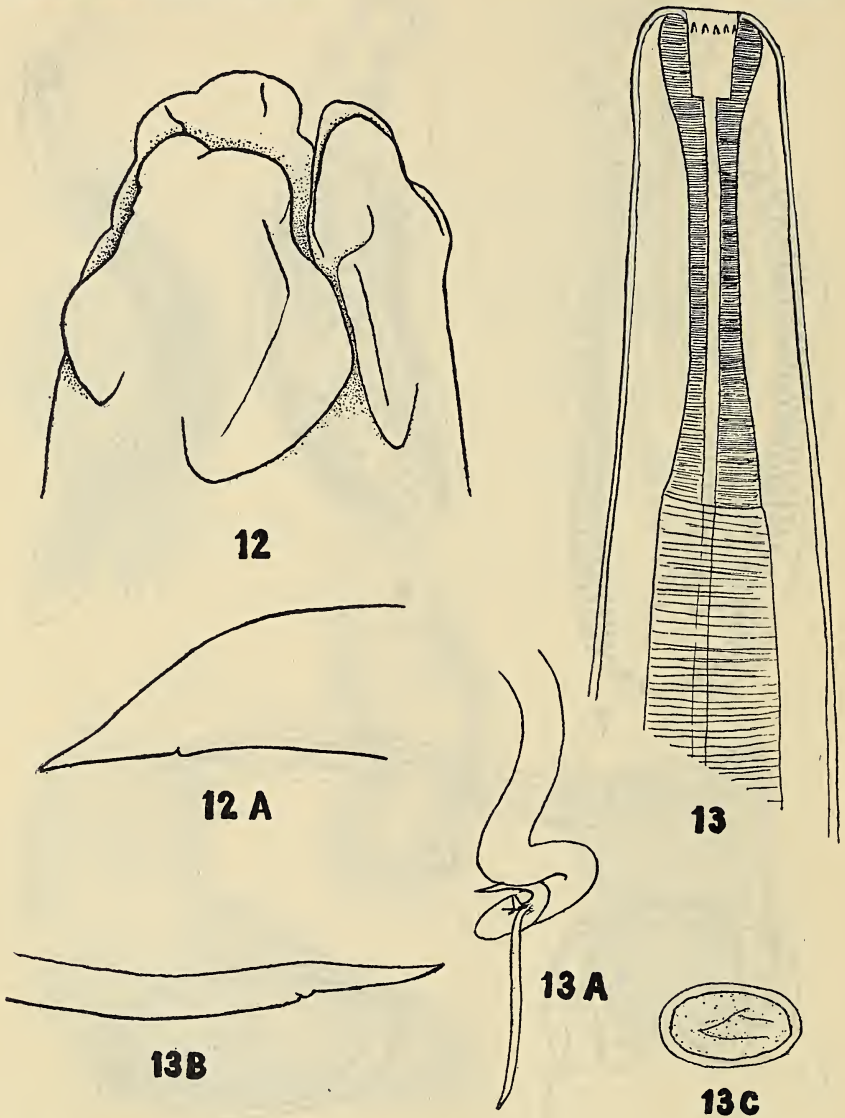
- Cooper, A. R. 1915. Trematodes from marine and fresh-water fishes, including one species of extoparasitic turbellarian. Trans. Roy. Soc. Canada, (3) 9: 181-206.
- Faust, E. C. 1918. Studies on American Stephanophialinae. Trans. Amer. Microscopical Soc. 37: 183-198.
- Goldberger, J. 1911. Some known and three new endoparasitic trematodes from American fresh-water fish. U. S. Publ. Health and Mar. Hospt. Serv., Hygienic Lab., Bull. 71: 7-35.
- MacCallum, W. G. 1915. On the anatomy of two distome parasites of fresh-water fish. Veterinary Mag. 2: 1-12.
- Marshall, W. S. and Gilbert, N. C. 1905. Three new trematodes found principally in black bass. Zool. Jahrb. Syst. 22: 479-488.
- Osborn, H. L. 1903. *Bunodera cornuta* sp. nov.: a new parasite from the crayfish and certain fishes of Lake Chautauqua, N. Y. Biol. Bull. 5: 63-73.
- Stafford, J. 1900. Some undescribed trematodes. Zool. Jahrb. Syst. 13: 399-414.
- 1904. Trematodes from Canadian fishes. Zool. Anzeig. 27: 481-495.
- Wallin, I. E. 1909. A new species of the trematode genus *Allocreadium*. Trans. Amer. Micr. Soc. 29: 50-66.
- Ward, H. B. and Magath, T. B. 1916. Notes on some nematodes from fresh-water fishes. J. Parasitol. 3: 57-64.
- Ward, H. B. and Whipple, G. C. 1918. Fresh-water biology. New York, x+1111.



1. *Phyllodistomum fausti* new species.
2. *Phyllodistomum superbum* Stafford.
3. *Phyllodistomum staffordi* new species.
- 3A. *Phyllodistomum staffordi*; anterior end showing oral sucker, esophagus, and intestinal rami.
4. *Allocreadium boleosomi* new species.
5. *Allocreadium ictaluri* new species.
6. *Acetodextra amiuri* (Stafford).



7. *Crepidostomum illinoiense* Faust.
8. *Allocreadium armatum* (MacCallum).
9. *Macroderoides spiniferus* new species.
10. *Capillaria catostomi* new species; portion of body showing esophagus, intestine, ulva, and uterus.
- 10A. *Capillaria catostomi* new species; egg.
11. *Ascaris scaphirhynchi* new species, anterior end.



12. *Ascaris lucii* new species; anterior end.  
12A. *Ascaris lucii* new species; posterior end.  
13. *Cystidicola serrata* (Wright); anterior end.  
13A. *Cystidicola serrata* (Wright); posterior end of male.  
13B. *Cystidicola serrata* (Wright); posterior end of female.  
13C. *Cystidicola serrata* (Wright); egg.

# THE PARASITES OF LAKE FISHES

---

A. S. PEARSE

## INTRODUCTION

Since the times of Van Beneden and Leuckilart animal parasites have been intensively studied, but little effort has been made to determine the amount or frequency of parasitic infection under natural conditions; except for those species directly related to man and his domestic animals. Many species of parasites that infest fishes have been, and are being, described, but few accurate observations that relate to their abundance and the factors which make them numerous or few have been made.

Van Cleave (1919) found that half the species of fishes that he examined from Douglas Lake, Michigan, were infected with acanthocephalans, and he determined the percentage of infection for sixteen species. La Rue (1914), Marshall and Gilbert (1905), Smallwood (1914), and Ward (1910) made incidental observations concerning the number of parasites present in certain fishes. Surber (1913) remarks on the small percentage of natural infections with glochidia. The white crappie, which carries more species of glochidia than any other fish, he found to show an infection of only 0.7 per cent, and the sheepshead, known to carry two species of glochidia, had 3.7 per cent.

Zschokke (1902) found that salmon lost a large number of their parasites while migrating up the Rhine. But Ward (1909) points out that such migrations are not always conducive to parasitic losses, for the Alaskan salmon during its journey inland acquires a copepod which is never found in salt water.

Little is known of the effects of seasonal succession on the life cycles of the parasites of fishes. Van Cleave (1916) states that acanthocephalans vary greatly in this respect and cites two species in one genus which, though occurring in the same host, mature at different seasons. Hausmann (1897) found that perch had very few trematodes in the spring. In studying frogs, Ward (1909) found the lowest percentage of infection in late spring or early

summer, and a maximum was reached during hibernation. There is a great need of more information concerning the seasonal prevalence of the parasites of all aquatic animals.

Of the factors that control the occurrence of fish parasites there is also a dearth of knowledge. Hausmann (1897) states that when fishes eat little on account of cold or heat, parasites are few; and he assigns an important role to temperature as a factor in parasitic infection. He also points out that most parasites enter fishes with food. Ward (1909) stresses the fact that parasites respond to changes in the habits of their hosts to such a degree that their presence or absence furnishes evidence of particular habits. Pratt (1919) affirms that epidemics of fish parasites are apt to occur when the water is warm and that small inclosed bodies of water harbor more parasites than those of larger size because fishes cannot escape by migration.

The present paper describes the results of statistical studies on the occurrence of fish parasites in different types of lakes. The writer was led to make such studies in attempting to discover why fishes fail to grow much in certain bodies of water while they may attain large size in other bodies near by. It seemed desirable to learn whether particular lakes showed specificities in regard to the numbers and kinds of parasites present and whether there is correlation between the presence and size of particular fishes and the presence or absence of parasites. The work began in 1917 and was at first confined to the yellow perch. Observations were made on specimens from sixteen lakes on three different river systems. Later, more extensive observations were made on five different types of lakes where the parasites of all available species of fishes were studied.

In studying fishes for parasites they were always examined while fresh, as it was found that results from old or preserved fishes were of little value. The skin, fins, mouth and gills were first scrutinized; then the specimen was opened from vent to throat, and the visceral organs were examined. The contents of the alimentary canal were stripped out on a glass plate and the canal itself was opened from end to end with scissors. The food and faecal matter were carefully teased across under a binocular microscope. The number and location of all parasites was entered on a form sheet, one sheet being used for each fish examined. Parasites were placed in corrosive sublimate solution and alcohol. Later they were stained and mounted. In this paper all measurements



of fishes are given in millimeters and do not include the tail fin. In the tables “+” indicates less than 0.05.

The work could never have been completed without the cheerful and excellent assistance rendered by Drs. George R. LaRue and H. J. Van Cleave, who identified Proteocephalidae and Acanthocephala, respectively. Others who deserve thanks for identifications are Dr. A. R. Cooper, tapeworms; Prof. H. S. Davis, Sporozoa; Dr. A. D. Howard, glochidia; Prof. J. P. Moore, leeches; and Prof. C. B. Wilson, copepods. Mr. Leslie Tasche assisted the writer in the field; Misses Henrietta Achtenberg and Marion E. Lamont, and Mr. J. C. Stucki mounted slides.

Before all the factors which influence parasitism in fishes are known, if they ever are, parasitologists and ecologists will have to labor for several generations. This paper is, of course, only a beginning in the ecology of fish parasites and is concerned particularly with certain Wisconsin lakes.

## PARASITES OF THE YELLOW PERCH

From June, 1917, to May, 1918, the yellow perch from the deep waters of Lake Mendota were examined each month, except during December. During the summer and at intervals throughout the year perch from four other lakes on the Yahara River and from the shallow waters of Lake Mendota were also examined. The results of these studies are given in table 1. The parasites found in the perch in these lakes were as follows:

### TREMATODA

#### *Diplostomum cuticola* Van Nordmann

This trematode was common, occurring in small cysts in the skin and fins, and sometimes on the gills. The cysts are easily seen on account of the black pigment that surrounds them and gives infected fishes a speckled appearance. Their distribution on the bodies of 335 perch from all the lakes studied averaged as follows: pectoral fins 1; pelvic fins 0.9; anal fin 0.5; caudal fin 1.3; dorsal fins 1; anterior dorsal 0.4; posterior dorsal 0.5; gills +; opercles 1.3; ventrum 1.4; tail +; dorsum 2.4; sides 3.3.

*Bunodera luciopercae* O. F. Müller

A parasite that was found only in the intestine and the intestinal caeca.

*Clinostomum* sp.?

Large white cysts enclosing this parasite occurred in the flesh just beneath the skin; sometimes on the gills and in the eye sockets.

ACANTHOCEPHALA

*Echinorhynchus thecatus* Linton

This hook-headed worm occurred as an intestinal parasite and in cysts in the peritoneum.

*Neoechinorhynchus cylindratus* (Van Cleave)

An intestinal parasite.

Acanthocephalan cysts

These cysts were mostly those of *Echinorhynchus thecatus* Linton, but as it is not certain that they all belonged to that species, they are not definitely assigned to it.

NEMATOIDEA

*Dacnitoides cotylophora* Ward and Magath

This nematode was an intestinal parasite in the perch.

*Ichthyonema cylindraceum* Ward and Magath

A filarial worm that occurred in cysts in the peritoneum and liver.

CESTOIDEA

*Proteocephalus* sp.?

Most of the intestinal proteocephalids were *P. pearsei* La Rue. Perhaps all belonged to this species.

Proteocephalid cysts

Encysted proteocephalids were commonly encountered; usually in the liver, but often in the peritoneum. Those identified were the cysts of *Proteocephalus ambloplitis* (Leidy).

*Bothriocephalus cuspidatus* Cooper

This tapeworm was found in the intestine of the perch.

## GLOCHIDIA

Probably all the glochidia observed were *Lampsilis luteola* Lamark, which is the most abundant species in the lakes along the Yahara River.

*Piscicolaria* sp. ?

This leech was usually attached about the bases of the fins.

## Unknown cysts

Very often cysts were encountered among the viscera that could not be identified.

The four lakes along the Yahara River decrease in size and depth downstream and come thus in the following order: Mendota, Monona, Waubesa, Kegonsa (Table 3). Lake Wingra is small, shallow, and is connected with Lake Monona through a narrow, swampy stream. In general the perch increase in size downstream, but average smaller in Lake Wingra than in Lake Mendota (Pearse and Achtenberg, 1920).

The results from the five Yahara lakes may properly be compared for the months of July, August, and September, when collections were made in all of them. During that time the total average parasitism\* for each lake was: Mendota, deep 66.7 (60.7); Mendota, shallow 120.9 (67.7); Monona 84.8 (18.8); Wingra 38.8 (38.6); Waubesa 24.9 (16.4); Kegonsa 40.9 (13.4). The figures in parenthesis represent the total average infection without the averages for *Diplostomum cuticola*, which, when it occurs in very large numbers on even one fish, may change the total very much. The figures in parenthesis are probably better as a basis for comparison. In any case it is apparent that a decrease in infection is generally correlated with larger size in these lakes. Before the writer had studied lakes along other rivers he thought that a greater infection might occur in deeper lakes, or in those nearer the headwaters of a stream.

The different kinds of parasites varied greatly in abundance in the lakes. Table 1 shows that the perch in the shallow water

\*Average total number of parasites per fish.

of Lake Mendota have more parasites than those at greater depths and that Lake Mendota has a higher percentage of infection than any of the other lakes. If the highest percentage of infection with a particular parasite makes a lake "first," the lakes rank about as follows:

Mendota, shallow: 6 firsts; 6 seconds; 2 thirds; all species present.

Mendota, deep: 5 firsts; 1 second; 2 thirds; 4 species absent.

Wingra: 3 firsts; 1 third; 1 fourth; 1 fifth; 2 sixths; 6 species absent.

Waubesa: 1 first; 2 seconds; 3 thirds; 2 fourths; 2 fifths; 4 species absent.

Kegonsa: 1 first; 2 seconds; 2 thirds; 1 fourth; 3 fifths; 3 species absent.

Monona: 1 first; 2 seconds; 1 third; 1 fourth; 2 sixths; 6 species absent.

That Monona ranks last is probably explained by the fact that it is heavily contaminated with organic matter from the city of Madison. It is on the whole the most barren of the lakes and contains fewest fishes.

Glochidia, leeches, intestinal proteocephalids, and acanthocephalans are apparently more abundant in shallow water. All encysted parasites are somewhat more abundant in deep water. Lake Kegonsa has a much higher infection with bothriocephalids than any other lake, and also has many Daenitoides.

The data in table 1 are rearranged in table 3 to show the average infection of the perch in the Yahara lakes by months. It will be noted that the maximum infections were in spring. This was due largely to the increase of acanthocephalans at that season. Winter came next, autumn was third, and summer showed the lowest infection. The different parasites reached their seasons of greatest numbers as follows:

Spring: acanthocephalans; Bunodera.

Summer: glochidia—which were found at no other season.

Autumn: bothriocephalids, Diplostomum, Clinostomum, Iethyonema, and proteocephalid cysts.

Winter: Dacnitoides; intestinal proteocephalids; unknown visceral cysts.

In order to compare other lakes with deep, fertile lakes along the Yahara, eleven lakes on the Oconomowoc and Fox Rivers were visited during August, 1917. The general characteristics of these lakes are given in table 3. Those on the Oconomowoc were deep, with sandy and pebbly shores. Those on the Fox (except Green Lake, which was much like those on the Oconomowoc River) were shallow with swampy shores.

Table 3 shows that the average infection was about equal on the Oconomowoc (15.2) and Fox (14.4) Rivers; the latter perhaps having a slight excess because eight parasites showed the highest infection average on it—to five on the former. The Yahara lakes showed about two-thirds the infection (9.3) of those on the other two rivers, and the infection average of only two parasites exceeded those of the same parasites in the lakes on the other rivers. In table 4 the lakes of each river system are arranged in order, with that nearest the headwaters on the left. It will be seen that only on the Yahara was infection greater toward the headwaters.

During August infection with all trematodes, intestinal proteocephalids, glochidia, and leeches was greater in the Fox River lakes; in the Oconomowoc lakes acanthocephalans, *Icthyonema* cysts, proteocephalid cysts, and unknown cysts were most abundant. The Yahara lakes showed the highest infections with acanthocephalan cysts and *Bothriocephalus*.

Except for *Diplostomum*, the trematodes were most abundant in the shallow lakes. *Acanthocephala* occurred in largest numbers in the deep, sandy, and rather barren Oconomowoc lakes; but acanthocephalan cysts reached their greatest numbers in the deep, fertile Yahara lakes. *Dacnitoides* was somewhat more abundant in the shallow lakes than in the sandy, barren, deep lakes and was absent from the deep, fertile lakes. *Icthyonema* cysts reached their maximum in Lake Poygan (shallow, swampy) but on the whole were slightly more abundant in the deep, sandy, Oconomowoc lakes. Intestinal proteocephalids (*P. pearsei* La Rue) also were prevalent in the shallow, swampy lakes, but encysted proteocephalids, mostly *P. ambloplitis* (Leidy), reached their maximum in the sandy, deep lakes. *Bothriocephalids* were most abundant in the deep fertile lakes. *Glochidia* and leeches reached their maxima in the shallow,

swampy lakes. Unknown visceral cysts were most common in the sandy, deep lakes.

According to their degree of average infection the sixteen lakes rank in the following order: Green 59.1; Monona 42.1; Beaver 32.7; Poygan 32.2; Mendota shallow 31.1; North 30; la Belle 30; Oconomowoc 25.5; Butte des Morts 19.2; Pine 17; Mendota deep 15.3; Okauchee 14.5; Puckaway 14.1; Wingra 9.5; Waubesa 6.5; Winnebago 3; Kegonsa 0.5. If Diplostomum cysts are disregarded the order is as follows: Beaver 32.1; Poygan 30.7; North 26; Mendota, shallow 23.3; Butte des Morts 19.1; Mendota, deep 14.7; Oconomowoc 14.2; Puckaway 14; Pine 10.8; Wingra 9.4; Monona 7.1; Green 7.1; la Belle 6.5; Okauchee 2.9; Waubesa 2.5; Winnebago 1; Kegonsa 0.2. There is no apparent relation between river systems, depth, fertility, character of shore and the general abundance of parasites. This appears to indicate that all parasites are not influenced by the same factors. There is also no apparent relation between the size of the perch in various lakes and the degree of parasitic infection, but when there are more fishes per unit of area there is a heavier infection.

*Phyllodistomum superbum* Stafford was found in the urinary bladders of many perch in the lakes along the Fox River, but was never observed in any of the two thousand perch that the writer has examined in the lakes on the Mississippi drainage. This parasite is apparently confined to the St. Lawrence drainage system.

The food of the perch examined was carefully recorded during August, 1917. For the three river systems it may be summarized as follows; the figures after the foods indicating the average percentage eaten:

	Yahara	Oconomowoc	Fox
Number examined.....	58	30	32
Average length.....	157	160	180
Insect eggs.....			0.1
Fish remains.....	10.3	32.7	6.8
Chironomid larvae.....	42.6	1.0	1.1
Caddis-fly larvae.....	1.8	2.3	7.0
Unidentified insect larvae.....			0.4
Chironomid pupae.....		0.2	1.3
Corixa .....	0.1		6.0
Grasshoppers .....			2.5
Sialis larvae.....			14.4
Mites .....	+		0.1
Crayfishes .....	0.7	22.0	43.6
Amphipods, unidentified.....	7.1	0.2	

	Yahara	Oconomowoc	Fox
Hyalella .....	2.0		1.9
Ostracods .....	0.2		
Cyclops .....	+		
Leptodora .....	2.9		2.4
Daphnia .....	21.4		0.4
Cladocera, unidentified.....	1.1		
Sphaeriidae .....	+		
Snails .....	3.0	20.9	2.0
Leeches .....	0.1	16.6	0.6
Bryozoa .....	1.5		
Plants .....	4.1	1.9	
Silt and sediment.....			3.3
Unidentified .....	0.1	2.1	4.0

From these figures it appears that a diet of fishes, insects, crayfishes, snails, and leeches is associated with parasitic infection more than chironomid larvae and cladocerans, but the observations cover too limited a period to be of much significance.

#### COMPARISON OF THE FISH PARASITES OF FIVE WISCONSIN LAKES

As the study of the yellow perch in sixteen lakes had not given results of particular value, it was decided to study the parasites of all the fishes available in several different types of lakes. According to this plan five Wisconsin lakes were studied intensively during the summers of 1919 and 1920. Accounts of the food and distribution of the fishes in these lakes have already been published (Pearse, 1921, 1921a). All the lakes were of considerable size and depth. Their general characteristics are given in table 5. Lake Geneva is deep, clear, and its deepest parts are without oxygen in summer. Mendota is deep, turbid and the water below 8 to 12 meters is without oxygen for three months during summer and early autumn. Pepin is the shallowest of the lakes, but it has the greatest area of any lake except Michigan. Its temperature is nearly uniform from top to bottom and it forms a part of the Mississippi River. Green Lake is deep and has a small surface area; it is sharply stratified thermally but has plenty of oxygen at the bottom at all seasons. Lake Michigan is clear, cool, and of course, has a very large volume of water compared to the other lakes. In regard to "fertility," as judged by the probable amount of food for fishes per unit of area, the lakes rank in about the following order: Mendota, Green, Geneva, Michigan, Pepin (Pearse,

1921, pp. 19, 58). Detailed accounts of the general characteristics of these lakes and of routine catches in them have been published (Pearse, 1921, 1921a).

Green Lake and Lake Mendota were studied during August, 1919. The lakes investigated in 1920 were studied as follows: Pepin: June 20 to July 25; Lake Michigan: July 27 to August 7; Geneva: August 8 to 25.

Attention will now be directed to a detailed consideration of the parasites that were found to infest Wisconsin lake fishes and the parts of fishes' bodies that they frequented. Although unidentified parasites of various groups occurred in a number of fishes, they are not given in the following lists.

#### PROTOZOA

*Myxobolus* cysts were found once in Lake Mendota on the gills of a yellow perch. Doubtless other protozoan parasites occurred, but were not observed.

#### TREMATODA

##### *Acetodextra amiuri* Pearse

Found in the swim bladders of the yellow, black, and speckled bullheads in Lake Pepin; in the black and speckled bullheads in Lake Michigan.

##### *Acrolechanus petalosa* (Lander)

Common in the sand sturgeon in Lake Pepin.

##### *Allocanthocasmus varius* Van Cleave

Occurred in the white bass in Lake Pepin; free in the intestine and encysted in the liver.

##### *Allocreadium armatum* (MacCallum)

Found in intestine of the sheepshead in Lake Pepin and Lake Michigan.

##### *Allocreadium boleosomi* Pearse

In intestines of the Johnny darter and log-perch in Lake Pepin.



*Allocreadium ictaluri* Pearse

In the intestine of the channel catfish in Lake Pepin.

*Allocreadium lobatum* Wallin

In the intestine of common sucker in Lake Mendota.

*Azygia* sp.?

An unidentifiable *Azygia* was found in the intestine of a yellow perch in Lake Michigan.

*Azygia acuminata* Goldberger

This species occurred in the stomachs and intestines of the dogfish, white bass, and wall-eyed pike in Lake Pepin.

*Azygia bulbosa* Goldberger

In the intestine of the wall-eyed pike in Lake Pepin.

*Azygia loosii* Marshall & Gilbert

Was found in the stomach and intestine of the rock bass in Lake Geneva; the pickerel in Lake Mendota; the pickerel and small-mouth black bass in Lake Pepin; the pickerel in Green Lake.

*Bunodera luciopercae* O. F. Müller

In the intestine and caeca of the yellow perch in Lake Geneva, Lake Mendota, and Green Lake.

*Caecincola parvulus* Marshall & Gilbert

In the intestine of the smallmouth black bass in Lake Pepin; in the rock bass in Lake Michigan.

*Centrovarium lobotes* MacCallum

In the intestine of the shiner, *Notropis hudsonius* (De Witt Clinton), in Lake Michigan.

*Clinostomum marginatum* Osborn

Found in cuticular cysts in the yellow bullhead in Lake Pepin. Cysts, probably of this species, were found on a yellow perch from

Lake Michigan. Cuticular cysts were also found in Green Lake on the speckled bullhead, Johnny darter, smallmouth black bass, largemouth black bass, and yellow perch. In the same lake visceral cysts were found in the speckled bullhead, pickerel, and yellow perch.

*Crepidostomum* sp.?

A single unidentified *Crepidostomum* was found in the intestine of a carp from Lake Pepin.

*Crepidostomum cornutum* (Osborn)

In the intestine of the channel cat in Lake Pepin; the rock bass, yellow and speckled bullheads, and one mud puppy in Lake Michigan.

*Crepidostomum illinoiense* Faust

In the intestine of the mooneye in Lake Pepin.

*Cryptognomius chyli* Osborn

Present in the intestine of the rock bass and smallmouth black bass in Lake Geneva; rock bass and pumpkinseed in Lake Michigan.

*Diplostomum* sp.?

Black cuticular cysts, which probably were *D. cuticola* van Nordmann, were found on the rock bass, pumpkinseed, bluegill, small and largemouth black bass, and wall-eyed pike in Lake Geneva; rock bass, Johnny darter, sucker, carp, pickerel, pumpkinseed, bluegill, both black bass, yellow perch, and wall-eyed pike in Lake Mendota; black bullhead, carp, pickerel, pumpkinseed, log perch in Lake Pepin; rock bass, pickerel, bluegill, smallmouth black bass, and yellow perch in Green Lake; on the yellow perch in Lake Michigan.

Visceral *Diplostomum* cysts commonly occurred in the liver and peritoneum; sometimes on the heart and in the muscles. In Lake Geneva they were found in the rock bass, pumpkinseed, bluegill, both species of black bass, yellow perch; in Lake Pepin in the pumpkinseed and log perch; Green Lake: rock bass, pumpkinseed, top minnow, bluegill, cisco, smallmouth black bass, and blunt-nosed minnow; Lake Michigan: rock bass, pumpkinseed, and log perch.

*Gasterostomum pusillum* Stafford

In the intestine of the sauger in Lake Pepin.

*Leucerthrus micropteri* Marshall & Gilbert

In the intestine of the smallmouth black bass in Lake Geneva; white bass in Lake Mendota and Lake Pepin.

*Macroderoides spiniferus* Pearse

In the intestine of the yellow and speckled bullheads, and short-billed gar in Lake Pepin.

*Microphallus opacus* Ward

In Lake Mendota this species occurred in the intestines of the yellow bullhead, dogfish, silversides, smallmouth black bass.

*Phyllodistomum fausti* Pearse

Found in the urinary bladder of the sheepshead in Lake Pepin.

*Phyllodistomum staffordi* Pearse

In the urinary bladder to the black and speckled bullheads, and the mud cat in Lake Pepin; black and speckled bullheads in Lake Michigan.

*Phyllodistomum superbum* Stafford

Found in the intestines of a bream and several perch in Lake Michigan.

*Plagiorchis corti* Lamont

In the intestine of the tadpole cat in Lake Mendota.

*Stephanophiala farionis* O. F. Müller

In the intestine of the Johnny darter and a shiner, *Notropis heterodon* (Cope) in Lake Mendota; the yellow perch in Lake Michigan; the pumpkinseed in Lake Geneva.

CESTOIDEA

*Abothrium crassum* (Bloch)

In the intestine of the largemouth black bass in Lake Geneva; lake trout and lota in Lake Michigan.

*Bothriocephalus claviceps* (Goeze)

In the intestine of the pumpkinseed in Lake Geneva; eel and pumpkinseed in Lake Pepin.

*Bothriocephalus cuspidatus* Cooper

In the intestine of the wall-eyed pike in Lake Mendota; sauger and wall-eyed pike in Lake Pepin.

*Corallobothrium* sp.?

Perhaps more than one species is represented in the following notes. Intestinal corallobothria were found in the speckled bullhead in Lake Mendota; black, yellow and speckled bullheads, Johnny darter, channel cat, tadpole cat, and mud cat in Lake Pepin; speckled bullhead in Green Lake and Lake Michigan.

Encysted corallobothria were found among the viscera of the Johnny darter in Lake Mendota.

*Cyathocephalus americanus* Cooper

In the intestine of the cisco in Green Lake and in one of the ciscoes, *Leucichthys hoyi* (Gill), in Lake Michigan.

*Glaridacris catostomi* Cooper

In the intestines of the sucker and pickerel in Lake Geneva; sucker in Lake Mendota; three species of quillbacks, three species of buffaloes, the white-nosed sucker, and log perch in Lake Pepin; sucker in Green Lake; sucker, long-nosed sucker, and mud puppy in Lake Michigan.

*Ligula intestinalis* Linnaeus

Immature ligulids were found in the peritoneal cavity of the perch in Green Lake.

*Marsipometra hastata* Linton

In the intestine of the spoonbill in Lake Pepin.

*Ophiotaenia lonnbergii* (Fuhrmann)

In the intestine of the mud puppy in Lake Michigan.

*Proteocephalus* sp.

Unidentified proteocephalids were found in the intestines of fishes in Lake Geneva as follows: bluegill and smallmouth black bass; Lake Pepin: yellow bullhead, smallmouth black bass, two species of shiners, yellow perch, log perch, white bass, sauger, and wall-eyed pike; Green Lake: pickerel, bluegill, smallmouth black bass, yellow perch, and blunt-nosed minnow; Lake Michigan: rock bass, sucker, three species of ciscoes, lota, perch, and cottid.

Proteocephalid cysts were found in the liver and peritoneum as follows: Lake Mendota: yellow perch and white bass; Lake Pepin: black and speckled bullheads, eel, sheepshead, channel cat, smallmouth black bass, short-nosed red-horse, black and white crappies, white bass, and wall-eyed pike; Green Lake: rock bass, bluegill, cisco, small and largemouth black bass, and yellow perch.

*Proteocephalus ambloplitis* (Leidy)

Intestinal representatives occurred as follows: Lake Geneva: both species of black bass; Lake Mendota: speckled bullhead, sucker, pickerel, long-nosed gar, and largemouth black bass; Lake Pepin: long-nosed gar and white bass; Green Lake: rock bass, pickerel, smallmouth black bass.

Visceral cysts were common in the liver and peritoneum. Their occurrence was as follows: Lake Geneva: rock bass, both black bass, and yellow perch; Lake Mendota: rock bass, yellow and black bullheads, sucker, pickerel, top minnow, long-nosed gar, both black bass, white bass, and wall-eyed pike; Lake Pepin: black, yellow and speckled bullheads, sheepshead, sucker, channel cat, bluegill, mud cat, both black bass, a shiner (*Notropis atherinoides* Rafinesque), yellow perch, black and white crappies, white bass, sauger, and wall-eyed pike; Green Lake: speckled bullhead and smallmouth black bass; Lake Michigan: smallmouth black bass and yellow perch.

*Proteocephalus exiguus* La Rue

In the intestine of the cisco in Green Lake, and in two of the ciscoes in Lake Michigan.

*Proteocephalus macrocephalus* (Creplin)

In the intestine of the eel in Lake Pepin.

*Proteocephalus pearsei* La Rue

In the intestines of fishes as follows: Lake Geneva: yellow perch; Lake Mendota: yellow perch and white bass; Lake Pepin: yellow perch and log perch. Green Lake: pickerel and yellow perch; Lake Michigan: yellow perch.

*Proteocephalus perplexus* La Rue

Occurred in the intestines of fishes. Lake Mendota: yellow bull-head, dogfish, and pickerel; Lake Pepin: rock bass; Green Lake: blunt-nosed minnow.

Visceral cysts were found in the white bass in Lake Mendota; in the speckled bullhead and blunt-nosed minnow in Lake Pepin.

*Proteocephalus pinguis* La Rue

Occurred in the intestines of the pickerel in all five of the lakes studied. Visceral cysts were found in the rock bass in Green Lake.

*Proteocephalus singularis* La Rue

Found in the intestine of the long-nosed gar in Lake Mendota and in the short-nosed gar in Lake Pepin.

*Trienophorus nodulosus* Pallas

Encysted visceral representatives of this species were found as follows: Lake Pepin: speckled bullhead and short-headed redhorse; Lake Michigan: sucker, long-nosed sucker, smallmouth black bass, and yellow perch.

*Trypanorhyncha*, gen.? sp.?

Visceral cysts occupied by representatives of this order were found in the yellow bass and skipjack in Lake Pepin; and in the top minnow in Lake Michigan.

## NEMATODA

*Ascaris* sp.?

An *Ascaris* that could not be identified was found in the intestine of a rock bass in Lake Geneva.

*Ascaris angulata* Rudolphi?

An ascarid that perhaps belonged to this species was taken from the intestine of a pumpkinseed caught in Lake Michigan.

*Ascaris labiata* Rudolphi

Found in the intestine of the rock bass in Lake Mendota.

*Ascaris lucii* Pearse

This species was the commonest intestinal ascarid found. Lake Geneva: pickerel; Lake Mendota: rock bass, pickerel; Green Lake: pickerel; Lake Michigan: pickerel.

*Ascaris scaphrhynchi* Pearse

Found in the intestine of the hackleback, or sand sturgeon, in Lake Pepin.

*Camallanus ancyloDIRUS* Ward & Magath

This species was found in the intestine of a lake carp (*Carpoides thompsoni* Agassiz) caught in Lake Pepin.

*Camallanus oxycephalus* Ward & Magath

This species was found in Lake Pepin only. It was usually hanging from the intestine out through the anus. The color in life was bright red. Occurred in the following fishes: moon-eye, mud cat, yellow bass, short-headed redhorse, log perch, black crap-pie, white bass, wall-eyed pike.

*Capillaria catostomi* Pearse

This species was found in the intestine of a sucker caught in Lake Michigan.

*Cystidicola serrata* (Wright)

Sixteen specimens were found in the intestine of a sheephead caught in Lake Pepin.

*Cystidicola sigmatura* (Leidy)

A single specimen was found in a mooneye caught in Lake Pepin. This species was abundant in the swim bladders of the ciscoes in Lake Michigan, occurring in all the species except the longjaw.

*Dacnitoides cotylophora* Ward & Magath

This species was often common in the yellow perch, occurring in the intestine of that species in all of the five lakes studied except Pepin. It was also found in the intestines of other fishes as follows: Lake Pepin: channel cat; Green Lake: speckled bullhead; Lake Michigan: black bullhead, sucker.

Cysts of this species were also found among the viscera of a cisco, *Leucichthys johanna*e (Wagner), in Lake Michigan.

*Haplonema immutatum* Ward & Magath

Found in the intestine of a dog fish in Lake Pepin.

*Histerothylacium brachyurum* Ward & Magath

Found in the intestines of the largemouth black bass and yellow perch in Lake Geneva.

*Ichthyonema cylindraceum* Ward & Magath

Cysts of this species were common in the liver and peritoneum of many fishes. Occurrence: Lake Geneva: smallmouth black bass, yellow perch; Lake Mendota: speckled bullhead, Johnny darter, top minnow, cisco, largemouth black bass, shiner—*Notropis heterodon* (Cope), yellow perch, white bass; Lake Pepin: black bullhead; Green Lake: rock bass, top minnow, yellow perch, blunt-nosed minnow; Lake Michigan: Johnny darter, Iowa darter, pumpkinseed, yellow perch, blunt-nosed minnow.

*Oxyuris* sp.?

A mutilated specimen, apparently belonging to this genus, came from a blue-gill caught in Lake Pepin.



*Spinitectus gracilis* Ward & Magath

This is an intestinal parasite of wide distribution. Occurrence: Lake Geneva: pumpkinseed, bluegill, smallmouth black bass; Lake Pepin: bluegill, smallmouth black bass; Lake Michigan: rock bass, pumpkinseed.

## ACANTHOCEPHALA

*Echinorhynchus coregoni* Linkins

In Lake Michigan in the intestines of long-nosed and common suckers, whitefish, lake trout, pickerel, five species of ciscoes, lota, yellow perch.

*Echinorhynchus salvelini* Linkins

In Lake Michigan in intestines of lake trout, four species of ciscoes, smallmouth black bass, yellow perch.

*Echinorhynchus thecatus* Linton

This was found to be a common and widely distributed intestinal parasite. Occurrence: Lake Geneva: rock bass, pickerel, bluegill, both black bass, yellow perch; Lake Mendota: rock bass, speckled bullhead, pumpkinseed, long-nosed gar, bluegill, both black bass, yellow perch; Lake Pepin: dogfish, eel, Johnny darter, pickerel, pumpkinseed, bluegill, both black bass, yellow perch, white bass, sauger; Green Lake: rock bass, speckled bullhead, sucker, top minnow, bluegill, both black bass, yellow perch; Lake Michigan: speckled bullhead, yellow perch.

Larval individuals were found in small white crappies in Lake Pepin; Green Lake: pickerel, top minnow, bluegill, smallmouth black bass, yellow perch.

Visceral cysts were found as follows: Lake Geneva: rock bass, pumpkinseed, both black bass; Lake Mendota: rock bass, speckled bullhead, pumpkinseed, largemouth black bass; Lake Pepin: sheepshead, pumpkinseed, channel cat, largemouth black bass, tadpole cat; Green Lake: rock bass, speckled bullhead, pumpkinseed, top minnow, bluegill, largemouth black bass, yellow perch; Lake Michigan: speckled bullhead, sucker, yellow perch.

*Neoechinorhynchus crassus* Van Cleave

Found in the intestine of the sucker in Lake Mendota, Lake Geneva, and Lake Michigan.

*Neoechinorhynchus cylindratu*s (Van Cleave)

In the intestines of fishes as follows: Lake Mendota: largemouth black bass; Lake Pepin: Johnny darter, pickerel, both black bass, yellow perch, white bass, sauger, wall-eyed pike; Lake Michigan: sucker.

Juvenile specimens occurred in the pickerel in Green Lake.

Visceral cysts were found as follows: Lake Mendota: rock bass; Lake Pepin: pickerel, smallmouth black bass, white bass, sauger, wall-eyed pike; Green Lake: pickerel, smallmouth black bass.

*Octospinifer macilentu*s Van Cleave

Occurred in the intestine of the sucker in Lake Geneva and Lake Michigan.

*Pomphorhynchus bulbocolli* Linkins

In the intestine of fishes: Lake Geneva: rock bass, sucker, both black bass; Lake Mendota: sucker, blunt-nosed minnow; Lake Pepin: sucker, a buffalo—*Ictiobus cyprinella* (Cuvier & Valenciennes), white-nosed and short-headed suckers, skipjack; Green Lake: sucker; Lake Michigan: black bullhead, sucker, Iowa darter.

Juvenile individuals were found in Green Lake in the following fishes: rock bass, speckled bullhead, top minnow, smallmouth black bass.

Visceral cysts occurred as follows: Lake Geneva: rock bass, sucker, both black bass; Lake Mendota: yellow and black bullheads; Lake Michigan: speckled bullhead, sucker.

HIRUDINEA

Unidentified leeches were found as follows: Lake Mendota: rock bass, speckled bullhead, largemouth black bass; Lake Pepin: black and yellow bullheads; Green Lake: rock bass, speckled bullhead, top minnow, largemouth black bass, yellow perch; Lake Michigan: lake trout, lota.

*Piscicola punctata* (Verrill)

Leeches, identified by the writer, occurred as follows: Lake Mendota: carp, bluegill, largemouth black bass; Green Lake: pumpkinseed.

*Piscicola milneri* (Verrill)

Found in Lake Michigan on a cisco—*Leucichthys hoyi* (Gill), and the lota.

*Piscolaria* sp.?

Professor J. P. Moore identified specimens from the following sources: Lake Geneva: rock bass, yellow perch; Lake Pepin: black and yellow bullheads, channel cat; Lake Michigan: rock bass, smallmouth black bass.

*Placobdella montifera* Moore

Occurrence: Lake Geneva: smallmouth black bass; Lake Pepin: carp and hackleback sturgeon.

*Placobdella parasitica* (Say)

Occurrence: Lake Mendota: bluegill; Green Lake: pickerel, top minnow.

*Placobdella picta* (Verrill)

Occurred in Lake Michigan on the sucker and perch.

## LAMELLIBRANCHIATA

During all the studies described in this paper glochidia were never found on any part of fishes except the gills. In Lake Mendota the yellow perch was infected with *Lampsilis luteola* (Lamarck). In Lake Pepin the yellow perch was infected with *Lampsilis luteola* (Lamarck) and *Quadrula plicata* (Say); the sauger, with *Quadrula metaneura* (Say) ("probably"), *Lampsilis recta* (Lamarck), *L. ligamentina* (Lamarck); the mud cat, with unidentified glochidia.

COPEPODA

*Achtheres ambloplitis* Kellicott

In Lake Michigan on the gills of a cisco—*Leucichthys harengus* (Richardson), the lota, and smallmouth black bass.

*Achtheres coregoni* (Smith)

On the gills of the lake trout in Lake Michigan.

*Achtheres corpulentus* Kellicott

On the gills of a cisco—*Leucichthys johannae* (Wagner), in Lake Michigan.

*Achtheres micropteri* Wright

On the gills of the smallmouth black bass in Lake Geneva.

*Achtheres pimelodi* Kroyer

On the gills of the channel cat in Lake Pepin.

*Argulus* sp.?

An unidentified *Argulus* was found on a carp in Lake Mendota.

*Argulus appendiculosus* Wilson

Found in Lake Pepin on the mud cat.

*Argulus catostomi* Dana and Herrick

Under the opercula and on the gills of suckers in Lake Geneva and Lake Mendota.

*Argulus maculosus* Wilson

On the yellow bullhead in Lake Pepin.

*Ergasilus caeruleus* Wilson

On the gills of fishes: Lake Mendota: yellow perch; Lake Michigan: rock bass, sucker, a cisco—*Leucichthys harengus* (Richardson), and yellow perch.

*Ergasilus centharchidium* Wright

In Lake Michigan on the gills of the rock bass.

## PISCES

*Ichthyomyzon concolor* (Kirtland)

This lamprey was taken in Lake Pepin on a spoonbill.

## DISCUSSION AND CONCLUSIONS

A summary of the parasites found in the five lakes studied is given in table 4. The writer had expected to publish six additional tables giving the number of fishes infected and total average infection for each parasite but the space available will not permit this. Those interested in such detailed information may obtain it by letter. Lake Mendota in all respects contained the smallest number of parasites—the average number in each fish being 2.0; the average number of species of fishes each parasite infected, 4.7; and the average number of individual fishes infected by each parasite, 1.4. Lake Pepin had the largest average number of parasites per fish (5.0); Green Lake the largest average number of species of fishes infected by each species of parasite (8.1); and Lake Geneva the largest average number of individuals infected by each parasite (2.2).

The lakes with the widest range of territory and opportunity for fishes to invade the greatest variety of habitats have the highest average infection per fish (Pepin, 5.0; Michigan, 3.9). However, the fishes in Pepin, with its shifting, sandy bottom and lack of thermal stratification, have 22 per cent more parasites than Michigan, with its soft mud bottom and cold deeper water. The two lakes with the largest average number of species of fishes infected per species of parasite include the one with a large number of species of fishes and habitats (Pepin, 8.1) and the one with the smallest number of species of fishes and the least variety of habitats (Geneva, 6.6). The lakes having the largest number of individuals infected by each parasite include one with the least range and variety of habitats (Geneva, 2.2), one with wide range and variety of habitats (Michigan, 2.1), and one in which there was little variety in the shore habitats and a sharp distinction between deep and shallow water habitats (Green, 2.1).

The lake in which there was the least infection by parasites (Mendota) had the largest number of fishes per unit of area (Pearse, 1921, p. 24), the most abundant food supply, the greatest degree of stagnation in the deeper water during summer. Table 4 shows, however, that this lake had the second largest number of species of parasites which showed the largest number of highest infection averages; and that it was excelled in this only by Lake Pepin, which had nearly twice as many species of fishes, the scantiest food supply, and the greatest parasitic infection. Taking the number of species of parasites that showed the highest average infections as a criterion, the lakes rank in the following order: Pepin, Mendota, Michigan, Green, Geneva. This order indicates that there is a direct relation between variety of habitat and amount of infection.

Taking the total number of species of fish parasites present as a criterion the lakes rank in the following order: Pepin 70, Michigan 60, Mendota and Green 44, Geneva 35. This indicates that variety of habitat is correlated with a large number of species of parasites (and fishes) as well as a large amount of infection. In other words the lake with the largest variety of habitats has the greatest variety of fishes and parasites.

Arranged in order of average infection the fishes in each of the five lakes in which extensive observations were made rank as follows:

**LAKE GENEVA:** Rock bass 9.4, pumpkinseed 5.0, smallmouth black bass 4.0, sucker 2.2, cisco 1.0, largemouth black bass 0.8, wall-eyed pike 0.6, pickerel 0.5, bluegill 0.5, perch 0.5, brook trout 0, shiner (*Notropis hudsonius*) 0.

**LAKE MENDOTA:** White bass 13.2, wall-eyed pike 12.7, dogfish 8.3, smallmouth black bass 6.6, sucker 4.0, long-billed gar 3.8, tadpole cat 2.8, pumpkinseed 2.6, speckled bullhead 2.4, largemouth black bass 2.4, Johnny darter 2.0, bluegill 1.6, perch 1.4, yellow bullhead 1.3, rock bass 1.1, pickerel 1.1, cisco 0.8, black crappie 0.7, top minnow 0.3, shiner (*Notropis heterodon*) 0.2, silversides 0.1, carp 0.1, blunt-nosed minnow +, bream 0, buffalo 0, miller's thumb 0.

**LAKE PEPIN:** Mud cat 462, lake carp 116.6, eel 40, dogfish 37, spoonbill 19, smallmouth buffalo 17, yellow bass 16, quillback 13.2, river carp 5, sucker 4.7, black bullhead 3.7, skipjack 3.3,

pickerel 3.1, speckled bullhead 2.9, white bass 2.9, channel cat 2.7, tadpole cat 2.5, mongrel buffalo 2, hackleback sturgeon 1.8, sauger 1.7, wall-eyed pike 1.6, pumpkinseed 1.3, white crappie 1, yellow perch 0.9, shiner (*Notropis heterodon*) 0.8, short-headed redhorse 0.7, long-billed gar 0.6, largemouth black bass 0.5, bluegill 0.5, mooneye 0.4, white-nosed sucker 0.4, black crappie 0.4, Johnny darter 0.2, shiner (*Notropis atherinoides*) 0.2, log perch 0.2, carp 0.1, shiners (*Notropis jejunus* and *N. hudsonius*) 0.1, pirate perch +, gizzard shad 0, lamprey 0.

GREEN LAKE: Pumpkinseed 29.7, blunt-nosed minnow 22.5, sucker 21.4, rock bass 8.9, bluegill 4.2, yellow bullhead 2.5, smallmouth black bass 2.5, cisco 2.4, carp 2, speckled bullhead 1.9, top minnow 1.1, largemouth black bass 0.8, yellow perch 0.4, pickerel 0.4, Johnny darter 0.1, shiner (*Notropis atherinoides*) 0.

LAKE MICHIGAN: Whitefish 31.1, smallmouth black bass 28.9, blackfin 27.8, pumpkinseed 18.9, carp 15, rock bass 12.6, lake trout 9.2, speckled bullhead 6.5, chub 5.8, mud puppy 5, black bullhead 4.1, bloater (*Leucichthys harengus*) 3.9, lota 3.9, bloater (*Leucichthys hoyi*) 2, log perch 1.5, pickerel 1.4, cottid 1.3, sucker 1.2, top minnow 1, Iowa darter 0.9, long-nosed sucker 0.8, Johnny darter 0.8, yellow perch 0.5, bream +, shiners (*Notropis atherinoides* and *N. hudsonius*) +, blunt-nosed minnow 0, yellow bullhead 0.

It would not be proper to add the average infections in different lakes in order to compare infection in different species of fishes, for the total infection in different lakes varies greatly. Each species should be given a rating which will compare it with all others in each lake. The writer has therefore used the following formula in order to give to each fish a relative percentage (P).

$$P=100-\frac{100}{N}\times R$$

$N$  is the number of fishes examined in the lake;  $R$ , the rank of the particular species of fish in the lake according to its average infection. For example twelve species were examined in Lake Geneva ( $\frac{100}{12}$ ). The largemouth black bass ranks sixth ( $\frac{100}{12}\times 6$ ). For this species  $P=100-\frac{100}{12}\times 6=50$ . Using this method for each lake and averaging the relative percentages for all species of fishes that occurred in two or more lakes, the fishes rank in the following order: dogfish 90, smallmouth black bass 78, white bass 78,

rock bass 73, pumpkinseed 71, sucker 68, black bullhead 66, tadpole cat 64, wall-eyed pike 61, speckled bullhead 60, long-billed gar 56, bluegill 55, yellow bullhead 55, all species of ciscoes 54, largemouth black bass 45, pickerel 42, carp 40, buffalo (*Ictiobus cyprinella*) 36, log perch 35, blunt-nosed minnow 32, top minnow 32, yellow perch 31, shiner (*Notropis heterodon*) 30, Johnny darter 30, black crappie 27, shiner (*Notropis atherinoides*) 14, bream 11, shiner (*Notropis hudsonius*) 11.

In general the fishes that frequent vegetation show the highest infection with parasites, those that frequent the bottom and open water are intermediate, and the small fishes that live in shallow water have fewest parasites. Doubtless many factors influence the prevalence of fish parasites, and much is yet to be learned before general laws that will enable one to predict the degree of infection that will be probable in a particular locality are formulated.

There are many ways in which parasites may infect fishes. The most important means of infection are: (1) food, (2) the active migration of the parasite to its host, (3) and accidental contamination from bottom mud, vegetation, or other material. Van Cleave (1920) and Mrázek (1891) have found parasites encysted in amphipods. The observations described in this paper show that the fishes in Lake Michigan that feed largely on amphipods are heavily infected with the parasites these crustaceans are known to carry. Several types of parasites are found encysted in fishes and fish-eaters often have a heavy infection. Hausmann (1897) believed that fishes acquired parasites chiefly through their food, and he was doubtless right, as intestinal parasites are most abundant. In general the fishes that eat the greatest variety of food have the most parasites, but there are some notable exceptions to this. The dogfish, wall-eyed pike, and gar, for example, subsist largely on fishes (Pearse 1918) and are heavily infected.

Little is known of the active migration of fish parasites to their hosts. The distribution of the cuticular cysts of *Diplostomum* indicates that infection may occur in such a way. Faust (1918) notes that *Bunodera* has been known to wander out of dead fishes. Perhaps parasites may infect a second host after leaving the first.

The acquiring of parasites from the accidental ingestion of eggs or other stages may be characteristic of certain parasites that are erratic in their occurrence—like intestinal nematodes.



The susceptibility of the host is an important factor in determining the degree and frequency of parasitic infection. *Proteocephalus pinguis* was never found by the writer except in the pickeral; *P. ambloplitis* was found in a number of hosts. Fasten (1913) has studied a parasitic copepod which kills brook trout in great numbers, but will not live on the German brown trout. Howard (1914) cites similar instances among glochidia. Fish parasites may show considerable specificity for certain hosts and hosts may possess a varying degree of immunity. The black crappie, for example, appears to be immune to many parasites that attack other Centrarchidae. The largemouth and smallmouth black bass are closely related, but during the present investigations the latter always carried more parasites. The pumpkinseed was always more heavily infected than the bluegill. Perhaps some of these differences are due to differences in habitats, but some are undoubtedly due to susceptibility. Furthermore, there is general similarity between the parasites of the Siluridae and certain Percidae which leads one to believe that infection may be limited at least in part by certain chemical substances which are present in or absent from the bodies of fishes.

Surber (1913) has remarked on the remarkably small percentage of fishes that carry glochidian parasites in nature. Van Cleave (1919) showed that only half the species of fishes in a Michigan lake were infected with acanthocephalans. Infection depends on so many factors and opportunities that it is to be expected that parasites will frequently fail to reach their hosts.

Most fish parasites do little harm to their hosts. Pratt (1919) states that nematodes are most injurious and that trematodes do the least harm. While his generalizations may apply to the parasites of certain marine fishes, like the cod, the writer does not believe they are generally applicable to the fresh-water fishes in the United States. The most injurious parasites (leaving out the Protozoa, which the writer has not studied) appear to be the larval tapeworms, which destroy liver tissue; acanthocephalans, which cause ulcers in the wall of the intestine; and copepods, which suck blood from the gills. Glochidia, nematodes, and leeches are usually too few in numbers to do serious damage. Tapeworms and trematodes often occur in enormous numbers but do not appear to do much injury. The writer has never examined a dogfish that did not contain numerous tapeworms; yet all appeared to be in good condition.

The migrations of fresh-water fishes doubtless afford them opportunity to acquire and shed parasites (Ward 1909): The fishes that travel most and invade the greatest variety of habitats in general have the most parasites.

Seasonal changes doubtless have a marked effect on certain fish parasites. It was found that perch have most parasites in spring, although some species of parasites were more abundant at other seasons. Ward (1909), Marshall and Gilbert (1905) and Van Cleave (1916) have also made observations on the abundance of parasites at various seasons, but such information is as yet too limited for generalization.

Hausmann (1897) thought that perch had few parasites when little food was eaten on account of low temperature. In the writer's experience perch have not been found to refrain from eating during winter and they have more parasites in winter than in autumn or summer. Pratt (1909) says that epidemics of trematodes are likely to occur when the water is warm. The writer has found no evidence that this is the case, at least in fresh-water fishes.

Some parasites are apparently limited to particular drainage systems. *Phyllodistomum superbum* Stafford was quite common in the urinary bladder of perch in several lakes on the St. Lawrence drainage but was never observed in a single one of the several thousand perch examined from the lakes on the Mississippi drainage. Perhaps this trematode entered the St. Lawrence drainage after the Mississippi separated from it. Other cases of this kind probably occur but too few specimens have yet been examined to demonstrate them.

Contrary to Pratt's (1919) assertion, the size of a lake does not appear to be correlated with the degree of parasitic infection of its fishes. The density of the population may sometimes be of importance. However, the fishes of Lake Mendota, which has the densest population of any of the five lakes studied extensively by the writer, has the fewest parasites and the fishes in the depth of Lake Michigan, where the population is scanty, have many: There is, in general, no direct relation between number of fishes and number of parasites.

The habitats of fishes are of course important in their relation to parasitic infection. While a variety of habitats is desirable for the growth of fishes, it gives opportunity for acquiring more parasites. A wide range also gives more opportunities for acquiring

parasites than a restricted one. Ward (1910) has pointed out that "the parasitic fauna of any animal is primarily a function of its habitat". The observations reported in this paper indicate that the fishes in comparatively barren lakes have an unusual number of visceral cysts and acanthocephalans—perhaps because they wander about more in search of food. Visceral cysts appear to be more abundant in deep water fishes than in those from shallow water. Linton (1910) found that marine fishes in shallow water had fewer parasites than those at greater depths. He believed this was because the former had less opportunity to wander about and become infected. In fresh-water the writer has found infection to be greater on the whole in shallow water—probably because there is a greater variety of habitats and secondary hosts there.

The ecological factors that appear to be important in relation to parasitic infection have now been discussed. Perhaps only one thing has been made clear—that, "now we see through a glass darkly". The writer makes no apology for this final conclusion. There is great need for more information in regard to the ecology of parasitism, not only among fishes but among all animals. It is hoped that this paper may help to interest fishermen, parasitologists, geographers, and ecologists in the opportunities that are open for research on the parasites of fishes. The fisherman must in the future learn to increase his catch by the control of parasites. There are many undescribed species and life histories that await discovery by the parasitologist. The zoogeographer has unusual opportunities for study—parasites depend on one or more hosts for their distribution and are hence conservative in their migrations. The ecologist may disclose the most intricate and interesting relations to be found in nature.

## BIBLIOGRAPHY

- Cooper, A. R. 1917. A morphological study of bothriocephalid cestodes from fishes. *Jour. Parasitol.* 4: 33-39. Urbana.
- Fasten, N. 1913. The behavior of a parasitic copepod, *Lernaepoda edwardsii* Olsson. *Jour. An. Behavior*, 3: 36-60. Cambridge.
- Faust, E. C. 1918. Studies on American Stephanophialinae. *Trans. Amer. Micro. Soc.* 37: 183-198. Menasha.
- Goldberger, J. 1911. Some known and three new endoparasitic trematodes from American fresh-water fish. *Bulletin U. S. Hygienic Laboratory*, No. 71: 7-35. Washington.
- Hausmann, L. 1897. Ueber Trematoden der Susswasserfische. *Revue suisse die Zoologie*, 5: 1-42, pl. 1. Geneva.

- Howard, A. D.** 1914. Some cases of narrowly restricted parasitism among commercial species of fresh-water mussels. *Trans. Amer. Fish. Soc.* 1914: 41-44.
- La Rue, G. R.** 1914. A revision of the cestode family Proteocephalidae. *Bul., Univ. Ill.* 12: 1-531. Urbana.
- Linton, E.** 1910. Notes on the distribution of entozoa of North American marine fishes. *Proceedings, Seventh International Zoological Congress, 1907: 1-11.* Cambridge.
- . 1911. Trematode parasites in the skin and flesh of fish and the agency of birds in their occurrence. *Trans. Amer. Fish. Soc.* 1911: 245-259.
- Marshall, W. S. and Gilbert, N. C.** 1905. Three new trematodes found principally in black bass. *Zoolog. Jahrb. Syst.*, 22: 447-488.
- Mrázek, A.** 1891. Příspěvky k vývojezpytu některých tasemnic ptáčích. Zvláštní otisk z *Věstníka královské české společnosti nauk, 1891: 97-131, tab. V.* Prag.
- Osborn, H. L.** 1911. On the distribution and mode of occurrence in the United States and in Canada of *Clinostomum marginatum*, a trematode parasite in fish, frogs. *Biolog. Bul.* 20: 350-364. Woods Hole.
- Pearse, A. S.** 1918. The food of the shore fishes of certain Wisconsin lakes. *Bulletin, U. S. Bureau of Fisheries.* 35: 247-292. Washington.
- . 1920. The fishes of Lake Valencia, Venezuela. *University of Wisconsin Studies in Science, No. 1: 1-51.* Madison.
- . 1921. The distribution and food of the fishes of three Wisconsin lakes in summer. *Ibid.*, No. 3: 1-61. Madison.
- . 1921a. Distribution and food of the fishes of Green Lake, Wisconsin, in summer. *Bulletin, U. S. Bureau of Fisheries,* 37: 255-272. Washington.
- Pearse, A. S., and Achtenberg, H.** 1920. Habits of yellow perch in Wisconsin lakes. *Bulletin, U. S. Bureau of Fisheries,* 36: 293-366. Washington.
- Pratt, H. S.** 1919. Parasites of fresh-water fishes. *Economic Circular, U. S. Bureau of Fisheries, No. 42: 1-8.* Washington.
- Smallwood, W. M.** 1914. Preliminary report on the diseases of fish in the Adirondacks, a contribution to the life history of *Clinostomum marginatum*. *Tech. Pub. N. Y. State Col. For., Syracuse University, No. 1: 1-27.* Syracuse.
- Surber, T.** 1912. Identification of the glochidia of fresh-water mussels. *U. S. Bureau of Fisheries, Doc. 771: 1-10, pls. 1-3.* Washington.
- . 1915. The identification of the glochidia of fresh-water mussels. *Report, U. S. Commissioner of Fisheries, 1914: 1-16.* Washington.
- Van Cleave, H. J.** 1916. Seasonal distribution of some Acanthocephala from fresh-water hosts. *Jour. Parasitol.* 2: 106-110. Urbana.
- . 1919. Acanthocephala from fishes of Douglas Lake, Michigan. *Occasional Papers of the Museum of Zoology, University of Michigan, No. 72: 1-12.* Ann Arbor.
- . 1919a. Acanthocephala from the Illinois River, with descriptions of species and a synopsis of the family Neoechinorhynchidae. *Bul. Ill. Nat. Hist. Sur.* 12: 225-271. Urbana.

- . 1920. Notes on the life cycle of two species of acanthocephalans from fresh-water fishes. *Jour. Parasitol.* 6: 167-172. Urbana.
- Ward, H. B. 1909. The influence of hibernation and migration on animal parasites. *Proceedings, Seventh International Zoological Congress, 1907: 1-12.* Cambridge.
- . 1910. Internal parasites of the Sebago salmon. *Bulletin, U. S. Bureau of Fisheries, 28: 1151-1194, pl. CXXI.* Washington.
- Ward, H. B. and Magath, T. B. 1916. Notes on some nematodes from fresh-water fishes. *Jour. Parasitol.* 3: 57-64. Urbana.
- Ward, H. B. and Whipple, G. C. 1918. *Fresh-water biology.* pp. x+1111. New York.
- Wilson, C. B. 1915. North American parasitic copepods belonging to the Lernaeopodidae, with a revision of the entire family. *Proceedings of the U. S. National Museum, 47: 565-729; pls. 25-56.* Washington.
- Zschokke, F. 1902. Marine Schmarotzer in Süßwasserfischen. *Verhandl. Naturforsch. Gesellsch. in Basel, 16: 118-157.*

TABLE 1. Total average infection of the yellow perch in the lakes along the Yahara River during July, August, September, 1917.

Parasite	Mendota, Deep	Mendota, Shallow	Monona	Wingra	Waubesa	Kegonsa
Number examined.....	30	44	30	26	36	26
<i>Diplostomum cuticola</i> .....	6.0	53.2	66.0	0.2	8.5	27.5
<i>Bunodera luciopercae</i> .....	0.3	7.2	.....	.....	.....	.....
<i>Clinostomum</i> .....	0.1	0.1	.....	.....	.....	.....
<i>Echinorhynchus thecatus</i> .....	.....	0.8	0.3	.....	0.3	0.1
<i>Neoechinorhynchus cylindricus</i> .....	.....	0.1	.....	.....	0.1	.....
<i>Acanthocephalan cysts</i> .....	3.9	5.0	.....	8.5	1.2	2.4
<i>Dacnitioides cotylophora</i> .....	3.8	2.1	0.1	0.6	1.0	3.6
<i>Icthyonema cysts</i> .....	16.1	8.6	0.3	1.5	2.8	0.7
<i>Proteocephalus, intestinal</i> .....	0.6	2.5	1.3	2.6	0.4	.....
<i>Proteocephalus, cysts</i> .....	32.4	26.1	14.1	24.5	1.4	1.0
<i>Bothriocephalus cuspidatus</i> .....	.....	0.1	0.9	.....	0.1	4.4
<i>Glochidia</i> .....	0.3	11.8	.....	.....	0.6	.....
<i>Piscicola</i> .....	.....	0.1	.....	0.2	.....	0.1
<i>Unknown cysts</i> .....	3.2	3.2	1.8	0.7	2.5	1.1
Total.....	66.7	120.9	84.8	38.8	24.9	40.9
Total without <i>Diplostomum</i> .....	60.7	67.7	18.8	38.6	16.4	13.4

TABLE 2. Showing average infection by months in the Yahara River lakes, 1917-1918. After October, perch were not examined from any lake except Mendota, with the exception of seven specimens from Kegonsa in November.

Month	Number examined	<i>Diplostomum cuiicola</i>	<i>Bunodera luctopercae</i>	<i>Clavostomum</i> cysts; skin, gills	<i>Echinorhynchus thecatus</i>	<i>Neoechinorhynchus cylindricus</i>	<i>Acanthocephalan</i> cysts, visceral	<i>Dacnitioides colyphophora</i>	<i>Ichthyonema</i> cysts, visceral	<i>Protocephalitis</i> , intestinal	<i>Protocephalitis</i> cysts, visceral	<i>Bothriocephalus cuspidatus</i>	<i>Glochidia</i> , gills	<i>Piscicola</i>	Unknown visceral cysts	Total
June.....	45	5.1	.....	+	.....	.....	.....	1.0	0.2	.....	6.2	0.2	2.1	.....	0.4	15.2
July.....	79	11.5	+	.....	0.2	+	1.0	1.3	0.7	0.1	7.9	+	2.1	+	0	525.3
August.....	62	8.9	1.2	.....	0.1	.....	0.3	0.1	1.5	0.4	5.5	0.1	.....	.....	0.4	18.5
September...	56	6.4	0.1	+	+	+	2.2	0.7	2.8	0.8	3.2	0.8	.....	0.1	1.2	18.2
October.....	31	6.3	2.0	.....	.....	0.3	0.3	0.3	4.3	0.3	3.3	0.2	.....	+	0.7	18.0
November...	13	19.1	1.0	0.2	0.2	.....	.....	.....	4.7	.....	13.8	.....	.....	.....	.....	39.0
January.....	20	4.5	1.8	.....	.....	23.7	0.3	21.5	2.1	0.9	3.5	0.1	.....	.....	1.3	59.7
February.....	10	0.5	0.9	.....	.....	5.3	2.8	.....	2.0	0.3	11.0	.....	.....	.....	0.4	23.2
March.....	20	0.4	3.1	.....	.....	18.4	17.6	.....	1.5	0.5	3.6	.....	.....	.....	.....	45.1
April.....	7	0.1	3.7	.....	7.5	9.1	114.6	.....	1.3	.....	0.7	.....	.....	.....	.....	137.0
May.....	8	1.5	2.7	.....	0.1	29.4	76.3	.....	5.4	0.3	1.6	.....	.....	0.1	.....	117.4
Total.....	.....	64.3	16.5	0.2	8.1	86.2	215.4	24.9	26.5	3.6	60.3	1.4	4.2	0.2	4.9	516.6
Average...	.....	5.8	1.5	+	0.7	7.8	19.6	2.3	2.4	0.3	5.5	0.1	0.4	+	0.4	46.8

TABLE 3. Showing average number of parasites infecting perch from 16 lakes during August, 1917. The results from lakes on three drainage systems are summarized.

	Yahara River						Oconomowoc River						Fox River							
	Men- dota,	Men- dota, shallow	Monona	Wingra	Waubesa	Kenzonsa	Average	Beaver	Pine	North	Okauchee	Oconomowoc	Lac la Belle	Average	Puckaway	Green	Poygan	Butte des Morts	Winnabago	Average
Depth, meters.....	25.6	25.6	22.5	4.3	11.1	9.6	14.6	15.0	27.4	23.7	28.6	19.1	14.2	21.3	1.6	72.2	3.3	3.4	6.4	17.4
Surface area, square kilometers.....	39.4	39.4	14.1	2.2	8.2	12.7	15.3	12.4	30.6	18.0	42.8	25.6	46.1	29.3	1.3	29.7	4.5	18.2	55.8	21.9
Number examined.....	10	10	10	10	11	7	10	10	4	1	3	10	2	5	7	6	8	10	1	6
Number infected.....	10	10	10	10	8	3	8	10	4	1	3	10	2	5	7	6	8	10	1	6
<i>Diplostomum cuticola</i> .....	0.6	7.8	35.0	0.1	4.0	0.3	8.0	0.6	6.2	4.0	11.6	11.3	23.5	9.5	0.1	52.0	1.5	0.1	10.7	
<i>Bufolella luciongae</i> .....		6.6					1.1	1.1						0.1	11.0	2.5	0.3	10.9	2.0	
<i>Cyrtostomum marginatum</i> .....																				
<i>Phyllostomum variegatum</i> .....																				
<i>Phyllostomum superbum</i> .....																				
<i>Allerodinium arcticum</i> .....																				
<i>Echinorhynchus flexilis</i> .....		0.1			0.2		+					0.6		0.1						
<i>Neoskincynchus cylindricus</i> .....												0.2								
<i>Acanthocephalus cyasi</i> , visceral.....	1.5	0.6		0.5	0.2	0.4	0.4	0.2	1.2			1.6		+	1.5	0.2			0.3	
<i>Dactylocephalus cyasi</i> , visceral.....		0.1										1.0		0.5	1.0	1.1	.05		0.5	
<i>Laklymones cyasi</i> , visceral.....	3.2	3.0		1.7	1.3	1.5	1.5	0.4	0.5	7.0	2.6	4.4		2.3	0.1	10.0	0.1		2.1	
<i>Proteocephalus inaequalis</i> .....			0.3							4.0				0.7	2.3	2.3				1.4
<i>Proteocephalus cyasi</i> , visceral.....	8.7	10.8	6.3	7.0		5.5	23.8	23.8	8.2	15.0		6.7	6.5	10.0	0.4	12.0	4.8	1.0	3.8	
<i>Echinocephalus caspiadus</i> .....		0.1	0.3				0.1													
<i>Glochidia</i> .....																				
<i>Piscicola</i> .....																				
Unknown <i>cyasi</i> , visceral.....	1.3	0.1		0.2	0.8	0.2	0.4	6.6	0.7		0.3	0.7		1.4		1.3	0.9	0.3		0.5
Total.....	15.3	31.1	42.1	9.5	6.5	0.5	17.3	32.7	17.0	30.0	14.5	25.5	30.0	24.7	14.1	59.1	32.2	19.2	3.0	25.1
Total without <i>diplostomum</i> .....	14.7	23.3	7.1	9.4	2.5	0.2	9.3	32.1	10.8	26.0	2.9	14.2	6.5	15.2	14.0	7.1	30.7	19.1	1.0	14.4

TABLE 4. *Summary of the average infection with fish parasites in five Wisconsin lakes during summer. + indicates less than 0.01 per cent.*

	Geneva	Mendota	Pepin	Green	Michigan
<i>Trematodes</i> .....	0.31	0.09	0.51	0.09	0.28
<i>Trematodes</i> , encysted.....	1.25	0.46	0.10	1.70	0.12
<i>Tapeworms</i> .....	0.39	0.23	0.67	0.45	0.50
<i>Tapeworms</i> , encysted.....	0.12	0.28	1.19	0.09	0.06
<i>Nematodes</i> .....	0.04	0.05	0.07	0.01	0.27
<i>Nematodes</i> , encysted.....	0.02	0.13	+	+	0.11
<i>Acanthocephalans</i> .....	0.24	0.12	0.18	0.41	1.79
<i>Acanthocephalans</i> , encysted.....	0.04	0.12	0.10	0.12	0.08
<i>Unknown cysts</i> .....	0.06	0.49	1.36	0.12	0.14
<i>Leeches</i> .....	0.01	0.02	0.02	0.02	0.03
<i>Glochidia</i> .....	—	+	0.80	—	0.01
<i>Copepods</i> .....	+	+	+	—	0.32
<i>Protozoan cysts</i> .....	—	+	—	—	—
<i>Parasitic fishes</i> .....	—	—	+	—	—
Total average infection <sup>5</sup> ; parasites per fish.....	2.3	2.0	5.0	3.0	3.9
Average number of species of fish infected by each parasite.....	6.6	4.7	5.0	8.1	5.3
Average number of infections by all species of parasites.....	2.2	1.4	1.5	2.1	2.1



# THE ANATOMY OF *TROCTES DIVINATORIUS* MUELL

RUTH CHASE NOLAND

## *Introduction*

The internal anatomy of *Troctes divinatorius* has never been carefully worked out, though the insect has frequently been described as a not uncommon household pest. In 1818 Nitzsch (18) published a description and figures of the digestive tract and reproductive organs of an insect which he called the book louse, *Psocus pulsatorius*. In a number of ways my descriptions differ from his, and it is probable that the insect which I have had is a different species, although of the same genus, for the generic names *Psocus*, *Troctes*, and *Atropos* have all been used in reference to the genus to which the book louse belongs. Since the time of Nitzsch, the only work which has been done on the book louse from an anatomical point of view has been that on the mouthparts, and is very little. However, considerable study has been made of the mouthparts of a closely related family, the *Psocidae*. This has been done by Burgess (6), Hagen (15), and others and has been of interest largely because of the light it throws on the relationships of these to other insects.

The studies made here of *Troctes* are based on examinations of hundreds of individuals in whole mounts, longitudinal, and cross sections and in dissections made in glycerine or in balsam under the dissecting microscope. The small size of the specimens, none of them more than a millimeter and a half in length, has made necessary the working out of many details by comparison in a large number of specimens. For the gross anatomy the micro-dissections stained in alum carmine, or haemalum gave most information; while the smaller details and histology could only be determined from sections. These were stained with Heidenhain's or Delafield's haematoxylin. A number of fixatives were used, but probably the best results came from Carnoy's I and II, and Kahle, Tower and Petrunkevitch. Very much assistance in the work was given by Professor W. S. Marshall, under whose direction it was carried out.

The specimens for use were easy to procure at certain times of the year, for during the summer and autumn months a sheet of paper left for a few days on one of the laboratory tables is sure to cover a number, large and small, but in the winter, beginning with November and continuing until May, the insects almost entirely disappear. Their favorite habitat is a dry and undisturbed place, and the tables of a laboratory, if dust-covered, suit them perfectly. It is useless to search for them on a clean table, even though it has been well sheltered by papers or books. Books infrequently used, or herbarium shelves, or dried grains packed away in boxes remote from sunlight are favorable habitats for them. As has often been noted in descriptions, the femur of the posterior pair of legs of *Troctes* is greatly enlarged, a characteristic of jumping insects, but observers have claimed this to be of no use to the animal. However, in escaping from the collector, as they probably do in eluding animals which prey upon them, they put this feature to good use by making leaps backward before fleeing swiftly into some dark crevice. Before they can hide, they are easily picked up with a moist brush and dropped into hot water.

#### MOUTHPARTS

The structure of the head and mouthparts of the Corrodentia has been of more interest to entomologists, particularly systematists, than any other feature of the anatomy of these insects, because of the similarity shown by them to corresponding parts of the Mallophaga. The oesophageal sclerite or "bonnet," the so-called maxillary fork, and the chitinous structures of the labium known as the lingual glands are similar, to a striking degree, in the two orders.

The first work which revealed to any extent the structure of the mouthparts of a form similar to *Troctes* was that of Burgess (5) in 1878 on the anatomy of the head in the Psocidae. In this he figured in detail some portions of the head and mouthparts of *Psocus*, with a few references to those of *Troctes* (called by him *Atropos*). Since his time the studies which have been made on these insects have been largely to determine the nature of the "lingual glands" and maxillary fork. Doubt has been expressed as to the glandular nature of the labial structures by Bertkau (4), Cummings (8) and Enderlein (10), and the true relationship of the maxillary fork is unknown. Is it an independent organ, not

maxillary in origin as Burgess concluded, or does it represent the inner lobe or lacinia of the maxilla, as claimed by Enderlein?

The head of *Troctes* is flattened dorso-ventrally with a large projecting clypeus filled with muscles which move the oesophageal sclerite. The internal support of the head is given it by the tentorium (fig. 1), which consists of a central plate and two pairs of arms; the anterior ones (fig. 1, a.t.) arise from the head capsule at the point of attachment of the mandibles, and the posterior pair (fig. 1, p.t.) appear to arise from the head capsule posterior to the muscles attaching the mandibles and maxillary fork to the posterior wall of the head in the occipital region.

In *Troctes* the inner surface of the clypeus, rather than the labrum as in *Psocus*, is furnished with tufts of hair (fig. 15, c.h.), and the labrum extends downward from the clypeus to meet the labium. The mandibles (fig. 2), heavy, chitinized structures, lie beneath the labrum. The dorsal portion of their inner or mesad surface is molar in nature for crushing (fig. 2, m.s.), while the ventral edge is made up of three sharply pointed teeth (fig. 2, v.p.), heavy enough to provide a satisfactory cutting surface. The dorso-lateral angle of each mandible is adapted to serve as the point of attachment to the lateral wall of the head capsule. The middle part of this area is rounded into a knob (fig. 2, m.p.) which fits into a corresponding socket in the wall of the capsule. Ventral to this is another projection (fig. 2, a.ab.) from which a small abductor muscle passes into the head just ventral to the base of the antenna. The mesad dorsal surface of the mandible is indented slightly (fig. 2, a.ad.) to form the point of attachment for a chitinous rod (fig. 1, c.m.) which is held in place by tendons. This rod spreads out posteriorly into several large bundles of adductor muscles (fig. m.m.) which fill a great part of the head cavity and are inserted in the posterior wall of the head. The maxillae and maxillary forks lie between the mandibles and labium. Each maxilla proper is composed of a main stipes (fig. 5, s.) which supports a four-jointed maxillary palp (fig. 5, m.p.) and a broad galea (fig. 5, g.). Burgess (6) describes a cardo in *Psocus*, but in *Troctes* this was not found. The inner edge of the galea is chitinized and has a few blunt teeth or ridges. This structure may be swung on the stipes by means of two muscles extending to the outer edge of the stipes (fig. 5, gme. and gmf.). The first muscle, attached to a place on the stipes anterior to the second, serves as the extensor, pulling the galea out laterally; the second acts as a

flexor to draw it inward toward the median line. The maxillary palp is pubescent. Its first or basal segment is very short, and the third is like it; while the second and fourth are longer, each fully three times the length of either of the other two. The largest muscles of the palp (fig. 5, f.p.) extend to the inner edge of the stipes, crossing it ventral to those of the galea. Thus their contraction would serve to draw the palp in toward the median line; a shorter muscle (fig. 5, ep.) attached near to those of the galea swings it out. On the stipes, just at the base of the galea, is a groove (fig. 5, fs.) through which the maxillary fork slides as if in a slot, and in which it is held in place by a band of tissue which arises from one wall of the slot and passes over the fork to attach on the other side. This slot has not been referred to before except as Hagen (15) described the fork as sliding "in the outer lobe as in a vagina"; yet this he did not figure. He spoke of the tip of the fork as sliding through a chitinous ring of the tip of the outer lobe, but this has not been seen in any of my preparations. The fork itself in *Troctes* is a straight rod ending distally in three sharp points of unequal length, the two outer longer than the inner. These ends are unlike the truncated tips of *Psocus*. At its base the fork is covered by strong muscles which in turn connect with a muscle (fig. 5, r.f.), not a ligament, as claimed by Burgess. This is probably the fork retractor, as it extends to the posterior wall of the head and would thus serve to draw the fork within the head by its contraction. The function of the forks is difficult to conceive, unless they could be used in so delicate a process as that of picking up mold spores and other small particles and drawing them into the mouth. With the close attachment which the maxillary fork bears through the slot to the stipes of the maxilla, it becomes possible to consider it the homologue of an inner lobe, since there is no other sign of one in connection with the stipes. However, even considering this, with the ultimate attachment of the fork to the posterior wall of the head, the old hypothesis of Burgess, that it is an independent organ, is still possible. In dissection it is so easy to separate the fork from the maxilla that its real attachment through the slot is difficult to ascertain. Until observation is made of its origin in development this question will remain a matter of doubt.

The labium is made up of a broad mentum (fig. 6, m.) which bears a pair of one-jointed labial palps (fig. 6, l.p.)—short, bluntly pointed, and covered with bristle-like hairs,—and two median, hair-

covered fleshy lobes which form the ligula (fig. 6, v.l.). The mentum is borne on a very short submentum (fig. 6, s.m.). So closely attached to the dorsal side of the labium as really to form a part of it, though designated by Burgess the tongue, is a thin plate (fig. 6, d.p.) which extends undivided as far forward as the tips of the lobes of the ligula, and in it and the labium itself the labial, or "lingual" glands (fig. 6, l.g.) are imbedded. The glandular nature of these structures has been doubted, but their appearance when examined in section is distinctly that of glandular cells. Each cell has a nucleus large in proportion to the size of the cell and containing a distinct nucleolus. It is difficult to explain the fact that the outer walls of these glands are of heavy chitin, but they are obviously neither reservoirs, nor merely chitinous supporting structures as has been supposed. Unlike the glands of *Psocus*, those of *Troctes* are not supported by any sort of cap or peduncle. They have no support except their position, imbedded in the labial tissue. From them chitinous ducts extend a short distance forward and then turn backward to unite with one-another between the two glands. The common duct so formed leads back between rows of gustatory cones (fig. 6, t.c.) or pegs, more rounded than hairs, into the oesophageal sclerite between its two anterior horns. This sclerite (figs. 4 and 6, o.s.) is a chitinous "bonnet-shaped" structure which extends two anterior arms, or horns, forward for support in the labium, and one backward onto a flat chitinous plate which is held on each side by two smaller rods extending out toward the sides of the head. The large masses of muscles of the clypeus, already mentioned, which are attached to the dorsal wall of the oesophageal sclerite, are said by Burgess (5) to function in closing the oesophagus, but it seems improbable that their contraction, situated as they are, could produce such an action.

#### THE DIGESTIVE SYSTEM

The mouth opens through the oesophageal sclerite into the long slender oesophagus, or fore-intestine. This extends through the thorax into the first or second abdominal segment where it joins the mid-intestine. The anterior portion of the oesophagus is narrow and has its origin at the oesophageal sclerite, turning in a slightly dorsal direction before passing posteriorly. In the thorax it enlarges into a crop-like structure (fig. 7, cr.) which has thin walls histologically the same as those of the oesophagus. At the

posterior end of the crop, lying close to this part of the digestive tract are four structures, presumably salivary glands, though it is impossible to find an outlet for them. The two of these lying in closest proximity to the crop are large and nearly oval in outline (fig. 7, l.g.); while the others are longer, more slender, and with rounded ends posteriorly. Their position is lateral and ventral to the larger ones. When studied in microscopic section, there appear to be six structures instead of four, for the anterior portion of the tubular pair is histologically distinct. The posterior part of each tubular organ (figs. 7 and 8, g.r.) has a broad lumen and the cells which make up its walls are probably syncytial, since no cell walls show, though nuclei are scattered throughout it at intervals. The structure of these leads to the conclusion that they are gland reservoirs rather than glands. The anterior part (fig. 8, s.g.) has no lumen, but is made up of cells which sometimes show droplets of secretion in their cytoplasm. The histological arrangement of these cells is similar to that of the large oval bodies mentioned above and the two pairs of structures are probably connected. The oval bodies have no lumen and are composed of large glandular cells, the nuclei of which are large and stain heavily, while the cytoplasm stains irregularly. These structures are glands and are connected with the reservoirs through their anterior ends, though this connection is not discernible. Their appearance suggests the three pairs of glands described by Uzel (22) in the thoracic region of the Thysanoptera. He does not show any ducts leading from them.

Fauré-Fremiet (13) describes in the *Hydrocorises* a pair of labial glands which lie in the thorax, even extending into the abdomen, and are composed of an anterior and posterior lobe uniting anteriorly, and, where they come together, joining the excretory duct of a gland reservoir. An arrangement similar to this is very possible in *Troctes*, because of the relation the various parts bear to each other.

The fore-intestine with its thin walls and wide channel, narrows abruptly at its posterior end to form the cardiac constriction, or valve (fig. 15, c.).

The mid-intestine (fig. 7, m.) beginning with this valve shows in section a sharp transition to thick glandular walls, markedly folded. The content of this part of the digestive tract reveals the food of the book louse, for it is often made up of the spores of molds and small particles of other organic matter. At times the contents of

the digestive tract is made up largely of brown crystals. The diet on the whole appears to be gained from the organic material in particles of dust, rather than from gnawing portions from dried grain or specimens. Frequently the mid-intestine is found to be two-thirds filled with large gregarines, the only parasites discovered in the digestive tract.

The hind-intestine is at its beginning much narrower than the mid-intestine. The anterior portion, or ileum, is the longest part, and is coiled once toward the dorsal wall of the abdomen. Immediately after coiling, the ileum enlarges into the short, broad rectum (fig. 7, rg.) which is fully as wide as the mid-intestine. Its walls contain four swellings which, in section, appear to be glandular. These rectal glands are composed of large cells with large nuclei, and both cells and nuclei stain heavily. The rectum narrows abruptly before it opens to the outside in the ninth segment of the abdomen.

At the beginning of the ileum four Malpighian tubules (fig. 7, m.t.) open. These extend anteriorly half or two-thirds of the length of the abdomen. Each tubule stretches anteriorly for about half of its length and then doubles back on itself, coiling about, with its blind end in the posterior part of the abdomen, near the rectum.

#### THE FEMALE REPRODUCTIVE SYSTEM

The two ovaries of the female reproductive system of *Troctes*, lying one on either side of the mid-intestine and between the intestine and the dorsal wall of the abdomen, are each made up of five ovarian tubules (fig. 9, o.). Each tubule is of the type in which nutritive cells alternate with egg cells. The young oöcyte (fig. 11, ov.) is found at the proximal end. Distal to it in the tubule are three or more large nutritive or nurse cells (fig. 11, n.c.) in a single chamber which supply nutriment to the oöcyte. The apex of the ovarian tubule forms a terminal chamber (fig. 11, t.c.) containing a mass of undifferentiated cells, and the tubule terminates distally in a long terminal filament which unites with those from the other ovarian tubules to form a single filament (figs. 9 and 11, f.) that serves to hold them in place in the abdomen. The proximal ends of the tubules are long and slender and unite to form the two short oviducts (fig. 9, od.) which join almost immediately in the broad vagina (fig. 9, v.) that opens to the outside at the posterior

ventral edge of the eighth segment. On the left side of the abdominal cavity lies the seminal receptacle (fig. 9, s.r.), a thin-walled sac, narrowed at each end and containing the spermatozoa. These can be readily seen through its walls in cleared whole mounts of the insect and in sections, and the thinness of its walls precludes the possibility of glandular structure. From the posterior end of the seminal receptacle a slender, delicate duct (fig. 9, d.) leads to the vagina, entering it midway between the point of union of the oviducts and its opening to the outside. No accessory glands are present in *Troctes*.

In older individuals than the one represented in the figure, the eggs are found in later stages of development. However no insect was found with more than one fully developed egg at a time. This egg is so large before laying that it occupies fully one-third of the abdominal cavity; in insects mounted in glycerine an outer chorion and yolk granules can be seen. In ovarian tubules on the other side of the abdomen from the well-developed egg, other eggs show considerable development, but none equal in size to the first. Though careful search was made during the breeding season, no eggs were ever found after they were laid.

#### THE MALE REPRODUCTIVE SYSTEM

The most conspicuous structures of the male reproductive system are not the testes, but the paired seminal vesicles (fig. 13, v.) which lie a little to the left of the median line of the abdomen. These are large, when fully matured extending nearly to the thorax, and they lie so close to each other as often to give the appearance of a single organ. An examination of transverse sections, however, proves it is a paired organ, its parts joining to form a single large duct at their proximal ends. This, the ejaculatory duct (fig. 13, e.d.), leads to the outside of the body through the copulatory apparatus (fig. 13, c.a.). The testes (fig. 13, t.) are round or oval bodies lying near the lateral abdominal walls. From a surface view they give the impression of being a mass of coiled tubes, and when sectioned, they appear to be separated into areas, representing coils, which contain the spermatozoa at different stages of development (fig. 12, s.). The central portion of each testis is formed of spermatogonia, and the posterior portion, from which the vas deferens (fig. 13, v.d.) arises, is filled with spermatozoa. At each end of the testis is a darkly staining mass (fig. 12,



d.b.) whose function was not determined. The vasa deferentia, which are long, slender, transparent tubes, lead by a somewhat winding course to the seminal vesicles, entering them laterally just anterior to their union in the ejaculatory duct.

The copulatory apparatus through which the ejaculatory duct passes is a complicated chitinous structure, the anterior end of which makes an acute angle; while the posterior part terminates in a pair of hooks which curve in toward each other and close about the end of the ejaculatory duct. When drawn well into the body, as figured, the anterior tip of the structure reaches as far anteriorly as the posterior ends of the seminal vesicles, but the apparatus can be thrust out of the abdomen to nearly one-half of its total length. This copulatory apparatus consists of three pairs of chitinous plates (fig. 13, prs. 1, 2, 3). The inner pair (fig. 13, pr. 1), broad and flat and slightly curved at the posterior ends, is in contact with the ejaculatory duct and forms the foundation to which the other two pairs are attached. The acute angle of the apparatus is formed by the second pair (fig. 13, pr. 2) which is more heavily chitinized and slender than the others and comes in contact with pair one at the anterior ends of the latter, ending there. The third pair (fig. 13, pr. 3) is heavy, like the first, and is attached to both of the other pairs, uniting with the first pair at its posterior end and forming there the outer portions of the terminal hooks (fig. 13, t.h.). The anterior parts of the third or outer pair unite with the second pair at about their middle. Thus the third pair virtually forms both a sheath for the posterior parts of the other two, and the posterior hooks or "forceps", themselves.

#### THE NERVOUS SYSTEM

The central nervous system of *Troctes* is of a simple type, composed of the supraoesophageal ganglion or brain (fig. 15, s.g.), the suboesophageal ganglion (fig. 15, sb.g.), and three thoracic ganglia (fig. 15, g.1, 2, 3). The last two thoracic ganglia are fused into a large mass which appears externally to be but one, though in section its compound nature is revealed. The length of this last ganglion and a slight constriction at its posterior end makes it appear as if a third ganglion, originally abdominal, may have taken part in its formation. This ganglion sends out a nerve, or group of nerves (fig. 15, n.) as a prolongation from its posterior

end which soon disappears in the abdomen and represents the total nerve supply of that part of the insect's body.

The supraoesophageal ganglion is broad, its central portion extending anteriorly in a projection which may be an ocellar lobe (fig. 14, o.1), though no ocelli are visible on the exterior of the head. Two lobes on the right and left of the median one send nerves to the mouthparts, and just lateral to these are the antennary lobes (fig. 14, a.n.). The largest lobes are the optic, (fig. 14, op.1.) reaching laterally almost to the eyes. The supraoesophageal ganglion ends posteriorly in two prominent projections which in sections seem largely cellular with little "punksubstanz", or medullary material, extending into them (fig. 14, p.1.). The function of these is not clear.

The supraoesophageal ganglion connects with the suboesophageal ganglion by the circumoesophageal commissures (fig. 15, c.o.c.) which pass from its anterior ventral surface around the oesophagus.

#### THE RESPIRATORY SYSTEM

The tracheal system can be distinguished only in specimens which have been a short time in glycerine. So treated the air is retained in the tracheal tubes and they appear black against a transparent background. Even when thus prepared only parts of the system are evident; so that any reconstruction of the tracheae must be a composite from many specimens.

The respiratory system of *Troctes* is of a simple type. In the abdomen are six pairs of stigmata or spiracles, one pair in each of the first six segments. From each a short trunk leads to a main lateral longitudinal one (fig. 16, l.t.) which extends the length of the abdomen and is continuous with one of the main trunks of the thorax and head. Each of the stigmatal trunks in the abdomen gives off typically a visceral branch (fig. 16, vs.b.) to the digestive and reproductive organs, a ventral branch (fig. 16, v.b.) to the ventral body wall, and a dorsal branch (fig. 16, d.b.) which supplies the dorsal region of the body with oxygen. In the posterior region of the abdomen the longitudinal trunks break up into numerous smaller branches which supply the last three segments. In the prothorax and in the head, the longitudinal trunks are connected to each other by transverse trunks (fig. 16, t.t. and h.t.), and in the head the tracheae are numerous and small, a large number of branches reaching into the mouthparts, antennae, and eyes.

## PARASITES OF TROCTES

In so small an insect, it was rather surprising to find parasites so common. As has already been mentioned, gregarines not infrequently are found in the mid-intestine. Once a parasitic protozoan was recognized in a longitudinal section of the testes.

The parasite most commonly found is a large nematode worm located in the body cavity. The small males and long, coiled females were found twisted about in the abdomen, even extending into the thorax. Sometimes one female nematode and as many as a half dozen of the small males were dissected out of a single *Troctes*. The males are short, less than one twenty-fifth the length of the females, whose long bodies are filled with eggs. All the specimens of the insect which contained this parasite were gathered from one place—a box which had for several years been kept filled with stalks of dried grain to make a breeding place. The hosts of the worms were as active as any of the non-parasitized individuals, but could usually be detected by their greater size.

## BIBLIOGRAPHY

1. **Banks, Nathan.** Catalogue of the Neuropteroid Insects (except Odonata) of the United States. Am. Ent. Soc., Philadelphia, 1907 (Separate publication).
2. **Banks, Nathan.** Two new species of *Troctes*. Entom. News, 11: 559. 1900.
3. **Berlese, A.** Gli Insetti, 1: Pt. 1.
4. **Bertkau, P.** Über die Speicheldrüsen der Psociden, Verh. Nat. Ver. Bonn, 39: 130. 1882.
5. **Burgess, Edward.** The anatomy of the head and the structure of the maxilla in the Psocidae. Pros. Bost. Ent. Soc. Nat. Hist. 19: 291. 1878.
6. ———— On the structure of the head of *Atropos*. Psyche, 2: 87. 1877-78.
7. **Butler, E. A.** Our household insects. London, 1893.
8. **Cummings, Bruce F.** On some points in the anatomy of the mouth-parts of the Mallophaga. Proc. Zool. Soc. London, Part 1: 128. 1913.
9. **Derham, W.** A letter concerning an insect that is commonly called the Death-watch. Phil. Trans. Roy. Soc. London, 22: 832. 1701.  
——— A supplement to the account of the *Pediculus Pulsatorius*, or Death-watch. Phil. Trans. Roy. Soc. London, 24: 1586. 1704.
10. **Enderlein, G.** Über die Morphologie, Gruppierung, und Systematische Stellung der Corrodentien. Zool. Anz. 26: 423. 1903.
11. ———— Morphologie, Systematik und Biologie der Atropiden und Troctiden. Results of Swedish Zool. Exped. to Egypt and the White Nile, 1901. Uppsala, Part I. 1904.

12. **Evans, A. M.** On the structures of maxillulae in insects. *Journ. Linn. Soc. London*, 34: 429. 1921.
13. **Fauré-Fremiet, E.** Contribution à l' étude des glandes labiales des Hydrocoris. *Ann. Se. Nat.*, 9 ser. 12: 217. 1910.
14. **Hagen, H. A.** Psocinorum et Embidinorum Synopsis Synonymica. *Verhandl. Zool.-Bot. Gesell. Wien.* 16: 201. 1866.
15. —————Some Psocina of the United States. *Psyche*, 3: 196, 206, 219. 1881.
16. —————Synopsis of Neuroptera of N. America. *Smithsonian Misc. Coll. Washington.* 1861.
17. **Jordan, Karl.** Anatomie und Biologie der Physapoda. *Hann. Münden.* 1888.
18. **Nitzsch, C. L.** Ueber die Eingeweide der Bücherlaus (*Psocus psicatorius*) und über das Verfahren bei der Zergliederung sehr kleiner Insekten. *Germa's Mag. Entom.* 4; 276. 1821.
19. **Rambur, M. P.** Histoire naturelle des insectes neuropteres. *Suites à Buffon. Paris.* 1842.
20. **Scudder, Samuel H.** On the structure of the head of *Atropos*. *Psyche*, 2: 49. 1877.
21. **Snodgrass, R. E.** A Revision of the mouth-parts of the Corrodentia and the Mallophaga. *Trans. Am. Ent. Soc.* 31: 297. 1905.
22. **Uzel, Jindrich.** Monographie Radu "Thysanoptera." *Königgratz.* 1895.
23. **Viallanes, H.** Centres nerveux et les organes des sens des animaux articulés. *Bib. de l'Ecole des Hautes Études*, 33: 1887.
24. **Westwood, J. B.** Introduction to the modern classification of insects. 2: 17.

EXPLANATION OF FIGURES

PLATE IV

All figures drawn with camera lucida.

FIG. 1. Outline of head and tentorium from the ventral side. X 160.

a.s. The first segment of the antenna. a.t. The anterior arm of the tentorium. c.m. The chitinous supports of the mandibles. e. The eye. l. The labrum. m. The mandibles. m.f. The maxillary fork. m.m. Mandibular adductor muscle. o.s. The oesophageal sclerite. p.t. The posterior arm of the tentorium.

FIG. 2. The Mandibles. X 250.

a. The right mandible. b. The left mandible. a.ab. The point of attachment of the abductor muscle. a.ad. The point of attachment of the adductor muscle. m.p. The pivotal knob which fits into the head capsule. m.s. The molar surface of the mandible. v.p. The ventral points of the mandible.

FIG. 3. Enlarged view of the cells of the right labial gland. X 930.

n. The nucleus. nu. The nucleolus.

FIG. 4. Lateral view of the oesophageal sclerite. X 250.

a.h. The anterior horn of the sclerite. c.d. The common duct of the labial glands. o. Oesophagus. o.s. The oesophageal sclerite. p.h. The posterior horn of the sclerite. t.c. The taste cones.

FIG. 5. Dorsal view of the maxilla and maxillary fork. X 250.

e.p. The extensor muscle of the maxillary palp. f.m. The muscles of the maxillary fork. f.p. The flexor muscle of the maxillary palp. f.s. The groove of the maxillary fork. g. The galea. g.m.e. The extensor muscles of the galea. g.m.f. The flexor muscle of the galea. h.w. The posterior wall of the head. m.f. The maxillary fork. m.p. The maxillary palp. p.m. The muscles of the second segment of the maxillary palp. r.f. The retractor muscle of the maxillary fork. s. The stipes.

FIG. 6. The labium and oesophageal sclerite from a dorsal view. X 250.

a.h. The anterior horn of the oesophageal sclerite. d.g. The duct of the gland. d.p. The dorsal plate of the labium which contains the glands. l.g. The labial gland. l.m. The labial muscles. l.p. The labial palp. m. The mentum. o.s. The oesophageal sclerite. p.h. The posterior horn of the oesophageal sclerite. s.a. The supports which help to attach the sclerite in the mouth. s.m. The submentum. t.c. The taste cones on either side of the common duct. v.l. The ventral lobe or ligula of labium as seen through the transparent dorsal plate.

PLATE V

FIG. 7. The dorsal view of the digestive system. X 160.

cr. The crop. i. The ileum. g.r. The reservoir of the salivary gland. l.g. The salivary gland. m. The mid-intestine. m.t. One of the Malpighian tubules. o. The oesophagus. o.s. The oesophageal sclerite. r.g. The rectal gland.

FIG. 8. Longitudinal section of one of the salivary glands and its reservoir.

X 160.

g. The salivary gland. g.r. The gland reservoir. s.g. The anterior end of gland reservoir.

FIG. 9. A dorsal view of the female reproductive system of a young specimen.

X 160

d. The duct of the seminal receptacle. f. The terminal filament. o. An ovarian tubule. od. An oviduct. s.r. The seminal receptacle. v. The vagina.

FIG. 10. A cross section of the salivary glands and reservoirs. X 250.

cr. The crop. g. The salivary gland. g.r. The gland reservoir.

FIG. 11. A single ovarian tubule. X 465.

f. The terminal filament. g. The nucleus. n. The nucleus of a nurse or nutritive cell. n.c. Nutritive cell. o.d. The duct of the tubule. ov. The oöcyte. t.c. The terminal chamber.

PLATE VI

FIG. 12. Longitudinal section of testis. X 465.

d.b. The dark body. s. Spermatozoa. sg. Spermatogonia. sp. Spermatids.

FIG. 13. The male reproductive system from a ventral view. X 160.

c.a. The copulatory apparatus. e.d. The ejaculatory duct. Pr.1, Pr.2, Pr.3. The first, second, and third pairs of chitinous structures of the copulatory apparatus. t. The testes. t.h. The terminal hooks of the copulatory apparatus. vd. The vas deferens. v. The seminal vesicle.

FIG. 14. Composite drawing of the brain. Outline of head. X 250.

a.l. The antennal lobe. a.n. The antennal nerve. e. The eye. lb. The labrum. o.l. An ocellar lobe. op.l. The optic lobe. p.l. The posterior lobe.

FIG. 15. Longitudinal section of the central nervous system. X 135.

c.h. Hairs on the clypeus. c.o.c. The circum-oesophageal commissure. c. The cardiac valve. g.1., g.2., and g.3. The first, second and third thoracic ganglia. n. The abdominal nerve. o.s. The oesophageal sclerite. sb.g. The suboesophageal ganglion. s.g. The supra-oesophageal ganglion or brain. t. A portion of the tentorium.

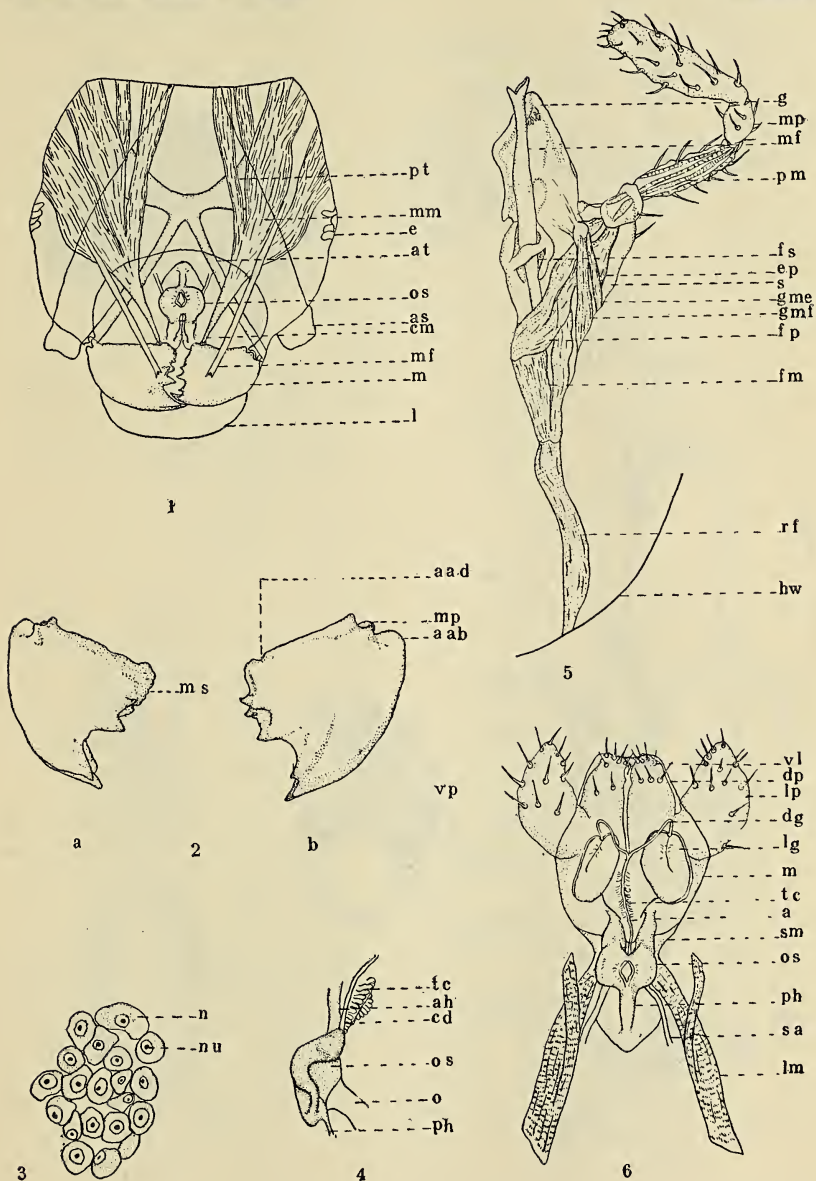
FIG. 16. A composite diagram of the tracheal system from a ventral view.

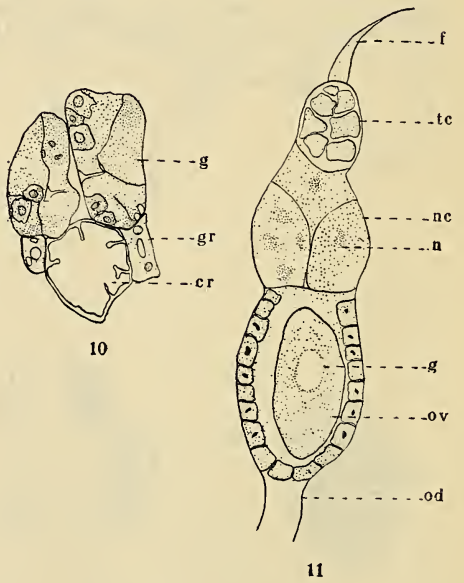
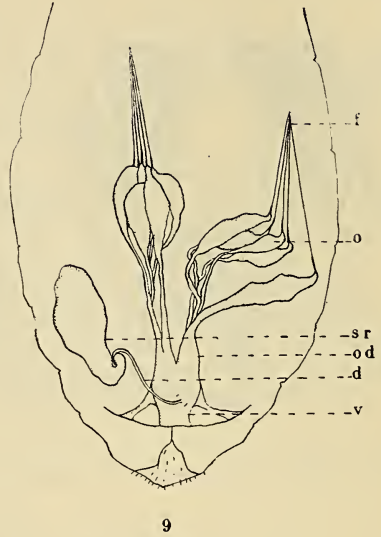
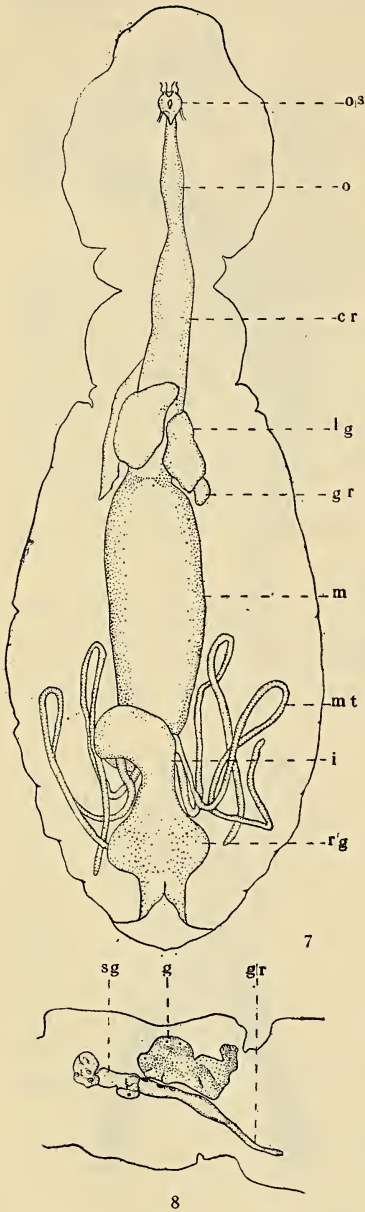
X 160.

a.b. The antennal branch. d.b. A dorsal abdominal branch. e.b. The branch to eye. h.t. The transverse connecting trunk of the head. lt. The main longitudinal trunk of the abdomen. t.s.t. A thoracic stigmal trunk. t.t. The transverse trunk of the thorax. v.b. A ventral branch. vs.b. A visceral branch.

TRANS. WIS. ACAD., VOL XXI

PLATE IV

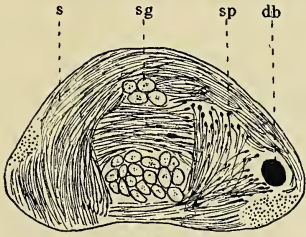




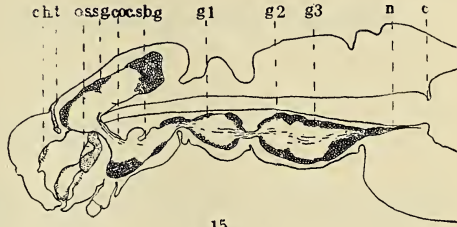


TRANS. WIS. ACAD., VOL. XXI

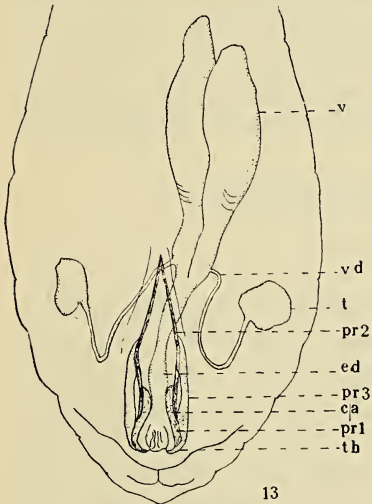
PLATE VI



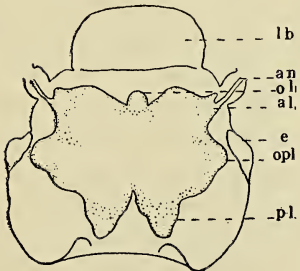
12



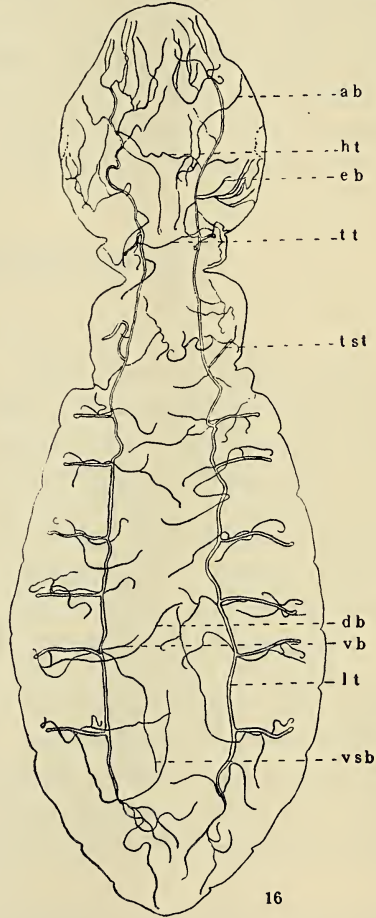
15



13



14



16



## ARRHENURI FROM WASHINGTON AND ALASKA

---

RUTH MARSHALL

In the summer of 1922 the author made an extended trip to Alaska, from Seattle to Kodiak Island. A number of localities in Alaska and the Canadian Northwest were visited and water mites were collected in many small bodies of water. The preliminary work on the study of this material has been done; it is proposed to publish in the near future a complete account of the species found and their distribution. The present paper is an account of the Arrhenuri of the collections.

### **Arrhenurus tacomaensis** nov. spec.

Pl. VII, fig. 1-5

While en route to Alaska, the author had an opportunity to make small collections of water mites in two localities in the state of Washington. The first place visited, July 7, 1922, was the inlet of Union Bay, at Seattle, near the University of Washington. In the shallow water, bordered by tall grasses and other plants, sixteen individuals were found, representing four different genera (*Limnesia*, *Neumania*, *Piona* and *Arrhenurus*). There was but one *Arrhenurus*, a male; this proved to be *A. krameri* Koenike, which has already been reported by the author from Oregon.

The second collecting ground was at Tacoma, September 4. Near the car-line at 52nd Street is a small shallow pond filled with yellow pond lilies in which seven individuals were found. Five of these are undetermined species of *Piona* and *Unionicola*. The remaining two specimens are *Arrhenurus* males of a new species which has been given a specific name indicative of the locality from which it was first reported.

*A. tacomaensis* belongs to the subgenus *Arrhenurus* and somewhat resembles *A. lautus* described by Dr. Koenike from Alberta. The body is stout; two sickle-shaped projections arise dorsally at the place where the body passes abruptly into the appendix. This

caudal appendix has pronounced lateral projections and a clearly defined hyaline appendage. The petiole is conspicuous; the sides roll over dorsally to enclose a central oblong structure arising out of it.

The palpi are stout, with a few large bristles. The fourth joint of the fourth leg has a well defined thumb-like projection. The color of the new species is dull red with indistinct brown areas where the internal organs show through the body wall. The legs have a greenish tinge. The total length is 1.15 mm., the greatest width, 0.9 mm.

***Arrhenurus elongatus* nov. spec.**

Pl. VII, fig. 6, 7; Pl. VIII, fig. 14, 15

It is a pleasure to be able to record the finding of a new species of *Arrhenurus* from Alaska, the first account of any work on the water mites from this territory that the author is aware of. Quite appropriately this species comes from the old Russian town and former capitol, Sitka. It was found in the border of a small shallow pond choked with yellow pond lilies and like plants, in a boggy meadow near the town. With it were a few individuals of other genera, the species not yet determined.

*A. elongatus* is a large mite belonging to the subgenus *Megaluracarus*. It is 1.5 mm. long, with a width of 0.73 mm. It resembles *A. solifer* Marshall and *A. pseudoconicus* Piersig, both American forms, and *A. conicus* Piersig, a European species. In this group of related species the appendix narrows conspicuously at the end. The new species, however, is more slender and has a more elongated appendix than in any of the nearly related species, a feature so characteristic that it has suggested the specific name.

Only one individual, a male, was found. The body is widest and most elevated in the anterior half; likewise, the appendix is largest in the proximal half, though constricted where it joins the body. The end of the appendix is bowed out and has several small humps and hairs, as shown in the figures. The three groups of the epimera are close together; the first and second pairs of plates have sharp projecting anterior corners, and the fourth epimera are very wide. The genital area is small and does not project beyond the body wall. The color of the animal is dull red.

***Arrhenurus acerformis* nov. spec.**

Pl. VIII, fig. 8, 9, 13

At Chitna, Alaska, about one hundred and thirty-five miles inland on the Copper River & Northwestern Railway from the seaport town of Cordova, a number of small ponds were examined. Only one of these yielded any *Arrhenuri*; this was a pond in the mountains, surrounded by the forest, and called Lost Lake. It is a circular body of water, perhaps a half mile in circumference, apparently shallow, with a border of yellow water lilies among sunken logs at one place. This pond is said to be seven hundred and fifty feet above the town, some two miles away. Only two *Arrhenuri* were found, both females, but representing two species. As this genus is usually very common in the quiet waters of lowlands and plains, much interest attaches to the finding of these specimens at this elevation. It is hoped that the males may be discovered in future collections by the aid of the accompanying figures, since the palpi are alike in the two sexes.

*A. acerformis*, female, is oval in form, 1.45 mm. long and 1.1 mm. across at the widest part. The color is dull olive green. The epimera of the first pair end in rather sharp points. The genital area is some distance from the fourth pair of epimera; in form, the wing-like areas bear a fanciful resemblance to the twin seeds of certain maples, and this has suggested the specific name.

***Arrhenurus hirsutus* nov. spec.**

Pl. VIII, fig. 10-12

This is a smaller species, found with the preceding species, and represented also by but one individual, a female. It is pyriform in shape, 1.2 mm. long and 0.96 mm. in the widest part. The genital area is close to the last epimera, and the wing-like expansions are short and inclined from the plates guarding the opening. The palpi have several long stout hairs or bristles on the second joint, a character which has suggested the name of the species. The color is the usual dull olive green.

## EXPLANATION OF THE PLATES

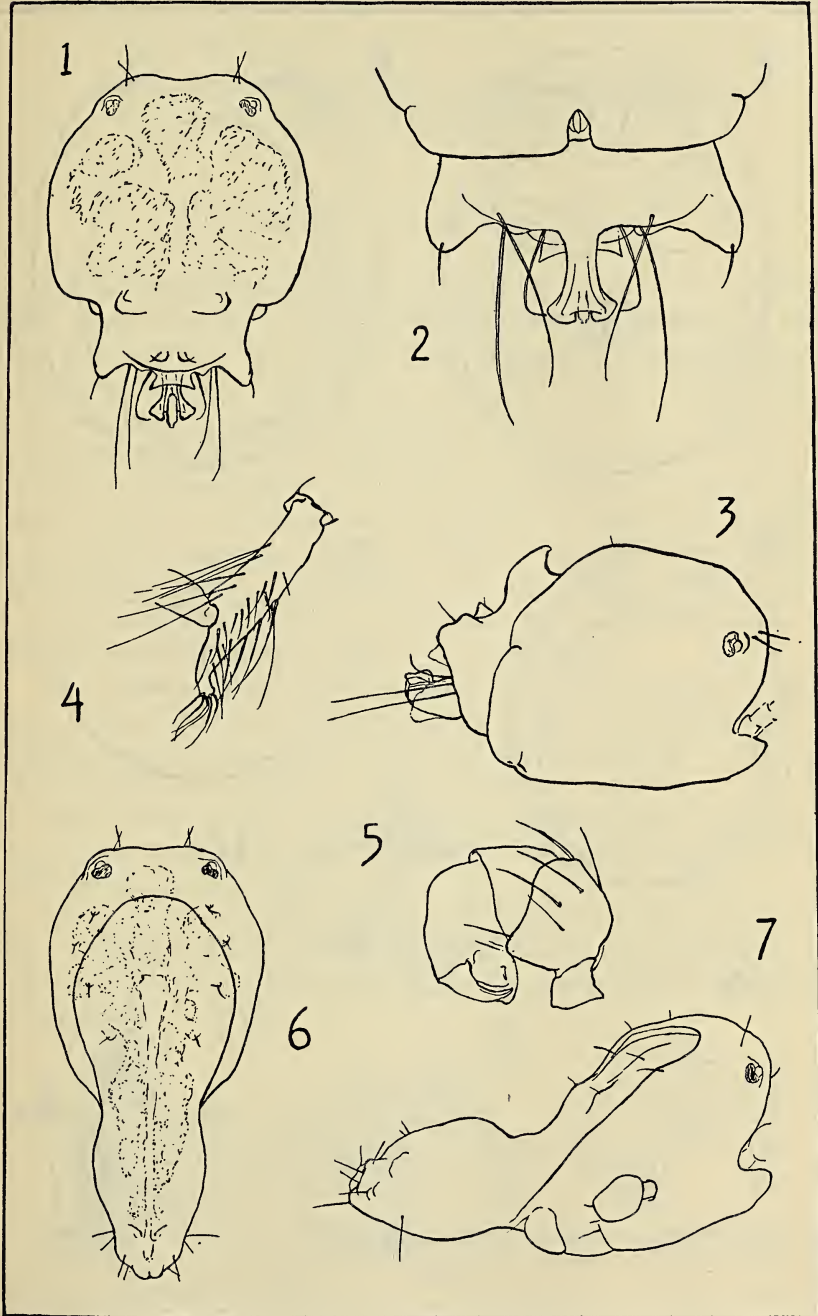
## PLATE VII

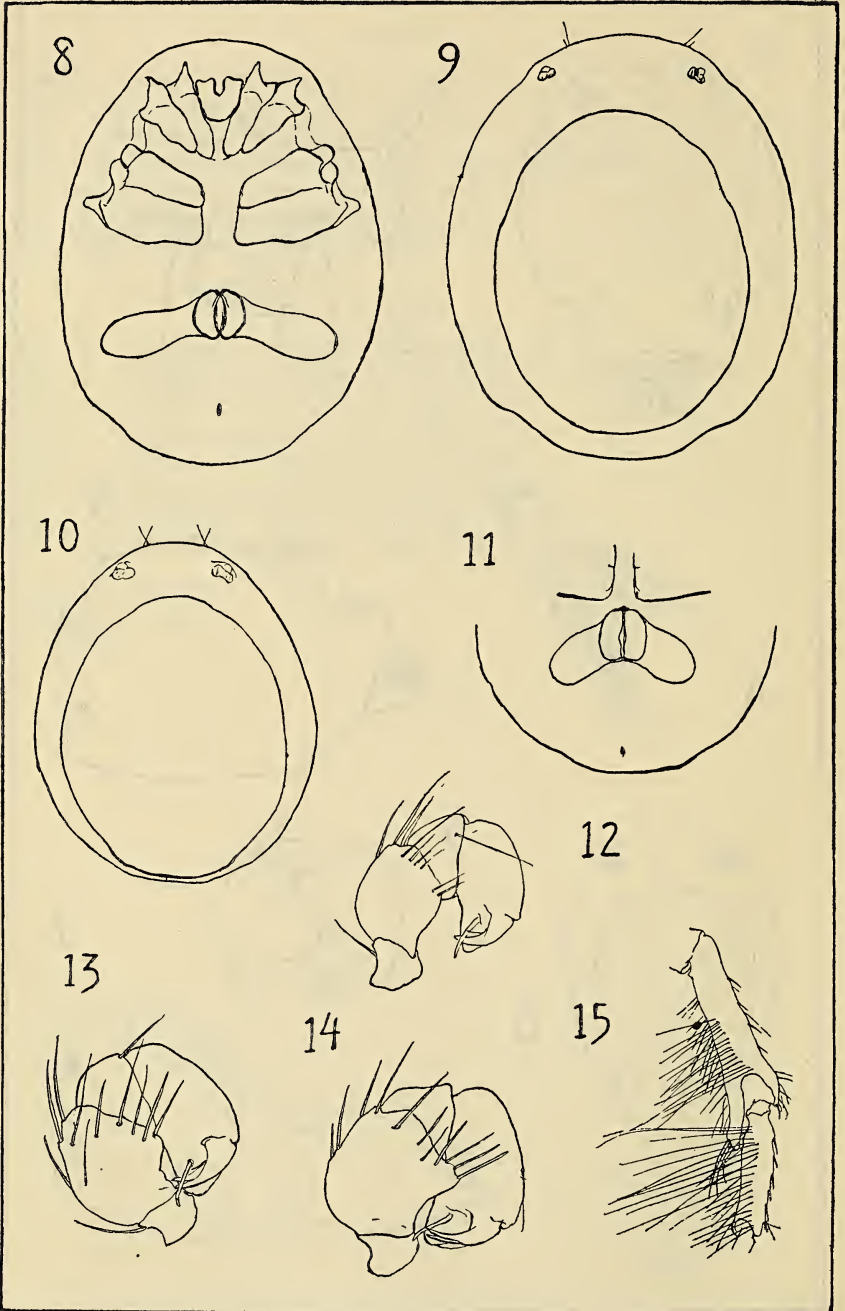
- FIG. 1. *Arrhenurus tacomaensis*, dorsal view.  
FIG. 2. *Arrhenurus tacomaensis*, appendix, ventral view.  
FIG. 3. *Arrhenurus tacomaensis*, lateral view.  
FIG. 4. *Arrhenurus tacomaensis*, fourth joint of fourth leg.  
FIG. 5. *Arrhenurus tacomaensis*, right palpus.  
FIG. 6. *Arrhenurus elongatus*, dorsal view.  
FIG. 7. *Arrhenurus elongatus*, lateral view.

## PLATE VIII

- FIG. 8. *Arrhenurus acerformis* fem., ventral view.  
FIG. 9. *Arrhenurus acerformis* fem., dorsal view.  
FIG. 10. *Arrhenurus hirsutus* fem., dorsal view.  
FIG. 11. *Arrhenurus hirsutus* fem., genital area.  
FIG. 12. *Arrhenurus hirsutus* fem., left palpus.  
FIG. 13. *Arrhenurus acerformis* fem., left palpus.  
FIG. 14. *Arrhenurus elongatus*, left palpus.  
FIG. 15. *Arrhenurus elongatus*, fourth joint of fourth leg.

ROCKFORD COLLEGE,  
ROCKFORD, ILLINOIS.







## NEW AND CORRECTED NAMES OF CERTAIN MILK BACTERIA\*

W. D. FROST AND RUTH CHASE NOLAND

We are not aware that there is anywhere a list of the bacteria that have been found in milk later than that of Conn, Esten and Stocking (1906). Since then, many species have been recognized and some new ones described as occurring in milk. Furthermore, the Society of American Bacteriologists, through their Committee on Characterization and Classification (1920), have so modified the genera that many species will have to be renamed. Few bacteriologists have ever bothered with synonyms so that there is really very great confusion in names. This is perhaps especially true with dairy bacteria because of the wide use of Conn's list in which he has paid little attention to synonymy and made general use of the unscientific trinomial system of nomenclature.

The adoption by the Society of American Bacteriologists of rules and a definite system of classification makes for progress and it would seem that the time is now ripe for an attempt to list the milk bacteria and assign to them the correct names.

Such a task is a long and difficult one and perhaps is only likely to be done piece-meal, yet if the work is carefully done, it should be welcomed and valuable.

We list below a number of species in which the usual names have been changed or new ones supplied because of the application of the priority rule and those that have been changed from one genus to another:

### NEW NAMES

#### **Bacillus involutus** (ADAMETZ)

*B. No. 15*, ADAMETZ, 1889, Landw. Jahrb. **18**: 247.

*Bact. turgidum* CHESTER, 1901, p. 195.

NOTE: This is now a bacillus but the name *turgidus* used by Chester is invalid because Duclaux has previously used the name. See Macé, 1897, p. 900, also Migula, 1900, p. 586.

\*Published by permission of the Director of the Wisconsin Agricultural Experiment Station.

**Bacillus septimus** (FLÜGGE)

No. VII. FLÜGGE, Zeitsch. f. Hygiene 17: 294. 1894.

*B. plicatus* CHESTER, 1901, p. 275.

*B. lactis* No. 7 (FLÜGGE), Swithinbank & Newman, 1903, p. 423.

NOTE: *Plicatus* is not tenable because this name was given to a bacillus by Deetjen in 1890.

**Bacillus sextus** (FLÜGGE)

No. VI. FLÜGGE, Zeitsch. f. Hygiene 17: 294. 1894.

*B. lactis* No. 6 (FLÜGGE), Swithinbank & Newman, 1903, p. 423.

**Bacillus tertius** (FLÜGGE)

No. III. FLÜGGE, Zeitsch. f. Hygiene 17: 272. 1894.

*B. lactis* No. 3 (FLÜGGE), Swithinbank & Newman, 1903, p. 422.

**Bacterium quintus** (FLÜGGE)

No. V. FLÜGGE, Zeitsch. f. Hygiene 17: 272. 1894.

*B. lactis* No. 5 (FLÜGGE), Swithinbank & Newman, 1903, p. 423.

NEW COMBINATIONS

**Bacterium circulans** (JORDAN)

*B. circulans* JORDAN, Report Mass. S. Board of Health, 1890, p. 831.

*B. circulans* II. CONN, 1899, p. 58.

*B. lactis circulans* I. & II. CONN, ESTEN & STOCKING, 1906, p. 174.

NOTE: Franklands' description of spores is probably an error.

**Bacterium cochleatus** (CONN, ESTEN & STOCKING)

*B. lactis cochleatus* CONN, ESTEN & STOCKING, 1906, p. 181.

**Bacterium liodermos** (FLÜGGE)

*B. liodermos* FLÜGGE, Die Mikroorganismen, 1886, (II. Aufl.), p. 323.

No. X. FLÜGGE, Zeitsch. f. Hygiene 17: 293. 1894.

*Gummibacillus* LOEFFLER, Migula, 1900, p. 577.

*B. cremoris* CHESTER, 1901, p. 274.

*B. lactis* No. 10 (FLÜGGE), Swithinbank & Newman, 1903, p. 423.

**Bacterium robertii** (CONN, ESTEN & STOCKING)

*B. lactis Robertii* CONN, ESTEN & STOCKING, 1906, p. 182.

NOTE: Description suggests *Bact. vermiculosum* (Zimmerman) Chester, 1901, p. 157, or *B. virmiculosus* Zimmerman, Die Bak. Nutz. u. Trinkwasser, 1890, p. 40.

**Bacterium tenuis** (DUCLAUX)

*Ty. tenuis* DUCLAUX, Le Lait, Paris, 1887.

*Ty. scaber* DUCLAUX, Le Lait, Paris, 1887.

*B. tenuis* TREVISAN, 1889.

*B. scaber* (DUCLAUX) MIGULA, 1900, p. 586.

*B. lactis tenuis* CONN, ESTEN & STOCKING, 1906, p. 176.

NOTE: We follow Conn who seems to regard *Ty. scaber* and *tenuis* as identical.

**Bacterium visco-symbioticum** (BUCHANAN & HAMMER)

*B. visco-symbioticum* BUCHANAN & HAMMER, 1915, p. 261.

**Chromobacterium ianthinum** (ZOPF)

*Bacterium ianthinum* ZOPF, 1885, Spaltzpilze, p. 68.

*Bact. ianthinum* (ZOPF), Com. S. A. B. 1920, p. 222.

*B. violaceus* MACÉ, 1887, Ann. d'Hyg. publ. et de Med. leg. XVII.

*B. violaceus* FRANKLAND, 1889, Zeitsch. f. Hygiene, p. 394.

*B. violaceus-laurentius* JORDAN, 1890, State Bd. of Health, Mass., p. 838.

*B. janthinus* ZIMMERMAN, 1890, Die Bakt. unser Trink. und Nutzwasser, I. Ruhe, p. 36.

*Ps. ianthina* (ZOPF) MIG., 1900, Migula, p. 94.

*Ps. ianthina* (ZOPF) CHESTER, 1901, Chester, p. 317.

*Bact. violaceum* (J. SCHROTER), 1901, Lehmann and Neumann, p. 277.

*B. lividus* (FLÜGGE and PROSKAUER), 1887, Zeitsch. f. Hygiene 2: 463.

*B. membranaceus amethystinus* EISENBERG, 1891, p. 421.

*B. membranaceus amethystinus mobilis* GERMANO, 1892, Centralb. f. Bakt. 12:516.

**Erythrobacillus aurantiacus** (FRANKLAND)

*B. aurantiacus* FRANKLAND, 1894, p. 449.

NOTE: Gr. and P. Frankland described but did not name it in an earlier communication, Über einige typische Organism im Wasser und im Boden, Zeitschr. f. Hygiene, Bd. VI., 1889, p. 390, also Frankland, 1894, p. 449.

**Erythrobacillus diffusus** (CONN, ESTEN & STOCKING)

*B. lactis diffusus* CONN, ESTEN & STOCKING, 1906, p. 181.

**Erythrobacillus aureus** (FRANKLAND)

*B. aureus* FRANKLAND, 1894, p. 448 (See Note below).

*B. aureus lactis II.* CONN, 1899, (No. 100), p. 39.

*Bact. aureum* (FRANKLAND) MIG., 1900, p. 480.

*Bact. lactis aureum II.* CONN, ESTEN & STOCKING, 1906, p. 130.

NOTE: The morphology of the form described by Frankland does not fully agree with that described by Conn, Esten & Stocking.

**Lactobacillus flocculus** (CONN, ESTEN & STOCKING)

*Bact. Lactis flocculus* CONN, ESTEN & STOCKING, 1906, p. 149.

**Lactobacillus gorinii** (CONN, ESTEN & STOCKING)

*Bact. C.* MULLER, Arch. Hyg. 67:127.

*Bact. lactis Gorinii* CONN, ESTEN & STOCKING, 1906, p. 148.

**Lactobacillus healii** (BUCHANAN & HAMMER)

*Bact. Healii* BUCHANAN & HAMMER, 1915, p. 249.

**Lactobacillus magnus** (CONN, ESTEN & STOCKING)

*Bact. lactis magnum* CONN, ESTEN & STOCKING, 1906, p. 149.

**Lactobacillus surgeri** (DORNIC & DAIRE)

*Bacillus surgeri* DORNIC & DAIRE, 1907, Bull. mens. de l'office de renseignements agricoles, 6:146.

*Bact. surgeri* (DORNIC & DAIRE) BUCHANAN and HAMMER, 1915, p. 254.

REFERENCES

- Buchanan and Hammer. 1915. Slimy and ropy milk. Research Bull. Iowa State Agr. Exp. Sta.
- Chester. 1901. Manual of determinative bacteriology. MacMillan Co., N. Y.
- Committee. 1920. Families and genera of the bacteria. Winslow, Broadhurst, Buchanan, Krumwiede, Rogers, and Smith. Jour. Bact. 5:191.
- Conn. 1899. 12th Annual Report Storrs Agric. Exp. Station, Storrs, Conn.
- Conn, Esten and Stocking. 1906. 18th Annual Report Storrs Agr. Exp. Sta.
- Frankland. 1894. Micro-organisms in water. Longmans, Green & Co., N. Y.
- Migula. 1900. System der Bakterien. Gustav Fischer, Jena.
- Swthinbank and Newman. 1903. Bacteriology of milk. John Murray, London.
- Trevisan. 1889. Schizomycetaceae in Sylloge Fungorum by A. P. Saccardo. Vol. III.

## THE CHARACTERISTICS OF CERTAIN FECAL BACTERIA AS SHOWN BY THE LITTLE PLATE METHOD.

OLA E. JOHNSTON AND WILLIAM D. FROST

(From the Department of Agricultural Bacteriology, University of Wisconsin, Madison, Wisconsin.)

In another paper we propose to discuss the "Use of the Little Plate Method for the Bacteriological Analysis of Feces." Here we describe and illustrate by means of photomicrographs the most commonly occurring colonies in the feces of infants, guinea pigs, puppies and rats.

**Infants.** The ages of the infants studied ranged from three days to eleven months. They were all breast fed except one.

Little plates made from the feces of these infants always showed the presence of many diplococci. These organisms varied in diameter from 0.6–0.8 microns, although occasionally smaller ones were found even down to 0.3 microns. Frequently these units grouped themselves in short chains. Some plates contained almost pure cultures of diplococci.

Usually colonies of staphylococci occurred in about the same numbers as the diplococci. Besides the irregular grouping, a few in tetrads and chains were found. The individual cells were about the same size as the streptococci or perhaps more frequently a little smaller.

With one exception all of the infant feces showed the presence of as many rods as diplococci or staphylococci. These bacilli were either Gram positive spore-bearers or Gram negative non-spore bearing rods. They were from 0.5 to 0.8 microns wide and from 1.0 to 3.5 microns long but most frequently about 1.5 microns.

Comparing these colonies with the colonies obtained by making little plates of pure cultures we have identified the following: *B.acidophilus*, *B.albolactis*, *B.bifidus*, *B.cereus*, *Staph.albus*(?), and *Strep.lacticus*. See figs. 1, 2, 3, 6, 11, 12, 13, 15, 16 and 19.

**Guinea pigs.** The fecal flora of fourteen guinea pigs was studied by this method.

A moderate number of colonies of diplococci was always found. The individual cells varied in diameter from 0.5 to 0.8 microns but were usually about 0.6 microns.

A few streptococci and a few staphylococci were found also.

Nearly as many colonies of small rods was found as diplococci. These colonies had dense centers and open edges where the individuals were grouped in pairs with a slight tendency to form short chains. The cells varied in width from 0.5 to 0.7 microns with a few as wide as 1.0 micron. In length they ranged from 1.0 to 3.5 microns, averaging about 2.0.

Several of the guinea pigs showed large rods which were arranged in extremely long chains. These lay parallel or interlacing and most generally radiating from the dense center of the colony.

About one-third of these animals showed the presence of smaller rods which grew into shorter chains than the foregoing.

Spores were quite abundant.

The dejecta of several scurvy guinea pigs was examined. The bacteria varied little here from those found in the normal animals. Except that the types were fewer and the colonies larger and more compact than usual.

By comparison with little plates of pure cultures the following species were recognized: *Staph.albus*(?), *Strep.lacticus*, *B.coli*, and *B.subtilis*. See figs. 9, 10, and 17.

**Puppies.** The fecal bacteria of the three puppies studied consisted of many diplococcus colonies, a moderate number of streptococcus colonies and a few staphylococcus colonies. Many large bacillus colonies and a few colonies of very short bacilli.

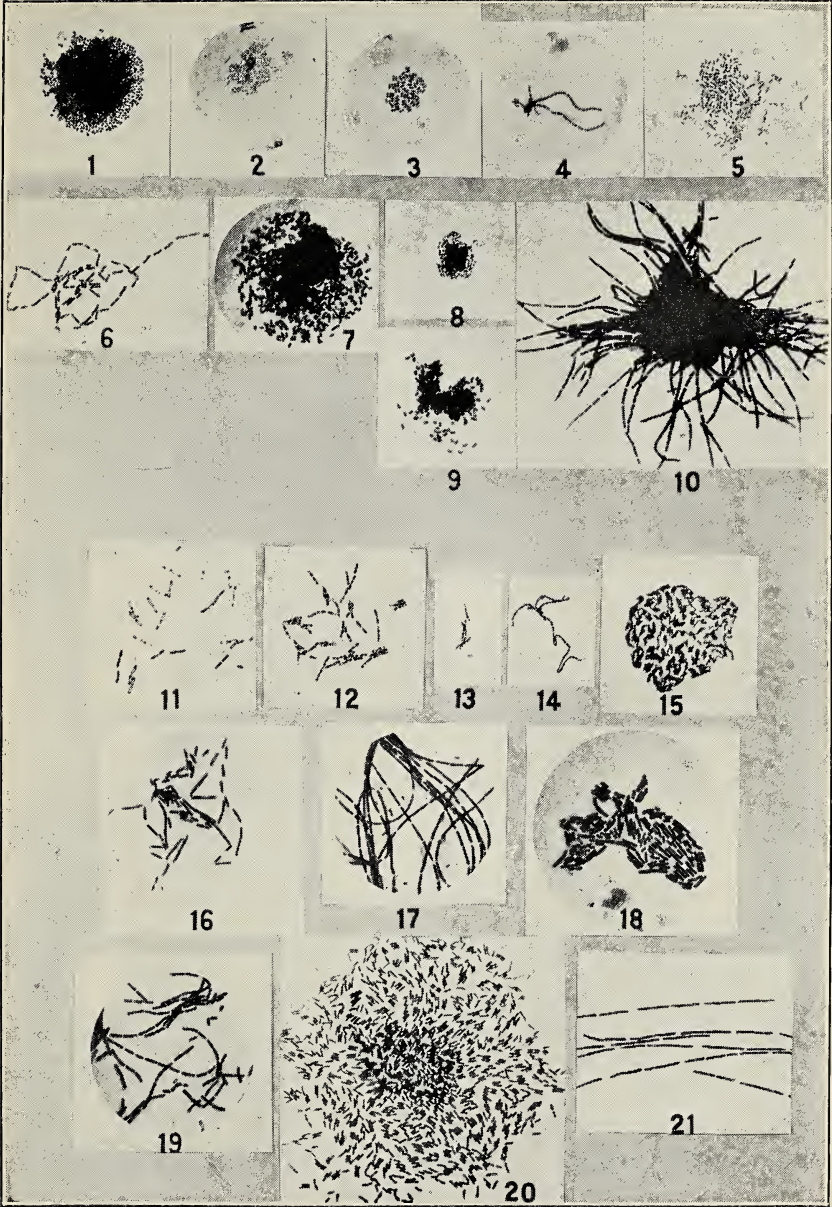
**Rats.** There were many colonies of diplococci, streptococci and staphylococci. Also many large bacilli of which some were arranged in spreading interlacing threads and others isolated or in pairs.

Some of the colonies were Gram positive and spore bearing and others Gram negative and non-sporulating.

The organisms found are believed to be: *Staph.albus*(?), *Strep.lacticus*, *B.acidophilus*, *B.bifidus*, *B.mesentericus*. See figs. 4, 5, 7, 8, 14, 18, 20, and 21.

Photomicrographs of some of the most frequently encountered colonies are given in the accompanying plate (No. IX).

Colonies from the stools of infants are reproduced in figures 1, 2, 3, 6, 11, 12, 13, 15, 16, and 19. Those from guinea pigs in 9, 10, and 17; and from rats in 4, 5, 7, 8, 14, 18, 20, and 21.







# ON THE NATURE OF DISEASE RESISTANCE IN PLANTS

J. C. WALKER

## INTRODUCTION

Since the pioneer work of DeBary (26) and Ward (87) upon the nature of parasitism, numerous contributions to our knowledge of the subject have been made. On the whole, however, we are still very much in the dark as to the nature of the complex relations which exist between the parasite and the host. Duggar (28) in 1911 remarked that, "in general, the physiology of penetration is poorly understood and it will reward investigation. . . . There is now at hand ample material for a thoroughgoing study of some of the factors governing resistance and susceptibility. The problem is doubtless extremely difficult, but it is believed by some the work may yield results. . . . At present there is no information respecting the cause of this difference in behavior as regards resistance." In connection with the writer's studies upon the nature of disease resistance in the onion (86), a review of previous work upon the general subject was found necessary. The results of this survey of the literature are presented at this time.

## TYPES OF DISEASE RESISTANCE

Orton (61), followed by Freeman (32) and Butler (16), calls attention to the distinction between avoidance of disease, endurance of disease, and true resistance to disease. It is the last of these three classes with which we are concerned in this paper. We shall include in this class, cases where through some inherent quality in its composition, the plant is capable of successfully resisting, to a greater or less extent, the attack of a given parasite. A survey of the studied cases of disease resistance in plants brings out at once the fact that all degrees are to be found, varying from complete immunity to a high degree of susceptibility. We have, for instance, in certain varieties of the potato complete immunity to the wart disease (*Synchytrium endobioticum* (Schil.)

Perc. (60). On the other hand, in the case of cabbage yellows (45) (*Fusarium conglutinans* Woll.) the resistant Wisconsin Hollander variety under extreme conditions (high soil temperature) shows a high percentage of plants slightly affected with the disease. However, such plants resist the parasite so successfully that they continue their growth, and with the return of somewhat cooler conditions all symptoms of the disease disappear and the plants mature normally. In contrast to this, plants of the common susceptible Hollander variety of cabbage may entirely succumb to the disease during the extreme conditions of high soil temperature. We thus have in the case of Wisconsin Hollander not a completely immune variety by any means, but unquestionably one which may be said to have a high degree of disease resistance. Moreover, as pointed out by Tisdale (78), this is a case of resistance acquired during the growth of the plant, since he has shown that very young seedlings of the Wisconsin Hollander variety are as susceptible as those of the common Hollander variety.

#### RELATION OF ENVIRONMENT TO RESISTANCE

The effect of environment upon resistance has been given only occasional attention by investigators. Vavilov (82) points out several cases where certain races of plants were equally resistant to given parasites when tried out under a variety of environments and in various parts of the world. However, we are not justified in concluding that in other cases environment does not have its effects.

Biffen (7) and Spinks (70) point out a distinct influence of various fertilizers upon the resistance of wheat to yellow rust (*Puccinia glumarum* (Schm.) Erikss. & Henn.). Stakman and Aamodt (73), on the other hand, found that in the case of wheat rust (*Puccinia graminis tritici* Erikss. & Henn.) "the amount of rust was not changed directly by any fertilizer or combination of fertilizers, although date of maturity, degree of lodging, crinkling, shrivelling of seed, percentage of yellow-berry, and yield were affected profoundly." Tisdale (79) states that a strain of flax, resistant to wilt (*Fusarium lini* Boll.) under normal field environment, showed a marked increase in susceptibility when grown at high greenhouse temperatures. The value of results recorded on the behavior of so-called resistant varieties in localities other than those in which they originated is often limited by the fact that there

often exist biologic strains of the parasite possessing distinct infective properties. This is especially true with the rusts where the existence of distinct biologic strains of *Puccinia graminis tritici* Erikss. & Henn. (74, 76), *Puccinia graminis avenae* Erikss. & Henn. (75), *Puccinia graminis secalis* Erikss. & Henn. (47), and *Puccinia triticina* Erikss. (51) has already been demonstrated. Kanred, a wheat resistant to *Puccinia graminis tritici* in Kansas, is not highly resistant in South Dakota nor in Minnesota. The difference in behavior is not attributed to any material difference in the host plant under the three environments, but to a difference in infective properties of the biologic strains of the parasite in the respective regions (54). In the case of the bean anthracnose organism (*Colletotrichum lindemuthianum* (Sacc. & Magn.) B. & C.) two biologic strains have been differentiated which behave quite differently in their infective properties on individual varieties of bean (5). Much more study is necessary on the effect of environing conditions upon parasitism and the expression of resistance over a wide range of cases.

#### GENETIC BEHAVIOR OF RESISTANCE

The hereditary nature of resistance has been shown to be a common phenomenon; its genetic behavior, however, from the limited results at hand, does not appear to follow any single genetic law. Chief limiting factors in the advancement of our knowledge of this phase of the subject have been the necessity of assuming an arbitrary division between resistance and susceptibility in analyzing the behavior of any group of plants, the present imperfect understanding of the effect of environmental factors upon the expression of resistant characters, and the lack of recognition, until recently, of the possible existence in many cases of several distinct biologic strains of the parasite. Biffen (7) found resistance in the case of yellow rust of wheat (*Puccinia glumarum*) to be recessive and determined by a single factor. Nilsson-Ehle (57), on the other hand, would explain the genetic behavior of resistance to yellow rust in his crosses of wheat on the basis of multiple factors. It is entirely possible that the variance in results in these two cases is due to the existence of different biologic strains in the two localities or to differences in environment. Recent work with black stem rust of wheat (*Puccinia graminis tritici*) (1, 55) and of oat (*Puccinia graminis*

*avenae*) (34) indicates that resistance to a given biologic strain is determined by a single dominant factor. Crosses between varieties of bean resistant and susceptible to anthracnose (*Colletotrichum lindemuthianum*) show that there is only a single factor difference between the two when a single strain of the parasite is considered (14, 49). Where two strains are involved a two factor difference is indicated (50). In both cases resistance is dominant over susceptibility. With two other diseases of bean, mosaic and root rot (*Fusarium martii* A. & W. var. *phaseoli* Burk.), susceptibility is at least partially dominant and resistance must be explained on the basis of more than one factor (50). Vavilov (81) in studying resistance of wheat to mildew (*Erysiphe graminis* DC.) found that from crosses between the immune Persian wheat (*Triticum vulgare* var. *fuliginosum* Al.) and common susceptible bread wheat varieties, F<sub>1</sub> hybrids were secured which were immune to the disease. Klaphaak and Bartlett (46) find that immunity to powdery mildew (*Erysiphe polygoni* DC.) in certain species of *Oenothera* is determined by a single factor, which is dominant. In the case of flax wilt (*Fusarium lini*) Tisdale (79) finds the behavior of resistance more readily explained on the basis of multiple factors. Gaines (33) reports there are different types of resistance to bunt (*Tilletia tritici* (Beij) Wint.) in different varieties of wheat and that in any particular case the resistant quality is composed of multiple factors. Johnson (40) finds that inheritance of resistance in tobacco to *Thielavia basicola* (B. & Br.) Zopf is best explained by a multiple-factor hypothesis.

#### CLASSES OF TRUE RESISTANCE

The causes of true resistance in plants have been grouped by Vavilov (82) into two classes: (1) mechanical or passive immunity and (2) physiological or active immunity. The first class includes those cases in which resistance depends upon certain mechanical differences in structure or habit of growth of the plant. The second class includes those cases in which resistance is due to inherent physiological qualities of the host cells which are sufficiently antagonistic to check the parasite. While this classification is convenient, it is obviously unwise at our present state of meagre knowledge of the subject to attempt to apply it too rigidly.

## CASES OF RESISTANCE DUE TO EXTERNAL STRUCTURE OF HOST

In a few instances disease resistance has been attributed to purely external differences in mechanical structure of the host plant. Hairiness of leaves and open habit of growth in certain varieties of potato are cited by Stuart (77) and by Appel (3) as facilitating more rapid evaporation of rain drops and hence as reducing liability to attack by *Phytophthora infestans* (Mont.) DeBary. Darnell-Smith (25) found a correlation between resistance to bunt (*Tilletia tritici*) in certain varieties of wheat and lack of hair on the terminal ends of kernels. Appel (3) noted that certain varieties of raspberries which were covered by a thick, blue, waxy layer remained free from attack by *Coniothyrium*, while other varieties were severely attacked. He suggests that the waxy layer may possibly influence infection by preventing penetration, or causing drops of water to run off. Freeman (32) noted higher resistance to stem rust (*Puccinia graminis* Pers.) in barley grown on alkali soils where the amount of "bloom" was increased.

The number and structure of stomata have been regarded in some cases as factors in disease resistance. In a study of numerous varieties of wheat in relation to rust (*Puccinia graminis*), Cobb (17) notes that in general the stomata were smaller and more numerous in the resistant than in the susceptible forms, and to these and certain other anatomical differences he attributes the cause of resistance. Eriksson and Henning (30), the first to test this theory, did not uphold it, and the more accurate studies of Ward (88) upon brome rust (*Puccinia dispersa* Erikss.) failed to confirm it. Norton (59) points out a correlation between small stomata and resistance to rust (*Puccinia asparagi* DC.) in the case of the resistant Martha Washington variety of asparagus, but the actual relation of this factor to penetration and infection was not studied. Allen (2) reports that only a very small percentage of the germ tubes of *Puccinia graminis tritici* enter the stomata of the highly resistant variety of wheat, Kanred, and points out that the stomatal slit of this variety is smaller and more slender than that of the very susceptible variety, Baart. Appel (3) cites a case in which resistance in "some Remontant carnations is due to the form of the stomata, which makes it impossible for the hyphae to penetrate them." Pool and McKay (63) point out that the immature leaves of beet are nearly immune to infection by *Cercospora beticola* Sacc. because the stomata are too small to permit

penetration by the fungus hyphae. Valteau (80) suggests that resistance to *Sclerotinia cinerea* (Bon.) Wor. in certain types of plums may be due to the fact that the stomata early become plugged with small parenchymatous cells which impede penetration.

The possible exclusion or retardation of parasites by means of unusual thickness of cuticle or by outer layers of corky cells has been suggested in a number of cases. Cobb (17) suggests that the thicker cuticle which is common in rust resistant varieties of wheat may contribute to resistance by preventing the maturation of the rust sori. Later work, such as that of Ward (88), indicates that this is not the important factor in rust resistance. An interesting case of correlation between thickness of cuticle in the tomato fruit and its resistance to *Macrosporium tomato* Cooke has recently been described by Rosenbaum and Sando (66). Young immature fruits are highly susceptible, while old fruits are resistant to attack. This difference does not appear to be due to changes within the host, since infection may readily be obtained in old fruits by first injuring the skin. There are no natural openings in the skin and the cuticle becomes thicker as the fruit matures. Moreover, the outer layer is shown to become gradually more resistant with age to mechanical puncture with a needle, and the authors suggest that resistance in the older fruits may be due to the ability of the thicker cuticle to resist puncture by the mycelium of the parasite. In discussing the pink disease of rubber (*Corticium salmonicolor* B. & Br.) in India, Butler (16) states that the attack is most marked on the shady side of the tree where the thinner cork offers less resistance to invasion. Appel (3) points out the importance of corky layers as a factor in resistance to certain parasites. In the case of the sweet potato, Weimer and Harter (91) have shown that wound cork layers may retard infection and that suberization of cell walls at the surface of the wound is often sufficient to prevent the entrance of microorganisms.

#### CASES OF RESISTANCE DUE TO INTERNAL CHARACTER OF THE HOST

In the foregoing cases, external differences in plant structure have been considered the determining factors in disease resistance. There is a much larger number of cases in which resistance is seemingly due to internal causes which have been sought either in the cell membranes or cell contents. The pioneer work of DeBary (26) upon *Sclerotinia* demonstrated the secretion of a

substance by the parasite which killed the host cells by diffusing in advance of the hyphae. As to the nature of this action he was not sure, but he considered the cell wall solution enzymic in character, and suggested the possible effects of a soluble oxalate. Ward (87) in his study of the *Botrytis* disease of lily likewise demonstrated the production of a wall-dissolving enzyme at the tips of the hyphae. Nordhausen (58) working with *Botrytis cinerea* Pers. also described its enzymic activity but in addition a toxic action of the fungus due possibly to oxalic acid. Smith (68) took the extreme position of attributing all of the action of *Botrytis* upon the host to oxalic acid. Jones (43), working with the soft rot bacillus (*B. carotovorus* Jones), ascribed the action of the parasite to a secreted enzyme, pectinase, and gave little importance to oxalic acid. Brown (9, 10, 11) improved greatly on methods previously used. He distinguished a macerating and a lethal effect of *Botrytis cinerea* upon the host. The former precedes the latter and is due to a cytolytic enzyme produced largely at the actively growing tips of the fungus hyphae. The nature of the lethal principle was not determined. Brown points out that there are chemical differences between cell walls and that a more thorough study of hemicellulose and pectins is needed. The significance attributed by earlier writers to oxalic acid or a soluble oxalate is definitely refuted.

In these early investigations the first stages of penetration were not made clear. Büsgen (15) did not consider that the parasite penetrated the cuticle by mechanical means alone. Miyoshi (56), however, showed that *Botrytis cinerea* was capable of penetrating paper, collodion, and other substances by mechanical pressure. More recent researches with the same fungus by Blackman and Welsford (8) and Brown (10) go to show that it does not secrete a cutin-dissolving enzyme but penetrates the cuticle by mechanical means alone. Further instances of apparent mechanical penetration have since been demonstrated by Dey (27) in the case of bean anthracnose, by Waterhouse (90) in the case of *Puccinia graminis* on barberry and by Curtis (24) in the case of invasion of potato by the zoospores of the wart organism.

#### IMPORTANCE OF CELL MEMBRANES

Hawkins and Harvey (39) give evidence to support their theory that in certain varieties of potato tubers, resistance to invasion by *Pythium debaryanum* Hesse is due to resistance of the cell

walls to mechanical puncture by the fungus hyphae. Tisdale (79) describes the formation of a layer of suberized cell walls in the cortex of resistant flax plants which checks further advance of the wilt fungus, *Fusarium lini*. He points out, however, that the actual resistant quality may possibly be contained in certain properties of the protoplasm of the normal cortical cells which retard the progress of the parasite during the suberization of the underlying cells, the latter being a natural host reaction. Valteau (80) considers it very possible that the slow development of *Sclerotinia cinerea* in resistant plums is due to a slight difference in the composition of the middle lamella which makes the latter less easily soluble in the secretions of the fungus. Further work by Willaman (93, 94) shows a higher crude fiber content in resistant than in susceptible plums.

#### THE NATURE OF RUST RESISTANCE

The nature of resistance to rusts has been studied by a number of investigators. The work of Cobb (17), stressing the importance of the anatomical features of the host, has already been cited. After a careful and comprehensive study of the question, Ward (88, 89) failed to find any correlation between external host features and infection. He showed (89) that in the case of wheat susceptible to *Puccinia glumarum* the hyphae of the latter "are typically stout, branched, and contain hundreds of nuclei. They also form numerous haustoria, and the attacked cells show no evident signs of injury to the chlorophyll-corpuscles or nuclei until a late stage of growth." In the case of highly resistant wheat, however, the substomatal chamber is invaded normally, but when the hyphae come to invade the cells they "show evident signs of degeneration in all respects and we conclude, from comparison with experimentally starved hyphae, that they are undergoing death-changes owing to one of two events, viz., they are either starving for want of food supplies or they are being poisoned." The same investigator (88) described earlier a similar condition existing between *Puccinia dispersa* and susceptible and highly resistant varieties of bromes. He (89) sums up his conclusions on the subject as follows:

In other words, infection, and resistance to infection depend on the power of the fungus-protoplasm to overcome the resistance of the cells of the host by means of enzymes or toxins; and, reciprocally, on that of the



protoplasm of the cells of the host to form anti-bodies which destroy such enzymes or toxins, or to excrete chemotactic substances which repel or attract the fungus-protoplasm.

Other work on the relation of rust fungi to their hosts has been carried on by Gibson (36) with *Puccinia (Uredo) chrysanthemi* Roze. on chrysanthemum, Marryat (52) with *Puccinia glumarum* on wheat, by Stakman (71, 72) with *Puccinia graminis* on wheat, by Reed and Crabill (65) with *Gymnosporangium juniperi-virginiana* Schw. on apple. In all cases the parasites were found to enter normally the substomatal chambers of both susceptible and highly resistant varieties of their respective hosts, but the difference in resistance lay in the reaction between the fungus hyphae and the mesophyll cells about the substomatal chamber. Giddings (37) describes a gradual development of resistance to rust (*Gymnosporangium juniperi-virginiana*) in the leaves of York Imperial, a susceptible variety of apple. He believes that this acquired immunity is due primarily to food factors and secondarily to differences in the composition of the cell wall.

The recent contribution by Miss Allen (2) advances considerably our knowledge of the nature of rust resistance. She has made a careful cytological study of infection of Baart, a very susceptible variety of wheat, and Kanred, a highly resistant variety, to a certain biological strain of *Puccinia graminis tritici*. We quote from her summary as follows:

The germination of the spores and the formation of the appressoria on the stomata take place in the same way in the susceptible and immune hosts.

In Baart the fungus enters freely and grows rapidly. In Kanred, under greenhouse conditions, only a few of the fungi pass through the stomata; the rest remain outside until they shrivel and die.

In a congenial host, numerous haustoria are formed. A slender-growing hypha strikes a host cell, swells at the tip, its pair of nuclei divide, and a septum is formed, marking off a short terminal cell. This haustorium mother cell is closely appressed to the host cell, forms a fine pore through its wall and the host wall, and its contents, including both the nuclei, which have decreased in size, and the cytoplasm, now pass in, forming the haustorium. The osmotic membrane of the host appears to be invaginated by the haustorium, but apparently is still intact.

In Kanred the process is similar until a small haustorium is formed, which, either by its presence, or, as is more likely, by secreting some substance in the host cell, sets up chemical reactions within that cell, causing its collapse and death. The further diffusion of toxic substances into healthy host tissues is checked by the formation of thickened contact walls. One or more of the substances formed in the host cell diffuse into

the haustorium, killing it, and causing collapse of the mother cell and the death and plasmolysis of the hypha back of it for some distance. If this reaction is rapid, the haustorium is destroyed while still very small; if more sluggish, a full-grown haustorium may be formed and some nourishment for further growth be extracted by the fungus.

She thus points out that the resistant variety Kanred possesses three means of defense against this strain of rust, namely, the stomata which exclude most of the fungi, the heavy contact walls adjoining the attacked cells which are interpreted as preventing the diffusion of toxic substances to uninvaded cells, and "a true immunity." In connection with the last the starvation theory discussed by Ward (89) and his students (36, 52, 70) does not seem tenable since the fungus hyphae appear to grow well in the intercellular spaces as long as the host cell is not penetrated. Upon invasion of the latter, there is evidence that the host cell undergoes chemical changes due to the invasion by the parasite and that, moreover, some substance diffuses into the fungus haustorium resulting in its death. That there is irregularity in the balance of forces of interaction between parasite and host is shown by the fact that in some cases the one collapses first while in other cases, the other dies first.

Preliminary studies of the reaction of Kanred to another biologic strain of *Puccinia graminis tritici* to which it is known to be less resistant, indicate that a higher percentage of appressoria enter the stomata. It will be interesting to learn the results of further study on the interactions between the host and this second strain of the parasite.

#### CHEMOTROPISM AS A FACTOR IN RESISTANCE

Massee (53) would explain the susceptibility or resistance of a plant by the presence or absence of a positively chemotropic substance in the host cells. The evidence is not convincing, however. Numerous cases have been recorded where fungi penetrated plants very resistant to their attack. Gibson (36), for instance, found that the germ tubes of a number of rust fungi readily entered a wide range of plants other than their respective hosts, but no further development of the fungus occurred. Wiltshire (95) found that the pear scab fungus (*Venturia pirina*) would invade apple fruit and that the apple scab fungus (*Venturia inaequalis*) would invade the pear, but each parasite was capable of producing the disease only upon its respective host. Tisdale (79) showed

that under certain conditions the cabbage yellows fungus (*Fusarium conglutinans*) would invade the root hairs of flax, but was incapable of progressing farther and producing a wilt similar to that caused by *Fusarium lini*. In a comparative study of two closely related organisms causing the leaf spots of alfalfa and red clover, respectively, Jones (41) showed that when sown under proper conditions upon clover leaves, the ascospores of *Pseudopeziza medicaginis* (Lib.) Sacc. germinated and the hyphae penetrated the epidermal cells, but the progress of the fungus was checked at this point; likewise when ascospores of the red clover organism, *Pseudopeziza trifolii* (Bernh.) Fcl., were sown upon alfalfa leaves, the germ tube penetrated but did not advance beyond the epidermal cell. Salmon (67) noted that the haustoria of the wheat mildew (*Erysiphe graminis*) penetrated the epidermal cells of the barley leaf, but that they eventually shriveled and died without producing the characteristic disease symptoms. Explanation of the cases just mentioned on the basis of the absence of positively chemotropic substances in the host cell is unsatisfactory, since several other possible explanations might be offered, such as the presence of inhibitive substances in the host cell, or the absence in the parasite of proper enzymes or toxins to bring about the chemical or physical changes in the host cell necessary to provide food for the growth of the invader.

#### OSMOTIC PRESSURE AS A FACTOR IN RESISTANCE

From his earlier experimental studies upon phanerogamic parasites, McDougal (48) concluded that an osmotic pressure of the parasite higher than that of the host was essential. In the light of more recent researches he believes that osmotic pressure may be of minor importance in the establishment of the haustorium, and that absorption by imbibition and the force of expansion of the invading protoplast are important factors at this early stage. In this connection the work of Hawkins (38) is significant. Using two potato-rotting fungi, and one strawberry-decaying fungus, he found that they would all grow on solutions of glucose, sucrose, potassium nitrate or calcium nitrate at diffusion tensions much higher than the total diffusion tensions of the dissolved substances in the juices of their respective host plants. Vavilov (82), after examining many species and varieties, was unable to establish any correlation between osmotic pressure and resistance.

## CELL SAP ACIDITY AS A FACTOR IN RESISTANCE

A correlation between resistance and a higher acidity of the cell sap of the host tissues has been pointed out by several investigators. Averna-Sacca (4) reports a higher acidity in grapes resistant to *Oidium* and *Peronospora*, and Comes (18, 19) reports a similar correlation for a variety of wheat (Rieti) resistant to rust. On the other hand, Vavilov (82) found no connection between the acidity of cell sap of many varieties of oats, wheat, and roses and their resistance to rusts and mildew. No such correlation was found in the potato by Jones and co-workers (44) in the case of late blight (*Phytophthora infestans*), by Hawkins and Harvey (39) in the case of leak (*Pythium debaryanum*), nor by Weiss and Harvey (92) in the case of black wart (*Sychitrium endobioticum*). Gardner and Kendrick (35) in their work upon a tomato fruit spot caused by *Bacterium exitiosum* G. & K. find a correlation between the hydrogen ion concentration of the plant tissues and their resistance to infection. The organism did not grow in culture media more acid than a P<sub>H</sub> value of 5. Examination of various tomato plant parts yielded P<sub>H</sub> values as follows: seedlings and leaves, 6.3 to 6.5; green fruits, 5 to 5.4; ripening and mature fruits, about 4.6. Seedlings, leaves, and green fruits were very susceptible to the disease, but inoculations of ripe fruits were usually unsuccessful. Aside from the last instance, we have as yet very little convincing evidence that cell sap acidity is an important factor in disease resistance.

## TANNIN AS A FACTOR IN RESISTANCE

The relation of tannin to the growth of a number of fungi was studied by Cook and Taubenhaus (21). They found that in general when tannin was added in increasing amounts to a favorable medium, germination was inhibited and finally spores were killed. Considerable variation in the reaction of different fungi was noted, and in general, parasitic fungi were less resistant to the toxicity of tannin than saprophytic fungi. Cook and coworkers (20) later claimed that tannin as such does not exist in the host cell, except in small amounts. There does exist a polyatomic phenol, which, upon injury to the cell, results in the formation of a tannin or tannin-like substance. They point out that conditions for such a reaction prevail in normal immature pomaceous fruits which are injured by the invading hyphae. A germicidal

fluid containing the soluble tannin is thus formed; on the basis of the germicidal action of this fluid, the resistance of such fruits to parasitic attack is explained. Cook and Taubenhau (22) in a later paper point out that many fruits lose their power of resistance very soon after removal from the plant. This loss of resistance is proportionate to the reduced activity of the enzyme. They extended their studies to the vegetable acids and found the toxicity of the latter to vary with the organisms used. Tannic acid was the most toxic, but the character and the true importance of this substance within the living plant remains to be determined by future investigations. Valleau (80) found no correlation between tannin content of plums and their resistance to *Sclerotinia cinerea*. The investigations upon tannin and organic acids in relation to resistance, while suggestive, are still inconclusive.

#### ANTHOCYANS AND FLAVONES IN RELATION TO RESISTANCE

The pigments of the anthocyan class have been suggested in several instances as substances contributing toward disease resistance, but in most cases the evidence is only observational and is not supported by experimental investigation. Sorauer (69) noted that red potatoes are in general more resistant than white. Jones (42) says that many potato experts, American and European, regard red, rough-skinned varieties of potatoes as less liable to rot than thin, white-skinned potatoes. He points out, however, that there is abundant evidence of high disease resistance coupled with a thin white skin. Voges (83) considered red color in apple fruits a protection against scab but the large amount of data to be found in literature does not bear out this statement. Comes (19) attributed certain cases of resistance to the occurrence of anthocyan but his evidence is not convincing. In this connection, it is interesting to note the work of Cook and Wilson (23) who studied the effect of "commercial" tannin and extracts from chestnut bark upon the growth of the chestnut blight organism, *Endothia parasitica* (Murr.) And. & And. Results with "commercial" tannin were of the same general nature as those secured with other fungi by Cook and Taubenhau (21, 22) noted above. Since "commercial" tannin was variable in composition and since it contained a certain percentage of impurities, extracts from chestnut bark were also used. Through the cooperation of Kerr, three extracts were made: "1-X", described as the water soluble

tannin, insoluble in alcohol; "2-X", described as similar in its reactions to "1-X", except that it is soluble both in water and in alcohol; and "3-X", described as the "coloring matter of the bark" . . . which "is estimated as tannin in bark analysis," but "its real nature is unknown." Extracts "1-X" and "2-X" were less toxic than "commercial" tannin while "3-X", the coloring matter, was very toxic. They point out further a statement from Kerr to the effect that "chestnut trees of northern growth, say on a line north of the southern boundary of Pennsylvania, contain very materially less coloring matter than the growth south of it, and, as we all know, the wood in the latitude referred to seems to have been more susceptible than that further south." The importance of the coloring matter as an inhibitive substance is thus suggested in this instance. Fromme and Wingard (31) in a study of varietal susceptibility of beans to rust (*Uromyces appendiculatus* (Pers.) Lév.) found that all varieties with solid red or red mottled seed were resistant, while those with white seed as a class were more susceptible than those of any other color. In the case of onion smudge (*Colletotrichum circinans* (Berk.) Vogl.), a bulb rot, Walker (84, 85, 86) has shown a very strict correlation between scale pigments and resistance. The white varieties are uniformly susceptible while the red and yellow varieties are only slightly attacked. The resistant principle can be secured by making a cold water extract of the dry, outer colored scale. This solution is highly toxic to the spores and mycelium of the fungus. A similar extract from white scales promotes normal germination and growth. When the dry outer scale is removed even colored bulbs are readily infected. The interpretation of this is found in the fact that the toxic substance is readily dissolved from the dead outer scales into the soil water thus deactivating the fungus before invasion. In the succulent scale the epidermal cells which are the ones containing the pigment show reduction of this pigment while the mycelium is still in the outer cell wall and has not actually invaded the cell lumen. This is due either to autolytic processes within the cell or to a diffusible substance secreted by the fungus. Resistance by the host, however, is accomplished by the dry outer scales which serve as a barrier to the fungus through the action of their soluble toxic substance.

## OTHER CELL CONTENTS IN RELATION TO RESISTANCE

Jones, Giddings, and Lutman (44) considered that resistance of certain varieties of potato to the late blight fungus (*Phytophthora infestans*) is due to something within the tissues of the leaf and the tuber, rather than to difference in epidermal structures. Their studies on the relation of the potato cell sap to the fungus indicate that acidity of the former has little to do with the disease resistant quality. Attempts to study the relation of the extracted juice from susceptible and from resistant varieties to the growth of the fungus yielded largely negative results. In conclusion they say "this (disease resistant) product may, therefore, be assumed to be either a compound, modified or destroyed by cooking and weakened or removed by filtration through porcelain, or else it may be so intimately associated with the living protoplasm as to be inseparable from it by the processes employed."

Wiltshire (95) studied the relation of apple and pear scab fungi to plants susceptible and plants highly resistant to their attack. Since these fungi penetrated the cuticle of both susceptible and resistant plants he concluded that immunity does not depend upon freedom from attack. A study of the germination and growth of spores of the apple scab fungus (*Venturia inaequalis*) in expressed juice of the host showed in one experiment that germination was inhibited in the sap of both susceptible and resistant varieties, while in the diluted sap no difference from germination in water was observed. In another experiment the germ tubes of the conidia appeared to grow better in the sap of susceptible than of resistant varieties. These experiments indicate that some chemical substance which had an inhibitive effect upon the fungus was present in the expressed cell sap, but Wiltshire apparently did not carry the investigation far enough to definitely establish the fact or to throw any light upon the nature of the inhibitive substance.

The fungicidal effect of volatile substances within the plant cell has received some attention. Pasteur (62) early noted the retarding effect of onion juice upon yeasts. Bernard (6) noted the fungicidal effect of volatile substances in the tissue of an orchid (*Loroglossum*) upon the mycorrhizal fungus from other closely related species. Walker (85, 86) noted that the volatile onion oil has a retarding effect upon germination and growth of the onion smudge fungus (*Colletotrichum circinans*). It was shown,

however, that although this may be a factor in limiting the parasitism of the latter fungus, it was not evidently a factor contributing to the difference in resistance between colored and white varieties. Brown (12, 13) has recently pointed out the effect on germinating of fungus spores of substance diffusing from the host cell into the infection drop; and in this work it was further shown that volatile oils from various plants may have in some cases detrimental and in other cases stimulative effects upon the spores.

#### SUMMARY

For purposes of convenience let us outline the main evidence to date as to the nature of disease resistance, remembering that since much of the work is fragmentary and not uniformly reliable this is merely a suggestive and tentative summary based wholly on statements in the original texts.

Orton (61) classifies the various known types of resistance into three classes: (1) avoidance of disease, (2) endurance of disease, and (3) true resistance to disease. We include in the discussion the latter class, in which we consider cases where through some inherent quality in its composition the plant is capable of successfully resisting the attack of a given parasite. In consideration of the subject the importance of environment as affecting the expression of resistant qualities is emphasized. In the few instances where the hereditary nature of resistance has been studied it is determined in some cases by a single factor, in other cases by multiple factors. Vavilov's (82) separation of the causes of true resistance into two groups, mechanical or passive and physiological or active is useful. Numerous instances where mechanical structures of the host plant are responsible for resistance have been noted. These include hairiness of leaves and open habit of growth in the case of potatoes resistant to blight, lack of hair on terminal end of kernels in case of wheat resistant to bunt, external waxy layers in case of raspberries resistant to *Coniothyrium* and of barley resistant to stem rust. Differences in stomatal structure or size have been cited in several cases as responsible for the resistant quality. The exclusion of parasites by means of thick cuticle or the formation of corky layers is quite well established in a few cases.

Physiological or internal factors as causes of resistance have been noted in a variety of instances. These internal differences are



found in the cell membranes or in the cell contents. In the first class are included (1) the internal cell walls as a factor in limiting the potato-rotting fungus (*Pythium debaryanum*), (2) the formation of a layer of suberized cell walls in the cortex of flax plants resistant to wilt, and (3) evidence of differences in cell wall composition in plums resistant or susceptible to attack by *Sclerotinia cinerea*.

In the second case—that of internal differences in the cell contents—we have first the examples in the various cases of rust resistance. While the physiology of the process is not clear we know that invasion of the cells of the resistant plant occurs but that progress is stopped either by lack of adjustment on the part of the fungus or by the presence of toxic substances in the host protoplasm. A theory of chemotropism to explain resistance has been offered by Masee (53) but it has never been well substantiated. The correlation between cell sap acidity and resistance was brought out by certain earlier workers; more recent investigations, however, with other diseases has failed to show such a relation. Tannins have been shown to be more or less toxic to fungi and there are suggestions that in some cases this may contribute to resistance. Correlation between the anthocyan or flavone pigments and resistance has been pointed out in a number of instances. In only one case, that of onion, is the evidence sufficient to justify the supposition that the coloring matter is the resistant principle, and even there further investigation is necessary to ascertain definitely whether it is the coloring matter or some other closely associated substance.

The presence within the host tissues of a volatile substance more or less toxic to parasites of the same tissue has been shown in the case of onion. Curiously enough this substance has not been correlated with resistance although it may play a rôle in limiting the parasitism of the smudge fungus.

The above summary is sufficient to show that the true nature of resistance has been exceedingly difficult to determine and, moreover, it is quite obvious that almost every case of resistance very probably presents a specific problem. In certain cases, no doubt, external factors, such as size of stomata, hairiness of leaf surface, or presence of bloom are factors contributing to resistance. In a larger number of cases, however, the underlying causes will be found in the interrelations between the parasite and the host cell membranes or the host cell contents. We can conceive of several

factors entering into this relationship. Resistance may be due to a substance (or substances) in the host tissue which is either toxic to the parasite or is capable of neutralizing or destroying the enzymes or toxins produced by the parasite and hence may preclude or check invasion; it may be due to a lack of proper nutrients in the host tissue for the development of the invader; or it may be due to a lack of ability on the part of the parasite, first, to penetrate the host plant or, secondly, so to adjust itself to the chemical and physical complex of its new substrate as to make food materials, even though present, available for absorption and assimilation. It is entirely possible that one or all of these factors may enter into a given case of disease resistance. It should also be recognized at the outset that a clear conception of the nature of the parasitism occurring in any given case is essential to a clear understanding of resistance. Indeed, the two processes are merely phases of a single phenomenon which involves the interrelation of two living organisms. Moreover, it should be made clear that, as Duggar (28) has pointed out, "there are all grades of parasitism and there must be a variety of effects induced in the host, including changes essentially autolytic." He compares, for instance, the effect of *Cystopus candidus* (Pers.) Lév. upon the host tissues with that of closely related fungi, as *Phytophthora infestans* or *Pythium debaryanum*; and again, the rusts which have "little tendency to kill immediately the tissues which they invade" with the large group of parasites which have no contact with the living protoplasm but kill the cells in advance by means of secreted diffusible substances. The greatest advance in our knowledge of the nature of disease resistance will therefore come from a thoroughgoing, persistent study of individual cases, and especially of those which seem to offer the most accessible approach.

## LITERATURE CITED

- (1). **Aamodt, Olaf S.** The inheritance of resistance to several biologic forms of *Puccinia graminis tritici* in a cross between Kanred and Marquis wheats. (Abstract.) *Phytopathology* 12: 32. 1922.
- (2). **Allen, Ruth F.** A cytological study of infection of Baart and Kanred wheats by *Puccinia graminis tritici*. *Jour. Agr. Research* 23: 131-152. 1923.
- (3). **Appel, Otto.** Disease resistance in plants. *Science* n. s. 41: 773-782. 1915.
- (4). **Averna-Sacca, Rosario.** L'acidita dei succhi delle piante in rapporto alla resistenza contro gli attachi dei parassiti. *Staz. Sper. Agr. Ital.* 43: 185-209. 1910.

- (5). **Barrus, M. F.** Varietal susceptibility of beans to strains of *Colletotrichum lindemuthianum* (Sacc. & Magn.) B. & C. *Phytopathology* 8: 589-614. 1918.
- (6). **Bernard, Noel.** Sur la fonction fungicide des bulbes d'Ophrydees. *Ann. Sci. Nat. Bot.* 9<sup>e</sup> serie 14: 221-234. 1911.
- (7). **Biffen, R. H.** Studies in the inheritance of disease resistance. *Jour. Agr. Sci.* 2: 109-128; 4: 421-429. 1907-1912.
- (8). **Blackman, V. H.** and **Welsford, E. J.** Studies in the physiology of parasitism. II. Infection by *Botrytis cinerea*. *Ann. Bot.* 30: 389-398. 1916.
- (9). **Brown, William.** Studies in the physiology of parasitism. I. The action of *Botrytis cinerea*. *Ann. Bot.* 29: 313-348. 1915.
- (10). ——— Studies in the physiology of parasitism. III. On the relation between the 'infection drop' and the underlying host tissue. *Ann. Bot.* 30: 399-406. 1916.
- (11). ——— Studies in the physiology of parasitism. IV. On the distribution of cytase in cultures of *Botrytis cinerea*. *Ann. Bot.* 31: 489-498. 1917.
- (12). ——— Studies in the physiology of parasitism. VIII. On the exosmosis of nutrient substances from the host tissue into the infection drop. *Ann. Bot.* 36: 101-119. 1922.
- (13). ——— Studies in the physiology of parasitism. IX. The effect on the germination of fungal spores of volatile substances arising from plant tissues. *Ann. Bot.* 36: 285-300. 1922.
- (14). **Burkholder, W. H.** The production of an anthracnose resistant white marrow bean. *Phytopathology* 8: 353-359. 1918.
- (15). **Büsgen, M.** Ueber einige Eigenschaften den keimlinge parasitischer Pilze. *Bot. Ztg.* 51: 53-72. 1893.
- (16). **Butler, E. J.** Immunity and disease in plants. *Agr. Jour. India* (Spec. Indian Sci. Cong. No.) 1918: 10-28. 1918.
- (17). **Cobb, N. A.** Contributions to an economic knowledge of the Australian rusts (Uredineae). *Agr. Gaz. N. S. Wales* 1: 185-214, 1890; 3: 44-68; 181-212. 1892. Literature cited 3: 190-200.
- (18). **Comes, Orazio.** Della resistenza dei frumenti alle ruggini. Stato attuale della quistione e provvedimenti. *Atti. R. Istituto d'Incorraggiamento Napoli.* Ser. 6, 64: 419-441. 1913. (Rev. in *Bul. Agr. Int. and Pl. Dis.* 4: 1117-1119. 1913.)
- (19). ——— Della resistenza dei frumenti alle ruggini ed in generale delle piante alle loro cause nemichi. *Ann. d. R. Scuola Sup. di Agricoltura.* Ser. 2, 12: 419-473. 1914.
- (20). **Cook, M. T., Bassett, H. P., Thompson, F., and Taubenhaus, J. J.** Protective enzymes. *Science* n. s. 33: 624-629. 1911.
- (21). ——— and **Taubenhaus, J. J.** The relation of parasitic fungi to the contents of the cells of the host plants (I. The toxicity of tannin). *Del. Agr. Exp. Sta. Bul.* 91. 77 p. 1911.
- (22). ——— and **Taubenhaus, J. J.** The relation of parasitic fungi to the contents of the cells of the host plants (II. The toxicity of vegetable acids and the oxidizing enzyme.) *Del. Agr. Exp. Sta. Bul.* 97: 53 p. 1912.

- (23). ——— and Wilson, G. W. The influence of the tannin content of the host plant on *Endothia parasitica* and related species. Bot. Gaz. 60: 346-361. 1915.
- (24). Curtis, K. M. The life-history and cytology of *Synchytrium endobioticum* (Schilb.) Perc., the cause of wart disease in potato. Phil. Trans. Roy. Soc. London. Ser. B, 210: 409-478. 1921.
- (25). Darnell-Smith, G. P. Some observations on bunt and fungicides. Agr. Gaz. N. S. Wales 21: 751-756. 1910.
- (26). DeBary, A. Ueber einige Sclerotinien und Sclerotienkrankheiten. Bot. Ztg. 44: 377-387; 393-404; 409-426; 433-441; 449-461; 465-474. 1886.
- (27). Dey, P. K. Studies in the physiology of parasitism. V. Infection by *Colletotrichum lindemuthianum*. Ann. Bot. 33: 305-312. 1919.
- (28). Duggar, B. M. Physiological plant pathology. Phytopathology 1: 71-78. 1911.
- (29). Durrell, L. W., and Parker, J. H. The comparative resistance of varieties of oats to crown and stem rusts. Iowa Agr. Exp. Sta. Res. Bul. 62: 25-56d. 1920.
- (30). Eriksson, J., and Henning, E. Die Getreideroste. 464 p. Stockholm, 1896. Literature cited, p. 355-363.
- (31). Fromme, F. D., and Wingard, S. A. Varietal susceptibility of beans to rust. Jour. Agr. Research 21: 385-404. 1921.
- (32). Freeman, E. M. Resistance and immunity in plant diseases. Phytopathology 1: 109-115. 1911.
- (33). Gaines, E. F. The inheritance of resistance to bunt or stinking smut of wheat. Jour. Amer. Soc. Agron. 12: 124-131. 1920.
- (34). Garber, R. J. A preliminary note on the inheritance of rust resistance in oats. Jour. Amer. Soc. Agron. 13: 41-43. 1921.
- (35). Gardner, M. W., and Kendrick, J. B. Bacterial spot of tomato. Jour. Agr. Research 21: 123-156. 1921.
- (36). Gibson, C. M. Notes on infection experiments with various Uredineae. New Phytologist 3: 184-191. 1904.
- (37). Giddings, N. J. Infection and immunity in apple rust. West Va. Agr. Exp. Sta. Bul. 170: 71 p. 1918.
- (38). Hawkins, L. A. Growth of parasitic fungi in concentrated solutions. Jour. Agr. Research 7: 255-260. 1916.
- (39). ———, and Harvey, R. B. Physiological study of the parasitism of *Pythium debaryanum* Hesse on the potato tuber. Jour. Agr. Research 18: 275-297. 1919.
- (40). Johnson, James. Inheritance of disease resistance to *Thielavia basicola*. (Abstract.) Phytopathology 11: 49. 1921.
- (41). Jones, F. R. The leaf-spot diseases of alfalfa and red clover caused by the fungi *Pseudopeziza medicaginis* and *Pseudopeziza trifolii*, respectively. U. S. Dept. Agr. Bul. 759: 38 p. 1919.
- (42). Jones, L. R. Disease resistance of potatoes. U. S. Dept. Agr., Bur. Pl. Ind. Bul. 87: 39 p. 1905.

- (43). ————Pectinase, the cytolytic enzyme produced by *Bacillus carotovorus* and certain other soft-rot organisms. N. Y. (Geneva) Agr. Exp. Sta. Tech. Bul. 11: 289-368. 1909; also Vt. Agr. Exp. Sta. Bul. 147: 289-360. 1909.
- (44). ————, Giddings, N. J., and Lutman, B. F. Investigations of the potato fungus *Phytophthora infestans*. U. S. Dept. of Agr. Bur. Pl. Ind. Bul. 245: 100 p. 1912.
- (45). ————, Walker, J. C., and Tisdale, W. B. Fusarium resistant cabbage. Wis. Agr. Exp. Sta. Res. Bul. 48. 34 p. 1920.
- (46). Klaphaak, P. J., and Bartlett, H. H. A preliminary notice of genetic studies of resistance to mildew in *Oenothera*. Amer. Jour. Bot. 9: 446-458. 1922.
- (47). Levine, M. N., and Stakman, E. C. Biologic specialization of *Puccinia graminis secalis*. (Abstract.) Phytopathology 13: 35. 1923.
- (48). MacDougal, D. T. The beginnings and physical basis of parasitism. Plant World 20: 238-244. 1917.
- (49). McRostie, G. P. Inheritance of anthracnose resistance as indicated by a cross between a resistant and a susceptible bean. Phytopathology 9: 141-148. 1919.
- (50). ————Inheritance of disease resistance in the common bean. Jour. Amer. Soc. Agron. 13: 15-32. 1921.
- (51). Mains, E. B., and Jackson, H. S. Strains of the leaf-rust of wheat, *Puccinia triticina*, in the United States. (Abstract.) Phytopathology 13: 36. 1923.
- (52). Marryat, Dorothea C. E. Notes on the infection and histology of two wheats immune to the attacks of *Puccinia glumarum*, yellow rust. Jour. Agr. Sci. 2: 129-138. 1907.
- (53). Massee, George. On the origin of parasitism in fungi. Phil. Trans. Roy. Soc. London. Ser. B, 197: 7-24. 1905.
- (54). Melchers, Leo E., and Parker, John H. Rust resistance in winter-wheat varieties. U. S. Dept. Agr. Bul. 1046: 32 p. 1922.
- (55). ———— Inheritance of disease resistance to black stem rust in crosses between varieties of common wheat (*Triticum vulgare*). (Abstract.) Phytopathology 12: 31-32. 1922.
- (56). Miyoshi, M. Die Durchbohrung von Membranen durch Pilzfäden. Jahrb. Wiss. Bot. (Pringsheim) 28: 269-289. 1895.
- (57). Nilsson-Ehle, H. Resistenz gegen Gelbrost beim Weisen. Kreuzungsuntersuchungen an Hafer und Weisen. II. Lund's Univ. Årsskr. n. f. afd. 2, 7: 57-82. 1911.
- (58). Nordhausen, M. Beiträge zur Biologie parasitärer Pilze. Jahrb. Wiss. Bot. (Pringsheim) 33: 1-46. 1898.
- (59). Norton, J. B. Methods used in breeding asparagus for rust resistance. U. S. Dept. Agr. Bul. Pl. Ind. Bul. 263: 60 p. 1913.
- (60). Orton, C. R., and Weiss, Freeman. The reaction of first generation hybrid potatoes to the wart disease. Phytopathology 11: 306-310. 1921.

- (61). **Orton, W. A.** The development of farm crops resistant to disease. U. S. Dept. Agr. Yearbook 1908: 453-464. 1909.
- (62). **Pasteur, L.** Memoire sur la fermentation appelee lactique. Ann. d. Chemie et d. Physique. Ser. 3, 52: 404-418. 1858.
- (63). **Pool, V. W., and McKay, M. B.** Relation of stomatal movement to infection by *Cercospora beticola*. Jour Agr. Research 5: 1011-1038. 1916.
- (64). **Reed, Geo. M.** Varietal resistance and susceptibility of oats to powdery mildew, crown rust, and smuts. Mo. Agr. Exp. Sta. Res. Bul. 37: 41 p. 1920.
- (65). **Reed, H. S., and Crabill, C. H.** The cedar rust disease of apples caused by *Gymnosporangium juniperi-virginianae* Schw. Va. Agr. Exp. Sta. Tech. Bul. 9: 106 p. 1915. Literature cited, p. 40-43.
- (66). **Rosenbaum, J. and Sando, C. E.** Correlation between size of the fruit and the resistance of the tomato skin to puncture and its relation to infection with *Macrosporium tomato* Cooke. Amer. Jour. Bot. 7: 78-82. 1920.
- (67). **Salmon, E. S.** On the stages of development reached by certain biologic forms of Erysiphe in cases of non-infection. New Phytologist 4: 217-222. 1905.
- (68). **Smith, R. E.** The parasitism of *Botrytis cinerea*. Bot. Gaz. 33: 421-436. 1902.
- (69). **Sorauer, P.** Ueber die prädisposition der Pflanzen für parasitäre Krankheiten. Arb. Deut. Landw. Gesell. Jahresber. Sonderaussch. Pflanzenschutz 12: 193-210. 1903. Literature cited, p. 198.
- (70). **Spinks, G. T.** Factors affecting susceptibility to disease in plants. Jour. Agr. Sci. 5: 231-247. 1913.
- (71). **Stakman, E. C.** A study in cereal rusts. Physiological races. Minn. Agr. Exp. Sta. Bul. 138: 56 p. 1914.
- (72). ————Relation between *Puccinia graminis* and plants highly resistant to its attack. Jour. Agr. Research 4: 193-199. 1915.
- (73). ————, and **Aamodt, Olaf S.** The effect of fertilizers on the development of stem rust of wheat. Phytopathology 12: 31. 1922.
- (74). ————, and **Levine, M. N.** The determination of biologic forms of *Puccinia graminis* on Triticum spp. Minn. Agr. Exp. Sta. Tech. Bul. 8: 10 p. 1922.
- (75). ————, and **Bailey, D. L.** Biologic specialization of *Puccinia graminis avenae*. (Abstract.) Phytopathology 13: 35. 1923.
- (76). ————, and **Leach, J. G.** New biologic forms of *Puccinia graminis*. Jour. Agr. Research 16: 103-105. 1919.
- (77). **Stuart, William.** Disease resistance of potatoes. Vt. Agr. Exp. Sta. Bul. 122: 105-136. 1906.
- (78). **Tisdale, W. B.** The influence of soil temperature and soil moisture upon the Fusarium disease in cabbage seedlings. Jour. Agr. Research. 24: 55-86. 1923.
- (79). **Tisdale, W. H.** Flaxwilt: a study of the nature and inheritance of wilt resistance. Jour. Agr. Research 11: 573-606. 1917.

- (80). **Valleau, W. D.** Varietal resistance of plums to brown-rot. Jour. Agr. Research 5: 365-396. 1915.
- (81). **Vavilov, N. I.** Breeding for resistance to rust and mildew in wheat. Jour. Gen. 4: 49-65. 1914.
- (82). **Vavilov, N. I.** Immunity of plants to infectious diseases. Proc. of the Petrovski Agricultural Academy 1918: 1-239. 1919. (With a resumé in English.)
- (83). **Voges, Ernst.** Die Bekämpfung des Fusicladium. Ztschr. Pflanzenkrank. 20: 385-393. 1910.
- (84). **Walker, J. C.** Notes on the resistance of onions to anthracnose. (Abstract.) Phytopathology 8: 70-71. 1918.
- (85). ————Onion smudge. Jour. Agr. Research 20: 685-722. 1921.
- (86). ————Disease resistance to onion smudge. Jour. Agr. Research. 24: 1019-1040. 1923.
- (87). **Ward, H. Marshall.** A lily-disease. Ann. Bot. 2: 319-382. 1888.
- (88). ————On the relations between host and parasite in the bromes and their brown rust, *Puccinia dispersa* (Erikss). Ann Bot. 16: 233--315. 1902.
- (89). ————Recent researches on the parasitism of fungi. Ann. Bot. 19: 1-54. 1905.
- (90). **Waterhouse, W. L.** Studies in the physiology of parasitism. VIII. Infection of *Berberis vulgaris* by sporidia of *Puccinia graminis*. Ann. Bot. 35: 557-564. 1921.
- (91). **Weimer, J. L., and Harter, L. L.** Wound-cork formation in the sweet potato. Jour. Agr. Research 21: 637-647. 1921.
- (92). **Weiss, F., and Harvey, R. B.** Catalase, hydrogen-ion concentration, and growth in the potato wart disease. Jour. Agr. Research 21: 589-592. 1921.
- (93). **Willaman, J. J., and Sandstrom, W. M.** Biochemistry of plant diseases III. Effect of *Sclerotinia cinerea* on plums. Bot. Gaz. 73: 287-307. 1922.
- (94). ————, and **Davison, F. R.** Biochemistry of plant diseases IV. Proximate analysis of plums rotted by *Sclerotinia cinerea*. Bot. Gaz. 74: 104-109. 1922.
- (95). **Wiltshire, S. P.** Infection and immunity studies on the apple and pear scab fungi (*Venturia inaequalis* and *V. pirina*). Ann. Appl. Biol. 1: 335-350. 1915.





## SOME FERNS OF SOUTHWESTERN WISCONSIN

---

SISTER M. ELLEN

An attempt to discover and to identify the pteridophytic flora in the vicinity of Sinsinawa Mound (Grant County) was both interesting and attractive. The types of habitat in this locality are so varied within a radius of three or four miles that a fern lover might hope to find almost any or all of the native, temperate forms. These various plant habitats may be classified as follows: deep moist woods, dry open woods, wet rocky bluffs, tall limestone cliffs, and waste lands.

It was somewhat disappointing but none the less interesting to find not a single plant of *Polypodium vulgare*, the common rock fern, which is so generally distributed throughout the state. The Woodsias, rock-loving Aspleniums, *Aspidium marginale*, the Lycopodiums, and other common forms were also hunted in vain.

In the following list the nomenclature follows Gray's Manual, seventh edition.

### POLYPODIACEAE

*Adiantum pedatum* L.

Common.

*Aspidium spinulosum* (O. F. Müller) Sw.

Occasional plants in deep woods.

*Asplenium Filix-femina* (L.) Bernh.

Common everywhere.

*Camptosorus rhizophyllus* (L.) Link.

Three places on rocks; (a) on Sinsinawa Mound; (b) about three and one-half miles west of the Mound; and (c) about four miles southwest of the Mound.

*Cystopteris bulbifera* (L.) Bernh.

Very abundant on rocks.

*Cystopteris fragilis* (L.) Bernh.

Common everywhere.

*Cryptogramma Stelleri* (Gmel.) Prantl.

Abundant on rocks.

*Pellaea atropurpurea* (L.) Link.

Very abundant on rocks.

*Onoclea sensibilis* L.

Abundant in moist woods.

*Onoclea Struthiopteris* (L.) Hoffm.

In wet fields and transplanted on the campus of St. Clara College.

*Pteris aquilina* L.

Abundant in open woods.

#### OSMUNDACEAE

*Osmunda Claytoniana* L.

Very abundant in moist woods.

#### OPHIOGLOSSACEAE

*Botrychium virginianum* (L.) Sw.

Common in deep woods.

#### EQUISETACEAE

*Equisetum arvense* L.

Common everywhere on roadsides and in margins of fields.

*Equisetum hyemale* L. var. *robustum* (A. Br.) A. A. Eaton.

On rocks.

DEPARTMENT OF BOTANY,

UNIVERSITY OF WISCONSIN

## NOTES ON PARASITIC FUNGI IN WISCONSIN—IX

J. J. DAVIS

The greater part of the field work in 1920 was done along the lower Wisconsin and the Mississippi river, the Chippewa and its tributaries, the Yellow, the Fisher, and the Jump rivers. The season was an unfavorable one because of low precipitation, which however allowed an unusual proportion of working days.

*Plasmopara acalyphae* Wilson previously known only from the type station at Madison was found in July 1920 at Caryville in the Chippewa valley. As usual the development of conidiophores was scanty. [Collected since at Lone Rock, Arena and Oconto but always scanty.]

*Plasmopara obducens* Schroet. in summer is sometimes confined to small angular leaf areas which become brown, thus causing spotting of the affected leaves. The summer development of this mildew is more common northward.

What is presumed to be mycelium and conidia of *Sphaerotheca humuli* (DC.) Burr. is sometimes abundant on leaves of *Rubus allegheniensis* at Madison during the early part of the season, disappearing in summer without development of perithecia. It has been noticed that the thickened leaves of the plants bearing *Caeoma* are especially liable to this infection.

In a collection on twigs and young leaves of *Physocarpus opulifolius* from Fish Creek referred to *Sphaerotheca humuli* (DC.) Burr. the perithecia bear long tapering appendages like those of *Podosphaera leucotricha* (E. & E.) Salmon in addition to short rhizoid basal ones. These long appendages are not apical, however, but basal or equatorial, and the spores are not crowded in the ascus. Nevertheless the *Sphaerotheca* would appear to be the "next of kin" to the apple mildew. The mildew on *Physocarpus* appears to over winter in the twigs or buds.

*Phyllachora oryzopsidis* Theiss. & Syd. has been collected on *Oryzopsis asperifolia* at Mosinee. The collection was made in

September and the spores are smaller than indicated in the description.

For the parasite recorded in "Notes" V, p. 696, under the name *Lophodermium lineare* Pk. (*Rhytisma lineare* Pk., *Hypoderma lineare* Pk.) von Hoehnel has proposed a new genus, *Bifusella* (*Ann. Mycol.* 15:318-19.)

In "Notes" IV pp. 683-4 reference was made to a group of variable Sphaerioidaceae on *Atriplex* and *Chenopodium* members of which have been referred to *Phyllosticta*, *Ascochyta*, *Diplodina*, *Septogloeum*, *Stagonospora*, *Phleospora* and *Septoria* and to the reference of the group as a whole to *Stagonospora atriplicis* West. by Lind and to *Septoria chenopodii* West. by Grove. In a discussion of some members of this group by J. B. Ellis the conclusion was reached that "This variability would seem to strengthen the supposition that all the forms here enumerated may be referred to *Septoria (Phyllosticta) atriplicis* Desm." (*Journ. Mycol.* 4:117-18 [1888].) A parasite collected on *Chenopodium album* at Caryville July 21, 1921, appears to be an extreme variant of this group because of the long and slender sporules. The following notes were made: Spots suborbicular, immarginate, light yellow to yellowish green, averaging about  $\frac{1}{2}$  cm. in diameter; pycnidia amphigenous, scattered evenly over the spots; sporules discharged in colorless cirri, hyaline, straight or curved, 1-3 septate,  $24-67 \times 2\frac{1}{2}-3\frac{1}{2}\mu$ . The sporules often appear continuous in a water mount. Apparently they are catenulate, their length depending upon the number of abstrictions of the primary sporule.

In a collection of *Septoria aquilegiae* Penz. & Sacc. from Durand (July 12, 1920) the sporules are mostly about twice the typical length but without noticeable increase in diameter.

*Septoria ampelopsidis* Ellis appears to be a better developed state of the parasite recorded in the provisional list under the name *Septogloeum ampelopsidis* (E. & E.) Sacc. This form with definite pycnidia and long and slender sporules has been collected on *Psedera* at Madison, Wausau and Durand. I have labeled it *Septoria ampelopsidis* (E. & E.) Ellis.

In a collection of *Septoria* on *Cicuta maculata* made at Weyerhaeuser, September 9, 1918, the pycnidia are borne on small (1 mm. or less) subcircular white arid spots having a dark reddish brown border; the globose pycnidia are 80-85 $\mu$  in diameter, the sporules

30–45x1–1½ $\mu$ . It was labeled provisionally *Septoria umbelliferarum* Kalchb.

In "Notes" V it was stated that while in *Gloeosporium caryae* Ell. & Dearn. as found on *Carya ovata* the acervuli are hypophyllous in the collections on *C. cordiformis* they are epiphyllous. In a collection on the latter host made at Caryville in 1920 they are amphigenous.

In a collection of *Marssonina fraxini* Ell. & Davis from the Mississippi river bottoms at Glen Haven the sporules range from 30–50x2½–4 $\mu$ . No matter what the length of the sporule but a single septum appears.

R. E. Stone states that the ascogenous state of *Marssonina potentillae* (Desm.) Magn. is *Mollisia earliana* (E. & E.) Sacc.

In the parasite recorded as *Cylindrosporium clematidis* in the provisional list the sporuligerous stroma, under favorable conditions, forms a hollow sphere and the spore body is therefore a pycnidium.

In "Notes" IV, p. 687 *Septocylindrium caricinum* Sacc. was recorded as occurring in Wisconsin. Examination of the specimen on *Carex grisea* from Blue Mounds however reveals only tufts of hyphae indistinguishable from the conidiophores of *Cercospora caricina* Ell. & Dearn. which are sometimes nearly or quite hyaline. The *Septocylindrium* record therefore should be stricken out.

*Cercospora apocyni* E. & K. and *Cylindrosporium apocyni* E. & E. sometimes occur on the same spots. May it be that they are conidial forms of one species?

Specimens of the parasite on *Populus tremuloides* referred to *Cladosporium subsessile* Ell. & Barth. have been collected in which the tufts are scattered over unaltered portions of the leaves.

W. B. Tisdale has shown the connection between *Heterosporium gracile* Sacc. and the ascigerous stage *Didymellina iridis* (Desm.) Hoehn. (*Phytopathology* 10:153–4.)

*Cercospora arctostaphyli* Davis (*Trans. Wis. Acad.* 18:268) seems to have been founded upon a misapprehension. There is no specimen in the University of Wisconsin herbarium and the characters ascribed are those of *Cercospora gaultheriae* E. & E. It should be stricken out.

In "Notes" V p. 694 reference was made to a small collection on *Ambrosia trifida* from Maiden Rock which was referred to *Entyloma polysporum* (Pk.) Farl. This form with definite, orbicular, yellow, thickened, concavo-convex spots is however merely a late stage of *E. compositarum* Farl. although it differs strikingly in appearance from the earlier conidiophorous state. The spore walls do not become thick. Field observation is said to indicate that *Entyloma calendulae* (Oud.) D By. as it occurs in Europe is composed of races adapted to various genera of Compositae and H. & P. Sydow have proposed eight binomials for the designation of these races (*Ann. Mycol.* 16:244). The same kind of evidence indicates that an equal number of races of *Entyloma compositarum* Farl. exist in Wisconsin but I see nothing to be gained by using binomials for them as it would tend to obscure their very close kinship. It would require a large amount of experimentation to demonstrate that under no circumstances is there passage from one host genus to another. There seems to be a very close adaptation of parasite to host in the Ustilaginales in general and with that in mind the citation of the host gives the information in this case that would be conveyed by a binomial without obscuring the conception of phylogenetic unity. It seems quite possible that no violence would be done in considering *E. calendulae* (Oud.) D By. and *E. compositarum* Farl. as two geographical series of races of a single species.

In Notes II p. 106 it was stated that *Uromyces graminicola* Burr. had been collected at Madison on the railroad right of way. It was not again observed until 1920 when it was found at Durand in the western part of the state.

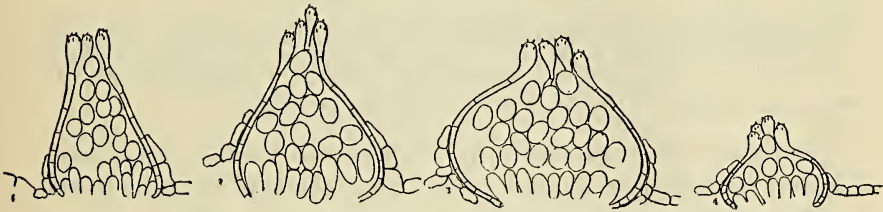
For the rust on *Koeleria cristata* having its aecial stage on *Liatris* I am using the designation *Puccinia koeleriae-liatridis* instead of *P. liatridis* Bethel. *P. koeleriae* Arth. with aecia on *Berberis* is considered to be distinct.

*Puccinia pustulata* (Curt.) Arth. with aecia on *Comandra* is treated as a race of *P. andropogonis* Schw. in *North American Flora*.

*Puccinia simillima* Arth. is united with *P. magnusiana* Koern. in *North American Flora*.

In the provisional list *Rubus idaeus aculeatissimus*, *R. occidentalis* and *R. triflorus* were given as hosts of *Pucciniastrum arcticum*

*americanum* Farl. The collections on *Rubus triflorus* however should be referred to the type while I find no specimens in the herbarium which I can determine as being on *R. occidentalis*. A specimen on this host collected by B. O. Dodge in Wisconsin at Algoma was reported by Arthur as *P. arcticum* but Dr. Arthur informs me that this was an error and that the specimen is of the *americanum* type which is not rare in Wisconsin on the red raspberry and that the host is *R. strigosus*. Arthur has proposed the raising of the variety *americanum* Farl. to specific rank (*Bull. Torr. Bot. Club* 47: 468) but certain forms on *Rubus idaeus aculeatissimus* having globose peridia seem closely allied to the type.



FIGS. 1-3. Sections through uredo sori of *Pucciniastrum* on *Rubus idaeus aculeatissimus*.

FIG. 4. Section through a uredo sorus of *Pucciniastrum* on *Rubus triflorus*.

Drawn by E. M. Gilbert with the aid of camera lucida. Fig. 4 was drawn from a small sorus and the disparity in size is somewhat exaggerated.

For the *Abies-Salix* rust recorded in "Notes" II & III under the binomial *Melampsora arctica* Rostr. Arthur proposes *M. americana* (*Bull. Torr. Bot. Club* 47:465-68.) Besides the localities which he gives the *Caeoma* has been collected in Wisconsin at Mountain and at Kelly lake in Oconto county and at Solon Springs. All of the localities are in either the northeastern or the northwestern corner of the state. Various collections of uredinia and telia on species of *Salix* have been referred to this species with doubt as they do not seem to be readily separable by their morphological characters from those of *Melampsora bigelowii* Thuem.

#### ADDITIONAL HOSTS<sup>o</sup>

Not previously recorded as bearing the parasites mentioned in Wisconsin.

*Synchytrium aureum* Schroet. On *Hydrocotyle americana* Caryville. Many leaves bore the parasite at this restricted station but the sori were much scattered; only one or very few on a leaf.

*Peronospora leptosperma* DBy. was collected at Jump River on a host that was referred to *Artemisia serrata*.

*Peronospora rubi* Rabh. was found in June, 1920, at Blue Mounds on *Rubus allegheniensis* growing along the railroad. The mildew was apparently confined to plants parasitized by *Caecoma*.

*Bremia lactucae* Regel. On *Lactuca Scariola integrata*, Madison.

*Basidiophora entospora* Roze & Cornu. On *Aster Tradescanti*. Madison. Rather abundant on this host in the autumn of 1920. .

*Gnomonia ulmea* (Schw.) Thuem. Immature material was collected on *Ulmus racemosa* at Nekoosa in September.

In September, 1919, *Phyllachora* on *Melica striata* was collected at Mosinee. The material is immature but the characters of the ascomata are not those of *Phyllachora melicae* Speg.

*Phyllosticta phomiformis* Sacc. On *Quercus bicolor*. La Crosse. Globose, dark brown, opaque cells 7-10 $\mu$  diameter are also found in this collection.

*Phyllosticta grossulariae* Sacc. On *Ribes oxycanthoides*. Durand. Sporules smoky tinted.

*Septoria noctiflorae* Ell. & Kell. On leaves and calyces of *Silene nivea*. Durand. In the collection referred to this species the sporules are 30-45x1 $\frac{1}{2}$ -2 $\frac{1}{2}$  $\mu$ , continuous, but the material is not mature.

*Septoria gei* Rob. & Desm. On *Geum canadense*. Glen Haven. The pycnidia are imperfect in these specimens.

*Septoria scrophulariae* Pk. On *Scrophularia leporella*. Glen Haven.

*Septoria stachydis* Rob. & Desm. On *Stachys palustris*. Coon Valley.

*Septoria commonsii* Ell. & Evht. On *Cirsium discolor*. Durand.

*Phleospora ulmi* (Fr.) Wallr. On *Ulmus fulva*. Fountain City.

In "Notes" VII mention was made of the fact that *Gloeosporium salicis* West. had been found in Wisconsin on foreign species of *Salix* only. In 1919 a tree of *Salix alba vitellina* bearing the *Gleo-*



*sporium* was observed at Fish Creek and under it a shrub of *Salix lucida* also bearing the *Gloeosporium*.

*Gloeosporium fraxineum* Pk. On *Fraxinus pennsylvanica*. Mosinee.

*Gloeosporium aridum* Ell. & Hol. On *Fraxinus nigra*. Caryville.

*Colletotrichum graminicolum* (Ces.) Wilson. On *Melica striata*. Mosinee. A *Colletotrichum* which was abundant on leaves of *Carex eburnea* at Fish Creek I do not distinguish from this species.

*Marssonina rhabdospora* (E. & E.) Magn. On *Populus tremuloides*. Millston, Cornell and Holcombe. My observation of this parasite does not lead me to look with favor on the suggestion of von Hoehnel that it is a form of *Septoria populi* Desm.

The parasite recorded under the name *Marssonina potentillae tormentillae* Trail in "Notes" III p. 259 was collected on *Rubus canadensis* at Tomahawk but immature or imperfectly developed as usual. Collections of a similar character were made on a host referred to *Rubus hispidus* at Millston in 1912.

*Cylindrosporium vermiforme* Davis. On *Alnus crispa*. Minocqua. In the collection on this host, which was made in August, the sporules are slender, being but about  $3\mu$  thick.

*Ramularia lysimachiae* Thuem. On *Lysimachia terrestris*. Vilas County and Holcombe. Conidiophores up to  $40\mu$  long.

*Ramularia virgaureae* Thuem. On *Solidago nemoralis*. Caryville.

*Ramularia asteris* (Phil. & Plowr.) Bubak. On *Aster lateriflorus*. Nekoosa. *Aster Tradescanti*. Caryville and Madison.

*Cercospora pyrina* Ell. & Evht. On *Pyrus ioensis*. Nekoosa.

A specimen on *Erigeron annuus* collected at Madison in September and referred to *Cercospora cana* Sacc. bears conidiophores  $50-100 \times 3-6\mu$ .

*Cladosporium subsessile* Ell. & Barth. On *Populus grandidentata*. Muscoda.

*Cladosporium triostei* Pk. On *Triosteum aurantiacum*. Glen Haven. In the material that I have seen the patches of conidio-

phores may precede the spotting, the conidia are devoid of apical papillae and the narrow base is truncate.

*Cercospora caricina* Ell. & Dearn. On culms, leaves and bracts of *Cyperus Schweinitzii*. Caryville.

*Cercospora oxybaphi* Ell. & Hals. On *Oxybaphus hirsutus*. Meridean.

*Cercospora velutina* Ell. & Kell. On leaves and stipules of *Baptisia bracteata*. Caryville.

The *Cercospora* that was tentatively referred to *C. flagellifera* Atk. in "Notes" VIII has been collected at Glen Haven on what was taken to be *Lespedeza frutescens*.

*Cercospora viciae* Ell. & Hol. On *Lathyrus palustris*. Caryville.

From the examination of a collection on *Solidago serotina* made at Durand August 18, 1920, the following notes were made: Spots angular, blackish brown becoming alutaceous and finally white and arid especially above, 1-2 mm. in diameter; conidiophores hypophyllous, single, in pairs or in small fascicles, erect, simple, terete and continuous or torulose and septate, fuligenous, 33-147x4-6 $\mu$ ; conidia obclavate, straight or but little curved, subhyaline, 67-200x4-6 $\mu$ . Although the spots are smaller and more definite and the conidiophores and conidia of a fuligenous cast rather than brown I have referred this provisionally to *Cercospora stomatica* Ell. & Davis as perhaps a modified form on a different species of host.

Of a collection on the same species of host made at La Crosse August 24, 1920, it was noted that the spots are definite, angular, brown, mostly 1-2mm. in diameter; the conidiophores having more or less of a fuligenous coloration, 33-63x4-6 $\mu$ , the conidia hyaline, upwardly attenuate, up to 110 $\mu$  or more in length by 3-4 $\mu$  thick. I was at first inclined to consider this to be a form of *Ramularia virgaureae* Thuem. modified by the dry weather but it can hardly be distinct from the collection referred to above.

On some of the leaves of the Durand material are small hypophyllous patches of *Ramularia* having straight, hyaline, subulate

conidiophores, 15–25x2 $\mu$  and catenulate, hyaline conidia which are straight, cylindrical with acute ends, 10–30x1½–2 $\mu$ . I have labeled this *Ramularia virgaureae* Thuem. Macroscopically the frost like patches look like those of *Cereosporella*.

*Schizonella melanogramma* (DC.) Schroet. On *Carex longirostris*. Madison. (J. R. Heddle.)

*Entyloma compositarum* Farl. On *Ambrosia psilostachya*. Tomahawk. This host was given in Trelease's Preliminary List and should have been included in the provisional list.

Of a *Uredo* collected at Cadott, July 23, 1920, on *Carex intumescens* Dr. Arthur reports, "appears to me to belong to *Uromyces minutus* Diet. rather than to *Puccinia minutissima*. I judge this from the fact that the pores are almost entirely equatorial and also because the host is more closely of the character of the *Uromyces* hosts than of the *Puccinia* forms. It is just possible that these two rusts are correlated but as to that we have made insufficient study to say with certainty."

*Uromyces hedysari-paniculati* (Schw.) Farl. Uredinia and telia on *Desmodium canadense*. Westby.

A single spot of *Aecidium fraxini* Schw. (*Puccinia peridermiospora* (E. & T.) Arth.) on a leaf of *Fraxinus nigra* was collected at Caryville.

*Puccinia graminis* Pers. Telia on *Agropyron tenerum*. Mosinee.

In "Notes" II *Puccinia gigantispora* Bubak was recorded from Glen Haven on a host that was not determined as between *Anemone virginiana* and *A. cylindrica*. A collection of aecia and telia from the same locality made in 1920 is on *A. virginiana*.

Dr. Arthur is of the opinion that the aecia and telia in these collections are not genetically related but are aecia of *Puccinia agropyri* E. & E. and telia of *Puccinia anemones-virginianae* Schw.

*Puccinia absinthii* DC. Uredinia on *Artemisia ludoviciana*. Prairie du Chien and Caryville.

*Sclerotium deciduum* Davis occurred at Caryville in 1920 on *Aster paniculatus* or an allied species.

## ADDITIONAL SPECIES

Not previously recorded as occurring in Wisconsin.

*Plasmopara cubensis* (B. & C.) Humphrey. On *Cucumis sativa* (cult.). Madison. The first collection of this parasite in Wisconsin, to my knowledge, was made in 1920. It is hoped that it was merely casual.

*Eocronartium muscicola* (Fr.) Fitzp. (*Typhula muscicola* (Pers.) Fr.) has been collected a number of times in Wisconsin on unidentified mosses. Most of the collections were made by Cheney in the northern part of the state.

*Cordyceps clavulata* (Schw.) Ell. & Evht. On scale insects (Lecanium) on *Fraxinus nigra* and *Ilex verticellata*. Hannibal. Very abundant on the black ash in 1920; seen on but two plants of Ilex. Immature specimens on *Lecanium corni* collected by J. G. Sanders in 1913 are probably of this species. Apparently parasitic on and destructive to the Lecanium.

*Phyllosticta phaseolina* Sacc. On *Strophostyles helvola*. Cassville. The flattened pycnidia with dark and much thickened upper wall and pale basal wall have a leptostromatoid appearance.

*Phyllosticta fraxinicola* Curr. On *Fraxinus pennsylvanica*. Durand. Spots along the midvein, angular, pale margined; sporules 3-6x2½-3μ, smoky hyaline.

On looking over a collection of *Cercospora dioscoreae* E. & M. one of the leaves was found to bear *Phyllosticta dioscoreae* Cke. Many of the sporules are two celled.

*Marssonina thomasiana* (Sacc.) Magn. On *Evonymus atropurpureus*. Glen Haven. In the Wisconsin collection the leaves are largely unspotted but pale spots appear late and red bordered ones are numerous. The subcuticular acervuli are mostly epiphyllous, quite variable in size and soon naked. The sporules are 17-23x7-14μ, the lower cell narrower. In the description of the variety or "subspecies" *fautreyana* the width of the sporules is given as 4μ, but in Vestergrens *Micromycetes rariores selecti* 1240, said to have been submitted to Saccardo, it approximates that of the sporules in the Wisconsin collection.

A parasite that is probably conspecific with *Septogloeum convolvuli* Ell. & Evht. was collected on *Convolvulus spithameus* at Tomahawk August 22, 1919. The small, circular, pale brown spots are clustered on dead or dying leaf areas. The hyaline, straight, cylindrical sporules are  $24-36 \times 3-3\frac{1}{2} \mu$  becoming triseptate.

**Ramularia tenuis n. sp.**

Spots yellowish, becoming black with age, subcircular to angular, immarginate, 2–10mm. in diameter; conidiophores epiphyllous, densely fasciculate from a prominent stromatoid base, hyaline, subulate to cylindrical, simple, continuous, usually straight, apex sometimes oblique,  $10-20 \times 2-3\frac{1}{2} \mu$ , conidia hyaline, cantenulate, usually straight, fusoid to cylindrical, acute, continuous to triseptate,  $7-37 \times 1-3 \mu$ . On leaves of *Solidago latifolia*. Holcombe, Wisconsin. August 9, 1920. This may prove to be a form of *Cercosprella reticulata* Pk.

*Botrytis epichloes* Ell. & Dearn. On *Epichloe typhina* growing on *Glyceria nervata*. Hannibal.

*Fusicladium effusum* Wint. On *Carya cordiformis* at Muscoda on both sides of the Wisconsin river.

In these collections are spots 2–4mm. in diameter which are light brown above but much darker and less regular in outline below and also dark dead areas following the veins as well as indefinite marginal areas; the conidiophores are hypophyllous, septate, usually curved or undulate,  $40-140 \times 3 \mu$  in places swollen to  $5 \mu$  thick; the conidia are obovate to fusoid or amygdaliform, subtruncate at base, continuous,  $13-23 \times 6-7 \mu$ . The host tissue affected becomes friable. *Fusicladium caryigenum* Ell. & Langlois is perhaps the same parasite.

*Fusicladium cerasi* (Rabh.) Sacc. (*Cladosporium carpophilum* Thuem.) On fruit of *Prunus americana*. Caryville and Durand. This was abundant on wild plums in August, 1920. *Venturia cerasi* Aderh. is said to be the ascigerous stage (*Ann. Mycol.* 16: 81). Dr. G. W. Keitt informs me that the conidial form has been observed on cherries and also on leaves in Door county.

*Cercospora moricola* Cke. On *Morus rubra*. Millville. Conidia  $40-75 \times 3-3\frac{1}{2} \mu$ , becoming 3–6 septate; spots immarginate, indefinite below.

*Cercospora euonymi* Ellis. On *Evonymus atropurpureus*. Durand.

In this collection the conidiophores are hyaline,  $35-50 \times 3 \mu$  the hyaline conidia cylindrical to obelavate-cylindrical,  $30-50 \times 3-4\frac{1}{2} \mu$ . Despite the Mucedinous character and the smaller conidiophores and conidia it is unquestionably the parasite described under this name by Ellis and issued in *Fungi Columbiani*, 2211. The white spots with the broad dark purple border are conspicuous.

*Cercospora teucrui* Ell. & Kell. On *Teucrium canadense*. Caryville.

*Ustilago hypodytes* (Schlecht.) Fr. On *Stipa spartea*. Meridean.

*Entyloma linariae* Schroet. var., *gratiolae* n. var. Causing spots which are orbicular, yellowish white, 1mm. or less in diameter or larger and indefinite; spores broadly elliptical to globose with epispore varying from nearly smooth to verrucose,  $13-18 \mu$  long. In leaves of *Gratiola virginiana*. Cadott, Wisconsin, July 22, 1920. The epispore in *Entyloma linariae* Schroet. is variously described by authors as being smooth, irregularly angularly thickened or as having a wavy outline because of low projections. In the collection referred to here some of the spores are studded with pale verrucosities which are perhaps the remains of the gelatinized hyphae. The form on this host is probably physiologically distinct from the var. *veronicae* Wint. (*E. veronicae* Lagh.) as well as from the type.

#### HERBARIUM OF THE UNIVERSITY OF WISCONSIN, MARCH, 1921

##### NOTES ON DISTRIBUTION AND ABUNDANCE

It is purposed to supplement the list of parasitic fungi occurring in Wisconsin with some notes on the distribution and frequency of the species in the state based upon the specimens preserved in the Davis and the University of Wisconsin herbaria and field observation. In attempting this one meets the fact that infection is dependent on variables and hence a parasitic flora is far from uniform. This seems to be especially true of those forms which infect by means of zoospores.

*Synchytrium cellulare* Davis. Where first found, at Devils Lake, (1913) the station, the bottom of a kettle hole, was very

restricted and the parasite disappeared therefrom in 3 or 4 years. It was not seen again until found at Babcock (1919) again very restricted in a low spot in the river bottoms. In 1920 it was found at Caryville, this time in more abundance, in an oxbow of Coon creek where it flows through the bottom lands along the Chippewa river and again in small quantity at Durand on the bank of the Eau Galle river near its mouth. From the situations in which this parasite has been observed it would appear that infection of the host is favored if the water in which the zoospores develop is impounded, thus preventing the carrying away of the infecting agents.

*Synchytrium scirpi* Davis. The collections of this form have been made only in the vicinity of Racine. It was first observed in 1904 southwest of the city and later northwest also, and appeared in the same places in successive years. It has been found upon the single species of host *Scirpus atrovirens*. It is possible that it is a form of the following species.

*Synchytrium aureum* Schroet. To this species are referred collections on a considerable number of hosts of widely different affinities and additions are made to the list yearly. When young and especially on succulent hosts the sori, as seen through a hand lens, are golden yellow, the color due apparently to the content of yellow oil. When older this disappears and the sori, in section are whitish. I have not seen an authentic specimen of *Synchytrium globosum* Schroet. but judging from the description some of the Wisconsin collections could be placed in that species. My observations lead me to suspect, however, that they represent a single species in different stages and on hosts of different character. The distribution is quite general as is indicated by the following list of collections:

*Clintonia borealis*, Athelstane, July 24, 1915.

*Geum virginianum*, Berryville, July 3, 7 and 14, 1892; August 30, 1892; June 10, 1894; October 9, 1894. Some of these are labelled "*Geum album*," (*G. canadense*.)

*Geum strictum*, Two Rivers, July 17, 1918.

*Rubus triflorus*, Turtle Lake, September 3, 1914; Solon Springs, August 6 and 14, 1915; Two Rivers, July 17, 1918; Bruce, September 4, 1918; Mosinee, September 1, 1919.

*Rubus hispidus*, Millston, August 26, 27, 28, 1912; August 17, 19, 1915; July 21, 22, 1916; Athelstane, August 26, 1913; Wild Rose, July 9, 1918.

*Rubus villosus* (?), Millston, September 26, 1912.

*Viola pallens*, Solon Springs, June 17 and 23, 1914; Athelstane, July 27, 1915.

*Viola pubescens*, Barryville, July 3 and 9, 1892; Somers, June 22, 1902; Wild Rose, July 3, 1918.

*Viola conspersa*, Solon Springs, August 14, 1915.

*Viola sp. indet.*, Solon Springs, August 7, 1915.

*Hydrocotyle americana*, Caryville, August 16, 1920.

*Lysimachia terrestris*, Millston, September 26 and 27, 1912.

*Halenia deflexa*, Solon Springs, August 7, 1915.

*Lycopus uniflorus*, Millston, September 26, 1912; Babcock, September 11, 1919.

*Pedicularis canadensis*, Racine, June 29, 1907.

*Rudbeckia laciniata*, Bruce, September 6 and 7, 1918.

*Petasites palmatus*, Prentice, August 18 and 19, 1918.

*Prenanthes alba*, Kenosha, July 4, 1907.

*Synchytrium asari* Arth. & Hol. This maintained itself from 1897 to 1902 at a station in southeastern Wisconsin. In 1908 it was observed in small quantity near Mellen in the northwestern part of the state. I have not seen it since.

*Synchytrium pulvereum* Davis. Found only in Rusk county in the north central part of the state. It was abundant at one station subject to overflow from a creek. [This has since been collected at White Lake and Sauk City.]

*Synchytrium anemones* (DC.) Wor. In Wisconsin, as elsewhere, this well marked species is of wide distribution and varying abundance. As is apt to be the case with common species it is not as well represented in the herbaria as are some that occur less frequently.

*Synchytrium decipiens* Farl. is the most frequent, abundant, and conspicuous species of the group. By some mycologists only



the first of these species is referred to *Synchytrium*, the last one to *Woroninella* and all of the others to *Pycnochytrium*. If one may borrow from the usage in the rusts and represent repeating spores by II and resting spores by III they could be presented thus:

II, III *Synchytrium*.

III *Pycnochytrium*

II *Woroninella*

*Physoderma menyanthis* (DBy). Collected but once (1902) near Found lake in the northern part of the state. But little was seen.

*Physoderma vagans* Schroet. But a single scanty collection has been made of this. It was found on bottom lands of the Wolf river. [Collected since at Spring Green.]

*Cladochytrium maculare* (Wallr.) has been collected only in the southern portion of the state (Kenosha, Racine, and Dane counties) where it is not frequent but sometimes rather abundant and able to maintain itself in one station for several successive years.

*Urophlyctis major* Schroet. Observed only in the northeastern part of the state in Kewaunee, Oconto and Marinette counties. It is infrequent.

*Urophlyctis pluriannulata* (B.&C.) Farl. Not frequent but sometimes locally abundant on *Sanicula* in both southern and northern Wisconsin. On *Zizia aurea* it has been seen in but one station. This was in 1907 and no trace of it was found on this host at the station in subsequent years.

*Albugo bliti* (Biv.) Kuntze. Frequent and abundant on *Amaranthus retroflexus* and *hybridus*, often with development of abundant and conspicuous oospores; infrequent on other species and on *Acnida*.

*Albugo portulacae* (DC.) Kuntze. Not infrequent and sometimes abundant.

*Albugo candida* (Pers.) O. Kuntze. Frequent and often abundant on various *Cruciferae*.

*Albugo tragopogonis* (DC.) S. F. Gray. Frequent, although on some of the hosts it is but rarely seen. It is more frequent prob-

ably on *Cirsium muticum* than on any other of the hosts. It is sometimes very abundant on cultivated *Tragopogon*.

*Phytophthora thalictri* Wilson & Davis. This occurs throughout the state and is collected every year. There are no collections on *Thalictrum dioicum*. As *T. revolutum* occurs in but the south-eastern corner of the state *T. dasycarpum* is the usual host.

*Phytophthora infestans* (Mont.) DBy. In Wisconsin, as elsewhere, there is wide fluctuation in the frequency and abundance of this parasite.

*Bremia lactucae* Regel. Frequent and abundant, especially on *Lactuca spicata*. It has not been collected often on cultivated lettuce in the open but is often abundant under glass.

*Plasmopara humuli* Miyabe & Takahashi. In southeastern and southwestern Wisconsin. A scanty development has been seen also in central Wisconsin. It appears to be indigenous. It was collected at Caryville in the Chippewa valley in July, 1920, with oospores.

*Plasmopara pygmaea* (Unger) Schroet. Frequent and abundant on *Hepatica* and *Anemone quinquefolia*. The var. *fusca* (Pk.) Davis has been collected in southern Wisconsin and on *Hepatica* only. This form is peculiar in not developing conidia.

*Plasmopara ribicola* Schroet. Although some of the hosts occur throughout the state this has been observed in the northern part of the state only, the southernmost localities being in Shawano county. Within its range it is not infrequent and fairly abundant on the hosts of northern range *Ribes prostratum* and *R. triste*.

*Plasmopara geranii* (Pk.) Berl. & DeToni. Widely distributed on *Geranium maculatum*.

*Plasmopara obducens* Schroet. Frequent throughout the state in spring, less so in summer when it is more often found northward.

*Plasmopara acalyphae* Wilson. This has been found only at a station near Madison and in very small quantity at Caryville. It is inconspicuous and as a rule very few conidiophores are developed. [Since collected at Arena and at Lone Rock and a trace at Oconto.]

*Plasmopara viticola* (B.&C.) Berl. & DeToni. A common and abundant species.

*Plasmopara australis* (Speg.) Swingle. Frequent and abundant in the southwestern quadrant of the state.

*Plasmopara viburni* Pk. The only Wisconsin collections were made at two localities in Marinette county in August, 1913.

*Plasmopara cephalophora* Davis. While this has been recognized but recently it has been collected on the banks of the Wolf, the Wisconsin, and the Chippewa rivers and is probably not rare.

*Plasmopara halstedii* (Farl.) Berl. & DeToni. Frequent and abundant. It is perhaps a congeries of host-linked races. It usually occurs upon a single species of host at any particular station.

*Peronospora schleideni* Unger. This is reported to have occurred sporadically and sparingly about Madison.

*Peronospora urticae* (Lib.) DBy. This was recorded by Trelease in the Preliminary List of Parasitic Fungi of Wisconsin (1884) as having been collected at Kirkland (now Devils Lake) and La Crosse. Dr. E. A. Burt kindly examined the Trelease herbarium at the Missouri Botanical Garden and found a specimen from "Kirkland." No collections have been made since in Wisconsin.

*Peronospora polygoni* Thuem. This has been collected in the southwestern part of the state along the Mississippi and lower Wisconsin and Chippewa rivers and in Kenosha county in southeastern Wisconsin.

*Peronospora effusa* (Grev.) Rabh. Frequent and abundant especially on *Chenopodium album*.

*Peronospora obovata* Bon. A single collection made in 1911. The host is rare in Wisconsin.

*Peronospora silenes* Wils. Collected at Necedah and Adams only. Local.

*Peronospora alsinearum* Casp. Observed at Racine and Madison only. Local and not permanently established.

*Peronospora ficariae* Tul. Rather common throughout the state.

*Peronospora corydalis* DBy. Rare and local. It has been collected in the southern part of the state only.

*Peronospora parasitica* (Pers.) Tul. Frequent and abundant on various species of Cruciferae. It is probably a group of host-linked races.

*Peronospora potentillae* DBy. Not infrequent on Agrimonia, Geum and Potentilla and perhaps includes three races which are host adapted.

*Peronospora rubi* Rabh. Infrequent. Most of the collections were made in northern Wisconsin but in 1920 it was found along the railroad at Blue Mounds where leaves infected by *Caeoma* seemed to be more susceptible. One of the specimens from north-western Wisconsin is on leaves bearing *Caeoma*.

*Peronospora trifoliorum* DBy. This is rather frequent in alfalfa fields but not destructive in Wisconsin. There is but a single specimen each on *Lupinus* and *Astragalus* in the herbarium, both from western Wisconsin.

*Peronospora viciae* (Berk.) DBy. This occurs rather frequently in the pea fields but does not do much damage to the crop.

*Peronospora viciae americana* Davis. Local on *Vicia americana* mostly in the western part of the state.

*Peronospora chamaesydis* Wils. This is probably more frequent than the small number of specimens would indicate as it is not conspicuous.

*Peronospora floerkeae* Kell. The collection made at St. Croix Falls by Holway in 1904 is the only one that has been made in Wisconsin.

*Peronospora arthuri* Farl. Not infrequent on *Oenothera biennis* to which it seems to be confined. It usually shows evidence of systemic infection of the host.

*Peronospora alta* Fckl. This is a frequent and abundant species.

*Peronospora calotheca* DBy. Not frequent but sometimes locally abundant. All of the specimens are from the southern half of the state.

*Peronospora leptosperma* DBy. This is a rare species in Wisconsin, being represented only from the following collections: Racine, 1897; Berryville, 1900; Shiocton, 1917.

*Basidiophora entospora* Roze & Cornu. This is probably more frequent than the specimens in the herbaria would indicate. It was especially abundant about Madison in 1920.

*Sclerospora graminicola* (Sacc.) Schroet. This again is doubtless more frequent than the few Wisconsin specimens would indicate.

*Protomyces andinus* Lagh. This was frequent and abundant on *Bidens* before 1911, but the only collections since were made along the Mississippi river. On *Ambrosia* it has continued to be frequent and sometimes abundant.

HERBARIUM OF THE UNIVERSITY OF WISCONSIN,  
MADISON, WISCONSIN, APRIL, 1921



## NOTES ON PARASITIC FUNGI IN WISCONSIN—X

J. J. DAVIS

The season of 1921 was characterized by high temperature and low humidity and was consequently unfavorable for the development of most fungous parasites. The low stage of water in the Wisconsin River, however, gave opportunity to explore bottom lands that are ordinarily difficult of access.

After one's conceptions of generalities have changed, there is a lag in the application of such changes to particulars. When the writer began the collection of data on the parasitic fungus flora of Wisconsin there was in his mind a conception of such a flora as something fixed, static; given time and application it could be fully set forth. The fact of quantitative variation was quickly brought home to him and was expressed in his first contribution. More slowly the conception of vegetation as dynamic and mutable has come to be applied to a special group in a local flora. The records are then seen as datum points having a time as well as a space value. This conception increases rather than lessens their value but shows no finality as a goal. It does not however at all lessen the importance of completeness in the record.

The downy mildews as they occur in Wisconsin are interesting from an evolutionary viewpoint. Typically they bear two kinds of spores, summer dispersion conidia and winter resting oospores, and cause local infections. In many species, however, general infection takes place and allows overwintering as mycelium. Such species show a tendency toward suppression of oospores and abundance of conidia. In *Plasmopara pygmaea* (Ung.) Schroet. each of these directions of change seems to have been followed. On *Hepatica* and *Anemone quinquefolia* and *A. canadensis* races producing local infections and both kinds of spores; on *Anemone quinquefolia* a race with general infections and suppression of oospores; on *Hepatica acutiloba* local infections, abundance of oospores and no conidia. The latter is what Peck described under the name *Protomyces fuscus* but which I have designated *Plasmopara pyg-*

*maea* var. *fusca* (Pk.). I take it that the state with local infections and both spore forms is the older and that the others have been derived therefrom.

*Synchytrium scirpi* Davis on *Scirpus atrovirens* previously known only from the vicinity of Racine was collected at Oconto in September, 1921, mostly in an abortive state, presumably because of the hot, dry summer. In examining sections of the leaves what appeared to be a Sphaerulina was observed and the following notes made: Perithecia sparse, innate, black, globose, 85–100 $\mu$  in diameter; asci sessile, fusoid-cylindrical, 60–70x16–18 $\mu$ ; spores long fusoid, slightly curved, hyaline, obtuse, 5-septate, 35–40x5–6 $\mu$ ; paraphyses none. The inconspicuous perithecia are too few to warrant taking the material as a type. [In 1922 *Synchytrium scirpi* was collected on the same species of host opposite Sauk City. There is also a specimen from Little Suamico.]

*Septoria rubi* West. was found by Roark to have an ascigerous stage for which he proposed the name *Mycosphaerella rubi* (*Phytopath.* 11:329, [1921]). Although the *Septoria* is abundant throughout the state he was able to find the *Mycosphaerella* only in Door county which lies between Green bay and lake Michigan.

*Piggotia vaccinii* Davis ("Notes" IX, p. 436, fig. 3) is doubtless conspecific with *Leptothyrium conspicuum* Dearn. & House (*N. Y. State Museum, Report of the Botanist for 1919*, p. 37, [1922] and is antedated thereby.

A parasite of *Gentiana Andrewsii* was collected in Wisconsin thirty odd years ago and sent to Ellis who identified it as *Depazea gentianaecola* Fr., but referred it to *Phyllosticta* (see N. A. *Phyllostictas* No. 176) and it was so recorded in the supplementary list. Baeumler in 1889 recorded as *Leptothyrium*, a fungus on *Gentiana* which he supposed to be the same as the one treated by De Candolle and Fries and used the specific name proposed by De Candolle. In compiling the provisional list there was no time to investigate such matters but simply to follow the Tom Johnson rule, "decide at once and be right half the time." On the principle that things that were equal to the same thing were equal to each other I used Baeumler's binomial. Dr. Brenckle sent me a specimen from North Dakota and I wrote him that it was the fungus recorded in the provisional list under the name *Leptothyrium gentianaecolum* (DC.) Baeuml. and he issued it in *Fungi Dakotenses* under that



name. This fall I took the matter up and find that it can not be referred to *Leptothyrium* but that it agrees with Allescher's description of *Asteroma gentianae* Fckl. (*Rabh. Krypt. fl. Pilze*: 7: 464). I have seen no specimens of *Sphaeria gentianaecola* DC., *Xyloma gentianaecola* DC., *Depazea gentianaecola* (DC.) Fr. and do not know their relationship to our parasite. Neither have I seen a specimen of Fuckel's *Asteroma gentianae*. As matters stand now, I am inclined to use Fuckel's name provisionally, as the fungus has the characters of *Asteroma*. [In 1922 this was collected on *Gentiana puberula* at Arena. Sometimes the proximal portion of the pycnidial wall is thin but distinct while the distal portion is thick and black while other pycnidia have a thick, black wall throughout.]

*Fusidium pteridis* Kalchbr. was recorded in Trelease's *Preliminary List of parasitic Fungi of Wisconsin* and was copied therefrom into the provisional list. In "Notes" V, p. 701, a parasite of *Pteris* was recorded under the name *Gloeosporium leptospermum* Pk. which is the same fungus. *Gloeosporium pteridis* Hark. as represented by Griffith's *West American Fungi* 324 and 324a and Jackson's No. 1688 is the same species. The synonymy is

*Fusidium pteridis* Kalchbr.

*Gloeosporium pteridis* Hark.

*Gloeosporium leptospermum* Pk.

*Gloeosporium pteridis* (Kalchbr.) Kabat & Bubak.

It is said to be a sporuligerous state of *Cryptomyces pteridis* (Reb.) Rehm. (*Gloeosporium obtegens* Syd. *Ann. Mycol.* 2:172), C. F. Baker, *Pacific Slope Fungi* 3757 can hardly be other than a profusely developed state of the same parasite. Another parasite of *Pteris* was recorded in the provisional list under the name *Marssonina necans* (E. & E.) Magn. The sporules of this fungus are developed in a pycnidium and it is referable to *Ascochyta* and does not differ from *Ascochyta pteridis* Bres. as represented in Krieger's *Fungi Saxonici* 989. The synonymy is:

*Gloeosporium necans* Ell. & Evht. *Journ. Mycol.* 4: 104, (October, 1888).

*Marsonia necans* (E. & E.) Sacc.

*Marssonina necans* (E. & E.) Magn.

*Ascochyta pteridis* Bres. *Hedwigia*, 1894.

*Ascochyta necans* (E. & E.) n. comb.

In specimens of *Ramularia desmodii* Cke. on *Desmodium illinoense* the penicillate conidiophoral fasciculi sometimes exceed  $100\mu$  in length.

In examining a collection of *Cerosporella cana* Sacc. on *Erigeron annuus* it was observed that the conidiophores ranged up to  $100\mu$  in length.

Specimens on leaves of *Crataegus* collected in 1890 were referred to Mr. J. B. Ellis for determination who reported as follows: "9039. *Phleospora oxyacanthae* (Kze. & Schm.) I think it must be, but your specimens are much better than any I have in my European collections." At the close of the letter he wrote: "I have had to examine the things in great haste but I think you will find them correct." In the Supplementary List the fungus was recorded under this name and carried from there to the Provisional List where by a slip the specific name was given as "crataegi". This was corrected in "Notes" III p. 254 and some remarks on the character of the parasite added which indicated that it could not be a *Phleospora*. To the notes there given, I would add that in some specimens the conidia have divided at some of the septa resulting in shorter conidia which sometimes becomes thicker,  $15-45 \times 3-7\mu$ . This is quite different from *Phleospora oxyacanthae* (Kze. & Schm.) Wallr., but appears to be *Cercospora mirabilis* Pk., for a specimen of which I am indebted to Dr. House which, however, lacks the differentiated conidiophores of *Cercospora*.

The first Wisconsin collection of *Cercospora* on *Smilax* was made at Racine. It was a form with small spots and preponderance of the dark border and was referred to *Cercospora mississippiensis* Tracy & Earle. Subsequent collections lead me to believe that there is but one species on *Smilax* in Wisconsin and that it is *C. smilacis* Thuem., as described and figured by Peck (*33d Report*, p. 29, figs. 1-3). In different collections the spots vary from 1 to 8 mm. in diameter, the border varies in width and intensity of color, the conidiophores are longer or shorter ( $30-83 \times 4\mu$ ) and the conidia are variable in size ( $30-115 \times 4-5\mu$ ) and depth of color. They may be attenuate or subcylindrical and obtuse and, with the conidiophores, vary in septation. *Fungi Columbiani 2208* labeled *Cercospora mississippiensis* Tracy & Earle I have referred to *C.*

*smilacis* Thuem. Saccardo however thought the parasite described and figured by Peck to be distinct from *Cercospora smilacis* Thuem. and called it *C. smilacina* Sacc. (*Michelia* 2: 364). I have not seen European specimens but Peck accepted von Thuemen's description as applying to his species (*33d Report*, explanation of plate 2, footnote).

A collection of *Cercospora davisii* E. & E. on *Melilotus alba* made at Madison in June 1921 (Bensaude, McFarland, & Davis) bears conidiophores up to  $140\mu$  in length. Evidence accumulates that length of conidiophores and conidia in this and similar genera as a specific character is to be used with caution. A *Cercospora* occurring on dark areas on branches of *Melilotus alba* at Gays Mills is referred to this species. The conidia seen were only about  $3\mu$  thick.

*Cercospora epigaeina* Davis (*Trans. Wis. Acad.* 16: 758) is evidently not distinct from *C. epigaeae* Ell. & Dearn, which is the older name.

Examination of a collection of *Cercospora saniculae* Davis from Blue Mounds shows that when not crowded the conidiophores are not always straight, that they sometimes occur on the upper leaf surface and that the longest ones may attain a length of  $60\mu$ .

*Cercospora platyspora* Ell. & Holw., is doubtfully distinct from *Cercospora sii* E. & E. and from *Fusicladium depressum* (B. & Br.) Sacc. Specimens on Angelica were issued in *Fungi Columbiani 1924* under the name *Didymaria platyspora* (Ell. & Holw.), but *F. Col.* 4230 on *Taenidia integerrima* is labeled *Fusicladium depressum* (B. & Br.) Sacc.

In a collection of *Cercospora stomatica* Ell. & Davis made at Woodman, July 4, 1921, the conidia are narrow (about  $3\mu$ ) and of nearly uniform diameter throughout. A result perhaps of the hot, dry season.

*Doassansia ranunculina* Davis which had not been seen in Wisconsin for upwards of 20 years was collected at Shiocton in September, 1921. Although the host was abundant there was but very scanty development of the parasite.

*Puccinia zygadeni* Trel. is merged into *P. atropuncta* Pk. & Cl. in *North American Flora*.

## ADDITIONAL HOSTS

Not previously recorded as bearing the fungi mentioned in Wisconsin.

It is customary in collecting in Wisconsin to find each year sori of *Synchytrium* on an additional host at a single station and in small quantity and they have usually been referred to *Synchytrium aureum* Schroet. Such a collection was made July 25, 1921, on leaves of *Acalypha virginica* in the Wisconsin River bottom lands at Lone Rock. In this collection the sori are first pale yellow becoming castaneous with age. The galls are hypophyllous, discrete, hemispherical, but little larger than the sori which are globose to elliptical, 125–175 $\mu$  in diameter with wall about 5 $\mu$  thick.

[Collected in 1922 at Arena and Prairie du Sac.]

*Peronospora ficariae* Tul. On *Ranunculus recurvatus*. Ridge-way.

*Peronospora calotheca* DBy. This was collected in small quantity on *Galium asprellum* at Madison in November, 1920.

*Basidiophora entospora* Roze & Cornu. On *Aster lateriflorus*. Muscoda.

*Erysiphe cichoracearum* DC. On *Vernonia fasciculata* and *Helenium autumnale*. Muscoda.

*Phyllactinia corylea* (Pers.) Karst. On *Betula nigra*. Richland County opposite Muscoda.

*Phyllachora graminis* (Pers.) Fkl. On *Elymus brachystachys*. Richland County opposite Muscoda.

A *Phyllachora* forming black patches with effused ascomata on leaves of *Panicum virgatum* has been collected at Muscoda. Provisionally it is labeled *Ph. graminis panici* (Schw.) Shear although it differs widely in macroscopic appearance from specimens on other species of *Panicum*.

*Phyllachora ambrosiae* (B. & C.) Sacc. (*Physalospora ambrosiae* E. & E.). On *Ambrosia psilostachya*. Muscoda.

*Pseudopeziza singularia* Pk. On *Ranunculus septentrionalis*. Blue River and Iowa County opposite Lone Rock.

*Phyllosticta apocyni* Trel. On *Apocynum androsaemifolium*. Ridgeway.

*Ascochyta pisi* Lib. On *Vicia angustifolia segetalis*. Barneveld and Ridgeway.

*Ascochyta lophanthi lycopina* Davis. This has been collected on *Lycopus virginicus* and it is quite possible that other collections are on this species of host.

*Darluca flum* (Biv.) Cast. On *Puccinia asteris* growing on *Aster Tradescanti*. Blue River. Two telial hosts were given in "Notes" VI, p. 707.

*Septoria annua* Ell. & Evht. On *Poa annua*. Black Earth. (McFarland & Davis.)

*Septoria caricinella* Sacc. & Roum. A specimen on *Carex chodorhiza* from Lost Lake, Vilas County (July 4, 1901) is referred to this species.

*Septoria polaris* Karst. Specimens on *Ranunculus septentrionalis* from Richland County opposite Muscoda are provisionally referred to this species. The sporules are  $20-30 \times 1-1\frac{1}{2} \mu$ .

*Septoria oenotherae* West. On *Oenothera rhombipetala*. Muscoda.

*Septoria sii* Rob. & Desm. On *Cicuta bulbifera*. Oconto.

*Septoria solidaginicola* Pk. On *Solidago patula*. Cecil. *Aster lateriflorus*. Woodman. Of the latter collection it was noted "not abundant on this host and some of the spots atypical".

*Septoria atropurpurea* Pk. On *Aster paniculatus*. Lone Rock. The strongly curved sporules range up to more than  $100 \times 1\frac{1}{2}-2 \mu$ .

*Phleospora ulmi* (Fr.) Wallr. On *Ulmus fulva*. Richland County opposite Boscobel. Sporules mostly about  $30 \times 7 \mu$ .

A Marssonina on leaves of *Salix lucida* collected at Shawano I do not distinguish from forms on *Populus* and have labeled it *Marssonina populi* (Lib.) Magn. The acervuli are amphigenous but more abundant and better developed below where they have a resinous appearance. The curved sporules are  $13-17 \times 3-4 \mu$ . A collection on *Populus balsamifera* from Little Suamico has hypophyllous subcuticular acervuli with sporules  $11-17 \times 3\frac{1}{2}-5 \mu$ .

*Marssonina potentillae* (Desm.) Magn. On *Fragaria virginiana*. Crandon and Little Suamico. Of the latter collection it was noted—Immaculate, sporules  $17-24 \times 3\frac{1}{2}-6\mu$ . On *Potentilla anserina*. Oconto.

*Septocylindrium concomitans* (Ell. & Holw.) Hals. On *Bidens vulgata puberula*. Wauzeka.

*Ramularia uredinis* (Voss) Sacc. On *Salix amygdaloides*. Oconto.

*Ramularia fraxinea* Davis. On *Fraxinus americana* (?) Gays Mills and Blue River. This parasite has been seen only in river bottom lands.

*Ramularia effusa* Pk. On *Gaylussacia baccata*. Ridgeway. Apparently causing defoliation.

*Ramularia dispar* Davis. A collection on *Eupatorium urticaefolium* from Crandon is referred to this species.

In a specimen on *Solidago serotina* from Gays Mills the conidiophores are mostly subulate,  $10-20 \times 3\mu$ , the conidia fusiform to cylindrical,  $7-36 \times 2\mu$ . This was referred to *Ramularia virgaureae* Thuem.

*Scolecotrichum graminis* Fkl. On *Dactylis glomerata*. Madison. (Bensaude, McFarland & Davis.)

*Cercospora diffusa* Ell. & Evht. On *Physalis heterophylla*. Oconto.

*Cercospora antipus* Ell. & Holw. On *Lonicera Sullivantii*. Werley. The brown, tufted conidiophores are  $40-70 \times 3\mu$ .

*Ustilago striaeformis*, (West.) Niessl. On *Agrostis alba*. Madison. (W. H. & J. J. Davis) Collected also on *Poa pratensis* at Madison by W. H. Davis.

*Urocystis agropyri* (Preuss) Schroet. On *Agrostis alba*. Madison. (W. H. Davis)

*Entyloma ranunculi* (Bon.) Schroet. Conidiophorous material on *Thalictrum dasycarpum* collected at Oconto September 8, 1921

I can not distinguish from this species either in the field or in the herbarium. Typical material of *E. thalictri* Schroet. was collected in the same locality.

*Uromyces appendiculatus* (Pers.) Lk. Uredinia on *Strophostyles helvola*. Richland County opposite Blue River.

*Puccinia graminis* Pers. Uredinia on *Poa annua*. Black Earth. (McFarland & Davis). Spores 17–24x13–17 $\mu$ .

*Puccinia peridermiospora* (E. & Tr.) Arth. On *Fraxinus pennsylvanica* and var. *lanceolata*. These are probably the most susceptible hosts of the *Aecidium* in Wisconsin.

*Puccinia polygoni-amphibii* Pers. Uredinia on *Polygonum Persicaria*. Oconto.

*Pucciniastrum myrtilli* (Schum.) Arth. Uredinia on *Gaylussacia baccata*. Oconto.

*Aecidium dicentrae* Trel. the type locality of which is in Wisconsin has been shown by Mains to be the aecial stage of a Melampsoraceous rust on *Laportea canadensis* (*Am. Journ. Bot.* 8: 445) which has been collected in Wisconsin at Hannibal, Jump River, Holcombe and Blue Mounds. For this Dr. Mains proposes the binomial *Cerotelium dicentrae* (Trel.) Mains & Anderson, a name which does not accord with the usage followed in this series of notes. [See Saccardo: *De Diagnostica et Nomenclatura Mycologica; admonita quaedam (Annales Mycologici* 2:197.) English translation in *Journal of Mycology* 10:111–2.] I am therefore using *Cerotelium urticastrum* Mains (*loc. cit.* 451).

#### ADDITIONAL SPECIES

Not previously recorded as occurring in Wisconsin.

In August 1892 a *Synchytrium* on *Ranunculus recurvatus* was collected in Kenosha County and the following description written and filed with the specimen. As it was not seen again, however, some doubt arose as to its being distinct and it was recorded under *S. aureum* Schroet. in the provisional list which is doubtless an aggregate species as treated in Wisconsin. In 1921 it was found on *Ranunculus septentrionalis* at the base of the Wisconsin River bluff in Iowa County opposite Spring Green readily recognizable as being the same as the original collection. I therefore publish the description.

**Synchytrium cinnamomeum** n. sp. Galls cinnamon brown, hemispherical to obtusely conical, scattered or aggregated, frequently confluent, 125–150 $\mu$  in diameter; resting sori solitary, globose to elliptical to pyriform, 42–66 $\mu$  in the longer diameter; wall brown, contents brown black, granular. On petioles and leaves of *Ranunculus recurvatus*, Somers, Wisconsin, August 13, 1892 (type). *Ranunculus septentrionalis*, Iowa County opposite Spring Green, July 20, 1921. Readily recognized by the brown color which suggests rust.

**Synchytrium nigrescens** n. sp. Sori hypophyllous, scattered, subepidermal, at first pale yellow with abundant oil content, becoming black with content in part black and granular, spherical to ovoid 80–180 $\mu$ ; wall thin, homogeneous, chitinous, black by reflected, fuscous by transmitted light, outer surface smooth or minutely tuberculate. But slight prominences are produced, the sori often extending through to the upper epidermis without causing hypertrophy. On *Aster lateriflorus* on bottom lands of the Wisconsin river at Spring Green, Lone Rock and Blue River.

**Plasmopara illinoensis** (Farl.) n. comb. On *Parietaria pennsylvanica*. This was described by Farlow (*Bot. Gaz.* 8: 332 [1883]) from collections made by Seymour at Quincy and Camp Point on the Mississippi river in southern Illinois. No further collections seem to have been made. Guy West Wilson gave a new description and referred it to his proposed genus *Rhysotheca* (*Bull. Torr. Bot. Club* 34: 407 [1907]). In 1921 it was collected at Blue Mounds, Ridgeway, Fennimore, Werley and Woodman. A collection from Blue Mounds made July 9 contains globose oospores 23–30 $\mu$  in diameter with wall 3–5 $\mu$  thick filling the rather thin-walled oogonia. Assuming that southern Wisconsin is the northern limit of this species its development was probably favored by the abnormally hot season of 1921.

**Phacidium taxi** Fr. On *Taxus canadensis*. Crandon. The ex-ciple is thick and black and ruptures irregularly in the center. The asci are clavate-cylindrical, about 50x6 $\mu$ . No mature spores were seen.

**Claviceps nigricans** Tul. Sclerotia on *Eleocharis palustris*. Sturgeon Bay (J. E. Sanders), Madison (J. R. Heddle).

**Phyllosticta congesta** Heald & Wolf (*Mycologia* 3: 8). On *Prunus pennsylvanica*. Devils Lake (C. E. Owens).



*Phyllosticta pyrolae* Ell. & Evht. Collected in small quantity and not quite mature on leaves of *Pyrola elliptica* at Blue Mounds.

*Phyllosticta steironematis* Dearn. & House. On *Steironema ciliatum*. Lone Rock.

*Phyllosticta verbascicola* Ell. & Kell. On *Verbascum Thapsus*. Barneveld.

*Phoma alliicola* Sacc. & Roum. A collection on *Allium canadense* from Madison is referred to this species. The ostiole is often gaping, the sporules 4–6x2–3 $\mu$ .

**Macrophoma arens** n. sp. Pycnidia black, scattered, subepidermal, globose, 130–150 $\mu$  in diameter; sporules narrow ovoid, becoming subfuligenous, 27x10 $\mu$  at maturity. On more or less of the distal portion of leaves of *Koeleria cristata* which become sere and involute. Boscobel, Wisconsin, July 5, 1921.

**Asteromella astericola** n. sp. Pycnidia epiphyllous on indefinite purple areas in compact orbicular groups, black, globose, 100–165 $\mu$  in diameter; wall parenchymatous of dark firm cells 6–10 $\mu$  in diameter; sporules sessile (?), hyaline, terete to fusoid-cylindrical, mostly straight, 20x30x3–4 $\mu$ . On *Aster lateriflorus*, Blue River, Wisconsin, August 3 and 4, 1921. It may be that this is a better developed form of *Asteromella asteris* Pk. (*Report for 1912*, p. 38).

**Stagonospora albescens** n. sp. Spots orbicular, sordid white, ½–2 mm. in diameter surrounded by a broad indeterminate reddish brown border; pycnidia few, innate, dark brown, globose, thick walled, about 150 $\mu$  in diameter; sporules hyaline, fusoid-cylindrical, straight or sometimes curved, 5–7 septate, 45–67x10–13 $\mu$ . On living leaves of *Carex tribuloides*. Muscoda, Wisconsin, October 1920. Macroscopically this resembles *Septoria caricinella* Sacc. sufficiently to have been mistaken for it in the field. The contents of the cells or cytoplasmic divisions are homogeneous.

May 13 and 19, 1921, spots were observed on leaves of a few plants of *Melilotus alba* at a station near Madison. The following notes have been made from these collections: Spots definite, circular to elliptical to irregular, argillaceous with a paler center, 1–10 mm. in diameter; pycnidia in the paler area, hypophyllous, exceptionally epiphyllous also, brown, globose to lenticular, ostiole circular with a dark margin about 30 $\mu$  across, 135–165 $\mu$  in diameter;

sporules cylindrical, hyaline, usually straight, sometimes slightly curved or bent, 1-3 septate, about 20 ("13-23", "10-27") $\times$ 3-3 $\frac{1}{2}$  $\mu$ . I have labeled it *Stagonospora meliloti* (Lasch) Petr.

Three collections on leaves of *Acer Negundo* were made in 1921 that were referred to *Septoria negundinis* Ell. & Evht. They are evidently members of the acericolous group referred to in "Notes" I, pp. 81-2. In the collection from Werley the round arid spots are but 2 to 3 times the diameter of the usually solitary pycnidia and the curved sporules 32-40 $\times$ 1 $\frac{1}{2}$ -2 $\frac{1}{2}$  $\mu$  indistinctly 3-septate. This is much like *Septoria saccharina* Ell. & Evht. The collection from Barneveld is similar with slightly greater range in spore length and septation not apparent. In the collection from Madison (Bensaude, McFarland & Davis) the spots are pale argillaceous with a narrow raised darker margin, amphigenous, circular to angular in outline, 1-3 mm. in diameter, often confluent; pycnidia one to few on the spot, hypophyllous, subepidermal, globose to lenticular, up to 180 $\mu$  in diameter; sporules hyaline becoming curved and 3-septate, 25-40 $\times$ 1 $\frac{1}{2}$ -2 $\frac{1}{2}$  $\mu$ . A collection made at Galesville in 1914 and recorded in "Notes" III, p. 264, as *Septoria acerella* Sacc. but belonging with these is similar, the sporules being 23-33 $\times$ 1 $\frac{1}{2}$ -2 $\frac{1}{2}$  $\mu$  becoming curved and triseptate. In this collection indefinite leaf areas upon which the small spots are numerous become dead and brown. In examining this epiphyllous subcuticular acervuli were seen bearing oblong hyaline sporules 10-13 $\times$ 4 $\mu$ . These collections are evidently *Septoria acerella* Sacc. as treated by Ellis in *Septorias of North America No. 160 (Journ. Mycol. 3: 79)* but subsequently described by Ellis & Everhart as a new species for which the name *Septoria negundinis* was proposed in the *Proceedings of the Academy of Natural Science, Phila.* for 1893, p. 165.

Of a *Septoria* on *Caeoma*-infected leaves of *Rubus allegheniensis* collected at Madison June 2, 1921, the following notes were made: Spots epiphyllous, circular to angular, subolivaceous, immarginate, 1-5 mm. in diameter, often confluent; sporules hyaline, usually curved, continuous, 30-50 $\times$ 1-2 $\mu$ . While it is possible that this is a form of *Septoria rubi* West. modified by the character of the substratum it has been kept separate under the name *Septoria comitata* n. sp. ad interim.

*Septoria lycopi* Pass. Collected on *Lycopus uniflorus* on the river bottoms opposite Muscoda in October 1920. This was a dry

season and the sporules are not well developed, being but about  $30 \times 1\frac{1}{2} \mu$ .

*Cylindrosporium caryogenum* Ell. & Evht. On *Carya cordiformis*, Werley and Woodman. This bears some resemblance to *Microstroma* in the field.

Of a collection on *Aster sagittifolius* obtained at Woodman July 4, 1921, and referred to *Septoria solidaginicola* Pk. the following notes have been made: Spots angular, limited by the veinlets, becoming confluent, reddish brown to pale brown, without halo, 2–7 mm. long, 1–2 mm. wide; pycnidia epiphyllous–innate, globose to ovoid, often with a black ring around the ostiole which is sometimes conical,  $60\text{--}90 \mu$  in diameter; sporules  $30\text{--}36 \times 1\text{--}1\frac{1}{2} \mu$ . *Septoria angularis* Tharp to which, judging from the description, this bears resemblance was described as having pycnidia  $75\text{--}80 \times 100\text{--}200 \mu$  and sporules  $35\text{--}50 \times 3 \mu$  (*Texas Parasitic Fungi, Mycologia* 9: 121). The name is antedated by *Septoria angularis* Dearn. & Barth. (*Mycologia*, 8: 103) on *Solidago latifolia* (Ontario, Dearness) in which the spots are said to be limited “when the pycnidia are well developed by a narrow, raised, sharply defined border”. The collection on *Aster sagittifolius* here referred to is quite similar to this as represented in *Fungi Columbiani* 4875. There seems warrant for the suspicion expressed by the authors that this may be *Septoria fumosa* Pk.

*Phleospora anemones* Ell. & Kell. On *Anemone virginiana*. Iowa County opposite Lone Rock. This forms a well-developed pycnidium and might be referred to *Septoria* without doing violence.

*Cylindrosporium guttatum* Wint. What is perhaps this species was collected on *Hypoxis hirsuta* at Blue Mounds bearing lunate sporules but  $18\text{--}24 \times 2 \mu$ . From the examination it was thought that the short sporules might have been formed by division as in the acervuli (?) were found longer straight ones.

*Cylindrosporium toxicodendri* (Curt.) Ell. & Evht. On *Rhus toxicodendron*. Barneveld and Lone Rock. *Septoria irregularis* Pk. as represented by a specimen collected by Peck at Bolton Landing, N. Y., is the same fungus.

**Septogloeum querceum** n. sp. Spots or areas indefinite, becoming mottled brown; acervuli hypophyllous, subcuticular, sporules sessile, hyaline, falcate, 7–9 septate,  $35\text{--}50 \times 5\text{--}7 \mu$ . On languishing

leaves of *Quercus bicolor*. Blue River, Wisconsin, August 2, 1921. Exceptionally straight conidia occur while some might perhaps be called rostrate.

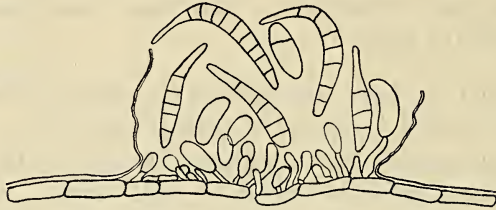


Fig. 1. Vertical section of acervulus of *Septogloeum querceum* n. sp. on leaf of *Quercus bicolor* with sporules in various stages of development. Drawn by E. M. Gilbert with the aid of camera lucida.

[This was collected again in 1922 and was grown on nutrient agar by Miss Helen Johann and in addition to the conidia there was development of pycnidia with spermatoid contents. Later a collection was made at Blue River that no longer bore conidia on the lower surface but with pycnidia on the upper surface with spermatoid, imperfectly developed, contents. Some of these leaves were kept in a moist chamber by Miss Johann and developed hyaline, globose, delicate walled sporules  $3-4\mu$  in diameter. When germinating in water these sporules developed first a bud and then bud and sporule developed each a germ tube. Often the bud was nearly and sometimes quite as large as the sporule. Later (Sept. 2) a collection was made at Arena with similar sporules in the pycnidia and acervuli on the lower leaf surface. For the purpose of filing I have designated this pycnidial state *Phyllosticta quercea* n. sp. ad interim.

In circular groups or later on orbicular brown spots or irregular areas; pycnidia epiphyllous, immersed in the palisade layer, dark brown, globose to elliptical, the longer axis parallel with the palisade cells,  $60-100\mu$  in diameter; sporules hyaline, globose, delicate walled,  $3-5\mu$  in diameter. On leaves of *Quercus bicolor*. Arena and Blue River, Wisconsin.

From observation of the cultures Miss Johann is of the opinion that the *Septogloeum* and the *Phyllosticta* represent distinct organisms, the mycelium of the former growing very slowly, that of the latter much more rapidly. By placing leaves in a moist chamber she brought about the development of sporules in which one or

two of the cells is divided by a vertical septum. She is quite sure that these are a further development of the sporules represented in fig. 1.]

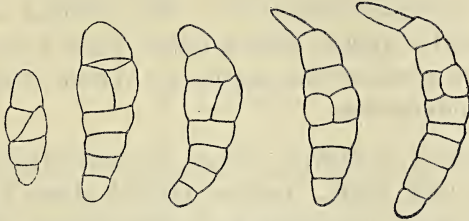


Fig. 2. Selected sporules from leaf of *Quercus bicolor* kept in a moist chamber. Drawn by Helen Johann with the aid of camera lucida.

*Ramularia tanacetii* Lind. On *Tanacetum vulgare*. Fennimore. Epiphyllous tufts sometimes occur.

*Cercospora celtidis* (Ell. & Kell.) n. comb. (*Ramularia celtidis* E. & K. *Journ. Mycol.* 1: 75). On *Celtis occidentalis*. Bank of Wisconsin river opposite Boscobel. Well characterized by the short conidiophores. The slender, filiform conidia up to  $75\mu$  in length are more nearly of the *Cercospora* type. To their description the authors appended the statement "approaches *Cercospora*".

Of a collection on ash leaves in 1921 the following notes were made: Spots epiphyllous, orbicular, sordid white with a reddish brown to black border, 1–2 mm. in diameter; conidiophores fuscous, single or in small fascicles, more or less irregularly undulate and finely denticulate toward the apex, simple, septate,  $40\text{--}100 \times 3\mu$ ; conidia brown, uniseptate, about  $13 \times 4\mu$ . On leaves of *Fraxinus pennsylvanica*. Blue River. This has been provisionally labeled *Cladosporium simplex* Schw. of which I have not seen an authentic specimen. It may be that the *Cladosporium* is not the cause of the spots.

*Cladosporium astericola* Davis. On leaves of *Solidago serotina*. Lone Rock.

*Cercospora molluginis* n. sp. Showing first small pallid spots but the infected leaves becoming sere and yellow before the appearance of the fasciculi which blacken the areas upon which they appear; conidiophores amphigenous, fasciculate, fuliginous, suberect or sometimes curved, undulate or geniculate, simple, usually con-

tinuous, 25–65x3–4 $\mu$ ; conidia subhyaline, slender, tapering, straight or slightly curved, 50–100x3 $\mu$ .

On leaves of *Mollugo verticillata*. Lone Rock, July 22, 1921.

*Cercospora verbenae-strictae* Pk. On *Verbena stricta*. Lone Rock. The conidia appear before tissue death has occurred and therefore before spotting has appeared. There is but a trace of color in the conidiophores.

Of a specimen on *Lepachys pinnata* from Fennimore the following notes have been made. Leaves mottled above with indefinite slightly paler areas; conidiophores amphigenous, solitary or in small fascicles, brown, straight, curved or undulate, sometimes septate, often subnodulose and geniculate distally, 50–100x3–4 $\mu$ ; conidia hyaline, straight, obclavate-cylindrical, becoming septate, 50–100x3 $\frac{1}{2}$ –5 $\mu$ . Pending opportunity to examine more material I have placed this with *Cercospora ratibidae* Ell. & Barth.

*Ustilago sphaerogena* Burrill was collected on *Echinochloa crus-galli* near Millville in 1913 but has not been recorded in the "Notes". It was collected again on the same species of host at Madison in 1921 by a class in mycology.

UNIVERSITY OF WISCONSIN HERBARIUM,  
MADISON, WISCONSIN, APRIL, 1922.

## NOTES ON PARASITIC FUNGI IN WISCONSIN—XI

J. J. DAVIS

The *Synchytrium* that has been reported as occurring in Wisconsin on *Lycopus* and referred to *Synchytrium aureum* Schroet. has been found to develop summer sori and consequently cannot be a form of that species. As the summer sori develop an empty basal cell I am now referring it to *Synchytrium cellulare* Davis. The galls of the summer sori are simpler than in the type of that species on *Boehmeria cylindrica*. The summer sporangia are globose to polyhedral, 18–24 $\mu$  in diameter. The resting sori sometimes develop in prominent multicellular galls. I am now labeling this var. **lycopodis** n. var. In addition to the ordinary host, *Lycopus uniflorus*, one collection has been made on *L. americanus*. Vestergren's *Micromycetes rariores selecti* 1673 is the form referred to. It may be that forms on other hosts in Wisconsin that have been referred to *S. aureum* will be found to form summer sori when collections have been made at the proper time.

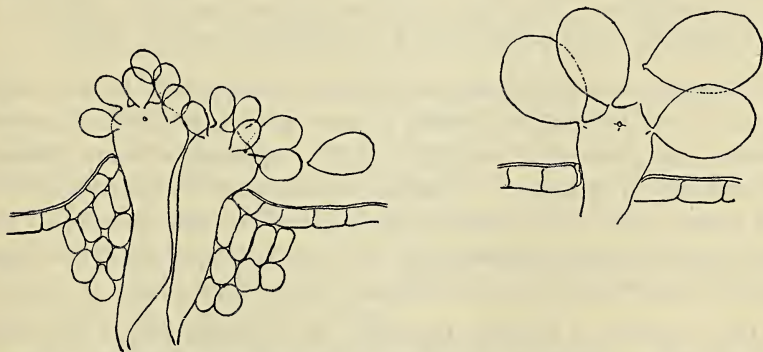


FIG. 1. Left, two conidiophores of *Plasmopara kellermani* bearing conidia. Right, apical portion of a conidiophore with conidia more highly magnified. Drawn by E. M. Gilbert with the aid of camera lucida.

The record of *Iva xanthifolia* as a host of *Albugo tragopogonis* (D.C.) S. F. Gray in the provisional list was an error, the fungus on that host being *Plasmopara kellermani* (Ell. & Hals.) Swingle.

It has been collected at Spooner, Dresser Junction and Alma. This differs from Basidiophora in the intrafoliar origin of the conidiophores and the absence of distinct basidia. From Albugo it differs in the conidia being borne in a cluster on the apex of the conidiophore instead of being catenulate.

Circular black spots 3–4 mm. in diameter sometimes occur on leaves of *Vitis vulpina* and *Vitis bicolor* in Wisconsin. They appear like a young stage of Rhytisma but have been seen only on living leaves in summer.

The parasite of *Ulmus americana* and *U. racemosa* recorded in "Notes" VI, p. 11, under the name *Phyllosticta ulmicola* Sacc. is referred to *Ph. melaleuca* E. & E. in *North American Flora* 6: 67.

In the provisional list a parasite of *Prunus virginiana* was recorded under the name *Phyllosticta destruens* Desm. regarding which a note was published in "Notes" I, p. 79. For this I am now using the binomial *Phyllosticta virginiana* (Ell. & Hals.) Seaver (*N. A. Flora* 6<sup>1</sup>: 70). This is not a typical *Phyllosticta* inasmuch as the sporules are formed by successive basipetal divisions of filaments the proximal, as yet undivided, portions of which I take to be the "long sporophores" mentioned in the description of the similar *Ph. innumerabilis* Pk. in *N. A. Flora* 6<sup>1</sup>: 52. The microconidia, of some species at least, of *Cylindrosporium* are produced in the same way. The form on Amelanchier has been collected in Wisconsin on hosts referred to *A. oblongifolia* and *A. spicata*.

The *Septoria* which occurs on *Cacalia atriplicifolia* in Wisconsin produces white arid spots with a more or less broad dark purple border like those of *S. nabali* B. & C. Specimens from Missouri and Kansas are similar. The single specimen on *Cacalia reniformis* has brown spots with a narrow darker border. This developed in a moist deeply shaded station while those on *C. atriplicifolia* developed in the open where they were exposed to the direct rays of the sun.

The parasite of *Spiraea* described by Trelease under the name *Ascochyta salicifoliae*, referred to *Septoria* by Berlese & Voglino and to *Cylindrosporium* in "Notes" IV, p. 673 is referred to *Phleospora* by Petrak (*Ann. Mycol.* 20: 210–11). I quite agree with those who see the genus *Phleospora* as a mixture of species referable to other genera and hence one that should be dropped as was done by Diedicke in *Kryptogamenflora der Mark Brandenburg* and by Migula in Thome's *Flora von Deutschland*.



For the species recorded in the provisional list as *Ovularia obliqua* (Cke.) Oud. the name *O. monosporia* (West.) Sacc. should be used because of priority (*Sylloge Fungorum* 22: 1296).

A collection on *Mentha arvensis canadensis* made at Arena in September and referred to *Ramularia variata* Davis bears conidia but about  $1\mu$  thick.

When well developed the conidia of *Cercospora ampelopsidis* Pk. are obclavate  $60-80 \times 5-6\mu$ .

The conidial tufts of *Cercospora galii* Ell. & Hol. are usually red until death of the host-tissue takes place. Fasciculi of this color are more often seen on the small leaved species of host.

There are a number of Compositae that bear *Cercospora* of a brown color in both Europe and America. In "Notes" VIII, p. 430 forms on *Rudbeckia* and *Prenanthes* were included in *Cercospora tabacina* Ell. & Evht. Until more is known of their relationship to each other it is perhaps better to keep the forms on the different host genera distinct. I am therefore labeling the specimens on *Prenanthes* *Cercospora brunnea* Pk., although it may be that this is not distinct from *C. prenanthis* Ell. & Kell. as the brown color is not always conspicuous. *C. rudbeckiae* Pk. seems to be a synonym of *C. tabacina* Ell. & Ev. which was published in 1888 not 1886 as given in the *Sylloge Fungorum*. I append notes of a specimen on *Prenanthes alba* collected in Iowa County July 1, 1922. Conidiophores in dense fascicles arising from substomatal, black, stromatoid tubercles, fuliginous, simple, flexuose, sometimes geniculate, continuous or sparingly septate,  $50 \times 80 \times 4\mu$ ; conidia cylindrical to subclavate, nearly hyaline, straight or curved,  $20 \times 60 \times 3-5\mu$ . Macroscopically the angular areas are tobacco brown. The form on *Ambrosia* issued in *Fungi Columbiani* 2117 under the name *Cercospora racemosa* E. & M. appears to be a member of this group which seems closely related to *C. ferruginea* Fekl. occurring on Compositae in Europe.

Although *Puccinia cryptotaeniae* Pk. was recorded in the fourth supplementary list I find that it was not included in the Provisional list. It has been collected at Racine, Ridgeway, and at the Dells of the Wisconsin River in Adams County.

If one reads the descriptions of *Septoria besseyi* Pk. on *Fraxinus pennsylvanica lanceolata* and *Marssonina fraxini* (Ell. & Davis) on *Fraxinus nigra* they appear to be quite distinct in their micro-

scopic characters while similar macroscopically. In the former the sporules are borne in pycnidia, are obtuse, continuous 40–55x about 4 $\mu$ . In the latter they are borne in acervuli, are acute, 1-septate, 17–33x2–3 $\mu$ . Examination of specimens, however, shows that the matter is not as simple as it appears. To illustrate I give some notes of various specimens.

On *Fraxinus pennsylvanica lanceolata*.

- 7-22-21. Pycnidia distally imperfect (hemispherical); sporules subacute to obtuse, becoming 1-septate, 27x50x3 $\mu$ .
- 7-21-22. Pycnidia more or less imperfect; sporules continuous, 40–60x3 $\mu$ .
- 7-7-20. Distal portion of pycnidia imperfect; sporules obtuse or acute at one end, continuous, 30–50x2 $\frac{1}{2}$ –4 $\mu$ .

On *Fraxinus nigra*.

- 7-29-20. Pycnidia more or less imperfect; sporules acute, continuous, 27–33x3 $\mu$ .
- 7-1-18. Pycnidia distally imperfect; sporules acute, continuous, 23–32x2 $\mu$ .
- 9-3-15. Pycnidia distally imperfect; sporules acute, continuous, 23–33x3 $\mu$ .
- 8-10-15. Spore bodies ranging from prominent acervuli to innate pycnidia; sporules acute, continuous, 24–36x2–3 $\mu$ .

*Fungi Columbiani 1526* on *Fraxinus pennsylvanica lanceolata* from Kansas, issued as *Cylindrosporium fraxini* E. & K., bears sporules which are obtuse, tapering toward one end, becoming 1-septate 33–45x3 $\mu$  and apparently belongs in this duplex. The character of the spore body in such groups as this appears to depend upon its position in the leaf. The beginning of a spore body is a spherical mass of hyphae in the leaf tissue. A wall develops on the periphery of the hyphal mass and under this protection a sporuligerous or hymenial layer is developed on the inner surface of the wall which gives rise to the reproductive bodies. Normally the pycnidium is globular and the entire inner surface of the wall is lined with hymenium except a small opening for the discharge of the sporules, the ostiole. When, however, the primary hyphal mass is in contact with the epidermis or by destruction of intervening host tissue becomes pressed against it no wall or hymenium is formed by the portion in contact with the epidermis. This results in a pycnidium the distal portion of which is defective. If the

deficiency is considerable the pressure of the mesophyll tends to flatten the remainder and produce an acervular structure. This is more likely to happen in the thinner leaf of *Fraxinus nigra*. In the normal pycnidium the length of the sporule may equal the radius of the pycnidial cavity but in the acervular condition it is limited to the distance from the hymenium to the epidermis.



FIG. 2. Diagram to illustrate influence of position of pycnidium with reference to epidermis on its development. Drawn by E. Dopp Jr., from a sketch by the author.

I have seen no specimen that corresponds to the description of *Cylindrosporium fraxini* (E. & K.) E. & E. (*Journ. Mycol.* 1:128), *Cercospora fraxini* E. & K. *loc. cit.* 1:2). As noted above *Fungi Columbiani* 1526 issued under this name appears to belong to the group of forms considered above.

Of the parasite of *Fraxinus oregana* of which *Fungi Columbiani* 4415, 4719, and 4816, issued as *Cylindrosporium fraxini* (E. & K.) E. & E., are examples, I have seen no description. It causes reddish brown spots with a paler margin of more or less circular outline quite variable in size and sometimes confluent. The acervuli are epiphyllous, subcuticular, and soon erumpent. The sporules are cylindrical, usually curved or undulate, becoming about 4-septulate, mostly 40–60x2–3 $\mu$ . The epiphyllous, subcuticular habit especially seems to remove this from the forms considered above.

As the range of species of Uredinales in *North American Flora* Vol. 7 is based on specimens in the Arthur herbarium there are sometimes considerable restrictions. For instance the range of *Puccinia aletridis* B. & C. (*Dicaeoma* (?) *aletridis* (B. & C.) Kuntze) is given as "The states bordering the Atlantic Ocean and Gulf of Mexico from Massachusetts to Texas". Its occurrence in northern Indiana was recorded by Burrill (*Parasitic Fungi of Illinois* pt. 1, p. 195) and in Wisconsin by Trelease (*Preliminary List of Wisconsin Parasitic Fungi*, p. 25). It has been collected in Wisconsin as recently as 1922.

## ADDITIONAL HOSTS

Synchytrium on *Acalypha virginica* has been collected at Lone Rock, Arena, and Prairie du Sac. Only resting sori were present which resemble those of *S. cellulare* Davis. The sori are first whitish, then pale yellow, then reddish brown as the wall develops. The contents are sordid white. Those measured were 80–135 $\mu$  in diameter.

*Bremia lactucae* Regel. On *Lactuca scariola integrata*. Madison.

*Peronospora parasitica* (Pers.) Tul. On *Cardamine pennsylvanica*. Lone Rock.

*Sphaerotheca mors-uvae* (Schw.) B. & C. On *Ribes lacustre*. White Lake.

*Microsphaera alni* (Wallr.) Wint. On *Quercus bicolor*. Chipewewa Falls.

*Erysiphe cichoracearum* DC. On *Verbena stricta*. Blue River.

*Phyllachora graminis panicis* Shear. On *Panicum Scribnerianum*. Prairie du Sac.

*Darlucia filum* (Biv.) Cast. On *Uromyces pyriformis* parasitic on *Acorus Calamus*. Arena.

The *Stagonospora* with 7-septate sporules referred to *S. intermixta* (Cke.) Sacc. was collected at Blue River on *Phyllachora* infected leaves of *Cinna latifolia*. The pycnidia are pale and thin walled throughout except the ostiolar ring. The sporules are variable in length the longest one seen being 90x4 $\mu$ .

*Stagonospora albescens* Davis. On *Carex vesicaria*. Arena. In this collection about 2 dm. of the apical portion of the leaves is dead and white with a ferruginous margin at the base. The sporules are 43–57x7–10 $\mu$ , 6-septate. With pycnidia of a *Coniothyrium* with elliptical to ovate fuscous sporules 7–10x3 $\frac{1}{2}$ –4 $\mu$ .

*Septoria graminum* Desm. On *Poa pratensis*. Madison (Geo. F. Weber).

*Septoria bromi* Sacc. var. *elymina* n. var. ad interim. On large indefinite areas that are first yellowish then brown with the death of the tissues; pycnidia scattered, globose or somewhat flattened,

dark walled, innate, 70–100 $\mu$  in diameter; sporules straight or slightly curved, acute, continuous, 30–45x1½–2 $\mu$ . On leaves of *Elymus virginicus*, Arena, Wisconsin, July 13, 1922.

*Septoria glumarum* Pass. On *Secale cereale*. Madison (G. F. Weber). It is said that this is not distinct from *Septoria nodorum* Berk.

*Septoria atropurpurea* Pk. On *Aster lateriflorus*. Arena and Blue River. Of the latter collection it was noted: "On the thin leaves of this species the spots are more or less angular and without a colored margin."

*Entomosporium thuemenii* (Cke.) Sacc. On "Paul's English Double Hawthorn". Racine (Mrs. W. H. Crosby). Reported as serious in its effects on the host.

*Gloeosporium ribis* (Lib.) Mont. & Desm. On *Ribes lacustre*. White Lake.

*Monilia cinerea* Bon. On fruit of *Pyrus melanocarpa*. Arena.

*Ramularia uredinis* (Voss) Sacc. With *Darluca* parasitic on *Melampsora bigelowii* on *Salix nigra*. Edgerton.

*Ramularia occidentalis* Ell. & Kell. has been collected at Chetek on a leaf of *Rumex verticillatus* that bears also the species that has been referred to *R. pratensis* Sacc.

*Ramularia repens* Ell. & Evht. On *Aralia racemosa*. Wyoming.

*Ramularia asteris* (Phil. & Plowr.) Bubak on *Aster azureus*. White Lake.

***Tuberculina argillacea* n. sp.**

Sporodochia epiphyllous on definite orbicular spots which sometimes become confluent and irregular, especially near the leaf margins, numerous, more or less prominent, mostly 50–100 $\mu$  in diameter; conidia hyaline, oblong, 8–16x2½–4 $\mu$ .

On Caecoma-infected leaves of *Rubus allegheniensis* or allied species. Madison and Blue Mounds. On *Rubus occidentalis* (cult.) Madison, Wisconsin. May and June. This was abundant at Madison in 1921, apparently parasitic on the Caecoma. The masses of conidia are argillaceous to whitish or, when fresh, honey colored.

*Cercospora caricina* Ell. & Dearn. On *Carex lupulina*. Blue River. In this collection the slender conidia range up to  $120\mu$  in length.

*Cercospora nasturtii* Pass. On *Radicula sylvestris*. Edgerton. In this collection from Lake Koshkonong the spots are mostly small (about 1 mm.) round, white and arid.

On withered leaves of *Radicula palustris*. Blue River.

*Cercospora zebrina* Pass. On *Trifolium dubium*. Mazomanie. The publication of this name seems to antedate that of *C. helvola* Sacc.

*Cercospora granuliformis* Ell. & Hol. On *Viola sagittata*. Arena.

*Cercospora clavata* (Ger.) Pk. On *Asclepias Meadii*. Arena.

*Coleosporium campanulae* (Pers.) Lev. Uredinia on *Campanula aparinoides*. Blue River. Confined to a single restricted station where it was abundant and destructive. The uredospores are but  $17-22\mu$  long.

*Puccinia graminis* Pers.

Uredinia on *Cinna arundinacea*. Saxon. Telia on *C. arundinacea*, Wonewoc. On *C. latifolia*, Madison and Cadott.

*Puccinia pruni-spinosae* Pers. Telia on *Prunus nigra*. Cadott.

An Aecidium on *Linaria canadensis* has been known in Wisconsin for a dozen years or more. Because of the relationship of the host and the resemblance to the Aecidium on Pentstemon it has been suspected that it is connected with *Puccinia andropogi* Schw. but the connection has not been demonstrated and no record has been made for this reason. It occurs along the Wisconsin River from above Mazomanie to Lone Rock and probably further.

*Urocystis agropyri* (Preuss) Schroet. On *Agrostis alba*. Madison. (W. H. Davis)

*Entyloma compositarum* Farl. On *Boltonia asteroides*. Richland County opposite Muscoda and at Blue River.

*Doassansia sagittariae* (West.) Fisch. On *Lophotocarpus calycinus*. Blue River. The parasite was not found on *Sagittaria* in this locality. In the irregularity of the spore balls this resembles

the forma *confluens* that occurs on *Sagittaria heterophylla*. Evidently the smut does not recognize *Lophotocarpus* as being generically distinct from *Sagittaria*.

*Sclerotium* (?) *globuliferum* Davis. On *Glyceria grandis*. Chetek.

#### ADDITIONAL SPECIES

In 1921 *Plasmopara cubensis* (B. & C.) Humphrey was collected in gardens at Madison on *Cucumis sativa*, *Cucurbita maxima* and *Cucurbita pepo* in September.

*Peronospora myosotidis* DBy. A very scanty collection on upper leaves of *Myosotis laxa* in July at Arena is supposed to be of this species but the material was not sufficient for proper examination.

*Pleosphaerulina briosiana* Pollacci. On *Medicago sativa* (cult.) Madison. (F. R. Jones)

*Phyllosticta oakesiae* Dearn. & House. On *Oakesia sessilifolia*. White Lake. In "Notes" VIII, p. 418 a collection of this was referred to *Phyllosticta cruenta* (Fr.) Kickx. As this occurs in Wisconsin the development is usually imperfect and I suspect it of being a state of *Diplodia uvulariae* Davis.

*Phyllosticta ludwigiae* Pk. On *Ludwigia polycarpa*. Blue River. In this collection the spots are usually elongate and the pycnidia prominent and often defective.

*Phyllosticta verbenicola* Martin. On *Verbena stricta*. Blue River. I have not seen an authentic specimen of this species and Dr. Seaver informs me that there is none in the Ellis herbarium. In this collection the spots are mostly somewhat larger than the description indicates and somewhat cinereous in color, the sporules 6-8x2-3 $\mu$ .

#### *Phyllosticta ambrosiae* n. sp.

Spots brown, suborbicular, immarginate, 3-12 mm. in diameter, mottled with small white arid areas on which the usually solitary pycnidia are located; pycnidia epiphyllous, dark brown, ostiolate, globose and about 100 $\mu$  in diameter to oval and 150 $\mu$  long; sporules hyaline, bacilliform, 3-6x1 $\mu$ . On *Ambrosia trifida*. Gays Mills, Wisconsin, July 30, 1921.

*Sclerotiopsis concava* (Desm.) Shear & Dodge. On *Fragaria virginiana*. Madison. *Steironema ciliatum*. Blue River. In the latter collection with the conidial form *Hainesia lythri* (Desm.) Hoehn. Connected with *Pezizella lythri* (Desm.) by Shear & Dodge. (*Mycologia* 13: 135 et seq.)

*Stagonospora sparganii* (Fekl.) Sacc. In leaves of *Sparganium eurycarpum*. Spring Green.

In the provisional list *Panicum depauperatum* was given as a host of *Septoria graminum* Desm. In this specimen the pycnidia are on indefinite pale leaf areas; they are black, globose to elliptical and lenticular, 100–150 $\mu$  in diameter with firm walls composed of very small cells; the sporules are usually curved, sometimes very strongly so, 50–70x1–1½ $\mu$ . I am now referring this to the South American *Septoria tandilensis* Speg. In his description the author notes resemblance to *Puccinia coronata*. The Wisconsin specimen came to me labeled *Puccinia emaculata*. The immersed pycnidia are sometimes laterally compressed.

***Septoria cenchrina* n. sp.**

Spots linear, cinereous, variable in size, often confluent; pycnidia amphigenous, brown-black, globose to depressed-globose to elliptical with a thick wall which is often defective distally, 60–115 $\mu$  in diameter; sporules filiform, continuous or indistinctly septulate, straight or more or less strongly curved, hyaline, 30–100x1½–3 $\mu$ . On leaves of *Cenchrus carolinianus*. Spring Green, Wisconsin, July 19, 1921. The longer sporules grow out through the widely open mouth of the pycnidium after the manner of those of *Cylindrosporium* and the species approaches that genus but the *Septoria* condition seems to be the normal state.

*Septoria didyma* Fekl. What is perhaps a short-spored form of this species is characterized as follows: Spots circular or sub-circular, brown with a raised purple border, becoming arid, about 1 mm. in diameter; pycnidia few, pale, globose, epiphyllous, subepidermal, inconspicuous, 50–70 $\mu$  in diameter; sporules hyaline, oblong, usually curved, uniseptate, 14–27x3 $\mu$ . On leaves of *Salix longifolia*. Lone Rock.

*Septoria aparines* Ell. & Evht. On *Galium asprellum*. Prairie du Sac. In the collection that I am recording under this name the pycnidia are scattered over the lower surface of the leaf



or sometimes confined to a lateral half. The leaf or half leaf becomes pale yellow and finally dead and brown. The pycnidia are somewhat flattened, about  $100 \times 75 \mu$  and extend through to the epidermis of the upper leaf surface. There are no pycnidia on the stems. The sporules are continuous, slightly curved, acute,  $30-60 \times 1\frac{1}{2} \mu$ . I have labeled this forma *asprelli*.

*Septoria erectitis* Ell. & Evht. On *Erechtities hieracifolia*. Blue River.

Of a collection on *Salix lucida* the following notes were made: Spots angular to orbicular, olivaceous to brown, becoming cinereous with a dark border, paler below, 1-3 mm. in diameter; acervuli mostly hypophyllous, small, scattered, subcuticular; sporules minute, hyaline,  $1-3 \times 1-1\frac{1}{2} \mu$  abstricted from hyaline, vertical, parallel hyphae,  $15-20 \times 1 \mu$ . Cadott, Wisconsin, September 19, 1922. This seems to be a microconidial state but for the purpose of filing I have labeled it **Gloeosporium egenum** n. sp.

*Colletotrichum pisi* Pat. On *Pisum sativum* (cult.) Marshall. (F. R. Jones)

**Colletotrichum violarum** n. sp.

Spots circular to angular or irregular in outline, arid with a slightly raised margin, 1-6 mm. in diameter, sometimes confluent, often lacerate; acervuli amphigenous, small, black; setae marginal, black, variable in size (up to  $165 \times 5 \mu$ ) and number, acute; sporules hyaline, oblong, somewhat curved or at least inequilateral, acute at each end, continuous,  $18-20 \times 3 \mu$ . On leaves of *Viola scabriuscula*, Spring Green, Wisconsin, July 3, 1922. I have not seen a specimen of the fungus on *Viola rotundifolia* collected by G. W. Clinton and referred to as a variety of *Vermicularia concentrica* P. & C. (*V. peckii* Sacc. nec *V. concentrica* Lev.) by Peck in 29th Report, p. 48.

**Septogloeum subnudum** n. sp.

Spots suborbicular, reddish brown with an olivaceous border, 2-5 mm. in diameter, becoming confluent; acervuli few, small, inconspicuous, epiphyllous, subcuticular; sporules hyaline, fusoid-oblong, straight, inequilateral or usually curved,  $20-40 \times 7-11 \mu$ , with a septum toward each end. On *Smilax herbacea*, Sauk City, Wisconsin, August 23, 1922. The development of the parasite seems

to be poor in this collection. One sporule was seen having a third septum in the middle.

*Ramularia canadensis* Ell. & Evht. On *Carex* sp. indet. Edgerton. In this collection the subulate conidiophores range up to  $65\mu$  in length, the conidia are fusiform, acute at each end,  $16-23 \times 3\frac{1}{2}-4\mu$ . In a collection on an undetermined species of *Carex* made at Madison in 1912 the conidia are oblong, acute, at least at one end,  $20-30 \times 4-6\mu$ . In both collections the conidia develop a median septum.

***Cladosporium caducum* n. sp.**

Spots hypophyllous, at first pale olivaceous, becoming yellow, finally brown, indeterminate, suborbicular, 1-4 mm. in diameter, when old showing on the upper surface; conidiophores hypophyllous, scattered or exceptionally in twos or very small fascicles, deep brown, ascending to erect, 3-4 septate, sometimes branched, often paler and torulose apically,  $50-80 \times 3\frac{1}{2}-4\mu$ ; conidia acro-pleurogenous, fuliginous or brown, limoniform, apiculate or acute and narrowly truncate at the extremities, sometimes catenulate and the chains sometimes branched, continuous,  $10-15 \times 4-7\mu$ . On leaves of *Betula nigra* along the Wisconsin river. The spots are usually multiple, the infected leaves fall and considerable defoliation is sometimes caused. This seems near *Cladosporium* but I have not seen septa in the conidia. They resemble those of *Monilia* in form. Although the parasite is abundant on the bottom lands and its effects conspicuous I have found it difficult to get good specimens as the conidiophores are very inconspicuous and soon fall away. The best specimens were obtained in July.

*Cladotrichum leersiae* Atk. On *Leersia oryzoides*. Blue River. In this collection oval, pale-avellaneous immarginate spots are produced which are sometimes confluent. The conidia are 13-17 $\mu$  in length and sometimes germinate without the formation of a septum.

*Napicladium arundinaceum* (Cda.) Sacc. On *Phragmites communis*. Madison.

***Cercospora crassoides* n. sp.**

Spots orbicular, alutaceous with a broad dark purple border, less distinct on the lanose lower surface of the leaf; conidiophores epiphyllous, sometimes a few on the lower surface, ferruginous, sub-

erect, more or less geniculate, septate, sometimes branched, 60–70x6–7 $\mu$ ; conidia ferruginous, lanceolate, 6–8 septate, tapering into a flagelliform distal portion about as long as the body, 100–165x13–7 $\mu$ . On leaves of *Froelichia floridana*, Lone Rock, Wisconsin, July 23 and 25, 1921. The spots are sometimes very abundant but mostly sterile. It is not unlikely that vertical septa appear at full maturity and that this therefore is an *Alternaria* like *A. crassa* (Sacc.) Rands (*Cercospora crassa* Sacc.) which it resembles in its conidia.

*Cercospora cucurbitae* Ell. & Evht. A parasite on leaves of *Cucurbita maxima* (cult.) collected at Madison, I have referred to this species although it is quite different from the type in appearance. In the Wisconsin material the spots are suborbicular, brown, with a distinct darker border above, whitish and immarginate below, 2–5 mm. in diameter, sometimes confluent; conidiophores scattered or in small tufts, amphigenous, fuscous, somewhat curved, sometimes septate, simple, more or less denticulate especially near the apex, 70–130x3–4 $\mu$ ; conidia flagelliform, straight or the slender distal portion curved, septate, hyaline, 87–123x3 $\mu$ . It was collected in October.

*Uromyces perigynius* Hals. var. **altiporus** n. var. Uredinia brown, erumpent, elliptical to linear 0.2–1 mm. long; uredospores brown, globose to elliptical, ovate, obovate or oblong, wall brown 1–1½ $\mu$  thick, echinulate, 12–23x12–15 $\mu$ , germ pores two, variously situated in the upper half of the spore; telia similar but darker; teliospores obovate to subfusoid, brown, rounded or often conical at the apex which is strongly thickened (up to 10 $\mu$ ), pedicel hyaline as long as the spore or longer. On leaves, bracts and perigynia of *Carex Grayii*, Blue River, Wisconsin, August 9, 1922. I am keeping this collection separate because the germ pores are uniformly further from the equator than in *U. perigynius* as I have seen it and as it is described. Often one pore lies higher than the other, sometimes both are subpolar.

Happening to be in a locality in which *Aecidium allenii* Clint. was abundant on *Shepherdia canadensis* attempt was made to get a clue to the alternate stages. The infected *Shepherdia* was confined to the small valley through which the waters of Fish creek flowed into Green Bay. The first step was to find a host having the same habitat as the *Shepherdia* and *Carex eburnea* was

hit upon as such a plant. Examination of the old leaves showed that they had borne a rust the previous year. Then began the watching of the *Carex eburnea* plants in the vicinity of infected *Shepherdia* plants. Soon a few uredinia appeared on the culms speedily followed by abundant telia on culms and leaves. The following autumn a trip to the locality was made and abundant telial material on the *Carex* secured and seeds of *Shepherdia* which were kept in a box outdoors during the winter. It was during this winter, while attending a meeting of the American Association for the Advancement of Science that it was learned that *Aecidium allenii* had been connected with a grass rust in Colorado. However the following spring attempts were made to secure plants of *Shepherdia canadensis* but without success. The seed would not germinate and no nursery was found that could supply plants. Some plants of *Shepherdia argentea* were obtained and attempts made to infect them but without success. Plants of *Artemisia dracunculoides* were also exposed to infection without result. Attempts to infect *Shepherdia argentea* using teliospores of *Puccinia coronata* on *Calamagrostis canadensis* also failed. The next autumn another trip to the locality was made and in addition to telial material small plants of *Shepherdia canadensis* were secured which were brought to Madison and heeled in for the winter in what was thought to be a safe situation. On looking for them in the spring it was found that trucks had been running over them during the winter but two of the plants proved to be still alive. These were potted and taken into the greenhouse and one of them used for the infection experiment. The weather was very warm and no spore germination was observed in slide cultures and it was still hotter in the greenhouse. Nevertheless attempts were made to secure infection but without result. Finally in despair, the *Shepherdia* plant was transplanted to the garden and before leaving it the wisp of wet *Carex* leaves that had been suspended over it was drawn across two of the leaves on both surfaces. As it happened it turned quite cold that night and typical *Aecidium allenii* developed on the two leaves that had been smeared and on those leaves only. Again the locality was visited the next autumn and telial material and small plants of *Shepherdia canadensis* obtained and again the following spring telial germination was not secured. Still an attempt to infect in the greenhouse was made which finally resulted in a single but well developed aecidial spot bearing numerous cups. Examining this one day it was thought to be ready for plucking and pre-

serving but as there were a few peripheral cups that were not yet open it was decided to leave it one more day. The next day it was found that some creature with epicurean taste had carefully eaten out each cup except three or four that were not open. The evidence seems to indicate that there is in Wisconsin a rust bearing aecidia on *Shepherdia canadensis* and uredinia and telia on *Carex eburnea*.

***Puccinia caricis-shepherdiae* n. sp.**

Aecia; "Spots large, indefinite, yellowish; peridia hypogenous, elongated, cylindrical, white, nestling among the tomentum of the leaf; spores bright orange, subglobose, 1-1000 in. in diameter." *Aecidium allenii* Clint. in *24th Rept. of the New York State Museum*, p. 93. Uredinia few, mostly culmicolous; uredospores elliptical, deep brown, wall  $1\frac{1}{2} \times 2\frac{1}{2} \mu$  thick, finely echinulate, germ pores two approximately equatorial,  $23-33 \times 17-27 \mu$ . Telia culmicolous and foliicolous, elliptical to linear, rupturing the epidermis, dark brown; teliospores brown, clavate, rounded to rounded-conical at the apex which is strongly thickened (up to  $13 \mu$ ) more or less constricted at the septum, the lower cell narrower and much paler than the upper,  $44-63 \times 17-23 \mu$ , pedicel hyaline, the length of the spore or shorter. This seems closely related to *Puccinia pringsheimiana* Kleb. but the uredo and teliospores are somewhat larger and the pedicels of the latter longer and more firmly attached. On *Carex eburnea*, Fish Creek, Wisconsin.

[In 1923 an attempt was made to infect *Shepherdia canadensis* with teliospores from *Carex eburnea* outdoors to see if the infections would not be more abundant than had been secured in the greenhouse. Old leaves of *Carex eburnea* bearing telia were obtained at Fish Creek May 14th. Rusted leaves were placed under and on a plant of *Shepherdia canadensis* in an open plot from time to time. Two leaves bearing aecia were removed June 28th. During my absence after July 3d the plant was watched by Dr. E. A. Baird who removed two leaves bearing aecia July 23d and one July 31st. A plant of *Shepherdia argentea* exposed to infection in the same manner bore no aecia. No infection of this species occurred in the greenhouse in previous years. So far as the evidence goes at present *S. argentea* does not bear this *Aecidium*.]

In June, 1922 a few uredinia were found on a leaf of *Rumex altissimus* growing beside the railroad at Madison. Later they were found in more abundance along the same railway line at

Arena and in September telia were found also. The rust agreed with the description of *Puccinia punctiformis* Diet. & Hol. and Dr. H. S. Jackson has identified it with that species through comparison with authentic material in the Arthur herbarium. As this had been known only from California, Mexico and Guatemala it was presumably a waif in Wisconsin and perhaps will not be able to maintain itself in this climate.

*Galium triflorum* as a host of *Puccinia punctata* Lk. should be stricken from the provisional list, the rust that has been collected on that host being *Puccinia troglodytes* Lindr. Collections have been made at Neopit, Athelstane and White Lake.

*Puccinia tumidipes* Pk. On *Lycium halimifolium* (cult.) Madison (Edward Kremers, com. R. B. Streets).

UNIVERSITY OF WISCONSIN HERBARIUM,  
MADISON, WISCONSIN, MARCH, 1923.

## INDEX TO "NOTES" IX, X, XI

Names of Fungi in *italics*.

- Acalypha virginica*, 276, 292  
*Acer Negundo*, 282  
*Acorus Calamus*, 292  
*Aecidium allenii*, 299  
*Aecidium dicentrae*, 279  
*Aecidium fraxini*, 259  
*Agropyron tenerum*, 259  
*Agrostis alba*, 278, 294  
*Albugo bliti*, 265  
*Albugo candida*, 265  
*Albugo portulacae*, 265  
*Albugo tragopogonis*, 265  
*Allium canadense*, 281  
*Alnus crispa*, 257  
*Amaranthus hybridus*, 265  
*Amaranthus retroflexus*, 265  
*Ambrosia*, 289  
*Ambrosia psilostachya*, 259, 276  
*Ambrosia trifida*, 254, 295  
*Amelanchier oblongifolia*, 288  
*Amelanchier spicata*, 288  
*Anemone canadensis*, 271  
*Anemone quinquefolia*, 266, 271  
*Anemone virginiana*, 259, 283  
*Apocynum androsaemifolium*, 277  
*Aralia racemosa*, 293  
*Artemisia ludoviciana*, 259  
*Artemisia serrata*, 256  
*Asclepias Meadii*, 294  
*Ascochyta lophanthi lycopina*, 277  
*Ascochyta necans*, 274  
*Ascochyta pisi*, 277  
*Ascochyta pteridis*, 273, 274  
*Ascochyta salicifoliae*, 288  
*Aster azureus*, 293  
*Aster lateriflorus*, 257, 276, 277, 280, 281, 293  
*Aster paniculatus*, 259, 277  
*Aster sagittifolius*, 283  
*Aster Tradescantii*, 256, 257, 277  
*Asteroma gentianae*, 273  
*Asteromella astericola*, 281  
*Baptisia bracteata*, 258  
*Basidiophora entospora*, 256, 269, 276  
*Betula nigra*, 276, 298  
*Bidens vulgata puberula*, 278  
*Bifusella lineare*, 252  
*Boehmeria cylindrica*, 287  
*Boltonia asteroides*, 294  
*Botrytis epichloes*, 261  
*Bremia lactucae*, 256, 266, 292  
*Cacalia atriplicifolia*, 288  
*Cacalia reniformis*, 288  
*Campanula aparinoides*, 294  
*Cardamine pennsylvanica*, 292  
*Carex*, 298  
*Carex chordorrhiza*, 277  
*Carex eburnea*, 257, 301  
*Carex Grayii*, 299  
*Carex grisea*, 253  
*Carex intumescens*, 259  
*Carex longirostris*, 259  
*Carex lupulina*, 294  
*Carex tribuloides*, 281  
*Carex vesicaria*, 292  
*Carya cordiformis*, 253, 261, 283  
*Carya ovata*, 253  
*Celtis occidentalis*, 285  
*Cenchrus carolinianus*, 296  
*Cercospora ampelopsidis*, 289  
*Cercospora antipus*, 278  
*Cercospora arctostaphyli*, 253  
*Cercospora brunnea*, 289  
*Cercospora caricina*, 253, 258, 294  
*Cercospora clavata*, 294  
*Cercospora crassoides*, 298  
*Cercospora cucurbitae*, 299  
*Cercospora davisii*, 275  
*Cercospora diffusa*, 278  
*Cercospora epigaeae*, 275  
*Cercospora epigaeina*, 275  
*Cercospora euonymi*, 262  
*Cercospora flagellifera*, 258  
*Cercospora fraxini*, 291  
*Cercospora galii*, 289  
*Cercospora granuliformis*, 294  
*Cercospora helvola*, 294  
*Cercospora medicaginis*, 278  
*Cercospora mississippiensis*, 274  
*Cercospora molluginis*, 285  
*Cercospora moricola*, 261  
*Cercospora nasturtii*, 294  
*Cercospora oxybaphi*, 258  
*Cercospora platyspora*, 275  
*Cercospora prenanthis*, 289  
*Cercospora racemosa*, 289  
*Cercospora ratibidae*, 286  
*Cercospora rudbeckiae*, 289  
*Cercospora saniculae*, 275  
*Cercospora sii*, 275  
*Cercospora smilacina*, 275  
*Cercospora smilacis*, 274-275  
*Cercospora stomatica*, 258, 275  
*Cercospora tabacina*, 289  
*Cercospora teucriti*, 262  
*Cercospora velutina*, 258  
*Cercospora verbenae-strictae*, 286  
*Cercospora viciae*, 258  
*Cercospora zebrina*, 294  
*Cercosporella apocyni*, 253

- Cercosporella cana*, 257, 274  
*Cercosporella celtidis*, 285  
*Cercosporella mirabilis*, 274  
*Cercosporella pyrina*, 257  
*Cercosporella reticulata*, 261  
*Cerotelium urticastris*, 279  
*Chenopodium album*, 252, 267  
*Cicuta bulbifera*, 277  
*Cicuta maculata*, 252  
*Cinna arundinaceae*, 294  
*Cinna latifolia*, 292, 294  
*Cirsium discolor*, 256  
*Cirsium muticum*, 266  
*Cladochytrium maculare*, 265  
*Cladosporium astericola*, 285  
*Cladosporium caducum*, 298  
*Cladosporium carpophilum*, 261  
*Cladosporium simplex*, 285  
*Cladosporium subsessile*, 253, 257  
*Cladosporium triostei*, 257  
*Cladotrichum leersiae*, 298  
*Claviceps nigricans*, 280  
*Clintonia borealis*, 263  
*Coleosporium campanulae*, 294  
*Colletotrichum graminicolum*, 257  
*Colletotrichum pisi*, 297  
*Colletotrichum violarum*, 297  
*Convolvulus spithameus*, 261  
*Cordyceps clavulata*, 260  
*Crataegus Oxyacantha*, 293  
*Cryptomyces pteridis*, 273  
*Cucumis sativa*, 260, 295  
*Cucurbita maxima*, 295, 299  
*Cucurbita Pepo*, 295  
*Cylindrosporium apocyni*, 253  
*Cylindrosporium caryogenum*, 283  
*Cylindrosporium clematidis*, 253  
*Cylindrosporium fraxini*, 290, 291  
*Cylindrosporium guttatum*, 283  
*Cylindrosporium salicifoliae*, 288  
*Cylindrosporium toxicodendri*, 283  
*Cylindrosporium vermiforme*, 257  
*Cyperus Schweinitzii*, 258  
*Dactylis glomerata*, 278  
*Darluca filum*, 277, 292  
*Depazea gentianaecola*, 272, 273  
*Desmodium canadense*, 259, 274  
*Desmodium illinoense*, 274  
*Didymaria platyospora*, 275  
*Didymellina iridis*, 253  
*Diplodia uvulariae*, 295  
*Doassansia ranunculina*, 275  
*Doassansia sagittariae*, 294  
*Echinochloa crusgalli*, 286  
*Eleocharis palustris*, 280  
*Elymus brachystachys*, 276  
*Elymus virginicus*, 293  
*Entomosporium thuementii*, 293  
*Entyloma calendulae*, 254  
*Entyloma compositarum*, 254, 259, 294  
*Entyloma linariae gratiolarum*, 262  
*Entyloma ranunculi*, 278  
*Eocronartium muscicola*, 260  
*Epichloe typhina*, 261  
*Erechtites hieracifolia*, 297  
*Erigeron annuus*, 257, 274  
*Erysiphe cichoracearum*, 276, 292  
*Eupatorium urticaefolium*, 278  
*Evonymus atropurpureus*, 260, 262  
*Fragaria virginiana*, 278, 296  
*Fraxinus americana*, 278  
*Fraxinus nigra*, 257, 259, 260, 289, 290  
*Fraxinus oregana*, 291  
*Fraxinus pennsylvanica*, 257, 260, 279, 285, 289, 290  
*Froelichia floridana*, 299  
*Fusicladium caryigenum*, 261  
*Fusicladium cerasi*, 261  
*Fusicladium depressum*, 275  
*Fusicladium efusum*, 261  
*Fusidium pteridis*, 273  
*Galium asprellum*, 276, 296  
*Galium triflorum*, 302  
*Gaylussacia baccata*, 278, 279  
*Gentiana Andrewsii*, 272  
*Gentiana puberula*, 273  
*Geranium maculatum*, 266  
*Geum canadense*, 256  
*Geum strictum*, 263  
*Geum virginianum*, 263  
*Gloeosporium aridum*, 257  
*Gloeosporium caryae*, 253  
*Gloeosporium egenum*, 297  
*Gloeosporium fraxineum*, 257  
*Gloeosporium leptospermum*, 273  
*Gloeosporium necans*, 273  
*Gloeosporium obtegens*, 273  
*Gloeosporium pteridis*, 273  
*Gloeosporium ribis*, 293  
*Gloeosporium salicis*, 256-257  
*Glyceria grandis*, 295  
*Glyceria nervata*, 261  
*Gnomonia ulmea*, 256  
*Gratiola virginiana*, 262  
*Hainesia lythri*, 296  
*Halenia deflexa*, 264  
*Helenium autumnale*, 276  
*Hepatica acutiloba*, 271  
*Heterosporium gracile*, 253  
*Iva xanthifolia*, 287  
*Hydrocotyle americana*, 255, 264  
*Hypoderma lineare*, 252  
*Hypoxis hirsuta*, 283  
*Ilex verticillata*, 260  
*Iva xanthifolia*, 287  
*Koeleria cristata*, 254, 281  
*Lactuca Scariola integrata*, 256, 292  
*Lactuca spicata*, 266  
*Laportea canadensis*, 279  
*Lathyrus palustris*, 258  
*Lecanium corni*, 260



- Leersia oryzoides*, 298  
*Lepachys pinnata*, 286  
*Leptothyrium conspicuum*, 272  
*Leptothyrium gentianaeecolum*, 272  
*Lespedeza frutescens*, 258  
*Linaria canadensis*, 294  
*Lonicera Sullivantii*, 278  
*Lophodermium lineare*, 252  
*Lophotocarpus calycinus*, 294  
*Ludwigia polycarpa*, 295  
*Lycium halimifolium*, 302  
*Lycopus americanus*, 287  
*Lycopus uniflorus*, 264, 282, 287  
*Lycopus virginicus*, 277  
*Lysimachia terrestris*, 257, 264  
*Macrophoma arens*, 281  
*Marssonina fragini*, 253, 289  
*Marssonina necans*, 273  
*Marssonina populi*, 277  
*Marssonina potentillae*, 253, 278  
*Marssonina potentillae tormentillae*, 257  
*Marssonina rhabdospora*, 257  
*Marssonina thomasiana*, 260  
*Medicago lupulina*, 278  
*Medicago sativa*, 295  
*Melampsora americana*, 255  
*Melampsora arctica*, 255  
*Melampsora bigelowii*, 293  
*Melica striata*, 256, 257  
*Melilotus alba*, 275, 281  
*Mentha arvensis canadensis*, 289  
*Microsphaera alni*, 292  
*Mollisia earliana*, 253  
*Mollugo verticillata*, 286.  
*Monilia cinerea*, 293  
*Morus rubra*, 261  
*Mycosphaerella rubi*, 272  
*Myosotis laxa*, 295  
*Napicladium arundinaceum*, 298  
*Oakesia sessilifolia*, 295  
*Oenothera biennis*, 268  
*Oenothera rhombipetala*, 277  
*Oryzopsis asperifolia*, 251  
*Ovularia monosporia*, 289  
*Ovularia obliqua*, 289  
*Oxybaphus hirsutus*, 258  
*Panicum depauperatum*, 296  
*Panicum Scribnerianum*, 292  
*Panicum virgatum*, 276  
*Parietaria pennsylvanica*, 280  
*Pedicularis canadensis*, 264  
*Peronospora alsinearum*, 267  
*Peronospora alta*, 268  
*Peronospora arthuri*, 268  
*Peronospora calotheca*, 268, 276  
*Peronospora chamaesydis*, 268  
*Peronospora corydalis*, 267  
*Peronospora effusa*, 267  
*Peronospora ficariae*, 267, 276  
*Peronospora floerkeae*, 268  
*Peronospora leptosperma*, 256, 268  
*Peronospora myosotidis*, 295  
*Peronospora obovata*, 267  
*Peronospora parasitica*, 268, 292  
*Peronospora polygoni*, 267  
*Peronospora potentillae*, 268  
*Peronospora rubi*, 256, 268  
*Peronospora schleideni*, 267  
*Peronospora silenes*, 267  
*Peronospora trifoliorum*, 268  
*Peronospora urticae*, 267  
*Peronospora viciae*, 268  
*Petasites palmatus*, 264  
*Pezizella lythri*, 296  
*Phacidium taxi*, 280  
*Phleospora anemones*, 283  
*Phleospora oayacanthae*, 274  
*Phleospora salicifoliae*, 288  
*Phleospora ulmi*, 256, 277  
*Phoma alliiola*, 281  
*Phragmites communis*, 298  
*Phyllachora ambrosiae*, 276  
*Phyllachora graminis*, 276  
*Phyllachora graminis panicis*, 276, 292  
*Phyllachora melicae*, 256  
*Phyllachora oryzopsidis*, 251  
*Phyllactinia corylea*, 276  
*Phyllosticta ambrosiae*, 295  
*Phyllosticta apocyni*, 277  
*Phyllosticta atriplicis*, 252  
*Phyllosticta congesta*, 280  
*Phyllosticta cruenta*, 295  
*Phyllosticta destruens*, 288  
*Phyllosticta dioscoreae*, 260  
*Phyllosticta fraxinicola*, 260  
*Phyllosticta grossulariae*, 256  
*Phyllosticta innumerabilis*, 288  
*Phyllosticta ludwigiae*, 295  
*Phyllosticta malaleuca*, 288  
*Phyllosticta oakesiae*, 295  
*Phyllosticta phaseolina*, 260  
*Phyllosticta phomiformis*, 256  
*Phyllosticta pyrolae*, 281  
*Phyllosticta quercea*, 284  
*Phyllosticta steironematis*, 281  
*Phyllosticta ulmicola*, 288  
*Phyllosticta verbascicola*, 281  
*Phyllosticta verbenicola*, 295  
*Phyllosticta virginiana*, 288  
*Physalis heterophylla*, 278  
*Physalospora ambrosiae*, 276  
*Physocarpus opulifolius*, 251  
*Physoderma vagans*, 265  
*Phytophthora infestans*, 266  
*Phytophthora thalictri*, 266  
*Phytophthora thalictri*, 266  
*Piggotia vaccinii*, 272  
*Pisum sativum*, 297  
*Plasmopara acalyphae*, 251, 266  
*Plasmopara australis*, 267

- Plasmopara cephalophora*, 267  
*Plasmopara cubensis*, 260, 295  
*Plasmopara geranii*, 266  
*Plasmopara halstedii*, 267  
*Plasmopara humuli*, 266  
*Plasmopara illinoensis*, 280  
*Plasmopara kellermani*, 287  
*Plasmopara obducens*, 251, 266  
*Plasmopara pygmaea*, 266, 271  
*Plasmopara ribicola*, 266  
*Plasmopara viburni*, 267  
*Plasmopara viticola*, 267  
*Pleosphaerulina briosiana*, 295  
*Poa annua*, 277, 279  
*Poa pratensis*, 278, 292  
*Polygonum Persicaria*, 279  
*Populus balsamifera*, 277  
*Populus grandidentata*, 257  
*Populus tremuloides*, 253, 257  
*Potentilla anserina*, 278  
*Prenanthes*, 289  
*Prenanthes alba*, 264, 289  
*Protomyces andinus*, 269  
*Prunus americana*, 261  
*Prunus nigra*, 294  
*Prunus pennsylvanica*, 280  
*Prunus virginiana*, 288  
*Psedera*, 252  
*Pseudopeziza singularia*, 276  
*Puccinia absinthii*, 259  
*Puccinia agropyri*, 259  
*Puccinia aletridis*, 291  
*Puccinia andropogonis*, 254  
*Puccinia anemones-virginianae*, 259  
*Puccinia asteris*, 277  
*Puccinia atropuncta*, 275  
*Puccinia caricis-shepherdiae*, 301  
*Puccinia cryptotaeniae*, 289  
*Puccinia gigantispora*, 259  
*Puccinia graminis*, 259, 279, 294  
*Puccinia koeleriae*, 254  
*Puccinia koeleriae-liatridis*, 254  
*Puccinia liatridis*, 254  
*Puccinia magnusiana*, 254  
*Puccinia peridermiospora*, 259, 279  
*Puccinia polygoni-amphibii*, 279  
*Puccinia pruni-spinosae*, 294  
*Puccinia punctiformis*, 302  
*Puccinia pustulata*, 254  
*Puccinia simillima*, 254  
*Puccinia troglodytes*, 302  
*Puccinia tumidipes*, 302  
*Puccinia zygadeni*, 275  
*Pucciniastrum arcticum americanum*, 254, 255  
*Pucciniastrum myrtilli*, 279  
*Pyrola elliptica*, 281  
*Pyrus ioensis*, 257  
*Pyrus melanocarpa*, 293  
*Quercus bicolor*, 256, 284, 292  
*Radicula palustris*, 294  
*Radicula sylvestris*, 294  
*Ramularia asteris*, 257, 293  
*Ramularia canadensis*, 298  
*Ramularia celtidis*, 285  
*Ramularia desmodii*, 274  
*Ramularia dispar*, 278  
*Ramularia efusa*, 278  
*Ramularia fraxinea*, 278  
*Ramularia lysimachiae*, 257  
*Ramularia occidentalis*, 293  
*Ramularia pratensis*, 293  
*Ramularia repens*, 289, 293  
*Ramularia tanacetii*, 285  
*Ramularia tenuis*, 261  
*Ramularia uredinis*, 278, 293  
*Ramularia variata*, 289  
*Ramularia virgaureae*, 257, 258, 259, 278  
*Ranunculus recurvatus*, 276, 279, 280  
*Ranunculus septentrionalis*, 276, 277, 279, 280  
*Rhus Toxicodendron*, 283  
*Rhizisma lineare*, 252  
*Ribes lacustre*, 292, 293  
*Ribes oxyacanthoides*, 256  
*Ribes prostratum*, 266  
*Ribes triste*, 266  
*Rubus allegheniensis*, 251, 256, 282, 293  
*Rubus canadensis*, 257  
*Rubus hispidus*, 257, 264  
*Rubus idaeus aculeatissimus*, 254  
*Rubus occidentalis*, 254, 255, 293  
*Rubus triflorus*, 254, 255, 263  
*Rubus villosus*, 264  
*Rudbeckia*, 289  
*Rudbeckia laciniata*, 264  
*Rumex altissimus*, 301  
*Rumex verticillatus*, 293  
*Salix alba vitellina*, 256  
*Salix amygdaloides*, 278  
*Salix longifolia*, 296  
*Salix lucida*, 257, 277, 297  
*Salix nigra*, 293  
*Schizonella melanogramma*, 259  
*Scirpus atrovirens*, 263, 272  
*Sclerospora graminicola*, 269  
*Sclerotopsis concava*, 296  
*Sclerotium deciduum*, 259  
*Sclerotium globuliferum*, 295  
*Scolecotrichum graminis*, 278  
*Scrophularia leporella*, 256  
*Secale cereale*, 293  
*Septocylindrium caricinum*, 253  
*Septocylindrium concomitans*, 278  
*Septogloeum ampelopsidis*, 252  
*Septogloeum convolvuli*, 261  
*Septogloeum quercuum*, 283  
*Septogloeum subnudum*, 297  
*Septoria acerella*, 282  
*Septoria ampelopsidis*, 252

- Septoria angularis*, 283  
*Septoria annua*, 277  
*Septoria aparines*, 296  
*Septoria aquilegiae*, 252  
*Septoria atriplicis*, 252  
*Septoria atropurpurea*, 277, 293  
*Septoria besseyi*, 289  
*Septoria bromi elymina*, 292  
*Septoria cacaliae*, 288  
*Septoria caricinella*, 277  
*Septoria cenchrina*, 296  
*Septoria chenopodii*, 252  
*Septoria comitata*, 282  
*Septoria commonsii*, 256  
*Septoria didyma*, 296  
*Septoria erechthitis*, 297  
*Septoria fumosa*, 283  
*Septoria gei*, 256  
*Septoria glumarum*, 293  
*Septoria graminum*, 292, 296  
*Septoria irregularis*, 283  
*Septoria lycopi*, 282  
*Septoria negundinis*, 282  
*Septoria noctiflorae*, 256  
*Septoria nodorum*, 293  
*Septoria oenotherae*, 277  
*Septoria polaris*, 277  
*Septoria populi*, 257  
*Septoria rubi*, 272, 282  
*Septoria salicifoliae*, 288  
*Septoria scrophulariae*, 256  
*Septoria sii*, 277  
*Septoria solidaginicola*, 277, 283  
*Septoria stachydis*, 256  
*Septoria tandilensis*, 296  
*Septoria umbelliferarum*, 253  
*Shepherdia argentea*, 301  
*Shepherdia canadensis*, 299, 301  
*Silene nivea*, 256  
*Smilax herbacea*, 297  
*Solidago latifolia*, 261, 283  
*Solidago memorialis*, 257  
*Solidago patula*, 277  
*Solidago serotina*, 258, 278, 285  
*Sparganium eurycarpum*, 296  
*Sphaeria gentianaecola*, 273  
*Sphaerotheca humuli*, 251  
*Sphaerotheca mors-uvae*, 292  
*Spiraea salicifolia*, 288  
*Stachys palustris*, 256  
*Stagonospora albescens*, 281, 292  
*Stagonospora atriplicis*, 252  
*Stagonospora intermixta*, 292  
*Stagonospora meliloti*, 282  
*Stagonospora sparganii*, 296  
*Steironema ciliatum*, 281, 296  
*Stipa spartea*, 262  
*Strophostyles helvola*, 260, 279  
*Synchytrium anemones*, 264  
*Synchytrium asari*, 264  
*Synchytrium aureum*, 255, 263, 276  
*Synchytrium cellulare*, 262, 287  
*Synchytrium cinnamomeum*, 280  
*Synchytrium decipiens*, 264  
*Synchytrium globosum*, 263  
*Synchytrium nigrescens*, 280  
*Synchytrium pulvereum*, 264  
*Synchytrium scirpi*, 263, 272  
*Taenidia integerrima*, 275  
*Tanacetum vulgare*, 285  
*Taxus canadensis*, 280  
*Teucrium canadense*, 262  
*Thalictrum dasycarpum*, 266, 278  
*Thalictrum revolutum*, 266  
*Trifolium dubium*, 294  
*Triosteum aurantiacum*, 257  
*Tuberculina argillacea*, 293  
*Typhula muscicola*, 260  
*Ulmus americana*, 288  
*Ulmus fulva*, 256, 277  
*Ulmus racemosa*, 256, 288  
*Urocystis agropyri*, 278, 294  
*Uromyces appendiculatus*, 279  
*Uromyces graminicola*, 254  
*Uromyces hedysari-paniculati*, 259  
*Uromyces minutus*, 259  
*Uromyces perigynius atiporulus*, 299  
*Uromyces pyriformis*, 292  
*Urophlyctis major*, 265  
*Urophlyctis pluriannulata*, 265  
*Ustilago hypodytes*, 262  
*Ustilago sphaerogena*, 286  
*Ustilago striaeformis*, 278  
*Venturia cerasi*, 261  
*Verbascum Thapsus*, 281  
*Verbena stricta*, 286, 292, 295  
*Vernonia fasciculata*, 276  
*Vicia americana*, 268  
*Vicia angustifolia segetalis*, 277  
*Viola conspersa*, 264  
*Viola pallens*, 264  
*Viola pubescens*, 264  
*Viola sagittata*, 294  
*Viola scabriuscula*, 297  
*Vitis bicolor*, 288  
*Vitis vulpina*, 288  
*Zizia aurea*, 265



# THE CYTOLOGY AND PHYSIOLOGY OF VENTURIA INEQUALIS (COOKE) WINTER

---

CHARLES N. FREY

## INTRODUCTION

During the last century our present conceptions of the nature and habits of the fungi have been developed. Fries 1819-22 began the systematic classification of the fungi. De Bary (1853) and Kühne (1856) demonstrated the parasitic nature of the fungi and laid the foundation of modern pathology. Pasteur (1858-60), Raulin (1869-70) and Nägeli (1882) studied the nutrition of fungi. In 1791 Bulliard described the asci as female organs. He believed that the asci were fertilized by the bursting of the paraphyses. It was de Bary (1863), however, who first studied and described the sexual organs of the fungi and observed fertilization. His critical observations form the basis of our knowledge as developed at the present time. De Bary (1863-70) discussed the origin of the fungi, the function of the archicarp and antheridium, which he considered as functional sex organs, and designated the ascus a spore mother cell. He believed that the archicarp should be regarded as the female sex organ and the antheridium as the male and that there occurred a material union of a male cell, or a part of its protoplasm and nuclear content, with a cell of the archicarp. From the archicarp the ascogenous hyphae originated, the latter developing the ascus which he designated a spore mother cell. According to de Bary it is possible that the lines of descent for the Ascomycetes came from divergent forms. The two groups, the Phycomycetes and Ascomycetes, converge, the Mucorineae and Peronosporae of the former being comparable to Eremascus among the Ascomycetes. Due to the insufficient knowledge of his time de Bary concluded the relationship and phylogeny of the higher fungi would remain in doubt until further research establishing more definite evidence as to their origin and character. He was struck by the similarity between the sex organs of the Florideae and the

Ascomycetes and in his lectures declared that a relationship might exist between the two groups.

Tulasne (1867) described the fusion of the sex organs of *Pyronema confluens*. Janczowski (1871) discovered the origin of the ascogenous hyphae in *Ascobolus furfuraceus* and established their relation to the asci, thereby verifying the predictions of de Bary. In 1883 Kuhlman substantiated the statements of Janzewski as to the origin of the asci. Sach (1875) developed views similar to de Bary's. He noted the similarity of the archicarp of the fungi to the procarp of the red algae, and believed the fungi were derived from the red algae.

Opposed to the views of de Bary were those of Brefeld (1879) and Van Tieghem (1891). Brefeld maintained that the fungi possessed no sexual characters. He attributed only a vegetative character to the fusions. The ascus was considered comparable to a sporangium of the lower fungi, the spores being produced endogenously in the ascus as in the sporangium. The Ascomycetes were derived from the Phycomycetes through such forms as *Thamnidium* and *Mortierella*. His theory was based on the assumption that the sporangium through evolution had become an ascus. As we shall see later, this theory rests on poor evidence. Due to the work of Harper and others, it was clearly shown that the two organs are not homologous. In the Oomycetes the spores are produced by progressive cleavage, whereas in Ascomycetes the spores are delimited by astral radiations from the centrosome-like body of the ascus nuclei.

Van Tieghem (1891) expressed the view that the archicarp is perhaps only an ascogenous hypha differentiated at an early period, and that the antheridia are part of the enveloping perithecium or serve as respiratory organs.

In 1894 Dangeard, while investigating *Peziza vesiculosa*, discovered fusion of nuclei in the ascus. He maintained that the sex organs were no longer functional and that the ascus may be considered an egg in which fertilization occurred. The archicarp and antheridium might be regarded as vestigial organs. Later he changed his views somewhat, stating that the ascogonium and ascogenous hyphae constitute a gametophore derived from a gametangium which formerly functioned in the production of motile gametes, but lost this function in adapting itself to the land habit. This conception involves the relationship of the Ascomycetes to the Oomycetes. He assumes that the ascogonium and

ascogenous hyphae are outgrowths from a parthenogenetic egg and the ascus is the result of this vegetative growth, an organ which has no equivalent in the lower fungi.

Harper (1895) began his studies of the Ascomycetes with *Peziza stevensonia* and *Ascobolus furfuraceus* and later investigated *Sphaerotheca castagnei*. He found that the asci arise from ascogenous hyphae substantially in the manner described by de Bary (1865-66), Janzewski (1871), and Kuhlman (1883), and described the fusion of two nuclei in the ascus of *Peziza stevensonia* to form the primary ascus nucleus. The fusion nucleus grows and either migrates to the periphery or remains in the center of the ascus. He followed the processes involved by the three successive divisions of the fusion nucleus resulting in the formation of eight nuclei. Harper found the chromosome number to be eight and believed that in the first division, which differs in appearance from the other two, a reduction in the chromosome number occurs. Further research indicated that the process of spore formation in *Ascobolus furfuraceus* was similar.

De Bary had described the formation of the antheridium and the ascogonium from the mycelium of *Sphaerotheca castagnei*. Harper (1896) found that the antheridium and ascogonium are produced on neighboring hyphae. Each sex organ has one nucleus at the beginning of development and each cell is cut off from the mycelium by a wall. When the ascogonium has completed its development the antheridial hypha elongates, its nucleus divides, one daughter nucleus passes to the tip of the cell and a partition wall is laid down between the two nuclei. The antheridium lies against the oogonium, the wall between the two organs is dissolved at the point of contact, and the male nucleus pushes through the pore and fuses with the egg nucleus. Sterile hyphae grow from the female stalk and surround the sex organs after the completion of nuclear fusion. Similar hyphae grow from the stalk cell of the antheridium; the antheridium itself disintegrates after fertilization.

The nucleus of the ascogone after fusion with the male nucleus divides and a wall is laid down which separates the two daughter nuclei. The upper cell nucleus divides again and a second wall is formed. Five or six uninucleate cells may be formed but the penultimate cell is binucleate. The two nuclei of the penultimate cell fuse, forming the primary ascus nucleus. Harper holds that this fusion is vegetative, the sexual fusion occurring in the ascogonium.

Three successive nuclear divisions of the primary ascus nucleus result in the formation of the eight nuclei of the spores.

The sex organs of *Erysiphe communis*, according to a later paper by Harper (1896), are borne on different hyphae, and the uninucleate oogonium is separated from the mycelium by a basal cell. The uninucleate antheridium is similar, but smaller and also has a basal cell. The nucleus of the antheridium divides and a wall is laid down between the daughter nuclei. The nucleus of the end cell of the antheridium passes into the oogonium through a pore formed by the dissolution of the cell wall at the point of contact between the two sex organs. The sterile hyphae arise from the stalk cell of the oogonium. The nucleus of the oogonium, formed by the fusion of the egg and the male nucleus, then divides. The daughter nuclei immediately divide again. The oogonium elongates and walls are formed between the nuclei, giving rise to a chain of five to seven cells. The chain of cells so formed is crooked and the penultimate cell has two nuclei and from this cell the ascogenous hyphae arise. The ascogenous hyphae branch, each branch forming two or three cells. One large intercalary cell in each branch has two nuclei; the two nuclei of this cell fuse and then the cell develops into an ascus. The remaining cells of the ascogenous hyphae degenerate.

The cells of the ascogonium of *Ascobolus furfuraceus* according to Harper (1896) are uninucleate in the early stages, but later seem to be connected by openings in the walls between them. The ascogonium becomes a bow-like row of cells. The nuclei in each cell divide many times. The fourth cell from the apical end of the ascogonium is the largest and from it ascogenous hyphae arise. The nuclei of the adjacent cells flow into the ascogenous hyphae and the empty ascogonium disintegrates. The nuclei gather at the tip of the ascogenous hyphae. The ascogenous hyphae branch, and nuclei pass into the branches which are then separated from the ascogenous hyphae by walls, thereby making the cells so cut off ascus mother cells from which asci arise.

In 1897 Harper described in detail the cytological phenomena connected with ascus development and spore formation in *Erysiphe communis*, *Peziza stevensoniana* and *Ascobolus furfuraceus*. Fusion of two nuclei to form the primary ascus nucleus takes place. The process is eventually the same in the three organisms. Harper does not regard the fusion in the ascus as sexual, for in *Ascobolus furfuraceus* cases occur of four nuclei fusing to form the ascus



nucleus. He believes that this fusion, since it involves more than two nuclei, is not sexual. The ascus is a new structure, the product of the asexual generation. The spores are cut out of the cytoplasm by kinoplasmic radiations from the central body. Harper found that reduction occurs in the first division of the ascus nucleus of *Erysiphe communis*.

The process of spore formation is similar in *Peziza stevensonia* and also in *Ascobolus furfuraceus*. The kinoplasm forms the spindle fibres and the astral radiations which cause the delimitation of the spores. The nucleus may be active in directing the process of spore delimitation as it moves to the periphery of the ascus. The central body may be only a distributing point of nuclear activity although it appears to be able to form new kinoplasmic fibres by its own activity. The nature of the kinoplasmic changes in forming a cell wall are not known. The chromosome number does not change but there seems to be a reduction in quantity. The chromosomes always remain attached to the central body by fibres.

Harper (1899) studied spore formation in the sporangia of certain Phycomyces. Brefeld (1873) held that the jelly of the Mucorineae, in which asexual spores are imbedded, is homologous with the epiplasm of the ascus, and that the sporangia of the Zygomycetes illustrate an ancestral type from which the ascus has developed. Harper's results utterly failed to corroborate Brefeld's theory. In *Synchytrium*, *Pilobolus* and *Sporodinia* the spores are cut out by progressive cleavage of the cytoplasm, as a result of which all the cytoplasm of the sporangia is used in the formation of the spores. There is, therefore, no structure in the molds comparable with the epiplasm of the ascus. Spore formation in the ascus of *Lachnea scutellata* was found to be similar to the corresponding process in *Peziza stevensonia* and *Ascobolus furfuraceus* except in slight details. The process in *Sporodinia* is spore formation by progressive cleavage; the process in *Lachnea scutellata* is free cell formation.

Tulasne (1866) had observed a fusion of oogone and antheridium by means of pores in *Pyronema confluens*. De Bary (1863) could not find the actual fusion, though he felt certain that it occurred. Harper (1900) figures an oogonium of *Pyronema confluens* with a trichogyne applied to the antheridium. At the point of application of the trichogyne to the wall of the antheridium a pore is formed by dissolution of the cell walls. The nuclei of the antheridium pass into the trichogyne and through a pore in the wall separating the

trichogyne from the oogonium. The opening in the basal cell wall of the trichogyne then closes. The male and female nuclei in the oogonium then fuse in pairs. As there are more egg nuclei than male nuclei many of the former fail to find mates and are later disorganized. The female nuclei aggregate in the center of the oogonium previous to fusion, but after fusion migrate to the ascogenous hyphae which are produced from bud-like outgrowths from the oogonium at the time of the formation of a pore in the basal wall of the trichogyne. The ascogenous hyphae grow and branch profusely, their ultimate branches giving rise to the asci. At first each branch contains two nuclei. These nuclei are not sister nuclei but come from different nuclei in the ascogenous hyphae, each nuclei having descended from one of the original pair in the ascogenous hyphae. Possibly each one is a direct descendant of one of the daughter nuclei of the fusion nucleus and the two nuclei in the ascus therefore represent two distinct lines of descent.

The two nuclei in the branch, which is curved, forming a shepherd's crook, divide simultaneously and form four nuclei. The spindles are so placed that a pair of nuclei are left in the crook, one from each spindle, so they are not sister nuclei. The other two nuclei, each the daughter of a different mother nucleus, migrate from the spindles, one going to the apical region of the branch, the other to the basal region. Two partition walls are then laid down making three cells out of the branch, the apical cell containing the single apical nucleus, the middle cell containing two nuclei, and the basal cell containing the nucleus that migrated to the basal region. The middle cell lies in the crook of the branch and is somewhat dome-shaped. It now forms the ascus, the two nuclei in it fuse to form the primary ascus nucleus. The nuclear fusion is followed by three successive divisions that are similar to those already described by Harper for other Ascomycetes.

The results of Harper's (1905) study of *Phyllactinia corylea* substantiated his earlier work. The sexual apparatus is formed where two hyphae cross or lie close to each other. The oogonium and antheridium become applied and spirally twist about each other. A portion of the walls between them is dissolved and the single nucleus of the antheridium migrates through the pore into the oogonium. It fuses with the somewhat larger nucleus of the oogonium and the pore through which it entered closes. After nuclear fusion, or just previous to the migration of the male nucleus, the stalk cell of the oogonium produces paraphyses to form

the perithecium. The stalk cell of the antheridium may also form paraphyses. The ascogonium increases in size, the fusion nucleus divides and a chain of three to five cells is formed. The end cell of the chain is uninucleate, the penultimate cell is generally binucleate but may contain more than two nuclei. Branches arise from the penultimate cell and perhaps from some of the others; these branches are the ascogenous hyphae. The asci are formed after the ascogenous hyphae have become septate. Each ascus arises from a terminal cell or as a lateral outgrowth from an intercalary cell of an ascogenous hypha. The cells that produce asci are at first binucleate. The ascogenous hyphae are multinucleate before they become septate which makes it possible to conceive that the two nuclei in the ascus are not sister nuclei. Following nuclear fusion in the ascus the ascogonium and the sterile cells of the ascogenous hyphae degenerate.

About the time of degeneration of the oogonium the perithecial envelope has made considerable growth. The wall formed by the perithecial hyphae consists of three layers: a peripheral, or outer layer of cells; a protective lignified layer, beneath the peripheral layer; and a layer of thin walled nutritive cells in the interior surrounding the asci. Harper has given a detailed account of the nuclear behavior in the ascus and the development of the spores; these are in agreement with his observations on other forms.

After the fusion of two nuclei to form the primary ascus nucleus, the cytoplasm of the ascus appears spongy but has no large vacuoles. Directly after fusion the chromatin of each of the fusing nuclei remains independent (retains its individuality), each group of chromatic structures consisting of about eight strands. The central bodies finally approach and unite, the nucleoli fuse, the two groups of chromatin strands intermingle and fusion is complete. At this time the ascus and the perithecium are about half grown. A synopsis stage now follows; later the chromatin fibres gradually become looser and a spireme appears. Harper always found eight chromatin strands at this stage. A period of rest intervenes previous to spindle formation, and the nucleus migrates from the base to the middle of the ascus. Each strand of the fibres then elongates, becomes bent and forms a chromosome. The chromosome contracts and thickens, leaving a fibrillar connection with the central body. The chromatin bodies seem to maintain a definite connection at all times with the central body. The central body now divides, the daughter bodies separate and a spindle is formed

between them. Eight chromosomes are found in the complete equatorial plate. In the three successive nuclear divisions in the ascus eight chromosomes always appear. The daughter nuclei of the first division are smaller than the mother nucleus. They divide at once or after a short period of rest. At the end of the third division each ascus contains eight nuclei. Only two spores are found in the ascus; the other six of the eight nuclei resulting from the three divisions of the fusion nucleus disintegrate. After the third division the polar asters persist, especially those connected with the two nuclei that are to form the spore nuclei. A nuclear beak is formed as in *Erysiphe* and the spores are delimited by the activity of kinoplasmic fibres that radiate from the central body. The remaining fibres now disappear; the central body breaks away from the plasma membrane of the young spore. The nucleus is reformed, becomes spherical, the central body lying against its membrane, and a spore wall is formed. Harper holds that the primary ascus nucleus contains quadrivalent chromosomes, which are separated into univalent chromosomes in the course of the three successive nuclear divisions. The fusion of nuclei in the ascus is a vegetative process and the ascus may be regarded as a spore mother cell. Harper considers that there is a true alternation of generations in the Ascomycetes.

I have taken up the work of Harper in detail as it represents the development of de Bary's fundamental conceptions in addition to Harper's own interpretation of the phylogeny and morphology of the fungi. His work developed the whole field of fungous morphology far beyond the grasp of the men of de Bary's time and his views have been, until recently, accepted as the best interpretation of the cytological processes concerned in the life history of the fungi. Dangeard (1903-04) on the other hand, inclines toward the views of Brefeld, regarding the sex organs as non-functional and the ascogenous hyphae as parthenogenetic outgrowths of functionless sex organs. The only nucleus fusion is in the ascus. He maintains that the union of gametes in the ascus has all the characteristics of a sexual fusion and the ascus all the characteristics of a sexual organ. The chromosome number doubled by fusion in the ascus is reduced by the first division, and the two succeeding divisions are homotypic.

Many contributions by various workers have been added to the literature substantiating one or the other of these views, but in the main supporting the ideas of Harper. Recently, however, a paper

by Clausen (1912) appeared in which he sets forth some new views. Clausen adopts an entirely new viewpoint. His theories combine the ideas of de Bary, Harper and Dangeard, and, if substantiated, will form a distinct advance in our knowledge of the sexuality of the fungi. Clausen retains the idea that the ascogonium and antheridium are sexual organs and that only one nuclear fusion occurs. This takes place in the ascus and may be considered comparable to the fusion occurring in the basidia and in teleutospores. The sexual act initiated in the sex organs is completed in the ascus.

It may be well to review in more detail the ideas of Clausen in order that a complete understanding of the various theories may be gained. The views of Blackman and Welsford (1912) are opposed to those of Clausen and will be reviewed later. Clausen (1905) described the formation of the sex organs in *Boudiera*. Short branches arise from the vegetative hyphae which branch dichotomously. The branches then twist about each other forming spiral coils, two branches in a coil, one forming the ascogonium and trichogyne, the other the antheridium. The ascogonium contains two or more nuclei. Ascogenous hyphae arise from the ascogonium after fusion with the antheridium has taken place. Nuclear behavior and the formation of the asci is similar to that of *Pyronema confluens*. Clausen (1906) states his belief in the sexuality of the fungi and opposes the views of Dangeard.

In a paper published in 1907 Clausen seems to have changed his views completely. He finds that the sexual organs of *Pyronema confluens* function, but nuclear fusion does not take place in the ascogonium. The male nuclei pass into the ascogonium, in the manner described by Harper, and a male nucleus pairs with a female nucleus but no fusion occurs. Conjugate divisions of the nuclei may occur as they migrate into the ascogenous hyphae. The ascus is formed in the manner described by Harper. The nuclei that fuse to form the primary ascus nucleus are, perhaps, direct descendants of the male nucleus on one side, and the female nucleus on the other, which paired in the ascogonium.

Clausen (1908) states that sexual fusion occurs in *Saproleginia monoica*. Degeneration of all the nuclei of the oogonium except those at the periphery occurs. The peripheral nuclei divide mitotically and from the daughter nuclei uninucleate eggs are formed. The antheridia apply themselves to the oogone, a pore is formed and nuclear fusion takes place between the male nucleus and the

egg. Each egg has a centrosome which may function like the central body of the Ascomycetes described by Harper.

In a later work Clausen (1912) confirms the results of his earlier research on *Pyronema confluens*. He agrees with Harper as to migration of nuclei from the antheridium to the ascogonium, but does not believe that nuclear fusion takes place in the ascogonium. The nuclei pair and migrate into the ascogenous hyphae. The ascogenous hyphae becomes septate and the cell nearest to the ascogonium may have eight pairs of nuclei, the other cells only one pair. The penultimate cell lying in the hook usually forms an ascus and the two nuclei lying in the hook fuse to form the primary ascus nucleus. In some cases the apical cell at the extremity fuses with the stalk cell and another ascus is formed. The cell usually forming an ascus may in some cases by budding produce a hook-like structure which forms another ascus in the usual way.

The first division in the ascus is heterotypic and the nuclei contain twelve chromosomes after the division. The second division is homotypic, twelve chromosomes appear at the equatorial plate and twelve pass to the poles. During the third division the astral rays appear at the poles, and twelve chromosomes pass to each pole. Clausen finds no centrosome as described by Harper in *Phyllactinia*. He believes the delayed fusion in *Pyronema confluens* may be due to toughness of the nuclear membrane. Clausen adheres to the idea of sexuality in *Erysiphe* and *Sphaerotheca* and holds that the ascus is a spore mother cell as stated by Harper. In accordance with the views of Clausen the Ascomycetes are similar to the Basidiomycetes and their phlogeny must be conceived from a new standpoint, preferably from some oomycete. It is simpler to consider the Ascomycetes from the viewpoint of Clausen but to do so we must disregard the work of so many investigators who believe they have observed nuclear fusion in the ascogonium, especially the critical work of Harper, that more evidence is necessary before these facts can be considered established.

Another point of view which may be considered as a reversion to the ideas of Brefeld has been brought out by Blackman and Welsford (1912) working with *Polystigma rubrum*. They maintain that the sexual organs have degenerated and that the ascogonium develops but does not function. The asci arise from the vegetative hyphae and the development then proceeds as described by Harper, Clausen, and others.

It is necessary at this point to take up the work of other investigators that we may determine to what extent the theories proposed by the leading workers or pioneers have been substantiated. Nichols (1896) holds with Harper that sexual fusion occurs in the Ascomycetes, but it may not occur in all of them. In *Ceratostoma* no sexual fusion occurs and in *Teichospora aspersa* and *Teichosporella sp.* the ascocarp is formed by the division of a single hyphal cell of the mycelium. The ascus arises from a single central cell.

Wager (1899–1900) described the formation of a single sexual nucleus in the ooplasm of the oogonium of *Peronospora parasitica*. The remaining nuclei of the female organ pass into the periplasm and degenerate. Both male and female nuclei undergo mitosis before fusion and a central body is present. The zygote is uninucleate. Stevens (1899) holds that the oogonia and antheridia of *Albugo bliti* are multinucleate when formed but later the oogonium is differentiated into oosphere and periplasm. All the nuclei pass into the periplasm and undergo mitosis. The nuclei that lie at the boundary between ooplasm and periplasm give one daughter nucleus to the ooplasm, the other to the periplasm. Fertilization occurs in this species; the male nuclei enter the ooplasm by means of the antheridial tube and fuse in pairs with the female nuclei.

Several sex organs are produced on *Cladonia crispum*. Baur (1898) thinks fertilization is necessary to produce asci. Baur (1901) states that he observed fertilization of the carpogonium by spermatia in *Parmelia acetabulum*. *Parmelia* and *Cladonia* according to Baur (1904) have ascogenous hyphae arising from the carpogonium. He observed fusion of spermatia with trichogynes in *Anaptychia* and *Endocarpion* but could discover no fusion in *Solarina* and declared it to be apogamous.

Juel (1902) holds that *Dipodascus*, which has multinucleate sex organs arising side by side from a single hypha, has functional oogonia and antheridia. One large male nucleus passes into the oogonium by a pore and fuses with a large nucleus in the oogonium. The oogonium produces a single ascogenous hypha, the latter producing a single ascus. The nuclei arising from the fusion nucleus decrease in size with each division and finally pass into the ascus. Juel thinks that *Dipodascus* is comparable to *Albugo* in the formation of the egg. Sexual fusion occurs in *Gymnoascus reesii* and *Gymnoascus candidus* according to Dale (1903). The ascogenous hyphae arise from cells which have paired and fused.

Barker (1903) describes sexual fusion in *Monascus*. The sex organs are small branches arising from the same hyphae and lie side by side. The oogonium consists of three cells; the stalk cell, central cell, and trichogyne. The male nuclei pass into the trichogyne by a pore and fuse in pairs with the female nuclei. The ascogenous hyphae arise from the central cell by budding but later grow back into it due to the pressure of the perithecial hyphae. The asci therefore appear to originate within the central cell. Barker tries to show that relationship exists between the Ascomycetes and the Oomycetes. He believes that the nuclei left in the periplasm of the oogonium of *Albugo candida* are comparable to those which degenerate in the central cell of *Monascus*.

Guilliermond (1903-04) points out that nuclear fusion accompanies cell fusion in some of the yeasts. This fusion he considers as sexual. He finds that conjugation of conidia and nuclear fusion precede spore formation in the Schizosaccharomycetes and Zygosaccharomycetes. Two cells are connected by a tube and in the tube nuclear fusion occurs. This is followed by one division and the daughter nuclei migrate, one going to each of the two original cells. Four spores are formed after the nucleus has made two successive divisions.

Maire (1903-04) and Dangeard (1903) hold that all Ascomycetes have four chromosomes. Guilliermond finds that the chromosome number in the nuclei of several Ascomycetes, *Peziza vesiculosis* and *Peziza catinus*, is not the same; therefore, the chromosome number varies with the species and the statements of Maire and Dangeard are invalid. Harper (1896, 1905) finds that the chromosome number varies with the species. He considers that there is a true alternation of generations in the Ascomycetes, the division in the ascus being purely vegetative, and states that it is impossible to determine when the two reductions in chromosome occur. It may be in the first and second division or in the second and third. The chromosomes are quadrivalent as they pass to the poles in the first division and bivalent in the second. The chromosome number remains constant during the three divisions, according to Harper (1905). The three divisions must, therefore, be necessary as two reductions must occur, and possibly arose in connection with inhibited cell and nuclear division due to increase in the nutritive material of the ascus. Fraser and Welsford (1908) hold that the first division of the primary ascus nucleus is the "meiotic" or reducing division, the synapsis occurring after the first contraction.



The third division is also a reducing division compensating for the vegetative fusion in the ascus. The tetravalent chromosome number before the first division in *Otidea aurantia* is four and following the first division each nucleus contains two chromosomes. In *Peziza vesiculosa* the first and second divisions constitute a "meiotic" phase. Eight chromosomes travel to the pole after the first division and on the spindle of the second, or homotypic division, four chromosomes appear and the resulting nucleus contains four chromosomes. Following the third, or "brachymeiotic" division, the nucleus contains four chromosomes which are regarded as univalent.

Fraser and Brooks (1909) hold that the first division in the ascus of *Humaria granulata* is synaptic and eight chromosomes migrate to each pole. In the second division four chromosomes appear and four migrate to each pole. The union of chromosomes takes place after the sexual, or pseudo-apogamous fusion in the ascogonium. The chromosomes of the asexual fusion, the fusion in the ascus, remain apart until the heterotypic division is complete and then pair in the prophases of the homotypic, or second division, separating in the "brachymeiotic", or third division in the ascus. *Ascobolus furfuraceus* is similar to *Humaria granulata* except that in the former vacuoles play an important part in delimiting the spores.

In *Lachnea stercorea* the nuclei fuse in pairs in the ascogonium and the chromosome number of the fusion nucleus is double that of the vegetative cell nucleus. In the second fusion in the ascus the chromosome number is doubled again making eight chromosomes in the primary ascus nucleus. The first division in the ascus is heterotypic and four univalent chromosomes appear at each pole. The second division is homotypic and four chromosomes pass to each pole. During the prophases of the third division there are still four chromosomes. In the metaphase the four chromosomes are still present but they do not divide and two chromosomes pass to each pole. The third division is, therefore, brachymeiotic and differs from meiosis in that there is seldom a synaptic contraction visible. When contraction does occur the reduced number of chromosomes is present in the prophase. If pairing occurs in the second prophase, reduction occurs in the second division. A second contraction never occurs during brachymeiosis. The absence of any pairing in the third division may indicate that the asexual fusions have little effect on the fungus. Perhaps the nuclei are too closely related. The spores are delimited after the manner

described by Harper with the exception that no fusion of ktoplasmic fibres was observed.

Olive (1905) finds that the central cell of *Monascus* described by Barker, is the nurse cell. The ascogenous hyphae arise from the trichogyne and grow into the central cell and form asci in the interior. Schikorra (1909) states that *Monascus* has paired nuclei and nuclear fusion takes place only in the ascus.

According to Trow (1895) there is no similarity in the development of *Saprolegnia diviea* to that of some of the Ascomycetes which have been described. He finds that the fertilized nucleus undergoes division into oospores directly after fusion. No nuclear division or fusion occurs in the sporangium. In the oogonium and the antheridium each nucleus undergoes one reduction before fusion.

Trow (1901) finds that the ooplasm of the mature oogonium of *Pythium ultimum* contains one nucleus, the remaining nuclei pass into the periplasm and degenerate. One male nucleus from the antheridium fuses with the nucleus in the ooplasm; fusion of the nuclei, however, is delayed until the oospore wall is formed.

Christman (1905) described the process of fertilization in *Caecoma nitens*. Pustules form containing hyphae with short thick cells, each cell having a single nucleus. The single nucleus divides, the cell elongates and a distal cell is cut off which dwindles in size. The basal cell keeps on growing and inclines toward another basal cell. Fusion occurs by the formation of a pore in the upper part of the adjacent sides making the apical ends continuous. The two nuclei lie in the apical end and conjugate divisions follow. Two daughter nuclei wander back into their respective cells, but the original nuclei remain side by side, move to the distal end and are cut off by a cell wall. The cell formed is an aecidiospore mother cell which may divide repeatedly. In the paired basal cells the process may be repeated.

Faull (1905) finds that the ascus of *Sordaria fimicola* does not always arise from the penultimate cell, but in many cases from the ultimate. In *Sordaria humana* and *Podospora acerina* the asci arise from the terminal cells of ascogenous hyphae. He holds that the ascus is homologous to the zoosporangium of the Oomycetes. Faull (1911-12) states that only one nuclear fusion occurs in the Laboulbeniales. In *Laboulbenia chaetophora* and *Laboulbenia gyridarium* no antheridia are produced. By a series of divisions the binucleate ascogenic cells are produced. The ascogenic cells

bud, and the buds form the asci. The nuclei of the ascogenic cells divide simultaneously and one of the daughters of each mother nucleus passes into the ascus, the pair left in the ascogenic cell may divide again. The two nuclei that enter the ascus fuse to form the primary ascus nucleus.

Miyake (1901) states that the multinucleate oogonium of *Pythium de baryanum* is differentiated into ooplasm and periplasm. A nucleus from the periphery migrates into the ooplasm to function as a female nucleus, which previous to fertilization divides. Only one antheridial nucleus functions.

It is interesting at this point to take up the yeasts, a group of Ascomycetes which have asci but no definite sex organs. Some yeasts, according to Guilliermond (1912), form the ascus by the fusion of two vegetative cells. A bud or beak is formed which fuses with the bud of another cell and the nuclei migrate into the tube and fuse. There is considerable variation in the manner of fusion and in the number of spores formed in the ascus. Wager and Peniston (1910) state that during spore formation in the Saccharomycetes the nuclear vacuole and network disappear. The nucleolus becomes closely surrounded by chromatin granules and then divides into two nearly equal, or equal, daughter nuclei each of which consists of a portion of the nucleolus with the surrounding chromatin. Each of the nuclei divides again to form the four spore nuclei of the ascus.

Guilliermond (1911, 1917, 1918) states that pairings of cells may occur in some forms of yeasts by the cells forming a beak and that nuclear fusion occurs, followed by migration of the fusion nucleus into one of the cells, leaving the other empty. The egg then forms an ascus. From the similarity of the developments of yeasts to *Endomyces* and *Eremascus* he thinks these forms are affiliated.

From the evidence available no definite phylogeny can be traced for the yeasts. It appears that only one nuclear fusion takes place and that the oogonium itself becomes the ascus. In such simple related forms as *Gymnoascus reesii* and *Gymnoascus candidus* Dale (1903) finds that sexual fusion occurs. The ascogenous hyphae arise from cells which have paired and fused.

Observations on *Saccharomyces cerevisiae* and related forms made by the writer indicate that dumb-bell forms are quite common in old cultures, especially if the culture solutions are of high acidity and unbalanced physiologically. Whether these forms have

any reproductive function has never been definitely determined. In nearly every case examined the cell contents were vacuolate and had apparently degenerated. When the cultures were dried no spores appeared and there was no indication of budding from the dumb-bell forms when nutrient solutions were added.

Investigations of the Basidiomycetes have brought forth some very interesting results, those of Christman (1905) having been considered, especially in relation to the ideas of Clausen on Ascomycetes. Blackman (1904) finds that in *Phragmidium violaceum* binucleate cells are formed in the aecidium. The spermatia are considered functionless. In the aecidium a group of special cells form the fertile cells; the fertile cells divide, each one cutting off a sterile cell above. The nuclei that enter the fertile cells migrate from undifferentiated mycelial cells and the binucleate fertile cell then produces aecidiospores which are binucleate. Nuclear fusion does not occur until the teleutospore is formed. Fusion is followed immediately by reduction and the formation of sporidia. Similar processes were observed in *Gymnosporangium clavariaeformae*. Blackman and Fraser (1906) state that the fertile cells of *Phragmidium violaceum* are female gametes which are fertilized by vegetative cell nuclei instead of spermatia. In *Puccinia poarum* nuclear migration begins before the fertile cells are formed. The nuclei migrate from one vegetative cell to another and later to the fertile cells. Two vegetative cells may form a fertile cell by fusion. In *Melampsora rostrupi* basal cells in the aecidium pair and form aecidiospores which are binucleate. *Puccinia malvacearum* is apogamous. From all the forms studied they conclude that nuclear fusion does not occur in the aecidiospore. The conjugate nuclei fuse in the teleutospore and reduction occurs during the formation of sporidia, a process which may be considered a true alternation of generations. In *Humaria rutilans* no male cells function, but the female nuclei of the multinucleate ascogonium fuse in pairs. Whether this process can be considered analogous to that of *Phragmidium violaceum* is questionable.

Bensaude (1918) investigated the nuclear behavior in certain Basidiomycetes. She finds that the mycelium is heterothallic, a + spore and a — spore must develop in sufficient proximity in order that fusion of the cells of the hyphae can be accomplished. Binucleate cells are formed but fusion of nuclei does not take place until the basidium stage is reached. Fitzpatrick (1918) and Gilbert (1910–11) (1921) have found that the hyphal cells of the

Basidiomycetes usually have a single nucleus in the early stages; later two nuclei may be found. The spores are uninucleate. The cells immediately beneath the hymenial layer always contain two nuclei. Fusion of nuclei occurs in the basidium. Gilbert (1921) states that the young spores of *Dacromyces* are one celled and uninucleate; later division occurs and an eight celled spore is formed. Uninucleate hyphae are produced from these cells.

The spermatogonia and ascogonia of *Polystigma rubrum* are functionless according to Blackman and Welsford (1912). They describe the formation of functionless spermatia on terminal hyphae. They state that large uninucleate cells surround the ascogonium but its cells are multinucleate. The ascogonium degenerates and perithecial hyphae arise in the neighborhood of the ascogonium, formed perhaps by vegetative hyphae, or special hyphae arising from or about the base of the degenerating ascogonium. The special hyphae are finger-like and grow together in a conical mass, the apex usually directed toward the lower epidermis of the leaf. The nuclei of the cells are arranged in pairs. From these hyphae the ascogenous hyphae arise, the nuclei of the latter arranged in pairs. The asci probably arise from the penultimate cells of the ascogenous hyphae for in these cells nuclear fusion seems to occur. There is evidence of nuclear fusion when the ascogenous hyphae are differentiated.

Welsford (1907) finds no antheridia taking part in the sexual fusion of *Ascobolus furfuraceus*. The female sex organs consist of a row of 6–10 cells. The middle cell is at first uninucleate but later becomes multinucleate and develops the ascogenous hyphae. The remaining cells of the ascogonium connect with the middle cell by pores through which the nuclei migrate and fuse in pairs in the ascogenous hyphae. The penultimate cells of the ascogenous hyphae contain two nuclei which fuse and from this cell the ascus is formed in the usual way.

Fraser (1913) states that the archicarp of *Lachnea creta* develops on one of the larger filaments; it forms two or three coils and becomes septate, each cell becoming multinucleate. The archicarp becomes differentiated into three regions; the stalk, the coiled ascogonium, and the septate trichogyne which elongates and branches. Antheridia are not present. Large pores form between the cells of the multinucleate ascogonial cells and nuclei migrate from one cell to another. The ascogenous hyphae arise from the cells of the ascogonium and asci are formed. Reduction occurs

during the first division in the ascus and in the telophase of the third division.

Many investigators fail to find antheridia in the forms they studied. Ramlow (1906) holds that *Thelebolus stercoreus* is apogamous and no antheridia are present. Cutting (1909) failed to find antheridia in *Ascophanus carneus*. He also states that any cell of the multinucleate and multicelled ascogonium may produce ascogenous hyphae.

Ramlow (1914) holds that the nuclei of *Ascophanus carneus* do not fuse but are paired in the ascogonium and wander into the ascogenous hyphae paired. Each cell of the ascogenous hyphae receives a pair of nuclei but only one cell develops into an ascus. Observations indicate that *Ascobolus immersus* is similar, except that each ascus contains sixteen spores.

Overton (1906) states that the ascogenous hphae of *Thecotheus pelletieri* may arise from any cell of the ascogonium. The cells of the ascogonium are not connected by pores. The ascus may contain sixteen or thirty-two spores. This seems to indicate that three divisions are not necessarily the limit and the number of divisions may have no special significance.

According to Brown (1908) the antheridium of *Pyronema confluens* is functionless, one fusion of nuclei occurs in the ascogonium. He holds (1910) that only one nuclear fusion occurs in *Leotia lubrica*, that being the fusion in the ascus.

The filaments of *Helvella elastica* form ascogenous hyphae according to McCubbin (1910). The nuclei of the cells in the fruiting body are paired. This organism is of great interest as no sexual organs function in the production of asci.

Carruthers (1911) holds with Harper that two nuclear fusions are necessary. In *Helvella crispa* the chromosome number in the vegetative nuclei is two and in the ascogenous hyphae four. The chromatin does not mingle during the first part of meiosis; only in the spireme stage is there a union and then perhaps an imperfect one. The chromosome number in the primary ascus nucleus is eight. Two contractions occur during the first, or heterotypic division and chromatin is extruded. The first and second divisions constitute a meiotic phase. The third division is simply a separation of nuclei which fused in the ascus. Sixteen nuclei may be formed but only eight spores are produced.

Bachman (1912-13) finds that the archicarp and spermatia of *Collema pulposum* function. The trichogyne grows toward the spermatia, coils about it and fertilization is accomplished.

Fraser (1913) describes the trichogyne of *Lachnea creta*. She holds that this form is apogamous, no antheridium having been found.

Nienburg (1914) opposes the views of Blackman and Welsford on *Polystigma rubrum*. He states that the archicarp has a coil at its base and a chain of long multinucleate cells forming a trichogyne. A long multinucleate cell, the antheridium, applied itself to the long uninucleate cell, the ascogonium, the walls dissolve and the nuclei migrate into the ascogonium where one increases in size and becomes the male nucleus. When this male nucleus is equal to the female nucleus in size the remaining cells of the archicarp have degenerated. The ascogenous hyphae arise from the ascogonium and contain paired nuclei but the development of the ascus could not be followed. The trichogyne is not a sexual organ, but may be regarded as a vegetative or nutritive structure. Nienburg did not observe fusion in the ascogonium or in the ascogenous hyphae and believes the only fusion that takes place is in the ascus.

Brooks (1910) described the development of *Gnomonia erythrotoma*. He finds spermatia are produced but they no longer function. Several hyphae entwine and a perithecium is formed. Later a trichogyne appears. A coil of deeply staining cells forms the ascogonium which, however, degenerates. The ascogenous hyphae arise de novo, probably from the vegetative hyphae. The only nuclear fusion takes place in the ascus. Reduction occurs in the first division

Moreau (1919) working with Pelligeraceae could find no spermatia which possessed the power to function as male cells. The ascogonium is multinucleate and no connection between the spermatia and the ascogonium was observed. The fusion in the ascus is the only nuclear fusion taking place.

Investigations of the development of *Pyronema confluens* were made by Brown (1915). He states that the form he studied produces a trichogyne which, however, does not fuse with the antheridium. He observed no fusion of nuclei in the ascogonium or in the ascogenous hyphae. The only fusion is in the ascus.

Welsford (1915) states that the reason paired nuclei are found in the ascogonium and ascogenous hyphae is due to better nutrition which causes rapid division. Nuclei in cells filled with large

quantities of food material proceed to divide, and before the nuclei can migrate another division occurs. This accounts for the figures observed by Clausen. There is, therefore, no significance to be attached to nuclei in this condition. In poorly nourished mycelia the paired nuclei are absent, as the nuclei have time to move apart before another division takes place.

Killian (1915) described the origin of the archicarp in *Venturia inaequalis*. He finds that a single coiled hyphae enlarges in the perithecium and forms an ascogonium. A trichogyne is produced which protrudes from the perithecium and grows toward the antheridium, but remains surrounded by a layer of cells. The two organs come into contact and pores are formed through which the male nuclei pass into the trichogyne. The walls of the ascogone are dissolved and the male nuclei pair with the female nuclei and aggregate in the end or basal cells of the ascogonium. Further observations were not made as the organism offers considerable difficulty for study.

*Cryptomyces pteridis* represents a type in which the trichogyne no longer functions. Pairing of equivalent cells in the fruiting body occurs and one of the cells may be regarded as an egg. The nucleus from the male cell migrates into the oogonium through a pore, but fusion with the egg nucleus does not take place for some time. The cell containing the egg does not produce ascogenous hyphae, although it elongates in an attempt to do so, but itself becomes the ascus. The process is essentially like that described by Guilliermond for yeasts. Only one nuclear fusion occurs.

The phylogeny of the Ascomycetes has been the subject of considerable controversy. Sachs (1868) and de Bary (1870-1899) noted the similarity of the sex organs of the Ascomycetes and the Florideae. Brefeld (1875) held that the Ascomycetes were derived from the Phycomycetes. He believed the sporangium evolved into an ascus, a view which Harper's work has shown to be extremely improbable. De Bary, (1881-84) states that the Ascomycetes may have originated from the Peronospora. He suggests that certain forms like *Eremascus* may have been derived from the Mucorales. Bucholz (1912) states that *Endogone* is a Phycomycete. The structure developed from the fusion of two unequally differentiated sex cells he designates a "zygosporocarp". Clausen (1912) prefers the view that the Oomycetes gave rise to the Ascomycetes. Dodge (1914) in a very able discussion of the literature concludes



that the Ascomycetes must have arisen from the Florideae. He bases his conception on the similarity of the archicarp, especially the trichogyne, to the corresponding organs in the Florideae. The difficulty in accepting this view arises from the lack of evidence as to the origin of the ascus, no equivalent organ having been found in the Florideae, unless we consider ooblastema filaments as homologous to ascogenous hyphae. Speculations, at present, are only worth while in so far as they stimulate further research. It is entirely possible that a large number of forms are present in nature, still undiscovered, which will supply the missing links. If such forms cannot be found our theories, like those on the origin of man, will ever remain the subject of dispute. The search for homologies in the evolution of the sex organs offers the most plausible method of attack. One would expect the vegetative organs to respond to immediate environmental changes whereas the generative organs or cells may not fundamentally alter.

Atkinson (1916) in a very detailed discussion attacks the views of Sachs on the origin of the Ascomycetes. He finds it impossible to accept the view of the origin of the Ascomycetes as being derived from the red algae. There is, according to him, no homology existing between the archicarp and the procarp. The ascus might develop from forms similar to Dipodascus by branching of the zyogametangium. By reducing the number of spores in the ascus of an organism of this type forms like Eremascus and Endomyces are produced. The trichogyne, Atkinson contends, is not a functional organ in most of the Ascomycetes studied, and may have developed rather as an outgrowth, or beak of the oogonium, a condition often found in certain oomycetes when the female organ is stimulated. In the Laboulbeniales the trichogyne is highly developed but does not always function. The septa prevent nuclear migration and thus it occurs that many Ascomycetes that retain the sexual organs may not have nuclear fusion. Many Ascomycetes that retain functioned gametangia do not possess a trichogyne. In cases in which the sperm enters the trichogyne there is no evidence that this process is necessary to initiate disintegration, as it may proceed without it and cannot be cited as proof of fertilization.

In such forms as *Monascus* he regards the antheridium as an elongated terminal cell of a hyphae and homologous with a chain of conidia. This conception harmonizes such anomalous forms as *Collema* in which the trichogyne fuses with a spermatium or conidium.

There is no evidence, according to Atkinson, to substantiate the view that ooblastema filaments are phylogenetically related to the ascogenous hyphae of the Ascomycetes. Pore formation is not connected with the presence of a trichogyne or antheridium as it is formed in *Ascobolus*, *Lachnea creta* and *Polystigma rubrum* forms in which one or both of these organs are absent. In the fusion of ooblastema filaments with auxiliary cells the diploid nucleus of the former never fuses with the haploid nucleus of the auxiliary cell but they actually repel each other.

Atkinson doubts whether the nuclear fusion in the ascus may be regarded as purely vegetative and believes it has greater significance. He cites Dangeard (1897) and W. H. Brown (1909) on *Pyronema* to substantiate his views that the sex organs do not always function. In *Lachnea scutellata* Brown (1911), the antheridium is absent, as also in *Ascophonas carneus*, and *Ascobolus immersus*. Ramlow (1914) and W. H. Brown (1910) maintain that no nuclear fusion occurs in the ascogonium of *Leotia* and Faul (1911-12) working on *Laboulbenia* holds the same view. The archicarp is absent in some forms and vegetative cells form ascogenous hyphae as in *Gnomonia erythrostoma* Brooks (1910) and *Helvella elastica* MucCubbin (1910). In *Polystigma rubrum* the archicarp, according to Blackman and Welsford (1912), does not function. In *Collema pulposum* observed by Bachman (1913), according to Atkinson, there is no evidence that the nucleus of the spermatia migrate to the ascogonium, although disintegration follows. The archicarp of *Gnomonia erythrostoma* Brooks (1910) has also ceased to function. If we accept the views of Clausen (1912) these results have no significance as only one fusion occurs and the sex organs are no longer necessary.

It is not difficult to bring up negations but the articles quoted by Atkinson to support one statement refute his claims in another. His argument that the trichogyne is of no fundamental importance from a phylogenetic standpoint and that the sex organs of many Ascomycetes are functionless or atrophied makes one doubt the wisdom of placing so much faith in the immutability of certain organs of the Phycomycetes as he apparently has. Progression and degeneration may go on together, and to discard one view or fact because it does not harmonize with preconceived notions does not solve the matter. More evidence is required before a generalization can be made.

From the literature reviewed one obtains no definite or uniformly accepted ideas of the phylogeny or cytology of the ascomycetes. The followers of de Bary have not succeeded in establishing his views beyond dispute. Harper's ideas are in line with those of de Bary and opposed to those of Brefeld and Dangeard. Clausen agrees with Harper except as to the fusion in the ascogonium. Fraser and Welsford, and Blackman and Welsford have taken a middle ground. On the one hand they resurrect the ideas of Brefeld as to the function of the sex organs. They agree that two nuclear fusions occur and describe the three divisions in the ascus. The difficulty of following nuclear behavior and the development of the sex organs may be the reason for much disagreement. A large number of forms have been studied, but it is possible that we have only begun the cytological work. The work of Harper indicates the complexity of the problem.

If we accept the views of Clausen it must be only upon incontrovertible evidence as the double fusion, if it occurs, may be considered an attempt in evolution which not other plants have undertaken. It would simplify the matter greatly to find that only one nuclear fusion occurred in the life history of the Ascomycetes, but mere simplicity should not mislead us nor prevent us from accepting conditions as they exist.

The divisions in the ascus have been studied in great detail by Harper (1905) and Fraser and Welsford (1909). Only a small number of forms have been studied and more research may bring out many more interesting phases. In some of the yeasts and lower Ascomycetes only two divisions in the ascus are recorded whereas in *Thecotheus*, (Overton 1906), *Rhyparobius*, (Barker 1905), and *Ascobolus immersus*, (Ramlow 1914), four and five divisions of the primary ascus nuclei may take place.

De Bary's idea that the sex organs of the fungi are functional becomes more plausible as cytological evidence accumulates in regard to the life history of the Lichens and Florideae. The law of function in a structure so important as the sex organs can only be viewed as due to a long cycle of evolutionary changes, to nutritional disturbances or to a sudden mutation. Paleobotanical studies indicate that the sex organs suffer little change through long cycles of time, whereas the vegetative organs may respond quickly to new environmental influences. Loss of function or suppression of an organ can scarcely be explained by the meager knowledge of physiology at our disposal. Such changes may be

influenced by nutrition, moisture, and temperature changes, but there is no evidence to indicate that such change of suppression is permanent.

It may be possible to view the ascus as homologous to the ooblastema of the red algae, but the fusion of the auxiliary cell with the filament brings in a phase of development which is not easily harmonized with the development of the ascus in the Ascomycetes.

### *Morphological Observations*

*Venturia inaequalis* (Cooke) Winter is an Ascomycete classified as a Pyrenomycete. Lindau (Engler and Prantl) places it in the order Sphaeriales, family Pleosporaceae. Fries (1819) named the conidial stages of the organism *Spilocoea pomi*. Fuckel transferred the fungus to the genus *Fusicladium*. Cooke (1866) described the stage in which asci are formed and named the organism *Sphaerella inaequalis*. Winter transferred the fungus to the genus *Venturia* naming it *Venturia inaequalis*. Aderhold (1897) connected the *Fusicladium* stage with the perithecial stage known as *Venturia inaequalis* by Winter and, not aware that Winter had transferred the organism, placed it in the genus *Venturia* naming it *Venturia inaequalis* (Cooke) Aderhold.

*Venturia inaequalis* is parasitic on the fruit and leaves of species of *Pyrus* and produces conidia during the spring and summer. As the leaves die and fall to the ground the mycelium, which is almost lacking and exists chiefly under the cuticle, penetrates the leaf tissue and during November in Wisconsin perithecial formation begins. The perithecium is not embedded in a stroma. The ascospores are found in March and April but do not ripen preparatory to discharge until May, discharge becoming active about the time the blossoms of the apple are opening.

The fungus is saprophytic from the time the leaf falls until the perithecium is formed. It is not known if the mycelium continues to function after the ascospores have been formed.

The mycelium is septate and branches irregularly. The uninucleate cells are from ten to forty microns in length and five to eight microns in diameter. The conidia are produced on conidiophores when the latter are from two to thirty microns in length. In cultures four or five conidia may be borne in a cluster at the apex of the conidiophore. As observed on the leaf only one conidium is borne at the apex of the conidiophores. As each coni-

dium is formed and abstricted the conidiophore grows further and produces another conidium, leaving a shoulder or node where the former was cut off. In culture several shoulders may be grouped; apparently the interspaces between the shoulders are extremely short, causing the conidia to appear in groups. The conidia are two-celled in most cases, each cell being uninucleate. The conidia measure about seven to ten microns in diameter and twenty-eight to forty microns in length. The color of the conidium is olive or brown.

Perithecial development, as previously stated, begins in autumn. The first evidence of perithecia was obtained from leaves fixed November 14, 1916. At that time the perithecia were approximately forty to seventy-five microns in diameter. Sections showed that considerable internal differentiation had occurred as each perithecium contained several large cells which stained more heavily than the surrounding tissue. The perithecia are spherical in form, each consisting of a dense mass of closely interwoven dark colored hyphae. The diameter of a mature perithecium varies but may exceed 150 microns. The perithecium may be formed in any part of the leaf but generally on the side lying uppermost. The perithecium is generally embedded in the spongy parenchyma and may be seen with the hand lens as it pushes up forming a small papilla or dome just before it discharges its spores. The spores are discharged through the opening known as the ostiole, but when ripe and suddenly wetted the whole upper portion of the perithecium may be lifted off. The discharge is produced, so far as could be ascertained, by the hydration of a colloidal gelatinous mass surrounding the asci which swells enormously.

The organism was grown in culture and observations were made to determine the course of development. Oatmeal agar proved to be a satisfactory medium for growth. Potato agar failed to produce perithecia. It was necessary to keep the cultures in the refrigerator to produce perithecia. The observations on the effect of temperature were first made by Jones (1913). A tube was inoculated and allowed to remain at room temperature for several weeks and then placed in the refrigerator which was held at a temperature of about 8° C.

Various fixatives were tried but Flemming's medium proved to be the most satisfactory. Urea was added to increase the rate of penetration when the perithecia were large and gelatinous. Fixations were made twice each week.

Staining proved to be very difficult as the fungus failed to retain the stain. Flemming's triple stain gave good results with young perithecia. Heidenhain's iron-alum haematoxylin gave good results when counter stained with Orange g. and was used for most of the cytological work.

To determine the development of the perithecium portions of oatmeal agar containing mycelium of the fungus were placed in a Van Tieghem cell and kept in the refrigerator. The appearance of short protuberances on the filaments of the mycelium were noted, as in figs. 1-6. Two branches arising from the same filament begin coiling about each other forming a compact, coiled mass. The branches become septate and it was possible to make out two and three cells. In most cases the coil soon becomes so intricate that it is impossible to follow its development. After the coil begins to form it is joined by other branches arising from the base of the stalk or the filament from which the stalk arose. Sometimes one branch begins to take a spiral form apparently without the assistance of another branch. It was also possible to obtain growth for a period of two weeks in oatmeal agar placed on a slide and covered with a cover glass, if the slide was placed in a petri dish and kept in a sterile condition and at low temperature, thereby making possible accurate observations of the early stages. In such cultures one often observes conjugations consisting of a short branch connecting adjacent or parallel hyphae. As far as could be determined these structures never gave rise to perithecia. Sometimes one finds a nucleus in the conjugating tube. Frequently one finds filaments forming perithecial structures in great abundance and branching profusely, while the neighboring filaments exhibit no tendency to branch or to form perithecia.

Sections of the young perithecium, fig. 10, indicate the presence of a large coil which stains more deeply than cells of the adjacent hyphae. This coil increases in size as the perithecium grows. Figs. 7, 8, 9, 10 and 11 show coils within the perithecium with part of the coil projecting beyond the limits of the wall.

From the similarity of my figures to those of Harper (1905), Clausen (1912), and Brooks (1910), one could not avoid concluding that the large coiled structures staining deeply were archi-carps. The coil within the perithecium resembles the ascogonium as described by Harper, and undoubtedly functions as such. There is evidence that a single branch enlarges to form the ascogonium as one can often follow the heavy staining cells to the periphery

of the perithecium, figs. 10, 11a and 14. The tongue-like structure emerging from the coil in the perithecium and extending beyond the margin is apparently a trichogyne. During the early stages the ascogonium and trichogyne seem to be non-septate, fig. 10. After fusion with the antherids the ascogonium becomes septate and paired nuclei are found in the cells, although some figures, fig. 14, indicate that the ascogonium may become septate without the presence of a trichogyne. Surrounding the trichogyne are numerous hyphae forming a wall around it. Most of the apical cells of the antheridial hyphae are swollen, have a bulb-like appearance, and arise from the filaments in the neighborhood of the perithecium. Some of these hyphae are applied to the trichogyne and seem to fuse with it, figs. 7, 8, 9, 10 and 12. Most of my figures show these bulb-like cells devoid of nuclei and highly vacuolate, as if the nuclei had migrated and the cells were disintegrating. Occasionally multinucleate cells were found as in figs. 7 and 12. These figures seem to indicate that some of these cells function as antheridia. The antheridium is found closely applied to the trichogyne and a pore is formed. Several nuclei lie immediately within the trichogyne and two nuclei appear to be within the antheridium in fig. 7. Paired nuclei are seldom found in the trichogyne. Apparently the nuclei migrate singly toward the ascogonium, but this may not always be the case for one occasionally finds paired nuclei in the trichogyne. The nuclei are approximately the diameter of the vegetative hyphae, 6-8 microns, and the membrane is sharply differentiated. Occasionally very little chromatin is visible but a large, dense nucleole is generally present. Sections of the perithecium cut after fertilization has occurred show that the coil has become septate, and that the cells of the ascogonium have greatly enlarged, stain more densely and contain two nuclei. Figs. 8, 11 and 12 indicate that the nuclei are paired. Perithecia found in leaves and those taken from cultures compare very closely in every morphological detail during all the stages observed.

In sections made from young perithecia grown on oatmeal agar one frequently observes the archicarp coiled but non-septate at its base, as in figs. 7 and 10. The trichogyne is non-septate and extends beyond the perithecium. It is not definitely known at what stage in the development of the coil fertilization occurs. The only disagreement with this type of structure and the ones described previously by other workers is the non-septate coil. If fertiliza-

tion occurred at this early non-septate stage, it would not be necessary for the nuclei to pass through pores from cell to cell. All the preparations indicate that fertilization occurs during the non-septate stage, for later stages show the nuclei paired in the cells of the coil of the ascogonium, figs. 11, 12 and 13.

An effort was made to discover if nuclear fusion occurred in the ascogonium. Sections cut from the coils as they formed and from the perithecium after it is fully mature, including the intermediate stages, failed to give evidence of fusion. Nuclei are found in pairs, fig. 12, and later in aggregates of four, fig. 23c. Figs. 7, 8 and 11 show sections of the perithecium. The ascogonium is coiled, four to six cells being visible, and the nuclei are paired. Fig. 8 shows the trichogyne still attached and the nuclei migrating toward the ascogonium each cell of which has paired nuclei. In none of the preparations of these early stages, however, was nuclear fusion apparent. Figs. 10, 11a and 11b indicate the condition of the structure. The basal or stalk cells are still visible and extend toward the periphery of the perithecium, while at the opposite end of the coil the trichogyne emerges. The stalk may be regarded as the basal remnant of the original branch. At the time the coil originates it appears as if two branches were concerned, one enlarging to form the ascogonial coil. What the function of the other hypha is could not be determined. It may be nutritive or sexual, but it is impossible to follow the development accurately as the vegetative hyphae enclose the coil and form a dense covering. The diameter of the perithecium is often 150 microns and one section or series of sections is difficult to interpret. The ascogonium is coiled and all portions do not lie in the same plane. In some figures, 11a and 11b, the coil is shown very distinctly. The cytoplasm is stained very densely and the nuclei stand out remarkably well. Each cell is binucleate, the cytoplasm is slightly granular in each cell. Fig. 12 also indicates the condition of the ascogonium when the nuclei are paired. As the perithecia enlarge and when they are from eight to nine weeks of age in cultures, the cells seem to increase in number and sections often show four nuclei in one cell, figs. 19, 23b and 23c. The cells of the coil increase in size until the perithecium has reached its maximum diameter. Following the four nucleate stage a large number of cells appear and extensive branching is apparent. There is considerable evidence to indicate that the large cells of the ascogonium branch, the branches become septate and form the asci,



figs. 16-20. The large cells of the ascogonium disappear gradually and lose their capacity to stain more densely than the surrounding hyphae.

As previously stated, at the time of fertilization the trichogyne is non-septate. The ascogonium has no definite cell walls. It was impossible to find sufficient evidence to indicate whether or not rapid nuclear division occurred in the coil, but a large number of nuclei are found later, fig. 12, indicating that division occurs. The evidence points to migration of nuclei from the trichogyne as initiating the multinucleate condition. There was no nuclear division apparent in any sections to indicate that the uninucleate cells of the ascogonium become multinucleate before fertilization. In the young trichogyne one can seldom find a nucleus. The ascogonial coil contains several nuclei, fig. 10, but after the trichogyne has fused with the antheridial cells it contains many nuclei; often a chain of them may be observed in the trichogyne extending from the apical end to the margin of the perithecium or beyond, figs. 8-12.

The nuclei of the ascogonium continue to grow in size until the cells no longer stain heavily, and there is apparent a great increase in the number of the cells. At this stage the perithecium is at its maximum size and it is difficult to make accurate observations of the various stages of development. Sections cut in March from material gathered February 27 in the orchard have no heavy staining material left and the nuclei are not much larger than the nuclei of the vegetative cells. The contents of the nucleus which at first stained very deeply become more and more difficult to stain about the time of ascus formation, figs. 16, 21, 22. A cross section of the perithecium gives very little indication of differentiation in any of the tissues not arising from the coil.

There is no evidence to indicate that typical ascogenous hyphae as described by Harper and Clausen occur. The whole content of the perithecium, with the exception of a layer of four or five cells at the periphery, seems to be occupied by asci and gelatinous material. All the large deeply staining cells of the ascogonium have disappeared, and the space formerly occupied by them is filled with asci which appear as if they originated from the basal portion of the perithecium, figs. 24 and 25ab. The only explanation formulated, and which agrees with the sections observed, is that apparently there is a breaking up and budding of the large cells of the ascogonium, forming a large number of small cells, the

initial ascus cells arising from some of these cells. The ascogonium immediately after fertilization may contain seven or eight cells. Later stages show the contents staining less densely, vacuoles appear and four nuclei are found in some cells. Distortion of all the cells is apparent and the inner contents of the perithecium are undoubtedly subjected to enormous pressure by the enveloping hyphae. By such intimate contact with the enveloping vegetative hyphae it is possible that the metamorphic tissue within receives nourishment. The cells of the enveloping tissue are uninucleate and are pressed into plates or rectangular polygons. At the time of fertilization they contain considerable food material but later this disappears.

As the ascogenous cells decrease in size, or rather as they bud and new cells are formed, the cells so formed are uninucleate or binucleate. It has not been possible to determine whether these cells form asci directly or by budding. The perithecium at this stage has reached its full size and it would be impossible for further budding and growth to take place unless some of the enveloping hyphae are absorbed, which seems, however, to occur at a later period. Possibly the cells elongate and by a process of rearrangement without much increase in the space occupied, the asci are finally developed to their full size.

There is a considerable gap in my series of developmental observations extending from the origin of the ascus to spore development. The ascus previous to the time the spores form is elongated and the nucleus or nuclei lie near the center, figs. 24-25. After the second nuclear division the ascus elongates still more and the nuclei migrate toward the periphery. About the time of the third division the ascus elongates again, the spores are delimited and the ascus is just wide enough at this time to hold the spore. Its length is approximately twice that of an ascus in the stage previous to the first division.

The spores are arranged in a chain and fill the ascus with the exception of a portion at the base. Practically all of the protoplasm of the ascus is exhausted, having been utilized in spore formation. A large number of cells forming the inner zone of the perithecium have been crowded aside, and their contents have disappeared. Many of the cells appear to be disintegrating. Three or four layers of heavy-walled cells constitute all that is left of the perithecium. Sometimes there is a cavity in the region below the ostiole as the perithecium elongates preparatory to discharg-

ing spores. The cavity may not be devoid of material as in some there is evidence of a gelatinous material which may take up water and swell thereby forcing out the spores. Whether an enzyme, or enzymes, are necessary to ripen the spores and digest the walls of the ascus is not known. Attempts to discharge spores by moistening and warming the perithecium after the spores appear to be mature fails to produce a discharge, even if considerable pressure is applied. When the perithecium is wetted and then punctured with a needle, considerable discharge occurs. The conditions for discharge are, however, very complex. During May the asci contain mature spores but neither wetting nor heating to room temperature would discharge the spores. July 6, 1917, leaves were obtained which had been lying on the sod and had not completely decayed. They contained perithecia full of asci and spores. The leaf was taken into the laboratory and placed in a moist chamber and a slide placed about an inch above the leaf. A tremendous discharge occurred. Several slides were then prepared and placed at various temperatures. About 80 per cent germination at 1-2° C. was obtained, but growth was extremely slow. At 2-3° C., 96 per cent germination was obtained. At 4° and 6° about the same per cent of germination resulted, but growth was more rapid. The optimum germination and growth occurred at 10-18° C. and then gradually decreased until 22° C. was reached when very little growth occurred, and the germination was greatly reduced. It may be well to state that the temperature control was only accurate to within a degree or more. The experiments conducted on spore discharge demonstrated rather conclusively that discharge of spores occurs only during rains or when the leaves are very wet, and that the discharge is greatest during the first two hours and gradually lessens. Temperature may influence the rate of discharge, but owing to lack of data at present it is not deemed possible to draw definite conclusions.

The ascospores when first delimited appear round or lens-shaped. When mature they are two-celled and each ascus usually contains eight spores. Each cell has one nucleus which is no larger than the nucleus of one of the cells of the filament. The wall of the spore consists of two layers. With Heidenhain's iron-alum haematoxylin the cytoplasm stains heavily, but the nucleus is much denser and more heavily stained. Evidently the protoplasm also contains considerable food material.

The ostiole is formed at the apex of the perithecium. The outer zone of cells becomes disorganized, and some of the cells appear plasmolyzed or devoid of staining material. Pressure due to swelling of the gelatinous material within the perithecium may rupture the upper portion and form the small opening known as the ostiole. If enzyme activity is necessary to dissolve some of the tissue, the inability to discharge spores before a certain maturity is reached might be explained. The gelatinous material within may require certain chemical changes to increase its swelling capacity, thereby limiting the period when spores may be discharged. If this material would simply by swelling cause the rupture of the perithecium, the discharge would be entirely a mechanical process. In the ostiole filaments appear as if the dissolution and pulling apart had left some of the fibres intact. The perithecia at this time are greatly elongated and have the appearance of forming a bottle neck at the upper end. There is very little staining capacity left in the tissue comprising the wall; evidently the cell contents have disappeared.

The nuclear behavior was not followed clearly owing to the difficulty of staining the chromatin. As previously stated, no nuclear fusion was observed in the ascogonium, although many preparations of the stages when fertilization occurred and those immediately following it were made. The nuclei in the ascogonium after fertilization increase tremendously in size and are paired. Two and four nuclei are found in a cell. The contents of the nucleus may stain densely or scarcely at all. No attempt was made to follow the behavior of the nuclear contents during growth and division. Some sections prepared at the time the spores are delimited in the ascus indicate that a central body exists whose fibres function in cutting out the spore, in a manner similar to that described by Harper (1897) (1905).

The work of Killian (1915) indicates that he found sections showing the large trichogyne and the coiled ascogonium. My preparations failed to show the antheridium branched as he figures it, but some of my sections show lobes of the tip or apical cell of the antheridium closely applied and partly surrounding the trichogyne. The nuclei aggregate near the pore and pass into the trichogyne sometimes in bead-like rows. Most of my sections indicate that the ascogonium is composed of five to eight cells and that these cells are formed after fusion with the antheridium. Killian's figures do not indicate that the ascogonium is divided

into cells, but his description leads one to believe that he observed pores in the cell walls through which the nuclei from the trichogyne passed, indicating that the archicarp is septate at the time of fusion.

The study of this organism gives further evidence of the correctness of de Bary's views in regard to the sexuality of the fungi. It is impossible to agree with Blackman and Welsford's idea that the sexual organs of the fungi do not function. The appearance of the trichogyne in connection with the perithecium and its conjugation with the antheridium cannot possibly be considered as non-functional. The trichogyne passes from a non-nucleate stage to one containing many nuclei at the time of fusion with the antheridium, and the cells of the ascogonium become binucleate, processes which must be shown to have no relation to the development of the asci if we are to accept the theories of Brefeld, Dangeard and Blackman and Welsford.

The figures of Blackman (1913) are similar to the stages observed in *Venturia inaequalis*. The similarity of the ascogonium of Collema to that of some of the Pyrenomycetes suggests that the Ascomycetes and Lichens may be rather closely related, more nearly, perhaps, than the Oomycetes and Ascomycetes. Further observations of the Pyrenomycetes may confirm the theories of Harper and Dodge as to the origin of the Ascomycetes from the red algae. The trichogyne is a prominent structure which cannot be disregarded, especially as it falls in line with the structures found in the Florideae. The multicelled ascogonium, the trichogyne and the ascogenous hyphae and asci have no homologue in the lower fungi. We do find some ground for comparison when we study the structure of the sex organs in the Florideae.

It has not been possible to follow the method of nuclear division or the development of the asci. Perhaps the interpretation of the processes observed can best be made from the assumption that the sex organs are functional, and that the nuclei pair in the ascogonium and then migrate into the ascus where fusion occurs. In some respects part of the sexual process is analogous to certain phases occurring in the Basidiomycetes where nuclear fusion is delayed. No evidence of a true sporophytic stage could be found in *Venturia*. Harper (1905) suggests that we consider the tetrasporange of the red algae as a progenitor of the ascus, the carpospores not being comparable to any stage in the Ascomycetes. In case the so-called nuclear fusion, which, according to some

workers on Ascomycetes occurs in the ascogonium, is found to be only pairing of nuclei, then new conceptions may be developed. The problem would be greatly simplified if the complex stages due to triple fusion were eliminated. Another helpful method which may aid in unraveling the nuclear history is the study of new forms. The list of new Wisconsin fungi compiled by the efforts and researches of Dr. J. J. Davis (1916-1921) continues to grow, and some of these forms may supply the missing link. At present we know so little about the effects of a physiological change caused by the environment on the morphology and sexual activity of organisms, and whether or not changes in the environment are immediately reflected in the offspring by morphological changes, that all speculations are futile. Until our conceptions rest upon more secure grounds, homologies and similarities may only lead us into scholastic discussions and far from the real nature of the underlying causes that find expression in these complex and truly marvelous forms of life.

It gives me great pleasure to express my gratitude and appreciation to Dr. E. M. Gilbert for many helpful suggestions and for the constructive criticism he has rendered during the course of this investigation.

## LITERATURE

- Bachman, F. M.** A new type of spermatogonium and fertilization in *Collema*. *Ann. Bot.* 26: 747-60 (1912).  
 ———The origin and development of the apothecium in *Collema pulposum* (Bernh) Ach. *Archiv. f. Zellforschung* 10: 369-430 (1913).  
**Barker, B. T. P.** Sexual spore formation in the Ascomycetes. *Ann. Bot.* 15: 759 (1901).  
 ———Morphology and development of the ascocarp of *Monascus*. *Ann. Bot.* 17: 167 (1903).  
**Bary, A. de.** *Über die Fruchtentwicklung der Ascomyceten.* Leipzig. 1863.  
 ———*Morphologie und Biologie der Pilze.* Leipzig. 1884.  
**Barrett, J. T.** Development and sexuality of some species of *Olpidiopsis* (Cornu) Fischer *Ann. Bot.* 26: 209-35 (1912).  
**Baur, E.** Zur Frage nach der Sexualität des Collemaceen. *Ber. Deut. Bot. Gesell.* 16: 363-67 (1898).  
 ———Untersuchungen über die Entwicklungsgeschichte der Flechten apothecien. *Bot. Zeit.* 62: 21-44 (1904).  
 ———Die Anlage und Entwicklung einiger Flechten apothecium. *Flora* 88: 319-32 (1901).  
**Bensaude, Mathilde.** *Recherches sur le cycle evolutif et la sexualite chez les Basidiomycetes.* Paris, 1918.

- Sur la sexualite chez les Champignons Basidiomycetes. Compt. Rend. Acad. Sci. Paris 165: 286 (1917).
- Blackman, V. H., and Welsford, E. J.** The development of the perithecium of *Polystigma rubrum* D. C. Ann. Bot. 26: 761-67 (1912).
- On the fertilization, alternation of generation, and general cytology of the Uredineae. Ann. Bot. 18: 323-73 (1904).
- Blackman, V. H., and Fraser, H. C. L.** Further studies on the sexuality of the Uredineae. Ann. Bot. 20: 35-48 (1906).
- Brefeld, O.** Untersuchungen aus dem Gesamtgebiete der Mykologie. Botanische Untersuchungen über Schimmelpilze. II. Die Entwicklungsgeschichte von *Penicillium*. Leipzig, 1874. Die Hemiasci und die Ascomyceten, IX Heft 1891, pp. 1-118; 340-51.
- Brooks, F. T.** The development of *Gnomonia erythrostoma* Pers. Ann. Bot. 24: 585-605 (1910).
- Brown, H. B.** Studies in the development of Xylaria. Ann. Myc. 11: 1-13 (1913).
- Brown, W. H.** The development of the ascocarp of *Lachnea scutellata*. Bot. Gaz. 52: 273-305 (1911).
- The development of *Pyronema confluens*. Amer. Jour. Bot. 2: 289-97 (1915).
- Bucholtz, F.** Beiträge zur Kenntnis der Gattung *Endogone*, Link. Beihefte Bot. Centralbl. 292: 147-225 (1912).
- Bulliard, P.** Histoire des Champignons de la France. 1791.
- Carruthers, D.** Contributions to the cytology of *Helvella crispa*. Ann. Bot. 25: 243 (1911).
- Christman, A. H.** Sexual reproduction in rusts. Bot. Gaz. 39: 207 (1905).
- Morphology of Rusts. Bot. Gaz. 44: 81 (1907).
- Claussen, P.** Zur Entwicklungsgeschichte der Ascomyceten Boudiera. Bot. Zeitg. 63: 1-28 (1905).
- Zur Kenntnis der Kernverhältnisse von *Pyronema confluens*. Ber. deut. Bot. Gesell. 25: 586-90 (1907).
- Über Entwicklung und Befruchtung bei *Saprolegnia monoica*. Ber. deut. Bot. Gesell, 26b: 144 (1908).
- Zur Entwicklungsgeschichte der Ascomyceten *Pyronema confluens*. Zeit. Bot. 4: 1-64 (1912).
- Clinton, G. P.** Apple Scab. III. Agr. Exp. Sta. Bull. 67: 109 (1901).
- Reproduction des Ascomycetes. Ann. d. Sci. Nat., Serie 6, T. 3. 1876.
- Cutting, E. M.** On the sexuality and development of the ascocarp in *Ascophanus carneus* Pers. Ann. Bot. 17: 399-417 (1909).
- Dale, E.** Observations on the Gymnoascaceae. Ann. Bot. 17: 591-96 (1903).
- On the Morphology and Cytology of *Aspergillus repens*. Ann. Myc. 7: 215-25 (1909).
- Dangeard, P. A.** La reproduction sexuelle des Ascomycetes. Le Botaniste 4: 21. 1894-95.
- Recherches sur le developpement du Perithece chez les Ascomycetes. Le Botaniste 10: 1-385. 1907.
- Recherches sur la reproduction sexuelle des Champignons. Le Botaniste 3: 222-278 (1893).

- La reproduction sexuelle des Ustilaginees. *Compt. Rend. l'Acad. des Sci.* Oct. 1893.
- Etude sur le developpement et la structure des organismes superieurs. *Le Botaniste* II serie, 1910.
- Davis, B. M.** The fertilization of *Batrochospermum*. *Ann. Bot.* 10: 49-76 (1896).
- Davis, J. J.** Notes on parasitic fungi in Wisconsin. *Trans. Wis. Acad. Sci.* 20: 389-413 (1921).
- Dodge, B. O.** Methods of culture and the morphology of the archicarp in certain species of the Ascobolaceae. *Bull. Torr. Bot. Club* 39: 139-97 (1912).
- The morphological relationships of the Florideae and the Ascomycetes. *Bull. Torr. Bot. Club* 41: 157-202 (1914).
- Faull, J. H.** The Cytology of the Laboulbeniales. *Ann. Bot.* 25: 649. 1911.
- Fitzpatrick, H. M.** The life history and parasitism of *Eocronartium muscicola*. *Phytopath.* 8: 197-218 (1918).
- The cytology of *Eocronartium muscicola*. *Amer. Jour. Bot.* 5: 397-499 (1918).
- Gilbert, E. M.** Studies on the Tremellineae of Wisconsin. *Trans. Wis. Acad. Sci.* 16: 1137-70 (1910).
- Cytological studies of the lower Basidiomycetes. *Trans. Wis. Acad. Sci.* 20: 387-9 (1921).
- Guilliermond, M. A.** Le developpement et la phylogenie des Levures. *Rev. gen. des Sciences* du 15 Raut. 1911.
- Contribution a l'etude cytologique des Ascomycetes. *Compt. Rend. de l'Acad. des Sci.* 137: 938-39, 1088 (1903).
- Zygosaccharomyces Nadsonii*, Nouvelle espees de levures a conjugaison heterogamique. *Annales de l'Institut Pasteur* 34: Fascicule. 1918.
- Sur la division nucleaire des levures. *Annales de l'Institut Pasteur* 31: No. 3, Mars. 1917.
- Sur la karyokinesic de *Peziza rutilaus*. *Compt. Rend. de l. Soc. Biol.* 56, 412 (1904).
- Les progres de la cytologie des Champignons *Prog. Rei. Bot.* 4: 389-542 (1911).
- Harper, R. A.** Beiträge zur Kenntniss der Kernteilung und Sporen Bildung in Ascus. *Ber. dent. Bot. Gesell.* 13: 67 (1895).
- Die entwicklung des Peritheciiums bei *Sphaerotheca castagnei*. *Ber. dent. Bot. Gesell.* 13: 475-81 (1895).
- Über das Verhalten des Kerne bei der Fruchtentwicklung einiger Ascomyceten. *Jahrb. f. Wiss. Bot.* 29: 656 (1896).
- Kernteilung u. freie Zellbildung im Ascus. *Jahrb. f. Wiss. Bot.* 30: 1-49 (1897).
- Nuclear phenomena in certain stages in the development of the smuts. *Trans. Wis. Acad. Sci.* 12: 475 (1899).
- Cell division in Sporangia and Asci. *Ann. Bot.* 13: 47-525 (1899).
- Sexual reproduction in *Pyronema confluens* and the morphology of the Ascocarp. *Ann. Bot.* 14: 321-400 (1900).
- Sexual reproduction and the organization of the nucleus in certain mildews. *Publ. Carnegie Inst., Washington, D. C.* 37: 1-92 (1905).



- Nuclear phenomena of sexual reproduction in fungi. Amer. Nat. 44: 533-46 (1910).
- Binucleate cells in certain Hymenomyces. Bot. Gaz. 33: 1-25 (1902).
- Ikeno, S.** Über die Sporenbildung und systematische Stellung von *Monascus purpureus*. Ber. dent. Bot. Gesell. 21: 259 (1904).
- Janczowski, E.** Recherches morphologique sur l'*Ascobolus furfuraceus*. Ann. des Sci. Nat. 5 E Serie 15: 197 (1892).
- Juell, O. H.** Über Zellinhalt, Befruchtung und Sporenbildung bei *Dipodascus*. Flora 91: 47 (1902).
- Jones, F. R.** Is the *Venturia* of the Wisconsin wild crab, *Pyrus coronarius* identical with the *Venturia inaequalis* of the cultivated apple? Thesis, MS. Univ. of Wis. 1914.
- Kihlman, O.** Zuz Entwicklungsgeschichte der Ascomyceten. Acta Soc. Sci. Fennicae 13: pt. 43, 1883.
- Killian, K.** Morphologie, Biologie und Entwicklungsgeschichte von *Cryptomyces pteridis* (Rebent.) Rehm. Zeit. f. Bot. 10, 48-126 (1913).
- Über die Entwicklung der Perithecia bei *Venturia inaequalis* (Cooke) Ad. Ber. dent. Bot. Gesell. Heft. 1: 164-68 (1915).
- Kunkel, O.** The production of a promycelium by the aecidiospores of *Caeoma nitens* Burrill. Bull. Torr. Bot. Club 40: 361-66 (1913).
- Kühn, J. G.** 1858. History of plant pathology by G. Whetzel. 1918.
- Levine, M.** Studies in the cytology of the Hymenomyces especially the *Boleti*. Bull. Torr. Bot. Club. 40: 137-81 (1913).
- Maire, R.** La formation des asques chez les Pezizes et l'évolution nucléaire des Ascomycetes. Compt. Rend. Soc. Biol. 55: 1401 (1903).
- Sur la cytologie des Hymenomyces. Compt. Rend. Acad. Sci. Paris 131: 121-4 (1900).
- Sur les divisions nucléaires dans l'Asque de la Morille et de quelques autres Ascomycetes. Compt. Rend. Soc. Biol. 56: 822 (1904).
- Recherches cytologiques sur le *Galactinia succosa*. Compt. Rend. de l'Académie der Sci. Paris 137: 769-71 (1903).
- Recherches cytologiques sur quelques Ascomycetes. Ann. Mycologici. 3: 123. 1905.
- Remarques sur la cytologie de quelque Ascomycetes. Compt. Rend. Soc. Biol. 56: 86 (1904).
- McCubbin, W. A.** Development of the Helvellinae. Bot. Gaz. 49: 195-205 (1910).
- Miyake, K.** The fertilization of *Pythium de Baryanum*. Ann. Bot. 15: 653-67 (1901).
- Nichols, M. A.** Morphology and development of certain pyrenomycetous fungi. Bot. Gaz. 22: 301-28 (1896).
- Nichols, S. P.** The nature and origin of the binucleated cells in some Basidiomycetes. Trans. Wis. Acad. Sci. 15: 30-70 (1905).
- Nienburg, W.** Beiträge zur Entwicklungsgeschichte einiger Flechtenapothecien. Flora 98: 1-40 (1907).
- Entwicklungsgeschichte von *Polystigma rubrum* DC. Zeit. f. Bot. 6: 369-400 (1914).

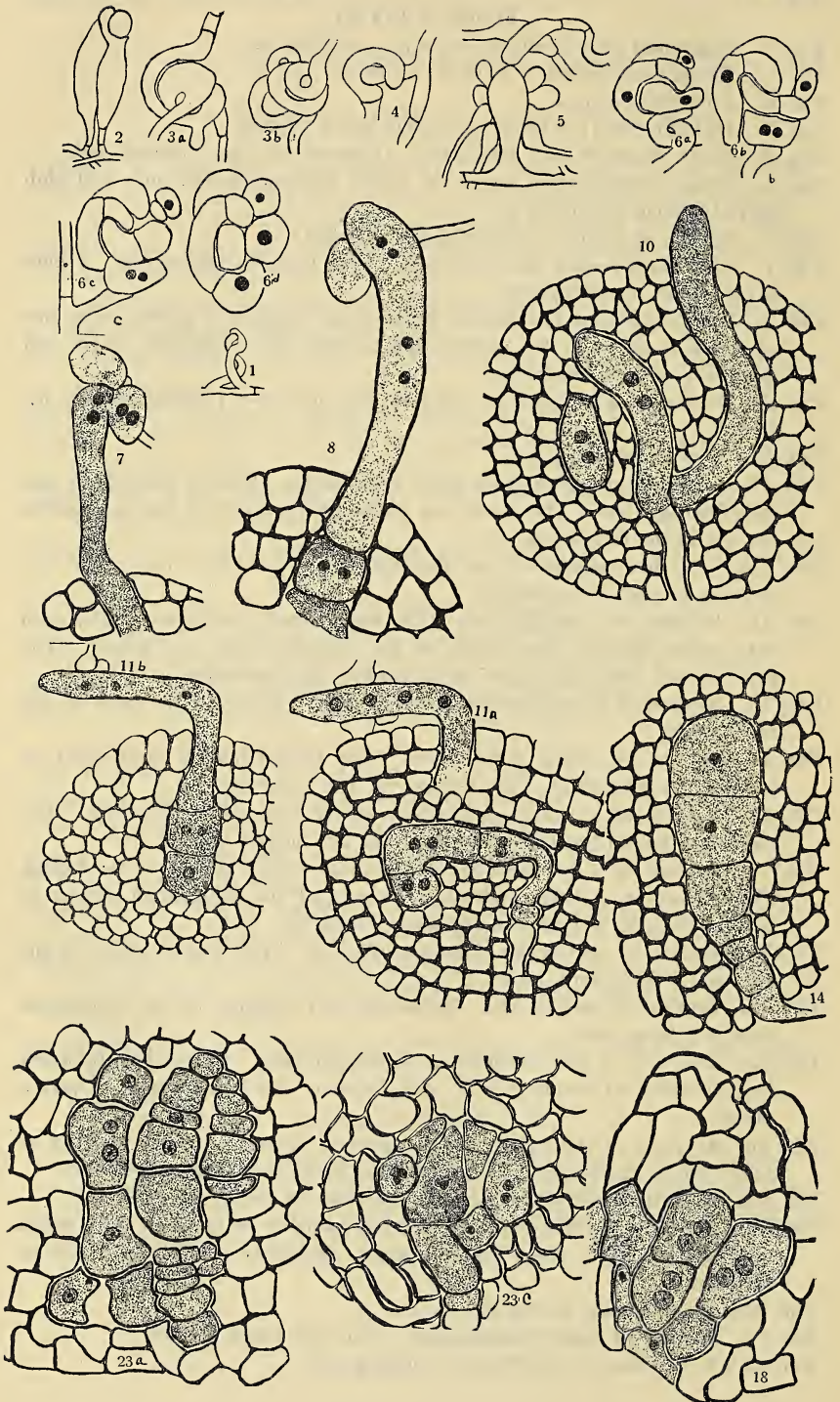
- Olive, E. W.** The morphology of *Monascus purpureus*. Bot. Gaz. 39: 56-60 (1905).  
 ——— Sexual cell fusions and vegetative nuclear divisions in the rusts. Ann. Bot. 22: 331-57 (1908).  
 ——— Nuclear conditions in certain short cycled rusts. Science N. S. 33: 194 (1911).
- Oltmans, F.** Über die Sexualität der Pilze. Biol. Centr. 21: 437-42 (1901).
- Overton, J. B.** The morphology of the ascocarp and spore formation in the many-spored asci of *Thecotheus pelletiera*. Bot. Gaz. 42: 450 (1906).
- Ramlow, G.** Zur Entwicklungsgeschichte von *Thelebolus stercoreus*. Bot. Zeitg. 64: 85-99 (1906).  
 ——— Beiträge zur Entwicklungsgeschichte der Ascobolen. Mycologisches Centrallblatt 5: Heft 4, Nov., 1919.
- Rawitscher, Felix.** Beiträge zur Kenntnis der Ustilagineen. Zeit. f. Bot. 4: 674 (1912).
- Sachs, J.** Lehrbuch der Botanik. 1-632. Leipzig, 1868.
- Schikorra, W.** Über die Entwicklungsgeschichte von *Monascus*. Zeit. f. Bot. 1: 397 (1909).
- Sutherland, G. K.** Additional notes on marine Pyrenomycetes. New. Phytologist 13-14: 183-93 (1914).
- Stevens, F. L.** The compound oosphere of *Albugo bliti*. Bot. Gaz. 28: 225 (1899).
- Trow, A. H.** Karyology of Saprolegnia. Ann. Bot. 9: 609 (1895).  
 ——— Cytology of *Pythium ultimum*. Ann. Bot. 15: 267. 1901.  
 ——— On fertilization in the Saprolegniae. Ann. Bot. 18: 541 (1904).
- Tulasne, R.** Selecta Fungorum Carpologia. 3: 197 (1865).  
 ——— Note sur les phenomenes de copulation que presentent quelques champignons. Ann. des. Sci. Nat. Bot. 6: 211 (1866).
- Van Tieghem, P.** Traite De Botanique. 2: 1129-56 (1891).
- Wager, H.** Sexuality of fungi. Ann. Bot. 13: 29-55; 575-97 (1899).  
 ——— Fertilization of *Peronospora parasitica*. Ann. Bot. 14: 263 (1900).
- Wager, H., and Peniston, A.** Cytological observations of the yeast plant. Ann. Bot. 24: 45 (1910).
- Welsford, E. J., and Blackman, V. H.** The development of *Polystigma rubrum* DC. Ann. Bot. 26: 761-67 (1912).
- Woronin, M.** Zur Entwicklungsgeschichte des *Ascobolus pulcherinum* und einiger Pezizen. De Bary and Waronin Beiträge Morph. u. Physiol. des Pilze 2: 1-11 (1866).
- Yamouchi, S.** The life history of Polysiphonia. Bot. Gaz. 42: 401-49 (1906).

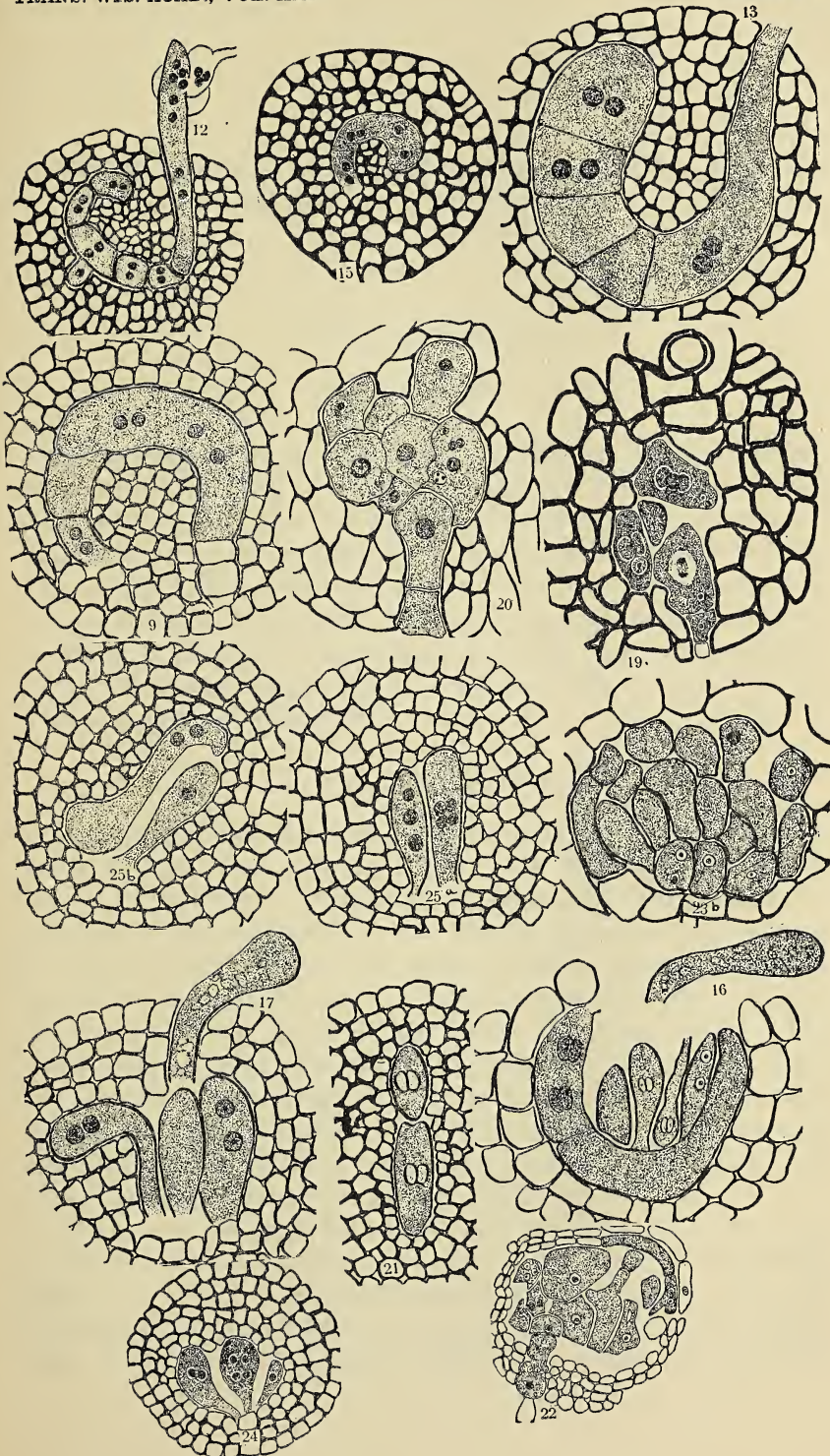
EXPLANATION OF FIGURES

All figures were made with the aid of a camera lucida. A Zeiss number 12 ocular and number 2.3 mm. apochromatic oil immersion objective were used for figures 7-18. The remaining figures were made with a Leitz  $\frac{1}{16}$  oil immersion and number 10 ocular.

## PLATES X AND XI

- FIG. 1. Beginnig of coil which results in a perithecium.  
FIG. 1a. Shows conjugation of adjacent filaments.  
FIG. 2. Formation of coil.  
FIG. 3. Coil enlarging; enveloping hyphae being formed.  
FIG. 4. Early stages in coil formation. Observed in Van Tieghem cell.  
FIG. 5. Large branch which forms the coiled ascogonium has bulb and club shaped hyphae applied to it.  
FIG. 6. Section of a coil. The nuclei are enlarged.  
FIG. 7. Club shaped cells, the antheridia, applied to the trichogyne. A pore is evident in the trichogyne.  
FIG. 8. The ascogonium has become septate and consists of several cells, one of which is shown. The nuclei migrate down the trichogyne singly and later pair in the ascogonium.  
FIG. 9. Section of a perithecium showing the coil after fertilization has occurred.  
FIG. 10. Section of young coil.  
FIG. 11a. Section of perithecium after fertilization showing trichogyne and coiled ascogonium. The nuclei are paired in the cells of the ascogonium but not in the trichogyne.  
FIG. 11b. Another section of perithecium shown in Fig. 11a. The remainder of the coil is evident.  
FIG. 12. Section of a perithecium. The ascogonium has several cells, each with paired nuclei. The nuclei of the trichogyne are not paired. The pore through which the male nuclei entered the trichogyne is visible.  
FIG. 13. Section of a perithecium showing paired nuclei in the cells of the ascogonium.  
FIG. 14. Section of young perithecium. The ascogonium is multicelled as in the previous figures. The trichogyne was not found.  
FIG. 15. Section of a young perithecium at the time of fertilization. The nuclei are paired but the ascogonium has not become septate.  
FIG. 16. Section of a perithecium. The paired nuclei appear to be fusing. The trichogyne is disintegrating. The cells of the ascogonium appear to be branching in preparation for ascus formation.  
FIG. 17. Section of perithecium shown in Fig. 16. Note paired nuclei in the cells which later form asci.  
FIG. 18. Section of perithecium. Branching and budding of the ascogenous cells is taking place.  
FIG. 19. The coil of the ascogonium is reorganizing. New cells are being formed either by budding or by cell division. Nuclear division is taking place.  
FIG. 20. In place of the coil of the ascogonium there are a large number of cells. From these compact cells branches arise which later form asci.  
FIG. 21. Cells in which nuclear fusion seems to be taking place.  
FIG. 22. Section of perithecium showing formation of many small cells, which later develop asci, from the coil which originally consisted of five or six cells.  
FIG. 23 a, b, c. Similar to Fig. 22.  
FIG. 24. Section of mature perithecium. Asci are being formed.  
FIG. 25 a, b. Section of perithecium showing asci.







# CYTOLOGICAL STUDIES OF TAPHRINA CORYLI NISHIDA ON CORYLUS AMERICANA

---

ELLA MAY MARTIN

## INTRODUCTION

The cytological work of Dangeard (1894) on *Exoascus deformans*, of Ikeno (1901) on various *Taphrina* forms, and of still later workers on other Ascomycetes, left unsettled various questions concerning the uninucleate or multinucleate condition of the cells, of the origin of the nuclei which fuse in the ascogenous cell, nuclear divisions in the ascus, and the formation of the ascospores. It was with the hope of throwing light upon some of these problems in *Taphrina coryli* Nishida, that the work described in the present paper was undertaken.

## MATERIALS AND METHODS

Leaves and twigs of *Corylus americana* infected with *Taphrina coryli* Nishida were collected by Dr. J. J. Davis and Dr. E. M. Gilbert in the vicinity of Madison, Wisconsin, in the spring of the years 1917, 1920, and 1921, and by the writer in the same location in 1920 and 1921. During the spring of 1921, material was fixed at various hours of the day and night in order that the condition of the nucleus and cell at different times might be studied. The parts collected were immediately dipped in Carnoy's fluid for a few seconds to remove the air, and were then placed in vials containing the desired fixative. A number of fixing reagents were used, but the best results were obtained with Merkel's fixative and with Flemming's weak chrom-osmic-acetic acid solution.

Spores were also germinated and kept growing for several days in sterile aqueous solutions made from hazel leaves. Germinating spores were fixed in Merkel's solution and attached to slides by stippling them into a thin film of egg albumen on the slides. These were then dried and stained. Imbedded material was cut from

three to seven microns in thickness. Flemming's triple stain was used for all preliminary studies, but all results with it were confirmed by the use of Heidenhain's iron-alum haematoxylin.

#### OBSERVATIONS

These studies show that the mycelium of *Taphrina coryli* Nishida may infect all parts of the leaf and the cortex of the youngest twigs of *Corylus americana*, as an intercellular parasite. It is found between the cells of the cortex of a one-year-old twig, but it is not found in older branches; apparently it grows out into the new cortex each season. In a young diseased leaf, the fungus may be traced along the veins, between spongy parenchyma and palisade cells, and frequently a layer of short thick cells is found between the cutin and the epidermis. In an older, badly diseased leaf, every available intercellular space is occupied by the fungal hyphae, and in addition, portions of the upper and lower surfaces of the leaf may be covered with asci. Instead of the classification of the mycelium given by Pierce (1900) for *Exoascus deformans*, namely vegetative, distributive, and fruiting hyphae, the writer will refer to only vegetative and fruiting hyphae; meaning, by the latter, asci and subcuticular ascogenous cells, and by the former, all other mycelia belonging to the fungus.

The vegetative cells of *Taphrina coryli* form long filaments, particularly where they follow the vessels in the leaves and between the palisade cells. In the air spaces between the spongy parenchyma cells, they broaden out and frequently branch. This dichotomous branching has been described by Pierce for *Exoascus deformans*, and is quite characteristic of *Taphrina coryli* (fig. 1). Each vegetative cell is long, cylindrical, thin-walled and contains a fine granular network of cytoplasm with either one or, more frequently, two nuclei (fig. 2). In a binucleate cell, the nuclei are small, each containing one prominent nucleole and a very small quantity of chromatin (fig. 3). This binucleate condition arises in the vegetative cells, and never in the ascogenous cells, of *Taphrina coryli* Nishida. Division figures were seen a number of times in the vegetative cells (figs. 4, 5). The spindles and centrosomes are extremely small, as are also the masses of chromatin material which pass to each pole. Ikeno observed binucleate cells in all forms of *Taphrina* studied by him, and Dangeard (1894) held that the mycelial cells of *Exoascus deformans* were originally binucleate



cells. Miss Adams (1915) and Miss Bitner (1915) found the binucleate condition only in ascogenous cells, where they found evidences that pairing of cells had taken place. It seems very probable, however, from my observations, that the binucleate condition which is later observed in the ascogenous cells has arisen in the vegetative cells (fig. 6, 7), although by what process, I am unable to determine.

As the fungus travels outward between cells of the palisade layer, the hyphae appear similar to those previously described, but the cells are usually longer and thinner. But as the mycelium passes between the epidermal cells, it becomes more difficult to determine the character of the vegetative cells, for they are only rarely seen and those observed become very slender as they force their way between the epidermal cells. Slender vegetative hyphae are also found in the cortex of the one-year-old twigs.

#### THE ASCOGENOUS CELLS AND NUCLEAR FUSION

By the time the fungus has reached the region between the epidermal cells and the cutin of the leaf, its cells have become much thickened and, being packed together, have become cuboidal in form. At times these fruiting or ascogenous cells are found in layers two or three cells thick, but as the outer layer develops, the cuticle is ruptured, the fungal cells increase in length and form asci. In the ascogenous cells, the cytoplasm is often more vacuolate than that of the vegetative cells, though this condition may vary. The binucleate condition which arose in the vegetative cells apparently does not continue long in the ascogenous cells, for most of these cells have only one large, fusion nucleus.

Nuclear fusion is found quite often in ascogenous cells of material collected at any time of day, but in material collected early in the morning the nuclei in the majority of ascogenous cells are fusing. It may be that moisture and low temperature stimulate the activity of the cell in such a way as to favor nuclear fusion. The two nuclei approach each other (figs. 6, 7), finally lying side by side in the cell (fig. 8). Their nucleoles (one in each nucleus) are at first some distance apart, but the thickened chromatin masses lie close together. As the two nuclei come into contact with each other, the nuclear membrane breaks down between them, so that there is formed a large double nucleus (figs. 9, 10, 11). The two chromatic systems remain separate for a time as described by

Harper for *Phyllactinia corylea* (1905), but eventually the elongated nucleus rounds up and assumes the form of a typical resting nucleus (figs. 12, 13). The two nucleoles gradually approach each other and unite, the large nucleole formed by the fusion staining deeply with safranin, but containing an unstained or lightly stained area at the center. The chromatic system becomes more clearly defined and is now a coarse network with thickened granules at intervals. Both the linin and the chromatin granules stain deeply with gentian violet. That this fusion may be a case of endokaryogamy similar to that found in the Basidiomycetes seems probable. By passing through a number of mitoses, in the vegetative cells, it may be that the nuclei which finally fuse have lost their originally similar characteristics.

#### DIVISION OF THE FUSION NUCLEUS

As the resting nucleus prepares for division, a spirem thread is gradually evolved from the reticulum of linin and chromatin, and very soon evidence of the pairing of the threads is apparent (fig. 14). They lie closely twisted about each other, and, since this synaptic stage is so clear, this division may be considered the heterotypic division. The condition of synapsis and that of the longitudinally split spirem (fig. 15) are frequently found, which fact may be an indication that the nucleus passes through these phases slowly. The nucleole, during this time, changes in staining properties, the outer zone taking much less stain than the inner. Another stage, showing the spirem thrown into loops which group at the center and spread out to the periphery of the nucleus, is frequently found (figs. 16, 17). Fitzpatrick (1918) suggested that these loops represent chromosomes in *Eocronartium muscicola*, but this is probably not the case in *Taphrina coryli* Nishida, for here five or six (the number of loops observed) does not represent either the haploid or the diploid number of chromosomes. The nucleus elongates considerably (fig. 20), and soon a definite spindle is noted which is larger than that found in the vegetative cells, but it, also, has a granular body or center at each end. This entire spindle is likewise surrounded by a clear area. It is impossible to make out the individual chromosomes; probably each mass of chromatin represents a number of chromosomes (figs. 21, 22, 23, 24).

These chromatin masses are in such position as to suggest the equatorial plate stage most frequently, though they appear at

other times to be in late metaphases and anaphases. The nucleole disappears at the time of the spindle formation, but no indications of the division of a central body to form two daughter centers, as described by Harper (1899, 1905), are seen. The reorganized nuclei are typical resting nuclei, each containing one nucleole (fig. 25).

#### THE FORMATION OF THE BASAL CELL

Each mature ascus of *Taphrina coryli* Nishida has a basal cell, but the time of the formation of the septum varies. Often before the division of the fusion nucleus is complete, the plasma membrane in the lower part of the ascogenous cell begins to constrict (fig. 23). Again, the plasma membrane may not begin to constrict until after the daughter nuclei are fully formed. It may be that vacuolar membranes also play a small part in the formation of the cell plate, for vacuoles are frequently in such a position that vacuolar membranes meet the constricting plasma membrane (fig. 25). Many cases were observed, however, which suggest that the constricting portions of the plasma membrane have stretched out to meet each other, forming a cleavage furrow in which will be laid down the cell wall (figs. 26, 27). From a study of a number of such cells, it seems safe to conclude that the process of separation of the ascus cell proper from the basal cell is initiated either before or just after the first nuclear division is complete. One of the nuclei formed by the division of the fusion nucleus passes to the upper part of the ascus where it later undergoes division, the repeated divisions of its daughter nuclei forming the nuclei for the eight primary spores. The other nucleus formed from the fusion nucleus remains in the lower part of the ascus, which becomes the basal cell. The nucleus of this cell persists for a while and then disintegrates; the only remains of it being in the form of chromatin granules which are left in the cytoplasm for a time (fig. 28). As the ascus grows older, even the chromatin granules disappear, and the cytoplasm, which has been quite dense, now becomes more and more vacuolate (fig. 29), until it, too, completely disappears in the basal cells of the older asci (figs. 31, 33). These would conform to the empty basal cells figured by Atkinson (1894) for *Exoascus deformans*, *Exoascus cerasi*, and *Exoascus decipiens*. Sadebeck (1893) in *Taphrina Sadebeckii* Johns. and Miss Bitner (1915) in *Taphrina coryli* also found empty basal cells with the older asci.

## THE FORMATION OF THE ASCOSPORES

As the ascus elongates, nuclear division proceeds within it. The second mitosis is probably homœotypic and the next two vegetative divisions, so that there are produced eventually eight spores for the eight nuclei. Since there was only one nuclear fusion, there is necessary only one reduction of chromatin material. Examples of the vegetative divisions in process are few, but those observed show the typical spindle with masses of chromatin passing toward the poles. Three divisions of the ascus nucleus have been mentioned for some of the Exoascaceae.

Ikeno (1903) in *Taphrina cerasi*, and Dangeard (1894) in *Exoascus deformans*, mention three divisions. This would be probable in types that have no basal cell, but where there is such a cell containing at some time a nucleus, it is evident that there must be four nuclear divisions: a division of the fusion nucleus and three successive divisions of the primary ascus nucleus and its derivatives. Nuclear division is seen more frequently in material collected in the early morning. Ikeno (1901) mentions many division figures at the time of the development of the spores of *Taphrina Johansonii*.

The nuclei formed are small and are often found in a resting condition. They contain a deeply staining nucleole and chromatin arranged upon a linin network (figs. 28, 29, 30). In a mature spore the nucleus occupies about one-third or one-fourth of its volume, and in the formation of the spores dense masses of cytoplasm collect about each of the eight nuclei. Sometimes this cytoplasm takes up so much stain that the nucleus can scarcely be seen through it (fig. 35). The plasma membrane of a spore seems to be formed by the union of membranes of vacuoles; this plasma membrane secretes a thick, clear wall, darkly stained only at intervals (figs. 31, 32). Vacuoles are especially conspicuous at the time of spore formation and are in such a position that each spore is entirely encircled by them, the inner vacuolar membranes uniting to form the boundary of the spore. This would conform to the description given by Brown (1911) for the delimiting of the spores of *Lachnea scutellata*. Faul (1912) considers this progressive method of delimiting the spore the characteristic method for Ascomycetes. He expresses the idea that astral rays would not naturally come together, but would rather tend to diverge. Fraser and Brooks (1909) report that vacuoles play an important part in

the formation of the spores of *Ascobolus furfuraceus*. No indication of astral rays as described by Harper (1899) in *Lachnea scutellata* and (1905) in *Erisyphe cichorearum*, *Erisyphe communis*, and *Phyllactinia corylea* have been found in *Taphrina coryli*. If present they may have been such fine threads as to be invisible with the magnification used. There are, however, many suggestions that vacuolar membranes are the active agents in forming membranes of spores (figs. 31, 32, 33, 34).

#### THE GERMINATION OF THE ASCOSPORES

Nishida (1912) ascribed to *Taphrina coryli* an irregular number of spores, and such is the case when each of the original eight spores comes to maturity and begins to form conidia. This process might be called fission, for, unlike the budding of yeasts, the spore lengthens and divides into conidia of equal size (fig. 37). When the spores begin to produce conidia, they become somewhat irregular in form, the constriction often being present earlier on one side of the spore than on the other (fig. 35). There must be a softening of the cell wall, for a spore lengthens and, as the cell wall and plasma membrane constrict, the whole assumes the form of a dumb-bell (fig. 36, A-G). At this time the nucleus begins to stretch out (fig. 36, G) and eventually divides, thus providing a new nucleus for each of the conidia so formed. The behavior of the nucleus was observed in the stained material, but the living spores were examined under the microscope for the rate of conidia formation. It was found that spores germinate to form conidia rapidly after they have been subjected to chilling.

Spores were placed in a hanging-drop of sterile solution made from hazel leaves, and the hanging-drop preparations were then placed in sterile Petri dishes. These were left in the refrigerator at a temperature of 10° C. for twelve hours. When taken out in the morning and placed in a room at about 20° C., germination took place almost immediately. Figure 37 shows what occurred in the course of one-half hour. A spore increased in size (compare figs. 37A and 37B) in the first ten minutes; in the next five minutes the stages represented in figure 37C, D, and E were passed through; and in another five minutes the constriction is complete between the two daughter conidia (fig. 37F). Within a few minutes one conidium may lengthen and furrow in on one side, and soon a secondary conidium is partly formed (fig. 37G). All the spores

do not germinate at once to form conidia, but one or two may lag behind and show no indication of germinating even after some of the others have produced secondary conidia (fig. 38).

The secondary conidia are very small, and it is these small conidia that produce the vegetative mycelium. The attempt to grow mycelium on artificial media was not successful. Short hyphae were produced but soon died. These hyphae were slender, having a diameter less than the diameter of the conidium and containing a very vacuolate cytoplasm (fig. 39).

#### SUMMARY

1. *Taphrina coryli* Nishida is an intercellular parasite infecting all parts of the leaves and the cortex of the one-year-old twigs of *Corylus americana*.

2. The vegetative cells form long filaments and frequently branch dichotomously. They serve to distribute the fungus through the leaf and through the twig.

3. The binucleate condition arises in the vegetative cells, and not in the ascogenous cells.

4. The division of the vegetative nucleus is mitotic, with small spindles and centrosomes. It is difficult to recognize individual chromosomes in the chromatin masses.

5. The binucleate condition continues into the ascogenous cells, and then nuclear fusion takes place. Nuclear fusion takes place most frequently early in the morning.

6. The fusion nucleus is a typical resting nucleus, containing a large nucleole, chromatin on a linin network, and a central mass of deeply staining chromatin.

7. The division of the fusion nucleus is a heterotypic reduction division, as is indicated by the occurrence of synapsis and of a later stage showing the spirem thrown into a definite, looplike arrangement from the center to the periphery.

8. Granular bodies are present at the ends of the spindle and a clear area surrounds the entire spindle. It is not definite how these granular bodies are formed.

9. The separation of the basal cell from the ascus proper takes place by the constriction of the plasma membrane.

10. One nucleus is left in the basal cell; the sister nucleus passes into the ascus proper. Gradually the former nucleus disintegrates, but the second and its derivatives divide to form nuclei for the eight primary spores.

11. Vacuolar membranes appear to be the active agents in the formation of the spores.

12. Conidia are produced by the lengthening of the spore, followed by its constriction into two cells of unequal size, the smaller growing to equal the larger before separation. The production of conidia is stimulated by chilling.

13. Primary conidia produce secondary conidia which germinate on artificial media to form short hyphae.

I wish to express my thanks to Professor E. M. Gilbert, who suggested this work, for his assistance and encouragement.

## LITERATURE CITED

- Adams, R. M. 1915. Studies in the life history of *Eoascus communis* on *Prunus cuneata*. 1-35. B. A. Thesis, Univ. of Wis.
- Atkinson, G. F. 1894. Leaf curl and plum pockets. Cornell Agr. Exp. Sta. Bull. 73: 319-355.
- Bitner, A. L. 1915. Studies on the life history of *Taphrina coryli* Nishida on *Corylus americana*. 1-39. B. A. Thesis, Univ. of Wis.
- Brown, W. H. 1911. The development of the ascocarp of *Lachnea scutellata*. Bot. Gaz. 52: 275-303.
- Dangeard, P. A. 1894. La reproduction sexuelle des Ascomycetes. Le Botaniste 4: 30-35.
- Faul, J. H. 1912. The cytology of *Laboulbenia chaetophora* and *L. gyrindarum*. Ann. Bot. 26: 325-355.
- Fisch, C. 1885. Ueber die Pilzgattung Ascomyces. Bot. Zeit. 43: 33-39 and 49-59.
- Fitzpatrick, H. M. 1918. The cytology of *Eocronartium muscicola*. Am. Jour. Bot. 5: 397-419.
- Fraser, H. C. I., and Brooks St. John. 1909. Studies in the cytology of the ascus. Ann. Bot. 23: 537-547.
- Harper, R. A. 1899. Cell division in sporangia and asci. Ann. Bot. 13: 467-525.
- 1905. Sexual reproduction and the organization of the nucleus in certain mildews. Carnegie Inst. Pub. 37: 1-97.
- Ikeno, S. 1901. Studies on the spore formation in *Taphrina Johansonii* Sad. Flora 88: 229-236.
- 1903. Sporenbildung von *Taphrina* Arten. Flora 92: 1-31.
- Nishida Y. 1912. On *Taphrina coryli* Nishida n. sp. Miyake Festschrift, 206, Tokyo.
- Pierce, N. B. 1900. Peach leaf curl. Its nature and treatment. U. S. Dept. Agr. Div. Veg. Phys. & Path. Bull. 20: 11-45.
- Sadebeck, R. 1893. Die Parasitischen Exoascen, eine Monographie. Jahrb. Hamb. Wiss. Bot. 10: 1-110, also Just. Bot. Jahrb. 21 Jahrg. I Abth. 196-199.

## EXPLANATION OF FIGURES

All drawings were made with a camera lucida at table level. Figures 3, 4, 5, 10, 12, 15, 23 were drawn with a Zeiss 2 mm. apochromatic oil immersion objective and 12 ocular (X2800); fig. 13 with Zeiss 2 mm. oil immersion objective and 18 ocular (X3600); figs. 1, 2, 8, 9, 14, 16-22, 24-29, 35, 38 with Zeiss 3 mm. oil immersion objective and 12 ocular (X1650). A Leitz oil immersion objective  $\frac{1}{16}$  and 4 ocular (X1600) was used with drawings 6, 7, 34, 36, 38, and the others, figs. 30-33, 37, 39, were drawn with a Leitz 7 objective and ocular 5 (X665).

## PLATES XII AND XIII

FIG. 1. Dichotomous branching of vegetative hyphae of *Traphina coryli* Nishida.

FIGS. 2, 3. Uninucleate and binucleate conditions shown in cross and longitudinal sections of vegetative cells.

FIGS. 4, 5. Mitosis in vegetative cells.

FIGS. 6, 7. Two nuclei are present in young ascogenous or fruiting cells.

FIGS. 8, 9, 10, 11. Stages in the fusion of nuclei in ascogenous cells.

FIGS. 12, 13. Typical fusion nucleus in resting condition.

FIGS. 14-24. Division of the fusion nucleus: fig. 14, synapsis; fig. 15, longitudinally split spirem; figs. 16, 17, spirem in loops; figs. 18, 19, 20, thickened spirem; figs. 21, 22, equatorial plate; fig. 23, metaphase and constriction of plasma membrane; fig. 24, anaphase.

FIG. 25. Reorganized nuclei; one, the primary ascus nucleus, and the other, the nucleus of the basal cell.

FIGS. 26, 27. Further constriction of the plasma membrane to separate basal cell from ascus proper.

FIG. 28. Binucleate ascus and disintegration of the nucleus in the basal cell.

FIG. 29. Second nuclear division of the ascus.

FIGS. 30-34. Asci containing spores. Large vacuoles surround the spores; fig. 32 represents the ascus in cross section.

FIG. 35. Early stage in formation of conidia.

FIG. 36, A, B, C, D, E, F, G. Successive stages in the budding of the primary ascospore showing behavior of nuclei and constriction of cell walls.

FIG. 37. A, B, C, D, E, F, G. Successive stages in the formation of primary and secondary conidia. Stages A-G represent development taking place in thirty minutes. Drawn as observed in living material grown on artificial media made from hazel leaves.

FIG. 38. Conidia and ascospore showing that all the ascospores do not divide simultaneously.

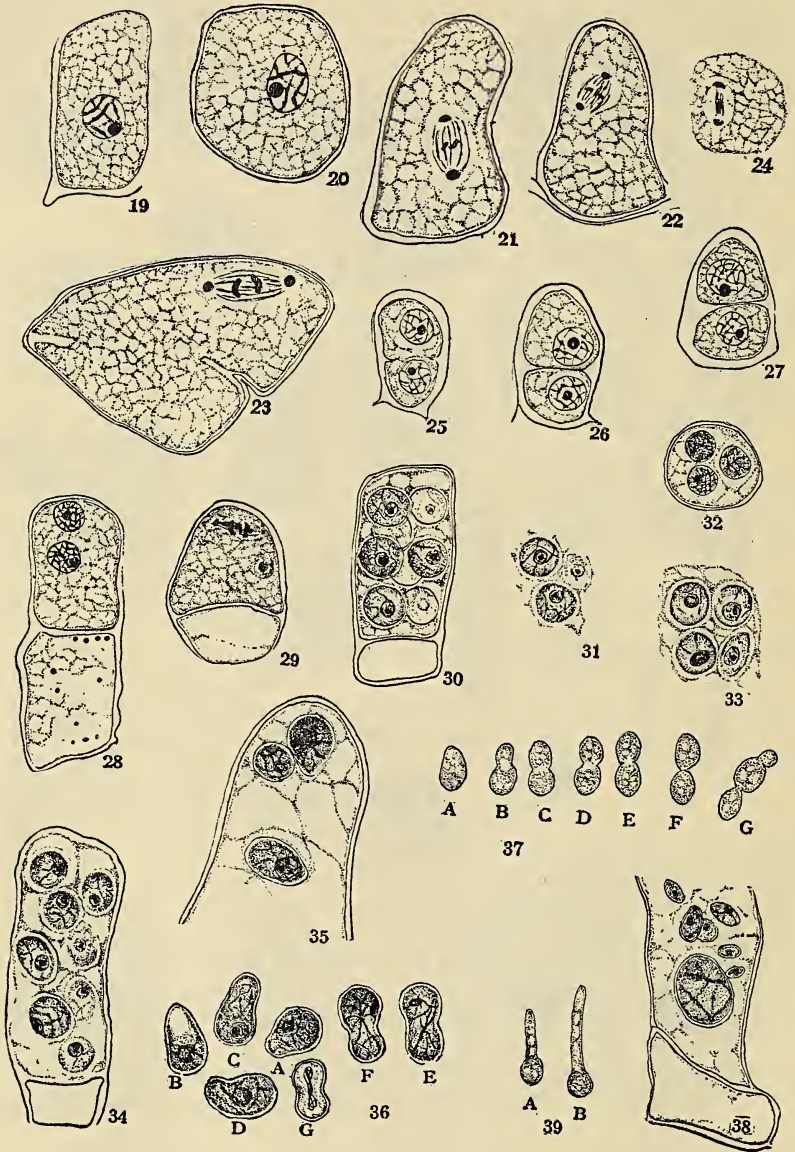
FIG. 39. Germinating conidia drawn from living material growing on the same media as the spores shown in fig. 37.



TRANS. WIS. ACAD., VOL XXI

PLATE XII





THE STRUCTURE AND BEHAVIOR OF THE NUCLEUS IN  
THE LIFE HISTORY OF PHYCOMYCES NITENS  
(AGARDH) KUNZE AND RHIZOPUS  
NIGRICANS EHRBG

---

E. A. BAIRD

Among the contributions to various phases of the life history of the Mucoraceae, a number of the writers do not include any clear statement of the structure of the nucleus or how it behaves in division. Most of the workers, who have attempted to follow closely the behavior and structure of the nucleus in zygospore formation, have described the resting nucleus in the forms studied as consisting of a nucleole, a nucleoplasm containing little or no stainable substance, and a nuclear membrane. In the consideration of nuclear division they have generally described a type of mitosis with a spindle formation, but in the details of this process the descriptions are incomplete. Many of these have described numerous nuclear fusions during the maturation of the zygospore together with a disorganization of other nuclei that do not fuse.

Dangeard and Léger (1894a) in a cytological study of zygospore formation in *Sporodinia grandis* and two species of *Mucor* have described the structure of the nucleus in the vegetative hyphae and the sexual branches of these forms as vesicular, consisting of a surrounding membrane and a centrally placed nucleole, which are separated by a non-staining "cytoplasm" containing a little chromatin. In the young zygospores of these forms they find two sizes of nuclei.

In another report, Dangeard and Léger (1894b) describe without figure the structure of the nuclei in *Mucor mucedo* and *M. racemosus* as similar to that described above. In the ripe zygospore of *Sporodinia* the small and, later, the large nuclei disappear. After their disappearance the zygospore contains a varying number of deep-staining bodies.

Léger (1895a) figures the nucleus of the vegetative mycelium as a vesicular body with a centrally placed nucleole. He describes

karyokinetic figures as occurring in the vegetative hyphae but does not figure nor describe the process of nuclear division. He finds that the nuclei, evident up to this time, begin to disintegrate as the zygospore matures and its protoplasm becomes spongy and filled with oil. This disintegration is a process in which the nucleole becomes smaller and finally disappears. The nucleus then becomes vacuole-like. A few nuclei, which are two or three times larger than those entering the zygospore at the time the gametes fuse, remain in the zygospores longer than do the other nuclei, but ultimately disappear. In another paper, without figures, Léger (1895b) has reported on the conditions he has found in species of *Pilobolus*, *Rhizopus*, *Chaetocladium* and *Mortierella*, together with those forms previously studied with Dangeard. He describes the structure of the nucleus in the vegetative hyphae in all the forms as similar to that described by Dangeard and himself. He indicates a point of interest as to the fate of the nucleus in the mycelium and the columella in that the nuclei become reduced to nucleoles which persist after all other traces of the protoplasm have disappeared.

Istvanffi (1895) describes the nucleus in *Mucor* sp. He finds that the nuclei are scattered thruout the entire protoplasm; that they are elliptical or spherical in shape and usually provided with a nucleole. In spore formation only one nucleus enters each spore. During preparation for germination, the spore is observed to have eight to ten nuclei. In the tips of hyphae where he considers that the nuclei are youngest, he states that they may consist of only a small homogeneously-stained body, not exceeding  $1\mu$  in diameter.

Harper (1899) in his description of spore formation of *Pilobolus* states that the vegetative nuclei of this form divide in the basal bulb, thus giving rise to the nuclei that enter the sporangium during its development. He also finds that the nuclei divide in the protospore and in the swelling spore in preparation for germination. In none of these references to nuclear division does he describe the structure of the nucleus or indicate how it divides. However, he figures several nuclei, each consisting of a dense central body enclosed by a granular nucleoplasm and a nuclear membrane. He also illustrates several division figures, each consisting of an elongated body, at the two poles of which are several dense granules; the two groups of granules are connected by one or more fibrous strands.

Swingle (1903) in a report of spore formation of *Phycomyces* and *Rhizopus* describes the nuclei in the sporangium of either form as in a resting condition. In either form each nucleus is approximately spherical in shape, and consists of one or two nucleoli, a finely granular chromatin, and a surrounding membrane. In the columella of *Rhizopus* he describes the nuclei as disintegrating. According to him the process of disintegration consists of the appearance of a red-stained mass on one side of the nucleus, followed by the nucleus taking on the appearance of a shrunken homogeneous mass often irregular in shape and staining much as do the crystalloids of the protoplasm. In *Phycomyces* the structure of the nucleus is similar except that it may have as many as three nucleoli, and in this form he has described the disintegration of the nuclei in the mycelium as in the columella of *Rhizopus*.

Gruber (1901) in a description of nuclear behavior in zygospore production of *Sporodinia grandis* agrees with Léger up to the point at which the protoplasm of the two gametes become mixed. From this point on he does not find nuclei of two sizes, nor fusions taking place between paired nuclei, nor evidence that nuclei are disintegrating, but rather that the nuclei are clearly in evidence after fourteen days of development of the zygospore. After five or six weeks and again at the end of six months he still finds nuclei in the same condition as when the zygospore was formed.

In a later paper, reporting on the sexual process of *Zygorhynchus Moelleri*, Gruber (1912) describes nuclear fusions as occurring between the nuclei of the male gamete and an equal number of those of the female gamete.

Dangeard (1903) describes the nuclear structure and behavior in a species of *Mucor* and in *Sporodinia*. In either of these forms a nucleus of the gametes consists of a small nucleole and a homogeneous achromatic nucleoplasm. After the fusion of the gametes the nuclei divide one or more times, then nuclear fusions occur. A daughter nucleus, thus arising in the zygospore, consists of a nucleole, a network of granular chromatin, and a nuclear membrane. In the process of nuclear fusion, the membranes fuse at the point of contact. At first the two nucleoles rest within the membrane thus formed and then fuse. Some of the nuclei do not fuse but disintegrate. In rather mature zygospores, this author finds large deep-staining bodies throughout the protoplasm, which he suggests have arisen from mucorine crystals.

Moreau (1911a) and 1911b) in describing cytological studies, especially in zygosporangium formation, of species of *Mucor*, *Zygorhynchus*, *Circinella*, *Rhizopus* and *Sporodinia* states that a nucleus of these mucors consists of a chromatin nucleole, a nucleoplasm, and a nuclear membrane. The nucleole, is either centrally, eccentrically, or laterally placed. In some cases in *Mucor* a centrosome, chromatic in nature, is observed on the external surface of the nuclear membrane. In the columella of *Rhizopus* he finds a modification of the nucleus in that there is no nuclear membrane and the nucleus consists simply of a homogeneous body. According to Moreau, the nucleus divides mitotically in the vegetative hyphae and in the zygosporangia of the forms studied. The process of mitosis is inaugurated by the disappearance of the nuclear membrane and of the nucleole. No other stages characteristic of prophase are described. He describes an equatorial plate stage in which double chromosomes are borne on a straight spindle, terminated at each pole by a centrosome. He describes and figures a later stage in which two daughter chromosomes are in process of moving toward each pole. Stages in the reorganization of the daughter nuclei are not described. In the zygosporangium, the mitotic nuclear divisions take place, according to Moreau, as if activated by the mixing of the protoplasm from the two fusing gametes. He also describes a form of amitotic nuclear division of the homogeneous nuclei in the columella of *Rhizopus*. In *Mucor*, following the nuclear divisions in the young zygosporangium, the nuclei fuse in pairs, giving rise to a large number of fusion nuclei. A number of nuclei fail to fuse and later disintegrate. In *Zygorhynchus* the nuclear disintegration takes place before fusion, and in the zygosporangia of this form, only two fusion nuclei are formed. The fusion nuclei of all the forms studied by Moreau are similar in structure. Each contains a single large nucleole. He states that the fusion nuclei persist in the mature zygosporangium and form the basis of the nuclei of the thallus arising from the germination of the zygosporangium.

Moreau (1913) has published the results of very extensive cytological research of a large number of the Mucoraceae. These later results are in accord with his previous work. In the case of *Phycomyces* he states that he saw clearly stages in the fusion of the nuclei in the young zygosporangium at the time the spiny exospore was being formed. The fusion of the nuclei in the zygosporangium, of those forms for which he describes the process, consists in the fusion of the two membranes at the point of contact, thus forming one

nuclear cavity. At first the two nucleoles lie separate, but later fuse. In his description of nuclear division in this paper, he conforms to his previous report.

Miss Keene (1914) in her cytological studies of *Sporodinia grandis* finds that the nucleus in this form is granular in structure and contains a centrally placed nucleole which she considers chromatin in nature. She believes that nuclear divisions occur in the tips of the two sexual branches. As the mixing of the two fusing gametes takes place, nuclear fusions occur. Miss Keene describes no divisions in the zygospore preceding nuclear fusions, as was described by Dangeard and Moreau. She describes nuclear degeneration of unfused nuclei in the zygospore, but her description of the process is somewhat different from that given by other workers. According to her, the process is first accompanied by an enlargement of the nucleole which does not stain as deeply as in preceding conditions. The nucleus eventually becomes a homogeneous-staining mass. According to her the fusion nuclei are in evidence in zygospores two and three months old.

Later, Miss Keene (1915) has contributed results of cytological studies of *Phycomyces nitens*. She has figured the nuclei in germinating asexual spores as containing one or two deep-staining bodies. The resting nucleus is described by her as bounded by a membrane and containing a deep-staining body, probably the nucleole, and chromatin granules throughout the nuclear cavity. She states that in the germinating spores, the young sporangia, suspensors, and progametes, the nuclei show conditions that are very suggestive of division figures. She suggests that in nuclear division figures containing three bodies, two may be chromosomes and the third the nucleole. In the young zygospore she finds that many of the nuclei are arranged in groups of twelve to sixteen. Some of these nuclei fuse in pairs; others do not fuse. Later the unfused nuclei of the zygospore coalesce to form one or two large amorphous masses that persist in the zygospore several months old. Similar masses are formed within the suspensors. The fused nuclei persist in the zygospore and are confined to a thin peripheral zone of the cytoplasm.

Burgeff (1915) has contributed a very interesting description, without figures, of his studies of the cytology of *Phycomyces nitens* and mutants of this species. His observations as to the structure of the nucleus or as to the facts of nuclear fusion are not fully in accord with those of either Keene or Moreau. He describes the

nucleus of the vegetative mycelium as consisting of a very small homogeneous body, and suggests that it is identical with a chromosome. Division of a nucleus in the vegetative hyphae consists simply in the separation of the chromatin body into two daughter nuclei. He finds that in spore formation in the sporangium from five to twelve of these chromatin bodies are enclosed within each spore. He describes no change in the structure of the nucleus during zygospore formation, except that after the fifth day of development the nucleus is spongy and contains a single chromatin body. He reports no nuclear divisions or fusion during the formation and maturation of the zygospore.

The nuclei in the zygospore preparing to germinate are surrounded by a membrane but have only one chromatin body and by the time the germ tube pushes out, eleven to twelve days after sowing, the nuclei are more or less irregular in outline and provided with several chromatin bodies and a nucleole. At this stage they are several times larger than the nuclei of the sexual generation. In the germ tube and sporangium, nuclear divisions occur among the large nuclei. Burgeff states that all stages in mitosis are difficult to make out. Clear prophases occur in which the nucleole disappears. The chromatin is separated into twenty-four (estimated) chromosomes. Twelve chromosomes move to each pole within the membrane; no equatorial plate stage is observed. Burgeff characterizes this as a heterotypic division, following which, he states, a homotypic division occurs in which distinct chromosomes are present. Following the homotypic division successive divisions take place, giving rise to a large number of membraneless nuclei. These nuclei, with a number of nuclei surrounded by membranes, become the nuclei of the spores formed within the germ-sporangium. He suggests that the nuclei with membranes are either unfused nuclei of the gametes or else nuclei that have not passed through reduction division. In spore formation only one nucleus enters into the formation of a spore. After spore formation, as they mature, the nucleus of each spore divides successively so that each mature spore contains a number of nuclei. In his summary, however, Burgeff states that he has not observed the division of nuclei with membranes within the spores of the germ-sporangium.

Burgeff (1920) describes the nuclei of the parasitic mould, *Chaetocladium*, and of its host, *Mucor*, as being very similar. The nucleus of either form consists of a deep-staining body with or without a clear zone surrounding it. The clear zone is more fre-



quently observed in poorly nourished hyphae. Burgeff calls the deep-staining body chromatin, states that it is nucleole like, and that it is frequently located eccentrically in the nucleus. In well-nourished hyphae the chromatin body is much larger than in poorly nourished hyphae. His special study of the nuclei has been in the galls formed at the point of attack of the parasite. He points out that the nuclei in the sporangiophores contain a much larger chromatin body than do those in the vegetative branches; he attributes this to the presence of reserve food in the sporangiophores. He states that the *Mucor* nuclei in the gall divide mitotically, but gives no figures nor details of the process. He also describes crystalloid bodies as arising from degenerating nuclei.

#### MATERIALS AND METHODS

The material from which the preparations were made was grown in petri dishes on potato-glucose agar prepared with distilled water. Flemming's medium fixing reagent was used almost exclusively, after a wide variety of reagents was tried out. The imbedded material was cut in sections  $4\mu$ – $12\mu$  thick and the preparations stained with Flemming's triple stain. Heidenhain's iron-alum-haematoxylin method of staining was also used, but in no case gave the minute differentiation obtained by the use of the triple-stain.

For the germination of the zygospores of *Phycomyces*, zygospores that had remained on the original substratum, upon which they grew, in a dark room at an average temperature of 20 degrees C., germinated readily when transferred to a non-nutrient 2% agar medium. The zygospores germinated, forming a single germ-sporangium within four or five days after transferring. The cultures of germinating zygospores were grown in a light room, at room temperature. On account of interruption in the work, the study of nuclear behavior in the germ spore and of the sex of the germ-sporangiospores has not been completed.

#### PHYCOMYCES NITENS

In the swollen spores of *Phycomyces* about to germinate there are one or more vacuoles with several (4–13) nuclei imbedded within the cytoplasm. After the germ tube has been formed (fig. 1) the nuclei are distributed throughout the enlarged cell by the increase of vacuolar volume. The nuclei show no change in structure up to this period. So far as I have observed the

nuclei show no change in structure until some time after the germination of the spore. As soon as the first hypha has several branches, one observes the first changes in the nuclei as described below.

A nucleus in the resting spore and during early stages after germination consists only of a homogeneous, deep-staining, approximately spherical body which I consider to be chromatin in nature. Its surface is undoubtedly membranaceous, although no membrane is differentiated. With the triple stain this body stains deeply with the safranin while the surrounding cytoplasm stains orange. The first change that occurs in such a nucleus is the swelling of the chromatin body accompanied by the formation of a vacuole within it. In some instances the chromatin becomes distributed for a time in the peripheral zone. With further growth of the vacuole the chromatin becomes separated at one or more points. If separated at one point, the chromatin may present a somewhat crescent-shaped optical section (fig. 2f). On the other hand, it may be separated so as to present a somewhat horseshoe-shaped section with a chromatin body in the opening of the horseshoe (fig. 2b). Usually the chromatin substance is separated into from three to six bodies, as the growth of the vacuole progresses (figs. 2a, 2c, and 2d). Figure 2 illustrates the distribution of such nuclei associated with vacuoles from a hyphae in the substratum of a three-day-old culture.

The question naturally arises in this connection concerning the nature of the membrane surrounding the nuclear vacuole. The vacuole evidently originates below the surface of the chromatin. But as soon as the chromatin is separated sufficiently at any point a thin membrane remains surrounding the vacuole; the membrane does not stain with the safranin as does the chromatin but stains more as does the surrounding cytoplasm. This may be due to the fact that it is so thin as not to appear differentiated from the surrounding cytoplasm, but I am inclined to believe that, while the membrane originates within the chromatin, its composition becomes changed and so differentiated from the chromatin.

The above-described vesicular body has undoubtedly been interpreted by most workers as the nucleus. Since, as I shall point out later, such a vesicular body functions as a single structure of the protoplasm at certain stages in the life history of the plant, perhaps it would not be incorrect to consider it a nucleus. However, on account of its behavior in connection with division and distribu-

tion of the chromatin in rapidly growing mycelium, I consider the vesicle a vacuole, and each portion of chromatin at its periphery a nucleus.

The nuclei that have been thus formed are destined soon to become disassociated from one another and in subsequent nuclear division give rise to daughter nuclei by a similar process.

There appear to be two different forces that bring about the ultimate separation of the daughter nuclei. One is the growth of the vacuole from within as just described. The other force is the streaming of the protoplasm within the hyphae, giving rise to elongated division figures and most frequently observed in the hyphae of the substratum where their tubular form is not uniform in outline and very angular in contour. In such hyphae of living cultures I have frequently observed that the rate of streaming is not uniform throughout a given diameter. This character of the streaming evidently accounts for the fact that the vesicular division figures are sometimes elongated and often curved in the hyphae of the substratum (figs. 2c, 2d).

Where the enlargement of the vacuole alone is operating, the daughter chromatin masses and the vacuole with which they are associated present a spherical figure (figs. 2a, 2e). While the outline of the vacuole is still unobliterated, one often finds the daughter nuclei beginning a subsequent division (fig. 2e). In this figure the daughter nuclei have lagged behind the progress of the vacuolar membrane and appear within the space bounded by the membrane that was carrying them apart. Here, too, the original vacuolar membrane is losing its identity and becoming thickened and evidently is about to be incorporated into the slimy portion of the cytoplasm. It is also observed that slimy cytoplasm is being formed within the cavity of the vacuole between the daughter nuclei.

In the sporangiophore and sporange one does not usually find division figures of the nucleus elongated or otherwise distorted, for evidently the protoplasm in which the nuclei are imbedded is moving uniformly or is at rest, as is the condition of the protoplasm of the sporange and sporangiophore as the sporange reaches maturity. In these structures, therefore, one usually finds the nuclei associated with approximately spherical vacuoles (figs. 3a and 3b). Figures of similar form are also found in the gametes, suspensors, and immature zygospores.

In some instances a vacuole associated with a nucleus may arise without bringing about a division of the nucleus. In such a case the vacuole originated below the surface of the chromatin mass and gradually enlarges eccentrically, giving rise to a vesicular structure consisting of a vacuole with a single chromatin body at its periphery (fig. 3a). In this case the vacuole is not destined to play a part in nuclear division. In some cases the vacuole enlarges uniformly around the chromatin body, leaving the chromatin suspended within the vacuole (figs. 4f, 4g and 5d). Thus it appears that numerous vacuoles of the cytoplasm arise from the chromatin bodies; they may or may not have divided nuclei as they were formed.

In figures 4a-4k are represented a number of nuclei taken from the two gametes of a sexual apparatus. All show stages in nuclear division except figure 4d where the vacuole was formed at one side as described above. Figures 4c, 4f and 4g represent the type of structure in which the vacuole was formed by progressing on all radii of the sphere, leaving the chromatin body within the vacuolar sap. A nucleus thus suspended within the vacuolar sap forms a second vacuole within itself to bring about division (figs. 4f and 4g).

During the process of nuclear division strands of protoplasm are frequently observed, extending across the vacuole from one chromatin body to another (fig. 4a). They vary considerably in different figures and do not always appear. Such strands are evidently formed by the chromatin. In some cases the strands connecting the daughter chromatin bodies appear to be so closely associated with the vacuolar membrane as to cause the membrane to be somewhat flattened, to conform to the straight lines of the connecting strands, and thus present a vacuole with a broken surface of flat faces rather than the curved surfaces of other vacuoles (figs. 4f, 4h and 4i).

In many cases the ultimate destiny of a vacuole of a division figure is that it becomes obliterated by an incorporation of the membrane with the slimy cytoplasm, and the space within becomes gradually filled with slimy cytoplasm, either reticulate or homogeneous. Figures 4j and 4k represent such groups of nuclei after the vacuole has thus become obliterated. The group of seven nuclei represented in figure 4k evidently originated from two sister nuclei. The three in the lower portion of the group and to the left are

evidently from one of the nuclei, and in this group each has begun to form a vacuole.

After the fusion of the gametes and during the growth of the resulting zygospore, I find no evidence of a pairing or fusing of the nuclei. During the growth of the zygospore, nuclear division occurs continuously until the protoplasm finally takes on its resting condition as described below. All of the nuclear division figures of the zygospore are of the spherical type. The only observed change in the protoplasm after the fusion of the gametes is the increased affinity of the cytoplasm for the safranin and gentian stains. As a result of this change in staining reaction, the differentiation of the nuclei is not as definite in the zygote as in the suspensors or the vegetative hyphae. The nuclear division figures of the zygospore are of the same form as has been described for them in the sporangia (figs. 5a–5e). Figure 5 represents a zygospore during the growing period while the exospore is being formed and shows the fragments of the walls of the gametes which fused to form the first wall of the zygospore.

During the growing period of the zygospore many of the dividing nuclei are found in groups of four to eight. In figure 5a six dividing nuclei of such a group, at the same optical level, are shown in their relative positions. Evidently these have originated from the same nucleus through two successive divisions, but, since the vacuoles bringing about the divisions have enlarged but little, the daughter nuclei of each division remain in close proximity to each other. On the other hand, the isolation of other daughter nuclei in the zygospore is accounted for by the greater expansion of the vacuole separating the nuclei. Figure 5b contains both isolated and grouped nuclei.

The nuclei of a zygospore which has attained nearly its full size are found associated with smaller vacuoles than are the nuclei of a zygospore during the rapidly growing period, or of the vegetative hyphae. Compare figures 5c and 5e of a full-grown zygospore with figures 3a and 3b from a sporangium, and with figures 6a and 6b from a growing zygospore.

In the stained preparation of the protoplasm I have found no evidence of fat, nor structures identified with its formation. However, a test with Sudan III of protoplasm crushed out of zygospores in all stages of development shows very clearly the presence of fat. Undoubtedly the fat in the zygospores occupies many of the larger spaces that appear as vacuoles in the preparations. The fat is

evidently dissolved by xylol or chloroform during the clearing and imbedding processes.

A mature zygospore two weeks old shows very little of the slimy portion of the cytoplasm. Figure 7 shows the condition of the protoplasm in a zygospore from an eleven-day-old culture, in which the zygospores would vary in age from three to seven days. At this stage one finds that the protoplasm consists of three distinct portions, vacuoles, the slimy portion of the cytoplasm, and nuclei. The vacuoles evidently represent spaces filled with oil, cell sap or gas. Some of the vacuoles contain a slightly-staining granular substance, as has frequently been described by other workers, but this is not so specially characteristic of the vacuoles of the zygospore as it is of the vacuoles of the vegetative hyphae. The slimy portion of the cytoplasm is still in evidence but in a much reduced proportion. Most of the nuclei together with the vacuoles associated with them present a different aspect than has been described for them heretofore in the life history of the plant. Some of the vacuoles associated with the nuclei appear as has been previously described; the others now contain a substance that stains with the same reaction as do the chromatin bodies at the periphery of the vacuoles. It appears that the chromatin substance has increased in volume accompanied by a reduction in the proportion of the cytoplasm.

In figure 7a a distinct vacuole is present, but the surrounding membrane has become thickened and stains deeper. Figure 7b illustrates a nuclear vacuole that has become filled with a stainable substance. Figure 7d represents the final stage in the development of such a nuclear structure in the mature zygospore, the form in which most of the protoplasm, except the fat, is found. These structures are often so closely crowded together that their surfaces are compressed flat against each other (fig. 7d). During this change the same stain-absorbing elements as are contained in the chromatin characterize all the material contained in the nuclear vacuoles. I call these structures "reserve food bodies". Each consists of a variable amount of food reserve, which occupies the space of the nuclear vacuoles, and one or more chromatin masses which may usually, though not always, be observed as deeper-staining bodies at the periphery (fig. 7b).

My interpretation is that during the process of maturation of the zygospore there are no nuclear fusions. After the fusion of the two gametes the nuclei continue to divide rapidly, as they do in

the actively growing vegetative mycelium, until the zygospore is mature. Then the nuclei, acting as metabolic centers, proceed to transform available food into a reserve form of protoplasm which is stored in the space previously occupied by the vacuolar sap of the associated vacuole. As for the fat, I am unable to conclude whether it is a metabolic product of the cytoplasm or of the nuclei.

In preparations of zygospores in which the protoplasm is in a resting condition, the proportion of stainable substances and of the spaces appearing as vacuoles varies considerably. This variation is undoubtedly due to a difference in the amount of nutrition available for the given zygospores. In some zygospores a comparatively large proportion of the space may be unoccupied by the deeply-stainable substances (fig. 7). In others the same substances occupy a much greater proportion of the space within the zygospores. In some cases this material is located largely in the peripheral zone, in others distributed more or less irregularly throughout.

In crushing zygospores under water, bubbles always appear from within the rupture of the inner, leathery spore wall. Therefore, I conclude that the clear spaces appearing in preparations are in some instances occupied by gas resulting from metabolism.

The protoplasts of zygospores five months old are unchanged in appearance from those that have matured up to the resting stage. After the zygospores are placed on moist agar for germination, one finds that many of the dense nuclear bodies become separated from each other by vacuolated cytoplasm. This change is most evident in the peripheral zone. In the more central region the nuclear structures stick together in large masses. In the peripheral zone there are many cases of a single nucleus with a vacuole or a group of several such nuclei surrounded by a very dense mass of slimy cytoplasm. The vacuoles associated with some of these nuclei have lost a large portion of their deep-staining substance. Figure 8 illustrates a section of a germinated zygospore with a portion of the germ tube. It contains many of the nuclear structures filled with food reserve as has been described for the zygospores before germination; many of them persist during zygospore germination and the formation of the sporangium. In the peripheral zone are many of the dense cytoplasmic masses surrounding one or more nuclei. Figure 8a shows such a cytoplasmic mass, wherein one nuclear structure is still unchanged, and from at least two of the nuclear vacuoles the reserve food has been dissolved. The later condition of the nuclear vacuoles is clearly illustrated in figures

8b, 8c and 8d. Such figures correspond very closely to those of nuclei observed in the zygospore during maturation when the vacuoles were beginning to receive the reserve substance.

An insufficient number of stages were fixed to warrant reporting on the process of spore formation in the germ sporange. However, it has been determined that nuclei of the type shown in figures 8a, 8b, 8c, and 8d pass into the sporangiophore and are found there before and after spore formation in the sporange. There appear to be no nuclear divisions in the germinating zygospore or in the germ sporangiophores either before or after spore formation.

#### RHIZOPUS NIGRICANS

A complete study of the nucleus of *Rhizopus nigricans* has been made in the vegetative mycelium, in the sporanges, in the mature and germinating spores, in the gametes, and in the zygospores during maturation. Since no germination of zygospores has been obtained, it has been impossible to follow the nuclear behavior through that process.

It is very evident that nuclear behavior is, in general, the same in *Rhizopus* as has been described for *Phycomyces* in the processes of nuclear division and in the formation of reserve protoplasm stored in the vacuoles associated with the nuclei of the zygospores.

The nuclear vacuoles do not become quite as large in *Rhizopus* as they do in *Phycomyces*. Compare figures 9a, 9b, and 9c taken from the sporange of *Rhizopus* with figures 3a and 3b taken from the sporange of *Phycomyces*; both sporanges were at about the same stage of development.

In *Rhizopus* the obliteration of the vacuole, causing the separation of the chromatin masses, takes place sooner after the separation of the daughter nuclei, and, therefore, in the case of *Rhizopus* one finds more frequently the nuclei disassociated from a vacuole.

Figure 9c illustrates a case in which two sister nuclei evidently were at first associated with the same vacuole and later one of them formed a second vacuole, which separated the two chromatin masses still further. A third small vacuole also has formed between them. A somewhat similar case is illustrated in figure 11b in which a nucleus from a young zygospore has divided and one of the daughter chromatin masses is forming a vacuole within another vacuole. Figures 10a, 10b, and 10c are dividing nuclei taken from a vegetative hypha.



Another minor variation in the process of nuclear division, occurring in *Rhizopus* as compared with *Phycomyces*, is that in *Rhizopus* the chromatin mass is separated more frequently into two portions rather than into three, four, or more as in *Phycomyces* (figs. 10a, 10b, 10c). In a few cases observed, however, in *Rhizopus* the chromatin may be separated into several portions (figs. 13a and 13b).

Figures 11a and 11c illustrate cases in each of which the vacuolar membrane has progressed further than the two daughter chromatin bodies, thus leaving them within the vacuole, and figure 13b shows one such chromatin body forming a second vacuole within itself. Figures 13a, 13b, and 13c represent nuclei from a zygospore at a time when the associated vacuoles are becoming filled with homogeneous reserve substance, as was described for the nuclear vacuoles of *Phycomyces*.

Figure 12 represents a spore from the sporangium of *Rhizopus* before the spores have shrunk and their walls have thickened. The nuclear structures observed here apparently shrink as the spore matures and shrinks. Each structure thus becomes one of the dense nuclei observed in the mature spore and that appear as soon as the spore germinates, as was figured for *Phycomyces* (fig. 1).

#### NUCLEI OF AGED MYCELIUM

The nuclei of the vegetative, aged mycelium behave very similarly to those in the maturing zygospores. Nuclear division continues in the vegetative hyphae up to a time which I conclude is determined by a change in water balance. For, at a time when no further growth of mycelium occurs, its nuclear vacuoles take on the appearance of those which contain reserve food in the zygospores (figs. 14a and 14b). In figure 14a, taken from a 36-day-old culture of *Phycomyces*, the vacuole has become filled with a homogeneously-staining substance, and some of the nuclei associated with the vacuole are still partially differentiated. Figure 14b represents a similar condition of a nuclear structure taken from a vegetative hypha of a 14-day-old culture of *Rhizopus*.

As the mycelium becomes dried out in aging cultures, the slimy cytoplasm does not disappear from the mycelium on a large scale as it does in the zygospores. However, in the aged mycelium partially dried out, some of the hyphae appear empty, except for a few of the deep-staining nuclear structures and a very slight

amount of slimy cytoplasm; other hyphae contain a large amount of slimy cytoplasm and nuclear structures filled with reserve food (fig. 16).

Mycelium of *Phycomyces* forty days old was placed on moist nutrient agar and after sixteen hours many hyphae had grown out from the old mycelium. Preparations made from sections of this material showed that nuclear structures of the type described above for aged mycelium were abundant in the new hyphae in the substratum. Some had lost completely the reserve food of the vacuoles and the nuclei were in a state of active division. Most of the nuclear structures were in a transitory condition in which the vacuolar portions had swollen considerably; the reserve food was partially dissolved and some of the nuclei were beginning division. Figure 15a shows several nuclei in a very dense cytoplasm which apparently has been formed from the reserve substance of the vacuolar portion. Figure 15b shows a nuclear structure in which most of the reserve food has been dissolved and the vacuole is quite clear; one of the nuclei is in progress of division and a second nucleus is apparently unchanged.

The foregoing nuclear behavior fits in well with the growth habits of these plants. The plant grows rapidly with a favorable water supply and during the growing period the nuclei divide rapidly and are distributed into the newly formed portions of the plant. As soon as a decrease in available water takes place or, at least, after a certain minimum is reached, growth stops and at the same time nuclear division ceases. As this change occurs most of the nuclei are at a certain stage in division. The nuclear vacuoles cease to expand but apparently proceed to absorb food reserve from the surrounding cytoplasm, giving rise to nuclear structures, filled with reserve food, as has been described above in old dried-out mycelium. When such mycelium is again supplied with water, new hyphae are observed growing out from the aged hyphae. The nuclei and associated structures resume activity, giving up the food reserve and dividing as previously described.

#### DISCUSSION

In the above report it has been difficult to use the term "nucleus" and convey the full idea that the writer holds as to its form and structure. It is evident that the fundamental unit of structure composing the nuclei is a small, homogeneous mass that stains

readily with safranin. This is undoubtedly the body seen and described by many writers as the nucleole. The vesicle that I have called a vacuole associated with one or more chromatin bodies seems to have been considered by others the nucleoplasm.

As I interpret the structure of the protoplasm of *Phycomyces* and *Rhizopus*, the homogeneous body is nucleus; it has the general nature of chromatin in that it stains readily and is present in all stages in the life history of these fungi.

Single masses of this chromatin may exist unassociated with others, as in the spores, where the single body appears to have originated from the reassembling of two or more small bodies that had previously been formed by the division of a single chromatin body, and in the vegetative hyphae, where individual bodies have become disassociated from others by the obliteration of a vacuole that previously had been active in bringing about division. Most frequently several nuclei are associated with a vacuole and these nuclei may or may not be connected by slender strands of protoplasm other than the vacuolar membrane. A vacuole thus associated with one or several nuclei seems to have been formed within the chromatin mass. Usually, the vacuole grows in such a way as to rearrange the chromatin substance into several bodies around its periphery. At other times, as it grows, the vacuole forms eccentrically in the chromatin body, leaving most of the chromatin undisturbed.

Although it has been observed that slimy cytoplasm seems to be formed in the immediate vicinity of the nuclei, as in the germinating zygospores and in the propagation of the mycelium from aged, dried plants, and that at the time this cytoplasm is being formed the nuclear vacuoles apparently lose their reserve, one can hardly conclude whether the nuclei are active metabolic centers contributing to this metabolism by forming cytoplasm from the reserve of fat outside of the nuclear structures, or whether the food has been stored in the nuclear vacuoles, and, later, cytoplasm formed directly from it. Possibly both the reserve in the nuclear vacuoles and the fat outside are used. But it appears evident that the nuclei are very intimately associated with the processes that bring about the renewed vegetative condition of the protoplasm.

The nuclei in the mature spores of the sporangium are dense, homogeneous bodies. When the spore is first formed in the sporangium it contains several nuclear vacuoles with two or more chromatin bodies associated with each. The condition of the nuclei in the

mature spore appears to come about through a reverse in the process of nuclear division brought about by the expansion of the nuclear vacuoles. At about the time the spores are formed there seems to be a change from expansion of their protoplasm to a contraction, due to a loss of water. At the same time the nuclear vacuoles shrink in size and the chromatin bodies of each nuclear structure reassemble to form a single chromatin mass. They remain in this condition until after spore germination, at which time they resume division.

Although it is impossible to state definitely which structures described by other workers correspond to structures that I have described, it is quite plain that most workers have found many of the same structures in different mucors.

The non-staining "cytoplasm" of Dangeard and Léger (1894) is undoubtedly the vacuole that I have described as associated with most nuclei. Léger (1895 a) believes that in aged hyphae the nuclei becomes reduced to nucleoli and persist after the rest of the protoplasm disappears. I find a similar condition in many of the aged hyphae, considering that the nucleole described by Léger is identical with what I have described as a nuclear structure, consisting of one or more nuclei associated with a vacuole which has become filled with a reserve protoplasm.

Istvanffi (1895) describes the nuclei in the growing tips of the mycelium as small homogeneous bodies. This conception of a nucleus is what I hold for the nucleus throughout the life history of the two forms I have studied.

I find no formations in the two forms I have studied that correspond to the dividing nuclei in the protospores of *Pilobolus* as figured by Harper (1899), in which he interprets fibrous strands between two nuclei as the remains of spindle fibers.

Swingle (1903) has described the nuclei of *Rhizopus* and *Phycomyces* as having two or three nucleoli. These are undoubtedly what I have described as the daughter chromatin bodies of a single nucleus. His description of disintegrating nuclei in the columella of *Rhizopus* and aged mycelium of *Phycomyces* corresponds very closely to my description of the nuclear structures with reserve material in aged mycelium, which later may become active upon resumption of growth on the part of such mycelium. Other workers have frequently referred to similar nuclear disintegration. It seems probable that the disintegrating nuclei in zygospores men-

tioned by Miss Keene (1915) are the same as the reserve food bodies of zygospores described by me.

As to the question of nuclear fusions in the zygospores of the various forms of the Mucoraceae, a review of the various reports shows that even in the same species there is little agreement as to when fusion takes place or how many nuclei take part. Several, as my review of the literature shows, do not find nuclear fusion at all in the early formation of the zygospore. Burgeff (1915) describes nuclear fusions as taking place at or shortly after zygospore germination. Many of the workers have described nuclear fusions as taking place soon after fusion of the gametes. For this period I have described rapid nuclear division.

Burgeff postulated a theory as a result of his work to account for the effects brought about by some nuclei fusing and others not fusing. If the nuclei do not fuse anywhere in the life history of the plants, as my results seem to indicate, the behavior of the nuclei in the germ sporangium remains to be demonstrated before any theory to explain the significance of sexual process in the Mucoraceae can be advanced.

#### SUMMARY

1. The nucleus in *Phycomyces nitens* and in *Rhizopus nigricans* is a dense, homogeneous, chromatin body.

2. The nucleus divides by a method of fragmentation into several portions; the complete separation of these fragments is brought about by growth of a vacuole formed within the body of the mother nucleus. In some instances the separation of the daughter nuclei is aided by the streaming of the protoplasm.

4. Vacuoles frequently form eccentrically in a nucleus in such a way as not to bring about nuclear division.

5. Nuclear division continues during the growth of the fungus in the sexual generation. In the vegetative hyphae nuclear division is arrested by the discontinuance of water absorption by the mycelium; in the spores of the sporangium, by a reverse of water absorption to water excretion; and in the zygospores by maturation, which is undoubtedly accompanied by cessation of water absorption.

5. In zygospore formation no nuclear fusions seem to occur.

6. When nuclear divisions stop in the zygospore and in the vegetative hyphae, reserve material is stored in the vacuoles associated with the nuclei.

7. The nuclei in process of division in the embryonic sporangiospores reverse their progress and the portions reassemble to form the nuclei of the mature spores.

8. Upon germination of the zygospores of *Phycomyces nitens* the reserve material in the nuclear vacuoles contributes to the formation of slimy cytoplasm. There is no evidence of nuclear division in the germ tube or in the zygospore.

9. Upon the resumption of growth of mycelium, the reserve of the nuclear vacuoles contributes to the formation of new cytoplasm, as do the similar structures of the germinating zygospores.

Sincere thanks are due Prof. E. M. Gilbert for his stimulating and encouraging interest and suggestions while this work was being carried on.

DEPARTMENT OF BOTANY,  
UNIVERSITY OF WISCONSIN

#### BIBLIOGRAPHY

- Burgeff, H.** (1915). Untersuchungen über Variabilität, Sexualität und Erblichkeit bei *Phycomyces nitens* Kunze. *Flora* 108:353-448.
- (1920). Ueber den Parasitismus des *Chaetocladium* und die heterocaryotische Natur der von ihm auf Mucorineen erzeugten Gallen. *Zeitschrift für. Bot.* 12: 1-35.
- Dangeard, P.-A.** (1903). Les ancêtres des Champignons suérieurs. *Botaniste* 9: 227-252.
- Dangeard, P.-A., and Léger, M.** (1894 a). Recherches sur la structure des Muconinées. *Botaniste* 4: 4-11.
- (1894 b). Recherches sur la structure des Muconinées. *Compt. Rend. Acad. Sci. Paris* 18: 430-432.
- Gruber, E.** (1901). Ueber das Verhalten der Zellkerne in den Zygosporen van *Sporodinia grandis* Link. *Ber. Deutsch. Bot. Ges.* 19: 51-55.
- (1912). Einige Beobachtungen über den Befruchtungsvorgang bei *Zygorynchus Moelleri* Vuill. *Ber. Deutsch. Bot. Ges.* 30: 126-133.
- Harper, R. A.** 1899). Cell division in sporangia and asci. *Annales Bot.* 13: 490-503.
- Istvanfi, Gy.** (1895). Ueber die Rolle der Zellkerne bei der Entwicklung der Pilze. *Ber. Deutsch. Bot. Ges.* 13: 452-467.
- Keene, M. L.** (1914). Cytological studies of the zygospores of *Sporodinia grandis*. *Annales Bot.* 28: 455-470.
- (1915). Studies of zygospore formation in *Phycomyces nitens* Kunze. *Trans. Wis. Acad. Sci., Arts, Letters* 19: 1195-1220.
- Léger, M.** (1895 a). Structure et développement de la zygospore du *Sporodinia grandis*. *Rev. Gen. Bot.* 7: 481-496.
- (1895 b). Recherches histologiques sur le développement des Muconinées. *Compt. Rend. Acad. Sci. Paris* 120: 647-649.

- Moreau, F. (1911 a). Première note sur les Mucorinées. Le noyau au repos. Le noyau en division. Mitose et amitose. Bull. Soc. Mycol. France 27: 204–210.
- (1911 b). Deuxième note sur les Mucorinées. Fusions de noyaux et dégénérescence nucléaire dans la zygospore. Fusions de noyaux sans signification sexuelle. Bull. Soc. Mycol. France 27: 334–341.
- (1913). Recherches sur la reproduction des Mucorinées et de quelques autres Thallophytes. Botaniste 13: 1–136.
- Swingle, D. B. (1903). Formation of spores in the sporanges of *Rhizopus nigricans* and *Phycomyces nitens*. Bull. U. S. Bur. Plant Ind. 37: 7–38.

#### EXPLANATION OF FIGURES

All figures drawn with the aid of the camera lucida.

Figs. 1—10, 14a, 15a, 15b and 16 are from *Phycomyces nitens*.

Figs. 11–13 and 14b are from *Rhizopus nigricans*.

Magnification of figures 7 and 8, 90 diameters; figure 5, 186 diameters; figures 2 and 16, 1050 diameters; figure 5b, 2100 diameters; and all other figures 3250 diameters.

#### PLATES XIV AND XV

- Fig. 1. Germinated spore.
- Fig. 2. Hypha from substratum, from culture 3 days old, grown from spore.
- Figs. 2a–2f. Nuclei from hyphae similar to that in fig. 2.
- Figs. 3a and 3b. Nuclei from sporange before spore formation.
- Figs. 4a–4k. Nuclei from gametes showing various stages in nuclear division.
- Fig. 5. Young zygospore during growing period, showing portion of a suspensor to the right.
- Fig. 5a. A group of nuclei from zygospore shown in fig. 5.
- Fig. 5b. Detail of protoplasm from zygospore in fig. 5.
- Figs. 5c and 5e. Dividing nuclei from zygospore in fig. 5.
- Fig. 5d. Nucleus of same zygospore around which a vacuole has formed.
- Figs. 6a and 6b. Nuclear division figures from a maturing zygospore and with comparatively large nuclear vacuoles.
- Fig. 7. Mature zygospore, about 5 days old. The numerous dense bodies are the nuclear structures, referred to in text, in which the nuclear vacuoles are filled with reserve material.
- Figs. 7a–7d. Nuclear structures with reserve material.
- Fig. 8. Germinated zygospore with dense cytoplasm around nuclear structures in peripheral region at the right; nuclear structures with reserve still unchanged in the central region. A small portion of germ tube appears.
- Fig. 8a. Cytoplasmic mass formed around nuclear bodies.
- Figs. 8b–8d. Nuclear structures from which reserve material has been dissolved.
- Figs. 9a–9c. Nuclear division figures from sporange before spore formation.
- Figs. 10a–10c. Nuclear division figures from vegetative hyphae.
- Figs. 11a–11c. Nuclear division figures from young zygospore.

Fig. 12. Embryonic spore. Nuclear division arrested in progress at about this stage.

Figs. 12a and 12b. Stages in the maturation of spores, and shrinking of nuclear vacuoles.

Figs. 13a and 13b. Showing nuclear vacuoles becoming filled with reserve material in a zygospore.

Fig. 13c. Four sister nuclei from zygospore; one is enlarged somewhat by a vacuole within, and is becoming filled with reserve material.

Figs. 14a and 14b. Nuclear vacuoles filled with reserve material, from aged hyphae.

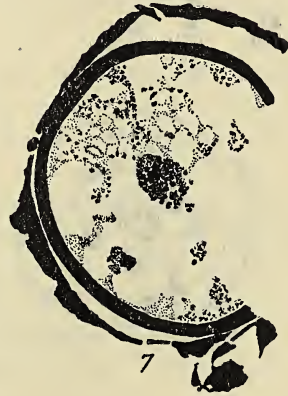
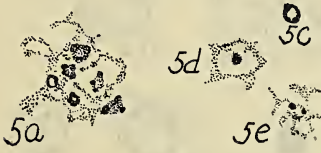
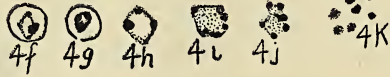
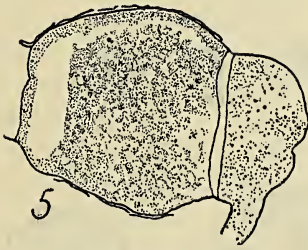
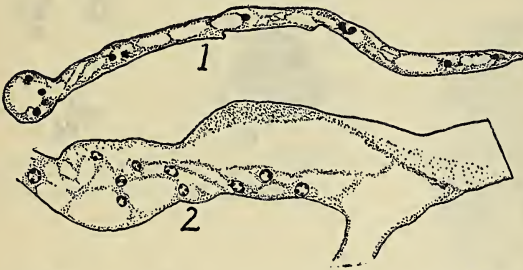
Figs. 15a and 15b. Nuclei from hypha propagated from aged mycelium. In 15a slimy cytoplasm is forming around the nuclear structure; in 15b the reserve material has been dissolved.

Fig. 16. Aged hypha after 16 hours on culture medium, after its protoplasm has renewed activity.



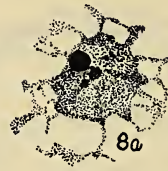
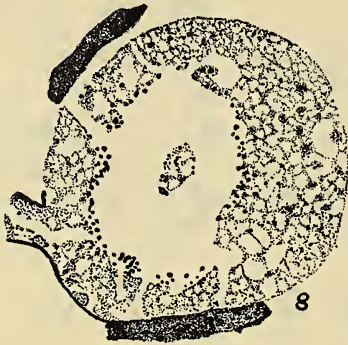
TRANS. WIS. ACAD., VOL. XXI

PLATE XIV



TRANS. WIS. ACAD., VOL. XXI

PLATE XV



# A QUANTITATIVE STUDY OF THE LARGER AQUATIC PLANTS OF GREEN LAKE, WISCONSIN<sup>1</sup>

---

H. W. RICKETT

Notes from the Biological Laboratory of the Wisconsin Geological and Natural History Survey. XXII.

## INTRODUCTION

In the summer of 1921 a survey was made of Green Lake, Wisconsin, with a view to the estimation of the amount of large aquatic plants produced by this body of water. This report embodies the results of the investigation. Besides the gross quantitative data, the study also furnished information on the distribution of various plants, their depth relations, and the vegetation of different parts of the lake.

A similar report has already been made (3) on Lake Mendota. The methods used and the nature of the information obtained in the study presently to be described were in general the same as those in the previous case.

The work was done for the Wisconsin Geological and Natural History Survey, under the supervision of Professor Chancey Juday. For assistance in identifying several of the plants collected, I am indebted to Dr. E. A. Baird, Dr. R. H. Denniston, Dr. G. M. Smith, and Dr. G. E. Nichols. For much assistance in collecting, I wish to thank Professor Juday and Mr. L. E. Noland.

## DESCRIPTION OF LAKE

Green Lake is a roughly oval body of water, seven and one-half miles in length and from one to two miles broad. It is 66 meters deep at its west end,—by far the greatest depth recorded for any Wisconsin lake. The east end is somewhat shallower. Its waters are cool, clear (compared, for instance, with those of Mendota), and of the bright tint which gives the lake its name. The color of

---

<sup>1</sup>This investigation was made in cooperation with the U. S. Bureau of Fisheries, and the results are published with the permission of the Commissioner of Fisheries.

the water is best seen on cloudy days; but even at other times, when most lakes reflect the blue of the sky, the surface of this lake is often a bright green. The same color is very noticeable when one is beneath the surface. The lake floor is in most places covered with a fine marl.

These conditions afford an interesting comparison with those in Lake Mendota. The waters of the latter are less transparent and warmer than those of Green Lake, and the bottom is of mud. There are striking differences in the underwater vegetation of the two lakes, which may be correlated to some extent with these environmental differences.

Various types of shore are found in different parts of Green Lake. Along most of the north side of the lake the land ends in smooth boulders of considerable size, behind which the shore slopes steeply upward for a short distance (fig. 1). A beach of smaller stones runs out a considerable distance beneath the water. Towards the northwest corner of the lake rises the hill known as Sugar Loaf (see the accompanying map), whose steep sides descend below the surface of the water at almost the same pitch, broken only by a narrow rocky beach at the water's edge. The opposite shore of Norwegian Bay, and a long stretch of the south shore of the lake (fig. 2), descend even more steeply into the water, and consist largely of more or less sheer rock walls. At both ends of the lake are wide sandy beaches, backed by gently rising meadows. Finally, at the mouths of the various streams that enter the lake, and around the outlet in Dartford Bay, there are extensive swamps and marshes (fig. 3). At the head of Norwegian Bay is found a muddy bog.

In general the shore line is very similar to that of Mendota, with the difference that the sandy beaches of the latter are much more extensive.

As in Mendota, the shore line is paralleled by a belt of submerged attached plants, extending in an unbroken line all around the lake. In Green Lake, however, this flora differs widely in nature and distribution from that of Mendota. The wide sandy beaches are not nearly so well covered. The rocks of the shore are nearly destitute of the tufts of *Cladophora* that are so characteristic of Mendota. The main axis of the lake lies parallel to the southwest winds that prevail in summer, and the consequent vigorous action of the waves is perhaps partly responsible for these

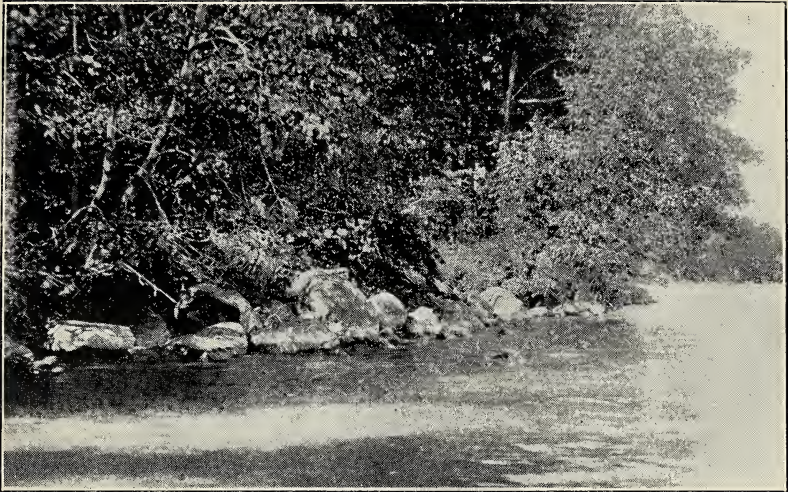


FIG. 1. A boulder-covered shore. Malcolm Bay.



FIG. 2. Precipitous shore. Near Dickinson Bay.





FIG. 3. Marshy shore, covered with *Typha* and *Sagittaria*. Near Silver Creek.





facts. On the other hand, vegetation is very abundant in the deeper waters, and descends to a greater depth than in Mendota.

Besides the main plant belt, consisting entirely of submerged plants, there are near the marshy shores regions well populated with emersed and floating forms, which merge gradually into the flora of the swamps themselves.

#### METHODS

The apparatus was the same as that used on Mendota. The various stations for collecting were reached by means of a rowboat equipped with a detachable motor. An iron frame, half a meter on a side, was let down to the bottom, and all plants falling within the area thus limited were gathered. Depths up to 3 meters were reached by ordinary diving. Collections in deeper water (up to 10 meters) were made by means of a diving hood, supplied with air by a hand pump in the boat. This device permitted almost as intimate an acquaintance with submerged plants in their habitat as can be enjoyed with land plants in theirs. It was found possible to stay down from 15 to 20 minutes, and to explore a considerable portion of the lake floor. The water of Green Lake being comparatively clear and admitting a fairly bright light to these depths, this method of survey furnished an accurate idea of the kinds of plants present, the uniformity of their distribution, and the downward extent of the plant belt. It is interesting to note that the decrease in illumination is very rapid in water deeper than 8 or 9 meters. At 7 meters there is what seems to be fairly bright sunlight; at 10 meters one is almost in darkness.

A section of shore of uniform general characteristics usually has opposite to it a section of the plant belt of fairly uniform nature throughout. Stations were therefore chosen on the basis of the character of the beach, and of the shallow water flora. The number of stations that can be made in this way of course depends largely upon convenience, since in many places the flora varies greatly within a small area (for instance, in the densely populated Stations 1 and 2). The plant belt was divided into 38 stations, with 3 additional stations representing the marshy bays. This was about the smallest number which would fairly represent every type of vegetation and at the same time include the whole circumference of the lake; it would not have been possible to collect thoroughly from a larger number. The stations used are shown by number on the map (fig. 4).

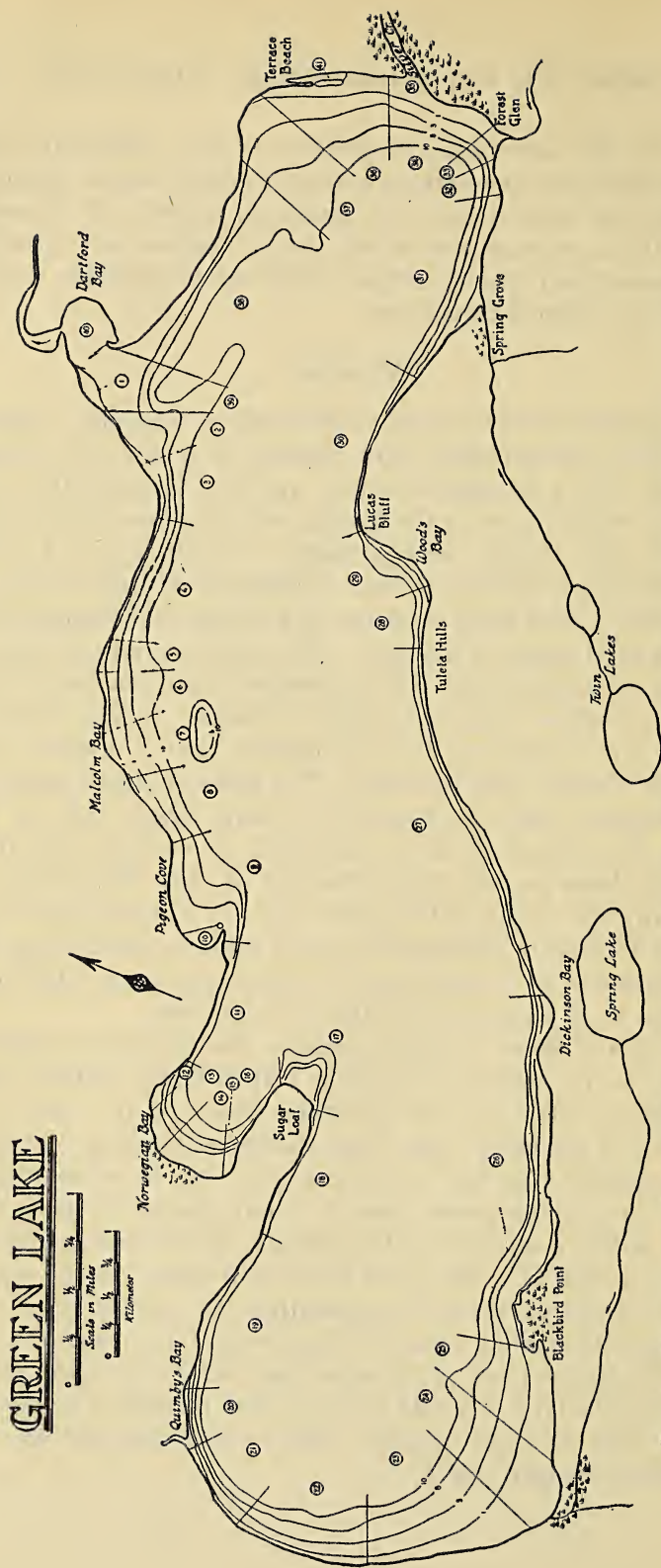


FIG. 4. Map of Green Lake showing 1, 3, 5, and 10 meter contour lines and the 41 stations from which plants were collected.

Experience with Lake Mendota profited to make the collection more systematic and more evenly distributed. An effort was made to collect from every region at the time of flowering, thus obtaining nearly the greatest weight attained by the plants, and making quantitative comparisons between different species and different localities more valuable. Plants in shallow water flower first; the time of flowering varies directly with the depth of the water. The early summer was therefore spent in collecting samples from the shallow water of the lake; then collections were made in water of medium depth; finally the deepest flora was sampled, using the diving hood. In the latter case it was not possible in the time remaining to visit all the stations; but this does not seriously impair the accuracy of the results, for the flora is more uniform in deeper water and the plant belt might here be divided into fewer stations. One station was therefore taken as representative of a group of several adjacent ones.

Because of the previous experience in this method of collecting it was possible, in spite of much stormy weather, to collect a larger number of samples than in Mendota—309 as against 221.

It soon became evident that the character of the flora varied at different depths. For convenience in handling the data, the plant belt was divided, as in Mendota, into three zones, within each of which the flora may be taken as fairly uniform, but between which there are great differences. The limits of the zones were the same as those used in Mendota, namely: Zone 1, 0–1 meter; Zone 2, 1–3 meters; Zone 3, 3 meters to the deepest limit of plant growth.

Samples were brought back to the lakeside laboratory (improvised from a boathouse), and there each was separated into its component species, the latter being numbered as sub-samples. These were weighed and spread out to dry. When air-dry, the smaller ones were dried in an oven at 60°C. for 48 hours. A few trials served to show that loss of water beyond this point was negligible.

From the wet and dry weights of a number of samples was obtained the percentage of moisture of each species. About twelve determinations were made for each species and averaged. In many cases, differences between the averages of different species were not significant, as shown by their probable errors; such species were therefore averaged together and considered as having the same percentage of moisture. Between some species, however, there were marked differences. The values for all species are shown

in table 2. It is curious that the plants of Green Lake show in all cases a slightly higher percentage of water than those of Mendota, although the method of determination was as nearly as possible the same in both cases.

#### THE FLORA

A list of the species collected is given in table 1.

Most of the genera are the same as those found in Mendota. There are more species of *Potamogeton* in Green Lake and a few genera not reported in Mendota. The list given does not pretend to include all of the species present in the lake; it shows only the predominating ones. Identification of rare forms was not thought to be of value in a quantitative study. Some other species may therefore be included in the quantitative data, among the ones named, with those they resemble most closely.

The dominant plant is *Chara*,—which in Mendota forms only a small fraction of the total vegetation. *Chara* grows almost everywhere in Green Lake, sometimes mixed with other plants, often forming great masses in which no other form can get a foothold.

*Radicula aquatica* deserves special mention. This plant was found only in two places (see table 4). It is usually described as having two kinds of leaves, the immersed ones pinnately dissected into capillary divisions, the emersed entire, serrate, or pinnatifid. In Green Lake the plant seems never to reach the surface and flowers were not observed; yet there are these two sorts of leaves, both under water (it was collected at a depth of two or three meters). The shape of the leaves would seem, therefore, not to be determined directly by the medium in which it grows. It may be conditioned by the intensity of the light.

*Drepanocladus pseudo-fluitans*, a moss, not collected in Mendota, grows in deep water at low temperatures, and in a few places forms immense mats or beds of close-growing stems and leaves, into which one may sink to the knees. Apparently it does not fruit in the lake, but depends wholly upon vegetative methods of reproduction.

*Castalia* is found in large quantities in Dartford Bay and the outlet and in the little bay behind Terrace Beach (Station 41). *Nymphaea* occurs at the other end of the lake, behind Blackbird Point; but in the open water of the marshes through which runs

the small stream that enters the lake here, *Castalia* is abundant, and there is less *Nymphaea*.

The marshes at the southwest corner of the lake have a rich and varied flora. Here one finds *Bidens Beckii*, various species of *Typha*, *Sagittaria*, and many others. *Sagittaria latifolia* is found mostly on land or at the water's edge; *S. heterophylla*, with its long lance-shaped leaves easily mistaken for those of a *Carex*, grows half submerged in shallow water. There is a *Carex* growing in a similar situation, both here and in several other places; in its young stages it may be mistaken for *Vallisneria*.

All the swampy or boggy parts of the shore are fronted by bars some distance out from shore. These bars have the usual shallow water flora and in addition large patches of *Scirpus*, of which several species were observed.

The attached algae form a smaller percentage of the total yield of the lake than they do in Mendota, owing chiefly to the comparatively small quantity of *Cladophora*. This plant, when present, is found on rocks at the water's edge, or only a few inches beneath the surface. In many places it is replaced by a thin fringe of *Oedogonium*. In some of the muddier stations (for example, Stations 32 and 33), there are quantities of *Spirogyra*, attached both to the mud and to rocks. The blue-greens, of which *Nostoc* and *Rivularia* were collected, are attached to the rocks near the shore and to the stems and leaves of many of the other plants, especially to the species of *Potamogeton*. *Vaucheria tuberosa* was found in one place (Station 37) in fairly deep water,—6.5 meters, averaging as high as 200 grams per square meter (wet weight) over a small area. It has been described as growing in a similar location in Lake George, N. Y., by Miss E. Moore (1).

As already indicated, the plant belt extends down to 8 meters beneath the surface, much deeper than that of Mendota. This is probably due largely to the greater transparency of the water. At the water's edge, there is, in all except the marshy places, a zone of rocks almost barren of plants. In Mendota, where a similar rocky beach exists, it is almost always densely covered with *Cladophora*. In Green Lake there are occasional patches of *Cladophora*, frequently a thin strip of *Oedogonium*, and here and there isolated plants of *Myriophyllum* arising from between the rocks. Outside of the border of rocks there is sometimes a thin strip of mud or sand bearing small, scattered plants, usually *Chara*, *Naias*, and *Heteranthera*. Here the water is about 1 meter in depth and this

is the limit of Zone 1. From this point the bottom falls away more or less gently to about 6 meters, the flora passing from that included in Zone 2 to that characteristic of deeper water. At about 6 meters the slope usually becomes much steeper and the outer strip of vegetation hangs, as it were, to the brow of a hill. The plants often cease quite sharply at 8 meters, as if an invisible boundary were holding them in check; on one side they rise two or three meters high, and packed closely together; on the other side there is nothing but the smooth mud sloping away towards the bottom of the lake.

In many places, however, the slope continues gentle to a much greater depth; in these cases the vegetation does not come to a sudden end, but thins out gradually down an imperceptible slope. In one such station (25) plants were found growing at a depth of 10 meters, though small and stunted in growth. Such gently sloping places are found around the entire west end of the lake, opposite Woods Bay, at Forest Glen, and thence up to Dartford Bay. In the west end of the lake and in parts of the east end, this gentle slope occurs in connection with wide sandy beaches. Figures 5 and 6 show the difference between these two sorts of stations.

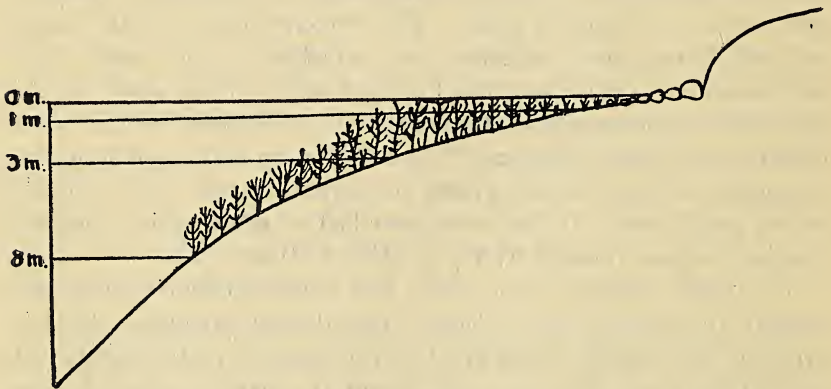


FIG. 5. Diagram of portion of lake floor bearing attached plants. Medium slope.

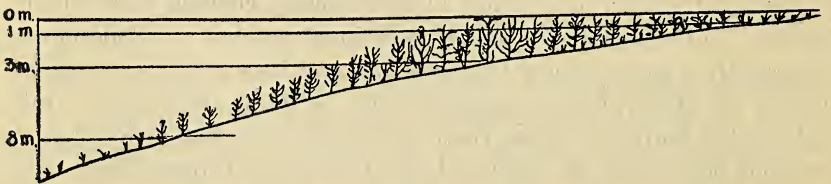


FIG. 6. Diagram of portion of lake floor bearing attached plants. Gentle slope.

In a few stations there is no flattening out from 1 to 6 meters, but the bottom drops steeply beneath the water (Stations 16 and 30). In these cases the vegetation extends only to 4 or 5 meters beneath the surface. This condition is represented in figure 7.

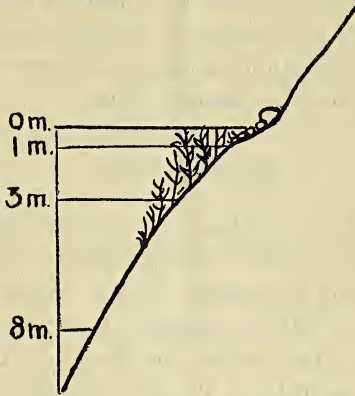


FIG. 7. Diagram of portion of lake floor bearing attached plants. Steep slope.

There is a certain degree of correspondence between the type of shore, the slope of the lake floor, and the vegetation. The type of slope represented in figure 5 is the most common, and is found opposite rocky shores of all sorts, such as those shown in figures 1 and 2. The steeper the shore, the steeper the slope of the bottom. The second kind of slope (figure 6) corresponds to low shores, either marshy or sandy (figure 3). The last type (figure 7) is found only opposite high land, such as Lucas Bluff and Sugar Loaf.

In Mendota it was found that there are well-defined patches of sand in various places, running into fairly deep water; and that some species were more or less limited to a sandy substrate, others to a muddy one. No such differentiation exists in Green Lake. The type of bottom is fairly uniform; it consists of a fine mud mixed with marl in deep water and with a small amount of sand in shallow water. The most important difference between stations is the presence or absence of rocks. Yet there is great regional variation in the vegetation, and although this cannot be correlated with any visible soil difference, it is probable that chemical analysis of soil from different places would tell a different story. In the few places where there are distinct sandy beaches, such as are more common in Mendota, these are not nearly so well covered with

plants as in the latter lake, nor, indeed, so well as are the muddier parts of Green Lake; nor do they display any species which do better there than on mud. The comparative scantiness of their vegetation may perhaps be explained by the violence of the waves in this lake; but it is interesting that species, such as *Potamogeton Richardsonii* and *P. pectinatus*, which grow decidedly better on sand in Mendota, attain their greatest development in Green Lake elsewhere than on these few sandy places.

#### CALCULATIONS

The data obtained by weighing the plants were treated in much the same way as in the case of Lake Mendota. The original weights obtained were reduced to common terms—grams per square meter—for each sample and all the samples in each zone of each station averaged together. The results are shown in tables 3, 4, and 5. The values for all the stations of each zone were then averaged, to give the weight per square meter of each species for each zone. Since the stations were of greatly differing sizes, it was judged best not to give them all the same weight in the average. One of the smallest stations was selected as a unit, and the other stations expressed in terms of this. The average weights in each station were multiplied by a factor for the station, its area in terms of the unit station, and the resulting figures averaged together, using the sum of all the factors as a divisor. The dimensions of the stations were obtained by measurement on the map. In Zone 1, for instance, the area of Station 23 was found to be 9, that of Station 36 was 6, Station 1 being the unit. The results of these calculations are given in table 6.

There were several plants that did not form part of the main plant belt, being found in scattered patches, and yet were present in considerable quantities. Such were *Scirpus*, *Carex*, *Castalia*, *Nymphaea*, and *Cladophora*. Of the first four of these, samples were collected in the usual way; the area of the particular spot sampled was estimated, in most cases by rowing around it and expressing it in terms of boat-lengths. From these data total weights were obtained directly. The same method was used for *Cladophora* in some cases, where there were large patches. In most cases, the fringe of *Cladophora* being thin, all of the growth for a certain distance was cleaned off, and measurement made of the length (instead of the area) of the strip or station from which



the sample came. The sample was converted to grams per meter, and this value multiplied by the length of the strip to give the total weight. The details of the data on these scattered plants are presented in table 7.

The areas of the different zones were measured on the map by means of a planimeter; these figures being checked up with data obtained by the Survey at other times. By multiplying the average weights of species (table 6) by the appropriate area, the total weight of each species in each zone was determined. These figures, together with those for the scattered plants (table 7) are shown in tables 8, 9, and 10. Total weights of the species for the whole lake flora were obtained by adding together the values for the three zones. These are given in table 11. In each case the total weight of a species is expressed also as a percentage of the total weight of all plants in the zone under consideration.

From tables 8, 9, and 10, table 12 was prepared. It shows the relative amounts of each species found at each depth, expressed as a percentage of the total weight of the species.

Table 13 summarizes the results shown in tables 6 and 11 and shows the average yield for each zone and for the lake as a whole, expressed in various units. The averages for the separate zones are the same as those in table 6, and hence disregard the weights of the scattered plants. The latter, however, are included in the average for the lake as a whole.

#### QUANTITATIVE RESULTS

The 309 samples, when divided into their species, gave 1,380 subsamples. This is an average of 4.5 species per sample,—which is nearly equivalent to 4.5 species per square meter. The corresponding value in Lake Mendota is only 3.5. Samples containing as many as twelve species were not uncommon in Green Lake, but a large number consisted of only one or two species.

The average yield of Green Lake is much smaller than that found for Mendota. Whether this would hold all seasons is, of course, unknown. The area of the plant zone is also less than that of Mendota, the total yield being, therefore, very much smaller in Green Lake.

The greatest difference between the two lakes is in the shallow water flora. In Green Lake Zone 1 is only a little more than one-third the area of that in Mendota. Its yield per unit area is less than one-third. The total yield is, therefore, very much less.

Zone 2 is of approximately the same size in both lakes, but has a considerably higher yield in Mendota. Zone 3, on the other hand, is slightly larger in Green Lake, and considerably more productive. Putting the facts in a different way, in Green Lake, about 9 per cent of the vegetation is in water less than 1 meter deep, about 40 per cent between 1 and 3 meters, and more than 50 per cent between 3 and 8 meters (table 12); whereas in Mendota 30 per cent is found in the shallowest water, 45 per cent between 1 and 3 meters, and only 25 per cent in water deeper than 3 meters.

About one-half of the entire vegetation (dry weight) is composed of *Chara* (table 11). In shallow water (table 3), this is everywhere fairly abundant except at the east end of the lake where the bottom is muddy (in the other swampy places there seems to be more sand mixed with the mud). It is most frequently associated with *Potamogeton heterophyllus* and small amounts of *Naias*; often it is mixed also with *P. pectinatus*, *Heteranthera*, and *Vallisneria*. In Zones 2 and 3 (tables 4 and 5), the distribution of *Chara* is about the same as in Zone 1, but it is usually mixed with most of the other species. Where it occurs unmixed, it is present in very great abundance. One sample of *Chara*, gathered from 0.25 square meter, weighed 2,700 grams (wet).

The various species of *Potamogeton* form about 20 per cent of the total flora. *Potamogeton* occurs abundantly in shallow water only in a few stations of different characteristics. In Zone 2, however, it thrives everywhere except for a few stations along the north and west shores. Restriction of *Potamogeton* in these places may be due to greater wave action. The shores here are of the type shown in fig. 1. In the northwest corner of the lake, *Potamogeton* is for some reason almost entirely replaced by *Drepanocladus*, here present in great quantity. In the deepest zone, species of *Potamogeton* are not abundant, except *P. zosterifolius*.

*Ceratophyllum* and *Myriophyllum* rank next in importance, each forming about 10 per cent of the vegetation. The former is found in abundance only in Zone 3, and is there universal. The distribution of *Myriophyllum* is similar, but its range is slightly shallower; it is found more commonly than *Ceratophyllum* in Zone 2 and does not extend down quite so far as the latter plant (table 12). A visit to the bottom 7 or 8 meters below the surface reveals a forest of almost pure *Ceratophyllum*; whereas at 5 or 6 meters, while the general appearance of things is the same, the vegetation is about half *Myriophyllum*.

*Potamogeton pectinatus* also forms about 10 per cent of the total weight of plants. It is distributed unevenly, but is locally very abundant. Elodea, Vallisneria, Drepanocladus, Scirpus, and *Potamogeton zosterifolius* each form between 2 and 10 per cent and all other species less than 2 per cent each.

In Mendota the situation is entirely different. Chara forms a negligible fraction of the vegetation. Vallisneria almost takes its place, composing about one-third of all the plants. Several species of *Potamogeton* bulk large,—*P. amplifolius* about 25 per cent, *P. Richardsonii* 10 per cent, *P. pectinatus* 8 per cent. Taken together the species of *Potamogeton* total about 50 per cent. *Myriophyllum* forms only 4 per cent of the total and *Ceratophyllum* still less.

It has been remarked already that both *Myriophyllum* and *Ceratophyllum* are deep water plants, as far as Green Lake is concerned; this may explain their relative scarcity in Mendota, where the whole deep flora is so much less luxuriant. The other differences, however, must be attributed to various factors. Temperature may perhaps hold down the *Vallisneria* in Green Lake, wave action the shallow water *Potamogetons*, and soil differences perhaps account for the immense development of Chara.

The distribution of species according to depth is well marked in some cases, in others less so. The cases of *Ceratophyllum* and *Myriophyllum* have been dealt with already. In Mendota the greater part of these plants is found in Zone 2. *Vallisneria* reaches its greatest abundance in Zone 2 in both lakes, but is hardly found in Zone 3 in Green Lake, while in Mendota about 25 per cent of it is found in deep water. *Ranunculus* reaches deeper water in Green Lake, half of it being found in Zone 2, and one-fourth in Zone 3; in Mendota it is confined to Zone 1. The same is true of Chara, which is nearly evenly distributed between Zones 2 and 3 in Green Lake, and between Zones 1 and 2 in Mendota. *Potamogeton amplifolius* and *P. zosterifolius* are similarly distributed in both lakes; but *P. Richardsonii* and *P. pectinatus* are found mostly in deeper water in Green Lake, while in Mendota their greatest growth occurs in Zone 1.

The final averages and totals of course conceal a great deal of regional variation. The varying characters of different stations may be seen in tables 3, 4, and 5, which present the stations separately. Two general kinds of stations may be distinguished. In one the vegetation is not very rich and is composed mostly of

Chara, with small amounts of *Potamogeton heterophyllus*, Naias, and Vallisneria; the other contains great quantities of the larger Potamogetons, often in addition to large amounts of Chara. The shallow water is most often of the first type. The deeper water is of the latter sort, grading out into almost pure Ceratophyllum and Myriophyllum. The medium depths vary the most. The species of Potamogeton often grow in great abundance mixed with Chara, Ranunculus, and others. Chara, as already mentioned, frequently grows alone in large patches. Drepanocladus also, in the few places where it attains abundance, grows in large patches almost unmixed with other plants, except that scattered stems of Myriophyllum are often found arising from it. There are in several stations absolutely barren patches irregularly distributed amidst luxuriant vegetation.

In some places samples of great weight were obtained. The largest came from Station 21, and yielded 2,700 grams (wet) from 0.25 square meter. There were several others almost as big. They were composed for the most part of Chara. There is, as far as I know, no single spot in Lake Mendota which yields as much as this. The smallest sample collected weighed 30 grams (wet) from 0.5 square meter. Most of the samples weighed about 200 to 300 grams (wet) from 0.25 square meter. In Mendota the general average was somewhat higher.

#### GENERAL DISCUSSION

Aside from its presentation of the quantitative data, this paper cannot do much more than suggest the ecological problems that await the botanist in this field. Pearsall (2) has attacked similar questions in the English lakes and in an excellent paper presents important evidence on the nature of the environmental factors that affect submerged vegetation. He considers that light is important only insofar as it limits the downward extension of the flora and that temperature has little effect in determining the kind of vegetation, at least within the limits found in one lake. Most of the variation in the kind of vegetation proves to be connected with soil differences, which often correspond to differences in their physical characteristics.

Nothing has as yet been done on Wisconsin lakes which is comparable to Pearsall's correlation of soil composition and type of vegetation. With regard to the other factors, light and tempera-

ture, there are abundant records from many Wisconsin lakes, which have been made available to me by Professor Juday. A brief comparison of Green Lake and Lake Mendota serves to bring out several interesting points.

The degree of transparency of the water was measured by means of a white disc, 10 centimeters in diameter, which was lowered into the water until it disappeared from view; the depth at which this occurred being recorded. This depth in Green Lake varied from 2.75 to 6.25 meters, the average being about 4.25 meters, during June, July and August. In Mendota, the range during the same months of the same year was from 1.75 to 3.8 meters, the average about 2.25 meters. When these figures are compared with the downward limits of the plants in the two lakes, it is evident that they confirm Pearsall's statement that light is a limiting factor in this respect; and, further, make it probable that it is the chief limiting factor.

Pearsall also showed, by an iodine method of measuring the light intensity, that plants grew in as little as 2 per cent of the light of the surface, but not in less. According to some figures kindly supplied me by Dr. E. A. Birge, the light intensity in Green Lake is reduced to 1 per cent of that at the surface at a depth of about 8 meters. The same light intensity in Mendota is found at a depth of about 4 meters. These depths correspond approximately with the limits of the plant zone in each case. Birge's determinations were made in an entirely different way from those of Pearsall, which may partially account for the discrepancy between the two sets of results.

With regard to temperature, table 14 shows the differences between Green Lake and Lake Mendota. The figures are averages of readings taken through June, July, and August. These differences in temperature evidently are not large enough to limit the plant zone, since plants grow in Green Lake in water 6°C. cooler than that at which they cease in Mendota; the temperatures at corresponding depths are also lower in Green Lake. It seems that the lower temperatures of Green Lake may partly account for the smaller productivity of its bottom by retarding the growth of plants to a slight extent.

The effect of low temperatures and low light intensity in retarding growth is illustrated by the reduced stature of plants in deep water. Most submerged plants flower at or near the surface. This is especially true of such plants as *Potamogeton*, *Vallisneria*, and

Ranunculus. Teleologically speaking, the plants in the deepest water should grow the tallest so as to obtain more light for the manufacture of food and for the formation of flowers and fruits. An "adaptation" to this effect has, however, not been provided by Nature. Plants growing 7 or 8 meters below the surface reach heights of 1 or 2 meters, those in deeper water still less; while those which are but 3 or 4 meters deep frequently reach the surface. These conditions are illustrated in figures 5 and 6.

Another interesting point in this connection is that in Green Lake many instances were observed of plants flowering before they reached the surface, even when they were growing in fairly shallow water. In Mendota this was not noticed, and indeed some of the larger plants grew 5 or 6 meters to the surface before they flowered. These facts suggest that there is a minimal light intensity for the production of flowers, which is of course realized further beneath the surface in Green Lake than in Mendota; so that in the latter lake some plants remain vegetatively active for a longer period and finally grow to reach the surface, in spite of the retarding effects of low temperature and low light intensity. Different plants probably vary in this respect. The whole argument does not, of course, concern such plants as *Ceratophyllum*, which regularly produces flowers under water.

## LITERATURE CITED

1. Needham, James G., Chancey Juday, Emmeline Moore, Charles K. Sibley, and John W. Titcomb. A biological survey of Lake George, N. Y. State of New York, Conservation Commission. 1922.
2. Pearsall, W. H. The aquatic vegetation of the English lakes. *Jour. Ecol.* 8: 163-199. 1920.
3. Rickett, H. W. A quantitative study of the larger aquatic plants of Lake Mendota. *Trans. Wis. Acad. Sci., Arts, and Let.* 20: 501-527. 1922.

TABLE 1. *List of plants collected.*

Submerged plants, forming main plant belt.

1. *Ceratophyllum demersum* L.
2. *Chara* sp.
3. *Drepanocladus*.
4. *Elodea canadensis* Michx.
5. *Myriophyllum verticillatum* L. var. *pectinatum* Wallbr.
6. *Najas flexilis* (Willd.) Rostk. & Schmidt.
7. *Potamogeton amplifolius* Tuckerm.
8. " *foliosus* Raf.
9. " *heterophyllum* Schreb.

- 10.        "        natans L.
  - 11.        "        pectinatus L.
  - 12.        "        Richardsonii (Benn.) Rydb.
  - 13.        "        zosterifolius Schumacher.
  - 14. *Radicula aquatica* (Eat.) Robinson.
  - 15. *Ranunculus aquatilis* L. var. *capillaceus* DC.
  - 16. *Vallisneria spiralis* L.
  - 17. *Heteranthera dubia* (Jacq.) MacM.
- Emerged or floating plants, growing in scattered patches.
- 18. *Bidens Beckii* Torr.
  - 19. *Carex* sp.
  - 20. *Castalia odorata* (Ait.) Woodville & Wood.
  - 21. *Lemna trisulca* L.
  - 22. *Nymphaea advena* Ait.
  - 23. *Sagittaria heterophylla* Pursh.
  - 24.        "        *latifolia* Willd.
  - 25. *Scirpus* spp.
  - 26. *Typha* sp.
  - 27. *Zizania aquatica* L.
- Attached algae.
- 28. *Cladophora* sp.
  - 29. *Nostoc* sp.
  - 30. *Oedogonium* sp.
  - 31. *Rivularia* sp.
  - 32. *Spirogyra* sp.
  - 33. *Vaucheria tuberosa*.

TABLE 2. *Percentage of water in plants.*

Species	Per Cent of Water
<i>Ceratophyllum</i> .....	92.9
<i>Chara</i> .....	84.9
<i>Drepanocladus</i> .....	81.1
<i>Elodea</i> .....	92.9
<i>Myriophyllum</i> .....	90.2
<i>Najas</i> .....	90.2
<i>Potamogeton</i> (all spp.).....	88.1
<i>Ranunculus</i> .....	88.6
<i>Vallisneria</i> .....	92.9
<i>Heteranthera</i> .....	90.2
<i>Scirpus</i> .....	88.6
<i>Cladophora</i> .....	89.2
Average.....	89.2





TABLE 3—Continued

Species:	Stations											
	22	23	24	25	28	30	31	33	35	36	39	41
1									50.0 3.6			987.0 70.0
2	200.0 30.1	358.0 54.0	153.0 23.1	54.0 7.8	315.0 48.4	x				160.0 34.0	260.0 39.2	
4												x
5			23.0 2.0									193.0 18.9
6	x	x	3.0 0.3	x	10.0 1.0	20.0 2.0			14.0 1.4		x	x
7												240.0 28.5
8					x				x			
9	20.0 2.4	131.0 15.6	123.0 17.2	18.0 2.1	150.0 17.8						370.0 48.4	
10			53.0 6.4		35.0 2.8							293.0 34.7
11	13.0 1.5	49.0 5.8	37.0 4.4		70.0 8.4				400.0 67.2	80.0 9.6		133.0 15.9
12		26.0 3.6			10.0 1.2							
13												493.0 61.6
15			50.0 4.7									x
16		28.0 2.0	237.0 16.8		65.0 4.5				310.0 28.2			
17			30.0 2.9		245.0 24.6	220.0 16.0	100.0 9.0	200.0 18.1	20.0 2.0			

TABLE 4. *Yield by stations, Zone 2, stated in grams per square meter. For explanation see heading of table 3.*

Species:	Stations											
	2	3	4	5	6	7	8	9	10	11	12	
1.....	625.0 44.4	20.0 1.5	10.0 0.7	100.0 6.6	..... .....	493.0 35.0	..... .....	..... .....	..... .....	..... .....	x .....	20.0 1.5
2.....	50.0 8.6	193.0 29.2	330.0 49.8	140.0 21.2	3980.0 601.0	107.0 18.6	1800.0 274.8	4100.0 619.0	310.0 44.7	540.0 81.6	4387.0 662.3	.....
3.....	.....	.....	.....	20.0 3.8	.....	.....	.....	.....	.....	.....	.....	.....
4.....	85.0 5.9	x	x	20.0 1.4	100.0 7.0	x	.....	.....	.....	.....	.....	200.0 23.9
5.....	800.0 78.4	100.0 9.5	.....	.....	.....	93.0 9.1	.....	.....	.....	.....	.....	x
6.....	10.0 1.0	280.0 30.0	60.0 5.8	120.0 11.6	90.0 8.8	40.0 3.8	x	6.0 0.6	5.0 0.5	60.0 6.0	x	.....
7.....	280.0 29.3	.....	.....	250.0 22.4	.....	170.0 29.2	.....	.....	20.0 2.4	.....	.....	.....
8.....	40.0 4.8	x	.....	x	.....	x	.....	.....	x	x	.....	.....
9.....	x	233.0 18.0	145.0 17.3	x	10.0 1.2	3.0 0.4	.....	20.0 2.4	80.0 9.5	.....	.....	7.0 0.7
10.....	70.0 10.2	.....	.....	170.0 20.2	.....	17.0 2.0	.....	.....	175.0 20.8	.....	.....	40.0 5.1
11.....	55.0 6.6	37.0 4.5	.....	700.0 83.2	70.0 8.4	150.0 17.8	.....	.....	5.0 0.5	60.0 7.2	133.0 16.5	.....
12.....	150.0 16.6	67.0 8.0	.....	.....	.....	153.0 18.1	.....	.....	55.0 8.0	.....	.....	.....
13.....	120.0 15.8	x	x	150.0 16.4	.....	247.0 29.4	.....	.....	.....	x	167.0 19.9	.....
14.....	180.0 18.0	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
15.....	x	7.0 0.8	.....	20.0 2.2	x	100.0 9.0	.....	.....	10.0 1.1	.....	.....	100.0 10.5
16.....	250.0 17.7	7.30 7.1	60.0 5.7	190.0 13.4	.....	40.0 2.8	.....	.....	x	.....	.....	.....
17.....	.....	.....	.....	.....	120.0 11.8	3.0 0.3	.....	.....	75.0 7.3	.....	.....	.....

TABLE 4—Continued

Species:	Stations											
	13	14	15	16	17	18	19	20	21	22	23	
1.....	7.0 0.5	23.0 1.7			23.0 1.7							x
2.....	83.0 12.6	2175.0 326.5		980.0 148.0	1066.0 209.2	520.0 78.4	967.0 145.9	890.0 134.2	1564.0 235.0	1107.0 167.2	400.0 60.4	
3.....	27.0 5.1	x			x		x	1400.0 260.2	460.0 89.4	547.0 89.6		
4.....		9.0 0.7							x		13.0 0.9	
5.....	23.0 2.3	884.0 78.1	x	x	44.0 4.4			650.0 63.8	20.0 2.0	x	x	
6.....	13.0 1.3	2.0 0.2	150.0 12.2	8.0 0.8	13.0 1.3		60.0 5.9		72.0 7.2	x	4.0 0.4	
7.....	137.0 16.3				60.0 7.1							
8.....	x	x	80.0 4.6		3.0 0.4				20.0 3.3		x	
9.....	5.0 0.5	90.0 8.7			x		53.0 6.1		60.0 8.2	x	87.0 8.4	
10.....	13.0 1.6	20.0 2.7			17.0 2.0						13.0 1.6	
11.....	1433.0 170.5	250.0 29.7	650.0 77.4		417.0 49.6		53.0 6.4		12.0 1.4		733.0 87.2	
12.....	30.0 6.3	30.0 6.6	200.0 22.4		47.0 5.5		53.0 6.4		x			
13. ...	33.0 4.0	58.0 7.8	150.0 15.8		198.0 23.5				4.0 0.5		7.0 0.8	
14.....												
15.....	x	x			x		40.0 4.8		12.0 1.8			
16.....	110.0 7.7		1160.0 58.8		467.0 32.9		7.0 0.4		20.0 1.4		13.0 0.9	
17.....						20.0 2.0						

TABLE 4—Continued

Species:	Stations										
	24	25	26	27	28	29	30	31	32	33	34
1.....	2.0 0.2	4.0 0.2	180.0 12.7	5.0 0.3	73.0 5.2	.....	63.0 4.4	380.0 27.4	240.0 17.2	117.0 9.4	.....
2.....	163.0 24.5	844.0 127.4	205.0 31.0	183.0 27.5	673.0 130.4	840.0 126.8	420.0 63.2	20.0 3.1	320.0 48.4	29.0 4.3	37.0 5.5
3.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
4.....	.....	.....	25.0 3.3	.....	.....	.....	.....	.....	.....	x	.....
5.....	8.0 0.8	x	950.0 93.1	.....	13.0 1.3	.....	90.0 8.9	x	80.0 8.0	29.0 2.8	.....
8.....	5.0 0.5	6.0 0.6	15.0 1.5	38.0 3.7	27.0 2.7	20.0 2.0	83.0 7.9	20.0 2.0	20.0 2.0	23.0 2.2	x
7.....	.....	4.0 0.5	40.0 4.8	.....	40.0 5.6	.....	20.0 2.3	x	.....	26.0 2.5	.....
8.....	.....	.....	x	x	67.0 8.0	.....	115.0 14.1	187.0 22.3	x	14.0 1.7	.....
9.....	125.0 15.3	8.0 0.9	.....	30.0 4.6	100.0 14.8	100.0 12.0	70.0 9.8	.....	.....	60.0 7.1	12.0 1.4
10.....	13.0 1.5	36.0 4.2	.....	.....	380.0 55.3	.....	70.0 8.4	27.0 2.8	.....	11.0 1.3	.....
11.....	98.0 11.2	4.0 0.5	160.0 19.0	55.0 6.5	407.0 48.4	.....	20.0 2.4	20.0 2.4	x	220.0 15.2	.....
12.....	70.0 8.4	.....	.....	300.0 35.7	80.0 9.6	.....	33.0 4.5	247.0 29.3	.....	6.0 0.7	.....
13.....	3.0 0.3	.....	8.0 1.0	.....	134.0 14.9	.....	95.0 11.3	67.0 11.3	.....	94.0 11.2	.....
14.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
15.....	.....	26.0 3.0	.....	8.0 0.9	13.0 1.5	.....	75.0 7.8	100.0 8.9	x	31.0 3.6	.....
16.....	85.0 3.6	88.0 6.2	.....	13.0 0.9	60.0 4.3	.....	80.0 5.7	247.0 17.2	.....	66.0 4.1	x
17.....	.....	.....	.....	90.0 8.8	27.0 2.7	.....	183.0 17.9	287.0 30.1	220.0 21.6	283.0 24.2	.....

TABLE 4—Continued

Species:	Stations				
	36	37	38	39	40
1.....	10.0	76.0	.....	724.0	270.0
	0.7	5.3	.....	50.9	18.4
2.....	298.0	140.0	237.0	1844.0	x
	44.9	21.1	35.7	322.9	.....
3.....					
4.....		8.0	.....	118.0	.....
		0.5	.....	9.3	.....
5.....	5.0	260.0	.....	311.0	117.0
	0.5	23.7	.....	30.4	11.4
6.....	x	60.0	5.0	9.0	3.3
		5.9	0.5	0.6	0.3
7.....		40.0	.....	16.0	430.0
		4.8	.....	1.9	51.2
8.....		120.0	.....	9.0	7.0
		14.3	.....	1.1	0.8
9.....	15.8	12.0	12.0	49.0	.....
	1.8	1.4	1.5	6.0	.....
10.....		12.0	.....	44.0	203.0
		1.4	.....	5.3	21.0
11.....	8.0	x	.....	138.0	387.0
	0.9		.....	16.7	46.9
12.....		8.0	.....	33.0	23.0
		1.0	.....	5.0	2.8
13.....		300.0	.....	209.0	230.0
		35.7	.....	24.9	27.7
14.....					
15.....				27.0	x
				3.0	.....
16.....	3.0	468.0	.....	49.0	2083.0
	0.2	33.2	.....	3.5	145.0
17.....	x	24.0	.....	x	143.0
		2.4	.....		14.1



TABLE 5—Continued

Species:	Stations									
	23	25	26	27	28	29	31	33	34	36
1.....	188.0 13.5	16.0 1.1	180.0 12.7	313.0 22.3	35.0 2.5	193.0 13.7	1490.0 105.7	1093.0 77.6	460.0 32.8	113.0 7.9
2.....	792.0 119.5	995.0 151.2	205.0 31.0	13.0 2.0	x .....	47.0 7.2	.....	.....	.....	160.0 23.8
3.....	64.0 14.6	.....	.....	.....	.....	.....	.....	.....	.....	.....
4.....	44.0 3.1	115.0 10.5	25.0 3.3	607.0 43.2	x .....	.....	55.0 3.9	.....	.....	18.0 1.3
5.....	156.0 17.7	.....	950.0 93.1	47.0 5.3	484.0 57.1	220.0 31.6	1380.0 134.7	x .....	.....	18.0 1.7
6.....	.....	10.0 1.0	15.0 1.5	7.0 0.7	71.0 6.9	27.0 2.7	x .....	.....	.....	x .....
7.....	.....	.....	40.0 4.8	73.0 7.9	60.0 7.1	.....	10.0 1.2	45.0 7.9	340.0 40.4	.....
8.....	x .....	.....	x .....	x .....	65.0 7.3	4.0 0.5	x .....	.....	.....	20.0 2.4
9.....	.....	.....	.....	60.0 5.6	.....	.....	.....	.....	.....	.....
10.....	.....	.....	.....	.....	.....	.....	70.0 8.3	.....	.....	.....
11.....	616.0 73.3	.....	160.0 19.0	333.0 29.7	145.0 17.2	.....	236.0 26.2	x .....	.....	288.0 34.2
12.....	.....	.....	.....	27.0 2.4	15.0 1.3	.....	.....	.....	.....	.....
13.....	12.0 1.4	20.0 2.4	8.0 1.0	47.0 5.6	74.0 8.9	354.0 44.4	103.0 12.3	1000.0 118.8	60.0 7.2	5.0 0.6
15.....	4.0 0.5	.....	.....	40.0 4.5	140.0 15.3	.....	x .....	.....	.....	.....
16.....	.....	.....	.....	.....	10.0 0.7	.....	x .....	.....	.....	.....
17.....	.....	.....	.....	x .....	465.0 45.8	53.0 4.7	.....	.....	.....	.....

TABLE 5—Continued

Species:.....	Stations		
	37	38	39
1.....	20.0 1.5	x	2460.0 174.7
2.....	67.0 10.0	10.0 1.2	
3.....	53.0 10.4		
4.....	7.0 0.4		513.0 34.8
5.....	x		587.0 56.8
6.....	40.0 3.9	20.0 2.0	
7.....			
8.....	153.0 14.9	x	x
9.....		x	
10.....			
11.....	53.0 6.4	370.0 48.8	
12.....			
13.....	40.0 5.7		60.0 8.5
15.....	7.0 0.8		47.0 5.3
16.....			
17.....			



TABLE 6. Average weights of species, stated in grams per square meter.  
(From tables 3, 4, and 5.)

Species	Zone 1		Zone 2		Zone 3	
	Wet	Dry	Wet	Dry	Wet	Dry
<i>Chara</i> .....	202	33.8	832	129.3	518	78.0
<i>Ceratophyllum</i> .....	28	2.0	114	8.1	429	29.7
<i>Drepanocladus</i> .....			35	6.1	15	3.0
<i>Elodea</i> .....			20	1.8	113	8.2
<i>Myriophyllum</i> .....	8	0.8	184	17.9	239	23.5
<i>Najas</i> .....	4	0.4	22	2.1	11	1.1
<i>Potamogeton amplifolius</i> .....	15	1.8	41	4.6	14	1.6
<i>Potamogeton foliosus</i> .....	4	0.4	12	1.4	21	2.2
<i>Potamogeton heterophyllum</i> .....	62	7.8	35	3.9	2	0.2
<i>Potamogeton natans</i> .....	18	2.2	26	3.1	1	0.1
<i>Potamogeton pectinatus</i> .....	52	6.8	158	18.3	171	20.5
<i>Potamogeton Richardsonii</i> .....	10	1.2	41	5.0	1	0.1
<i>Potamogeton zosterifolius</i> .....	13	1.6	48	5.8	69	7.9
<i>Ranunculus</i> .....	13	1.4	11	1.2	5	0.5
<i>Vallisneria</i> .....	52	3.9	125	8.4		
<i>Heteranthera</i> .....	29	2.7	27	2.6	3	0.3
Total.....	510	66.8	1,731	219.6	1,612	176.8

TABLE 7. *Weight of scattered plants.*

Species	Station	Area in Square Meters	Average Weight, Grams per Square Meter		Total Weight in Kilograms	
			Wet	Dry	Wet	Dry
<i>Scirpus</i> .....M	24	150,000	393	44.7	58,950	6,705
	25	255,000	867	102.9	221,085	26,265
	24 and 25	4,800	1,000	115.2	4,800	553
	34	3,685	2,000	228.0	7,370	840
	39	3,500	5,400	615.6	18,900	2,155
<i>Carex</i> .....	3	5,000	283	28.3	1,698	170
	24	25,000	23	1.2	575	30
	25	25,500	76	7.6	1,938	194
<i>Castalia</i> .....	40	25,000	960	81.6	24,000	2,040
<i>Nymphaea</i> .....	24	25,000	2,400	205.2	60,000	4,925
<i>Cladophora</i> .....	7	12.5	2,900	324.0	36	4
	24	1,125	100	10.8	113	4
		Length in Meters	Grams per Meter			
	1	700	220	23.8	154	17
	2	600	150	16.2	90	10
	4	1,000	14	1.4	14	1
	5	60	760	85.2	46	5
	7	25	35	3.8	1	.....
	16	600	50	5.4	30	3
	28	400	50	5.4	20	2
	30	1,200	100	10.8	120	13
	31	2,000	75	8.1	150	16
	32	300	60	6.5	18	2

TABLE 8. Total weight and percentage of each species in Zone 1 (0-1 meter).  
Area: 1.424 square kilometers. From tables 6 and 7.

Species	Kilograms		Per Cent	
	Wet	Dry	Wet	Dry
<i>Ceratophyllum</i> .....	39,900	2,900	3.6	2.1
<i>Chara</i> .....	287,600	48,100	26.1	35.1
<i>Drepanocladus</i> .....				
<i>Elodea</i> .....				
<i>Myriophyllum</i> .....	11,400	1,100	1.0	0.8
<i>Najas</i> .....	5,700	600	0.5	0.4
<i>Potamogeton amplifolius</i> .....	21,400	2,600	1.9	1.9
<i>Potamogeton foliosus</i> .....	5,700	600	0.5	0.4
<i>Potamogeton heterophyllum</i> .....	88,300	11,100	0.8	8.1
<i>Potamogeton natans</i> .....	25,600	3,100	2.3	2.3
<i>Potamogeton pectinatus</i> .....	74,000	9,700	6.7	7.1
<i>Potamogeton Richardsonii</i> .....	14,200	1,700	1.3	1.2
<i>Potamogeton zosterifolius</i> .....	18,500	2,300	1.7	1.7
<i>Radicula</i> .....				
<i>Ranunculus</i> .....	18,500	2,000	1.7	1.4
<i>Vallisneria</i> .....	74,000	5,600	6.7	4.1
<i>Heteranthera</i> .....	41,300	3,800	3.8	2.8
<i>Carex</i> .....	4,200	400	0.4	0.3
<i>Castalia</i> .....				
<i>Cladophora</i> .....	800	100	0.1	0.1
<i>Nymphaea</i> .....	60,000	4,900	5.5	3.6
<i>Scirpus</i> .....	311,100	36,500	28.2	26.2
<b>Total</b> .....	<b>1,102,200</b>	<b>137,100</b>	<b>100.0</b>	<b>100.0</b>

TABLE 9. Total weight and percentage of each species in Zone 2 (1-3 meters). Area: 2.905 square kilometers. From tables 6 and 7.

Species	Kilograms		Per Cent	
	Wet	Dry	Wet	Dry
<i>Ceratophyllum</i> .....	331,100	23,500	6.5	3.7
<i>Chara</i> .....	2,417,000	375,600	47.6	58.2
<i>Drepanocladus</i> .....	101,700	17,700	2.0	2.8
<i>Eldoea</i> .....	58,100	5,200	1.2	0.8
<i>Myriophyllum</i> .....	534,500	52,000	10.5	8.1
<i>Najas</i> .....	63,900	6,100	1.3	1.0
<i>Potamogeton amplifolius</i> .....	119,100	13,400	2.4	2.1
<i>Potamogeton foliosus</i> .....	34,900	4,100	0.6	0.6
<i>Potamogeton heterophyllum</i> .....	101,800	11,300	2.0	1.8
<i>Potamogeton natans</i> .....	75,500	9,000	1.5	1.4
<i>Potamogeton pectinatus</i> .....	459,000	53,200	9.0	8.3
<i>Potamogeton Richardsonii</i> .....	119,100	14,500	2.4	2.3
<i>Potamogeton zosterifolius</i> .....	135,400	16,900	2.7	2.6
<i>Radicula</i> .....	22,500	2,200	0.4	0.4
<i>Ranunculus</i> .....	32,000	3,500	0.6	0.6
<i>Vallisneria</i> .....	363,100	24,400	7.2	3.8
<i>Heteranthera</i> .....	78,400	7,600	1.2	1.2
<i>Carex</i> .....				
<i>Castalia</i> .....	24,000	2,000	0.5	0.3
<i>Cladophora</i> .....				
<i>Nymphaea</i> .....				
<i>Scirpus</i> .....				
Total.....	5,075,100	642,200	100.0	100.0

TABLE 10. Total weight and percentage of each species in Zone 3 (3–8 meters).  
Area: 4,234 square kilometers. From tables 6 and 7.

Species	Kilograms		Per Cent	
	Wet	Dry	Wet	Dry
<i>Ceratophyllum</i> .....	1,816,400	125,700	26.6	16.8
<i>Chara</i> .....	2,193,200	330,300	32.1	44.1
<i>Drepanocladus</i> .....	63,500	12,700	0.9	1.7
<i>Elodea</i> .....	478,400	34,700	7.0	4.6
<i>Myriophyllum</i> .....	1,011,900	99,500	14.8	13.3
<i>Najas</i> .....	46,600	4,700	0.7	0.6
<i>Potamogeton zosterifolius</i> .....	135,400	16,900	2.7	2.6
<i>Potamogeton foliosus</i> .....	88,900	8,900	1.3	1.2
<i>Potamogeton heterophyllum</i> .....	8,500	800	0.1	0.1
<i>Potamogeton natans</i> .....	4,200	400	0.1	0.1
<i>Potamogeton pectinatus</i> .....	724,000	86,800	10.6	11.6
<i>Potamogeton Richardsonii</i> .....	4,200	400	0.1	0.1
<i>Potamogeton zosterifolius</i> .....	292,200	33,500	4.3	4.4
<i>Radicula</i> .....				
<i>Ranunculus</i> .....	21,200	2,100	0.3	0.3
<i>Vallisneria</i> .....				
<i>Heteranthera</i> .....	12,700	1,300	0.2	0.2
<i>Carex</i> .....				
<i>Castalia</i> .....				
<i>Cladophora</i> .....				
<i>Nymphaea</i> .....				
<i>Scirpus</i> .....				
Total.....	6,825,200	748,600	100.0	100.0

TABLE 11. *Total weight at all depths and percentage of each species. Area: 8.573 square kilometers. From tables 8, 9, and 10.*

Species	Kilograms		Per Cent	
	Wet	Dry	Wet	Dry
<i>Ceratophyllum</i> .....	2,187,400	152,100	16.8	9.9
<i>Chara</i> .....	4,897,800	754,000	37.7	49.3
<i>Drepanocladus</i> .....	165,200	30,400	1.3	2.0
<i>Elodea</i> .....	536,500	39,900	4.1	2.6
<i>Myriophyllum</i> .....	1,557,800	152,600	12.0	10.0
<i>Najas</i> .....	116,200	11,400	0.9	0.7
<i>Potamogeton amplifolius</i> .....	199,700	22,800	1.5	1.5
<i>Potamogeton foliosus</i> .....	129,500	13,600	1.0	0.9
<i>Potamogeton heterophyllum</i> .....	198,600	23,300	1.5	1.5
<i>Potamogeton natans</i> .....	105,300	12,500	0.8	0.8
<i>Potamogeton pectinatus</i> .....	1,257,000	149,700	9.7	10.0
<i>Potamogeton Richardsonii</i> .....	137,600	16,600	1.0	1.1
<i>Potamogeton zosterifolius</i> .....	450,100	52,700	3.5	3.5
<i>Radicula</i> .....	22,500	2,200	0.2	0.1
<i>Ranunculus</i> .....	71,700	7,600	0.5	0.5
<i>Vallisneria</i> .....	437,100	30,000	3.4	2.0
<i>Heteranthera</i> .....	132,400	12,700	1.0	0.8
<i>Carex</i> .....	4,200	400	.....	.....
<i>Castalia</i> .....	24,000	2,000	0.2	0.1
<i>Cladophora</i> .....	800	100	.....	.....
<i>Nymphaea</i> .....	60,000	4,900	0.5	0.3
<i>Scirpus</i> .....	311,100	36,500	2.4	2.4
Total.....	13,002,500	1,527,900	100.0	100.0

TABLE 12. *Distribution of species by depth, stated in percentages.*  
*From tables 8, 9, 10, and 11.*

Species	0—1 M.		1—3 M.		3—8 M.	
	Wet	Dry	Wet	Dry	Wet	Dry
<i>Ceratophyllum</i> .....	1.8	1.9	15.1	15.5	83.1	82.6
<i>Chara</i> .....	5.9	6.4	49.3	49.8	44.8	43.8
<i>Drepanocladus</i> .....			61.6	58.2	38.4	41.8
<i>Elodea</i> .....			10.8	13.0	89.2	87.0
<i>Myriophyllum</i> .....	0.8	0.7	34.3	34.1	64.9	65.2
<i>Naïas</i> .....	4.9	5.3	50.0	53.5	40.1	41.2
<i>Potamogeton amplifolius</i> .....	10.7	11.4	59.6	58.8	29.7	29.8
<i>Potamogeton foliosus</i> .....	4.4	4.4	27.0	30.2	68.6	65.4
<i>Potamogeton heterophyllum</i> .....	44.4	47.8	51.2	48.7	4.4	3.5
<i>Potamogeton naïans</i> .....	24.3	24.8	71.7	72.0	4.0	3.2
<i>Potamogeton pectinatus</i> .....	5.9	6.4	36.5	35.5	57.6	58.1
<i>Potamogeton Richardsoni</i> .....	10.3	10.2	86.6	87.4	3.1	2.4
<i>Potamogeton zosterifolius</i> .....	4.2	4.4	30.3	32.0	65.5	63.6
<i>Radicula</i> .....			100.0	100.0		
<i>Ranunculus</i> .....	25.8	26.3	44.6	46.1	29.6	27.6
<i>Vallisneria</i> .....	16.9	18.7	83.1	81.3		
<i>Heteranthera</i> .....	31.2	29.9	59.2	59.9	9.6	10.2
<i>Carex</i> .....	100.0	100.0				
<i>Castalia</i> .....			100.0	100.0		
<i>Cladophora</i> .....	100.0	100.0				
<i>Nymphaea</i> .....	100.0	100.0				
<i>Scirpus</i> .....	100.0	100.0				
All species.....	8.4	9.0	39.1	42.0	52.5	49.0

TABLE 13. *Average yield of Green Lake. From tables 6 and 11.*

Depth	Grams per Square Meter		Kilograms per Hectare		Pounds per Acre	
	Wet	Dry	Wet	Dry	Wet	Dry
0-1 M.....	510	67	5,100	670	4,550	600
1-3 M.....	1,731	220	17,310	2,200	15,440	1,960
3-8 M.....	1,612	177	16,120	1,771	14,380	1,580
All depths.....	1,518	178	15,180	1,780	13,540	1,590

TABLE 14. *Temperature of the water at different depths in summer.*

Depth	Mendota	Green Lake
	Degrees C.	Degrees C.
0 M.....	26.1	24.3
5 M.....	23.7	23.5
8 M.....	20.4	17.7
10 M.....	16.9	14.0



## THE ROTIFER FAUNA OF WISCONSIN.—II.

---

### A REVISION OF THE NOTOMMATID ROTIFERS, EXCLUSIVE OF THE DICRANOPHORINAE

H. K. HARRING AND F. J. MYERS

Notes from the Biological Laboratory of the Wisconsin Geological and Natural History Survey. XXIII.

#### INTRODUCTION.

At the beginning of the survey of the Wisconsin rotifer fauna a promise was made to publish descriptions and figures of all the species found. We soon realized that this was likely to prove quite an ambitious program, and especially so in the case of the Notommatid rotifers, the largest and also the most chaotic group of all. Ever since this family was first proposed, there has been a steady accretion of new species and a periodic shifting of the old ones, until it has become a veritable Serbonian bog, carefully avoided by everybody or, at least, trespassed upon only under compulsion. We do not make any pretense to superior virtue or to being considered exceptions to the rule; the compulsion was, however, greater and became, under the circumstances, a seemingly unavoidable necessity. A beginning was made with the review of the central group of the Notommatids appended to the preliminary list of the rotifers of Wisconsin published in volume twenty of the Transactions. In the present paper the remaining species are described, as far as material has been obtainable.

No definition was given in part one of what was meant to be included among the Notommatids, and it becomes necessary to explain our conception of the family. No usable diagnosis has ever been given and none was possible until a more detailed study of the group became available. The tendency in the past has been to include in the family Notommatidae nearly all the slow-moving, plant-feeding, illoricate Ploima, without any serious attempt to define it more precisely. We have endeavored to maintain this

general idea in so far as it could be done without violating accepted principles of classification and with proper deference to the necessarily hypothetical nature of present-day ideas of the interrelations of the various rotifer groups.

The family Notommatidae may then be characterized as a family of pliomate rotifers with moderately elongate, prismatic or spindle-shaped, illoricate or partially loricate body, ending in a short, normally two-jointed, tubular foot with two toes, in rare cases fused; with a corona composed of simple cilia, primarily forming a marginal wreath composed of strong cilia adapted to the propulsion of the animal, and enclosing the unciliated apical plate and a buccal field with short cilia for bringing food to the mouth, which is near the ventral margin of the corona; the ciliation may be continued beyond the mouth as a so-called chin. The mastax is a more or less specialized form of the malleate type, and we have divided the family into six subfamilies, according to the degree of departure from the type. The stomach and intestine are usually without distinct separation; the ovary is nearly always an irregularly oval, disc-shaped organ with the normal number of nuclei, eight; the excretory system consists of two lateral canals with 3-5 flame cells, opening into the bladder, which is either an expansion of the cloaca or a separate, pyriform vesicle discharging into the cloaca through a short duct. The ganglion is large and saccate; the retrocerebral organ is very unequally developed in the different genera. The eyespot is usually cervical, but may be frontal or absent.

The subfamily Proalinae is characterized by a type of mastax very closely related to the malleate; the unci are adapted to the crushing or grinding of the food; a weak "piston" is usually present, but it is attached to the ventral floor of the mastax, and not to the fulcrum. The retrocerebral organ is absent or limited to a rudimentary sac.

The subfamily Notommatinae has a mastax to which De Beuchamp applied the name *virgate*, first used by Hudson and Gosse with ambiguous definition; it is characterized by the development on its ventral surface of a powerful muscle, the hypopharynx, attached to the fulcrum and acting as the piston of a pump, the entire mastax forming the cylinder of the "pump", thus enabling the animal to extract the contents of plant cells or of the bodies of small animals without swallowing them. A well-developed retrocerebral organ is present in the majority of the genera.

The subfamily Tetrasiphoninae includes only a single species; the mastax is notable for the unusual development of the epipharynx; a weak piston is present, but it is not attached to the fulcrum. The retrocerebral organ consists of a large sac and two long subcerebral glands.

The subfamily Lindiinae has a highly specialized type of mastax, for which we propose the name "cardate"; like the virgate it functions by suction, but the structure is very different; the mastax oscillates as a unit on a transverse axis, while a complicated epipharynx supports the mouth. The retrocerebral organ is limited to a ductless sac surrounding the eyespot.

The subfamily Birgeinae with a single genus and species has a remarkable type of mastax, characterized by the virtual atrophy of the normal elements and their replacement by a pair of "pseudunci", hook-shaped organs of epipharyngeal origin, which may be protruded from the mouth to seize the prey. No retrocerebral organ is present.

The subfamily Dicranophorinae includes Notommatid rotifers having a forcipate mastax; the entire organ is strongly compressed dorso-ventrally and adapted to the capture and tearing apart of prey by protrusion through the mouth. The retrocerebral organ is usually present, either as sac or glands. This subfamily includes a very large number of species, the great majority still undescribed, and we have not been able to include them in this paper.

The distribution of the various genera among the proposed subfamilies is indicated in the list below, as well as the species included in each and a reference to the description. This arrangement will no doubt need modification as more detailed information becomes available, but if it be permitted to serve as a foundation upon which to erect a more permanent structure, it will have answered its purpose and accomplished all that was expected of it.

Family NOTOMMATIDAE.

Subfamily PROALINAE.

Genus *Proales*.

<i>decepiens</i> (Ehrenberg)	.....Vol. XX, p. 603
<i>sordida</i> Gosse	.....XX, p. 605
<i>parasita</i> (Ehrenberg)	.....XX, p. 607
<i>gigantea</i> (Glasscott)	.....XXI, p. 424
<i>werneckii</i> (Ehrenberg)	.....XXI, p. 426
<i>brevipes</i> Harring and Myers	.....XXI, p. 428
<i>daphnicola</i> Thompson	.....XXI, p. 430

<i>reinhardti</i> (Ehrenberg) .....	XXI, p. 431
<i>similis</i> De Beauchamp .....	XXI, p. 434
<i>minima</i> (Montet) .....	XXI, p. 435
<i>doliaris</i> (Roussélet) .....	XXI, p. 437

Genus *Proalinopsis*.

<i>caudatus</i> (Collins) .....	Vol. XX, p. 603
<i>staurus</i> Harring and Myers .....	XXI, p. 439

Subfamily NOTOMMATINAE.

Genus *Notommata*.

<i>copeus</i> Ehrenberg .....	Vol. XX, p. 562
<i>pachyura</i> (Gosse) .....	XX, p. 565
<i>collaris</i> Ehrenberg .....	XX, p. 568
<i>pseudocerberus</i> De Beauchamp .....	XX, p. 598
<i>falcinella</i> Harring and Myers .....	XX, p. 570
<i>saccigera</i> Ehrenberg .....	XX, p. 594
<i>cerberus</i> (Gosse) .....	XX, p. 572
<i>galena</i> Harring and Myers .....	XX, p. 574
<i>aurita</i> (Müller) .....	XX, p. 578
<i>codonella</i> Harring and Myers .....	XXI, p. 444
<i>thopica</i> Harring and Myers .....	XXI, p. 446
<i>peridia</i> Harring and Myers .....	XX, p. 576
<i>lenis</i> Harring and Myers .....	XX, p. 586
<i>placida</i> Harring and Myers .....	XX, p. 587
<i>pygmaea</i> Harring and Myers .....	XX, p. 593
<i>epaxia</i> Harring and Myers .....	XXI, p. 443
<i>angusta</i> Harring and Myers .....	XX, p. 580
<i>cyrtopus</i> (Gosse) .....	XX, p. 582
<i>doneta</i> Harring and Myers .....	XXI, p. 448
<i>telmata</i> Harring and Myers .....	XX, p. 584
<i>tripus</i> Ehrenberg .....	XX, p. 589
<i>venusta</i> Harring and Myers .....	XX, p. 591
<i>tithasa</i> Harring and Myers .....	XXI, p. 450
<i>contorta</i> (Stokes) .....	XX, p. 600
<i>silpha</i> (Gosse) .....	XX, p. 596
<i>trypeta</i> Harring and Myers .....	XX, p. 602

Genus *Taphrocampa*.

<i>annulosa</i> Gosse .....	Vol. XXI, p. 452
<i>clavigera</i> Stokes .....	XXI, p. 455
<i>selenura</i> Gosse .....	XXI, p. 454

Genus *Drilophaga*.

<i>judayi</i> Harring and Myers .....	Vol. XX, p. 612
---------------------------------------	-----------------

Genus *Pleurotrocha*.

<i>petromyzon</i> Ehrenberg .....	Vol. XXI, p. 459
<i>robusta</i> (Glasscott) .....	XXI, p. 461

Genus *Cephalodella*.

Group A; eyespot frontal, double.

<i>catellina</i> (Müller) .....	Vol. XXI, p. 465
<i>angusta</i> Myers .....	XXI, p. 467
<i>epitedia</i> Myers .....	XXI, p. 468
<i>paxilla</i> Myers .....	XXI, p. 468
<i>marina</i> Myers .....	XXI, p. 469
<i>innesi</i> Myers .....	XXI, p. 470
<i>mineri</i> Myers .....	XXI, p. 471
<i>elongata</i> Myers .....	XXI, p. 471

Group B; eyespot frontal, single.

<i>gibba</i> (Ehrenberg) .....	XXI, p. 472
<i>gracilis</i> (Ehrenberg) .....	XXI, p. 473
<i>sterea</i> (Gosse) .....	XXI, p. 474
<i>globata</i> (Gosse) .....	XXI, p. 475
<i>forficula</i> (Ehrenberg) .....	XXI, p. 476
<i>panarista</i> Myers .....	XXI, p. 478

Group C; eyespot cervical.

<i>auriculata</i> (Müller) .....	XXI, p. 479
<i>exigua</i> (Gosse) .....	XXI, p. 481
<i>hoodii</i> (Gosse) .....	XXI, p. 482
<i>plicata</i> Myers .....	XXI, p. 483
<i>ventripes</i> (Dixon-Nuttall) .....	XXI, p. 484
<i>physalis</i> Myers .....	XXI, p. 484
<i>strigosa</i> Myers .....	XXI, p. 485
<i>tantilla</i> Myers .....	XXI, p. 486
<i>compressa</i> Myers .....	XXI, p. 487
<i>dorseyi</i> Myers .....	XXI, p. 487
<i>hiulca</i> Myers .....	XXI, p. 488
<i>elegans</i> Myers .....	XII, p. 489
<i>galbina</i> Myers .....	XXI, p. 490
<i>belone</i> Myers .....	XXI, p. 490
<i>nana</i> Myers .....	XXI, p. 491
<i>xenica</i> Myers .....	XXI, p. 492

Group D; eyespot absent.

<i>nelitis</i> Myers .....	XXI, p. 493
<i>melia</i> , Myers .....	XXI, p. 493
<i>megalocephala</i> (Glasscott) .....	XXI, p. 494
<i>pheloma</i> Myers .....	XXI, p. 496
<i>tenuior</i> (Gosse) .....	XXI, p. 497
<i>retusa</i> Myers .....	XXI, p. 498
<i>dixon-nuttalli</i> Myers .....	XXI, p. 498
<i>forficata</i> (Ehrenberg) .....	XXI, p. 499
<i>intuta</i> Myers .....	XXI, p. 500
<i>collactea</i> Myers .....	XXI, p. 501
<i>inquilina</i> Myers .....	XXI, p. 502
<i>licinia</i> Myers .....	XXI, p. 503

<i>vacuna</i> Myers.....	XXI, p. 503
<i>speciosa</i> Myers.....	XXI, p. 504
<i>cuneata</i> Myers.....	XXI, p. 505
<i>hyalina</i> Myers.....	XXI, p. 505
<i>papillosa</i> Myers.....	XXI, p. 506
<i>eva</i> (Gosse).....	XXI, p. 507
<i>tenuiseta</i> (Burn).....	XXI, p. 508
<i>apocolea</i> Myers.....	XXI, p. 509
<i>strepta</i> Myers.....	XXI, p. 509
<i>mucronata</i> Myers.....	XXI, p. 510
<i>parasitica</i> (Jennings).....	XXI, p. 511
<i>eupoda</i> Myers.....	XXI, p. 512
<i>lipara</i> Myers.....	XXI, p. 512
Genus <i>Dbrystoma</i> .	
<i>caudata</i> (Bilfinger).....	Vol. XXI, p. 513
Genus <i>Rousseletia</i> .	
<i>corniculata</i> Harring.....	Vol. XXI, p. 514
Genus <i>Tylotrocha</i> .	
<i>monopus</i> (Jennings).....	Vol. XXI, p. 516
Genus <i>Resticula</i> .	
<i>melandocus</i> (Gosse).....	Vol. XX, p. 644
<i>gelida</i> (Harring and Myers).....	XX, p. 642
<i>anceps</i> Harring and Myers.....	XXI, p. 519
<i>nyssa</i> Harring and Myers.....	XXI, p. 521
Genus <i>Eosphora</i> .	
<i>najas</i> Ehrenberg.....	Vol. XX, p. 634
<i>ehrenbergi</i> Weber.....	XX, p. 637
<i>therina</i> Harring and Myers.....	XX, p. 639
<i>thoa</i> Harring and Myers.....	XXI, p. 523
<i>anthadis</i> Harring and Myers.....	XX, p. 641
Genus <i>Enteroplea</i> .	
<i>lacustris</i> Ehrenberg.....	Vol. XXI, p. 526
Genus <i>Eothimia</i> .	
<i>elongata</i> (Ehrenberg).....	XX, p. 646
<i>triphaea</i> Harring and Myers.....	XXI, p. 528
<i>argus</i> Harring and Myers.....	XXI, p. 530
Genus <i>Sphyrias</i> .	
<i>lofuana</i> (Rousselet).....	Vol. XXI, p. 532
Genus <i>Monommata</i> .	
<i>longiseta</i> (Müller).....	Vol. XXI, p. 535
<i>grandis</i> Tessin.....	XXI, p. 538

Subfamily TETRASIPHONINAE.

Genus *Tetrasiphon*.

*hydrocora* Ehrenberg .....Vol. XX, p. 630

Subfamily LINDIINAE.

Genus *Lindia*.

*torulosa* Dujardin.....Vol. XX, p. 618  
*pallida* Harring and Myers.....XX, p. 620  
*annecta* Harring and Myers.....XX, p. 622  
*producta* Harring and Myers.....XX, p. 616  
*candida* Harring and Myers.....XX, p. 614  
*tecusa* Harring and Myers.....XX, p. 624  
*truncata* (Jennings).....XX, p. 626  
*fulva* Harring and Myers.....XX, p. 628

Subfamily BIRGEINAE.

Genus *Birgea*.

*enantia* Harring and Myers.....Vol. XX, p. 610

Subfamily DICRANOPHORINAE.

Genera: *Dicranophorus*, *Encentrum*, *Erignatha*, *Albertia*.

In this regrouping we have endeavored to avoid two extremes, the one of including so many species in a genus that it becomes unnatural and lacking in homogeneity, and the other of splitting up the group into enough genera to make each one absolutely homogeneous; the latter course would probably require in this instance at least a dozen new genera. The result must therefore be accepted as a compromise, which obviously precludes the application of any hard and fast rule. The precept we have tried to observe is: when only a single structural feature in one species is involved, a new genus is not proposed unless the departure is very striking; if, however, the same modification occurs in several species, in other respects apparently closely related, a new generic name is introduced.

Some concrete examples may help to make this clear. *Notommata pseudocerberus* has a peculiar form of mastax, quite different from other members of the genus, but it agrees so well with the normal in every other respect that it has not been separated. Much the same is true of *N. saccigera*; the pumping function of the mastax has all but disappeared, but it is so obviously derived from the normal virgate mastax that it seems advisable to leave it in the genus *Notommata*. Three of the smaller species, *Notommata venusta*, *contorta* and *tithasa*, have the same type of corona, with-

out evertile auricles, but the mastax is so different in these species that they do not appear to form a natural group. The genus *Eothinia* is separated from *Eosphora* on account of the form of the mastax, virgate trophi with regularly denticulate rami, because this occurs in three species which are very similar in other features. A second genus, *Resticula*, has been created for four species, closely related to *Eosphora*, but with a type of mastax intermediate between this genus and *Notommata*, adapted to prehension, but retaining the pumping action unimpaired; there is also close agreement in the form of the body, retrocerebral organ and eyespot.

The compromise arrived at must be justified by the evidence of a common ancestry brought out by a detailed study of each group. It is quite true that extreme species often differ considerably in their characteristics, but their actual relationship appears in a clearer light when the entire series of intermediates are taken into consideration.

There is also something to be said against the very fashionable subdivision of existing genera; it may, and if carried far enough does, lead to homogeneous and "natural" genera, but this advantage is obtained at the price of a more comprehensive view of the actual relationship of the species concerned. A partial remedy is then introduced in the form of various higher groupings, tribes, sections, etc., but the total gain by this process does not seem to justify the more cumbersome machinery and the burden of additional generic and other names.

A misleading typographical error occurs several times in volume twenty; on page 577, line 22, page 583, line 31, page 585, line 20, page 587, line 7, and page 590, line 38, for "ramus" read "uncus".

### **Subfamily PROALINAE.**

#### **Genus PROALES Gosse.**

Notommatid rotifers with spindle-shaped, illoricate body, with a slight constriction behind the mastax separating the head and abdomen; there is usually a distinct reduction in diameter of the body at the base of the foot, which has two very short toes.

The corona is an oblique disc with well developed marginal cilia and two lateral tufts of densely set, long cilia, especially adapted to swimming; they resemble auricles, but are not retractile. The apical plate is not usually enclosed by the marginal ciliation and



may be dorsal. The buccal field is large and evenly ciliated; the mouth is at the ventral margin.

The mastax is a modification of the malleate type; the piston is small and not attached to the fulcrum, but to the ventral wall of the mastax. The fulcrum is short and nearly in a straight line with the flat, roughly triangular rami, which are usually dentate on the inner edges and have large basal apophyses. The manubria are as long as in the normal virgate mastax; the unci have four or more well-developed teeth. The epipharynx consists of two very irregularly shaped pieces, imbedded in the walls of the mastax at the sides of the mouth.

The retrocerebral organ is rudimentary or absent. The eyespot is usually cervical, rarely frontal or absent.

*Type of the genus*.—*Proales decipiens* (Ehrenberg)=*Notommata decipiens* Ehrenberg.

We have not seen *Proales aureus* Zavadovsky, parasitic in colonies of *Volvox aureus*, or *P. quadrangularis* (Glasscott); Dr. E. Penard kindly sent us a slide with a balsam-mounted specimen of his *P. latrunculus*, but we did not succeed in isolating the trophi of the contracted specimen. A number of species, so poorly described that there is little hope of identifying them, have been referred to this genus. They are listed here only to complete the record.

*Proales aureus* ZAVADOVSKY, Uchen. Zap. Moskovsk. Gor. Univ. Shaniavskago, vol. 1, 1916, p. 278, pl. 4, figs. 1-9.

*Proales algicola* KELLICOTT, Trans. Amer. Micr. Soc., vol. 19, 1897, p. 48 [= *Cephalodella catellina* (Müller)?]

*Proales coryneger* GOSSE, Journ. Royal Micr. Soc., 1887, p. 863, pl. 14, fig. 4.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 24, pl. 31, fig. 10.

*Proales inflata* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 51, pl. 4, fig. 1.

*Proales latrunculus* PENARD, Mikrokosmos, vol. 2, 1909, p. 142, figs. 1-7.

*Proales micropus* (Gosse).

*Furcularia micropus* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 46, pl. 19, fig. 2.

*Proales micropus* JENNINGS, Amer. Natural., vol. 35, 1901, p. 743, pl. 5, fig. 82.

*Proales othodon*, GOSSE, Journ. Royal Micr. Soc., 1887, p. 366, pl. 8, fig. 11.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 24, pl. 31, fig. 11.

*Proales prehensor*, GOSSE, Journ. Royal Micr. Soc., 1887, p. 366, pl. 8, fig. 12.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 24, pl. 31, fig. 12. (= *Lecane depressa* Bryce?)

*Proales quadrangularis* (Glasscott).

*Notops quadrangularis* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 43, pl. 3, fig. 3.—HAUER, Mitt. Bad. Landesver. Naturk., Freiburg i. Br., new ser., vol. 1, 1921, p. 184, text fig.

*Furcularia quadrangularis* MURRAY, Trans. Royal Soc. Edinburgh, vol. 45, 1906, p. 180.

*Furcularia globulifera* HAUER, Mitt. Bad. Landesver. Naturk., Freiburg i. Br., new ser., vol. 1, 1921, p. 185

The last-named species is evidently valid, and, judging from the figures and description given by Hauer, it should be included in this genus.

**PROALES GIGANTEA (Glasscott).**

Plate XVII, figures 6-10.

*Notommata gigantea* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 80, pl. 7, fig. 1.

? *Proales ovicola* GIARD, Feuilles jeunes Nat., vol. 38, 1908, p. 184.

*Proales gigantea* STEVENS, Journ. Quekett Mier. Club, ser. 2, vol. 11, 1912, p. 481, pl. 24, figs. 1-5.

The body of the free-swimming animal is nearly cylindrical, short and stout; its greatest width is about one fourth of the entire length. The integument is very soft and flexible and the outline constantly changing.

The head is short and broad; the neck is represented by two or three indistinct folds, which do not encircle the body completely. The abdomen is elongate ovoid and slightly constricted at the base of the foot; the tail is distinct, but not very prominent. The foot has two short joints, both very large in diameter, and terminates in a hemispherical bulb with the two very small toes set far apart; on the posterior dorsal margin of the foot there is a prominent spur, projecting at a nearly right angle with the longitudinal axis of the body; the toes are abruptly reduced to short, needle-like points.

The dorsal antenna is a small, setigerous papilla in the normal position; the lateral antennae have not been observed.

The corona is oblique and weakly ciliated with the exception of two lateral, auricle-like areas provided with strong cilia adapted to propelling the animal through the water. The mouth is at the posterior margin of the corona.

The mastax is closely related to the primitive malleate type. The incus is nearly straight; the fulcrum is long, slender and slightly

decurved at the anterior end. The rami are broad and triangular with a large basal apophysis; on the right ramus there is immediately behind the basal apophysis a broad, shear-like, striated and denticulate blade projecting towards the left and opposing the first tooth of the left uncus; it has no counterpart on the left side. The inner edges of the rami are not denticulate. The right uncus has six long teeth, gradually decreasing in size from the ventral margin; to the first tooth is joined an additional rudimentary tooth, which is only half the length of the main tooth; the two dorsal teeth are very slender and joined for their entire length. The left uncus has five principal teeth, one very slender supplementary, full length tooth and the tip of a second both joined to the first ventral tooth; to the last, or dorsal, tooth is joined the tip of another imperfectly developed tooth. The middle cell of the manubrium is long and very broad and has the usual sigmoid curvature; the ventral and dorsal cells are broad and plate-like. The epipharynx consists of two irregular, conchoidal structures, imbedded in the walls of the mastax at the sides of the mouth. The piston is rudimentary and attached to the ventral wall of the mastax.

The oesophagus is fairly long and quite slender. The gastric glands are small and nearer the ventral side than is usually the case. There is no constriction between the stomach and intestine. The ovary is very large and in the mature animal contains usually from one to three developing eggs at the same time. The bladder is very small. The foot glands are huge and completely fill the foot; they discharge into large mucus reservoirs, contained in the hemispherical bulb on which the toes are seated.

The ganglion is rather small and saccate; the minute eyespot is at the posterior end. A large retrocerebral sac is present, but no subcerebral glands.

Total length of the free-swimming animal  $200\mu$ ; toes  $8\mu$ .

*Proales gigantea* is parasitic in the eggs of the pond snail, *Lymnaea*, possibly in several species. Stevens has given an account of its development in the eggs of *Lymnaea auricularia* and it is possible that the notes in the following articles may be based on either the eggs or the fully developed animals:

- BOMME, L., 1773. Bericht aangaande verscheiden zonderlinge zee-insecten, gevonden aan de zeewieren, op het strand van 't eiland Walcheren.—Verh. Zeeuwsch Genootsch. Wetensch. te Vlissingen. Middelburg, vol. 3, pp. 283-318, 1 pl. ("Raderdiertje" in snails' eggs pp. 302-305)

- KARSCH, A. F. F., 1846. Die Entwicklungsgeschichte des *Limnaeus stagnalis*, ovatus und palustris, nach eignen Beobachtungen dargestellt.—Arch. Naturg., Berlin, Jahrg. 12, vol. 1, pp. 236–276, pl. 9.
- ECKER, A., 1851. Zur Entwicklungsgeschichte der Infusorien.—Zeitschr. Wis. Zool., vol. 3, pp. 412–415; Froriep's Tagesber. Fortschr. Nat.-u. Heilk., Abt. Zool., vol. 2 (for 1852), pp. 273–275.

We have not seen the living animal; the foregoing description is from material kindly furnished us by the late Mr. John Stevens, of Exeter, England, who gave the first adequate account of this species. The free-swimming young female pierces the shell of the snails' egg, feeds on the contents and lays its eggs within the shell, where the young continue the destruction of the embryo snail. The fully grown female *Proales gigantea* is very much larger than in the free-swimming stage, reaching a size of fully 500 $\mu$ , and becomes a shapeless, distended bag, hardly recognizable as a rotifer. A full account of the development of the eggs is given by Stevens.

**PROALES WERNECKII (Ehrenberg).**

Plate XVII, figures 1–5.

- Cyclops lupula* VAUCHER, Hist. Conf. d'Eau Douce, 1803, p. 18, pl. 3, figs. 8r, 11s; not *Cyclops* Müller.
- Notommata werneckii* EHRENBURG, Abh. Akad. Wiss. Berlin (for 1833), 1834, p. 216; Infusionsthierchen, 1838, p. 429.—OLIVER, Trans. Tyneside Nat. Field Club, vol. 4, 1860, p. 263, pl. 14.—MAGNUS, Verh. Botan. Ver. Prov. Brandenburg, vol. 18, 1876, p. 125.—WOLLNY, Hedwigia, vol. 16, 1877, p. 163; vol. 17, 1877, pp. 5, 97.—BALBIANI, Ann. Sci. Nat., Zool., ser. 6, vol. 7, No. 2, p. 1, pl. 4, figs. 1–18; Journ. Royal Micr. Soc., 1879, p. 530, pl. 18.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 134.—DEBRAY, Bull. Sci. France et Belgique, vol. 22, 1890, p. 222, pl. 11.—ROTHERT, Zool. Jahrb., Syst., vol. 9, 1896, p. 673, figs. A–D; Jahrb. Wiss. Bot., vol. 29, 1896, p. 525, pls. 8, 9.
- Copeus werneckii* EHRENBURG, Infusionsthierchen, 1838, p. 441.
- Proales werneckii* HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 23, pl. 32, fig. 18.—ROUSSELET, Journ. Quekett Micr. Club, ser. 2, vol. 6, 1897, p. 415, pl. 19, figs. 1–4.—LUCKS, Rotatorienfauna Westpreussens, 1912, p. 52, fig. 8.—VOIGT, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 89, fig. 157.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 102, fig. 29.

The body of the free-swimming female is elongate, spindle-shaped and very slender, its greatest width is about one sixth of the total length. The integument is very flexible and the outline constantly changing. The body is very transparent.

The head segment is considerably longer than wide; it is rounded anteriorly, and this portion is separated from the head proper by

a slight transverse fold; this corresponds to the rostrum of the forcipate Notommatids. There is no distinct neck. The abdomen is nearly cylindric in its anterior half; from there it tapers gradually to an inconspicuous tail. The foot is short and relatively slender, continuing the general spindle-shaped outline of the body; it has two joints of nearly equal length. The toes are moderately long, about one twelfth of the total length, slender, conical and slightly decurved.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae have not been observed.

The corona is oblique and has two strongly ciliated areas corresponding to the auricles of other Notommatids. The ciliation of the buccal field does not extend beyond the mouth; the circumapical band has disappeared, as in the forcipate Notommatids.

The mastax is closely related to the malleate type. The incus is straight; on the upper side of the fulcrum is a broad rib, which curves around the end and continues for a very short distance on the lower side; the web is thin and lamellar. The rami are triangular and decurved at their posterior ends; the inner edges do not come into contact. The unci have only a single tooth, expanded into a triangular basal plate, into which it gradually merges without quite reaching the malleus; this has a very small basal plate and a rod-shaped main stem, which at the posterior end is curved diagonally forwards and inwards. The epipharynx consists of two sigmoid plates with a slender rib on the lower edge; they are imbedded in the walls of the mastax near the base of the rami. The piston seems to be very weak; it is attached to the anterior wall of the mastax and not to the fulcrum. Two huge, vacuolate salivary glands, each nearly as large as the mastax itself, are attached to it by a short, narrow neck.

The oesophagus is very long and slender. The gastric glands are large and filled with highly refractive globules. The stomach is not separated from the intestine. The ovary of the free-swimming female is normal.

The ganglion is very large and saccate. A retrocerebral sac appears to be present, but no duct has been observed. The eyespot is at the posterior end of the ganglion.

Total length 140–175 $\mu$ ; toes 11–14 $\mu$ ; trophi 18 $\mu$  wide, 12 $\mu$  long.

*Proales werneckii* is parasitic in galls on various species of *Vaucheria*. The free-swimming young, to which the description

exclusively refers, probably enters the *Vaucheria*-filament through the point, and the alga forms a gall around it. The rotifer feeds on the protoplasm within reach, and when mature begins to lay eggs; as many as 50-60 may be laid by a single individual. Simultaneously the body swells enormously, becoming almost spherical; this is caused principally by the enlargement of the stomach, which is probably the result of the accumulation of waste materials. Apparently no discharge of faecal matter takes place in the mature animal.

The male has been described by Rousselet; it is remarkable in possessing a functional mastax.

Rothert has made a very complete study of *Proales werneckii*, describing the rotifer in *Zoologische Jahrbücher* (see synonymy), and the formation of the galls in *Jahrbücher f. wissenschaftliche Botanik*. We give a short summary of his conclusions.

The parasite appears to enter the thallus by way of the growing point, where the cell-wall is thin and readily pierced by the trophi; the galls are formed only where the parasite is present. When the point of the growing thallus is injured, it starts a new growth at the base of the gall, giving to this the appearance of a lateral branch. The "cap" of the gall is structurally different from the walls. The rotifer finally eats up the entire contents, both protoplasm and chromatophores, and the gall dies; at the same time the cap falls off and the young animals find their way out. After the death of the gall a new supply of protoplasm will restore the injured section to normal life. The female is unable to complete its development outside of the gall.

We have not had an opportunity to study the living animal; the description is based on preserved material contributed by the late C. F. Rousselet, and no doubt will need correction in some details.

**PROALES BREVIPIES** Harring and Myers, new species.

Plate XIX, figures 1, 2.

The body of this species is elongate, spindle-shaped and very slender; its greatest width is less than one fifth of the total length. The integument is very flexible and the outline constantly changing. The body is very transparent.

The length of the head segment is considerably greater than its width; the anterior portion is separated from the head proper by a slight transverse fold and is the equivalent of the rostrum of the

forcepsate Notommatids. The neck segment is fairly long and nearly as wide as the body at its widest point. The anterior transverse folds are well marked. The abdomen is very nearly parallel-sided and ends in a slightly projecting tail, under which the cloaca opens. The foot is very stout, but little smaller in diameter than the abdomen; the anterior joint is twice as long as the nearly hemispherical posterior joint. The toes are minute, slender and conical, set wide apart, and freely movable, so that their tips may be brought into actual contact in the manner of a pair of forceps.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae have not been found.

The corona is obliquely ventral and weakly ciliated with the exception of the two frontal, auricle-like areas, which are furnished with strong cilia adapted to swimming. The mouth is at the posterior margin of the corona. The rostrum is outside of the corona, as the circumapical band has disappeared.

The mastax is very nearly identical with that of *Proales decipiens*, and consequently no figure is given. The incus is almost straight; the fulcrum is slightly tapering from the base towards the ventral end. The rami are triangular and have a large basal apophysis; the inner edges are obscurely dentate. The manubria are elongate, rod-shaped, and expanded anteriorly into broad plates; the unci have each five well-developed teeth. An epipharynx has not been found, but may be present; on account of the very small size it is difficult to make out the true form of the various elements of the mastax.

The oesophagus is very long and slender. The gastric glands, ovary and bladder are normal. The stomach and intestine are not separated by a constriction. The foot glands are pyriform and rather small.

The ganglion is large and saccate. A retrocerebral sac is present, but there are no subcerebral glands; the sac is partly fused to the ganglion and apparently ductless. No eyespot has been found.

Total length 90–120 $\mu$ ; toes 5–7 $\mu$ , distance apart 7–8 $\mu$ ; trophi 12 $\mu$ .

A few specimens of this species have been found in sphagnum growing on the banks of ditches at Glen Burnie, Maryland; Mr. David Bryce has found it in sphagnum collected in Otsego county, New York, by Mrs. A. C. Clarke, and sent to him. It is closely related to *Proales decipiens*, but is easily distinguished by its peculiar toes, smaller size and more slender body.

## PROALES DAPHNICOLA Thompson.

Plate XVIII, figures 1-5.

*Proales daphnicola* THOMPSON, Science Gossip, vol. 28, 1892, p. 220, fig. 125.—MURRAY, Trans. Royal Soc. Edinburgh, vol. 45, 1906, p. 179, pl. 6, fig. 26.

? *Pleurotrocha sigmoidea* SKORIKOV, Trav. Soc. Nat. Kharkov, vol. 30, 1896, p. 284, pl. 7, fig. 8.

*Pleurotrocha daphnicola* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 84.—MYERS, Proc. U. S. Nat. Mus., vol. 52, 1917, p. 478, pl. 41, figs. 4-9.

The body is spindle-shaped, short and stout; its greatest width is about one third of the total length. The integument is soft and flexible, but the outline is fairly constant. It is a moderately transparent species.

The head is short, broad and truncate anteriorly; it is separated from the abdomen by a well-marked constriction. Its width is about two thirds of the greatest width of the body and the length considerably less. The abdomen is somewhat pyriform, ending in a broad, but not very prominent tail. The foot is short and very stout; it has two joints, the basal somewhat longer and broader than the terminal, which is obliquely truncate posteriorly. The two toes are short, stout, and bluntly conical, ending in a minute tubule, through which the mucus glands discharge their contents.

The dorsal antenna is a small, setigerous papilla in the normal position; the lateral antennae are near the middle of the body.

The corona is very slightly oblique; the marginal ciliation is relatively weak, with the exception of two lateral auricle-like areas with very strong cilia adapted to swimming. The apical plate is large and unciliated; the buccal field is evenly covered with short, close-set cilia. The mouth is near the ventral edge of the corona.

The mastax is very robust and furnished with powerful trophi, closely resembling the malleate type. The fulcrum is short and very broad. The rami are of an unusual form. The basal apophysis is very large and almost as long as the ramus itself, from which it is separated by a very deep sinus; the dorsal end curves downwards. The main portion of the rami is a broad, nearly rectangular plate; the inner margins are not dentate, but form small projecting cones at their junction with the dorsal margin. The right uncus has three clubbed teeth, gradually decreasing in size from the ventral margin, followed by three linear teeth; the basal plate is nearly square. The left uncus has three clubbed and two linear teeth. The manubria are roughly equilateral triangles; the ventral



angle curves downwards and the posterior angle towards the dorsal side; the unci are hinged near the dorsal angle of the anterior margin. There is no epipharynx and apparently no piston.

The oesophagus is moderately long and slender. There is no constriction between the stomach and intestine. The gastric glands are large and strongly compressed laterally. The ovary is normal. The foot glands are very large, pyriform and somewhat compressed; they open into large mucus reservoirs, which extend almost to the tips of the toes. There is no bladder.

The ganglion is very large and saccate. There is no eyespot and no trace of a retrocerebral organ.

Total length 300–400 $\mu$ ; toes 25–35 $\mu$ ; trophi 36 $\mu$  wide, 30 $\mu$  long.

*Proales daphnicola* is not very common; since first found by Thompson it has been recorded only by Murray from Scotland and by Myers from California; Mr. C. F. Rousselet sent us specimens collected at Totteridge, Herts, England. It is commensal or, more correctly, synoecious on Daphnids and, according to Murray, on oligochaete worms; it seems to obtain nothing but transportation from the host.

PROALES REINHARDTI (Ehrenberg).

Plate XVI, figures 6–10.

? *Vorticella succolata* MÜLLER, Anim. Infus., 1786, p. 287, pl. 40, figs. 8–12.

? *Furcularia succolata* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 2, 1816, p. 38.

*Furcularia reinhardti* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1833), 1834, p. 208; Infusionsthierchen, 1838, p. 420, pl. 18, fig. 4.—DUJARDIN, Hist. Nat. Zooph., Inf., 1841, p. 651.—EICHWALD, Bull. Soc. Imp. Nat., Moscou, vol. 22, pt. 1, 1849, p. 529.—DADAY, Ertek. Termész. Köreböl, vol. 19, No. 17, p. 11, pl. 1, figs. 4, 13, 19–21, 27, 31.—LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 33, pl. 2, fig. 15.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 44; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 103, fig. 191.—LAUTERBORN, Mitt. Pollichia, vol. 60, No. 19, 1904, p. 116.—LIE-PETTERSEN, Bergens Mus. Aarbog, 1905, No. 10, p. 31, pl. 2, fig. 8.—MURRAY, Trans. Royal Soc. Edinburgh, vol. 45, 1906, p. 180.—SACHSE, Arch. Hydrobiol., vol. 9, 1914, p. 498, fig. 1.—HAUER, Mitt. Bad. Landesver. Naturk., Freiburg i. Br., new ser., vol. 1, 1921, p. 184.

? *Distemma marinum* EHRENBERG, Infusionsthierchen, 1838, p. 450, pl. 56, fig. 4.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 32, pl. 33, fig. 16.

? *Endesma (marinum)* EHRENBERG, Infusionsthierchen, 1838, p. 450.

? *Furcularia gammari* PLATE, Zeitschr. Wiss. Zool., vol. 43, 1886, p. 236, pl. 7, fig. 42; HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 61, pl. 34, fig. 8.

- Mytilia tavina* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 110, pl. 26, fig. 8.
- Mytilia teresa* GOSSE, Journ. Royal Micr. Soc., 1887, p. 3, pl. 1, fig. 7; HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 49, pl. 31, fig. 8.
- Notommata theodora* GOSSE, Journ. Royal Micr. Soc., 1887, p. 862, pl. 14, fig. 2; HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 21, pl. 31, fig. 8.
- Mytilia poecilops* GOSSE, Journ. Royal Micr. Soc., 1887, p. 869, pl. 15, fig. 21; HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 49, pl. 31, fig. 51.
- Mytilia producta* GOSSE, Journ. Royal Micr. Soc., 1887, p. 870, pl. 15, fig. 22; HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 49, pl. 31, fig. 53.
- Notommata reinhardti* HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 22.
- Diops marina* BERGENDAL, Acta Univ. Lundensis, vol. 28, 1892, sect. 2, No. 4, p. 83, pls. 4, 5, fig. 27.
- Pleurotrocha reinhardti* VON HOFSTEN, Zool. Bidr. Uppsala, vol. 1, 1912, p. 187, fig. 1; HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 85; KOZAR, Zool. Anz., vol. 44, 1914, p. 416.

The body is elongate, slender and spindle-shaped; its greatest width is less than one fourth of the total length. The integument is very flexible and the outline is constantly changing. The entire body is very transparent.

There is a well marked transverse fold separating the head and abdomen. The head segment is subsquare; its length is slightly greater than the width. The abdomen increases rather rapidly in width for about one-third of its length; from this point it tapers gradually to the tail, which is prominent and rounded posteriorly. The foot is two-jointed and very long; the basal joint is short and stout, about one-third of the length of the terminal joint, which is very slender; the length of the foot is one fourth of the total length. It is very contractile and may be completely telescoped within the body. The toes are long and slender and have a characteristic lanceolate form; their length is one twelfth of the total length.

The dorsal antenna is in the normal position; the lateral antennae are near the base of the tail.

The corona is slightly oblique. The marginal wreath has laterally two strongly ciliated, auricle-like areas; the apical plate is unciliated and fairly large; the buccal field is covered with short, close-set cilia. The mouth is near the ventral edge of the corona.

The mastax is of the typical form of the genus. The fulcrum is short, slender and tapering, its extreme end curving slightly forward. The rami are broadly triangular with a large basal apophysis and the inner margins have blunt, knoblike, interlocking teeth. The left uncus has a large ventral tooth, clubbed at the tip; this

is followed by three linear teeth of nearly equal length; the basal plate is subsquare. The right uncus has a large ventral, clubbed tooth, followed by a much more slender, minutely clubbed tooth and three linear teeth; the basal plate is sub-triangular. The manubria are very long and strongly curved posteriorly, so that the ends are directed inwards and towards the dorsal side of the mastax; the two lateral cells are small, so that three fourths of the entire length of the manubrium belongs to the central cell only. The epipharynx consists of two thin, curved plates, imbedded in the walls of the mastax at the sides of the mouth. There are indications of the presence of a rudimentary piston, attached to the ventral wall of the mastax, but not to the fulcrum.

The oesophagus is moderately long and slender. The stomach and intestine are not separated by a constriction. The gastric glands, ovary and bladder are normal. The foot glands are excessively long, the gland itself being within the body and the duct as long as the foot.

The ganglion is moderately large and saccate. The eyespot is near the anterior margin; it is double, composed of two triangular pigment cells. No retrocerebral organ is present.

Total length 250–300 $\mu$ ; toes 20–25 $\mu$ ; trophi 32 $\mu$ .

*Proales reinhardti* is not rare in brackish tidepools; we have collected it near Atlantic City, New Jersey. It seems to occur also in fresh water, according to Voigt, Lauterborn, Murray, Von Hofsten, Sachse and Hauer.

It may be questioned whether *Furcularia gammari* Plate should be considered a synonym of this species; with the exception of the length of the foot there is complete agreement in everything else, and, as the foot of *Proales reinhardti* is highly contractile, it is not unlikely that Plate may have had a specimen of this species before him.

According to Von Hofsten *Distyla weissei* Eichwald is "undoubtedly" a synonym of *P. reinhardti*; we are unable to see a single character in Eichwald's description or figures that belongs unmistakably to this species and the extrapolation required is far too great to make it advisable to displace the generic name *Proales* by *Distyla*. If a guessing contest is to be admitted, *Endesma* Ehrenberg has a far better claim to consideration, but many naturalists will question the wisdom of assigning to any animal char-

acteristics in direct opposition to those claimed for it by the original discoverer.

**PROALES SIMILIS** De Beauchamp.

Plate XVI, figures 1-5.

*Proales similis* DE BEAUCHAMP, Bull. Soc. Zool. France, vol. 32, 1908, p. 153, fig. 2.

*Pleurotrocha similis* VON HOFSTEN, Zool. Bidr. Uppsala, vol. 1, 1912, p. 186; HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 85.

The body is elongate, slender and fusiform; its greatest width is one-fifth of the total length. The integument is very soft and flexible, and the outline is somewhat variable on account of the contractility of the animal. It is a very transparent species.

The length of the head segment is very slightly greater than its width and a little less than the greatest width of the body. The abdomen is separated from the head by a slight transverse fold and increases slightly in width for one half its length; from this point it tapers gradually to the foot, ending in a minute tail, projecting but very slightly beyond the general outline of the body. The foot is relatively long, about one sixth the total length, slightly compressed dorso-ventrally and tapering towards the posterior end; it is without any joints, but is frequently wrinkled. The toes are moderately long, robust and conical; near mid-length they taper a little more rapidly and end in acute points; their length is about one twentieth of the total length.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae are unusually far forward and only a short distance beyond mid-length of the body.

The corona is slightly oblique and has laterally two strongly ciliated, auricle-like areas. The apical plate is unciliated and rather small; the buccal field is covered with short, closely set cilia. The mouth is near the ventral edge of the corona.

The mastax is intermediate between the virgate and the malleate type. The fulcrum is short, broad at the base and tapers gradually towards the slightly fan-shaped ventral end. The rami are roughly triangular and have a large basal apophysis; the alulae are two acutely pointed cones at the external angles. No denticulations are present on the inner edges of the rami. The unci have each six teeth; the last two on the dorsal margin are partly fused. The manubria are broad and lamellar at the base, ending in a

slender posterior section. The epipharynx consists of two long, slender, slightly curved rods imbedded in the anterior walls of the mastax at the sides of the mouth. The piston is small and attached to the ventral wall of the mastax.

The oesophagus is moderately long and slender. The gastric glands are large, somewhat triangular and strongly compressed. There is no distinct separation between the stomach and intestine. The ovary and bladder are normal. The foot glands are rather small and pyriform; at the base of the toes there is a minute mucus reservoir.

The ganglion is moderately large and saccate. The retrocerebral sac is small and ductless. The large eyespot is at the posterior end of the ganglion.

Total length 140–180 $\mu$  toes 15–20 $\mu$ ; trophi 24 $\mu$  wide, 15 $\mu$  long.

*Proales similis* was described by De Beauchamp from material collected in brackish tidepools at Saint-Jean-de-Luz, Basses-Pyrénées, France. We find it common in similar places near Atlantic City, New Jersey; it does not occur in freshwater ponds, as far as we know.

#### PROALES MINIMA (Montet).

Plate XX, figures 1–4.

*Pleurotrocha minima* MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 323, pl. 13, fig. 33.

*Proales minima* WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 103.

The body is short, saccate and very stout; its greatest width is nearly equal to half the length of the body proper. The integument is very delicate and flexible, but the outline remains virtually unchanged. The entire body is very hyaline.

The head is short, broad, and truncate anteriorly; its length is about one half the greatest width of the body. It is separated from the abdomen by a well defined constriction immediately behind the mastax. The abdomen is ovate in outline and ends posteriorly in a short tail. The foot is two-jointed, long and slender; the basal joint is only half the length of the terminal joint and somewhat larger in diameter. The toes are long and very slender; they are nearly cylindrical for one half their length, and from there taper gradually to long, needle-like points; their length is one fifth of the total length.

The dorsal and lateral antennae are minute setigerous papillae in the normal positions.

The corona is slightly oblique; the marginal wreath has laterally two auricle-like tufts of strong cilia for propulsion through the water. The apical plate is small and unciliated; the buccal field is covered with closely set, short cilia. The mouth is near the ventral edge of the corona.

The mastax is closely related to the malleate type, but appears to have a weak piston, attached to the ventral wall and not to the fulcrum. The incus is nearly straight; the rami are broadly triangular and crenate on their inner margins; the basal apophysis is very large and projects above the general surface of the rami. The fulcrum is very short and all but rudimentary. The right uncus has five, and the left four teeth; the ventral tooth is large and slightly clubbed at the tip, while the remaining teeth are much smaller and more slender. The manubrium is unusual in form, as only the central cell, or stem, is developed; there is no trace of the lateral, usually lamellar cells; it tapers from the base to near mid-length and ends in a slender, rod-like distal portion, slightly incurved at the tip. The epipharynx consists of two fairly large, triangular plates, imbedded in the anterior walls of the mastax, above the basal apophysis of the rami and immediately in front of the unci.

The oesophagus is relatively short and slender. The gastric glands are small and rounded. There is no distinct separation between the stomach and intestine. The ovary and bladder are normal. The foot glands are very minute and probably not functional.

The ganglion is fairly large and saccate. A rudimentary sac is fused to the posterior end of the ganglion; the duct is present, but does not reach the anterior surface of the head. There is no eye-spot.

Total length 80–100 $\mu$ ; toes 12–18 $\mu$ ; trophi 12 $\mu$  long, 10 $\mu$  wide.

*Proales minima* seems to be rare; it was found by Montet in moss that had been kept for months; we have found it under similar circumstances. The sphagnum in which it occurred had been collected in Long Pond on the Pocono plateau by Paul Lukenbach, of Bethlehem, Pennsylvania.

PROALES DOLIARIS (Rousselet).

Plate XIX, figures 3-7.

*Microcodides doliaris* ROUSSELET, Journ. Quekett Micr. Club, ser. 2, vol. 6, 1895, p. 120, pl. 7, fig. 6. VOIGT, Forschungsber. Biol. Stat. Plön, vo. 11, 1904, p. 20, pl. 2, fig. 9.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 86.—STEVENS, Trans. Devonshire Ass. Sci., 1912, p. 686. COLLIN, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 60, fig. 95.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 11. *Mikrocodides doliaris* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 70.

The body is short, extremely stout and gibbous; its greatest width is nearly equal to one half the total length. The integument is very flexible, but the outline is nevertheless quite constant. The entire body is hyaline.

The head is short, broad and obliquely truncate, joining the abdomen without any constriction; its width is about one half of the greatest width of the body. The abdomen is ovoid or nearly spherical; it terminates in a short, sleeve-like tail surrounding the base of the foot. The dorsal surface is marked with five or six indistinct, transverse folds. The foot is short and two-jointed; the length of the terminal joint is barely equal to its width, of the basal joint nearly twice the width. The toe is single, acutely pointed and fusiform; its length is about one twelfth of the total length. As two normal foot glands are present, it is evident that the single toe originated by the fusion of two separate toes and is not to be considered as an unpaired toe; it would therefore be erroneous to attach any special significance to this distinctive feature.

The dorsal antenna is a small setigerous papilla at the junction of the head and abdomen; the lateral antennae are somewhat farther back than usual.

The corona is strongly oblique and consists of a circumapical band of relatively short cilia with two lateral, auricle-like tufts of long cilia adapted to swimming. On the unciliated apical plate are two minute papillae with a few sensory setae; the buccal field is evenly ciliated. The mouth is near the ventral edge of the corona.

The mastax represents a somewhat unusual modification of the intermediate type common to this genus. The fulcrum is a nearly parallel-sided, thin lamella. The medial portion of the rami form a roughly lyrate forceps; this is extended laterally by very thin lamellae, thus giving the incus a triangular outline. The basal

apophyses take the form of long, conical, divergent, hornlike prongs. The right ramus has near the base a lamellar projection, curving towards the left and with five or six marginal denticles; this is followed by four widely spaced, short, conical teeth on the inner edge, the last one terminal. The left ramus has, opposite the lamellar projection of the right ramus, two short teeth, very close together, followed by three widely spaced teeth. The right uncus has seven, and the left six, well developed teeth, clubbed at the tips and united by a thin basal plate; each ramus has an additional, imperfect tooth at the ventral margin. The manubria are moderately long and have a broad basal plate. The piston is rudimentary.

The oesophagus is long and slender. The stomach and intestine are separated by a slight constriction. The gastric glands, ovary and bladder are normal. The two pyriform foot glands are within the body and discharge through long, very slender ducts through the single toe.

The ganglion is very large and saccate; the eyespot is on the ventral side, close to the mastax and apparently affected by its movements. No retrocerebral organ is present.

Total length 250–300 $\mu$ ; toes 20–25 $\mu$ ; trophi 25 $\mu$ .

*Proales doliaris* is not rare in regions with very soft water; we have found it in ponds and pools in Oneida and Vilas Counties, Wisconsin, and around Atlantic City, New Jersey.

The propriety of placing this species in the genus *Proales* may be open to question; there can be none as to its removal from *Mikrocodides*, which is related to *Cyrtonia* and not at all to the Notommatids. However, if it is not to be made the type of a new genus, on account of the somewhat aberrant structure of the mastax, the assignment to *Proales* seems unobjectionable.

#### Genus **PROALINOPSIS** Weber.

Notommatid rotifers with fusiform, illoricate body, with a well-marked constriction separating head and abdomen; there is a gradual reduction of the diameter of the body towards the tail; the foot is short and two-jointed, with two fairly long toes; on the tail or the basal foot joint is a knoblike papilla with a tuft of setae or a spine.

The corona is an oblique disc with short marginal cilia and two lateral, auricle-like areas with very long cilia; the apical plate is



small and enclosed by the marginal wreath; the buccal field is evenly ciliated and the mouth is at or near the ventral margin.

The mastax is intermediate between the malleate and the virgate types; the fulcrum may be either short or long; the rami are symmetrical, large and triangular, with a well developed basal apophysis; the unci have about eight slender teeth, clubbed at the tips; the manubria are long. No epipharynx is present; the piston is partly or wholly attached to the fulcrum.

The retrocerebral organ is rudimentary or absent; the eyespot, when present, is cervical.

*Type of the genus.*—*Proalinopsis caudatus* (Collins) = *Notomata caudata* Collins.

**PROALINOPSIS STAURUS** Harring and Myers, new species.

Plate XX, figures 5-9.

The body is fairly slender and spindle-shaped; its greatest width is about one fourth of the entire length. The integument is very flexible and the outline constantly changing in response to the contractions of the animal. The entire body is as hyaline as *P. caudatus*.

The head and abdomen are separated by a deep constriction. The head segment is somewhat longer than wide and convex anteriorly; its width is about two thirds of the greatest width of the body. The abdomen is spindle-shaped and widest near the middle; from there it tapers gradually to the tail, a small, knoblike papilla bearing a stiff spine, one fifth as long as the body. The foot is stout and fairly long; it has two joints, the terminal somewhat longer than the basal. The toes are rather stout at the base and end in very slender, acute points; their length is a little less than one fifth of the total length.

The dorsal antenna is a large, knoblike elevation in the normal position; it has a funnel-shaped central depression with a small tuft of sensory setae. The lateral antennae have not been observed.

The corona is an elongate oval area covering the oblique anterior surface of the head and terminating a short distance below the mouth on the ventral side. The marginal cilia are rather short, except on two lateral, auricle-like areas, which are provided with long and powerful cilia for swimming. The unciliated apical plate is small; the buccal field is evenly ciliated.

The mastax is of a type intermediate between the malleate and virgate; the primary function of the unci is evidently to crush the food, but there is also a piston, in this instance attached to the ventral floor of the mastax and perhaps incidentally to the fulcrum. The rami are triangular and apparently without teeth on the inner edges; the basal apophysis is large and immediately behind it there is a shallow groove across the rami. The fulcrum is short and tapers to the posterior end, which is slightly expanded. The unci have eight or nine long, slender teeth, clubbed at the tips and decreasing in size towards the posterior margin. The manubrium is very long and well developed; the dorsal cell continues almost to the posterior end as a thin lamella.

The oesophagus is short and slender. There is no distinct constriction between the stomach and intestine. The ovary is of normal form; the nuclei are large and as hyaline as the plasma, but of higher refractive index. The posterior portion of the cloaca appears to function as a bladder. The gastric glands are small and nearly spherical. The foot glands are large and pyriform.

The ganglion is large and saccate. There is no trace of a retro-cerebral organ or eyespot.

Total length  $100\mu$ ; toes  $18\mu$ ; spine  $22\mu$ ; trophi  $15\mu$ .

*Proalinopsis staurus* is not rare among floating and submerged sphagnum in soft water lakes and ponds. We have collected it at Mamie Lake, Eagle River and Lac Vieux Desert, Vilas County, Wisconsin, in lakes and ponds near Atlantic City, New Jersey, and in sphagnum ditches in Polk County, Florida. While closely related to *P. caudatus*, it is readily distinguished by the long, slender toes, lack of an eyespot and the conspicuous posterior spine. It is difficult to narcotize and usually rolls itself up into a ball, armadillo-fashion.

### Subfamily NOTOMMATINAE.

#### Genus NOTOMMATA Ehrenberg.

Notommatid rotifers with spindle-shaped, illoricate body, having a distinct constriction or neck behind the mastax, separating the head and the abdomen; posteriorly the body is abruptly reduced to a very short, usually two-jointed foot with two short, pointed toes; the cloaca opens dorsally at the base of the foot, under a projecting fold of the integument, or "tail."

The corona is an elongate oval area covering the oblique anterior surface of the head and continuing beyond the mouth on the ventral surface as a projecting chin; the marginal cilia are relatively short, except on two latero-frontal areas, provided with long and powerful cilia adapted to swimming, in the majority of species seated on auricles, short tubular, retractile evaginations of the integument. The apical plate is nearly always enclosed by the marginal ciliation and has frequently a projecting skinfold or rostrum, at the base of which are the openings of the ducts of the retro-cerebral organ; the buccal field and chin are covered with very short, dense cilia; the mouth is approximately in the center.

The mastax is virgate and usually somewhat asymmetric; the fulcrum is very large and nearly at a right angle to the roughly hemispherical rami, which are occasionally faintly denticulate on the inner edges; the manubria are long and expanded anteriorly into broad plates; the unci have at least one strongly developed ventral tooth and usually some additional, more or less rudimentary teeth. The piston is a powerful, muscular organ, filling the entire cavity of the mastax and attached to the fulcrum. Two rod-shaped transverse supports are imbedded in the walls of the mastax below the posterior margin of the rami; some very small, accessory teeth are frequently attached to the ventral margin of the unci; an epipharynx is rarely present.

The retrocerebral organ is highly developed; the sac is always present and the subcerebral glands are found in all but a very few species. The eyespot is at the posterior end of the ganglion.

*Type of the genus.*—*Notommata aurita* (Müller) = *Vorticella aurita* Müller.

A large number of species have been described which we have not been able to identify satisfactorily with any of the species known to us. The majority are probably now to be considered as hopeless; in some cases, at least, it is clear that the same name has been used for a number of actually quite different species. *Notommata brachyota* is apparently a valid species, if we may judge from the number of records, but we have not found an animal that could be made to agree with Ehrenberg's description.

*Notommata brachyota* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, pp. 51, 132, pl. 4, fig. 8; Infusionsthierchen, 1838, p. 435, pl. 51, fig. 3.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 24, pl. 17, fig. 1.—WIERZEJSKI, Rozpr. Akad. Umiej., Wyd. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 228.

- WEBER, *Rev. Suisse Zool.*, vol. 5, 1898, p. 446, pl. 18, figs. 1, 3.—VOIGT, *Forschungsber. Biol. Stat. Plön*, vol. 11, 1904, p. 39; *Süsswasserfauna Deutschlands*, pt. 14, 1912, p. 101, fig. 186.—WEBER and MONTET, *Cat. Invert. Suisse*, pt. 11, 1918, p. 114.
- Notommata celer* BERGENDAL, *Acta Univ. Lundensis*, vol. 28, 1892, sect. 2, No. 4, p. 60.
- Notommata constricta* (Müller).
- Vorticella constricta* MÜLLER, *Animalcula Infusoria*, 1786, p. 293, pl. 42, figs. 6, 7.
- Furcularia constricta* LAMARCK, *Hist. Nat. Anim. sans Vert.*, vol. 2, 1816, p. 38.
- Notommata constricta* EHRENBERG, *Isis* (Oken), vol. 26, 1833, col. 247.
- Notommata cylindriciformis* GLASSCOTT, *Proc. Royal Dublin Soc.*, new ser., vol. 8, 1893, p. 47, pl. 3, fig. 5.
- Notommata granularis* EHRENBERG, *Abh. Akad. Wiss. Berlin* (for 1831), 1832, p. 133; *Infusionsthierchen*, 1838, p. 427, pl. 50, fig. 2.
- Notommata gravitata* LIE-PETTERSEN, *Bergens Mus. Aarb.*, 1905, No. 10, p. 29, pl. 2, figs. 3-5. (See *Lindia tecusa*).
- Notommata grönländica* BERGENDAL, *Acta Univ. Lundensis*, vol. 28, 1892, sect. 2, No. 4, p. 56, pls. 2, 3, fig. 21.—LUCKS, *Rotatorienfauna Westpreussens*, 1912, p. 52.
- Notommata larviformis* GLASSCOTT, *Proc. Royal Dublin Soc.*, new ser., vol. 8, 1893, p. 48, pl. 3, fig. 6.
- Notommata limax* GOSSE, *Journ. Royal Mier. Soc.*, 1887, p. 862, pl. 14, fig. 3.—HUDSON and GOSSE, *Rotifera*, *Suppl.* 1889, p. 20, pl. 31, fig. 6.
- Notommata longipes* BERGENDAL, *Acta Univ. Lundensis*, vol. 28, 1892, sect. 2, No. 4, p. 66, pl. 2, fig. 20.
- Notommata lucens* GLASSCOTT, *Proc. Royal Dublin Soc.*, new ser., vol. 8, 1893, p. 79, pl. 6, fig. 6.
- Notommata megaladena* SCHMARDA, *Neue wirbellose Thiere*, 1859, vol. 1, p. 54, pl. 13, fig. 111.
- Notommata melanoglena* SCHMARDA, *Neue wirbellose Thiere*, 1859, vol. 1, p. 53, pl. 12, fig. 109.
- Notommata pentophthalma* HILGENDORF, *Trans. New Zealand Inst.*, vol. 31, 1899, p. 116, pl. 9, fig. 4.
- Notommata pleurotrocha* EHRENBERG, *Ber. Verh. Akad. Wiss. Berlin*, 1840, p. 218.
- Notommata rapax* GOSSE, *Journ. Royal Mier. Soc.*, 1887, p. 865.
- Notommata sulcata* SCHMARDA, *Neue wirbellose Thiere*, 1859, vol. 1, p. 53, pl. 13, fig. 110.
- Notommata symbiotica* KOZAR, *Kosmos* (Lwów), vol. 36, 1911, pp. 401, 407, figs. 14, 15. [= *Dicranophorus auritus* (Ehrenberg)?].
- Notommata tarda* BERGENDAL, *Acta Univ. Lundensis*, vol. 28, 1892, sect. 2, No. 4, p. 55, pl. 2, fig. 16.
- Notommata volitans* GLASSCOTT, *Proc. Royal Dublin Soc.*, new ser., vol. 8, 1893, p. 47, pl. 3, fig. 4.

NOTOMMATA EPAXIA Harring and Myers, new species.

Plate XXI, figures 1-5.

The body is very slender and almost cylindrical; its greatest width is less than one fifth of the total length. The integument is very flexible, but the outline is quite constant. It is a very transparent species.

The head and neck segments are separated by a slight transverse fold and a second and somewhat deeper fold divides the neck from the abdomen; the length of these two segments is nearly equal to their width. The abdomen is cylindrical for nearly its entire length; posteriorly it is rapidly reduced to the base of the foot. The tail has a single, moderately large, rounded lobe. The foot has two joints, the posterior very short, the anterior somewhat broader and longer. The toes are short, straight cones; their length is about one twentieth of the total length. The abdomen is longitudinally fluted dorsally and laterally; the ventral surface is smooth.

The dorsal antenna is a small setigerous pit in the normal position; the lateral antennae have not been observed.

The corona extends down on the ventral side about one fourth of the length of the body; the post-oral portion projects slightly from the body, forming a chin. The rostrum or cuticular fold on the apical plate is well marked. The auricles are rather small and provided with strong tufts of cilia, continuous with the corona.

The mastax is of the virgate or pumping type, but differs from the normal in having two large salivary glands on the ventral side, in the angles between the mallei and fulcrum. The trophi are robust and slightly asymmetric. The fulcrum is long, slender and tapering towards the posterior end, which is slightly expanded and incurved. The ventral portion of the rami is triangular; at the apex there is a strong, blunt tooth, and the inner margin of the dorsal portion is denticulate. There is a narrow, oval opening between the rami on the ventral side, below the anterior tooth; the edge of the right ramus opposite this opening is smooth, while the left ramus is denticulate and striate. The unci have a sub-square, lamellar basal plate; the ventral tooth is large and clubbed at the tip. The right uncus has two small, slender teeth close to the ventral tooth; from their base a diagonal rib crosses the uncus to the dorsal margin, where it joins a very slender fourth tooth.

The right uncus has only one slender tooth following the ventral tooth, but is otherwise identical with the left. At the point of the right uncus there are three very small accessory teeth; the left uncus has four similar teeth, gradually decreasing in size. The manubria are nearly straight, with a broad, subsquare lamella at their anterior ends. A pair of slightly curved rods are imbedded in the walls of the mastax near the posterior edge of the rami and parallel with the dorsal branch; their function is to aid in keeping the cavity open during the pumping action.

The oesophagus is long and slender. There is a slight constriction between the stomach and intestine. The gastric glands, ovary and bladder are normal. The foot glands are small and club-shaped; they discharge into a minute, spherical mucus reservoir at the base of the toes.

The ganglion is large and saccate. The retrocerebral sac is nearly spherical and the spaces between its vacuoles are crowded with bacteroids, giving it the appearance of being filled with small, black globules. The subcerebral glands are large and vacuolate, but ductless and fused with the ganglion. The eyespot is at the posterior end of the ganglion.

Total length 225–250 $\mu$ ; toes 12–14 $\mu$ ; trophi 38 $\mu$ .

*Notommata epaxia* was collected at Oceanville, near Atlantic City, New Jersey, where it occasionally occurs in small numbers. It is closely related to *N. aurita*, but is readily distinguished by its much more slender form, the striation and the much smaller retrocerebral sac, as well as the large mastax with its salivary glands.

**NOTOMMATA CODONELLA** Harring and Myers, new species.

Plate XXI, figures 6–10.

The body is elongate, slender and spindle-shaped; its greatest width is less than one fourth of the total length. The integument is very flexible, but the outline remains quite constant. The entire body is very transparent.

The transverse folds limiting the head and neck segments are well marked. The head segment is short and broad; the neck segment increases very slightly in width towards the posterior end; its length is somewhat greater than the width. The abdomen continues the outline of the neck segment and increases in width for about three fourths of its length; it is rounded posteriorly and ends in a very broad tail with a large, truncate median lobe and

two minute lateral lobes. The foot is two-jointed and very short; the basal joint does not project beyond the tail. The two toes are short, slender and conical; their inner margins are nearly straight and the outer slightly curved; the length is about one sixteenth of the total length.

The corona extends down on the ventral side about one fourth the length of the body; the post-oral portion projects from the body as a fairly prominent chin. The auricles are short and stout, with robust tufts of cilia, continuous with the corona.

The dorsal and lateral antennae are small setigerous papillae in the normal positions.

The mastax is of the normal virgate type and the trophi somewhat asymmetric. The fulcrum is long and slender and tapers towards the posterior end, which is slightly expanded and incurved. The rami have fairly deep transverse grooves below the accessory teeth of the unci; the right ramus has in front of this groove a broad, subsquare, lamellar tooth, projecting diagonally towards the left; the anterior margin is coarsely dentate. The dorsal section of the rami immediately below the unci is strongly curved and the inner, opposing edges crenate. The right uncus has a linear ventral tooth, followed by a strong, clubshaped tooth; behind this are two smaller, clubshaped teeth, very close together, and from their base a diagonal rib crosses the uncus to unite with a linear, rudimentary tooth just inside the dorsal margin of the basal plate uniting all the teeth. The left uncus has a linear ventral tooth and a stout, clubshaped tooth, larger than its mate on the opposite side; close to this there is a second, somewhat smaller tooth. From the base of this a somewhat curved, rudimentary fourth tooth crosses the basal plate diagonally; nearly parallel to this and separated from it by a considerable space is a rudimentary fifth tooth.

Short accessory teeth are attached to the ventral edges of the unci at their tips; the right uncus has four very slender teeth, and the left three broad, obtuse teeth, successively decreasing in size. The central section of the manubrium is very stout and curves towards the ventral side at the tip; the basal plate is large and irregular in outline. A pair of curved rods, attached at their ventral ends to the inner surfaces of the rami, pass under the manubria and terminate below the dorsal tips of the rami; they are imbedded in the walls of the mastax and assist in supporting them during the pumping action.

The oesophagus is long and slender. The gastric glands are small and rounded. There is no constriction between the stomach and intestine. The ovary and bladder are normal. The foot glands are short and pyriform.

The retrocerebral sac is elongate conical and truncate posteriorly; including the duct its length is fully one third of the length of the entire body. The subcerebral glands are elongate and fusiform; their length is one half the length of the sac. Bacteroids are abundant in the posterior end of the sac and in the glands beyond the level of the eyespot. The ganglion is relatively small and saccate; the eyespot is at its posterior end.

Total length 300–350 $\mu$ ; toes 18–21 $\mu$ ; trophi 38 $\mu$  long, 45 $\mu$  wide.

*Notommata codonella* is locally fairly common, but seems to be found only in neutral or slightly acid waters. We have collected it in a shallow bay of Range Line Lake, near Three Lakes, Oneida County, Wisconsin, and in ponds in Atlantic County, New Jersey. It is closely related to *N. cerberus*, *N. galena*, *N. collaris*, etc.; but is readily recognized by the retrocerebral sac and the broad, truncate tail.

**NOTOMMATA THOPICA** Harring and Myers, new species.

Plate XXII, figures 5–9.

The body is elongate, slender and spindle-shaped; its greatest width is less than one fourth of the total length. The integument is very flexible, but the outline remains fairly constant. The body is transparent, but somewhat milky.

The transverse folds limiting the head and neck segments are well marked. The head segment is short and broad; the neck segment is almost parallel-sided and its width nearly equal to its length. The abdomen is deeply striate longitudinally and increases very slightly in width for about two thirds of its length; it is rounded posteriorly and ends in a short tail with a very broad, rounded median lobe and two minute lateral lobes. The foot has two very short joints; the basal joint projects by about one half of its length beyond the tail. The two toes are short, slender and conical, ending in fairly acute points; their length is about one sixteenth of the total length.

The corona extends down on the ventral side about one fourth of the length of the body; the post-oral portion projects from the



body as a fairly prominent chin. The auricles are moderately large and the ciliation continuous with the corona.

The dorsal antenna is a large, circular papilla with a shallow central depression bearing a minute tuft of setae; the lateral antennae are minute tubules with a few long setae in the normal positions.

The mastax is virgate and slightly asymmetric. The fulcrum is long and moderately stout, tapering slightly towards the posterior end, which is somewhat enlarged and incurved. The ventral portion of the rami is roughly semicircular; at the apex there is on the left ramus a single, blunt tooth, interlocking with two similar teeth on the right ramus. The dorsal portion of the rami is not denticulate. There is a narrow opening between the ventral edges of the rami, beginning above the inconspicuous basal apophysis of the right ramus and limited anteriorly by the apical teeth; the edge of the right ramus opposite this opening is smooth, while the left has about 8 or 9 minute, close-set teeth or denticles. The alula of the left ramus, which is somewhat longer than the right, ends in a needle-like, slightly curved spur, which is characteristic for this species. The unci are asymmetric and have only one well developed tooth. The left uncus has a subsquare basal plate with a linear rudimentary tooth crossing diagonally from the base of the ventral tooth to a point close to the two parallel, rudimentary teeth at the dorsal margin. Close to the ventral tooth are two very small teeth, which are reduced to little more than the clubshaped points; between these and the diagonal tooth there is an additional, blunt, marginal tooth. The right uncus has a strongly curved, rudimentary tooth limiting the basal plate on the dorsal side; the diagonal tooth does not project beyond the margin of the basal plate. Following the ventral tooth are three rudimentary teeth, of which only the middle one can be traced beyond the margin of the basal plate. Four accessory teeth, gradually decreasing in size, are attached to the point of the left uncus; the right has three similar, but more slender teeth. The manubria are nearly straight, with a broad, subsquare basal plate; the posterior ends are slightly incurved and decurved posteriorly. A pair of supporting rods are imbedded in the walls of the mastax behind the posterior edges of the dorsal branch of the rami; their dorsal ends are slightly expanded and upcurved. The piston is large and muscular, filling the entire cavity of the mastax. There

are two large salivary glands in the ventral angles of the mastax, between the fulcrum and manubria.

The oesophagus is very long and slender. There is a slight reduction in diameter marking the separation of the stomach and intestine, but no distinct constriction. The gastric glands are large, thin and disc-shaped. The ovary and bladder are normal. The foot glands are small and pyriform; they discharge into a mucus reservoir at the base of the toe, nearly half as large as the gland itself.

The ganglion is moderately large and saccate. The retrocerebral sac is very long and pyriform; bacteroids are occasionally present, scattered through the posterior half of the sac. The subcerebral glands are saccate and almost as long as the sac; they always contain bacteroids, collected into very dense, globular masses, thus simulating an additional pair of eyespots. The true eyespot is at the posterior end of the ganglion, just below the dorsal antenna.

Total length 250–300 $\mu$ ; toes 15–18 $\mu$ ; trophi 36 $\mu$ .

*Notommata thopica* was first found by Mr. L. M. Dorsey, of the Philadelphia Academy of Natural Sciences, in a pond in Fairmount Park, Philadelphia, Pennsylvania. It is common at Bargaintown, near Atlantic City, New Jersey. It is closely related to *N. epaxia*, *N. codonella* and other species of the central group of the genus, but readily distinguished by the two globular aggregations of bacteroids in the subcerebral glands, as well as by the salivary glands. It is possible that this may be Ehrenberg's *Triophthalmus dorsualis*, but as he insists that the two additional eyespots are not to be confused with the black, granular masses of other Notommatids and *Otoglena*, it seems best not to use his name for this species, especially as it is not known whether it occurs in Germany at all. If his drawing really looks like the animal he saw, it is probably an *Eosphora*-species.

**NOTOMMATATA DONETA** Harring and Myers, new species.

Plate XXII, figures 1–4.

The body is slender and spindle-shaped; its greatest width is about one fifth of the total length. The integument is very flexible, but the outline is quite constant. It is a very transparent species.

The head and neck segments are of nearly equal length, a little less than their width. The anterior transverse folds are well marked. The abdomen increases very gradually in width for about

three fourths of its length and is rounded posteriorly; it is faintly plicate longitudinally. The tail is prominent and has a single, median, rounded lobe. The foot has two very short joints, the terminal smaller than the basal joint. The toes are long and very slender; the basal portion, about one third of the total length, is straight, and from this point they curve somewhat abruptly outwards and downwards, ending in very acute points. Their length is about one sixth of the total length.

The dorsal and lateral antennae are small setigerous papillae in the normal positions.

The corona extends down on the ventral side somewhat more than one fourth of the length of the body; the post-oral portion projects from the body as a small chin. The auricles are moderately large, and the ciliation is continuous with the corona.

The mastax is virgate and the trophi very nearly symmetrical. The rami are broadly triangular in ventral view and curve gradually from the base to the dorsal points. The basal apophysis is very prominent and is separated from the main portion of the ramus by a deep sinus. The inner margins of the rami are armed with about twelve minute teeth, beginning a short distance behind the basal sinus and continuing to the point of attachment of the unci, gradually increasing in length. The fulcrum is long and slender, tapering gradually to the posterior end, which is slightly incurved. The unci have a single, well developed ventral tooth and a rudimentary second tooth, crossing the basal plate diagonally to its dorsal angle. Seven small accessory teeth are attached to the point of the left uncus and six to the right uncus. The manubria are long and slender, with a small basal plate. A pair of slightly curved, slender rods are imbedded in the walls of the mastax below the posterior edge of the rami and assist in its support during the pumping action. The epipharynx consists of two very slender, tapering and decurved rods immediately in front of the unci.

The oesophagus is moderately long and slender. The gastric glands, ovary and bladder are normal. There is no distinct separation between stomach and intestine. The foot glands are small and pyriform.

The retrocerebral sac is large and rounded; bacteroids are not abundant. The subcerebral glands are very large, vacuolate and ductless; they are fused to the posterior end of the large, saccate

ganglion at the level of the eyespot without any distinct junction line.

Total length 275–300 $\mu$ ; toes 45–50 $\mu$ ; trophi 40 $\mu$ .

*Notommata doneta* is rare; we have found only a few specimens in Starvation Lake, about 4 miles south of Eagle River, Vilas County, Wisconsin, and at Oceanville, near Atlantic City, New Jersey. Its closest relatives are *N. aurita*, *N. cyrtopus* and *N. telmata*; the unusually long and peculiar toes are sufficient to distinguish it from these species.

**NOTOMMATA TITHASA** Harring and Myers, new species.

Plate XXIII, figures 1–5.

The body is elongate, spindle-shaped and slender; its greatest width is about one fifth of the total length. The integument is very flexible and the outline is constantly changing in response to the contractions of the animal. The entire body is transparent, but has a very faint yellowish tinge.

The neck is very slightly constricted, but no anterior transverse folds are present. The head is rather small and triangular in dorsal view on account of a large, slightly obtuse rostrum. The abdomen increases very gradually in width for about three fourths of its length and then tapers somewhat more rapidly to a broad tail projecting very slightly from the body. The foot is stout, fairly long and obscurely wrinkled. The toes are very long and stout, incurved and decurved; the ventral edge does not curve evenly, but is faintly indented near the tip and a short distance from the base. Their length is one eighth of the total length.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae are somewhat farther back than usual.

The corona has two large, strongly ciliated areas corresponding to the auricles of other Notommatids, but not evertile. The buccal field is evenly ciliated and continues down on the ventral side of the body for about one fourth of its length, forming posteriorly a slight chin. The dorsal arc of the circumapical band has disappeared.

The mastax is of a very simple virgate type and the trophi very small. The fulcrum is rodlike and very slender, slightly curved posteriorly. The rami are triangular and without denticulations on the inner margins, which do not quite meet, but enclose

a narrow, elongate, ventral opening; the alulae are very large and curved. The unci are small, triangular lamellae with a very faint median tooth. The manubria show no indication of cellular division; the basal plate is triangular and the posterior portion rodlike, ending in a small crutch. Instead of being approximately parallel to the longitudinal axis of the mastax, as in other species of the genus, the manubria are nearly at right angles to it. The epipharynx consists of two small, very thin, triangular plates, imbedded in the walls of the mastax at the sides of the mouth. The piston is large, but very weak.

The oesophagus is moderately long and slender. There is no constriction between stomach and intestine. The gastric glands are small and rounded. The ovary and bladder are normal. The foot glands are pyriform and nearly as long as the foot.

The ganglion is an elongate, pyriform sac; at its posterior end is a rounded, moderately large, ductless retrocerebral sac, which does not contain bacteroids. No eyespot is present.

Total length 175–200 $\mu$ ; toes 25–28 $\mu$ ; trophi 15 $\mu$ .

*Notommata tithasa* is not common; we have found it at Three Lakes, Oneida County, Wisconsin, and in ponds around Atlantic City, New Jersey; a few specimens occurred in some collections made by Dr. H. S. Jennings in the Huron River at Ann Arbor, Michigan. This species is readily recognized by the unusually long and robust toes.

#### Genus TAPHROCAMPA Gosse.

Notommatid rotifers with cylindric or spindle-shaped, illoricate or semiloricate body, marked with permanent or evanescent transverse folds; the foot is rudimentary and the cloaca opens dorsally at the base of the toes, under a projecting fold of the integument or tail.

The corona is an elongate oval area covering the oblique anterior surface of the head and continuing beyond the mouth on the ventral surface; the marginal cilia are relatively short, except on the auricles, which have long and powerful cilia adapted to swimming. The apical plate is enclosed by the marginal ciliation; a rostrum may be present; the buccal field is covered with short, dense cilia; the mouth is approximately in the center of the corona.

The mastax is virgate with strongly asymmetric trophi; the fulcrum is long and slender and nearly at a right angle to the

roughly hemispherical rami; the manubria are long and slender with a rudimentary basal plate; the unci have a strongly developed ventral tooth and one or two additional, rudimentary teeth. The piston is very large and fills the entire cavity of the mastax. The rodshaped transverse supports, which are found imbedded in the walls of the mastax below the posterior margin of the rami in many Notommatids, are absent in this genus.

The retrocerebral sac is present in all of the species, but there are no subcerebral glands. The eyespot is at the posterior end of the ganglion.

*Type of the genus.*—*Taphrocampa annulosa* Gosse.

TAPHROCAMPA ANNULOSA Gosse.

Plate XXIII, figures 6-10.

*Taphrocampa annulosa* GOSSE, Ann. Mag. Nat. Hist., ser. 2, vol. 8, 1851, p. 199.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 16, pl. 17, fig. 12.—PETR, Sitzungsber. Böhm. Ges. Wiss. (for 1890), 1891, p. 220.—TERNETZ, Rotat. Umg. Basels, 1892, p. 11.—GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 43.—WIERZEJSKI, Rozpr. Akad. Umiej., Wyzd. Mat.-Pryzr., Krakow, ser. 2, vol. 6, 1893, p. 227.—LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 26.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 433, pl. 17, figs. 11-13.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 123. HEMPEL, Bull. Illinois State Lab. Nat. Hist., vol. 5, 1898, p. 369.—JENNINGS, Bull. U. S. Fish Comm., vol. 19 (for 1899), 1900, p. 84, pl. 16, figs. 13, 14.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 38; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 92, fig. 165.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 197.—KOFOD, Bull. Illinois State Lab. Nat. Hist., vol. 8, No. 1, 1908, p. 217.—LIE-PETTERSEN, Bergens Mus. Aarb. (for 1909), 1910, No. 15, p. 38.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 240.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 105.

The body is elongate, slender and very nearly cylindric, tapering slightly to the foot; its greatest width is about one fourth of the total length. The integument is leathery and almost semiloriculate; its dorsal surface is viscous and usually covered with adhering particles of floccose material.

There is no distinct separation between the head and abdomen; both are transversely plicate, about ten ridges in the entire length, of which three may be taken as belonging to the head. The plications do not form rings around the body; the lateral ridges alternate with those of the dorsal surface, forming a sort of "bellows"-fold. The ventral surface is very faintly plicate. The tail is as

wide as the body and rounded posteriorly; it is separated from the abdomen by a deep transverse groove. The foot is short and very broad; it has no joints. The toes are rather short, slender, conical and slightly decurved; their length is about one fifteenth of the length of the body, and they are separated by an interspace of nearly half their length.

The dorsal antenna is a minute setigerous pit in the normal position; the lateral antennae have not been observed.

The corona is strongly oblique and extends down on the ventral side about one fourth of the length of the body; the post-oral portion projects very slightly from the body, but does not form a chin. The auricles are small and rounded; the ciliation is continuous with the corona. The mouth is nearly in the center.

The mastax is virgate with very slender and slightly asymmetric trophi of a simple type. The fulcrum is long and slender, tapering gradually to the posterior end, which is expanded into an oval plate for the attachment of the muscles of the piston. The rami are approximately triangular in ventral view and have well developed alulae, ending in acute points; the right ramus has below the apex a small, blunt tooth, fitting into a recess on the left ramus. On the external edge of the rami there is a strongly curved dorsal extension, which forms a nearly right angle with the rami; a deep sinus separates it anteriorly from the points of the rami. The unci have two teeth, of which the ventral one is more robust than the second tooth; the basal plate is very narrow and lamellar, with a rudimentary tooth at its dorsal edge. The manubria are slightly curved near the base; the posterior portion is straight and very slender, ending in a spatulate expansion, which curves slightly inwards. The piston is very large and fills the entire cavity of the mastax.

The oesophagus is moderately long and begins high up on the mastax. The gastric glands, ovary and bladder are normal. There is a slight constriction between the stomach and intestine. The foot glands are small and pyriform.

The ganglion is large and saccate. The retrocerebral organ consists of a small, pyriform sac, usually filled with bacteroids. The eyespot is at the posterior end of the ganglion.

Total length 175–200 $\mu$ ; toes 12–15 $\mu$ ; trophi 26 $\mu$ .

*Taphrocampa annulosa* is common everywhere in ponds and among wet mosses. It is closely related to *Taphrocampa selenura*,

but is readily distinguished by its smaller size and short toes, as well as by the differences in the trophi.

**TAPHROCAMPA SELENURA** Gosse.

Plate XXIV, figures 5-9.

- Taphrocampa selenura* GOSSE, Journ. Royal Micr. Soc., 1887, p. 1, pl. 1, fig. 1.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 20, pl. 31, fig. 5.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 227.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 436, pl. 17, figs. 14, 15.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 38; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 92, fig. 166.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 95.—MONTET, Rev. Suisse Zool. vol. 23, 1915, p. 325.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 106.
- Taphrocampa viscosa* LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 26, pl. 2, fig. 14.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 123.

The body is elongate, slender and very nearly cylindrical, tapering slightly to the foot; its greatest width is about one fifth of the total length. The integument is leathery and almost semiorlicate; its surface is viscous and usually covered with adhering particles of floccose material.

There is no distinct separation between the head and abdomen; both are transversely plicate, about eleven ridges in the entire length, of which three may be considered as belonging to the head. The plications do not form rings around the body; the lateral ridges alternate with those on the dorsal surface and meet them in a "bellows"-fold. The ventral surface is very faintly plicate. The tail is slightly narrower than the body and rounded posteriorly; it is separated from the abdomen by a deep transverse groove. The foot is rudimentary, the anus opening just above the toes; these are long, slender, tapering and decurved; they are far apart at the base and form nearly a semicircle, when seen from the dorsal or ventral side; their length is about one ninth of the total length.

The dorsal antenna is a minute setigerous pit in the normal position; the lateral antennae have not been observed.

The corona is strongly oblique and extends down on the ventral side for nearly one third of the length of the body; there is no chin. The auricles are small and rounded; the ciliation is continuous with the corona. The mouth is a little below the center.



The mastax is virgate and the trophi slender and strongly asymmetric, the left side being more strongly developed than the right. The fulcrum is long and slender and tapers towards the posterior end, which is slightly enlarged and bent inwards, providing attachment for the muscles of the piston. The rami appear triangular in ventral view and are bent nearly at a right angle at the extreme anterior point. The left ramus has near the base a prominent, blunt tooth on its inner edge, and immediately behind this a broad, lamellar and finely striated tooth. Near the anterior angle there are two large teeth, separated by a slight interspace. The right ramus is coarsely denticulate; about eight rudimentary teeth are present. The left uncus has a large ventral tooth, followed by a much smaller and shorter second tooth; the right uncus has a similar ventral tooth, followed by two smaller teeth; the basal plates are somewhat triangular in outline and bordered by a marginal rib. The manubria have a subsquare basal plate, with a straight posterior branch ending in a triangular, plate-like expansion. The piston is large and fills the entire cavity of the mastax.

The oesophagus is moderately long and begins high up on the mastax. The gastric glands, ovary and bladder are normal. There is no distinct separation between the stomach and intestine. The foot glands are small and pyriform.

The ganglion is moderately large and saccate. The retrocerebral organ consists of a rather small, pyriform sac, usually opaque with bacteroids. The eyespot is at the posterior end of the ganglion.

Total length 225–275 $\mu$ ; toes 25–30 $\mu$ ; trophi 36 $\mu$ .

*Taphrocampa selenura* is widely distributed, but always in small numbers. It is closely related to *Taphrocampa annulosa*, but is readily distinguished by its larger size, as well as by the peculiar form of the toes and the more robust trophi.

#### TAPHROCAMPA CLAVIGERA Stokes.

Plate XXIV, figures 1–4.

*Taphrocampa clavigera* STOKES, Ann. Mag. Nat. Hist., ser. 6, vol. 18, 1896, p. 18, pl. 7, fig. 2.

The body is elongate, fusiform and very slender; its greatest width is about one sixth of the total length. The integument is soft and very flexible and the outline is constantly changing.

There is no distinct separation between the head and abdomen; the contracted animal is marked with evanescent annulations,

which disappear when the body is fully extended in swimming. There is no true foot and the tail is a small fold above the toes; between the toes is a minute, but quite distinct, rounded papilla. The toes are short, slightly decurved and emarginate on their inner edges, which gives them the appearance of being clawed; their length is about one twentieth of the length of the body.

The dorsal antenna is a minute setigerous papilla in the normal position; the lateral antennæ have not been observed.

The corona extends down on the ventral side somewhat more than one fourth of the length of the body. The auricles are small and rounded; a fairly prominent rostrum is present and curves down over the corona. The mouth is a little below the center.

The mastax is virgate with strongly asymmetric trophi of a simple type. The fulcrum is very long and slender, tapering gradually towards the posterior end, which is expanded into an oval plate for the attachment of the muscles of the piston. The rami are roughly triangular in ventral view; the dorsal branch forms an acute angle with the ventral portion. The alula of the left ramus is nearly as long as the ventral part of the ramus itself and forms a very acute angle with the fulcrum. The right alula is smaller and somewhat more divergent; it is excavate dorsally and the sinus is reinforced by a strong rib, easily seen in the ventral view. The unci have a strong ventral tooth, followed by a much smaller second tooth. The manubria are rodlike and formed entirely by the median cell, only a slight ventral hump indicating the normal posterior limit of the ventral cell. The right manubrium is only two thirds as long as the left, and both are slightly expanded at the posterior end. The piston is very large and fills the entire cavity of the mastax. Two salivary glands are present; the left gland is very large and curves under the mastax, while the right gland is rudimentary and apparently not functional.

The oesophagus is long and slender. The gastric glands are very small and rounded. There is no distinct separation between stomach and intestine. The bladder is formed by an expansion of the cloaca. The foot glands are large and slightly club-shaped. The ovary is normal.

The ganglion is large and elongate saccate. The retrocerebral organ consists of a small, pyriform sac, usually opaque with bacteroids; no subcerebral glands are present. The eyespot is a granular mass of red pigment at the posterior end of the ganglion.

Total length 150–200 $\mu$  toes 8–10 $\mu$  trophi 28 $\mu$ .

*Taphrocampa clavigera* was collected by Stokes at Trenton, New Jersey; our material is from Bargaintown, near Atlantic City, where it occurs occasionally in small numbers. While without the pronounced, permanent annulations of *T. annulosa* and *selenura*, it is evidently closely related to these two species; the mastax differs only in details from that of *T. annulosa*.

Genus **DRILOPHAGA** Vejdovský.

Notommatid rotifers with elongate, slender, spindle-shaped, illoricate body, usually without distinct separation of head and body and with very flexible integument; the head is cylindric and elongate, with the mouth at a considerable distance from the front; the tail is rudimentary and the foot very short and apparently unjointed; the toes are minute and conical.

The corona is reduced to a simple, circumapical ring of cilia.

The mastax is virgate and the trophi of very simple form, usually protrusile and adapted as organs of attachment to the body of the host; rami large and strongly curved, without denticulation on the inner margin; mallei slender and rodshaped, unci reduced to small, oval plates; salivary glands very large.

Neither retrocerebral organ nor eyespot are present.

At least two of the species are ectoparasitic on oligochaete worms; the third species appears to be free-living.

*Type of the genus.*—*Drilophaga bucephalus* Vejdovský.

This genus includes, in addition to *D. judayi*, described in volume twenty, two other species, listed below. Neither has been studied by anybody but the original discoverer.

*Drilophaga bucephalus* VEJDOVSKY, Sitzungsber. Böhm. Ges. Wiss. Prag (for 1882), 1883, p. 390, pl. 1, figs. 1-8.—DE BEAUCHAMP, Bull. Soc. Zool. France, vol. 29, 1904, p. 157, figs. A, B.

*Drilophaga delagei* DE BEAUCHAMP, Bull. Soc. Zool. France, vol. 29, 1904, p. 159, fig. C; vol. 30, 1905, p. 121, fig. 3.

Genus **PLEUROTROCHA** Ehrenberg.

Notommatid rotifers with short, stout, illoricate, ovoid or globose body, with a distinct neck separating the head and abdomen; the foot is long and cylindric or slightly tapering; the toes are very short and conical and may be either separate or fused.

The corona is slightly oblique and consists of a marginal wreath of cilia with lateral, auricle-like tufts of long cilia adapted to swimming; the apical plate is unciliated and the buccal field evenly covered with short, close-set cilia; the mouth is near the ventral edge of the corona.

The mastax is virgate and the trophi very simple; the fulcrum is long and rodlike, the rami triangular, curved and not denticulate; the manubria are very long and the basal plate much reduced; the unci are feeble and have only a single distinct tooth; the piston is very large.

The eyespot is single and at the posterior end or on the lower surface of the ganglion; there is no trace of the retrocerebral organ.

*Type of the genus.*—*Pleurotrocha petromyzon* Ehrenberg.

This genus was created by Ehrenberg for *P. petromyzon*, which he supposed to be without an eyespot. When the error was discovered, he transferred this species to his "Noah's Ark," the genus *Notommata*, into which he thrust all illoricate, freeswimming rotifers with cervical eyespot. He then proceeded, in accordance with his usual custom, to use the generic name for other species without eyespots and subsequent authors have followed him in this change of concept. As *P. petromyzon* does not belong to *Notommata* as now understood, the original generic name must be used for it, and the obscure species later referred to *Pleurotrocha*, listed below, must be placed on a firm foundation or dropped as insufficiently described.

*Pleurotrocha aurita* BERGENDAL, Acta Univ. Lundensis, vol. 28, 1892, sect. 2, No. 4, p. 49, pl. 2, fig. 15.

*Pleurotrocha constricta* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 129; Infusionsthierchen, 1838, p. 419, pl. 48, fig. 1.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 19, pl. 18, fig. 3.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 12.

*Pleurotrocha gibba* (Ehrenberg).

*Hydatina gibba* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 127.

*Pleurotrocha gibba* EHRENBERG, Infusionsthierchen, 1838, p. 418, pl. 47, fig. 4.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 20, pl. 18, fig. 5.

*Theora gibba* EYFERTH, Mikroskopische Süßwasserbewohner, 1877, p. 51; Einfachsten Lebensformen, 1878, p. 83; 1885, p. 108.

*Pleurotrocha renalis* EHRENBERG, Monatsber. Akad. Wiss. Berlin, 1840, p. 218.

*Pleurotrocha truncata* Gosse.

*Pleurotrocha truncata* GOSSE, Ann. Mag. Nat. Hist., ser. 2, vol. 8, 1851, p. 199.

*Theora truncata* ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 372.

**PLEUROTROCHA PETROMYZON Ehrenberg.**

Plate XXV, figures 1-4.

*Pleurotrocha petromyzon* EHRENBERG, Abh. Akad. Wiss. Berlin, 1830, p. 46.—  
VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 12.

? *Notommata gibba* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 132, pl. 4, fig. 15; Infusionsthierchen, 1838, p. 430, pl. 52, fig. 4.

*Notommata petromyzon* EHRENBERG, Infusionsthierchen, 1838, p. 427, pl. 50, fig. 7.—GOSSE, Phil. Trans. Royal Soc. London, vol. 146, 1856, p. 432, pl. 17, figs. 27-31.

*Proales petromyzon* HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 37, pl. 18, fig. 9.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 30.—HOOD, Proc. Royal Irish Acad., ser. 3, vol. 3, 1895, p. 680.—SKORIKOV, Trav. Soc. Nat. Khar-kow, vol. 30, 1896, p. 291.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 469, pl. 18, figs. 21-23.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 42; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 90, fig. 160.—DE BEAUCHAMP, Arch. Zool. Expér., ser. 4, vol. 6, 1907, p. 9, fig. 5.—LIE-PETERSEN, Bergens Mus. Aarbog (for 1909), 1910, No. 15, p. 43.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 243.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 322.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 16.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 99.

*Notops laurentinus* JENNINGS, Bull. Michigan Fish Comm., No. 3, 1894, p. 12, figs. 3, 4.

*Proales laurentinus* JENNINGS, Bull. Michigan Fish Comm., No. 6, 1896, p. 91.  
*Pleurotrocha laurentina* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 85.

The body is short, stout and gibbous; its greatest width is about one third of the entire length. The integument is soft and very flexible, but the general outline is nevertheless quite constant. The body is very transparent.

The head and abdomen are separated by a rather shallow constriction. The head is small and short and somewhat oblique anteriorly. The abdomen is pyriform and tapers posteriorly to the base of the foot; there is no tail. The foot is long, cylindric and two-jointed; the length of the basal joint is equal to its width and the terminal joint is twice the length of the basal. The toes are very short, conical, acutely pointed and very slightly recurved at the tips; their length is about one twentieth of the length of the body.

The antennae are minute setigerous papillae, the dorsal in the normal position, the lateral just beyond mid-length.

The corona is frontal and consists of a circumapical band of cilia with two strongly developed lateral, auricle-like tufts of cilia adapted to swimming; the buccal field is evenly ciliated and the mouth is near the ventral edge of the corona.

The mastax is virgate and the trophi of very simple form. The rami are approximately triangular, strongly curved longitudinally and have large, rounded alulae. The fulcrum is a very long, slender, tapering rod, incurved and slightly expanded at the posterior end. The unci are triangular plates with one weak ventral and a rudimentary second tooth; additional teeth are represented by three faint striae. The manubria are long and double-curved, tapering gradually from the broad base to the posterior end; near mid-length there is a small projecting lobe on the ventral edge; their longitudinal direction is nearly at right angles to the fulcrum. Two small curved rods are imbedded in the anterior walls of the mastax and serve to support the edges of the mouth during the pumping action.

The oesophagus is short and slender. The gastric glands are elongate oval and strongly compressed laterally. There is no constriction separating the stomach and intestine. The ovary is large and of a somewhat irregularly oval outline. A small bladder is present. The foot glands are very long and nearly cylindrical; they discharge into a large mucus reservoir at the base of the toes.

The ganglion is large and saccate, reaching nearly to the posterior end of the mastax. No retrocerebral organ is present. The eyespot is at the extreme end of the ganglion and consists of a very small sphere of minute pigment granules.

Total length 225–250 $\mu$ ; toes 12 $\mu$ ; trophi 32 $\mu$ .

*Pleurotrocha petromyzon* is cosmopolitan in its distribution, but does not usually occur in large numbers. It has been reported as attaching itself to other living organisms (Infusoria, Entomotraca); we have not observed it in this condition and do not know under what circumstances it occurs. It is evidently not a case of parasitism, in the proper sense of this word, but rather one of synœcia or "Raumparasitismus"; the rotifer obtains free transportation and probably nothing more. The highly developed foot glands point to the possibility of an adaptation of this kind; they are found in all rotifers that are known to be synœcious or pseudo-parasitic.

PLEUROTROCHA ROBUSTA (Glasscott).

Plate XXV, figures 5-8.

*Microcodon robustus* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 40, pl. 3, fig. 2.

*Microcodides robustus* ROUSSELET, Journ. Quekett Micr. Club, ser. 2, vol. 6, 1895, p. 121, pl. 6, fig. 1.

? *Microcodides abbreviatus* STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 113, pl. 1, fig. 20.

*Mikrocodides robustus* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 71.

The body is short, stout and gibbous; its greatest width is about two fifths of the entire length. The integument is leathery and the outline remains quite constant. The entire body is very transparent.

The head and abdomen are separated by a deep constriction. The head segment is short and very broad; its width is about two thirds of the greatest width of the body. The abdomen is globose and ends in a short, sleeve-like tail surrounding the base of the foot. On the posterior half of the abdomen are five or six well marked longitudinal folds; they are continuous from side to side and not interrupted posteriorly. The foot is long, stout and slightly tapering; it has three joints of approximately equal length. The toe is single and abruptly reduced near the middle; its length is a little less than one tenth of the total length of the animal. As there are two well developed foot glands it is evident that the single toe is a result of the fusion of two originally separate toes.

The dorsal antenna is a large, knoblike elevation on the posterior part of the head, immediately in front of the neck; it has a funnel-shaped central depression with a small tuft of sensory setae. The lateral antennae are minute tubules with a few very short setae in the normal position.

The corona is oblique and consists of a circumapical band of cilia with two lateral, auricle-like tufts of strong cilia adapted to swimming; the buccal field is evenly ciliated. The mouth is in the normal position, near the ventral margin of the corona, and not in the center, as stated by Rousselet.

The mastax is virgate and of very simple form. The fulcrum is very long, slender and tapering; the posterior end is slightly expanded for the attachment of the muscles of the piston. The rami are roughly triangular and without teeth or denticulations; a somewhat abrupt bend divides them into a rather short ventral

and a long dorsal section. The alulae are very prominent. The unci have only one tooth, slender and clubbed at the tip; there is no basal plate. The manubria are very long and their general direction is nearly at right angles to the fulcrum, so that they almost reach the dorsal side; the basal plate is small and its edges are parallel to the strongly curved anterior end of the principal rib; the posterior branch is very slender and slightly recurved. The piston is bulky, but not very powerful. The epipharynx consists of two slender, strongly curved rods, imbedded in the walls of the mastax at the sides of the mouth.

The oesophagus is short and slender. There is no constriction between stomach and intestine. The gastric glands are small and nearly spherical. The ovary is irregularly elongate and reaches from the bladder nearly to the mastax; the nuclei are large and irregularly polygonal. A fairly large bladder is present. The two foot glands are tapering and fully as long as the foot.

The ganglion is large and saccate. There is no trace of the retrocerebral organ. The eyespot is well towards the front of the head and seems to be seated on the mastax instead of the lower surface of the ganglion, as it follows the movements of the mastax.

Total length 180–200 $\mu$ ; foot and toes 55–60 $\mu$ ; toes 16–18 $\mu$ ; trophi 22 $\mu$ .

*Pleurotrocha robusta* is rather rare; we have found it in Oneida and Vilas Counties, Wisconsin, and in ponds and ditches around Atlantic City, New Jersey. As this species has nothing in common with *Mikrocodides chlaena* except the fused toes, it has been transferred to *Pleurotrocha*, with which it seems to agree fairly well. No good reasons ever existed for referring it to *Mikrocodides*; the fused toes can not be considered a generic character to the exclusion of everything else. The supposed identity of the corona in the two species is an error; neither *M. chlaena* nor *P. robusta* has the mouth at the center of the corona; as pointed out by De Beauchamp, *M. chlaena* has a corona of the type of *Cyrtonia*, and the mastax is malleate.

#### Genus CEPHALODELLA Bory de St. Vincent.

Notommatid rotifers with prismatic or spindle-shaped, illoricate or partly loricate body, having a slight constriction or neck separating the head and abdomen and passing without definite limit to the rudimentary foot, which is not jointed and has two slender toes.



The corona is an obliquely frontal disc with long marginal cilia and two lateral tufts of densely set long cilia, especially adapted to swimming; the apical plate is enclosed by the marginal ciliation; the buccal field is sparsely ciliated. The mouth is slightly below the center of the corona and the lips occasionally project as a "beak."

The mastax is virgate; the fulcrum is long and straight, nearly always slightly expanded at the posterior end to provide a greater surface for the attachment of the muscles of the piston; the rami are imperfectly developed, the uncus having only a single, slender tooth and the manubrium usually rodshaped, with or without a terminal crutch; the piston is a large, powerful muscle attached to the fulcrum and filling the entire cavity of the mastax.

The retrocerebral organ is absent in nearly all the species and rudimentary when present, being limited to a small sac with partially atrophied duct, which does not reach the surface of the corona. The eyespot may be cervical, frontal (single or double) or absent.

*Type of the genus.*—*Cephalodella catellina* (Müller)=*Cercaria catellina* Müller.

The definition of this genus, which includes all the species of *Diaschiza* Gosse, as revised by Dixon-Nuttall and Freeman, has been broadened sufficiently to admit some evidently closely related species. We have based it on the peculiar form of the body, a head segment separated from the abdomen by a slight constriction, no distinct separation between the abdomen and foot, corona slightly oblique with mouth near the center, and the specialized type of the virgate mastax, which varies only in minute details throughout the genus as here constituted. We do not consider the divided lorica as a generic character; in many species it is only a polite fiction. Neither can the small tuft of setae at the base of the toes be accepted as such; it is so difficult to find that we have made no use of it; although the genus includes a great many species, they are readily distinguished by easily ascertainable differences.

The "beak" must be observed in the living animal; in preserved material the lips nearly always project somewhat. We have not figured the trophi of all the species included, as the differences are slight, but enough have been given to show the range of variation within the genus.

The change of the familiar name *Diaschiza* is regrettable, but is seemingly made unavoidable by the inclusion of *Diglena catellina*, of Ehrenberg and Gosse. De Beauchamp\* objects to identifying Ehrenberg's animal with Müller's *Cercaria catellina*, reproducing the figures of Müller and Weber. We are quite willing to admit that Müller's figure is, to say the least, poor, but Weber's is not a great deal better, especially if consideration is given to the improvements made in optical instruments in the interval between 1786 and 1888. The usual custom in similar doubtful cases is to abide by the choice of the "first reviser", a distinction clearly belonging to Ehrenberg. As he claims to have recognized *Cercaria catellina* Müller, the simplest and most consistent procedure is to accept the identification as correct. Denying it would not dispose of the generic name *Diglena*; although this was originally defined by a synonymic citation only, there is no doubt about the identity of the animal for which Ehrenberg created the genus. His figure in the *Infusionsthierchen* of 1838 is unmistakable and this species must remain the type of *Diglena*, whether it retains the specific name *catellina* (Müller) or the next available, probably *granularis* Weisse, used for the male; for the reasons given above it seems preferable to use *catellina* (Müller). However, this had already been made the type of a genus *Cephalodella* by Bory de St. Vincent in his compilation of 1826, which under the circumstances may be considered fortunate, as it obviates the displacement of the name *Diaschiza* by *Diglena* Ehrenberg, which has long been used for the forcipate Notommatids. Such transpositions are very confusing, even when absolutely unavoidable.

*Diaschiza* Gosse is not tenable under any circumstances; Dujardin created a genus *Plagiognatha* in 1841, designating as type *P. felis*, in his opinion identical with Müller's *Vorticella felis*, but his figure shows beyond reasonable doubt that the animal he actually studied was Ehrenberg's *Furcularia gibba*, more familiar as *Diaschiza gibba*. Consequently, as *Diaschiza* can not possibly be retained, the least objectionable solution appears to be the resurrection of *Cephalodella* Bory de St. Vincent, a course already suggested by Eyferth (*Einfachsten Lebensformen*, 1878, p. 83, *Diglena*):

“ . . . *D. catellina*, die gemeinste von allen, ist jedenfalls abzutrennen. In der Form des Kauers und der Derbheit der Cuticula steht sie (wie *Notom-*

\*Bull. Soc. Zool. France, vol. 38, 1914, p. 291 ff.

*mata lacinulata*) der *Furcularia* näher, von der sie aber durch den sehr kurzen Fuss zu stark abweicht. Am besten würde sie unter dem alten Namen *Cephalodella* Bory als besondere Gattung abzusondern sein.''

The three species listed below evidently belong to this genus. They have not occurred in our collections and all appear to be rare; *C. crassipes* and *C. leptodactyla* were described from single specimens.

**CEPHALODELLA CRASSIPES (Lord)**

*Diaschiza crassipes* LORD, Trans. Manchester Micr. Soc. (for 1903), 1904, p. 78, pl. 3, fig. 3.

**CEPHALODELLA DERBYI (Dixon-Nuttall and Freeman).**

*Diaschiza derbyi* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 131, pl. 4, fig. 13.

**CEPHALODELLA LEPTODACTYLA (Hauer).**

*Furcularia leptodactyla* HAUER, Mitt. Bad. Landesver. Naturk., Freiburg i. Br., new ser., vol. 1, 1921, p. 183; Arch. Hydrobiol., vol. 13, 1922, p. 693, pl. 9, fig. 1.

**CEPHALODELLA CAPELLINA (Müller).**

Plate XXVII, figures 3-5.

- Cercaria catellina* MÜLLER, Anim. Infus., 1786, p. 130, pl. 20, figs. 12, 13.  
*Vorticella larva* MÜLLER, Anim. Infus., 1786, p. 286, pl. 40, figs. 1-3.  
*Furcocerca catellina* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 1, 1815, p. 448.  
*Furcularia larva* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 2, 1816, p. 37.  
*Cephalodella catellina* BORY DE ST. VINCENT, Class. Anim. Micr., 1826, p. 43.  
 —HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 24.—KOZAR, Zool. Anz., vol. 44, 1914, p. 416.  
*Dicranophorus catellinus* NITZSCH, Enc. Wiss. u. Künste, sect. 1, vol. 16, 1827, p. 68.  
*Diglena catellina* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1829), 1830, p. 8; (for 1831), 1832, p. 137, pl. 4, fig. 17; Infusionsthierchen, 1838, p. 444, pl. 55, fig. 3.—BARTSCH, Jahresh. Ver. Naturk. Württemberg, vol. 26, 1870, p. 39.—DADAY, Erdélyi Múz.-Egyt. Evkôn., new ser., vol. 2, pp. 198, 217, pl. 9, figs. 1-3.—ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 371, pl. 26, figs. 40, 41.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 53, pl. 19, fig. 10.—WEBER, Arch. Biol., Liège, vol. 8, 1888, p. 46, pl. 34, figs. 1-6; Rev. Suisse Zool., vol. 5, 1898, p. 492, pl. 19, figs. 12-14.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 232.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 31.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 48.—DE BEAUCHAMP, Arch. Zool. Expér., ser. 4, vol. 10, 1909, p. 280; Bull. Soc. Zool. France, vol. 38, 1914, p. 297, fig. 1.—LUCKS, Rotatorienfauna Westpreussens, 1912, p. 56.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912,

- p. 106, fig. 199.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 246.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 329.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 19.—WHITNEY, Journ. Exper. Zool., vol. 20, 1916, p. 274, figs. 4, 5.
- ? *Leiodina capitata* MORREN, Ann. Sci. Nat., vol. 21, 1830, p. 124, pl. 3, fig. 2; Bijdr. Natuurk. Wetensch., vol. 5, 1830, p. 211, fig.
- Furcularia catellina* BLAINVILLE, Dict. Sci. Nat., vol. 60, 1830, p. 152.
- Typhlina furca* EHRENBERG, in Hemprich and Ehrenberg, Symb. Phys. Anim. Evert., 1831 (1832?), pl. 1, figs. 17 b, 2, 3; not *Cercaria furca* Müller.
- Plagiognatha catellina* DUJARDIN, Hist. Nat. Zooph., Inf., 1841, p. 652.
- Plagiognatha hyptopus* DUJARDIN, Hist. Nat. Zooph., Inf., 1841, p. 653, pl. 21, fig. 8; not *Notommata hyptopus* Ehrenberg.
- Diglina granularis* WEISSE, Bull. Phys.-Math. Acad. St. Petersburg, vol. 8, 1849, col. 300.
- ? *Heterognathus diglenus* SCHMARDA, Neue wirbellose Thiere, vol. 1, 1859, p. 52, pl. 12, fig. 107.
- ? *Notops forcipita* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 79, pl. 6, fig. 5.
- ? *Proales algicola* KELLICOTT, Trans. Amer. Micr. Soc., vol. 19, 1897, p. 48.
- ? *Diaschiza tenuior* MURRAY, Brit. Antarctic Exped. 1907-9. Rep. Sci. Inv., vol. 1, 1910, p. 57, pl. 13, fig. 16.
- ? *Diglina volvocicola* ZAVADOVSKI, Uchen. Zap. Moskovsk. Gor. Univ. Shaniavskago, vol. 1, 1916, p. 246, pl. 3, text figs. 1-19.
- ? *Diglina catellina parasitica* ZAVADOVSKI, Uchen. Zap. Moskovsk. Gor. Univ. Shaniavskago, vol. 1, pt. 2, 1916, App., p. 4.
- Diaschiza catellina* WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 143.

The body is short, stout and strongly gibbous dorsally. The head is very large and oblique anteriorly. The neck is not very strongly marked. The abdomen is strongly compressed laterally; the ventral edge is nearly straight, the dorsal gently curved for about two thirds of its length and the posterior third rounded. The lorica is rather flexible, and the plates somewhat indistinct; the lateral clefts are wide and parallel-sided. The small, short foot is wholly ventral and the posterior portion of the abdomen projects over and beyond it as a huge tail. The toes are short, almost straight and taper gradually to acute points; when closely appressed to the body, they project very little beyond the tail; their length is about one fifth of the total length.

The corona is very strongly oblique and distinctly convex without projecting lips.

The mastax is very large and the trophi of the normal type; the fulcrum is very long and slightly expanded at the posterior end; the manubria are rodshaped and decurved, ending in a semi-circular, dorsal expansion.

The ganglion is very large and saccate. The retrocerebral organ is absent and the eyespot frontal and double, consisting of two closely approximated spheres of red pigment.

Total length 105—110 $\mu$ ; toes 18—20 $\mu$ ; trophi 45 $\mu$ .

*Cephalodella catellina* is apparently of worldwide, but somewhat erratic distribution; this is probably to be attributed to unusually narrow limits of the conditions necessary for its existence; when these are satisfied, it will be found in great profusion.

*Diglena volvocicola* Zavadovski is at least very closely related to *C. catellina* and probably identical with it; the figures given by the author do not show any differences that might be considered of specific value. Some physiological dissimilarities are described, the most striking one being the parasitism of the animal in Volvox colonies. The author suggests the alternative name *catellina parasitica* for this form, if it should prove to be only a variety.

**CEPHALODELLA ANGUSTA** Myers, new species.

Plate XXVII, figure 2.

The body is small, stout and gibbous dorsally. The head is very large, slightly deflexed, and strongly oblique anteriorly. The neck is indistinctly marked. The abdomen increases slightly in width for about two thirds of its length; the posterior third is rounded dorsally. The lorica is very flexible, but the plates well marked; the lateral clefts are fairly wide anteriorly and the edges diverge slightly and gradually towards the posterior end. The foot is small and conical with a minute tail somewhat beyond mid-length. The toes are very short, slender and slightly recurved, tapering gradually to acute points; their length is one sixth of the total length.

The corona is strongly oblique and convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded posteriorly, the manubria rodlike with ends strongly decurved, but not crutched. The gastric glands are small.

The ganglion is very long and pyriform. The eyespot is frontal and double, the two halves very close together; the retrocerebral organ is absent.

Total length 90—95 $\mu$ ; toes 15—18 $\mu$ .

*Cephalodella angusta* is not common; we have collected it only in a large pond at Oceanville, New Jersey, among *Riccia* and floating sphagnum in soft, acid water.

**CEPHALODELLA EPITEDIA** Myers, new species.

Plate XXVII, figure 7.

The body is fairly slender, laterally compressed and slightly gibbous dorsally. The head is long and convex anteriorly. The neck is somewhat indistinct. The abdomen increases gradually in width for about two thirds of its length; the posterior third is gently rounded. The integument is very flexible and the plates ill-defined; the lateral clefts are very obscure, but apparently parallel-sided and rather narrow. The foot is conical and rather narrow at the base; the small tail is near the posterior end. The toes are short, straight and slender, nearly parallel-sided for about three fourths of their length and somewhat abruptly reduced to acute, slightly recurved, clawlike points; their length is less than one fifth of the total length. The foot glands are very small and pyriform.

The corona is moderately oblique and strongly convex without projecting lips.

The mastax is large and of the typical form; the fulcrum is slender and slightly expanded at the extreme posterior end, the manubria very slender, rodlike and not crutched. The gastric glands are small and rounded.

The ganglion is very long and saccate; the retrocerebral organ is absent and the eyespot frontal and double, the two small pigment spheres fairly wide apart.

Total length 135-140 $\mu$ ; toes 24-26 $\mu$ .

*Cephalodella epitedia* is found among algae and detritus in brackish and saltwater ditches near Atlantic City, New Jersey. It resembles *C. angusta* and *gracilis* in general form, but differs in the shape of the toes and in never being found in fresh water, to which these two species appear to be confined.

**CEPHALODELLA PAXILLA** Myers, new species.

Plate XXVI, figure 6.

The body is elongate, slender, cylindric and very nearly parallel-sided. The head is large and slightly oblique anteriorly. The neck is not very strongly marked. The abdomen is cylindric for nearly its entire length, abruptly rounded at the extreme posterior end; the integument is thin and flexible and the plates indistinct; the lateral clefts are fairly wide anteriorly and the edges diverge very

slightly and gradually towards the extreme posterior end, which is oblique and flaring. The foot is relatively small, conical and longer on the ventral side than on the dorsal; the tail is small and near mid-length. The toes are short and nearly straight, the anterior half cylindric and the posterior tapering, ending in acute points; the dorsal edge is very slightly decurved, the ventral straight for half its length, converging gradually towards the dorsal margin; their length is less than one fifth of the total length. The foot glands are small and pyriform.

The corona is only slightly oblique, convex and without projecting lips.

The mastax is large and of the typical form, but the trophi are delicate; the fulcrum is a long, straight, very slender rod, not expanded posteriorly, the manubria not crutched. The gastric glands are small and rounded.

The ganglion is moderately long and saccate; the retrocerebral organ is absent. The eyespot is frontal and double, the two spheres fairly wide apart.

Total length 210–220 $\mu$ ; toes 36–40 $\mu$ .

*Cephalodella paxilla* is rare; we have collected it among floating sphagnum in a soft, acid-water pond at Gravelly Run, near Mays Landing, New Jersey.

**CEPHALODELLA MARINA** Myers, new species.

Plate XXVI, figure 7.

The body is moderately elongate, spindle-shaped, very slightly compressed laterally and faintly gibbous dorsally. The head is large, slightly deflexed and oblique anteriorly. The neck is somewhat indistinct. The abdomen is slightly convex dorsally and deepest near mid-length; the lorica is very thin and flexible and the plates ill-defined; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The foot is fairly long, stout and conical; the small tail is a little beyond mid-length. The toes are short, very slender, slightly decurved and taper gradually to very acute points; their length is somewhat less than one fifth of the total length. The foot glands are rather small and elongate ovate.

The corona is decidedly oblique and somewhat convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is slightly expanded posteriorly, the manubria slender, rodlike and not crutched. The gastric glands are small.

The ganglion is elongate and saccate; the eyespot is frontal and double, the two spheres rather wide apart. No retrocerebral organ is present. The dorsal antenna is unusually far back on the head. Total length 160–165 $\mu$ ; toes 28–30 $\mu$ .

*Cephalodella marina* is common among algae and vegetable detritus in shallow tidepools near Atlantic City, New Jersey. It is related to *C. mineri*, but is readily distinguished by the very slender toes and the uncrutched manubria, the more oblique corona and larger head.

**CEPHALODELLA INNESI** Myers, new species.

Plate XXVI, figures 3–5.

The body is elongate, slightly compressed laterally and strongly gibbous dorsally. The head is small, distinctly deflexed and strongly oblique anteriorly. The neck is well marked. The abdomen increases rapidly in width for about two thirds of its length; at this point the dorso-ventral depth is almost twice the depth of the anterior margin; the posterior third of the dorsal edge curves slightly downward. The lorica is flexible, but the plates are fairly distinct; the lateral clefts are narrow anteriorly and increase slightly in width towards the posterior end. The foot is long, conical and extremely broad at the base; the tail is small and somewhat beyond mid-length. The toes are relatively short and robust, very slightly enlarged at the base and taper gradually to slender, acute points; their length is about one fifth of the total length. The foot glands are very large and pyriform.

The corona is strongly oblique and convex without projecting lips.

The mastax is fairly large and of the typical form; the fulcrum is relatively short, stout and parallel-sided without any expansion at the posterior end; the manubria are long and crutched. The gastric glands are small.

The ganglion is moderately long and saccate; the eyespot is frontal and double, the two halves fairly wide apart. No retrocerebral organ is present. The dorsal antenna is far back on the head, a short distance in front of the neck.

Total length 200–210 $\mu$ ; toes 40–44 $\mu$ ; trophi 40 $\mu$ .



*Cephalodella innesi* has been collected around Atlantic City, New Jersey, in weedy ponds with soft, acid water. It is readily distinguished by the small head and gibbous body and also by its rapid, restless mode of swimming.

**CEPHALODELLA MINERI** Myers, new species.

Plate XXVI, figure 1.

The body is rather short and nearly cylindric, slightly gibbous dorsally. The head is moderately large and somewhat deflexed. The neck is not very distinctly marked. The abdomen is nearly parallel-sided, slightly convex dorsally; the lorica is very thin and flexible, but the plates are fairly well defined; the lateral clefts are very narrow and parallel-sided, slightly flaring at the extreme posterior end. The foot is relatively short, conical and robust; the very small tail is a little beyond mid-length. The toes are short, strongly decurved, extremely broad at the base and taper gradually and regularly to acute points; their length is about one fifth of the total length. The foot glands are large and ovate.

The corona is slightly oblique and convex without projecting lips.

The mastax is fairly large and of the typical form; the fulcrum is rather stout and slightly expanded posteriorly, the manubria long, very slender and crutched. The gastric glands are small.

The ganglion is elongate and saccate; the eyespot is double and frontal, the two pigment spheres fairly wide apart, and the retrocerebral organ absent.

Total length  $125\mu$ ; toes  $27\mu$ .

*Cephalodella mineri* is very abundant among *Fontinalis novae-angliae* in a brackish stream near Tuckahoe, Atlantic County, New Jersey.

**CEPHALODELLA ELONGATA** Myers, new species.

Plate XXVI, figure 2.

The body is elongate, cylindric and extremely slender. The head is unusually long and convex anteriorly. The neck is indistinct. The abdomen is cylindric throughout its length; the lorica is very thin and flexible and the plates ill-defined; the lateral clefts are very obscure, but apparently very narrow and parallel-sided. The foot is short and conical; the small tail is near the posterior end. The toes are short, slightly decurved, and taper gradually and

evenly to very acute points. The foot glands are very small and pyriform.

The corona is only slightly oblique, but strongly convex and without projecting lips.

The mastax is moderately large and of the typical form; the fulcrum is slender and slightly recurved at the posterior end; the manubria are crutched. The gastric glands are elongate pyriform, the obtuse end forward.

The ganglion is very long and saccate; the retrocerebral organ is absent and the eyespot frontal and double, the two pigment spheres fairly wide apart.

Total length 105–115 $\mu$ ; toes 21–25 $\mu$ .

*Cephalodella elongata* is not common; we find it occasionally in weedy ponds and sphagnum bogs around Atlantic City, New Jersey. It is readily recognized by the very slender body, as well as the pyriform gastric glands.

#### CEPHALODELLA GIBBA (Ehrenberg).

Plate XXX, figures 4–6.

- Furcularia gibba* EHRENBURG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 130, pl. 4, fig. 16; Infusionsthierchen, 1838, p. 420, pl. 48, fig. 3.—GOSSE, Phil. Trans. Royal Soc. London, vol. 146, 1856, p. 433, pl. 17, figs. 35–37.—ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 374.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 43, pl. 19, fig. 13.—TESSIN, Arch. Naturg. Mecklenburg, vol. 43, 1890, p. 150.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 230.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 31.—SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 294.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 133.
- Plagiognatha felis* DUJARDIN, Hist. Nat. Zooph., Inf., 1841, p. 652, pl. 18, fig. 3; not *Vorticella felis* Müller.
- Diaschiza semiaperta* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 80, pl. 22, fig. 10.—BILFINGER, Jahresh. Ver. Naturk. Württemberg, vol. 48, 1892, p. 116; *ibid.*, vol. 50, 1894, p. 54.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 237.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 35.—LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 44.—STENROOS, Acta Soc. Fauna et Flora Fennica, 17, No. 1, 1898, p. 155.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 551, pl. 21, figs. 1–3.—RUNNSTRÖM, Zool. Anz., vol. 34, 1909, p. 270.—LIE-PETTERSEN, Bergens Mus. Aarbog (for 1909), 1910, No. 15, p. 59.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 255.
- Diaschiza gibba* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 6, pl. 1, fig. 1.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 63.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2,

1907, p. 105.—DE BEAUCHAMP, Arch. Zool. Expér., ser. 4, vol. 10, 1909, p. 203, fig. XXI A.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 50.—LUCKS, Rotatorienfauna Westpreussens, 1912, p. 92.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 223, fig. 227.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 330.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 21.—WEBER and MONTET, Cat. Invert Suisse, pt. 11, 1918, p. 135.

The body is moderately elongate, slightly compressed laterally and gibbous dorsally. The head is large and oblique anteriorly. The neck is well marked. The abdomen increases slightly in width for about two thirds of its length and is rounded posteriorly; the lorica is firm and the plates very distinct; the lateral clefts are rather narrow anteriorly and increase gradually in width towards the posterior end. The foot is small and conical; the small tail is near mid-length. The toes are very long, straight or recurved and very slender; the basal portion is broad and tapers rapidly to the nearly parallel-sided, very slightly tapering main portion; the extreme tips are conical. The length of the toes is about one third of the total length.

The corona is oblique and strongly convex without projecting lips.

The mastax is very large and the trophi of the normal type. The inner ventral edges of the rami are near the apex provided with comblike, denticulate lamellae; the fulcrum is broadly expanded at the posterior end and the manubria are strongly crutched; the unci have only a single tooth. The gastric glands are rather small.

The ganglion is very long and saccate; no retrocerebral organ is present. The eyespot is frontal and consists of a spherical capsule, the anterior half transparent, the posterior filled with pigment granules.

Total length 250-300 $\mu$ ; toes 70-80 $\mu$ ; trophi 60 $\mu$ .

*Cephalodella gibba* is abundant in weedy ponds everywhere. It is somewhat variable, especially in the curvature of the toes; specimens with virtually straight toes are not rare and in the early spring months they predominate over the curved toed variety.

#### CEPHALODELLA GRACILIS (Ehrenberg).

Plate XXVII, figure 1.

*Furcularia gracilis* EHRENBURG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 130; Infusionsthierchen, 1838, p. 421, pl. 48, fig. 6.—ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 374, pl. 26, fig. 43.—HUDSON and

- GOSSE, Rotifera, 1886, vol. 2, p. 42, pl. 19, fig. 14.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 229.—SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 294.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 133.
- ? *Diaschiza taurocephalus tenua* HILGENDORF, Trans. New Zealand Inst., vol. 31, 1899, p. 124, pl. 10, fig. 9c-d.
- Diaschiza gracilis* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 10, pl. 1, fig. 4.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 64.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 105.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 50.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 119, fig. 228.—HARRING, Proc. U. S. Nat. Mus., vol. 47, 1913, p. 528.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 330.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 21.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 137.

The body is rather short, laterally compressed and slightly gibbous dorsally. The head is relatively short, broad and convex anteriorly. The neck is well marked. The abdomen increases gradually in width for about two thirds of its length; the posterior third is gently rounded; the lorica is thin and flexible, but the plates are fairly distinct; the lateral clefts are rather narrow anteriorly and increase slightly in width towards the posterior end. The foot is conical and rather short; the very small tail is somewhat beyond mid-length. The toes are short, fairly slender, very slightly recurved and taper gradually and evenly to acute points; their length is about one fifth of the total length. The foot glands are moderately large and pyriform.

The corona is oblique and strongly convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is very slender and slightly recurved posteriorly, but not expanded; the manubria are slender, rodlike, decurved at the ends and not crutched. The gastric glands are small.

The ganglion is elongate and saccate; the retrocerebral organ is absent and the eyespot frontal.

Total length 125-130 $\mu$ ; toes 22-25 $\mu$ .

*Cephalodella gracilis* is common everywhere in weedy ponds. It has a certain resemblance to *C. sterea*, but is readily distinguished by the form of the toes and its much smaller size and stouter body.

#### CEPHALODELLA STEREA (Gosse).

Plate XXVII, figure 6.

- Furcularia sterea* GOSSE, Journ. Royal Micr. Soc., 1887, p. 864, pl. 14, fig. 8.  
—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 25, pl. 31, fig. 15.—

WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 230.

*Diaschiza sterea* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 8, pl. 1, fig. 3.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 105.—WHITNEY, Journ. Exper. Zool., vol. 20, 1916, p. 273, figs. 3, 4.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 136, fig. 37.

The body is moderately stout and slightly gibbous dorsally. The head is large and strongly oblique anteriorly. The neck is well marked. The abdomen increases gradually and regularly in width for about three fourths of its length and diminishes rapidly from this point to the base of the foot; the lorica is relatively firm and the plates well marked; the lateral clefts are somewhat wider than usual and nearly parallel-sided. The foot is large and robust; the tail is very prominent and extends very slightly beyond the end of the foot. The toes are rather short, stout, minutely recurved posteriorly and taper gradually to very acute points; the dorsal and ventral edges are very slightly undulate; their length is less than one fourth of the total length. The foot glands are large and pyriform.

The corona is strongly oblique and convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is slightly expanded at the posterior end and the manubria strongly crutched. The gastric glands are rather small.

The ganglion is very large and saccate; some specimens appear to possess a rudiment of the retrocerebral sac at the posterior end of the ganglion. The eyespot is frontal and consists of two hemispherical pigment masses within a single capsule.

Total length 180–190 $\mu$ ; toes 40–45 $\mu$ .

*Cephalodella sterea* is somewhat sporadically distributed; when found, it is usually very abundant. It is readily distinguished by the large tail.

#### CEPHALODELLA GLOBATA (Gosse).

Plate XXXI, figure 3.

*Diaschiza globata* GOSSE, Journ. Royal Micr. Soc., 1887, p. 362, pl. 8, fig. 4.

—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 37, pl. 31, fig. 30.—

DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 7, pl. 3, fig. 9.

*Furcularia sphaerica* GOSSE, Journ. Royal Micr. Soc., 1887, p. 864, pl. 14,

fig. 7.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 26, pl. 31, fig. 16.

The body is short, stout and gibbous dorsally. The head is rather short, very broad, slightly deflexed and oblique anteriorly. The neck is not very strongly marked. The abdomen is short and very broad; the dorsal edge is strongly convex. The lorica is relatively firm and the plates well marked; the lateral clefts are narrow anteriorly and increase very slightly in width towards the posterior end. The foot is very short and broad; the small tail reaches nearly to the posterior end. The toes are short, rather slender, slightly decurved and taper gradually to acute points; their length is about one fifth of the total length. The foot glands are small and pyriform.

The corona is oblique and somewhat convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded at the posterior end and the manubria long and strongly crutched. The gastric glands are small.

The ganglion is very long and saccate; no retrocerebral organ is present. The eyespot is frontal and consists of a somewhat diffuse cluster of very pale pigment granules.

Total length 125–130 $\mu$ ; toes 22–25 $\mu$ .

*Cephalodella globata* is very widely, but somewhat sporadically distributed and is not often found in large numbers. It resembles *C. physalis*, but the toes are different, the head is smaller and the eye is frontal; *physalis* has a cervical eyespot, is considerably larger and has relatively longer toes.

#### CEPHALODELLA FORFICULA (Ehrenberg).

Plate XXXIV, figures 1-3.

- ? *Distemma forficula* EHRENBURG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 139; Infusionsthierchen, 1838, p. 449, pl. 56, fig. 2.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 41; Suppl., 1889, p. 31, pl. 33, fig. 19.
- Furcularia forficula* EHRENBURG, Infusionsthierchen, 1838, p. 421, pl. 48, fig. 5.—BARTSCH, Jahresh. Ver. Naturk. Württemberg, vol. 26, 1870, p. 41.—ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 375, pl. 26, fig. 44.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 41, pl. 20, fig. 1.—KELLCOTT, Proc. Amer. Soc. Micr., vol. 10, 1888, p. 94.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 229.—JENNINGS, Bull. Michigan Fish Comm., No. 3, 1894, p. 17.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 31.—SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 293.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 473, pl. 19, figs. 1, 2.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 132, pl. 1, fig. 29.—VOIGT, Forschungsber. Biol. Stat. Plön,

- vol. 11, 1904, p. 44, pl. 3, fig. 21; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 103, fig. 192.—DE BEAUCHAMP, Arch. Zool. Expér.; ser. 4, vol. 6, 1907, p. 8, fig. 4.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 16, fig. 1.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 244.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 18.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 117.
- Distemma laeve* EICHWALD, Bull. Soc. Imp. Nat. Moscou, vol. 20, 1847, pt. 2, p. 343, pl. 9, fig. 4.
- Furcularia tubiformis* KING, Journ. Quekett Micr. Club, ser. 2, vol. 5, 1893, p. 139, pl. 8, figs. 1-5.
- Furcularia trihamata* STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 133, pl. 2, fig. 14.
- Notops falcipes* LINDER, Rev. Suisse Zool., vol. 12, 1904, p. 238, pl. 4, fig. 6.
- Cephalodella forficula* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 25.

The body is spindle-shaped, elongate and fairly slender. The head is relatively large and slightly oblique anteriorly. The neck is marked by a shallow constriction. The anterior half of the abdomen is very nearly cylindric, the posterior slightly tapering; the integument is very flexible and the characteristic, discontinuous lorica seems to be totally lacking. The foot is ill-defined, but a slight basal constriction is usually present; the tail is small, but fairly prominent, and belongs to the abdomen rather than to the foot. The toes are short, stout, recurved and acutely pointed; the bases are somewhat swollen and near mid-length there is on the dorsal side a prominent, toothlike spine, preceded by a transverse row of small, acute spicules, from two to four in number. The length of the toes is about one fifth of the total length. The foot glands are very long and slightly clubshaped.

The corona is slightly oblique and convex without projecting lips.

The mastax is relatively large and of the normal type; the inner edges of the rami are serrate at the apex; the fulcrum is very slightly expanded at the posterior end. The manubria are somewhat unusual on account of the presence of a well developed, oval basal plate; the posterior ends are very slightly enlarged, but not crutched. The gastric glands are small. There is a very faint constriction between the stomach and intestine.

The ganglion is elongate and saccate; no retrocerebral organ is present. The eyespot is frontal and of somewhat unusual structure; its anterior half is transparent and the posterior pigment mass is divided into two segments by a median, clear space.

Total length 160-165 $\mu$ ; toes 30-35 $\mu$ ; trophi 45 $\mu$ .

*Cephalodella forficula* is common in weedy ponds everywhere. The propriety of including this species in the genus *Cephalodella*, which is virtually equivalent to Gosse's *Diaschiza*, as emended by Dixon-Nuttall and Freeman, will probably not be questioned by anybody, as the presence or absence of a lorica is now generally conceded to be of small importance.

**CEPHALODELLA PANARISTA** Myers, new species.

Plate XXXI, figures 5-7.

The body is very large, elongate and slender. The head is fairly large and oblique anteriorly. The neck is marked by a slight constriction. The abdomen increases gradually and very slightly in width for about three fourths of its length; the dorsal edge curves downwards posteriorly to the base of the foot. The integument is very flexible and the plates indistinct; the lateral clefts are very obscure, but apparently fairly wide and parallel-sided. The foot is short, stout and conical; the very small tail is near mid-length. The toes are very long, stout and recurved, tapering gradually to acute points; their length is a little less than one third of the total length. On the dorsal edge there is occasionally a single, toothlike spine; its distance from the base of the toe is about one third of the length. The foot glands are extremely long and slightly club-shaped.

The corona is strongly oblique, convex and without projecting lips.

The mastax is large and the trophi robust. On the inner ventral edges of the rami there are near the apex two denticulate, comblike lamellae, the left one much larger than the right. The fulcrum is long and straight, slightly expanded posteriorly; the manubria are short, recurved posteriorly, but not crutched, and have a large basal plate. The unci have the typical single tooth. The gastric glands are small.

The ganglion is elongate and pyriform; no retrocerebral organ is present. The eyespot is frontal and the anterior part of the capsule is without pigment, simulating a "lens".

Total length 360-375 $\mu$ ; toes 102-105 $\mu$ ; trophi 65 $\mu$ .

*Cephalodella panarista* is rare; we have found a few specimens at Four Mile Run, near Washington, District of Columbia, and in ponds at Tuckerton, Ocean County, New Jersey, as well as in col-



lections made by Dr. Birge at the Fish Hatchery, Bass Island, Lake Erie, during the Great Lakes Biological Investigations in 1901.

CEPHALODELLA AURICULATA (Müller).

Plate XXVIII, figure 6.

- Vorticella auriculata* MÜLLER, Verm. Terr. Fluv., vol. 1, pt. 1, 1773, p. 111.  
*Vorticella lacunculata* MÜLLER, Anim. Infus. 1786, p. 292, pl. 42, figs. 1-5=  
*Vorticella auriculata* renamed.
- Eccelissa lacunculata* SCHRANK, Fauna Boica, vol. 3, pt. 2, 1803, p. 107.  
*Eccelissa hermanni* SCHRANK, Fauna Boica, vol. 3, pt. 2, 1803, p. 109.
- Furcularia lacunculata* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 2, 1816,  
 p. 38.  
*Furcularia lobata* BORY DE ST. VINCENT, Enc. Méth., Zooph. (pt. 2), 1827,  
 p. 425=*Vorticella lacunculata* renamed.
- Notommata lacunculata* EHRENBERG, Abh. Akad. Wiss. Berlin, 1830, p. 46;  
 (for 1831), 1832, p. 134; Infusionsthierchen, 1838, p. 428, pl. 48, fig. 1+,  
 pl. 51, fig. 4.—LEYDIG, Zeitschr. Wiss. Zool., vol. 6, 1854, p. 38.—GOSSE,  
 Phil. Trans. Royal Soc. London, vol. 146, 1856, p. 432, pl. 17, figs. 32-34.  
 —BARTSCH, Jahresh. Ver. Naturk. Württemberg, vol. 26, 1870, p. 338.—  
 ECKSTEIN, Zeitschr. Wiss. Zool., vol. 39, 1883, p. 364, pl. 24, fig. 22.—  
 PLATE, Jenaische Zeitschr. Naturw., vol. 19, 1885, p. 23, pl. 1, fig. 6.—  
 HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 26, pl. 17, fig. 9.—  
 WIERZEJSKI, Rozpr. Akad. Umiej., Wyzd. Mat.-Przyr., Krakow, ser. 2,  
 vol. 6, 1893, p. 228.
- ? *Dekinia calopodaria* MORREN, Ann. Sci. Nat., vol. 21, 1830, p. 139, pl. 3,  
 fig. 4; Bijdr. Natuurk. Wetensch., vol. 5, 1830, p. 225, fig.
- ? *Dekinia minutula* MORREN, Ann. Sci. Nat., vol. 21, 1830, p. 144, pl. 3, fig.  
 5; Bijdr. Natuurk. Wetensch., vol. 5, 1830, p. 230, fig.
- ? *Dekinia compta* MORREN, Ann. Sci. Nat., vol. 21, 1830, p. 146, pl. 3, fig. 7;  
 Bijdr. Natuurk. Wetensch., vol. 5, 1830, p. 231, fig.
- Proales gibba* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 37,  
 pl. 18, fig. 8.—SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 290.
- Notommata ovulum* GOSSE, Journ. Royal Micr. Soc., 1887, p. 2, pl. 1, fig. 3;  
 HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 20, pl. 31, fig. 7.
- Plagiognatha lacunculata* TESSIN, Arch. Naturg. Mecklenburg, vol. 43, 1890,  
 p. 149, pl. 1, fig. 9.
- Notommata cuneata* THORPE, Journ. Royal Micr. Soc., 1891, p. 305, pl. 7,  
 fig. 5.
- ? *Notostemma makrocephala* BERGENDAL, Acta Univ. Lundensis, vol. 28,  
 1892, sect. 2, No. 4, pl. 69, pls. 2, 3, fig. 19.
- ? *Notostemma bicarinata* BERGENDAL, Acta Univ. Lundensis, vol. 28, 1892,  
 sect. 2, No. 4, p. 70, pl. 2, fig. 18.
- Diaschiza lacunculata* LEVANDER, Acat. Soc. Fauna et Flora Fennica, vol. 12,  
 No. 3, 1895, p. 43.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 545, pl. 18,  
 figs. 5-7.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1,  
 1898, p. 156.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc.,  
 1903, p. 11, pl. 2, fig. 6.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11,

- 1904, p. 64.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 106.—RUNNSTRÖM, Zool. Anz., vol. 34, 1909, p. 270.—LIE-PETERSEN, Bergens Mus. Aarbog (for 1909), 1910, No. 15, p. 58.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 119, figs. 229, 230.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 256.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 330.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 21.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 138.
- Plagiognatcha lacinulata* SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 292, pl. 7, fig. 9.
- ? *Diaschiza taurocephalus* HILGENDORF, Trans. New Zealand Inst., vol. 31, 1899, p. 123, pl. 10, fig. 9.
- Diaschiza auriculata* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 33; Proc. U. S. Nat. Mus., vol. 47, 1913, p. 528.

The body is short, stout and somewhat prismatic; its greatest depth is just behind the neck. The head is very large, oblique anteriorly and slightly deflexed. The neck is well marked. The abdomen is nearly parallel-sided, slightly narrower at the posterior end. The lorica is fairly rigid and the plates distinct; the lateral clefts are narrow anteriorly and widen slightly and gradually towards the posterior end. The foot is short, stout and broadly conical; the fairly large tail is somewhat beyond mid-length. The toes are short, moderately stout and decurved, tapering gradually to acute points; their length is about one fifth of the total length. The foot glands are fairly large and pyriform.

The corona is oblique and strongly convex with prominent, beak-like lips.

The mastax is very large and of the normal type; the fulcrum is long and expanded posteriorly; the manubria very slender and strongly recurved. The gastric glands are small and usually tinted brownish-red in mature animals.

The ganglion is very large and saccate; the eyespot is at the posterior end. The retrocerebral organ is absent.

Total length 120-130 $\mu$ ; toes 22-25 $\mu$ .

*Cephalodella auriculata* is common everywhere in weedy ponds. In spite of its small size it is readily recognized by the peculiar, jerky manner of swimming.

This species was first described by Müller under the name of *Vorticella auriculata*; in his *Animalcula Infusoria* the specific name was changed to *lacinulata*, seemingly under the impression that it was fashioned somewhat like the flowers of the "Bluebell", hollow

and the margin cut into lappets or "lacinulae". As *auriculata* is the oldest name, it will have to take the place of *lacinulata*; both are obviously misnomers.

CEPHALODELLA EXIGUA (Gosse).

Plate XXVIII, figure 2.

*Diaschiza exigua* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 78, pl. 22, fig. 15.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 133, pl. 3, fig. 10.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 52.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 121, figs. 233-234.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 330.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 20.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 140.

The body is rather short, stout and oblique anteriorly. The head is very large and deflexed. The neck is well marked. The abdomen is laterally compressed at the posterior end; the dorsal and ventral edges are almost parallel, the dorsal slightly arched; the lorica is flexible, but the plates are fairly distinct; the lateral clefts are wide and parallel-sided anteriorly, the posterior ends slightly flaring. The foot is very small, almost tubular, and gives the abdomen the appearance of being squarely truncate posteriorly; the tail is very small and not far from the end of the foot. The toes are short, slender, slightly decurved and taper gradually to acute points; their length is a little more than one fifth of the total length. The foot glands are small and pyriform.

The corona is strongly oblique and distinctly convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is very slightly expanded at the posterior end; the manubria are very slender and strongly recurved posteriorly, but not crutched. The gastric glands are moderately large.

The ganglion is very elongate and saccate; the retrocerebral organ is absent. The large eyespot is at the posterior end of the ganglion.

Total length 90-95 $\mu$ ; toes 20-22 $\mu$ .

*Cephalodella exigua* is present in weedy ponds everywhere, usually in large numbers.

## CEPHALODELLA HOODII (Gosse).

Plate XXVIII, figure 1.

- ? *Plagiognatha lacinulata* DUJARDIN, Hist. Nat. Zooph., Inf., 1841, pl. 18, fig. 6; not *Vorticella lacinulata* Müller.
- Diaschiza hoodii* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 79, pl. 22, fig. 15.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 129, pl. 2, fig. 5.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 120, figs. 231-232.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 21.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 139.
- Diaschiza rhamphigera* GOSSE, Journ. Royal Micr. Soc., 1887, p. 6, pl. 2, fig. 20.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 38, pl. 31, fig. 32.
- Plagiognatha gracilis* TESSIN, Arch. Naturg. Mecklenburg, vol. 43, 1890, p. 150, pl. 1, fig. 10.
- Diaschiza valga* BILFINGER, Jahresh. Ver. Naturk. Württemberg, vol. 50, 1894, p. 53.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 549, pl. 20, figs. 26-28.—LIE-PETTERSEN, Bergens Mus. Aarbog (for 1909), 1910, No. 15, p. 58.—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 256.

The body is fairly slender and somewhat gibbous dorsally. The head is fairly large, oblique anteriorly and slightly deflexed. The neck is well marked. The abdomen is unusually elongate and the dorsal line arched and rounded posteriorly; its greatest depth is at mid-length; the lorica is firm and the plates well marked. The lateral clefts are narrow and parallel-sided in the anterior half of their length and widen gradually towards the posterior end. The foot is rather small and conical; the tail is fairly prominent and near mid-length. The toes are rather short, fairly stout and decurved, tapering gradually to acute points; their length is a little less than one fourth of the total length. The foot glands are rather small and pyriform.

The corona is moderately oblique and strongly convex with prominent, beaklike lips.

The mastax is fairly large and of the normal type; the fulcrum is very slightly expanded posteriorly, the manubria short, very slender, rodlike and slightly recurved at the ends, but not crutched. The gastric glands are small and ovate.

The ganglion is very large and saccate; the eyespot is fairly large and at the posterior end of the ganglion. The retrocerebral organ is absent.

Total length 140-145 $\mu$ ; toes 32-35 $\mu$ .

*Cephalodella hoodii* is not common; we have collected it at Madison, Wisconsin, in Fairmount Park, Philadelphia, Pennsylvania, and near Los Angeles, California.

CEPHALODELLA Plicata Myers, new species.

Plate XXVIII, figures, 3-4.

The body is rather short and strongly gibbous dorsally. The head is fairly large and somewhat deflexed. The neck is well marked. The abdomen is strongly arched dorsally, with its greatest depth near mid-length; the lorica is very firm and the plates well marked; posteriorly it projects over the foot nearly to the base of the toes. The dorsal and lateral clefts are abnormally deep and their edges project as very distinct ridges, as shown in the optical section of the body in figure 4; the dorsal cleft is straight-sided and acute-angled, the lateral clefts rounded at the bottom. Symbiotic zoochlorellae are invariably present and arranged in a fairly regular and quite constant pattern. The foot is rather small; the minute tail is near the posterior end. The toes are rather short, fairly stout, tapering, and slightly decurved; their length is about one fourth of the total length. The foot glands are rather small and pyriform.

The corona is moderately oblique and convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is very slightly expanded at the posterior end; the manubria are short, slender and without terminal crutch. No gastric glands are present.

The ganglion is moderately elongate and saccate; no retrocerebral organ is present. The eyespot is at the posterior end of the ganglion.

Total length 105-110 $\mu$ ; toes 24-27 $\mu$ .

*Cephalodella plicata* is not rare in soft, acid water ponds among Fontinalis and submerged sphagnum; we have collected it in Loon Lake, Vilas County, and Starvation Lake, Oneida County, Wisconsin, and also at Bargaintown, near Atlantic City, New Jersey. It has a superficial resemblance to *C. hoodii* and *C. ventripes*, but the projecting beak is absent; the exceptionally deep dorsal and lateral clefts and the symbiotic zoochlorellae are sufficient to distinguish it from these species.

**CEPHALODELLA VENTRIPES (Dixon-Nuttall).**

Plate XXVIII, figure 5.

*Diaschiza ventripes* DIXON-NUTTALL, Journ. Quekett Micr. Club, ser. 2, vol. 8, 1901, p. 25, pl. 2, figs. 1-3.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 14, pl. 2, fig. 7.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 105.

The body is moderately stout and gibbous dorsally. The head is large, strongly oblique anteriorly and slightly deflexed. The neck is well marked. The abdomen is arched dorsally and the ventral line straight; the lorica is very firm and the plates distinct, overhanging the foot. The lateral clefts are rather narrow anteriorly and increase gradually in width towards the posterior end. The foot is small and broadly conical; the tail is prominent and near the end of the foot. The toes are rather short, stout and decurved, tapering gradually to acute points; their length is a little less than one fifth of the entire length. The foot glands are very small and pyriform.

The corona is strongly oblique and convex with prominent, beak-like lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded posteriorly, the manubria are short, very slender and the ends strongly recurved, but not crutched. The gastric glands are fairly large and elongate ovate.

The ganglion is large and saccate; the large, lens-shaped eyespot is at the posterior end. No retrocerebral organ is present.

Total length 135-140 $\mu$ ; toes 25-28 $\mu$ .

*Cephalodella ventripes* is widely distributed in weedy ponds, but is not usually found in large numbers. It is readily distinguished by the overhanging lorica and its large size.

**CEPHALODELLA PHYSALIS Myers, new species.**

Plate XXIX, figures 3-5.

The body is very short, stout and gibbous dorsally. The head is very large and obliquely truncate anteriorly; its length is less than the dorso-ventral depth. The neck is well marked. The abdomen is but little longer than wide, somewhat prismatic and deepest near mid-length. The lorica is quite firm and the lateral cleft is wide. The foot is very short and stout; the tail is small and knoblike and near the posterior end of the foot. The toes

are blade-shaped, decurved and acutely pointed; the dorsal edge is evenly curved and the ventral edge has a blunt cusp about one third of its length from the base; the length of the toes is one fourth of the total length.

The corona is strongly oblique and the lips project as a small beak.

The mastax is large and the trophi of normal type; the fulcrum is slightly expanded posteriorly and the manubria rodlike, not crutched.

The ganglion is very large and saccate; the eyespot is at the posterior end. There is no retrocerebral organ.

Total length 150–160 $\mu$ ; toes 35–40 $\mu$ ; trophi 45 $\mu$ .

*Cephalodella physalis* is not rare among sphagnum and submerged plants in soft-water ponds around Atlantic City, New Jersey. It resembles *C. lipara*, but the body is not as stout; the much longer toes and the presence of an eyespot are sufficient to separate it from this species.

CEPHALODELLA STRIGOSA Myers, new species.

Plate XXIX, figure 7.

The body is moderately elongate, nearly cylindric and slightly gibbous dorsally. The head is relatively long and strongly oblique anteriorly. The neck is marked by a shallow constriction. The abdomen increases very slightly and gradually in width for about three fourths of its length; from this point the dorsal edge curves downward to the base of the foot. The integument is very flexible and the plates ill-defined; the lateral clefts are somewhat obscure, apparently narrow and parallel-sided throughout their length. The foot is short and broadly conical; the tail is a small, rounded boss near mid-length. The toes are very long, slender, slightly decurved and taper gradually to extremely acute, needle-like points; their length is about one fourth of the total length. The foot glands are rather small and pyriform.

The corona is strongly oblique, decidedly convex and without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is slightly expanded posteriorly, the manubria very slender and not crutched. The gastric glands are small and rounded.

The ganglion is elongate and saccate; no retrocerebral organ is present. The eyespot is at the extreme posterior end of the ganglion.

Total length  $125\mu$ ; toes  $33\mu$ .

*Cephalodella strigosa* is not common; we have found it in weedy ponds and among submerged sphagnum in Vilas County, Wisconsin, and around Atlantic City, New Jersey. There is a slide of this species in the U. S. National Museum, mounted by C. F. Rousselet and according to the label collected in Epping Forest; it is erroneously determined as *Diaschiza derbyi* Dixon-Nuttall and Freeman. This is probably the nearest relative of *C. strigosa*, but differs in having recurved toes.

**CEPHALODELLA TANTILLA** Myers, new species.

Plate XXX, figure 2.

The body is moderately elongate, laterally compressed and strongly gibbous dorsally. The head is large and slightly deflexed. The neck is not very strongly marked. The abdomen increases gradually in width for two thirds of its length and is somewhat abruptly rounded posteriorly; the lorica is firm and the plates well marked. The lateral clefts are rather narrow anteriorly and increase gradually in width towards the posterior ends, which are somewhat flaring. The foot is short and broad; the fairly prominent tail is a little beyond mid-length. The toes are wide apart at the base, long, slender and recurved, tapering gradually from the base to acute points; their length is about one third of the total length. The foot glands are small and pyriform.

The corona is oblique and strongly convex without projecting lips.

The mastax is relatively large and of the normal type; the fulcrum is very stout and slightly expanded at the extreme end, the manubria very slender, rodshaped and recurved, but not crutched. The gastric glands are rather small.

The ganglion is long and saccate; no retrocerebral organ is present. The eyespot is at the posterior end of the ganglion.

Total length  $115-120\mu$ ; toes  $38-40\mu$ .

*Cephalodella tantilla* is common in weedy ponds with soft, acid water; we have collected it in Vilas and Oneida Counties, Wisconsin, around Atlantic City, New Jersey, and in Polk County,



- Florida. It bears a striking resemblance to *C. gibba*, from which it differs in the much smaller size, cervical eyespot, acutely pointed toes and the form of the trophi.

**CEPHALODELLA COMPRESSA** Myers, new species.

Plate XXX, figure 1.

The body is moderately elongate, slightly gibbous dorsally and strongly compressed laterally. The head is rather small and distinctly deflexed. The neck is well marked. The abdomen increases gradually in width towards the posterior end. The lorica is fairly rigid and the plates distinct; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The foot is broad at the base and fairly stout. The toes are long, slender and cylindric for about two thirds of their length; the posterior third tapers gradually to very acute points; the dorsal edge is straight throughout and the ventral bends upwards to meet it. The length of the toes is about one third of the total length.

The corona is oblique and distinctly convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is long, stout and slightly expanded at the posterior end; the manubria are very slender, rodlike and strongly recurved posteriorly. The gastric glands are small and irregularly ovate.

The ganglion is long and saccate; the eyespot is at the posterior end, well towards the ventral side. The retrocerebral organ is absent.

Total length 140–145 $\mu$ ; toes 45–48 $\mu$ .

*Cephalodella compressa* is common in sphagnum and among submerged plants in soft, acid water ponds and bogs in Vilas and Oneida Counties, Wisconsin, and around Atlantic City, New Jersey. It is readily recognized by the strongly compressed body.

**CEPHALODELLA DORSEYI** Myers, new species.

Plate XXX, figure 7.

The body is relatively short, stout and slightly gibbous dorsally. The head is large, slightly deflexed and strongly oblique anteriorly. The neck is well marked. The abdomen increases gradually in width for about two thirds of its length and is gently rounded posteriorly; the lorica is firm and the plates distinct; the

lateral clefts are fairly wide at the ends and slightly narrower at mid-length. The foot is short and stout; the tail is fairly prominent and near the posterior end. The toes are very long and wide apart at the base, fairly stout and tapering for about one fifth of their length; from this point they are very nearly cylindrical and end in acute, conical tips, the dorsal edge straight and the ventral bending abruptly upwards to meet it. The length of the toes is about one third of the total length. The foot glands are small and pyriform.

The corona is strongly oblique and distinctly convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is moderately long and slightly expanded at the posterior end; the manubria are slender, rodshaped, slightly clubbed and decurved posteriorly, but not crutched. The gastric glands are small and ovate.

The ganglion is long and saccate; the eyespot is very large and saucer-shaped and at the posterior end of the ganglion. The retro-cerebral organ is absent.

Total length 145–150 $\mu$ ; toes 50–54 $\mu$ .

*Cephalodella dorseyi* is not very common. We have collected it among submerged sphagnum and other plants in soft, acid water ponds around Atlantic City, New Jersey. It is readily recognized by the long, very slender toes with their peculiar, clawlike points.

**CEPHALODELLA PIULCA** Myers, new species.

Plate XXX, figure 3.

The body is elongate, slender, slightly curved and laterally compressed. The head is relatively small and short and distinctly deflexed. The neck is not strongly marked. The abdomen is nearly parallel-sided, very slightly gibbous dorsally and concave ventrally; the lorica is firm and the plates well marked. The lateral clefts are narrow anteriorly and increase slightly in width towards the posterior end. The foot is fairly long and stout; the small tail is near the posterior end. The toes are long, slender and slightly recurved, moderately stout at the base and taper gradually to extremely slender, acute points; their length is a little less than one third of the total length. The foot glands are rather small and pyriform.

The corona is oblique and strongly convex without projecting lips.

The mastax is small and of the normal type; the fulcrum is very slightly expanded posteriorly and the manubria distinctly crutched. The gastric glands are small and somewhat triangular.

The ganglion is long and saccate; the small eyespot is at the posterior end, on the dorsal side. No retrocerebral sac is present.

Total length 130–135 $\mu$ ; toes 38–40 $\mu$ .

*Cephalodella hiulca* is not rare in soft, acid water ponds among Fontinalis, Riccia and sphagnum; we have collected it at Bargaintown and Oceanville, New Jersey. It resembles superficially *C. strepta*, but is much larger and without the head sheath of this species; an additional distinction is the presence of an eyespot in *C. hiulca*.

**CEPHALODELLA ELEGANS** Myers, new species.

Plate XXXI, figure 8.

The body is elongate, very slender, somewhat curved and slightly compressed dorso-ventrally. The head is relatively large and very slightly deflexed. The neck is not very strongly marked. The abdomen is slightly curved dorsally and nearly straight ventrally; the lorica is firm and the plates distinct. The lateral clefts are narrow anteriorly and increase gradually and considerably in width towards the posterior end. The foot is small and terminates in a short, cylindric section; the tail is very minute and only a short distance beyond the lorica. The toes are very long and slightly decurved, fairly stout at the base and tapering rapidly to slender, nearly cylindric, acutely pointed rods; their length is about one third of the total length. The foot glands are rather small and pyriform.

The corona is slightly oblique and moderately convex without projecting lips.

The mastax is small and of the normal type; the fulcrum is slightly expanded at the posterior end and the manubria are distinctly recurved and increase somewhat in width towards the ends. The gastric glands are small and oval.

The ganglion is long and pyriform; the eyespot is fairly large and at the posterior end of the ganglion; no retrocerebral organ is present.

Total length 135–140 $\mu$ ; toes 48–50 $\mu$ .

*Cephalodella elegans* is not common; we have collected it in small numbers among sphagnum and other submerged plants in a swamp near Oceanville, New Jersey. It is readily distinguished by the very slender, depressed body and the long toes.

**CEPHALODELLA GALBINA** Myers, new species.

Plate XXXI, figure 1.

The body is very short, stout and gibbous dorsally. The head is relatively short, very broad and slightly deflexed. The neck is not strongly marked. The abdomen is short and very broad, with its greatest width near mid-length. The lorica is very flexible, but the plates are well marked; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The foot is short and stout; the tail is fairly prominent and somewhat beyond mid-length. The toes are very long, slender, slightly decurved, rather stout at the base and taper gradually to very acute points; their length is about two fifths of the total length. The foot glands are small and pyriform.

The corona is slightly oblique and strongly convex without projecting lips.

The mastax is huge and of the normal type; the fulcrum is nearly half the length of the entire body and the posterior end very slightly expanded, the manubria short, slender, slightly recurved and clubbed posteriorly, but not crutched. The gastric glands are very small and ovate.

The ganglion is very long and saccate; no retrocerebral organ is present. The eyespot is at the posterior end of the ganglion.

Total length 100–110 $\mu$ ; toes 38–42 $\mu$ .

*Cephalodella galbina* is rather rare; we have collected it only among submerged sphagnum in a soft, acid water pond at Gravelly Run, near Mays Landing, New Jersey. Its nearest relative is probably *C. dorseyi*, from which it differs in the much shorter and stouter body, huge mastax and long, decurved toes.

**CEPHALODELLA BELONE** Myers, new species.

Plate XXXI, figure 2.

The body is small and conical, tapering increasingly from the head towards the foot. The head is very large, fully one third the length of the entire body and somewhat wider than the abdomen.

The neck is well marked. The abdomen tapers rapidly and increasingly from the neck to the base of the foot; the lorica is fairly rigid and the plates are well marked; the lateral clefts are very narrow and parallel-sided. The foot is moderately long, conical and rather small at the base; the tail is small and a little beyond mid-length. The toes are extremely long, straight and slender, slightly enlarged at the base and tapering very gradually to the minutely rounded tips; their length is about two fifths of the entire length.

The corona is somewhat oblique and convex with prominent beaklike lips.

The mastax is large and of the normal type; the fulcrum is relatively stout and slightly expanded posteriorly; the manubria slender, rodlike and slightly recurved, but not crutched. The gastric glands are small.

The ganglion is long and pyriform; the eyespot is cervical, at the posterior end of the ganglion; no retrocerebral organ is present.

Total length 120–125 $\mu$ ; toes 45–50 $\mu$ .

*Cephalodella belone* is not common; we have collected it among Fontinalis in a decadent lake two miles east of Eagle River, Vilas County, Wisconsin, and in a bog pool at Bargaintown, near Atlantic City, New Jersey. The appearance of the animal is at first somewhat puzzling, whether alive or dead: when swimming the toes are never separated and it looks very much like a diminutive *Trichocerca* (= *Rattulus*); when death occurs, the toes are thrown out sidewise, thus resembling a small *Monommata*. It is probably related to *C. cuneata*, but readily distinguished by the presence of the eyespot, as well as by its peculiar behavior.

**CEPHALODELLA NANA** Myers, new species.

Plate XXIX, figure 1.

The body is relatively short and conical, tapering evenly and gradually from the corona to the base of the toes; the dorsal edge is gently curved. The head is very large, nearly half the length of the entire body and much wider than the abdomen. The neck is well marked. The abdomen is very short, little more than one third of the length of the body and tapers gradually towards the foot; the lorica is moderately flexible and the plates distinct; the lateral clefts are narrowest near mid-length and wide at the posterior end. The foot is fairly large and conical; the small tail is unusually far

back on the foot. The toes are long, slender, wide apart at the base, double-curved and taper gradually to acute, bristle-like points; their length is about one third of the total length. The foot glands are small and pyriform.

The corona is strongly oblique and convex with prominent, beak-like lips.

The mastax is very large and of the normal type; the fulcrum is slightly expanded at the posterior end; the manubria are slender, slightly clubbed and recurved at the ends, but not crutched. The gastric glands are small.

The ganglion is very long and somewhat pyriform; the eyespot is at the posterior end. No retrocerebral organ is present.

Total length 105–110 $\mu$ ; toes 35–40 $\mu$ .

*Cephalodella nana* has been collected only in sphagnum along the marshy edges of Corduroy Creek, near Absecon, New Jersey. It resembles *C. cuneata*, but the presence of an eyespot and the sigmoid curvature of the toes is sufficient to distinguish it.

**CEPHALODELLA XENICA** Myers, new species.

Plate XXIX, figure 6.

The body is moderately elongate and gibbous dorsally. The head is large and oblique anteriorly. The neck is marked by a rather shallow constriction. The abdomen is arched dorsally, its greatest depth near mid-length; the lorica is fairly rigid and the plates well marked; the lateral clefts are wide and parallel-sided. The foot is large and robust; the prominent tail is near the posterior end. The toes are short, blade-shaped and very broad; they increase slightly in width for about half their length, then decrease rather suddenly to very slender, conical tips, slightly blunted at the extreme ends; their length is less than one fifth of the total length. The foot glands are rather small and ovate.

The corona is oblique and strongly convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is very slightly expanded at the posterior end; the manubria are long and have a very pronounced terminal crutch. The gastric glands are small and oval.

The ganglion is elongate and pyriform; no retrocerebral organ is present. The eyespot is at the posterior end of the ganglion.

Total length 128 $\mu$ ; toes 22 $\mu$ .

*Cephalodella xenica* was found in considerable numbers in material collected by Dr. H. S. Jennings in Huron River at Ann Arbor, Michigan, in 1901. Its nearest relative is *C. eupoda*, which differs in its greater size and in the absence of the eyespot, as well as the flexible integument.

**CEPHALODELLA NELITIS** Myers, new species.

Plate XXXII, figure 1.

The body is elongate, very slender and somewhat prismatic. The head is fairly small and strongly oblique anteriorly. The neck is not strongly marked. The abdomen increases slightly in width for about two thirds of its length and from this point tapers slightly to the base of the foot; it is somewhat variable in width and specimens with parallel-sided body are occasionally met with. The lorica is very thin and flexible, but the plates are fairly well marked; the lateral clefts are rather narrow and parallel-sided for nearly their entire length; the extreme posterior ends are slightly flaring. The foot is short and conical, but broad at the base; the tail is very small. The toes are short, strongly decurved and very slender; from the slightly bulbous base they taper very gradually to acute points; their length is about one fifth of the total length. The foot glands are small and pyriform.

The corona is oblique, strongly convex and without projecting lips.

The mastax is rather small and of the normal type; the fulcrum is stout and slightly expanded posteriorly, the manubria rodlike, very slender and not crutched. The bladder is large.

The ganglion is elongate and saccate; eyespot and retrocerebral organ are absent.

Total length  $135\mu$ ; toes  $22\mu$ .

*Cephalodella nelitis* was collected in a pond with soft, acid water among submerged sphagnum, at Gravelly Run, near Mays Landing, New Jersey. Its nearest relative is *C. melia*; a comparison is given under this species.

**CEPHALODELLA MELIA** Myers, new species.

Plate XXXII, figure 2.

The body is elongate, somewhat prismatic and gibbous dorsally. The head is rather small, but relatively long in comparison with

its width, and obliquely truncate anteriorly. The neck is well marked. The abdomen increases gradually and considerably in width for about three fourths of its length; the dorsal line curves rapidly downward in the posterior fourth. The lorica is very thin and flexible and the edges of the plates rather difficult to trace; the lateral clefts are very narrow anteriorly and increase gradually in width towards the posterior end. The foot is long and conical and the tail prominent. The toes are fairly long and slender, enlarged at the base, parallel-sided for about four fifths of their length, decurved and end in small conical points, prolonged by a fairly long, bristle-like nib, continuing the line of the dorsal edge; their length is about one fourth of the total length. The foot glands are fairly large and pyriform.

The corona is oblique, strongly convex and without projecting lips.

The mastax is moderately large and of the normal type; the fulcrum curves upwards at the posterior end; the manubria are not crutched. Symbiotic zoochlorellae are present in abundance in the walls of the stomach. The bladder is very large.

The ganglion is long and saccate; eyespot and retrocerebral organ are absent.

Total length 130–145 $\mu$ ; toes 28–32 $\mu$ .

*Cephalodella melia* was originally collected in soft, acid water ponds and bogs in the neighborhood of Atlantic City, New Jersey; it has not been seen for two years, but was until then fairly common. Its nearest relative is probably *C. nelitis*, from which it is readily distinguished by the form and length of the toes and the shorter and strongly gibbous body, as well as by the presence of zoochlorellae.

#### CEPHALODELLA MEGALOCEPHALA (Glasscott).

Plate XXXII, figures 5-7.

- ? *Pleurotrocha leptura* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 129, pl. 4, fig. 18; Infusionsthierchen, 1838, p. 419, pl. 48, fig. 2.  
 ? HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 20, pl. 18, fig. 4.—  
 ? VOIGT, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 86, fig. 149.  
 ? *Furcularia lactistes* GOSSE, Journ. Royal Mier. Soc., 1887, p. 863, pl. 14, fig. 5.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 25, pl. 31, fig. 13.  
*Furcularia megaloccephala* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 56, pl. 4, fig. 3.



? *Diglena inflata* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 60, pl. 4, fig. 6.

*Diaschiza megalcephala* ROUSSELET, Journ. Quekett Micr. Club, ser. 2, vol. 6, 1895, p. 123, pl. 7, fig. 5.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 139, pl. 4, fig. 14.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 65.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 123, figs. 240-242.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, p. 21.—HAUER, Mitt. Bad. Landesver. Naturk., Freiburg i. Br., new ser., vol. 1, 1921, p. 179.

The body is fairly stout and gibbous dorsally. The head is very large and extremely oblique. The neck is not strongly marked. The abdomen increases considerably in width for about two thirds of its length and from this point the dorsal line curves rapidly to the base of the foot. The lorica is very thin and flexible and the edges of the plates ill-defined; the lateral clefts are narrow and parallel-sided. The presence of a dorsal cleft is denied by Dixon-Nuttall and Freeman; according to Hauer it is really present, but the connecting portion of the integument is convex instead of forming a deep groove, as in other species of this genus. The foot is stout and conical, but its base is ill-defined; the knoblike tail is near mid-length. The toes are short, stout and decurved, tapering gradually to acute points; their length is about one sixth of the total length. The foot glands are large and pyriform.

The corona is extremely oblique, very slightly convex and without projecting lips.

The mastax is large and differs very little from the typical form, except in the feeble development of the mallei.

The ganglion is very elongate and saccate; eyespot and retro-cerebral organ are absent.

Total length 195–210 $\mu$ ; toes 34–38 $\mu$ ; trophi 30 $\mu$ .

*Cephalodella megalcephala* is very widely distributed, if not cosmopolitan; it is common in weedy ponds wherever we have collected. Dixon-Nuttall and Freeman included this species in the genus *Diaschiza* under protest; this was not unreasonable under their somewhat narrow and artificial definition of this genus. No objection can be raised against its inclusion in *Cephalodella*, if the definition given above is accepted for this genus, basing it primarily on the form of the corona and the mastax, secondarily on the form of the head, body and foot, and neglecting the degree of development of the lorica, even its total absence, as well as the

presence of the minute and all but invisible tuft of setae at the base of the toes, which we consider trivial.

Ehrenberg's figure and description of *Pleurotrocha leptura* probably refer to this species; his figure of the mastax accompanying the original description shows that it belongs to *Cephalodella*. As his name has never been used by anybody else for the species under consideration and the identification is not absolutely certain, its resurrection at this time is probably unnecessary.

**CEPHALODELLA PHELOMA** Myers, new species.

Plate XXXII, figure 3.

The body is elongate, slender and nearly cylindrical. The head is unusually long and extremely oblique. The neck is slightly constricted dorso-ventrally and excessively compressed transversely, its width being less than half the width of the head. The abdomen is fusiform and increases slightly in width towards the base of the foot; the integument is so flexible that it can hardly be called a lorica, and the plates are very obscure; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The foot is large and robust; the tail is fairly prominent. The toes are short, stout and decurved, with the ventral edges somewhat undulate; the basal portion is nearly cylindrical and the posterior tapers gradually to acute points; their length is about one sixth of the total length. The foot glands are very long and tubular.

The corona is excessively oblique and slightly convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is broad and very slightly expanded posteriorly, the manubria unusually long, nearly straight, rodlike and stout. The bladder is very large.

The ganglion is very long and pyriform; eyespot and retrocerebral organ are absent.

Total length  $200\mu$ ; toes  $35\mu$ .

*Cephalodella pheloma* is rare; we have found only a few specimens among *Fontinalis* and submerged sphagnum growing in soft, acid water in a shallow pond at Estellville, near Atlantic City, New Jersey. It appears to be closely related to *C. megalcephala*, but is readily distinguished by the more slender body, long foot

glands, the form of the toes, as well as the remarkable compression of the neck, so striking in a dorsal view of the animal; when the species was first found, we assumed this to be caused by a pathological condition, but this was evidently an error, as it is always present in perfectly healthy individuals.

**CEPHALODELLA TENUIOR (Gosse).**

Plate XXXIII, figure 3.

*Diaschiza tenuior* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 81, pl. 22, fig. 14.—DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 135, pl. 4, fig. 12.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 123, fig. 239.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 21.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1915, p. 141.

The body is elongate, slender and nearly cylindric. The head is large, slightly deflexed and oblique anteriorly. The neck is not strongly marked. The abdomen is very nearly parallel-sided, slightly gibbous posteriorly; the lorica is very flexible and the plates indistinct; the lateral clefts are narrow anteriorly and increase slightly and evenly in width for about two thirds of their length; at this point the dorsal plates become rounded and the cleft widens rapidly. The foot is relatively short and broadly conical; the tail is near the end of the foot and fairly prominent. The toes are short, very nearly straight and parallel-sided for about two thirds of their length; beginning here the ventral edge curves upwards to meet the dorsal edge in an acute point; the length of the toes is one fifth of the total length. The foot glands are very small.

The corona is oblique, strongly convex and without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded posteriorly and the manubria crutched. The gastric glands are small and occasionally have a brownish tint.

The ganglion is very long and pyriform; eyespot and retrocerebral organ are absent.

Total length, 120-125 $\mu$ ; toes 22-24 $\mu$ .

*Cephalodella tenuior* is fairly common in weedy ponds everywhere. It is closely related to *C. forcicata*, from which it differs in the form of the toes, the much smaller size, flexible lorica and the form of the lateral clefts.

**CEPHALODELLA RETUSA** Myers, new species.

Plate XXXIII, figure 6.

The body is rather short, fusiform and fairly stout. The head is large and obliquely truncate anteriorly. The neck is not very strongly marked. The abdomen is nearly parallel-sided and very slightly gibbous dorsally; the lorica is fairly rigid and the plates well marked; the lateral clefts are narrow and parallel-sided for about one half of their length, increasing slightly in width towards the posterior end. The foot is moderately large and robust; the tail is very small. The toes are short and stout; the ventral edge is straight in its entire length, the dorsal for about three fourths of its length, and from this point it curves rapidly towards the ventral edge, meeting it in an acute point; the length of the toes is about one fourth of the entire length. The foot glands are small and pyriform.

The corona is strongly oblique and convex without projecting lips.

The mastax is fairly large and of the normal type; the fulcrum is expanded posteriorly and the manubria crutched.

The ganglion is very large and saccate; eyespot and retrocerebral organ are absent.

Total length  $100\mu$ ; toes  $24\mu$ .

*Cephalodella retusa* is not common; we have collected it among sphagnum growing on the bottom in shallow water of Doughty's Mill Pond, about two miles west of Absecon, New Jersey. It is related to *C. forficata*, but is much smaller and the form of the toes is quite different.

**CEPHALODELLA DIXON-NUTTALLI** Myers, new species.

Plate XXXIII, figures 4-5.

The body is elongate, fairly slender and laterally compressed. The head is rather small, slightly deflexed, and obliquely truncate anteriorly. The neck is not strongly marked. The abdomen increases gradually and very regularly in width from the neck to the posterior end; the dorsal and ventral edges are almost straight lines. The lorica is very thin and flexible and the plates are difficult to trace; the lateral clefts are narrow anteriorly and the edges diverge rapidly and regularly towards the posterior end, where their distance apart is half the width of the abdomen. The foot

is nearly half as long as the abdomen and very stout; the tail is small and somewhat beyond mid-length. The toes are short and taper very slightly for one half of their length, changing abruptly to conical, acute points; their length is a little less than one fifth of the total length. The foot glands are very small and pyriform.

The corona is oblique, slightly convex and without projecting lips.

The mastax is rather small and of the normal type; the fulcrum is very slightly expanded posteriorly, the manubria very slender and not crutched. The gastric glands are very small.

The ganglion is moderately elongate and pyriform; eyespot and retrocerebral organ are absent.

Total length  $160\mu$ ; toes  $30\mu$ .

*Cephalodella dixon-nuttalli* is known only from Lake Kathan, Oneida County, Wisconsin; it was collected among submerged sphagnum and other small aquatic plants. All the specimens seen had the toes closely appressed, producing the appearance of a single toe.

**CEPHALODELLA FORFICATA (Ehrenberg).**

Plate XXXIII, figure 7.

- Notommata forficata* EHRENBURG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 134.
- Notommata forcipata* EHRENBURG, Infusionsthierchen, 1838, p. 428, pl. 51, fig. 5.
- Furcularia caeca* GOSSE, Ann. Mag. Nat. Hist., ser. 2, vol. 8, 1851, p. 199.  
—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 42, pl. 20, fig. 4.
- Furcularia ensifera* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 43, pl. 20, fig. 3.
- Diaschiza paeta* GOSSE, in Hudson and Gosse, Rotifera, 1886, vol. 2, p. 79, pl. 22, fig. 11.—BILFINGER, Jahresh. Ver. Naturk. Württemberg, vol. 50, 1894, p. 53.—LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 44.—RUNNSTRÖM, Zool. Anz., vol. 34, 1909, p. 270.—LIE-PETTERSEN, Bergens Mus. Aarbog (for 1909), 1910, p. 59.
- Diaschiza acronota* GOSSE, Journ. Royal Micr. Soc., 1887, p. 867, pl. 15, fig. 15.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 37, pl. 31, fig. 29.
- Diaschiza caeca* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 134, pl. 4, fig. 11.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 64.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 105.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 53.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 121, figs. 235, 236.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 20.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 141.
- Diaschiza forficata* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 34; Proc. U. S. Nat. Mus., vol. 47, 1913, p. 528.

The body is elongate, fairly slender, somewhat prismatic and slightly compressed laterally. The head is large and obliquely truncate anteriorly. The neck is well marked. The abdomen is very nearly parallel-sided and slightly convex dorsally; the lorica is firm and the plates well marked; the lateral clefts are narrow and parallel-sided. The foot is conical and rather short; the tail is small and rounded. The toes are fairly wide apart at the base, moderately short, stout, very slightly recurved and taper gradually to acute points; their length is a little less than one fourth of the total length. The foot glands are moderately large and pyriform.

The corona is strongly oblique and convex without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded at the posterior end and the manubria are crutched. The gastric glands are large and pigmented red.

The ganglion is long and saccate; at its posterior end is a small retrocerebral sac with a distinct duct, bifurcate anteriorly, but not reaching the surface of the corona. There is no eyespot.

Total length 175–184 $\mu$ ; toes 36–40 $\mu$ .

*Cephalodella forficata* is common everywhere in weedy ponds. We have used Ehrenberg's name for this species, as it is undoubtedly the same as Gosse's *Diaschiza caeca*; the form of the toes, often crossed, size 150 $\mu$ , and the very large "eye," that is: gastric glands, all agree with Gosse's description.

*C. forficata*, *tenuior*, *collactea* and *intuta* show considerable similarity; the form of the body is approximately the same, all have pigmented gastric glands and crutched manubria. They are readily distinguished by the form of the toes; *C. tenuior*, *collactea* and *intuta* are also much smaller than normal specimens of *C. forficata*.

CEPHALODELLA INTUTA Myers, new species.

Plate XXXV, figures 2–5.

The body is moderately elongate and slender, laterally compressed and slightly gibbous posteriorly. The head is relatively long on the dorsal side and short on the ventral side on account of the strongly oblique corona. The neck is well marked. The abdomen increases gradually in depth for about two thirds of its length and from there tapers rapidly towards the short, conical foot; the

tail is small and rounded. The lorica is fairly rigid and the plates well marked. The lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end of the lorica. The toes are faintly recurved, wide apart at the base, very long and slender, tapering slightly to acute, clawlike points with transverse basal septa; their length is about one fourth of the total length.

The corona is convex and strongly oblique, without projecting lips.

The mastax is large and of the normal type; the fulcrum is broadly expanded at the posterior end and the manubria crutched. The gastric glands are tinted red.

The ganglion is long and saccate; at its posterior end is a small sac with well marked duct, bifurcate at the anterior end, but not reaching the surface of the corona. There is no eyespot.

Total length 115–125 $\mu$ ; toes 30–35 $\mu$ ; trophi 40 $\mu$ .

*Cephalodella intuta* has been collected among submerged sphagnum and other aquatic vegetation in Loon Lake, about one mile south of Eagle River, Vilas County, Wisconsin, and in soft, acid water ponds around Atlantic City, New Jersey. Its nearest relative is *C. forficata*, from which it differs in the form of the body, shorter foot and much longer and more slender toes, as well as in its smaller size.

**CEPHALODELLA COLLECTEA** Myers, new species.

Plate XXXIV, figure 5.

The body is moderately elongate, nearly cylindrical and slightly gibbous dorsally. The head is very short and strongly oblique anteriorly. The neck is well marked. The abdomen increases gradually in width for nearly three fourths of its length and from this point tapers rapidly to the large, robust foot; the tail is a small rounded boss. The lorica is fairly rigid and the plates well marked; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The toes are long, straight, slender and very slightly tapering; the dorsal edge is straight throughout; the ventral edge is straight for about five sixths of the length of the toe; at this point it bends abruptly at an obtuse angle to meet the dorsal line and this tapering portion of the toe ends in a bristle-like point. The length of the toes is

one fourth of the total length. The foot glands are fairly large and pyriform.

The corona is oblique and strongly convex without projecting lips.

The mastax is small; the fulcrum is straight and slightly expanded posteriorly, the manubria slender and crutched. The gastric glands are frequently tinted red.

The ganglion is moderately long and saccate; eyespot and retro-cerebral organ are absent.

Total length  $130\mu$ ; toes  $32\mu$ .

*Cephalodella collectea* has been found only in Loon Lake, Vilas County, Wisconsin. Its nearest relative is *C. intuta*, from which it is readily distinguished by the form of the toes.

**CEPHALODELLA INQUILINA** Myers, new species.

Plate XXXVI, figure 1.

The body is moderately elongate, nearly parallel-sided and laterally compressed. The head is short and broad, somewhat longer dorsally than ventrally. The neck is well marked. The abdomen is either parallel-sided or slightly wider posteriorly; the lorica is very thin and flexible and the edges of the plates indistinct; the lateral clefts are narrow anteriorly and increase gradually in width towards the posterior end. The foot is large and very broad at the base; the tail is very small. The toes are long, slender, nearly straight, somewhat enlarged at the base and very slightly tapering, suddenly reduced at the ends to minute, but very distinct claws; their length is about one fourth of the total length. The foot glands are moderately large and pyriform.

The corona is decidedly oblique and strongly convex without projecting lips.

The mastax is relatively small; the posterior end of the fulcrum is broadly and abruptly expanded; the manubria are crutched.

The ganglion is long and saccate; eyespot and retro-cerebral organ are absent.

Total length  $250-270\mu$ ; toes  $62-68\mu$ .

*Cephalodella inquilina* is common among sphagnum and submerged plants in soft-water ponds; we have collected it in Vilas and Oneida Counties, Wisconsin, and around Atlantic City, New Jer-



sey. It is a very rapid swimmer, readily recognized by its large size and the peculiar, clawed toes.

**CEPHALODELLA LICINIA** Myers, new species.

Plate XXXIV, figure 4.

The body is elongate, slender and somewhat prismatic. The head is a little longer than wide and obliquely truncate anteriorly. The neck is not strongly marked. The abdomen is very slightly arched dorsally, almost parallel-sided; the lorica is fairly rigid and the plates well marked; the lateral clefts are rather narrow anteriorly and increase in width towards the posterior end. The foot is conical and moderately large; the tail is small and rounded and unusually far back on the foot. The toes are long and slender; they are nearly parallel-sided and straight for about three fourths of their length; the terminal portion is strongly decurved and tapers to very slender, bristle-like points; their length is about one fourth of the total length. The foot glands are small and pyriform.

The corona is oblique and slightly convex without projecting lips.

The mastax is relatively small and weak; the fulcrum is slightly expanded at the posterior end and the manubria are slender, rod-like and not crutched. The gastric glands are small.

The ganglion is very long and saccate. The eyespot and retro-cerebral organ are absent.

Total length  $105\mu$ ; toes  $28\mu$ .

*Cephalodella licinia* is found in small numbers among *Fontinalis novae-angliae* in bog pools at Bargaintown, near Atlantic City, New Jersey.

**CEPHALODELLA VACUNA** Myers, new species.

Plate XXXV, figure 6.

The body is elongate, fairly slender, nearly parallel-sided and somewhat prismatic. The head is long and obliquely truncate anteriorly. The neck is well marked. The abdomen increases very slightly in size towards the posterior end and is faintly curved dorsally; the lorica is flexible and the plates well marked; the lateral clefts are fairly wide anteriorly and become more so towards the posterior end. The body is obliquely truncate posteriorly; the

foot is large and conical, projecting slightly beyond the small, rounded tail. The toes are very long, faintly recurved and slender, tapering gradually to acute points; their length is more than one fourth of the total length. The foot glands are small.

The corona is convex and strongly oblique without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded posteriorly and the manubria strongly crutched.

The ganglion is large and elongate saccate. Neither eyespot nor retrocerebral organ are present.

Total length  $220\mu$ ; toes  $62\mu$ .

*Cephalodella vacuna* has been collected in small numbers among submerged sphagnum in a pond with soft, acid water at Gravelly Run, near Atlantic City, New Jersey.

**CEPHALODELLA SPECIOSA Myers, new species.**

Plate XXXIV, figure 6.

The body is moderately elongate and tapers gradually to the base of the toes. The head is very large; its dorso-ventral width is greater than the width of the abdomen. The neck is well marked. The abdomen tapers rapidly from the neck to the base of the foot; the plates of the lorica are moderately flexible and separated by well marked lateral clefts. The foot is of normal length; the tail is small and knoblike and does not quite reach the posterior end of the foot. The toes are very long, slender, tapering and very slightly decurved; near the blunt tip is a transverse septum, giving the toes an appearance of being clawed; their length is but little less than half the length of the body.

The corona is oblique and without projecting lips.

The mastax is large and of normal type; the fulcrum is crutched and the manubria slender and rodlike.

The ganglion is large and saccate; neither eyespot nor retrocerebral organ are present.

Total length  $145-155\mu$ ; toes  $45-47\mu$ .

*Cephalodella speciosa* is found in a large pond at Oceanville, New Jersey, among *Riccia* and floating sphagnum in soft, acid water.

**CEPHALODELLA CUNEATA** Myers, new species.

Plate XXIX, figure 2.

The body is fairly short and conical, tapering gradually from the corona to the base of the toes. The head is very large, nearly half the length of the entire body and considerably wider than the abdomen. The neck is indicated by a slight constriction. The abdomen is very short and tapers evenly and rapidly to the base of the foot; the lorica is very flexible, but the plates are well marked; the lateral clefts are fairly wide and flaring at the posterior end. The foot is relatively long and conical and rather small at the base; the tail is rudimentary. The toes are very long, slender and decurved, slightly expanded at the base and gradually tapering to acute, bristle-like points; their length is one third of the total length. The foot glands are very small and pyriform.

The corona is strongly oblique and convex with prominent, beak-like lips.

The mastax is huge; the fulcrum is nearly half as long as the entire body; the manubria are very slender and not crutched.

The ganglion is elongate and saccate; neither eyespot nor retro-cerebral organ are present.

Total length  $105\mu$ ; toes  $32\mu$ .

*Cephalodella cuneata* is fairly common among sphagnum in a shallow ditch with soft, acid water, about five miles north of Egg Harbor, New Jersey. It has considerable resemblance to *C. speciosa*, but is much smaller, the head is relatively larger and the toes quite different.

**CEPHALODELLA HYALINA** Myers, new species.

Plate XXXII, figure 4.

The body is elongate, fairly slender and slightly compressed laterally. The head is large and strongly oblique anteriorly. The neck is well marked. The abdomen is very nearly parallel-sided, slightly rounded dorsally at the extreme posterior end; the integument is very flexible and the body virtually illoricate; the edges of the plates are very obscure and difficult to trace; the lateral clefts appear to be narrow and parallel-sided. The foot is fairly large and robust; the tail is prominent and near mid-length. The toes are long, slender, wide apart at the base, recurved and slightly tapering, with conical points formed by an abrupt downward

curvature of the dorsal edge; at the apex is a short, bristle-like nib forming a continuation of the ventral edge; the length of the toe is about one fourth of the total length. The foot glands are large and pyriform.

The corona is strongly oblique and decidedly convex without projecting lips.

The mastax is large and of the normal type; the fulcrum ends in a triangular expansion and the manubria are strongly crutched.

The ganglion is very long and saccate; eyespot and retrocerebral organ are absent.

Total length 200-215 $\mu$ ; toes 45-50 $\mu$ .

*Cephalodella hyalina* is not rare in ponds with soft, acid water; we have collected it among submerged sphagnum in Lake Kathan and Starvation Lake, Oneida County, Wisconsin, and in *Fontinalis novae-angliae* at Bargaintown, near Atlantic City, New Jersey.

**CEPHALODELLA PAPILOSA** Myers, new species.

Plate XXXIV, figure 7.

The body is relatively short, laterally compressed and strongly gibbous dorsally. The head is fairly large and obliquely truncate anteriorly. The neck is deeply constricted. The abdomen increases rapidly in depth for about two thirds of its length and is gently rounded posteriorly; the transverse width is only one half of the dorso-ventral depth of the body at its highest point. The lorica is fairly rigid and the plates well marked; the lateral clefts are fairly wide and nearly parallel-sided throughout their length. The foot is moderately short and broad at the base; the tail is very small. The toes are very long, slender and slightly decurved; from the base they taper evenly and gradually to acute points; their length is nearly half the length of the body.

The lateral antennae are of unusual form; small tufts of sensory setae are seated on small, slender conical tubules.

The corona is oblique and strongly convex without projecting lips.

The mastax is rather large and of the normal type; the fulcrum is slightly expanded posteriorly; the manubria are rodlike and not crutched.

The ganglion is elongate saccate; retrocerebral organ and eyespot are absent.

Total length 135 $\mu$ ; toes 43 $\mu$ .

*Cephalodella papillosa* is rare; we have collected it only in a large pond at Oceanville, New Jersey, among *Riccia* and floating sphagnum.

CEPHALODELLA EVA (Gosse).

Plate XXXV, figure 8.

*Furcularia eva* GOSSE, Journ. Royal Micr. Soc., 1887, p. 864, pl. 14, fig. 9.

—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 26, pl. 31, fig. 17.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 230, pl. 5, fig. 41.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 134.—RUNNSTRÖM, Zool. Anz., vol. 34, 1909, p. 269.

*Furcularia semisetifera* GLASSCOTT, Proc. Royal Dublin Soc., new ser., vol. 8, 1893, p. 55, pl. 4, fig. 2.

*Proales tigridia* WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 468, pl. 18, figs. 18–20; not *Proales tigridia* Gosse.

*Diaschiza eva* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 137, pl. 3, fig. 8.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 64.—VON HOFSTEN, Arkiv Zool., Stockholm, vol. 6, No. 1, 1909, p. 54. LUCKS, Rotatorienfauna Westpreussens, 1912, p. 93, fig. 26.—SACHSE, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 122, figs. 237, 238.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 331.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3–4, 1915, p. 20.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 142.

The body is moderately slender, strongly compressed laterally and gibbous dorsally. The head is short, broad and obliquely truncate anteriorly. The neck is well marked. The abdomen is arched dorsally and widest at mid-length; the lorica is very flexible, but the plates are well marked; the lateral clefts are very wide posteriorly. The foot is large and conical and the tail minute; the foot glands are large and pyriform. The toes are very long, nearly one third of the total length; the proximal third is tapering and the remainder very slender, almost bristle-like, flexible and strongly decurved. The foot glands are large and ovate.

The corona is oblique and without projecting lips.

The mastax is large and of the normal type; the manubria are nearly as long as the fulcrum and strongly crutched.

The ganglion is large and elongate saccate; eyespot and retrocerebral organ are absent.

Total length 275–285 $\mu$ ; toes 80–85 $\mu$ .

*Cephalodella eva* is fairly common in weedy ponds with soft water. We have collected it in Vilas and Oneida Counties, Wisconsin, and around Atlantic City, New Jersey. According to Dixon-Nuttall and Freeman this species is very variable, especially in the form of the toes; we have not found this to be the case: all the specimens that we have seen are very constant, both in form and size. We are inclined to believe that the varieties described by them may belong to one or more different species.

**CEPHALODELLA TENUISETA (Burn).**

Plate XXXV, figure 7.

*Furcularia tenuiseta* BURN, Science Gossip, vol. 26, 1890, p. 34, text fig.

*Diaschiza tenuiseta* DIXON-NUTTALL and FREEMAN, Journ. Royal Micr. Soc., 1903, p. 138, pl. 1, fig. 2.

The body is elongate, fairly slender and nearly cylindrical. The head is large, but relatively short, and obliquely truncate anteriorly. The neck is well marked. The abdomen is unusually long and slightly gibbous posteriorly; the lorica is very flexible and the plates faintly marked; the lateral clefts are narrow anteriorly and slightly wider at the extreme posterior end of the lorica. The foot is short and bluntly conical with a small, rounded tail at mid-length. The foot glands are very small and pyriform. The toes are half as long as the body, very slender, slightly recurved, and gradually tapering to acute, conical points.

The corona is convex and slightly oblique without projecting lips.

The mastax is large and of the normal type; the fulcrum is slightly expanded posteriorly and the manubria rodlike, not crutched. The oesophagus is very long and slender.

The ganglion is very long and saccate. The retrocerebral organ and eyespot are absent.

Total length 380–390 $\mu$ ; toes 120–125 $\mu$ .

*Cephalodella tenuiseta* was originally described from freshwater; we have found it only among algae and detritus in brackish and saltwater ditches around Atlantic City, New Jersey. Specimens collected by the late C. F. Rousselet at Stowmarket, Suffolk, England, agree with our material in every way except in having much longer toes. We have not been able to find any other differences and believe that they are simply local variations of the same species.

CEPHALODELLA APOCOLEA Myers, new species.

Plate XXXIII, figures 1-2.

The body is moderately elongate, nearly cylindrical and slightly compressed laterally. The head is large and relatively short. The neck is not strongly marked. The abdomen is nearly parallel-sided and slightly convex dorsally; the lorica is very thin and flexible, but the plates are well marked; the lateral clefts are moderately wide and parallel-sided. The foot is large and robust; the small tail is near the posterior end. The toes are extremely far apart at the base, cylindrical and straight for about two thirds of their length, abruptly recurved and ending in slender, sickle-shaped, acute points; their length is about one fourth of the total length. The foot glands are very large and pyriform.

The corona is oblique, moderately convex and without projecting lips.

The mastax is large and of the normal type, but the trophi are slender; the fulcrum is slightly incurved at the extreme end, but not expanded; the manubria are delicate, slightly curved rods, and not crutched. The gastric glands are small.

The ganglion is moderately elongate and pyriform; eyespot and retrocerebral organ are absent.

Total length 125-135 $\mu$ ; toes 32-35 $\mu$ .

*Cephalodella apocolea* is common in weedy ponds and bogs; we have collected it in Vilas and Oneida Counties, Wisconsin; around Washington, District of Columbia; Atlantic and Ocean counties, New Jersey, and Polk County, Florida; also in material collected by Dr. H. S. Jennings around Ann Arbor, Michigan.

CEPHALODELLA STREPTA Myers, new species.

Plate XXXV, figure 1.

? *Furcularia macrodactyla* STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 134, pl. 2, fig. 15.

The body is elongate, fairly slender, slightly gibbous dorsally and faintly curved. The head is relatively long and tapers very slightly from the neck towards the corona; it is protected by a distinct lorica, which falls into definite folds when the head is retracted, as in the genus *Diurella* and others. The neck is well marked. The abdomen is somewhat prismatic and slightly arched dorsally; its greatest depth is near mid-length. The plates of the

lorica are very firm and the lateral cleft wide. The foot is large and conical; the tail is very small and near the middle of the foot. The toes are very long, recurved, stout at the base and taper gradually to acute points; their length is about two fifths of the total length. The foot glands are large and pyriform.

The corona is slightly oblique and without projecting lips.

The mastax is moderately large and of the normal type, the fulcrum and manubria rodshaped and slightly curved, but not crutched. The gastric glands are large and usually of a deep pink color.

The ganglion is fairly large and saccate. Neither eyespot nor retrocerebral organ are present.

Total length 100–110 $\mu$ ; toes 40–45 $\mu$ .

*Cephalodella strepta* is not rare in weedy ponds with soft, acid water. We have collected it at Eagle River, Vilas County, Wisconsin, and around Atlantic City, New Jersey. It swims very slowly and deliberately, nearly always in a straight course, so that, when once seen, it is easily recognized in spite of its minute size; its behavior suggests the movements of a mechanical toy rather than the erratic course of other rotifers. It is possible that Stenroos's *Furcularia macrodactyla* may have been described from specimens of this species; according to his description and figure his animal differs in the form of the body and foot, as well as in its greater size and relatively longer toes.

**CEPHALODELLA MUCRONATA** Myers, new species.

Plate XXXVI, figures 2–4.

The body is elongate, slender and slightly gibbous dorsally. The head is moderately long and obliquely truncate anteriorly. The neck is well marked. The abdomen is protected by a very rigid lorica, extending over the foot and projecting beyond it; the longitudinal clefts are deep and terminate at the foot sheath, which has a triangular ventral point and a stout dorsal spine, separated by a deep, rounded sinus. The foot does not project beyond the ventral point of the foot sheath. The toes are nearly as long as the body, unusually slender, slightly recurved and taper very gradually to acute points.

The corona is slightly oblique without projecting lips.



The mastax is of the normal type of the genus; the inner edges of the rami are finely denticulate; the fulcrum is slightly expanded posteriorly and the rami are crutched.

The ganglion is large and saccate; there is a small retrocerebral sac, curving over the posterior end of the ganglion; the duct approaches the corona, but does not quite reach it. There is no eyespot.

Total length 265–275 $\mu$ ; toes 120–125 $\mu$ ; trophi 36 $\mu$ .

*Cephalodella mucronata* is not rare in weedy, soft-water ponds; we have collected it in Vilas and Oneida Counties, Wisconsin, around Atlantic City, New Jersey, and in Polk County, Florida. It was first found by the late James Murray in preserved material brought home from New Zealand; the contracted specimens, one of which he sent to us, were believed by him to be *Monommata appendiculata* Stenroos.

CEPHALODELLA PARASITICA (Jennings).

Plate XXXVI, figure 6.

*Pleurotrocha constricta* JENNINGS, Bull. Michigan Fish Comm., No. 3, 1894, p. 14; not *Pleurotrocha constricta* Ehrenberg.

*Pleurotrocha parasitica* JENNINGS, Bull. U. S. Fish Comm., vol. 19 (for 1899), 1900, p. 84, pl. 16, figs. 13, 14.—DE BEAUCHAMP, Bull. Soc. Zool. France, vol. 30, 1905, p. 117, figs. 1, 2; Arch. Zool. Expér., ser. 4, vol. 10, 1909, p. 202.

*Diaschiza parasitica* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 34.

The body is fairly slender, distinctly curved and gibbous dorsally. The head is unusually long and tapers from the neck towards the corona. The neck is well marked. The abdomen increases gradually in width for about two thirds of its length and from this point tapers rapidly to the base of the foot. The integument is very flexible and there is no trace of the usual fissured lorica. The foot is short and conical, its base somewhat smaller than the posterior end of the abdomen; the tail is rudimentary. The toes are very slightly decurved; the anterior half is nearly cylindrical and the posterior tapers gradually to acute points; their length is about one sixth of the total length. The foot glands are minute and virtually atrophied.

The corona is strongly oblique and without projecting lips.

The mastax is large and the trophi of normal type; two large salivary glands are attached to its posterior end.

The ganglion is relatively small and saccate; neither eyespot nor retrocerebral organ are present.

Total length 200 $\mu$ ; toes 35 $\mu$ .

*Cephalodella parasitica* is usually found attached to the cuticle of various oligochaetes (*Stylaria*, *Chaetogaster*). There is no reason for considering it a true parasite; it leaves the host readily and swims as well as other members of the genus; in all probability the temporary attachment is simply a method of transportation. We have collected this species in shallow bays of Mamie Lake, Vilas County, and Lake Kathan, Oneida County, Wisconsin.

**CEPHALODELLA EUPODA** Myers, new species.

Plate XXXVI, figure 7.

The body is moderately slender and gibbous dorsally. The head is large, somewhat longer than wide. The neck is well marked. The abdomen increases gradually in width for about half its length, and from this point tapers towards the base of the foot, which is marked by a slight constriction. The integument is very flexible and there is no trace of the lorica. The foot is large and conical; the minute tail is somewhat beyond mid-length. The toes are blade-shaped, short and slightly decurved; they increase slowly in width for nearly half their length, then decrease more rapidly to conical, acute points about one third the length of the toes; their entire length is one seventh of the total length.

The corona is very slightly oblique and without projecting lips.

The mastax is fairly large and of normal type; the manubria are somewhat stouter than usual and bent at an obtuse angle near mid-length. The oesophagus is very long and convoluted.

The ganglion is large and saccate; there is no eyespot and no trace of the retrocerebral organ.

Total length 150 $\mu$ ; toes 22 $\mu$ .

A few specimens of *Cephalodella eupoda* were collected some years ago at Four Mile Run, near Washington, District of Columbia; it has not been found elsewhere.

**CEPHALODELLA LIPARA** Myers, new species.

Plate XXXVI, figure 5.

The body is extremely short, stout and nearly cylindrical. The head is enormous; its length is nearly half the length of the body.

The neck is marked by a slight constriction. The abdomen is very short and abruptly truncate posteriorly; the lorica is very flexible, and the dorsal and ventral plates separated by a very wide cleft. The foot is indistinct and the tail very small. The toes are short, stout and blade-shaped; the dorsal edge is decurved and the ventral nearly straight, with a slightly decurved, clawlike tip; their length is about one sixth of the total length of the body.

The corona is slightly oblique without projecting lips.

The mastax is huge, but of the normal type of the genus; the fulcrum is slightly expanded and decurved at the posterior end; the manubria are slender and rodlike. The total length of the mastax is fully half the length of the body.

The ganglion is very large and saccate; there is no eyespot and no trace of the retrocerebral organ.

Total length 130–140 $\mu$ ; toes 22–24 $\mu$ .

*Cephalodella lipara* was collected among floating sphagnum in a ditch with soft, acid water, about five miles north of Egg Harbor, New Jersey. It has a superficial resemblance to *C. physalis*, but is readily distinguished by the short toes, very stout body and the absence of the eyespot.

#### Genus DORYSTOMA Harring and Myers.

Notommatid rotifers with short, stout, gibbous, illoricate body, with a distinct constriction between head and abdomen; the foot is very short and apparently two-jointed; the toes are short and decurved; at the base of the foot there is a short spine.

The corona is oblique and consists of a marginal wreath of cilia with lateral, auricle-like tufts of cilia adapted to propulsion.

The mastax is a specialized form of the virgate type; the trophi are modified as supports for the walls and a highly specialized epipharynx is present and serves to pierce the body wall of the prey by projection through the mouth.

The eyespot is single and at the posterior end of the ganglion.

*Type of the genus.*—*Dorystoma caudata* (Bilfinger) = *Proales caudata* Bilfinger.

This species was listed in volume twenty as a member of the Wisconsin rotifer fauna on the strength of a preliminary identification, which later proved to be incorrect. However, enough is

known of this species to warrant the provision of a separate genus for it. The external form has been well described by Bilfinger, Voigt and Lie-Pettersen, and the mastax by De Beauchamp.

**Genus ROUSSELETIA Harring.**

Notommatid rotifers with short, gibbous, illoricate body, with a slight constriction separating head and abdomen; the tail is large and collar-like, surrounding the base of the long, unjointed foot; the two toes are short and conical.

The corona is slightly oblique; the marginal cilia are short, except on two lateral, auricle-like areas; on the unciliated apical plate are two slightly decurved papillae; the mouth is near the ventral edge.

The mastax is virgate and very large; the fulcrum expands fan-wise towards the posterior end and is in the transverse plane of the body; the rami are large and dome-shaped, without marginal denticulations; the mallei are simple, curved rods with a ventral spur; unci are absent; a rodshaped epipharynx, decurved at the ends, is imbedded in the anterior wall of the mastax.

The retrocerebral sac is large and pyriform; no subcerebral glands are present. The eyespot is cervical.

*Type of the genus.*—*Rousseletia corniculata* Harring.

**ROUSSELETIA CORNICULATA Harring.**

Plate XXXVII, figures 1-4.

*Rousseletia corniculata* HARRING, Proc. U. S. Nat. Mus., vol. 46, 1913, p. 393, pl. 37, figs. 1-3.

The body is short, moderately stout and gibbous dorsally; its greatest width is nearly one third of the total length. The integument is very flexible, but the outline is quite constant. The entire body is colored green by symbiotic zoochlorellae.

The head and abdomen are separated by a well marked constriction. The width of the head segment is nearly equal to its length, about two thirds of the greatest width of the body. The abdomen increases gradually in width for about two thirds of its length and is rounded posteriorly; a short, sleeve-like tail surrounds the base of the foot. The dorsal surface is marked with faint longitudinal striations, continued about half way down the sides. The foot is relatively long, slightly tapering and without

joints. The toes are short, conical and acutely pointed; their length is about one twelfth of the total length. Only the ventral half of the truncate posterior end of the foot is occupied by the toes; on the dorsal margin is a minute papilla with a few long setae.

The dorsal antenna is a small, setigerous pit in the normal position; the lateral antennae are on minute tubules, only a short distance above and in front of the tail.

The corona is very slightly oblique; the circumapical band of cilia is without any dorsal gap and has laterally two strongly ciliated, auricle-like areas. The buccal field is evenly covered with very short cilia. On the unciliated apical plate are two conspicuous, slightly decurved papillae, resembling those of the genus *Ploesoma*. The mouth is near the ventral margin of the corona.

The mastax is virgate and almost half as long as the body proper. The fulcrum is narrow at the base and its sides gradually diverge towards the posterior end, enclosing a thin, ovate lamella with fanshaped striations; it is unique on account of being in the transverse plane of the body. The rami are large and roughly triangular in ventral view; the edges are curved towards the dorsal side, so that a roughly dome-shaped cavity is formed. The mallei are simple, strongly curved rods, with a short spur near mid-length; there is no trace of the unci. The epipharynx is rod-shaped, with decurved ends. The piston is very large and fills the entire cavity of the mastax.

The oesophagus is slender and moderately long. There is no constriction between the stomach and intestine. The gastric glands, ovary and bladder are normal. The foot glands are long and clubshaped.

The retrocerebral organ consists of a large, pyriform sac, which never contains bacteroids; there are no subcerebral glands. The ganglion is large and saccate, and the small eyespot is at the posterior end.

Total length  $130\mu$ ; toes  $10\mu$ ; trophi  $40\mu$ .

*Rousseletia corniculata* occurs in weedy ponds, but never in large numbers. It seems to be widely distributed; we have collected it at Washington, District of Columbia, at Atlantic City, New Jersey, in Oneida and Vilas Counties, Wisconsin, in Fairmount Park, Philadelphia, Pennsylvania, and Polk County, Florida.

**Genus TYLOTROCHA Haring and Myers.**

Notommatid rotifers with spindle-shaped, illoricate body, with a distinct constriction between the head and abdomen; two lateral, knoblike, retractile processes near mid-length; the tail is rudimentary, the foot fairly long and unjointed; the toe is single, formed by the fusion of two originally separate toes. The dorsal antenna is double.

The corona is slightly oblique and has a marginal row of moderately long cilia and two lateral, auricle-like tufts of long cilia; the buccal field is sparsely ciliated; on the apical plate are two unciliated, retractile elevations without definite form.

The mastax is a specialized form of the virgate type; all the normal elements are fused into a dome-shaped structure, serving for the support of the walls of the mastax during the pumping action.

At the posterior end of the ganglion is a lenticular pigment body, which is probably a rudimentary retrocerebral sac enclosing the eyespot.

*Type of the genus.*—*Tylotrocha monopus* (Jennings) = *Notommatata monopus* Jennings.

**TYLOTROCHA MONOPUS (Jennings).**

Plate XXXVII, figures 5-8.

*Notommatata monopus* JENNINGS, Bull. Michigan Fish Comm., No. 3, 1894, p. 14, figs. 5, 6; No. 6, 1896, p. 87.

*Tylotrocha monopus* HARRING and MYERS, Trans. Wisconsin Acad. Sci., vol. 20, 1922, p. 555.

The body of this peculiar species is spindle-shaped and slender; its greatest width is about one fourth of the total length. The integument is very flexible and the outline varies constantly in response to the contractions of the animal. The entire body is of a brilliant, translucent reddish-purple or crimson color.

The head and abdomen are separated by a shallow constriction; there is no distinct transverse fold. The head segment decreases slightly in width towards the neck; its length is nearly equal to the width. The abdomen is fusiform, largest in the middle and tapering to the rudimentary tail. Near the middle are two knoblike lateral elevations, retractile at the will of the animal and constantly changing in form. The foot is relatively long and conical, continuing the outline of the body; it is without joints, but deeply

wrinkled. The toe is single, slender and conical, slightly reduced at the base and apparently formed by the fusion of the two normal toes, as there are two well developed mucus glands; its length is one twentieth of the total length.

There are two dorsal antennae, slightly elevated papillae with a minute tuft of sensory setae; they are on the posterior part of the head and about  $15\mu$  apart. The lateral antennae are in the normal position and very small.

The corona consists of a circumapical band of moderately long cilia; laterally there are two tufts of long cilia, resembling auricles. The buccal field is evenly and somewhat sparsely ciliated; on its upper edge there is a median tuft of long cilia or setae. The mouth is near the ventral edge. Near the lateral margins of the apical plate are two unciliated retractile elevations without any very definite form; they are constantly being thrust out and withdrawn, thus resembling the enigmatic lateral humps; when fully extended, they appear to be bluntly conical.

The mastax is a highly specialized form of the virgate type; all the normal elements are firmly fused into a roughly dome-shaped structure. The outlines of the incus are still recognizable: a very slender, rodshaped fulcrum and two elongate triangular rami, separated by an elongate oval space. The mallei are no longer divisible in unci and manubria; a single, roughly semicircular lamella with a posterior, rodlike extension representing the posterior part of the median cell, is all that is actually present, and the ventral margin is firmly united to the rami. The animal has not been observed while feeding, and the operation of the mastax is unknown; the sclerified framework may act simply as a support to the walls of a pump, the piston moving in the cavity. The possibility is not excluded that it may serve as the real piston, as in the genus *Lindia*, and produce the vacuum necessary for suction by a rocking motion; this would, however, appear to require some form of an epipharynx, and no trace of this has been found.

The oesophagus is long and slender. The stomach and intestine are separated by a deep constriction. The gastric glands are replaced by a cluster of small rounded bodies of high refractive index, apparently enclosed in a membranous investment; these highly refractive globules are also found floating freely in the body cavity, and there is always a cluster in the lateral humps; their nature and function are unknown. The bladder is a simple expansion of

the cloaca. Two well developed foot glands are present, indicating that the single toe is of recent origin. The ovary is normal.

The ganglion is large and nearly circular; at its posterior end is a lenticular, pigmented body which seems to be partly eyespot and partly a rudimentary retrocerebral sac.

Total length 175–250 $\mu$ ; toes 18–24 $\mu$ ; trophi 18 $\mu$ .

*Tylostrocha monopus* is fairly common in certain localities. We have collected it in shallow ponds in Vilas and Oneida Counties, and limnetic in lakes in Washburn and Sawyer Counties, Wisconsin, and Polk County, Florida; it is common in ponds around Atlantic City, New Jersey. Jennings found it in Lake Michigan, as well as in inland lakes in Michigan.

#### Genus **RESTICULA** Harring and Myers, new genus.

Notommatid rotifers with very slender, spindle-shaped, illoricate body, nearly cylindric anteriorly and tapering gradually from mid-length to the base of the toes, without reduction in diameter of the foot; the two toes are short and usually have a bulbous enlargement at the base, containing a small mucus reservoir.

The corona is frontal or slightly oblique, with a marginal wreath of short cilia and two lateral, auricle-like tufts of long cilia for propulsion; the buccal field is covered with short, close-set cilia.

The mastax is virgate and adapted to prehension, but still retains the pumping action unimpaired; the fulcrum is long and slender; the rami are triangular and nearly symmetrical, with a right-angled bend near mid-length; the unci have a single well developed tooth; the epipharynx is rudimentary or absent. Two large salivary glands are present.

The retrocerebral organ consists of a small, rounded, ductless sac. The eyespot, when present, is a loosely aggregated mass of red pigment granules, diffusing among the vacuoles of the sac.

*Type of the genus.*—*Resticula melandocus* (Gosse) = *Furcularia melandocus* Gosse.

#### **RESTICULA MELANDOCUS** (Gosse).

*Furcularia melandocus* GOSSE, Journ. Royal Micr. Soc., 1887, p. 2, pl. 1, fig. 4.—HUDSON and GOSSE, Rotifera, Suppl., 1889, p. 27, pl. 31, fig. 18.

—BILFINGER, Jahresh. Naturk. Württemberg, vol. 50, 1894, p. 47.—VOIGT, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 102, fig. 189.

*Notommata melandocus* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 79.



*Eosphora melandocus* HARRING and MYERS, Trans. Wisconsin Acad. Sci., vol. 20, 1922, p. 644, pl. 59, figs. 6-10.

For description of this species see volume twenty, cited above; we have finally come to the conclusion that a new genus is necessary for this and related species.

**BESTICULA GELIDA** (Harring and Myers).

*Eosphora gelida* HARRING and MYERS, Trans. Wisconsin Acad. Sci., vol. 20, 1922, p. 642, pl. 60, figs. 1-6.

For description of this species see volume twenty, cited above. It is closely related to *R. melandocus*, especially in the structure of the mastax.

**BESTICULA ANCEPS** Harring and Myers, new species.

Plate XXXVIII, figures 5-8.

The body is elongated, spindle-shaped and very slender; its greatest width is about one fifth of the total length. The integument is very flexible and the outline is constantly changing in response to the contractions of the animal. The entire body is very transparent.

The head and neck segments are of about equal length and width, approximately three fourths of the greatest width of the body. The transverse folds limiting the two anterior segments are well marked. The abdomen is very nearly parallel-sided for half its length; from there it tapers very gradually to the base of the foot, ending in an indistinct, broadly rounded tail. The foot continues the general outline of the body without any marked reduction; it has two joints, the proximal very large and tapering to the short terminal joint. The toes are short and conical; their external margins are slightly curved and the inner straight; their length is about one twentieth of the total length.

The dorsal and lateral antennae are small setigerous papillae in the normal positions.

The corona is slightly oblique and consists of a marginal wreath of cilia, closed on the ventral side immediately below the mouth; laterally there are two strong, auricle-like tufts especially adapted to swimming. The buccal field is covered with short, close-set cilia; the small apical plate is unciliated.

The mastax is virgate, but of a modified type; although it still retains the pumping action seemingly unimpaired, the unci may

be used for prehension. The fulcrum is very long and slender, slightly incurved and expanded at the posterior end for the attachment of the muscles of the piston. The rami are broadly triangular in ventral view and have large, somewhat asymmetric alulae with a complicated system of reinforcing ribs. The basal apophysis is prominent and very broad; behind this there is a large oval ventral opening between the rami, continuing to the point where the teeth of the unci normally rest. The dorsal, curved portion of the rami is deeply striate and obtusely dentate on its inner margin. The unci have a very small, subsquare basal plate, traversed diagonally by a rudimentary tooth, finely striate at the tip; only one tooth in each uncus is functional. Five or six very short accessory teeth are attached to the tip of the left uncus, but none to the right. The central section of the manubrium tapers gradually to the posterior end; the basal plate is somewhat pentagonal in outline. A slender, curved rod is imbedded in the walls of the mastax on each side just below, and parallel to, the posterior edge of the ramus; these rods assist in the support of the mastax during the pumping action. The salivary glands are very large and nearly of the same size.

The oesophagus is slender and moderately long. The gastric glands are very small. A slight constriction separates the stomach from the intestine. The ovary and bladder are normal. The foot glands are small and pyriform; they discharge into a very small, spherical mucus reservoir at the base of the toes.

The ganglion is large and saccate. The retrocerebral sac is fairly large, pyriform and vacuolate; it does not appear to contain bacteroids. No subcerebral glands are present. The eyespot is a huge, lens-shaped disc attached to the posterior end of the ganglion; its diameter is two thirds of the width of the ganglion itself.

Total length 250-300 $\mu$ ; toes 12-15 $\mu$ ; trophi 45 $\mu$ .

*Resticula anceps* is rare; we have only found a few specimens in a boggy area along Helen Creek, near Mamie Lake, Vilas County, Wisconsin. Its nearest relative is *R. nyssa*, but it is readily recognized by its smaller size, the form of the corona and the eyespot, as well as the simpler toes.

RESTICULA NYSSA Harring and Myers, new species.

Plate XXXVIII, figures 1-4.

The body is elongate, spindle-shaped or subcylindric and very slender; its greatest width is only one sixth of the total length. The integument is very flexible and the outline changes with the contortions of the animal. The body is transparent.

The head segment is rounded anteriorly and this portion is separated from the head proper by a slight constriction; it corresponds to the rostrum of other Notommatids. The length of the neck segment is a little greater than its width; the transverse folds limiting it anteriorly and posteriorly are well marked. The abdomen is very nearly cylindric; it is longitudinally striate and has three indistinct, transverse folds. The tail is quite prominent, short and very broad. The foot has two very short, broad joints of about equal length. The toes have a large basal, bulbous enlargement, similar to, but smaller than *R. melandocus*; the posterior half is conical, acute and slightly decurved. A very faint transverse line separates the basal bulb and the clawlike tip of the toes; their length is about one twentieth of the total length.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae have not been observed.

The corona is virtually ventral and consists of a simple, evenly ciliated oval area without any auricles or any cilia specialized for swimming. The mouth is near the posterior edge.

The mastax is virgate with modifications adapting it for prehension. The fulcrum is long and slender, slightly incurved and expanded at the posterior end for the attachment of the muscles of the piston. The rami are roughly triangular in ventral view and have large asymmetric alulae. The basal apophysis is very prominent; above this there is a large oval ventral opening between the rami. At the apex of the rami there are three or four very small teeth, traceable for some distance from the inner edges of the rami as faint striae. The dorsal portion of the rami is marked with a marginal band of fine, closely spaced, convergent striae; near the dorsal tips there appears to be complete fusion of the rami. The unci have two teeth each; the ventral tooth is well developed, but not clubbed at the tip. The second tooth is strongly curved and only half the length of the main tooth; it rests in a well marked depression or socket in the ramus and evidently serves only as a hinge for the entire malleus. Five acces-

sory teeth are attached to the tip of the left uncus; there are none on the right side. The basal plate of the manubria is rather small and rounded; the central portion is long and slender, somewhat irregularly curved and tapers gradually towards the posterior end. The slender reenforcing rods imbedded in the walls of the mastax of so many Notommatids are in this species fibrillate at the ends and fused to the rami. The piston is very large and powerful and, as far as can be judged from the structure of the mastax, the pumping function is of primary importance and prehension secondary. The salivary glands are very large and of the same size.

The oesophagus is very long and slender. The gastric glands, ovary and bladder are normal. There is no distinct separation between stomach and intestine. The foot glands are small and pyriform; a minute mucus reservoir may be concealed in the basal enlargement of the toes.

The ganglion is large and saccate; the spherical, ductless, vacuolate retrocerebral sac is attached to its posterior end. No sub-cerebral glands are present. There is no true eyespot; the anterior portion of the sac is filled with a mass of red pigment granules, diffusing among its vacuoles, but not enclosed in any capsule.

Total length 300–350 $\mu$ ; toes 14–18 $\mu$ ; trophi 50 $\mu$ .

*Resticula nyssa* has been found only at Bargaintown, near Atlantic City, New Jersey. Its nearest relatives are *R. melandocus* and *R. anceps*; it is readily recognized by its large size, slender body and the very simple, ventral corona, as well as the structure of the eyespot.

#### Genus **EOSPHORA** Ehrenberg.

Notommatid rotifers with fusiform, illoricate body, nearly cylindrical anteriorly and tapering to a distinct tail; the foot is usually tubular and moderately long; the two toes are short.

The corona is frontal, with a marginal wreath and a lateral, inner arc of cilia joined to it and simulating auricles; the mouth is at the ventral margin of the buccal field and the intra-marginal ciliation has largely disappeared.

The mastax is virgate, but the pumping action has been partly lost; the fulcrum is short and very broad; the rami are triangular and bent at a right angle near mid-length, where one or two large, blunt teeth are usually present; the unci have a single, very large

tooth, adapted to prehension; a rudimentary epipharynx is usually present. There are two salivary glands, the right much larger than the left and frequently curving under the fulcrum.

The retrocerebral organ is small, but both sac and glands are present. The eyespot is cervical, at the posterior end of the ganglion; two accessory frontal eyespots are found in some species.

*Type of the genus.*—*Eosphora najas* Ehrenberg.

The genera *Eothinia* and *Resticula* are very closely related to *Eosphora*, but seem to form natural groups with the included species agreeing in so many important characters (corona, mastax, retrocerebral organ, form of body, etc.), that generic separation appears advisable.

**EOSPORA THOA** Harring and Myers, new species.

Plate XXXIX, figures 1-5.

The body is broad and very robust; its greatest width is one third of the total length. The integument is very flexible and the animal highly contractile. The entire body is hyaline.

The head and neck segments are fused and separated from the abdomen by a well marked constriction; the corona is as wide as the body at its widest point. The abdomen tapers gradually from a point near mid-length to the base of the foot, and ends in a broad, but not very prominent tail. The foot is conical and very stout; it is without joints, but irregularly wrinkled. Its length is about one fourth of the entire length. The two toes are heart-shaped in dorsal view, ending in very fine points; the ventral edge is straight, while the dorsal is strongly curved; their length is about one fifteenth of the total length. In young animals the abdomen is faintly striate or plicate dorsally.

The corona is frontal and consists of a marginal wreath of cilia, interrupted dorsally and passing in a curve to the lateral angles where it is joined by an inner arc, starting also from the dorsal gap; from the angles the corona continues as a single band, closed ventrally and passing immediately below the mouth. The buccal field is evenly ciliated. On the apical plate are two large papillae, each with a tuft of sensory setae. There is no indication of the accessory eyespots usually present on these papillae in other species of this genus.

The dorsal antenna is on the posterior portion of the head segment, just in front of the transverse neck fold; the distance from the neck to the lateral antennae is about two thirds of the length of the abdomen.

The mastax is of a modified virgate type, in which the pumping action has become subordinate and the trophi adapted to the seizure of prey by prehension. The fulcrum is very short and broad. The rami are elongate, roughly triangular and strongly curved longitudinally; near the base there is a very large apophysis, projecting as a double spur towards the ventral side. The inner edges of the rami have near mid-length a blunt tooth, interlocking with its mate on the opposite side; immediately in front of this tooth there are some faint denticulations, and nearer the base a strong transverse rib forms a slightly projecting knob. The posterior half of the rami are armed with about twenty small, conical teeth, separated by relatively large interspaces. The unci have a single, very robust, clubshaped ventral tooth, which is connected to the upper end of the manubrium by an excessively thin lamella of irregular outline. The central section of the manubrium is nearly parallel-sided and slightly curved; the basal plate is triangular. The epipharynx consists of two symmetrical, roughly I-shaped pieces, imbedded in the walls of the mastax; the shorter branch is directed diagonally outwards and towards the ventral side; the longer, broadly expanded posteriorly, is nearly parallel to the longitudinal axis of the mastax.

The epipharynx has been turned through an angle of approximately 90 degrees in figure 5, to avoid obscuring the form of the rami; it is consequently somewhat foreshortened, and its true length is shown in figure 4. The right lobe of the mastax is considerably larger than the left; this condition usually indicates the presence of a salivary gland, but there are no structural remains of it.

The oesophagus is relatively short. The gastric glands are very large and rounded. There is no constriction between the stomach and intestine. The nuclei of the ovary are unusually large and irregular in outline; they appear to have separate yolk-masses. The bladder is normal. The foot glands are nearly cylindrical and as long as the foot itself; they discharge into a minute, spherical mucus reservoir at the base of the toes.

The ganglion is large and saccate. The retrocerebral organ consists of a small, vacuolate sac and two very small subcerebral

glands. The eyespot is large and at the posterior end of the ganglion.

Total length 300–500 $\mu$ ; toes 20–35 $\mu$ ; trophi 50 $\mu$  long, 60 $\mu$  wide.

*Eosphora thoa* is rare; we have found only a few specimens in "Cemetery pond," near Eagle River, Vilas County, Wisconsin, and at Bargaintown, near Atlantic City, New Jersey. In external appearance it resembles *E. anthadis* so closely that it is virtually impossible to separate them. However, their behavior is very different; *E. anthadis* is a very slow swimmer and generally sluggish in its movements, while *E. thoa* swims very fast and is constantly changing its direction. The eyespot is sufficient to distinguish the species, and the trophi show but slight resemblances. It should be noted that *E. anthadis* is found only in moderately hard waters, while *E. thoa* occurs only in very soft water, so that there is really no great danger of confusion.

#### Genus ENTEROPLEA Ehrenberg.

Notommatid rotifers with short, very stout, saccate, illoricate body; the head is short and broad, the neck well marked; the abdomen is slightly pyriform and ends in a short, sleeve-like tail; two deep dorsal grooves at the points of attachment of the retractor muscles; the foot is short and indistinctly two-jointed; the toes are short and bladeshaped.

The corona is frontal and consists of a marginal wreath of strong cilia and a transverse arc of moderately long cilia separating the apical plate and the unciliated buccal field.

The mastax is a modified form of the virgate type, adapted to prehension; the fulcrum is short and broad, the rami lyrate and very powerful, denticulate on the inner margin; the unci have a single, very large tooth, clubbed at the point; the manubria are short and broad; two rudimentary salivary glands are present.

The gastric glands are very long and ribbonlike; on the dorsal side of the stomach are four long, tubular, glandular appendages.

The retrocerebral organ is rudimentary; both sac and glands are present. Two eyespots are seated on small knobs on the apical plate.

*Type of the genus.*—*Enteroplea lacustris* Ehrenberg.

## ENTEROPLEA LACUSTRIS Ehrenberg.

Plate XL, figures 1-5.

- Enteroplea lacustris* EHRENBURG, Abh. Akad. Wiss. Berlin, 1830, p. 46; in Hemprich and Ehrenberg, Symb. Phys. Anim. Evert., Phytozoa, 1832 (?), pl. 3, fig. IV, 11.—HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 44.
- Diglena lacustris* EHRENBURG, in Hemprich and Ehrenberg, Symb. Phys. Anim. Evert., Phytozoa Polypi, 1832 (?), fol. *b* (second page); Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 136, pl. 3, fig. 10, pl. 4, fig. 14; (for 1833), 1834, p. 335, pl. 10, fig. 2; Infusionsthierchen, 1838, p. 442, pl. 54, fig. 4.—DUJARDIN, Hist. Nat. Zooph., 1841, p. 652.—TÓTH, Math. Termész. Közl., vol. 1, 1861, p. 187, (pl. 4) fig. 32.
- Triphylus lacustris* HUDSON, in Hudson and Gosse, Rotifera, Suppl., 1889, p. 19, pl. 32, fig. 16.—WESTERN, Journ. Quekett Micr. Club, ser. 2, vol. 4, 1890, p. 107, pl. 10, fig. 1; 1892, p. 374, pl. 25, fig. 5.—BILFINGER, Jahresh. Ver. Naturk. Württemberg, vol. 48, 1892, p. 113.—WIERZEJSKI, Rozpr. Akad. Umiej., Wydz. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 224.—KERTÉSZ, Budapest Rotat. Faun., 1894, p. 28.—JENNINGS, Bull. U. S. Fish Comm., vol. 19 (for 1899), 1900, p. 84.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 40; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 110, figs. 207, 208.—VORONKOV, Trudy Hidrobiol. Stants. Glubokom Oz., vol. 2, 1907, p. 95.—DE BEAUCHAMP, Arch. Zool. Expér., ser. 4, vol. 10, 1909, pp. 24, 228, 341, figs. II 4, XXXVI, LVII, pl. 9, figs. 124-131.—LUCKS, Rotatorienfauna Westpreussens, 1912, p. 47, fig. 6.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 124, fig. 35.

The body is short, saccate and very stout; its greatest width is nearly two thirds of the length of the body proper. The integument is very soft and flexible, but the outline remains quite constant. The entire body is very hyaline.

The head is short and very broad; it is separated from the abdomen by a well defined constriction or neck immediately behind the mastax. The abdomen is slightly pyriform, ending posteriorly in a short, sleeve-like tail surrounding the base of the foot; posterodorsally it has two parallel, deep, V-shaped grooves, caused by the pull of the dorsal retractor muscles, the broadened ends of which are attached to the internal apex of the V. The foot is indistinctly two-jointed, tapering and rather short, about one fifth of the length of the body; the terminal joint is nearly twice as long as the basal joint. The toes are nearly cylindrical for one half of their length, with conical, acute points; their length is about one sixteenth of the total length.

The dorsal antenna is a small, setigerous papilla in the normal position; the lateral antennae are quite close together, immediately in front of and above the tail.



The corona is frontal and consists of a marginal wreath of strong cilia, interrupted dorsally and closed behind the mouth, which is near the ventral edge. The buccal field is in this species unciliated and somewhat depressed; its margin is indicated by a horseshoe-shaped band of cilia, separating it dorsally from the apical plate.

The mastax belongs to the virgate type, but is somewhat modified, as the animal is carnivorous and the mallei have become adapted to the seizure of prey by prehension through the mouth opening. The rami are lyrate in ventral view and have prominent basal apophyses for the attachment of the abductor muscles; laterally they are expanded into broad, thin, somewhat asymmetric lamellae. Near mid-length they are bent at a right angle; this median section is lamellar and denticulate on its inner edge, with fine striae continuing for some distance from the base of the denticles. At the apex of the angle there is on each ramus a strongly developed tooth, fitting into a groove on the opposite side. The dorsal ends of the rami form two powerful, curved, opposing teeth, separated from the central, denticulate section by an elongate oval opening. The fulcrum is a moderately long, broad lamella, expanded at the base of the rami and nearly parallel-sided posteriorly. The unci have a single, powerful tooth, somewhat curved and clubbed at the point, and a small accessory tooth, only half the length of the main tooth; the basal plate is roughly triangular. The manubria have a subsquare basal plate; the central section is continued as a nearly straight, slightly compressed rod, curved towards the ventral side at the extreme end. The epipharynx consists of two triangular plates, bent at a somewhat obtuse angle along the median line, and projecting forward at a right angle to the rami at the anterior apex. The piston is very large and almost completely fills the cavity of the mastax. There are two rudimentary salivary glands in the ventral angles of the mastax.

The oesophagus begins high up on the dorsal side of the mastax; its walls are muscular and may be greatly distended to allow the passage of entire animals into the stomach. The gastric glands are long and ribbon-like; their ends are bifurcate. In addition to the glands there are four very long, slender gastric appendages, no doubt glandular in nature; two of these are a short distance below the gastric glands, the others near the posterior end of the stomach. There is no constriction between the stomach and in-

testine. The bladder is large. The foot glands are very long and slender, extending almost the entire length of the foot.

The ganglion is relatively small and saccate. The retrocerebral sac is rudimentary and fused to the lower surface of the ganglion. Two small subcerebral glands are present; in the young animals they contain bacteroids and are consequently opaque, but with age they gradually become transparent. The two eyespots are on small knobs on the apical plate, a short distance below and outside the arc of cilia limiting the buccal field dorsally.

Total length 500–600 $\mu$ ; toes 30–35 $\mu$ ; trophi 70 $\mu$  long, 60 $\mu$  wide.

*Enteroplea lacustris* is widely, but somewhat sporadically distributed; where it does occur, it is usually present in enormous numbers. It is very often found in company with *Epiphanes* (= *Notops*) *clavulata*, although they are not to be considered inseparable.

#### Genus EOTHINIA Harring and Myers.

Notommatid rotifers with moderately elongate, fusiform, illoricate body, a distinct neck segment separating head and abdomen; the tail is moderately large or rudimentary, the foot two-jointed and short; the toes are rather short.

The corona is obliquely frontal and may have a ventral chin; the marginal cilia are fairly short except on two lateral, auricle-like areas.

The mastax is virgate, but somewhat specialized; the inner<sup>s</sup> edges of the rami are provided with numerous short, closely spaced, needlelike teeth; the piston is well developed.

The retrocerebral organ is well developed; both sac and glands are present; there is a cervical eyespot at the posterior end of the ganglion and two frontal eyespots on the apical plate.

*Type of the genus.*—*Eothinia elongata* (Ehrenberg) = *Eosphora elongata* Ehrenberg.

EOTHINIA TRIPHAEA Harring and Myers, new species.

Plate XLI, figures 1–5.

The body of this species is fusiform and moderately elongate; its greatest width is about one fourth of the total length. The in-

tegument is very flexible and the outline changes according to the contractions of the animal. The body is very transparent.

The transverse folds limiting the head and neck segments are unusually deep. The head segment is broadest anteriorly and tapers towards the neck; its width is but little less than the width of the abdomen. The neck segment is a little narrower than the head, but approximately the same length, slightly more than half the width. The abdomen increases very slightly in width for about half its length and then tapers gradually to the base of the foot; the tail is represented by a very slight dorsal elevation. The two short foot joints continue the outline of the abdomen without any sudden reduction in width. The two toes are very long and slender, slightly decurved and incurved; they have a nearly hemispherical, slightly compressed, bulbous enlargement at the base. The length of the toes is about one seventh of the total length.

The corona extends down on the ventral side about one fourth of the length of the body; the post-oral portion projects as a minute chin. The unciated apical plate is strongly convex; the buccal field has a well marked, troughlike median depression in which the mouth is located. The marginal cilia are short except on two lateral, auricle-like areas.

The dorsal antenna is a short, stubby boss with a central depression, at the center of which is a tuft of sensory setae. The lateral antennae have not been observed.

The mastax is virgate and resembles closely the type of the genus, but in the development of the unci it is a little nearer the normal *Notommata*-type. The fulcrum is extremely broad at the base and tapers somewhat abruptly to a slender, rodlike, slightly incurved posterior section. The rami are broadly triangular and nearly symmetrical; their inner edges are provided with short, close-set, needle-like teeth, beginning near the base and continuing to the apex. The unci have a subsquare basal plate with a well developed ventral tooth, clubbed at the tip, and a rudimentary second tooth, beginning near the base of the ventral tooth and crossing the basal plate diagonally to its dorsal edge. Two short and very slender accessory teeth are attached to the ventral edge of the principal tooth in each unci. The basal plate of the manubrium is large and subsquare; the posterior portion is fairly stout and decurved at the tip. Two slender, slightly curved rods are imbedded in the walls of the mastax below the posterior edges of

the rami; they serve as supports during the pumping action. The piston is well developed.

The oesophagus is slender and moderately long. The stomach and intestine are not separated by any constriction. The gastric glands and ovary are normal. The cloaca appears to function as a bladder. The foot glands are large, nearly circular and slightly compressed; they discharge into a small, spherical mucus reservoir, which is partly in the bulbous, basal enlargement of the toe.

The ganglion is moderately large and nearly spherical. The retrocerebral sac is pyriform and very small; the subcerebral glands are short and always contain a rounded mass of bacteroids at the level of the cervical eyespot, thus producing the appearance of three eyespots in a transverse row. There are two accessory frontal eyespots on the apical plate in addition to the cervical eyespot at the posterior end of the ganglion.

Total length 175–250 $\mu$ ; toes 25–35 $\mu$ ; trophi 28 $\mu$  long, 35 wide.

*Eothinia triphaea* occurs in small numbers among sphagnum growing on the margins of shallow ponds. We have found it widely distributed in Vilas and Oneida Counties, Wisconsin, and also in ponds around Atlantic City, New Jersey, and at Hyattsville, near Washington, District of Columbia.

**EOTHINIA ARGUS** Harring and Myers, new species.

Plate XLI, figures 6–11.

The body of this species is fusiform and moderately elongate; its greatest width is about one fourth of the total length. The integument is moderately flexible and the outline fairly constant. It is a very transparent animal.

The transverse folds limiting the head and neck segments are well marked. The head segment is very broad anteriorly and tapers towards the neck; its width is equal to the width of the abdomen. The neck segment is considerably narrower than the head. The abdomen is nearly cylindrical for three fourths of its length and rounded posteriorly. The tail is small and three-lobed; the median lobe is subsquare and the lateral lobes rounded. The foot has two short joints of nearly equal length. The toes are slender, conical, acutely pointed and slightly decurved; their length is about one fourteenth of the total length.

The corona is slightly oblique and terminates a short distance behind the mouth. The apical plate is strongly convex and un-

ciliated; the buccal field is covered with very short, close-set cilia and has a median depression around the mouth. The marginal cilia are short except on two laterally projecting, auricle-like areas.

The dorsal and lateral antennae are small setigerous papillae in the normal positions.

The mastax is virgate and slightly asymmetric. The fulcrum is long and broad at the base, tapering gradually to the slightly incurved posterior end. The rami are roughly triangular and have moderately large alulae. There is a heartshaped opening just above the fulcrum; this is followed in the right ramus by four small teeth, two strong, apical teeth and two small teeth on the dorsal portion; the left ramus has five small teeth above the ventral opening and one large, apical tooth, followed by two small dorsal teeth. The rami are prolonged dorsally by two thin, blade-like curved pieces, not observed in the mastax of any other Notommatid. The unci have a single, large tooth with two small accessory teeth attached to the clubbed tip on the ventral side; the basal plate is irregularly oval and has a narrow, denticulate portion adjoining the tooth on the dorsal side. The basal plate of the manubria is large; the posterior branch is nearly straight and has a slight terminal expansion. Two slender, double-curved rods are imbedded in the walls of the mastax just below the posterior edges of the rami; they serve as supports during the pumping action. The piston is large and muscular. On the left side is a granular area which appears to represent an atrophied salivary gland.

The oesophagus is very long and slender. There is no constriction between the stomach and intestine. The gastric glands and ovary are normal. The cloaca functions as a bladder. The foot glands are pyriform and very small.

The ganglion is large and saccate. The retrocerebral organ consists of a very small, pyriform sac and two short subserebral glands, which contain a rounded mass of bacteroids at the level of the eyespot. There are two accessory frontal eyespots on the apical plate in addition to the cervical eyespot at the posterior end of the ganglion.

Total length 250–300 $\mu$ ; toes 18–22 $\mu$ ; trophi 38 $\mu$ .

*Eothinia argus* was collected in small numbers in Lenape Lake, at Mays Landing, New Jersey. It is very closely related to *E. triphaea*, but is readily distinguished by the much shorter toes and the long retrocerebral sac.

Genus **SPHYRIAS** Harring.

Notommatid rotifers with short, broad, saccate, illoricate body; the head is very broad and truncate anteriorly and has two short, stumplike lateral projections; it is separated from the abdomen by a well marked constriction; the abdomen is subsquare and ends in a collarlike tail; the foot is long and wrinkled; the toes are short, conical and obtusely pointed.

The corona consists of two roughly circular wreaths of long cilia at the edges of the short, lateral projections of the head; the anterior surface of the head is unciliated; the mouth is near the ventral margin and strongly protrusile.

The mastax is virgate; the rami are roughly triangular and strongly curved, the inner margins armed with numerous short, closely spaced, needlelike teeth; the fulcrum and manubria are long, straight rods; the unci have only a single functional tooth; the piston is very large.

The retrocerebral organ is rudimentary; the two eyespots are on the lateral projections of the head.

*Type of the genus.*—*Sphyrias lofuana* (Rousselet) = *Notops lofuana* Rousselet.

**SPHYRIAS LOFUANA** (Rousselet).

Plate XLII, figures 1-5.

*Notops lofuana* ROUSSELET, Proc. Zool. Soc. London, 1910, p. 795, pl. 75, figs. 1-3.

*Sphyrias lofuana* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 96; Proc. U. S. Nat. Mus., vol. 46, 1913, p. 400, pl. 37, figs. 4-8.

The body of this species is short, stout and truncate anteriorly; its greatest width is about one half of the total length. The integument is moderately flexible and the outline is constantly changing in response to the violent contractions of the animal. It is a moderately transparent species.

The head and abdomen are separated by a deep transverse fold. The outline of the head is variable; when the animal is at rest (as represented in the figures), it is broadly triangular and wider than the abdomen; when it is swimming, the mouth region is retracted and the head becomes squarely truncate. The abdomen is subsquare in dorsal view, truncate posteriorly and ends in a short, very wide, collar-like tail, surrounding the base of the foot; it is

marked dorsally with strong, longitudinal folds, gradually disappearing on the sides. The foot is fairly long and wrinkled, but not jointed. The two toes are somewhat obtusely pointed, slightly decurved and laterally compressed; their length is about one tenth of the total length.

The tubular dorsal antenna is on the abdomen, immediately behind the transverse fold, and joined to the integument in its entire length. The lateral antennae are small, rounded, knoblike, setigerous papillae just above and in front of the tail.

The corona is perhaps easier to understand if it is considered as a simplified or specialized *Eosphora*-corona. As explained under this genus, its corona consists of a circumapical band of cilia, interrupted dorsally, with a lateral arc of very long cilia for propulsion, and an inner arc of fairly long cilia joined to the circumapical band at both ends. In *Sphyrias* the dorsal gap in the corona is almost equal to the width of the head, and all that remains of the circumapical band is the lateral, auricle-like arc of long cilia; in front of this is a short arc of fairly long cilia, representing the inner arc of *Eosphora*. Nothing remains of the latero-ventral arc of the circumapical band normally joining the auricles and passing below the mouth except a few short cilia at the sides of the vertical, slitlike mouth. The mouth region is retracted when the animal swims, and the inner arc of cilia thus forced out even with the external or posterior arc; this produces an appearance recalling the form of the hammerhead shark (*Sphyrna*, in Rafinesque's Greek!). At the point of attachment of the dorsal longitudinal muscles are four small tufts of sensory setae.

The mastax is virgate, but adapted also to prehension. The fulcrum is very long and straight; it is formed of two plates joined together at the edges and forming a V-shaped trough with the apex dorsal. The rami are symmetrical and roughly triangular; their inner edges are armed with about twenty long, needle-like teeth. The unci have only a single, long tooth, clubbed at the tip and with a minute basal plate. The manubria are long, rodlike and nearly straight; they diverge from the incus at an angle of nearly 45 degrees. Two straight rods, expanded at their dorsal ends into triangular plates, are imbedded in the walls of the mastax below the dorsal branch of the rami and aid in the support of the mastax during the pumping action. The piston is large and powerful; its striate longitudinal muscles are very conspicuous.

In the ventral angles of the mastax are two well developed salivary glands.

The oesophagus is moderately long and slender. There is no constriction between the stomach and intestine. The ovary is very long and ribbon-shaped and passes dorsally over the stomach into the head segment. The gastric glands and bladder are normal. The foot glands are slender, slightly clubshaped and nearly as long as the foot.

The ganglion is large and saccate. At its posterior end is a small, spherical, ductless retrocerebral sac and two granular areas at the external angles of the ganglion appear to represent the remains of the subcerebral glands. The two eyespots are on rounded, knoblike projections between the lateral arcs of cilia.

Total length 275–300 $\mu$ ; toes 35–30 $\mu$ ; trophi 62 $\mu$ .

*Sphyrias lofuana* is not rare in weedy ponds around Washington, District of Columbia; we have found it also near Atlantic City, New Jersey, and at Dock Lake, near Spooner, Wisconsin.

In spite of the somewhat aberrant external form this species is closely related to *Eosphora* and *Eothinia*, as shown by a comparison of the mastax and corona. Its food seems to consist principally of the smaller Bdelloids and *Conochilus*, whose trophi are often found in the stomach.

#### Genus **MONOMMATA** Bartsch.

Notommatid rotifers with slender, elongate ovate, spindle-shaped, illoricate body, with a slight constriction behind the mastax, separating the head and abdomen; the foot is very short and obscurely two-jointed; the toes are extremely long, nearly twice the length of the body, and unequal, the right toe longer than the left.

The corona is slightly oblique and consists of a marginal wreath of cilia with lateral, auricle-like tufts of longer cilia adapted to propulsion; the apical plate is unciliated and the buccal field evenly covered with short, close-set cilia; the mouth is somewhat below the center of the corona.

The mastax is intermediate between the virgate and forcipate type; the rami are lyrate and the inner margins armed with one or more strong teeth immediately below the mouth opening; the unci have three unequally developed, long, slender, clubbed teeth; the manubria are broad and lamellar at the base; the piston is



weak and plays only a subordinate part in the operation of the mastax.

The retrocerebral organ is imperfectly developed; the sac is ductless and the glands rudimentary or absent; the eyespot is at the posterior end of the ganglion.

*Type of the genus.*—*Monommata longiseta* (Müller) = *Vorticella longiseta* Müller.

One of the most interesting results of this survey of the notomatid rotifers is the discovery of the remarkable type of mastax of this genus; a more perfect intermediate or "missing link" between the forcipate and virgate mastax than that of *Monommata grandis* could hardly be imagined. If only the ventral view were available, it would unhesitatingly be called forcipate; its real affinities become evident at once in the lateral view, showing the curvature of the rami found only in the virgate mastax and also the large basal plate of the manubria. Both are developed as supports for the walls of the pumping type of mastax. However, the changes necessary to transform it into a perfectly good forcipate mastax are small indeed.

MONOMMATA LONGISETA (Müller).

Plate XLIII, figures 1-5.

? *Cercaria orbis* MÜLLER, Zool. Dan. Prodr., 1776, p. 280; Anim. Infus., 1786, p. 138, pl. 20, fig. 7.

*Vorticella longiseta* MÜLLER, Anim. Infus., 1786, p. 295, pl. 42, figs. 9, 10.

? *Trichoda bicaudata* SCHRANK, Fauna Boica, vol. 3, pt. 2, 1803, p. 87.

? *Vaginaria brachiura* SCHRANK, Fauna Boica, vol. 3, pt. 2, 1803, p. 144.

? *Furcocerca orbis* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 1, 1815, p. 448.

*Furcularia longiseta* LAMARCK, Hist. Nat. Anim. sans Vert., vol. 2, 1816, p. 39.—HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 46, pl. 18, fig. 16.

—ANDERSON, Journ. Asiatic Soc. Bengal, vol. 58, pt. 2, 1889, p. 53.

—WIERZEJSKI, Rozpr. Akad. Umiej., Wyd. Mat.-Przyr., Krakow, ser. 2, vol. 6, 1893, p. 230.—SKORIKOV, Trav. Soc. Nat. Kharkow, vol. 30, 1896, p. 295.—WEBER, Rev. Suisse Zool., vol. 5, 1898, p. 476, pl. 19, fig. 3.

—HEMPPEL, Bull. Illinois State Lab. Nat. Hist., vol. 5, 1898, p. 370.

—LIE-PETTERSEN, Bergens Mus. Aarbog (for 1909), 1910, No. 15, p. 46.

—MOLA, Ann. Biol. Lac., vol. 6, 1913, p. 245.

? *Trichocerca orbis* BORY DE ST. VINCENT, Class. Anim. Mier., 1826, p. 42.

? *Lecane orbis* NITZSCH, Enc. Wiss. u. Künste, sect. 1, vol. 16, 1827, p. 68.

? *Brachionus orbis* BLAINVILLE, Dict. Sci. Nat., vol. 60, 1830, p. 149.

? *Trichocerca longiseta* BLAINVILLE, Dict. Sci. Nat., vol. 60, 1830, p. 150.

- Notommata longiseta* EHRENBERG, Abh. Akad. Wiss. Berlin, 1830, p. 46; Infusionsthierchen, 1838, p. 432, pl. 53, fig. 2.
- Notommata longiseta aequalis* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831), 1832, p. 134.
- Notommata longiseta inaequalis* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831) 1832, p. 134.
- Notommata aequalis* EHRENBERG, Abh. Akad. Wiss. Berlin (for 1831) 1832, p. 134; Infusionsthierchen, 1838, p. 432, pl. 53, fig. 3.
- Scaridium longisetum* SCHOCH, Micr. Thiere Süßw.-Aqua., 1868, p. 30.
- Monommata longiseta* BARTSCH, Jahresh. Naturk. Württemberg, vol. 26, 1870, p. 344.—EYFERTH, Einf. Lebensf., 1878, p. 84, pl. 5, fig. 12; 1885, p. 109, pl. 7, fig. 12.—BERGENDAL, Acta Univ. Lundensis, vol. 28, 1892, sect. 2, No. 4, p. 75, pl. 1, fig. 14.—STENROOS, Acta Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 134.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 45; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 104, fig. 193.—LUCKS, Rotarienfauna Westpreussens, 1912, p. 54.—MONTET, Rev. Suisse Zool., vol. 23, 1915, p. 324.—JAKUBSKI, Rozpr. Wiad. Muz. Dzieduszyckich, vol. 1, No. 3-4, 1915, p. 18.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 118.
- Monommata aequalis* EYFERTH, Einf. Lebensf., 1878, p. 84; 1885, p. 109.—VOIGT, Süßwasserfauna Deutschlands, pt. 14, 1912, p. 104, fig. 194.
- Furcularia aequalis* HUDSON and GOSSE, Rotifera, 1886, vol. 2, p. 46, pl. 18, fig. 5.
- Monommata orbis* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 72.

The body of this species is slender, elongate ovate and spindle-shaped; its greatest width is less than one fourth of the length. The integument is very flexible, but the outline is fairly constant. The entire body is very transparent.

The head segment is relatively short and broad; the length is slightly greater than the width. It is separated from the abdomen by a well marked constriction. The abdomen is elongate and ovate, slightly gibbous dorsally and rounded posteriorly; the integument is covered with minute, interrupted, very closely spaced longitudinal striae. The foot is short, stout and obscurely two-jointed. The toes are extremely long and unequal; the left toe is always shorter than the right, but the relative length is variable, the usual proportion being four to five, but may be as much as one to two and individuals are occasionally found with nearly equal toes. The basal portion of the toes is fairly stout and very nearly cylindrical, tapering gradually to the cylindrical, extremely slender posterior portion, which is fully half the length of the entire toe. The right toe is virtually straight and in the axis of the body; the left toe curves slightly upwards and to the left.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae are on the posterior fourth of the body.

The corona is very slightly oblique and consists of a marginal wreath of cilia with lateral, auricle-like tufts of longer cilia for propulsion; the apical plate is unciolated and the buccal field evenly covered with short, close-set cilia.

The mastax is of a modified virgate type. The fulcrum is long and slender and tapers gradually towards the posterior end. The rami are triangular at the base and bent near mid-length at an approximately right angle; the dorsal portion is long, slender, tapering and slightly incurved. Each ramus has at the angle a long, slender tooth, interlocking with its mate on the opposite side. The right uncus has three very long, slender teeth, the posterior resting on the tip of the ramus, the two anterior on the ramus just below the inner tooth; the left uncus has two teeth, one resting on the posterior tip of the ramus and the other just below the inner tooth. The manubria are broad and lamellar, ending in a rod-shaped posterior portion, slightly recurved at the end. The piston is large, but apparently not very powerful.

The oesophagus is rather short. The gastric glands are small and rounded. There is no constriction between stomach and intestine. The ovary and bladder are normal. The foot glands are very small and pyriform.

The ganglion is moderately large and saccate. The retrocerebral sac is small and apparently ductless; it contains a small number of transparent, globular bodies and can not be stained. Near mid-length of the ganglion are two small, rounded masses representing the subcerebral glands, indicated in the figures, but invisible without intra-vitam staining. The eyespot is at the posterior end of the ganglion.

Total length 200–250 $\mu$ ; length of body 75–95 $\mu$ ; length of right toe 125–155 $\mu$ ; left toe two thirds to four fifths of right toe; trophi 18 $\mu$ .

*Monommata longiseta* is abundant everywhere in weedy ponds all over the world.

Müller's *Cercaria orbis* was undoubtedly a contracted *Monommata*. Accepting as fact the frequently asserted identity of the two "varieties" in every respect except size, the species was listed as *Monommata orbis* by Harring in the Synopsis of the Rotatoria

in accordance with accepted rules of nomenclature. However, it is very evident that the genus includes two perfectly distinct species and it is not now possible to refer *C. orbis* definitely to one or the other. For this reason we have used the later name *longiseta*, as it unquestionably belongs to the smaller species.

**MONOMMATA GRANDIS** TESSIN.

Plate XLIII, figures 6-10.

*Monommata grandis* TESSIN, Arch. Naturg. Mecklenburg, vol. 43, 1890, p. 151, pl. 1, figs. 11, 12.—LEVANDER, Acta Soc. Fauna et Flora Fennica, vol. 12, No. 3, 1895, p. 35.

*Furcularia longiseta grandis* ROUSSELET, Journ. Quekett Micr. Club, ser. 2, vol. 6, 1895, p. 124, pl. 7, fig. 3.

*Monommata longiseta grandis* STENROOS, Acta. Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 135.—VOIGT, Forschungsber. Biol. Stat. Plön, vol. 11, 1904, p. 56; Süßwasserfauna Deutschlands, pt. 14, 1912, p. 104.—WEBER and MONTET, Cat. Invert. Suisse, pt. 11, 1918, p. 119.

? *Monommata appendiculata* STENROOS, Acta. Soc. Fauna et Flora Fennica, vol. 17, No. 1, 1898, p. 135, pl. 1, figs. 33, 34.

*Monommata orbis grandis* HARRING, Bull. 81 U. S. Nat. Mus., 1913, p. 72.

The body of this species is moderately slender, elongate ovate and spindle-shaped; its greatest width is less than one third of the length. The integument is rather flexible and the outline is quite constant. The body is moderately transparent.

The head segment is moderately large and the width nearly equal to the length. It is separated from the abdomen by a well marked constriction. The abdomen is elongate and ovate, distinctly gibbous dorsally and rounded posteriorly; the integument is marked with very closely spaced, unbroken longitudinal striae, acute-angled at the bottom of the grooves and the top of the ridges. The foot is short, stout and obscurely two-jointed. The toes are extremely long and unequal; their length, both absolute and relative, is highly variable; the left toe is always shorter than the right, the difference varying between one third and one fifth of the length of the right toe. The basal portion of the toes, from one third to one half of its length, is very nearly straight for the greater part of its length; this is followed by a tapering section, which passes into the very nearly cylindrical, extremely slender posterior portion, which is from one half to two thirds of the entire length. The right toe is straight and in the axis of the body; the left toe curves slightly upwards and to the left.

The dorsal antenna is a small setigerous papilla in the normal position; the lateral antennae are on the posterior fourth of the body.

The corona is very slightly oblique and consists of a marginal wreath of cilia with lateral, auricle-like tufts of longer cilia for propulsion; the apical plate is unciliated and the buccal field evenly covered with short, close-set cilia.

The mastax belongs to a type intermediate between the virgate and the forcipate, the piston playing but a very subordinate rôle in its function. The fulcrum is rather short and very broad at the base, tapering rapidly to the blunt posterior end. The rami are broadly triangular at the base and the posterior portion lyrate; the basal apophysis is abnormally large, somewhat curved and separated from the rami proper by a deep, rounded sinus. The inner margins of the rami are equipped with a unique and complicated dental armature. The teeth are naturally divisible into three groups: ventral, oral and posterior. The ventral group consists of 12–14 comblike teeth; their length increases gradually to a point somewhat beyond mid-length, decreasing from there towards the oral group. This consists of four extremely large, stout, slightly curved and acutely pointed, interlocking teeth; the relative length and development of the individual teeth is somewhat variable, especially in the case of the second and third tooth on each side. The posterior group consists of three long, slender, acutely pointed, interlocking needle-like teeth in each ramus. Each uncus has three long, slender, unequal teeth, clubbed at the tips; two rest on the rami at the base of the comb-like teeth and one on the posterior end, beyond the oral group of teeth. In the right uncus the ventral tooth is largest and the second somewhat smaller; in the left uncus the ventral tooth is relatively small and the second as large as the right ventral. The basal portion of the manubria is broad and plate-like, the posterior rod-like and decurved at the end. The piston is relatively small and weak.

The oesophagus is short. The gastric glands are rather small and rounded. There is no constriction between the stomach and instine. The ovary and bladder are normal. The foot glands are small and pyriform.

The ganglion is large and saccate. The retrocerebral sac is fairly large and pyriform; it is usually crowded with bacteroids and opaque to transmitted light. The duct can not be traced be-

yond the dorsal antenna; subcerebral glands are not present. The eyespot is at the posterior end of the ganglion.

Greatest length 680 $\mu$ ; body 210 $\mu$ ; right toe 470 $\mu$  trophi

*Monommata grandis* is abundant everywhere in weedy ponds in the United States; judging from published records it is not common in Europe, but it is uncertain whether this is to be attributed to actual rarity or to reiterated assertions of its specific identity with *M. longiseta*.

### Subfamily TETRASIPHONINAE.

Genus TETRASIPHON Ehrenberg.

Notommatid rotifers with fusiform, illoricate body, without constriction between head and abdomen; the tail is rudimentary; the foot is short and two-jointed, with two long, slender toes.

The corona is an oblique, weakly ciliated area without auricles and used for carrying food to the mouth only, not for propulsion; the mouth is a little below the center of the corona.

The antennae are long and tubular, the dorsal antenna double.

The mastax is an aberrant form of the virgate type; the fulcrum is short and the rami very large and dome-shaped; the mallei are imperfectly developed. The epipharynx consists of four pieces of complicated form, which apparently serve to expand the mouth opening. The piston is very bulky, but weak; it is attached to the ventral floor of the mastax.

The retrocerebral organ is well developed; the subcerebral glands are longer than the sac. The eyespot is at the posterior end of the ganglion.

*Type of the genus.*—*Tetrasiphon hydrocora* Ehrenberg.

### Subfamily LINDIINAE.

Genus LINDIA Dujardin.

Notommatid rotifers with spindle-shaped, elongate, illoricate body, usually with several indistinct annulations, and without constriction at the base of the foot, which has two very small toes; the cloaca opens under a small tail, at the base of the foot.

The corona is an elongate, oval area covering the oblique anterior surface of the head and continuing beyond the mouth on the ven-

tral surface as a slightly projecting chin; the marginal cilia are relatively short, except on two latero-frontal areas provided with long and powerful cilia adapted to swimming, in the majority of species seated on evertile auricles; the apical plate is enclosed by the marginal ciliation and has occasionally a projecting rostrum; the mouth is near the center of the corona.

The mastax is adapted to suction or "pumping" by oscillating as a complete unit on a transverse axis near the posterior end of the fulcrum; the name "cardate" is proposed for this peculiar type. The fulcrum is short and narrow, usually tapering towards the posterior end; the rami are lyrate, resembling the forcipate type; the ventral branch or cell of the manubria is very large, equaling or exceeding in length the median or principal cell, with which it forms a rather acute angle; the unci are feebly developed, the teeth being rudimentary and usually united into a thin plate. Nearly all the species included have an epipharynx of very complicated form; it may consist of one, two or four separate pieces, which act as supports for the edges of the mouth, while the oscillation of the entire mastax produces behind it the vacuum necessary for the pumping action. Two salivary glands occupy the posterior portion of the mastax in some species.

The retrocerebral organ consists of a rather small, hemispherical, ductless sac at the posterior end of the ganglion; it is filled with red pigment granules and encloses the large, disc-shaped eyespot, seated on the ganglion.

*Type of the genus.*—*Lindia torulosa* Dujardin.

### Subfamily **BIRGEINAE.**

Genus **BIRGEA** Harring and Myers.

Notommatid rotifers with short, broad, illoricate, anteriorly truncate body; the head is short and very broad, separated from the abdomen by a slight constriction; the abdomen is ovate and ends posteriorly in a short, broad tail; the foot is long, very slender and three-jointed; the toes are fairly long and lanceolate.

The corona is frontal with a circumapical band of short cilia, interrupted dorsally, and two lateral, auricle-like areas with long cilia adapted to propulsion; the buccal field is evenly ciliated and the mouth is near the ventral edge.

The mastax is very aberrant; the trophi, which normally seize and subdivide the food, are virtually atrophied and their functions transferred to a pair of hooked "pseudunci", probably a highly specialized form of the epipharynx; no gastric glands are present, but the walls of the stomach are produced into a number of gastric caeca and contain symbiotic zoochlorellae.

No retrocerebral organ is present; the ganglion is small and the eyespot at its posterior margin.

*Type of the genus.*—*Birgea enantia* Harring and Myers.



EXPLANATION OF PLATES.

All the figures are highly magnified. For actual measurements see text. The epipharynx is stippled in order to distinguish it more readily from the trophi proper.

PLATE XVI.

- FIG. 1. *Proales similis*, dorsal view; page 434.
- FIG. 2. *Proales similis*, lateral view.
- FIG. 3. *Proales similis*, trophi, ventral view.
- FIG. 4. *Proales similis*, trophi, lateral view.
- FIG. 5. *Proales similis*, trophi, frontal view.
- FIG. 6. *Proales reinhardti*, dorsal view; page 431.
- FIG. 7. *Proales reinhardti*, lateral view.
- FIG. 8. *Proales reinhardti*, trophi, ventral view.
- FIG. 9. *Proales reinhardti*, trophi, lateral view.
- FIG. 10. *Proales reinhardti*, unci, frontal view.

PLATE XVII.

- FIG. 1. *Proales werneckii*, dorsal view; page 426.
- FIG. 2. *Proales werneckii*, lateral view.
- FIG. 3. *Proales werneckii*, trophi, ventral view.
- FIG. 4. *Proales werneckii*, trophi, lateral view.
- FIG. 5. *Proales werneckii*, trophi, frontal view.
- FIG. 6. *Proales gigantea*, dorsal view; page 424.
- FIG. 7. *Proales gigantea*, lateral view.
- FIG. 8. *Proales gigantea*, trophi, ventral view.
- FIG. 9. *Proales gigantea*, trophi, lateral view.
- FIG. 10. *Proales gigantea*, trophi, frontal view.

PLATE XVIII.

- FIG. 1. *Proales daphnicola*, dorsal view; page 430.
- FIG. 2. *Proales daphnicola*, lateral view.
- FIG. 3. *Proales daphnicola*, trophi, ventral view.
- FIG. 4. *Proales daphnicola*, trophi, lateral view.
- FIG. 5. *Proales daphnicola*, trophi, frontal view.

PLATE XIX.

- FIG. 1. *Proales brevipes*, dorsal view; page 428.
- FIG. 2. *Proales brevipes*, lateral view.
- FIG. 3. *Proales doliaris*, dorsal view; page 437.
- FIG. 4. *Proales doliaris*, lateral view.
- FIG. 5. *Proales doliaris*, trophi, ventral view.

EXPLANATION OF PLATES—Continued

- FIG. 6. *Proales doliaris*, trophi, lateral view.  
 FIG. 7. *Proales doliaris*, rami, frontal view.

PLATE XX.

- FIG. 1. *Proales minima*, dorsal view; page 435.  
 FIG. 2. *Proales minima*, lateral view.  
 FIG. 3. *Proales minima*, trophi, ventral view.  
 FIG. 4. *Proales minima*, trophi, lateral view.  
 FIG. 5. *Proalinopsis staurus*, dorsal view; page 439.  
 FIG. 6. *Proalinopsis staurus*, lateral view.  
 FIG. 7. *Proalinopsis staurus*, trophi, ventral view.  
 FIG. 8. *Proalinopsis staurus*, trophi, lateral view.  
 FIG. 9. *Proalinopsis staurus*, trophi, frontal view.

PLATE XXI.

- FIG. 1. *Notommata epaxia*, dorsal view; page 443.  
 FIG. 2. *Notommata epaxia*, lateral view.  
 FIG. 3. *Notommata epaxia*, trophi, ventral view.  
 FIG. 4. *Notommata epaxia*, trophi, lateral view.  
 FIG. 5. *Notommata epaxia*, unci, frontal view.  
 FIG. 6. *Notommata codonella*, dorsal view; page 444.  
 FIG. 7. *Notommata codonella*, lateral view.  
 FIG. 8. *Notommata codonella*, trophi, ventral view.  
 FIG. 9. *Notommata codonella*, trophi, lateral view.  
 FIG. 10. *Notommata codonella*, unci, frontal view.

PLATE XXII.

- FIG. 1. *Notommata doneta*, dorsal view; page 448.  
 FIG. 2. *Notommata doneta*, lateral view.  
 FIG. 3. *Notommata doneta*, trophi, ventral view.  
 FIG. 4. *Notommata doneta*, trophi, lateral view.  
 FIG. 5. *Notommata thopica*, dorsal view; page 446.  
 FIG. 6. *Notommata thopica*, lateral view.  
 FIG. 7. *Notommata thopica*, trophi, ventral view.  
 FIG. 8. *Notommata thopica*, trophi, lateral view.  
 FIG. 9. *Notommata thopica*, unci, frontal view.

PLATE XXIII.

- FIG. 1. *Notommata tithasa*, dorsal view; page 450.  
 FIG. 2. *Notommata tithasa*, lateral view.  
 FIG. 3. *Notommata tithasa*, trophi, ventral view.  
 FIG. 4. *Notommata tithasa*, trophi, lateral view.  
 FIG. 5. *Notommata tithasa*, trophi, frontal view.  
 FIG. 6. *Taphrocampa annulosa*, dorsal view; page 452.

EXPLANATION OF PLATES—Continued

- FIG. 7. *Taphrocampa annulosa*, lateral view.
- FIG. 8. *Taphrocampa annulosa*, trophi, ventral view.
- FIG. 9. *Taphrocampa annulosa*, trophi, lateral view.
- FIG. 10. *Taphrocampa annulosa*, unci, frontal view.

PLATE XXIV.

- FIG. 1. *Taphrocampa clavigera*, dorsal view; page 455.
- FIG. 2. *Taphrocampa clavigera*, lateral view.
- FIG. 3. *Taphrocampa clavigera*, trophi, ventral view.
- FIG. 4. *Taphrocampa clavigera*, trophi, lateral view.
- FIG. 5. *Taphrocampa selenura*, dorsal view; page 454.
- FIG. 6. *Taphrocampa selenura*, lateral view.
- FIG. 7. *Taphrocampa selenura*, trophi, ventral view.
- FIG. 8. *Taphrocampa selenura*, trophi, lateral view.
- FIG. 9. *Taphrocampa selenura*, unci, frontal view.

PLATE XXV.

- FIG. 1. *Pleurotrocha petromyzon*, dorsal view; page 459.
- FIG. 2. *Pleurotrocha petromyzon*, lateral view.
- FIG. 3. *Pleurotrocha petromyzon*, trophi, ventral view.
- FIG. 4. *Pleurotrocha petromyzon*, trophi, lateral view.
- FIG. 5. *Pleurotrocha robusta*, dorsal view; page 461.
- FIG. 6. *Pleurotrocha robusta*, lateral view.
- FIG. 7. *Pleurotrocha robusta*, trophi, ventral view.
- FIG. 8. *Pleurotrocha robusta*, trophi, lateral view.

PLATE XXVI.

- FIG. 1. *Cephalodella mineri*, lateral view; page 471.
- FIG. 2. *Cephalodella elongata*, lateral view; page 471.
- FIG. 3. *Cephalodella innesi*, lateral view; page 470.
- FIG. 4. *Cephalodella innesi*, trophi, ventral view.
- FIG. 5. *Cephalodella innesi*, trophi, lateral view.
- FIG. 6. *Cephalodella paxilla*, lateral view; page 468.
- FIG. 7. *Cephalodella marina*, lateral view; page 469.

PLATE XXVII.

- FIG. 1. *Cephalodella gracilis*, lateral view; page 473.
- FIG. 2. *Cephalodella angusta*, lateral view; page 467.
- FIG. 3. *Cephalodella catellina*, lateral view; page 465.
- FIG. 4. *Cephalodella catellina*, trophi, ventral view.
- FIG. 5. *Cephalodella catellina*, trophi, lateral view.
- FIG. 6. *Cephalodella sterea*, lateral view; page 474.
- FIG. 7. *Cephalodella epitedia*, lateral view; page 468.

## EXPLANATION OF PLATES—Continued

## PLATE XXVIII.

- FIG. 1. *Cephalodella hoodii*, lateral view; page 482.  
 FIG. 2. *Cephalodella exigua*, lateral view; page 481.  
 FIG. 3. *Cephalodella plicata*, lateral view; page 483.  
 FIG. 4. *Cephalodella plicata*, cross section.  
 FIG. 5. *Cephalodella ventripes*, lateral view; page 484.  
 FIG. 6. *Cephalodella auriculata*, lateral view; page 479.

## PLATE XXIX.

- FIG. 1. *Cephalodella nana*, lateral view; page 491.  
 FIG. 2. *Cephalodella cuneata*, lateral view; page 505.  
 FIG. 3. *Cephalodella physalis*, lateral view; page 484.  
 FIG. 4. *Cephalodella physalis*, trophi, ventral view.  
 FIG. 5. *Cephalodella physalis*, trophi, lateral view.  
 FIG. 6. *Cephalodella xenica*, lateral view; page 492.  
 FIG. 7. *Cephalodella strigosa*, lateral view; page 485.

## PLATE XXX.

- FIG. 1. *Cephalodella compressa*, lateral view; page 487.  
 FIG. 2. *Cephalodella tantilla*, lateral view; page 486.  
 FIG. 3. *Cephalodella piulca*, lateral view; page 488.  
 FIG. 4. *Cephalodella gibba*, lateral view; page 472.  
 FIG. 5. *Cephalodella gibba*, trophi, ventral view.  
 FIG. 6. *Cephalodella gibba*, trophi, lateral view.  
 FIG. 7. *Cephalodella dorseyi*, lateral view; page 487.

## PLATE XXXI.

- FIG. 1. *Cephalodella galbina*, lateral view; page 490.  
 FIG. 2. *Cephalodella belone*, lateral view; page 490.  
 FIG. 3. *Cephalodella globata*, lateral view; page 475.  
 FIG. 4. *Cephalodella panarista*, lateral view; page 478.  
 FIG. 5. *Cephalodella panarista*, trophi, ventral view.  
 FIG. 6. *Cephalodella panarista*, trophi, lateral view.  
 FIG. 7. *Cephalodella panarista*, toe with spine.  
 FIG. 8. *Cephalodella elegans*, lateral view; page 489.

## PLATE XXXII.

- FIG. 1. *Cephalodella nelitis*, lateral view; page 493.  
 FIG. 2. *Cephalodella melia*, lateral view; page 493.  
 FIG. 3. *Cephalodella pheloma*, lateral view; page 496.  
 FIG. 4. *Cephalodella hyalina*, lateral view; page 505.  
 FIG. 5. *Cephalodella megalcephala*, lateral view; page 494.  
 FIG. 6. *Cephalodella megalcephala*, trophi, ventral view.  
 FIG. 7. *Cephalodella megalcephala*, trophi, lateral view.

EXPLANATION OF PLATES—Continued

PLATE XXXIII.

- FIG. 1. *Cephalodella apocolea*, lateral view; page 509.
- FIG. 2. *Cephalodella apocolea*, toes, dorsal view.
- FIG. 3. *Cephalodella tenuior*, lateral view; page 497.
- FIG. 4. *Cephalodella dixon-nuttalli*, lateral view; page 498.
- FIG. 5. *Cephalodella dixon-nuttalli*, toes, dorsal view.
- FIG. 6. *Cephalodella retusa*, lateral view; page 498.
- FIG. 7. *Cephalodella forficata*, lateral view; page 499.

PLATE XXXIV.

- FIG. 1. *Cephalodella forficula*, lateral view; page 476.
- FIG. 2. *Cephalodella forficula*, trophi, ventral view.
- FIG. 3. *Cephalodella forficula*, trophi, lateral view.
- FIG. 4. *Cephalodella licinia*, lateral view; page 503.
- FIG. 5. *Cephalodella collactea*, lateral view; page 501.
- FIG. 6. *Cephalodella speciosa*, lateral view; page 504.
- FIG. 7. *Cephalodella papillosa*, lateral view; page 506.

PLATE XXXV.

- FIG. 1. *Cephalodella strepta*, lateral view; page 509.
- FIG. 2. *Cephalodella intuta*, lateral view; page 500.
- FIG. 3. *Cephalodella intuta*, trophi, ventral view.
- FIG. 4. *Cephalodella intuta*, trophi, lateral view.
- FIG. 5. *Cephalodella intuta*, toes, dorsal view.
- FIG. 6. *Cephalodella vacuna*, lateral view; page 503.
- FIG. 7. *Cephalodella tenuiseta*, lateral view; page 508.
- FIG. 8. *Cephalodella eva*, lateral view; page 507.

PLATE XXXVI.

- FIG. 1. *Cephalodella inquilina*, lateral view; page 502.
- FIG. 2. *Cephalodella mucronata*, lateral view; page 510.
- FIG. 3. *Cephalodella mucronata*, trophi, ventral view.
- FIG. 4. *Cephalodella mucronata*, trophi, lateral view.
- FIG. 5. *Cephalodella lipara*, lateral view; page 512.
- FIG. 6. *Cephalodella parasitica*, lateral view; page 511.
- FIG. 7. *Cephalodella eupoda*, lateral view; page 512.

PLATE XXXVII.

- FIG. 1. *Rousseletia corniculata*, dorsal view; page 514.
- FIG. 2. *Rousseletia corniculata*, lateral view.
- FIG. 3. *Rousseletia corniculata*, trophi, ventral view.
- FIG. 4. *Rousseletia corniculata*, trophi, lateral view.
- FIG. 5. *Tylotrocha monopus*, dorsal view; page 516.

## EXPLANATION OF PLATES—Continued

- FIG. 6. *Tylotrocha monopus*, lateral view.  
 FIG. 7. *Tylotrocha monopus*, trophi, ventral view.  
 FIG. 8. *Tylotrocha monopus*, trophi, lateral view.

## PLATE XXXVIII.

- FIG. 1. *Resticula nyssa*, dorsal view; page 521.  
 FIG. 2. *Resticula nyssa*, lateral view.  
 FIG. 3. *Resticula nyssa*, trophi, ventral view.  
 FIG. 4. *Resticula nyssa*, trophi, lateral view.  
 FIG. 5. *Resticula anceps*, dorsal view; page 519.  
 FIG. 6. *Resticula anceps*, lateral view.  
 FIG. 7. *Resticula anceps*, trophi, ventral view.  
 FIG. 8. *Resticula anceps*, trophi, lateral view.

## PLATE XXXIX.

- FIG. 1. *Eosphora thoa*, dorsal view; page 523.  
 FIG. 2. *Eosphora thoa*, lateral view.  
 FIG. 3. *Eosphora thoa*, trophi, ventral view.  
 FIG. 4. *Eosphora thoa*, trophi, lateral view.  
 FIG. 5. *Eosphora thoa*, trophi, frontal view.

## PLATE XL.

- FIG. 1. *Enteroplea lacustris*, dorsal view; page 526.  
 FIG. 2. *Enteroplea lacustris*, lateral view.  
 FIG. 3. *Enteroplea lacustris*, trophi, ventral view.  
 FIG. 4. *Enteroplea lacustris*, trophi, lateral view.  
 FIG. 5. *Enteroplea lacustris*, incus, oblique frontal view.

## PLATE XLI.

- FIG. 1. *Eothinia triphaea*, dorsal view; page 528.  
 FIG. 2. *Eothinia triphaea*, lateral view.  
 FIG. 3. *Eothinia triphaea*, trophi, ventral view.  
 FIG. 4. *Eothinia triphaea*, trophi, lateral view.  
 FIG. 5. *Eothinia triphaea*, unci, frontal view.  
 FIG. 6. *Eothinia argus*, dorsal view; page 530.  
 FIG. 7. *Eothinia argus*, lateral view.  
 FIG. 8. *Eothinia argus*, trophi, ventral view.  
 FIG. 9. *Eothinia argus*, trophi, lateral view.  
 FIG. 10. *Eothinia argus*, incus, oblique frontal view.  
 FIG. 11. *Eothinia argus*, unci, frontal view.

## PLATE XLII.

- FIG. 1. *Sphyrias lofuana*, dorsal view; page 532.  
 FIG. 2. *Sphyrias lofuana*, lateral view.

EXPLANATION OF PLATES—Continued

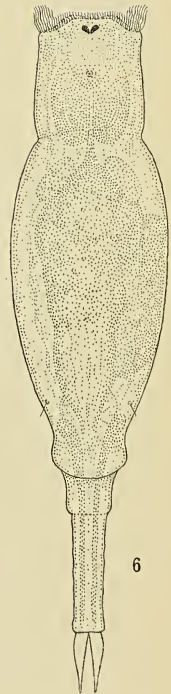
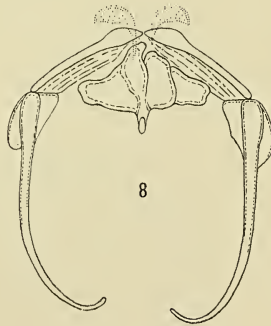
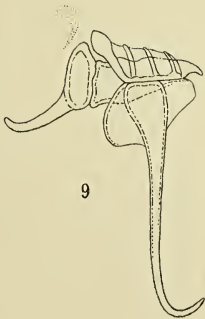
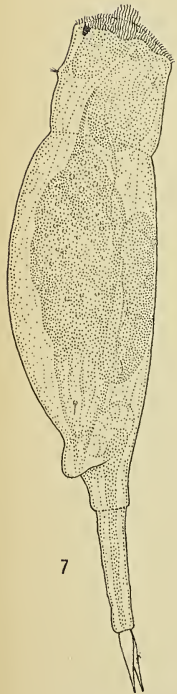
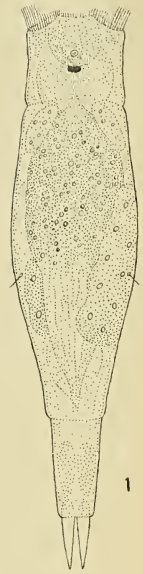
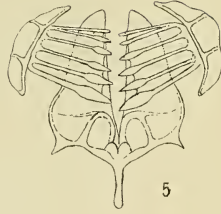
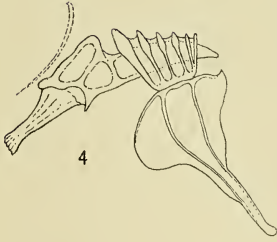
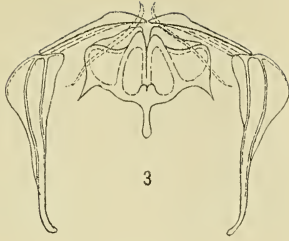
- FIG. 3. *Sphyrias lofuana*, trophi, ventral view.  
FIG. 4. *Sphyrias lofuana*, trophi, lateral view.  
FIG. 5. *Sphyrias lofuana*, trophi, oblique frontal view.

PLATE XLIII.

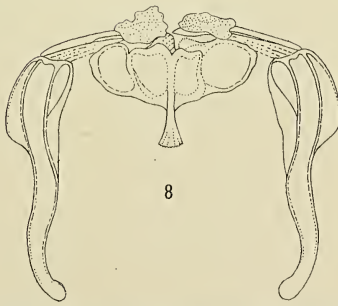
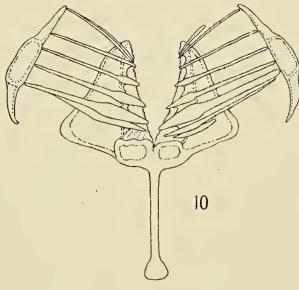
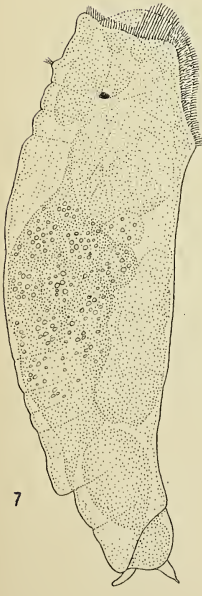
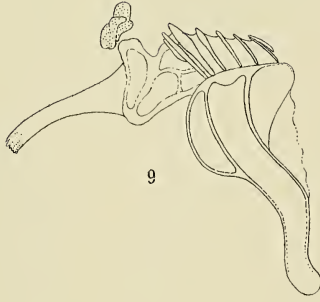
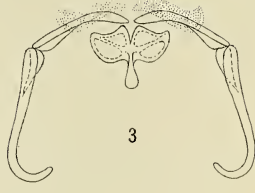
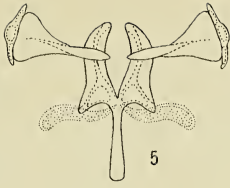
- FIG. 1. *Monommata longiseta*, dorsal view; page 535.  
FIG. 2. *Monommata longiseta*, lateral view.  
FIG. 3. *Monommata longiseta*, trophi, ventral view.  
FIG. 4. *Monommata longiseta*, trophi, lateral view.  
FIG. 5. *Monommata longiseta*, trophi, oblique frontal view.  
FIG. 6. *Monommata grandis*, dorsal view; page 538.  
FIG. 7. *Monommata grandis*, lateral view.  
FIG. 8. *Monommata grandis*, trophi, ventral view.  
FIG. 9. *Monommata grandis*, trophi, lateral view.  
FIG. 10. *Monommata grandis*, trophi, oblique frontal view.



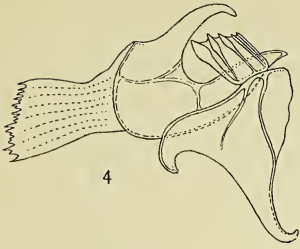




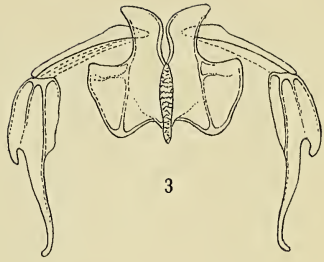




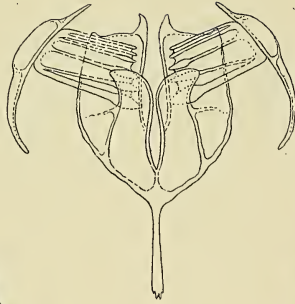




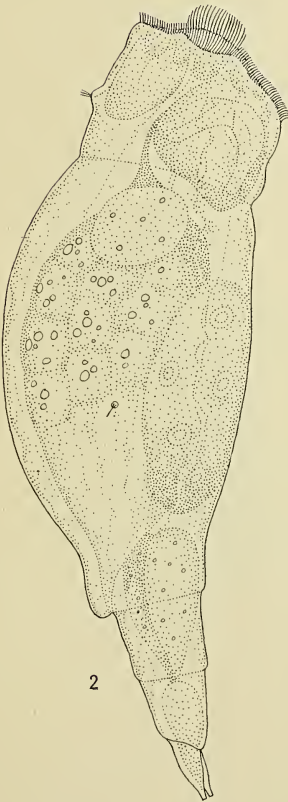
4



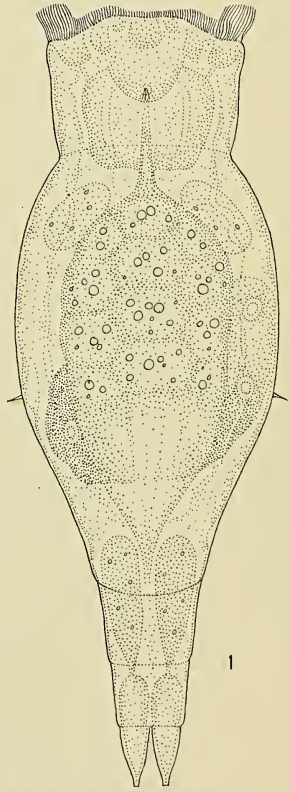
3



5

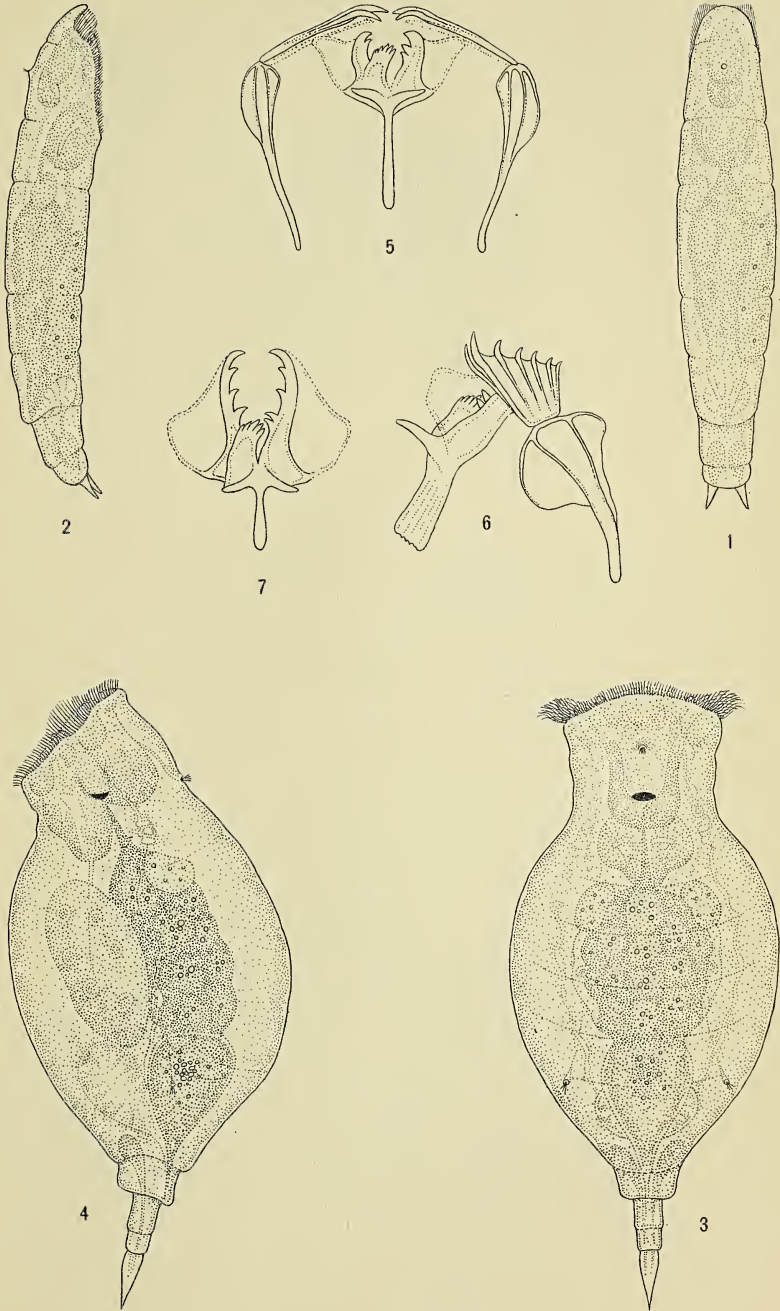


2



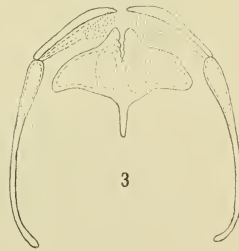
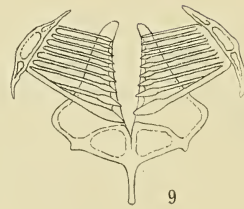
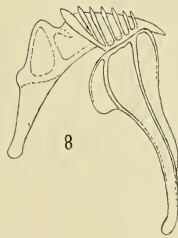
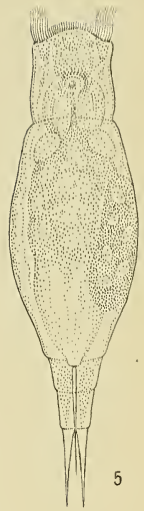
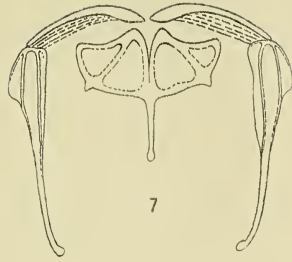
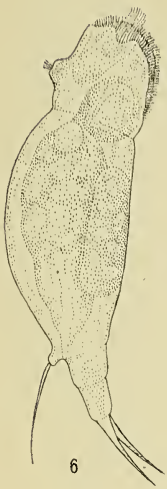
1



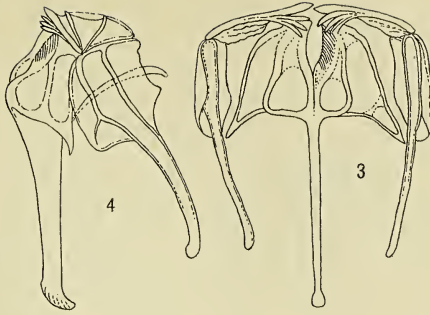
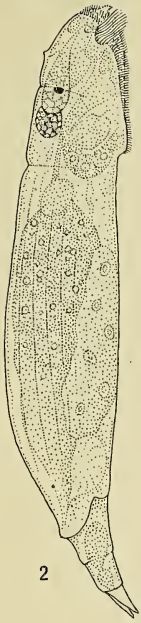




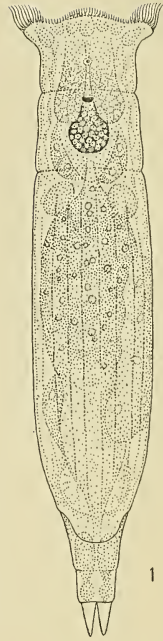




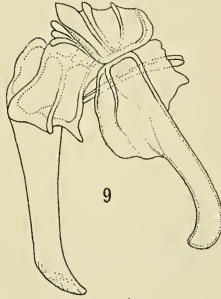




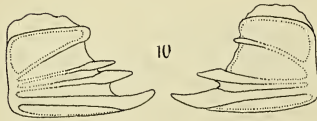
5



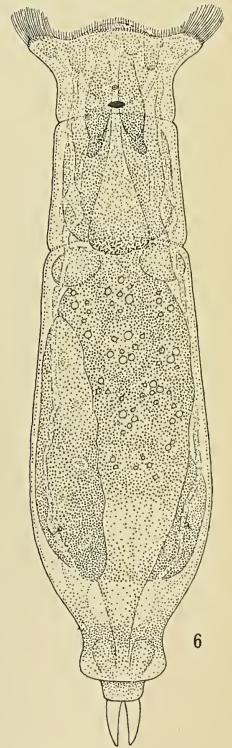
1



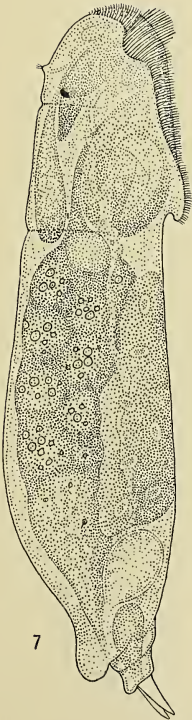
9



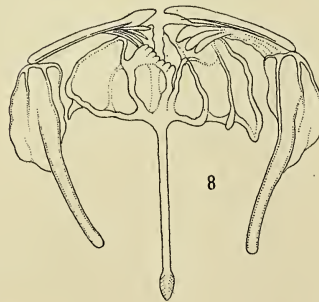
10



6

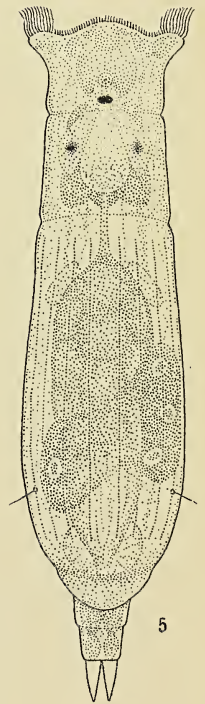
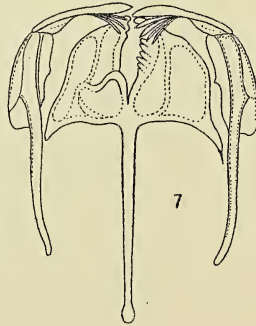
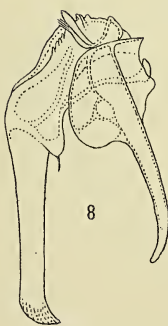
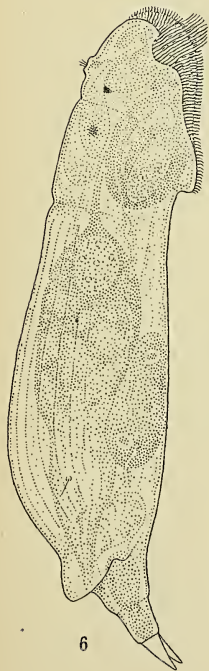
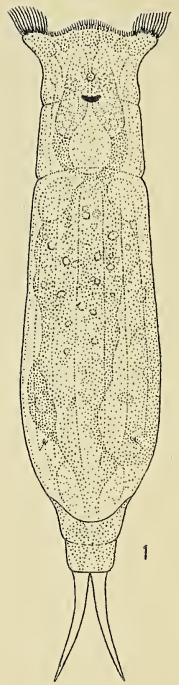
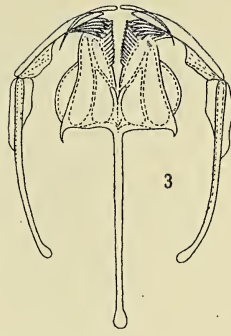
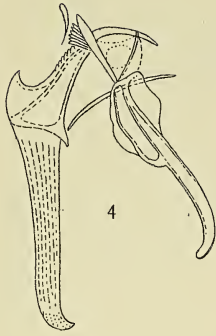
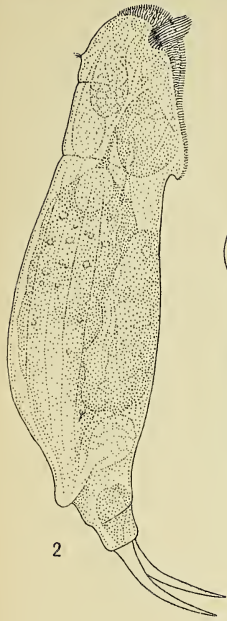


7



8

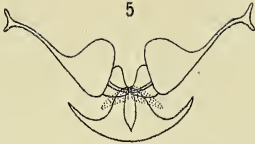




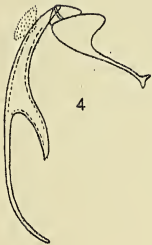




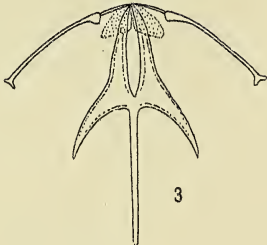
2



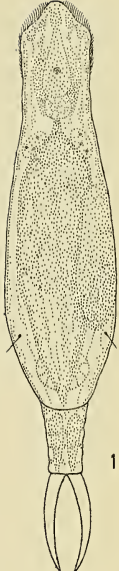
5



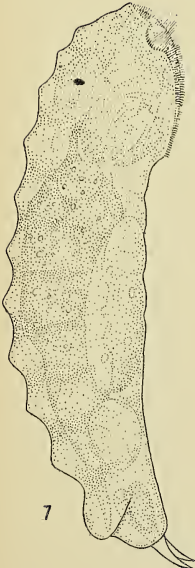
4



3



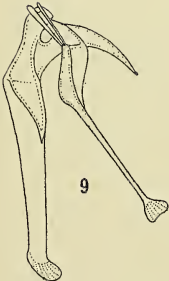
1



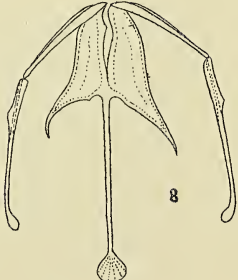
7



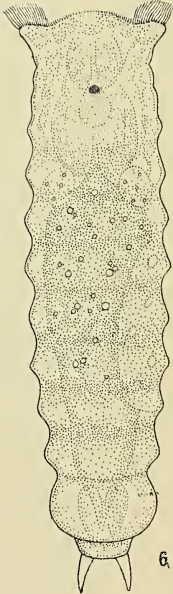
10



9



8



6



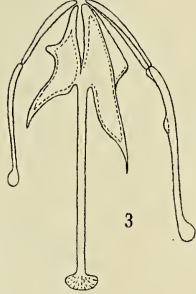




2



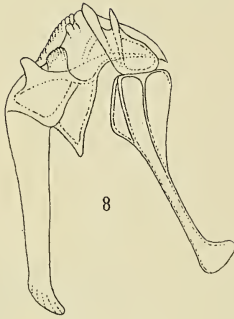
4



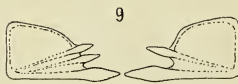
3



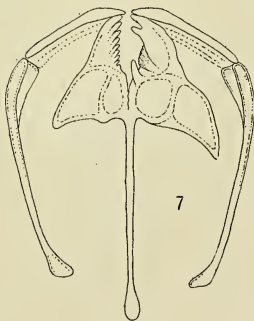
1



8



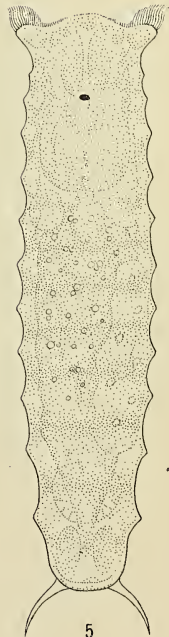
9



7

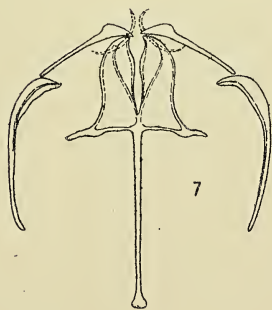
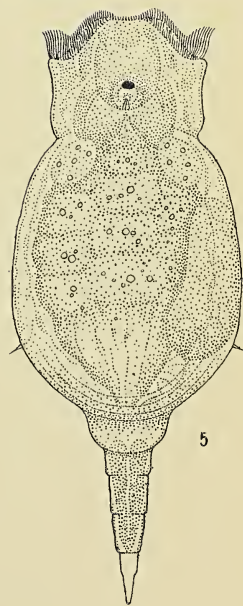
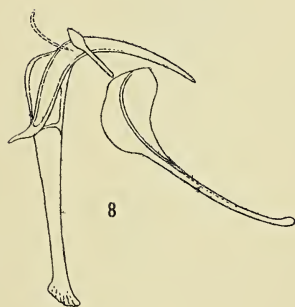
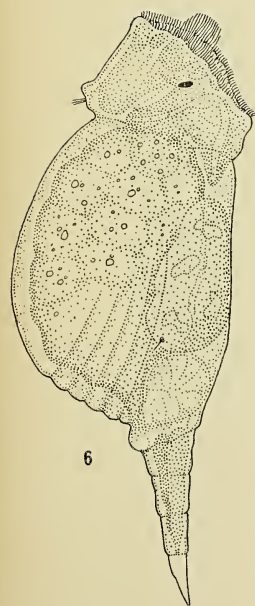
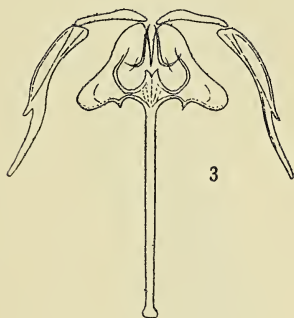
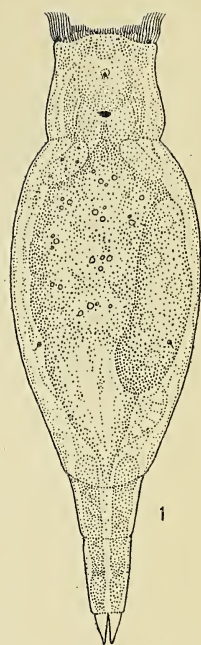
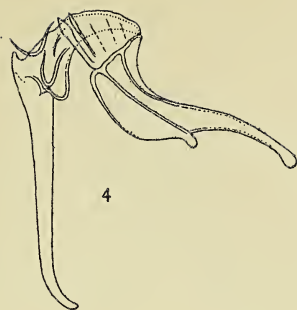
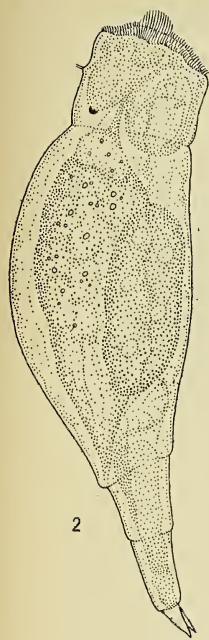


6

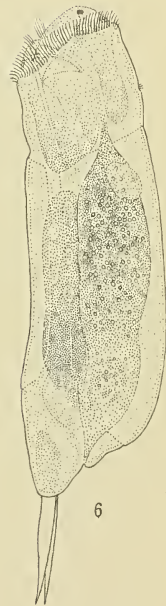


5

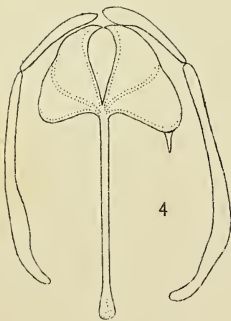
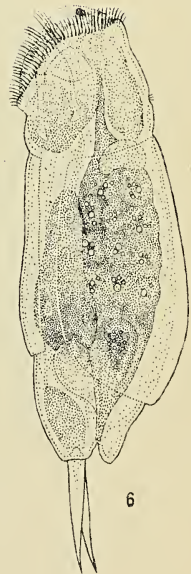
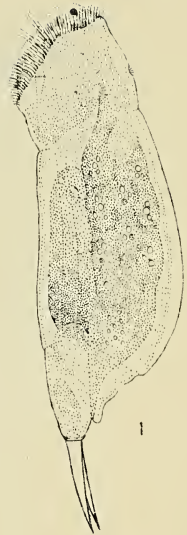
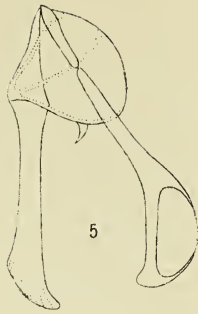






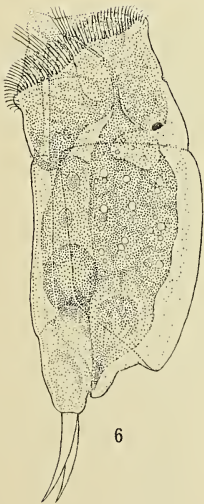
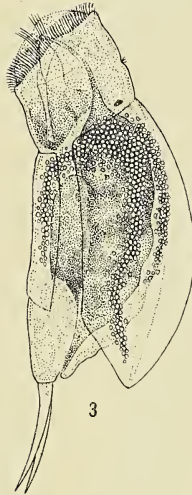
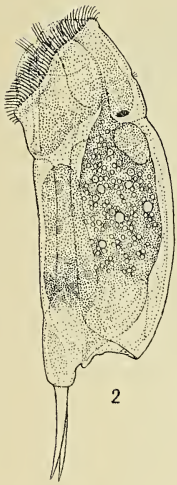




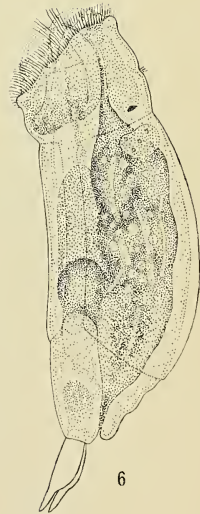
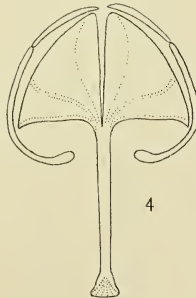
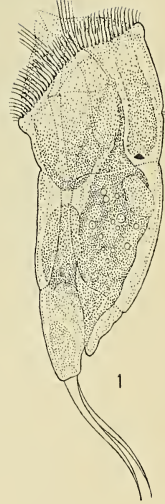
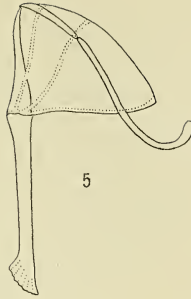
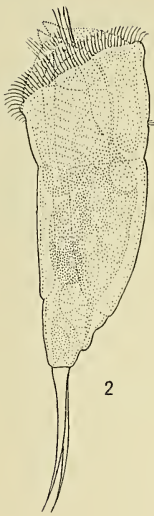




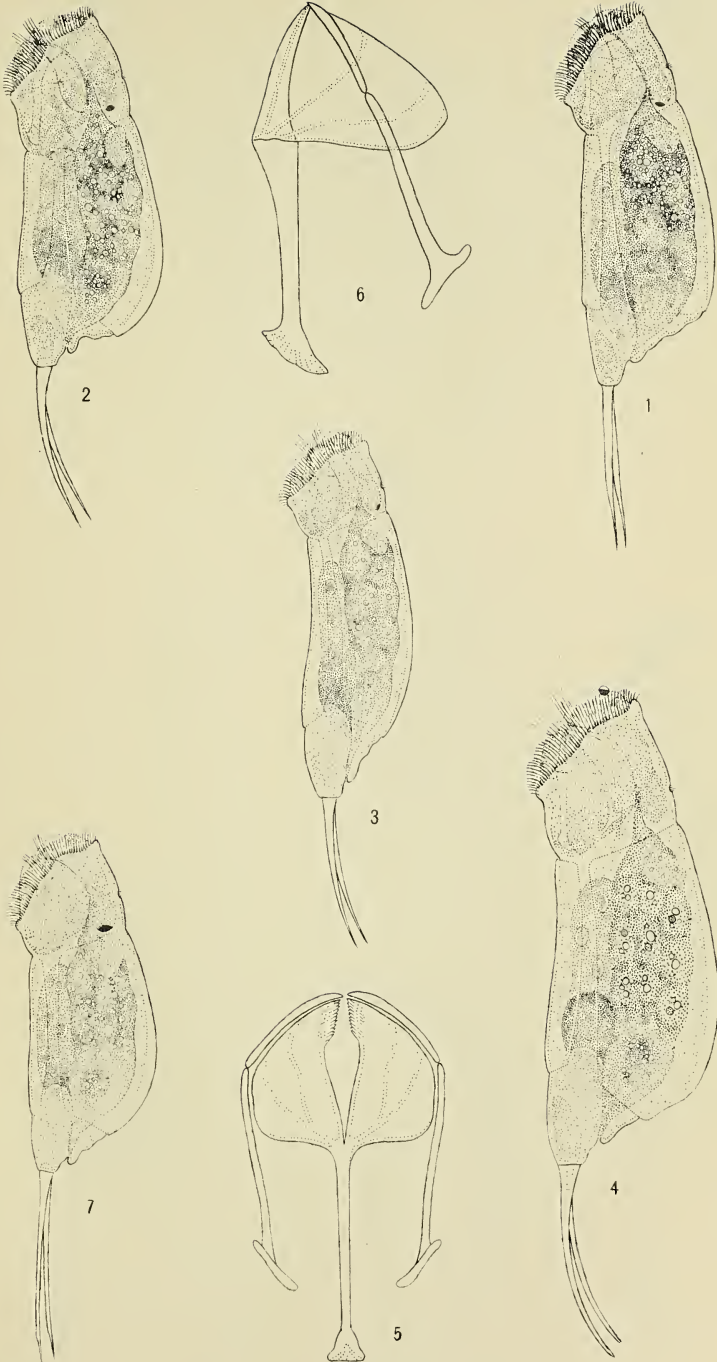




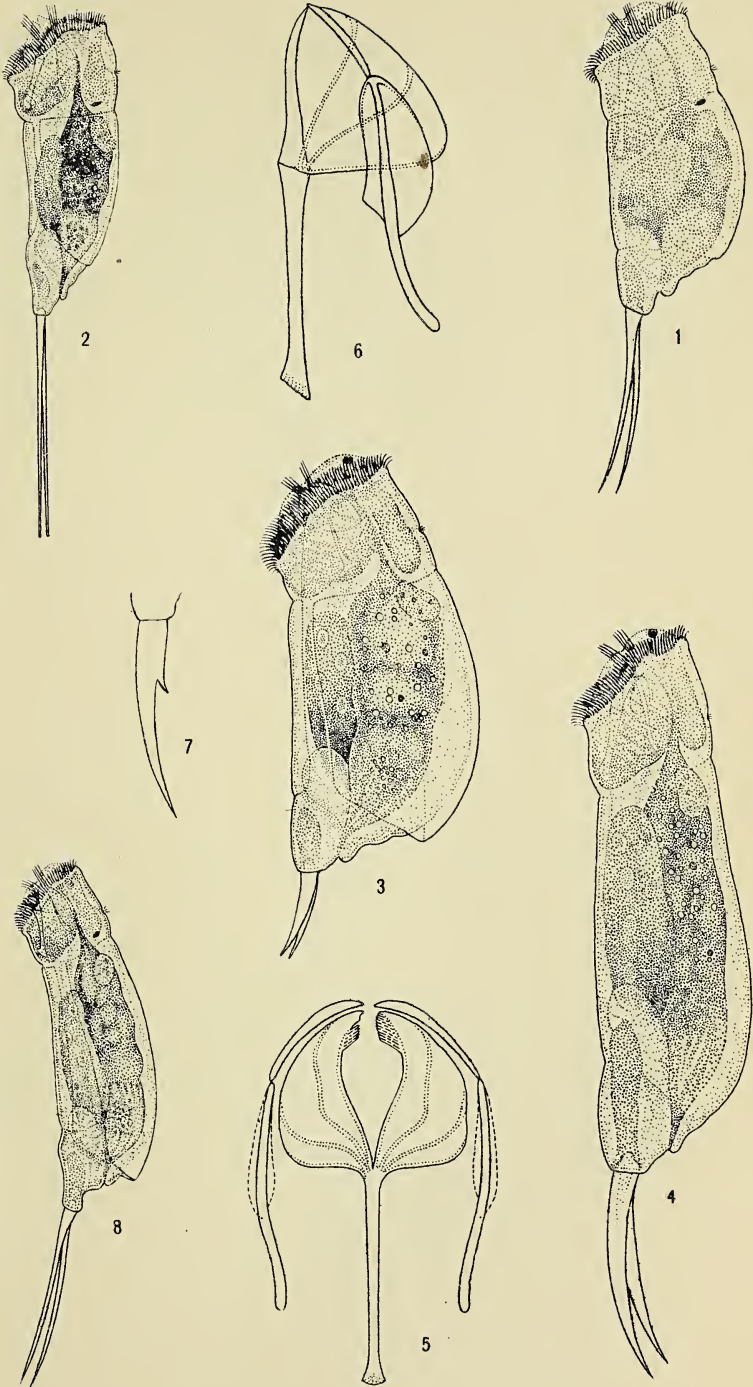






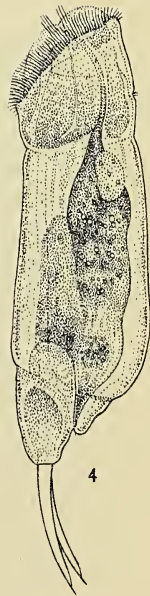
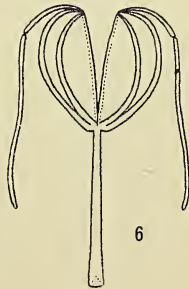
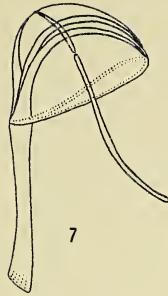




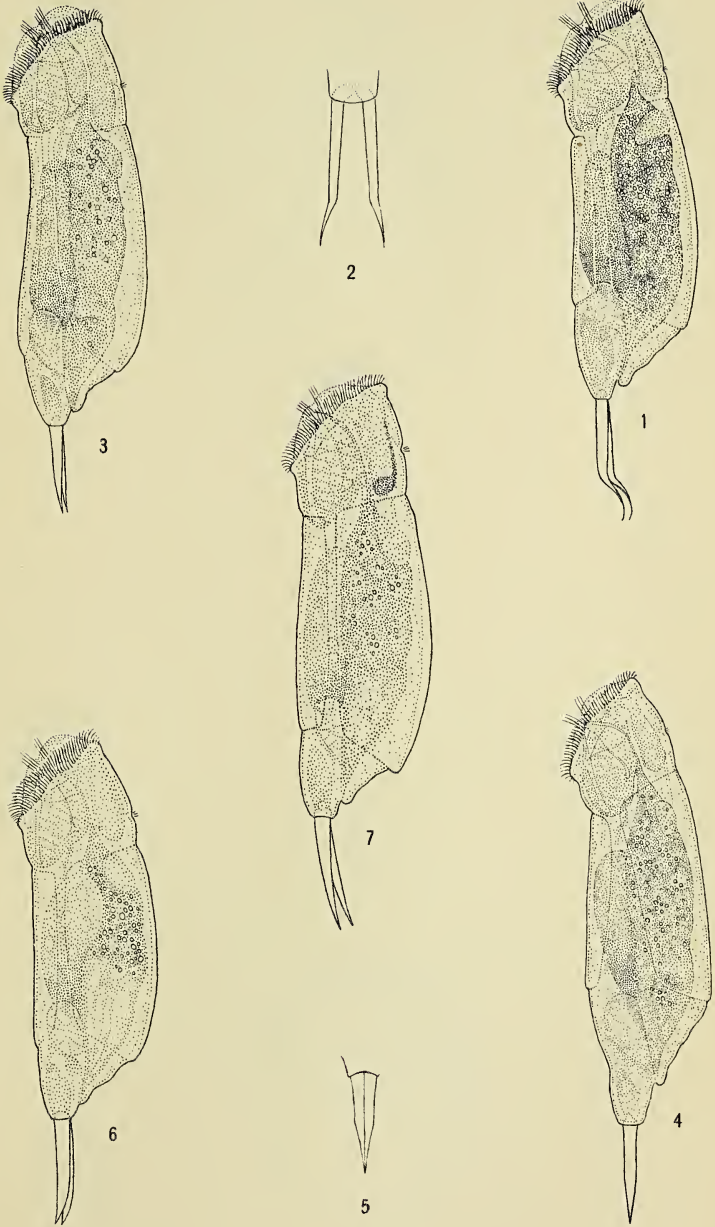








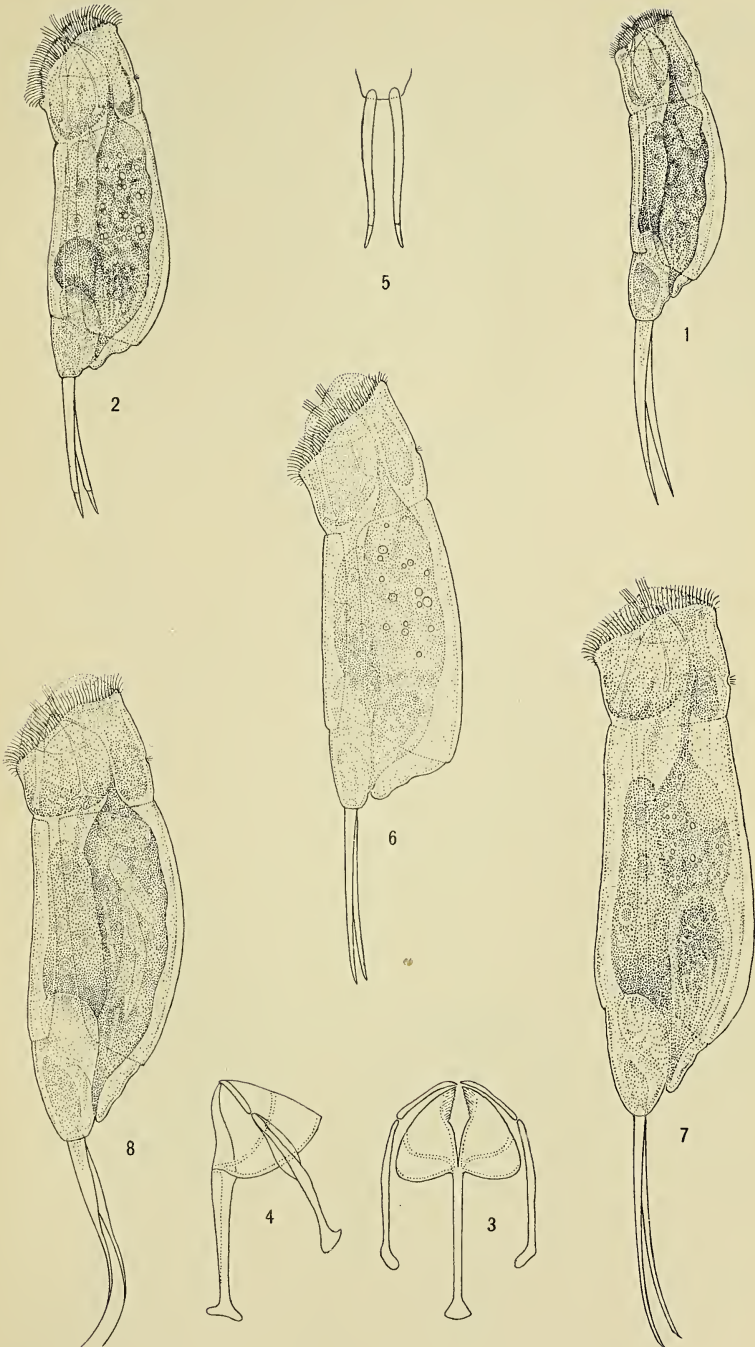






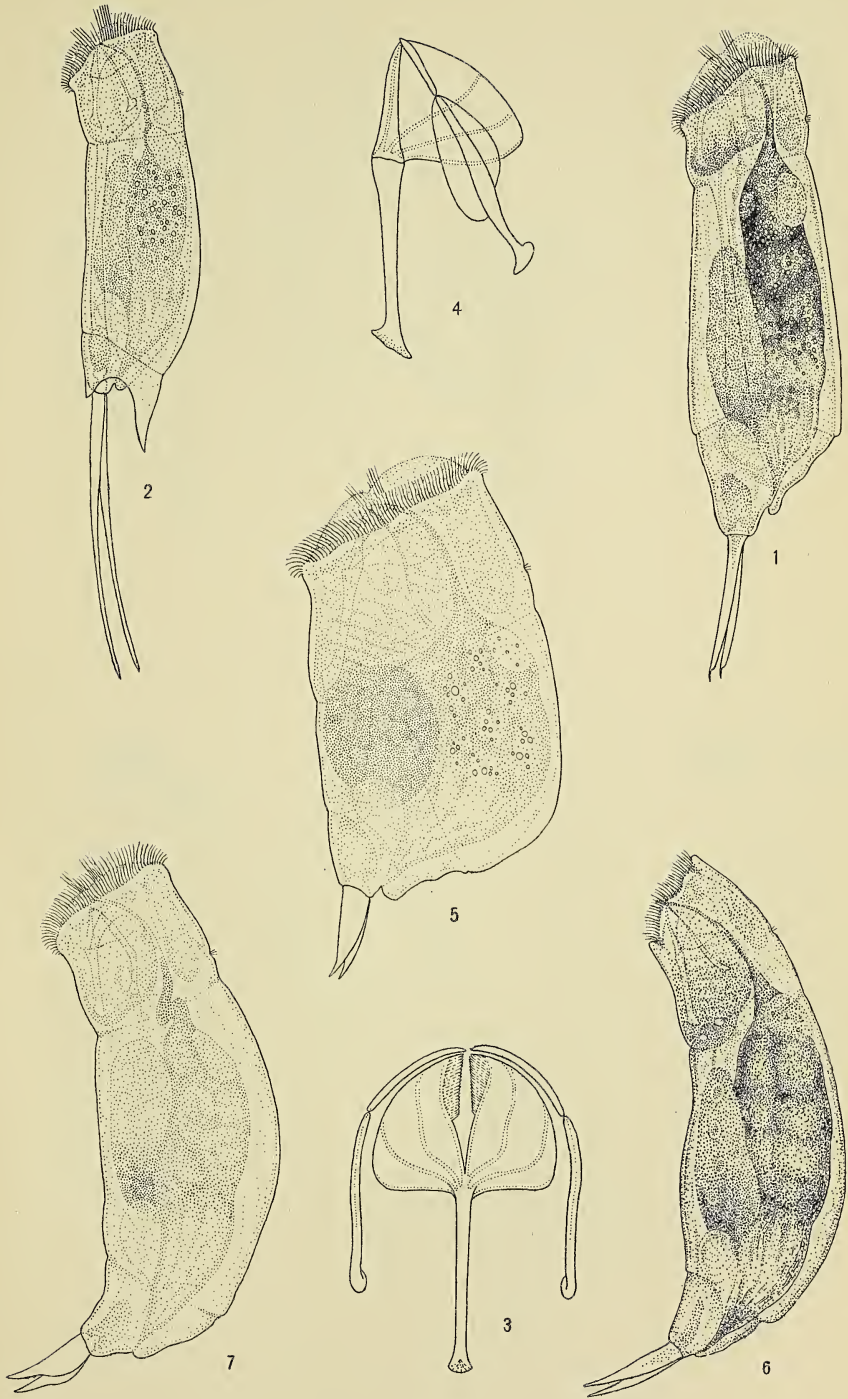




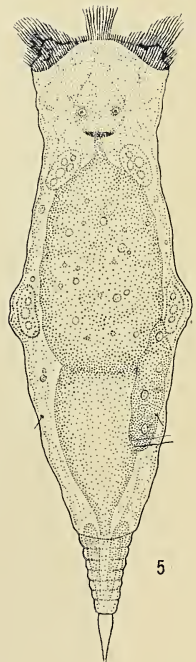
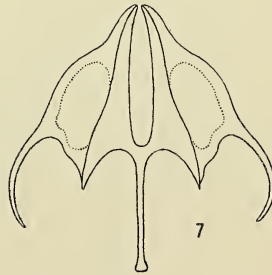
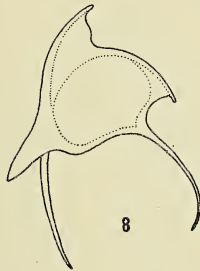
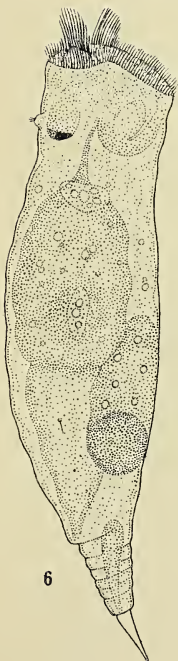
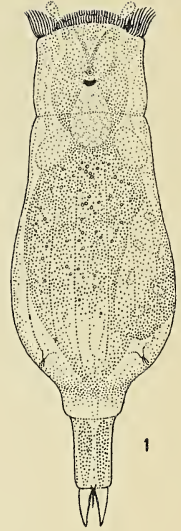
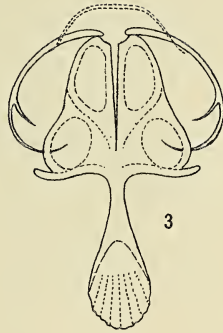
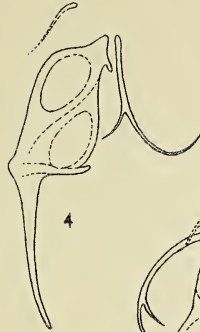
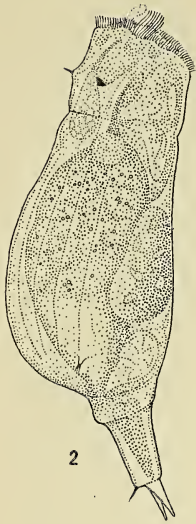




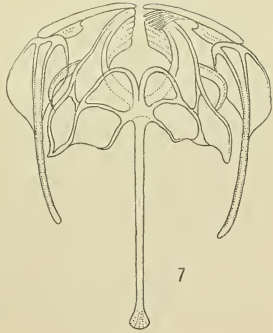
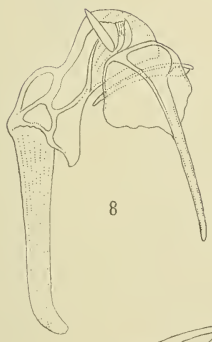
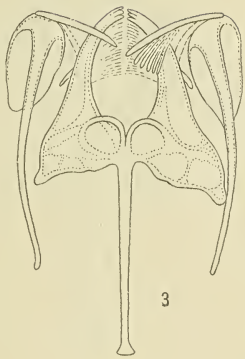
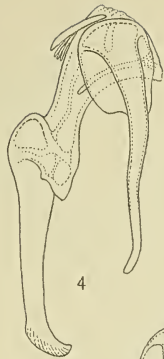
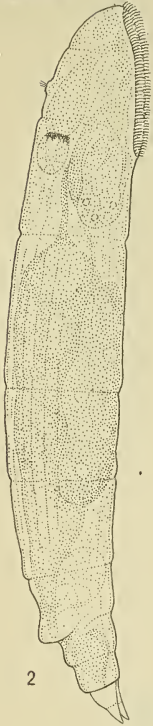




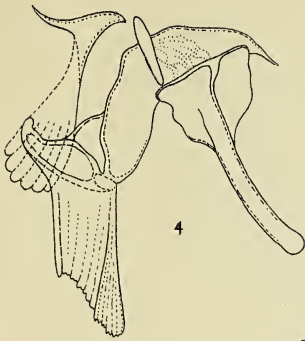




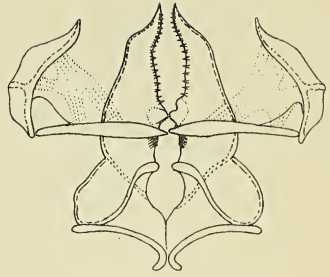




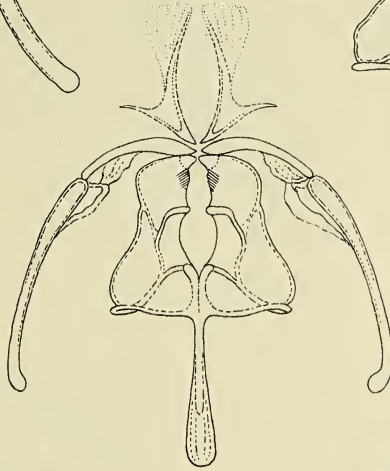




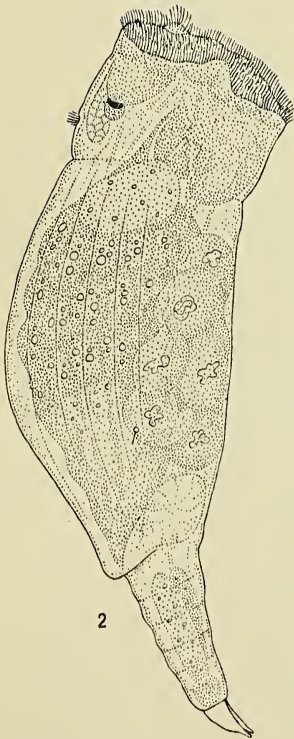
4



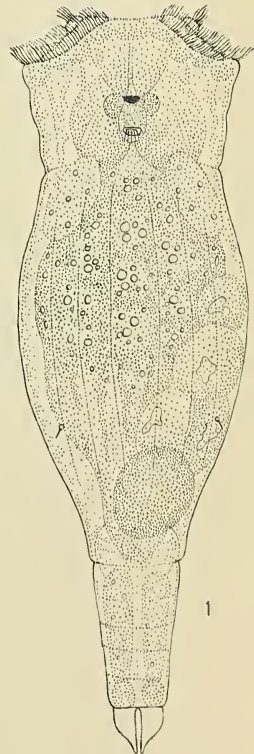
5



3



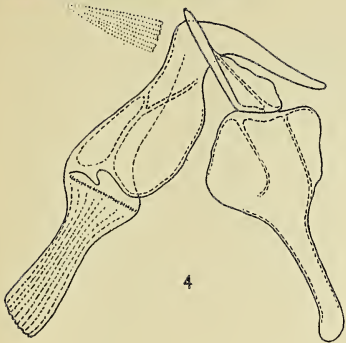
2



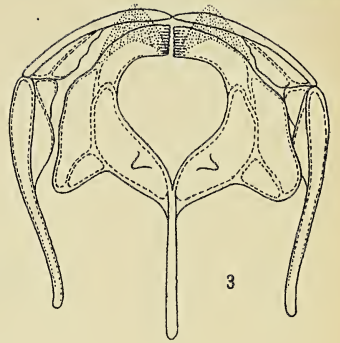
1



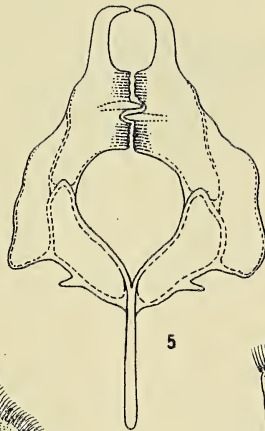




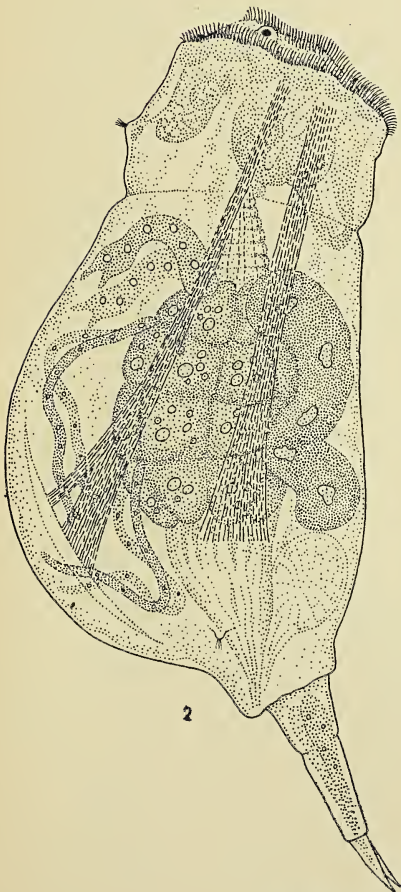
4



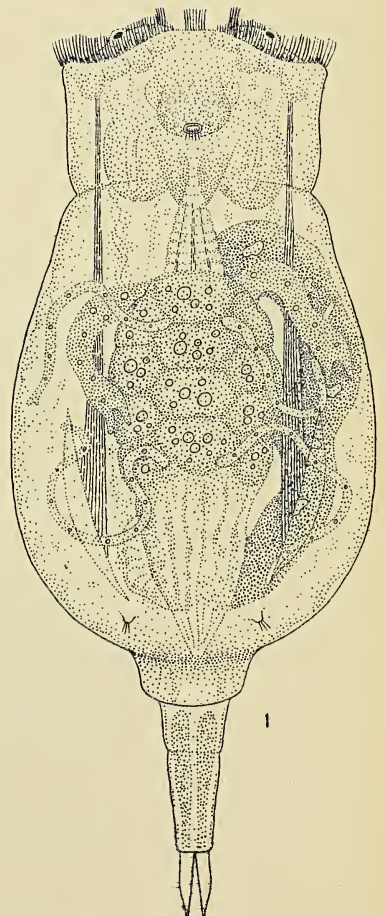
3



5

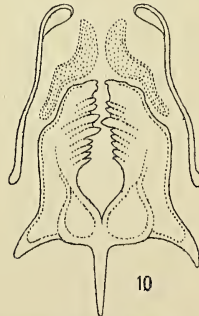
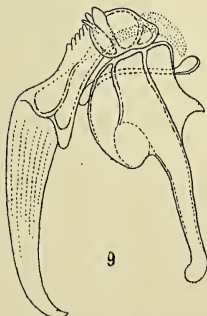
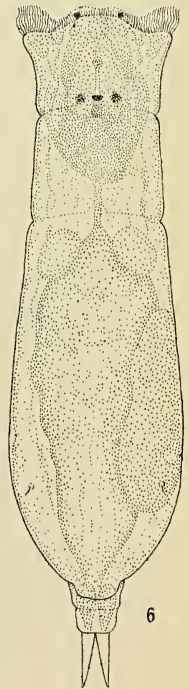
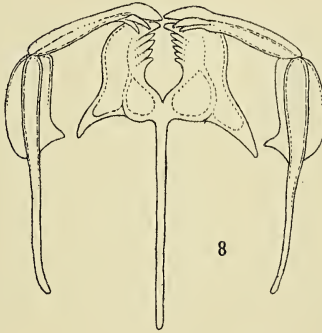
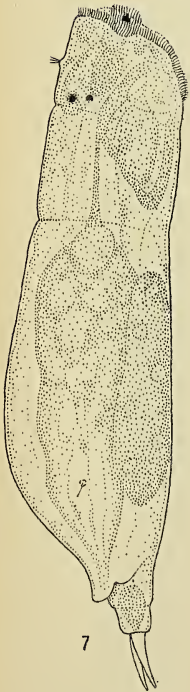
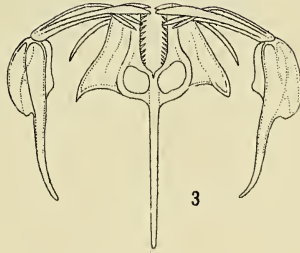
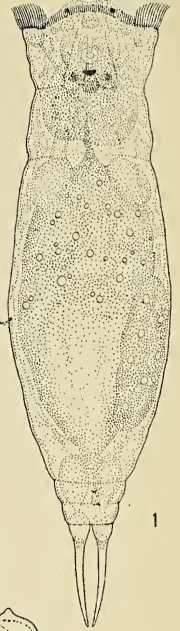
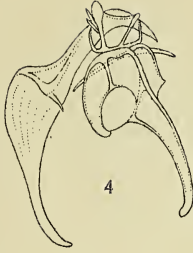
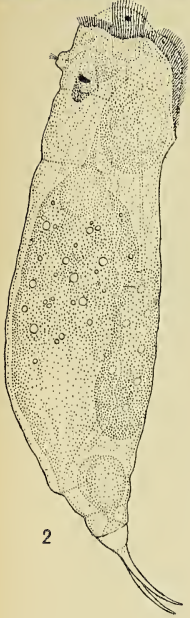


2

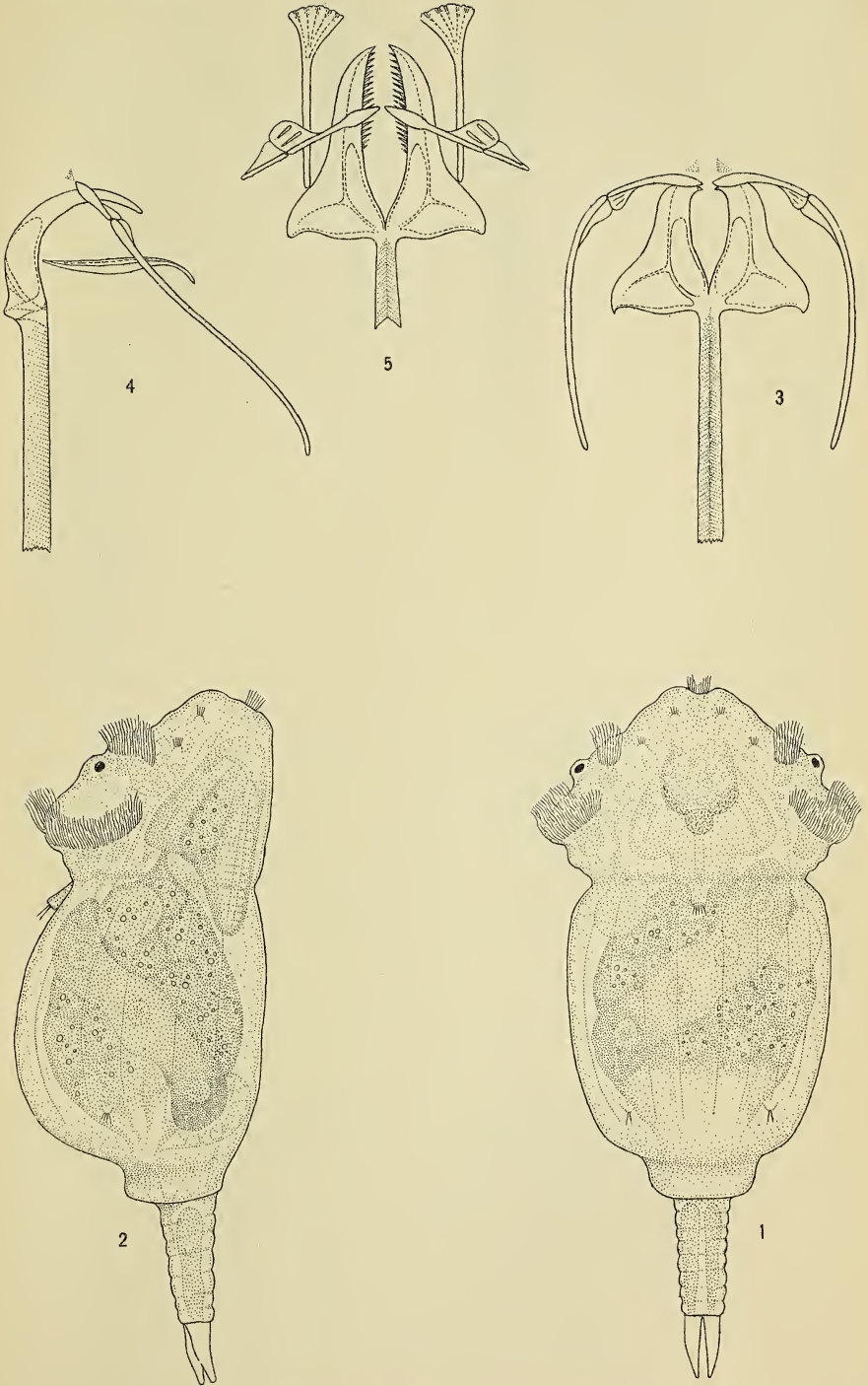


1

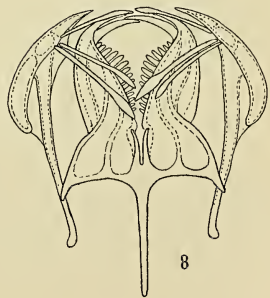
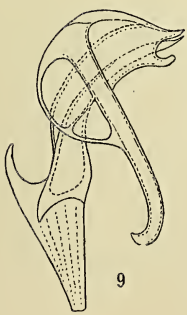
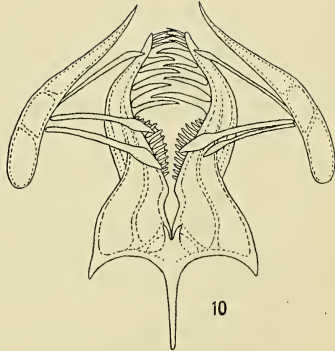
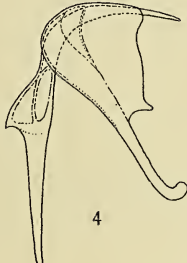
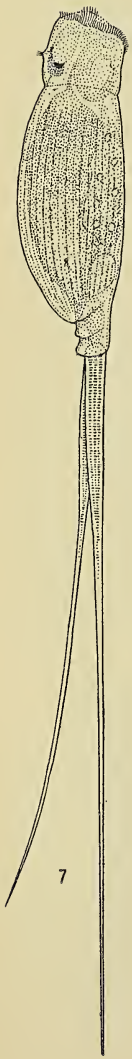
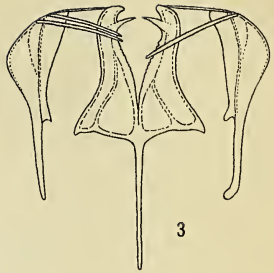
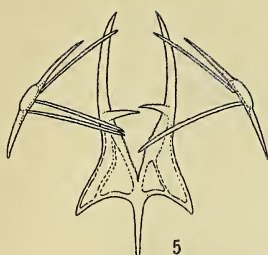
















# PROCEEDINGS OF THE ACADEMY

1921 TO 1923

---

## FIFTY-FIRST ANNUAL MEETING, 1921

The fifty-first meeting of the Wisconsin Academy of Sciences, Arts, and Letters, in joint session with the Wisconsin Archeological Society, was held at Madison, in Room 301, Biology Building, University of Wisconsin, on Friday and Saturday, April 15 and 16, 1921.

Under the direction of the president the following program was presented:

### First Session, Friday, April 15, 3:00 P. M.

General Business.

Presentation of Papers.

1. Food Value of some Aquatic Organisms found in Lake Mendota. CHANCEY JUDAY.
2. Notes on the Herpetology of Wisconsin. GEORGE WAGNER.
3. The Distribution of the Fishes in Six Wisconsin Lakes. A. S. PEARSE.
4. The Radiation Hypothesis of Chemical Action. FARRINGTON DANIELS. Illustrated.
5. The Polarization Method of Measuring the Gloss of Paper. L. R. INGERSOLL. Illustrated.
6. Notes on the Chemical Composition of some of the Larger Aquatic Vegetation of Lake Mendota. HENRY A. SCHUETTE. By title.
7. A Preliminary List of the Water Mites of Wisconsin. RUTH MARSHALL. By title.

### Second Session, Saturday, April 16, 9:30 A. M.

8. Bisexual Organs in *Bryum medium*. GEORGE S. BRYAN. Illustrated.
9. Some Cytological Studies on *Beloniella Dehnii*. E. M. GILBERT.
10. Aquatic Fungi of the Madison Lakes. Progress Report. E. M. GILBERT.
11. The Antherozoid of *Riccardia pinguis*. W. N. STEIL.
12. Notes on Parasitic Fungi in Wisconsin, IX. J. J. DAVIS.
13. Stone Celts from Southern Colorado. C. E. BROWN. Effigy Mound Photographs. GEORGE R. FOX.
14. Jacob Wimpfelings Germania, Strassburg 1501 and Thomas Murners Germania Nova, 1502. A Controversy about the Nationality of Alsace (at the beginning of the Sixteenth Century). ERNST VOSS.

**Third Session, Saturday, April 16, 2:30 P. M.**

11. The American Housing Situation. LEONARD S. SMITH.
12. The Declining Use of Lake Michigan as a Waterway. R. H. WHITBECK.
13. Some Observations on the Volcano of Kilauea. G. E. CULVER. Illustrated.
14. Road Oil and Its Use. A. F. GALMAN. By title.
15. Carl Winkler and his Meteorological Observations. EDWARD KREMERS. By title.

The Secretary presented the following applications for membership. On motion he was instructed to cast the ballot in their favor :

- Lloyd Slote Dancey, Waukesha
- Howard Greene, Milwaukee
- E. E. Hubert, Madison
- F. F. Lewis, Janesville
- Stanley Walker Rockwood, Waukesha
- James Elcana Rogers, Waukesha
- Harry Linn Starr, Waukesha
- Clarence L. Turner, Beloit

He then presented the secretary's report for the year, which was approved :

**Report of the Secretary for the Year 1920**

Honorary Members .....	7	
Life Members .....	17	
Corresponding Members .....	34	
Active Members .....	247	
		263
Total .....	305	
Changes since last report:		
Active members reported for 1919 .....	244	
Members reinstated .....	3	
New Memberships enrolled in 1920.....	16	
		263
Deaths of Active Members.....	5	
Resignations .....	1	
Dropped for non-payment of dues.....	7	
Active Members made Life Members.....	3	16
		16
Present Active Membership.....		247

Mr. George Merrick was enrolled as an Honorary Member in 1920. Seven new Life Members were enrolled in 1920: Thomas E. Brittingham, Madison; Frank P. Hixon, La Crosse; A. J. Hor-

lick, Racine; C. K. Leith, Madison; Frank A. Logan, Chicago; Mrs. Charles M. Norris, Milwaukee; and M. S. Slaughter, Madison.

During 1920 arrangements were completed whereby the Academy and the American Association for the Advancement of Science were affiliated.

There are 66 new members who have paid their dues to be enrolled after their applications have been acted upon by this meeting. Of this number, 58 will become members of both societies.

I regret to report the loss of five active members by death: E. T. Harper, Geneseo, Ill.; Herman W. Kunz, Milwaukee; Publius V. Lawson, Menasha; W. A. P. Morris, Madison; and Dr. C. H. Vilas, Madison.

ARTHUR BEATTY,  
*Secretary.*

The treasurer's report for the year was next presented, adopted, and audited, as follows:

**Report of the Treasurer for the Year 1920**

RECEIPTS

Received from Dues and Initiations.....	\$1,034.50
Received from sale of Transactions.....	14.58
Received from Interest on Certificates of Deposit.....	16.00
Received from Interest on Liberty Bonds.....	31.25
Received from Interest on City of Madison Bonds.....	118.00
Received from 5 City of Madison Bonds matured April 1, 1921.....	500.00
	<hr/>
Total .....	\$1,714.33
Balance on hand April 23, 1920.....	152.95
	<hr/>
Total .....	\$1,867.28

DISBURSEMENTS

Secretary-Treasurer's Allowance .....	\$200.00
6 City of Madison Bonds purchased April 1, 1921.....	600.00
Warrant sent A. A. A. S. in adjustment of dues.....	540.00
	<hr/>
	1,340.00
	<hr/>
Balance on hand April 16, 1921.....	\$ 527.28

ARTHUR BEATTY,  
*Treasurer.*

We have examined the securities owned by the Academy and find them in accord with the Treasurer's record.

We approve the statement of Receipts and Disbursements of the Treasurer as shown by his record.

R. H. WHITEBECK,  
E. G. SMITH,  
*Auditors.*

The next order of business was the report of the nominating committee:

Your committee on nominations reports the following nominations for officers and committees for the ensuing term:

President, Melvin A. Brannon, Beloit.  
Vice President, Sciences, S. A. Barrett, Milwaukee.  
Vice President, Arts, Grant Showerman, Madison.  
Vice President, Letters, Karl Young, Madison.  
Secretary, C. Juday, Madison.  
Treasurer, C. Juday, Madison.  
Curator, C. E. Brown, Madison.  
Librarian, W. M. Smith, Madison.

COMMITTEE ON PUBLICATIONS

The Secretary, *ex-officio*.  
The President, *ex-officio*.  
W. E. Tottingham, Madison.

COMMITTEE ON LIBRARY

The Librarian, *ex-officio*.  
George Wagner, Madison.  
W. Harley Barber, Ripon.  
A. E. Whitford, Milton.  
A. A. Trever, Appleton.

COMMITTEE ON MEMBERSHIP

The Secretary, *ex-officio*.  
P. W. Boutwell, Beloit.  
V. E. McCaskill, Superior.  
H. H. Smith, Milwaukee.  
G. S. Bryan, Madison.

We also recommend that the present Secretary and C. E. Allen of the Committee on Publication be continued for a period of six months.

Respectfully submitted,  
CHARLES E. BROWN,  
E. M. GILBERT,  
WM. S. MARSHALL.  
*Committee on Nominations.*

The report of the Nominating Committee was adopted and the Secretary was instructed to cast the ballot for these officers.

It was moved by W. S. Marshall that the Nominating Committee be continued and be directed to draft an amendment to Article 6 of the constitution of the Academy, relating to the appointment of committees by the President. Carried.

It was moved by Edward A. Birge that those who contributed \$100 to the Fiftieth Anniversary Medal be placed on the list of the Life Members of the Academy, in accordance with the earlier practice of the Academy. Carried.

This motion applies to the following persons, who were duly elected Life Members:

Hon. Thomas E. Brittingham, Madison  
Hon. F. P. Hixon, La Crosse  
Hon. A. J. Horlick, Racine  
Dr. Charles K. Leith, Madison  
Hon. Frank A. Logan, Chicago  
Mrs. Charles M. Norris, Milwaukee  
Dr. M. S. Slaughter, Madison

Dr. E. A. Birge, Madison, and Dr. C. S. Slichter, Madison, who donated \$100 each to the Medal Fund, were already Life Members of the Academy.

#### **Fourth Session, Saturday, 6:30 P. M.**

The annual dinner was held at the University Club, at which 54 persons were present. The retiring President, Edward A. Birge, delivered an address on "A Lake as a Going Concern."

The President had specimens of the Fiftieth Anniversary Medal, which were inspected and highly approved by the guests.

The 1921 meeting was then adjourned.

**FIFTY-SECOND ANNUAL MEETING, 1922**

The fifty-second annual meeting of the Wisconsin Academy was held in the Trustee's Room of the Public Museum, Milwaukee, Wisconsin, on Thursday and Friday, April 13 and 14, 1922.

**First Session, Thursday, April 13, 2:00 P. M.**

Presentation of Papers.

1. Some Aspects of British Colonial Policy during the Nineteenth Century. PAUL KNAPLUND.
2. An Aspect of Samuel Johnson's Criticism of Shakespear. KARL YOUNG.
3. An Experimental Study of the Relativity of Spacial Perception. MARGARET WOOSTER.
4. Home Economics and the College of Classical Traditions. FLORENCE P. ROBINSON.
5. A Blackfoot Sweat Lodge. S. A. BARRETT. Illustrated.
6. A New Method of Museum Technique. R. E. TYRRELL. Illustrated with specimens.
7. Notes on the Distribution and Occurrences of Insects in Wisconsin. T. E. B. POPE. Illustrated with specimens.
8. Development of the Eye of the Confused Flour Beetle, *Tribolium confusum*. W. S. MARSHALL.
9. On the Anatomy of *Atropos divinatoria* Müll. RUTH W. CHASE.
10. Typhoid Agglutinins in Rabbits. ELIZABETH A. SMITH.
11. Some Phenomena in a Dying Lake. M. A. BRANNON.
12. The Sangamon River—A Study in Stream Pollution. MINNA E. JEWELL.
13. Crayfishes in the Eastern United States, with Special Reference to Ohio. C. L. TURNER.

**Second Session, Friday, April 14, 9:00 A. M.**

Presentation of Papers.

14. The Piskum or Plains Indian Buffalo Drive. S. A. BARRETT. Illustrated.
15. Menominee Customs Concerning Children. ALANSON SKINNER.
16. A Preliminary Report on the Ethno-botany of the Menominee Indians. HURON H. SMITH. Illustrated.
17. Notes on Parasitic Fungi in Wisconsin, X. J. J. DAVIS.
18. Cytological Studies on the Lower Basidiomycetes, II. *Auricularia*. E. M. GILBERT.
19. A Census of the Water Molds of a Portion of Lake Monona. E. M. GILBERT.
20. Inheritance in a Simple Plant. C. E. ALLEN. Illustrated.
21. Progress Report on the Flora of Wisconsin. HURON H. SMITH.
22. Notes on the Occurrences of Certain Wisconsin Fishes. T. E. B. POPE.
23. The Parasites of Lake Fishes. A. S. PEARSE.

24. Observations Concerning the Respiration of Turtles. FRANCES E. DIEBOLD.
25. A Quantitative Study of the Bacteria of Lake Mendota. E. B. FRED and FRANK C. WILSON.
26. The Hydrogen Ion Concentration in Wisconsin Lake Waters. FRANK C. WILSON, E. B. FRED, and C. JUDAY.

**Third Session, Friday, April 14, 2:00 P. M.**

Presentation of Papers.

27. The Significance of an Economic Fisheries Exhibit and Its Relation to Conservation. T. E. B. POPE.
28. The Analytical Chemistry of Selenium and Tellurium. V. LENHER.
29. The Summer Temperature of the Bottom Water in Some Deep Lakes of the Western United States. GEO. I. KEMMERER.
30. Unusual Veinings in the Richardton Meteorite. R. N. BUCKSTAFF. Illustrated with specimens.
31. The Progress of Topographic Mappings in Wisconsin. W. O. HOTCHKISS.
32. Road Material Surveys in Wisconsin. E. F. BEAN.
33. The Lime Industry in Wisconsin. E. STEIDTMANN.
34. The Mining of Sulphur at Freeport, Texas. IRA EDWARDS. Illustrated.
35. The Upper Mississippi River as a Commercial Waterway. R. H. WHITBECK.
36. The Cytology of *Venturia*. C. N. FREY.

The annual dinner was held on Thursday evening at the Hotel Wisconsin, with 86 persons in attendance.

Following the dinner brief addresses were made in honor of three of the early members of the Academy who are commemorated on the Semi-centennial Medallion. President E. A. Birge spoke on Dr. George W. Peckham, Mr. William W. Wight on Dr. I. A. Lapham, and Dr. John J. Davis on Dr. P. R. Hoy.

The Secretary presented the following applications for membership. On motion he was instructed to cast the ballot in their favor:

Irving M. Addleman, Wausau  
B. P. Churchill, Milwaukee  
H. H. Conwell, Beloit  
Percy M. Dawson, Madison  
H. D. Densmore, Beloit  
Edward Evans, La Crosse  
Geo. J. Fiebiger, Waterloo  
Arthur C. Foster, Raleigh, N. C.  
Edwin B. Fred, Madison  
Chas. N. Frey, New York, N. Y.  
W. A. Hamilton, Beloit  
E. G. Hastings, Madison

Thomas M. Jasper, Urbana, Ill.  
 W. A. Kenyon, Madison  
 Clifford S. Leonard, Madison  
 Fred. L. Musbach, Marshfield  
 Lowell E. Noland, Madison  
 Henry V. Ogden, Milwaukee  
 C. E. Patzer, Milwaukee  
 Geo. F. Potter, Durham, N. H.  
 John Walker Powell, Milwaukee  
 Jessie P. Rose, Madison  
 Arthur Simon, Milwaukee  
 Kurt Stock, Fish Creek  
 Noel F. Thompson, Madison  
 Fred. T. Ullrich, Platteville  
 David E. W. Wenstrand, Milwaukee  
 J. W. White, Platteville  
 Clyde M. Woodworth, Urbana, Ill.  
 John A. Jeske, Milwaukee  
 Chas. R. Porteus, Milwaukee  
 Stephen J. Majerowski, Milwaukee  
 Edward R. Tyrrell, Milwaukee  
 Tenus Tuttrup, Milwaukee  
 S. Cheifetz, Milwaukee  
 George Peter, Milwaukee  
 E. S. Haynes, Beloit  
 G. D. Shallenberger, Beloit  
 Clarence L. Clark, Beloit  
 Kenneth B. Barnes, Beloit  
 Florence P. Robinson, Beloit  
 Wm. J. Trautman, Beloit  
 R. N. Buckstaff, Oshkosh  
 E. A. Goessl, Milwaukee

The following individuals were elected to Life Membership:

Arthur Beatty, Madison  
 Mrs. Elizabeth G. Peckham, Milwaukee

### Report of Secretary, November 1, 1921 to April 10, 1922

Honorary Members .....	6
Life Members .....	17
Corresponding Members .....	33
Active Members—Old .....	275
Active Members—New .....	44
Members reinstated .....	3
<b>Total .....</b>	<b>378</b>
Resigned .....	4



The Illinois State Academy of Science extended a cordial invitation to the members of the Wisconsin Academy to attend its meeting at Rockford, Illinois, April 27 to 29, 1922. It was voted that greetings and good wishes for a successful meeting be extended to the Illinois State Academy of Science.

Being an affiliated society, the Wisconsin Academy is entitled to a representative on the Council of the American Association for the Advancement of Science. It was voted that the Secretary represent the Wisconsin Academy on the Council of the American Association and that he be authorized to appoint some member to represent the Academy when he does not attend the meetings of the American Association.

It was voted that the Academy express its thanks to the Milwaukee Public Museum for its interest in the meeting and for the use of a room for the sessions.

CHANCEY JUDAY,  
*Secretary.*

**Report of Treasurer for 1922**

RECEIPTS

Received from previous Treasurer, November 15, 1921.....	\$ 367.58
Received from Dues and Initiations.....	944.10
Received from sale of Transactions.....	96.00
Received from Interest on Bonds.....	50.62
	<hr/>
	\$1,458.30

DISBURSEMENTS

Patterns for Medallion.....	\$ 12.10
Postage .....	58.00
Printing .....	13.36
Safety Deposit Box Rent.....	4.00
Warrant sent A. A. A. S. in Adjustment of Dues.....	671.10
	<hr/>
	\$ 758.56
Balance April 10, 1922.....	699.74
	<hr/>
	\$1,458.30

Audited and found correct.

C. E. ALLEN,  
IRA EDWARDS,  
*Auditors.*

Securities owned by the Academy April 10, 1922:

Government Bonds .....	\$ 700.00
City of Madison Bonds.....	2,600.00
Certificate of Deposit.....	76.38

\$3,376.38

CHANCEY JUDAY,  
*Treasurer.*

### FIFTY-THIRD ANNUAL MEETING, 1923

The fifty-third annual meeting of the Wisconsin Academy was held at Beloit College, Beloit, Wisconsin, on April 6 and 7, 1923, in joint session with the Wisconsin Archeological Society.

The following program was presented:

#### First Session, Friday, April 6, 10:00 A. M.

Presentation of Papers.

1. Augustine of Hippo *qua* Patriot. R. K. RICHARDSON.
2. Chartiludium Institute Summarrie Doctore *Thoma Murner* Memorante et Ludente. Strassburg, 1518. ERNST VOSS.
3. The Sentimental Return to Nature in the Eighteenth Century. WILLIAM E. ALDERMAN.
4. Botanical Collecting in Southwestern Wisconsin in 1922. HURON H. SMITH. Illustrated.
5. Racial Characters in *Sphaerocarpus* and their Inheritance. C. E. ALLEN. Illustrated.
6. Physiological Stability in Maize. W. E. TOTTINGHAM.
7. Notes on Parasitic Fungi in Wisconsin. J. J. DAVIS.
8. On the Nature of Disease Resistance in Plants. J. C. WALKER.
9. The Nuclear Phenomena in Some of the Short-cycled Rusts. E. M. GILBERT.
10. The Corrected Names of Certain Milk Bacteria. RUTH W. CHASE and W. D. FROST.
11. The Characteristics of Certain Fecal Bacteria as shown by the Little Plate Method. OLA E. JOHNSTON and W. D. FROST.

#### Second Session, Friday, April 6, 2:00 P. M.

Presentation of Papers.

12. Beloit Mound Groups. GEORGE L. COLLIE.
13. Winnebago Chieftains and Villages of the Lower Rock River Region. N. W. JIPSON.
14. Removal of the Rock River Winnebago in 1833. LOUISE P. KELLOGG.
15. The Applications of Amerind Decorative Art. MRS. W. R. TYLOR.
16. Prehistoric Archeology in France. A. W. POND. Illustrated.

17. Stage Coaches and Taverns of the Baraboo Region. H. E. COLE.
18. Wood County Potawatomi. A. GEREND.
19. The Manufacture of Stone Axes and Celts. H. L. SKAVLEM.
20. Indian Cave, Richland County. C. E. BROWN.
21. Wisconsin Caves. W. C. ENGLISH.
22. The Glaciation of Northern Illinois. M. M. LEIGHTON, University of Illinois.
23. Some Recent Discoveries of Wisconsin Graptolites. RUFUS M. BAGG.
24. The Diplomatic Crisis of our Civil War. R. B. WAY.

**Third Session, Saturday, April 7, 9:00 A. M.**

Presentation of Papers.

25. Floundering in Modernity. GEORGE C. CLANCY.
26. Scientific Pupil-classification. C. G. F. FRANZEN.
27. Milton as a Writer on Education. OLIVER M. AINSWORTH.
28. Symposium on Eugenics.
  - a. General Statement of Problems. M. F. GUYER.
  - b. Pauperism and Crime in Wisconsin. J. L. GILLIN.
  - c. The Inheritance of Mental Traits. V. A. C. HENMON.

**Fourth Session, Saturday, April 7, 1:30 P. M.**

29. Further Notes on Wisconsin Reptiles. GEORGE WAGNER.
30. A Case of Arrested Development in a Frog's Heart. GEORGE WAGNER.
31. Notes on the Biology of the Book Louse. RUTH W. CHASE.
32. The Amount of Food Eaten by Four Wisconsin Fishes. A. S. PEARSE. Illustrated.
33. The Chemical Composition of Trout and Perch. A. S. PEARSE.
34. A Mutation in the Moth Fly (*Psychoda*) and its Method of Inheritance. C. L. TURNER. Illustrated with specimens.
35. A new *Arrhenurus* from Washington State. RUTH MARSHALL. By title.
36. Water Mites from Alaska and The Canadian Northwest, with an Account of the Collecting Grounds. RUTH MARSHALL. Illustrated.
37. Landmarks Work in Winnebago County. A. P. KANNENBERG.

The annual dinner was held on Friday evening, April 6, at Beloit College. Following the dinner Professor W. S. Bayley, President of the Illinois State Academy of Science, gave an address on The Function of a State Academy of Science.

The Secretary presented the following applications for membership. On motion he was instructed to cast the ballot in their favor:

- R. A. Brink, Madison
- Wm. A. Clark, Stevens Point
- Thos. A. Rogers, Stevens Point
- G. Steiner, Washington, D. C.

**Report of Secretary, April 10, 1922 to April 2, 1923**

Honorary Members .....	7
Life Members .....	17
Corresponding Members .....	32
Active Members .....	328

384

Resigned .....	3
Deaths .....	4

The following deaths have been reported to the Secretary: Professor Henry Prentiss Armsby, Corresponding Member, State College, Pa.; Professor A. S. Flint, Life Member, Madison; Dr. Paul H. Dernehl, Active Member, Milwaukee; Professor Fritz Wilhelm Woll, Active Member, Berkeley, California.

The Winnebago County Archeological and Historical Society extended a cordial invitation to the members of the Wisconsin Academy and the Wisconsin Archeological Society to attend its field meeting at Oshkosh on June 8 and 9, 1923.

The following resolution was presented:

Whereas there are in the State of Wisconsin a considerable number of interesting caves, and

Whereas some of these, of notable size and beauty, containing stalactites and other interesting geological formations as well as Indian pictographs and petroglyphs of scenic and historical interest to the general public and to tourists, are being mutilated and otherwise defaced by thoughtless persons,

Be it resolved that the Wisconsin Academy of Sciences, Arts and Letters and the Wisconsin Archeological Society, in joint meeting assembled at Beloit College, Beloit, Wisconsin, on this sixth day of April, 1923, greatly deplore the neglect into which these scenic monuments have fallen and the continuance of such destructive practices and depredations and urge upon the owners of these caves that they in every way protect them against further mutilations and misuse, and upon the State of Wisconsin itself to take such measures as shall make such vandalism an offense against its laws.

CHARLES E. BROWN,  
W. O. HOTCHKISS,  
A. S. PEARSE,  
*Committee on Resolutions.*

The resolution was unanimously adopted.

It was moved that the thanks of the Wisconsin Academy of Sciences, Arts, and Letters and of the Wisconsin Archeological Society be extended to Beloit College for its great interest in the meetings and for the hospitality shown to the members of the two societies. The motion was unanimously adopted.

CHANCEY JUDAY,  
*Secretary.*

**Report of Treasurer, April 10, 1922 to April 2, 1923**

The publication of Volume XX of the Transactions left a deficit of nearly \$700 so that it was necessary to cash the certificate of deposit amounting to \$76.38 and to sell \$600 in government bonds in order to pay the printing deficit. This action was approved by the Council of the Academy.

RECEIPTS

Balance in State Treasury, July 1, 1922.....	\$ 28.48
Annual appropriation for fiscal year 1922-1923.....	1,500.00
Sale of Transactions.....	29.95
Annual dues of Active Members.....	912.00
	<hr/>
	\$2,470.43

DISBURSEMENTS

Dues of members of A. A. A. S.....	\$ 668.00
Freight on Transactions to Washington, D. C.....	13.09
Labor in packing and mailing Transactions.....	13.60
Postage on letters and Transactions.....	29.48
Allowance of Secretary for 1922.....	200.00
	<hr/>
	\$ 924.17
Balance in State Treasury, April 2, 1923.....	1,546.26
	<hr/>
	\$2,470.43

Owing to the high cost of printing and to the limited funds, it has been thought best to omit the membership list in this volume of the Transactions. It will be printed in the next volume.

CHANCEY JUDAY,  
*Treasurer.*

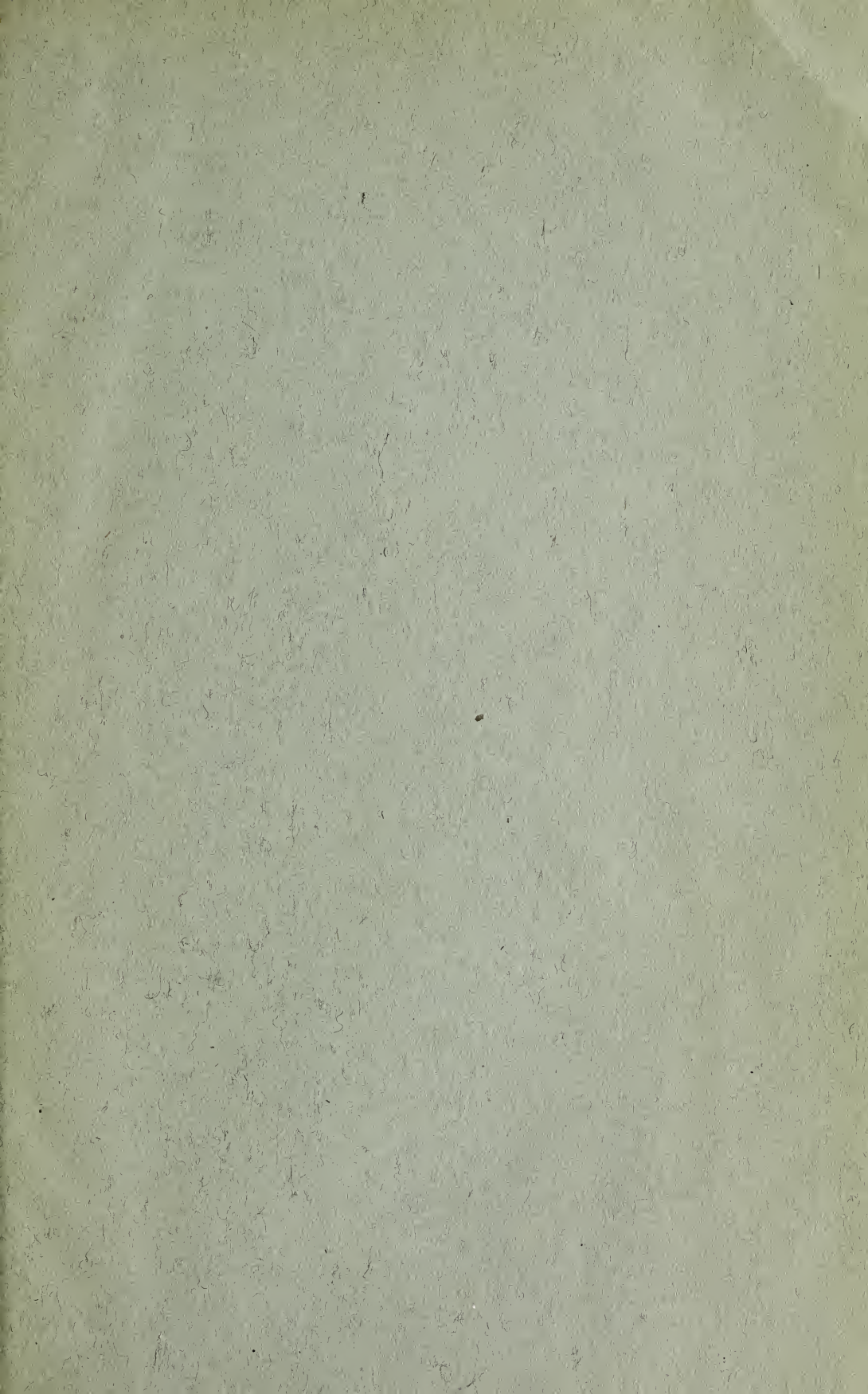
Audited and found correct.  
C. E. ALLEN,  
IRA EDWARDS,  
*Auditors.*





























SMITHSONIAN INSTITUTION LIBRARIES



3 9088 00897 5104