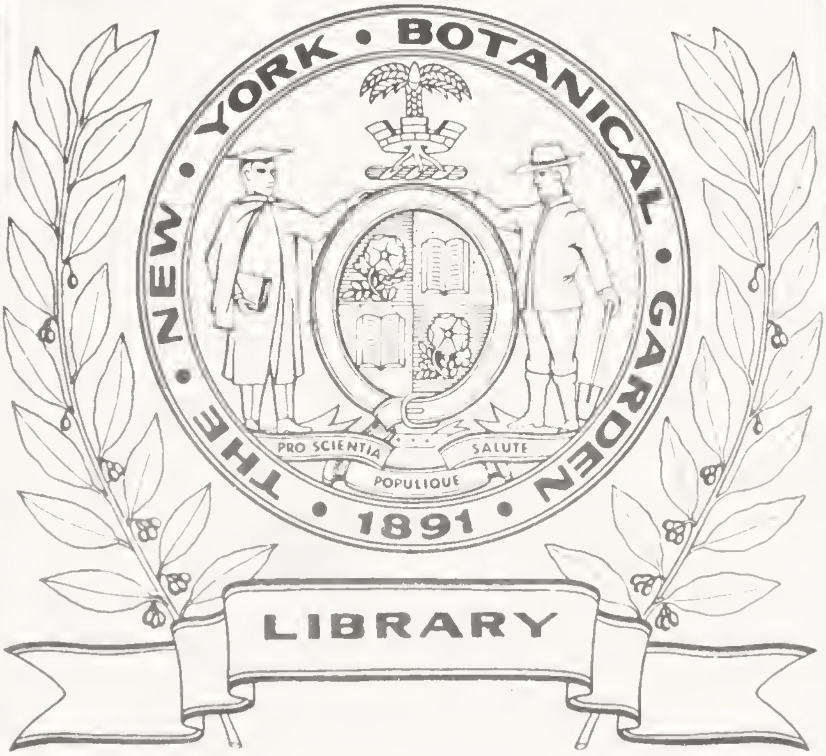
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of the

Torrey Botanical Club

VOLUME 19

Editor

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Volume 19 Number 1

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M. A. Chrysler

The cytology of the Chytridiales with special reference to Cladochytrium replicatum

By

JOHN S. KARLING

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The cytology of the Chytridiales with special reference to Cladochytrium replicatum

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The cytology of the Chytridiales with special reference to Cladochytrium replicatum

John S. Karling

(with six plates and two text-figures)

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I. CLADOCHYTRIUM REPLICATUM KARLING

INTRODUCTION

The species, genera, and families of fungi which are collectively grouped under the order Chytridiales are unusually diverse in structure, life cycles, habitat and method of development; and for a group of organisms which show so many widely different indications as to origin, descent, and phylogenetic relationships they have received comparatively little attention from cytologists. The majority of students of these fungi have for the most part been concerned with recording the occurrence of old and new species throughout the world and describing their developmental stages. Furthermore, the larger number of such descriptions have been only fragmentary and based on isolated stages of development, and have thus left wide gaps in our knowledge of the life cycles of the chytrids. This scarcity of cytological data is primarily due without doubt to the fact that the majority of the species are markedly evanescent and difficult to procure in sufficient quantities for intensive investigation, as well as unusually minute in size. In addition, very few of them are economically important as parasites, and have thus attracted but little attention from pathologists.

A general survey of the literature of the Chytridiales shows that scarcely more than six genera and less than two dozen species have so far been studied cytologically with any degree of intensity. As a consequence, very little is known about the details of karyokinesis, cytokinesis, asexual and sexual reproduction, pathogenicity, host and parasite relationship, etc., as a whole in the widely divergent families of the group. Meiosis or reduction division, for example, has been described in only one species, while chromosome counts have been made in only six. Furthermore, the accounts of these various cytological processes which have been given in the literature are directly conflicting in many instances, while others are scarcely more than a revival in modified form of the old theories of Schleiden and Schwann as to the origin of the nuclei and cell division.

The first part of this contribution will deal with the processes of nuclear and cell division, zoosporogenesis, resting spore development, and structure and organization of the thallus of *Cladochytrium replicatum* Karling, while the second will review the accounts of these processes as they are given in the literature of the Chytridiales as a whole. In the latter, the literature is quite extensive, and for the sake of convenience it may perhaps be best summarized and analyzed chronologically by separate families. The Plasmodiophoraceae are excluded from this discussion on the ground that there is little or no agreement among students of the so-called Archimycetes as to their exact relation to the chytrids. The order in which the families are presented is not to be interpreted as indicating the author's conception of their phylogeny and relationship. This analysis is not primarily concerned with these problems, and for this reason the order of presentation is immaterial. Furthermore, a number of genera included here are very doubtful as far as their validity and relation to the chytrids are concerned, but in view of the fact that our knowledge of this group of fungi is at present so imperfect and fragmentary it is impossible to establish well-defined limits. While the majority of species and genera may possibly be grouped into vague and poorly delimited families, the order as a whole is scarcely more than a dumping ground for relatively simple fungi. At least it cannot be regarded as a phylogenetic group in our present state of knowledge.

MATERIALS AND METHODS

Among the various genera and species investigated by the author during the past ten years, none lends itself more favorably to cytological study than *Cladochytrium replicatum* Karling. Not only is it widely distributed in nature and thus readily available, but it can be easily grown in abundance as a saprophyte in sterilized plant tissues, thus eliminating most of the difficulties usually encountered in fixing, embedding, and staining these minute organisms. Furthermore, its nuclei and other cell organs are fairly large, clear and conspicuous in fixed and stained preparations. In this study *C. replicatum* was isolated from dead leaves of *Eriocaulon septangulare* and cultured in sterilized roots of *Panicum variegatum*, succulent internodes of *Tradescantia*, and cells of *Nitella flexilis*, as has been described in previous publications (1931b, 1935) by the author. These tissues were first boiled in water until fairly soft and then placed in small battery jars containing infected leaves of the pipewort. Within a few days they usually became heavily infected with the saprophyte, and by fixing such soft and fleshy tissues an abundance of thalli in all stages of development were secured. It is thus obvious that by this method *C. replicatum* can be manipulated as easily as root tips, anthers, etc., throughout the steps of killing, washing, dehydration, and imbedding.

A wide variety of fixing agents were employed, including Flemming's medium and weak solutions at full strength as well as in dilutions of $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, and $\frac{1}{10}$ with distilled water, chrom-acetic, Merkle's, osmic acid vapor, absolute alcohol, Bouin's, and Allen's and Wilson's modifications of Bouin's solution in various dilutions. Regaud's, Němec's, and Benda's fixatives were used for the study of chondriosomes and checked in each case against intra-vitam staining with Janus green. Material killed in these latter solutions was stained in Heidenhain's iron haematoxylin, Benda's sulfalizarine crystal violet, and acid fuchsin-toluidin blue and aurantia, according to Champy-Kull's method. For the more general cytological structures Flemming's $\frac{1}{2}$ weak and $\frac{1}{4}$ medium solutions with a fixation period of 48 hours have given the best and most consistent results, particularly when followed by the triple stain. Likewise Allen's and Wilson's modifications of Bouin's solution when used in combination with Heidenhain's iron alum haematoxylin and counter-stained with dilute Orange G gave excellent preparations. Feulgen's nuclear and Newton's gentian violet stains were also employed to good effect, especially in relation to the origin and structure of the chromosomes. In all cases the appearance of the rhizomycelium, spindle organs, zoosporangia and resting spores in the fixed and stained preparations were continually compared with living and intra-vitam stained material, so as to check as far as possible the degree of alteration and artifact incurred.

METHOD OF INFECTION, DEVELOPMENT, STRUCTURE AND ORGANIZATION OF THE THALLUS

As has been described and figured in my previous papers on *C. replicatum*, the zoospores in the free swimming stage are uniciliate, hyaline, and spherical with a conspicuous, highly refractive, golden red globule lying in or near the center. This body frequently appears to lie in a vacuole, and is usually the only structure that can be seen with certainty in living material. In fixed and stained preparations, on the other hand, the appearance and structure are quite different. The refractive globule is no longer visible as such, and in the center of the zoospore lies a comparatively large nucleus with a small nucleole and a large densely stained external nuclear cap. The nucleus is generally connected with the point of attachment of the cilium by delicate and faint cytoplasmic strands.

Following the active swimming period the zoospore becomes sluggish and frequently amoeboid, loses its cilium and comes to rest on the host tissue, as is shown in figure 1. Very shortly afterwards, unless degeneration occurs, a very fine germ tube is produced which penetrates the wall of the host cell. The diameter and size of this tube depend to some degree on the character of the wall. If the host material has been cooked for a long time so that the walls are quite soft, the germ tube is relatively large, but when the wall is comparatively hard and compact the tube has an appearance like that shown in figure 2. Oftentimes under such circumstances the wall may appear slightly thicker in the region of penetration as if it has undergone local gelatinization. As soon as the tube has passed through the wall it increases considerably in diameter, as is illustrated in figures 2 and 3. At this stage the nucleus and nuclear cap still lie in the spore body on the outside, and the cytoplasm usually appears more vacuolated. Shortly afterwards the nucleus migrates through the wall into the enlarged tube in the host cell. As is illustrated in figure 3, it appears extremely dense and heavily stained during this passage, and it is usually almost impossible to differentiate between the nucleole and nuclear cap. As to the history of the latter during this initial nuclear migration and the early developmental stages of the rhizomycelium, our knowledge at present is very fragmentary. In the majority of germinating zoospores so far observed very little remained behind in the external spore cases, and the suggestion becomes obvious that the nuclear cap passes with the nucleus into the germ tube. However, the fact that it is not usually evident and sharply defined in association with the nucleus in the incipient primary spindle organ, as is shown in figure 4, militates against this general assumption. It is not altogether improbable that it may be reserve food which is gradually used up in germination, although I have no concrete data in support of this hypothesis. If, as Debaisieux (1920) and Hatch (1935) claim, in *Coelomycidium Simulii* and *Allomyces arbuscula* it is formed by condensation and fusion of chondriosomes during the maturation and cleavage of the zoosporangium, it may break up into fragments and become dispersed in the elongating germ tube and young rhizomycelium as chondriosome *anlagen*. This again is purely hypothetical and I have so far failed to find any conclusive evidence to substantiate this supposition.

As the germ tube elongates it usually increases considerably in diameter near the tip, and a comparatively short spindle-shaped region is thereby formed. This is the rudiment of the initial spindle organ. The nucleus migrates into this region (fig. 4) and the first vegetative center of thallus replication is thus established. In a number of cases, however, no previous enlargement behind the tip of the germ tube has been found prior to the arrival of the nucleus. In such instances the tube merely enlarges in the region where the nucleus lies to form the spindle organ. As this goes on the elongated densely stained nucleus begins to shorten, vesiculate and round up, loses its intense chromaticity and assumes its characteristic appearance and structure. In this transformation, however, some changes apparently take place, because the nucleole emerges much larger in size than it was in the zoospore. The nucleus shown in figure 4 is considerably elongated and somewhat pear-shaped with the pointed end toward the old zoospore case, giving an appearance which suggests that it has but recently arrived in the incipient spindle organ. The nucleole is quite conspicuous and shaped like a broad flat ring lying around the inner periphery of the pointed end. The chromatin is in the form of a faint reticulum and is not particularly clear and abundant. Such pear-shaped nuclei have often been encountered in young spindle organs, and from such preparations I have come to associate this peculiar shape with recent nuclear migration. The evidence for this, however, is more indirect and circumstantial than directly conclusive, as will appear shortly.

It is to be noted from the above description that in germination the center of gravity, so to speak, of growth, development, and organization is not retained in the spore, as in the families Synchytriaceae, Olpidiaceae, Woroninaceae, and some members of the Rhizidiaceae, but carried away to an outgrowth of it, the spindle organ. Up to this stage the thallus is monocentric in organization. After the first center has been established the thallus begins to extend rather rapidly. Rhizoids and branches begin to develop (fig. 4) and the spindle organ begins to increase in diameter. The nucleus keeps pace with its growth to a certain degree and then usually undergoes division as is shown in figure 5. This is followed very shortly by cell division, and the spindle organ becomes two-celled (fig. 6). One of the nuclei generally remains behind, while the other migrates out into the tenuous portion of the rhizomycelium and establishes a second center for growth and organization. In a few instances, however, both nuclei have been observed to travel on before cell division occurred, leaving the primary spindle organ empty.

Successive stages in the migration of the second nucleus from the initial spindle organ into the filamentous part of the thallus are shown in figures 6 to 11. The organ illustrated in figure 6 has undergone cytokinesis and is quite large. The lower nucleus has begun to enter the filament and is drawn to a sharp point at the apex. This portion is as densely stained as the nucleole, which can be clearly distinguished at one side of the nucleus as a somewhat hemispherical body. The cytoplasm toward the median wall has become more vacuolated. A slightly later stage perhaps is shown in figure 7. The apex of the nucleus lies in the filament and is drawn out into a dense pointed rod, while the nucleole and the remainder of the nucleus still lie in the spindle organ. The greater portion of the cytoplasm has also migrated with the nucleus and appears quite dense around it. Usually at this stage, the cytoplasm in the immediate vicinity of the nucleus is filled with round, irregular and angular, deeply stained bodies, which frequently tend to obscure the nuclear membrane. Figure 8 shows a nucleus in transit. It appears like a densely stained rod, slightly pointed at the apex and almost completely filling the filament. Quite often a break appears in it, as is shown so well in figure 8, which I have interpreted as a line of separation between the nucleole and the remainder of the nucleus. The nuclei shown in figures 8 and 9 are rather short and thick, but it is not uncommon to find them more filamentous and drawn out. Figure 9 shows a nucleus about to enter the incipient secondary spindle organ, while in figure 10 is shown a full-grown organ of the same type in which the nucleus has become vesicular again and attained mature proportions. The nucleus in this latter figure is, none the less, still quite pointed at one end and markedly pear-shaped. From its pointed end a granular cytoplasmic strand runs through the organ into the filament. Such strands have frequently been observed, but their significance and functions are still obscure. They may possibly represent a line of flow or path along which the nucleus traveled, as Gilbert (1935) has suggested and illustrated in *Ceratiomyxa*. However, in a few spindle organs I have observed pear-shaped nuclei lying at right angles rather than parallel to the long axis, as in figure 10. The nucleole in this figure is again in the shape of a broad flat ring near the pointed end, while the chromatin reticulum is quite conspicuous and dense.

In figure 12 is shown a two-celled primary and an incipient unicellular secondary spindle organ together with some of the more filamentous portion of the rhizomycelium. One of the nuclei has migrated from the primary to the secondary spindle organ, while the other has remained behind and been blocked off by a cell wall. It is to be noted in this figure that the thallus has branched repeatedly and formed a number of rhizoids. The latter filaments are generally developed in abundance and are doubtless the chief organs of absorption. Structurally, they may often be of the same diameter and appearance as the main branch or axis, but very shortly run out to a fine filament and eventually end. Figure 11 also brings out sharply the wide variation in diameter and contour of the main axis and its branches. When first described by the author in 1931 from cells of *Eriocaulon septangulare* the filamentous portion of the rhizomycelium was reported to be very finely drawn out, and in the same year Sparrow described it (*C. Nowakowskii*) in several algae as "exceedingly tenuous, never attaining a diameter of more than 1.5 μ." However, when grown under the conditions used in this study the tenuous filaments may vary from 1.5 to 6 μ and sometimes become almost vesicular in certain regions, as is well illustrated in figure 12. Furthermore, the thallus spreads and proliferates so profusely that the host tissue may become filled with a meshwork of branches, rhizoids, spindle organs, zoosporangia, and resting spores. This is especially true in boiled internodes of *Nitella flexilis*, where the number of globular zoosporangia alone may run into thousands within a single cell.

The cytoplasm in the main axis, its branches and the rhizoids is usually quite vacuolated and contains a few scattered, densely stained fragments, bodies, or granules of varying sizes and shapes. These stain rather intensely in all of the basic stains, and so far have shown no specific affinity for chondriosomal dyes. In the young spindle organs the cytoplasm is generally more dense, and the number of granules much greater. The latter are usually aggregated around the nucleus, suggesting perhaps a nuclear origin. Their appearance, size, and distribution will be discussed more in detail under the consideration of nuclear division. As the spindle organ matures and one or both nuclei migrate out, as has been noted above, the cytoplasm becomes more and more vacuolated and sparse and may often be reduced to a thin primordial utricle surrounding a central vacuole.

Following the stage illustrated in figure 12 the nucleus in the secondary spindle organ divides and one, and occasionally both, daughter nuclei migrate out into tertiary and quaternary spindle organs, and successively new centers of organization, growth, and development are thus established. In this fashion the thallus is continually reduplicated as it spreads in the host tissue. With the view of presenting more graphically the organization, type of development, and profuseness of the rhizomycelium of *C. replicatum*, I have drawn in plate 6 a portion of a thallus as it occurred in an internode of *Nitella flexilis*. This drawing is accurate as far as the general appearance, distribution, structure, and maturity of the thallus are concerned, but reconstructed with respect to the cytological details of nuclear migration, division, cleavage in the zoosporangia, etc. As will become apparent later, these details were added and the whole interior reconstructed from stages observed in other fixed and stained preparations in order to summarize more objectively in diagrammatic form the processes of nuclear and cell division and their relation to growth and development. The profuseness and variability in diameter of the rhizomycelium with its zoosporangia, spindle organs and resting spores are in no sense exaggerated in this figure. In fact many thalli have been found in internodes of *N. flexilis* which have been even more profuse and extended.

A careful analysis of this figure will emphasize the structural characteristics and organization of the thallus of *C. replicatum*. In the first place it is polycentric and continually replicated, and in this respect it is like the mycelium or thallus of the higher fungi. Spindle organs may follow spindle organs or alternate with tenuous filaments, zoosporangia, and, at maturity, with resting spores; and except for the rhizoids, the type of development is distinctly homeotic. In the early stages of growth the thallus is essentially trophocentric with the spindle organs as the vegetative centers of replication, but with the development of zoosporangia and resting spores at maturity it becomes more and more reproducto- or genocentric, as has been described in a previous paper (1932).

The second outstanding characteristic, and perhaps the most significant in comparison with the mycelium of the higher fungi, shown in plate 6 is that the nuclei are not regularly distributed along the length of the thallus, but are localized and confined to the spindle organs, zoosporangia, and resting spores. Nuclei may occasionally be seen in the filamentous portion of the rhizomycelium, but only in transit. As has been described above, they are migrating to new centers. This characteristic is of fundamental significance, it seems to me, from the standpoint of development and organization. In the thallus of the higher fungi the nuclei are distributed more or less regularly along the length of the mycelium, according to the figures in the literature, while in *C. replicatum* they are localized; and it is doubtless by virtue of this localization that the spindle organs become the vegetative centers of replication.

The rhizomycelium of this chytrid is, on the other hand, strikingly different from the thallus in the Synchytriaceae, Olpidiaceae, Woroninaceae, and Rhizidiaceae also. As has been previously described, the thalli of these four families are monocentric in contrast to the polycentricity of the Cladochytriaceae. This difference in structure and organization seems at present to be fundamentally and directly correlated with the extent of distribution of the nuclei in the thallus. In the first three families the entire thallus at maturity is holocarpic or transformed into zoospores, gametes or resting sporangia, while in the Rhizidiaceae there is considerable differentiation into vegetative and fertile portions. The vegetative parts may be limited to a simple unbranched absorbing organ as in species of *Phlyctidium* or greatly extended into a rhizoidal system as in *Diplophlyctis;* nevertheless, only a single zoosporangium, resting spore or center of organization is developed. This may be due to the fact that the nuclei remain in this center and never migrate out into the rhizoids, according to the figures in the literature. While the number of illustrations bearing directly on this point are limited (Lowenthal, 1905; Serbinow, 1907; Němec, 1912; Wager, 1913; Couch, 1935; Hovasse, 1936), they nevertheless show the nuclei as being confined to the reproductive portion of the thallus and never migrating into vegetative parts. In species of *Entophlyctis* and *Diplophlyctis* (Karling, 1930, 1931a) where the rhizoids may be as much as 6μ in diameter at their point of origin and extend over a radius of 700μ the author has never found nuclei except in the sporangia or resting spores. Monocentricity in organization appears to be thus directly correlated with localization in nuclear distribution. This is naturally to be expected since the nucleus is without doubt the dominating sphere of influence in metabolism, reproduction and organization.

In the family Cladochytriaceae on the other hand, as has been shown by Tisdale, Jones and Dreschler, Bartlett and myself, the nuclei migrate out into the tenuous filaments, and where they come to rest new and successive centers of organization are formed. The thallus is thus continually replicated and becomes polycentric. The nuclei are nevertheless localized and confined to the turbinate and spindle organs during the strictly vegetative stage, and by virtue of this fact such structures become the centers of duplication. In *Physoderma Zeae-maydis*, *Ph. Menyanthis* (Sparrow, 1934), *Ph. maculare* and *Ph. pulposa*, however, evanescent monocentric rhizidiaceous zoosporangia are occasionally formed as in the family Rhizidiaceae, but unfortunately no cytological work has been done on such structures to show the distribution of the nuclei. In *Catenaria* sp., which the author is now studying cytologically, such monocentric thalli are frequently formed, and in all cases so far observed the nuclei are confined to the zoosporangia alone. In other cases where the successively divided nuclei migrate out into the filaments additional sporangia develop, and very shortly the thallus becomes polycentric. In this form it is thus possible to note the transition from monocentric to polycentric thalli and its relation to nuclear distribution.

Thus as far as our knowledge of the chytrids extends at the present time, the rhizomycelium of *C. replicatum* stands midway in organization between the mycelium of the higher fungi and the thallus of the Rhizidiaceae. On one hand it possesses rhizoids like species of the latter family, and on the other it is polycentric and continually replicated like a true mycelium. These similarities together with the fundamental differences noted above are justifications, in my opinion, for designating the thallus of this chytrid and most known members of the family Cladochytriaceae as a rhizomycelium. Quite recently, however, Bessey (1935, pp. 45-46) has given the impression that the term is to be applied only to the enucleate filamentous portion, but such a limitation is incorrect and does not conform to the author's original and present intention. The term applies to the thallus as a whole and includes the spindle organs, zoosporangia, resting spores, and rhizoids as well as the more tenuous part.

While the rhizomycelium appears at the present time to occupy a position more or less midway between the rhizoidal system and a true mycelium as far as structure, method of development and organization are concerned, there is no good evidence to indicate that it represents an evolutionary transitional type of thallus. It is to be particularly noted in this connection that *Physoderma* and *Catenaria* sometimes form evanescent monocentric thalli with rhizoids as in the family Rhizidiaceae, and the suggestion immediately arises that this is the more primitive type of development which is occasionally recapitulated in the life cycles of typically rhizomycelioid species; and, furthermore, that the Cladochytriaceae have probably evolved from this family through the migration of the nuclei into the filamentous rhizoids and the acquisition of a polycentric mode of development. This conception, however, is purely hypothetical, and there are no concrete data to support it. As used in this and my previous papers the term rhizomycelium carries no phylogenetic connotation, and is primarily employed to emphasize some of the fundamental differences in structure and organization that exist among the various chytrids. Many mycologists make no distinction between the round protoplasts or plasmodium-like thalli of the Olpidiaceae, Woroninaceae and Synchytriaceae, the rhizoids of the Rhizidiaceae and the mycelium of the higher fungi, and designate them all by the latter term. Schwartz and Cook (1929), for example, speak of the oval thallus of *Olpidium radicale* as "a definite mycelium . . . . from which sex organs are formed . . . . ," while Fitzpatrick (1930) describes the rhizoids of the Rhizidiaceae as a mycelium regardless of whether they are minute, single, absorbing, or anchoring pegs as in *Phlyctidium brevipes* or greatly branched systems as in *Diplophlyctis*. Such broad and general use of terms, it seems to me, robs them of their significance. In the Chytridiales striking differences in structure, development, and organization do exist, and wherever possible they should be clearly recognized and properly designated.

Cladochytrium replicatum is primarily a saprophyte and does not develop in normal, healthy growing cells as far as my observations go. Consequently it is impossible to determine its effect on the nucleus and cytoplasm of the host cells. It is obvious from the methods employed during this study in preparing the host tissues for inoculation and infection that the cellular content is dead, badly distorted and frequently quite macerated in appearance. Thus the most conspicuous changes which appear in infected cells are not due to the presence of the fungus. Sparrow (1931) reports that *C. replicatum* (*C. Nowakowskii*) is a virulent parasite of *Spirogyra*, but I have so far failed to find it as such. In fact, as has been shown in a previous paper by the author (1935), it is very widely distributed and ubiquitous in nature and may infect the dead fleshy tissues of almost any plant.

NUCLEAR AND CELL DIVISION IN THE SPINDLE ORGANS

The nucleus of *C. replicatum* is quite large, well defined and shows definite structural characteristics as is shown in figure 13. Except when in transit it is usually spherical, oval, or somewhat citriform. Its most conspicuous element is a large nucleole which generally lies at one side near the nuclear membrane and stains intensely dark in the ordinary basic dyes.

The nucleole varies considerably in size and shape from a broad round band around the inner periphery of the nucleus (figs. 12, 15 16) to a more or less flattened spherical disk (figs. 17, 18, 22, 27, 32) or an oval body as in figures 13, 21, and 24. In the majority of nuclei studied it appears homogeneous throughout and even in contour, but occasionally it may be irregular, variable in density, and seemingly composed of a number of granules, as is suggested in figure 20. Whether or not in such exceptional cases this appearance is correlated with prophase nuclear changes has not been determined, but it seems unlikely. In preparations which have been poorly fixed and stained, the nucleole appears to lie in a conspicuous central vacuole, and is often the only visible structure in the nucleus, but such appearances are largely due to artifact.

In addition to the nucleole a definite chromatin reticulum or network is usually clearly visible in the resting nucleus, as is well illustrated in figures 13 to 16. In median sections of the nucleus, the reticulum appears denser and more abundant at the nuclear membrane, and in exceptional cases may leave the center almost devoid of chromatin (fig. 13). It is usually quite irregular in appearance, and seems to be made up of chromatin granules, net knots, and irregular bodies distributed on a linin framework. In good triple-stained preparations it stains deeply blue or violet in contrast to the ruby red nucleole, which thus suggests a fundamental difference in composition from the latter. The presence of this well defined chromatin reticulum in the resting nucleus militates against the general assumption and contention that the nucleole in the Chytridiales is the storehouse of chromatin and ultimate source of the chromosomes.

Quite often in the spindle organs and particularly in the young zoosporangia and resting spores the cytoplasm surrounding the nuclear membrane is filled with densely stained globules and granules of various sizes and shapes as is shown in figures 14 to 20; and it is not uncommon to find them in such abundance that the membrane is almost completely obscured and indistinguishable. In such cases the nucleus usually stands out in sharp contrast as a comparatively clear oval or circular region with the deeply stained nucleole at one side (fig. 33). These granules may be round, angular, or elongated and extremely variable in size. Figures 17, 18, and 26 show them as quite large, while in figure 24 they are of more or less uniform size and evenly distributed. In some spindle organs they may be lacking entirely, as is shown in figures 29, 32, 34, 35, and 36. It is primarily because of these granules that it is so difficult to determine with certainty the presence and structure of centrosomes and astral rays. Such granules are very common in the cells of the chytrids, and to date have been described in *Synchytrium* (Stevens and Stevens, 1903; Kusano, 1907; Percival, 1910; Curtis, 1921; Kohler, 1923; Quintanilha, 1926), *Olpidium* (Kusano, 1912; Schwartz and Cook, 1928), *Polyphagus* (Wager, 1913; Dangeard, 1900), *Olpidiopsis* (Barrett, 1912), and *Urophlyctis* (Fron and Lasnier, 1920; Jones and Dreschler, 1920; Bartlett, 1926). Their source and manner of origin are not clearly known, but the majority of students of *Synchytrium*, *Olpidium*, and *Polyphagus* describe them as originating from the nucleole and being extruded from the nucleus preparatory to and during division. In the resting spores of *Polyphagus Euglenae* Wager (1913) regards them as chromidia or tropho-chromatin which represent the vegetative element in the nucleus, while in the zoospores and young thalli they are concerned with the elaboration of oil. Griggs (1909), Percival, Bally, Curtis, and others, on the other hand, claim that they enlarge in the cytoplasm and become the secondary nuclei and primordia of the zoospores. Kusano regards them as reserve food substance which is absorbed in the growth of the resting spore. Whether in *C. replicatum* they are chromidia extruded from the nucleus during division or chondriosomes aggregated around the nuclear membrane has not been determined with certainty. In material killed in ordinary non-chondriosomal fixatives containing acetic acid and stained in haematoxylin and Flemming's triple stain they show a marked affinity for basic dyes and have much the same staining capacity as the nucleole. The same is true when Feulgen's nuclear stain is employed, which supports perhaps the contention that they are of nucleolar origin. However, no marked and characteristic correlative change in the nucleole during the prophases of division such as Kusano, Stevens (1907), Bally, Percival, Curtis, and others have described for *Synchytrium*, have been observed in *C. replicatum*. In the former genus the nucleole is described and figured as periodically extruding globules of chromatin which first accumulate on its periphery and then migrate out into the cytoplasm. As a result the nucleole becomes periodically vacuolated and less basophilic. In chondriosomal fixatives and stains these granules in our species do not appear as sharp, well defined, and specific as chondriosomes. Minute mitochondria may be found in *C. replicatum*, but the larger bodies seem to be distinct from them.

The changes which occur in the nuclear reticulum during the early prophases of division are not very clear and are difficult to interpret correctly. The nucleus increases perceptibly in size, while the chromatin bodies become larger, more basophilic and less highly dispersed. Quite frequently the whole reticulum is more or less withdrawn from the nuclear membrane into a dense and somewhat crescentic or half-moon-shaped network, which appears oriented to some degree on the nucleole as is shown in figures 17 and 18. Such nuclei are strikingly similar in many respects to those of *Synchytrium* and *Polyphagus* as they have been figured by Guttenberg (1909), Percival (1910), Bally (1911), Tobler (1913), and Wager (1913). Whether this appearance is largely an artifact of fixation in *C. replicatum* or a normal early prophase stage is not altogether certain. In poorly fixed and heavily stained material the chromatin network or reticulum may be highly shrunken and appear as a more or less solid crescentic mass as in figure 17. The degree of aggregation and density varies considerably with the quality of fixation, and it is thus possible to make up a series of stages from that shown in figure 17 to the more normal appearance illustrated in figure 20. Such a series, however, does not seem to constitute a progressive succession of prophase stages, and for this reason I am inclined to regard the contraction as largely an artifact. On the other hand, the orientation of the network on and to some degree around the nucleole is quite common and pronounced during the prophases in the best of preparations and thus seems to be a more normal characteristic. In all such cases the nucleole is separated from the chromatin meshwork by a clear space, which may vary considerably in extent with the quality of fixation.

A network of this type appears to be quite common in *Synchytrium*, *Polyphagus*, and *Olpidium*. In *S. endobioticum*, *S. Anemones*, *S. Puerariae*, *S. fulgens*, *S. anomalum*, and *Olipidium radicale*, Guttenberg, Percival, Tobler, Schwartz and Cook (1928), and Kusano (1930) figure the reticulum as a crescentic and amoeboid body with pseudopod-like extensions connecting it with the nuclear membrane and cytoplasm. Wager (1913, fig. 60) likewise figures it as such in the female gamete nucleus of *P. Euglenae*. They describe it as a condensed network with basophilic chromatic particles lying within its meshes, but do not regard the shape and orientation as essentially characteristic of the prophases. In figure 20 is shown what I consider a fairly early prophase stage in *C. replicatum*, which shows a minimum of contraction from the nuclear membrane. The chromatin granules, angular fragments or bodies, are somewhat larger and denser than in resting nuclei, while the nucleole is rather irregular in outline and denser in certain regions. A somewhat later stage is shown in the nucleus on the left of figure 21. This figure shows a binucleate incipient zoosporangium, but it is interpolated here because both of its nuclei are in early prophase stages of division. The nucleus on the left side contains a number of elongated chromatin strands which doubtless represent an early stage in the development of the spireme. The nucleole is comparatively small, but whether this diminution in size is to be taken as an index that the nucleole has given up chromatin to the spireme is highly uncertain. Quite commonly in more advanced stages after the chromosomes have been fully formed there appears to have been no reduction in size and staining capacity of the nucleole.

As has been noted before, the majority of cytologists dealing with Chytridiales maintain that the chromatin of the resting nucleus is contained in the large densely basophilic nucleole and extruded into the fine network or nuclear cavity as the prophase stages progress. In *Polyphagus Euglenae, Synchytrium endobioticum, S. Taraxaci, S. Puerariae, S. fulgens, Olipidium radicale,* etc., Wager, Dangeard, Kusano (1907, 1930), Bally, Curtis, Schwartz and Cook, and others describe the chromosomes as being largely derived from the karyosome. In *S. endobioticum,* according to Miss Curtis, the linin strands are attached to the surface of the nucleole, and during the growth of the prosorus three distinct discharges of chromatin from the nucleolus occur. These chromatin globules travel along the strands, and are eventually discharged into the cytoplasm. The prophases of division begin with the third discharge, and Miss Curtis believes that the chromosomes are formed directly from chromatin buds extruded from the nucleole. Kusano found essentially the same type of nucleolar extrusion in *S. fulgens*, but describes the chromosomes as being formed from the nucleolar substance present in the reticulum. In *P. Euglenae* Wager does not show the origin of the chromosomes. Little or no evidence of nucleolar extrusion and the formation of the chromosomes from such material has been found in *C. replicatum*, and I am strongly of the opinion that the nucleole contributes very little if any directly to the chromosomes. The evidence at hand indicates that they arise from the chromatin reticulum entirely. No nucleolar discharges such as those described for *Synchytrium* have been observed, and in the majority of successive prophase stages studied the nucleole has undergone but little change in size and shape.

The nucleus on the right side of figure 21 shows the spireme fully formed. The three strands lying in the plane of focus are definitely oriented on the nucleole and show a zigzag or spiral structure. In their orientation they are strikingly similar to the prophase strands in *S. endobioticum* as they have been figured by Miss Curtis. So far no evidence of longitudinal splitting or doubling has been observed in my material, and it is not yet clear where this process occurs. In figure 21 is also shown the best evidence I have so far found for the presence of centrosomes and astral rays. Deeply staining granules at the poles of the nucleus are not uncommon, but it is usually impossible to differentiate them from the others present or to see any evidence of cytoplasmic radiation in connection with them. In figure 21, however, are shown granules on the membrane of each nucleus with lines radiating from them. On the left-hand nucleus five beaded radiating strands are present, while on the one to the right only two are visible. Whether or not these granules and cytoplasmic strands are centrosomes and astral rays I am at present uncertain. They are strikingly similar to such structures, but in view of the fact that I have found them so seldom and that they seem to play no visible part in the formation of the spindle and the division of the nucleus and chromosomes I am somewhat doubtful at present as to the presence of centrosomes in *C. replicatum*. Among the Chytridiales which have been studied cytologically centrosomes have been found only in *Synchytrium* amd *Rhizophidium*. Neither Kusano, Wager, Barrett, Němec, nor Schwartz and Cook found them in *Olpidium*, *Olpidiopsis*, and *Polyphagus*. In various species of *Synchytrium*, however, according to Stevens (1907), Griggs, and Kusano, centrosomes and enlarged asters appear in the cytoplasm during the telophasic reconstruction of the daughter nuclei, but never during the prophases, metaphases, and anaphases. Quite often they may appear spontaneously in the cytoplasm quite apart from the daughter groups of chromosomes. In *S. Puerariae* and *S. fulgens* Kusano describes the astral rays as bending around the chromosome groups and fusing to form the daughter nuclear membranes. In view of their activity in this respect he called these structures *karyodermatoplasts*. In *Rhizophidium Beauchampi* Hovasse (1936) figures centrosomes lying at the poles of the nucleus but inside of the nuclear membrane. No astral radiations in the cytoplasm occur in connection with these bodies.

In figure 22 is shown a later prophase stage in which the spireme strands have apparently contracted and are shortening to form the chromosomes. The whole mass is, nevertheless, oriented to some degree on the large disk-shaped nucleole. The nucleus is somewhat lemon-shaped, and at one pole lie two large granules, but they are hardly, it seems to me, to be regarded as centrosomes. A slightly later stage is shown in figure 23. The nucleus appears to be at its maximum diameter, and the nucleole in the shape of a flat ring lies at one side. In the center of the nucleus and apparently imbedded in a light staining karyoplasm lie three elongated and three short discrete bodies which are doubtless the chromosomes. The tip of the longest one lies over the nucleole. While only six bodies are shown in this nucleus I am not certain that this is the correct number of chromosomes for the species. They are usually so small and closely crowded that it is almost impossible to arrive at a definite number. Figure 24 shows eight bodies, while in figures 28 and 29 are shown six and seven, respectively. I am thus inclined at present to put the number of chromosomes in *C. replicatum* between six and nine. The correct number will doubtless be very small and close to those of other chytrids in which the chromosomes have been counted. As far as I am aware, this has been done for only four genera and seven species, including *C. replicatum*. For the sake of comparison I am presenting these data here in tabular form.

Author	*Species*	*Chromosome number*	
		n	2*n*
Stevens and Stevens (1903)	*Synchytrium decipiens*	4(?)	—
Griggs (1908)	*Synchytrium decipiens*	4	—
Griggs (1909)	*Synchytrium decipiens*	4	—
Kusano (1907)	*Synchytrium Puerariae*	5	—
Kusano (1909)	*Synchytrium Puerariae*	5	—
Kusano (1930)	*Synchytrium fulgens*	5	10
Curtis (1921)	*Synchytrium endobioticum*	5	—
Barrett (1912)	*Olpidiopsis vexans*	6	—
Wager (1913)	*Polyphagus Euglenae*	10–12	—

I have so far been unable to determine the origin of the division spindle. No evidence of polar caps or radial kinoplasm has been found; nor have I seen any entering cones or bundles of fibers in connection with centrosomes such as Harper (1897, 1905) has described in *Erysiphe* and *Phyllactinia*. The source and manner of origin of the spindle in the other chytrids which have been studied cytologically are likewise obscure and little understood. In *Synchytrium decipiens* Stevens and Stevens describe the linin as aggregating near the center of the nucleus, and from which the threads gradually assume the form of a spindle. Kusano (1907, 1909, 1930) is uncertain as to its origin in *S. Puerariae*, but states that it is formed in the center of the achromatic striations. Bally likewise describes it as being formed from the linin in *S. endobioticum*. Curtis, on the other hand, as has been noted above, figures and describes fine linin threads attached to the nucleole in the resting nuclei and prophase stages of *S. endobioticum*, which later on converge at the two ends and thus form the spindle. The number of linin threads is the same as that of the chromosomes, and in most of her figures they look like irregular spireme bands or strands. Her illustrations as to the origin of the spindle are not at all convincing, and I am inclined to agree with Kusano (1930) that her five so-called linin threads are actually fine elongated spireme strands or chromosomes oriented on the nucleole. In *Polyphagus Euglenae* Wager failed to observe the origin of the spindle, while in *Olpidiopsis vexans* Barrett claims that "the chromosomes become massed together into a large, deeply staining body from which the tips of the spindle appear to emerge." The best evidence which I have supporting the *linin origin* of the spindle is illustrated in figure 24. The chromosomes lie more or less in the center of the nucleus, and extending out from them are faint, irregular granular lines, which perhaps constitute the residual linin. However, I have not observed any further development stages that show the transformation and rearrangement of these lines into the spindle. It is thus quite obvious from this figure and the above description as well as from the survey of the literature that the problem of the source and manner of origin of the spindle in the Chytridiales is still quite obscure. However, there can be no doubt that in the majority of species it is entirely intranuclear until the late anaphases. The only exceptions to this rule occur in the zoosporangia of *Olpidium Brassicae* (Němec, 1912), *O. radicale* (Schwartz and Cook, 1928), and *Cystochytrium radicale* (Cook, 1932), and in the resting spores of *O. Viciae* (Kusano, 1912).

In figure 25 is shown the primary nucleus of a zoosporangium in the late prophases. The intranuclear spindle is completely formed, and the indistinct chromosomes are apparently being drawn into the equator. The nuclear membrane is well defined and clear, and the spindle fills approximately a half of the nuclear cavity. It is comparatively narrow and distinctly spindle-shaped, and its poles are centered on two somewhat disk-shaped bodies lying on the nuclear membrane. From these bodies radiate faint and irregular lines which suggest the presence of astral rays, but here again the evidence is not particularly convincing. Figure 26 shows an equatorial plate stage. In this spindle organ the nucleus has doubtless been distorted during fixation and sectioning, so that the membrane appears abnormal. The division spindle is quite broad in the equatorial region and then tapers rather quickly to the poles, which are again centered on two deeply stained granules. The chromosomes are so closely crowded that they form almost a continuous irregular band across the equator. As a general rule the nucleus becomes somewhat elongated and oval in shape during the late prophases, metaphases, and anaphases as is illustrated in figures 25, 31, 33, and 34, but round nuclei may occasionally be found (figs. 23, 27, 32). In figure 27 the spindle is quite broad and tapers only slightly toward the poles. This figure illustrates very well the arrangement of the chromosomes in a circular band around the outer periphery of the spindle. The nucleole at this stage usually lies at the side of the nucleus and is distinctly crescentic when viewed from the side. In many nuclei it may appear to push the nuclear membrane out or distend it, and in some preparations such as are shown in figures 27, 30, and 32 it may even seem to lie on the outside. This is doubtless an optical illusion, since it is very difficult to distinguish the membrane in that particular region. It is to be particularly noted that the nucleole is still quite large and densely basophilic.

A polar view of the equatorial plate stage is shown in figure 28. Six distinct bodies lie in a flat loop in the center of the nucleus, while the more or less cup-shaped nucleole occupies the side. Occasionally one pole of the spindle may be centered on the nucleole as is shown in figure 29. The division figure in this cell has doubtless been displaced by the microtome knife in sectioning, which accounts for its unorthodox appearance. This figure shows a 2-celled spindle organ in which one nucleus has migrated to other parts of the thallus, while the remaining one is dividing. So far the actual separation of the individual chromosomes has not been observed, but in figure 30 is shown a very early anaphase stage. The two daughter groups of chromosomes are rather compact and have begun to draw apart, so that a clear space is visible between them. At the upper pole of the spindle lies a flat curved body which stains heavily. The nucleole is very conspicuous, basophilic, and somewhat pyramidal in shape. In over-stained preparations the chromosome groups may look like two irregular but optically homogeneous bands across the spindle as is shown in figure 31, and it is then impossible to differentiate the limits of the individual chromosomes. This figure is particularly noteworthy in that it suggests that the chromosomes separate first in the middle and then progressively towards the periphery. As a result the two groups form a somewhat flat loop with the two ends pulling apart. Figure 32 shows the clearest and best defined case of early anaphase so far seen. The nucleus is quite large and round, while the achromatic spindle is comparatively narrow. The two groups of chromosomes are quite conspicuous, but the individual bodies are still so close together that they form irregular bands. The nuclear membrane is bulged out in the vicinity of the nucleole, and the ends of the latter appear somewhat stretched or drawn out in the direction of the two poles. A later anaphase stage is illustrated in figure 33, in which the individual chromosomes are fairly distinct. Between the two groups run faint central spindle fibers, while the mantle fibers taper quickly at the poles. This nucleus is surrounded by such a dense mass of granules that its membrane is hardly distinguishable, and as a consequence the nuclear region stands out in contrast as a comparatively clear oval space with the division figure clearly defined and sharp. In figure 34 the chromosome groups have reached the poles of the spindle and form two more or less flattened crescentic bands which conform to the boundary of the nucleus at those points. The spindle is quite barrel-shaped in this figure and fills most of the nuclear cavity, which is rather exceptional. This preparation was considerably overstained, which doubtless accounts largely for the density and optical homogeneity of the two chromosome groups. Occasionally in division figures like this there is slight resemblance to some of the so-called promitotic stages which have been described for the Plasmodiophorales, particularly when looking directly down upon the nucleole. This is doubtless due, however, to poor fixation and overstaining, and so far no evidence has been found as far as the method of nuclear division is concerned that would indicate a possible relationship between this polycentric chytrid and the so-called parasitic slime molds.

Following the arrival of the chromosomes at the poles, the spindle begins to elongate rapidly, and as a result it apparently pushes through the nuclear membrane in these two regions. I have never actually observed this occurrence in *C. replicatum*, but indirect evidence supports this conclusion. The nuclear membrane disappears first at the poles, while in the equatorial region it may persist for some time. In *Polyphagus Euglenae*, according to Wager (1913), the spindle elongates tremendously and pushes through at the poles, while the rest of the nuclear membrane remains intact and becomes compressed like a flattened drum. The same kind of elongation of the spindle has been described for *Synchytrium* by various workers. Figure 35 shows the elongated straight spindle with a remnant of the nuclear membrane on the right side. The chromosome groups are quite compact but not optically homogeneous. The nucleole is here seen in surface view and appears quite large, oval, and densely basophilic. With the breakdown of the nuclear membrane it is liberated into the cytoplasm and persists for a long time. A later anaphase stage is shown in figure 36. The central portion of the cell formerly occupied by the nucleus is comparatively clear, although it has elongated and is being encroached upon by the more dense cytoplasm. No evidence of the nuclear membrane is visible, and the large nucleole lies clear and distinct in the cytoplasm. The spindle is even more elongated and narrow, and consists of but a few fibers connecting the daughter chromosome groups. Furthermore, it is slightly curved and strikingly similar to the spindles in *Olpidiopsis vexans*, the rusts, and other fungi, as figured by Barrett, Blackman (1904), Colley (1918), Dodge and Gaiser (1926), and others. Similarly marked polar radiations in the cytoplasm occur around the groups of chromosomes. Wager (1913) has described and figured such radiations in *P. Euglneae* likewise. A somewhat exceptional case is shown in figure 38. The spindle is still rather broad and well developed, while the nucleole which lies on its periphery is greatly extended and drawn out at the edges. No evidence of the nuclear membrane is visible, and the chromosomes are aggregated into compact optically homogeneous oval bodies. They lie at the bottom respectively of two clear spaces which seem to be partly delimited by thin cytoplasmic membranes or borders. There is thus here a faint suggestion of an early stage in nuclear membrane formation, and for this reason I am inclined to regard this stage as more advanced than the one shown in figure 37, although the spindle is still quite broad.

As to the manner of reorganization of the chromosome groups and the formation of the daughter nuclei there are but few concrete data in the literature and much less agreement of opinion. In *Synchytrium Puerariae* and *S. fulgens*, Kusano describes the chromosome masses as being transformed into a nucleole and then becoming surrounded by a clear space. The astral rays then fold over and fuse and thus progressively build the nuclear membrane around this cavity. Stevens and Griggs' figures on *S. decipiens* support Kusano as to the presence of centrosomes and astral rays during the telophases, but Bally and Curtis failed to find such structures in the cytoplasm of *S. endobioticum* and *S. Taraxaci*. In the latter species Bally reports that the chromosomes unite to form the nucleole, which then becomes surrounded by a clear space and eventually a nuclear membrane. The spindle, however, persists as a fine filament connecting the daughter nuclei long after they have been reconstituted. The so-called nucleole then begins to divide into secondary ones, and very shortly the reticulum appears. Miss Curtis' account for *S. endobioticum* is essentially the same as Bally's. Barrett and Wager contribute nothing to our knowledge of this reorganization from their study of nuclear division in *Olpidiopsis* and *Polyphagus*. As has been noted above I have been unable to add anything of marked significance from my study of *C. replicatum*. The chromosome groups become united into a compact body as is shown in figures 37 to 39, and above and below each group respectively develop clear areas which eventually appear to become surrounded by a membrane. The clear areas and membrane seem to develop and progress gradually from the chromosome masses onward as is shown in figure 37, which suggests at least that they may be directly concerned with the formation of the nuclear membrane. Figure 38 shows the two daughter nuclei completely formed. The chromatin masses constitute two large densely basophilic oval bodies which are similar in every respect to the nucleoli of resting nuclei. No chromatin reticulum is yet visible. The spindle has disappeared entirely, and in its former place is a clear region. The nucleole is still quite large and densely stained and lies in the cytoplasm. However, it usually decreases gradually in size (fig. 39), and may eventually be broken up into a number of small granules (fig. 40) and disappear entirely, as is shown in figure 41. In two instances so far observed it persisted until after cell division had been completed, and as a result was included in one of the daughter cells of the spindle organ.

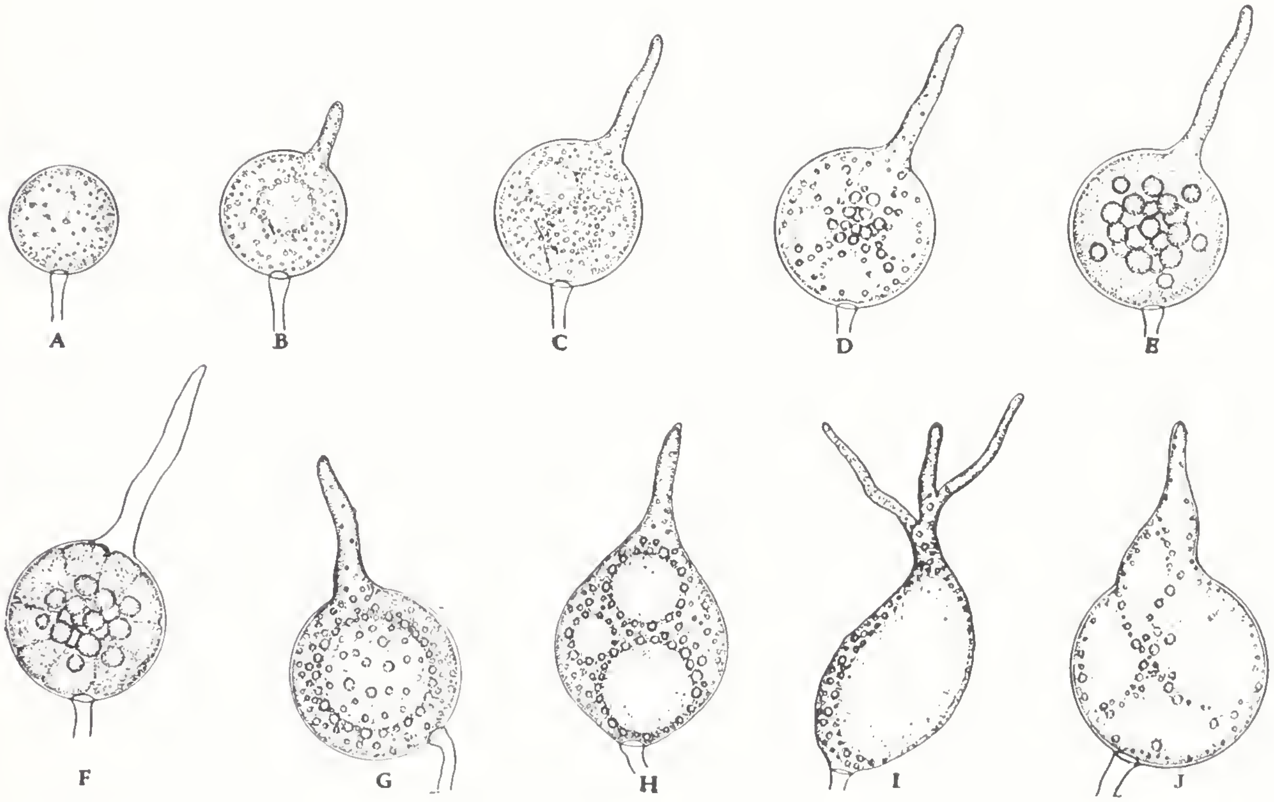
While the early prophase stages seemed to show that the spireme and chromosomes were formed from the chromatin reticulum rather than the nucleole, the telophase changes suggest the opposite. The evidence at hand indicates that the chromosomes unite to form large nucleole-like bodies which in some unknown manner become enveloped by a nuclear membrane. At first there is little or no reticulum visible, but as reconstruction continues a faint one develops as is shown in figure 39. Although the nucleole-like chromatin masses show no marked change in staining capacity, shape, or size during the process, this reticulum is undoubtedly formed from it in some fashion. In no cases so far observed have the telophase chromosome masses become alveolated or broken up into smaller and smaller units and gradually dispersed as is the general rule in higher plants; nor have the nucleoli been found to arise *de novo*. The author is at present of the opinion that the nucleole constitutes the residue of the chromosome masses after the reticulum has been formed in the reconstructed daughter nuclei. Very often the space between the two daughter nuclei is highly vacuolated, and occasionally both may move into this region and lie close together as is illustrated in figure 40.

Cytokinesis in the spindle organs and zoosporangia occurs after nuclear division is complete and appears to be entirely independent of the activity of the achromatic spindle. In the former only a few stages have been found to date, so that at present the story is far from complete. As has been noted before, the equatorial region of the cell formerly occupied by the nucleus and spindle is often highly vacuolate, and nothing is to be seen of the fibers by the time cell division begins. In figure 41 is shown the earliest indication of cytokinesis so far observed. The equatorial region of this cell is non-vacuolated, and at the periphery are two faint open furrows which appear to be progressing centripetally. A slightly later stage is shown in figure 42. The furrows are considerably wider and more open at the periphery, and within them have now been formed a thin membrane or cell plate, which is in direct connection with the cell walls and extends almost up to the apex of the furrow. I am still uncertain as to how this membrane is formed at its encroaching tip; no conspicuous, deeply stained cytoplasmic masses or plugs have been found enveloping and preceding it, as Lutman (1911) has shown in *Closterium*. Its development is more similar in superficial appearance at least to the so-called girdle wall formation in *Cladophora* as figured by Brand (1908), although no accumulation of slimy wall substance in the regions where cell division begins has yet been observed. The furrows and cell plate progress deeper and deeper, as is shown in figure 43, until they meet in the center and thus divide the cell (fig. 44). No kinoplasmic material in the form of spindle fibers or astral rays has thus been seen in relation with cytokinesis in the spindle organs. Nuclear division may not always be followed immediately by cell division. In a few instances elongated multinucleate spindle organs, such as are illustrated in figure 45, have been found in which no cross septa were present. Such cases, however, appear to be exceptional. Whether cross walls are developed at all in such organs or all of the nuclei migrate out is not known.

As has been shown elsewhere, the spindle organs vary considerably in size, shape, and number of cells. They are predominantly spindle-shaped, but occasionally irregular and somewhat rectangular-shaped ones with several tenuous filaments, such as is illustrated in figure 46, occur. The division spindle in one of these cells is at right angles to the long axis of the organ, and as a result, when cytokinesis is completed the structure may become dictyosporous in appearance. Oftentimes the individual cells may become greatly enlarged and vesicular or transformed directly into zoosporangia. In figure 47 is shown what was doubtless originally a five-celled spindle organ, but two of its cells have developed into sporangia. In exceptional cases the zoosporangia may bud out from the surface of the spindle organ as is shown in figure 48. This figure is of further significance in that it also shows the division of the primary nucleus of the young sporangium.

DEVELOPMENT OF THE ZOOSPORANGIA

The zoosporangia occur terminally and intercalary in the rhizomycelium, and may also arise from the surface of a spindle organ or directly by the transformation of its cells. They vary considerably in size and somewhat in shape, but are predominantly oval or spherical. Occasionally the shape of larger ones is determined by that of the host cell. At maturity they are filled with large, round, refractive, golden-red globules. Their development and maturation can be readily followed in the living condition, and for the sake of comparison with fixed and stained preparations I shall describe the processes first in living material. The most pronounced visible changes involve increase in size of the zoosporangium itself and the genesis of the refractive globules. The visible and physical changes which the latter undergo in the development and maturation of the zoosporangium are quite characteristic and can be followed with readiness. With the view of presenting these changes more concretely, I have drawn in text-figure 1 successive developmental stages of a terminal sporangium at different time intervals. At first these droplets are hyaline or grayish-white in color with a faint tinge of pale orange, and appear to be more or less evenly distributed in the hyaloplasm, as is shown in text-figure 1A. At this stage they vary from minute points at the limits of microscopic visibility to well-defined and fair-sized globules. As the zoosporangium grows in size (text-fig. 1B), they increase in number and size also, and quite often in this uninucleate stage they may be grouped more numerously about the centrally located nucleus. In living material the nucleus cannot, of course, be clearly seen, but its outline as a hyaline sphere is rather well defined by these globules. Their increased number around the nuclear membrane does not necessarily indicate, in my opinion, a specific affinity between the two, but is doubtless primarily a matter of displacement. Assuming them to be evenly distributed in a more or less viscid hyaloplasm, it is obvious that those in the center around the nucleus will become more closely crowded as it grows in size preparatory to division. This view is supported by observation on the developmental stages of vacuolated zoosporangia, such as are shown in text-figure 1G to 1I. In these sporangia the globules were densely crowded at the periphery of the vacuoles, and as the latter increased in size the crowding became more and more pronounced. Grouping of refractive droplets around the nuclear membrane as described above is not always visible, however. Sometimes it is quite pronounced, but at other times it appears to be lacking. This may possibly be associated with the disappearance of the nuclear membrane in the late anaphases of division and its subsequent reformation in the telophases. It is not inconceivable that the refractive globules may invade the nuclear region after the membrane has broken down; and then as the daughter nuclei are reconstituted and grow in size the crowding again becomes evident.



Text-figure 1, showing changes in the refractive golden-red globules during the maturation of the zoosporangium in living material.

The increase in number of globules as well as their individual growth continues apace with the growth of the zoosporangium, but when it reaches mature size (text-fig. 1C), there appears to be no further multiplication of droplets. Hand in hand with this growth a marked change in color occurs. As the droplets increase in size the orange tint becomes more and more intense, and by the time the zoosporangium has reached the stage shown in text-figure 1D, the globules are golden red and highly refractive. At this stage (text-fig. 1D) and also earlier, the number of globules begin to decrease in number and increase markedly in size. The latter change is primarily due to coalescence, and as this goes on the globules seem to move toward and aggregate in the center of the zoosporangium. Coalescence of the globules continues until a limited number are formed, as is shown in text-figure 1E, which almost always corresponds to the number of zoospores developed in the sporangium, although a few exceptions have been observed. By this time the hyaloplasm is completely free of granules and droplets, and the mature zoosporangium has the appearance of a pellucid sphere with a large number of brilliantly refractive, golden-red globules suspended in the center. Shortly thereafter cleavage begins (text-fig. 1F), and occurs in such a fashion as usually to include a single globule in each segment. The position of the globule relative to the nucleus is difficult to determine, because the latter is generally invisible in living material.

So far no Brownian movement of these droplets and globules has been observed, except in pathological, dying, and dead zoosporangia. As the zoosporangia begin to die and degenerate, movement may become quite pronounced and active, but never in healthy protoplasm. From superficial appearance these globules appear to be fatty or lipoidal in composition, and they have been almost universally referred to in chytrid literature as oil droplets. Their reaction to various acids and agents, however, indicate a more complex nature. When treated with a 2% osmic acid solution they retain their golden-red color for several hours, and do not blacken conspicuously until two days or more have elapsed. They slowly undergo a change in color from red to reddish green, olive green and finally dark olive. In full strength glacial acetic they change to orange and light olive orange in color, and finally after approximately three-quarters of an hour they become completely hyaline. This change is not accompanied by any marked increase in size or dissolution, and appears to be nothing more than a bleaching process. After 18 hours immersion no further change occurred in these globules. In ether and chloroform the changes were essentially the same. In absolute alcohol immediate coagulation and clumping of the globules took place, and within approximately six hours they had lost all color and become hyaline without undergoing any perceptible change in size and shape.

The exit tube usually begins to form quite early, and it is not uncommon to find it almost fully developed while a zoosporangium is still uni- or binucleate, as is shown in figures 48, 49 and text-figure 1B. Its length varies from that of a short papilla to a cylindrical tube sometimes 30 μ in length, and it may occasionally branch one to several times (text-fig. 1I).

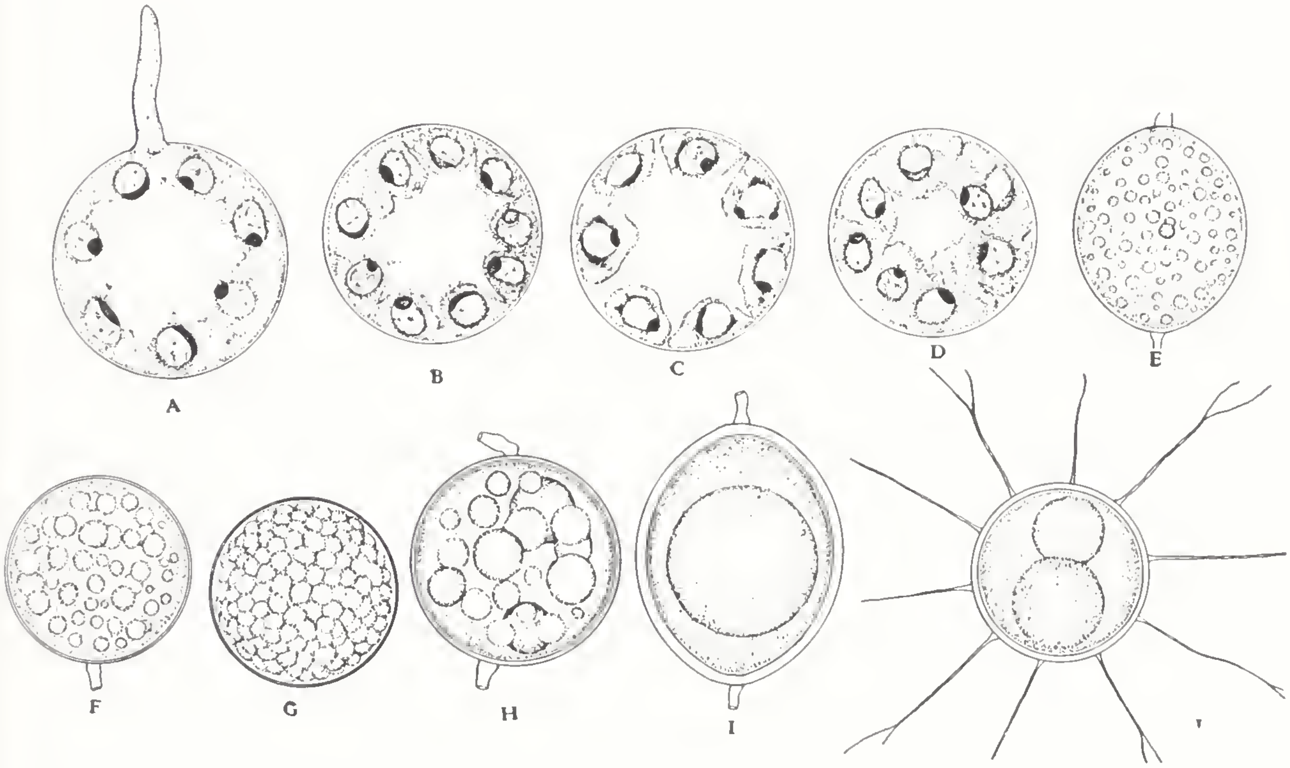
In fixed and stained preparations these globules as such are no longer visible and appear to have been destroyed or altered markedly during the process of fixation. A young uninucleate incipient zoosporangium is shown in figure 48 in which the nuclear membrane is surrounded by a layer of irregular, densely basophilic granules and fragments of varying sizes and shapes. Do these bodies represent the modified refractive globules of living material, or are they chromidia and chondriosomes? In view of the fact that the refringent globules as such are no longer visible in fixed and stained preparations, and that the angular, irregular and oval granules around the nuclear membrane are not destroyed by fixatives containing acetic acid and are densely basophilic and stain like the nucleole and chromosomes, it seems improbable that they are chondriosomes or the residue of the globules. The nucleus of the zoosporangium shown in figure 48 has doubtless come directly from the upper cell of the spindle organ. The primary nuclei are comparatively large (6 μ to 7.5 μ), but their size in proportion to the secondary nuclei is not even near the magnitude exhibited by *Synchytrium*. They divide mitotically with an intranuclear spindle in the same manner as in the spindle organs. The cytoplasm at this stage is usually quite dense, particularly around the nucleus, and relatively free of large granules at the periphery of the sporangium. Figures 21 and 49 show binucleate stages. In the former there are very few granules in the cytoplasm and none around the nuclei, but in the latter they are unusually abundant and large. They form a broad, dense, and somewhat constricted layer around both nuclei, which have apparently moved closer together after division and now lie in the more or less vacuolated region formerly occupied by the primary nucleus and division spindle. This figure is of further significance in that it also illustrates proliferation of the zoosporangia, which is quite common in *C. replicatum*.

In figure 50 is shown a tetra-nucleate sporangium whose four nuclei are all in the late prophases of division. Definite spireme bands are visible in the two upper ones. Figure 51 shows another zoosporangium of the same stage in which only three of the nuclei are present in the plane of the section. These are markedly globe-like in shape, and are clearly in the equatorial plate stage of division with the poles of the intranuclear spindles centered on rather well-defined bodies or granules lying on the nuclear membrane. In two of the nuclei these bodies appear flattened and disk-like in shape. In the third nucleus one end of the spindle is centered on the nucleole. Around none of them, however, are astral or polar radiations visible. Figure 52 shows a portion of an elongated eight-nucleate zoosporangium. Five of the nuclei are clearly visible, while at the base of the figure are faint evidences of two others. Two of the five plainly visible nuclei present profile views of equatorial plate stages, while the remainder show polar views of the same stage. It is thus obvious from these figures that nuclear division in the zoosporangia is distinctly mitotic and completely simultaneous, as is usually the case of zoosporangia in general. Large zoosporangia with sixteen nuclei in the equatorial plate stage of division have been found several times. The number of divisions is directly correlated with the growth and size attained, and as a result the number of nuclei present in mature sporangia varies accordingly. As the number increases the nuclei become gradually smaller, and at the time of cleavage in unusually large sporangia they may be only slightly more than half the size of the primary nucleus. The cytoplasm of the zoosporangia shown in figures 48 to 52 is comparatively homogeneous with no large conspicuous vacuoles. Vacuolated ones, however, are not uncommon, and at maturity the more or less irregularly distributed vacuoles usually flow together to form a larger central one as is shown in figure 53. The cytoplasm in this sporangium is unusually sparse and scant, and the tonoplast of the vacuole is not particularly sharp and well defined. The nuclei of such zoosporangia lie in the peripheral layer of the cytoplasm.

CYTOKINESIS AND ZOOSPOROGENESIS

Cytokinesis in the zoosporangia occurs by the process of progressive cleavage in which furrows cut the protoplasm up into uninucleated segments. It may be centrifugal or centripetal, or in rare cases a combination of both, depending on the size and vacuolation of the sporangium. Figure 54 shows a portion of a 16-nucleated zoosporangium in which cleavage has just begun at the periphery. This preparation is somewhat shrunken, and doubtless as a consequence the furrows are more open than usual. In such a homogeneous sporangium they travel in a more or less radial direction, but may occasionally become curved or bent. In figure 55 is shown a smaller zoosporangium in which the cleavage furrows have progressed almost to the center of the section. In cases where the center is occupied by a nucleus the furrows stop short of it, divide, and the two arms travel almost at right angles to the original direction, as is shown in figure 56.

They then take a more curved path, and as they meet with similar arms of other furrows a more or less round uninucleate segment is delimited in the center. In other cases where the central nucleus is lacking the furrows meet in the center (fig. 57), and as a consequence the cleavage segments are typically wedge-shaped. Figure 58 shows a section of a large zoosporangium in which cleavage is complete, and the segments are primarily pentagonal in shape. The furrows or lines of demarcation are quite marked and clear, and each zoospore initial is surrounded by a faint membrane which seems to be hardly more dense and conspicuous than the remainder of the cytoplasm. In unusually large zoosporangia bi- and trinucleate segments may occasionally be delimited first, but they are subsequently divided by secondary furrows. Following the stage shown in figure 58 the segments may increase in size and volume and almost completely fill the zoosporangium again. In such instances the lines of demarcation are scarcely distinguishable.



Text-figure 2, showing progressive cleavage in vacuolated zoosporangia from fixed and stained preparations, and the development of the resting spores in living material.

In highly vacuolated zoosporangia cleavage is usually centripetal. Such types are comparatively rare, but for the sake of comparison I have drawn in text-figure 2 successive stages of the process. In figure 2A is shown a median section of a sporangium with a large central vacuole, in which at one side there is some evidence of cleavage furrows. These begin at the tonoplast of the vacuole as rather broad V's and progress outwards between the peripherally disposed nuclei. A slightly later stage is shown in text-figure 2A. The furrows are quite conspicuous and have deepened considerably. In the zoosporangium illustrated in text-figure 2C, four of the furrows have reached the boundary, while the other three are at the stage of cutting through the plasma membrane. As a result some of the segments are already fully delimited. After cleavage is complete the central vacuole disappears, and the zoospore initials gradually move toward the center of the zoosporangium. This type of centripetal cleavage is exactly similar to what Schwarze (1922), Scherffel (1925), and Couch (1935) have described for *Olpidiopsis*, *Eurychasma*, *Ectrogella*, *Pythiella*, and the Saprolegniales. In two zoosporangia of *C. replicatum* both centripetal and centrifugal cleavage furrows have been found, but such cases appear to be comparatively rare according to my observations. As is shown in figure 2D the central vacuole is relatively small, but from its border furrows are beginning to develop. At the same time, they have also formed at the periphery of the sporangium and are progressing inwards.

It is thus obvious from this description that cytokinesis in the zoosporangia of *C. replicatum* does not occur by a simultaneous fragmentation or cleavage of the protoplasm into polyhedral segments as Dangeard (1890), Kusano (1909), Curtis, Barrett, Schwartz and Cook, and others have described for *Synchytrium*, *Olpidiopsis*, and *Olpidium*, but by progressive cleavage, as Harper (1899), Swingle (1903), Timberlake (1902), Schwarze (1922) and Bold (1933), have so clearly shown in the sporangia of fungi and algae. The claim that it is simultaneous is based, primarily, it seems to me, on the fact that the observers have not seen the initial stages of cleavage. As Harper, Schwarze, and myself have shown, the cleavage segments or spore initials may grow or swell up by rehydration after cleavage is over and often completely fill the sporangium. As a result of this increase in size the lines of demarcation become faint and less conspicuous and look as if they had but recently been formed. The whole sporangium thus appears as if it had at once undergone simultaneous division into polyhedral segments throughout. It is thus apparent that if observations are made at that stage the impression is deceptive.

As has been noted above, the cleavage segments or zoospore initials in sections are usually pentagonal, hexagonal, or triangular in shape. During the late stages of cleavage and the transformation of the segments into zoospores the nucleoli appear to become greatly reduced in size as is shown in figures 57 and 59. This change is not accompanied by budding or fragmentation and nuclear extrusion as far as I have been able to determine. The reduced nucleoli are usually homogeneous in appearance and even in contour, while the cytoplasm may occasionally be comparatively free of basophilic granules (figs. 51–56). At this stage, however, granules and dark staining substances are usually very abundant, particularly around the nucleus, as is shown in figures 57–59, but whether or not they are of nucleolar origin is uncertain. Oftentimes they may be so dense as to almost obscure a portion of the nuclear membrane. The extranuclear substance or granules shown in these figures are very finely divided, but in the slightly older segments shown in figures 60 to 69 they are very large and coarse and lie around that portion of the nuclear membrane opposite the nucleole. Figure 60 shows five conspicuous bodies or granules of this type. This segment as well as those shown in figures 61 and 62 are from sporangia fixed in Flemming's medium solution and triple stained. When treated thus the granules are usually ruby red in color like the small round nucleole. In figure 61 is shown a later stage of zoosporogenesis in which the number and amount of extranuclear substance and granules have increased markedly. Apparently the bodies fuse as maturation continues (fig. 62), since at maturity their place is occupied by a densely stained, more or less optically homogeneous, somewhat hemispherical cap which envelops the upper portion of the nucleus, as Kniep (1929) and Hatch have recently described in *Allomyces*. At this stage the zoosporangium with its zoospore segments may frequently have the appearance shown in figure 63. The nuclei may look like clear spaces or vacuoles surrounded at the apex by a densely stained crescentic mass or cap.

Nuclear caps of this type seem to be fairly common in the zoospores of the Oomycetes, according to the observations of Thaxter (1896), Barrett (1912b), Kniep, Cotner (1930) and Hatch; but with the exception of Debaisieux's (1920) account of *Coelomycidium* this description of their presence in *C. replicatum* is the first conclusive report for the Chytridiales. I have also found them in the zoospores of *Catenaria* and *Diplophlyctis*. The figures of Hovasse (1936) suggest that they may be present in *Rhizophidium*, and it is not improbable that the crescentic shaped body or nucleole described by Wager as lying inside of the nuclear membrane of *Polyphagus Euglenae* may possibly be a nuclear cap.

There is, however, considerable difference of opinion as to whether the nuclear caps are intra- or extra-nuclear. Thaxter, Cotner and Sparrow (1933b) interpreted the densely basophilic crescentic bodies which they observed as constituting the greater part of the nuclei, while Barrett described them as food bodies in which the nucleus is partially imbedded. Kniep and Hatch claim that they are entirely extramatrical and fit as a more or less hemispherical hood over the nucleus of the zoospores and gametes. My observations on *C. replicatum* confirm their account as to its spatial relation to the nucleus, but differs somewhat from that of

Debaisieux and Hatch as to its composition. After cleavage has been completed in *Coelomycidium Simulii*, according to Debaisieux, and the segments have begun to round up large angular, round, or elongated basophilic bodies appear in the cytoplasm and gradually fuse into a large body, which usual lies at the apex of the nucleus on the side opposite the point of attachment of the cilium. He regards this extranuclear body as an accessory nucleus which results from the fusion of chondriosomal granules and is in some way connected with the formation and development of the cilium. In *Olipidium*-like parasites of *Saprolegnia* Varitchak (1931) describes and figures the chondriosomes as aggregating around the nuclei during zoosporogenesis, but he does not show their fusion to form an extra-nuclear cap. Hatch has subsequently presented a viewpoint somewhat similar to that of Debaisieux as to the origin of the cap, although apparently unaware of the former's account. He describes the extranuclear cap as originating by the aggregation, vesiculation and fusion of chondriosomes around the nuclear membrane during gametogenesis in *Allomyces arbuscula*, and believes it is equivalent to the so-called limosphere which appears during spermatogenesis in certain mosses. Figures 27, 28, and 32 of Hatch are fundamentally similar to my figures 60, 61, 62 and 63 of *C. replicatum*, but in the latter these extranuclear granules which eventually form the cap show much the same reaction, staining capacity and affinity as the nucleole and chromatin. It is to be noted in this connection that Debaisieux also demonstrated their presence without the aid of chondriosomal fixatives and that they appeared densely basophilic when ordinary killing agents and stains were employed. In *C. replicatum*, as has been noted previously, I have so far been unable to demonstrate with conclusive certainty and to my own satisfaction that they are chondriosomal in appearance and composition. It is to be noted, however, that in *A. arbuscula*, according to Hatch, the chondriosomes are conspicuous in the living hyphae and young zoosporangia as elongated rods, and such material is apparently more favorable for study than *C. replicatum*. Furthermore, the use of Feulgen's nuclear stain has not differentiated the cap specifically in our species. In the best of preparations it has not appeared as a colorless region in contrast to the densely stained chromatin, as Hatch has shown in figure 20 of *A. arbuscula*. The author thus feels that before any definite conclusion can be reached as to the composition of the nuclear cap an intensive study of its occurrence in a large number of species must be made. In *Rhizophidium Beauchampi*, for instance, Hovasse (fig. 4C) figures a densely stained mass at the anterior end of the cleavage segment which in living material blackens intensely with osmic acid, and appears later in zoospores as an oil globule where it is ultimately used up as food. Whether or not this mass is equivalent to the nuclear cap is uncertain, but its presence, nevertheless, emphasizes the need for more intensive study of the cytoplasmic constituents of the sporangia and zoospores of the lower fungi.

In some zoospores the cap may be reduced and small in size, while in others it may envelop the large part of the nucleus, as is shown in figures 64A and 64B. The nucleole usually lies at the opposite pole of the nucleus, which by this time has become somewhat elongated and even peaked, and is quite small in comparison with its former size. As the zoospore initials mature and begin to glide about in the zoosporangium, the cilia are formed. These are apparently developed before the zoospores escape, since numerous ones have been found with well-developed organs of locomotion while still within the sporangium. Figure 65 shows the structure of the zoospore after it has escaped. The cilium is posteriorly attached, and from its point of insertion runs a faint cytoplasm strand to the nucleole. This strand is not always clearly visible, but it is doubtless equivalent to the rhizoplasts which occur in the zoospores of the Myxomycetes, water molds, and protozoa.

DEVELOPMENT OF THE RESTING SPORANGIA

The resting sporangia of *C. replicatum* are predominantly spherical in shape, and vary from 9 to 21 μ in diameter, but oval, lemon-shaped and elongated ones are not uncommon. They are hyaline and possess a fairly thick wall which is often quite smooth, but in a large number of sporangia fine hyaline, single, and sometimes branched filaments or spines radiate from the surface, as has been described previously by Sparrow (1933) and myself (1934). As many as thirty such threads varying from 4 to 15 μ in length have been found in a single sporangium. It thus seems that both smooth and spiny resting spores are formed in this species. In living material a large spherical, hyaline, and somewhat refractive globule occupies the center of the cell, and in elongated sporangia two or more such globules may be present.

The resting sporangia may be borne terminal or intercalary on the rhizomycelium, and generally make their appearance as the thallus matures. So far no fusion of motile isogametes such as occurs in *Olpidium* and *Synchytrium* have been observed in relation to the genesis of these spores. This possibility, however, must not be excluded, in spite of the evidence at hand that their early development is fundamentally similar to that of the zoosporangia. They begin as enlargements in the rhizomycelium, and in their early stages are indistinguishable from the ordinary evanescent zoosporangia. Very shortly, however, it becomes obvious that the suspended globules in the cytoplasm do not acquire the brilliantly golden red color as in the case of the zoosporangia, but remain hyaline or faint yellow. This seems to be the first recognizable difference. Text-figure 2E shows an early developmental stage in which the globules are still quite small. In text-figure 2F they have begun to coalesce into larger bodies, and their number has been somewhat reduced. The wall has also thickened considerably. It is not uncommon, however, to find young spores which are completely filled with hyaline bodies of more or less the same size as is shown in text-figure 2G. A fairly late stage is shown in text-figure 2H in which the wall is markedly thicker. The hyaline globules are further reduced in number but much larger in size. Eventually they coalesce to form one or two large central globules as is illustrated in text-figure 2I. This figure shows a mature, thick, smooth-walled spore, while text-figure 2J shows one with the slender radiating filaments or spines. So far I have not followed the development of the latter type and determined the manner of origin of the spines. Occasionally the central globule may have a faintly yellow or orange tinge.

In fixed and stained material, on the other hand, the appearance of the developing spores is somewhat different. The globules are apparently destroyed or greatly modified as such by fixation and their places appear to be occupied by vacuoles. Here it becomes apparent that the spores attain mature size without nuclear multiplication ordinarily, and the first visible change is in the thickening of the wall. In figure 66 is shown an incipient uninucleate spore in which the wall is only slightly heavier than in the zoosporangia. The cytoplasm is relatively dense, particularly around the nuclear membrane. The nucleus is large and round with a well-defined nucleole, but the chromatin reticulum appears denser and more basophilic. As the spore matures this change becomes more conspicuous, and the nucleus may be filled with large irregular granules. A later stage in development is shown in figure 67. The wall has thickened perceptibly, large vacuoles have appeared in the cytoplasm, and the nucleus has been slightly displaced from its central position. Furthermore, it is enveloped in a rather dense layer of cytoplasm in which granules are beginning to appear. While the resting spores are predominantly uninucleate, occasional bi- and tetranucleate ones may be found as is shown in figures 68, 69, and 70. Figure 68 shows a binucleate spore in which the wall is comparatively thick. Most of the cytoplasm is aggregated around the two nuclei and is filled with densely stained granules. As a result, the nuclei in such cells appear as relatively clear spaces in which lie the nucleole and other large dense chromatic bodies. In the nuclei shown in figure 68 the chromatin reticulum is condensed into a more or less solid homogeneous body.

I do not interpret this binucleate condition as delayed karyogamy following cell fusion, as Kusano, Griggs, Wager, Schwartz and Cook, and Sampson (1932) claim in *Olpidium*, *Monochytrium*, and *Polyphagus*. It seems to me we are here dealing with an incipient binucleate, arrested zoosporangium which encysted and became a resting spore. This view is supported by evidence of the type presented in figures 69 and 72. In figure 69 a partly developed but unopened sporangial neck is present, which was doubtless formed in the early stages of development and would have served as the exit tube of a zoosporangium. Instead of developing into such a structure, however, its content retracted somewhat, encysted, and formed a thick wall. Here again conspicuous vacuoles are present, and the denser cytoplasm is aggregated around and between the two nuclei. Figure 72 shows a uninucleate but somewhat similar cell in which the exit tube is longer and the spore wall thicker. These figures are fundamentally similar to those of Buckley and Clapham (1929) for *Catenaria anguillulae,* in which they show that the resting sporangia are nothing but encysted zoosporangia. Occasional tetranucleate spores may also be found, as is shown in figure 70. Such sporangia are hardly to be regarded as stages in germination, since the wall is not fully developed. Without doubt, this represents again an incipient four-nucleate zoosporangium which has encysted.

Quite often the spindle organs themselves may develop thick walls and become transformed into resting sporangia, as is shown in figure 71. This is additional indirect evidence, it seems to me, that no sexual fusion is involved in the formation of the resting spores. In figures 73 and 74 are shown fully mature dormant sporangia. The nucleus generally lies flattened at one side (fig. 74) in the primordial utricle and is surrounded by a dense layer of cytoplasm in which a large number of granules are suspended. The large refractive globule which is usually so conspicuous in living material has apparently been destroyed or greatly modified in fixation, since it is no longer present as such. Its position is usually occupied by a large central vacuole. Figure 73 shows the same kind of spore as seen from above. The flattened nucleus here appears quite large and round, with a conspicuous nucleole at one side and a large angular densely stained body lying in the reticulum. The granules in the cytoplasm are very numerous and form a dense layer around the nucleus. At this stage the resting sporangium may be described as mature. So far no germination stages have been found in fixed and stained material.

II. CYTOLOGY OF THE CHYTRIDIALES IN GENERAL

SYNCHYTRIACEAE

The species of this family were the first to receive serious attention from cytologists and have without doubt been most extensively and intensively studied. It is primarily for this reason that I take this family first for consideration. At present it is generally regarded as including only three genera, *Synchytrium*, *Micromyces* and *Micromycopsis*.

In 1890 Dangeard described and figured the nuclei of *Synchytrium Taraxaci* as dividing both by successive bipartition, or amitotically, and indirectly, and from his description and drawings it appears as if mitosis and amitosis occur simultaneously and side by side in the same thallus. Three years later in the same species Rosen (1893) reported direct division of the primary nucleus, in which the chromatin spins out into a spireme, the nucleole divides, and its two halves then migrate apart. Finally the nucleus with its spireme and two nucleolar portions constricts and divides into two daughter nuclei without the formation of an achromatic spindle. Subsequently, the successive divisions of the secondary nuclei assume more and more the character of mitosis, and eventually divide entirely by this method. Thus, according to Rosen, mitosis gradually evolves from amitosis in the growth and maturation of the sorus.

As to the mode of cell division Dangeard described the prosorus of *S. Taraxaci* as fragmenting simultaneously into a large number of polyhedric segments which subsequently form thin membranes, separate, and develop into sporangia. In 1899 Harper, however, demonstrated the inaccuracy of Dangeard's description, and showed in *S. Taraxaci* and *S. decipiens* that cell division is accomplished by progressive cleavage, rather than by simultaneous fragmentation. Cleavage furrows begin at the surface and progress deeper and deeper in a more or less radial direction until they intersect and thus divide the protoplasmic mass into irregular segments. At first the furrows or grooves are so narrow as to appear as thin plates, or lines; but as the result of shrinkage which usually accompanies cleavage the segments begin to separate, and the cleavage lines become open furrows. After cleavage has been completed the prosorus swells to its original proportions, and the segments thus become closely pressed together. The lines of demarcation are nevertheless evident, but at this stage the whole prosorus looks as if it had undergone simultaneous cleavage or fragmentation. From this description it is evident that what Dangeard and subsequent workers saw was only the rehydrated stage of the prosorus after cleavage had been completed, and this doubtless explains the oft-repeated description in the literature that cell division in the zoosporangia of the chytrids occurs by simultaneous cleavage.

The problem of the method of nuclear division remained as Dangeard and Rosen had described it until 1903, when Stevens and Stevens undertook a study of karyokinesis in *S. decipiens*. They described the primary nucleus as decreasing tremendously in size preparatory to division, but none the less dividing mitotically with the formation of a definite spireme, chromosomes, and an intranuclear spindle. Lowenthal made a cytological study of *S. Anemone* in 1905, showed the hypertrophy of the infected host cell, and figured the primary nucleus of the resting spore as continuous with the cytoplasm and totally devoid of a membrane. Beyond this peculiarity, which is undoubtedly an artifact, he contributed nothing of significance to our knowledge of nuclear and cell division. Two years later Rytz (1907) published an extensive account of the host range of species of *Synchytrium* and dealt in some detail with the cytology of *S. Succisae*, in which he confirms Harper's description of progressive cleavage in detail. Although he figures a typical mitotic spindle for one of the secondary nuclei, he is, nevertheless, somewhat doubtful as to the universality of this method of nuclear division. Kusano (1907–1908) in *S. Puerariae* confirmed the account of Stevens and Stevens as to the indirect division of primary nucleus, and in the same year F. L. Stevens (1907) independently gave another account of the nuclei and their method of division in *S. decipiens*, *S. fulgens*, and *S. papillatum*. In these species he figured and described not only nuclei without limiting membranes, but centrosomes, astral rays, and mitotic division of some secondary nuclei. He was unable to find intermediate and progressive division stages in the latter, and because of this fact he postulated that a single nucleus may often fragment simultaneously into several smaller ones. Stevens apparently turned over his material of *S. decipiens* to Griggs, who in 1908 described in detail the relation of the centrosome and astral rays to the reconstruction of the nucleus. In the following year (1909a), however, Griggs confirmed Stevens' hypothesis as to amitosis or fragmentation of the secondary nuclei and described two types of nuclear origin, heteroschizis and nuclear gemmation. In the latter process the karyosome breaks up into bodies which then migrate through the nuclear membrane, becomes enveloped in a vacuole, and then becomes surrounded by a membrane. In heteroschizis, on the other hand, the nucleus undergoes direct multiple division or fragmentation to form a somewhat compact morula-like cluster of daughter nuclei. These remain close together, and eventually divide mitotically to form a group of small division spindles. Subsequently in the same year Griggs published another paper (1909b) dealing with these latter mitotic divisions and the individuality of the chromosomes. From the fact that nuclei derived by amitosis also show the characteristic four chromosomes he concluded that there is no continuity of these bodies from one nuclear generation to another, and "that the chromosome number is a physiological constant, like the other hereditary characters of the species."

In the meantime, Kusano (1909) published a long account of the cytology of *S. Puerariae* and showed again that the division of the primary and secondary nuclei is distinctly mitotic, although he did not find all of the successive stages of the process and also gave some figures of small nuclei which are strikingly similar to those of Griggs. Cell division in the prosorus occurs by simultaneous cleavage, and the sporangial walls are precipitated from the cytoplasm. It seems obvious, however, from his description and figures that he is describing the rehydrated stage of the prosorus which Harper found to occur after cleavage has been completed. At the same time Guttenberg (1909) described and figured a peculiar looking mitotic figure in *S. anomalum*. The nucleus appears to be surrounded by an extraordinarily thick membrane or wall and contains a number of nucleolar fragments. Its upper end, however, is broken open and through this large aperture extrudes the greater part of a division figure apparently in late anaphase. At the exterior pole of the latter lies a large centrosphere. From the appearance of this one figure Guttenberg, nonetheless, concluded that nuclear division in *S. anomalum* is mitotic. In the following year (1910) appeared Percival's study on the life history and cytology of the potato wart disease organism which he transferred to the genus *Synchytrium* under the name *S. endobioticum*. He gave a brief but rather well-illustrated account of the development of the summer sorus, figured what appears to be early prophase changes of primary nucleus, but failed to find metaphase, anaphase, and telophase division stages. According to his description, the primary nucleus begins to shrink as chromatin is extruded into the cytoplasm and gradually disappears altogether. The extruded chromatin granules or chromidia in the cytoplasm then become surrounded by vacuoles and develop into small secondary nuclei, which subsequently undergo mitotic division. This is essentially like the process of nuclear gemmation described by Griggs. In view of the fact presumably that he could not find any sharply defined division figures of the primary nucleus, Percival came to the same conclusion as Dangeard and Rosen that a gradual evolution of typical mitosis occurs in the later divisions of the secondary nuclei. On the other hand, he confirmed Harper as to cell division by progressive cleavage in the prosorus. With respect to the maturation of the thick-walled winter spores or sporangia his account is essentially the same and as curious as for the prosorus, particularly in relation to the nuclei. The primary nucleus lacks a membrane until it reaches maximum size. Chromatin is then apparently extruded into the meshes of the cytoplasm and eventually gives rise to the nuclei of the zoospores. While this is going on the primary nucleus shrinks in size, the nuclear membrane dissolves and disappears, and at the times the zoospores are formed only a residue consisting of the remnants of the nucleole and chromatin remains.

Percival's work was shortly followed by that of Bally in 1911 on *S. Taraxaci* and *S. endobioticum.* In the former species Bally failed to find any division of the primary nucleus and reported not only nuclear gemmation of the type described by Griggs for *S. decipiens* but also the presence of macro- and micronuclei, and fusion of the small secondary nuclei as well. Later on such nuclei in the sorus and sporangia were found to undergo typical simultaneous mitosis. Cell division was found to occur fundamentally by progressive cleavage, although he does not give any convincing figures of the process. For *S. endobioticum* Bally confirmed Percival's account of the nuclei in detail, but failed to find any division figures of the secondary nuclei. Two years later Tobler (1913) monographed the genus *Synchytrium*, and while her study was largely morphological and taxonomic, she none the less reviews the cytology of the group and in *S. aurantiacum*, confirms Lowenthal's, Stevens', and Percival's description of primary nuclei without membranes. In *S. mercurialis* as well as in *S. aurantiacum* she described and figured migration of secondary nucleoli through the nuclear membrane into the cytoplasm where they develop into small secondary nuclei.

Rytz resumed his study on the cytology of *S. Taraxaci* in 1916 and 1917 with an extensive description and illustration of young sori and micro- and macronuclei similar to those figured by Stevens (1909), Griggs, and Bally. He described these size differences as possibly due either to non-synchronous nuclear division or reunion of recently divided nuclei, and refuted emphatically the views of Griggs, Percival, and Bally that secondary nucleoli normally migrate through the nuclear membrane and develop into nuclei in the cytoplasm. Such phenomena are nothing but abnormal and pathological appearances induced by the fixing agents employed. Likewise, he denied the claim of Dangeard, Rosen, Griggs, Percival, and others that amitosis and mitosis of the secondary nuclei alternate during the growth of the prosorus. He found numerous nuclei which appeared to be dividing directly, but attributed this entirely to artifact induced by the killing solution. Although he did not observe division of the primary nucleus, Rytz, nevertheless, maintained that mitosis is the only method of division of both the primary and secondary nuclei. In 1919, however, Bally refuted these claims of Rytz, and reiterated his previous views as to chromidial extrusion, methods of nuclear division and zoosporogenesis. In answer to the contention that regular mitosis is essential to equal and proper distribution of hereditary characters he claimed that these were very few in *Synchytrium*, and that the small number of genes which determined them required no elaborate process like meiosis and mitosis for their segregation and distribution. Accordingly, he regarded the chromidia which are extruded from the primary nucleus of the zygote or resting spore as the bearers of hereditary factors.

Following Rytz's and Bally's publications came Miss Curtis' extensive cytological study of *S. endobioticum* in 1921. As to the prophasic changes in the primary nucleus, she described three periodic discharges of chromatin from the nucleolus into the cytoplasm during the growth of the prosorus. According to her report the nucleus then divides mitotically and is followed by similar divisions of the daughter and successive secondary nuclei. Curtis, nevertheless, figures large and small secondary nuclei in the sorus like those described by previous workers. Cleavage in both the prosorus and sorus is described as simultaneous instead of progressive. Perhaps the most outstanding contribution by Curtis was the demonstration of the relationship between the fused gametes and the resting spore. Copulation of motile cells had been first figured in *S. Taraxaci* by Lowenthal in 1905a, but its significance had not been fully recognized. Curtis figured abundant fusion in *S. endobioticum* and claimed that the zygote develops into the resting spore. Her account of the development of the latter and the zoospores, however, is very unusual, and confirms in essential details that of Percival. In the early stage of host infection and growth of the zygote, the nucleus is "represented by a single chromatic globule lying free in the mass of the cytoplasm," which becomes surrounded by a vacuole and develops into a normal nucleus. As the latter assumes mature proportions the nucleole periodically discharges chromatin into the nuclear cavity and cytoplasm. Following the final discharge the primary nucleus shrinks in size and finally becomes functionless without undergoing division. The extruded chromatin granules in the cytoplasm grow somewhat in size and become the primordia of the zoospores, discharging, in the meantime, smaller granules of their own into the surrounding cytoplasm. The zoospores are thus not formed at all by cleavage of the sporangium into uninucleate segments, but develop and enlarge around extruded chromatin granules. The latter, as far as can be made out from Miss Curtis' ambiguous description, eventually enlarge themselves and become the nuclei of the zoospores.

In the same year, on the other hand, Welsford (1921) described and figured normal intranuclear mitotic figures of the secondary nuclei in the resting sporangium of the same species. However, there has been some doubt expressed (Kusano, 1930) as to whether he was dealing with the resting spore. The results of Miss Curtis as to the degeneration of the primary nucleus and the origin of the secondary nuclei and zoospores were fully confirmed by Köhler in 1923 for *S. endobioticum* and *S. anomalum*, and in 1926 Quintanilha reported and figured nucleolar extrusions and amitosis of the secondary nuclei in the sorus of *S. papillatum*, which were then followed by regular mitosis.

The cytology of *Synchytrium* remained thus until Kusano (1930) published his account of nuclear and cell division in *S. fulgens*. He found not only indirect division of the primary and secondary nuclei of the sorus but in the resting spore as well. Fusion of gametes occurred abundantly to form diploid zygotes. Accordingly, the first division of the primary resting spore nucleus proved to be heterotypic and the subsequent ones homoeotypic. Abundant extrusion of chromatin into the cytoplasm occurred, but instead of the granules becoming secondary nuclei and primordia of zoospores, as most of the earlier workers had claimed, he found them enlarging to form reserve food globules, which are consumed in the germination of the resting spore. As to the method of cell division, Kusano is somewhat obscure. He merely states that the sorus undergoes segmentation by "the formation of the plasmic walls between the segments." Nothing is known apparently concerning the delimitation of zoospores during germination of the resting spore.

Nothing of significance has appeared in the literature on the cytology of *Synchytrium* since Kusano's latest contribution. In a neighboring genus, *Micromyces*, however, Couch (1932) has shown the developmental stages and the host-parasite relationship of *M. Zygogonii* in *Spirogyra*. As soon as the parasite enters the host cell it moves toward the nucleus, and throughout its whole development usually lies closely appressed to the latter. The content of the prosorus escapes into a vesicle, nuclear division, and cleavage into zoosporangia follow. The sporangia then cleave into minute uniciliate zoospores, which Couch claims are planogametes and fuse to form diploid biciliate zygotes. These infect the host cell, but Couch has not so far observed their development into resting spores. No details as to the mode of nuclear division and type of cleavage are given. The genus *Micromycopsis* was established and described by Scherffel in 1926 and confirmed by Sparrow and by Cejp in 1932 and 1933. Nothing is known concerning nuclear division, cytokinesis, and sexuality in this genus.

It is quite obvious from this brief résumé of the literature that there is little agreement on the manner of nuclear and cell division in the family Synchytriaceae. All but three of the investigators who studied these problems describe the nuclei as dividing either amitotically in one stage of development or mitotically in another, and there is only one detailed and accurate account of cytokinesis for the whole group. The descriptions and views of Griggs, Percival, Bally, and Curtis on nuclear and zoospore development in various species of *Synchytrium* are fundamentally hardly more than a revival in slightly modified form of Schleiden's (1838) and Schwann's (1839) archaic account of "free cell formation" around a "cytoblast," which proved to be such an enigma and stumbling block to a correct interpretation of the manner of origin of new cells. According to these students of *Synchytrium*, neither meiosis nor mitosis occurs in the zygotic primary nucleus of the resting spore; and the secondary nuclei arise from extruded granules in the cytoplasm around which are subsequently developed the zoospores. We see further in these accounts a return in essence to the views of R. Hertwig, Schaudinn, Dobell, Schaxel and other students of the protozoa on the extrusion of chromatin or chromidia from the nucleus in *Arcella*, *Arachnula*, *Actinosphaerium*, etc., and their subsequent union and growth to form the nuclei of the daughter cells. These observations were the basis for the elaborated chromidial hypothesis of Hertwig, Goldschmidt, and others as to the duality of the nucleus, which has been greatly discredited by the development of chondriosomal and Golgi body fixatives and the demonstration of such structures in the cell. If the observation of Griggs, Percival, Bally, Curtis, Köhler, and others on nuclear formation in *Synchytrium* are correct what becomes then of the universal doctrine of *omnis nucleus e nucleo* and its concomitant relations to the present-day concepts of heredity?

As to sexuality in this family fusion of motile isogametes has been described in three species of *Synchytrium* and one of *Micromyces*. In all cases reported the gametes are formed in the same sporangia and there seems to be no genotypic sex differentiation and segregation. Köhler (1930, 1932) has found in *S. endobioticum* that fusion may occur between three or more gametes with the result that the zygotes may become tri- and tetranucleate. He is uncertain as to whether or not all of the nuclei fuse and has not followed the development of such zygotes beyond the early stages, so that nothing is known as to their chromosome number. In *S. fulgens* Kusano regards the sexuality exhibited as relative rather than fixed and absolute, and thus brings this species in line with what Hartmann (1925) and Jollos (1926) have claimed for species of *Ectocarpus* and *Dasycladus*. The gametes all behave as male in the active swimming stage and as female after becoming quiescent. Each gamete is furthermore unstable in sex character and may act as female in relation to one gamete and as male toward another. Köhler (1936) has reported the same type of sexuality in *S. endobioticum*.

The majority of workers on this chytrid family are more or less agreed on the mass effects of the host-parasite relationship, particularly in *Synchytrium*, but differ somewhat as to the cytological changes incurred. The presence of the parasite leads very shortly to a marked increase in size of the infected host cells and does not inhibit but may actually stimulate neighboring cells to divide also, if the latter are young and meristematic. Lowenthal, however, denies this in *S. Anemones*, but Bally, Curtis, Tobler, and Kusano have shown in *S. endobioticum* and other species that the infected host cells together with the healthy ones surrounding them may divide a number of times, and as a consequence the resting spores often become deeply imbedded in the tissues. Galls or enlargements are accordingly formed in the infected regions, which are thus the result of both auxesis (cell enlargement) and meresis (cell multiplication). Auxesis, however, seems to be the dominant factor in their development. In *S. Puerariae* Kusano (1907, 1909) maintains that the epidermal cells are never attacked, and the zoospores infect only the non-chlorophyll bearing parenchyma by entering the intercellular spaces beneath the stomata. After entering the host cell, the parasite stimulates it to enlarge slightly, but the growth of the *Synchytrium* thallus is proportionally much greater. As a result the parasite soon completely fills it, and the host nucleus and cytoplasm form a thin enveloping layer. With continued growth of the parasite the adjacent host cells are compressed, and an enzyme presumably is then secreted by the former which dissolves the cell walls. The cytoplasm and nuclei of these surrounding cells flow out and unite with that of the initial infected cell to form a dense living protoplasmic layer, which Kusano calls the "symplast." According to this description the cytoplasm and nuclei of the affected host cells are only slightly deformed and enlarged in size and volume by the parasite and remain alive and normal until after zoosporogenesis. The cells of *Oenothera sinuata*, however, fail to enlarge to any appreciable extent when infected with *S. fulgens*, which is primarily due to the relative resistance of the host. The cell is, nevertheless, killed and its nucleus and cytoplasm degenerate simultaneously with the parasite.

In other species, however, the reaction between host and parasite is quite different, according to the accounts in the literature. In *S. Anemones*, *S. mercurialis*, *S. Succisae*, *S. endobioticum*, etc., Lowenthal, Rytz, Guttenberg, Percival, Tobler, and others describe and figure the host nucleus as becoming greatly enlarged and irregular and finally disintegrating.

Guttenberg and Tobler in particular describe host nuclei which have attained a diameter of more than 50 μ and are quite irregular in outline and extensively ramified by furrows and canals. Such changes are usually accompanied by a marked increase in size of the nucleole and its subsequent fragmentation and division into a great number of secondary nucleoli and granules, which then enlarge and become intensely basophilic. Similar but less marked changes may also occur in the neighboring uninfected cells. In some species the host cytoplasm is described as more dense and alveolar than normal, but as the cell enlarges it becomes highly vacuolated. The figures in the literature thus indicate that parasitism may be accompanied by some protoplasmic accretion, but vacuolation without doubt plays the significant rôle in subsequent enlargement or auxesis.

All species of *Micromyces* so far described cause marked local hypertrophy of the infected cells but do not stimulate them or adjacent ones to divide. The chloroplasts soon change to light yellow and brown and together with the rest of the cytoplasm soon become disorganized, degenerate and clumped about the prosorus. *Micromycopsis*, on the other hand, is not particularly destructive, according to Scherffel (1926) and Cejp (1932, 1933) and does not cause any enlargement of the parasitized cells.

WORONINACEAE

This family is a heterogeneous collection of species with biciliate zoospores, and in the present state of our knowledge should perhaps be regarded more as a dumping ground for the *Olpidium*-like forms with swarm cells of this type rather than a group of phylogenetically related species. In recent years many genera and species of the Olpidiaceae have been transferred to this family with the discovery that the zoospores are biciliate. In several species the swarm cells are diplanetic and somewhat reniform in shape with the cilia laterally attached, while sexual reproduction is distinctly heterogamous; and for these reasons they are regarded by many mycologists as distantly related to or the direct ancestors of the Saprolegniales.

It was in a genus of this family that sexuality was first demonstrated for the Chytridiales. In 1872 Cornu showed that the resting spore of *Olpidiopsis* is formed by the fusion of the contents of two unequal thalli. Pringsheim had observed and figured the male thallus attached to the resting spore as early as 1860 and assumed that some type of sexual fusion had occurred, but he, none the less, mistook the zoosporangia for the antheridia of *Saprolegnia*. He showed the conspicuous hypertrophy of the host cells, followed the development of the zoosporangia in this form as well as in what we now recognize as *Rozella* and *Woronina*, and described zoospore formation as occurring directly (*unmittelbar*). Cornu likewise describes it as such. In 1878 Reinsch observed for the first time actual fertilization and fusion of the male and female thalli. However, in 1880 and 1882 Fischer denied Cornu's and Reinsch's claims as to sexual reproduction in *Olpidiopsis* and described cytokinesis in the zoosporangia as a breaking up of the protoplasm into polyhedral masses. In 1890 Dangeard likewise failed to observe fusion and described cytokinesis as a grouping of the protoplasm around each nucleus. His figures, however, certainly suggest cell division by progressive cleavage. Ten years later Fischer realized his confusion, segregated all *Olpidiopsis*-like species in which sexuality had not been observed in a new genus *Pseudolpidium*, and confirmed the accounts of Cornu and Reinsch. Since that time sexual reproduction in various species of *Olpidiopsis* has been observed again and again. In 1895 Maurizio described it in *O. major* and reported cytokinesis in the zoosporangia as occurring by cell plate development, although his figure 8 shows conspicuous progressive cleavage furrows. At that time cytokinesis by cell plates had been shown in the pollen mother cells of a large number of plants, and Maurizio was doubtless influenced by these accounts in his interpretation of the process in *Olpidiopsis*. Butler likewise observed sexuality in 1907.

The most intensive cytological study of this genus, however, was made by Barrett in 1912. He illustrated and described infection of the host, its relation and reaction to the presence of the parasite, nuclear and cell division, and fertilization. The nuclei divide mitotically and simultaneously with intranuclear spindles in the developing zoosporangia. As to cell division, Barrett describes it as a simultaneous fragmentation of the protoplasm throughout the sporangia "much as described by Dangeard for the primitive cell of *Synchytrium Taraxaci*." Barrett showed the passage of the contents of multinucleate male gametes into the female thallus through a small opening in the respective walls, and the subsequent development of the zygotic resting spore. He was unable, however, to determine definitely whether the male and female nuclei fuse in pairs or all but one of each degenerate. Similarly he observed neither meiosis nor germination of the resting spores. It is thus obvious that the fundamental problems of fertilization in this genus are yet to be solved in spite of Barrett's excellent contribution.

In 1922 Schwarze studied cleavage in living zoosporangia of *O. Saprolegniae* and found it to occur by progressive cleavage. The more or less centrally placed vacuoles fuse into a large central one, and from the border of the latter cleavage furrows arise which progress outward until they reach and cut through the plasma membrane. As the contents of the central vacuole thus escape, it disappears completely and as a result the cleavage segments contract and become visible. They may then increase considerably in size, presumably by the imbibition of water, press against each other and become polygonal. The original cleavage lines thus become less distinct as furrows, and the whole mass looks as if it had undergone simultaneous division into polyhedral bodies. Following this another contraction stage occurs, and the segments again separate and become distinct. It is doubtless the appearance of the rehydrated and subsequent contraction stages which has led most of the investigators to believe that cleavage is simultaneous throughout.

Diehl's study in 1935 on this species is apparently the latest for the genus, as far as I am aware. He studied only living material and confined his attention primarily to the effect of the parasite on the host. He found, as had all previous workers, a marked enlargement but no division of the hyphae in the region of infection, and the envelopment of the parasite in a dense layer of host protoplasm. The latter accumulates to such an extent around the chytrid thallus that the surrounding area becomes highly vacuolated and ramified by fine cytoplasmic strands which extend to the primordial utricle, as Barrett has also shown. From the appearance of his figures as well as those of previous workers there is doubtless some increase in the more viscid nitrogenous protoplasm of the host hyphae as the result of infection, but vacuolation seems to play the dominant rôle in enlargement. Neither Reinsch, Fischer, Barrett, nor Diehl shows the effect of the parasite on the host nuclei. That the host cell is stretched, however, is indicated from Diehl's plasmolytic experiments. Diehl also found that sexual reproduction occurs more abundantly at low temperatures, and that the male and female thalli may often be of the same size at the time of fusion. Furthermore, several male thalli may fuse with one female as Reinsch, Maurizio, and Barrett have also shown.

No intensive cytological study has yet been made of species of *Rozella* and *Woronina*. As noted before, Pringsheim, Cornu, and Fischer described the cytokinesis as occurring directly and simultaneously by the breaking up of the protoplasm into segments which then round up to become the zoospores. In 1890 Dangeard figured and described nuclear division in *Rozella septigina* as amitotic, but contributed nothing to our knowledge of cytokinesis. Cook and Nicholson (1933), on the other hand, describe the thallus of *W. polycystis* as becoming furrowed, and in these grooves is laid down cellulin, which thus divides the so-called plasmodium into a number of sporangia. Later the contents of these sporangia divide up into zoospores; but Cook and Nicholson say nothing as to whether it occurs by simultaneous or progressive cleavage. Their contribution is none the less noteworthy in showing that the two cilia are attached apically rather than laterally. Most students of these genera describe the young thallus as being entirely naked or devoid of a membrane and so enveloped by the host protoplasm that the two are almost indistinguishable in the living condition. If these accounts are correct the association between host and parasite is very intimate and without any marked visible evidence of antagonism in the early stages. However, that the two protoplasts are immiscible is hardly to be doubted. None of the studies show the ultimate effect on the host nuclei and cytoplasm, although Cook and Nicholson maintain that *W. polycystis* feeds on and thus extracts the oil globules from the cytoplasm. The most conspicuous effect of these parasites is the enlargement of the host cell, but it is impossible to determine from the figures in the literature whether this is primarily due to vacuolation or an increase in the number of nuclei and the amount of dense viscid cytoplasm. The host hyphae are also stimulated to divide transversely, which suggests an attempt on their part to limit the spread of the parasite. No sexual reproduction has so far been described for these genera.

The genera *Eurychasma*, *Sirolpidium*, *Pontisma*, *Ectrogella*, *Aphanomycopsis*, *Pseudosphaerita*, *Petersenia*, and *Blastulidiopsis* must doubtless be transferred from the Olpidiaceae to this family on the basis of the discovery by Scherffel (1925), Sigot (1931), Dangeard (1933) and Sparrow (1934) that their zoospores are biciliate. The limits of these genera are not well established and defined, and some of them will perhaps with further study be merged. In fact Scherffel, Sparrow (1933) and others regard *Ectrogella*, *Eurychasma*, and *Aphanomycopsis* as primitive or reduced members of the family Saprolegniaceae. However, for the sake of convenience in this discussion they will be retained here and treated as valid and separate genera. Lowenthal (1905b) studied *Eurychasma Dicksonii* cytologically but figured neither nuclear nor cell division. As relating possibly to the latter he shows the mature thallus as consisting of a large central vacuole and a relatively thin peripheral scalloped layer in which the nuclei lie. This layer becomes more and more scalloped on the inner periphery, and finally the zoospores are formed simultaneously and directly. In the same year Petersen studied the development of the sporangia of the same species, and listed four stages of development which he believes are characteristic not only for this species but for the Chytridiales in general: (1) *Stade protoplasmique ordinaire* in which the protoplasm is very dense, comparatively non-vacuolate, and the nuclei are dividing; (2) *Stade globuleux* in which nuclear division has been completed and the sporangium is filled with numerous, closely pressed, spherical globules; (3) *Stade écumeux* when the protoplasm is filled with numerous large vacuoles separated only by thin cytoplasmic bridges in which the nuclei lie, as well as in the peripheral layer; and finally, a fourth stage in which the zoospores lie peripherally disposed inside of the sporangial wall. In the transition from the third stage he noted a brief marked contraction of the protoplasm which is immediately followed by an expansion as the vacuoles disappear and the zoospore initials become visible. After the latter have been fully formed they become violently active for a short time, and then come to rest and encyst; so that the interior of the zoosporangium presents the appearance of a reticulum of polygonal segments. Sparrow (1934), on the other hand, believes that the encysted stage is the result of adverse conditions and that ordinarily the zoospores escape directly and at once. In any event the encysted zoospores germinate by escaping from their cysts in the same manner as *Achlya* and other Oomycetes. Scherffel maintains that the method of zoosporogenesis described by Lowenthal and Petersen is not characteristic of true chytrids, and hence *Eurychasma* should be removed to the Saprolegniaceae. Petersen's claim that the developmental stages which he enumerated are characteristic for the Chytridiales as a whole is certainly open to question, since his conclusions are based entirely on the study of living material. In such material, according to the author's experience, it is practically impossible to determine at what stages nuclear division is occurring. Furthermore, the peripheral disposition of the nuclei and the subsequent cleavage segments is characteristic only of such forms as have highly vacuolate zoosporangia.

The young parasite is described as naked and occupying a position adjacent to the host nucleus when young, but becoming invested with a definite membrane at maturity. The host cell becomes somewhat enlarged as Wright (1879), Rattray (1885), Wille (1899), and Magnus (1905) had previously shown, but the cytoplasm, plastids, and nucleus are not markedly distorted or injured until the parasite matures, according to Lowenthal. Pierre Dangeard and Sparrow (1934), on the other hand, describe the host cell as enlarging very shortly after infection, while the plastids soon become discolored and integrated and thus form a residual layer around the parasite.

In *Pseudosphaerita Euglenae* Dangeard (1933) describes a type of cytokinesis that is most unusual for the Chytridiales. The division of the initial nucleus is followed at once by bipartition of the thallus, and as the two resultant daughter nuclei divide the thallus undergoes division into four cells, etc. Cytokinesis thus immediately follows each division of the nuclei until the thallus or zoosporangium is divided into a large number of polygonal zoospore segments. Dangeard shows no nuclear division figures and consequently nothing of the relation of the spindle to the formation of the cell boundaries. Hence, it is not evident from his description and figures whether cytokinesis occurs by constriction, furrowing, or cell plate formation. The time relations of mitosis and cytokinesis in this species is the same as in the meristematic tissues of higher plants, and consequently entirely different from that of all other chytrids.

In *Sirolpidium*, according to Sparrow, the elongated thallus fragments into a number of bodies which separate and become isolated zoosporangia and eventually form zoospores, but he gives no description as to how this process occurs. Similarly nothing is known of cytokinesis and nuclear division in *Pontisma* and *Petersenia*. In *Ectrogella bacillariaracearum* and other species of this genus, however, Scherffel (1925) has figured in detail the manner of origin of the zoospores. Vacuoles are more or less evenly distributed in the protoplasm at first, but as the thallus enlarges they aggregate to form a central row, as Zopf had earlier shown, and at maturity fuse into a single elongated and irregular central vacuole. From its border then develop furrows which progress outward and eventually reach the periphery. The central vacuole disappears, and shortly thereafter the cleavage segments swell to fill the entire thallus so that the lines of demarcation become less distinct and conspicuous. Scherffel is very sparing in the description of his figures and does not at any time refer to the process as progressive cleavage. It is to be noted that his figures are fundamentally similar to those of Schwarze for *Olpidiopsis Saprolegniae*, but he is apparently unaware of this paper. Scherffel stresses at length his view, as in the case of *Eurychasma Dicksonii*, that this mode of cytokinesis or zoospore formation is not characteristic of true chytrids but principally of the Saprolegniaceae, and is accordingly a criterion of relationship. He thus obviously avoids reference to the studies of Harper, Swingle, and Schwarze who have shown that progressive cleavage, whether centripetal or centrifugal, is not characteristic for a particular group but is the universal method of cytokinesis in the sporangia of the Mycetozoa, Chytridiales, Oomycetes, and Zygomycetes in general. The particular point which Scherffel is trying to stress, although he does not seem to be clearly aware of it, in my opinion, is not that cleavage is not progressive in the Woroninaceae and Saprolegniaceae but primarily centrifugal in direction because of the presence of a large central vacuole. Scherffel also figures many stages of what is undoubtedly progressive cleavage in *Aphanomycopsis*, but he does not describe them as such.

The species of *Ectrogella*, *Sirolpidium*, *Pontisma*, and *Petersenia* cause no enlargement or distortion of the host cell according to the figures of

Zopf, Scherffel, de Bruyne (1890), Petersen, and Sparrow. Zopf and de Bruyne show the host protoplasm closely aggregated around the parasites and undergoing discoloration and degeneration, but nothing further of a specific nature is known. In the early stages the parasites seem to be fairly naked, but there is no universal agreement on this point. In this group of genera sexual reproduction has been described for *E. Licmophorae* only, and according to Scherffel it is essentially similar to that of *Olpidiopsis Saprolegniae.*

Sigot's study of *Blastulidiopsis* while relating to fixed and stained material shows nothing of nuclear and cell division. The mature thallus consists of a large central vacuole, a peripheral layer of cytoplasm in which the nuclei lie, and at maturity, according to Sigot, the cytoplasm around each nucleus rounds up simultaneously to form the zoospores which then move into the central vacuole and become very active. As to host-parasite relationship, he figures *B. Chattoni* as lying in a clear space or cavity of the *Cyclops* egg and not immediately enveloped by the host protoplasm. This clear space may possibly be a digestion cavity, as in the case of plants parasitized by members of the Erysiphaceae, into which ferments flow and digest the host protoplasm. On the other hand, it may be nothing more than the result of shrinkage from fixation.

The genus *Pseudolpidium* as recognized at the present time has been studied only in the living condition, and as a consequence little or nothing specific is known about nuclear and cell division. Sexual reproduction has never been observed. Butler followed the maturation of the zoosporangia in several species but does not describe cytokinesis, while Cornu and Fischer, as noted before, figure vacuolated zoosporangia and report the formation of zoospores as occurring directly. The effect of the parasite on the host hyphae is quite marked. They enlarge and become more or less vesicular as when parasitized with *Olpidiopsis*, *Rozella*, and *Woronina*, and may be stimulated to divide transversely. According to the descriptions of Cornu, Fischer, and Butler, the relation between the young parasite and the host protoplasm is apparently very similar to that of these genera and equally as little known or understood.

In the genus *Pythiella*, parasitic on *Pythium*, Couch (1935) has given an excellent illustrated account of cytokinesis and sexual reproduction from a study of living material, but he contributes nothing about nuclear division and the behavior of the gamete nuclei during fusion. Cell division in the zoosporangia is progressive and centrifugal from the border of a large central vacuole, as Schwarze has described it in *Olpidiopsis Saprolegniae.* The zoospores are somewhat reniform in shape with two laterally attached cilia. After escaping from the zoosporangium they lie quiescent at the mouth of the exit tube for some time and then germinate in the same fashion as in *Achlya*. Sexual reproduction consists of the fusion of a small male and a large female thallus through a short conjugation tube or canal. More than one male thallus or gamete (fig. 25) may fuse with the female thallus as in *O. Saprolegniae*. After fertilization the zygote rounds up and becomes invested with a comparatively thick wall. As to its effect on the host, *Pythiella* causes conspicuous hypertrophy of the *Pythium* hyphae in the region of infection, but no transverse septation, according to Couch.

This résumé shows that nuclear division has been well figured and described in only one genus; cytokinesis in five, and sexual reproduction in three genera. The majority of species cause marked enlargement of the host cell, but the cytological changes involved and the details of hypertrophy as well as the intimate relation of the parasites and host protoplasm are but imperfectly known.

OLPIDIACEAE

The members of this family have not been studied as intensively as those of the Synchytriaceae, although the number of genera is considerably greater. None the less, the same degree of uncertainty and conflict of opinion as to methods of nuclear and cell division occurs in the literature, and the accounts of sexual reproduction are equally diverse. In 1878 Woronin postulated on the basis of Cornu's (1872) and Nowakowski's (1877b) demonstrations of sexuality in *Olpidiopsis* and *Polyphagus* that the resting spores of *Olpidium Brassicae* arise from the fusion of motile isogametes, and six years later Fisch (1884) reported it to occur in *Reessia amoeboides*, which is perhaps a species of *Olpidium*. Fisch also described fusion of unequal thalli to form the resting spores in what has since been recognized as *Pseudolpidiopsis parasitica*. In the same year Zopf described and figured fusion of small male and large female thalli to form resting sporangia in *Pseudolpidiopsis Schenkiana*.

This type of sexual reproduction was confirmed by Fischer in 1892 and Wildeman in 1895 for other species of the same genus, and since that time has been observed again and again (Butler, 1907; Tokunagu, 1933). Very little was contributed to the cytology of the strictly olpidiaceous species of this family, however, until 1910, when Griggs described a new species, *Monochytrium stevensianum* in which the young uninucleate thalli fuse within the host cell to form binucleate, thick-walled resting spores. Although this is doubtless a species of *Olpidium* the present binomial will be retained in this discussion. Fusion of the gametic nuclei is apparently delayed until shortly before germination, although it was not observed by Griggs. The thalli which do not fuse develop into thin-walled evanescent zoosporangia. During the early growth of such thalli the primary nucleus fragments by constriction into four daughter nuclei, but no further multiplication occurs until the incipient zoosporangia have attained almost mature size. Then, according to Griggs, follows a period of rapid amitosis, although he is not certain that this is the universal method of nuclear division. Nothing is said or known as to the mode of cell division. The parasite causes only slight hypertrophy of host cell, does not injure it perceptibly for a long time, and lives to some extent in a mutualistic relationship with its host, according to Griggs. In the following year Němec (1911) reported a new species, *Olpidium Salicorniae*, with both evanescent zoosporangia and smooth thick-walled resting spores. In the former the nuclei were found to divide mitotically and simultaneously. The resting spores were either uni- or binucleate, and in the former cases the nuclei always appeared peculiarly constricted, like two nuclei in the process of fusion. From such appearances Němec postulated the possibility that the resting spores are formed by the fusion of two small naked uninucleate thalli in the host cell, as in *M. stevensianum*, and that the binucleate character and constricted nuclei of the resting spore might be stages in nuclear fusion. During the next year Němec (1912) also reported and figured regular mitosis of the nuclei and progressive cleavage in the evanescent zoosporangia of *O. Brassicae*. The cleavage grooves or furrows usually begin at the periphery and progress inwards, but if the zoosporangium has a large central vacuole centrifugal furrows may also form.

At the same time Kusano (1912) published an extensive account on the cytology of a new species, *O. Viciae*, in which he reports the fusion of motile isogametes to form binucleate motile zygotes which infect the host cell and develop into smooth, thick-walled resting spores. Karyogamy or nuclear fusion, however, does not occur until the spores begin to germinate. In the growth and maturation of the resting spore the gamete nuclei undergo remarkable changes, according to Kusano. The nucleole migrates to the outside of the nuclear membrane, and the nucleus then buds at the tip of the nucleole. This bud gradually increases in size and attains almost the same form, volume, and appearance of the main body, forming thus a dumbell-shaped structure with the nucleole between. The membrane of the bud then disintegrates, and the contents pass into the central vacuole of the spore. Kusano regards this budding as an unusual type of amitosis, since in the process the median nucleole is divided into two halves, one going into the bud and the other returning to the mother nucleus. However, the subsequent degeneration of the bud indicates that this is only a peculiar type of nuclear extrusion. The first stage of germination of the resting spore is initiated by the conjugation of the gamete nuclei. The diploid fusion nucleus then divides, but Kusano was unable to determine conclusively whether or not the first division is indirect and meiotic. He figures two metaphase spindles of the daughter nuclei, but failed to find any others and is therefore uncertain as to the universal mode of division. The zoospores which fail to fuse infect the host and form zoosporangia. During this development the nuclei multiply by an unusual type of amitosis in which the nuclear membrane breaks down and the chromatin granules as such disappear. New nuclei are then formed, which subsequently divide mitotically, as is well shown in his figures. In *O. Viciae*, thus, mitosis follows amitosis in the development of the zoosporangium. Kusano is quite ambiguous as to the method of cell division, but states definitely that it is not progressive cleavage. "Clear spaces appear in the cytoplasm all at once between each two nuclei, cutting off the cytoplasm in as many polygonal parts as the nuclei." In 1922 Němec described fusion of motile isogametes in *O. Brassicae*, confirming thus Woronin's assumption that the resting spores in this species are formed sexually. In the same year Sawada (1922) likewise reported the same type of sexual reproduction in *O. Bothriospermi*. In 1927 Guyot published a lengthy account on the systematic position, host range structure and development of *Asterocystis radicis* but contributed nothing of significance cytologically.

Schwartz and Cook (1928) reported a new species, *O. radicale*, in which the zoospores become motile again after entering the host cell. Later on fusion between small and large thalli, which are designated as antheridia and oogonia, occurs, which is followed by immediate karyogamy and the development of a thick wall around the zygote or resting sporangium. Although they did not actually observe the processes, they none the less describe the fusion nucleus as first dividing meiotically and later homeotypically a great number of times to form a large multinucleate zoosporangium. The thalli which fail to fuse develop into thin-walled evanescent zoosporangia. Cell division or zoospore delimitation in both types of sporangia occurs by vacuolation of the cytoplasm, according to their description. It is to be particularly noted that their observations were not made from fixed and sectioned material but only from mounts stained in toto. They failed to observe conclusive cases of cell fusion, karyogamy, and meiosis, and although they figure a few mitoses they are not certain but that amitosis may also occur. Their whole account of the life history and cytology of this species is woefully uncertain as to the critical stages, and seems to be largely a description by analogy to bring it in line with those of other observers.

In 1929 Kusano described the life history of *O. Trifolii* in which he found copulation of motile isogametes to form resting sporangia as in

O. Viciae. Fusion occurs only between gametes from different zoosporangia. In this species Kusano contributes nothing to our knowledge of nuclear and cell division. In 1931 de Wildeman described a new species, *O. Stigeoclonii* which causes marked hypertrophy of the infected *Stigeoclonium* cells. They may become five and seven times their normal diameter and length respectively and are more or less completely filled by the chytrid zoosporangia. The presence of the parasite, however, does not stimulate them to division as has been noted above in cases of infection by *Synchytrium.* The young parasite takes up a central position in the cell adjacent to and partly surrounded by the band-shaped chloroplast, and as it enlarges the latter is compressed and flattened against the cell wall. The plastid is not particularly injured at first and does not become disorganized until after the parasite has matured, according to de Wildeman. Cytokinesis or the formation of the zoospores is quite unique and so unlike that of other species that one is inclined to regard it as abnormal. The protoplasm of the zoosporangium oozes out of the neck, and successively from this mass individual rounded globules separate or are pinched off one by one. Cilia may develop while the globules are still attached to central mass, but they are lost almost at once so that the zoospores never swim about actively. Movement is accordingly only amoeboid.

Miss Sampson recorded a new species, *O. Agrostidis,* in 1932, and followed carefully its developmental stages in the host cell. No fusion of gametes was observed, but since the resting spores are invariably binucleate until maturity she believes they originate by copulation of zoospores. Nothing is reported on the type of nuclear and cell division, although Miss Sampson gives a number of figures of fixed and stained thalli. The latest contribution to the cytology of the *Olpidium,* as far as I am aware, is by Cook and Collins in 1935 on *O. majus.* They reported fusion of thalli in the root hairs of cucumber to form diploid resting spores as in *O. radicale.* They did not, however, actually observe the process of fusion, but only figured resting spores with a smaller empty thallus attached, which is interpreted as the male gamete. No nuclear fusion was seen, but karyogamy apparently occurs at once, since no binucleate spores were found. Neither was nuclear division observed. Cook and Collins described cleavage furrows which delimit the zoospores, but it is not obvious from either their drawings or account whether the furrows occur simultaneously throughout or develop progressively.

In another genus, *Cystochytrium,* whose taxonomic position and relationship with the chytrids is still obscure but which nevertheless resembles *Olpidium* to some degree, Cook (1929, 1932) described and illustrated clearly defined simultaneous mitotic figures in the equatorial or metaphase stage. No other stages were observed, and nothing further is known regarding cytokinesis, host-parasite relationship, and sexual reproduction.

In *Pleolpidium*, *Septolpidium*, *Pleotrachelus*, *Plasmophagus*, *Sphaerita*, and *Nucleophaga* nothing is known of nuclear division, and the fragmentary accounts of cytokinesis are based primarily on living material. The young protoplast of *Pleolpidium*, according to Cornu, Fischer, Butler and others lies more or less naked in the host hyphae and completely surrounded by but immiscible with their protoplasm. As it grows in size the host hyphae and sporangia enlarge and eventually become vesicular in the region of infection, but with the exception of parasitism by *P. irregulare* (Butler, 1907) the former are not stimulated to divide, according to the descriptions in the literature. At maturity the parasite completely fills the host vesicle or gall, and its wall or membrane is reported to fuse with or become so closely appressed to the host wall that the two are indistinguishable. None of the species have been studied cytologically from fixed and stained material, so that the exact relation of the host and parasite walls as well as the nuclei and cytoplasm is yet unknown. No sexuality has yet been described in this genus, but according to Butler a number of protoplasts from separate and individual zoospore infections may fuse inside of the host and form a plasmodium. He does not, however, state whether or not any nuclear union results from such fusion. In *Septolpidium* the division of the elongated thallus into a linear series of zoosporangia is progressive and centripetal, according to Sparrow (1936b), while the zoospores are delimited by progressive cleavage.

It is doubtless questionable whether all species of the genus *Pleotrachelus* should be included here in light of Petersen's (1905) and Sparrow's (1936b) observations that the zoospores of *P. Andreei* are biciliate. Since this character has been found in only one species, *P. Andreei* should perhaps be removed from the genus as Sparrow has recently done. *Pleotrachelus fulgens* on *Pilobolus* has much the same effect as *Pleopidium*, *Olpidiopsis*, and *Pseudolpidium* on the host cells. The infected host hyphae and sporangia enlarge and become somewhat vesicular and may occasionally be delimited by cross septa, according to Zopf's figures. It is not obvious, however, whether the enlargement is accompanied by an increment of host protoplasm or by marked vacuolation. At any rate the host protoplasm becomes conspicuously discolored and may change to yellow and intensely orange or golden red with the growth and development of the parasite. In the other species of *Pleotrachelus* described by de Wildeman (1893), Petersen (1905), Lund (1930) and Sparrow (1934), hypertrophy of the host cell may be very slight or lacking entirely, according to the reports. In a species closely similar to *P. Andreei* Sparrow found small companion cells or thalli attached to the developing and mature resting spores, and although he did not see actual fusion he believes the latter are formed as the result of fertilization.

The genus *Plasmophagus* has been even less studied than the two preceding ones and contains only a single species, *P. Oedogoniorum*, which was first reported by de Wildeman in 1895. He described it as almost completely filling the *Oedogonium* cells at maturity and being to a certain degree indistinguishable from the host protoplasm. Its walls, however, always remain distinct from those of the host. According to de Wildeman the nuclei of the host cell may continue to divide for some time, but cell division is inhibited. As a result greatly elongated and multinucleate cells are formed, and in *Tribonema* these may enlarge to almost twice their normal diameter, according to Sparrow (1933). The host protoplasm is almost completely consumed by the parasite at maturity and may occasionally form a thin discolored disintegrating residual layer around the periphery. Neither de Wildeman nor Sparrow contributes anything to our knowledge of nuclear and cell division of the parasite.

The genus *Sphaerita* has been recorded rather extensively, particularly by protozoologists, since its discovery by Dangeard in 1886, but in spite of this we know very little as to the cytology of its critical stages. While a large number of these studies (Chatton and Brodsky, 1909; Dobell, 1919; Dobell and O'Connor, 1921; Cunha and Muniz, 1923; Kessel, 1924a and b; Brumpt, 1926; Becker, 1926; Li-Yuan-Po, 1928; Jirovec, 1933; Crouch, 1933; Brumpt and Lavier, 1935) relate to fixed and stained preparations they nevertheless fail to show anything significant about the processes of nuclear and cell division. These studies have been primarily concerned with the cytology of the host, and their discourses on *Sphaerita* and *Nucleophaga* relate only indirectly to isolated stages of development which occurred sporadically in their material. Dangeard (1886, 1889, 1895) described cytokinesis in *S. endogena* as a simultaneous breaking up or fragmentation of the protoplasm in the zoosporangia into polyhedral segments, and in 1889 showed stages in the fusion of uniciliate zoospores to form biciliate zygotes (fig. 8, pl. 3). He was not certain, however, that resting spores always result from such fusion, and finally in 1933 after describing the biciliate character of the zoospores of *Pseudosphaerita* he raised the question whether the zygote previously described for *Sphaerita* may be nothing but the zoospores of the other genus. In the same species apparently, Nägler (1911) describes the nucleus as undergoing constriction and promitosis, and later fragmentation, while his account of cytokinesis and zoospore formation is very confusing and difficult to interpret in light of Dangeard's description. Chatton and Brodsky failed to observe zoospore fusion in a species of *Sphaerita* which they found in *Amoeba limax*, but nevertheless believe it occurs in this form also and is general for the whole genus. As to cell division, they describe the cytoplasm as condensing around the nuclei and secreting a thin spore membrane. Penard (1912), on the other hand, while studying the same species apparently saw what he claims to be conjugation of quiescent (fig. 33) swarmspores. In *S. endamoeba* Becker describes and figures the nuclei as deeply staining bodies lacking membranes or any other structural differentiation, which divide more or less simultaneously in bipartite fashion without any evidence of spindle figures. When the sporangia are mature the nuclei enlarge somewhat, stain less intensely, develop membranes, and become the zoospores directly. This account of Becker is quite unlike that of any previous and subsequent investigator, and it is not improbable that his unusual description is based on poorly fixed and stained material. Crouch on the other hand, describes and figures the thallus of *S. trichomonadis* as undergoing more or less regular and simultaneous bipartition to form the spores, while the nucleus is represented as a small black dot surrounded by a clear space.

The relation between *Sphaerita* and its host is rather unusual in many respects, since the parasite does not kill the active host cell until quite late. *Sphaerita endogena* in *Euglena* may often reach maturity, according to Dangeard (1895) and produce zoospores before any marked effect is visible in the host cell, and in many cases the *Euglena* may return to normal appearance and activity after the parasite has been expelled. Puymaly (1927), however, denies this and maintains that the ciliary motion of *Euglena* almost always ceases after infection, but spasmodic action may continue until the zoospores of the parasite are liberated. He furthermore describes the zoospores as biciliate with a long posterior and a shorter anterior cilium, and fails to confirm Dangeard's account of fusion. In light of the fact that *Pseudosphaerita* parasitizes the same host and has biciliate zoospores, according to Dangeard (1933), it is not improbable that Puymaly may have confused this organism with *Sphaerita*. Sometimes the hosts encyst and thus inhibit the development of the sporangia. Usually, however, the host nucleus becomes spongy, the chromatin condenses, the nucleole disappears, the chromatophores turn yellow and disintegrate, while the cytoplasm becomes thinner and less in quantity, and finally the cell bursts. In *Nuclearia* and *Heterophyra* (Dangeard, 1886a and b), on the other hand, *S. endogena* has but little deleterious effect at first, and the host cells may continue to divide so that the parasite is distributed to one of the daughter cells. Later, however, it inhibits division. In the cells of various amoebae, according to Chatton and Brodsky, Mattes

(1924), Becker and Dobell, *Sphaerita* has no marked toxic effect, and injures primarily by encumbering and impoverishing the host. In its young stages the ingested spore is indistinguishable from ordinary food particles lying in the vacuoles, and the membrane around the developing parasite is scarcely perceptible. The amoeboid motion of the host continues unchanged for a considerable length of time, but gradually becomes slower. At the same time the amoeba becomes more spherical in shape with the pseudopods assuming a radial direction. The contractile vacuole continues to function for a long time, but eventually its rhythmic pulsation ceases and it disappears altogether. However, the fundamental structural appearance of the cytoplasm and nucleus is retained for a long time, and the nucleus may often remain intact after the rest of the host has been destroyed. According to Penard the amoebae may often rid themselves of the parasites like extraneous food particles and continue to live normally.

Nucleophaga, a questionable genus which may perhaps be related to *Sphaerita*, was first described by Dangeard in 1895 as a parasite in the nuclei and nucleolus of various rhizopods, and since that time a large number of additional species have been reported by Gruber (1904), Penard (1905), Mercier (1907, 1910), Elpatiewsky (1907), Doflein (1907), Epstein (1922), Brug (1926), Kirby (1927), Lavier (1935a, 1935b), Brumpt and Lavier (1935) and others. According to Dangeard and subsequent workers the parasite enters the nucleus and nucleole and appears first as a small vacuole with a central granule which represents its nucleus. It grows at the expense of the chromatin, karyolymph, and nucleole and soon fills the nuclear cavity, and with subsequent development the nucleus becomes greatly distended and enlarged. In cases where the nucleole is not infected it is shoved aside by the developing parasite and flattened against the nuclear membrane into a crescentic disk. Later it may break up into fragments and disintegrate or be partially consumed. At maturity the entire thallus of the parasite is transformed into zoospores. The manner in which this occurs is as yet little understood in spite of all the studies which have been made. Dangeard describes cytokinesis as taking place simultaneously, but none of the subsequent investigators have contributed anything further on the process. Likewise nothing is known as to the method of nuclear division. Doflein was the first to observe the motility of the zoospores, and described their fusion to form biciliate zygotes. These encyst and later on germinate to form amoeboid thalli. Doflein's account is the only report so far of sexual reproduction in this genus.

As to the effect of *Nucleophaga* on the activity of its host, most investigators are agreed that parasitized amoebae show little if any immediate effect. Dangeard and Gruby in particular report that the host moves about and feeds normally even when the nucleus is enormously distended and filled with parasites. Normal activity may continue for some time after the nucleus has been completely destroyed, but the pseudopodial movement gradually becomes slower and ceases entirely. The amoebae eventually round up, and as the zoosporangia of the parasite open and the zoospores escape the host cell begins to disintegrate. *Nucleophaga* feeds primarily on the chromatin reticulum and nucleole, but according to Dangeard it may also draw nourishment from the cytoplasm outside. In this process the nuclear reticulum is gradually absorbed and disappears as such, while the nucleole may become less basophilic and finally disintegrate into fragments.

Whether *Blastulidium*, *Endoblastidium*, *Coelomycidium*, *Chytridiopsis*, and *Chytridioides* belong in this family or are to be considered as chytrids at all is highly problematical. In the last three decades many protozoologists have tentatively assigned a number of genera and species to this family which do not appear to fit into any groups of the Protozoa. In some respects their development and life histories are similar to *Olpidium*, *Nucleophaga*, and *Sphaerita*, but they are as yet imperfectly known. *Blastulidium paedophthorum* was first described as a parasite of eggs and young embryos of *Daphnia obtusa* by Perez in 1903 and 1905. Its thallus is oval with a thin limiting membrane and a large central vacuole, and at maturity is divided up completely, as in the Olpidiaceae, into polyhedral segments which round up to become spores. Perez does not report any evidence of sexuality nor describe nuclear and cell division, but his figures suggest at least that the latter process occurs by progressive cleavage. He placed this species in the family Haplosporidiidae, but in 1905 Caullery and Mesnil transferred it to the Coelosporidiidae. Finally in 1908 Chatton found the uniciliate zoospores, and on this basis primarily assigned the genus provisionally to the chytrids in the neighborhood of the Olpidiaceae.

Coelomycidium attacks and destroys the proximal adipose tissue of the larvae of *Simulium*, according to Debaisieux (1920), and is strikingly similar to *Olpidium* in vegetative structure and asexual reproduction. Debaisieux was unable to differentiate the successive stages of mitosis in his fixed and stained material of the incipient zoosporangia, but nevertheless describes division as indirect and bipolar and figures numerous nuclei which are undoubtedly in various phases of division. He describes the thallus as a plasmodium and figures a number of stages of progressive cleavage in the formation of the zoospores. No sexual reproduction was observed, and the thick-walled hyaline resting spores which appear in the winter may occur singly or in groups held together by a common membrane. They may be uni- or multinucleate, and the nuclei are described as dividing by bipartition, although Debaisieux found one case of indirect division. From his figures it seems probable that karyokinesis is indirect throughout and that the stages of bipartition are abnormal, as Rytz observed for *Synchytrium*.

Endoblastidium was first described by Codreanu in 1931 as a parasite in the coelomic cavities of larvae of *Baetis Rhodani* and *Rhitogena semicolorata* and bears considerable resemblance to *Coelomycidium* and *Olpidium* in some respects. It is primarily an inhibitory parasite, according to Codreanu, which suppresses the growth and development of the organs, and at maturity is ejected from the anus of the host. In its vegetative stage the thallus is somewhat irregular in shape and plasmodium-like, but becomes oval and surrounded by a fairly thick membrane at maturity. After ejection from the host it is completely divided up into uniciliate oval zoospores which escape through an elongated slit or cleft. Codreanu figures a number of nuclear changes which suggest early prophases of mitosis, but does not describe the manner of cytokinesis or report any evidence of sexuality.

Chytridiopsis, according to Schneider (1884) and Leger and Duboscq (1902, 1909), is a parasite of the intestinal cells of *Blaps mucronata* which causes marked distention of the epithelial cells and leads to the destruction of their cytoplasm and nucleus. The thallus begins as a small uninucleate oval corpuscle in the basal part of the cell which increases rapidly in size and at maturity divides into a large number of spores. In this process the nucleus of the host cell becomes flattened on one side and begins to degenerate, and when zoosporogenesis is complete the degenerated host cell and parasite are expelled from the epithelial layer. The spores are thus liberated into the intestine, become amoeboid, and infect other cells. No flagellated stage has so far been observed. According to Leger and Duboscq certain thalli form amoeboid micro- and macrogametes which fuse to form a zygote. The latter develops into thick-walled resting cysts which are eventually expelled with other excrement from the intestines. Neither of the observers describes nuclear and cell division, and their account of sexuality is rather obscure and unconvincing. Schneider considered this genus as a primitive chytrid, while Caullery and Mesnil, regarded it as a member of the family Haplosporidiidiae. Leger and Duboscq, on the other hand, believe it to be related to primitive mycetozoa resembling the Monadinae. *Chytriodes Schizophylli* is closely similar to *Chytridiopsis socius* according to Tregouboff (1913) and parasitizes the epithelial cells of the middle intestine of *Schizophyllum mediterraneum*. The young thallus is more or less spherical with a single nucleus which is represented by a granule and completely devoid of a membrane. As it increases in size the nuclei multiply, and at maturity it is cut up into uninucleate polyhedral segments, which become amoeboid and are expelled from the sporangium and the infected epithelial cell. No cilia have so far been observed and Tregouboff shows nothing of nuclear and cell division. As to its relation to the host cell, *Ch. Schizophylli* distends the latter considerably and depresses the nucleus to one side. However, no marked changes occur in the nucleus and cytoplasm according to Tregouboff's figures and description. A thick-walled resting spore or cyst is frequently formed, and Tregouboff believes it arises from the union of small and large fusiform gametes, although he did not observe the process of fusion. The young zygote or cyst increases in size, but instead of giving rise to spores directly divides into locules or compartments in a fashion very suggestive of sporange formation in the sorus of *Synchytrium*. Each compartment gives rise to spores, but in the process the partitioning walls are gradually resorbed, so that the mature resting cyst is unilocular and filled with round spores. It is quite obvious from these descriptions of Schneider, Leger and Duboscq and Tregouboff that *Chytridiopsis* and *Chytridioides* are very questionable chytrid genera, and in our present state of knowledge they should perhaps be excluded entirely.

From this summary of the literature on the Olpidiaceae it is apparent that no adequate and detailed description of nuclear and cell division has yet been given in any of the numerous species. The nuclei have been described as fragmenting, budding, and dividing both directly and indirectly, and for the latter type only a few isolated equatorial plate stages have been shown. For cytokinesis we find, with only one or two exceptions, scarcely more than the general descriptive terms. "Clear spaces appear in the cytoplasm . . . cutting the cytoplasm into as many polygonal parts as the nuclei"; "whole structure becomes cut up into a large number of uninucleate zoospores"; "contents divide up into a large number of separate areas," etc., without any convincing figures to accompany them.

In no species has meiosis yet been described, although fertilization has been reported in more than half a dozen members of this family. As to the types of sexual reproduction, fusion between motile isogametes has been reported in five species, and copulation of small male and larger female thalli or so-called antheridia and oogonia has been described for four additional members, excluding *Chytridiopsis* and *Chytridioides*. In all of these cases the gametes are uninucleate at the time of fusion. Sexual reproduction in *Pseudolpidiopsis Schenkiana* and other species of this genus, however, is identical with that of *Olpidiopsis Saprolegniae* of the family Woroninaceae in which the gametes are multinucleate, but no cytological study has yet been made to determine whether or not it is similar in this latter respect also and that the gametic nuclei fuse in pairs. Karyogamy may immediately follow plasmogamy, but in the majority of described species it is delayed until germination of the zygote or resting spore.

The host-parasite relationship in this family has not been studied as intensively as in the Synchytriaceae, with the exception perhaps of *Sphaerita* and *Nucleophaga*, but it is apparent from the literature that the reaction of the host in the majority of cases is not as marked as in the latter family. In most species which have been studied cytologically the host cells and cell organs have been reported to enlarge to several times their natural size, particularly if young at the time of infection, and the adjacent healthy cells become greatly compressed, distorted, and elongated. The mass enlargement of an infected region is thus due primarily to hypertrophy of the parasitized cells. However, the production of galls is not nearly as pronounced as in the Synchytriaceae. Furthermore, the host nuclei are not conspicuously enlarged, distorted, nor do they become reticulated and furrowed. No nucleolar growth and fragmentation has been described as the result of parasitism. In *Monochytrium stevensianum*, according to Griggs, the host nucleus retains its finer structure and staining reaction until the cell is killed, and the relation between host and parasite appears to be somewhat mutualistic. In *Olpidium Viciae* and *O. Trifolii* Kusano reports the host nucleus as becoming only slightly enlarged or compressed, while the increased cytoplasm is scarcely perceptible. In *O. Sphacellarum*, according to Sparrow (1936) the young thallus attaches itself to the nucleus of the host cell, and in the lateral branches of *Sphacelaria* causes pronounced swelling of the infected region. Similar swellings or hypertrophy of the infected host cells has been reported by de Wildeman (1895) for *Pseudolpidiopsis Zopfii* and *P. fibrillosa*. It is not certain, however, that these species belong in the genus *Pseudolpidiopsis*, since the zoospores and the number of cilia which they bear have never been observed.

In *Olpidium Salicorniae* Němec has described and figured marked hypertrophy of the infected host cells also. Furthermore, as the germ tube penetrates the host wall, the latter develops internal cellulose excresences or caps which envelop it and may become elongated into tubular canals which traverse the lumen of the cell. These excrescences are quite similar to those described by Scherffel for algal cells parasitized by rhizidiaceous species, and their formation is apparently a reaction on the part of the host which prevents the entry and spread of the parasites. Cellulose caps of a similar nature but reduced in size have also been described by Griggs for *M. stevensianum*.

RHIZIDIACEAE

This family contains without doubt the largest number of genera and species, and is the second of the chytrid families in which indisputable sexuality was first observed. In 1877 (b) and 1878 Nowakowski described in detail the life history and development of *Polyphagus Euglenae* and *P. parasiticus* and showed that the spiny and smooth-walled resting sporangia are formed by the conjugation of male and female thalli of unequal size. The smaller or male thallus sends out a long conjugation tube which comes in contact with the larger female thallus, and a zygospore is formed at the tip of this fusion canal. Very little further was contributed to the cytology of this family until 1898 and 1899, when Wager gave a short preliminary account of the structure and behavior of the nuclei in resting spore formation in *P. Euglenae.* The male nucleus and cytoplasm enter the incipient zygospore or swelling first, and are then followed by the female protoplast. The former is at first smaller and less chromatic, but with continued growth of the zygospore it gradually attains the same size and appearance as the female nucleus. Karyogamy is delayed until germination. The zygospore forms a tubular vesicle or sporangium into which both gamete nuclei migrate and finally fuse. In the next year Dangeard (1900) published an extended cytological account of the same species in which he showed that the nuclei of the zoosporangia divide mitotically and simultaneously but without centrosomes or astral radiations. The division spindle is completely intranuclear, and after karyokinesis is completed the sporangium is cut up into polyhedral segments simultaneously. He confirmed in general Wager's description as to nuclear behavior during fertilization, but maintained that the female nucleus was the first to enter the incipient zygospore.

Finally in 1913 Wager gave his completed report on the cytology of *P. Euglenae.* Nuclear division in both zoosporangia is mitotic and simultaneous with intra-nuclear spindles. Wager describes the structure of the resting nucleus and the later stages of mitosis but contributes very little to our knowledge of the prophases. No evidence of centrosomes was observed in the prophases, but after the spindles have been fully formed, they push through the nuclear membrane at the poles, and polar radiations then appear in the cytoplasm. His account of cell division in the sporangia is not particularly elucidating as to the exact manner by which it occurs, but from his figures together with the description given it appears to be identical to the process of progressive cleavage as described by Harper for *Synchytrium decipiens.* The two gametic nuclei in the young zygote begin to extrude two large separate masses of chromidia which ultimately fuse in the cytoplasm. In this process the nuclei become quite small, and Wager describes them accordingly as generative nuclei. As the zoosporangium is formed in germination they pass out of the spore and fuse likewise. Thus, according to Wager, double fusion occurs in *P. Euglenae*—chromidial fusion in the spore and nuclear fusion in the sporangium. The nucleus is thus regarded as having a dual character: the chromidia represent the trophic or somatic element and the small nuclei the hereditary or generative element. Wager thus adopts Hertwig's, Schaudinn's and Goldschmidt's "chromidial hypothesis" to explain the peculiar behavior of the nuclei in the germination of the zygospore of *Polyphagus Euglenae.* In 1925 Scherffel confirmed the observations of Nowakowski (1878) on *P. parasiticus* as to its development and sexuality, but contributed no further cytological details.

According to Nowakowski, Fisch (1884), Dangeard (1900) and Scherffel the prosporangium may encyst and develop into a resting spore without fusion. Such spores, according to Dangeard, may be readily distinguished from the zygote by their uninucleate character, thin, single-layered wall, and fewer, minute refractive globules. He and Scherffel regard this as parthogenetic development. The latter has also figured smaller spiny spores which appear as if they were the encysted prosporangia of the small so-called male thalli. If such thalli are definitely male it is obvious that the small spores have been formed androgenetically.

Fisch has cast considerable doubt on the sexuality of the resting spores by the observations that in rich cultures of *Polyphagus* numerous thalli may anastomose and form an intricate network with numerous spores between them. He believes that fusion between two thalli is either fortuitous and accidental or a means of nourishing and rejuvenating a small weak thallus which is incapable of independent existence. Zopf (1890, p. 561) takes the same viewpoint. This conception, however, was formed before anything was known concerning the behavior of the nuclei in fusing thalli.

In the meantime Lowenthal (1905) had described a new Chytridium-like, operculate species, *Zygorhizidium Willei*, whose sexual reproduction is somewhat similar to that of *P. Euglenae*. Small uninucleate male and larger female thalli or gametangia occur on the same host cell; and the former then develops a lateral, continuous conjugation tube of varying length in the direction of the female, with which it eventually fuses. The uninucleate protoplast of the so-called antheridium migrates through the tube into the larger thallus, and plasmogamy occurs at once. Nuclear fusion apparently does not immediately follow, since Lowenthal has observed binucleate zygotes long after fusion had occurred. In any event a thick wall soon envelops the diploid cell, and the smooth mature resting spore is formed. Both Lowenthal and Scherffel (1925) believe that the female thallus may occasionally encyst and develop into a resting spore parthenogenetically, and it is not improbable that the male thalli may likewise do so. The sexuality of these so-called male and female thalli does not appear too strongly fixed, since if they fail to copulate they may develop directly into vegetative zoosporangia. As to where in the life cycle sex segregation occurs nothing is known. Neither Lowenthal nor Scherffel has determined whether the zoospores which develop into male and female thalli respectively come from the same or different zoosporangia.

Scherffel maintains that *Zygorhizidium* is but a form of *Chytridium* which develops its resting spores sexually and extramatrically. Accordingly he proposes the alternative sub-generic name *Ectochytridium* for it and includes tentatively *Chytridium Confervae* Wille, *Ch. chaetophilum* Scherff., *Ch. Characii* Scherff. and *Ch. Spirotaeniae* Scherff, with it.

Lowenthal describes nuclear division in the zoosporangia as being mitotic, although he did not observe any sharp and well-defined figures. As to cell division, the cytoplasm first clumps or concentrates around the nuclei, and then the whole protoplast breaks up into uninucleate segments.

In 1907 Serbinow described the life history, development, and sexuality of a new completely extramatrical species, *Sporophlyctis rostrata*, which may well be considered in this place, although its taxonomic position and relationship are obscure. Sexual reproduction occurs by the fusion of a small male and a larger female thallus. The smaller attaches to the larger, and the content of the latter migrates through a pore into the former, which then forms a spiny outer wall. Karyogamy follows plasmogamy at once. The thalli which do not fuse develop into evanescent sporangia and form uniciliate but non-motile spores. These are liberated when the sporangium wall breaks and develop into thalli. Serbinov does not figure or describe nuclear division, meiosis or cytokinesis. Petersen established a new rhizidiaceous genus, *Siphonaria*, in 1910 for which he described and figured an unusual type of reproduction. "A rhizoid-like thread from a sporangium fuses with a similar thread from another," forming presumably a conjugation canal through which the content of one sporangium passes completely into the other. The latter then becomes larger and invests itself with a thick, brown, smooth wall. Sparrow confirmed this account of sexual reproduction in *Siphonaria variabilis* in 1935 and extended it to the closely related genus *Rhizoclimatium* also, and in 1936 Ledingham described sexual fusion through the rhizoids of separate thalli in *Rhizophidium graminis*. However, he only observed the intermingling and contact of rhizoids and did not actually see fusion of the two protoplasts.

Ledingham also found fusion of zoospores in this species but he apparently does not believe that this leads to the formation of resting spores. Recently Sparrow (1936c) has presented data to show that the resting sporangia of *Diplophlyctis intestina* are formed as the result of fusion of two thalli by anastomosis of their rhizoids and the migration of the protoplasm of one into the other in the same manner as in *Siphonaria* and *Rhizodosmatium*. Although I have had this species under more or less continual observation for a number of years I am unable at the present time to confirm his report. Minute empty thalli have frequently been found in the vicinity of young developing resting sporangia, but it has been impossible to determine with certainty anastomosis between the rhizoids because of the opacity of the host cell wall. More favorable methods of growing this chytrid must be developed before Sparrow's contention can be conclusively settled. As has been described in a previous paper (1936a) I have frequently found individual thalli bearing micro- and macrozoospores respectively, and there is thus the possibility that *D. intestina* is heterothallic. So far, however, no fusion between the two types of motile cells has been observed, and it is likewise probable that the two thalli represent distinct species.

With the exception of these studies on *Polyphagus*, *Zygorhizidium*, and *Sporophlyctis* very little additional has been contributed to the cytology of this widely diverse group. Němec described and figured a few curious uninucleate, rhizidiaceous and amoeboid thalli of his new species, *Entophlyctis Salicorniae* in 1912, about which there is still considerable doubt. Subsequent papers have dealt primarily with morphological development and occasional records of sexual reproduction. In 1924 Gimesi figured what looks like fusion of motile gametes in *Phlyctidium Eudorinae* which is followed by resting spore development from the zygote. Scherffel (1925) reported and figured the conjugation of male and female thalli in *Chytridium Characii*, *C. Spirotaeniae*, *C. Confervae*, *C. chaetophilum*, *Rhizophidium asterosporium*, *R. parasitans*, *Rhizophidium* sp., *R. goniosporium* and *R. fallax*. In the first two species long conjugation tubes are formed by the male thallus which eventually fuse with the female as in *Z. Willei*. In the other species the female thallus is figured as attached to the host cell, while the motile male gamete fuses with it. It is to be noted, however, that Scherffel does not show the actual fusion and development of the resting spores in all of these species, but merely figures such cysts with small empty adhering vesicles or companion cells which he interprets as having been the male gametes. In *Rhizophidium granulosporium*, on the other hand, the motile male gamete apparently comes to rest and germinates on the host cell, and then fuses with a motile female gamete which becomes attached to it in this sessile condition. In 1932 Couch described "oogonia and antheridia" and their fusion to form resting spores in *Rhizophidium globosum*. In 1933 and 1935 Sparrow reported and figured an unidentified species of *Rhizophidium* in which motile isogametes germinate and infect the host cell side by side, and then develop a definite conjugation canal between them through which the contents of one moves into the other. The latter then grows in size to become the resting spore. Later in 1936 (b) he figured a somewhat similar type of sexual reproduction in *R. goniosporium* but in which the conjugation canal is not evident, confirming thus Scherffel's earlier account. In 1935 Couch described the motile male gamete in *R. ovatum* as germinating on the host cell and subsequently fusing with an active female gamete which becomes attached to it in the same fashion as Scherffel described for *R. granulosum*. The content of the minute male thallus migrates into the female gamete, nuclear fusion occurs, and a diploid resting spore is thus formed on top of the empty male gamete. In *Phlyctidium anatropum* fusion of motile isogametes or zoospores side by side is figured and described, although Couch did not observe and follow their development into zygotes or resting spores. Scherffel's, Couch's, and Sparrow's observations are confined largely to living material or thalli fixed and stained in toto and as a consequence show nothing of nuclear structure, mitosis, and very little of cell division.

In *Rhizophidium Beauchampi*, which may possibly be a species of *Phlyctochytrium* because of the presence of a sub-sporangial swelling or apophysis, Hovasse (1936) has recently shown that nuclear division in the zoosporangia is distinctly mitotic and simultaneous. While he has not described and figured the prophase stages, he nevertheless shows that the division spindle is intranuclear and oriented on two granules or centrosomes which lie inside of the nuclear membrane. He does not, however, describe cytokinesis, but merely states that it is preceded by the appearance of osmiophilic vacuoles at the poles of the nucleus.

In two recent papers (1936a and b) Sparrow has described sporangial proliferation in his new genus and species *Traustochytrium proliferum* and *Rhizophidium simplex*. In the latter species he figures a number of small incipient zoosporangia developing within the old empty ones. In view of what I have frequently observed in other rhizidiaceous chytrids I am inclined to believe that this is nothing but germination *in situ* of trapped zoospores. In *Diplophlyctis, Chytridium, Phlyctochytrium* and *Endochytrium* I have (1936b, 1937a, 1937b) often found zoospores which failed to escape and later germinated in the old sporangium. In numerous cases the germ tubes have grown down into the apophysis and rhizoidal system, and with subsequent development the thalli have attained maturity. If only the later developmental stages of such thalli are observed one may readily get the impression that the old sporangia are proliferating. Secondary and tertiary sporangia within each other, such as I have observed in these genera, have also been described by Raitchenko (1902) in *Rhizophidium sphaerocarpum*. Previous to this time, however, Nowakowski (1877a), Rosen (1887) and de Wildeman (1895a) had reported sporangial proliferation in *Rhizidium mycophilum*, *Phlyctochytrium Zygnematis* and *Rhizidiomyces Spirogyrae*, but their accounts have not been confirmed.

True sporangial proliferation, as it has been described for *Cladochytrium*, *Nowakowskiella* and members of the Saprolegniales, is quite different from this and involves either: (1) the penetration of empty sporangia by a portion of the thallus beneath and its subsequent development into a sporangium itself; or (2) unequal and incomplete cleavage whereby a part of the nucleated protoplasm remains behind and in continuity with the remainder of the thallus and later grows and matures into an organ of reproduction. In the first category it is essential that the mycelium, rhizomycelium or rhizoids apart from the sporangia are nucleated; otherwise no proliferation could occur. As has already been noted elsewhere, however, the meager evidence in the literature on the rhizidiaceous chytrids does not support this assumption. In the few species which have been studied cytologically the nuclei are confined to the zoosporangia and resting spores and do not occur in the rhizoids.

Proliferation of the first type or category appears at present to occur only in polycentric thalli whose nuclei are variously distributed and not localized entirely in the organs of reproduction.

The second type of proliferation, on the other hand, does apparently occur in the Rhizidiaceae, and has been repeatedly described for *Harpochytrium*. While this genus does not appear to be a valid member of the chytrids it has many characteristics in common with them. The protoplasm in the lower part of the sporangium is delimited at the time of zoosporogenesis and remains undifferentiated, while that in the upper two-thirds undergoes cleavage into zoospores. The former subsequently grows and fills up the initial sporangium, and the same process is again duplicated. Gobi (1899), however, disagrees and maintains that this is nothing more than the germination and development of a zoospore which has been kept behind in the sporangium. Dangeard (1903) describes the zoosporangia as sometimes being completely emptied, and later rejuvenated to form additional secondary sporangia. This is obviously impossible when no nucleated protoplasm is left behind in the stalk or flattened holdfast and foot. Proliferation in *Traustochytrium proliferum* is apparently of the *Harpochytrium* type. According to Sparrow a large globular portion of protoplasm in the base of the sporangium remains unchanged, while the remainder undergoes cleavage into zoospores. After these have been carried away it increases in size and becomes transformed into a secondary zoosporangium.

Extensive proliferation of the rare monocentric, rhizidiaceous thalli in *Physoderma maculare*, *P. Zeae-maydis* and *Ph. Menyanthis* has been described by Clinton, and Sparrow (1934), but neither of them indicate of what type it may be. In view of the fact that these thalli have the same organization as the true Rhizidiaceae it is improbable that the rhizoids are nucleated, and hence the proliferation may be similar to that in *Harpochytrium* and *Traustochytrium*. It is quite obvious from this discussion that the whole problem of sporangial proliferation in relation to the rhizoidal system in the Rhizidiaceae needs to be studied from fixed and stained material before any adequate conclusions can be drawn.

At this point we may perhaps best consider the two unusual saprophytic genera *Tetrachytrium* and *Zygochytrium*, described by Sorokin (1874), although there is no good evidence for including them among the Rhizidiaceae. In the latter sexual reproduction occurs by lateral conjugation between branches of the same thallus and appears to be identical in superficial appearances at least to the same process in the Zygomycetes. The thalli are thus homothallic. In *Tetrachytrium*, on the other hand, fusion between uniciliate motile isogametes occurs, forming an active biciliate zygote. The gametes come from the same sporangia and are thus not genotypically differentiated. In neither of these forms has the cytology of sexual reproduction, nuclear division, and meiosis been studied. However, in his figures of *Tetrachytrium*, Sorokin shows that cleavage in the zoosporangia is progressive from the center outwards.

It is thus obvious from this résumé that there are only three accounts of nuclear division of any significance in this large family of chytrids, while cytokinesis has scarcely been studied at all in detail. Sexual reproduction, however, has been reported in almost a score of species and exhibits a variety of differences. In the majority of species, long conjugation canals between the thalli are developed, while in others the content of the adjacent male gamete passes directly into the female through a small opening or pore. In a few species fusion between motile isogametes occurs. The cytological details of fertilization, however, such as nuclear fusion have been described in only three species, and in none of these or any member of this family has reduction division been observed. Consequently, very little conclusive evidence is known regarding the alternation of generations.

The cytology of host-parasite relationship in this family has scarcely been studied at all in fixed and stained material, and then only indirectly. The species such as *Sporophlyctis rostrata* and *Polyphagus Euglenae* which have been investigated cytologically are completely extramatrical, except for the tips of the rhizoids, and polyphagus, and are thus less favorable for the study of this problem. The cytological data on these two forms so far relate primarily to the parasite and not the host. The majority of species in the Rhizidiaceae are quite small, evanescent, and occur chiefly on single algal cells, and it is accordingly difficult to determine the degree of pathogeneity. In many cases it is not certain from the descriptions in the literature whether the pathological conditions of the infected cells are due to the so-called parasite, or that the latter is only capable of attacking dying and dead cells.

There are, however, numerous cases on record where the effect of the parasite on the host is quite marked. In the case of parasitism on green algae the plastids are soon discolored, turn yellowish brown and red and finally degenerate as they become more or less clumped with the remainder of the protoplasm around the rhizoids or haustoria of the parasite. Sometimes marked plasmolysis may accompany such degeneration. Effects of this kind have been reported by Zopf (1887) for *Rhizophidium Sciadii* and *R. Cyclotellae* and *R. agile; Phlyctidium Bumilleriae* (Couch, 1932); *Chytridium perniciosum*, and *Podochytrium lanceolatum* (Sparrow, 1933, 1936) and numerous other workers. *Rhizophidium Sphaerotheca* and *R. pollinis*, according to Zopf (1888) cause a fatty degeneration of the protoplasm of pollen grains. Numerous other changes of a similar nature have been reported.

The reaction of the host cell wall to the presence of the parasite is often quite marked and characteristic. Braun (1855) early noted that the walls of the host cells became thickened when parasitized but he did not regard this as a protective reaction. More recently Scherffel (1925, 1926) has reviewed the literature in relation to this occurrence and shown that a great number of algae when attacked by rhizidiaceous chytrids form cellulose caps or plugs in the region of infection which prevent the entry and spread of the parasite. This is particularly evident in the case of *Chytridium Confervae* and *C. lagenula* on *Tribonema*, and *Rhizophidium fallax* on *Mougeotia*. In the former, as the rhizoids come into contact with the cross walls the host nucleus and cytoplasm become clumped together at that point and build a large conspicuous cellulose plug. Numerous other cases are cited by Scherffel where the host reaction is essentially the same. It appears nonetheless to be rather specific, since one host may react quite differently or not at all to the same or different parasites.

In contrast to the condition in the Synchytriaceae and Olipidiaceae, however, no galls or malformations of the host tissues are produced, nor are the infected and adjacent cells stimulated to divide. *Rhizophidium fungicolum*, for instance, cause enlargement, elongation of *Gloeosporium* cells, according to Zimmermann (1902); while *Zygorhizidium* or *Ectochytridium Willei* may bring about a distinct bending of *Mougeotia* cells in addition to elongation and a slight increase in diameter (Scherffel, 1925). These changes in the host cells do not involve meresis or hyperplasia but only auxesis, cell expansion or enlargement.

CLADOCHYTRIACEAE

The meager cytological data at hand for this family are almost as conflicting as in the Synchytriaceae. The most significant contributions bearing directly on the problems of host-parasite relationship, nuclear and cell division, sexual reproduction, etc., are those of Prunet (1894), Maire and Tison (1911), Bally (1911), Tisdale (1919), Wilson (1915, 1920), Fron and Lasnier (1920), Jones and Dreschler (1920) and Bartlett (1926). Much earlier, however, Schroeter (1889, 1897) and Magnus (1897, 1901) had maintained for several species of *Urophlyctis* that the resting sporangia arose by the fusion of antheridia and oogonia. Fischer (1892) at once pointed out that what had been called the antheridia were nothing but empty vegetative "sammelzellen" such as Nowakowski (1877a) and Büsgen (1887) had shown in *Cladochytrium* and *Physoderma*, and that the so-called oogonium was only another such cell which had developed into a zoosporangium. He was confirmed by Ludi (1901) and Clinton (1902), and we now know that what the earlier students regarded as the conjugation tube in *Urophlyctis* is nothing but the isthmus connecting the resting spore with the turbinate organ cell from which it originated. Prunet, none the less, is inclined to regard the zoosporangia in *Cladochytrium viticolum* as originating from the fusion of adjacent spindle organ cells. Furthermore, in this species he describes the zoospores as being formed by the simultaneous division of the protoplasm into a number of equal masses.

Maire and Tison were the first to study cytologically the development of the thallus of *Urophlyctis Kriegeriana*, and described nuclear division in the turbinate organs and growing sporangia as strictly amitotic. In the latter structures they also observed nuclei of unusual size which degenerate and whose content aggregates in the central vacuole. No evidence of antheridia and oogonia was observed. Bally confirmed their results on this species, and in *U. Rübsaameni* also described nuclear division as amitotic. In addition he observed macro- and micronuclei, occasional fusion between the smaller ones, and nuclear multiplication by heteroschizis and gemmation in the same manner as he, Percival, and Griggs had described in *Synchytrium*. The chromatin granules which are extruded from the nucleole during nuclear gemmation increase in size and gradually undergo hydration in the cytoplasm, and eventually the zoospores are formed around them. Thus as far as nuclear and cell division are concerned, *U. Rübsaameni* shows the same characteristics and aberrations as he had previously described for *S. Taraxaci* and *S. endobioticum*.

Tisdale showed the initial infection stages of *Physoderma Zeae-maydis*, the development of the rhizomycelium in the host cells and the germination of the resting sporangia without giving any particular cytological details of the processes. As to cell division and zoospore formation in the sporangia he merely states that "the granular content of the endosporangium begins rounding up into nuclei or oil droplets," which finally become the central bodies of the zoospores. Wilson's account of the development and cytology of *Urophlyctis Alfalfae* is comparatively unorthodox and unusual to say the least. The mature resting sporangium undergoes progressive cleavage during germination and forms both large and small zoospores which are biciliate, with one flagellum much longer than the other. These heterogamous gametes may fuse to form a motile zygote, or infect the host directly. Both the zygotes and zoospores produce amoebae, and later develop into an extended plasmodium in the host tissue, from which presumably the resting sporangia develop. No evidence of the rhizomycelium was observed. Abundant mitotic figures were seen only in the plasmodial stage. In relation to Wilson's unusual account of *U. Alfalfae* attention is also called to Scott's (1920) description of the germination of the resting spores. Each resting spore forms from one to fifteen zoosporangia which give rise to uniciliate zoospores, and is accordingly to be regarded as a prosporangium, similar in most respects to the same type of structure in *Synchytrium*. In the light of previous and subsequent descriptions of the life history of *Urophlyctis* species, it is highly probable that both Wilson and Scott were dealing with more than one organism.

Jones' and Dreschler's work on the same species appeared a little later in the same year. They showed some early infection stages, the immediate enlargement of the infected host cells, extensive replication of the rhizomycelium, and the development of the resting sporangia. Rapid amitotic division of the nuclei occurs in the turbinate organs, which is then apparently followed by cytokinesis, although nothing was observed as to the mode of this process. The organs thus become multicellular, and from these cells grow out secondary, tertiary, etc., turbinate organs, tenuous filaments and resting sporangia. No nuclei occur in the filaments except in transit, and are confined exclusively to the turbinate organs and sporangia, in the same manner as I have described for *Cl. replicatum*. No nuclear division was observed in the latter structures, but enlarged nuclei which subsequently degenerated into the central vacuole were frequently seen.

Fron and Lasnier confirmed Jones and Dreschler as to amitosis in the turbinate organs, but in *U. Potterii* Bartlett found one typical mitotic figure in a developing turbinate organ. In the genus *Catenaria* Buckley and Clapham (1929) have shown that the resting sporangia are formed by the contraction and retraction of the contents of the zoosporangia and their investment with a thick, smooth, double-contoured wall. Occasional fusion of zoospores has been observed by the author (1934) in a saprophytic species of *Catenaria* and by Miss Ojerholm (1934) in *Physoderma Zeae-maydis*, but it is still questionable whether such fusion occurs universally and is of general significance in resting spore development.

The genera *Hypochytrium* and *Rhizidiocystis* are generally regarded as doubtful chytrids, but they have nevertheless been occasionally grouped with the Cladochytriaceae. Until more is known, however, of their structure and development they must accordingly occupy a dubious position. *Rhizidiocystis* (Sideris, 1929) is a destructive parasite in the root hairs of pineapples, being to some degree responsible for "pineapple wilt." The only distinct characteristic which it has in common with members of this family is the presence of intercalary swellings or "turbinate organs," since, according to Sideris, no zoospores are produced. *Hypochytrium* parasitizes the ascocarps of *Helotium* (Zopf, 1884) and cells of *Hydrodictyon* (Valkanov, 1929). It is likewise characterized by the presence of intercalary swellings, but possesses anteriorly ciliate zoospores. Both of these genera have only been studied in the living condition, and as a consequence nothing is known of nuclear and cell division and the cytological effects of the parasites on the hosts.

This résumé shows clearly the inadequacy and lack of cytological data for the family Cladochytriaceae. Bartlett's lone mitotic figure in a developing turbinate organ is the only one in the literature showing indirect nuclear division in this family, outside of those of Wilson in the dubious plasmodium of *Urophlyctis* and my own in *Cl. replicatum*. The presence of this figure and the abundance of regular mitosis in *Cl. replicatum* convinces me that this will undoubtedly prove to be the normal and universal mode of nuclear division in all species of the Cladochytriaceae when they have been studied intensively, although the reports of Maire and Tison, Bally, and Jones and Dreschler are to the contrary. Cell division in the zoosporangia is generally described as simultaneous when considered at all, and as to the manner in which the turbinate and spindle organs become multicellular nothing is known, except in *Cl. replicatum.* Furthermore, there are no conclusive and indisputable accounts of sexuality.

The reaction of the host to the presence of the parasite is not particularly marked except when infected with species which are commonly assigned to the genus *Urophlyctis.* In fact, such action on the host is regarded by many mycologists as the criterion for separating this genus from *Cladochytrium* and *Physoderma.* While the author does not agree with this distinction fundamentally, it is nevertheless convenient for the purposes of this discussion. Schroeter, Fischer, Magnus, and all of the later students of *Urophlyctis* have described pronounced enlargement of the infected host cells; and when such infections occur close together and spread profusely conspicuous galls are formed. The parasite has a predilection for young meristematic cells, and infection of mature differentiated tissues occurs very seldom if at all. The infected cells do not divide, but those immediately surrounding are stimulated to rapid multiplication. This is particularly true of the vascular strand of infected growing points. As a consequence layers of thin, meristematic, and more or less isodiametric cells are formed by the host, apparently limiting the spread of the disease. These may become infected very shortly, or differentiate into vascular elements. The mature galls may thus be composed of various kinds of cells, and are the combined results of auxesis and meresis, with the latter apparently playing by far the dominant rôle.

As to the effect of the parasite on the host cell walls, nucleus and cytoplasm, there are only a few specific cytological data in the literature. Schroeter and Magnus early noted that in some species the host cell wall became greatly thickened and swollen and finally extensively perforated, somewhat similar to sieve plates, as the rhizomycelium grows through to adjacent cells. In *U. Alfalfae* particularly, Magnus described the walls as being locally absorbed in certain regions, and in others forming conical and coralloid cellulose plugs which extend out into the lumen of the cell. Bally also noted a thickening of the cell walls of *Rumex scutatus* when parasitized by *U. Rübsaameni* but no cellulose plugs. On the other hand, such thickened and swollen walls showed no cellulose but rather a marked pectic reaction with various microchemical tests. Bally is thus of the opinion that the first step in the breakdown of the wall is the secretion of an enzyme by the fungus which dissolves the cellulose and leaves only a pectic residue. However, many years previously Saccardo and Mattirolo (1895) had claimed that the walls of infected cells of alfalfa were typically cellulose in composition, while Lagerheim (1898) maintained that they became lignified. Bartlett supports Lagerheim's contention for *Lotus corniculatus* when parasitized by *U. Potteri*. Jones and Dreschler, on the other hand, noted only a thickening of the wall, but made no tests as to its fundamental composition. Walls of adjacent enlarged cells may be dissolved or absorbed, so that the replicated rhizomycelium may often lie in a multinucleate symplast, according to Bally. The nucleus of the host cell usually enlarges considerably and may become quite irregular in outline. The latter change, however, is not as marked as in the case of cells infected with *Synchytrium*. The increase in size, on the other hand, may not be entirely due to the presence of the parasite, but primarily to an effort to maintain the nucleo-cytoplasmic ratio in the enlarging cell. Magnus, Bally, and Jones and Dreschler, however, believe it is chiefly due to the former. The nucleoli enlarge and multiply, become intensely basophilic, and are the last of the nuclear elements to disintegrate, while the chromatin and linin become more sparse and gradually disappear. Very little definite is known about the effect on the host cytoplasm. None of the students of *Urophlyctis* discuss this problem, but Jones' and Dreschler's figures indicate that it becomes highly vacuolated as the infected cells enlarge.

The majority of species of *Cladochytrium*, *Amoebochytrium*, and *Catenaria* are saprophytic, and for those which are weakly parasitic little or nothing is known about their effect on the host. On the other hand, *Cl. viticolum*, according to Prunet (1894), is a destructive parasite of grape vines and causes definite swellings and spots in the infected regions. It is not certain, however, from his descriptions whether these galls are the result of auxesis or meresis or a combination of both. On the basis of its effect on the host this species will perhaps be transferred to *Physoderma* if Minden's (1911) classification is widely accepted.

The species of *Physoderma* are parasitic and cause only slight enlargement and discoloration of the host tissues, according to Minden's (1911) limitations of the genus. As noted above, they have been studied somewhat extensively from the structural standpoint, but none of these studies have contributed much to our knowledge of the cytology of host-parasite relationship. The contributions of Schroeter, De Bary (1874, 1884), Büsgen, Clinton and Tisdale on various species of this genus are notably lacking in this respect.

SUMMARY

1. The zoospores of *Cladochytrichum replicatum* penetrate the host cell by a small germ tube into which the nucleus migrates. It usually comes to rest near the tip of the tube, and the latter then enlarges in that region and becomes the initial uninucleate spindle organ. One or more tenuous

filaments and rhizoids develop from this organ and pass into adjacent cells. The nucleus divides very shortly, and one and occasionally both daughter nuclei migrate out into these filaments and thus secondary and tertiary spindle organs or "sammelzellen," etc., are established. Accordingly, as this continues the thallus is continually replicated as it spreads in the host tissue and soon becomes polycentric in structure and organization. Its development and replication is thus distinctly homoeotic.

2. Rhizoids are abundantly developed on the tenuous filaments and often from the surface of the spindle organs and zoosporangia and soon run out to fine points and end shortly. They appear to be the primary organs of absorption.

3. The nuclei in mature thalli are localized in distribution and confined to the spindle organs, zoosporangia and resting spores. They may be found in the tenuous filaments only in transit or during migration to establish successively new centers. They are thus not more or less evenly distributed along the entire length of the thallus as appears to be the condition in the mycelium of the higher fungi. Doubtless as a result of such localization of the nuclei in the spindle organs during the growth period, these enlargements become the vegetative centers of thallus replication.

4. The thallus or rhizomycelium of *C. replicatum* at maturity thus consists of rhizoids, tenuous filamentous portions, spindle organs, zoosporangia and resting spores. The so-called tenuous filaments connecting the more or less globular structures vary considerably in diameter and may become quite large under certain conditions. The rhizomycelium possesses many characteristics in common with rhizidiaceous thalli of the family Rhizidiaceae and the mycelium of the higher fungi, and as far as our knowledge of the chytrids goes at the present time appears to stand more or less midway between the two. On one hand it develops numerous enucleate rhizoids, and on the other hand it is polycentric in structure and organization. There is, however, no good evidence at hand to show that it is a transitional evolutionary type of thallus which has evolved from the rhizidiaceous forms and then in turn given rise to a true mycelium.

5. Nuclear division in the spindle organs and zoosporangia is mitotic with well-defined achromatic spindle and chromosomes. The resting nucleus possesses a large nucleole and a faint chromatin reticulum oriented to some degree on the former. During the prophase changes the reticulum becomes denser and more basophilic, but the nucleole does not undergo much change in size, shape, and staining capacity. No conspicuous nucleolar discharges of chromatin have been observed, and at present it is not certain that the large nucleole is to be regarded as karyosome. The chromosomes are quite small, and in cases of faulty fixation and staining may

become indistinct as individual bodies. The number falls between six and nine. The division spindles are intranuclear but their origin is obscure. Some evidence of centrosomes and astral rays has been found, but the data at hand are not sufficient to warrant the general conclusion that they are universally present. So far they have not been found to play any part in the origin of the spindle and the division of the cell. In the late anaphases and telophases the daughter chromosomes usually fuse into two compact, optically homogeneous oval masses which have an appearance strikingly similar to the nucleoli of the resting nucleus and eventually become surrounded in some unknown manner by a membrane. The nucleole of the mother nucleus generally retains its size and staining reaction during division and finally with the disappearance of the nuclear membrane is liberated into the cytoplasm where it gradually diminishes in size and disintegrates.

6. Cytokinesis occurs after nuclear division has been completed and is independent of the activity of the spindle fibers or other similar kinoplasmic material. In the spindle organs circular clefts or furrows develop centripetally and within them are formed delicate plates or membranes which gradually progress with the clefts toward and meet in the center of the cell. In the zoosporangia cell division is accomplished by progressive cleavage. In non-vacuolated sporangia the cleavage furrows begin at the periphery and progress more or less radially between the nuclei until the protoplasmic mass is cut up into polyhedral segments. Cleavage may be accompanied by shrinkage, but after the process is completed the segments may rehydrate and fill up the zoosporangium again. The lines of demarcation thus become finer and less distinct, and the sporangium frequently has the appearance of having undergone simultaneous fragmentation. In sporangia with large central vacuoles the cleavage furrows usually start at the boundary of the vacuole and progress centrifugally. In a few instances both centripetal and centrifugal cleavage have been observed within the same sporangium.

7. During the process of cleavage and the maturation of the segments the nucleole usually diminishes in size, and numerous basophilic granules or bodies appear in the cytoplasm near the nuclear membrane at the pole opposite the nucleole. Whether these are chromidia extruded from the nucleole during its diminution in size or chondriosomes has not been definitely determined, but they nevertheless appear to increase in size and volume and eventually fuse to form a dense staining extra-nuclear cap. This varies considerably in size but usually sits as a more or less hemispherical hood over the apex of the nucleus. The mature zoospores possess thus a well-defined nucleus with a small nucleole, a conspicuous nuclear cap

and a single posteriorly attached cilium. The point of attachment of the cilium and the nuclear membrane are frequently connected by delicate cytoplasmic strands.

8. No fusion of motile or quiescent gametes has so far been observed. From the data at hand the more or less spherical, hyaline resting spores appear to be formed asexually. They are predominantly uninucleate, although occasional bi- and tetranucleate spores may be formed. Their method of development seems to be similar to that of the evanescent zoosporangia, with the exception that the golden-red globules are not conspicuously developed and nuclear division is ordinarily suppressed. As the spore grows in size the more or less hyaline globules fuse to form a large central one, and the wall begins to thicken and soon attains mature proportions.

9. The Chytridiales in general have been but little studied cytologically. Less than two dozen species have been investigated, and very little is known of the processes of sexual reproduction, nuclear division, cytokinesis, etc., in the group as a whole. Amitosis, nuclear budding and fragmentation, and the origin of nuclei from granules in the cytoplasm has been described in a large number of species, while cell division is reported to occur by cell plate formation, simultaneous fragmentation of the protoplasm, and progressive cleavage. Chromosome counts have been made in only seven species, and there are scarcely half a dozen detailed accounts of indirect nuclear division for the whole group. While sexual reproduction has been observed in a large number of species, meiosis has been found and described in only one species.

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Literature cited

Atkinson, G. F. 1909. Some fungus parasites of algae. Bot. Gaz. **48**: 321–338.

Bally, W. 1911. Cytologische Studien an Chytridineen. Jahrb. wiss. Bot. **50**: 95–156.

————. 1919. Einige Bemerkungen zu den amitotischen Kernteilung der Chytridineen. Ber. deut. bot. Ges. **37**: 115–122.

Barrett, J. T. 1912a. Development and sexuality of some species of *Olpidiopsis* (Cornu) Fischer. Ann. Bot. **26**: 209–238.

————. 1912b. The development of *Blastocladia strangulata* n. sp. Bot. Gaz. **54**: 353–371.

Bartlett, A. W. 1926. On a new species of *Urophlyctis* producing galls on *Lotus corniculatus* Linn. Trans. Brit. Mycol. Soc. **11**: 266–281.

Bary de, A. 1874. *Protomyces microsporus* und seine Verwandten. Bot. Zeit. **32**: 97–108.

————. 1884. Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien. Leipzig.

Becker, F. R. 1926. *Endamoeba Citelli* sp. nov. from the striped ground squirrel *Citellus tridecemlineatus*, and the life history of its parasite, *Sphaerita Endamoebae* sp. nov. Biol. Bull. **50**: 444–454.

Bessey, E. A. 1935. A text-book of mycology. Phila.

Blackman, V. H. 1904. On the fertilization, alternation of generations and general cytology of the Uredineae. Ann. Bot. **18**: 323–373.

Bold, H. C. 1933. The life history and cytology of *Protosiphon botryoides*. Bull. Torrey Club **60**: 241–299.

Brand, F. 1908. Über Membran, Scheidewände und Gelenke der Algengattung *Cladophora*. Ber. deut. bot. Gesell. **26**: 114–143.

Braun, A. 1855. Über *Chytridium*, eine Gattung einzelliger Schmarotzgewäsche auf Algen und Infusorien. Abh. Kgl. Akad. Wiss. Berlin 1855: 21–83.

Brug, S. L. 1926. *Nucleophaga intestinalis* n. sp. parasitic in the nucleus of *Endolimax Williamsi* (Prow.) [*Iodamoeba Bütschli* (Prow.)] *Sphaerita* as a parasiste of *Entamoeba coli*. Med. Dienst. Volks. Nederl.-Indie **4**: 466–468.

Brumpt, E., and G. Lavier. 1935. Sur une *Nucleophaga* parasite d'*Endolimax nana*. Ann. Parasit. **13**: 439–444.

Bruyne de, C. 1890. Monadines et Chytridicées, parasites des algues du Golfe de Naples. Arch. Biol. **10**: 43–104.

Buckley, J. J. C., and P. A. Clapham. 1929. The invasion of helminth eggs by chytridiacean fungi. Jour. Helminth. **7**: 1–14.

Büsgen, M. 1887. Beitrag zur Kenntnis der Cladochytrien. Cohn's Beitr. Biol. Pflanz. **4**: 269–283.

Butler, E. J. 1907. An account of the genus *Pythium* and some Chytridiaceae. Mem. Dep't. Agric. India, Bot. I., no. 5: 1–160.

Caullery, M., and F. Mesnil. 1905. Recherches sur les Haplosporidies. Arch. Zool. Exp. Gen. 4th ser. **4**: 101–181.

Cejp, K. 1932. Some remarks to the knowledge of the parasitic Phycomycetes of Conjugates in Bohemia. Bull. Int. Acad. Sci. Bohême 1932: 1–6. pls. 1, 2.

———. 1933. Further studies on the parasites of Conjugates in Bohemia. Ibid. 1933: 1–11. pls. 1, 2.

Chatton, E. 1908. Sur la reproduction et les affinities du *Blastulidium paedophthorum* Ch. Perez. Comp. Rend. Soc. Biol. **64**: 34–36.

———, **and A. Brodsky.** 1909. Le parasitisme d'une Chytridinée du genre *Sphaerita* Dangeard chez *Amoeba limax* Dujard. Etude comparative. Arch. Protistk. **17**: 1–18.

Clinton, G. P. 1902. *Cladochytrium Alismatis*. Bot. Gaz. **33**: 49–60.

Codreanu, R. 1931. Sur l'évolution des *Endoblastidium*, nouveau genre de protiste parasite coelomique des larves d'Ephémères. C. R. Acad. Sci. Paris **192**: 772–775.

Colley, R. H. 1918. Parasitism, morphology and cytology of *Cronartium ribicola* Jour. Agr. Res. **15**: 619–660.

Cook, W. R. J. 1929. A preliminary account of a new species of the Protista. Arch. Protistk. **66**: 285–289.

———. 1932. The life history of *Cystochytrium radicale* occurring in the roots of *Veronica beccabunga*. Trans. Brit. Mycol. Soc. **16**: 246–252.

———, **and W. B. Collins.** 1935. The life history of *Olpidium majus* sp. nov. with notes on *Olpidium radicale* Schwarze and Cook. Ann. Mycol. **33**: 72–77.

————, **and W. H. Nicholson.** 1933. A contribution to our knowledge of *Woronina polycystis.* Ann. Bot. **47:** 851–859.

Cornu, M. 1872. Monographie des Saprolegniées, deuxième partie. Chytridinées parasites des Saprolegniées. Ann. Sci. Nat. ser. 5, **15:** 112–198.

Cotner, F. B. 1930. Cytological study of the zoospores of *Blastocladia.* Bot. Gaz. **79:** 295–309.

Couch, J. N. 1931. *Micromyces Zygogonii* Dang., parasitic on *Spirogyra.* Jour. Elisha Mitchell Soc. **46:** 231–239.

————. 1932. *Rhizophidium, Phlyctochytrium* and *Phlyctidium* in the United States. Jour. Elisha Mitchell Sci. Soc. **42:** 245–260.

————. 1935. New or little known Chytridiales. Mycologia **27:** 160–175.

Crouch, H. B. 1933. Four new species of *Trichomonas* from the woodchuck (*Marmota monax* Linn.). Jour. Parasit. **19:** 293–300.

Cunha, A. Da., and J. Muniz. 1923. Parasitismo de *Trichomonas* por Chytridiaceae do genero *Sphaerita* Dangeard. Brazil-Medico. **37:** 19.

Curtis, K. M. 1921. The life history and cytology of *Synchytrium endobioticum* (Schilb.) Perc., the cause of wart disease in potato. Phil. Trans. Roy. Soc. Soc. London B. **210:** 409–478.

Dangeard, P. A. 1886a. Sur un nouveau genre de Chytridiacées parasite des rhizopodes et des flagellates. Bull. Soc. Bot. France **33:** 240–241.

————. 1886b. Recherches sur les organismes inferieurs. Ann. Sci. Nat. ser. 7 **4:** 241–341.

————. 1889. Mémoire sur les Chytridinées. Le Bot. **1:** 39–74.

————. 1890. Recherches histologiques sur les Champignons. Ibid. **2:** 63–149.

————. 1895. Mémoire sur les parasites du noyau et du protoplasma. Ibid. **4:** 199–256.

————. 1900. Recherches sur la structure du *Polyphagus Euglenae* Nowak. et sa reproduction sexuelle. Ibid. **7:** 213–258.

————. 1903. Un nouveau genre de Chytridiacées: le *Rhabdium acutum.* Ann. Mycol. **1:** 61–64.

————. 1933. Nouvelles observations sur les parasites des Eugleniens. Le Bot. **25:** 1–46.

Dangeard, Pierre. 1934. Sur la présence à Roscoff d'une Chytriadale des Ectocarpées l'*Eurychasma Dicksonii* (Wright) Magnus. Ann. Protist. **4:** 69–71.

Debaisieux, P. 1920. *Coelomycidium Simulii* nov. gen., nov. spec., et remarques sur l'*Amoebidium* des larves de *Simulium.* La Cellule **30:** 249–276.

Diehl, H. 1935. Beiträge zur Biologie von *Olpidiopsis Saprolegniae* Barrett. Zentralb. Bakt. Parasitk. u. Infekt. **92:** 229–249.

Dobell, C. 1919. The amoebae living in man. London.

————, **and F. W. O'Connor.** 1921. The intestinal protozoa of man. London.

Dodge, B. O., and L. O. Gaiser. 1926. The question of nuclear fusions in the blackberry rust *Ceoma nitens.* Jour. Agric. Res. **22:** 1003–1024.

Doflein, F. 1907. Studien zur Naturgeschichte der Protozoen. Arch. Protistk. Suppl. **1:** 250–293.

Elpatiewsky, W. 1907. Zur Fortpflanzung von *Arcella vulgaris* Ehrbg. Arch. Protistk. **10:** 441–466.

Epstein, H. 1922. Ueber parasitische Infektion bei Darmamöben. (Russian text, German Résumé.) Arch. Soc. Russ. Protist. **1:** 46.

Fisch, C. 1884. Beiträge zur Kenntniss der Chytridiaceen. Sitz'b. phys.-med. Soc. Erlangen **16**: 29–66.

Fischer, A. 1880. Ueber die Stachelkugeln in Saprolegiaschläuchen. Bot. Zeit. **38**: 689–696, 705–711, 721–726.

———. 1882. Untersuchungen über die Parasiten der Saprolegnieen. Jahrb. wiss. Bot. **13**: 286–371.

———. 1892. Phycomycetes. Rabenhorst's Kryptogamenflora 1^4.

FitzPatrick, H. M. 1930. The lower fungi—Phycomycetes.

Fron, G., and Lasnier, E. 1920. Sur un Chytridinée parasite de la Luzerne. Bull. Soc. Mycol. France. **36**: 53–61.

Gilbert, H. C. 1935. Critical events in the life history of *Ceratiomyxa* Am. Jour. Bot. **22**: 52–70.

Gimesi, N. O. C. F. 1924. Hydrobiologiai Tanulmányok (Hydrobiologische Studien) 2. Budapest.

Gobi, C. 1899. *Fulminaria mucophila* nov. gen., et sp. Scripta Bot. Horti. Univ. Imp. Petrop. Fasc. **15**: 283–292.

Griggs, R. F. 1908. On the cytology of *Synchytrium*. III. The rôle of the centrosome in the reconstruction of the nucleus. Ohio Nat. **8**: 277–283.

———. 1909a. Some aspects of amitosis in *Synchytrium*. Bot. Gaz. **47**: 127–138.

———. 1909b. Mitosis in *Synchytrium* with some observations on the individuality of the chromosomes. Bot. Gaz. **48**: 339–358.

———. 1910. *Monochytrium*, a new genus of the Chytridiales, its life history and cytology. Ohio Nat. **10**: 44–54.

Gruber, A. 1904. Ueber *Amoeba viridis* Leidy. Zool. Jahrb. Supp. **7**: 67–76.

Guttenberg, H. R. 1909. Cytologische Studien an *Synchytrium*—Gallen. Jahrb. wiss. Bot. **46**: 453–477.

Guyot, A. L. 1927. Contribution à l'étude systematique et biologique de l'*Asterocystis radicis*. Ann. Epiph. **13**: 79–93.

Harper, R. A. 1897. Kerntheilung und freie Zellbildung im Ascus. Jahrb. wiss. Bot. **30**: 249–284.

———. 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.

———. 1914. Cleavage in *Didymium melanospermum* (Pers.) Macbr. Am. Jour. Bot. **1**: 127–144.

Hartmann, M. 1925. Untersuchungen über relative Sexualität. I. Versuche an *Ectocarpus siliculosus*. Biol. Zentralbl. **45**: 449.

Hatch, W. R. 1935. Gametogenesis in *Allomyces arbuscula*. Ann. Bot. **49**: 623–649.

Hovasse, R. 1936. *Rhizophidium Beauchampi* sp. nov., Chytridinée parasite de la Volvocinée *Eudorina* (*Pleodorina*) *illinoisensis* (Kofoid). Ann. Parasit **5**: 73–81.

Jollos, V. 1926. Untersuchungen über die Sexualitätsverhältnisse von *Dasycladus clavaeformis*. Biol. Zentralbl. **46**: 279.

Jones, F. R., and C. Dreschler. 1920. Crownwart of alfalfa caused by *Urophlyctis Alfalfae*. Jour. Agric. Res. **20**: 295–325.

Karling, J. S. 1928a. Studies in the Chytridiales I. The life history and occurrence of *Entophlyctis heliomorpha* (Dang.) Fischer. Am. Jour. Bot. **15**: 32–42.

————. 1928b. Studies in the Chytridiales II. Contribution to the life history and occurrence of *Diplophlyctis intestina* (Schenk) Schroeter in cells of American Characeae. Ibid. **15**: 204–214.

————. 1930. Studies in the Chytridiales IV. A further study of *Diplophlyctis intestina* (Schenk) Schroeter. Ibid. **17**: 770–778.

————. 1931a. Studies in the Chytridiales V. A further study of the species of the genus *Entophlyctis*. Ibid. **18**: 443–464.

————. 1931b. Studies in the Chytridiales VI. The occurrence and life history of a new species of *Cladochytrium* in cells of *Eriocaulon septangulare*. Ibid. **18**: 526–557.

————. 1932. Studies in the Chytridiales VII. The organization of the chytrid thallus. Ibid. **29**: 41–74.

————. 1934a. A saprophytic species of *Catenaria* isolated from the roots of *Panicum variegatum*. Mycologia **26**: 528–543.

————. 1934b. Resting sporangia of *Cladochytrium*. Sci. n. s. **79**: 390.

————. 1935. A further study of *Cladochytrium replicatum* with special reference to its distribution, host range, and culture on artificial media. Am. Jour. Bot. **22**: 439–452.

————. 1936a. Germination of the resting sporangia in *Diplophlyctis intestina*. Bull. Torrey Club **63**: 467–471.

————. 1936b. The endo-exogenous method of growth and development of *Chytridium lagenaria* Schenk. Amer. Jour. Bot. **23**: 619–626.

————. 1937a. A new species of *Phlyctochytrium* on *Hydrodictyon reticulatum*. Mycologia **29**: 178–186.

————. 1937b. The structure, development, identity and relationship of *Endochytrium*. Am. Jour. Bot. **23**: (In press).

Kessel, J. F. 1924a. Experimental infection of rats and mice with the common intestinal amoebae of man. Univ. of Calif. Pub. Zool. **20**: 409–430.

————. 1924b. The distinguishing characteristics of the parasitic amoebae of culture rats and mice. Univ. of Calif. Ibid. **20**: 489–544.

Kirby, H. 1927. Studies on some amoebae from the termite *Microtermes*, with notes on some other protozoa from the Termitidae. Quart. Jour. Micro. Soc. n. s. **71**: 190–219.

Kniep, H. 1929. *Allomyces javanicus* n. sp. ein anisogamer Phycomycet mit Planogameten. Ber. deut. bot. Gesell. **47**: 199–212.

Köhler, E. 1923. Ueber den derzeitegen Stand der Erforschung des Kartoffelkrebses. Arbeit. Biol. Reichanst. Land. Forstwirt. **11**: 289.

————. 1930. Beobachtungen an Zoosporenaufschwemmungen von *Synchytrium endobioticum* (Schilb.) Percival. Zentralb. Bakt. Parasitk. II. **82**: 1–10.

————. 1932. Zur Biologie und Cytologie von *Synchytrium endobioticum* (Schilb.) Perc. Phytopath. Zeitschr. **4**: 43–55.

————. 1936. Untersuchungen über *Synchytrium endobioticum* (Schlussbericht). Zeitschr. Pflanzkr. u. Pflanzsch. **46**: 214–223.

Kusano, S. 1907a. On the nucleus of *Synchytrium puerariae* Miyabe. Bot. Mag. Tokyo Bot. Soc. **21**: 118–121.

————. 1907b. On the cytology of *Synchytrium*. Centralb. Bakt. Parasitenk. **19**: 538–543.

———. 1908a. Studies on a disease caused by *Synchytrium Puerariae*. Bot. Mag. Tokyo Bot. Soc. **22**: 1–2.

———. 1908b. On karyodermatoplast, a nuclear-membrane-forming body. Bot. Mag. Tokyo Bot. Soc. **22**: (205).

———. 1909. Contribution to the cytology of *Synchytrium* and its hosts. Bull. Coll. Agric. Imp. Univ. Tokyo **8**: 80–147.

———. 1912. On the life history and cytology of a new *Olpidium* with special reference to the copulation of motile isogametes. Jour. Tokyo Coll. Agric. **4**: 141–199.

———. 1928. The relative sexuality in *Synchytrium*. Proc. Imp. Acad. **4**: 497–499.

———. 1929. Observations on *Olpidium Trifolii*. Jour. Coll. Agric. Imp. Univ. Tokyo **10**: 83–99.

———. 1930. Cytology of *Synchytrium fulgens* Schroet. Jour. Coll. Agric. Univ. Tokyo **10**: 347–388.

Lagerheim, G. 1898. Mycologische Studien. Beitrag zur Kenntniss der parasitischen Pilze, 1–3. Bih. Sven. Vet. Akad. Hand. Stockholm **24,** III, no. 4: 1–22.

Lavier, G. 1935a. Action, sur la biologie d'une Entamibe, du parasitisme intranucléaire par une *Nucleophaga*. Comp. Rend. Soc. Biol. **118**: 457–459.

———. 1935b. Sur une *Nucleophaga parasite* d'*Entamoeba Ranarum*. Ann. Parasit. **13**: 351–361.

Ledingham, G. A. 1936. *Rhizophidium graminis* n. sp., a parasite of wheat roots. Canad. Jour. Res. **14**: 117–121.

Leger, L., and O. Duboscq. 1902. Les grégarines et l'épithélium intestinal chez les tracheates. Arch. Parasit. **6**: 377–473.

———, ———. 1909. Sur les *Chytridiopsis* et leur évolution. Arch. Zool. Exp. Gen. **5** Ser. 1: IX–XIII.

Löwenthal, W. 1905a. Tierversuche mit *Plasmodiophora Brassicae* and *Synchytrium Taraxaci* nebst Beiträgen des letzeren. Zeit. Krebsf. **3**: 46–60.

———. 1905b. Weitere Untersuchungen an Chytridiaceen. Arch. Protistk. **5**: 221–239.

Ludi, R. 1901. Beiträge zur Kenntniss der Chytridiaceen. Hedwigia **40**: 1–44.

Lund, A. 1930. A new species of *Pleotrachelus* with remarks on the genus. Bot. Tideskr. **41**: 240–243.

Lutman, B. F. 1911. Cell and nuclear division in *Closterium*. Bot. Gaz. **51**: 401–430.

L-Yuan-Po. 1928. *Entamoeba Bobaci* n. sp. des tarabagans (*Marmota bobac*). Ann. Parasit. **6**: 330–342.

Maire, R., and A. Tison. 1911. Recherches sur quelques Cladochytriacées. Compt. Rend. Acad. Sci. Paris **152**: 106–107.

Magnus, P. 1897. On some species of the genus *Urophlyctis*. Ann. Bot. **11**: 87–96.

———. 1901. Ueber eine neue unteriridisch lebende Art der Gattung *Urophlyctis*. Ber. deut. bot. Gesell. **19**: (145)–(153).

———. 1905. Über die Gattung zu der *Rhizophidium Dicksonii* Wright gehört. Hedwigia **44**: 347–349.

Mattes, O. 1924. Über Chytridineen im plasma und Kern von *Amoeba sphaeronucleus* und *Amoeba terricola*. Arch. Protistk. **47**: 414–429.

Maurizio, A. 1895. Zur Kenntniss der schweizerischen Wasserpilze nebst Angaben über eine neue Chytridine. Jahresb. Naturf. Ges. Graubünden Chur. **38:** 9–38.

Mercier, L. 1907. Un parasite de noyau d'*Amoeba Blattae* Bütschli. Comp. Rend. Soc. Biol. Paris. **62:** 1132–1134.

————. 1910. Contribution à l'étude de l'Amibe de la Blatte (*Entamoeba Blattae* Bütschli). Arch. Protistk. **20:** 143–145.

Minden, M. v. 1911. Chytridineae. Krypt. Fl. Mark Brandenburg. **5:** 209–422.

Nägler, K. 1911. Studien über Protozoen aus einem Almtümpel. II. Parasitische Chytridiaceen in *Euglena sanguinea*. Arch. Protistk. **23:** 262–268.

Němec, B. 1911. Zur Kenntniss der niederen Pilze. III. *Olpidium Salicorniae* n. sp. Bull. Internat. Acad. Sci. Boheme. **16:** 136–144, 157.

————. 1912. Zur Kenntniss der niederen Pilze. IV. *Olpidium Brassicae* Wor. und zwei *Entophlyctis*—Arten. Ibid. **17:** 16–25.

————. 1922. O pohlavnosti u *Olpidium brassicae*. Zolast. otisk ze Sborniku Klubu, Praze. 1922: 1–3.

Nowakowski, L. 1877a. Beitrag zur Kenntniss der Chytridiaceen. Cohn's Beitr. Biol. Pflanz. **2:** 73–100.

————. 1877b. Beitrag zur Kenntniss der Chytridiaceen II. *Polyphagus Euglenae*, eine Chytridiacee mit geschlechticher Fortpflanzung. Ibid. **2:** 201–219.

————. 1878. Przyczynek do morfologii i systematyki Skoczków (Chytridiaceae). Pamietník Akad. Umiejetnošci w Krakowie Wydzia Matem.-Przyród. **4:** 174.

Ojerholm, E. 1934. Multiciliate zoospores in *Physoderma Zeae-maydis*. Bull. Torrey Club **61:** 13–18.

Penard, E. 1905. Observations sur les Amibes à pellicule. Arch. Protistk. **7:** 175–207.

————. 1912. Nouvelles recherches sur les amibes de groupe Terricola. Ibid. **28:** 78–140.

Percival, J. 1910. Potato "wart" disease: The life history and the cytology of *Synchytrium endobioticum* (Schieb.) Perc. Centralb. Bakt. Parasitk. II. **25:** 440–447.

Perez, C. 1903. Sur un organisme nouveau, *Blastulidium paedophthorum*, parasite des embryons de Daphnies. Mem. Soc. Biol. **55:** 715–716.

————. 1905. Nouvelles observations sur le *Blastulidium paedophthorum*. Ibid. **58:** 1027–1029.

Petersen, H. P. 1905. Contributions à la connaissance des phycomycètes marins (Chytridinae Fischer). Oversigt Kgl. Danske Videns Selsk. Forh. 1905, no. 5: 440–488.

————. 1910. An account of Danish freshwater-phycomycetes with biological and systematical remarks. Ann. Mycol. **8:** 494–560.

Pringsheim, N. 1860. Beiträge zur Morphologie und Systematik der Algen. IV. Nachträge zur Morphologie der Saprolegnieen. Jahrb. wiss. Bot. **2:** 205–236.

Prunet, A. 1894. Sur une Chytridinée de la vigne. Compt. Rend. Acad. Sci. Paris **119:** 572–574.

Puymaly, A. de. 1927. Sur le *Sphaerita endogena* Dangeard, Chytridiaceae parasitic des Euglenes. Bull. Soc. Bot. France **74:** 472–476.

Quintanilha, A. 1926. Contribuçao ao estodo des *Synchytrium*. Bolet. Soc. Broteriana 2nd ser., **3**: 88–194.

Raitschenko, A. 1902. Über eine Chytridiacee: *Rhizophidium sphaerocarpum* (Zopf) Fischer. Bull. Jard. Imp. St. Petersburg **2**: 119–126.

Rattray, J. 1885. Note on *Ectocarpus*. Trans. Roy. Soc. Edinburgh **32**: 589–600.

Reinsch, P. F. 1878. Beobachtungen über einige neue Saprolegnieae, über die Parasiten in Desmidienzellen und über Stachelkugeln in Achlyaschlauchen. Jahrb. wiss. Bot. **11**: 281–311.

Rosen, F. 1887. Ein Beitrag zur Kenntniss der Chytridiaceen. Cohn's Beitr. Biol. Pflanz. **4**: 253–282.

————. 1893. Beiträge zur Kenntniss der Pflanzenzelle II. Studien über die Kerne und die Membranbildung bei Myxomyceten und Pilzen. Ibid. **6**: 237–266.

Rytz, W. 1907. Beiträge zur Kenntniss der Gattung *Synchytrium*. Centralb. Bakt. Parasitk. II. **18**: 635–655, 799–825.

————. 1916. Cytologische Untersuchungen an *Synchytrium Taraxaci* de Bary et Woronin. Ber. schweiz. bot. Ges. **24, 25.**

————. 1917. Beiträge zur Kenntniss der Gattung *Synchytrium* I. Die cytologischen Verhältnisse bei *Synchytrium Taraxaci* De By. et Wor. Beih. Bot. Centralb. **34**: 343–372.

Saccardo, P. A., and O. Mattirolo. 1895. Contribuzione allo studio dell'*Oedomyces leproides* Sacc. Nuovo parassita della Barbabietola. Malpighia **9**: 399–408.

Sampson, K. 1932. Observations on a species of *Olpidium* occurring in the roots of *Agrostis*. Trans. Brit. Mycol. Soc. **17**: 182–193.

Sawada, K. 1922. Descriptive catalogue of the Formosan fungi, II. Dept. Agric. Govt. Res. Inst., Formosa, Rept. 2.

Scherffel, A. 1925. Zur Sexualität der Chytrideen. Arch. Protistk. **53**: 1–58.

————. 1926a. Einiges über neue oder ungenügend bekannte Chytridineen. Ibid. **54**: 167–260.

————. 1926b. Beiträge zur Kenntniss der Chytridineen. Teil III. Ibid. **54**: 510–528.

————. 1931. Über einige Phycomyceten. Ibid. **73**: 37–146.

Schleiden, M. 1838. Ueber Phytogenesis.

Schneider, A. 1884. Sur le developpement de *Stylorhynchus longicollis*. Arch. Zool. Exp. Gen. 2nd ser. **2**: 1–36.

Schroeter, J. 1889. Chytridiei. Cohn's Krypt.-Fl. Schlesiens **3**: 175–197.

————. 1897. Chytridineae. Engler & Prantl, Die Nat. Pflanzf. **I**^{1}: 64–87.

Schwann, T. 1839. Mikroscopische Untersuchungen über die Uebereinstimmung in der Structur und dem Wachstum der Thiere und Pflanzen.

Schwartz, E. J., and Cook, W. R. J. 1928. Life history and cytology of a new species of *Olpidium; Olpidium radicale* sp. nov. Trans. Brit. Mycol. Soc. **13**: 205–221.

Schwarze, C. A. 1922. The method of cleavage in the sporangia of certain fungi. Mycologia **14**: 143–172.

Scott, C. E. 1920. A preliminary note on the germination of *Urophlyctis Alfalfae*. Science n. s. **52**: 225–226.

Serbinow, J. L. 1907. Beiträge zur Kenntniss der Phycomyceten. Organization und Enwickelungsgeschichte einiger Chytrydeenpilze. Scripta Bot. Horti. Univ. Imp. Petropol. **24**: 149–173.

Sideris, C. P. 1929. *Rhizidiocystis Ananasi.* nov. gen. et sp., a root parasite of pineapples. Phytopath. **19**: 367–382.

Sigot, A. 1931. Une Chytridiacée nouvelle, parasite des œufs de *Cyclops.* Comp. Rend. Soc. Biol. **108**: 34–37.

Sorokin, N. W. 1874. Einige neue Wasserpilze. Bot. Zeit. **32**: 305–315.

Sparrow, F. K. 1931. Two new Chytridiaceous fungi from Cold Spring Harbor. Am. Jour. Bot. **18**: 615–623.

————. 1933a. Inoperculate chytridiaceous organisms collected in the vicinity of Ithaca, N. Y., with notes on other aquatic fungi. Mycologia **25**: 513–535.

————. 1933b. The Monobleparidales. Ann. Bot. **47**: 517–542.

————. 1934a. The occurrence of true sporangia in the *Physoderma* disease of corn. Sci. n. s. **79**: 563–564.

————. 1934b. Observations on marine Phycomycetes collected in Denmark. Dansk Bot. Ark. **8**, no. 6: 1–24.

————. 1935. Recent contributions to our knowledge of the aquatic Phycomycetes. Biol. Rev. **10**: 150–186.

————. 1936a. Biological observations on the marine fungi of Woods Hole waters. Biol. Bull. **70**: 236–263.

————. 1936b. A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. Jour. Linn. Soc. London **50**: 417–478.

————. 1936c. Evidence for the possible occurrence of sexuality in *Diplophlyctis.* Mycologia **28**: 321–324.

Stevens, F. L. 1907. Some remarkable nuclear structures in *Synchytrium.* Ann. Mycol. **5**: 480–484.

————, **and Stevens, A. C.** 1903. Mitosis of the primary nucleus in *Synchytrium decipiens.* Bot. Gaz. **35**: 405–415.

Swingle, D. B. 1903. Formation of the spores in the sporangia of *Rhizopus nigricans* and of *Phycomyces nitens.* U. S. Bur. Pl. Ind. Bull. 37: 1–40.

Thaxter, R. 1896. New or peculiar aquatic fungi III. *Blastocladia.* Bot. Gaz. **21**: 45–52.

Timberlake, H. G. 1902. Development and structure of the swarm spores of *Hydrodictyon.* Trans. Wisconsin Acad. Sci. **13**: 486–522.

Tisdale, W. H. 1919. *Physoderma* disease of corn. Jour. Agric. Res. **16**: 137–154.

Tobler, G. 1913. Die Synchytrien. Arch. Protistk. **28**: 141–238.

Tokunaga, Y. 1933. Studies in the aquatic chytrids of Japan. Trans. Sapporo Nat. Hist. Soc. **13**: 20–28.

Tregouboff, G. 1913. Sur un Chytriopside nouveau, *Chytridioides Schizophylli* n. g., n. sp., parasite de l'intestin de *Schizophyllum mediterraneum* Latzel. Arch. Zool. Exp. Gen. **52**: 25–31.

Valkanov, A. 1929. Protistenstudien 5. *Hyphochytrium Hydrodictyii*—ein neuer Algenpilz. Arch. Protistk. **67**: 122–127.

Varitchak, B. 1931. Remarques sur la répartition du cytome au moment de la formation des zoospores. Comp. Rend. Acad. Sci. Paris. **192**: 371–372.

Wager, H. 1898. The formation of the zygospore in *Polyphagus Euglenae.* Rept. Brit. Assn. Adv. Sci. Bristol **1898**: 1064.

————. 1899. The sexuality of the fungi. Ann. Bot. **13**: 575–597.

————. 1913. The life history and cytology of *Polyphagus Euglenae.* Ann. Bot. **27**: 173–202.

Welsford, E. J. 1921. Division of the nuclei in *Synchytrium endobioticum* Perc. Ann. Bot. **35**: 298–299.

Wenyon, C. M. 1907. Observations on the protozoa in the intestine of mice. Arch. Protist. Supl. **1**: 169.

————. 1926. Protozoology—A manual for medical men, veterinarians and zoologists. New York.

Wildeman de, E. 1895a. Notes Mycologiques XV. Mem. Soc. Belge Micro. **19**: 88–117.

————, 1895b. Quelques Cytridiacées nouvelles parasites d'algues. La Notarisia **10** (3): 33–35.

————. 1931. Sur quelques Chytridinées parasites d'algues. Bull. Class. Sci. Roy. Belgique 5th ser., **17**, no. 3: 291–298.

Wille, N. 1899. Om nogle Vandsoppe. Vidensk. Selskabets. Skrift. Kristiania Math. Nat. Kl. 1, **3**: 1.

Wilson, O. T. 1915. The crown gall of alfalfa. Sci. n. s. **41**: 797.

————. 1920. Crown-gall of alfalfa. Bot. Gaz. **70**: 51–68.

Woronin, M. 1878. *Plasmodiophora Brassicae*, Urheber der Kohlpflanzen-Hernie. Jahrb. wiss. Bot. **11**: 548–574.

Wright, E. P. 1879. On a species of *Rhizophydium* parasitic on a species of *Ectocarpus*, with notes on the fructification of the Ectocarpi. Trans. Roy. Irish Acad. Sci. **26**: 369–379.

Zimmermann, A. 1902. Ueber einige an tropischen Kulturpflanzen beobachtete Pilze II. Centralbl. Bakt. Parasitk. **8**: 148–152.

Zopf, W. 1884. Zur Kenntniss der Phycomyceten. Nova Acta Ksl. Leop.-Carol. Deut. Akad. Nat. **47**: 143–236.

————. 1887. Über einige niedere Algenpilze (Phycomyceten) und eine neue Methode ihre Keime aus dem Wasser zu isoliren. Abh. Nat. Ges. Halle **17**: 77–107.

————. 1888. Zur Kenntniss der Infections—Krankheiten niederer Thiere und Pflanzen. Nova. Acta. Ksl. Leop.-Carol. Deut. Akad. Nat. **52**: 313–376.

————. 1890. Die Pilze. Schenk's Handbuch der Botanik **4**: 561.

Explanation of Plates

All figures refer to *Cladochytrium replicatum* and were drawn from fixed and stained preparations with the aid of a Spencer camera lucida, a Zeiss 2 mm. N. A. 1.30 apochromatic objective, and compensating oculars nos. 6 and 8.

Plate 1

Fig. 1. A zoospore with a large nuclear cap lying on the surface of an epidermal cell of *Panicum variegatum.*

Fig. 2. An early germination stage.

Fig. 3. A later stage showing the migration of the nucleus into the elongated germ tube.

Fig. 4. A very young thallus showing the primary pear-shaped nucleus in the initial spindle organ.

Fig. 5. Equatorial plate stage of division of the primary nucleus in the initial spindle organ.

Fig. 6. A primary two-celled spindle organ showing an early stage of the migration of a daughter nucleus into the tenuous portion of the rhizomycelium.

Fig. 7. A slightly later stage in which the apex of the nucleus is drawn out into a densely stained rod.

Fig. 8–10. Nuclei in transit to secondary spindle organs.

Fig. 11. A secondary spindle organ with a pear-shaped nucleus. The nucleole is in the form of a broad circular band, and from the pointed end of the nucleus runs a conspicuous cytoplasmic strand which may possibly indicate the path taken by the nucleus in entering.

Fig. 12. A portion of a rhizomycelium showing the primary and secondary spindle organs, rhizoids, and habit of branching and variations in diameter of the filamentous portions.

Plate 2

Fig. 13. A secondary spindle organ showing the structure of the resting nucleus.

Fig. 14. A median section of an enlarged resting nucleus showing the structure of the chromatin reticulum. The nucleole was not visible in this section.

Fig. 15, 16. Surface and side views of resting nuclei with circular band-shaped nucleoli.

Fig. 17. An early prophase nucleus from poorly fixed and overstained material. The chromatin reticulum is highly shrunken and densely stained.

Fig. 18. A similar stage from the same type of material, but less densely stained. The reticulum is slightly oriented on the nucleole.

Fig. 20. A very early prophase stage in well-fixed and stained material. The reticulum is fairly dense, while the nucleole has an uneven contour and appears to be composite.

Fig. 21. A binucleate zoosporangium with both nuclei in the spireme stage of division. In the right-hand nucleus the spireme bands appear coiled or zigzag in appearance and are definitely oriented on the nucleole. On the membrane of each nucleus lies a densely stained body with cytoplasmic strands radiating from it, which suggests the presence of centrosomes and astral rays.

Fig. 22. A later prophase nucleus showing the shortening and thickening of the spireme strands.

Fig. 23. A slightly later stage showing three small and three larger discrete bodies. The nucleole lies at the left side in the shape of a ring.

Fig. 24. A late prophase nucleus with seven discrete bodies or chromosomes. The achromatic spindle appears to be forming.

Fig. 25. A very late prophase stage in the primary nucleus of a zoosporangium. The intra-nuclear spindle has been fully formed, and the chromosomes are being drawn into the equator of the nucleus. The poles of the spindle converge on two densely stained bodies lying on the nuclear membrane, and from the latter radiate faint irregular cytoplasmic lines.

Fig. 26. An equatorial plate stage in which the chromosomes appear more or less merged into an irregular band across the equator of the spindle.

Fig. 27. A similar stage showing a broad spindle with the chromosomes arranged in a ring around its periphery.

Fig. 28. Polar view of an equatorial plate stage showing six chromosomes arranged in a flat loop. The nucleole is irregular in contour and somewhat cup-shaped.

Fig. 29. A two-celled spindle organ showing the division of the remaining nucleus. One pole of the distorted spindle is centered on the nucleole.

Fig. 30. An early anaphase stage. The triangular-shaped nucleole lies at one side and has apparently distended the nuclear membrane in that region.

Fig. 31. A slightly later stage in which, due to overstaining, the two chromosome groups appear as homogeneous, irregular curved bands.

Fig. 32. An anaphase stage with a narrow intra-nuclear spindle.

Fig. 33. A later stage in which the individual chromosomes are fairly distinct. The nucleus is surrounded by a dense mass of granules which tend to obscure the nuclear membrane.

Fig. 34. A late anaphase stage in which the chromosomes have arrived at the poles of the spindle.

Fig. 35. A later stage in which the nuclear membrane has almost completely disappeared. The spindle has elongated considerably; the nucleole lies free, and the chromosomes have united into two compact groups.

Fig. 36. A further anaphase stage. The elongated spindle is represented by a few strands and is slightly bent, while around the chromosome groups are distinct polar radiations. The nucleole is still present in the cytoplasm as a densely basophilic globule.

Plate 3

Fig. 37. An early telophase stage, perhaps, in which the spindle is still faintly evident. The chromosomes have united into two compact, optically homogeneous groups, and above them appear clear spaces partly surrounded by a faint boundary which suggests the origin of the nuclear membrane. The edges of the nucleole are drawn out along the spindle.

Fig. 38. A spindle organ showing the completion of nuclear division. The daughter chromosome groups look like two large nucleoli, while the old nucleolus lies in the cytoplasm. No well-defined nuclear reticulum is visible.

Fig. 39. Doubtless a later stage showing the diminution in the size of the old nucleole and the development of a reticulum in the daughter nuclei.

Fig. 40. A spindle organ showing the two daughter nuclei lying close together in the region formerly occupied by the mother nucleus. The old nucleole lies as a disintegrating mass at the right side.

Fig. 41. An early stage of cell division in which two faint furrows or clefts are visible.

Fig. 42. A further advanced stage showing the faint membranes which have been laid down in the advancing grooves.

Fig. 43. A later stage of cytokinesis.

Fig. 44. Cytokinesis has been completed.

Fig. 45. An elongated unicellular spindle organ with four nuclei in which karyokinesis has apparently not been followed immediately by cell division.

Fig. 46. An odd-shaped spindle organ with one of the nuclei dividing at right angles to the long axis.

Fig. 47. A five-celled spindle organ, two of whose cells have developed into zoosporangia.

Fig. 48. A two-celled spindle organ with a zoosporangium developing directly from the surface of one of its cells.

Plate 4

Fig. 49. A bi-nucleate zoosporangium showing proliferation.

Fig. 50. A cross section of a four-nucleate zoosporangium, all nuclei of which are in the prophases of division.

Fig. 51. A longitudinal section of a similar structure with the three visible nuclei in the equatorial plate stage of division.

Fig. 52. An eight-nucleate zoosporangium in longitudinal section with six nuclei in division.

Fig. 53. An oval zoosporangium with a large central vacuole.

Fig. 54. An early stage of progressive cleavage in a medium-sized sporangium.

Fig. 55, 56. More advanced stages of cleavage in small zoosporangia.

Fig. 57, 58. Small and large sporangia showing the completion of progressive cleavage and the presence of large masses of densely basophilic granules around the nuclei.

Fig. 59. A peripheral cleavage segment showing the position of the nucleus and the small nucleole.

Fig. 60. A cleavage segment showing five densely basophilic bodies in the cytoplasm.

Fig. 61. A cleavage segment showing an increase in the number of such bodies and their aggregation at the pole of the nucleus opposite the nucleole.

Fig. 62. A later stage of aggregation and fusion of bodies to form the extra-nuclear cap.

Plate 5

Fig. 63. A mature sporangium with zoospore initials whose nuclei appear as clear spaces surmounted by densely stainable nuclear caps.

Fig. 64A, 64B, and 65. Zoospores showing the variations in size and extent of the nuclear cap.

Fig. 66. An early stage in resting spore formation.

Fig. 67. A later stage showing the increased vacuolation of the cytoplasm and thickening of the cell wall.

Fig. 68. A bi-nucleate incipient resting spore.

Fig. 69. A similar spore which has apparently been formed from a young zoosporangium, whose exit tube is still present.

Fig. 70. A four-nucleate resting spore.

Fig. 71. A two-celled resting spore formed from an encysted spindle organ.

Fig. 72. An almost mature resting spore which has apparently developed from a young uninucleate zoosporangium. The exit tube of the latter is still intact.

Fig. 73, 74. Mature resting spores showing the flattened nucleus from the side and above.

Plate 6

Showing the structure, cytology, distribution and organization of the rhizomycelium of *C. replicatum* in a portion of an internode of *Nitella flexilis*.

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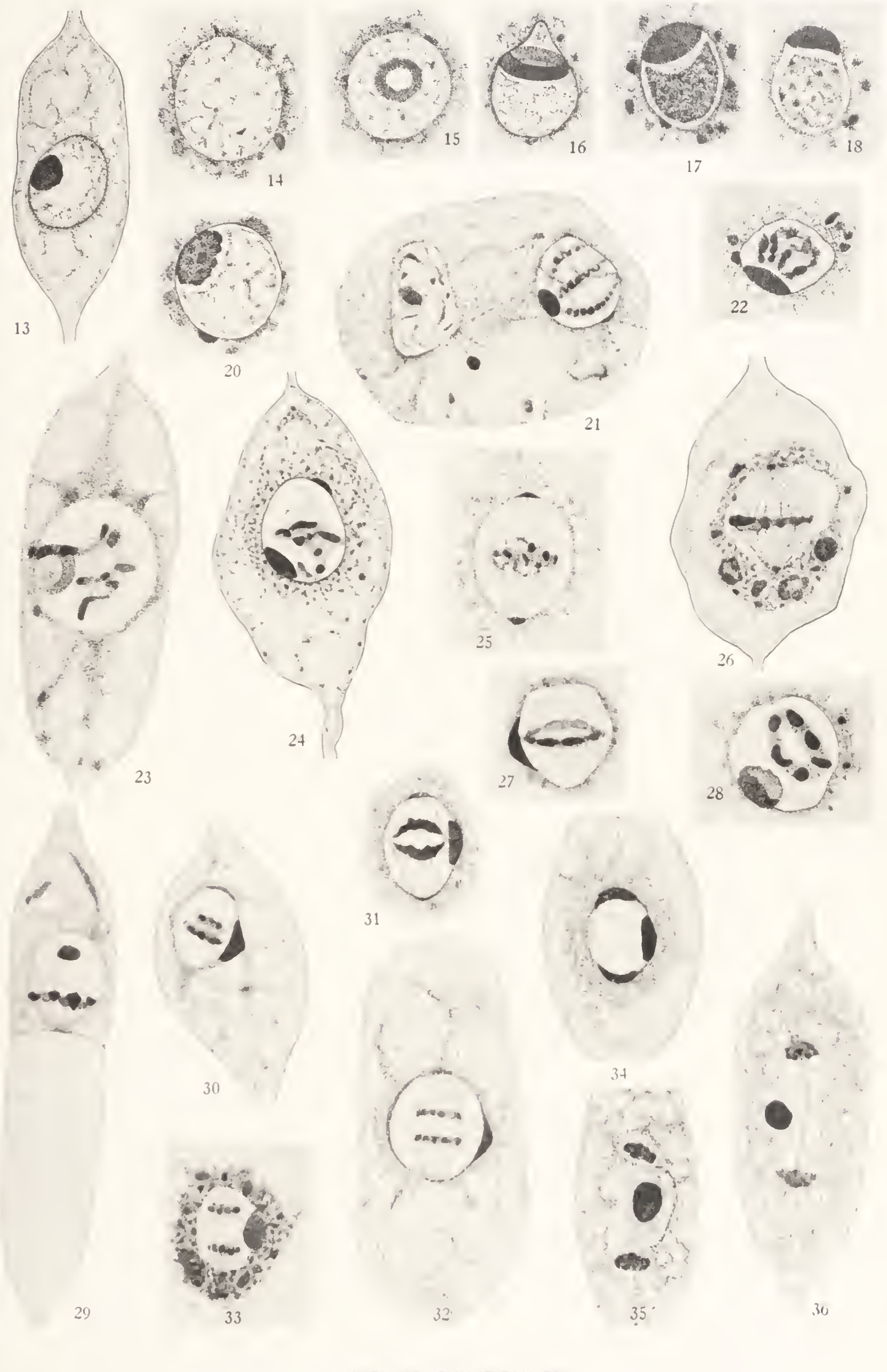

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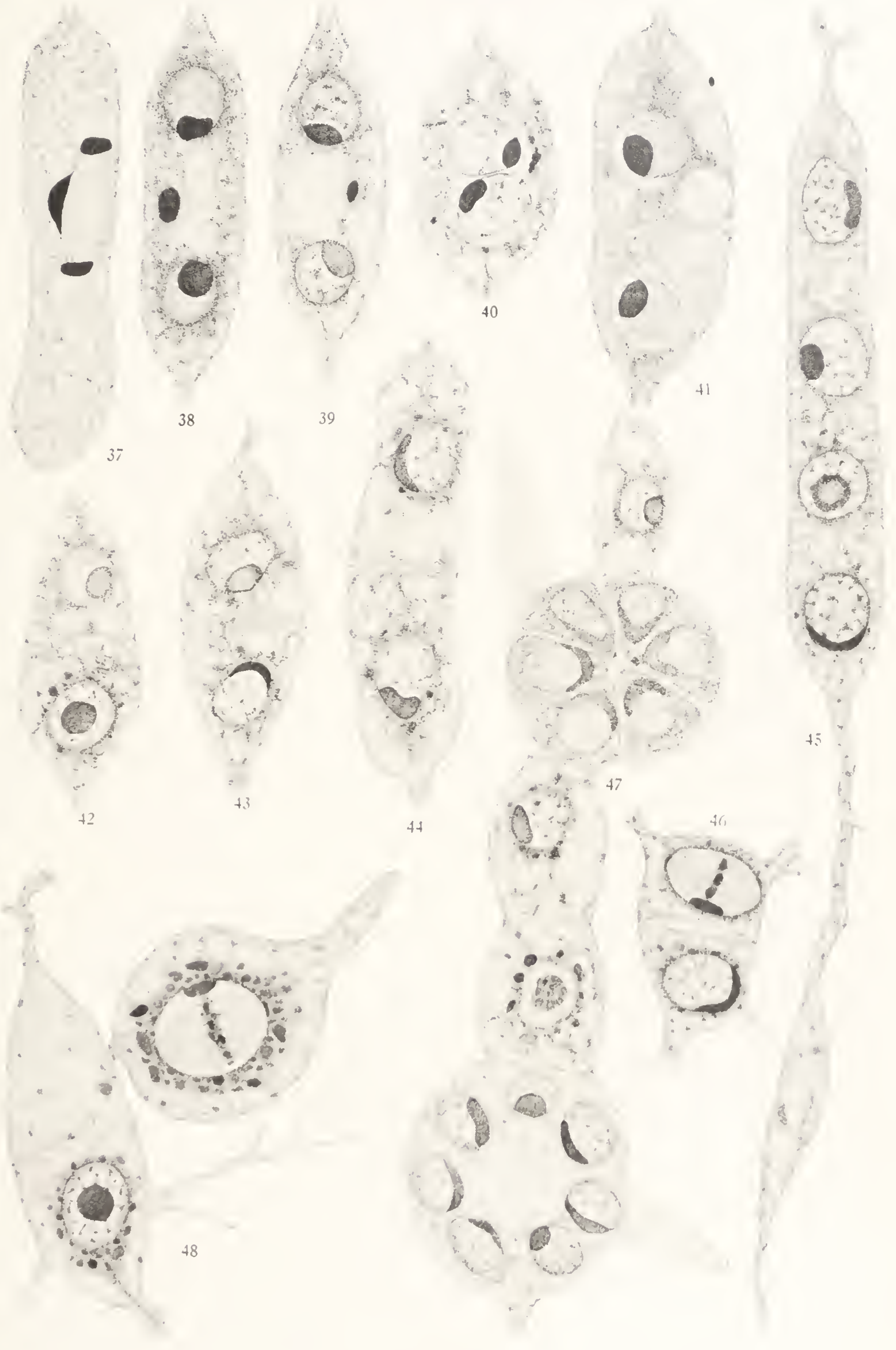

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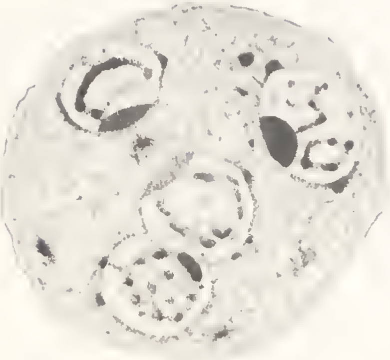
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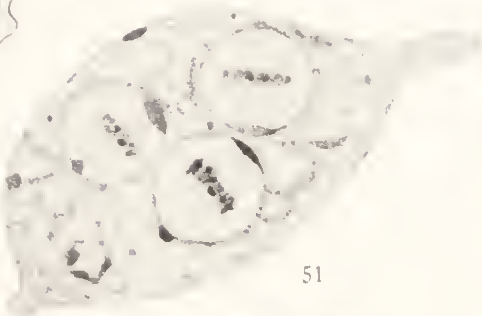
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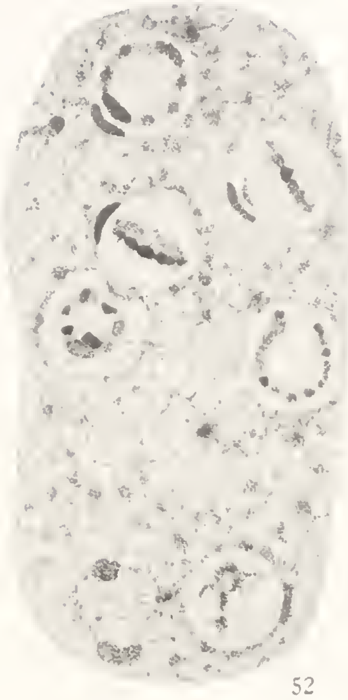
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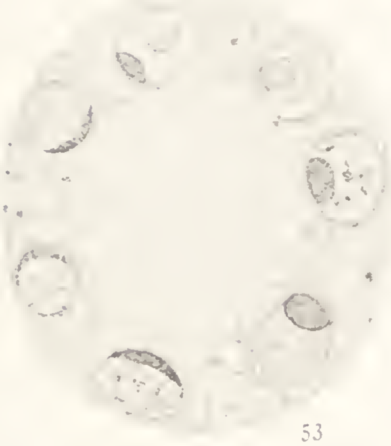
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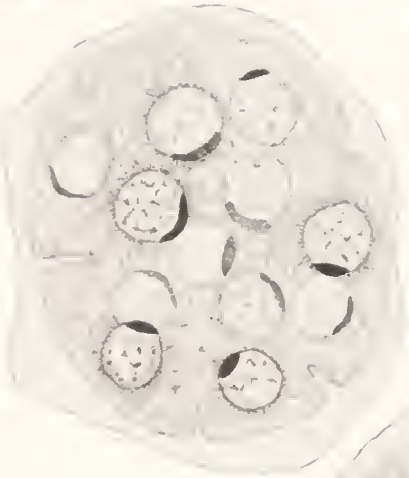
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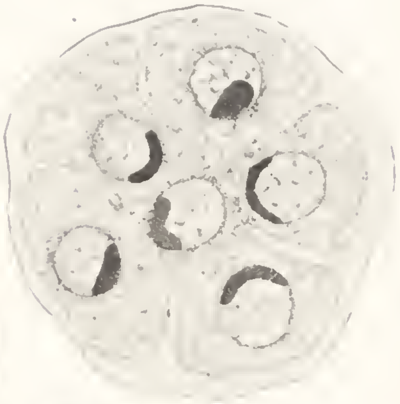
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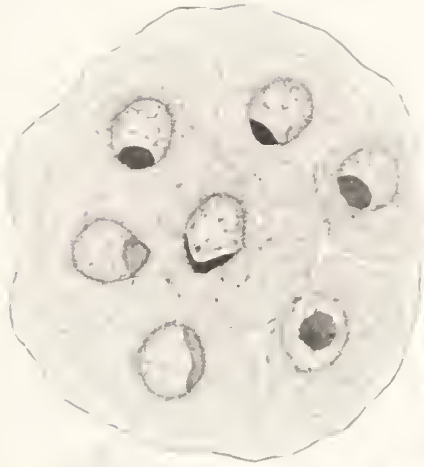
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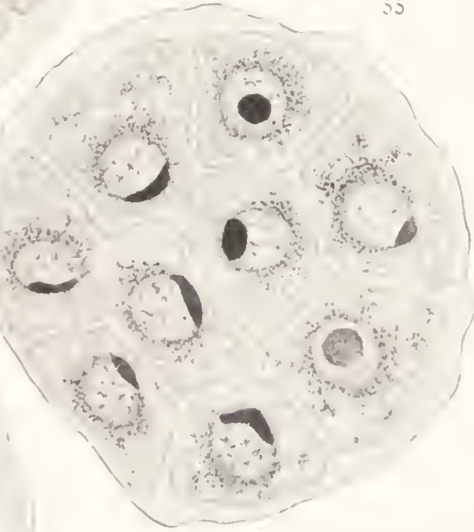
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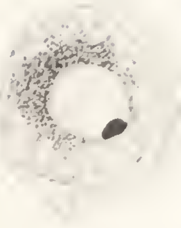
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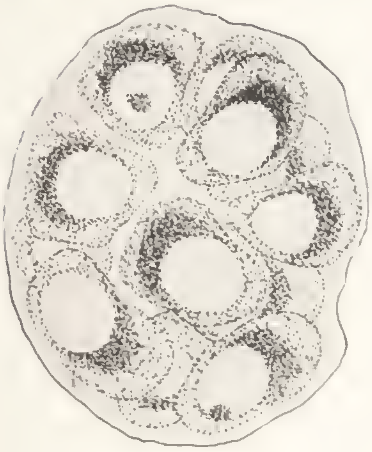
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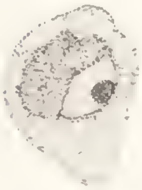
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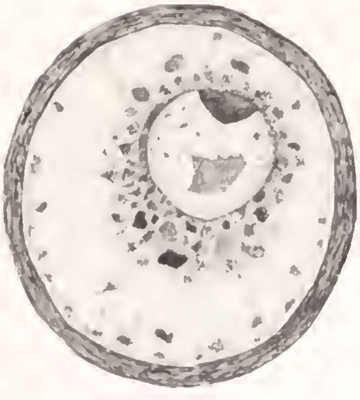
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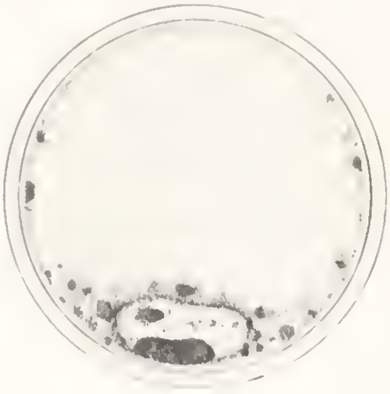
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KARLING: CHYTRIDIALES

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Memoirs of the Torrey Botanical Club

Volume 19 Number 2

Editor
M. A. Chrysler

A Monograph of the Ophioglossaceae

By
ROBERT T. CLAUSEN

Published for the Club by
GEORGE BANTA PUBLISHING COMPANY
MENASHA, WISCONSIN
1938

MEMOIRS OF THE TORREY BOTANICAL CLUB

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Robert T. Clausen

(with thirty-three figures)

CONTENTS

INTRODUCTION

PRELIMINARY STATEMENT

Among all the pteropsid groups, the *Ophioglossaceae* perhaps represent the most primitive division and the best example of simple morphological development. It is not surprising, therefore, that the systematology of the family should be attended with certain difficulties and peculiarities which must perplex the student who is accustomed to the problems encountered in the taxonomy of higher and structurally more complicated orders.

Those characters which are available for use in classification are few and of a type that may not be relied upon too closely. Since the group is an old one, species have had time to become exceedingly widespread. Indeed, some of the most widely distributed vascular plants are found in the *Ophioglossaceae*, and these in almost the same form throughout the world. This condition must constantly be borne in mind when dealing with this family. Its ancient lineage and extreme conservatism are practically unparalleled in the other fern groups.

The small number of characters available for systematic purposes in the *Ophioglossaceae* has forced workers, in developing their classifications, to base conclusions concerning species often on trivial details such as leaf cutting and size, characters which would not ordinarily be considered of fundamental importance in other groups. Since the entire aerial plant commonly is represented only by a single leaf which at once functions as stalk, leaf, and sporophyll, the classification must be based in large part on characters afforded by these single leaves, which to be sure are of a more specialized type than most ordinary angiosperm leaves, but morphologically their equivalent. If one were to base a classification of the genus *Quercus* entirely on leaf characters, with all other parts of the plants buried under the ground and not available for systematic purposes, there would result either myriads of species or utter chaos. Such has been somewhat the case in the *Ophioglossaceae*. Lacking better characters, minute variations in leaf cutting, venation, size and texture have been used as bases for species differentiation with the consequence that the number of species has become quite large.

The present study has developed from a desire to discover more fundamental characters on which to base a new classification of the group. Unfortunately, these more fundamental characters have not been found. It appears that here is a family in which the structure is so simple that it affords no set of organs or parts that can be designated as furnishing the ideal characters which might serve as a sound basis for systematic work. Hence, like other students of the family, the writer has been forced, with considerable misgiving, to accept at least to a certain degree such characters as leaf cutting, pubescence, size and habit as sufficient for species differentiation. He has tried to be reasonable in his use of these characters, however, and to bring his treatment so far as possible into accord with what might be termed conservative practice in dealing with fern groups. If these characters were not adopted as criteria for species, it would be necessary to reduce the species to a very small number and thereby remove the opportunity to keep apart populations which appear to be really distinct enough, but for which the characters available for species differentiation do not seem fundamental.

The undertaking of such a study with the thought of eventual publication, either as a whole or in parts, has seemed justified since there is not available in the English language any world monograph of this group and since the last such monograph in any language, that of Prantl, written in German, was published over fifty years ago. It now seems appropriate that a new treatment should be available, brought up to date in the light of the additional information that has accumuated during the last half century.

NOMENCLATURE

The Approach

In a systematic investigation of this type, nomenclature should not be an end in itself, but rather an incidental by-product resulting from the taxonomic work. It should not be thought, however, that the nomenclature is of little importance. Many workers may judge an investigation entirely on a basis of the nomenclature employed. Since the names are the labels or tags by which the systematist designates his organisms, they represent the guide posts or clues to his entire treatment. It therefore seems highly desirable for the writer to explain at the beginning of this paper exactly what have been his general views on this subject.

The General Statement

Since the nomenclature of any group of organisms depends largely upon the concepts of the fundamental taxonomic units adhered to by the workers dealing with that group, it is first necessary to consider what units should be recognized and how these should be defined.

Among biologists, there seems to be rather general acceptance of the existence in nature of groups of organisms which represent distinct kinds of things and hence merit recognition as species. These species might be defined after the manner of Du Rietz (1930) as "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes." To be sure, not all taxonomists would probably subscribe to this definition, but it seems the best and most practical one that has until now been offered. In biological literature there is now complete agreement that names of species should be written as binomials consisting of the generic name followed by the specific designation.

Treatment of groups of less than specific value has not been so uniform. Unfortunately, the International Botanical Congress has made no rulings rigidly defining subspecific categories. As a result, practice has been extremely diverse. On a basis of method of treatment of subspecific populations, workers may be divided into at least five distinct classes:

1. The extreme splitters and lumpers, who recognize only species. These have no subspecies, varieties or forms, but consider that a population is *worth recognizing either as a species or not at all.* Although the chief exponents of this school have been segregators, this same type of philosophy might lead to the lumping of the minor subdivisions of other workers.

2. The extreme conservatives, who have large species with a multiplicity of subspecies, varieties and forms; usually employ *polynomial nomenclature;* and always use the subspecific epithets.

3. Middle-course group. These workers have species with varieties and forms, but not subspecies; rarely use any name longer than a trinomial; *always* use the epithets *var.* or *forma;* and define a variety as a somewhat geographically segregated extreme (Fernald, 1936).

4. Progressive group which recognizes subspecies and rarely varieties. Workers of this group often write names of subspecies as trinomials and consider the subspecies to be equivalent to geographical races.

5. The horticulturists and botanists who have treated minor variations of species, not necessarily correlated with range, as varieties, designated by adding after the ordinary binomial the epithet *var.* followed by the Latin name of the variety. These seldom have forms or subspecies.

To the writer, the practice of those who recognize no subspecific categories appears decidedly unsatisfactory because it does not seem in accord with the actual state of affairs in nature. Just as genera are made up of a number of species, so species are usually composed of a number of closely related subdivisions or subspecies. To ignore these lesser divisions or to elevate them to the status of species destroys the opportunity to show the relationships which exist between closely allied groups. The practice of the conservatives, on the other hand, while it leads to an ideal expression of relationships, results in a style of nomenclature that is at once awkward and impractical.

The style of treatment adopted by the middle-course group seems unsatisfactory because it not only leads to an entirely different interpretation of variety from the historical meaning of the term, but it tends to produce a gulf between botanical and zoological practice. This school of taxonomists seems to have developed, particularly in England, during the latter part of the last century, after the advent of the evolutionary theory, when the practice arose among certain systematic botanists of considering varieties to be variations of species correlated with range, that is geographical races. This school of botanists thereby gave the term variety a technical meaning not at all implied by the word itself and quite different from the sense in which it had been employed for so long a time in horticultural usage and by many workers dealing with wild plants. This technical use of the term variety has become increasingly popular among certain American systematists, who have been reducing all minor variations of species not correlated with range to the rank of *forma*. Meanwhile, systematic zoologists have almost throughout the world standardized the category of subspecies for geographical variations of species, while a not inconsiderable group of botanists, including a few Americans, but most of them Europeans, representing what we have termed the progressive, school, have taken up the subspecies in the same sense as the zoologists.

If one were to follow the practice of those who give the term variety a technical meaning, then it would be necessary to reduce all horticultural variations based on botanical characters, not fancy variations, to the rank of *forma*, unless a range correlation could be demonstrated. This is impossible. Horticulturists would never permit such a procedure and a considerable block of systematists would be irreconcilable. Further, zoological and botanical practice would be definitely divorced. In view of these considerations, it seems apparent that some sort of compromise arrangement must be made.

It is here suggested that a type of nomenclature be adopted that is based upon two primary taxonomic units of less than specific rank and worthy of nomenclatorial distinction, the subspecies and the variety, A subspecies would be defined as a major division of a species, usually differing from the other divisions of the species in several characters and having a definite geographical range. A variety would be defined as a minor variation of a species, made up of individuals varying from a more typical condition in only one or two trivial characters and generally without any geographical correlation. Varieties might be found among either wild or cultivated plants, but in both cases would be based on the same sort of characters.

It is thought that two subspecific units are sufficient for practical purposes. Any more than two leads to a complicated system of polynomials which does not seem justifiable. In the present suggestion, it is further proposed that no name of greater length than a trinomial be employed.

There may thus be both varieties and subspecies of species, but although there might be theoretical varieties of subspecies, these would be written in practice as ternary combinations, leaving out the subspecific name. If *forma* is to be used at all, it might best be reserved for teratological conditions, but ordinarily such conditions would not seem to warrant formal nomenclatorial designation.

Some have suggested that popular names be taken up for all minor variations of species, but Latin names for horticultural varieties and their equivalents among wild plants have become so firmly established that it probably would be impossible to get rid of them. These Latin names have the advantage of being more precise than popular names, of being capable of greater standardization and of being available to people in all lands, regardless of the native tongue.

Since the international code of nomenclature, although it does not require the use of subspecific prefixes, by suggestion implies that the various epithets are best employed, it seems most proper, for the present at least, that we should continue to employ the *var.* or *ssp.* in designating less than specific categories. This seems particularly desirable because of the great disagreement which now exists among workers. It is sincerely hoped that eventually this divergence of opinion may disappear and that some particular system may be definitely taken up and standardized by the International Congress. It is hoped too that there might be a definite ruling to legalize trinomials, with a statement that any third name in such a combination should automatically be interpreted as a subspecies.

These suggestions would insure the traditional use of the term variety for horticultural purposes and for minor variations among wild plants. By establishing the major botanical divisions of species correlated with geographical range as subspecies, the practices in zoology and botany might be brought into harmony.

The mention of horticultural practice in this paper is not considered out of place since several species of *Botrychium* and at least one *Ophioglossum* are regularly mentioned in standard horticultural manuals. Further, in the case of at least two sub-specific elements, there has been just that sort of reduction, by certain middle-course systematists, from the rank of variety, as considered by the horticulturists, to the rank of *forma*, which the writer desires to avoid.

HISTORICAL ACCOUNT

Knowledge of the *Ophioglossaceae* begins perhaps with the description and illustration by Leonhard Fuchs (1542) of *Lunaria minor*, the species that we now call *Botrychium Lunaria* (L.) Sw. In the two centuries that followed this publication by Fuchs, various other authors became interested in the moonworts and adder's tongues, and, as well as redescribing *Lunaria minor,* added other species to the group. Among the outstanding students of the family during this pre-Linnean period were the two Bauhin brothers in France. Caspar Bauhin (1620) in his *Prodromus theatri botanicae* and later in his *Pinax* listed three kinds of *Ophioglossum* and five kinds of *Lunaria.* In his *Historia plantarum universalis,* J. Bauhin and J. H. Cherlero (1651) treated *Ophioglossum* (*Ophioglossum vulgatum*) and three kinds of *Lunaria,* all illustrated by line drawings. The Lunarias are *L. botrytis,* which is typical *Botrychium Lunaria; L. botrytis minor multifolia,* which is an abnormal form, also of *B. Lunaria;* and *L. botrytes ramosa silesiaca* which is *B. multifidum.*

In the initial edition of *Species Plantarum,* Linnaeus (1753) provided the first really comprehensive world treatment of the group. Under *Ophioglossum* he listed six species, two of which we now refer to *Lygodium,* but the other four we still maintain in the genus. These are *O. vulgatum, O. lusitanicum, O. reticulatum* and *O. palmatum.* In the disposal of the other two genera of the family, Linnaeus did not fare so happily. He lumped in one genus, *Osmunda,* along with a variety of other things, plants which we now place in *Helminthostachys* and *Botrychium.* Our only species of *Helminthostachys* was described as *Osmunda zeylanica* from Ceylon. Of *Botrychium,* only two were listed, *Osmunda Lunaria* from Europe and *O. virginiana* from America. Under the former he included most of the European species described by earlier workers. In the second edition of the *Species Plantarum,* an additional species of *Ophioglossum, O. pendulum,* was described, but no new moonworts were added.

Four years after the appearance of the first edition of *Species Plantarum,* Trew (1757) published a discussion of *Lunaria,* with illustrations of four species, three of which can be clearly made out. There is some slight doubt about the other, which is probably a small form of *Botrychium virginianum.* Trew seems to have worked quite independently of Linnaeus. He based his treatment on that of the Bauhins and used descriptive phrases for designating his species, after the style of the prelinnean herbalists. Recently Woynar (1913) has tried to bring up one of Trew's names, *Lunaria silesiaca,* stating that it represented the first binary combination to be applied to the species which we now know as *Botrychium multifidum,* but it seems that this combination resulted as a chance abbreviation in the text and not as an intentional binomial. In any event, it can not be considered to constitute valid publication since Trew did not consistently follow the principle of binomial nomenclature throughout his paper, as required by the international rules.

Gmelin (1768), working in Russia, added two species to the group, *Osmunda lanceolata* and *Osmunda multifida*. These were both illustrated. Somewhat after this, Swartz (1800) established the genus *Botrychium* based on five species: *Lunaria*, *rutaceum*, *virginianum*, *ternatum* and *zeylanica* (*Helminthostachys*).

The first real student of the *Ophioglossaceae*, who might be designated as a specialist and expert on the group, was the Hungarian, Karel Boriwog Presl (1845). In his treatment of the family, which included descriptions of several new species, he recognized six genera: *Botrychium* with 17 species, *Rhizoglossum* 1, *Ophioglossum* 25, *Ophioderma* 1, *Cheiroglossa* 1, and *Helminthostachys* 3. Each of the two large genera, *Botrychium* and *Ophioglossum*, was divided into two major subdivisions according to the nature of the venation. Although we do not today follow Presl in the grouping of species in *Botrychium* and *Ophioglossum*, we do divide the family into essentially the same major groups. Further, no new generic names have been taken up since Presl's time. The present treatment, so far as genera are concerned, differs from Presl's only in the reduction of *Rhizophyllum*, *Ophioderma* and *Cheiroglossa* from the rank of genera to that of subgenera under *Ophioglossum*. Presl developed the framework on which all later workers have based their classifications. In addition to this taxonomic contribution, Presl (1847) studied the internal anatomy of the stipes of ferns, including the *Ophioglossaceae*, and published a paper with descriptions and drawings of the number and nature of the vascular bundles in transverse sections of the stem.

At about the same time as Presl was working, Ruprecht (1845 and 1859) in Russia and Angström (1854) in Sweden were interested in the *Ophioglossaceae* along with other groups and made various nomenclatorial changes and innovations.

The great student of *Botrychium* during the middle of the nineteenth century was Dr. Julius Milde (1858a, 1858b, 1864, 1868, 1869), a school teacher at Breslau in Silesia, Germany. He made numerous contributions to the literature of the genus, including a comprehensive monograph. Milde seems to have had a philosophical approach to his subject and was apparently quicker to see similarities and relationships between plants than he was to see differences. This is mirrored throughout his work, particularly in his extreme tendency in the direction of lumping. In the *Botrychiorum Monographia*, a world study, only ten species were treated, but under many of these were included a great array of varieties and forms. Milde's nomenclature was cumbersome, founded as it was on a taxonomic philosophy that considered species to be made up of a large number of subgroups and sub-subgroups. Although Milde did not have great series of specimens on which to base his conclusions, yet he seems to have seen most of the forms that had been described up to his time. These he in most cases clearly differentiated, but usually awarded to them no more than the rank of form or variety. He particularly was proficient in working out the minute details of external morphology, excellent drawings of which appeared in some of his papers. Further, he had a keen sense of the variation of species in nature and, in one of his papers, published series of illustrations to show the normal range of variation of the species treated.

In England, Hooker and Baker (1868), like Milde, were very conservative students and much inclined towards lumping. In their *Synopsis Filicum* they admitted only 17 species under the *Ophioglossaceae*, 10 of these in *Ophioglossum*, 1 in *Helminthostachys* and only 6 in *Botrychium*. Theirs was quite a different treatment of the family from that of Presl, who recognized 48 species. That some of Presl's species were not maintained, was to be expected, but men like Milde, Hooker, and Baker went decidedly too far in the other direction. Unfortunately this often uncritical lumping misled many contemporary workers and the influence of these nineteenth century conservatives has persisted to a certain extent up to the present time.

In America, D. C. Eaton (1878) and G. E. Davenport (1897) followed Milde, Hooker, and Baker in reducing to synonymy numerous previously described species. While a small part of this was justified, much of it was uncritical and has merely produced confusion in our knowledge of the North American forms. Eaton, for example, in his treatment of the ternate-leaved grape-ferns, reduced them all to varieties of *B. ternatum* of eastern Asia, then treated the large-leaved, typically North American plant, described by Presl as *B. silaifolium*, under the name of var. *australe*, based on *B. australe* R. Br. of New Zealand and Australia, which is usually small leaved and quite unlike *B. silaifolium*. The two great contributions of G. E. Davenport (1877, 1878, 1881) were first to work out rather elaborately the characters and range of variation in *Botrychium simplex* and second to describe and demonstrate the value of the buds in classifying and identifying species of *Botrychium*.

Although Milde published much concerning *Botrychium*, he seems not to have been interested in *Ophioglossum*, but Prantl (1883 and 1884), like Presl, studied the entire family. Throughout all time, perhaps, Prantl has been the greatest student of the *Ophioglossaceae*. His monograph stands as the basis for all modern work in the family and represents at the same time the most recent general treatment of the group to be published. Although papers have been written concerning the various divisions of the family and concerning all the forms found in particular geographical areas, no one since Prantl has ventured to monograph the whole group, hence the present attempt.

In his treatment Prantl demonstrated a healthy swing away from the over enthusiastic lumping of some of his predecessors, but he did not go too far in the other direction. He recognized 15 species of *Botrychium* and 29 of *Ophioglossum*. All but one of the Botrychia are maintained in the present study, although it has been necessary to change the names of three of these and to redefine many of the others. As characters for his classification of *Botrychium*, Prantl used leaf architecture, venation and the sculpture of the spore coat. In *Ophioglossum* much emphasis was placed on venation and characters afforded by the spores. In the present investigation, there has been an indication that sometimes these characters are not as reliable as Prantl had thought. The venation, though variable, can be used to a certain extent as a primary character for species differentiation. The spores are in most cases so small that it is exceedingly difficult to make out the nature of the outer coat and since they vary in size almost as much as their entire diameter, it has been concluded that while a study of the spores might be of considerable theoretical interest, spore characters would not be of great practical value in the *Ophioglossaceae*, as they have been in certain other groups, particularly in *Isoetes* and *Lycopodium*.

In America, towards the close of the nineteenth century and the beginning of the twentieth, a new school of fern students arose, foremost among whom was Dr. L. M. Underwood (1903) who carried on intensive studies in *Botrychium*, both at home and abroad. His chief contribution in the *Ophioglossaceae* was an *Index to the described species of Botrychium*, in which he brought up to date Prantl's treatment. At the same time, Mrs. E. G. Britton (1897), wife of Dr. N. L. Britton, first director of the New York Botanical Garden, studied *Ophioglossum* and published a revision of the North American forms, including some new species, but these have been reduced to synonymy by later workers.

E. B. Copeland (1909) and C. R. W. K. van Alderwerelt van Rosenburgh (1909) in their studies of the fern floras of the Malay-Asiatic region, described various new species and worked out in detail the characters for distinguishing the forms found in that part of the world. Copeland's treatment was more conservative than that of van Alderwerelt van Rosenburgh, who seems to have been a little too extreme in his splitting tendencies.

In modern times the *Ophioglossaceae* have not received as much attention as during the period towards the turn of the century. Abroad, the contemporary students of the group are Christensen (1906, 1932) who, in addition to the listing of species in *Index filicum*, has made a critical study of the Madagascarian forms; d'Almeida (1922) in India, who has studied the forms of his native land and also the European species; and Nakai (1926) in Japan, who has specialized on the eastern Asiatic species. In America, Butters (1917) has studied the variations of *Botrychium virginianum*, while recently the late E. W. Graves (1931, 1935), an amateur, has made various interesting field investigations. At the present time, the American authorities on the whole family are C. A. Weatherby at the Gray Herbarium and W. R. Maxon at the National Herbarium; and, on *Botrychium*, Brother Victorin at Montreal.

Morphological studies of the *Ophioglossaceae*, as of other groups, have been pursued largely by workers who have had little or no interest in the taxonomy of the family. Hofmeister (1855, 1857) worked out the life cycle of *Botrychium Lunaria*, describing the gametophytes and the development of the young sporophytes. At the same time, Stengel (1858) investigated the anatomy of the stem and root of *Ophioglossum vulgatum*, while Roeper (1859) published on both the classification and gross anatomy of the family, providing the first general morphological treatment of the group with an attempt to interpret structures and to understand relationships.

Somewhat later, Holle (1875) published a study on the vegetative anatomy of *Ophioglossum* and *Botrychium*, providing a review of work up until his time and figures illustrating the various details of structure discussed in the text. In 1902, Bitter, in the treatment of the Ophioglossales in *Die Naturlichen Pflanzenfamilien* provided a good summary of all the work that had been done in the family up until the end of the nineteenth century.

Reviewing the work of Hofmeister and carrying on even more elaborate studies of a similar type, Bruchmann (1904, 1906) made important contributions to the knowledge of the embryogeny and later development of *Botrychium Lunaria* and *Ophioglossum vulgatum*.

In England, Lang (1902, 1913) has described the gametophyte of *Ophioglossum pendulum* and *Helminthostachys* and has studied branching in *Botrychium Lunaria*, while Bower (1894, 1896, 1903, 1926) has made numerous contributions to the knowledge of the morphology of the family. Some of the anatomical evidence which he has made available has helped substantially in determining the relationships of various species within the group. During the earlier period of his work, Bower was the leading proponent of the strobilus theory, according to which *Ophioglossum* represented the simplest development in the family, related to the bryophytes, with the fertile segment representing a large partitioned sporangium, while the sterile blade represented an enlarged photosynthetic lobe of the sporangium base. Campbell (1886, 1895, 1904, 1911, 1920, 1921, 1922), in America, thought that the fertile segment of the *Ophioglossaceae* represented an enlarged ventral sporangium, and that the line of development had been from *Lycopodium*-like types; but these theories of both Bower and Campbell have now been largely abandoned because of the work of Chrysler (1910, 1926), who has conclusively demonstrated the lateral foliar nature of the fertile segment in this group.

Jeffrey (1897, 1898) described the gametophytes and development in *Botrychium virginianum*, while Lyon (1905) discovered and described the gametophytes of *B. dissectum* var. *obliquum*. In the last, the presence of a suspensor and the development of the root down through the gametophyte, rather than to the side and around it as in *B. virginianum*, seemed of such importance that Lyon ventured to describe a new genus, *Sceptridium*, for those species which had this type of development. Although Lyon had studied only a single variety of one species, yet he proceeded to make combinations under *Sceptridium* for all previously described forms of the ternate type of grape-ferns, apparently on the assumption that these would have a similar development. Actually, the gametophytes of most of these species are still unknown today, although we have found gametophytes for several of the other varieties of *B. dissectum* and these are all the same. In 1858, Milde described a forma *tuberosum* of *B. rutaefolium* which is really based on young sporophytes with gametophytes attached. His figures show the root emerging from the base of the gametophyte, hence we may assume that development in this species (our *B. multifidum*) proceeds in essentially the same manner as in *B. dissectum*. The gametophytes of all other species placed in *Sceptridium* apparently must still be found.

Recent American morphological research in the *Ophioglossaceae* has been conducted by Petry (1914, 1915) who worked out the anatomy of *Ophioglossum pendulum* and investigated branching throughout the family, and Baas-Becking (1920) who has studied the origin of the vascular structure in *Botrychium* and various other details of the general anatomy of the group.

To summarize, the history of research in the *Ophioglossaceae* may be divided roughly into four general periods:

1. The pioneer period (1542–1849) during which the herbalists and early post-Linnaean writers described the basic species and gave names to the generic groups. The studies during this period culminated in 1845 in the world monograph of the family by Presl.

2. The eighteenth century conservative period (1850–1880) during

which workers like Milde and Hooker and Baker summarized what the earlier students had done and the first morphological investigators, like Hofmeister, began to study the detailed structure of the group.

3. The progressive period of investigation (1881–1915) when Prantl monographed the family and numerous researchers, both taxonomists and morphologists, were studying the group.

4. The modern or contemporary period (1916–), difficult to characterize, but apparently decadent, with little work being done.

MATERIALS AND PROCEDURE

It was about six years ago that the writer first became interested in the *Ophioglossaceae.* While studying the vascular floras of New Jersey and central New York, he collected occasional specimens of *Botrychium* which were rather difficult, if not impossible, to determine with the aid of the usual manuals. Besides, the statements in the manuals concerning distribution, relative frequency, habitat and diagnostic characteristics did not seem in accord with the conditions as they appeared in nature. Hence a desire developed to gain more information concerning this interesting, but apparently little known group. Investigation of the literature has demonstrated that the group is not so little known as was at first supposed, for the array of papers available on the *Ophioglossaceae* is decidedly formidable. Realizing that all of this material had never before been brought together and that many new facts were appearing which required exposition, the writer has continued his studies and enlarged them until now they have become of world scope.

When the author (Clausen 1934) wrote his paper on the Botrychia of northeastern North America, he was able to discuss almost all of the forms treated with actual field experience to guide him in his conclusions. Now, unfortunately, in this world paper, conclusions concerning many forms must be based on an interpretation of herbarium material. This is the great handicap of any student who attempts to investigate a group or flora that is outside of his own local region.

The writer has examined all of the material of *Ophioglossaceae* available in the following herbaria, which have been abbreviated in the text as:

B—Herbarium of the Brooklyn Botanic Garden
C—Cornell University Herbarium
Claus—Private herbarium of R. T. Clausen
Deam—Private herbarium of C. C. Deam
Edw—Private herbarium of J. L. Edwards
G—Gray Herbarium
Gris—Private herbarium of L. Griscom

H—Herbarium of the Bailey Hortorium
Har—Herbarium of the Pennsylvania State Museum
Lyon—Private herbarium of M. W. Lyon, Jr.
M—Herbarium of the Missouri Botanical Garden
Mont—Herbarium of the University of Montreal
N—Herbarium of the New England Botanical Club
NY—Herbarium of the New York Botanical Garden
Ot—National Herbarium of Canada
Penn—University of Pennsylvania Herbarium
Ph—Herbarium of the Academy of Natural Sciences of Philadelphia
Prince—Princeton University Herbarium
Rut—Rutgers University Herbarium
U—United States National Herbarium

The taxonomic conclusions that will be presented here have been arrived at largely as a result of the study of the several thousand sheets on hand at the above named institutions, as well as of a rather complete survey of the available literature and of continued field work in the northeastern United States. Also, fresh material of several species of *Ophioglossum* and of one *Botrychium* has been available from Florida. In a few critical cases, photographs of types have been obtained from European herbaria.

Spore studies have been made to a limited extent, mostly of those species of which it was possible to collect mature spores in the field. These were collected in dry vials in which they were brought to the laboratory, where they were either mounted in glycerine jelly on glass slides or placed between two pieces of white mica fastened together by a good quality mending cement and sealed about the edges with strips of adhesive tape. This last method has the advantage that the mica slide may be slipped into a paper pocket and mounted on the same herbarium sheet with the specimen from which the spores were obtained, whereas glass slides are so heavy that they must be kept in special slide boxes and hence are separated from the specimens. The use of mica for spore mounts was first brought to the writer's attention by Mr. C. A. Weatherby of the Gray Herbarium.

Gametophytes, buds and other structures which it has seemed desirable to preserve in an unpressed condition, have been placed in small bottles, in 70% alcohol, or in a mixture of glycerine and 70% alcohol.

Most of the plants collected by the writer have been preserved as herbarium specimens after the usual manner. Particular attention has been given to noting full data for each specimen. Besides exact locality, various ecological details such as associated species, types of soil, relative acidity, and drainage have been noted whenever possible.

Ranges have been worked out rather elaborately on outline maps which are used through the courtesy of the McKinley Map Company of Philadelphia. On these maps, each dot or cross represents a collection, from the place indicated, that has been studied by the writer. Because of the great disagreement concerning the definitions and limits of many of the species, no records based only on references in the literature have been designated on the maps. This practice has been followed to insure accuracy. Locality records in the literature are mentioned in the text whenever these have seemed to be particularly significant. For common species of wide distribution, no attempt has been made to list all specimens examined, but instead, the writer has simply indicated the regions (states, provinces, counties, or districts) from which material has been seen, whereas for less common species or for those of more restricted distribution, fuller data are provided. Complete citations of specimens examined may be found in manuscript copies of the writer's (Clausen, 1937b) doctorate thesis, which are filed in the library at Cornell University.

The writer here wishes to thank all those who have at various times contributed to the progress of this study. He particularly desires to express appreciation to Professor K. M. Wiegand, who has given kindly guidance and suggestions throughout this investigation; to Dean L. H. Bailey, who has offered many suggestions and helped in obtaining photographs of several type specimens; to Mr. J. L. Edwards, who has given freely of his first hand information concerning the northeastern North American forms; to Messrs. E. P. and R. P. St. John who have contributed excellent series of specimens from Florida; to Mr. Glen Chamberlain for certain valuable material from the Gaspé Peninsula and Aroostook County, Maine; to Profs. A. J. Eames, W. C. Muenscher, L. C. Petry, and A. H. Wright, also to Mr. S. H. Burnham, all of whom have ever been ready to encourage and make easier the path of a younger worker; to Miss E. Z. Bailey and Mr. Harold Trapido for reading and criticizing the manuscript; and finally, to all those institutions and individuals whose collections and facilities have generously been placed at his disposal.

SYSTEMATIC TREATMENT

ORDER OPHIOGLOSSALES

FAMILY OPHIOGLOSSACEAE

Ophioglossaceae, Presl. Tent. Pterid. p. 10. 1836.

Ophioglosseae, R. Brown, Prodromus Florae N. Holl. p. 163. 1810.

Perennial herbs, terrestrial or epiphytic; the sporophytes consisting of a short, usually erect rhizome bearing a cluster of stout fibrous roots and one or several leaves, with a bud containing the undeveloped succeeding leaves commonly enclosed in the sheathing base of the stalk of the last expanded leaf; the leaves erect or pendent, usually divided into a sterile leaf-like segment, the blade, and an apparently ventral, but truly lateral, fertile segment or segments; occasionally the leaves either all fertile or all sterile; the venation free or netted; the blades stalked or sessile, simple, lobed, or variously decompound; the fertile segments various, simple, racemose, or paniculate, bearing the naked eusporangiate sporangia laterally, either on the surface of the branches or imbedded in the tissue of the spike; the sporangia bivalvate, producing numerous thick-walled spores; the gametophytes subterranean, branched or unbranched, cylindrical or flattened, normally without chlorophyll, apparently dependent for nourishment upon an endophytic fungus which is found throughout the prothallia as well as in various structures of the mature sporophytes. A family of three distinct genera, widely distributed over the earth, in almost all regions and on all continents.

KEY TO THE GENERA

A. Venation dichotomous, open; the sterile blades usually pinnately or palmately once or several times divided, rarely simple; the sporangia distinct, stalked or sessile, in simple, racemose, paniculate or glomerate spikes. B

  B. Sporangia globose, dehiscing horizontally; the fertile segment usually pinnately divided, paniculate or racemose, rarely simple; the blades either pinnately or palmately decompound, sometimes simple. Gametophytes unbranched or unlobed, simple, cylindrical, or oblong and flattened. I. *Botrychium*

  B. Sporangia ovoid, almost sessile, dehiscing vertically, borne on the many glomerate lobes of the spicate fertile segment; the blades palmately once compound. Gametophytes stout, erect, and lobed below. II. *Helminthostachys*

A. Venation reticulate; the sterile blades simple, sometimes bifurcate towards the apex or palmately lobed; the sporangia dehiscing horizontally, arranged in two lateral rows, sunken in the tissue of the simple, spike-like, fertile segment. Gametophytes branched, cylindrical, usually slender, linear, oblong, ovate or even stellate. III. *Ophioglossum*

The genera of the *Ophioglossaceae* are sometimes considered to represent three progressive stages in an evolutionary reduction series. In such an arrangement, based on characters afforded by the sporophytes, *Botrychium* with open venation and relatively much divided leaf, is accounted the most primitive; *Helminthostachys* intermediate; and *Ophioglossum,* with reticulate venation and little divided leaf, the most advanced.

When the gametophytes are employed as criteria for determining possible phylogeny, the series is reversed, since *Ophioglossum* is primitive with cylindrical branched prothallia, while *Botrychium* has gametophytes which are at once simple unbranched and often somewhat flattened, which is thought to represent a rather advanced or more specialized condition. *Helminthostachys*, with stout somewhat lobed prothallia, would again be intermediate in such a series.

A third arrangement is also possible. If we give credence to the theory of Willis (1922, 1923) that, all other factors being equal (which they are not), the older an organism is, the more time it will have had to spread in all directions over the earth's surface, then we can use present day geographical distribution as an index to possible phylogeny. In such a series, *Ophioglossum*, represented on every continent and major land mass on which conditions permit the growth of vegetation, would seem to be the primitive group. *Botrychium* would then also be primitive, but not so much so as *Ophioglossum*, since this genus is very poorly represented in several of the major land masses, only one species being found in all Africa and only two species in Australia and New Zealand. *Ophioglossum* is widespread and well represented throughout both of these areas. On such a basis, *Helminthostachys*, with its rather more restricted range in the Australasian region, thus might be considered the most advanced genus. Such a consideration might receive some further support from the suggestion of Bower (1896) that in *Helminthostachys* the fertile segment with its short sporangiophores seems to represent a condition derived from *Ophioglossum*.

Bower (1926) has maintained, however, that *Ophioglossum*, particularly because of the reticulate venation and despite the branching gametophytes, represents a more advanced condition than does *Botrychium*. This is the view adopted in this paper, although it is felt that the three modern genera represent widely separated lines of development which must have parted from a hypothetical ancestral stock at a very early period. Probably those forms which exist today represent merely the remnants of a once much more important element of the earth's vegetation, which has disappeared to a large extent because of an inability to adapt itself to the changing environmental conditions, and because of the critical protracted life cycle, which makes the development of these plants extremely slow and possible only under particularly favorable conditions.

Certain species of *Botrychium* are among the most wide-ranging of all vascular plants. *B. Lunaria*, for example, is found on all continents except Africa, both in arctic and antarctic regions. Likewise, forms of *B. multifidum* are almost as widely distributed and there is still question whether some of the geographically isolated elements of the ternate *Botrychia* really deserve specific recognition. These wide-ranging forms of *Botrychium* are here considered to represent the primitive types of the genus, from which the other species have perhaps been derived. It is not postulated that *Ophioglossum* has arisen from such types, but merely that certain of these *Botrychium* species seem to represent a less advanced condition than most of the *Ophioglossum* series.

Helminthostachys is considered somewhat intermediate between *Botrychium* and *Ophioglossum*, but morphologically so unique in many respects that it seems to represent a separate line of development. Its ovoid sporangia which dehisce vertically, its creeping rhizome, and the open venation furnish a combination of characters which render derivation from either *Botrychium* or *Ophioglossum* exceedingly difficult to imagine.

Unfortunately, since the *Ophioglossaceae* are herbaceous forms, they have not been adapted for preservation in the rock strata, hence we have almost no fossil record to help us in determining the phylogeny of the group. Cytological work has been difficult because the chromosome numbers, as in other fern groups, run high. As in the case of the fossil record, cytology has afforded us no clue to the phylogeny of the family. Our speculation must be based solely upon what we know concerning the morphology, taxonomy, and distribution of the modern forms and on what has seemed to be the course of development in other groups.

Although best placed in the *Pteropsida* and considered a true fern group the *Ophioglossaceae* undoubtedly approach the *Lycopodiaceae* in many respects. As Bower (1896) has pointed out and formerly believed, the lycopods most nearly represent the modern prototypes of this primitive family. Additional support might be given to Bower's old hypothesis by what we know of the distribution of the forms in the two families. In both cases there are several species which are unusually wide-ranging and found in nearly all regions of the earth in an almost identical, unmodified form. Such extensive ranges for species is abnormal among vascular plants, and when these ranges coincide to the extent that they do in these two cases, they would seem to indicate a similar past history for the groups involved.

I. Botrychium

Botrychium, Swartz, Journ. für die Botanik. **2**: 110. 1800. Genotype, *B. Lunaria* (L.) Swartz (*Osmunda Lunaria* L.), the first species listed under *Botrychium* by Swartz and apparently the one on which he based his generic concept. Since *B. Lunaria*, which was described in 1542 by Fuchs as *Lunaria minor*, is the oldest known form, it seems also to deserve designation as the type species because of historical priority. The name, which is from the Greek, as given by Swartz, has reference to the resemblance of the fertile segment to a cluster of grapes; hence the common designation, grape-ferns.

Perennial herbs; the sporophytes consisting of a short erect usually unbranched rootstock, thick fleshy roots, and one or several leaves, in the sheathing base of the stalk of the most recent of which, and borne terminally on the rhizome, is the bud from which the leaves for succeeding seasons develop; the leaves consisting of a common stalk and a fertile and sterile segment; the fertile segment seeming to arise from the adaxial surface of the leaf, but truly lateral and morphologically equivalent to the two basal divisions of the blade which have fused and are sporangia bearing, although, in one species, arising, above the base, laterally, from the rachis of the blade, in place of one of the sterile pinnae; the blades sessile or stalked, exceedingly diverse in form, varying from simple and entire to pinnately or palmately once to many times decompound; the venation dichotomous, open; the fertile segment of two parts, a stalk and the "spike" which is either simple or more frequently branched, with the naked globular distinct sporangia borne laterally on its branches; the sporangia dehiscent horizontally by two valves, producing numerous reticulate or verrucose yellowish thick-walled spores; the gametophytes small subterranean bodies, cylindrical or oblong and flattened, unbranched, entirely destitute of chlorophyll and dependent for nourishment on a mycorrhizic fungus. A genus of 23 species, found in suitable places in all of the major geographical regions of the earth.

The species of *Botrychium* fall naturally into three subgenera, based on characters afforded by vernation, the division of the leaf, and the gametophytes. The ternate-leaved forms are here placed in the subgenus *Sceptridium*. Because of their very wide and general distribution, their relatively large much divided leaves, and the type of development of the sporophyte with the presence of a suspensor and the primary root developing down through the gametophyte, they seem to represent the most primitive division of the genus. Lyon (1905) proposed this group of species as a new genus on a basis of the presence of the suspensor, the penetration of the gametophyte by the primary root, and the almost basal parting of the fertile and sterile segments, but Eames (1936) has recently pointed out that these characters are scarcely sufficient to warrant generic segregation. Since we know the gametophytes of only two of the twelve species in this subdivision, and since detailed anatomical studies have been made of only one variety of one of these species, a non-taxonomist who meddles with the classification of this group in the light of such information, is indeed on dangerous ground. Certainly, the gross morphological details of the twelve species constituting *Sceptridium* do not afford a basis for generic segregation. Further, there are species in this subgenus which have characters tending towards *Eubotrychium* and other species with characters tending towards *Osmundopteris.* Sharp lines can not be drawn, therefore, between genera that may be segregated from *Botrychium.* It has consequently seemed better to retain the three major groups of species as subgenera.

The subgenus *Eubotrychium* has a much more limited distribution than does *Sceptridium*, being largely Holarctic, although two species are also represented in southern South America and Australia. The sterile blades in this subgenus are small, perhaps as a result of reduction. In the case of one variety of *Botrychium simplex*, the sterile lamina is regularly very poorly developed and mature sporophytes, shedding spores, have been found with the gametophytes still attached and perhaps serving as a source of nourishment for the reduced aerial portions. The gametophytes are small, somewhat flattened bodies; the embryos are without suspensors and the primary roots develop without penetration of the prothallia.

Osmundopteris, with large much divided leaves and buds which are exposed at least in part and usually hairy, is the most fern-like of the *Botrychium* subgenera and perhaps represents the most advanced division of the genus. Although the much divided leaf and cylindrical gametophytes are indeed primitive characters, yet a suspensor is absent, while in the bud, the fertile and sterile segments are both completely reflexed as in *B. lanceolatum* and most species of *Sceptridium.* It has been thought that this reflexed condition of the leaf represents a derived condition and that the condition as found in *B. Lunaria* and *B. simplex*, in which the leaves are erect in vernation, is more primitive. The fact that *Osmundopteris* has never been found in the Australian Region or in southern South America has seemed another indication that this group of species is not as old as the others.

Just as the three genera of the Ophioglossaceae seem to represent three widely separated lines of development, so the three major subdivisions of *Botrychium* likewise represent distinct evolutionary series, but there do exist species which at least in part bridge the gap between these series, hence these divisions are treated as subgenera.

KEY TO THE SUBGENERA OF BOTRYCHIUM

I. Sterile blades various, but not at once lax and membranous, broadly deltoid and sessile. Bud hairy or smooth, completely enclosed by the sheathing base of the stalk. II

II. Sterile blades rather large, ternately decompound, long stalked to sessile, usually inserted towards the base of the plant, but sometimes arising rather high up; the buds commonly hairy, but rarely almost glabrous, with the leaves sometimes completely reflexed. Gametophytes where known, flattened dorsiventrally, with a suspensor present in the embryo and the root emerging from the lower surface of the prothallium. A. Subgenus *Sceptridium*

II. Sterile blades usually small, pinnately or palmately divided, rarely simple, sessile or short stalked, parting from the common stalk at various heights. Buds glabrous, with the leaves erect, partially inclined or completely reflexed, depending upon the species. Gametophytes small, somewhat flattened; the primary root developing above and to the side of the prothallium. B. Subgenus *Eubotrychium*

I. Sterile blades sessile, large, deltoid, much divided, often rather thin in texture. Bud hairy, partially exposed by the sheathing base of the stalk, which is open on one side. Gametophytes short cylindrical. C. Subgenus *Osmundopteris*

A. Subgenus **Sceptridium** (Lyon) Clausen, n. stat.

Botrychium, section *Phyllotrichium*, subsection *Ternata* Prantl, Jahrb. Bot. Gart. Berlin **3**: 336. 1884.

Sceptridium Lyon, Bot. Gaz. **40**: 457. 1905. Genotype *Botrychium obliquum* Muhl. *Sceptridium* is derived from the Greek and is in allusion to the scepter like fertile segment.

This, the section of the ternate grape ferns, includes twelve species, some of which are of extremely wide distribution.

KEY TO THE SPECIES OF SCEPTRIDIUM

A. Segments of blade all of about same size and shape; ovate, obovate, rhomboid, or oblong; the chief terminal divisions not elongate. Blades fleshy or membranous. B

B. Ultimate divisions of the sterile blade ovate, rhomboid, oblong, or oblanceolate, rarely flabellate, and if so, then all of the divisions not uniform in this respect. Tips of the chief terminal divisions acutish or obtuse, rarely rounded. a. Section *Multifidae* C

C. Sterile blades either very fleshy or somewhat so, with the margins slightly hyaline and with the ultimate divisions acutish or obtuse at the tips and either crenate or entire. D

D. Ultimate divisions of blade relatively large, 4–20 mm. long, 3–10 mm. broad. 1. *B. multifidum*

D. Ultimate divisions of blade small, 1–8 mm. long, 1-5 mm. broad. E

E. The three major divisions of the blade relatively (in proportion to the size of the plants) long stalked, 0.5–7 cm., the ultimate divisions obtuse or acutish. Plants of New Zealand, Australia, and southern South America. 2. *B. australe*

E. The three major divisions of the blade not particularly long stalked, 0.7–4 cm.; the ultimate divisions obtuse. Plants of Central America and of northern and central South America. 3. *B. Schaffneri*

C. Sterile blades membranous, with the margins *not* hyaline and with the ultimate divisions ovate to oblong, *acutish*, usually serrate, rarely entire. Plants lax. 4. *B. ternatum*

B. Ultimate divisions of the sterile blade decidedly and consistently flabellate, broad and rounded at the apex, but contracted to an abrupt cuneate base. Tips of the chief terminal divisions broad and rounded. b. Section *Biternatae* F

F. Buds only sparsely hairy, almost glabrous; plants low, with the blades short stalked, almost prostrate on the ground; spores maturing in late winter or early spring. Plants of the southeastern United States. 5. *B. biternatum*

F. Buds very hairy; plants various, usually rather large and often lax. G

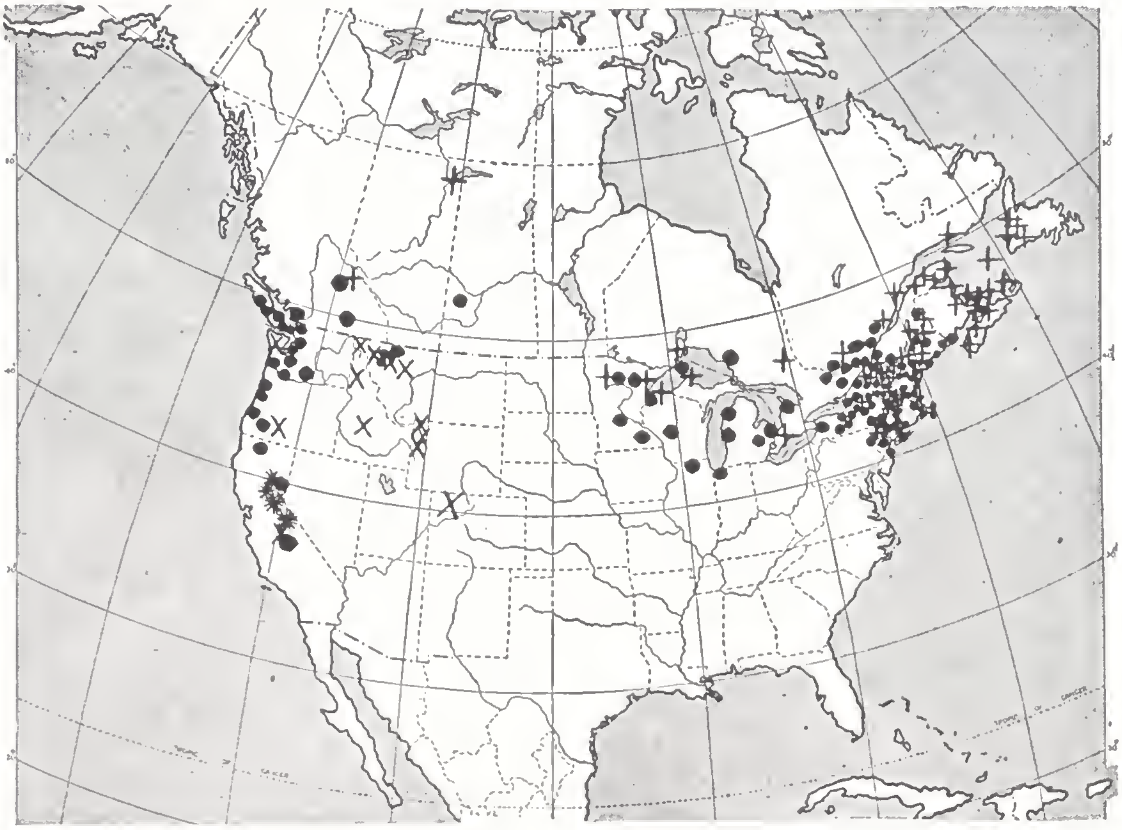


Fig. 1 (above). *Botrychium multifidum* in North America; ssp. *silaifolium* (•), ssp. *typicum* (+), ssp. *Coulteri* (X), and ssp. *californicum* (*).

Fig. 2 (lower left). *Botrychium Schaffneri* var. *typicum* (•), var. *pusillum* (+).

Fig. 3 (lower right). *Botrychium dissectum* var. *oneidense.*

G. Plants *slender*, with the blades membranous and lax; the ultimate divisions obovate or flabellate. H

  H. Blade inserted basally, far surpassed by the fertile segment, which is commonly two to four times the length of the sterile segment. Sterile stalk averaging about 2 cm. in length. 6. *B. Jenmani*

  H. Blade inserted suprabasally, surpassed by the fertile segment for only one half its length. Sterile stalk averaging about 6 cm. in length. 7. B. *alabamense*

G. Plants rather stout, with the blades leathery and firm; the ultimate divisions obovate to spatulate. 8. *B. Underwoodianum*

A. Segments of blade not all of the same size and shape, but with the chief terminal divisions usually elongate and little divided. Blades either membranous or slightly fleshy. c. Section *Elongatae*

I. Sterile blade inserted towards the base of the plant, never medianly. J

  J. Ultimate divisions of blade ovate, oblong, or lanceolate, entire or finely toothed, in one form much dissected. Usually only one leaf expanded during a season. K

    K. Plants somewhat fleshy or membranous; the divisions of the blade entire, finely serrate, or crenate, in one form much dissected. Plants of eastern North America. 9. *B. dissectum*

    K. Plants delicate and membranous; the divisions of the blade prominently and *sharply* serrate. Plants of Japan and eastern Asia. 10. *B. japonicum*

  J. Ultimate divisions of blade oblong to obovate, lacerate at apex; the rachis winged. Two leaves commonly expanded during a season. Plants of the Hawaiian Islands. 11. *B. subbifoliatum*

I. Sterile blade usually inserted medianly, the fertile segment either equalling or only slightly exceeding the sterile segment; the ultimate divisions conspicuously and sharply toothed. 12. *B. daucifolium*

a. Section **Multifidae,** n. sect.

Multifidae, sectio nova subgeneris *Sceptridii* segmentis ultimis laminae sterilis in amplitudine et forma omnibus similibus, ovatis obovatis vel rhombeis, divisionibus penultimis non elongatis, laminis carnosis aut membranaceis.

This section is characterized by the division of the sterile blade into ultimate segments of essentially uniform size and shape, with the penultimate segments not elongate. It includes three species of temperate regions and one found in tropical lands only at high altitudes.

1. BOTRYCHIUM MULTIFIDUM (Gmel.) Rupr. *Figure 1.*

This circumboreal species is composed of five distinct elements, which in their extreme conditions are decidedly dissimilar, but which, since they pass insensibly from one into the other, can not be kept apart or sharply differentiated. The species is characterized by its rather fleshy texture, which attains its most decided development in the ssp. *Coulteri* of the Rocky Mountain Region of western North America. The fleshy blade is ternately compound, with the ultimate divisions varying from ovate to rhomboid, obovate, or even rarely flabellate. In the large size of these divisions, 4–20 mm. long by 3–10 mm. broad, the species is easily separable from both *B. Schaffneri* and *B. australe*, which commonly have much smaller ultimate segments, while the stout habit at once distinguishes it from *B. ternatum* of eastern Asia.

The widespread large-leaved ssp. *silaifolium* is considered the morphological type of the species, from which the smaller more compacted ssps. *robustum* and *typicum* seem to have been derived, while in northern California, the large lax-leaved ssp. *californicum* seems to have developed as a response to an extremely favorable environmental condition. The five subspecies may be distinguished as follows:

A. Blades coriaceous, large or small, with the ultimate divisions usually of moderate size, 3–10 mm. long, 3–8 mm. wide. B

B. Plants stout and fleshy, but not extremely so; the sterile blades relatively long stalked, the stalks 1–11 cm. long. C

C. Plants rather large, 15–42 cm. high; the blades 7–15 cm. long, 3–21 cm. wide; the ultimate divisions usually rather remote and not imbricate. 1a. *B. multifidum* ssp. *silaifolium*

C. Plants of medium or small size, 5–25 cm. high; the blades 1–7 cm. long, 1–8 cm. wide; the ultimate divisions usually somewhat crowded and sometimes overlapping. D

D. The divisions of the sterile blade commonly obtuse or rounded at the tips; the plants mostly glabrous. 1b. *B. multifidum* ssp. *typicum*

D. The divisions of the sterile blade acutish; the plants sparingly hairy. 1c. *B. multifidum* ssp. *robustum*

B. Plants very stout and decidedly fleshy; the common stalks 0.5–1.5 cm. thick; the divisions of the blade small and closely crowded, often imbricate; the sterile blades short stalked, the stalks 1–4 cm. long. 1d. *B. multifidum* ssp. *Coulteri*

A. Blades semi-membranous, large and lax, 15–24 cm. long, 21–35 cm. wide, with the ultimate divisions oblong-obovate, blunt, minutely serrate, 1–2 cm. long, 0.5–1 cm. wide. 1e. *B. multifidum* ssp. *californicum*

1a. BOTRYCHIUM MULTIFIDUM ssp. SILAIFOLIUM (Presl) Clausen

Botrychium silaifolium Presl, Rel. Haenk. **1**: 76. 1825. Based on a specimen from the region of Nootka Sound, which is preserved in the herbarium at Prague. A rather poor photograph of the type specimen is filed in the herbarium at the New York Botanical Garden.

Botrychium ternatum B) *Australasiaticum* α *vulgare* Milde (in part), in Verh. zool. bot. Ges., Wien. **19**: 157. 1869.

Botrychium ternatum var. *australe* (in part) and subvar. *intermedium* D. C. Eaton, Ferns of North America. **1**: 149. 1879. Eaton erroneously considered our two largest North American grape ferns to be the same as Robert Brown's *B. australe* of New Zealand. In the plate illustrating these two varieties, three drawings are presented, the one superimposed upon the other. The uppermost of these is designated as subvar. *intermedium* and is based on a plant collected in New Hampshire. This clearly represents the subspecies that is widespread across the northern United States and southern Canada and which is the same as Presl's *B. silaifolium*. The middle figure is designated as var. *australe*, based on a specimen from northern New York, but it is simply a somewhat larger, better developed example of the same thing that is illustrated in the top figure. The bottom drawing is of a specimen collected in Plumas County, California, by Mrs. Lewis. This too is labelled var. *australe*, but it is the plant which was later described as *B. californicum* by Underwood, who cited this illustration in his original description of the species. Eaton's var. *australe*, then, consists of two elements, the one well developed *B. silaifolium* of Presl and the other *B. californicum* of Underwood, while the subvar. *intermedium* represents a somewhat less well developed *silaifolium*. The var. *intermedium* is here dropped because it seems to possess no distinctive characters of its own, but simply represents an intermediate condition between large forms of ssp. *silaifolium* and the small ssp. *typicum*. Such intermediates are to be expected in a region where the ranges of two subspecies overlap.

Botrychium occidentale Underwood, in Bull. Torrey Club **25**: 538. 1898. Based on specimens collected at New Westminister, British Columbia, by Mr. A. J. Hill. The type is at the New York Botanical Garden. Underwood at first wrongly interpreted Presl's *B. silaifolium* as the same as the large subspecies from California and accordingly described the plants from British Columbia as new. Later, realizing that his species and *silaifolium* were the same, he relegated *occidentale* to synonymy and described the California plants as a new species, *B. californicum*.

Botrychium obliquum intermedium Underwood, Native Ferns, ed. 6. p. 72. 1900.

Botrychium ternatum obliquum f. *intermedium* (D. C. Eaton) Clute, in Fern Bull. **11**: 116. 1903.

Botrychium ternatum silaifolium Clute, in Fern Bull. **11**: 117. 1903.

Sceptridium silaifolium (Presl) Lyon, in Bot. Gaz. **40**: 458. 1905.

Sceptridium obliquum intermedium (Underw.) Lyon, in Bot. Gaz. **40**: 458. 1905.

Botrychium ternatum obliquum f. *silaifolium* (Presl) Clute, in Fern Bull. **13**: 118. 1905.

Botrychium ternatum var. *intermedium* D. C. Eaton of Gray's Manual. ed. 7. p. 49. 1908.

Botrychium ternatum var. *silaifolium* (Presl) M. E. Jones, in Bull. Univ. Montana, Biol. Ser. **15**: 8. 1910.

Botrychium multifidum var. *australe* (D. C. Eaton) O. A. Farwell, in Rep. Mich. Acad. Sci. **18**: 86. 1916.

Botrychium multifidum var. *intermedium* (D. C. Eaton) O. A. Farwell, in Rep. Mich. Acad. Sci. **18**: 87. 1916.

Botrychium multifidum ssp. *silaifolium* (Presl) Clausen, in Bull. Torrey Club **64**: 271. 1937.

Plant fleshy, rather large, 10–45 cm. high; sterile blade coriaceous, 7–21 cm. broad, 3–15 cm. long, ternately decompound, with the ultimate divisions not closely crowded, varying from oblong to obovate or ovate, 4–10 mm. long by 4–8 mm. wide, usually slightly crenate; blade parting from the fertile portion low down, with the sterile stalk 1–11 cm. long; fertile spike long stalked, decompound; bud very hairy, both the blade and the fertile portion completely reflexed in vernation. The gametophyte has never been described.

The spores are shed commonly during August and September, which is one to two months earlier than the fruiting time of the varieties of *B. dissectum*. Since *B. dissectum* is the only other species of *Sceptridium* that occurs within the range of this subspecies, early fruiting can be used as a field character indicating ssp. *silaifolium*.

Besides the other subspecies of *B. multifidum*, with all of which the ssp. *silaifolium* intergrades freely, the only other form with which it might be confused is the var. *oneidense* of *B. dissectum*, which is easily distinguished by the elongate penultimate segments, membranous texture, and later fruiting period. While there is no evidence that ssp. *silaifolium* and var. *oneidense* intergrade, occasional specimens are found that are difficult to place. Whether these represent hydrids, an actual intermediate population, or otherwise, is not known. Since these puzzling specimens are usually small undeveloped forms, it has been thought that they represent abnormal variations of the one species or the other and hence no great significance has been attached to their occurrence. Further, no fully developed specimens have been seen which could not easily be placed in the one species or the other.

This is a plant of open fields and pastures in southern Canada and the northern United States, but at the southern part of its range it prefers wooded hillsides and rich woods where it often becomes quite lax and the blade loses much of its leathery quality. This subspecies ranges from western New Brunswick, Maine, and central Quebec south to northern New Jersey and Pennsylvania and west to British Columbia, Washington, Oregon, and northern California. In New England and eastern Canada it passes insensibly into the ssp. *typicum*, while in northwestern British Columbia it passes into ssp. *robustum*. The northern limits of its range are still poorly worked out, while its status between Minnesota and western Montana is not known. The available data would seem to indicate that this subspecies reaches its greatest abundance in New England, central and northern New York, southern Quebec, and on the Pacific coast in western Washington, Oregon, and southern British Columbia. According to Mr. E. W. Graves (1931), who studied material at several of the mid-western herbaria which have not been available to the writer, there are specimens indicating that this subspecies is fairly common in northern Wisconsin and Minnesota, also that it occurs in Iowa.

NEW BRUNSWICK. Charlotte: Grand Manan, *C. A. & U. F. Weatherby 5546* (G, Ot).

QUEBEC. Southern, central, and western counties: Valcartier, Quebec County, and Hatley, Stanstead County; Chambly, Champlain, Deux Montagnes, Gatineau, Missisquoi, Montcalm, Montreal, Papineau, Pontiac, Richelieu, Terrebonne, and Vercheres Counties.

ONTARIO. Algoma, Grey, Leeds, Renfrew, and Russel Counties.

MANITOBA. ———: *E. S. Thompson* (M).

SASKATCHEWAN. South Battleford: Battleford, *J. M. Macoun 28586* (Ot).

British Columbia. Alberni, Cariboo, Nanaimo, and West Kootenay Counties.

Maine. The writer has examined specimens from all counties except Knox, Sagadahoc, and Waldo.

New Hampshire. All counties except Belknap, Strafford, and Sullivan.

Vermont. All counties except Essex, Franklin, Grand Isle, and Orange.

Massachusetts. Barnstable, Berkshire, Bristol, Essex, Franklin, Hampshire, Middlesex, Nantucket, and Norfolk Counties.

Connecticut. Fairfield, Litchfield, and New Haven Counties.

New York. Cayuga, Chemung, Delaware, Dutchess, Essex, Franklin, Greene, Hamilton, Herkimer, Lewis, Oneida, Onondaga, Oswego, Otsego, St. Lawrence, Saratoga, Steuben, Tompkins, Ulster, Warren, and Washington Counties; also, there is questionable material from Erie, Orange, and Suffolk Counties.

New Jersey. Monmouth, Morris, Sussex, and Warren Counties; see Clausen (1937a).

Pennsylvania. Monroe?: Pocono Plateau, *J. W. Harshberger* (G, M, Penn, Ph). The writer has also seen a doubtful specimen from Berks County.

Ohio. Listed from the northern part by Graves (1935), but no specimens have been seen by the writer.

Indiana. Porter: Tremont, *M. W. Lyon, Jr.* (Lyon); Dunes State Park, *R. M. Tryon, Jr. 2355* (Deam). According to Graves (1931), there is in the herbarium of the University of Indiana, a specimen from Millers, Lake County.

Illinois. Winnebago: Shirland, *H. A. Gleason* (G).

Michigan. Keweenaw, Leelanau, Muskegon, Oakland, and Saint Clair Counties.

Wisconsin. Bayfield, Douglas, Florence, and Juneau Counties.

Minnesota. Hubbard, Itasca, and Wright Counties.

Iowa. Graves (1931) cites a specimen from Fayette, Fayette County, in the herbarium at the State Agricultural College at Ames.

Montana. Flathead and Lake Counties.

California. The writer has seen typical material from Plumas and Tulare Counties, also a doubtful specimen from Siskiyou County.

Oregon. Coos, Lane, Klamath, and Lincoln Counties.

Washington. Clarke, Pierce, Snohomish, Wahkiakum, Whatcom, and Yakima Counties.

1b. BOTRYCHIUM MULTIFIDUM (Gmel.) Rupr., ssp. TYPICUM

Osmunda multifida Gmel., in Nov. Comment, Acad. Petrop. **12**: 517. 1768. Described from Russian material and based on *Lunaria racemosa multifido folio* Breyn. Cent. I, p. 184, pl. 95. The name is apparently in allusion to the division of the blade into many small segments.

Osmunda Matricariae Schrank, Baier. Flora **2**: 419. 1789. Based on specimens from Bavaria and on *Lunaria racemosa multifido folio* CBP, 355.

Botrychium rutaceum Swartz (in part), in Schrad, Journ. für die Botanik **2**: 110. 1800. Based on *Lunaria racemosa multifido folio* Breyn., *Osmunda Lunaria* $\beta\gamma$ L., *Osmunda lanceolata* Gmel., and *Osmunda Matricariae* Schrank.

Osmunda bavarica Schmid, in Hoppe, Bot. Taschenb. p. 7. 1803. Based on material from Bavaria and said to fruit there from July to September.

Botrychium matricarioides Willd., Sp. pl. **5**: 62. 1810. Based on *Osmunda Matricariae* Schrank.

Osmunda matricarioides (Willd.) Poir., in Lam., Enc. Suppl. **4**: 233. 1816.

Botrychium matricarianum J. E. Smith, in Rees, The Cyclopaedia **39**: no. 3. 1819.

Botrychium Matricariae (Schrank) Spr., Syst. veg., ed. 16, **4** (part 1): 23. 1827.

Botrychium rutaefolium A. Br. in Döll, Rhein. Flora. p. 24. 1843. Described from the upper Rhine Valley. *B. matricarioides* Willd. and *B. Matricariae* (Schrank) Sprengel are listed as synonyms.

Botrychium Breynii Fries, Summa Vegetabilium **1**: 252. 1846. *B. matricarioides* Willd. is given as a synonym.

Botrychium silesiacum Kirschleger, Flora d'Alsace, v. **2**: 401. 1857. Based on *Lunaria botrytes ramosa silesiaca* of J. Bauhin. *B. matricarioides* Willd., *B. rutaefolium* A. Br., *B. rutaceum* Wahl., and *Lunaria racemosa multifido folio* Breyn. are also listed as synonyms.

Botrychium multifidum (Gmel.) Rupr., in Beitr. zur Pflanzenkunde des Russ. Reiches. **11**: 40. 1859.

Botrychium Backeanum Brockmuller, in Arch. Ver. Fr. Nat. Mecklb. **17**: 170. 1863.

Botrychium ternatum a) *Europaeum* Milde, in Verh. zool. bot. Ges. **19**: 146. 1869.

Botrychium ternatum var. *rutaefolium* (A. Br.) D. C. Eaton, Ferns of North America. **1**: 149. 1879.

Botrychium obliquum var. *rutaceum* (Sw.) Waters, Ferns. p. 335. 1903.

Botrychium ternatum obliquum f. *matricariae* (Schrank) Clute, in Fern Bull. **13**: 118. 1905.

Sceptridium matricariae (Schrank) Lyon, in Bot. Gaz. **40**: 458. 1905.

Botrychium multifidum var. *dichotomum* Farwell, in Rep. Mich. Acad. Sci. **18**: 87. 1916. The accompanying plate depicts a specimen which is obviously a monstrosity.

Botrychium multifidum var. *simplicius* Farwell, in Papers Mich. Acad. Sci. Arts and Letters **3**: 89. 1924. Based on small specimens from Keweenaw County and Algonac, Saint Clair County, Mich. Dr. O. A. Farwell has kindly loaned, from his private herbarium, the type of this variety, which the writer has been unable to distinguish from *B. multifidum* ssp. *typicum*.

Woynar (1913) has argued that *Lunaria Silesiaca* C. J. Trew (1757) is the earliest binomial name to have been applied to the species, but this designation, occurring as it does in the text of a paper in which binomial nomenclature has not been followed, represents a chance abbreviation and not a valid binary combination. According to Art. 68, Sect. 4 of the International Rules of Botanical Nomenclature, "specific names are illegitimate and must be rejected when they were published in works in which the Linnaean system of binary nomenclature for species was not consistently employed."

Plant 5–20 cm. high; common stalk short, 4–35 mm. long; sterile stalk 1–4 cm. long; blade 1–5 cm. long, 1–8 cm. wide, with the ultimate divisions crowded, sometimes imbricate, varying from flabellate to ovate and acutish; fertile stalk 2.5–11 cm. long; fruiting spike paniculate, 1.2–7 cm. long; sporangia 0.8–1 mm. in diam.; spores maturing during August and September. The gametophytes were figured by Milde (1858a), who named plants with these present as forma *tuberosum*.

This subspecies is similar to ssp. *silaifolium*, but much smaller and more compact, with the ultimate divisions of the blade blunter and more crowded. In the area where the ranges of these two subspecies overlap, there is a complete intergradation between the two forms and it is frequently impossible to place specimens in the one category or the other. Small, compacted individuals of the varieties of *B. dissectum* are sometimes difficult to separate from this, but usually in that species some of the divisions of the blade are elongate, while the spores are shed at a later period.

This is a plant of exposed meadows, sterile fields, beaches, sandy open places, and grassy hillsides. It is widely distributed in northern Europe and Asia, but apparently nowhere common. In North America it ranges from Labrador and Newfoundland south to Maine, New Hampshire, Vermont, western Massachusetts (doubtfully), and northern New York, with one questionable outpost in the western Catskills; and west to northern Wisconsin, Minnesota, and Alberta. There is also a collection from eastern British Columbia which has seemed best referred here. It is thought that this subspecies probably has a continuous distribution across central Canada, but insufficient collecting probably explains the present lack of data concerning this region. The ssp. *typicum* definitely does not occur as far south in North America as Virginia, as stated by Christensen and Hultén (1928). The northern limits of the range are entirely unknown, as are the relationships between this form and the ssp. *robustum*.

LABRADOR. Sand beaches among grass near salt water, *W. Palmer* (U).

NEWFOUNDLAND. Districts of Bonne Bay, Burgeo and La Poile, and St. Georges Bay.

PRINCE EDWARD ISLAND. Kings, Prince, and Queens Counties.

NOVA SCOTIA. Cape Breton, Colchester, Cumberland, Digby, Inverness, and Kings Counties.

NEW BRUNSWICK. Gloucester and Kent Counties.

QUEBEC. Bonaventure, Chambly, Gaspé (including Magdalen Islands), Labelle, Matane, Quebec, Rimouski, Saguenay and Stanstead Counties.

ONTARIO. Elgin County, also Nippissing and Thunder Bay Districts.

ALBERTA. Sand Point, Lake Athabasca, *H. M. Raup* and *E. C. Abbe 601* (H, Ny, Ot).

BRITISH COLUMBIA. East Kootenay: Glacier, *S. Brown 647* (Ph).

MAINE. Aroostook, Franklin, Kennebec, Penobscot, Piscataquis, and Somerset Counties.

NEW HAMPSHIRE. Coos and Hillsborough Counties.

VERMONT. Addison, Bennington, Caledonia, Chittenden, Orleans, Rutland, and Washington Counties.

MASSACHUSETTS. Berkshire: questionable material from Tyringham, *F. Kobbe* (N).

Fig. 4. *Botrychium multifidum* ssp. *robustum* from Alaska ($\times \frac{1}{3}$).

New York. Essex, Franklin, and Herkimer Counties. The writer has also studied doubtful material from Lake Shandelee, Sullivan County, *P. Wilson* (NY).

Michigan. Keweenaw: Allouez, *F. J. Hermann 7677* (NY).

Wisconsin. Ashland: LaPointe, ——— (M).

Minnesota. Clearwater and St. Louis Counties.

Norway. The writer has examined material from Isterdalm and from Storboekken, District of Hedmark.

Sweden. The writer has examined specimens from the Läns of Alfsborg, Gafleborg, Gotland, Kopparberg, Norrbotten, Västerbotten, and Västernorrland.

France. Reported by various authors from the eastern districts.

Denmark. In wet sand, *C. Baun* (M).

Germany. The writer has seen specimens from Pomerania and Silesia.

Danzig. (M).

Austria. Salzburg: Salzburg, ——— (M).

Czechoslovakia. Districts of Moravia and Szepes.

Roumania. Bukowina: Pojana-Stampi, *J. Dörfler 2303* (G, M).

Finland. District of Oulon, also Savonia Borealis.

Russia. Leningrad: Luga, *E. Czerniakovska-Reinecke 149* (Ph). Cykarbon, ——— *2598* (Ph).

Siberia. Tomsk: Tomsk, *L. Sergievskaja* (NY).

China. Yunnan: ———, *M. l'abbé Delavay 2921* (NY). District of Tchen-keou-tin, Su-tchuen, *R. P. Farges* (NY).

1c. BOTRYCHIUM MULTIFIDUM ssp. ROBUSTUM (Ruprecht) Clausen. *Figure 4.*

Botrychium rutaefolium var. *robustum* Rupr., according to Milde, in Nova Acta **26**: 763. pl. 55, f. 9. 1858. The figure illustrates the form which is the characteristic element in eastern Siberia and Alaska.

Botrychium rutaceum var. *robustum* Rupr., in Beitr. zur Pflanzenkunde des Russ. Reiches. **11**: 40. 1859.

Botrychium robustum (Rupr.) Und., in Bull. Torrey Club **30**: 51. 1903. Stated to occur in Kamtchatka and Unalaska.

Sceptridium robustum (Rupr.) Lyon, in Bot. Gaz. **40**: 458. 1905.

Botrychium ternatum obliquum f. *robustum* (Rupr.) Clute, in Fern Bull. **13**: 118. 1905.

"*Botrychium ternatum* ssp. *robustum* (Rupr.) Komarov, Fl Pen. Kamtchatka **1**: 77. 1927."

Botrychium multifidum var. *robustum* (Rupr.) C. Chr., in Kungl. Sv. Vet. Akademiens Handlingar. **5** (1): 49. pl. 3. 1928.

Botrychium multifidum ssp. *robustum* (Rupr.) Clausen, in Bull. Torrey Club **64**: 272. 1937.

Plant similar to ssp. *typicum*, but larger, with blade and fertile stalk sparingly covered with lax brownish hairs and with blade differently cut. Sterile stalk 2–6 cm. long; blade 5–8 cm. broad, 4–7 cm. long, with the apices of the penultimate divisions usually not divided to the midrib, *acutish* and crenulate. Fertile stalk 6–12 cm. long; spike 3–4.5 cm. long, 2–3 cm. wide; sporangia 0.5–1.0 mm. in diameter.

Fig. 5. *Botrychium multifidum* ssp. *californicum* from Plumas County, California. Specimen from the type collection ($\times\frac{1}{3}$).

A little known subspecies, whose relationships with ssp. *typicum* and ssp. *silaifolium* are still not clear. It is poorly represented in American herbaria. From the literature it is inferred that this subspecies ranges from southern and western Alaska west to eastern Siberia and south to Kamtchatka, northern Japan, and Corea.

Christensen and Hultén (1928) state that it is characteristic of the meadow association in South Kamtchatka, also that "the Kamtchatkan form is intermediate between *B. silaifolium* and the European *B. multifidum.*"

ALASKA. Unalaska Island, *L. M. Turner* (Deam, G, M, NY, Ph).

1d. **Botrychium multifidum** ssp. **Coulteri** (Underwood), n. comb.

Botrychium Coulteri Underwood, in Bull. Torrey Club **25**: 537. 1898. The type specimen is at the New York Botanical Garden. It is the collection of P. A. Rydberg and E. A. Bessey, Aug. 7, 1897, from geyser formations, near a stream, in open places in Yellowstone National Park. The species was named in honor of its original collector, Dr. John M. Coulter, who first secured specimens at Lower Fire Hole Basin in 1872.

Botrychium ternatum obliquum f. *Coulteri* (Underw.) Clute, in Fern Bull. **11**: 116. 1903.

Sceptridium Coulteri (Underwood) Lyon, in Bot. Gaz. **40**: 457. 1905.

Botrychium ternatum var. *Coulteri* (Underw.) Jones, in Bull. Univ. Montana, Biol. Series **15**: 7. 1910.

Botrychium silaifolium var. *Coulteri* (Underw.) Jepson, Manual of the Flowering Plants of California, p. 26. 1923.

Plant very stout and decidedly fleshy, compact, 15–23 cm. high; common stalk 2–5.5 cm. long, 0.6–1.5 (2.) cm. thick; sterile stalk 1–4 cm. long; blade 7–15 cm. wide, 6–9 cm. long, with the ultimate divisions small and crowded, often imbricate, ovate, oblong or obovate, 4–6 (10) mm. long, 3–6 mm. wide; fertile stalk 6–17 cm. long; fruiting spike dense, about 5 cm. long; sporangia averaging about 1.2 mm. in diameter The spores are shed during July and August. Apparently the gametophyte is unknown.

In its extreme condition, the ssp. *Coulteri* is easily distinguished from any of the other *multifidum* subspecies by its decidedly stout character, but it passes by a series of almost insensible intergradations into the ssp. *silaifolium*, which is the prevailing form of the species along the Pacific Coast from British Columbia to northern California. In this far western region, the ssp. *Coulteri* is known at present only from scattered localities in Washington, Oregon, and California, also perhaps Colorado, while it reaches its best development in northwestern Wyoming, Idaho, and western Montana, where it is characteristically a plant of geyser formations and grassy meadows.

MONTANA. Flathead: Columbia Falls, *R. S. Williams 1044* (NY). Teton: Teton Range, *J. S. Coulter* (U).

IDAHO. Blaine: Redfish Lake, *L. F. Henderson 3715* (U). Bonner: Priest Lake, *D. T. MacDougal 234* (NY). Latah: Moscow, *L. F. Henderson* (U).

WYOMING. Teton: Leigh's Lake, *E. D. Merrill & E. N. Wilcox 1175* (G, NY). Yellowstone National Park: *P. A. Rydberg & E. A. Bessey* (G, NY, Ph).

COLORADO. Routt: Steamboat Springs, *Alice Eastwood* (Herb. Univ. Colo.).

CALIFORNIA. Placer: ? Tahoe, *F. J. Smiley 386* (G). Tulare: Sequoia National Park, *H. E. & S. T. Parks 0398* (C, G, M, Herb. Univ. Colo.).

OREGON. Klamath: Klamath Marsh, *W. C. Cusick 2996* (C, G, M, NY, U). This collection matches the type in all respects.

WASHINGTON. Foothills of the Olympic Range, *J. M. Grant 115* (G).

1e. **Botrychium multifidum** ssp. **californicum** (Underwood), n. comb. *Figure 5.*

Botrychium ternatum var. *australe* D. C. Eaton (in part), Ferns of North America. **1**: 149. 1879.

Botrychium californicum Underwood, in Torreya **5**: 107. 1905. Based on a series of specimens collected at Quincy, in the Sierra Nevada Mountains, Plumas County, California, by Mrs. R. M. Austin on July 2, 1897. Three sheets of this series in the herbarium of the New York Botanical Garden have been designated as types. The blades of these plants are rather membranous, very large, and with the ultimate segments large and conspicuously serrate. The specific name alludes to the state of California.

Sceptridium californicum (Underwood) Lyon, in Bot. Gaz. **40**: 457. 1905.

Botrychium silaifolium var. *californicum* (Underw.) Jepson, Manual of the Flowering Plants of California, p. 26. 1923. Said by Jepson to range from Mariposa County to Plumas and Modoc Counties and to be rather stout and fleshy, but Underwood's types are decidedly not fleshy, although his original description might give the impression that they were. Jepson has described a plant which is often seen in collections from California, which is a large, rather fleshy affair, somewhat intermediate in appearance between ssps. *silaifolium* and *Coulteri*, with short common stalk and well developed blade, but this does not match the type of *californicum*. In the present treatment, some of the collections of *californicum* sensu Jepson have been referred to ssp. *silaifolium*, others to ssp. *Coulteri*. The ssp. *californicum* is here reserved only for the kind of specimens typified by Mrs. Austin's Plumas County material.

Plant very large; blade 20–35 cm. broad, 15–25 cm. long, lax, semi-membranous, with the ultimate divisions oblong-ovate, elliptical or oblong, acute to obtuse, minutely serrate to denticulate, large, 1–2 cm. long, 0.5–1 cm. wide; sporangia 0.6–0.8 mm. in diameter, brown, with the valves wide spreading in dehiscence. Apparently matures spores during July and August. The gametophyte is unknown.

Although the ssp. *californicum* differs from all of the other subspecies in its large size, yet it intergrades with both ssps. *Coulteri* and *silaifolium*. Many California plants, because of their intermediate character, can not be placed satisfactorily in any one of the recognized subspecies. Careful field study of such puzzling material is necessary before we can really understand the status and relationships of the various races of *B. multifidum* represented in California.

CALIFORNIA. Placer: Emigrant Gap, *Dr. A. Kellogg* (NY). Plumas: Quincy, Mrs. *R. M. Austin 358* (G, M, NY, U). Sierra: ———, *J. G. Lemmon* (G). Siskiyou: Sisson, *M. A. Howe* (NY). Tulare: Sequoia National Park, *Mrs. H. P. Bracelin 718* (NY). Yosemite Valley, *E. Michael* (U).

2. BOTRYCHIUM AUSTRALE R. Brown

In temperate regions in the southern hemisphere, this species is the counterpart of *B. multifidum* in the north. Although, in some of its forms it approaches various other species, it has seemed best to retain it because of the usually small ultimate divisions and the relatively long-stalked major divisions of the sterile blade, the distinct range, and the occurrence of a dissected leaf form. The other species with which this might be confused do not possess such a dissected leaf form, which fact seems significant.

Widely variable in texture and leaf cutting, *B. australe* may be divided into four elements. The species is first divisible into two subspecies on a basis of leaf architecture and range. The one of these, which is found in southern South America, in several respects closely simulates forms of *B. multifidum* and is only doubtfully distinct from that species. The other race, confined to New Zealand and eastern Australia, may be divided into three varieties: the typical rather stout form, which most closely resembles the South American subspecies and *B. Schaffneri;* a dissected leaf form; and a lax, almost membranous leaved shade form which is very close to *B. ternatum* of eastern Asia. These various subdivisions may be separated as follows:

A. Ultimate divisions of the sterile blade very small, 0.5–4 mm. long by 0.5–2 mm. wide, or if larger, the plants not very stout and with the divisions of the blade not rhomboid and obtuse. (*B. australe* ssp. *typicum*)
  B. Plants usually stout and somewhat fleshy; the venation obscure; the ultimate divisions of the blade oblong to oblanceolate, 0.5–4 mm. long by 0.5–2 mm. wide. C
    C. Sterile blade not deeply incised or dissected. 2a. *B. australe* var. *typicum*
    C. Sterile blade deeply incised and dissected. 2b. *B. australe* var. *Millefolium*
  B. Plants usually lax and slender; the venation evident; the ultimate divisions of the blade larger, acutish, unevenly crenate or serrate; the penultimate divisions broadly cuneate at the base. 2c. *B. australe* var. *erosum*
A. Ultimate divisions of the blade rather large, 8 mm. long by 5 mm. wide, rhomboid and obtuse at the tips; the plants stout and fleshy. 2d. *B. australe* ssp. *Negeri*

2a. BOTRYCHIUM AUSTRALE R. Brown, var. TYPICUM

Botrychium australe Robert Brown, Prod. Fl. Nov. Holl. **1**: 164. 1810. Based on specimens collected at Port Jackson, Parramatta, New Zealand. The types, according to James Britten (Journ. of Bot. **36**: 491. 1898) are deposited in the British National Herbarium, while duplicates were sent to Kew and Edinburgh. In one of the types the sterile blade is 13 cm. long and 9 cm. wide. The name probably alludes to the occurrence of the species in the southern hemisphere.

Botrychium virginicum J. D. Hooker, Fl. Nov. Zeal. **2** (2): 50. 1855.

Botrychium cicutarium J. D. Hooker, Handbook of the New Zealand Flora, p. 387. 1867.

Botrychium ternatum B) *Australasiaticum α vulgare* Milde (in part), in Verh. zool. bot. Ges., Wien. **19**: 157. 1869.

Sceptridium australe (R. Br.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant rather stout and fleshy, 10–30 cm. high; sterile blade 3.5–25 cm. wide, 2.5–20 cm. long; ultimate divisions oblong to oblanceolate or ovate, acutish or obtuse at the apex, crenate or entire, 0.5–4 mm. long, 0.5–2 mm. wide. Matures spores during March and April. The gametophyte is unknown.

According to Cheeseman (1925) this form is abundant in New Zealand from the North Cape to south of Otago, while Ewart (1930) states that it is widely distributed in Victoria except in the northwestern part, and ranges from Tasmania to Queensland; but it is not well represented in American herbaria and the few specimens available are not all provided with specific locality data. Although the species is said to range throughout eastern Australia, the writer has seen specimens only from New South Wales and Victoria.

AUSTRALIA

NEW SOUTH WALES. Paterson, ——— (U); Lord Howe Island, *J. L. B* ——— (U).

VICTORIA. Mt. Baker, *Oldfield* (NY).

NEW ZEALAND

NORTH ISLAND. Te Pahi, *T. Kirk 346* (G, U); Auckland, *T. F. Cheeseman* (U).

SOUTH ISLAND. Canterbury, *T. F. Cheeseman* (U).

2b. BOTRYCHIUM AUSTRALE var. MILLEFOLIUM (Hochst.) Prantl

"*Botrychium Millefolium* Hochst. mscr. in hb. Vindob."

Botrychium ternatum B) *Australasiaticum δ Millefolium* (Hochst.) Milde, in Verh. zool. bot. Ges., Wien. **19**: 158. 1869. *B. millefolium* Hochst. is given as a synonym.

Botrychium australe var. *Millefolium* (Hochst.) Prantl, in Jahrb. Bot. Gart., Berlin. **3**: 341. 1884.

Botrychium biforme Colenso, in Trans. New Zeal. Inst., Wellington. **18**: 223. 1886. Based on the collections of Mr. H. Hill in swamps near Tahoraiti, county of Waipawa, New Zealand, April, 1885.

Sceptridium biforme (Col.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Similar to var. *typicum*, but more slender and with the ultimate divisions of the blade deeply incised and dissected.

Although Underwood (1898) rightly pointed out that this dissected form from New Zealand is not the same as *B. dissectum* Sprengel, he failed to appreciate that this was part of the normal variation of *B. australe*, as New Zealand botanists seem to have been aware, even from early times, for they have rather consistently treated this form as a variety of their one native species of the subgenus *Sceptridium.*

This plant is apparently known only from New Zealand, where it is widely distributed, but according to the published statements of the local botanists, is less common than the typical variety.

NEW ZEALAND
NORTH ISLAND. Mt. Egmont, ——— (NY); Taupa, *T. Kirk 539* (U).
SOUTH ISLAND. Marlborough, ——— (C).

2c. BOTRYCHIUM AUSTRALE var. EROSUM (Milde) Prantl

Botrychium erosum Milde, in Bot. Zeit. **22**: 102. 1864. Based on a specimen collected during the Novara Expedition by Hay at Auckland, New Zealand. The type is preserved in the herbarium of the k.k. Hofmuseum, Vienna. The name alludes to the erose nature of the divisions of the sterile blade.

Botrychium ternatum B) *Australasiaticum y erosum* Milde, in Verh. zool. bot. Ges., Wien **19**: 157. 1869.

Botrychium australe var. *erosum* (Milde) Prantl, in Jahrb. Bot. Gart., Berlin. **3**: 340. 1884.

Plant more slender and lax than var. *typicum;* blade semimembranous, with the ultimate divisions oblong, ovate, or lanceolate, acutish, unevenly crenate or serrate; penultimate divisions broadly cuneate towards the base.

During the course of the present study, the writer has seen only one specimen that could be referred definitely to this variety. It was the collection of *E. Craig 2629* (M), for which the locality is given simply as New Zealand. The specimen consists merely of a single sterile segment. This variety requires careful investigation by field botanists in New Zealand.

2d. **Botrychium australe** ssp. **Negeri** (Christ) n. comb.

Botrychium Negeri Christ, in Arkiv för Botanik. **6**: 2. fig 1. 1906. Based on a specimen collected in 1897 by Dr. Neger at Valdivia in southern Chile. The species was named in Dr. Neger's honor.

Plant rather stout and fleshy; the blade with the major divisions relatively long stalked as in the ssp. *typicum* and with the ultimate divisions nearly rhomboid, obtuse at the apex, broad at the base, minutely denticulate on the margins, averaging 8 mm. long and 5 mm. wide.

No specimens of this subspecies have been seen by the writer and so far as can be determined, it seems to be known only from the type collection. It is here tentatively placed as a subspecies of *B. australe,* as a result of study of the original description with the accompanying figure.

3. BOTRYCHIUM SCHAFFNERI Underwood. *Figure 2.*

This species, representing the section *Multifidae* in Mexico, Central

America, and northern South America, may be divided into two varieties, distinguished as follows:

A. Plants lax and large, 10–35 cm. high. 3a. *B. Schaffneri* var. *typicum*
A. Plants stout, compact and small, less than 10 cm. high. 3b. *B. Schaffneri* var. *pusillum*

3a. Botrychium Schaffneri Underwood, var. typicum

Botrychium Schaffneri Underwood, in Bull. Torrey Club **30**: 51. 1903. Type specimen in the herbarium of the New York Botanical Garden; *J. G. Schaffner 9*, collected in 1875 in mountains near San Luis Potosi, State of San Luis Potosi, Mexico. The species was named in honor of its original discoverer, Dr. Schaffner.

Sceptridium Schaffneri (Underwood) Lyon, in Bot. Gaz. **40**: 458. 1905.

Mature plant 20–35 cm. high, rather fleshy; roots stout, 1–4 mm. in diam.; bud densely pilose; common stalk 2–4.5 mm. in diam.; sterile stalk 2–12 cm. long; blade rather lax and sometimes membranous, ternately divided, with the ultimate divisions oblong or obovate, small, 1–6 mm. long, 1–5 mm. broad; fertile stalk 13–26 cm. long; fruiting spike decompound, 3–10 cm. long; sporangia yellowish brown, 0.6–1 mm. in diam., with the lobes not strongly reflexed in dehiscence; spores maturing during August and September. The gametophyte is unknown.

Of all the American species of the subgenus *Sceptridium*, this perhaps is more nearly like *B. ternatum* of Asia. It is usually not quite so lax a plant as the Asiatic species, while the ultimate divisions of the blade are both smaller and blunter. In *B. ternatum* the divisions of the sterile segment are ovate or oblong, acute and often dentate. In some specimens, *B. Schaffneri* approaches forms of *B. multifidum* ssp. *silaifolium*, but it can usually be separated from these by its less fleshy texture and by the very small ultimate divisions of the blade which are always obtuse, never acutish.

B. Schaffneri var. *typicum* is a plant of the mountains of Mexico, Central America and northern South America, found at altitudes from 5000 to 10,000 feet. It ranges from Chihuahua and Durango in Mexico south through the state of Oaxaca and Guatemala to Colombia, Peru, and Bolivia.

Mexico. Chihuahua; Chuichupa, Sierra Madre Mts., *M. E. Jones* (M, U). Durango: El Salto, Sierra Madre Occidental, *F. W. Pennell 18365* (Ph). Hidalgo: near Trinidad Iron Works, *C. G. Pringle 8922* (C, G, H, M, Ph, U). Mexico: Cima, *J. N. Rose & J. H. Painter 7197* (U). Oaxaca: Sierra de San Felipe, *C. L. Smith 2029* (M, U). San Luis Potosi: San Luis Potosi, *J. G. Schaffner 9* (NY).

Guatemala. ———, *E. Seler 2738* (U).

Colombia. ———, *Bro. Ariste-Joseph A470* (U).

Peru. Panticalla Pass, *O. F. Cook & G. B. Gilbert 1845* (U).

Bolivia. ———, *A. M. Bang 2595* (NY, U).

Argentina. Two fragments of sterile blades collected by *Hieronymus, nos. 1174 & 1876*, perhaps represent this species (NY).

3b. **Botrychium Schaffneri** var. **pusillum** (Underwood), n. comb.

Botrychium pusillum Underwood, in Bull. Torrey Club **30**: 50. 1903. The type collection is in the herbarium of the New York Botanical Garden and consists of five small plants, several still immature and obviously not fully developed. This is *C. G. Pringle, no. 5192*, from wet meadows, altitude 10,000 feet, Sierra de las Cruces, State of Mexico, Mexico, Sept. 11, 1892. The specific name alludes to the small size of the plants.

Sceptridium pusillum (Underwood) Lyon, in Bot. Gaz., **48**: 458. 1905.

Plant small, stout, 4–8.5 cm. high; common stalk 0.6–3 cm.; sterile stalk 0.7–1.2 (–4) cm.; blade 1.8–2.7 cm long, 3–4 cm. wide, coriaceous, with the ultimate divisions small, oblong or obovate, 2–3 mm. long, 1–2 mm. wide; fertile stalk 2–5 (–11) cm. long; fruiting spike 1.5–4.5 cm. long; sporangia 0.8 mm. in diameter.

This differs from typical *B. Schaffneri* in being smaller and stouter, with the ultimate segments of the blade rounder. All of the specimens that the writer has examined look suspiciously like reduced or undeveloped forms of the var. *typicum*. Further, certain specimens are somewhat intermediate between the two forms and on that account it has not seemed possible to retain this population as of specific rank. It is consequently considered tentatively as a variation derived from typical *B. Schaffneri*. More material and field study are required to clear up its status.

Mexico. Hidalgo: Trinidad, *C. G. Pringle 11,879* (U). Mexico: Sierra de las Cruces, *C. G. Pringle 5192* (NY, U). San Luis Potosi: San Miguelita, *J. G. Schaffner 944* (U). Also Sierra de Pachuca, *C. G. Pringle 11359* (U).

4. Botrychium ternatum (Thunberg) Swartz. *Figure 6.*

Osmunda ternata Thunberg, Flora Japonica, p. 329. pl. 32. 1784. Based on a specimen collected from the region of Nagasaki, Japan. The specific name alludes to the ternate nature of the sterile blade.

Botrychium ternatum (Thunberg) Swartz, in Schrad. Journ. für die Botanik. **2**: 111. 1800.

Botrychium ternatum B) *Australasiaticum α vulgare* Milde (in part), in Verh. Zool. bot. Ges. **19**: 157. 1869.

Sceptridium ternatum (Thunberg) Lyon, in Bot. Gaz. **40**: 458. 1905.

Plant rather lax, 18–41 cm. high, usually thin in texture, rarely subfleshy, with the blade inserted towards the base; common stalk 1–6 cm. long; sterile stalk 4–11 cm. long; blade 5–16 cm. wide, 4–15 cm. long, with the three major divisions on stalks 0.5–2 cm. long and with the ultimate segments 3–4 mm. wide, 2–5 mm. long, ovate to oblong, acutish or rarely obovate, mostly serrate or entire; fertile stalk 13–27 cm. long; fruiting spike 3–10 cm. long; sporangia 0.5–1.2mm. in diameter. Matures spores largely from August to October. The gametophyte is unknown.

Botrychium ternatum may be distinguished from any of the other species of the section *Multifidae* by its thin texture, the small acutish ultimate segments, and the relatively short stalked three major divisions of the

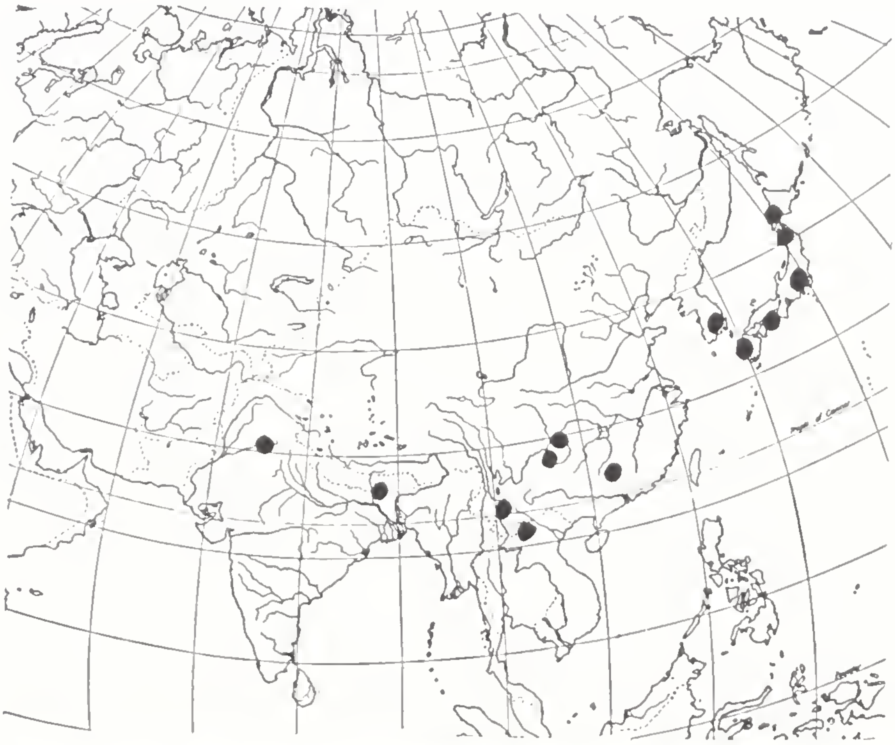


Fig. 6 (above). *Botrychium ternatum.*
Fig. 7 (below). *Botrychium daucifolium* (•) and *B. subbifoliatum* (+).

sterile blade. Of the two species with which it might be confused, *B. Schaffneri* differs in being more *fleshy* and in having the ultimate divisions of the blade blunt and *rounded*, while *B. australe* differs in being stouter and in having the three major portions of the blade relatively longer stalked, as well as differently cut.

According to data compiled from herbarium labels, this is a plant of meadows, fields, grassy slopes, and occasionally woods, ranging from northern Japan south and west through Corea and the uplands of southern China to the Himalayas.

JAPAN. Hokkaido: Sapporo, *S. Arimoto* (G, M). Honshu: Aomori, *U. Faur 16* (NY); Tokyo, *Y. Yabe* (G, NY). Shikoku: Tosa, *K. Watanabe* (G). Kioshu: Nagasaki, *Maximowicz* (G).

COREA. ———, *Taouet 2269* (NY).

CHINA. Kwantung: Put Wan Tsz, Loh Fau Mountain, *E. D. Merrill 11018* (NY). Kweichow: Schuicheng, *Y. Tsiang 9434* (NY); Ta Ho Yen, Fan Ching Ku-chin-shen, *A. Henry* (NY).

FRENCH INDO CHINA. Brousailles, Chapa, U. S. *1551552* (U).

INDIA. British Sikkim: Darjiling, *H. C. Levinge* (NY). Punjab: Simla, *H. F. Blanford* (NY).

b. Section **Biternatae,** n. sect.

Biternatae, sectio nova subgeneris *Sceptridii* segmentis ultimis laminae sterilis certe et congruenter flabellatis, latis et rotundatis ad apicem, sed ad basem abruptam cuneatamque contractis; apicibus divisionum penultimarum latis et rotundatis.

This section, comprising four species of the West Indies, Central and northern South America, and the southeastern United States, is characterized by the flabellate ultimate divisions and the broad rounded tips of the penultimate divisions of the sterile blade. The species included form a very compact group, sharply set off from the other two sections of *Sceptridium* by this characteristic leaf architecture.

5. BOTRYCHIUM BITERNATUM (Savigny) Underwood

Osmunda biternata Savigny, in Lamarck, Enc. **4**: 650. 1797. Based on a specimen collected by Michaux in South Carolina. According to Underwood (1898) the type specimen is in the Michaux Herbarium in Paris and the label bears the data, "in pascuis sabulosis juxta Charleston."

Botrypus lunarioides Michaux, Flora Boreali-Americana. **2**: 274. 1803. Based on a specimen collected in a pasture near Charleston, South Carolina.

Botrychium lunarioides (Michx.) Swartz, Synopsis Filicum. p. 172. 1806.

Botrychium fumarioides Willdenow, in Sp. pl. ed. 4. **5** (pt. 1): 63. 1810. *Botrychium lunarioides* Swartz, *Botrypus lunarioides* Michx., and *Osmunda ternata* Lam. are listed as synonyms.

Botrychium fumarianum J. E. Smith, in Rees, The Cyclopaedia **39,** no. 4. 1819.

Botrychium Fumariae Sprengel, in Linnaeus, Systema Vegetabilium. ed. 16. **4** (pt. 1): 23. 1827. *B. fumarioides* Willd., *B. lunarioides* Sw., *Osmunda* *biternata* Lam., and *Botrypus Lunarioides* Michx. are all listed as synonyms. The native region is given as Carolina.

Botrychium ternatum (C) *Americanum α lunarioides* (Michx.) Milde, in Verh. zool. bot. Ges., Wien. **19**: 162. 1869.

Botrychium ternatum var. *lunarioides* D. C. Eaton, Ferns of North America **1**: 148. pl. 20, fig. 3. 1879.

Botrychium biternatum (Sav.) Underwood, in Bot. Gaz. **22**: 407. pl. 21. 1896.

Septridium biternatum (Sav.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant low and compact; common stalk short, 1–1.5 cm. long; sterile stalk 1–2.5 cm. or none; blade subfleshy to membranous, 3.5–4.5 cm. long, 5–10 cm. wide, with the ultimate divisions 5–8 mm. wide, 4–5 mm. long, rather symmetrically flabellate or reniform, contracted to narrow bases, irregularly and coarsely crenate, with 12–25 small teeth and often a larger terminal sinus on the broadly rounded tips; fertile stalk 4.5–8 cm. long; sporangia 1 mm. in diameter; bud glabrous or almost so, with the segments essentially erect. Matures spores from February to March. The gametophyte is unknown.

This is a plant of dry situations, preferring grassy knolls, wooded banks, and dry pastures. It ranges from central and southern South Carolina and Georgia south to northern Florida and west to southern Alabama and doubtfully to Louisiana.

South Carolina. Aiken: Aiken, *H. W. R.* (G). Charleston: Charleston, *L. DeWitte* (NY). Richland: Columbia, *K. A. Taylor* (G, NY).

Georgia. Burke: ———, ——— (G).

Florida. *A. W. Chapman* (G, Ph). Filed in the herbarium of the New York Botanical Garden is a letter from Hugh O'Neill to Dr. J. K. Small, referring to a specimen of *B. biternatum* from "grassy banks of Hogtown Creek, about two miles west of Gainesville, Jan., 1925, no. 1313."

Alabama. Mobile: Spring Hill, *W. C. Dukes* (G, NY, Ph, U).

Louisiana. According to the Louisiana Conservation Review (v. **5**: 18. 1936), this was collected by Drummond about 1833, but apparently has not since been found.

6. Botrychium Jenmani Underwood

Botrychium Jenmani Underwood, in Fern Bull. **8**: 59. 1900. Based on material from the island of Jamaica. The type sheet is in the herbarium at the New York Botanical Garden and bears five plants which represent the collection of *W. N. Clute, no. 63*, at Cinchona, at an elevation of 5000 ft., on Feb. 6, 1900. The species is named in honor of Mr. Jenman, who had earlier communicated a specimen to the Kew Herbarium.

Sceptridium Jenmani (Underwood) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant slender, 4–22.5 cm. high, with the blade usually inserted basally, far surpassed by the fertile segment, which is commonly 2–4 times the length of the sterile portion; common stalk 0.5–2.5 cm. long; sterile stalk 0.3–4 cm. long; blade membranous and lax, with the major divisions mostly alternate in arrangement and the ultimate divisions obovate, ovate, or flabellate, finely crenate, 4–8 mm. broad, 4–12 mm. long; fertile stalk 3–17 cm.; fruiting spike 0.5–4 cm. long; sporangia 1 mm. in diameter; bud densely hairy. Matures spores during August, September, October, January, February, and March. The gametophyte is unknown.

B. Jenmani is easily distinguished from the continental *B. biternatum* by the more slender habit, larger size, and densely hairy bud. It is most closely related to *B. alabamense* of the mainland, from which it differs in having the blade inserted basally or even subbasally, rather than suprabasally, and in having the fertile segment far surpassing the sterile (i.e. by 2–4 times), whereas in *B. alabamense* the fertile segment is only half again as long as the sterile portion. In *B. alabamense*, also, the sterile stalk is usually longer than in the present species.

Botrychium Jenmani is a plant of dry grasslands in the West Indies at elevations from 2000 to 6000 feet.

CUBA. Oriente: La Perla to Santa Ana, *J. A. Shafer 8626* (NY, U).

JAMAICA. Surrey: Cinchona, *W. N. Clute 63* (NY, U).

HISPANIOLA. Constanza, *H. von Turckheim 3130* (NY); La Vega, Cordillera Central, *E. L. Ekman H13816* (U).

PORTO RICO. Mayaguez: Maricao, *F. L. Stevens* and *W. E. Hess 4703* (NY).

7. BOTRYCHIUM ALABAMENSE Maxon

Botrychium alabamense Maxon, in Proc. Biol. Soc. Wash. **19**: 23. 1906. Based on material collected by W. C. Dukes in August, 1905, at an altitude of 200 feet, at Spring Hill, seven miles west of Mobile, Alabama. The type is in the United States National Herbarium. The specific name alludes to the state of Alabama.

Plant slender, lax and membranous, 20–44 cm. high; blade inserted suprabasally, surpassed by the fertile segment for only about half its length; common stalk 2–4 cm. long; sterile stalk 2.5–6 cm.; blade ternately decompound, 5–16.5 cm. wide, 5–14 cm. long, membranous, venation evident; ultimate divisions flabellate or lunulate, broadly rounded at the apex, constricted at the base, 4–11 mm. wide, 5–8 mm. long, crenate; fertile stalk 17–28 cm. long; fruiting spike lax; sporangia 0.8–1 mm. in diameter; bud densely hairy. Matures spores during the autumn, from September to December, but mostly in October. The gametophyte is unknown.

This species is closely related to both *B. biternatum* and *B. Jenmani*. It is distinguished from the former by its densely hairy bud, more slender habit, and autumnal fruiting period; and from the latter in having the fertile segment only about half again the length of the sterile, not two to four times longer, and in the suprabasal insertion of the blade. Although *B. alabamense* and *B. biternatum* seem distinct enough when typical specimens of both are compared, further field study is necessary to determine their actual relationship. There is still the possibility that these plants represent a species which fruits from the early autumn, through the winter and into the early spring, and that the habit characters may be explained on a basis of the season and the age of the individuals. There would still remain the essentially different bud, which is almost glabrous in *B. biternatum*, but the range of variation in pubescence of the bud in this species must still be investigated.

Botrychium alabamense is a plant of wooded slopes, thickets, pine woods and old fields, ranging from central and western North Carolina south to northern Florida and southern Alabama.

North Carolina. Mecklenburg: Charlotte, *A. N. Leeds 3585* (Ph). Polk: Columbus, *E. C. Townsend 15* (C).

Georgia. Clarke: Athens, *J. H. Pyron* and *R. McVaugh 141* (Ph). DeKalb: ———, *P. Wilson* (NY). Dougherty: Albany, *C. L. Pollard* & *W. R. Maxon 507* (U).

Florida. Gadsden: Aspalaga, ex herb. A. W. Chapman, in part (M). Also, *A. W. Chapman* (Ph).

Alabama. Lee: Auburn, *L. M. Underwood* (NY). Mobile: Spring Hill, *W. C. Dukes* (G, Ph, U).

8. Botrychium Underwoodianum Maxon

Botrychium Underwoodianum Maxon, in Bull. Torrey Club **32**: 222. pl. 6. 1905. Based on specimens collected in Jamaica by Jenman during 1874–79. The type is in the herbarium of the New York Botanical Garden and a cotype in the United States National Herbarium. The species was named in honor of Dr. L. M. Underwood, who collected an excellent series of the plants in 1906.

Sceptridium Underwoodianum (Maxon) Lyon, in Bot. Gaz. **40**: 458. 1905.

Plant rather stout, averaging 22 cm. high; common stalk 1–3 cm. long; sterile stalk brown, pilose to glabrous, 2–7 cm. long; blade ternate, 7–21 cm. broad, 6–16 cm. long, with the ultimate divisions obovate to spatulate, crenate, 2–7 mm. wide, 2–15 mm. long; fertile stalk 6–15 cm. long; fruiting spike decompound, 3–6 cm. long; sporangia yellowish brown, 0.8 mm. in diameter. Spores mature from September to February. The gametophyte is unknown.

This striking species, native in the West Indies and northern South America, is most closely related to *B. Jenmani* and *B. alabamense*. From the former it is at once distinguished by its stouter character, larger size, spatulate (never ovate) divisions of the blade and its autumnal fruiting period. From *alabamense*, it differs in having the divisions of the blade spatulate, not lunulate, and in its much stouter and more leathery character.

Botrychium Underwoodianum is found on bushy slopes, in the forest, and in meadows, in the mountains of Jamaica, Central and northern South America. It occurs mostly at altitudes from 3000 to 12,000 feet.

Jamaica. Surrey: Cinhona, *L. M. Underwood 3151* (NY, U). Also, Chestervale, near Newcastle, *M. Carhart* (NY).

Costa Rica. San José: Santa Maria de Dota, *P. C. Standley 41567* (U). Heredia: Volcan Barba, *M. Valerio A35 & 118* (U).

Colombia. Santander: Paramo de Romeral, *E. P. Killip* & *A. C. Smith 18540* (U).
Venezuela. Los Andes: Tovar, *A. Fendler 4* (U).

c. Section **Elongatae,** n. sect.

Elongatae, sectio nova subgeneris *Sceptridii* segmentis laminae sterilis in amplitudine et forma non similibus, sed cum divisionibus penultimis semper fere elongatis et paullum partitis; laminis aut membranaceis aut aliquantulum carnosis.

The section *Elongatae* is represented in eastern North America, the West Indies, eastern Asia, and on various of the islands in the Pacific Ocean. All of the four species included in this group are characterized by the decidedly elongate penultimate segments of the sterile blade.

9. Botrychium dissectum Sprengel

This species, although in the literature reported in one or more of its forms from eastern Asia, seems to represent a strictly North American population. No specimens from the Old World have been seen by the writer.

B. dissectum ranges from southern Nova Scotia and New Brunswick west to the Mississippi Valley and south to Florida and Texas. It is also found in Jamaica and in central and southern Mexico and Guatemala. Throughout this range it exists in a large variety of habitats. The species is exceedingly variable in texture, size, and the cutting of the leaf. As here considered, it may be divided into two rather well marked subspecies: the typical race, which is common and widely distributed in the eastern United States, with one outpost on the island of Jamaica in the West Indies; and a Mexican race, which extends from central Mexico to Guatemala. Although the ranges of these two subspecies do not truly overlap, yet, since certain individuals of both approach each other very closely and since the area in which true intermediates might be expected is practically unknown botanically, it has seemed best, for the present at least, to treat these two elements as subspecies.

The extreme variation in the cutting of the sterile blade and the great difference in the appearance of the plants due to the influence of the environment have been important and misleading factors resulting in the description of many spurious species and varieties which have been segregated from this population. If the writer were to follow the treatments of some authors who have dealt with this group, he would need to name many new varieties and species, perhaps as many as a hundred, in order to be consistent in naming every minor variation of leaf cutting. Such a procedure would have neither practical nor scientific value. It has seemed best to adopt here a conservative course, recognizing only those most extreme variations which have either some slight range correlation or some other distinction to support the leaf character. On this basis, it has seemed feasible to maintain four varieties of the subspecies *typicum*. These are distinguished from one another and from the subspecies *decompositum* in the following key:

A. Plants slender, with the blades large and lax, or compact, with the blades small and coriaceous; the chief terminal divisions of the blades usually lanceolate or oblong in outline, not decidedly broadened towards the base; the ultimate divisions oblong, ovate or rhomboid, rarely lanceolate. Plants of eastern Canada, the United States, and Jamaica. (*B. dissectum* ssp. *typicum*)

  B. Chief terminal divisions of the blade broad and *rounded;* the blades normally remaining green throughout the winter. 9a. *B. dissectum* var. *oneidense*

  B. Chief terminal divisions of the blade usually narrower and *acute* or *acutish;* the blades becoming bronze colored during the late autumn and winter. C

    C. The divisions of the blade not deeply and finely lacerate or divided. D

      D. Blades usually somewhat coriaceous, with the margins of the segments entire or inconspicuously crenate; the penultimate divisions somewhat divided below and with a truncate or adnate base. 9b. *B. dissectum* var. *obliquum*

      D. Blades lax and membranous, with the margins of the segments conspicuously serrate; the penultimate divisions not or little divided and contracted to a cuneate base. 9c. *B. dissectum* var. *tenuifolium*

    C. The divisions of the blade deeply and finely lacerate or divided. 9d. *B dissectum* var. *typicum*

A. Plants slender, with the blades large and lax; the chief terminal divisions of the blade usually ovate in outline, decidedly broadened towards the base; the ultimate divisions flabellate, ovate, oblong, or lanceolate. Plants of Mexico and Guatemala. 9e. *B. dissectum* ssp. *decompositum*

9a. BOTRYCHIUM DISSECTUM var. ONEIDENSE (Gilbert) Farwell. *Figure 3.*

Botrychium ternatum var. *oneidense* Gilbert, in Fern Bull. **9:** 27. 1901. Based on specimens collected on the flat of a stream at Deerfield, N. Y.

Botrychium dissectum var. *obliquum* f. *oneidense* (Gilb.) Clute, in Fern Bull. **10:** 76. 1902.

Botrychium obliquum f. *oneidense* Clute, in Fern Bull. **10:** 77. 1902.

Botrychium obliquum var. *oneidense* (Gilbert) Waters, Ferns, p. 334. 1903.

Botrychium ternatum obliquum f. *oneidense* Clute, in Fern Bull. **13:** 118. 1905.

Sceptridium obliquum oneidense Lyon, in Bot. Gaz. **40:** 458. 1905.

Botrychium multifidum var. *oneidense* (Gilbert) Farwell, in Rep. Mich. Acad. of Science. **18:** 86. 1916.

Botrychium oneidense House, in Amer. Midl. Naturalist **7:** 126. 1931.

Botrychium dissectum var. *oneidense* (Gilbert) Farwell, in Papers Mich. Acad. Sci. Arts and Letters. **3:** 89. 1924.

Plant 24–41 cm. high; common stalk 1.5–6 cm.; sterile stalk 4–10 cm.; blade 6–14 cm. long, 8–23 cm. wide, ternately decompound, little divided, with the chief terminal divisions broad and blunt-tipped; fertile stalk 13–22 cm.; fruiting spike 5–14 cm. long; sporangia 0.6–1.0 mm. in diameter. Matures spores largely during September and October. The gametophytes are small tuberous flattened bodies, with the root emerging from the base and the stem differentiating above.

This is one of the most distinct and least divided leaf forms of the *B. dissectum* group, distinguished from *B. multifidum* by the thin texture of the blade, the elongate penultimate segments, the late fruiting time, and the regular association with the other varieties of *B. dissectum*. Several recent authors (Farwell, 1916, and Graves, 1935) have treated this as a variety of *B. multifidum*, since it does suggest that species in the blunt divisions of the blade and in retaining the green leaf color throughout the winter, but it seems always to be readily separated from it by the other characters mentioned above. Although no true intergradation has been observed, the var. *oneidense* seems to represent that form of *B. dissectum* which is most nearly related to *B. multifidum*. Careful study of the retention of the green color of the blades throughout the winter indicates that although the majority of the plants of *B. dissectum*, vars. *typicum* and *obliquum* turn to bronze in the late autumn, a rather considerable number of them remain quite green, hence too much significance should not be attached to this character.

The var. *oneidense* is a plant of rich moist woodlands, where it occurs either alone or in association with the other varieties of *B. dissectum* ssp. *typicum*. It ranges from western New Brunswick, southern Quebec, and northern Maine west to Michigan, and according to Graves (1931) to Wisconsin and Minnesota, and south in the mountains to North Carolina. Occasional specimens show a tendency towards a dissected leaf condition.

NEW BRUNSWICK. Carleton: Woodstock, *J. Macoun 22691* (Ot).

QUEBEC. Southern Gatineau and Stanstead Counties.

ONTARIO. Leeds, Lincoln, Middlesex, Peel, and Russel Counties.

MAINE. Aroostook, Cumberland, and Kennebec Counties.

NEW HAMPSHIRE. Cheshire, Coos, and Rockingham Counties.

VERMONT. Essex and Windsor Counties.

MASSACHUSETTS. Berkshire, Dukes, Essex, Hampden, Middlesex, Norfolk, and Suffolk Counties.

RHODE ISLAND. Providence: Providence, *E. B. Chamberlain* (N).

CONNECTICUT. Hartford and New London Counties.

NEW YORK. Albany, Cattaraugus, Cayuga, Cortland, Delaware, Erie, Herkimer, Madison, Nassau, Oneida, Seneca, Steuben, Tioga, Tompkins, and Ulster Counties.

NEW JERSEY. Bergen, Camden, Somerset, and Sussex Counties.

PENNSYLVANIA. Berks, Columbia, Luzerne, McKean, Tioga, and Wayne Counties.

NORTH CAROLINA. Graham: Yellowcreek, *J. H. Ferriss* (M) ?

OHIO. Lorrain and Portage Counties.

INDIANA. DeKalb, Howard, Porter, and Steuben Counties.

MICHIGAN. Van Buren and Wayne Counties.

WISCONSIN. According to Graves (1931) this variety is represented in the herbarium of the University of Minnesota by collections from Milwaukee, Rush, Shawano, and Wood Counties.

MINNESOTA. Represented in the herbarium of the University of Minnesota, according to Graves (1931), by specimens from Chisago and Houston Counties.

9b. BOTRYCHIUM DISSECTUM var. OBLIQUUM (Muhlenberg) Clute. *Figure 9.*

Botrychium lunarioides Schkuhr, Kryptogamische Gewächse **1**: 158. pl. 157. 1809. Based on the same material as *Osmunda obliqua* Willd. *Botrypus lunarioides* Michx. is listed as a synonym, but this is not that species.

Botrychium obliquum Muhl., in Willd., Sp. pl. **5**: 63. 1810. Based on a specimen collected in Pennsylvania by Muhlenberg.

Osmunda obliqua Poiret, in Lam., Enc. Suppl. **4**: 233. 1816.

Botrychium cuneatum Desv., in Mém. Soc. Linn. Paris **6**: 195. 1827.

Botrychium lunarioides var. *obliquum* Gray, Manual, ed. 1. p. 635. 1848.

Botrychium ternatum C) *Americanum* β *obliquum* Milde, in Verh. zool. bot. Ges., Wien. **19**: 163. 1869.

Botrychium ternatum var. *obliquum* D. C. Eaton, Ferns N. Amer. **1**: 149. 1878.

Botrychium dissectum var. *obliquum* Clute, in Fern Bull. **10**: 76. 1902.

Botrychium obliquum var. *elongatum* Gilbert & Haberer, in Fern Bull. **11**: 89. 1903. Based on specimens collected by J. V. Haberer near Utica, N. Y. This mere leaf form does not merit nomenclatorial distinction.

Sceptridium obliquum (Muhl.) Lyon, in Bot. Gaz. **40**: 458. 1905.

Botrychium dissectum f. *obliquum* (Muhl.) Fernald, in Rhodora **23**: 151. 1921.

Botrychium obliquum var. *oblongifolium* Graves, in Amer. Fern Journ. **22**: 50. pl. 4. 1932. Based on a specimen collected by W. S. Blatchley in Marion County, Indiana, and deposited in the herbarium of Mr. C. C. Deam. The illustration of the type accompanying the original description represents a plant that is occasionally found in otherwise normal colonies of *B. dissectum* var. *obliquum*. This seems to represent merely an extreme variation in leaf cutting and as such does not deserve nomenclatorial distinction.

Botrychium obliquum var. *pennsylvanicum* Graves, in Amer. Fern Journ. **25**: 118. 1935. Based on a specimen collected by W. L. Dix near Morrisville, Pennsylvania. This is the weakest of the named leaf forms of the *B. dissectum* complex and certainly does not merit the rank of variety or even of form.

Plant 12–32 cm. high; common stalk 1.5–5 cm.; sterile stalk 3–7 cm.; blade somewhat coriaceous, ternately decompound, averaging 2–14 cm. long, 3–16 cm. wide; penultimate divisions elongate, acutish, somewhat divided below, with the margins entire or inconspicuously crenate; fertile stalk 6–21 cm. long; fruiting spike 2–10 cm. long; sporangia 0.6–1 mm. in diameter. Matures spores during September, October, November, and, in the south, December. The gametophytes are small subterranean tuberous bodies, flattened dorsiventrally and entirely without chlorophyll.

Lyon (1905) has studied and described the development in this variety. The reproductive organs are borne on the flattened dorsal side of the gametophyte. After segmentation, a long suspensor is developed, which burrows down into the tissue of the prothallium. At the tip of the suspensor a spherical protocorm is produced, from which stem and root apices soon develop. The embryo does not possess a lateral cotyledonary structure, as in *B. virginianum.* The root grows downward and emerges from the lower side of the gametophyte, while the first leaf later appears from the upper side of the structure. This represents a condition quite different from that in those species of *Eubotrychium* and *Osmundopteris* in which the development is known. In these, the roots develop to the side or above the gametophyte. Since the axis of the archegonium is oblique, there is a marked curvature in the embryo of *B. dissectum* var. *obliquum* to insure the downward emergence of the root and the upward orientation of the stem apex.

The var. *obliquum* is widely variable in the cutting of the foliage blade and in general appearance. It grows in a variety of habitats: sterile hilltop fields, dry pastures, meadows, thickets, dry woodlands, rich swampy woods, and rarely sandy banks in pine barrens. It ranges from southern Nova Scotia and New Brunswick west to Wisconsin and Iowa and south to South Carolina, Georgia, and Louisiana, with an outlying population in the Blue Ridge Mountains of Jamaica. Some of the plants from Florida, Alabama, and Texas, which in this discussion are treated as var. *tenuifolium,* may perhaps belong here.

NOVA SCOTIA. Digby, Lunenberg, Shelburne, and Yarmouth Counties.

NEW BRUNSWICK. York: Fredericton, *J. Fowler* (G).

QUEBEC. Deux Montagnes, Gatineau, Jacques Cartier, Montcalm, Richelieu, Stanstead, Vercheres, and Wolfe Counties.

ONTARIO. Hastings, Nipissing, and Welland Counties.

MAINE. The writer has examined specimens from all counties except Aroostook, Sagadahoc, Somerset, and Washington.

NEW HAMPSHIRE. All counties except Belknap, Grafton, and Strafford.

VERMONT. Addison, Bennington, Caledonia, Lamoille, Orange, Orleans, Rutland, and Windsor Counties.

MASSACHUSETTS. All counties except Hampshire.

RHODE ISLAND. Newport, Providence, and Washington Counties.

CONNECTICUT. All counties.

NEW YORK. Albany, Bronx, Cayuga, Chemung, Chenango, Clinton, Cortland, Delaware, Erie, Essex, Greene, Hamilton, Herkimer, Jefferson, Madison, Nassau, Niagara, Oneida, Onondaga, Orange, Oswego, Otsego, Queens, Richmond, Rockland, St. Lawrence, Saratoga, Schoharie, Seneca, Steuben, Suffolk, Tioga, Tompkins, Ulster, Warren, Washington, and Westchester Counties.

NEW JERSEY. All counties except Somerset; see Clausen (1937a).

PENNSYLVANIA. Adams, Allegheny, Berks, Blair, Bucks, Cambria, Carbon, Centre, Chester, Columbia, Dauphin, Delaware, Erie, Fayette, Forest, Franklin, Indiana, Juniata, Lackawanna, Lancaster, Lehigh, Luzerne, McKean, Mifflin, Monroe, Montgomery, Montour, Northampton, Perry, Philadelphia, Pike, Sullivan, Susquehanna, Tioga, Venango, Warren, Wayne, Westmoreland, and York Counties.

Delaware. Kent and New Castle Counties.

Maryland. Allegany, Baltimore, Cecil, Garrett, Harford, Kent, Montgomery, Prince Georges, Queen Annes, St. Marys, Talbot, Wicomico, and Worcester Counties.

District of Columbia.

Virginia. Accomac, Augusta, Campbell, Fairfax, Grayson, Greensville, Henrico, James City, Loudon, Louisa, Mathews, Princess Anne, Roanoke, Shenandoah, and Warwick Counties.

West Virginia. Cabell and Tucker Counties.

Kentucky. Barren, Bell, Boyd, Kenton, Lawrence, Todd, and Warren Counties.

Tennessee. Carroll, Roane, and Unicoi Counties.

North Carolina. Avery, Buncombe, Burke, Davie, Forsyth, Haywood, Henderson, McDowell, Mecklenburg, Nash, Orange, Rutherford, Swain, Transylvania, Wake, and Watauga Counties.

South Carolina. Anderson, Beaufort, Charleston, Horry, and Richland Counties.

Georgia. Cobb, Gwinett, Morgan, and Walton Counties.

Alabama. Jackson: Long Island, *E. W. Graves* (U).

Louisiana. Jefferson Parish and Tangipahoa County.

Ohio. Hamilton, Mahoning, Miami, and Portage Counties.

Indiana. Allen, Cass, Clark, Decatur, Franklin, Jackson, Jefferson, Jennings, Knox, Kosciusko, La Porte, Marion, Orange, Perry, Posey, Scott, Shelby, Spencer, Wayne, and Wells Counties.

Illinois. Gallatin: Equality, *E. J. Palmer 17053* (M). According to Graves (1931) there are in the herbarium of the University of Illinois sheets from three stations in the southern half of Illinois: Carlinville, Olmstead, and Mt. Carmel. Also, Mr. E. J. Palmer found it in Franklin County.

Michigan. Saint Clair, Van Buren, and Washtenau Counties.

Wisconsin. Buffalo: Cochrane, *N. C. Fassett 2834* (G).

Iowa. Van Buren: Bentonsport, *E. W. Graves* (M, U). According to Graves (1931), Prof. B. Shimek has collected this variety at Cedar Rapids, Linn County.

Missouri. Dunklin, Jackson, Jasper, Jefferson, New Madrid, St. Louis, and Ste. Genevieve Counties; also reported from Franklin and Iron Counties.

Arkansas. Hempstead and Howard Counties.

Oklahoma. Creek: Sapulpa, *B. F. Bush 855* (M).

Jamaica. Surrey: Cinchona, *L. M. Underwood* (NY, U).

9c. Botrychium dissectum var. tenuifolium (Underwood) Farwell. *Figure 9.*

Botrychium tenuifolium Underwood, in Bull. Torrey Club **30**: 52. 1903. Based on a specimen collected by Hale at Alexandria, Louisiana. The type is at the New York Botanical Garden.

Botrychium obliquum tenuifolium (Underw.) Gilbert, in Fern Bull. **12**: 99. 1903.

Botrychium ternatum obliquum f. *tenuifolium* (Underw.) Clute, in Fern Bull. **13**: 118. 1905.

Sceptridium tenuifolium (Underw.) Lyon, in Bot. Gaz. **40**: 458. 1905.

Botrychium dissectum var. *tenuifolium* (Underw.) Farwell, in Papers Mich. Acad. Sci. Arts and Letters **3**: 89. 1924.

Plant slender and lax, 15–36 cm. high; common stalk 2–7 cm.; sterile stalk 2.5–8 cm. long; blade membranous, 3–19 cm. long, 3–25 cm. wide;

penultimate divisions much elongate, little or not at all divided, often contracted to a cuneate base, with the margins conspicuously and sharply serrate; fertile stalk 6–32 cm. long; fruiting spike 2.5–11 cm. long; sporangia 0.6–0.8 mm. in diameter. Matures spores from September to December. The gametophyte is unknown.

In its extreme form, this variety has the appearance of a very distinct species, but it is connected with the var. *obliquum* by such a complete series of intermediates that it has not been possible to give it specific status. Since certain forms from the north closely approach the var. *tenuifolium*, while the typical var. *obliquum* occurs on the mainland at least as far south as South Carolina, Georgia and Louisiana, there has seemed not enough range correlation to warrant designation of *tenuifolium* as a subspecies. Further, the two races are not very different structurally. Certain specimens exhibit a slight tendency towards a dissected condition, as in var. *typicum*, while others have the penultimate divisions more or less blunt lobed and in this respect approach the var. *oneidense*.

This is a plant of open woodlands, ranging from eastern Texas to Florida and north at least to Missouri, southern Indiana, and the coastal plain of Virginia and Maryland. Certain specimens from southern and eastern New Jersey and Long Island should perhaps also be included here. Farwell (1924) has reported this variety from St. Clair County, Mich., but the writer has not examined the specimens on which this record is based.

MARYLAND. Wicomico: Salisbury, *E. T. Wherry* & *A. N. Leeds 3696* (Ph).

DISTRICT OF COLUMBIA. Washington, ex N. M. Glatfelter Herb. (M).

VIRGINIA. James City: Williamsburg, *E. J. Grimes 3113* (G). New Kent: Lanexa, *E. T. Wherry* (G).

TENNESSEE. Tennessee Mts. (eastern Tenn.), *J. H. Ferriss* (M).

NORTH CAROLINA. Haywood: Balsam Mt., *J. H. Redfield 1755* (M). Watauga: Blowing Rock, *G. F. Atkinson 12873* (C).

SOUTH CAROLINA. Anderson: Anderson, *J. Davis* in part (M). Darlington: Society Hill, ——— (Princ). Georgetown: Georgetown, *F. G. Tarbox 820* (U).

GEORGIA. McDuffie: Branch Swamp, *H. H. Bartlett 1473* (Deam). Troup: Gabbetville, *Catherine Stewart* (Har).

FLORIDA. Duval: Jacksonville, *Mrs. W. D. Diddell 830* (Herb. E. P. St. John). Hernando: Brooksville, *R. P. St. John* (Claus, Ph). Washington: Chipley, *E. Pleas* (M).

ALABAMA. Lee: Auburn, *F. S. Earle* & *C. F. Baker* (M). Mobile: Spring Hill, *W. C. Dukes* (G, M, Ph).

MISSISSIPPI. Simpson: Saratoga, *S. M. Tracy 8643* (C, G, M, Penn).

LOUISIANA. Bossier: Alden Bridge, *W. Trelease* (M). Natchitoches: Natchitoches, *E. J. Palmer 8756* (M, Ph). Orleans: New Orleans, *T. Drummond 484* (C). Rapides: Alexandria, *Hale* (G). West Feliciana: Catalpa, *F. W. Pennell 4291* (Penn).

INDIANA. Crawford: Leavenworth, *C. C. Deam 18564* (Deam).

Fig. 8 (left). *Botrychium dissectum* var. *typicum*.
Fig. 9 (right). *Botrychium dissectum* var. *obliquum* (•), var. *tenuifolium* (+), and ssp. *decompositum* (X).

MISSOURI. Butler: Poplar Bluff, *E. J. Palmer 16, 438* (M). Dunklin: E. Bertig, *W. Trelease 10, 728* (M). Sullivan: Paw Paw Jn., *B. F. Bush* (M).

ARKANSAS. Hempstead: McNab, *J. M. Greenman 4349* (M). Pulaski: Little Rock, *G. Engelmann 26* (M).

TEXAS. Hardin: Voth, *V. L. Cory 11, 135* (G). Harrison: Marshall, *E. J. Palmer 8644* (M, Ph). San Augustine: San Augustine, *E. J. Palmer 14, 465* (M).

9d. BOTRYCHIUM DISSECTUM Sprengel, var. TYPICUM. *Figure 8.*

Botrychium dissectum Sprengel. Anleitung zur Kenntniss der Gewächse. **3**: 172. 1804. Based on a specimen collected in Virginia.

Osmunda dissecta Poiret, in Lam., Enc. Suppl. **4**: 233. 1816.

Botrychium fumarioides var. *dissectum* (Spreng.) Oakes, in Thompson, Hist. Vermont. p. 207. 1842.

Botrychium lunarioides var. *dissectum* Gray, Manual, ed. 1. p. 635. 1848.

Botrychium ternatum C) *Americanum* γ *dissectum* Milde, in Verh. zool. bot. Ges., Wien. **19**: 164. 1869.

Botrychium ternatum var. *dissectum* D. C. Eaton, Ferns N. Amer. **1**: 150. 1878.

Botrychium obliquum var. *dissectum* (Spreng.) Prantl, in Jahrb. Bot. Gart. Berlin. **3**: 342. 1884.

Botrychium ternatum obliquum f. *dissectum* Clute, in Fern Bull. **11**: 116. 1903.

Sceptridium dissectum (Spreng.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Sceptridium ternatum dissectum Clute, in Fern Bull. **14**: 48. 1906.

Botrychium obliquum f. *dissectum* (Spreng.) House, N. Y. State Mus. Bull. **36**: 243–244. 1933.

This is similar to the var. *obliquum*, but the divisions of the blade are deeply and finely lacerate. According to Dr. A. J. Eames, the gametophyte is apparently in all respects like that of the var. *obliquum*.

It is most regrettable that this, the atypical form of a widely distributed and variable species, should stand as the nomenclatorial type for the species, but if one is to abide by the International Rules of Nomenclature which state that the first validly published name to be applied to any part of a species must be considered as the proper name for that species, no other alternative is possible. To the writer it seems more likely that the wide ranging *B. obliquum* of Muhlenberg represents the morphological type of the species, from which variation has taken place in various directions. This dissected leaf form, although not supported by other characters, seems worth maintaining as distinct from the var. *obliquum* because of its strikingly different appearance.

The var. *typicum* is a plant of essentially the same habitats as the undissected variety. Usually the two varieties grow together in colonies and in the northeastern United States they intergrade freely, while farther south and in the middle west they seem to be quite distinct. The range of the var. *typicum* is from southern Nova Scotia, New Brunswick, and Quebec west to Minnesota and Iowa and south to North Carolina and Tennessee. It is also reported from Florida. Occasional specimens of var.

tenuifolium show a tendency towards a dissected condition, but not extreme enough to warrant placing them here.

Nova Scotia. Digby, Shelburne, and Yarmouth Counties.

New Brunswick. Charlotte: Grand Manan, *C. A.* and *U. F. Weatherby 5774* (G).

Quebec. Gatineau and Stanstead Counties.

Ontario. Lincoln and Russell Counties.

Maine. All counties except Somerset, Waldo, and Washington.

New Hampshire. All counties except Belknap, Merrimack, and Strafford.

Vermont. Addison, Bennington, Caledonia, Lamoille, Orleans, Rutland, and Windsor Counties.

Massachusetts. All counties.

Rhode Island. Newport, Providence, and Washington Counties.

Connecticut. All counties.

New York. Bronx, Cayuga, Chautauqua, Chemung, Chenango, Dutchess, Erie, Essex, Greene, Hamilton, Herkimer, Madison, Nassau, Oneida, Onondaga, Orange, Oswego, Otsego, Queens, Richmond, St. Lawrence, Saratoga, Schoharie, Seneca, Steuben, Suffolk, Tioga, Tompkins, Washington, and Westchester Counties.

New Jersey. All counties except Cumberland, Hunterdon, and Warren: see Clausen (1937a).

Pennsylvania. Adams, Allegheny, Berks, Blair, Bucks, Cambria, Carbon, Centre, Chester, Clearfield, Clinton, Dauphin, Delaware, Erie, Huntingdon, Juniata, Lackawanna, Lancaster, Lebanon, Lehigh, Luzerne, Mifflin, Monroe, Montgomery, Montour, Northampton, Perry, Philadelphia, Pike, Sullivan, Susquehanna, Wayne, Wyoming, and York Counties.

Delaware. Kent and New Castle Counties.

Maryland. Baltimore, Cecil, Garrett, Harford, Howard, Kent, Prince Georges, Queen Annes, St. Marys, and Washington Counties.

District of Columbia.

Virginia. Augusta, Fairfax, Gloucester, Henrico, Princess Anne, Roanoke, and Shenandoah Counties.

West Virginia. Tucker: Parsons, *J. M. Greenman 20* (G).

Kentucky. Boone and Warren Counties.

Tennessee. Smoky Mts., *J. H. Ferriss* (G). Also reported from Cades Cove.

North Carolina. Forsyth: Winston-Salem, *E. T. Wherry* (Ph).

Florida. In the herbarium of the N. Y. Botanical Garden is a letter from Elizabeth Pinkerton to J. K. Small in which is mentioned the collection of this variety from Chipley by Mr. E. Pleas, 1896. According to Graves (1931) Miss Sadie Price also collected two plants at Chipley, but the writer has seen no Florida material except some specimens of var. *tenuifolium* collected by the Messrs. E. P. and R. P. St. John, which somewhat approach this variety.

Ohio. Ashtabula, Clermont, Delaware, Montgomery, and Portage Counties.

Indiana. Allen, Cass, Delaware, Henry, LaPorte, Owen, Porter, Posey, Spencer, and Wells Counties.

Illinois. Reported by Graves (1931) from Franklin County and the northern part of the state.

Michigan. Saint Clair and Van Buren Counties.

MINNESOTA. Graves (Amer. Fern Journ. **21**: 21–24, 1931) cites the collection of E. O. Rosendahl from five miles east of Faribault, Rice County.

IOWA. Van Buren: Bentonsport, *E. W. Graves* (U).

MISSOURI. Reported by E. J. Palmer and J. A. Steyermark (Amer. Fern Journ. **22**: 119. 1932) from Iron, Jefferson, and St. Louis Counties.

9e. **Botrychium dissectum** ssp. **decompositum** (Mart. & Gal.), n. comb. *Figure 9.*

Botrychium decompositum Mart. et Gal., in Mém. Ac. Brux. **15**: 51. pl. 1. 1842. Based on the collection of H. Galeotti, no. 6452, from the forests of the peak of Orizaba at an altitude of 5000–6000 feet. The type is in the herbarium at Bruxelles and photographs of the type specimen are deposited at the Gray Herbarium and at the U. S. National Herbarium.

Botrychium ternatum B) *Australasiaticum α vulgare* Milde (in part), in Verh. zool. bot. Ges., Wien. **19**: 157. 1869.

Sceptridium decompositum (Mart. et Gal.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant slender, 27–59 cm. high; common stalk 3–5 cm. long; sterile stalk 6–25 cm. long; blade large and lax, 5–15 cm. long, 7–23 cm. wide; penultimate divisions of the sterile blade usually acute, ovate in outline, often divided almost to the main vein; ultimate divisions ovate, oblong or lanceolate, irregularly and conspicuously crenate; fertile stalk 20–49 cm.; fruiting spike 9–20 cm. long; sporangia 0.6–0.8 mm. in diameter. Matures spores from August to November. The gametophyte is unknown.

Although Prantl (1884) treated *B. decompositum* as a synonym of *B. silaifolium* Presl and stated that the original illustration of the Mexican plant agrees fully and certainly with specimens of Presl's species, it has seemed to the writer that these two forms are decidedly dissimilar and do not have any affinity at all. The illustration of the type of *B. decompositum* and the series of specimens available from Mexico and Guatemala indicate quite clearly that the affinity of this "species" is not with *B. silaifolium*, but rather with the large lax forms of *B. dissectum* var. *tenuifolium* that occur in the southern United States.

This is a plant of woodlands and shrubby thickets in southern Mexico and Guatemala, ranging from Hidalgo and Vera Cruz to Baja Verapaz.

MEXICO. Chiapas: Coapilla, *J. N. Rovirosa 1063* (G, Ph). Hidalgo: Trinidad Iron Works, *C. G. Pringle 8922* in part (G, NY). Vera Cruz: Orizaba, *Müller* (NY). Jalapa, *C. G. Pringle* (U).

GUATEMALA. Alta Verapaz: Coban, *H. von Turckheim 1731* (NY). Baja Verapaz: Purula, *H. von Turckheim 1168* (U). Huehuetenango, Cuesta de la Concepcion, *Caec. & E. Seler 2738* (NY).

10. BOTRYCHIUM JAPONICUM (Prantl) Underwood

Botrychium daucifolium β japonicum Prantl, in Jahrb. Bot. Gart. Berl. **3**: 340. 1884. Based on the collection of Wichura, no. 1368, from Nagasaki, Japan.

Botrychium japonicum (Prantl) Underwood, in Bull. Torrey Club **25**: 538. 1898. Underwood studied, in the Berlin Herbarium, specimens marked in Prantl's own writing.

Sceptridium japonicum (Prantl) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant delicate and membranous, 22–42 cm. high; common stalk 3–7 cm.; sterile stalk 3–10 cm. long, blade membranous, 7–13 cm. long, 9–16 cm. wide, with the penultimate segments acute and finely prominently and sharply serrate; fertile stalk 13–22 cm. long; spike 6–14 cm. long; sporangia 0.8–1 mm. in diameter. Matures spores from August to November. The gametophyte is unknown.

This differs from *B. daucifolium* in having the blade inserted below the middle of the plant, in the finer cutting of the blade, and in the more delicate texture. From the varieties of *B. dissectum* it differs in the prominently and sharply serrate margins of the divisions of the blade and in the thinner texture.

B. japonicum is a plant of woodlands in central and southern Japan and eastern China.

JAPAN. Honshu: Tokyo, *J. Matsumuru* (NY); Kyoto, *A. W. Stanford* (U). Shikoku: Tosa, *K. Watanabe* (G). Kioshu: Nagaski, *R. Oldham 1368* in part (G); Satsuma Province, *G. Masamune* (NY). Also Nyakoji, *Stanford* (M).

CHINA. Kwantung: Chong Uen Shan near Kau Fung (Loh Ch'ang Dist.), *W. T. Tsang 20953* (NY).

11. BOTRYCHIUM SUBBIFOLIATUM Brackenridge. *Figure 7.*

Botrychium subbifoliatum Brackenridge, in U. S. Expl. Exp. **16**: 317. pl. 44, f. 2. 1854. Based on specimens from the Hawaiian Islands. The type is in the U. S. National Herbarium at Washington.

Botrychium ternatum B) *Australasiaticum α vulgare* f. *subbifoliata* (Brack.) Milde, in Verh. zool. bot. Ges., Wien. **19**: 157. 1869.

Sceptridium subbifoliatum (Brack.) Lyon, in Bot. Gaz. **40**: 458. 1905.

Plant 23–40 cm. high, regularly producing two leaves in a season; sterile segment parting from the fertile near the base of the plant; common stalk 2–5 cm.; sterile stalk 6–17.5 cm. long; blade 15–25 cm. wide, 11–18 cm. long, with the penultimate segments elliptical and unevenly lacerate; rachis winged; ultimate divisions of the blade oblong, obovate, or ovate, obtuse, lacerate at apex; fertile segment surpassing the sterile; fertile stalk 15–28 cm. long; spike 6–7 cm. long; sporangia 0.6 mm. in diameter. Matures spores from August to November. The gametophyte is unknown.

This species is most closely related to *B. daucifolium*, from which it differs in the essentially basal insertion of the sterile segment and in the blunt tips of the divisions of the blade. It is not likely to be confused with any other species.

Botrychium subbifoliatum is a plant of shady places in the Hawaiian Islands.

HAWAIIAN ISLANDS. Hawaii: ———, *F. W. Thrum* (NY). Kauai: Wahiawa Mts., *C. N. Forbes 262* (NY). Lanai: Mts., east end, *C. N. Forbes 2172* (M). Oahu: *H. Mann* & *W. T. Brigham* (C).

12. BOTRYCHIUM DAUCIFOLIUM Wallich. *Figure 7.*

Botrychium subcarnosum Wall., List, no. 49. 1828. Nomen nudum.
Botrychium daucifolium Wall.; Hooker et Greville, Ic. Fil., pl. 161. 1829.
Sceptridium daucifolium (Wall.) Lyon, in Bot. Gaz. **40**: 457. 1905.

Plant lax to rather stout, hairy, 23–47 cm. high; common stalk 4–26 cm.; sterile stalk 1–5 cm. long; blade ternately divided, subcoriaceous, 6–22 cm. wide, 8–17 cm. long; penultimate segments elongate, acute and coarsely serrate; ultimate divisions oblong and blunt; fertile stalk 6–15 cm. long; fruiting spike 2–8 cm. long; sporangia 0.5–0.8 mm. in diameter. Matures spores from November to March. The gametophyte is unknown.

This is distinguished from all the other species of *Sceptridium* by the short stalked sterile blade which is inserted towards the middle of the plant and is little or not at all exceeded by the fertile segment.

Van Alderwerelt van Rosenburgh (1911 & 1913) has described from Java a var. *parvum*, with very small leaves, and a forma *subbasilis*, which is even smaller, with the blade long stalked and basally inserted. The forma *subbasilis* is illustrated. To the writer it appears so different that it would seem to merit specific recognition, but judgment is here withheld until actual material can be examined.

Botrychium daucifolium is a plant of the mountains of India, southern China, Ceylon, Java, Borneo, the Philippines, and Fiji, where it usually occurs at altitudes from 2500–5000 feet.

INDIA. Assam: Dibrugarh, Lakhimpur, *G. Mann* (M, NY). Sikkim: ———, *J. D. Hooker* (G). Central Prov., *G. Wall* (NY). Coimbatore Mts., in groves, *Fairbank 1600* (M). Burma, Herb. Griffith (G).

CEYLON. Central Prov., *G. Wall* (NY).

CHINA. Yunnan: Meng-tsze, *A. Henry 11951* (NY).

JAVA. Preanger: Tjibodas, Mt. Gedde, *W. Palmer* & *O. Bryant 211* (U).

BRITISH NORTH BORNEO. Tenompok, Mt. Kinabalu, *J. & M. S. Clemens 27982* (NY).

PHILIPPINES. Luzon: ———, *A. Loher* (U). Mindanao: Mt. Apo, *R. S. Williams 2518* (NY).

FIJI. Nadarivatu, *Sir Everard im Thurn 278* (U).

B. Subgenus **Eubotrychium** (Milde) Clausen, n. stat.

Botrychium, suborder *Botrychiaceae*, § *Flabellovenata* Presl (in part), in Abh. Böhm. Ges. Wiss. Ser. 5. **4**: 303. 1845–46.

Botrychium, §, I, *Eubotrychium*, a) *Affinia* Milde, in Verh. zool. bot. Ges., Wien. **19**: 96. 1869. In this subdivision Milde placed *B. Lunaria*, *crassinervium*, *boreale*, *matricariaefolium*, and *lanceolatum*. *B. simplex* was placed with *B. ternatum* in the subdivision b) *Ternata*.

Botrychium, section *Eubotrychium* (Milde) Prantl, in Berichte deutsch. bot. Ges. 1: 348. 1883.

The subgenus *Eubotrychium* is characterized by the small size of the sporophytes; the always *glabrous* buds and leaves; the sterile blades, which are simple or variously lobed, rarely more than bipinnate; the somewhat flattened small gametophytes with the primary root developing above and to the side of the prothallium; and the bud, which is completely enclosed by the sheathing base of the leaf stalk. The six species belonging in this group are widely distributed throughout the north temperate zone in North America, Asia, and Europe, with two of them in extreme southern South America and one of these in New Zealand and Australia. The plants are known popularly as moonworts.

KEY TO THE SPECIES OF EUBOTRYCHIUM

A. Sterile blade oblong or ovate in outline, very rarely deltoid, sessile or stalked; the fertile and sterile segments in the bud either erect or with their tips variously inclined, but never both completely reflexed. *a*. Section *Lunariae*

B. Both segments of the leaf erect in vernation or the fertile segment erect and the extreme tip of the sterile just slightly inclined over it; the blade simple or once pinnate, sometimes with the basal divisions again divided, thus appearing ternate. C

C. Sterile blade sessile or short stalked, with the divisions either imbricate or somewhat remote, usually decidedly flabellate, but sometimes obovate or oblong, generally all similar; the basal lobes rarely again divided; the spores 25–40μ in diameter. 13. *B. Lunaria*

C. Sterile blade usually stalked, but sometimes sessile, with the divisions either somewhat remote or imbricate, usually obovate or oblong, seldom flabellate, generally dissimilar in shape; the basal lobes often again divided, giving the blade a ternate appearance; the spores 30–45μ in diameter. D

D. Sterile blade simple or pinnate, sometimes subternately divided, stalked, inserted at various heights. Plants stout and leathery or lax and membranous. 14. *B. simplex*

D. Sterile blade pinnately divided, with the basal divisions again divided, producing a ternate appearance; the blade sessile, inserted above the middle of the plant. Plants very stout and fleshy. 15. *B. pumicola*

B. The fertile segment usually erect in the bud or with the tip slightly inclined towards the sterile; the upper part of the sterile portion commonly bent down over and covering the fertile segment; the blades variously divided, usually bipinnate in mature specimens. E

E. The apex of the sterile segment not clasping the fertile in vernation; the blade either palmately or pinnately divided, either ovate or broadly ovate oblong in outline, usually sessile. 16. *B. boreale*

E. The apex of the sterile segment regularly clasping the fertile in vernation; the blade usually pinnately, sometimes ternately divided, commonly oblong in outline, usually stalked, inserted at various heights. 17. *B. matricariaefolium*

A. Sterile blade deltoid, usually sessile; the fertile and sterile segments both completely reflexed in vernation. *b*. Section *Lanceolatae*
18. *B. lanceolatum*

a. Section **Lunariae**, n. sect.

Lunariae, sectio nova subgeneris *Eubotrychii* lamina sterili oblonga aut ovata, raro deltoidea, sessili aut petiolata; segmentis fertilibus et sterilibus in gemma aut erectibus aut apicibus varie inflexis, sed numquam ambis omnino reflexis.

The five species included in this section all have the fertile and sterile segments essentially erect in the bud. Since the species are very closely related and with little structural difference, the determination of material in this group is often decidedly difficult. The characters afforded by the buds seem most reliable, after which the shape and cutting of the blade, the spore size and spore coat architecture, texture, and the height of insertion of the sterile blade are respectively of diminishing importance.

13. Botrychium Lunaria (L.) Swartz. *Figure 11.*

Of all the *Ophioglossaceae* this is probably the most widely distributed species; ranging throughout northern Europe, Asia, where it occurs southward to northern India, and boreal North America, where it extends southward in the Rocky Mts. to California. It also appears in an almost unchanged form in extreme southern South America, and in Australia and New Zealand. Since over all this vast area the species exhibits about the same sort of variation, it has not been possible to divide it into subspecies correlated with range. The four principal variants have accordingly been treated as varieties. These are distinguished in the following key:

A. Common stalk not greatly enlarged (swollen) towards the base; the blade inserted usually at or below the middle of the plant, with the lobes proximate or remote, flabellate or oblong in outline. B

B. Spores 25–35μ in diameter; blade inserted towards the middle of the plant, usually broadly oblong in outline. C

C. Blade coriaceous, with the flabellate divisions often imbricate. 13a. *B. Lunaria*, var. *typicum*

C. Blade membranous, with the flabellate or oblong divisions rather remote. 13b. *B. Lunaria*, var. *onondagense*

B. Spores 30–40μ in diameter; the blade often inserted somewhat below the middle of the plant, *much* longer than wide, with the divisions various in shape. 13c. *B. Lunaria*, var. *minganense*

A. Common stalk greatly enlarged (swollen) towards the base; the blade inserted above the middle of the plant, with the lobes rather remote and obtuse or truncate. 13d. *B. Lunaria*, var. *Dusenii*

13a. Botrychium Lunaria (L.) Swartz, var. typicum. *Figure 10.*

Osmunda Lunaria L., Sp. pl. **2**: 1064. 1753.

Ophioglossum pinnatum Lamarck, Flore francoise. **1**: 9. 1779. Based on *Osmunda Lunaria* L.

Osmunda ramosa Roth, Tent. Fl. Germ. **1**: 444. 1788.

Osmunda lunata Salisbury, Prodromus. p. 401. 1796.

Botrychium Lunaria (L.) Swartz, in Schrader's Journ. für die Botanik. **2**: 110. 1800.

Botrypus Lunaria Richard, in Marthe, Cat. Jard. Med., Paris. p. 120. 1801.

Botrychium lunatum Gray, A natural arrangement of British plants. **2**: 19. 1821.

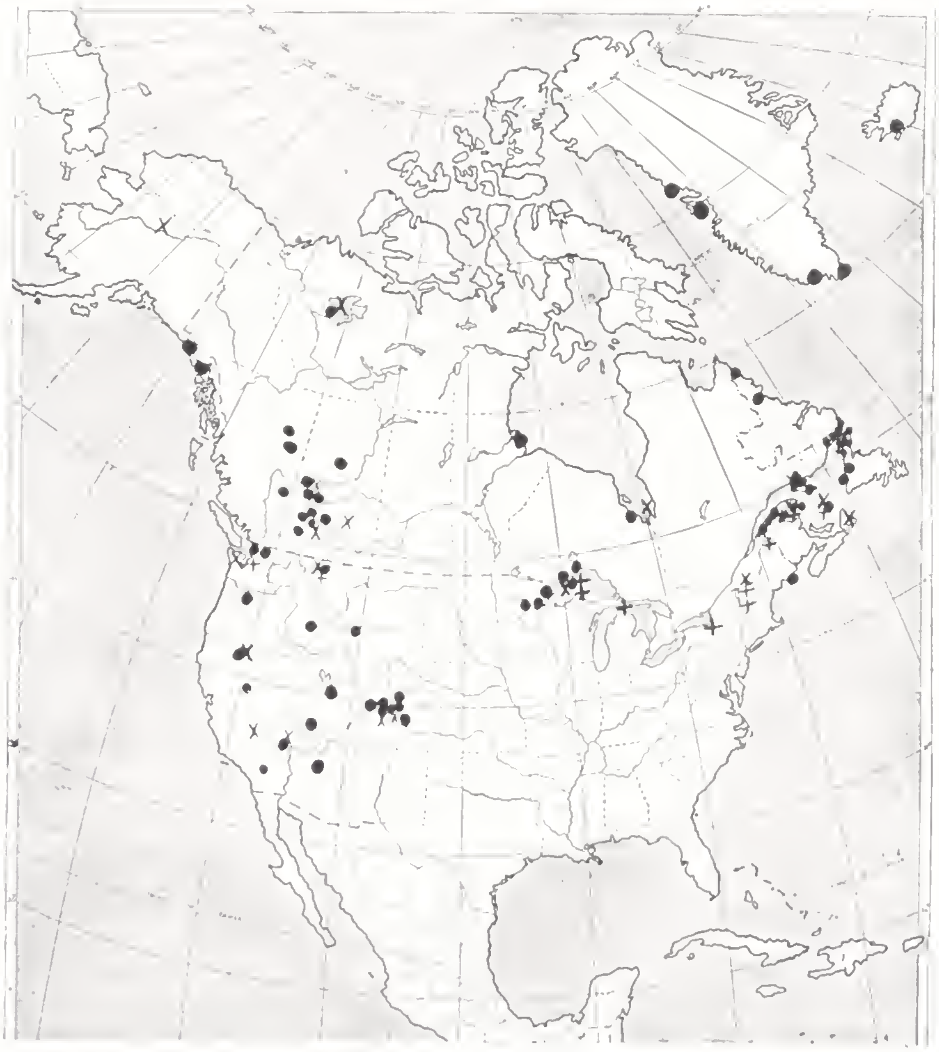


Fig. 10 (above). *Botrychium Lunaria* var. *typicum*.

Fig. 11 (below). *Botrychium Lunaria* in North America; var. *typicum* (•), var. *onondagense* (+), and var. *minganense* (X).

Botrychium racemosum (Fuchs) Bubani, Fl. Pyr. **4**: 438. 1901. Based on *Lunaria minor* of Fuchs, Hist. stirp. p. 481–482. 1542.

Plant rather stout, 4–25 cm. high; bud smooth, with both the fertile and sterile segments erect in vernation, but with the apex of the blade usually slightly inclined over the tip of the fertile spike; common stalk 2–13 cm. long; blade commonly sessile, coriaceous, 0.7–3 cm. wide, 1–6 cm. long, pinnately divided, with the lobes flabellate and often overlapping, their margins either entire or somewhat incised; fertile stalk 1–5 cm. long; fruiting spike racemose or paniculate, 0.4–8 cm. long; sporangia 0.5–1 mm. in diameter. Matures spores in the north temperate regions from mid June to early August. The gametophytes are small, brownish or yellowish, subterranean bodies, provided with rhizoids.

Hofmeister (1855, 1857) and Bruchman (1906) have described the prothallia and development of *Botrychium Lunaria*. In this species, the embryo early differentiates a primary root, which grows in a horizontal direction and emerges from the side of the gametophyte, while the rest of the embryo, remaining within the prothallium, produces a rather large foot. On this foot and opposite the old archegonium, a stem apex appears, which is immediately overarched by a small structure that has been likened to a rudimentary cotyledon. More roots are developed, but the growth of the bud remains almost at a standstill while about eight small leaves are produced in succession. About the last of these is the first to appear above ground. This development differs from that of *B. dissectum* var. *obliquum* in the absence of a suspensor, the lack of curvature of the embryo, and the emergence of the primary root from the side rather than from the lower surface of the gametophyte.

Various trivial leaf forms of the typical *Botrychium Lunaria* have been described, but to the writer these do not seem worthy of nomenclatorial distinction, since they possess neither range correlation nor additional distinctive characters other than the minute details of the architecture of the sterile blade.

In early times this species was sometimes used as a drug. According to S. F. Gray (1821), when it is "made into an ointment with butter and rubbed in opposite to the kidneys, it is esteemed as a certain remedy for a dysentery." Eaton (1878) states that "the moonwort was anciently employed in alchemy and magic, and until a comparatively recent period it was considered singular to heal green and fresh wounds; but its virtues were never rightly manifested unless the plant was collected by moonlight, —probably not an easy task."

Botrychium Lunaria var. *typicum* is a plant of open places, alpine meadows, open fields, turfy slopes, and gravelly banks. It seems to reach its best development in regions overlying limestone rock. The distribution is extensive: Iceland, southern and western Greenland, Labrador, Newfoundland, eastern Quebec in the region of the Gulf of the St. Lawrence, western Ontario north of Lake Superior, Maine, northern Michigan, and extreme northeastern Minnesota. It occurs also in Manitoba and Mackenzie, and in the mountains of Alberta and British Columbia southward through Montana and Washington to Colorado, Arizona, and California; also along the coast of southern Alaska, in the Pribilof Islands, and westward through the Aleutian Chain to the Commander Islands. In Asia it ranges southward to Mount Fuji in central Japan and to the mountains of northern India and Afghanistan and probably occurs throughout central Siberia. In Europe it is found from Ireland, Scotland, and northern Scandinavia southward to northern Spain, southern France, northern Italy, and Austria, and eastward to eastern Czechoslavakia, Esthonia, and northwestern Russia. It has also been collected in Patagonia, New Zealand, southern Australia, and Tasmania.

GREENLAND. Southern and western coasts from Frederiksdal, 59° 55′ N., to Disko and Svarenhuk Halve, Manitsoqut, 71° 30′ N.

LABRADOR. Region of Straits of Belle Isle, Chateau, Nain, Ramah, and along Ungava River.

NEWFOUNDLAND. Districts of Petit Nord Peninsula and St. Georges Bay; also region of Hannah's Head and St. Johns Island.

QUEBEC. Bonaventure, Gaspé, Matane, Rimouski, and Saguenay Counties; also the Mingan Islands and Anticosti Island.

ONTARIO. Thunder Bay County and region of James Bay.

MANITOBA. Fort Churchill, *R. Bell 28561* (Ot).

ALBERTA. Calgary West, Peace River, and Red Deer Counties.

BRITISH COLUMBIA. Cariboo, East Kootenay, and West Kootenay Counties; also Peace River Block.

MACKENZIE. Great Bear Lake, *J. M. Bell* (Ot).

ALASKA. Region of Glacier Bay, Yakutat Bay, Shumagin Islands, Unalaska, and St. Paul Island.

COMMANDER ISLANDS. *L. Stejneger 143* (H, U). Bering Island, *J. M. Macoun 204* (G).

MAINE. Hancock: Cranberry Island, July 4, 1937, *Mrs. Edward W. Evans* (Claus, Ph). These specimens are somewhat unusual because of their large size, the rather long stalks of the sterile blade, and the tremendously well developed and much branched fertile segments.

MICHIGAN. Keweenaw: Isle Royal, *W. S. Cooper 129* in part (G).

MINNESOTA. Aitkin, Carlton, and Lake Counties.

MONTANA. Glacier National Park, Grinnell Glacier, *P. C. Standley 16766* (U).

IDAHO. Custer: Bonanza, *J. F. Macbride* and *E. B. Payson* (G).

WYOMING. Yellowstone National Park: Yellowstone Lake, *J. N. Rose 508* (U).

COLORADO. Clear Creek, El Paso, Garfield, Grand, and Larimer Counties.

Utah. Iron and Salt Lake Counties.

Nevada. Clark and Ormsby Counties.

Arizona. Coconino: Mt. Agassiz, *J. G. Lemmon* (NY); also San Francisco Peaks, elev. 10,500–11,000 ft., *T. H. Kearney* and *R. H. Peebles 12123* (U).

California. Modoc and San Bernardino Counties.

Oregon. ? Mt. Hood, *L. F. Henderson* (G).

Washington. Okanogan and Whatcom Counties.

Argentina. Patagonia: ———, *C. W. Furlong 10* (C, NY).

Iceland. Reykjavik, *R. Bartlett 29* (NY). Hals, *Miss E. Taylor* (C, G, Ph, U).

Faroe Islands. Momafjeld, Videro, *Miss E. Taylor* (G).

Ireland. Antrim and Donegal Counties.

Scotland. Aberdeen, Edinburgh, Forfarshire, and Kincardineshire Counties.

England. Cheshire and Suffolk Counties.

Norway. Counties of Christiana, Hamar and Tromsö.

Sweden. Läns of Bohnstan, Gafleborg, Jamtland, Norrbotten, Oelandia, Scania, Södermanland, and Stockholm.

Denmark. Gallöbben, ——— (M). Storeklint, *A. Ingerslev 56835* (Ot).

France. Departments of Hautes Alpes, Hautes Pyrenees, and Vosges.

Spain. Asturias: Pico de Aryas, *Durieu* (G).

Italy. Eneto: Belluno, *R. Pampanini* (G).

Switzerland. Cantons of Geneva, Grisons, Uri, and Valais.

Austria. Districts of Lower Austria, Salzburg, and Upper Austria.

Roumania. Districts of Temes and Zip.

Czechoslovakia. Districts of Bohemia, Moravia, and Slovakia.

Germany. Provinces of Baden, Bavaria, Brandenburg, Pommern, Saxony, Schlesien, Silesia, and Thuringia.

Esthonia. Narva, *M. S. Baxter* (Herb. I. W. Clokey).

Finland. Uleaborg: Sordavala, *H. Pullinen, A. Türikka,* and *H. Tulla 1005* (Ot).

Russia. Karelia Onegensis, *V. P. Sancz 192* (Ph). Karelia pomorica occidentalis, *M. M. Iljin 263* (G).

Siberia. Siberia occident., ex Herb. Univ. Tomskensis (NY). Kamtchatka, reported by Christensen and Hultén (1928).

Afghanistan. Kurrum Valley, *J. E. T. Aitchison 1002* (G).

India. Kashmir: Gulmorg, *R. R. Stewart 10357a* (Ph); Chamba, Tarloknath, *W. Koelz 1058* (NY); *Souamarg, R. R. Stewart 7180* (U).

Japan. Islands of Honshu and Yizo.

Australia. Reported, but no specimens have been seen by the writer.

Tasmania. ———, *R. C. Gunn* (G).

New Zealand. Reported, but no specimens have been seen by the writer

13b. Botrychium Lunaria var. onondagense (Underwood) House

Botrychium onondagense Underwood, in Bull. Torrey Club **30:** 47. 1903. Based on specimens from the vicinity of Syracuse, Onondaga Co., N. Y. The type, collected by L. M. Underwood, at Split Rock, near Syracuse, is in the herbarium of the New York Botanical Garden. The species is named for Onondaga County, where Dr. Underwood states that he commenced the study of ferns in 1875.

Botrychium Lunaria onondagense (Underw.) Clute, in Fern Bull. **14**: 80. 1906.
Botrychium Lunaria var. *onondagense* (Underw.) House, in Bull. N. Y. State Mus. Nos. 243–244: p. 47. 1923.

Similar to the var. *typicum*, but the plants lax and membranous, with the divisions of the sterile blade either flabellate or oblong, rather remote; the blade sometimes short-stalked.

This is a plant of rich soils in rocky woodlands, where the slender habit and membranous lax blade seem a direct response to shade conditions. The writer considers this population to represent a variety rather than a subspecies of *B. Lunaria* because it is distributed in woodlands quite generally throughout the range of var. *typicum* and because, although it occurs farther south than the typical form in the northeastern United States, it seems to be merely an ecological variation and not a major subdivision of the species.

Labrador. ———, *Butler* (M).

Newfoundland. Straits of Belle Isle, Flower Cover, *M. L. Fernald, B. Long & B. H. Dunbar 26161* (G). St. John Island, *M. L. Fernald, K. M. Wiegand, B. Long, F. A. Gilbert, Jr. & N. Hotchkiss 27272* (C, G, Ph).

Quebec. Bonaventure: between Balde and the Baie des Chaleurs, *J. F. Collins, M. L. Fernald & A. S. Pease* (G). Gaspé: Percé, Mt. Percé, *E. F. Williams, J. F. Collins & M. L. Fernald* (G); Magdalen Islands: Basin Island, *Fernald, Bartram, Long & St. John 6674* in part (G, NY, U). Labelle: Nomingue, Lac Blanc, *H. Laflamme* (Mont). Rimouski: Bic, *E. F. Williams, J. F. Collins & M. L. Fernald* (G). Sherbrooke: Sherbrooke, *H. Mousley* (Mont, Ot).

Maine. Aroostook: Fort Kent, *K. K. Mackenzie 3567* (NY).

Vermont. Orleans: Willoughby, *G. H. Tilton* (N). Windsor: Woodstock, Mt. Tom, *A. N. Leeds 775* (Ph).

New York. Onondaga: Jamesville, *H. E. Ransier* (Deam, Ph, U).

Michigan. Cheboygan: Mackinac Island, *W. H. Manning* (G). Keweenaw: near Copper Point, Keweenaw Point, *O. A. Farwell* (NY); Isle Royale, *H. Gillman* in part (G, Princ).

Montana. Lambert Valley, Mission Mts., *M. E. Jones 644,004* (Ph). Box Elder Creek, Belt Mts., ——— *525* (NY). Stanton Lake, *R. S. Williams 525* (U).

Washington. Snohomish: Mt. Dickerman, *J. W. Thompson 8781* (G).

Hungary. ———, ——— (G).

Germany. ———, *Reichardt* (G).

India. Kashmir: Pahlgam, *R. R. Stewart 9232* (NY).

13c. Botrychium Lunaria, var. minganense (Victorin) Dole

Botrychium minganense Victorin, Contrib. Lab. Bot. Univ. Montreal. No. **11**: 331. 1927. Based particularly on specimens from the Mingan Islands in the Gulf of the St. Lawrence. The type collection, *Victorin and Rolland 18122*, from the Isle Niapisca, is in the herbarium of F. M. -Victorin. Cotypes are in the Gray Herbarium, University of Montreal, New York Botanical Garden and the Philadelphia Academy of Natural Sciences, also elsewhere. The species is named for the Mingan Islands, where it seems to reach its best development.

"*Botrychium Lunaria* var. *minganense* (Victorin) Dole, in Flora of Vermont, ed. 3. p. 1. 1937." *Fide* F. M.-Victorin.

This differs from the var. *typicum* in the somewhat larger spores, 30–40μ in diameter, and in the variability of the sterile blade, which is regularly much longer than wide, is sometimes inserted below the middle of the plant, and rarely has the basal pair of lobes again divided. The lobes are various in shape, usually not decidedly flabellate, but more often obovate, rhomboidal or oblong, frequently incised and either distant or proximate.

Despite the careful studies of Victorin (1927, 1932), it has not seemed possible to maintain *B. minganense* either as a species or as a subspecies, since it is found almost throughout the North American range of *B. Lunaria* var. *typicum* and passes imperceptibly into that variety. Although Victorin has stated that in the Mingan Islands the two forms do not seem to intergrade, collections from Michigan, Alberta, and various places in the Rocky Mountains indicate that, at least in those areas, a complete transition occurs.

Victorin has maintained that *B. Lunaria* is a species remarkably constant in its characters, but studies by the writer do not support this contention. Herbarium specimens from all over the range of the species indicate that *B. Lunaria* is quite as variable as other species of *Botrychium* in the cutting and height of insertion of the sterile blade, in texture, and in the general habit of growth. Forms like *B. onondagense* Underw. and *B. minganense* Vict. come within this natural range of variation for the species and since they are without geographical correlation, they must be treated as varieties.

B. Lunaria var. *minganense* may be known by its yellowish green appearance and its tendency to grow in clumps, with the roots of many plants closely interwoven. The blades are pinnately divided, with the lateral lobes obovate or rhomboidal, cuneate at the base and often much incised or even again divided. The spores average several microns larger than do those of typical *B. Lunaria*, but spore size is not of great significance in *Botrychium* since variation is very great. Since spores from the same plant may vary as much as their entire diameter, it is necessary to make hundreds of measurements in order to obtain the average spore size for a particular specimen. A variable character, which must be worked out in this manner, is not of practical value and should not be used as a primary basis for species differentiation.

The var. *minganense* is a plant of marly meadows, where it may grow either by itself or in association with other forms of *B. Lunaria*. In North America the range is essentially the same as for the typical variety; from the Straits of Belle Isle to Hudson Bay, southern Quebec, northern Michigan, Wisconsin, Alberta, Montana, Colorado, Nevada, California, central Mackenzie, and central Alaska.

Labrador. Straits of Belle Isle, Blanc Sablon, *M. L. Fernald* & *K. M. Wiegand 2346* in part (C, G, Ph).

Nova Scotia. Cape Breton Island, ? New Campbelltown, *D. White* & *C. Schuchert 8* (U).

Quebec. Archipel de Mingan: Ile Niapisca, *Ff. M. -Victorin* & *R. -Germain 18,122* (Deam, G, Mont, NY, Ot ,Ph); Ile a la Proie, *Ff. M. -Victorin* & *R. -Germain 22,016* (G, Mont, NY, Ot, Ph). Bonaventure: ? between the Forks and Brulé Brook, Little Cascapedia River, *J. F. Collins, M. L. Fernald* & *A. S. Pease* (G). Gaspé: Mont Saint-Pierre, *Ff. M. -Victorin, R. -Germain* & *E. Jacques 33,581* (G, Mont, NY); Magdalen Islands, Basin Island, *M. L. Fernald, E. B. Bartram, B. Long* & *H. St. John 6674* in part (G, Ot, U). Rimouski: Bic. *M. L. Fernald* & *J. F. Collins* (G). Stanstead: Hatley, *L. Griscom 9869* (Gris). James Bay, Charlton Island, *D. Potter* (G).

Ontario. Thunder Bay: Peninsula Island, Lake Nipigon, *J. Macoun 28,575* in part (Ot).

Manitoba. Churchill, Hudson Bay, Lat. 58°, 50′, *J. M. Macoun 79,227* (G, Ot).

Saskatchewan. Boss Hill Creek, *J. Macoun 28,543* (Ot).

Alberta. Bow River: Rosedale, *Marion E. Moodie 1073* (G, NY, U). Peace River: Shovel Pass, Jasper Park, *W. C. Wilson 234* (C, Claus, H).

British Columbia. East Kootenay: Stephen, *Miss D. Pelluet 352* (Ot), a single doubtful specimen. Cascade Range, near head of McGillivray Creek, alt. 4500 ft., *J. M. Macoun 92,735* (Ot).

Mackenzie. Great Bear Lake: Etacho Point (Big Point); alt. about 1500 feet. 66° N., 121°30′ W. Aug. 24, 1928, *A. E.* & *R. T. Porsild 3458* (Mont); also north shore of Smith Arm, Olmsted Bay, *A. E.* & *R. T. Porsild 5054* (Mont).

Alaska. Kokrines Mountains: north side of divide towards Metozitna River, 65°20′ N., 154°30′ W., alt. 800–4000 feet, June 23–July 5, 1926, *A. E.* & *R. T. Porsild 687* (Mont).

Michigan. Keweenaw: Isle Royal, *W. S. Cooper 129* in part (G).

Wisconsin. Bayfield: Bark Point, shore of Lake Superior, *Conklin* & *Knowlton 2* (Mont), a single poor specimen.

Montana. Glacier National Park, *P. C. Standley 16,039* (U).

Wyoming. Park: Beartooth Butte, Shoshone National Forest, *L. O.* & *R. P. Williams 3667* (G).

Colorado. Boulder: Bryan Mt., *F. Ramaley 10749* (Herb. Univ. Colo.). Clear Creek: Graymont, *I. W. Clokey 3631* in part (U). Ouray: Ouray, *J. C. Arthur 2* (NY). ? Spur of Mt. Anters, Sawatch Range, *T. S. Brandegee 2349* (M).

Nevada. Clark: Charleston Mts., *I. W. Clokey 7462, 7463*, and *7464* (Clokey).

California. Modoc: Warner Valley, *Mrs. R. M. Austin 1220* (U). Tulare: eight miles northwest of Whitney Meadows, Sierra Nevada, *F. V. Coville* & *F. Funston 1703* (NY, U). San Antonio Mts., Coldwater Fork of Lytle Creek, *I. M. Johnston 1757* (U).

Washington. Olympic Mountains, *C. V. Piper 928* (M, NY).

13d. Botrychium Lunaria var. Dusenii Christ

Botrychium Lunaria var. *Dusenii* Christ, in Ark. för Bot. **6**, no. 3: 5–6. 1906. Based on specimens collected by Dr. P. Dusen at Rio Fosiles, not far from Lake San Martin, in Patagonia. The variety is named in honor of Dr. Dusen.

This differs from var. *typicum* in the smaller size, the swollen base of the common stalk, and the character of the sterile blade, which is inserted high up, with the rachis broad and the lateral lobes only 4–5 pairs, rather distant, cuneate-rhomboid, and obtuse or truncate at the apex.

Since the typical form of the species occurs in southern South America along with the present variety, it has not been possible to designate this as a geographical race or subspecies. The relation of the var. *Dusenii* to var. *typicum* must still be worked out. Scant material is available from South America, while there are almost no data concerning the status of the two varieties in the field. Dr. Christ, in his original description of the Patagonian variety, indicated that one of his reasons for giving it a name was to make Chilean and Argentine botanists more interested to collect additional specimens, but up until now this objective has not been achieved.

B. Lunaria var. *Dusenii* is at present known only from Patagonia, where according to Christ, it is found on denuded slopes.

ARGENTINA. Patagonia. ———, *Vieuna* (G).

14. BOTRYCHIUM SIMPLEX Hitchcock. *Figure 12.*

This is perhaps the most variable of all the species of *Eubotrychium*. Unfortunately, the several major variations can be only poorly correlated with range and must accordingly be treated as varieties rather than as subspecies. These are differentiated in the following key:

A. Plants stout and leathery; the blade inserted at or below the middle of the plant, with the divisions proximate, often imbricate. B
  B. Blade simple, entire or once pinnate, inserted either basally or suprabasally; sterile segment in vernation either erect or with its tip slightly inclined over the apex of the fertile portion. 14a. *B. simplex* var. *typicum*
  B. Blade ternate, i.e. pinnate with the two basal divisions again pinnate, inserted basally; sterile segment entirely erect in the bud. 14b. *B. simplex* var. *compositum*
A. Plants lax and membranous; the blade inserted at or above the middle of the plant, with the divisions typically remote. C
  C. Sterile blade inserted towards the middle of the plant. Plants of dry woodlands. 14c. *B. simplex* var. *laxifolium*
  C. Sterile blade extremely slender, inserted towards the summit of the plant. Plants of swamps and wet woods. 14d. *B. simplex* var. *tenebrosum*

14a. BOTRYCHIUM SIMPLEX Hitchcock, var. TYPICUM

Botrychium simplex Hitchcock, in Amer. Journ. Sci. **6**: 103. pl. 8. 1823. Based on specimens collected in dry hilly pastures in Massachusetts. The figure accompanying the original description depicts a small juvenile plant of the kind that is fairly common in northern New England, southern Quebec, and western Europe. The specific name alludes to the simple blade and fertile spike.

Botrychium Lunaria var. *cordatum* Fries, Summa Vegatab. Scand. **1**: 251. 1846. Based on material from the old province of Scania, Sweden.

Botrychium Kannenbergii Klinsmann, in Bot. Zeit. **10** (22): 379. pl. 6a. 1852. Based on specimens collected at Memel by Kannenberg. The plate shows two specimens, one rather immature and the other large and well developed. The species is named in honor of its discoverer, Kannenberg, a Peplin apothecary.

Botrychium virginicum var. ? *simplex* (Hitchcock) Gray, in Manual, ed. 2. p. 602. 1856.

Botrychium Reuteri Payot, Cat. Foug. Mont-Blanc. p. 15. 1860.

Botrychium Lunaria var. *simplex* (Hitchc.) Watt, in Can. Nat. 2. **3**: 160. 1866.

Botrychium simplex var. *cordatum* (Fries) Wherry, in Amer. Fern Journ. **27**: 58. 1937. This combination is contrary to the spirit of Recommendation 18 under Article 30 of the International Rules of Botanical Nomenclature, in which botanists are urged to designate the nomenclatorially typical element of a species either by employing tautonymy or by using one of the conventional epithets.

Plant compact, rather fleshy, 3–16 cm. high; bud glabrous with both the fertile and sterile segments erect or with the tip of the sterile slightly inclined over the tip of the fertile; blade inserted almost basally or towards the middle of the plant; common stalk 0.5–6 cm. long; sterile stalk 0.2–2 cm. long; blade simple, lobed, or pinnately divided, 0.5–4 cm. long, 0.3–3.2 cm. wide; divisions oblong, rhomboid, or reniform, usually overlapping; basal divisions rarely again divided; fertile stalk 0.5–8 cm. long; fruiting spike simple or compound, 0.3–5 cm. long; sporangia 0.8–1.2 mm. in diameter; spores finely and irregularly reticulate, 33–52μ in diameter, averaging 40–46μ. Matures spores during late May and June.

Lasch (1856) and Milde (1869) described a number of varieties which were mostly age forms of the same population and as such do not merit formal Latin designation. The one variety of Lasch which does seem to merit recognition, var. *compositum*, is treated below.

Campbell (1922) studied and described the gametophytes of plants which he identified as *B. simplex*, but the drawing accompanying his paper represents two specimens which belong more likely to the var. *tenebrosum*. The fact that this material was collected in swampy ground further indicates that variety.

Since Milde's time many botanists have studied the variation in this species. Davenport (1877) and Luerssen (1889) described and illustrated the principal leaf forms. These seem to the writer to be explained largely on a basis of age, but also by the influence of the environment upon the habit of the plants.

Botrychium simplex and other species of moonworts frequently occur in colonies made up of individuals all of approximately the same size and age. This is probably because the spores are widely distributed by the wind and, when they happen to fall in a suitable spot, they may germinate and produce a large number of gametophytes. All the plants in such a place might develop at about the same rate of growth. Hence they would be all of the same general type and size. Once a colony should become established, it might maintain itself for a long period, but this does not seem to be true everywhere. Apparently the conditions favorable for spore germination are rather critical and not always maintained, for instead of colonies perpetuating themselves for indefinite periods in the same locality, they may mature and gradually die out. Conditions evidently become unsuitable for spore germination on the old site, while new colonies are established elsewhere. This theory may explain, at least in part, why species like *Botrychium simplex* seem to fluctuate greatly in abundance in particular localities.

The var. *typicum* is a plant of open places; growing in pastures and meadows, and on shores and gravelly slopes. In the south it passes into the var. *laxifolium*, which is a slender woodland shade form. The typical variety has the following known distribution in North America; from Newfoundland, Nova Scotia, and Quebec southward to Massachusetts, New York, and northern Pennsylvania; westward to Ontario, Wisconsin, and British Columbia; and southward through Oregon and Montana to Colorado, New Mexico, and California. It is also found in northern Europe, on the island of Corsica, and in Japan.

Newfoundland. Regions of Bay of Islands, Notre Dame Bay, and Exploits Bay.

Nova Scotia. Cumberland, Lunenberg, and Yarmouth Counties.

Quebec. Bonaventure, Gaspé, Matane, Montcalm, and Vercheres Counties; also reported from Chicoutimi and Stanstead Counties.

Ontario. Bruce and Thunder Bay Counties.

British Columbia. Vancouver Island: Nanaimo Mountain, *J. Macoun* (G); Mt. Benson, *J. Macoun 92,732* (G, Ot, U). Summit of Burgess Trail, Selkirk and Rocky Mts. near 51°30′ N. lat., *E. R. Heacock 593* (B, Ph).

Maine. Androscoggin, Aroostook, Franklin, Hancock, Oxford, Penobscot, Somerset, and Washington Counties.

New Hampshire. Carroll, Coos, Grafton, Rockingham, and Sullivan Counties.

Vermont. Addison, Bennington, Caledonia, Chittenden, Lamoille, Orleans, and Windsor Counties.

Massachusetts. Franklin and Worcester Counties.

New York. Essex, Jefferson, Lewis, Oneida, Onondaga, Oswego, Otsego, St. Lawrence, Schuyler, Suffolk, Tompkins, Ulster, and Washington Counties.

New Jersey. Union: Plainfield, *J. Porter* (NY).

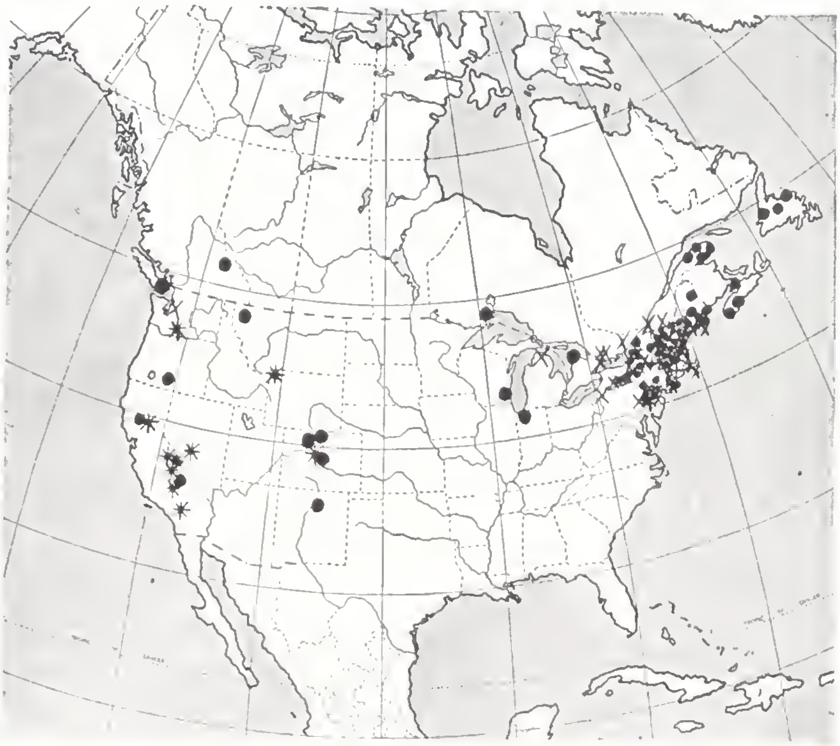
Pennsylvania. Monroe, Northampton, and Wayne Counties.

Indiana. Porter: Dune Park, *M. W. Lyon, Jr.* (Herb. M. W. Lyon, Jr.).

Wisconsin. Milwaukee: Milwaukee, *H. E. Hasse* (NY).

Montana. Flathead: Columbia Falls, *R. S. Williams* (G, M, NY).

Colorado. El Paso and Gilpin Counties, also doubtfully Boulder County.



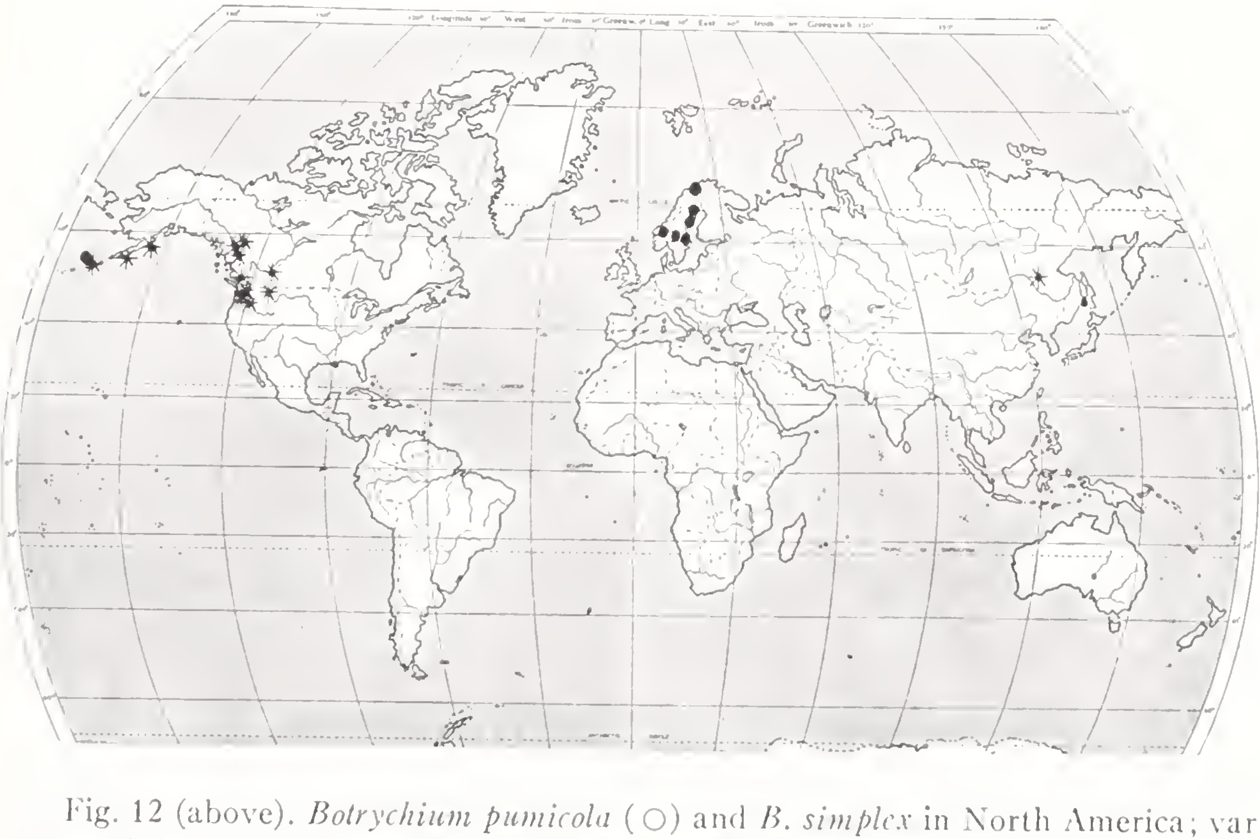


Fig. 12 (above). *Botrychium pumicola* (○) and *B. simplex* in North America; var. *typicum* (•), var. *laxifolium* (+), var. *tenebrosum* (X), and var. *compositum* (*).

Fig. 13 (below). *Botrychium boreale* ssp. *typicum* (•) and ssp. *obtusilobum* (*).

NEW MEXICO. Santa Fe: Santa Fe Creek Valley, *A. Fendler 1014* (G).

CALIFORNIA. Butte and Tulare Counties.

OREGON. Lake: Warner Range, *F. V. Coville* and *J. B. Leiberg 41* (U).

SCANDINAVIA. Reported by various authors, but no specimens have been seen by the writer.

DENMARK. Sjellandia: Saltbökvig, *J. Hartz, O. Möller*, and *C. H. Ostenfeld 4199* (Mont).

GERMANY. Provinces of Brandenburg and East Prussia.

FINLAND. Isthmus Karelicus, par Valkjarvi, Punstinlahti ad Pasuri, *G. Lang* (M, NY, Ot).

CORSICA. Reported by Litardiere (1927). The illustration clearly shows that the Corsican material belongs to var. *typicum*.

JAPAN. Reported by Nakai (1926) from Yizo.

14b. BOTRYCHIUM SIMPLEX var. COMPOSITUM (Lasch) Milde

Botrychium Kannenbergii var. *compositum* Lasch, in Bot. Zeit. **14** (no. 35): 608. 1856. Based on specimens from Germany with the blade divided into two or three major divisions and the fruiting spike paniculate.

Botrychium simplex var. *compositum* (Lasch) Milde, in Verh. zool. bot. Ges., Wien. **19**: 140. 1869.

Differing from var. *typicum* in having the sterile blade ternately divided and inserted basally, and in having the fertile and sterile segments entirely erect in the bud.

Although all the other varieties of *B. simplex* described by Lasch seem to represent mere age forms of the var. *typicum*, the var. *compositum* seems to be something more than such a form. This contention is based on the fact that in the western United States the ternately divided *B. simplex* is the dominant and often the only form. It seems to possess its characteristic habit and blade from an early age. This western material has in general the appearance of a distinct race, characterized by the basal insertion of the sterile segment, the ternate nature of the blade, and the stout bud with both the fertile and sterile segments erect. Large series of specimens from Colorado and elsewhere show, however, that there is a complete intergradation between the typical form and this variety. In eastern North America and Europe the ternately divided *B. simplex* is extremely rare and probably represents only an age form. Since the European var. *compositum* and the plants from western North America are essentially the same, Lasch's name has been retained for this population, which is here treated as a variety only weakly correlated with range.

B. simplex var. *compositum* is characteristically a plant of grassy open slopes and meadows. It is found sparingly in northern Europe and New England; while in the western United States it occurs in Wyoming, Colorado, Nevada, California, and Washington.

Fig. 14 (left). *Botrychium simplex* var. *tenebrosum* from Springdale, Sussex County, New Jersey ($\times \frac{1}{4}$).
Fig. 15 (right). Type specimens of *Botrychium matricariaefolium* ssp. *hesperium* ($\times \frac{1}{3}$).

MAINE. Hancock: Mt. Desert Island, *E. L. Rand* (N).

NEW HAMPSHIRE. Coos: W. Milan, *A. S. Pease 14,122* (N).

MASSACHUSETTS. Franklin: Sunderland, *W. H. Chapin* in part (N).

WYOMING. Yellowstone National Park, Yellowstone Lake, *C. C. Parry 306* (G, M, NY, Ph).

COLORADO. El Paso: Pikes Peak, *I. M. Johnston 2415* in part (G).

NEVADA. Esmeralda: Chiatovitch Creek, White Mountains, *V. Duran 3080* (B, C, M, NY, U).

CALIFORNIA. Butte: Jonesville, *E. B. Copeland 601* in part (B, C, M, NY). Fresno: Kearsage Pass, *Mrs. J. Clemens* (NY). Mariposa: Yosemite, *A. A. & A. H. Wright* (C, Claus). Mono: Mt. Lyell, *J. Muir* (G). San Bernardino: Bluff Lake, San Bernardino Mts., *P. A. Munz 10,673* (G). Tulare: Kaweah Mds., C. A. Purpus *5646* (G, M). Tuolumne: Tuolumne Meadows, *H. L. Mason 676* (Herb. Univ. Colo.).

WASHINGTON. Yakima: Mt. Paddo (Adams), 1880, *W. N. Suksdorf* in part (G).

GERMANY. Brandenburg: Frankfurt, *W. Lasch* in part (NY).

14c. BOTRYCHIUM SIMPLEX var. LAXIFOLIUM Clausen

Botrychium simplex var. *laxifolium* Clausen, in Bull. Torrey Club **64**: 277. pl. 7. 1937.

"Plant lax, with the blade membranous and inserted medianly; the divisions of the blade obovate and rather remote.—Dry woodlands of Vermont, Massachusetts, Connecticut, New York and New Jersey. Type in Clausen Herbarium, from dry shady woods over limestone rocks, Johnsonburg, Warren Co., N. J., June 24, 1933, *J. L Edwards* & *R. T. Clausen*, no. 80."

The var. *laxifolium* differs from both the vars. *typicum* and *compositum* in its more slender habit and its membranous blade with the divisions rather remote, and from the var. *tenebrosum* in having the blade much better developed and inserted medianly rather than towards the summit of the plant. This is a woodland, shade form which, in central and northern New York and New England, passes into var. *tenebrosum* on the one hand, and into var. *typicum* on the other. Since Milde's many described varieties of *B. simplex* seem to represent mere age forms of the same thing, while the present population represents a distinct local variation, it has seemed best to assign to it a new name. The var. *subcompositum* (Lasch) Milde is most like the var. *laxifolium*, but it differs in being of stouter habit and in having the blade more coriaceous, with the divisions rather crowded, not remote. For ecological data and further discussion, see Clausen (1937a).

As at present known, the var. *laxifolium* is limited to dry, deciduous woodlands in Vermont, Massachusetts, Connecticut, New York, New Jersey, and Pennsylvania.

VERMONT. Addison: Middlebury, *E. Brainerd* in part (G, NY, Ph). Bennington: Manchester, *M. A. Day 246* (G).

MASSACHUSETTS. Berkshire: Pittsfield, *G. G. Kennedy* (G).

CONNECTICUT. Windham: Woodstock, *C. A. Weatherby* & *A. W. Upham* (G), this not entirely typical, but approaching the variety.

NEW YORK. Chemung: Erin, *S. J. Smith* (C). Lewis: Lowville, *Mrs. K. L. Barnes* in part (NY, Ph). Saratoga: West Charlton, *H. K. Svenson* (B). Tompkins: Danby, *F. C. Curtice* (C, NY). Washington: Fort Ann, *S. H. Burnham* (C).

NEW JERSEY. Sussex: Springdale, *B. Long 8580* (Ph). Warren: Johnsonburg, *L. Griscom & K. K. Mackenzie 10602* (Gris, NY).

PENNSYLVANIA. Berks: Kutztown, *C. L. Gruber* (Herb. C. L. Gruber). Also reported from Bucks County.

14d. BOTRYCHIUM SIMPLEX var. TENEBROSUM (A. A. Eaton) Clausen. *Figure 14.*

Botrychium tenebrosum A. A. Eaton, in Fern Bull. **7**: 8. 1899. Based on abundant material collected in shady situations in Rockingham Co., N. H., and Essex Co., Mass. Specimens from Kensington, N. H., filed in the Gray Herbarium and at the New York Botanical Garden, bear the inscription that they are types. Series of specimens from Amesbury, Byfield and West Newbury, Mass. have been widely distributed to various herbaria and marked either "type specimens" or "type collection." The actual type, so labelled by A. A. Eaton himself, is in the herbarium of the New England Botanical Club. It was collected by Eaton at Byfield, Mass., on July 3, 1898, and is a plant 13.5 cm. high (without root system); the sterile blade is elongate, with two pairs of simple subopposite distant lobes, and is inserted at about 8 cm. from the base; the fertile portion is divided into two spikes, both simple, with few and scattered sporangia. The specific name probably alludes to the dark shady places in which the plant characteristically grows.

Botrychium matricariaefolium var. *tenebrosum* (A. A. Eaton) Clute, Our Ferns in their Haunts. p. 62. 1901. This combination was based on the erroneous assumption that *B. tenebrosum* represents a depauperate form of *B. matricariaefolium*, but such forms of the latter are not at all like *tenebrosum*. Further, the buds do not show the apex of the sterile segment completely bent over and grasping the tip of the fertile portion, as they do in *matricariaefolium*, and the spores average considerably larger than in that species.

Botrychium simplex var. *tenebrosum* (A. A Eaton) Clausen, in Bull. Torrey Club **64**: 275. 1937.

Plant glabrous, very slender, 1–25 cm. high; base of stalk enclosing bud, the whole covered by the brown sheathing bases of the stalks of preceding years; fertile segment erect in the bud; sterile segment usually with the apex slightly inclined over (but not covering) tip of fertile spike; sterile blade not sessile, inserted above the middle, usually towards the summit of the plant, simple or lobed, in old plants with two or three pairs of subopposite, obovate-oblong lobes; fertile spike simple or once pinnate; spores finely vermiculated or verrucose, large, 38–52μ in diameter, averaging about 42μ.

Gametophytes with young sporophytes attached have been found in low wet woods at Springdale and at Mud Pond, both in Sussex Co., N. J. These are small flattened brownish bodies, 3–4 mm. long and about 1.5 mm. wide. The roots are developed from the dorsal surface, growing to the side of the prothallium, while the stem apex differentiates from the center where the roots originate and grows upwards from this point. Thus, the sporophyte is developed entirely on the upper surface of the gametophyte, which probably remains attached to the young plant for several years, before it disappears completely through decay. Sporophytes with gametophytes attached ranged from minute to quite large. At Mud Pond the largest specimen obtained with an undecayed gametophyte attached was 17 cm. high, with a pinnately divided spike 3.3 cm. long, in the process of shedding abundant spores. The foliage blade in this specimen was as well developed as is ever the case in the var. *tenebrosum*.

Campbell (1922) has described the development of plants which he determined as *B. simplex*, but his drawings indicate that he had material of var. *tenebrosum*. The specimens on which his work was based were collected by Dr. H. C. Lyon in swampy ground on the shore of Echo Lake, near White Bear Lake, Minnesota. According to Campbell, the development is similar to that in *B. Lunaria*, except that the differentiation of root and stem apices in the embryo occurs much earlier in this variety.

Many recent authors have merged Eaton's *B. tenebrosum* with *B. simplex*, not considering it worthy of any nomenclatorial distinction; yet, in northern New Jersey, eastern Pennsylvania, and parts of central and southern New York, *B. tenebrosum* forms a very distinct population, quite constant in its characters and not intergrading with any other forms. Farther north, however, in northern New York, northern New England, and southern Canada, there is a complete intergradation between this population and typical *B. simplex*. Since *tenebrosum* also occurs at various places throughout the entire range of the *B. simplex* complex, it has not been possible to consider it as a geographical race, but it is here treated as a decidedly distinct variety. The var. *angustum* of Milde resembles the var. *tenebrosum* in some respects, but does not seem to the writer to be exactly the same.

B. simplex var. *tenebrosum* occurs in damp heavily shaded woods and at the edges of deep swamps. It is often found in slightly acid soil on rich swampy bottom lands, where it may grow in the moss on hummocks and on old decaying logs. Its range is largely within that of the variety *typicum*, except that it extends farther to the south; Quebec and southern Ontario south to northern New Jersey, northern Pennsylvania, and Michigan; Minnesota; Washington; and Austria.

QUEBEC. Chambly and Stanstead Counties.

ONTARIO. Durham, Lanark, Peterborough, Victoria, and Welland Counties.

MAINE. Hancock, Kennebec, Oxford, Penobscot, and Somerset Counties. The writer has also seen doubtful material from Knox County.

NEW HAMPSHIRE. Grafton, Merrimack, Hillsborough, Rockingham, and Sullivan Counties.

Vermont. Addison, Bennington, Caledonia, Chittenden, Orleans, Rutland, Windham, and Windsor Counties.

Massachusetts. Berkshire, Essex, Franklin, Nantucket, Norfolk, and Plymouth Counties.

Connecticut. Fairfield, Hartford, Litchfield, New Haven, and Windham Counties.

New York. Allegany, Herkimer, Oneida, Onondaga, Oswego, St. Lawrence, Schuyler, Suffolk, Tompkins, and Washington Counties.

New Jersey. Hunterdon, Passaic, Sussex and Warren Counties.

Pennsylvania. Berks, Bucks, Lehigh, Monroe, Pike, and Warren Counties.

Maryland. Doubtful material from Ellicott City, Howard Co., *J. B. Egerton* (G).

Michigan. Cheboygan: vicinity of Douglas Lake, northern end of the Lower Peninsula, *H. A. Gleason* & *H. A. Gleason, Jr. 127* (Deam, NY).

Minnesota. The drawings of two specimens accompanying the paper of Campbell (1922) represent the var. *tenebrosum*. The plants were collected on the shore of Echo Lake near White Bear Lake. No specimens have been seen by the writer.

Washington. Snohomish: Snohomish, *J. W. Thompson 8781a* (G).

Austria. Tyrol: Windisch Matrei, ——— *703* (G).

15. BOTRYCHIUM PUMICOLA Coville. *Figure 12.*

Botrychium pumicola Coville; in Underwood, Our Native Ferns, ed. 6. p. 69. 1900; Coville, in Bull. Torrey Club **28**: 109. pl. 7. 1901. Based on specimens collected on August 5, 1898, by F. V. Coville & E. I. Applegate. The type specimens are in the National Herbarium; cotypes in the Gray Herbarium and the New York Botanical Garden. The specific name alludes to the pumice gravel in which the plants grow.

Plant stout and fleshy, 7.5–10 cm. high; bud glabrous; fertile and sterile segments both erect in vernation or the apex of the sterile portion slightly inclined; bases of leaves of previous years persisting as a prominent sheath about the lower half of the plant; common stalk 5.5–8 cm. long; blade sessile or almost so, coriaceous, glaucous, 1–3 cm. long, 1.3–2.5 cm. wide, usually ternately divided with each of the three major divisions ovate-deltoid; ultimate segments flabellate or obovate, lobulate, decidedly overlapping; fertile stalk about 5 mm. long; fruiting spike dense, paniculate, 1–2.5 cm. long; sporangia 0.8 mm. in diameter. Victorin (1932) gives the spore measurement as 33–36μ.

B. pumicola was described from Crater Lake, Klamath County, Oregon where it grows in the pumice gravel about fifty yards west of the highest point of Llao Rock, at an altitude of 8148 ft. Recently Victorin (1932) has cited the additional collection of L. E. Detling, no. 226 from the gravel-scoria of Mt. Newberry, Pauline Mts., Deschutes National Forest, Oregon. Specimens from this collection have not been seen by the writer. Outside of Oregon the species is apparently unknown.

Oregon. Klamath: Llao Rock, *F. V. Coville* & *E. I. Applegate 417* (G, NY, U); Llao Rock, *J. W. Thompson 12307* (NY).

16. BOTRYCHIUM BOREALE Milde. *Figure 13.*

As most other species of *Botrychium*, *B. boreale* is decidedly variable in size, texture, and the cutting of the sterile blade. It may be known by the almost sessile, ovate or ovate-oblong blade, which is inserted above the middle of the plant, and by the bud, in which the fertile segment is erect and the sterile is also erect except for the apex, which is bent towards, but does not clasp, the fertile portion. It differs from *B. lanceolatum* in vernation and in the cutting of the blade, which is usually pinnate, with the lateral segments rather broad. From *B. matricariaefolium* it differs in the bud; also in the sessile nature and the shape of the blade, which is ovate or ovate-oblong, with the ultimate divisions ovate-rhombic or rhombic-oblong, acute or obtuse at the apex.

This species may be divided into two rather well marked subspecies; the one ranging from the northwestern United States north through British Columbia and Alaska and westward across the Aleutian Islands to eastern Siberia; and the other ranging from Scandinavia and Finland east to Siberia. The last may be subdivided into two leaf forms of varietal rank. These elements are differentiated in the following key:

A. Divisions of the blade pinnately or palmately divided, ovate or rhomboid, acute at the apex. (*B. boreale* ssp. *typicum*) B
  B. Blade typically ovate, with the divisions palmately lobed or crenate; veins not very prominent. 16a. *B. boreale* var. *typicum*
  B. Blade typically oblong-triangular, with the divisions closely imbricate and pinnately lobed; veins very prominent. 16b. *B. boreale* var. *crassinervium*
A. Divisions of the blade pinnately divided, oblong, obtuse at the apex. 16c. *B. boreale* ssp. *obtusilobum*

16a. BOTRYCHIUM BOREALE Milde, var. TYPICUM

Botrychium boreale Milde, in Bot. Zeit. **15** (51): 880. 1857. Based on specimens from Sweden and Finland. The specific name alludes to the fact that this is a plant of northern regions.

Botrychium brevifolium Angström, in Bot. Notis. Nos. 3 & 4: 40. 1886. Based on material from Koddis in Västerbotten. According to Milde, Angström later declared that his species was merely a form of *B. boreale*.

Plant usually stout and fleshy, 4–26 cm. high; bud glabrous; fertile segment erect in vernation; sterile segment with the apex inclined towards, but not clasping, the fertile portion; common stalk 3–14 cm. long; blade inserted above middle of plant, usually sessile, 1–4 cm. wide, 1–9 cm. long, pinnately divided, with the primary divisions palmately lobed or crenate, acute at the apex; fertile stalk 0.2–2 cm. long; fruiting spike simple or paniculate, 0.5–5 cm. long; sporangia 1.2 mm. in diameter. Matures spores during June and July. The gametophyte is unknown.

Holmberg (1922) has described a supposed hybrid of *B. boreale*×*B. Lunaria* as *B. intermedium*, but specimens of this from Kongsvold, N.

Dovre, Norway, which have been examined by the writer, appear to be typical *B. boreale.*

B. boreale var. *typicum* is a plant of open places in Scandinavia, Finland, Russia, northern Asia, and Unalaska. There is abundant material in American herbaria from Norway and Sweden, but very little from elsewhere.

Alaska. Unalaska Island, *L. M. Turner* in part (G, Ph).

Norway. Hamar: Dovre, *J. E. Zetterstedt* (H); Kongsvold (Dovre Fjeld), *C. Baenitz* (U). Tromsö: Kongsli Farm, near Lake Ruostavand, *E. Taylor* (Ph).

Sweden. Gafleborg: Hille, Edskon, *S. Ahlner* (G). Jamtland: Tannäs, Tanndalen, *S. Ahlner* in part (G). Norrbotten: Pitholoreen, near Pitea, *C. Håkansson* (G, NY). Västerbotten: Koddis, Umea, *C. Håkansson* (G, NY); Skelleftea, *V. F. Holm* in part (M).

Lapland. E. Lajeponia Lutens, *Carling* (Ph).

Russia. Konud, *H. Cobur* (Ot).

Siberia. Kamtchatka, reported by Christensen and Hultén (1928).

Corea. Nakai (1926) cites the collection of T. Ikuma 173 from Mt. Paiktusan.

16b. BOTRYCHIUM BOREALE var. CRASSINERVIUM (Ruprecht) Christensen

Botrychium crassinervium Ruprecht; Milde, in Nova Acta **26** (2): 763. pl. 55, f. 10 & 11. 1858; Ruprecht in Beitr. zur Pflanzenkunde des Russ. Reiches. **11**: 42. pl. 11. 1859. Based on three specimens from Siberia. The specific name alludes to the prominent thick veins of the sterile blade. The plate accompanying the original description represents two of the type specimens.

Botrychium boreale var. *crassinervium* (Ruprecht) Christensen, Index Fil., Suppl. p. 99. 1913.

Similar to var. *typicum*, but with the divisions of the oblong-triangular blade pinnately lobed or divided, acute at the apex; veins very thick and prominent.

The var. *crassinervium* was based on three plants collected in Siberia. When Ruprecht wrote, there were probably not enough specimens available to show that this variation was connected by a complete series of intermediates with the typical form of the species. With such a series now available, the writer feels that this form is best given only varietal status.

Certain large specimens from Scandinavia surely match the plants depicted in the drawing accompanying the original description, while many other Scandinavian specimens are intermediate between these and the var. *typicum.* No material from Siberia has been available for the present study.

Sweden. *G. Lidman* in part (U).

16c. **Botrychium boreale** ssp. **obtusilobum** (Ruprecht), n. comb.

Botrychium crassinervium var. *obtusilobum* Ruprecht, in Beitr. zur Pflanzenkunde des Russ. Reiches. **11**: 42. 1859. Based on a specimen collected by

Eschscholtz in Unalaska. The specific name alludes to the blunt divisions or lobes of the sterile blade.

Botrychium pinnatum St. John, in Amer. Fern Journ. **19**: 11. 1929. Based on the collection of W. N. Suksdorf, no. 7075, from Mt. Paddo (Adams), Yakima Co., Wash.; also on other Washington collections. Cotypes have been examined by the writer in the U. S. National Herbarium and in the herbarium of the Philadelphia Academy of Natural Sciences. In the discussion accompanying the original description, St. John says that this does not closely simulate any described species and although he mentions how it may be distinguished from *B. ramosum* (i.e. *matricariaefolium*), *Lunaria*, *lanceolatum* and *pumicola*, he makes no reference to either *B. boreale* or *B. crassinervium*, with which his species is definitely to be associated. The specific name alludes to the pinnate divisions of the sterile blade.

Similar to var. *crassinervium*, but with the divisions of the blade oblong and obtuse, pinnately divided or lobed; veins very stout and conspicuous; bud as in var. *typicum*, with the apex of the sterile portion bent down over the tip of the fertile segment. The lamina is not entirely reflexed in vernation as stated by St. John. Specimens in eastern American herbaria representing collections cited by St. John all show only the apex of the lamina bent in vernation; none show it entirely reflexed. Matures spores from July to September.

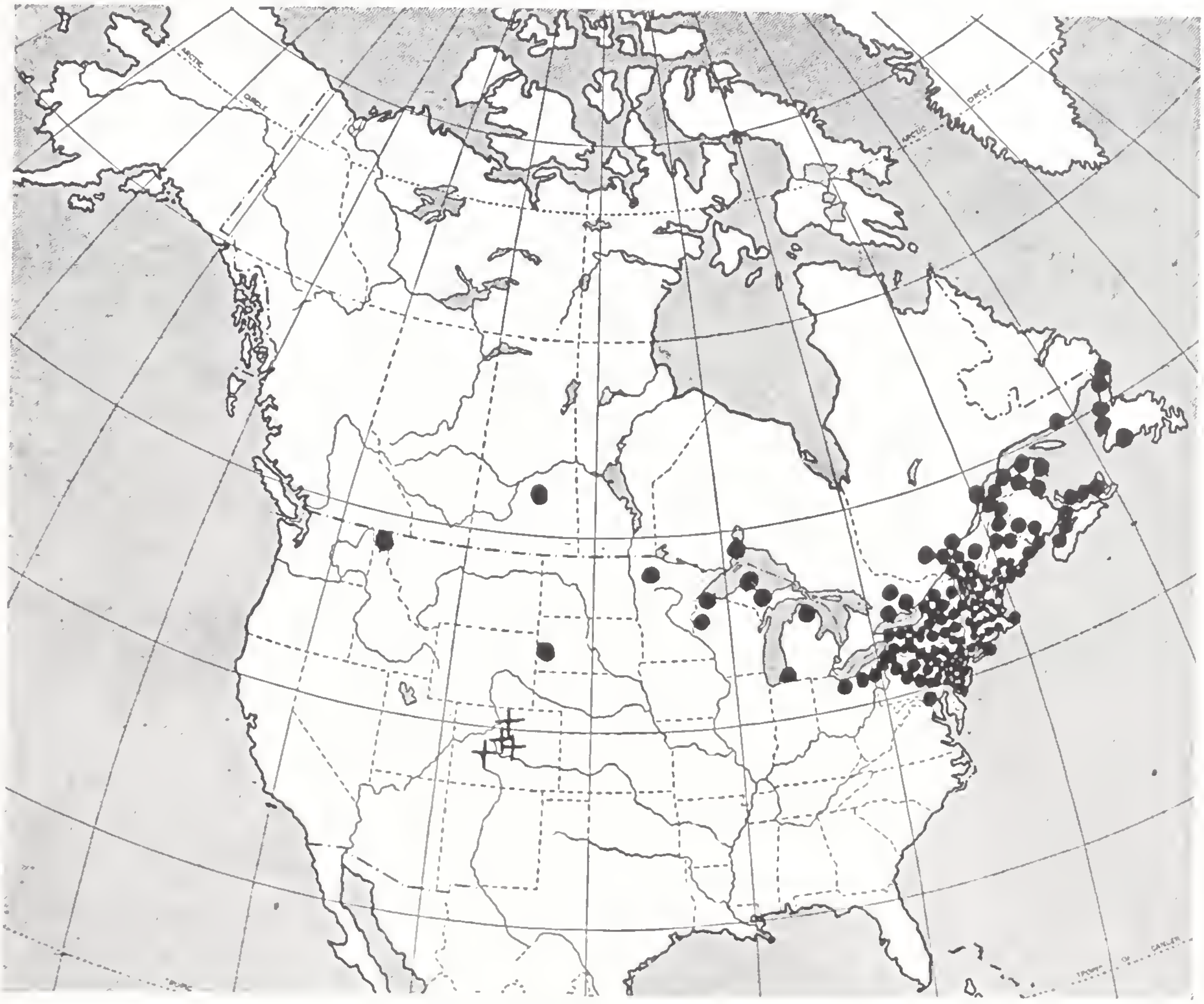
Representative series of specimens from British Columbia, Unalaska, and Siberia demonstrate that this population can not be kept specifically distinct from *B. boreale* Milde. There are places where both forms occur together and apparently intergrade freely, while away from the area in which the two races overlap, occasional forms are produced which indicate the close relationship of the two populations.

In some respects this subspecies resembles *B. matricariaefolium*, but it differs in the more coarsely divided, larger lobes of the sterile blade, which are more proximate, in the stouter more conspicuous venation; and in the yellow green color of the whole plant. *B. matricariaefolium* is characteristically dark blue green or glaucous; with the lobes of the blades often finely divided, rather small and somewhat distant; and the veins generally delicate, not striking.

The ssp. *obtusilobum* represents a very distinct race of *B. boreale*, ranging from Montana, Oregon, and Washington northward and westward through Alberta and British Columbia to the islands of the Aleutian Chain, and in eastern Asia southwards to the Amur River region. This is typically a plant of grassy open places.

Fig. 16 (above). *Botrychium matricariaefolium* in North America; ssp. *typicum* (•) and ssp. *hesperium* (+).

Fig. 17 (below). *Botrychium lanceolatum* in North America; ssp. *typicum* (*) and ssp. *angustisegmentum* (•).


ARCTIC CIRCLE
ARCTIC CIRCLE
TROPIC OF CANCER


ARCTIC CIRCLE
ARCTIC CIRCLE
TROPIC OF CANCER

ALBERTA. Red Deer: Brazeau Lake, *S. Brown 1074* (Ph). In the Gray Herbarium is a photograph of three herbarium specimens collected by H. L. Lyon at Moraine Lake.

BRITISH COLUMBIA. Skeena: Cassiar District, near head of Ispatseeza River, a head branch of Stikine River, *E. A. Preble & G. Mixter* (U); Cassiar District, mountains near head of Ingenika River, *E. A. Preble & G. Mixter 688* (U). South fork of Nelson River, *Mrs. J. N. Henry 160* (Ph). Northern British Columbia, *Rothrock* (C). Cascade Range, near head of McGillivray Creek, *J. M. Macoun 92,733* (Ot) and *92,735* in part (U).

ALASKA. Shumagin Islands: Popoff Island, *D. A. Saunders 2644a* (M). Kodiak Island: Karluk, *W. T. Horne* (NY). Unalaska Island, *L. M. Turner* in part (G, NY).

MONTANA. Glacier: Swift Current Creek below Lake McDermott, Glacier National Park, *P. C. Standley 15939* (U). Glacier Park, Bald Mt., *J. M. Fogg, Jr. 1132* (G).

OREGON. Wallowa: bog along Lostine River 17 miles above Lostine, *M. E. Peck 17771* (G).

WASHINGTON. Skamania: Mt. St. Helens, 4650 ft., *D. D. Lawrence* (U). Snohomish: Mt. Dickerman, *J. W. Thompson 8782* (Ph, U). Yakima: Mt. Paddo (Adams), *W. N. Suksdorf 7075* (Ph, U); also *W. N. Suksdorf 1* (G).

SIBERIA. Amur: Zejskaya Pristan on Zeia River, *F. Karo 468* (NY).

17. BOTRYCHIUM MATRICARIAEFOLIUM Al. Braun. *Figure 16.*

Widely variable in texture and the cutting of the sterile blade, this species can always be determined by the characteristic bud with the fertile segment erect or with its tip slightly inclined and the apex of the sterile segment bent down over and clasping the fertile portion. The only species with which this might be confused is *B. boreale*, but in that species the blade is usually sessile and yellow green, not glaucous, while the apex of the blade does not clasp the fertile segment in vernation. The cutting of the blade is also quite different. *B. simplex* and *B. Lunaria* may be distinguished by their entirely different buds and by the major divisions of the sterile blade, which are in those species typically flabellate, obovate or oblong; and little divided.

Botrychium matricariaefolium may be divided into three rather distinct subspecies, which are distinguished in the following key:

A. Plants lax and membranous or stout and fleshy; sterile blade either sessile or short-stalked, usually oblong in outline, with the major divisions *pinnately divided* or *crenately lobed*.
17a. *B. matricariaefolium* ssp. *typicum*

A. Plants stout and fleshy; sterile blade sessile or almost so, with the major divisions either entire or rarely lobed. B

  B. Blade leathery, oblong-ovate; the divisions rhomboid or oblong, obtuse or acutish, entire or coarsely and bluntly lobed, often overlapping. Plants of western North America.
  17b. *B. matricariaefolium* ssp. *hesperium*

  B. Blade fleshy; the divisions oblong, very blunt (almost truncate), rather remote; common stalk very stout at the base. Plants of South America.
  17c. *B. matricariaefolium* ssp. *patagonicum*

17a. Botrychium matricariaefolium Al. Braun, ssp. typicum

Osmunda Lunaria γ L., Flor. Suec. ed. 2. p. 369. 1755. Based on *Lunaria racemosa minor, matricariae folio* Breyn., Cent. 184. pl. 94.

Botrychium rutaceum Swartz (in part), in Schrader's Journ. für die Bot. **2**: 110. 1800.

Osmunda rutacea Poiret, in Lam., Enc. meth., Suppl. **4**: 232. 1816. Based on *B. rutaceum* Swartz.

Botrychium Lunaria β *rutaceum* E. Fries, Novit. Flor. Suec. p. 289. 1828. Based on specimens from Femjö, Denmark. *B. rutaceum* is given as a synonym.

Botrychium simplex Hooker & Greville in part, Icones Filicum **1**: pl. 82. 1831. The description is of *B. simplex* Hitchc., but the left hand figure of the plate is *B. matricariaefolium* A. Br. from Canada.

Botrychium matricariaefolium Al. Braun, in Döll, Rheinische Flora. p. 24. 1843. Based on specimens from the Rhine Valley. *B. rutaceum* Swartz is listed as a synonym.

Botrychium (*Lunaria*) *lanceolatum* Ruprecht, in Beitr. zur Pflanzenkunde des Russ. Reiches. **3**: 33. 1845.

Botrychium neglectum Wood, Class-book, ed. 2. p. 635. 1847. Based on specimens collected at Meriden, New Hampshire.

Botrychium tenellum Angström, in Botaniska Notiser, Nos. 5 & 6. p. 69, f. 1–4. 1854. Based on specimens from Sättna, Sweden. The figures represent small plants which are certainly to be referred here.

Botrychium Lunaria β *matricariaefolium* Döll, Flora des Grossherzogthmus Baden. v. **1**: 51. 1857. *Lunaria racemosa minor, matricariae folio* Breyn.; *Osmunda Lunaria* L.; and *B. rutaceum* Swartz are given as synonyms.

Botrychium Lunaria β *ramosum* F. W. Schultz, in Pollichia **20, 21**: 286. 1863.

Botrychium ramosum (Roth) Aschers., Flor. Prov. Brandenburg. p. 906. 1864. Ascherson's description as to plant described, not as to name bringing synonym, *Osmunda ramosa* Roth, clearly indicates that his plant should be referred here, but this is not the same as *B. ramosum* Roth, which represents a form of *B. Lunaria*.

Botrychium ramosum var. *neglectum* (Wood) Farwell, in Ann. Rep. Mich. Acad. Sci. **6**: 200. 1904. Designated as smaller than the typical form and with the blade oblong-ovate, divided into nearly equal, more or less crenate or toothed lobes. This is merely one of the many trivial forms of the species which does not merit nomenclatorial distinction.

Botrychium matricariaefolium var. *rhombeum* Farwell, in Ann. Rep. Mich. Acad. Sci. **18**: 85. 1916. *B. ramosum* var. *neglectum* (Wood) Farwell is given as a synonym.

Botrychium neglectum f. *gracile* House, in Bull. N. Y. State Museum. No. 254: 13. 1924. A small form that occurs throughout the range of the species. It does not deserve recognition.

Plant lax and membranous or stout and fleshy, 3.5–28 cm. high; bud glabrous, with the fertile segment erect or with its tip slightly inclined and the apex of the sterile segment bent down over and clasping the fertile portion; common stalk 2–16 cm. long; sterile stalk none or to 2.5 cm. long, averaging 2–3 mm.; sterile blade inserted above the middle or near the summit of the plant, 0.4–7 cm. wide, 0.8–9 cm. long, pinnately divided, rarely with the lowest pair of divisions again divided, then ternate; blade typically oblong in outline, with the lateral divisions oblong and obtuse, crenate or obtusely lobed; fertile stalk 0.3–5 cm. long; fruiting spike generally paniculate, 0.4–8 cm. long; sporangia 0.6–1 mm. in diameter; spores 26–48μ in diameter. Matures spores commonly during June and July. According to Campbell (1922), Lyon collected the gametophytes, but these apparently have never been described.

No constant difference has been found to separate the American from the European material of this species. Specimens from northern North America and from northern Europe are rather coriaceous and much alike, while specimens from farther south on both continents are more lax and likewise similar. In general the European plants are more compact and fleshy, with the fertile spikes dense, while the American plants are more slender, with lax fruiting segments. A number of minor variants have been described. These have been based on the cutting of the sterile blade, but since such variants may occur in any large colony of the species and since there are no other characters to support the leaf architecture, these are not considered here as worthy of nomenclatorial distinction.

In the pre-fruiting condition and until the time when the spores are shed, plants of *B. matricariaefolium* are decidedly glaucous, but later in the season they loose the bloom and become yellowish green. During the early part of the season, however, the presence of the bloom may be used as a field character indicating this species.

The habit and texture are greatly influenced by the environment. In dry sterile fields the plants assume a leathery compact character, while in rich shaded woodlands they become tall and slender. In any one region the specimens found in exposed open places will fruit several weeks before the woodland forms. After the fruiting period, the leaf withers, and, by late summer, has usually completely disappeared.

B. matricariaefolium ssp. *typicum* grows in a variety of habitats; dry woodland slopes, dry sandy woods, rich swamps, rocky woods, sandy thickets, and dry sterile fields. The range of the subspecies is extensive; Newfoundland and New Brunswick south to New Jersey, Pennsylvania, and Maryland; west to Minnesota; also in northern Europe and northern Asia.

LABRADOR. In the herbarium of the Missouri Botanical Garden is a sheet labelled Labrador, 1869, Mr. Butler. It bears four specimens, one of which is *B. matricariaefolium* ssp. *typicum*.

NEWFOUNDLAND. Regions of Burgeo and La Poile, Bay of Islands, Bonne Bay, Sacred Bay, and Straits of Belle Isle.

PRINCE EDWARD ISLAND. Kings and Queens Counties.

NOVA SCOTIA. Annapolis, Cumberland, Inverness, and Kings Counties.

NEW BRUNSWICK. Carleton, Charlotte, Gloucester, Madawaska, and York Counties.

QUEBEC. Bonaventure, Chambly, Drummond, Gaspé, Labelle, Maskinongé, Matane, Montcalm, Rimouski, Saguenay, Sherbrooke, Stanstead, Temiscouata, Terrebonne, and Vercheres Counties.

Ontario. Durham, Hastings, Nipissing, and Thunder Bay Counties.

Alberta. Camrose: ? Galahad, *A. H. Brinkman 2751* (U).

Maine. All counties except Cumberland, Sagadahoc, and Waldo.

New Hampshire. All counties except Belknap and Strafford.

Vermont. All counties except Grand Isle.

Massachusetts. Barnstable, Berkshire, Essex, Franklin, Hampden, Hampshire, Middlesex, and Worcester Counties.

Rhode Island. Providence: Cranston, *J. F. Collins* (N, U).

Connecticut. Hartford, Litchfield, New Haven, and Windham Counties.

New York. Albany, Cattaraugus, Cayuga, Chemung, Cortland, Delaware, Essex, Greene, Hamilton, Herkimer, Jefferson, Lewis, Monroe, Niagara, Oneida, Onondaga, Orange, Otsego, St. Lawrence, Saratoga, Suffolk, Tioga, Tompkins, Ulster, Washington, Wayne, and Westchester Counties.

New Jersey. Bergen, Burlington, Gloucester, Middlesex, Monmouth, Morris, Passaic, Salem, Sussex, and Warren Counties.

Pennsylvania. Berks, Bucks, Carbon, Chester, Clearfield, Columbia, Crawford, Dauphin, Delaware, Elk, Forest, Huntingdon, Lackawanna, Lancaster, Lawrence, Lebanon, Lehigh, Lycoming, Monroe, Montgomery, Perry, Philadelphia, Pike, Sullivan, Susquehanna, Tioga, Warren, Wayne, and Westmoreland Counties.

Maryland. Baltimore: Towson, *C. E. Waters* (G, NY, U).

District of Columbia. Reported by Tidestrom (1905) from within four miles of Washington.

Ohio. Erie and Portage Counties.

Michigan. Alger, Berrien, Cheboygan, and Keweenaw Counties.

Wisconsin. Bayfield and Polk Counties.

Minnesota. Clearwater: Itasca Park, *J. B. Moyle 598* (C, G, M, U).

South Dakota. Black Hills, *P. A. Rydberg 1186* (U).

Idaho. Kootenai: Upper Priest River, *C. C. Epling 7457* (U).

England. According to W. Whitwell (1898), Dr. St. Brody collected this in July, 1887, on the sandy sea-shore of Stevenston, Ayrshire.

Sweden. Läns of Scania and Vasterbotten.

Italy. Reported from Mt. Majore, Tuscany, by Levier (Bull. Soc. Bot. Ital. 1900: 133–137); also from Lombardy.

Switzerland. Grisons: St. Moritz, ex herb. G. E. Davenport (G).

Germany. Provinces of Brandenburg, Saxony, Silesia, and Thuringia.

Czechoslovakia. Bohemia: Lysa, *I. Velenowski* (Ph).

Corea. Nakai (1926) cites the collection of Y. Ikuma, n. 174, from Mt. Paiktusan.

In the Gray Herbarium are specimens collected by *C. G. Pringle no. 5193*, in a wet canyon, Volcano of Toluca, State of Mexico, Mexico. These plants were identified by G. E. Davenport as *B. matricariaefolium* and are so labelled. The specimens are very poor and difficult to make out. Only two sterile blades are present and, since these are both heavily sporangia-bearing towards the base, they are not typical. In vernation, the apex of the sterile blade is inclined over the fertile segment. To the writer it appears possible that this material may represent either depauperate *B. Lunaria*, *B. matricariaefolium*, or even perhaps an undescribed species, but judgment seems best withheld until better specimens may be available.

17b. **Botrychium matricariaefolium** ssp. **hesperium** Maxon and Clausen, n. ssp. *Figure* 15.

Botrychium matricariaefolium A. Br. ssp. *hesperium* Maxon et Clausen, ssp. nov.—Planta robusta et fere carnosa, 5–20 cm. alta; gemma glabra, apice segmenti fertilis parum inclinato et apice segmenti sterilis deflexo supra et portionem fertilem amplexo; caulis communis 3–11 cm. longus, 2–4 mm. crassus si premitur; petiolus sterilis 1–15 mm. longus; lamina super medium vel versum culmen plantae inserta, coriacea, ovato- oblonga, 1–5 cm. longa et 0.6–4 cm. lata, pinnata cum sex vel pluribus lateralibus divisionibus; his rhomboideis vel oblongis, obtusis vel aliquando acutulis, integris vel crasse crenatis, vel imbricatis vel remotis infra, supra imbricatis; si divisiones inferae laminae, ut aliquando, iterum divisae, lamina ovato-deltoidea et ternata; petiolus fertilis 0.3–6 cm. longus; spica fertilis paniculata, multo divisa, 1–6 cm. longa; rami sporangiferi longe petiolati; sporangia 0.6–1 mm. lata; sporae 41–52μ latae.

Plant stout and rather fleshy, 5–20 cm. high; bud glabrous, with the tip of the fertile segment slightly inclined and the apex of the sterile segment bent down over and clasping the fertile portion; common stalk 3–11 cm. long, 2–4 mm. thick when pressed; sterile stalk 1–15 mm. long; blade inserted above the middle or towards the summit of the plant, coriaceous, ovate-oblong in outline, 1–5 cm. long, 0.6–4 cm. wide, pinnately divided into six or more lateral divisions which are rhomboid or oblong, obtuse or sometimes acutish, entire or coarsely lobed, either imbricate or distant below and crowded above; basal divisions of blade sometimes again divided, the blade then ovate-deltoid and ternate; fertile stalk 0.3–6 cm. long; fruiting spike paniculate, much divided, 1–6 cm. long; sporangia-bearing branches long stalked; sporangia 0.6–1 mm. in diameter; spores 41–52μ in diameter.—Type in the U. S. National Herbarium, from Glacier Lake, Boulder County, Colorado, July, 1914, *E. Bethel* (U.S.N.H. 984953).

This subspecies differs from the typical form of *B. matricariaefolium* in having the sterile blade more leathery, almost sessile or short-stalked, with the lateral divisions either entire, or less divided with coarser lobes. The divisions of the blade are often ascending, rather than arranged at right angles to the main axis, and frequently overlap. The sporangia are very broad at the base. In dehiscence the sporangial valves split only one half the distance from the apex, leaving the broad lower portion undivided, like an inverted hat. The spores are regularly somewhat larger than in ssp. *typicum.*

H. L. Shantz was probably the first to collect this subspecies. In 1904 he obtained specimens at Pikes Peak, in Colorado. Since then, abundant material has been collected from Glacier Lake, Boulder Co., Colo., by E. Bethel and I. W. Clokey, and from the vicinity of Pikes Peak, by I. M. Johnston. These collections show that variation in colonies of the ssp. *hesperium* is apparently very great. At one end of the series the forms are so distinct that they would seem to merit specific designation, while at the other end of the series are specimens which can be matched almost exactly by material of ssp. *typicum* from Europe, eastern Canada, and the northeastern United States. In consideration of this variation in the *hesperium* population, the Colorado plants seem best treated as a geographical race of *B. matricariaefolium*. As at present known, this subspecies is confined to dry gravelly slopes and grassy open places in central and northern Colorado, where it occurs at elevations of 8,000 to 11,000 feet, in association with *B. Lunaria* and *B. simplex*.

COLORADO. Boulder: Glacier Lake, *E. Bethel* (U); also *E. Bethel & I. W. Clokey 3987* (U, Herb. I. W. Clokey). El Paso: Pikes Peak, various stations, *I. M. Johnston* (G); also *H. L. Shantz 52* (U). Larimer: Rocky Mt. National Park, *A. & W. C. Wilson 71b* (Claus). Summit: Breckenridge, *K. K. Mackenzie 99* (M). Sawatch Range, *T. S. Brandegee 2350* in part (M).

17c. **Botrychium matricariaefolium** ssp. **patagonicum** (Christ), n. comb.

Botrychium ramosum var. *patagonicum* Christ, in Ark. för bot. 6 (no. 3): 4–5. fig. 2, 3. 1906. Based on specimens collected by Dr. P. Dusen at Rio Fosiles, not far from Lake San Martin, in Patagonia. The figures accompanying the original description portray two typical plants.

This differs from the other two subspecies in the smaller size, in the very stout base of the common stalk, and in the cutting of the fleshy blade, of which the divisions are oblong, very blunt (almost truncate), and rather remote. Also, the rachis of the blade is strikingly broader.

The ssp. *patagonicum* was found on denuded slopes at Rio Fosiles, where it was growing in association with *B. Lunaria* var. *Dusenii*. It is apparently known only from the type collection. No specimens have been seen by the writer.

b. Section **Lanceolatae,** n. sect.

Lanceolatae, sectio nova subgeneris *Eubotrychii* lamina sterili deltoidea plerumque sessili; segmentis fertilibus et sterilibus ambis gemma omnino reflexis.

This section, containing only one species, is distinguished from the *Lunariae* by the characteristic bud, in which the fertile and sterile segments are both completely reflexed, and by the sterile blade, which is commonly deltoid and sessile. In the bud character, the section is most like the subgenus *Osmundopteris*, to which it seems rather closely related.

On this basis, *B. lanceolatum* may be considered as the most likely connecting link between the species of *Eubotrychium* and *Osmundopteris.*

18. Botrychium lanceolatum (Gmelin) Angström. *Figure 17.*

Confined to the northern hemisphere, this species has a range somewhat like that of *B. multifidum*, except that in western North America it is not as well represented and there does not extend as far southward. The distinguishing characters are those of the section. On a basis of the cutting of the blade, texture, and the size of the sporangia and spores, the species may be divided into two subspecies, which are differentiated in the following key:

A. Plants stout and fleshy; divisions of blade 1–5 mm. wide; spores averaging 35μ in diameter. 18a. *B. lanceolatum* ssp. *typicum*

A. Plants lax and rather membranous; divisions of blade 1–2.5 mm. wide; spores averaging 30μ in diameter. 18b. *B. lanceolatum* ssp. *angustisegmentum*

18a. Botrychium lanceolatum (Gmel.) Angstr., ssp. typicum

Osmunda lanceolata Gmelin, in Nov. Comment. Acad. Petrop. **12**: 516. pl. 11, fig. 2. 1768. Based on European material. The figure accompanying the original description may be considered to typify the species. The specific name alludes to the lanceolate divisions of the sterile blade.

Botrychium palmatum Presl, in Abh. Böhm. Ges. Wiss. 5. **4**: 303. 1845. Based on specimens from the mountains of Scandinavia and from Unalaska. The specific name alludes to the palmate division of the blade into three or five major segments.

Botrychium Lunaria var. *lanceolatum* (Gmel.) Rupr., Distr. Cryp. Vasc. Ross. p. 332. 1845.

Botrychium matricariaefolium Fries, excl. synonymy, Summa Veg. **1**: 252. 1846. Said to occur sporadically in Sweden and considered by Angström to be a distinct species.

Botrychium rutaceum β tripartitum Ledeb., Fl. Rossica **4**: 505. 1853. Based on specimens collected by Chamisso and Eschscholtz on the island of Unalaska.

Botrychium lanceolatum (Gmel.) Angstr., in Bot. Notiser. Nos. **5** & **6**: 68. 1854.

Botrychium rutaceum var. *lanceolatum* (Gmel.) Moore, Index Fil. p. 211. 1858.

Botrychium matricariaefolium var. *lanceolatum* (Gmel.) Watt, in Can. Nat. 2. **3**: 16. 1866.

Plant stout and fleshy, glabrous, 6–42 cm. high; sterile blade and fertile spike both completely reflexed in vernation; common stalk 4–15 cm. long; blade sessile or nearly so, inserted near the summit of the plant, 1–9 cm. wide, 1–6 cm. long, deltoid, with lanceolate segments 1–6 mm. wide, of which the lowest pair is longest; fertile stalk 0.5–1 cm. long; fruiting spike paniculate, 1–5 cm. long; sporangia 0.8–1.5 mm. in diameter; spores 29–42μ, averaging about 35μ in diameter. Matures spores in midsummer, during July and August. The gametophyte is unknown.

As stated by Prof. Fernald (1915), this is a plant of the subarctic and arctic-alpine floras. It is found in a variety of habitats, including dry slopes, alpine meadows, sandy open places, and even swampy forests. In North America the subspecies *typicum* ranges in the northeast from Greenland, Newfoundland, and Quebec south to northern Maine; while in the northwest it occurs from the Aleutian Islands southward through British Columbia to Washington, Wyoming, and Colorado. It is also found in Scotland, Scandinavia, France, Switzerland, Austria, Finland, Russia, Siberia, and Japan. The writer has seen Old World specimens only from Sweden and Japan. In the western United States this subspecies becomes quite variable and some of the plants in the *Thuja* forests of the state of Washington attain a truly huge size. A specimen from Mt. Fujiyama, Japan, is somewhat intermediate between ssp. *typicum* and ssp. *angustisegmentum*.

Greenland. Ameralik Fjord, 64°9′ N., *A. E. & M. P. Porsild* (G, U). S. F. Kiagtut, Tunugdliarfik Fjord, 61°10′ N., *A. E. & M. P. Porsild 117712* (G, M, NY, Ot, U).

Labrador. Mingan River, sandy beaches among grasses, *W. Palmer* (U).

Newfoundland. Sacred Bay, Ship Cove, *M. L. Fernald, K. M. Wiegand, & B. Long 27273* (C, G, Penn, Ph).

Quebec. Gaspé: Mt. Au Clair, Tabletop Mts., *M. L. Fernald & L. B. Smith 25396* (G). Matane: Pease Basin, between Mts. Logan and Pembroke, *A. S. Pease & L. B. Smith 25395* (G). Saguenay: Natashquan, *Ff. M. -Victorin & R. -Germain 28200* (G, Mont, Ot); Pt. Aux Basques, Seven Islands, *C. B. Robinson 836* (NY).

British Columbia. Fraser Valley: Agassiz, *J. Macoun 28573* (Ot). Vancouver: North Brackendale, *J. M. Macoun 92736* (G, Ot, U). North moraine, Sanford Glacier, lat. 51°41′, *F. K. Butters & E. W. D. Holway 558* (G).

Alaska. Shumagin Islands: Popoff Island, *De Alton Saunders 2644* (M). Unalaska Island, *L. M. Turner* (G, M, Ph, U).

Maine. Aroostook: Red River, *Josephine F. Clark* (G, U).

Wyoming. Yellowstone National Park, *F. Tweedy* (U).

Colorado. Boulder: Glacier Lake, *E. Bethel* (U). El Paso: Pikes Peak, *I. M. Johnston 2413, 2416, & 2419* (G). Summit: Breckenridge, *K. K. Mackenzie 99* in part (M, NY); Gray's Peak, *H. N. Patterson 164* in part (G). Sawatch Range, *T. S. Brandegee 2550* in part (M); also (G).

Washington. Jefferson: Mt. Olympus, *J. B. Flett 3091* in part (U). Pierce: Mt. Rainier, *J. B. Flett 1904* (U); also *J. A. Allen* (NY). Skamania: Mt. St. Helens, *D. D. Lawrence* (U). Snohomish: Mt. Dickerman, *J. W. Thompson 8781c* (G). Whatcom: Mt. Baker, *W. C. Muenscher 7502* (C, Claus).

Scotland. Reported by W. Whitwell (1898) from "the Sands of Barry, near Dundee."

Sweden. Norrbotten: Pitea, *C. Håkansson* (G, M, NY). Vasterbotten: Skelleftea, *V. F. Holm* in part (G, M); Umea, *C. Håkansson* in part (M).

Siberia. Kamtchatka, reported by Christensen and Hultén (1928).

Japan. Honshu: Mt. Fuji, *J. Matsumura* (NY), intermediate towards ssp. *angustisegmentum*.

18b. BOTRYCHIUM LANCEOLATUM ssp. ANGUSTISEGMENTUM (Pease and Moore) Clausen

Botrychium lanceolatum var. *angustisegmentum* Pease and Moore, in Rhodora **8**: 229. 1906. Based on abundant material from the northeastern United States. The type is in the herbarium of the New England Botanical Club. It is the collection of *E. B. Chamberlain, no. 354*, from Bristol, Maine. The varietal name alludes to the narrow segments of the sterile blade.

Botrychium angustisegmentum (Pease and Moore) Fernald, in Rhodora **17**: 87. 1915.

Botrychium lanceolatum ssp. *angustisegmentum* (Pease and Moore) Clausen, in Bull. Torrey Club **64**: 280. 1937.

Differing from ssp. *typicum* in being lax and membranous, with the divisions of the blade narrow, often more acute, 1–2.5 mm. wide, and with the spores slightly smaller, averaging 30μ in diameter.

The writer has been unable to follow Prof. Fernald in considering the more lax, woodland plant of the northeastern United States and southern Canada as representing a species distinct from the boreal ssp. *typicum*. All of the characters used to separate *angustisegmentum* from *lanceolatum* fall down on close examination. The cutting of the sterile blade and the general appearance of the plants seem to be the best criteria for determing specimens as the one form or the other. Difference in spore size was given as one of the characters on which the segregation of *angustisegmentum* was based, but measurements of spores made by the writer do not correspond with those furnished by Prof. Fernald (1915) in his paper on the species. He stated that the spores of *B. angustisegmentum* measured from 21–28 μ in diameter, while those of *B. lanceolatum* were from 35–45μ. These measurements of the spores of the two species are considerably farther apart than the writer's investigations would indicate. The writer's data show that the spores of the two forms overlap considerably in size, although the extremes of typical *lanceolatum* are slightly larger than those of *angustisegmentum*. The averages show the spores of the boreal plant to be about 5μ larger than those of the more southern form. According to these measurements, *B. lanceolatum* ssp. *typicum* has spores 29–42μ in diameter, av. 35μ; while ssp. *angustisegmentum* has spores 24–37μ, av. 30μ.

The size of the sporangia and the manner in which they are immersed in the sides of the branches of the fertile segment have not seemed constant enough characters for specific segregation, while the nature of the blade, with its narrower, thinner segments, seems to be a definite response to the habitat in rich, shaded woods. Further, a number of specimens from southern Canada and the western United States have seemed somewhat intermediate between the two forms. In the light of all of this evidence, the writer feels that *angustisegmentum* is best treated as a very distinct geographical race or subspecies of *B. lanceolatum.*

The ssp. *angustisegmentum* is characteristically a plant of shaded woodlands or moist situations about the edges of swamps and along streams, but it is also occasionally found in open fields, particularly towards the northern part of its range. It occurs from Newfoundland, New Brunswick, and Quebec south to central New Jersey, Pennsylvania, and Ohio; and west to Michigan.

Newfoundland. Humber Arm, Bay of Islands, *M. L. Fernald & B. Long 1174* (G).

Nova Scotia. Cumberland and Inverness Counties.

New Brunswick. Charlotte and York Counties.

Quebec. Chambly, Labelle, Rimouski, and Saguenay Counties.

Ontario. Nipissing, Peel, and Welland Counties.

Maine. Aroostook, Cumberland, Franklin, Knox, Lincoln, Oxford, Piscataquis, Somerset, and York Counties.

New Hampshire. Carroll, Cheshire, Coos, Grafton, Hillsborough, and Sullivan Counties.

Vermont. Addision, Bennington, Caledonia, Chittenden, Rutland, Washington, Windham, and Windsor Counties.

Massachusetts. Barnstable, Berkshire, Essex, Franklin, Hampden, Hampshire, Middlesex, Norfolk, and Worcester Counties.

Connecticut. Fairfield, Hartford, Litchfield, New London, Tolland, and Windham Counties.

New York. Cattaraugus, Cayuga, Chautauqua, Chemung, Chenango, Cortland, Delaware, Dutchess, Greene, Herkimer, Niagara, Oneida, Orange, Oswego, Otsego, Rockland, St. Lawrence, Schuyler, Steuben, Sullivan, Tioga, Tompkins, Ulster, Washington, Westchester, and Wyoming Counties.

New Jersey. Bergen, Middlesex, Morris, Passaic, Sussex, and Warren Counties.

Pennsylvania. Berks, Bradford, Centre, Chester, Columbia, Crawford, Indiana, Lancaster, Lehigh, Luzerne, Lycoming, Monroe, Pike, Somerset, Sullivan, Susquehanna, Tioga, and Wayne Counties.

West Virginia. According to Maurice Brooks (Castanea **3**(2): 27. 1938), there is a specimen in the herbarium of the University of West Virginia from Pocahontas County.

Ohio. Portage: Garrettsville, *R. J. Webb 343* (G).

Michigan. Ontonagon ?: near West Sleeping River, *H. Gillman* (Princ).

Wisconsin. Bayfield: Bark Point, shore of Lake Superior, *C* ——— and *Knowlton* (Mont).

C. Subgenus **Osmundopteris** (Milde) Clausen, n. stat.

Botrychium, suborder *Botrychiaceae*, § *Pinnato-venato* Presl (in part), in Abh. Böhm. Ges. Wiss. Ser. 5. **4**: 306. 1845–46.

Botrychium, § II, *Osmundopteris* Milde, in Verh. zool. bot. Ges. Wien. **19**: 96. 1869. In this section Milde placed only *B. virginianum*. He classified *B. lanuginosum* with *B. daucifolium* in the subsection *Elata* of *Eubotrychium*.

Botrychium, section *Phyllotrichium*, subsection *Cicutaria* Prantl, in Jahrb. Bot. Gart. Berlin **3**: 337. 1884. Prantl placed here *B. lanuginosum* and *B. virginianum*.

The species included in *Osmundopteris* are the most fern like of the *Botrychia*. The subgenus is characterized by the hairy buds which are often exposed; by the large sterile blades which are typically deltoid, many times decompound, usually thin in texture, and sometimes hairy; and by the cylindrical gametophytes, with the primary root developing either from the side or from the upper surface. Five species are included here. These are of wide distribution in the north temperate zone and at high altitudes in the tropics. No species is known from the south temperate or antarctic regions.

KEY TO THE SPECIES OF OSMUNDOPTERIS

A. Fertile segment arising laterally as a division of the foliage blade; plants rather stout, fleshy, often very hairy. a. Section *Lanuginosae*
19. *B. lanuginosum*

A. Fertile segment obviously arising from base of sterile blade; plants membranous to subfleshy, glabrous or sparingly pubescent. b. Section *Virginianae* B

  B. Ultimate divisions of blade ovate, oblong, or lanceolate, acutely or obtusely toothed or lobed; blades usually ternately divided. Plants of North and South America, Europe and Asia. C

    C. Fertile spike relatively long stalked, usually much exceeding the blade in length. Only one leaf commonly produced during a season. 20. *B. virginianum*

    C. Fertile spike short stalked, rarely exceeding the blade in length. Either one or two leaves produced during a season. D

      D. Fruiting spike paniculate, not strict. Divisions of the blade confluent along the main veins. Two leaves usually produced during a season. 21. *B. cicutarium*

      D. Divisions of fruiting spike short, 3–10 mm. long, giving that structure a strict appearance. Divisions of the blade not confluent along the main veins. Only one leaf produced during a season. 22. *B. strictum*

  B. Ultimate divisions of blade ovate or oblong. bluntly toothed or lobed; blades usually pinnately divided. Plants of Africa. 23. *B. chamaeconium*

a. Section **Lanuginosae**, n. sect.

Lanuginosae, sectio nova subgeneris *Osmundopteris*, segmento fertili ex latere laminae sterilis emergente; plantae fere robustae, carnosae, saepe summe pubescentes.

This section includes only one species, *B. lanuginosum*. It is a unique division of *Botrychium* because, in this section, the fertile segment arises as a lateral branch or pinna of the sterile blade. In all other sections of the genus, the fertile segment appears to emerge from the base or below the base of the sterile blade.

Because of its extreme variability and the lateral insertion of the fertile segment, Chrysler (1925) has considered *B. lanuginosum* to represent most closely the primitive type of *Botrychium*. According to his theory, in early representatives of the genus, of which this is a living fossil, all parts or pinnae of the leaf were fertile, then special regions were modified to bear

Fig. 18 (above). *Botrychium virginianum* ssp. *typicum* (•), ssp. *europaeum* (+), and ssp. *meridionale* (*).

Fig. 19 (below). *Botrychium lanuginosum* var. *typicum* (*), *B. cicutarium* (•), *B. strictum* (+), and *B. chamaeconium* (X).

sporangia. Later, opposite pairs of leaflets became fertile, and finally the basal leaflets always were the fertile ones. These basal leaflets then became fused and were raised erect, thus producing the type of fertile segment that is found in *B. virginianum* and in most of the other species of *Botrychium*. From this viewpoint, *B. lanuginosum* clearly is a primitive type, and the section *Lanuginosae* certainly represents the more primitive division of *Osmundopteris*, from which the section *Virginianae* has been derived. On a basis of this theory, the present section may also represent the most primitive part of the whole genus, but, in this paper, the writer has preferred to consider the subgenus *Sceptridium* as more primitive because of the wide and broken geographical distribution of its members, the great variation within the group, and the presence of a suspensor in the embryo of at least one of the species.

19. BOTRYCHIUM LANUGINOSUM (Wall.) Hk. et Grev. *Figure 19.*

The characters distinguishing this very distinct species are the same as those for the section. On a basis of pubescence and habit, the population may be divided into two varieties, as indicated in the key:

A. Plant stout and fleshy; sterile blade and stalk usually more or less pilose. 19a. *B. lanuginosum* var. *typicum*
A. Plant slender, rather membranous, glabrous. 19b. *B. lanuginosum* var. *leptostachyum*

19a. BOTRYCHIUM LANUGINOSUM (Wall.) Hk. et Grev., var. TYPICUM

Botrychium lanuginosum Wall., List, no. 48. 1828, nomen nudum.
Botrychium lanuginosum Wall.; Hooker & Greville, Icones filicum. **1**: t. 79. 1831. The plate accompanying the original description may be taken to typify the species. The specific name alludes to a woolly substance which is attached to the upper part of the bulbous base of the plant.

Plant stout and fleshy, 37–54 cm. high; roots stout and numerous, clustered; stalk of blade 23–35 cm. long; blade ternately divided, 20–37 cm. wide, 21–29 cm. long, mostly three to four times decompound, with the ultimate divisions obtuse or acute; fertile segment arising, above the base, laterally from the rhachis of the blade, in the place of one of the sterile pinnae; fertile stalk 7–10 cm. long; fruiting panicle 7–10 cm. long; sporangia 0.8–1 mm. in diameter.

B. lanuginosum is decidedly variable in texture and in the amount of pubescence of the leaf. The fertile spike arises at various points, usually in place of one of the lateral pinnae between the second and fifth from the base of the blade.

The typical form of the species is native in rich woods, at altitudes from 4,000 to 7,000 feet, in southeastern Asia and in various of the islands of the East Indies. It is occasionally somewhat epiphytic.

INDIA. Assam: Khasi Hills, *G. Mann* (M, NY, U). Bissar and Orissa: Nilgiri, ——— (G). Bombay: Ahmedabad, *J. Martin* (U). Punjab: Simla, *Mrs. Col. Lyell* (M, Ph, Princ); also *H. F. Blanford* (NY). United Provinces of Agra and Oudh: Saharanpur, ex herb. J. F. Duthie (U); Landour, *L. Kenoyer* & *W. Dudgeon 58* (Ph). Pulney Mts., *Fairbank 1603* (M).

NEPAL. *Wallich 48* (U).

CEYLON. *W. T. Ferguson 225* (M); *Thwaites* (G).

SUMATRA. Habinsaran, between Panapparan and Pager Batoe, *H. H. Bartlett 7912* (U).

JAVA. Reported by van Alderwerelt van Rosenburgh (1916), but no specimens have been seen by the writer.

PHILIPPINES. Luzon: Prov. Benguet, Baguio, *R. S. Williams 1598 & 1599* (NY).

CHINA. Yunnan: Talifu, *J. F. Rock 6655* (U); Meng-tsz, *W. Hancock 18* (U).

19b. BOTRYCHIUM LANUGINOSUM var. LEPTOSTACHYUM (Hayata) Nakai

Botrychium leptostachyum Hayata, Icones Plantarum Formosanarum. **4**: 134. fig. 71. 1914. Based on slender, glabrous material from Formosa. The type is the collection of U. Mori. no. 6291, from Nokosan, Formosa.

Botrychium lanuginosum var. *leptostachyum* (Hayata) Nakai, in Bot. Mag. Tokyo **39**: 192. 1925.

Differing from var. *typicum* in being entirely glabrous and more slender.

According to Nakai (1926), this variety is found in Formosa, China, and the Himalayas. No specimens have been seen by the writer.

b. Section **Virginianae**, n. sect.

Virginianae, sectio nova subgeneris *Osmundopteris*, segmento fertili manifeste ex basi laminae sterilis emergente; plantae membranaceae vel subcarnosae, glabrae vel parum pubescentes.

This section is characterized by the emergence of the fertile segment from the base of the sterile blade, not as a lateral branch or pinna of the blade itself. The four species included are various in habit and of wide distribution.

20. BOTRYCHIUM VIRGINIANUM (L.) Swartz. *Figure 18.*

To laymen and field botanists, this is perhaps the most familiar species of *Botrychium*. Known popularly as Rattlesnake Fern, it is a prominent feature of the woodland vegetation throughout north temperate regions. In its wide range, the species may be subdivided into at least three geographical races. These are differentiated in the following key:

A. Blade appearing ternate, with the basal pinnae much larger than the second pair; pinnae rather finely divided, with the ultimate divisions usually toothed or lobed. B

  B. Blade large, lax, and membranous, with the pinnae divided to the midrib and the ultimate divisions not overlapping; sporangia 0.5–1 mm. in diameter, with the valves recurving widely in dehiscence 20a. *B. virginianum* ssp. *typicum*

B. Blade compact and leathery, with the pinnae not so deeply divided and the ultimate divisions often crowded or imbricate; sporangia 0.5–1.8 mm. in diameter, with the valves usually not widespreading or recurving in dehiscence. 20b. *B. virginianum* ssp. *europaeum*

A. Blade appearing pinnate, with the basal pinnae little larger than the second pair; pinnae coarsely divided, with the ultimate divisions oblong and entire.
20c. *B. virginianum* ssp. *meridionale*

20a. BOTRYCHIUM VIRGINIANUM (L.) Swartz, ssp. TYPICUM

Osmunda virginiana L. Sp. pl., ed. 1. **2**: 1064. 1753. Based on American material. The type is in the Linnaean Herbarium.

Osmunda virginica L., Syst. nat. ed. 12. **2**: 685. 1767. This represents simply a respelling of the specific name.

Botrychium virginianum (L.) Swartz, in Schrad. Journ. für die Bot. **2**: 111. 1800.

Botrypus virginicus (L.) Michx., Fl. bor. Am. **2**: 274. 1803. Based on *Osmunda virginica* L.

Botrychium virginicum (L.) Willd., Sp. pl. **5**: 64. 1810.

Botrychium gracile Pursh, Fl. Amer. Sept. **2**: 655. 1814. Based on specimens from Virginia. This represents merely a small slender form of typical *B. virginianum*, which does not merit nomenclatorial recognition.

Botrychium virginicum β gracile (Pursh) Presl, Suppl. Tent. Pterid. p. 46. 1845.

Botrychium virginianum var. *gracile* (Pursh) Milde, in Verh. zool. bot. Ges., Wien. **19**: 179. 1869.

Botrychium virginianum var. *intermedium* Butters in part, in Rhodora **19**: 210. 1917. Based on material from Nova Scotia, New England, northern New York, Illinois, and Missouri. The type is in the Gray Herbarium and is represented by the collection of *Orra P. Phelps, no. 47*, from moist woods, Canton, N. Y. The varietal name alludes to the intermediate character of the variety between the typical form and the ssp. *europaeum*. The writer has been quite unable to recognize var. *intermedium*. He would refer the type collection to ssp. *typicum*.

Botrychium virginianum var. *occidentale* Butters in part, in Rhodora **19**: 213. 1917. Based on material from Montana, Idaho, Oregon, and California. The type is in the Gray Herbarium and is represented by the collection of *J. H. Sandberg, D. T. MacDougal,* and *A. A. Heller, no. 762*, from deep woods near the south end of Lake Pend d'Oreille, Idaho. Butters supposed this to differ from the typical form and the ssp. *europaeum* in the broad herbaceous bases of the sporangia. The writer has been unable to distinguish this variety and is inclined to consider the type merely as a trivial form of the variable ssp. *typicum*.

Plant erect, 5–76 cm. high, glabrous or sparsely pubescent; bud pilose and, at least late in the season, partially exposed by the sheathing base of the stalk, which is open on one side; fertile and sterile segments both completely reflexed in vernation; common stalk 7–25 cm. long; blade sessile, thin and membranous, deltoid, large, 4–21 cm. long, 5–36 cm. wide, ternately decompound, much divided, with the ultimate divisions oblong-lanceolate, variously toothed or lobed, blunt or acutish; fertile stalk 1–23 cm. long; fruiting spike pinnately decompound, 2–16.5 cm. long; sporangia 0.5–1 mm. in diameter, with the valves recurving widely in dehiscence. Matures spores chiefly from May to

July, depending on the latitude and altitude. Gametophyte a brown subterranean tuberous body, 2–18 mm. long, 1.5–8 mm. wide.

Although D. H. Campbell probably discovered the gametophytes of this species, it was E. C. Jeffrey (1897, 1898) who first critically described them and worked out the details of development. As in other species of *Botrychium*, the prothallia are infected throughout with a mycorrhizic fungus. The reproductive organs are borne on the upper surface of the gametophytes, with the antheridia arranged in a series along the median ridge and the archegonia on either side. In the developing embryo, a root apex early differentiates. This grows out horizontally, as in *B. Lunaria*, and emerges from the side of the gametophyte. Meanwhile, a foot develops and from this the stem apex originates. In *B. virginianum*, the stem apex is immediately overarched by a cotyledonary structure, as in *B. Lunaria*. The first leaf of the young sporophyte regularly expands above ground, whereas in *B. Lunaria*, it is about the eighth leaf produced by the plant, which first appears above ground. Otherwise, the embryo of *B. virginianum* is essentially like that of *B. Lunaria*, except that all the structures are larger.

Since this is a common species, botanists have had good opportunity to notice and describe minute variations from the typical condition. Numerous malformations and monstrosities are known, commonest of which are forms with several fertile spikes and forms with sporangia-bearing divisions of the sterile blade.

Botrychium virginianum ssp. *typicum* is characteristically a plant of dry or somewhat moist deciduous woodlands. Its distribution is extensive. In North America it ranges from Prince Edward Island, New Brunswick, and Quebec west to southern British Columbia and south to central Florida, the "Gulf states," Arizona, California, and doubtfully Mexico. It is also found in northern India, China, and Japan, while certain specimens from central Europe perhaps should also be referred here. The status of this subspecies in Mexico and its relation to ssp. *meridionale* and *B. cicutarium* still remain doubtful. Further field study is necessary before the Mexican material can be properly interpreted.

PRINCE EDWARD ISLAND. Kings and Prince Counties.

NOVA SCOTIA. Annapolis: Middleton, *B. Long 19499* (G, Ph).

NEW BRUNSWICK. Kent: Bass River, *J. Fowler* (M).

QUEBEC. Beauce, Brome, Chambly, Deux Montagnes, Gaspé, Montreal, Papineau, Richmond, Rimouski, Sherbrooke, Stanstead, and Wolfe Counties.

ONTARIO. Bruce, Grey, Lanark, Lincoln, Nipissing, Northumberland, Thunder Bay, Wellington, and Wentworth Counties.

BRITISH COLUMBIA. Alberni and Nanaimo Counties.

MAINE. Androscoggin, Aroostook, Cumberland, Franklin, Kennebec, Oxford, Penobscot, Piscataquis, Somerset, Washington, and York Counties.

NEW HAMPSHIRE. All counties except Belknap and Strafford.

VERMONT. All counties except Grand Isle and Lamoille.

MASSACHUSETTS. All counties except Dukes, Nantucket, and Plymouth.

RHODE ISLAND. Providence: North Smithfield, *E. B. Chamberlain 138* (N).

CONNECTICUT. All counties.

NEW YORK. Bronx, Cattaraugus, Cayuga, Chautauqua, Chemung, Columbia, Cortland, Delaware, Dutchess, Erie, Essex, Genesee, Greene, Hamilton, Herkimer, Jefferson, Livingston, Madison, Niagara, Oneida, Onondaga, Ontario, Orange, Oswego, Otsego, Queens, Richmond, Rockland, Saint Lawrence, Schuyler, Seneca, Steuben, Suffolk, Tioga, Tompkins, Ulster, Washington, Wayne, Westchester, and Yates Counties.

NEW JERSEY. All counties except Atlantic and Union; see Clausen (1937a).

PENNSYLVANIA. Adams, Allegheny, Beaver, Berks, Blair, Bradford, Bucks, Cameron, Centre, Chester, Clearfield, Crawford, Cumberland, Dauphin, Delaware, Elk, Forest, Franklin, Greene, Huntingdon, Indiana, Juniata, Lancaster, Lebanon, Lehigh, Luzerne, Lycoming, McKean, Mifflin, Monroe, Montgomery, Northampton, Northumberland, Perry, Philadelphia, Pike, Potter, Snyder, Somerset, Sullivan, Susquehanna, Tioga, Union, Warren, Wayne, Westmoreland, and York Counties.

DELAWARE. Kent and New Castle Counties.

MARYLAND. Anne Arundel, Baltimore, Cecil, Garrett, Harford, Montgomery, Talbot, and Washington Counties.

DISTRICT OF COLUMBIA. Washington and Reno.

VIRGINIA. Amelia, Arlington, Bath, Culpepper, Dinwiddie, Fairfax, Fauquier, Giles, Gloucester, James City, Louisa, Madison, Mathews, Page, Prince William, Princess Anne, Rockbridge, Smyth, and Stafford Counties.

WEST VIRGINIA. Jefferson: Shepherdstown, *E. T. Wherry* (Ph). Dent's Run, *E. J. Smith* (Penn).

KENTUCKY. Barren, Bell, Carter, Christian, Edmonson, Franklin, Graves, Greenup, Hancock, Harlan, Muhlenberg, and Warren Counties.

TENNESSEE. Carroll, Davidson, Franklin, Knox, and Shelby Counties.

NORTH CAROLINA. Avery, Buncombe, Caswell, Craven, Davie, Haywood, Jackson, McDowell, Orange, Person, Polk, Rockingham, Swain, and Watauga Counties.

SOUTH CAROLINA. Anderson and Berkley Counties.

GEORGIA. Burke, Gwinnett, Polk, and Thomas Counties.

FLORIDA. Hernando: Brooksville, *E. P. St. John* (Claus., Herb. E. P. St. John). ———, *Chapman* (Ph). ———, ——— (G).

ALABAMA. ———, *S. B. Buckley* (M); ———, herb. C. Mohr (U).

LOUISIANA. East Feliciana, Natchitoches, and Rapides Counties.

OHIO. Butler, Erie, Holmes, Mahoning, Montgomery, Portage, and Scioto Counties.

INDIANA. Dubois, Jefferson, Kosciusko, La Porte, Lawrence, Montgomery, Porter, and St. Joseph Counties.

ILLINOIS. Cook, Hardin, Jackson, Johnson, Lawrence, Macon, Marion, Peoria, Pope, Richland, St. Clair, Union, Vermilion, and Winnebago Counties.

MICHIGAN. Alger, Berrien, Cheboygan, Emmet, Gogebic, Gratiot, Ingham, Keweenaw, Marquette, Ontonagan, Presque Isle, Roscommon, and Washtenaw Counties.

Wisconsin. Bayfield, Brown, Dane, Door, Douglas, Lafayette, Oneida, and Sauk Counties.

Minnesota. Becker, Clearwater, Cook, Dakota, Hennepin, Houston, Itasca, Nicollet, Nobles, and St. Louis Counties.

Iowa. Allamakee, Jefferson and Webster Counties.

Missouri. Adair, Audrain, Benton, Butler, Camden, Cape Girardeau, Carroll, Carter, Clark, Clay, Dade, Douglas, Dunklin, Gasconade, Greene, Jackson, Jasper, Jefferson, Johnson, Laclede, Lincoln, McDonald, Macon, Madison, Maries, Marion, Mercer, Pettis, Phelps, Pike, Putnam, Ralls, St. Louis, Schuyler, Shannon, Shelby, Stoddard, Sullivan, Taney, and Webster Counties.

Arkansas. Garland, Hempstead, Izard, Newton, and Washington Counties.

South Dakota. Lawrence and Roberts Counties.

Nebraska. Cass, Dawes, Otoe, Richardson, and Thomas Counties.

Kansas. Riley and Wilson Counties.

Oklahoma. Creek and McCurtain Counties.

Idaho. Kootenai: Lakeview, southern end of Lake Pend d'Oreille, *J. H. Sandberg, D. T. MacDougal, & A. A. Heller 762* (G, Ph, U).

Texas. Anderson, Dallas, Harrison, Kerr, Polk, San Augustine, and Upshur Counties.

Arizona. Pima: Santa Rita Mts., *C. G. Pringle* (G).

California. Specimens without locality data, *Miller* (G).

Mexico. Doubtful specimens from the states of Hidalgo, Mexico, Michoacan, and Puebla.

India. Kashmir: Lolob Valley, *R. C. Wroughton* (U).

China. Hupeh: ———, *E. H. Wilson 1033* (NY); also *A. Henry 5799a* (G) and *2568* (U). Tchenkeou-tin, 1400 m., *R. P. Farges 473* (NY).

Japan: Hokkaido: Sapporo, *K. Miyabe* (Ph). Honshu: Yokohama, *Maximowicz 129* (NY), Shikoku: Nanokarva, Tosa, *K. Watanabe* (G). Musashi: Mt. Mitare, ——— (U).

20b. **Botrychium virginianum** ssp. **europaeum** (Angström), n. comb.

Botrychium charcoviense Portenschl.; Presl in Suppl. Tentaminis Pteridographiae, p. 47. 1845. Based on a specimen collected near Charkow, Ukrainia. Presl states that *B. virginianum* is native in Europe and that the Ukrainian plant is not different from that species. This name thus can not be considered to be validly published, since it appears in the discussion as a synonym of *B. virginianum* and is not accompanied by a formal description.

Botrychium anthemoides Presl, in Abh. Böhm. Ges. Wiss. 5. **5**: 323. 1847. Based on specimens from near Spital, Upper Austria.

Botrychium virginianum var. *europaeum* Angström, in Botaniska Notiser. Nos. 5 & 6. p. 68. 1854. Based on specimens collected in northern Europe.

Botrychium virginianum var. *laurentianum* Butters, in Rhodora **19**: 208. 1917. Based on numerous specimens from Labrador, Newfoundland, Quebec, Maine, and Michigan. The type collection, which is in the Gray Herbarium, is that of *Fernald and Collins, no. 794*, from meadows and swamps in the slaty region south of Bic, Rimouski Co., Quebec. This represents merely an extreme form of ssp. *europaeum* in which the sporangia are very large and the divisions of the blade are decidedly imbricate. It occurs in Scandinavia as well as in North America.

Botrychium virginianum var. *intermedium* Butters in part, in Rhodora **19**: 210. 1917. Although the type specimens definitely belong to the ssp. *typicum*, many of the plants which have been referred to this variety represent ssp. *europaeum*.

Botrychium virginianum var. *occidentale* Butters in part, in Rhodora **19**: 213. 1917. Much of the material which has been referred to this variety belongs to ssp. *europaeum*.

Differing from ssp. *typicum* in the more compact and leathery blade, with the pinnae not so deeply or finely divided, and with the ultimate divisions often crowded or imbricate; and in the larger sporangia, which are 0.5–1.8 mm. in diameter, with the valves usually not widely spread open or recurved in dehiscence.

The writer entirely agrees with Weatherby (1935) in uniting the vars. *europaeum* and *laurentianum*, particularly since the latter variety represents only an extreme phase of the former, due in part to the habitat and in part to the age of the plants at the time of collection. Practically all of the characters used by Butters in separating his several varieties of *B. virginianum* fail upon close inspection. The nature and size of the sporangia and the method of dehiscence are definitely influenced by moisture and light conditions as well as by the stage of development of the fertile segment. The sporangia in most species of *Botrychium* regularly average larger in the north than in the south, while, because of the short growing season, most of the specimens collected in the north are at an earlier or younger stage than those obtained from places farther south. This probably explains to a certain extent why the valves of the sporangia are not widely reflexed in many of the northern specimens filed in American herbaria. Such characters as those used by Butters (1917) seem to the writer to be of little value in a variable and diverse group such as the present one.

This is typically a plant of coniferous forests, moist meadows and mossy open places. It is found in North America and Asia in the region north of that where the ssp. *typicum* occurs, also in northern Europe. In North America it ranges from Labrador and Newfoundland west to Alberta and British Columbia and south to northern New England, Michigan, Wisconsin, Minnesota, Colorado, and Oregon.

LABRADOR. Blanc Sablon, *M. L. Fernald* & *B. Long 27,280* (C, G, Ph); also *2356* (G).

NEWFOUNDLAND. Regions of Straits of Belle Isle, Ingornachoix Bay, Port a Port, and Back Cove.

NEW BRUNSWICK. Madawaska and Restigouche Counties.

QUEBEC. Gaspé, Matane, Quebec, Rimouski, and Saguenay Counties; also the Mingan Islands and Anticosti Island.

ONTARIO. Bruce and Thunder Bay Counties.

MANITOBA. Winnipeg: Fort Garry, *H. E. Niles* (Ph). Moose Mt., *J. Macoun* (U).

ALBERTA. Counties of Calgary West and Peace River.

BRITISH COLUMBIA. Counties of Alberni, East Kootenay, and West Kootenay. Also reported from Hudson Hope in Contr. Arn. Arboretum. **6**: 113. 1934.

MAINE. Aroostook, Piscataquis, and Washington Counties.

NEW HAMPSHIRE. Coos: Colebrook, *M. L. Fernald* & *A. S. Pease 16,839* (N).

VERMONT. Orleans: Willoughby, *G. G. Kennedy* (N).

MASSACHUSETTS. Franklin: ? Sunderland, *R. A. Ware 787* (C), intermediate towards ssp. *typicum*.

MICHIGAN. Cheboygan, Gogebic, Keweenaw, and Mackinac Counties.

WISCONSIN. Oneonta, Lake Superior, *H. Gillman* (Princ).

MINNESOTA. Cook: Poplar Lake, *E. T. Wherry* & *A. N. Leeds 3242* (Ph).

MONTANA. Lake and Lewis and Clark Counties; also Glacier National Park.

IDAHO. Bonner: Upper Priest River, *C. C. Epling 7175* (M). West Fork of Priest River, *J. B. Leiberg 2812* (U).

COLORADO. Snowy Range, Wet Mountain Valley, *T. S. Brandegee* (Princ).

OREGON. Hood River: Hood River, *Mrs. E. P. Barrett* (G).

WASHINGTON. Clarke and Whatcom Counties.

SWEDEN. Läns of Gafleborg, Jamtland, and Vasternorrland.

RUSSIA. Districts of Leningrad, Novgorod, and Olonets.

20c. **Botrychium virginianum** ssp. **meridionale** (Butters), n. comb.

Botrychium virginianum var. *meridionale* Butters, in Rhodora **19**: 213. 1917. Based on specimens from Mexico. Type in the Gray Herbarium; Chiapas, *Dr. Ghiesbreght, no. 252*.

Differing from ssp. *typicum* in the coarser cutting of the sterile blade, with the divisions of the pinnules oblong and entire; in the acute or acuminate pinnae; in the basal pinnae little larger than the second pair; and in having the midribs conspicuously pilose. Matures spores in July and August.

This represents a very distinct geographically segregated population of the circumboreal *B. virginianum*. At present it is known only from the mountains of central and southern Mexico, but is to be expected also in the mountains from both farther north and south. The relation of this subspecies to ssp. *typicum* and to *B. cicutarium* is as yet poorly understood. Much collecting must still be done in the areas where these races overlap before the relationships can be more definitely stated.

MEXICO. Chiapas: ———, *Ghiesbreght 252* (G). Hidalgo: Cuyamaloya, *C. G. Pringle 13467* (U). Mexico: Temascaltepec, *G. B. Hinton 1531* (NY). Morelos: Cuernavaca, *W. Trelease* (M). San Luis Potosi: Alvarez, Sierra de Alvares, *F. W. Pennell 17882* (Ph, U); Mt. San Miguelito, *J. G. Schaffner 943* (G).

21. BOTRYCHIUM CICUTARIUM (Savigny) Swartz. *Figure 19.*

Osmunda cicutaria Savigny, in Lamarck, Encycl. meth. bot. **4**: 650. 1797. Based on plants collected by Plumier in the forests of Santo Domingo. *Osmunda asphodeli radice*, Plum. fil. 136, t. 159, is listed as a synonym.

Botrychium cicutarium (Savigny) Swartz, Synopsis Filicum. p. 171. 1806.

Botrychium Virginicum β mexicanum Hooker & Greville, in Bot. Misc. **3**: 223. 1833. Based on specimens from Jalapa, Mexico, collected by Chamisso, and from Rigla, Mexico, obtained by Captain Veitch. The blade is said to be less finely divided than in typical *B. Virginicum*.

Botrychium brachystachys Kunze, in Linnaea **18**: 305. 1844. Based on Mexican specimens with the fertile segment shorter than the sterile. The type is the collection of Roemer, no. 35. *B. virginicum β mexicanum* Hook. and *B. virginicum* Schlectend. are listed as synonyms. Kunze states that this fern stands near *B. virginianum*, as *B. decompositum* Mart. & Gal. does *B. obliquum*.

Botrychium dichronum Underwood, in Bull. Torrey Club **30**: 45. 1903. Based on material from Jamaica. Type in the herbarium of the N. Y. Bot. Gard.; the collection of W. N. Clute 96, from Morce's Gap, alt. 1500 m., Feb. 7, 1900. The specific name alludes to the two growing leaves present at the time of maturity.

Plant 25 to 50 cm. high; roots stout; common stalk 17–26 cm. long; blade sessile or short-stalked, membranous, ternately divided, with the lowest pinnae far exceeding the others in length; pinnae acuminate, with the midrib often winged, practically glabrous; fertile stalk 5–13 cm. long; fruiting spike to 11 cm. long, decompound; sporangia 0.5–0.8 mm. in diameter, brownish; valves wide spreading in dehiscence. Spores maturing from February to June. Gametophyte apparently unknown.

This differs from *B. virginianum* so decidedly in the cutting of the sterile blade, as well as in the length of the fertile stalk, that since there seems to be discontinuity in the series between that species and this, it seems desirable to maintain the present form as a species. If it is found however, when more Mexican material shall be available, that *B. virginianum* passes by gradual stages into *B. cicutarium*, then it would be best to designate this as a subspecies.

Specimens from Bolivia differ from typical *B. cicutarium* in that the fertile spike considerably exceeds the sterile segment and that the ultimate divisions of the blade are oblong or broad, elliptical or obtuse, not finely divided. These Bolivian plants may perhaps represent a new species, but until more material is available from South America, they are tentatively included here.

B. cicutarium is a plant of rich woodlands in the New World tropics, where it occurs at altitudes from 2500–12,000 feet. It ranges from the mountains of central Mexico south through Central America to Colombia, Ecuador, Peru, and Brazil; also in various of the islands of the West Indies, including Cuba, Jamaica, and Hispaniola.

CUBA. Santa Clara: Buenos Aires, Trinidad Hills, *J. G. Jack 7266* (U).

JAMAICA. John Crow Peak, *W. R. Maxon* & *E. P. Killip 995* (G, Penn, U). Morce's Gap, *W. N. Clute 96* (NY).

SANTO DOMINGO. Barahona: Tal Mingo, *Padre Miguel Fuertes 1540* (G). Constanza, *H. von Tuerckheim 2963* (G).

HAITI. Artibonite: Ennery, ——— (U). Mission at Fonds Varettes, *E. C. Leonard* (U). Furcy, ——— (U). Massif de la Selle, Petionville, *E. L. Ekman 1538* (U).

MEXICO. Chiapas: ———, *Gheisbreght 430* (G). Chihuhuahua: Chuhuichupa, alt. 8000′, *H. Le Sueur 1131* (U). Mexico: Salazar, *J. N. Rose* & *J. H. Painter 7045* (U). Morelos: Cuajimalco, *F. Salazar* (U). Vera Cruz: Jalapa, *C. G. Pringle 7753* (G, M); also *C. L. Smith 2141* (G).

GUATEMALA. Chimaltenango: Volcan de Agua, *O. Salvin* (G).

COSTA RICA. Cartago: Cerro de la Carpintera, *P. C. Standley 34276* (G). Canddaria, *Brade 153* (NY).

PANAMA. Several collections from deep woods and humid forests (U).

COLOMBIA. Antioquia: Medellin, *Bro. Henri-Stanislaus 1667* (U). Santander: in dense woods between Pamplona and Toledo, *E. P. Killip & A. C. Smith 19968* (U); Paramo de Romeral, *E. P. Killip & A. C. Smith 21177* (U). Cascada de Buitre, *Bro. Ariste-Joseph A469* (U).

ECUADOR. ———, *W. Jameson* (U). ———, *Mille* (U).

PERU. Junin: Huacapistana, *E. P. Killip* & *A. C. Smith 24308* (U).

BRAZIL. Minas Geraes: ———, *A. F. Regnell* (U). Santa Catharina: Lages, *L. Spannagel* (U).

BOLIVIA. *O. Buchtien* (U); *A. M. Bang 2596* (U). These specimens are not typical and probably represent an undescribed species or variety.

22. BOTRYCHIUM STRICTUM Underwood. *Figure 19.*

Botrychium strictum Underwood, in Bull. Torrey Club **30**: 52. 1903. Based on specimens from Japan. The type is in the herbarium of the New York Botanical Garden; the collection of *A. W. Stanford*, Sapporo, Japan. Aug., 1894. The specific name alludes to the strict, spike-like fruiting panicle.

Plant lax, 30–40 cm. high; common stalk averaging 25–28 cm. long; sterile blade sessile, 28–31 cm. wide, 17–19 cm. long, ternately parted, with each of the major divisions pinnately again divided and with the ultimate segments oblong and obtuse; fertile stalk 5–6 cm. long; fruiting panicle strict and spike like, 6–15 cm. long, with the sporangia crowded on the short branches, which are 3–10 mm. long and strongly ascending; sporangia 0.6–1 mm. in diameter. Apparently matures spores during July and August. The gametophyte is unknown.

This species is native in woodlands in Japan and China. It is easily distinguished from any of its relatives by the strict spicate fertile segment, which rarely surpasses the blade in length. Only one leaf is regularly expanded during a growing season.

CHINA. "District de Tchen-keou-tin," *R. P. Farges* (NY).

JAPAN. Hokkaido: Sapporo, *A. W. Stanford* (M, NY). Honshu: Yokohama, *Maximowicz* (G); Prov. Musashi, Takaosan, *J. Matsumuru* (NY). ———, *W. Hancock 70* (U).

23. BOTRYCHIUM CHAMAECONIUM Bitter & Hieronymus. *Figure 19.*

Botrychium chamaeconium Bitter & Hieronymus, in Engler & Prantl, Die Nat. Pflanzenfam. 1 (4 Abt.): 471. 1900. Based on material collected by Preusz, no. 1037, on Cameroons Mt., near Buea, British Cameroons.

Since no specimens of this species have been seen by the writer, the following description has been adapted from that supplied by Ballard (1934): plant 8–28 cm. high; roots numerous, stout; common stalk 5–12 cm. long, with a few weak whitish hairs, particularly towards the base; bud completely inclosed by the more or less persistent stipular base of the leaf stalk; sterile blade membranous, broadly subdeltoid or pentagonal, to 18 cm. broad, bipinnate with the pinnules pinnatifid, and the basal pinnae tripinnate with the rachises narrowly winged; ultimate segments broadly elliptical or ovate, much lobed, with the lobes oblong or suboblong, dentate at the apex, with the teeth ovate or ovate-lanceolate, acute; fertile segment arising from the base or towards the base of the sterile blade, bi- or tripinnate, to 15 cm. long, with the stalk to 5 cm. long; sporangia globose, pale brown, to 1.5 mm. in diameter at maturity, with the valves broadly reflexed in dehiscence; spores pale yellow, 35–40μ in diameter.

B. chamaeconium was originally described in 1900, based upon somewhat poor material collected by Preusz in the Cameroons Mts. According to Bitter and Hieronymus, and also to Ballard, this species is most nearly related to *B. lanuginosum* (Wall.) Hk. & Grev., to which it is supposed to bear a strong resemblance, but is smaller, more slender, with the fertile segment surpassing the sterile and the stalk of the sporophyll arising from the base of the sterile stalk. In the present treatment, because of this last character (the basal origin of the fertile segment) the species is placed in the section *Virginianae*, rather than in the *Lanuginosae*. It differs from other species of *Virginianae* in the pinnate, rather than ternate, division of the blade, and in the slender fertile spike. The divisions of the blade are not decurrent, while the ultimate divisions are ovate or oblong, and bluntly toothed or parted.

Ballard (1934) cites two collections: British Cameroons, Cameroons Mt., Buea, 2200 m., *Preusz* 1037; and Uganda, Bulago District, Mt. Elgon, Bugishu, 1970 m., *A. S. Thomas* 350.

D. Dubious and Rejected Names

1. *Botrychium obliquum* var. *Habereri* Gilbert, in Fern Bull. **11**: 88–89. 1903. Based on material from Whitesboro and Oriskany, Oneida Co.; Ilion, Herkimer Co.; and Shandaken, Ulster Co., N. Y. This is stated by Gilbert to be the same as *B. ternatum* var. *australe*, but material distributed as *Habereri* has been rather various. Some of it, including the type collection, is somewhat intermediate between *B. dissectum* var. *oneidense* and *B. multifidum* ssp. *silaifolium*, while the rest is either straight var. *oneidense* or ssp. *silaifolium*. In consideration of

this confusion, it seems desirable to drop the name *Habereri* completely, rather than arbitrarily to assign it to synonymy under one or the other of the two elements mentioned above.

2. *Botrychium ternatum* var. *Agnetis* Mackay, in Proc. Nov. Scot. Inst. Sci. **10**: 99. 1903. Like Weatherby (Amer. Fern. Journ. **27** (2): 55. 1937), the writer has been unable to place this name.
3. *Botrychium ternatum* var. *daedaleum* Christ; H. Pittier, in Primitiae Florae Costaricensis. **3** (fasc. 1): 46. 1901. According to Pittier, this is a curious form with the divisions of the sterile blade rounded, tripinnatifid, with the ultimate lobes obtuse, cuneate at the base, and rounded and serrate at the apex. Based on a collection from Cerros de Velirla, 2200 m., in the valley of the Copey, Costa Rica. The writer has been unable to place this variety, although he strongly suspects that it may represent a peculiar form of *B. dissectum* ssp. *decompositum*.
4. *Japanobotrychium arisanense* Masamune, in Journ. Soc. Trop. Agric. Formosa **3**: 246. 1931. Based on specimens from Formosa. The type is in the herbarium of the Imperial University at Taihoku. This is the collection of Mori and Masamune, no. 1345, from near Arisan, Formosa. Since this new genus seems to depend for recognition on the epiphytic habit alone, it seems quite likely that it is properly a *Botrychium* and perhaps not even distinguishable from *B. lanuginosum*, which the original description strongly suggests. Since no material has been available in the present study, judgment must be temporarily withheld.

II. HELMINTHOSTACHYS

Helminthostachys, Kaulfuss, in Flora, p. 103. 1822. Genotype and only species, *H. zeylanica* (L.) Hooker (*Osmunda zeylanica* L.). Kaulfuss based the genus on *H. dulcis*, but this is merely a later synonym of the older *Osmunda zeylanica* of Linnaeus.

Botryopteris Presl, Rel. Haenk. **1**: 76. 1825. Based on *B. crenata* and *B. mexicana*, both later synonyms of *Osmunda zeylanica* L.

Ophiala Desvaux, in Mém. Soc. Linn. Paris. **6**: 195. 1827. Based on *O. zeylanica*.

Perennial herbs; sporophytes consisting of a stout elongate unbranched horizontal rootstock, numerous thick fleshy roots, and commonly one leaf, in the sheathing base of the stalk of which is the bud, from which the leaves for succeeding seasons develop; leaf consisting of a common stalk and a fertile and sterile segment; sterile blade sessile, palmately compound; venation open, dichotomous; fertile segment consisting of a short stalk and a long fruiting spike, bearing numerous very short branches or lobes on which the crested naked sporangia are borne in crowded glomerules; sporangia ovoid, dehiscent vertically by two valves, producing numerous yellowish thick-walled spores; gametophyte cylindrical, erect, stout and lobed below. A genus containing one variable species in the Indo-Malayan and Australian Regions.

1. HELMINTHOSTACHYS ZEYLANICA (L.) Hooker. *Figure 20.*

Osmunda zeylanica L., Sp. pl. ed. 1. **2**: 1063. 1753. Based on material from Ceylon.

Botrychium zeylanicum (L.) Swartz, in Schrad. Journ. für die Botanik. p. 111. 1800.

Helminthostachys dulcis Kaulfuss, Flora. p. 103. 1822. Based on the description and illustration of Rumphius (Herb. amboin. **6**: 153. pl. 68, f. 3).

Botryopteris mexicana Presl, Rel. Haenk. **1**: 76. t. 12, f. 1. 1825.

Helminthostachys mexicana (Presl) Sprengel, Systema veg. ed. 16. **4**: 23. 1827.

Ophiala zeylanica (L.) Desvaux, in Mém. Soc. Linn. Paris. **6**: 195. 1827.

Helminthostachys zeylanica (L.) Hooker, Genera Filicum. pl. 47b. 1842.

Helminthostachys crenata Presl, Suppl. Tent. Pterid. p. 60. 1845. Based on material from the island of Guam and from the Philippine Islands. The specific name alludes to the crenate margins of the divisions of the sterile blade. This is a renaming of *Botryopteris mexicana*, which Presl earlier erroneously had designated as native in Mexico.

Helminthostachys integrifolia Presl, Suppl. Tent. Pterid. p. 60. 1845. Based on material from the island of Luzon in the Philippines. The specific name alludes to the entire margins of the divisions of the sterile blade.

Botryopteris crenata Presl, Abh. Böhm. Ges. Wiss. 5. **5**: 324. 1847. *Botryopteris mexicana* Presl and *Helminthostachys crenata* Presl are listed as synonyms.

Plant perennial with a stout horizontal rootstock bearing numerous thick fleshy roots and producing above ground, each season, a single palmately divided leaf, 18–64 cm. high; common stalk 11–36 cm. long, stout or rather slender; blade sessile, 11–30 cm. wide, 8–22 cm. long, palmately divided, with the three major divisions palmately lobed or forked; divisions of blade oblong lanceolate, acutish, or obtuse, 3–20 cm. long, 1–3.5 cm. wide, with entire or

Fig. 20 (above). *Helminthostachys zeylanica.*
Fig. 21 (below). *Ophioglossum palmatum.*

crenate margins; venation open, pinnate, with the numerous lateral veins parallel and almost at right angles to the midvein, mostly once forking, rarely twice or thrice forking; fertile stalk 4–11 cm. long; fruiting panicle spike-like, 3–16 cm. long, with the numerous sporangia borne in glomerules on the very short (0.5 mm.) lateral branches; sporangia dark brown, capitate, dehiscing by an apparently vertical suture, 0.6–1.2 mm. in diameter; spores yellowish, finely granulose on the surface, averaging 35μ in diameter. Gametophyte cylindrical, erect, stout and lobed below.

According to Presl (1847) the number of vascular bundles in the stalk of this species varies between 10 and 12, which is the highest number found in any species of the *Ophioglossaceae.* R. de Litardiere (1921) lists the diploid chromosome number, as determined by Beer, as between 80 and 120. Beer (1906) has also worked out the details of spore development, while Farmer and Freeman (1899) investigated the general anatomy.

Helminthostachys zeylanica is widely distributed in thickets and woods at low altitudes throughout the Australasian region.

INDIA. Assam: Sibsagar (Bungpore) Station, *G. Mann* (M, NY, U).

CEYLON. Colombo, *G. Wall* (NY). *Wight 30* (NY); *Thwaites* (G); *W. Ferguson 223* (M).

INDO-CHINA. Laos: Mekong, below Paklai, *F. K. Ward 9027* (NY); also Phu-Domrek, Bassin d'Attapu, *Harmanden 306* (NY).

BRITISH MALAYA. Pahang, ——— (U).

SUMATRA. Subdiv. Laboehan Batoe, Dist. Kota Pinang, Saboengan, *R. Si Toroes 3773* (NY). Div. Padang Si Dimpoean, subdiv. Padang Lawas, Tapianoeli, *R. Si Toroes 4815* (NY). Indragiri, *I. W. Burchardt 48* (NY).

JAVA. ——— (U).

BORNEO. British North Borneo: Mt. Kinabalu, *J. & M. S. Clemens 27666* (NY, U). Sarawak: Sabakix, base of Mt. Poi, *J. & M. S. Clemens* (NY); Selungo, upper Baram, ——— *2809* (NY).

PHILIPPINE ISLANDS.

Island of Luzon. La Laguna: Dayap, *J. Agati 7799* (M). Morong: Antipolo, *E. D. Merrill 776* (G, M, NY). Nueva Ecija: ———, *E. B. Copeland* (G). Pangasanan: Umingan, *F. Otanes 1788* (G).

Island of Mindanao. Davao: Davao, *E. B. Copeland 461* (NY); Catalnan, *R. Kanehira 2495* (NY). Surigao: Butnan, *C. N. Weber 1187* (G). Subprov. Bukidnon: Tanculan, *E. Fenix 24981* (G). Agusan: Cabadbaran (Mt. Urdaneta) *A. D. E. Elmer 13547* (*M*, NY).

CHINA. Kwantung: Hainan Island, west of Fan Tá, *Tsang & Fung 463* (NY); also Lin Fa Shan, *Tso* (NY); Canton, *Reed 2050* (M, Ph).

JAPAN. Liu Kiu Islands, *L. Boehmer* & *Co.* (NY). Formosa: reported by various authors, but no specimens have been seen by the writer.

NEW GUINEA AND SOLOMON ISLANDS. Reported by Baker (1891), but no specimens have been seen by the writer.

NEW CALEDONIA. Plateau d'Unio, *Franc 710* (NY, Ph); also *M. Gandoger* (M).

AUSTRALIA. Queensland: Innisfail, *M. Michael 127* (G).

III. OPHIOGLOSSUM

Ophioglossum L., Sp. pl., ed. 1, 2: 1063. 1753. Genotype, *Ophioglossum vulgatum* L. The name is derived from the Greek and means literally snake-tongue, hence the common designation of the group as Adder's-Tongue Ferns.

Perennial herbs, terrestrial or epiphytic; sporophytes consisting of a short erect or prostrate unbranched rootstock with an erect exposed bud borne apically, rather thick fleshy roots, and one or several glabrous somewhat fleshy leaves which consist of a common stalk and a fertile and a sterile segment; blade sessile or stalked, usually simple, sometimes palmately lobed or bifurcate towards the apex; venation reticulate; fertile segment consisting of a stalk and a simple spike in which the naked coalescent subspherical sporangia are borne in two rows; sporangia dehiscent by a transverse suture, producing numerous yellowish thick-walled spores; gametophytes small, subterranean, cylindrical or ovoid, branched or unbranched, entirely destitute of chlorophyll and dependent for nourishment upon a mycorrhizal fungus. A genus of 26 species, found in a variety of habitats in all of the major geographical regions of the earth.

The genus *Ophioglossum* may be divided into four rather natural subgenera based on the nature and division of the blade, habit, and the condition of the fertile segment. Some students have preferred to consider these subgenera as distinct genera, but to the writer the argument for merging them under *Ophioglossum* seems much stronger than the argument in favor of segregation.

The subgenus *Cheiroglossa* includes only one species, which is an epiphyte, with the blade either palmately lobed or divided, and with each leaf regularly bearing several pendent fertile spikes.

The subgenus *Ophioderma* includes three species which seem to represent successive stages in a reduction series from the *Cheiroglossa* type to the condition in the subgenus *Euophioglossum*. *O. pendulum* is epiphytic, with long strap-shaped blades, but with each leaf bearing only one pendent fertile spike, instead of several, as in *Cheiroglossa*. The blade is occasionally furcate towards the apex, but never palmately lobed. This species and *O. intermedium* seem to be connecting links between *Cheiroglossa* and the typical terrestrial species of *Euophioglossum*. Further, *O. intermedium* definitely represents the intermediate condition between *O. pendulum* and these terrestrial types. In the former species, the habit is various, either epiphytic or terrestrial, while the blade is intermediate in character between the condition in *O. pendulum* and species of *Euophioglossum*. *Ophioglossum simplex*, apparently at the end of a side-line of development in *Ophioderma*, represents the extreme example of reduction in this series, in which only a fertile leaf is developed. A sterile segment is apparently not produced.

The subgenus *Euophioglossum* includes the majority of the species of *Ophioglossum*. These are terrestrial plants, mostly small in size, with the leaf divided into a simple sterile blade and an erect fertile segment. The subgenus *Rhizoglossum*, with only one species, represents an extreme variation from this condition. In this the leaves are of two types, some fertile and others sterile, but none of the leaves is divided into both fertile and sterile segments.

KEY TO THE SUBGENERA OF OPHIOGLOSSUM

I. Fertile segment commonly arising medianly from considerably above the base of the face of the sterile blade, or if basally or subbasally, then several spikes produced laterally on a single leaf; fruiting spikes pendent or erect; blades variously lobed or undivided; plants mostly epiphytic, but sometimes terrestrial. II

  II. Blade palmately lobed or divided, usually with several fertile spikes borne laterally on the stalk or towards the base of the expanded portion of the sterile segment. A Subgenus *Cheiroglossa*

  II. Blade undivided, usually much elongate, occasionally bifurcate towards the apex, but never palmately lobed, rarely lacking; leaf with only one fertile spike borne medianly somewhat above the base on the face of the blade; plants epiphytic or sometimes terrestrial. B Subgenus *Ophioderma*

I. Fertile segment arising medianly from or below the base of the sterile blade; fruiting spikes erect; blades simple; plants terrestrial. III

  III. Leaves regularly divided into a fertile and a sterile segment; plants never scapose, with the leaves dimorphic. C Subgenus *Euophioglossum*

  III. Leaves regularly of two distinct types, fertile and sterile; plants scapose, with the sporangia-bearing leaves surrounded by the sterile ones. D Subgenus *Rhizoglossum*

A. Subgenus **Cheiroglossa** (Presl) Clausen, n. stat.

Cheiroglossa Presl, Suppl. Tent. Pterid. p. 56. 1845; also in Abh. Böhm. Ges. Wiss. 5. **4**: 317. 1845. Genotype, *Ophioglossum palmatum* L. The specific name, derived from the Greek, alludes to the resemblance of the blade to a hand and of the fertile segments to tongues.

Ophioglossum, section *Cheiroglossa* (Presl) Prantl, in Ber. deutsch. bot. Ges. **1**: 353. 1883.

In this section is included only a single species, *O. palmatum*. Although this is exceedingly variable, the writer has been unable to find differences, even of varietal rank, for separating the various forms which occur. The species is of wide distribution throughout the American tropics, but occurs also in Réunion and French Indo-China.

1. OPHIOGLOSSUM PALMATUM L. *Figure 21.*

Ophioglossum palmatum L., Sp. pl. ed. 1. **2**: 1063. 1753. Based on *O. palmatum* Plum. fil. 139. t. 163. The specific name alludes to the palmate nature of the sterile blade.

Cheiroglossa palmata (L.) Presl, Suppl. Tent. Pterid. p. 57. 1845.

Ophioderma palmata (L.) Nakai, in Bot. Mag. Tokyo. **39**: 193. 1925.

Cheiroglossa palmata var. *malgassica* C. Christensen, in Dansk Bot. Ark. **7**: 185. 1932. Based on material from the island of Réunion. The type, the collection of Perrier 17047, from near the junction of the rivers Onive and Mangoro, is deposited in the Herb. Perrier.

Plant epiphytic; rootstock prostrate, elongate, 1–2 cm. long, bearing numerous fleshy roots and usually several leaves; rootstock and bases of leaf stalks regularly densely paleaceous; leaves (including stalks) 12–76 cm. long; sterile stalks 5–42 cm. long; blades 4–35 cm. long, 4–30 cm. wide, palmately lobed or divided, with the oblong-lanceolate divisions usually acute or acutish; leaves with several fruiting spikes arising along the margin of the stalk or near the base of the blade, rarely only a single spike borne medianly; fertile segments 1–9 cm. long; fertile stalks 0.2–6 cm. long; fruiting spikes rather stout, 1–3 cm. long; sporangia 0.6–1 mm. in diameter; spores yellowish, finely verrucose, 45–60μ in diameter. Gametophyte apparently unknown.

Christensen (1932) has described, as var. *malgassica*, the form of this species occurring in Réunion. This variety is based on the supposed smaller size of the Réunion plants, the firmer texture, and the very short brown scales of the rhizome. The new variety is also said to be distinguished by the origin of all of the fertile segments from the sides of the sterile stalk and not from the base of the blade. Since examination of abundant American material reveals that the illustrations and description of var. *malgassica* can be matched exactly by certain New World forms, this variety is not here recognized. The American plants display a wide range of variation in size and in texture. The leaves of some specimens are lax and membranous, while those of others are almost coriaceous. The hair-like scales investing the rhizome vary greatly in length and abundance, and range in color from very pale brown or buffy to deep reddish brown. The venation is diffuse and rather variable, but the areoles formed, though varying greatly in size, are rather consistently elongate-hexagonal.

In certain small specimens the leaf bears only one fertile segment, which arises medianly. Normally, a single leaf may have from three to twelve or more fertile segments borne laterally on the margins of the leaf stalk or towards the base of the blade.

In many respects, this species is very closely allied to *O. pendulum*. Nakai (loc. cit.) has been so strongly impressed by this relationship that he has combined *Ophioderma* and *Cheiroglossa* to form one genus, *Ophioderma*, including *O. palmatum*, *O. pendulum*, and related species. Since *O. pendulum* is definitely connected with *Euophioglossum* by intermediate forms, and since *O. palmatum* is in many respects (i.e. in the prostrate paleaceous rootstock, epiphytic habit, and stout pendent fertile segments) closely related to *O. pendulum*, the argument for placing *O. palmatum* in a distinct genus, separated from *O. pendulum*, seems decidedly weak.

Ophioglossum palmatum is a plant of the dense forests of the West Indies, Central America, and South America. It is also found in central and southern Florida, Réunion, and French Indo-China.

FLORIDA. Collier, Dade, Indian River, Lee, Manatee, Monroe, Orange, and Seminole Counties.

WEST INDIES. Islands of Cuba, Guadeloupe, Hispaniola, Jamaica, Montserrat, and Porto Rico.

MEXICO. Reported by Martens & Galeotti (Mém. sur les fougères du Mexique, p. 14, 1842) from Petlapa, Oaxaca.

HONDURAS. Cortes: El Jural, Lake Yojoa, *J. B. Edwards y50* (G). Puerto Sierra, *P. Wilson 308* (NY).

COSTA RICA. Provinces of Guanacaste and San José.

COLOMBIA. Departments of Magdalena and "El Valle."

PERU. Cuzco: Prov. La Convericion, *C. B. Quillabamba 1561* (NY).

BRITISH GUIANA. Demerara, *G. S Jenman* (NY).

BRAZIL. State of Santa Catharina, *A. Schmalz 131* (NY).

RÉUNION. Reported by various authors, but no specimens have been seen by the writer.

FRENCH INDO-CHINA. Annam: Tourane, *Parture 7083* (G).

B. Subgenus **Ophioderma** (Blume) Clausen, n. stat.

Ophioglossum, Sect. *Ophioderma* Blume, Enumeratio plantarum Javae. fasc. 2: 259. 1828.

Ophioderma (Blume) Endlicher, Genera plantarum secundum ordines naturalis disposita. p. 66. 1836. Based on *Ophioglossum pendulum* Linn.

Under *Ophioderma* are included three species. The subgenus is characterized by the median origin of the single fertile segment from considerably above the base of the sterile blade; by the horizontal tuberous rhizome; and by the usually long and narrow blade, which is absent only in *O. simplex*. *Ophioglossum pendulum*, the commonest and most widely distributed of the three species, is an epiphyte.

KEY TO THE SPECIES OF OPHIODERMA

A. Plant epiphytic; rhizome elongate, horizontal; fertile segment pendulous, inserted medianly on the face of the sterile blade, considerably above its base, but still usually far surpassed by the sterile segment. 2. *Ophioglossum pendulum*

A. Plant characteristically terrestrial, erect; rhizome stout and tuberous; fertile segment erect, surpassing or overtopping the sterile segment; blade elongate-oblanceolate or wanting. B

  B. Leaf usually consisting of both a fertile and a sterile segment; sterile blade always present. 3. *Ophioglossum intermedium*

  B. Leaf consisting of only a fertile segment; sterile blade always lacking. 4. *Ophioglossum simplex*

Fig. 22 (above). *Ophioglossum pendulum* ssp. *typicum* (•) and ssp. *falcatum* (+).
Fig. 23 (below). *Ophioglossum vulgatum* in North America.

2. OPHIOGLOSSUM PENDULUM L. *Figure 22.*

This is the largest and most widely distributed of the epiphytic species of *Ophioglossum.* In tropical countries it is frequently cultivated for its attractive foliage.

The species may be divided into two rather distinct subspecies which are distinguished in the following key:

A. Sterile blade lax and membranous, 12–170 cm. long; fertile spike with slender stalk, 0.8–10 cm long. 2a. *O. pendulum* ssp. *typicum*

A. Sterile blade falcate, of firm texture, subcoriaceous and rigid, 25–35 cm. long, oblanceolate, blunt at the apex, gradually tapering to the rhizome without a definite stalk; fertile spike long and stout, with a short stalk, 0.6–2.5 cm. long. 2b. *O. pendulum* ssp. *falcatum*

2a. OPHIOGLOSSUM PENDULUM L., SSP. TYPICUM

Ophioglossum pendulum L., Sp. pl., ed. 2. **2**: 1518. 1763. Based on *Scolopendra major* of Rumphius and stated to be native in India, where it is parasitic on trees. The specific name alludes to the hanging or epiphytic habit.

Ophioderma pendulum (L.) Presl, Suppl. Tent. Pterid. p. 56. 1845. Based on *Ophioglossum pendulum* L., Sp. pl. **2**: 1518. 1763.

Ophioglossum furcatum John Smith; Ferns, British and Foreign, p. 272. 1866. No description is furnished, but *Ophioglossum pendulum β furcatum* Presl, Suppl. Tent. Pterid., p. 56, is listed as a synonym. The species is said to be native in Queensland. The specific name alludes to the furcate apex of the blade. This is simply a trivial form which certainly does not merit nomenclatorial distinction.

Ophioglossum Moultoni Copeland, Journ. Straits Branch Roy. Asiatic Soc. no. 63: 72. 1912. Based on specimens from Bukit Buyo and Bukit Lawi, Borneo. This is a small form with winged stipe. Although Copeland has designated it as an "amply distinct and apparently very constant species," the writer has been unable to distinguish it from small plants of typical *O. pendulum.* Not only is the original description decidedly brief, but no attempt was made to differentiate this species from related forms.

Plant epiphytic, 15–180 cm. high; rhizome horizontal, 1–2.5 cm. long, somewhat paleaceous, bearing one to several leaves; sterile stalk little differentiated from base of blade, 3–25 cm. long, sometimes not apparent, blade long and strap-shaped, 12–170 cm. long, 1–6 cm. wide, lax and membranous, acutish or obtuse at the apex, sometimes bifurcate above, but never palmately divided; venation reticulate; leaf bearing only a single medianly inserted fertile segment arising from 6–40 cm. above the base of the blade; fertile stalk rather slender, 0.8–10 cm. long; fruiting spike 1.5–12 (–25) cm. long; sporangia 0.8–1.3 mm. in diameter, bearing numerous yellowish spores; gametophyte a free branched tuberous body.

Lang (1902) studied and described the gametophyte of this species, while Petry (1914) made a detailed investigation of the general anatomy of the sporophyte.

Various trivial forms have been described, but these do not seem worthy of nomenclatorial designation. Among such may be mentioned forma *nutans* v. A. v. Rosenburgh, forma *angustata* v. A. v. Rosenburgh, and forma *ramosa* Nakai.

The ssp. *typicum* is widely distributed throughout the Old World tropics where it characteristically grows on trees in open woods or in other places where there is considerable light. It occurs in Madagascar, the Mascarenes, India, Ceylon, Malay Peninsula, Formosa, Philippines, Sumatra, Java, Borneo, the Moluccas, New Guinea, Guam, Caroline Islands, Australia, New Hebrides, Fiji, Samoa, Tahiti, and rarely in the Hawaiian Islands.

Madagascar. Reported by Christensen (1932), but no specimens have been seen by the writer.

Réunion. Reported by Cordemoy (Flore de L'Ile de Réunion. p. 102. 1895), but no specimens have been seen by the writer.

Mauritius *Sieber* 16 (M, NY). *N. Reke* (NY, U).

India. Reported from various provinces by d'Almeida (1922), but no specimens have been seen by the writer.

Ceylon. *W. Ferguson* (G, M); ex herb. Oldfield (NY); *Walker* (G).

Malay Peninsula. Johore; Lungei Tersap, *R. E. Holttum 24911* (U).

Formosa. Kusukusu, *T. Kawakami, Y. Shimada, & T. Ito 82* (NY). *S. Cefe 1348* (NY).

Philippines. Islands of Luzon, Mindanao, and Mindoro.

Sumatra. Toba Lake, *W. N. & C. M. Bangham 1229* (G); also *1159* (G). Badakerlande, *Hinklern 124* (NY).

Java. Mt. Gedé. Aoove Tjibodas, *M. Fleischer* (M).

British North Borneo. Kiau, Mount Kinabalu, *Mary S. Clemens 9993* (NY); also Tenompok, Mount Kinabalu, *J. & M. S. Clemens 24768* (NY, U).

Moluccas. Amboina, *J. B. Steere 2822* (G, M); also *C. B. Robinson 440* (U).

British New Guinea. Mafulu, Central Division, *L. J. Brass 5274, 5325, 5439, & 5550* (NY).

Guam. Santa Rosa, *W. E. Safford & A. Seale 1055* (U).

Caroline Islands. Kusai: Mt. Hinkern, *P. Kanehira 1398* (NY); also Mt. Matante, *P. Kanehira 1445* (NY).

Australia. New South Wales: Coffs Harbor, *J. L. Boorman* (NY, U). Queensland: Moreton Bay, ——— (NY).

New Hebrides. Aneitum Island, Anelgauhat Bay, *S. F. Kajewski 825* (NY). Tanna Island, Lenakel, *S. F. Kajewski 139* (NY).

Fiji Islands. Levuka, *F. C. Prince* (G). *J. Horne 155* (G); *B. Seeman 794* (G); *Capt. Wilkes 6* (NY).

Samoa. *V. Pendulum* (G).

Tahiti. Teahupoo, Toanoano Valley, *M. L. Grant 3875* (NY). Aiurura, Tautira, *B. Leland, E. W. B. Chase, & J. E. Tilden 54* (NY). *W. A. Setchell & H. E. Parks 501* (G).

Hawaiian Islands. Kauai: Kilohana, *W. Wendte* (G).

2b. **Ophioglossum pendulum** ssp. **falcatum** (Presl), n. comb.

Ophioglossum pendulum β fronde falcata, R. K. Greville & W. J. Hooker in

Bot. Misc. **3**: 220. 1833. Based on specimens from the Sandwich (Hawaiian) Islands "with a falcate, more rigid, and apparently more simple frond, as well as a shorter spike."

Ophioderma pendulum β falcatum Presl, Suppl. Tent. Pterid. p. 55, 1845; also in Abh. Böhm. Ges. Wis. 5. **4**: 315. 1845. Based on specimens with the "frond" falcate, shorter, more rigid, and simpler.

Ophioderma falcatum Degener, Flora Hawaiiensis, 1932. Based on specimens from the Hawaiian Islands. The type locality is given as "undoubtedly Oahu." The species is stated also to be found elsewhere in Polynesia. Although the name *falcatum* had been used by Presl as early as 1845, no mention is made by Degener of this previous publication, nor is there, in the original description, any attempt made to indicate how this species may be distinguished from *Ophioglossum pendulum* L.

Ophioglossum pendulum var. (?) Christensen, Index Filicum Suppl. Tent. p. 200. 1934.

Differing from ssp. *typicum* in the falcate, more leathery blade, and in the shorter fertile stalk, which is 0.6–2.5 cm. long.

The subspecies *falcatum* is the dominant form of *Ophioglossum pendulum* in the Hawaiian Islands, although the typical subspecies also does occur there sparingly. The falcate-leaved subspecies is otherwise rare, but widely distributed, in the islands of the East Indies and Polynesia. Numerous forms occur which are intermediate between this and the typical race. In its extreme form in the Hawaiian Islands, the ssp. *falcatum* has all the distinctness of a good species, but the presence of the many intermediates demonstrates that it is merely a phase of the variable *O. pendulum.* Since this population seems to be at present somewhat geographically segregated, with its center in Hawaii, it is here treated as a subspecies.

According to Degener (loc. cit.) this plant grows, in the Hawaiian Islands, among decayed moss on trees or fallen logs at middle elevations.

HAWAIIAN ISLANDS. Kauai: Kilohana, *W. Wendte* (G);———,ex herb. W. H. Dole (NY). Oahu: lower slopes of Konahuanui, above Manoa, *A. A. Heller 2217* (C, G, Ph); Tantalus, *O. Degener 9242* (G). Molokai: ———, *C. N. Forbes 272* (M).

GUAM. *U.S.N.H. 516057* in part (U).

NEW HEBRIDES. Aneitum, *T. Moore 68* (G).

Also, intermediate specimens have been seen from the Philippines, Sumatra, and elsewhere.

3. OPHIOGLOSSUM INTERMEDIUM Hooker

Ophioglossum intermedium Hooker, Icones plantarum. **10**: pl. 995. 1854. Based on specimens collected by Thomas Lobb in Sarawak, Borneo. The illustration accompanying the original description may be assumed to typify the species. The specific name alludes to the intermediate nature of this species between *Euophioglossum* and *O. pendulum.*

The following description is based on two plants studied by the writer. One of these was from British North Borneo and the other from Sumatra. Plant terrestrial, erect, 18–21 cm. high; leaf stalk 9 cm. long; sterile blade membranous, 12 cm. long, 1 cm. wide, linear-oblong, broadest above, obtuse at apex, gradually tapering towards base; fertile segment inserted medianly, arising from upper half of face of blade and surpassing that structure; fertile stalk 3.5–16 cm. long; fruiting spike erect 2–6 cm. long; sporangia 1 mm. in diameter; gametophyte apparently unknown.

Hooker (loc. cit.) states that this species differs from *Ophioglossum pendulum* in the following respects: the frond is not dichotomous; the stipe is narrow; and the peduncle is elongate, equaling the spike. He also says that the plant seems to be an epiphyte and to grow erect.

Campbell (1907) emphasizes the rigidly upright habit of the plant. He adds that the peduncle is longer, while the blade is much smaller and more sharply separated from the petiole than in *O. pendulum*. With J. J. Smith he collected a series of the species near Buitenzorg, Java. The plants were growing in a plantation of bamboo, usually in the accumulation of humus and earth about the roots of the clumps of this woody grass. The rhizomes of these plants were small tuberous bodies, while the spores were somewhat smaller than in *O. pendulum*, with the spore coats delicately reticulate.

Some authors have preferred to consider this species as merely an extreme variant of the *O. pendulum* population, but, to the writer, its characters appear so distinctive that it seems to merit specific rank. As already mentioned, the species clearly represents an intermediate condition between the typically epiphytic, large *O. pendulum* and the small, terrestrial types included in *Euophioglossum*.

O. intermedium occurs in rich woodlands in the Philippines, Sumatra, Java, Borneo, and New Guinea.

Philippines. Mindoro: Mt. Halion, *E. D. Merrill 6039* (U).

Sumatra. *Fr. Nagiri* (NY); ? Fodragiri, near Lalah River, *I. W. Burchard 59* (G).

Java. Reported by Campbell (1907) from near Buitenzorg.

British North Borneo. Kiau, Mount Kinabalu, *M. S. Clemens 10243* (NY).

New Guinea. Reported from Mindoro, but no specimens have been seen by the writer.

4. Ophioglossum simplex Ridley

Ophioglossum simplex Ridley; Bower, in Annals of Botany **18**: 205. pl. 15. 1904. Based on material collected in 1897 by Mr. Ridley in dense wet woods on the Kelantan River, Siak, Sumatra. The illustration accompanying the original description may be assumed to typify the species. The specific name alludes to the simple "reduced" character of the sporophyte.

Since no authentic material of this species has been examined by the writer, the original description has been copied.

"*Ophioglossum simplex*, n. sp. Terrestrial, rhizome short, and tuberous, with few roots. Fertile fronds solitary, or two together, slender flattened, with a blunt apex, 4 to 6 inches long, $\frac{1}{8}$ inch wide, dark green, sterile division represented by a very small lateral process or quite absent. Fertile portion about an inch long.

"Hab.—dense wet woods on the Kelantan River, Siak, eastern Sumatra."

On a basis of the vascular anatomy, Bower (loc. cit.) has demonstrated that this species is related to *Ophioglossum pendulum* and thus properly a member of the subgenus *Ophioderma*, of which it is morphologically the most reduced and simplest member. The plants consist only of a fertile segment. Apparently a sterile blade is never developed, since close anatomical investigation has failed to reveal such a structure.

Ophioglossum simplex seems to be known only from the type locality and collection.

C. Subgenus **Euophioglossum** (Prantl) Clausen, n. stat.

Ophioglossum, section *Euophioglossum* Prantl, in Ber. deutsch. bot. Ges. **1**: 350. 1883.

Euophioglossum includes 21 or more species. These are the familiar terrestrial adder's tongues which are widely distributed over the earth's surface. The subgenus is characterized by the terrestrial habit, the short erect rhizome, the division of the leaf into a fertile and a sterile segment, the small size of the plants, and the simple undivided sterile segment.

Of all the *Ophioglossaceae*, this is by far the most difficult division to treat taxonomically. Many authors have struggled with it, but none seems to have succeeded in settling the numerous puzzling problems that exist. The present treatment represents yet another effort to interpret what sometimes appears to be an almost continuous series of forms without any clear cut specific lines or breaks in the continuity between the various populations.

The last serious attempt critically to interpret the *Ophioglossum* flora of the world was made by Prantl, who published the results of his studies in 1884. In that treatment, much emphasis was placed upon characters afforded by the venation and also on the size and markings of the spores. Twenty-six species of *Euophioglossum* were recognized, of which several were described as new.

At an early stage in the present study, the writer discovered that venation in *Ophioglossum* is not always reliable for species differentiation, and that variation of this character within a particular species population may be tremendous. Only in a relative manner may venation be considered useful for purposes of classification. The division of *Euophioglossum* by Prantl into two subsections, *Paraneura* and *Ptiloneura*, on characters of venation, had to be abandoned by the writer, as by Christensen (Hultén, 1928) because, in certain species, some individuals properly belong to the

Paraneura, while others definitely belong to the *Ptiloneura*. Obviously, in consideration of such a condition, these two subsections can not now be maintained.

The writer has also found spore characters to be quite unsatisfactory in this group. Not only is the range of variation in size very great, but the markings are not sufficiently different and distinctive to be of much use for identification purposes. With such an array of material as has been examined in this study, no such clear-cut spore characters have been apparent as Prantl found and described in his paper.

Absolute shape of the sterile blade, height of insertion of that structure, and size of the plant have also proved entirely unreliable. In short, almost, every character previously employed in the classification of the small species of *Ophioglossum* seems to be unsatisfactory for systematic purposes. Such a situation in a group of simple structure is not surprising, but must be treated by the taxonomist in a way that is both practical and comparable with the treatment of other similar groups.

Various amateurs and others who have not given critical study to *Ophioglossum* from a world viewpoint, have been ready to describe new species on minor variations in venation and size, but such workers are dealing with and describing not species populations, but single specimens or small groups of individuals. The extreme variability of the plants has caused even many seasoned taxonomists to describe, as new, forms which never should have received nomenclatorial recognition. For these reasons, the number of described species has now become very large.

In the present treatment the writer has found it necessary to reject a large number of previously accepted species. All too often these have been based on single collections, while the descriptions have frequently been scant, since it has apparently not been realized that it is the duty of a student who describes a new species to tell how that species differs from other related forms and what are its nearest relatives. The literature of *Ophioglossum* abounds in isolated unrelated descriptions of new species which would never have been published if the authors had conscientiously fulfilled their duties in the above respect. The same species have been described again and again, thus increasing the synonymy.

For characters in *Euophioglossum*, the writer has tried to employ a combination of all the morphological evidence that is available, realizing that no one single structure here affords a key or solution to the classification and trying, so far as possible, to interpret the forms in what is hoped may be considered a reasonable, common-sense manner.

ARTIFICIAL KEY TO THE SPECIES OF EUOPHIOGLOSSUM

A. Leaves consisting only of a single fertile segment; a sterile segment apparently never produced. 26. *O. lineare*

A. Fertile leaves always bearing a sterile segment; sterile leaves also frequently produced, but never fertile leaves without blades. B

B. Rootstock definitely and conspicuously globose-bulbous. C

C. Fertile segment equaling or slightly shorter than the sterile in length. 21. *O. opacum*

C. Fertile segment usually far surpassing the sterile. 22. *O. crotalophoroides*

B. Rootstocks cylindrical, subglobose, or tuberous, but never globose-bulbous. D

D. Principal veins characteristically forming large primary areoles in which are included numerous veinlets forming secondary areoles. E

E. Rhizome cylindrical; blade not with a pale median band. 13. *O. Engelmanni*

E. Rhizome subglobose or tuberous; blade usually with a prominent pale median band. F

F. Rhizome elongate-tuberous; plants of the Old World. 14. *O. pedunculosum*

F. Rhizome short, subglobose; plants of South America. 15. *O. ellipticum*

D. Principal veins forming areoles not enclosing smaller secondary areoles, but occasionally with included free veinlets. G

G. Blade linear, linear-lanceolate, or rarely lanceolate. H

H. Blade narrowly elongate, linear, 1–3 mm. wide, with only 2 or 3 parallel veins. 25. *O. gramineum*

H. Blade linear-lanceolate or lanceolate, 3–6 mm. wide, with several parallel veins. I (see third I).

I. Veins usually few; principal parallel veins 3–7; plants of somewhat fleshy texture; common stalk 0.5–3.5 cm. long. 24. *O. lusitanicum*

I. Veins very numerous; principal parallel veins 5–15; plants of membranous texture; common stalk 2.5–5 cm. long. 23. *O. lancifolium*

I. Veins numerous, reticulate; plants of rather membranous texture; common stalk 2.5–6 (–13.5) cm. long. 7. *O. angustatum*

G. Blade elliptical, ovate-lanceolate, cordate, oblong, or even suborbicular, rarely linear, or linear-lanceolate. J

J. Rootstock usually subglobose; blade 4–35 mm. long, ovate, oblong-ovate, suborbicular, or elliptical, inserted towards base of plant. K

K. Sterile blade sessile or rarely stalked; fertile and sterile stalk, as well as most of the common-stalk, regularly epigaean. L

L. Blade ovate, suborbicular, or elliptical, acute at apex or, if blunt, then minutely apiculate. 16. *O. nudicaule*

L. Blade obovate or suborbicular, with rounded apex. 17. *O. rubellum*

K. Sterile blade conspicuously stalked; common stalk, sterile stalk, and most or base of fertile stalk hypogean. M

M. Sterile blade rarely overtopped by fertile spike; most of fertile stalk hypogean. 18. *O. fernandezianum*

M. Sterile blade considerably surpassed by the fertile segment; only base of fertile stalk hypogean. 19. *O. scariosum*

J. Rootstock cylindrical; blade large or small, of various shapes, usually inserted towards middle of plant. N

N. Fertile segment flattened, up to 1.8 mm. wide between the two lateral rows of sporangia, which are only 0.25 mm. in diameter. 20. *O. Schlechteri*

N. Fertile segment not conspicuously flattened and usually less than 1.5 mm. wide between the 2 lateral rows of sporangia, which are rather large, 0.6–1.0 mm. in diameter. O

O. Rhizome with persistent brown sheaths formed by the bases of the old leaf stalks. 12. *O. Aitchisonii*

O. Rhizome without persistent brown sheaths. P

P. Blade elliptical or lanceolate, rarely ovate or suborbicular. Q

Q. Blade narrowly lanceolate, oblong-lanceolate, or elliptical; plant very slender; usually with 4–8 parallel veins passing down through the base of the blade. 7. *O. angustatum*

Q. Blade elliptical or oblong-elliptical, rarely ovate; usually with 8–20 parallel veins passing down through the base of the blade. R

R. Fertile segment far surpassing the sterile. 5. *O. vulgatum*

R. Fertile segment equaling or slightly exceeding the sterile. 6. *O. sarcophyllum*

P. Blade ovate, deltoid, or cordate; usually with only 4–8 parallel veins passing down through the base of the blade. S

S. Blade cordate at the base; veins usually numerous. 8. *O. reticulatum*

S. Blade truncate or contracted at the base. T

T. Blade acute or cuneate at base; plant usually rather coriaceous. 11. *O. concinnum*

T. Blade truncate or obtuse at base; plant usually more lax. U

U. Blade rather short ovate; veins numerous, forming small areoles. 9. *O. Harrisii*

U. Blade lance-ovate; veins not numerous, forming large areoles. 10. *O. petiolatum*

5. OPHIOGLOSSUM VULGATUM L. *Figure 23.*

Ophioglossum vulgatum L., Sp. pl. **2**: 1062. 1753. Based on European material. Type in the Linnaean Herbarium.

Ophioglossum unifolium Gilibert, Exercitia phytologica **2**: 544. 1790.

Ophioglossum ovatum Salisbury, Prodromus stirpium in horto ad Chapel Allerton vigentium. p. 401. 1796 (nomen); "Opiz, Kratos. **14**: 12. 1819."

Ophioglossum polyphyllum A. Braun, in Seubert, Flora Azorica. p. 17. 1844. Based on material from the Azores. Said to differ from *O. vulgatum* in its smaller size and in having several fronds produced in a single year, but these characters are scarcely of specific importance.

Ophioglossum azoricum Presl, Suppl. Tent. Pterid. p. 49. 1845. Also based on material from the Azores.

?*Ophioglossum lanceolatum* Watelet, in Bull. Soc. Fr. **5**: 16. 1858. Based on specimens collected in the vicinity of Laon in northeastern France. May represent either a form of *O. vulgatum*, as suggested by Christensen, or of *O. lusitanicum*. Described as differing from *O. vulgatum* in the cespitose habit, the presence of brownish scales about the base of the plant, the narrow oval blade, and the very short slender fertile segment. The writer has not seen the type collection.

"*Ophioglossum sabulicolum* Sauze & Maillard, Fl. des Deux-Sèvres. p. 451. 1880."

Ophioglossum arenarium E. G. Britton, in Bull. Torrey Club **24**: 555. pl. 318 & 319, f. 3. 1897. Based on specimens collected at Holly Beach, N. J., July 3, 1897, by J. Crawford and C. L. Pollard. This seems to be a purely ecological variation. Since plants of typical *O. arenarium* are not unlike slender or depauperate individuals which occasionally occur farther north in otherwise normal colonies of *O. vulgatum*, this minor strain does not seem worthy of nomenclatorial distinction.

Ophioglossum alaskanum E. G. Britton, in Bull. Torrey Club **24**: 556. 1897. Based on specimens collected on Unalaska Island in 1878, by L. M. Turner. It was based on a supposed distinctive difference in venation. The

Alaskan plants are less lax than most forms from the eastern United States, while the venation is coarser, with the areoles larger and with only three to five parallel veins passing down into the petiolate base of the blade. Since, however, occasional plants from the eastern United States, eastern Canada, and Scandinavia exactly match this Alaskan material, *O. alaskanum* does not seem worthy even of varietal rank. All of its supposedly distinctive characters fail upon close inspection and can be duplicated in *O. vulgatum* from elsewhere.

Ophioglossum microstichum Acharius, in Vet. Acad. Nya Handl. **30**: 64. pl. 3A. 1899.

Ophioglossum vulgatum f. *alaskanum* (E. G. Britton) Gilbert, List N. Am. Pterid. p. 12. 1901.

Ophioglossum vulgatum f. *arenarium* (E. G. Britton) Clute, Our ferns in their haunts. p. 316. 1901.

Ophioglossum thermale Komarov, in Fedde Repert. **13**: 85. 1914. Based on specimens collected in the vicinity of warm springs in the crater of the volcano Uzon in Kamtchatka. Christensen, in Index Filicum, Suppl. 3, p. 134, considers this to be a synonym of *O. vulgatum*. The writer has not seen any authentic specimens.

Ophioglossum nipponicum Miyabe & Kudo, in Trans. Sapporo Nat. Hist. Soc. **6**: 122. 1916. Based on specimens from the island of Hokkaido, Japan. Although this was supposed to represent simply a renaming of *O. japonicum* Prantl, Christensen and Nakai have both indicated that it is not synonymous with that species, but rather with *O. vulgatum*. The writer has not seen the collections cited by Miyabe & Kudo.

Ophioglossum vulgatum var. *alaskanum* (E. Britt.) C. Chr., in Kungl. Sv. Vet. Akad. Handl. **5** (1): 45. 1928.

Ophioglossum vulgatum var. *thermale* (Komarov) C. Chr., in Kungl. Sv. Vet. Akad. Handl. **5** (1): 45. 1928. From the data presented, this might be interpreted as an ecological variant.

Perennial herb, 7–36 cm. high, with short erect cylindrical rootstock bearing numerous stout fleshy roots and one or several leaves; bud regularly exposed, not enclosed in the base of the leaf of the season; common stalk 1.5–19 cm. long; blade 1–10 cm. long, 0.8–4 cm. broad, oblong-elliptical, elliptical, oblanceolate, suborbicular or even ovate, usually blunt at apex, sessile or sometimes with a distinct haft*; venation various, usually with 4–18 parallel veins passing up through the base of the blade and often continuing almost to the apex with few connecting veinlets, but with the veins between these and the margin of the blade numerous and freely anastomosing, thus forming many small areoles; fertile stalk 3–17 cm. long; fertile spike 1–4 cm. long; sporangia 0.6–1.2 mm. in diameter; spores yellowish, numerous, variously sculptured. Gametophyte slender and elongate, rarely branching.

Various trivial forms and varieties, based largely upon size of plant and shape of sterile blade, have been described, but since these seem to represent normal variations of any local population of this species, they are not considered in this discussion.

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* haft = stalk or foot of the sterile blade in *Ophioglossum*.

Ophioglossum vulgatum occurs in a variety of habitats: in moist meadows, shady fields, grassy thickets, moist woods, rich swamplands, and occasionally on sandy beaches. The species is widely distributed throughout North America, Europe, and Asia. In North America it ranges from Prince Edward Island, southern Nova Scotia, and New Brunswick west to northern Michigan, Minnesota, and Nebraska, and south to North Carolina, northern Florida, Mississippi, Louisiana, and Texas. It also occurs in southern Arizona, northwestern Montana, Washington, on the island of Unalaska, and in the mountains of central Mexico. The Mexican specimens are from the states of Hidalgo and Puebla. These have been distributed as *O. Pringlei* Underwood, but the writer has been unable to distinguish this from typical *O. vulgatum* from the northeastern United States and elsewhere. In the Old World *O. vulgatum* occurs in Iceland, the British Isles, the Azores, Madeira, and on the European continent from Scandinavia south to Portugal, southern France, Italy, Austria, Hungary, and Roumania, and east to Finland and central Russia. It is also known from Syria, Persia, the mountains of northern India, Kamtchatka, and Japan.

PRINCE EDWARD ISLAND. Queens: Brackley Point, *J. Macoun* (G, NY, Ot).

NOVA SCOTIA. Digby and Yarmouth Counties.

NEW BRUNSWICK. Charlotte: Grand Manan, *C. A. & U. F. Weatherby 5617* (G, Ot, U).

QUEBEC. Deux-Montagnes, Gatineau, Shefford, Stanstead, and Terrebonne Counties.

ONTARIO. Carleton, Durham, Hastings, Lambton, Nipissing, Norfolk, and Northumberland Counties.

ALASKA. Unalaska Island, *L. M. Turner* (G, M, NY, Ph, U).

MAINE. All counties except Aroostook, Knox, and Waldo.

NEW HAMPSHIRE. All counties except Grand Isle, Orange, and Orleans.

MASSACHUSETTS. All counties.

RHODE ISLAND. Providence: Grotto, ex herb. G. Thurber (G).

CONNECTICUT. Fairfield, Hartford, Litchfield, New London, and Windham Counties.

NEW YORK. Bronx, Cayuga, Chautauqua, Dutchess, Essex, Genesee, Herkimer, Jefferson, Lewis, Madison, Nassau, Oneida, Onondaga, Oswego, Otsego, Rensselaer, St. Lawrence, Saratoga, Schuyler, Seneca, Suffolk, Sullivan, Tioga, Tompkins, Washington, Wayne, and Westchester Counties.

NEW JERSEY. Atlantic, Bergen, Burlington, Camden, Cape May, Essex, Gloucester, Morris, Ocean, Passaic, Salem, Somerset, Sussex, Union, and Warren Counties.

PENNSYLVANIA. Berks, Bradford, Bucks, Chester, Dauphin, Delaware, Erie, Franklin, Juniata, Lancaster, Lebanon, Lehigh, Luzerne, Mifflin, Monroe, Montgomery, Northampton, Perry, Susquehanna, Tioga, Warren, Wayne, Westmoreland, and York Counties.

DELAWARE. New Castle: Centerville, *A. Commons* (M, Ph, U).

MARYLAND. Carroll, Cecil, Prince Georges, and St. Mary's Counties.

DISTRICT OF COLUMBIA. Washington, *L. F. Ward* (Ph).

VIRGINIA. Albemarle, Amelia, Highland, and James City Counties.

KENTUCKY. Muhlenberg and Warren Counties.

TENNESSEE. Reported from Haywood Co. by W. A. Anderson, Jr. (Amer. Fern. Journ. **21**: 67. 1931). No specimens have been seen by the writer.

NORTH CAROLINA. Bertie, Buncombe, Durham, and Halifax Counties.

FLORIDA. Apparently collected somewhere in northern Florida be Le Conte. A photograph of a drawing of this specimen has been distributed to various herbaria by Dr. J. K. Small.

MISSISSIPPI. Marion: Columbia, *E. T. Wherry* (U).

LOUISIANA. Natchitoches: Natchitoches, *E. J. Palmer 9417* (M); also *7482* (Ph).

OHIO. Ashtabula, Clermont, Cuyahoga, Hamilton, Lake, Mahoning, Portage, and Ross Counties.

INDIANA. Clark, Daviess, Dearborn, Jackson, Jefferson, Knox, Lake, Lawrence, Monroe, Owen, Perry, Porter, St. Joseph, Scott, Spencer, Warrick, and Washington Counties.

ILLINOIS. Jackson: Carbondale, *E. J. Palmer 14961* (M).

MICHIGAN. Cheboygan, Delta, Keweenaw, and Saint Clair Counties.

MINNESOTA. Washington: Echo Lake, *H. L. Lyon* (G).

MISSOURI. Bollinger, Butler, St. Louis, and Stoddard Counties.

ARKANSAS. Arkansas and Hempstead Counties.

NEBRASKA. Cherry: Kennedy, *J. M. Bates 5679* (NY).

KANSAS. Crawford: Pittsburgh, *F. A. Riedel* (NY).

MONTANA. Yellow Bay, Flathead Lake, *Gertrude Norton 995* (U).

TEXAS. Harrison, Smith, and Upshur Counties; also reported from Denton and Harris Counties.

ARIZONA. Cochise: Huachuca Mts., *Lemmon* (G).

WASHINGTON. Mason and Skamania Counties.

MEXICO. States of Hidalgo and Puebla.

ICELAND. Reykjahlid, *E. Taylor* (C). Although the material from Iceland has been referred to the var. *polyphyllum* because of the smaller size of the plants and the presence during a single season of several leaves on a rootstock, the writer has not considered this sufficiently distinct to warrant nomenclatorial distinction.

IRELAND. County Derry: Kilrea, *M. J. Leebody* (G).

SCOTLAND. Kincardineshire: Den Fenellay, *Mr. Roy* (G). Cheshire, *W. Wilson* (Ph).

ENGLAND. Counties of Cambridge, Derby, Hereford, Leicester, and York.

NORWAY. Stapenden, *O. Nykiins* (G). Christiana, ——— (G).

SWEDEN. Läns of Oelandia and Södermanland.

FRANCE. Departments of Alpes Maritimes, Bas Rhin, Indre, Haute-Savoie, Seine et Oise, and Vosges.

BELGIUM. Liege: Ensival, *M. Mairlot* (G). ——— (U).

SPAIN. Reported by Prantl (1884), but no specimens have been seen by the writer.

PORTUGAL. ———, *W. D. Brackenridge* (Ph).

AZORES. ———, *Watson* (NY).

MADEIRA. ———, *G. Mandon* (NY). ———, *A. Fényes* (NY).

ITALY. Venezia: Treviso, *C. Spegazzini* (NY); Venice, *R. Pampanini 207* (G); Verona, *Rigo* (G).

SWITZERLAND. Branson, *Fr. Castella* (U).

GERMANY. Provinces of Bavaria, Brandenburg, and Saxony; also the East Frisian Islands.

DENMARK. ———, *H. Mortensen* (M). Sjoll, Alindelille.

AUSTRIA. Lower Austria: Wien, *J. Dorfler* (G).

CZECHOSLOVAKIA. Eastern Moravia, *G. Rican 702* (U). Mittelgel: Milleschan, *R. Suissbach* (G).

HUNGARY. Fadd, *Haynald 1505* (G, M, U).

ROUMANIA. Bucovina, Cernauti, *E. Topa 1001* (M, U).

POLAND. Zakopane and Stryj.

FINLAND. Nylandia, Ekenäs, Island of Langholmen, *Inga Ström 411* (M, Ot).

RUSSIA. ———, *Pycanab* (Ph).

SYRIA. Zebdaine, near Damascus, *T. Kotschy 89* (G).

PERSIA. Azerbaijan: Aldshi Talysh, *N. Pastuchov 403* (NY).

INDIA. Provinces of Bengal, Kashmir, Northwest Frontier, and Punjab.

JAPAN. Musashi: Todahara, *K. Watanabe* (G, U), not typical. Also reported from Sapporo, island of Hokkaido, by Miyabe and Kudo (Trans. Sapporo Nat. Hist. Soc. **6**: 122. 1916).

KAMTCHATKA. Reported and described from the crater of the volcano Uzon by Komarov (Fedde Repert. **13**: 85. 1914) as *O. thermale;* also reported from South, Central, and East Kamtchatka by Christensen and Hultén (1928).

Since preparing the above list of citations, the writer has had opportunity to examine, on loan from the British Museum, very typical, large specimens of *O. vulgatum* from São Tomé, off the west coast of Africa, *A. W. Exell 307;* also additional small specimens, representing *O. polyphyllum* A. Braun, from Madeira.

6. OPHIOGLOSSUM SARCOPHYLLUM* Desvaux

> *Ophioglossum ovatum* Bory de Saint Vincent, Voyage dans les quatre principales îles des mers d'Afrique. **2**: 206. 1804. Based on specimens from the island of Réunion in the Indian Ocean. The type collection is in the De Candollean Herbarium at Geneva, Switzerland. A photograph of the type is at hand and is now filed in the herbarium at the Bailey Hortorium. Although the original description, "*O.* (ovatum) *fronde ovata, acuta, nervuris laxis,*" indicates a plant similar to *O. petiolatum*, the type specimen clearly represents a somewhat different species that is also fairly frequent in

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* Through the kindness of Mr. C. A. Weatherby of the Gray Herbarium, the writer has recently had opportunity to study photographs of the type sheet and another authentic collection of *O. sarcophyllum* Desvaux from the herbarium of the Paris Museum. These clearly indicate that the species of Desvaux and *O. ovatum* Bory are identical, and, since Bory's name is invalidated by the earlier homonym, *O. ovatum* Salisbury, 1796, *O. sarcophyllum* Desv. should now be employed as the proper designation for this population.

southeastern Africa and in various of the islands of the Indian Ocean. This species seems very closely related to *O. vulgatum*, but differs particularly in the shorter fertile segment. The specific name alludes to the sometimes ovate sterile blade.

Ophioglossum sarcophyllum Desvaux, in Mém. Soc. Linn. Paris. **6**: 193. 1827. Based on material from the Mascarene Islands. The blade is described as ovate, acute, laxly reticulated, and subfleshy. The specific name alludes to the fleshy nature of the blade. This is identical with *O. ovatum* Bory, so far as can be determined from the description.

Perennial herb, 9–14 cm. high, with erect cylindrical rootstock and usually numerous reddish roots; common stalk 3.5–7 cm. long; blade sessile, subfleshy, ovate, or elliptical, tapering at both ends, obtuse or subacute at apex, weakly mucronate (tipped), 3–7.5 cm. long, 1–4.5 cm. wide; venation either lax or rather fine, often difficult to determine because of the fleshy nature of the lamina; fertile stalk 4–6 cm. long; fruiting spike 1.5–3 cm. long; sporangia closely crowded, 0.6–0.8 mm. in diameter. Gametophyte unknown.

This species differs from *O. vulgatum* in the shorter fertile segment, the usually more lax venation, and the reddish nature of the plants. Christensen (1932) states that, from the other species of *Ophioglossum* found in Madagascar, this differs "by the sterile blade being broadest at the middle, elliptic, 5–6 cm. long, 2 cm. wide, and by the rather short (4–6 cm.) peduncle."

On a specimen in the herbarium at the Missouri Botanical Garden is the following information, sent in a letter by the Rev. J. Buchanan, who studied the species in the field in Natal, "Our plant supposed to be *Oph. vulgatum* does not seem to me to be such at all. I would sooner take our *O. reticulatum* to be *O. vulgatum*, for it is a very variable plant and often very like *O. vulgatum*. Our supposed *O. vulgatum* is a slender growing plant, pretty uniform in character and affects only very light sandy soil near the coast, tapers at both ends and is always more or less tinged with an orange red color. This color is very marked in the stipes near the ground, but it seems to pervade the plant, giving a very peculiar greenish to the lamina, almost as if it were blighted."

Some authors have identified the African material of this species as *O. capense* Schlecht., but the venation is entirely different in that species, with the primary veins forming numerous areoles in which are included fine networks of secondary veinlets forming secondary areoles.

As here considered, *O. sarcophyllum* is a plant of the Mascarenes, Madagascar southeastern Africa, and perhaps Ceylon. Little is known of its habitat preferences, although it has been found variously on moist rocks, on palm and Caffre plains, and in sand near the coast.

NATAL. *J. Buchanan* (M, Princ, U).

MADAGASCAR. Reported by Christensen (1932) from Tanala, Nossi Bé, Ambovombe, and Fort Dauphin. No specimens have been seen by the writer.

MAURITIUS. Reported by Prantl (1884).

RÉUNION. The type collection is from moist rocks at the foot of Piton de Crac. Cordemoy (Flora of the Island of Réunion. p. 101. 1895) reports the species as rather common on the palm and Caffre plains of Réunion.

CEYLON. "About Newera Ellia plains, in the open," *G. Wall* (NY). This is doubtfully *O. sarcophyllum*.

7. OPHIOGLOSSUM ANGUSTATUM Maxon

Ophioglossum vulgatum Franchet & Savatier (non L.), Enum. Pl. Jap. **2**: 252. 1879. Based on material from the base of Mt. Fujiyama. The writer has not seen these specimens, but Nakai (1925) refers them to his *O. nipponicum* which is the same as *O. angustatum*.

Ophioglossum japonicum Prantl (non Thunberg, 1784, which is *Lygodium japonicum*), in Ber. Deutsch. Bot. Ges. **1**: 353. 1883. Based on specimens from Japan. Type in the herbarium at Berlin, not seen by the writer.

Ophioglossum nudicaule Christ (non L. f.), in Bull. Herb. Boiss. **4**: 675. 1896. Based on the collection of Père Urbain Faurie 4294, from the dunes of Sendai. Specimens of this collection have been studied by the writer and are clearly *O. angustatum*.

Ophioglossum angustatum Maxon, in Proc. Biol. Soc. Wash. **36**: 169. 1923. This is a renaming of *O. japonicum* Prantl which is untenable because of the earlier homonym of Thunberg. *O. angustatum* is founded on two collections from Japan and also on material from central China. The new specific name alludes to the narrow sterile blade.

Ophioglossum bucharicum, O. A. & B. A. Fedtschenko, in Not. Syst. Herb. Hort. Bot. Petrop. **4**: 8. 1923. No specimens of this have been seen by the writer, but the original description strongly suggests *O. angustatum* and Christensen considers it a synonym of that in Index Filicum, Suppl. 3, p. 133, 1934.

Ophioglossum nipponicum Nakai (non Miyabe & Kudo, 1916, which is *O. vulgatum* L.), in Bot. Mag. Tokyo **39**: 193. 1925. This represents another renaming of *O. japonicum* Prantl, but the name *nipponicum* is superseded both by *O. angustatum* Maxon and by the slightly earlier homonym of Miyabe and Kudo, which is *O. vulgatum* L.

Ophioglossum Savatieri Nakai, in Bot. Mag. Tokyo **40**: 374. 1926. This is a renaming of *O. nipponicum* Nakai because of the earlier homonym of Miyabe and Kudo, but this name is also untenable because of the earlier *O. angustatum* of Maxon. The specific name honors the botanist Savatier who was among the first to collect this species in Japan.

Plant slender, 10–25 cm. high; rhizome cylindrical, erect; common stalk 2.5–6 (–13.5) cm. long; blade seemingly inserted at or just below the middle of the plant, lanceolate, oblong or even linear-lanceolate, acute, or obtuse and mucronate at the apex, 1.4–4.5 (–8) cm. long, 3–10 mm. wide, margin entire or slightly crenulate; venation loosely reticulate with the midvein usually disappearing towards the apex, but in its lower half emitting a few lateral veins; fertile stalk 3.5–14 cm. long; fruiting spike 1–3.5 cm. long; sporangia 0.6–1.0 mm. in diameter. Gametophyte unknown.

Despite its complicated nomenclatorial history, authors have seemed generally in agreement concerning the distinctness of this species. The narrow lanceolate sterile blade at once distinguishes it from most of its near allies. It is true that certain slender forms of *O. vulgatum*, particularly some of those which have been referred to the *O. arenarium* of Mrs. Britton, somewhat approach this species, but in these the blade is never so narrow as in *O. angustatum*, nor is the venation so loosely reticulate. Otherwise, the only other species which approach this are *O. gramineum* and *O. lancifolium*, in which the blade is elongate-linear, or linear-lanceolate, and *O. lusitanicum*, which differs markedly in its much smaller size and in the more fleshy texture.

The species is apparently partial to sandy soils, in which it is frequently found near the coast. It is widely distributed throughout the Japanese Islands and also is found in eastern central China and India. Questionable material has been seen from the Philippine Islands.

CHINA. Anhwei: Chuchow, *A. N. Steward 2324* (M, U); also *E. D. Merrill 11225* (NY). Kiangsu: Peitaiho, *N. H. Cowdry* (NY, U).

JAPAN. Honshu: Tokyo, ——— 529 (U), also *K. Miyake* (C); Prov. Ugo, *J. Matsumuru* (NY); Prov. Mimasaka, Mt. Nagi, *S. Arimoto* (G, M); Sendai, *Père Urbain Faurie 4294* (M). Loo Choo Islands, *C. Wright* (G, U). Also reported from Shikoku and Bonin Islands by Nakai (1926).

INDIA. Shurtleff Herb. (U).

8. OPHIOGLOSSUM RETICULATUM L. *Figure 24.*

Ophioglossum reticulatum L., Sp. pl. **2**: 1063. 1763. Based on material from Middle America. Described as an *Ophioglossum* with cordate base. Type in the Linnaean Herbarium, not seen by the writer. The specific name alludes to the prominently reticulated venation.

Ophioglossum peruvianum Presl, Suppl. Tent. Pterid. p. 52. 1845. Based on material from Peru. No specimens have been seen by the writer, but authors seem generally agreed that this is simply a form of *O. reticulatum*.

Perennial herb, 5–39 cm. high, with short erect rootstock bearing during a season one or rarely several leaves; common stalk 3–16 cm. long; blade either sessile or with a short haft to 10 mm. long; blade usually rather membranous, cordate, broadly ovate, ovate-orbicular, or even subreniform, either cordate or very broad-truncate at base, obtuse, rounded or sometimes acutish at apex, 1.5–9 cm. long, 1.2–5 cm. wide; venation lax and diffuse, veins forming areoles 0.5–15 mm. long and 0.5–3 mm. wide; fertile stalk 5–18 cm. long; fruiting spike 1–5.5 cm. long; sporangia 0.5–1.0 mm. in diameter; spores 30–40μ in diameter. Gametophyte apparently unknown.

In its typical condition, *O. reticulatum* is readily distinguished from related species by the rather broad, thin cordate sterile blade, but forms also occur in which the blade is simply truncate at the base. These last are

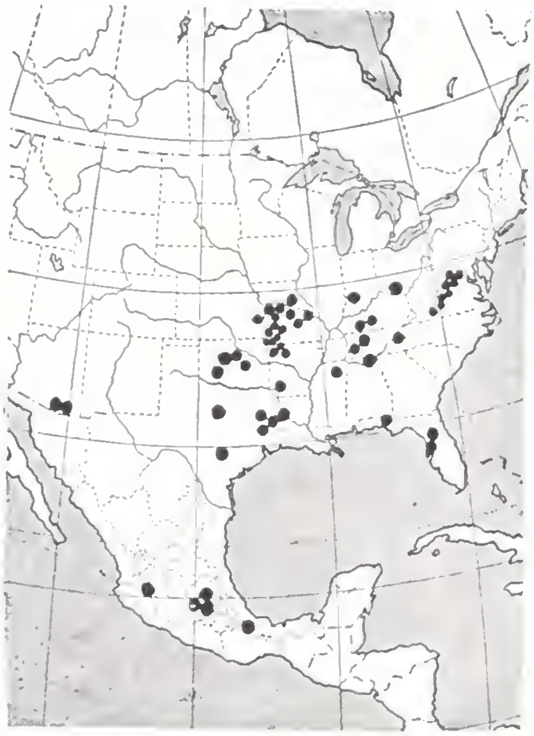

Fig. 24 (above). *Ophioglossum reticulatum.*
Fig. 25 (lower left). *Ophioglossum Engelmanni.*
Fig. 26 (lower right). *Ophioglossum crotalophoroides.*

sometimes difficult to distinguish from specimens of *O. petiolatum*, although in that species the blade is characteristically lance-ovate, not broadly ovate, the apex of the lamina is almost always acute, not obtuse or rounded, and the areoles are usually larger since the veins are less numerous. That *O. reticulatum*, *O. Harrisii*, and *O. petiolatum* may all represent forms of the same species is quite likely, but until more field investigations have been made to determine the actual relationship of these types, it seems desirable to maintain them as distinct, particularly since most specimens or local populations are quite readily placed in the one or the other of these three categories.

D'Almeida (1922) has considered *O. vulgatum* and *O. reticulatum* to be forms of the same species, these being connected by a number of transitional stages, but the writer has been unable to reach this conclusion. *O. vulgatum* is a species of the north temperate zone, with a range overlapping that of the tropical *O. reticulatum* only slightly, if at all. Although it is true that occasional individuals are found in either species population that somewhat approach the other, yet *bona fide* intermediates seem not to exist, or at least to be very rare. The great majority of specimens of either species are quite distinct, differing widely from each other in the shape of the blade, the venation, the position of the lamina, and somewhat in texture. To summarize, *O. reticulatum* may usually be distinguished from *O. vulgatum* by the broad cordate blade, the thinner texture, and the larger size.

As here considered, *O. reticulatum* itself varies widely in size, shape of lamina, and venation, but since these variations seem not to be correlated with range and are entirely of a trivial sort, they seem unworthy of varietal designation.

Litardiere (1921), in his paper on cytological studies in the ferns, lists the diploid chromosome number for this species as between 200 and 240 (i.e., between 100 and 120×2).

O. reticulatum grows in a variety of habitats, displaying a wide range of tolerance for different environmental conditions. In a survey of data secured from herbarium labels, the following diverse habitats were indicated: swampy woods, shaded banks, moist grassy slopes, clearings, moist grassy places under shrubs, dry sandy soil, dry open places and even steep cultivated slopes. The species is pantropical, being found in tropical regions in both the Old and New World, at altitudes from 60 to 4000 feet. It also occurs inexplicably at several places in temperate regions in the Old World. This temperate zone material requires further study and may perhaps represent an undescribed species. The detailed range includes central and southern Mexico, Central America, the islands of the West

Indies, northern and central South America from Colombia to Peru, Bolivia, and southern Brazil; the island of Madeira, the Cape Verde Islands, Liberia, Cameroons, Nyassaland, Natal, Mauritius, India, Ceylon, China, the island of Luzon in the Philippines, and doubtfully Corea and Japan. The species has also been reported from Samoa, the Caroline Islands, and Madagascar, but no material from these places has been seen by the writer.

In the following list, collections tending towards *O. petiolatum* are prefixed by a question mark.

West Indies. Islands of Cuba, Grenada, Guadeloupe, Hispaniola, Jamaica, Martinique, Porto Rico, and St. Thomas.

Mexico. States of Jalisco, Mexico, San Luis Potosi, and Vera Cruz.

Central America. Costa Rica, Guatemala, Honduras, and Panama.

South America. Colombia, Venezuela, British Guiana, Dutch Guiana, Brazil, Peru, and Bolivia, also, *fide* Mr. C. A. Weatherby, northern Argentina.

Isle of Pascua. La Peiruse Bay, *C. & I. Skottsberg 638* (NY, U).

Galapagos Islands. Through the kindness of Mr. C. A. Weatherby, the writer has had opportunity to study specimens collected by *J. T. Howell, no. 9001*, on Villamil Mt. above Santo Tomas, Albemarle Island.

Madeira. U. S. So. Pacific Explor. Exped. under Capt. Wilkes, *no. 2* (U).

Cape Verde Islands. ———, *L. Nicolao* (NY).

Liberia. ? ———, *O. F. Cook 405* (U).

Cameroons. Bipinde, *G. Zenker 1939* (M); also *4606* (M); this material not typical.

Nyassaland. Kyimbila, *A. Stolz 1812* (M); also *1901* (M).

Natal. *J. Buchanan 1590* (M); also *498* (U). Basutoland: Berea, *J. M. Wood 8331* (U).

Réunion. Reported by E. J. de Cordemoy (in Flora of Réunion, p. 101, 1895) from the meadows by the river Saint-Denis.

Mauritius. ———, *W. Arnott* (NY).

India. Assam: ? Khasi Hills, *G. Mann* in part (M, NY). Darjiling: ? Observatory Hill, *G. C. Levinge* (NY). Kashmir: ? Dehra Dun District, Jamsar-Kathian, *J. S. Gamble 25510* (NY). Madras: Palni Hills, *C. L. Noyes* (G), Nilgiris District, *J. S. Gamble 18008* (NY).

Ceylon. ———, *W. Ferguson 221* (M).

Philippines. Island of Luzon: Provinces of Bataan, Batangas, Benguet, and Ilocos Norte.

China. Hupeh: ......, *A. Henry 5953* in part (G).

Corea. ? Alnelpacrt, Hatisan, *Tagnet 2470* (NY).

Japan. Reported by Nakai (1926) from Hondo, Formosa, and Bonin.

9. Ophioglossum Harrisii Underwood

Ophioglossum Harrisii Underwood, in North American Flora **16**: 11. 1909. Based on material from Jamaica. Type in the herbarium of the New York Botanical Garden, collected near Cinchona, at 1600 meters, Jan. 30, 1903, *L. M. Underwood 169.* Named in honor of W. Harris, who several times collected the species in Jamaica.

Ophioglossum Ekmani C. Chr., in Kungl. Sv. Vet. Akad. Handl., Ser. 3, **16** (2): 89. 1936. Based on the collection of *E. L. Ekman, no. 6852*, from H. Selle: Gr. Morne des Commissaires, Grand Gosier, Savane Jombi, 1425 m., Sept. 3, 1926. A sheet of the type collection is in the U. S. National Herbarium. Although Christensen tells how to separate this from *O. ypanemense* Mart., to which it is scarcely related, he fails to indicate how to distinguish it from *O. Harrisii*. The writer has been completely unable to distinguish between the types of *O. Ekmani* and specimens labeled in Christensen's own writing, *O. Harrisii*.

Plant 4–18 cm. high, often reproducing vegetatively by sending out specialized rootlets from which arise new individuals; rhizome short, stout, subbulbous, erect, bearing one or sometimes several leaves; common stalk 1.5–9 cm. long; blade sessile, ovate-cordate, deltoid, or suborbicular, usually truncate below, obtuse or rounded at apex, 1.5–3.5 cm. long, 1.3–2.5 cm. broad; venation diffuse, veins forming numerous small areoles; fertile stalk 2.2–11.5 cm. long; spike 0.7–2.5 cm. long; spores 35–40μ in diameter.

O. Harrisii may be merely a dry ground form of *O. reticulatum*, found at high altitudes in Jamaica, Hispaniola, and Grenada. It differs from typical *O. reticulatum* in the shape of the blade, which is regularly truncate rather than cordate at the base, in its smaller size, in the smaller areoles formed by the veins, and also in the stouter rhizome. On a basis of these characters, it seems best for the present to retain this as a separate species, although future studies may show it to be only an ecological variant of *O. reticulatum*.

This species grows typically in clay soil among grasses on exposed slopes in the mountains of Jamaica, Hispaniola, and Grenada at 2400–5000 ft. elevation.

JAMAICA. Cinchona Plantation, 5000 ft., *L. M. Underwood 169*, type (NY); also *W. Harris 9146* (NY) & *11428* (NY, U). Between Hardware Gap and Silver Hill, *D. E. Watt* (NY). Silver Hill Gap, *W. R. Maxon 1134* & *1137* (U).

HISPANIOLA. Haiti. Massif de la Selle, *E. L. Ekman 6852* and *10076* (U).

GRENADA. Belvidere, ——— (NY).

10. OPHIOGLOSSUM PETIOLATUM Hooker

Ophioglossum petiolatum Hooker, Exotic Flora **1**: 56. 1823. Based on specimens sent from the West Indies to the Liverpool Botanical Garden, where the plants were cultivated. The exact place of collection of the types is apparently unknown. The two specimens shown in the illustration accompanying the original description may be considered as typifying the species. Hooker states that it differs from *O. ovatum* and *O. vulgatum* in the long pedunculated fertile spike, the slender habit, and the narrower much more acuminate lamina.

Ophioglossum moluccanum Schlecht., Adumbratio Filicum in promontorio

Bonae Spei provenientium p. 9. 1825. Based on *O. simplex* Rumphius, Herb. Amboinense **6**: 152. pl. 68, fig. 2. 1750.

Ophioglossum cordifolium Roxb., Wall., List, no. 47. 1828.

Ophioglossum elongatum A. Cunningham, in Hooker's Companion to the Botanical Magazine. **2**: 361. 1836. Based on material from North Island, New Zealand.

Ophioglossum cognatum Presl, Suppl. Tent. Pterid. p. 53. 1845. Based on material from Calcutta, Bengal, India.

Ophioglossum Cumingianum Presl, Suppl. Tent. Pterid. p. 52. 1845. Based on the collection of Cuming, no. 284, from the island of Corregidor in Manila Bay, the Philippines. The writer has examined material from the type collection at the Gray Herbarium. This is the same as *O. petiolatum*, but a sheet of this number in the U. S. National Herbarium is *O. reticulatum*.

Ophioglossum obovatum and *O. timorense* Miquel, in Ann. Mus. Bot. Lugd.-Bat. **4**: 93. 1868–69. Based on material from the island of Timor. So far as can be determined from the original descriptions, both of these names probably should be considered synonyms of *O. petiolatum*. The types have not been available for examination in this study.

Ophioglossum vulgatum L. var. *australasiaticum* Luerssen in part, in Journ. des Museum Godeffroy. **3**: 246c. 1875. This includes both *O. petiolatum* Hooker and *O. pumilum* Raciborski.

Ophioglossum pedunculosum sensu Prantl (not Desvaux, 1811), in Jahrb. Bot. Gart. Berlin **3**: 328. 1884. The type of *O. pedunculosum* Desvaux is filed in the herbarium at the Museum of Natural History in Paris, while a photograph of the type sheet is now available at the Gray Herbarium. As Weatherby (Contr. Gray Herb. **114**: 29. 1936) has already indicated, this plant of Desvaux is not the same as *O. pedunculosum* as interpreted by Prantl. The Desvaux type is a plant about 18 cm. high, with a much enlarged bulbous rootstock bearing numerous roots and two leaves with the blades basally inserted. The expanded portion of one of these blades is about 4 cm. long by 1.8 cm. broad, oblong-elliptical and apiculate, with a conspicuous pale median band extending the length of the lamina. The fertile stalk is 12 cm. long and the spike about 2 cm. This plant is the same as *O. fibrosum* Schumacher of Africa, India, and the East Indies. Since *O. pedunculosum* Desv. is the first name to have been applied to this eastern species, it must now replace *O. fibrosum*, while *O. petiolatum*, the next earliest available name, must be used for the population erroneously designated as *O. pedunculosum* by Prantl.

Ophioglossum Raciborskii van Alderwerelt van Rosenburgh, in Bull. Jard. Bot. Buit. Series 2, no. 28: 35. 1918. Based on *O. moluccanum* Schl. forma *lanceolatum* Raciborski, in Nat. Tijdschrift Ned.-Ind. **59**: 236. tab. 2, fig. 4. 1900. The original description is based on a specimen from Klappa Noenggal, near Buitenzorg, Java, the collection of C. A. Backer 23403. This represents a narrow-bladed form of *O. petiolatum*, which does not merit nomenclatorial recognition. The venation characters mentioned by van Rosenburgh are of trivial consequence. The species was named in honor of M. Raciborski who studied *Ophioglossum* in the Dutch East Indies.

Ophioglossum pedunculatum Nakai, in Bot. Mag. Tokyo **39**: 193. 1925. This name is an error for *O. pedunculosum*, supposedly of Desvaux, in Berl. Mag. **5**: 306. 1811. The spelling was not corrected, but rather was perpetuated in a later paper by the same author. According to Nakai (1925) this species resembles smaller specimens of *O. reticulatum*, but the margins of the leaves, instead of being entire, are crenate.

Ophioglossum littorale Makino, in Journ. Jap. Bot. **6**: 27. 1929. Although the writer has not yet had opportunity to study authentic material of this, Makino's original description so strongly suggests *O. petiolatum* that it seems best tentatively to list the name in the synonymy of this species

Ophioglossum floridanum E. P. St. John (including forma *favosum* and f. *reticulosum*), in Amer. Fern. Journ. **26**: 52–55, figs. 1–3; 1936. Based on abundant material from near Gainesville, Fla., and on specimens from many other stations in central Florida. Plants of this population are in every respect identical with material of *O. petiolatum* from Java, Sumatra, and elsewhere. Not even varietal separation of the East Indian and Florida plants seems possible. The plate accompanying the original description of *O. petiolatum* shows plants which are entirely like *O. floridanum* except that the blades have longer hafts, but the length, or the presence or absence of a haft on the sterile blade, is a character of slight taxonomic consequence in *Ophioglossum* and certainly should not be used here as a basis for the separation of species. Further, although the venation in *O. floridanum* is highly variable, since it is in every respect like that of *O. petiolatum* from all parts of its range, there seems little basis for according nomenclatorial distinction to the Florida plants. The minor variations in shape of blade and venation within the American populations scarcely deserve naming.

Plant 6–21 cm. high, with short slender erect rhizome bearing several long fleshy roots and one or usually several leaves during a single growing season; vegetative reproduction common, by means of modified long slender roots, buds from these giving rise to new plants; common stalk 2–9 cm. long; blade rather thin in texture, lance-ovate, ovate, or elliptical-ovate, acute at apex, obtuse or subtruncate at base, cuneate into a short haft or sessile, 1.5–6 cm. long, 0.6–1.7 cm. wide; venation lax, veins few, areoles large; fertile stalk 1.5–9 cm. long; fruiting spike 1–4 cm. long; sporangia 0.5–1 mm. in diameter. Gametophyte apparently unknown.

The history of *Ophioglossum petiolatum* is one of taxonomic blundering and misinterpretation. Although the species was already known somewhat before the publication of the first edition of the *Species plantarum*, yet there seems to have been no end of misunderstanding concerning its proper status, its distribution, and its range of variation. It has been almost periodically described as new, each time with a different name and usually without any mention of the previous descriptions or an examination of the considerable literature which should always be consulted before a new name is placed on record, to avoid renaming long known species.

The first description was by Rumphius in 1750. He clearly described plants from Amboina as *O. simplex* and provided a drawing showing that he unquestionably was dealing with the present population. Unfortunately the name *O. simplex* was not used by later writers. Instead, new names were introduced, while rather recently *O. simplex* has been assigned to an entirely different species from Sumatra. This last application of the name is tenable under the International Rules of Nomenclature, since *O.simplex* Rumphius, having been published before 1753, is not valid.

Hooker, in 1823, described and illustrated *O. petiolatum* from plants cultivated in England, which were originally obtained from somewhere in the West Indies. Hooker's description is entirely adequate and his name should have been used subsequently as the proper designation for this species. Other workers, however, misinterpreted *O. pedunculosum* Desvaux, a quite different species, and have used this name for the *O. petiolatum* population, which was thought to be entirely of Old World distribution. Actually, *O. petiolatum* has a rather wide distribution in the New World, but seems to be less common here than in the Old World, where it is apparently fairly abundant. Since much of the American material in herbaria lacks specific locality data, it has not been possible to work out the detailed range of this species in the Americas, but the evidence available indicates that, besides being found in central Florida, it occurs on various islands of the West Indies, in Central America, and in northern South America. The American plants exactly match Old World specimens.

In the Old World, there has been much misconception concerning the range of variation in this species. Enthusiastic "splitters" have frequently described minor variants as new species, thus greatly adding to the synonymy. None of these trivial variations in leaf shape or in the minute details of venation seems worthy of naming. Often all of the supposed different species may occur in the same patch or colony, as a few large series demonstrate.

O. petiolatum really is very closely related to *O. reticulatum* and in certain parts of the world, notably in India, China, and Mexico, the two populations seem somewhat to intergrade. Usually, however, they appear distinct and are readily separable. *O. petiolatum* generally may be distinguished by its lance-ovate blade which is acute at the apex, by the rather long slender fertile segment, and by the lax venation. Typically, also, it is somewhat smaller than *O. reticulatum*.

O. petiolatum is a plant of moist meadows, damp grassy places, and occasionally of moist woodlands and thickets. The range includes central Florida, Trinidad and elsewhere in the West Indies, Mexico, northern South America, tropical Africa and Madagascar (*fide* Christensen, 1932), India, Ceylon, Siam, China, Japan, Philippines, Borneo, Sumatra, Java, New Guinea, New Caledonia, New Zealand, Fiji, and Samoa. For a detailed discussion of the distribution see Clausen (1938).

11. OPHIOGLOSSUM CONCINNUM Brackenridge

Ophioglossum concinnum Brackenridge, in Charles Wilkes, U. S. Exploring

Expedition **16**: 315. p. 44. fig. 1. 1854. Based on plants collected on sandhills near Wailuku, island of Maui, Hawaiian Islands. Type in the U. S. National Herbarium.

Plant 7–16 cm. high with rather stout cylindrical rootstock bearing several fibrous roots and one or several leaves; old leaf stalks persisting as a brown sheath about base of plant; common stalk 2–7 cm. long; blade subcoriaceous, elliptic-lanceolate, ovate-elliptic, or suborbicular, tapering at base, 1–4 cm. long, 0.8–1.5 cm. wide; veins numerous, forming many small areoles; fertile stalk 2–8 cm. long; fruiting spike 1–1.5 cm. long; sporangia 0.6–0.8 mm. in diameter.

This species has been much tossed about by fern students, having been at various times relegated to synonymy under one or the other of several different species, or sometimes completely disregarded. Actually, its characters seem sufficiently distinctive to warrant its maintenance as a separate species, based on the coriaceous nature of the elliptical blade, the characteristic venation, and the rather small size of the plants. Most nearly related are *O. petiolatum*, in which the blade is lance-ovate and membranous, with the areoles large, and *O. nudicaule*, in which the blade is also rather membranous, ovate-orbicular to elliptical, and inserted either basally or almost so. It is not likely that *O. concinnum* would be confused with any other species in the genus. Except for *O. pendulum* ssp. *falcatum*, it is the only species of *Ophioglossum* found in the Hawaiian Islands.

HAWAIIAN ISLANDS. Kaui: ———, *W. H. Dole* (NY). Oahu: Honolulu, *C. N. Forbes* (M, NY). Maui: Haleakala, ——— (U). Hawaii: ———, *M. J. Remy* 99 (G).

12. OPHIOGLOSSUM AITCHISONII (Clarke) d'Almeida

Ophioglossum vulgatum var. *Aitchisoni* Clarke, in Trans. Linn. Soc. London II. **1**: 586. 1880. Based on specimens collected by J. E. T. Aitchison at 2400 ft. in Punjab. Described as "Rhizome elongate, bearing annually 4–10 fronds in succession, 2–$2\frac{1}{4}$ by $\frac{2}{3}$–$\frac{3}{4}$ in., oblong, texture stout."

Ophioglossum lusitanicum C. W. Hope (non L.), in Journ. Bombay Nat. Hist. Soc. **15**: 106. 1903. Based on material from Afghanistan and Punjab. *O. vulgatum* var. *Aitchisoni* is listed as a synonym.

Ophioglossum Aitchisoni (Clarke) d'Almeida, Journ. Ind. Bot. **3**: 63. f. 12. 1922. Based on specimens from the northwestern Himalayas and from Abyssinia. The figure accompanying the original description may be taken to typify the species.

Since no specimens of this species have been available for the present study, the original description is here copied. "Rhizome elongated, not tuberous, with several fibrous rootlets and crowned with a tuft of brown persistent sheaths surrounding the bases of the fronds; fronds several on the rhizome, sterile division $1\frac{1}{2}$–$2\frac{1}{2}$ inches long, $\frac{1}{2}$–$\frac{3}{4}$ inch broad, linear lanceolate, acute or mucronate; veins visible in dry specimens, but not quite distinct; no midrib;

texture stout; fertile division arising from a little above the base of the sterile lamina, fertile spike 1 inch long on a peduncle 2 inches long."

According to the literature, *O. Aitchisonii* occurs only in the mountains of northern and western India, Afghanistan, and Abyssinia.

13. OPHIOGLOSSUM ENGELMANNI Prantl. *Figure 25.*

Ophioglossum Engelmanni Prantl, in Ber. deutsch. bot. Ges. **1**: 351. 1883. Based on plants from Texas and Missouri. The writer has examined specimens from the type collection, *G. Lindeheimer 53*, from New Braunfels, Comal Co., Texas. This cotypic material has been rather widely distributed in American herbaria.

Ophioglossum vulgatum f. *Engelmanni* (Prantl) Clute, Our ferns in their haunts. p. 316. 1901.

Plant 5–22 cm. high with stout erect cylindrical rhizome bearing numerous clustered roots and usually several leaves in a single season; bases of old leaves persisting as a sheath about the rootstock; common stalk 1–9 cm. long; blade elliptical or rarely oblong, acute or cuneate at each end, apiculate, 1–12 cm. long, 0.5–3.5 cm. wide; veins numerous, forming large areoles in which are included networks of secondary veinlets forming small secondary areoles; fertile stalk 2–12 cm. long; fruiting spike 1.2–3.5 cm. long; sporangia 0.5–1 mm. in diameter. Matures spores from Feb.–July, also in Nov., but mostly during April and May.

O. Engelmanni is easily distinguished from all other species of the genus by the characteristic venation with primary and secondary areoles, by the absence on the blade of a pale median band, by the short cylindrical rootstock, and by the elliptical apiculate lamina.

This is a species of limestone regions, being found particularly in clayey depressions between limestone ledges, in clay barrens, in pastures, in open and grassy woodlands, and also in cedar barrens and glades. It ranges from northwestern Virginia westwards through southern Ohio and Illinois to Missouri and southwards to central Florida, Louisiana, Texas, Arizona, and central and southern Mexico.

Wherry (1935) has discussed the status of the species in Virginia, while Palmer (1932) has published on its habitat requirements and has summarized the distributional data from the United States. Couch (1937) has recently called attention to the autumnal development of this species in Oklahoma.

VIRGINIA. Augusta, Botetourt, Montgomery, Page, Rockbridge, Rockingham, Shenandoah, and Warren Counties.

KENTUCKY. Barren, Marshall, Simpson, and Warren Counties.

TENNESSEE. Knox and Rutherford Counties.

FLORIDA. Citrus, Hernando, and Jackson Counties.

ALABAMA. Madison: on limestone shelves above the sandstone, Smithers Mountain, *R. M. Harper 3556* (H).

MISSISSIPPI. Lee: Tupelo, *E. J. Palmer 39010* (G, M, U).

LOUISIANA. Natchitoches, *J. Hale* (NY). Red River, *J. Hale* (G).

OHIO. Adams: Beaver Pond, *E. Lucy Braun* (G).

INDIANA. Monroe: Bloomington, *L. M. Underwood* (NY).

ILLINOIS. Hardin: Cave-in-Rock, *E. J. Palmer 15469* (M).

MISSOURI. Barry, Benton, Boone, Cedar, Dade, Franklin, Greene, Iron, Jackson, Jasper, Jefferson, McDonald, Miller, Newton, Oregon, Ozard, Pettis, Phelps, St. Louis, Stone, and Taney Counties.

ARKANSAS. Baxter, Benton, Carroll, Hempstead, and Washington Counties.

KANSAS. Linn: La Cygne, *F. C. Greeve* (U). Also reported from Wilson County.

OKLAHOMA. Choctaw, Comanche, Logan, Payne, and Pittsburg Counties.

TEXAS. Anderson, Brazos, Brown, Comal, Dallas, Harris, San Augustine, Travis, and Walker Counties; also reported from Gonzales County.

ARIZONA. Cochise: Hereford, *G. J. Harrison 8267* (U). Huachuca Mts., ex Lemmon Herb. (G). Mustang Mts., *C. G. Pringle* (G, Ph).

MEXICO. States of Baja California, Chihuahua, Federal District, Hidalgo, Jalisco, Mexico, and Oaxaca.

14. OPHIOGLOSSUM PEDUNCULOSUM Desvaux

Ophioglossum pedunculosum Desvaux, in Magazin Gesellschaft Naturforsch. Freunde Berlin **5**: 306. 1811. Based on material which Desvaux designated as doubtfully collected in America, although most of the plants which he described were from the Old World. The type is preserved in the herbarium of the Museum of Natural History in Paris. At the Gray Herbarium, and also at the U. S. National Herbarium, is a photograph of the type. This has been studied by the writer. It clearly represents a species which is rather widely distributed in the Old World tropics and which has been passing under the name of *O. fibrosum* Schum. The type specimen is about 18 cm. high, with enlarged bulbous rootstock with numerous roots and two blades inserted basally. The blades are about 4 cm. long and 1.8 cm. broad, oblong-elliptical and apiculate, with a conspicuous pale median stripe. The fertile portion is about 14 cm. long with the sporangia-bearing spike 2 cm. long. Since this is the same as *O. fibrosum* Schum., it seems likely that Desvaux had somehow confused his data concerning the native region for his species. The question marks after America both in the original description and on the label accompanying the type specimen indicate that he himself was aware of this confusion.

Ophioglossum capense α regulare Schlechtendal, Adumbratio filicum in promontorio Bonae Spei provenientum. p. 9. pl. 1, fig. 2. 1825. Based on specimens from South Africa. This seems to the writer to be only a trivial form of *O. pedunculosum*. *O. capense* Swartz, in Schrader's Journ. Bot., 1801, p. 308, 1803, is doubtfully the same as this. The original description is quite unsatisfactory and until more evidence is available, it seems best to drop the name of Swartz entirely, regarding it as a nomen dubium. In herbaria, much of the material which has been passing as *O. capense* is *O. sarcophyllum*, but some of it is *O. pedunculosum*.

Ophioglossum fibrosum Schumacher, in K. Danske Videnskabernes Naturvidenskabelige og Mathematiske Afhandlingar. **4:** 226. 1827. Based on material from South Africa.

Ophioglossum Wightii Greville & Hooker, in Bot. Misc. **3:** 218. 1833. Based on material collected by Dr. Wight near Negapatam in the peninsula of India.

Ophioglossum brevipes Beddome, Ferns of Southern India. p. 23. pl. 72. 1863. Based on material from southern India. The illustration accompanying the original description may be taken to typify the species, which is clearly the same as *O. pedunculosum* Desv.

Ophioglossum cuspidatum Milde, in Bot. Zeit. 1864. p. 107. Based on specimens from Abyssinia.

Ophioglossum bulbosum Beddome, Ferns of British India, Suppl. p. 28. 1876. This is a substitution for *O. brevipes*, which Beddome erroneously thought to be the same as *O. bulbosum* Michx., from America.

Ophioglossum regulare (Schlechtendal) C. Christensen, Index Filicum. p. 471. 1906.

Plant 11–18 cm. high, with stout elongate tuberous rootstock bearing numerous fleshy roots and usually several leaves during a single season; common stalk 3–6 cm. long; blade oblong-elliptical, elliptical, or ovate, apiculate, cuneate to subtruncate at base, averaging 4 cm. long and 1.8 cm. wide, with a prominent pale median band; venation double, with primary veins forming large oblong areoles in which are included networks of secondary veinlets; fertile stalk 1.5–15 cm. long; fruiting spike 1–3.5 cm. long. Gametophyte apparently unknown.

An American student, without opportunity for studying the series of *O. pedunculosum* represented in the various Old World herbaria, is at a decided disadvantage in interpreting the range of variation and the relationships of this puzzling species. Since only scant material has reached American herbaria, and since most of this is of an unsatisfactory nature, the conclusions reached here as a result of the study of these specimens must be considered as quite tentative and likely to be changed whenever more material may be available.

Sim (Ferns of South Africa, p. 321 & 322, 1915) indicates that he considers *O. capense* Swartz and *O. fibrosum* Schum. to be the same, although Christensen has made two species out of *O. capense* Schlecht., namely *O. regulare* Schl. and *O. capense* Swartz, and has also maintained *O. fibrosum* Schum. The writer has been unable to satisfy himself concerning the proper interpretation of *O. capense* Swartz, although he is inclined to agree with Christensen in considering it as different from *O. regulare* and *O. fibrosum*, which last two the writer considers synonymous. *O. capense* Schl., except for the rather short fertile segments, seems to be the same as *O. fibrosum* Schum, and *O. pedunculosum* Desv., but whether the earlier homonym of Swartz also represents this, or is a robust form of

O. lusitanicum, or perhaps really is a distinct species, is a problem which requires more investigation.

As here considered *O. pedunculosum* is a plant of dry grassy places. It is apparently widely distributed in central and southern Africa, southern India, and the East Indies.

ABYSSINIA. Reported and described as *O. cuspidatum* by Milde, also listed from here by Prantl (1884).

CAPE OF GOOD HOPE. Oudeberg, *W. M. Canby 1692* (Ph).

SOUTHWEST AFRICA. Halenberg, *K. Dinter 6650* (G).

CENTRAL AND SOUTH AFRICA. Reported by various writers from numerous localities. Quorra Border. ——— (G). Without locality (M).

MADAGASCAR. Reported by Prantl (1884) and by Christensen (1932).

INDIA. Madras: Canara, *Stocks* (G); Malabar, *Stocks 4* (G).

CEYLON AND SUMATRA. Reported by Prantl (1884).

Since preparing the above, the writer has had opportunity to study a suite of ten collections of this species, loaned through the kindness of the Keeper of Botany at the British Museum. This material is interesting because the specimens either lack the pale median band completely or possess it so obscurely that it is scarcely visible. The rhizome, in most of the plants, is surrounded by a sheath composed of the leaf bases of previous seasons. In many respects these African plants closely approach *O. Engelmanni* of North America, with which they indeed may be identical. In addition to the regions listed above, the writer has now examined specimens from the Cape Verde Islands, the Nubian coast, Natal, and southeastern Madagascar.

15. OPHIOGLOSSUM ELLIPTICUM Hooker and Greville

Ophioglossum ellipticum Hooker and Greville, Icones Filicum. **1**: pl. 40 A. 1831. Based on specimens collected by C. S. Parker in Demerara, British Guiana. The illustration accompanying the original description may be considered to typify the species, which the plate shows to be characterized by the double venation, the pale median band of the sterile blade, and the subglobose rootstock bearing regularly several leaves during a season.

Ophioglossum vulgatum var. *surinamense* Luerssen, Journ. Mus. Godeff. **8**: 247c. fig. 1875.

Plant 4.5–15 cm. high with subglobose rootstock bearing only a few roots and usually two or several leaves during a single season; common stalk 4–60 mm. long; blade elliptical or lanceolate-elliptical, cuneate or subtruncate at base, acute to blunt at apex, 1.3–7 cm. long, 0.5–2.0 cm. wide, with a conspicuous median band or midrib; venation double, with primary veins forming large oblong areoles in which are included networks of secondary veinlets forming small rhombic areoles; fertile stalk slender, (2) 5–9 cm. long; fertile spike 1–3 cm. long. Gametophyte apparently unknown.

In its double venation and habit, this species is most like *O. pedunculosum* Desv. and *O. Engelmanni* Prantl. From the former it differs in its subglobose rootstock which bears only sparse roots. From the latter it is distinguished by the pale median band of the lamina, also by its smaller size. The characteristic venation distinguishes it from all other species of *Ophioglossum*.

O. ellipticum occurs in damp grassy places in the New World tropics. Authentic specimens have been examined from Brazil, and from British, Dutch, and French Guiana; also doubtful material from Panama and Bolivia.

?PANAMA. Panama: Savana de Alhajuela, Chagres Valley, *H. Pittier 3483* (U).

BRITISH GUIANA. Demerara, *G. S. Jenman* (NY, U).

SURINAM. Paramaribo, *Forbes* (G). *Hering* (Ph). *Schweinitz* (Ph).

FRENCH GUIANA. Ouessa, *Leprieur 149* (G, U). Near Cayenne, *Leprieur 151* (G, U); also *148* (G, NY, U). Karouany, *Sagot 706* (NY).

BRAZIL. Pernambuco: Tapera, *D. B. Pickel 3044* (U). Rio de Janeirio: Piauhy, *Gardner 2991* (U).

?BOLIVIA. Reyes, Rosario Hacienda, *White 1223* (NY).

16. OPHIOGLOSSUM NUDICAULE L. fil. *Figure 27*

Plant perennial, 1.3–13 cm. high, with sub-bulbous or rarely cylindrical rootstock bearing several fibrous roots and one or several leaves during a single growing season; common stalk 0.1–4.2 cm. long; blade ovate, orbicular, elliptical, oblong, or rarely elliptic-lanceolate, usually apiculate at apex, cordate to cuneate at base, 0.4–3.5 cm. long, 0.3–1.6 cm. wide; venation rather lax with a primary set of veins forming large or small areoles in which are sometimes included occasional free veinlets; fertile stalk 0.6–8.2 cm. long; fruiting spike 0.3–2.5 (–4) cm. long; sporangia 0.2–1.0 mm. in diameter. Gametophyte apparently unknown.

Ophioglossum nudicaule is an exceedingly variable form from which many spurious species have been segregated. Since the several extremes of development within this species population freely intergrade and since these variations cannot be satisfactorily correlated with range, it has seemed impossible to consider these here either as species or as subspecies. These are, therefore, treated as varieties, which are distinguished in the following key:

A. Plant small, 2.5–7.5 (–12) cm. high. B
  B. Sterile blade inserted basally or almost so. C
    C. Blade truncate or cuneate at base. D
      D. Blade ovate-orbicular, usually about as broad as long; fertile segment 2–4 times as long as sterile blade. 16a. *O. nudicaule* var. *typicum*
      D. Blade ovate, elliptical, or elliptic-lanceolate, usually longer than broad; fertile segment 4–8 times as long as sterile blade. E

E. Mature plant rather large, 4–12 cm. high. 16b. *O. nudicaule* var. *tenerum*

E. Mature plant small, 3–8 cm. high, with very slender fertile segment. 16c. *O. nudicaule* var. *minus*

C. Blade cordate clasping, subcordate, or broadly truncate at base. 16d. *O. nudicaule* var. *vulcanicum*

B. Sterile blade inserted almost at middle of plant (i.e. about half way between rootstock and fertile spike). 16e. *O. nudicaule* var. *macrorrhizum*

A. Plant rather large, 4–13 cm. high, with the blade 1–3.5 cm. long and 0.5–1.5 cm. wide. F

F. Blade elliptical, opaque when dried, with numerous veins forming small areoles. 16f. *O. nudicaule* var. *laxum*

F. Blade orbicular or almost so, membranous when dried, with few veins forming large areoles. 16g. *O. nudicaule* var. *grandifolium*

16a. OPHIOGLOSSUM NUDICAULE L. fil., var. TYPICUM

Ophioglossum nudicaule L. fil., Suppl. p. 443. 1781. Based on a specimen from the Cape of Good Hope. Christensen (1932) states that the type in the Linnean Herbarium is scanty, but can be matched by specimens from Madagascar, two of which he illustrates.

Ophioglossum parvifolium Greville and Hooker, in Bot. Misc. **3**: 218. 1833. Based on specimens from Negapatam, India.

Ophioglossum Luersseni Prantl, in Ber. deut. bot. Ges. **1**: 352. 1883. Based on material from Queensland, Australia. No specimens have been available for this study. The writer has been unable to determine from Prantl's description how this is to be distinguished from typical *O. nudicaule*.

Ophioglossum moluccanum f. *pumilum* Raciborski, in Nat. Tijdschr. Ned. Ind. **59**: 237. t. 2. f. 2–3. 1900. Based on material from Java. The two figures accompanying the original description may be considered to typify the species.

Ophioglossum pumilum (Rac.) van Alderwerelt van Rosenburgh, Malay Ferns Suppl. **1**: 453. 1916. Based on material from Buitenzorg, Java.

Plant small, 1–4.5 cm. high; sterile blade inserted almost basally, ovate-orbicular or orbicular, about as broad as long, 2–10 mm. long, 2–10 mm. wide, usually apiculate; fertile stalk rather short, 1–3.5 cm. long, surpassing the lamina only by 2–4 times.

Christensen (1932) has illustrated two specimens from Madagascar, which, he states, match the scanty type in the Linnean Herbarium. Only meagre material of this variety is available in American herbaria. The writer has seen specimens from Florida, India, China, Australia, New Caledonia, Lombok, and Samoa, but nothing from South Africa or Madagascar. The Indian and Chinese specimens closely match the plants illustrated by Christensen and are to be classified with these. Many speci-

Fig. 27 (above). *Ophioglossum nudicaule* var. *typicum* (+), var. *tenerum* (•), var. *minus* (X), var. *vulcanicum* (*), var. *macrorrhizum* (‡), var. *laxum* (○), and var. *grandifolium* (φ).

Fig. 28 (below). *Ophioglossum lusitanicum* ssp. *typicum* (•), ssp. *californicum* (X), and ssp. *coriaceum* (+).


TROPIC OF CAPRICORN
EQUATOR
TROPIC OF CANCER


TROPIC OF CAPRICORN
EQUATOR
TROPIC OF CANCER
ARCTIC CIRCLE

mens from the New World should, perhaps, also be referred to this variety, but because of their more slender habit and larger size, with the blade more elliptical than orbicular, most of these American plants are here treated under var. *tenerum*.

O. nudicaule var. *typicum* is a plant of grassy places and is to be expected throughout the range of the species.

FLORIDA. Polk: Fort Meade, *E. P. St. John 622* (Claus. U); these specimens exactly match the collection cited below from Yunnan Province, China.

AFRICA. Described from the Cape of Good Hope.

MADAGASCAR. Reported from Boina by Christensen (1932).

INDIA. Puling Hills, near Fairy Parlor, *S. B. Fairbank* (C). Pulney Mts., *S. B. Fairbank 1587* (M). Also reported by various authors.

CHINA. Yunnan: along Yangtse River north of Likiang, *Handel-Mazzetti 7599* (U).

JAVA. Reported from near Buitenzorg as *O. moluccanum* f. *pumila* by Raciborski (loc. cit.).

LOMBOK. Plawangen, *C. N. A. de Voogl. 2597* (NY).

AUSTRALIA. Queensland: reported by Prantl (1884) as *O. Luersseni*. South Australia: Androisan, *O. J. G. Tepper* (NY).

NEW CALEDONIA. ———, *I. Franc* 487 (U).

SAMOA, Upolu, *Reinecke 116* (U). ———, *F. Vaupel 307* (U).

Since preparing the above, the writer has had opportunity to examine four collections loaned from the herbarium of the British Museum: Cape Colony, *Sieber 125;* Southwest Africa, *Schlechter 10842;* Central Africa, *G. Schweinfurth 1922;* and Fernando Po, *Barter*. Of these, the Schweinfurth specimens are definitely to be referred to the var. *tenerum*, while the Schlechter and Barter specimens are somewhat intermediate between this and var. *typicum*. On a basis of this material, the separation of the varieties *tenerum* and *typicum* seems scarcely justifiable, and they might best be treated as the same.

16b. **Ophioglossum nudicaule** var. **tenerum** (Mettenius) n. comb.

Ophioglossum ypanemense Martius, Icones Plant. Crypt. Bras. p. 39, 130. pl. 73. f. 1. 1834. Based on specimens collected in pastured fields near Ypanema, Prov. of Sao Paulo, Brazil. The plate accompanying the original description depicts two plants with very small basally inserted sterile blades and long slender peduncles. These can be matched by specimens from various parts of South America and from the West Indies. They are not sufficiently distinct to warrant even varietal recognition. The length of the fertile stalk is exceedingly variable and should not be employed as a taxonomic character.

Ophioglossum Schmidii Kunze, in Linnaea **24**: 246. 1851. Based on specimens from southern India. The original description seems to indicate that this is intermediate between vars. *typicum* and *tenerum*.

Ophioglossum melipillense Remy, in Gay, Fl. Chil. **6**: 542. 1853. Based on specimens from Chile. The original description, referring to the ovate acute lamina and very long fertile stalk, strongly suggests this variety. The writer has not seen the type collection.

Ophioglossum Gomezianum Welw.; A. Br. apud Kuhn, Fil. Afr. p. 176. 1868. Based on specimens from Angola with the sterile blades elliptical or lanceolate. The writer is doubtful whether this should be referred here or to var. *typicum*. No specimens have been available for study.

"*Ophioglossum Spruceanum* Fée, Cr. vasc. Br. **1**: 218. pl. 52, fig. 3. 1869."

Ophioglossum tenerum Mett.; Prantl, in Ber. Deut. Bot. Ges. **1**: 352. 1883. Based on a collection from Georgia. The type sheet is deposited in the herbarium at Berlin. The writer has studied a photograph of this sheet. The Georgia specimen, presumably the type, is so scant that it can not be satisfactorily placed, since only a part of a fertile spike and stalk is evident. On the same sheet, however, are specimens gathered by Chapman in Florida. Since these two collections were placed together by Mettenius, it seems probable that he considered both to be the same and to represent his new species. The Florida plants are slender, with ovate-elliptical sterile blades, which are far surpassed by the tall fertile segments.

Plant rather large, (2) 4–12 cm. high, with the rootstock subglobose and the blade ovate, elliptical, or elliptic-lanceolate, typically longer than broad, much (4–8 [–10] times) surpassed by the fertile segment.

It is doubtful whether this population, in which the lamina is typically elliptical and the fertile segment is much elongated, really is sufficiently different from the var. *typicum* to warrant even varietal designation. It is here maintained, however, for practical convenience, until more material of var. *typicum* from the Old World may be available for comparison with the American plants. The name *tenerum* has been chosen to designate the variety because it is more appropriate than the other available names, all of which have been used to designate this population as a species. When it is necessary to choose a name in reducing a species to varietal rank, it would seem desirable to select the most appropriate of several possible epithets, rather than rigidly to apply the rule of priority, which here would recommend the adoption of the rather inappropriate appellation, var. *ypanemense*.

The present population presents a great range of variation in size of plant, in the shape of the sterile blade, and particularly in venation. The extremes of the numerous variations that occur, however, are connected by an almost complete series of intermediate specimens. Further, since venation, size, and shape of blade are all decidedly unreliable and inconstant in this group, these trivial forms do not merit nomenclatorial recognition.

The var. *tenerum* is a plant of wet meadows, swales, and moist open woods. It is found in Florida, Alabama, Mississippi, Texas, Mexico, various islands of the West Indies, northern and central South America, the Philippines, and Sumatra. It has not been possible positively to identify certain scrappy specimens from Georgia.

Georgia. A doubtful scrap from near Savannah River, *Beyrich* (NY).

Florida. Alachua, Citrus, Dade, Duval, Hernando, and Jackson Counties.

Alabama. Mobile and Pike Counties.

Mississippi. Jackson: Ocean Springs, *S. M. Tracy* (NY, U).

Louisiana. Orleans: New Orleans, *T. Drummond 1* (G).

Texas. Hardin: ———, *J. S. Holmes* (U).

West Indies. Cuba and Hispaniola.

Mexico. States of Sinaloa and Federal District, also doubtful material from San Luis Potosi.

Colombia. Tolima: ———, *F. C. Lehmann 6124* (U).

Venezuela. Los Andes: Tovar, *A. Fendler 342* (M), this tending towards var. *grandifolium*.

British Guiana. Kamakusa, along upper Mazaruni River, *H. Lang 366* (NY).

French Guiana. Cayenne, *Leprieur 150* (G, U); also *187* in part (G, U). Sinnamary, *Leprieur* (G, U).

Brazil. States of Matto Grosso, Minas Geraes, Pernambuco, and Rio Grande do Sul, and São Paulo, also Amazon Basin.

Bolivia. On plains between Rio Pirai and Rio Cuchi, *T. Herzog 1451* (U).

Argentina. Gob. de Chaco y Formosa: Mapalpi, *A. Donat 14* (G, M, Ph, U).

Africa. Reported from Angola as *O. gomezianum* by Prantl (1884).

Philippines. Island of Luzon.

Sumatra. Padang Sidimpoeuan, *R. Si Toroes 5529* (NY).

16c. **Ophioglossum nudicaule** var. **minus,** n. var. *Figure 29.*

Planta parva et tenuis, 3–8 cm. alta, lamina parvissima, 4–13 mm. longa, 2–5 mm. lata, elliptica, ovata, vel obovata; rhizoma cylindricum vel raro subglobosum; pedunculo gracillimo, 2–6 cm. longo; sporangiis 0.2–0.4 mm. latis.

Plant small and slender, 3–8 cm. high, with the sterile blade very small, 4–13 mm. long, 2–5 mm. wide, elliptical, ovate, or obovate; rootstock cylindrical or rarely subglobose; fertile stalk very slender, 2–6 cm. long; sporangia 0.2–0.4 mm. in diameter—Type in U. S. National Herbarium; cotypes in Gray Herb. and N. Y. Bot. Gard. Herb. Low pineland in the vicinity of Fort Myers, Lee County, Fla., Sept. 4, 1916, *Miss J. P. Standley, no. 354.*

The var. *minus* is a small form which is occasionally produced almost throughout the range of the *O. nudicaule* population. It perhaps represents a juvenile condition of var. *tenerum*. Many collections of var. *tenerum* contain specimens which either belong to or somewhat tend towards this variety. No attempt has been made to list these here. Only a few collections, which exactly match the type specimens, are cited.

Florida. Citrus: roadside between Lecanto and Crystal River, *E. P. St. John 570* (U). Dade: Miami, *A. P. Garber 2259* (M). Levy: Rosewood, *A. P. Garber* (G, M, NY, Ph, U) Nassau: Yulee, *Mrs. W. D. Diddell 536* (Herb. E. P. St. John).

French Guiana. Cayenne, *Leprieur 187* in part (U). Sinnamary, *Leprieur* (U).

Fig. 29 (upper left). Type specimens of *Ophioglossum nudicaule* var. *minus* ($\times\frac{3}{5}$).

Fig. 30 (upper right). Type specimens of *Ophioglossum nudicaule* var. *laxum* ($\times\frac{1}{3}$).

Figs. 31 & 32 (below). Type specimens of *Ophioglossum nudicaule* var. *vulcanicum* ($\times\frac{2}{3}$).

16d. **Ophioglossum nudicaule** var. **vulcanicum,** n. var. *Figures 31 and 32.*

Planta parva, 1.3–6 cm. alta, rhizoma cylindricum vel subglobosum, vaginibus fulvis e basibus perserverantibus foliorum factis; lamina sterili truncata vel subcordata, oblonga, ovata, vel orbiculari, apiculata, 5–9 mm. longa, 3–6 mm. lata, venis paucis; pedunculo fere oriundo e 1 mm. supra base laminae, breve, 0.6–3.2 cm. longo.

Plant small, 1.3–6 cm. high, with cylindrical or subglobose rootstock surrounded by a brown sheath formed by the persistent bases of the leaves; sterile blade truncate or subcordate, oblong, ovate, or orbicular, mucronate at apex, 5–9 mm. long, 3–6 mm. wide, with the veins few; fertile stalk usually arising about 1 mm. above the base of the blade, short, 0.6–3.2 cm. long.—Type in U. S. National Herbarium, at 1300 m., Llanos del Volcan, Province of Chiriqui, Panama, July 14, 1935, *G. W. Martin 2798.*

From the type locality may also be cited, at 1300 m., *G. W. Martin, nos. 2057* (U) and *2052* (U), and, at 1120–1200 m., *R. J. Seibert 127* (U).

The var. *vulcanicum* is known only from Llanos del Volcan, where it occurs in moist decomposed lava from 1120–1300 meters. Although it perhaps represents only an ecological variant of the *O. nudicaule* population, its characters are so distinctive that it seems to merit at least varietal recognition. From var. *typicum* it differs in the lax venation with larger areoles, in the frequently cylindrical rootstock, and in the origin of the fertile stalk from about 1 mm. above the base of the blade, so that the lamina seems to clasp or form a minute collar about the common stalk. From var. *tenerum,* it is distinguished by the somewhat smaller size, by the oblong or orbicular blade, and by the short fertile stalk, also by the rootstock and the place of insertion of the fertile stalk.

In the four collections examined, there were a few specimens which tended towards var. *typicum* and one which rather closely approached var. *macrorrhizum.* These intermediate plants indicate that the Panama population is not of specific rank.

16e. **Ophioglossum nudicaule** var. **macrorrhizum** (Kunze), n. comb.

Ophioglossum macrorrhizum Kunze, Die Farrnkräuter. **1**: 57. pl. 29, f. 1. 1840. Based on specimens collected in French Guiana by Leprieur. The figures accompanying the original description may be considered to typify the species.

Plant with small ovate or orbicular sterile blade, 2–5 mm. long, 1–2 mm. wide, inserted at or towards the middle of the plant.

This diminutive form may be expected to occur anywhere in the range of the *O. nudicaule* population, in association with the other varieties. In addition to the following typical specimens, plants which closely approach var. *macrorrhizum* have been seen from Florida, the West Indies, and Panama.

British Guiana. On the shore of the Mazaruni River, Demarara, *G. S. Jenman* (NY).

French Guiana. Various collections of Leprieur which have been widely distributed as *O. pusillum* Lepr.

Brazil. Amazonas: Rio Negro, *E. Rosenstock* (G, NY). Santa Catharina: Capivare Serra-Geral, *E. Ule* (G).

Paraguay. Listed by R. Chodat and E. Hassler (in Bull. Herb. Boiss., Ser. II, **3**: 619. 1903) from near Santa Elisa, Gran Chaco, Mart., n. 2951, Teg. Rojas.

India. Madras: Pulney Mts., *S. B. Fairbank* (Princ).

16f. **Ophioglossum nudicaule** var. **laxum,** n. var. *Figure 30.*

Planta grandis, 4–13 cm. alta, rhizoma subglobosum vel elongatum cylindricum, radicibus numerosis; lamina elliptica vel oblonga, acutiuscula vel obtusa, 1–4 cm. longa, 0.5–1.3 cm. lata, opaca si sicca.

Plant large, 4–13 cm. high, with subglobose or elongate cylindrical rootstock bearing numerous roots; sterile blade elliptical or oblong, acutish or obtuse, 1–4 cm. long by 0.5–1.3 cm. wide, opaque when dry.—Type in U. S. National Herbarium from near Carnicerias, Tolima, Colombia, *F. C. Lehmann 6124* (U).

In addition to the type, two collections from Brazil may be cited: Minas Geraes: ———, *A. F. Regnell 429* (U). Pernambuco: Tapera, *B. Pickel 3262* (U).

Ophioglossum tapinum Peter (Fedde Rep. Beih. **40**:86. pl. 4, fig. 3. 1929) may be tentatively mentioned as a synonym of this variety. It is based on material from East Africa. The figure accompanying the original description closely resembles the Colombian plants on which var. *laxum* is based.

More material is necessary before the relationships of this distinct variety may be properly understood.

16g. **Ophioglossum nudicaule** var. **grandifolium,** n. var.

Planta grandis et tenuis, 10–14 cm. alta, lamina cuneata, obovata, orbiculare, vel oblonga-elliptica, acuta vel rotundata ad apicem, 1.5–2.3 cm. longa, 0.7–1.6 cm. lata; areolibus magnis a venis paucis formatis.

Plant large and slender, 10–14 cm. high, with blade cuneate, obovate, orbicular, or oblong-elliptical, acute or rounded at apex; veins few forming large aeroles.—Type in Herbarium of the New York Botanical Garden, at 2200 ft., Todaya, District of Davao, Island of Mindanao, Philippines, Oct. 21, 1904, *E. B. Copeland 1448* (U, NY).

Besides the type, the following additional collections may be cited:

Philippines. Island of Leyte, *C. A. Wenzel 465* (M). Luzon, Prov. of Cavite, *M. Ramos & D. Deroy 22550* (U).

This variety is easily distinguished by the large size, the slender habit, and the usually almost round blade with lax venation. The areoles formed by the veins are 2–5 mm. long and 1–2 mm. broad.

17. OPHIOGLOSSUM RUBELLUM Welw.

> *Ophioglossum rubellum* Welw.; A. Braun apud Kuhn, Filices Africanae. p. 179. 1868. Based on specimens collected in 1857 by Welwitsch, no. 33, from pastures in the district of Pungo Andongo, Angola. Type was not seen by the writer. The specific name alludes to the reddish color of the plants.

Plant reddish, 2–2.5 (–4) cm. high with subglobose rootstock and numerous roots; common stalk 3–10 mm. long; blade inserted basally or towards middle of plant, obovate or suborbicular, blunt or abruptly apiculate, 5–10 mm. long, 3–6 mm. broad, with lax venation; fertile stalk very slender, 4–16 mm. long; fruiting spike 5 mm. long; sporangia 0.4 mm. in diameter. Gametophyte unknown.

Ophioglossum rubellum is most nearly related to *O. nudicaule*, from which it is readily distinguishable by the diminutive size, the obovate or suborbicular sterile blade, and the reddish color of the whole plant.

Little is known concerning the species since only scant material has been collected. It grows in grassy open places in Angola and Uganda.

Uganda Protectorate. Mulange, 4000 ft., *R. A. Dummer 5619* (U).

Recently the writer has received from Mr. A. H. G. Alston, of the British Museum of Natural History, specimens collected at Kabaka's Lake, Kampala, Uganda, *Thomas, no. 1903.* These plants probably represent an undescribed species which differs from *O. rubellum* in the cylindrical rootstock, the very small oblong or oblanceolate sterile blade which is 2–3 mm. long, the longer (2–3 cm.) fertile stalk, and the short fruiting spike with large sporangia, 0.5–0.6 mm. in diameter.

Ophioglossum Thomasii, sp. nov.

Planta minima, 1.5–3.5 cm. alta, rhizomato brevissimo cylindrico, radicibus tribus vel quatuor filiformibus et uno vel duobus foliis; caulis communis 2–5 mm. longa; lamina oblanceolata, rotundata ad apicem, 1–4 mm. longa, 0.3–1.0 mm. lata; venae paucae, vena media et venae laterales duae convergentes cum vena media ad apicem; petiolus fertilis gracilissimus et filiformis, 1–3 cm. longus; spica fertilis 1–4 mm. longa, jugis sporangiorum 2–6; sporangia 0.5–0.6 mm. lata; apex sterilis spicae 0.5–1.0 mm. longus; sporae tetrahedrales, verrucosae, 50–70μ latae.

Ophioglossum Thomasii, n. sp.

Plant very small, 1.5–3.5 cm. high; rootstock very short cylindrical, bearing three or four thread-like roots and one or two leaves; common stalk 2–5 mm. long; blade oblanceolate, rounded at apex, 1–4 mm. long, 0.3–1.0 mm. wide; veins few, a median vein and two lateral veins converging with the median vein towards the apex; fertile stalk very slender, thread-like, 1–3 cm. long; fertile spike 1–4 mm. long, of 2–6 pairs of sporangia, 0.4 mm. in diameter; sterile tip of fertile spike 0.5–1.0 mm. long; spores tetrahedral, verrucose, 50–70μ in diameter.—TYPE in the herbarium of the British Museum of Natural History; locally frequent in swamp, Kabaka's Lake, Kampala, Uganda, March, 1936, *Thomas 1903.*

18. OPHIOGLOSSUM FERNANDEZIANUM C. Christensen

Ophioglossum fernandezianum C. Christensen, in Skottsberg Nat. Hist. Juan Fernandez and Easter Island. **2**:44. fig. 7. 1920. Based on specimens collected in August, 1917, by Bäckström, no. 1126, on slopes in the western part of the island of Masatierra. Two plants and the details of venation in a sterile blade are illustrated in the figure accompanying the original description.

Since no material of this species has been available for study, the original description is here reproduced. "*Ophioglossum fernandezianum* C. Chr. nov. spec. Rhizoma parvum, 3–4 mm. latum, hypogaeum, radiculas numerosas brunneas emittens. Folia saepe bina. Petiolus communis hypogaeus, tenuis, pallidus, compressus, rarius ad 2 cm. longus. Lamina sterilis petiole hypogaeo 0.5–1.5 cm. longo, pallido, complanato, ovata, 1.5–2.5 cm. longa, paulo supra basin rotundatam 10–14 mm. lata, apiculata, carnosula. Vena mediana indistincta, quam laterales vix crassior, interdum subnulla; areolae magnae. Vitta deest. Pedunculus spicae lamina sterili brevior vel subaequens, fere ad apicem hypogaeus et pallidus. Sporangia 7–10 juga, apice sterili spicae ovato-acuto."

Christensen states that this species belongs in the aggregation of forms called by Baker *O. nudicaule*, but that it can not be referred to any species listed in Prantl's monograph. He says that it differs from all other species of the genus in the long stalk of the sterile lamina and in the short fertile segment, which scarcely overtops the sterile blade. Further, he states that the whole common stalk, as well as the stalk of the sterile blade and nearly the whole fertile stalk are, at least in all specimens collected, hypogaeous and without chlorophyll.

Christensen's statement that this is most like *O. ypanemense* Mart. seems unjustified, since, in the plate accompanying the original description of that species, Martius portrays plants with small, basally inserted, sessile sterile blades far surpassed by the fertile segments, quite unlike the condition in *O. fernandezianum.*

19. **Ophioglossum scariosum,** n. sp. *Figure 33.*

Ophioglossum scariosum sp. nov.—Planta parva, 3.4–6 cm. alta, rhizomato subgloboso, 2–4 mm. crasso, radicibus carnosis numerosis et una aut plerumque duabus laminis fertilibus quoque tempore anni, basis plantae circumdata basibus persistentibus brunis foliorum temporis anni prioris; gemma nuda, circa 5 mm. longa; caulis communis, petiolus sterilis, et basis petioli fertilis, hypogeae et scariosae; caulis communis 0.4–1.5 cm. longus; petiolus sterilis 0.4–0.9 cm. longus; lamina coriacea. suborbicularis, oblonga-orbicularis, aut oblonga-ovata, apiculata ad apicem, plus vel minus truncata ad basim, 0.8–1.7 cm. longa, 0.9–1.3 cm. lata, ut videtur horizontalis; venae indistinctae, sine vena media valida et venis 8–12 emergentibus e basi laminae cedentibus in reticulum et formantibus areolas 2–4 mm. longas; petiolus fertilis 1.3–4.0 cm. longus; interdum ramis sporangiferis brevibus; spica fertilis 0.6–1.1 cm. longa, jugis sporangiorum 9–12; sporae recentes non valentes studi causa; prothallium incognitum.

Plant small, 3.4–6 cm. high, with subglobose rhizome, 2–4 mm. thick, bearing numerous fleshy roots and one or usually two fertile leaves during a single growing season; base of plant surrounded by persistent brown bases of leaves of previous seasons; bud exposed, about 5 mm. long; common stalk, sterile stalk, and base of fertile stalk hypogean and scarious; common stalk 0.4–1.5 cm. long; sterile stalk 0.4–0.9 cm. long; blade coriaceous, suborbicular, oblong-orbicular, or oblong-ovate, apiculate at apex, truncate or almost so at base, 0.8–1.7 cm. long, 0.9–1.3 cm. wide, apparently borne horizontally; venation indistinct, without a strong midvein and with the 8–10 veins arising from the base of the blade passing into an anastomosing network forming areoles 2–4 mm. long; fertile stalk 1.3–4.0 cm. long, occasionally with short sporangia-bearing branches; fertile spike 0.6–1.1 cm. long, with 9–12 pairs of sporangia; fresh spores not available for study; gametophyte unknown.—Type in the U. S. National Herbarium, from the vicinity of Oroya, Dept. of Junin, Peru, *A. S. Kalenborn 125* (U).

This species is most similar to *Ophioglossum fernandezianum* C. Christ., of the Juan Fernandez Islands, from which it differs in the shape of the sterile blade, which relatively, in proportion to the length, is much wider than in that species; in the long fertile stalk which regularly surpasses the blade in length; and in the occasional short sporangia-bearing branches of the fertile peduncle. In the shape and the apparently horizontal orientation of the blade, the species bears some resemblance to *O. crotalophoroides*, but it can be easily separated from that by the absence of a prominent globose rootstock and by the scarious stalk of the sterile blade. In this scarious character of the hypogean common stalk, sterile stalk, and base of the fertile stalk, *O. fernandezianum* and *O. scariosum* may be distinguished from all other species of *Ophioglossum*.

Besides the type collection may be cited the collection of *O. Buchtien 876* (U), Mar. 25, 1907, at 3900 m., La Paz, Bolivia, and additional material from Oroya, Peru, *Margaret Kalenborn 125* (G, NY).

Fig. 33. Type collection of *Ophioglossum scariosum.* No. 4 is the type specimen (×1).

20. OPHIOGLOSSUM SCHLECHTERI Brause

> *Ophioglossum Schlechteri* Brause, in Engl. Bot. Jahrb. **49:** 58–59. Fig. 3 E. 1913. Based on specimens collected on July 16, 1907 by Schlechter, no. 16280, in humus of the virgin forest of Kelel, Kaiser-Wilhelmsland, northeastern New Guinea. A single specimen and the summit of a fertile spike are illustrated.

Since no material of this species has been available for study, the original description is here reproduced. "*O. Schlechteri* Brause n. sp.—*O.* e turma *paraneura* Prantl. Rhizoma cylindricum. Folia singula, rarius bina. Petiolus epigaeus, 1–2,5 cm. longus, 0,5–0,8 mm. latus. Pedunculus e petiolo ortus. Lamina sterilis e basi breviter lateque cuneata ovata vel cordata, acutiuscula, 3–4 mm. longa, 2–3,5 mm. lata, subcarnosa, sicca vix pellucida, margine integra vel leviter crenata, nervo mediano validiore, substricto, ad laminae apicem versus indistincto, nervis lateralibus inconspicuis, 1–2 in utroque mediani nervi latere, subparallelis, venis transversis interdum conjunctis. Pedunculus petiolo plerumque paulum brevior, 0,9–2,3 cm. longus, subcuneatus, basi 0,7 mm., inter sporangia usque ad 1,8 mm. latus, in apicem acutiusculum desinens. Sporangia parva, angusta, 5–14—juga, cr. 0,25 mm. lata."

Brause states that this species is in habit and size nearest to *O. Schmidii* Kze., but in that the sterile blade is inserted lower down and the fertile portion is linear, very narrow between the sporangia, while in *O. Schlechteri* the free surface between the sporangia is perhaps wider than in any other *Ophioglossum*. The comparatively great width of the fertile spike, the small size of the sporangia which are 0.25 mm. in diam., and the small sterile blade which is inserted at the middle or even above the middle of the plant, distinguish this from all related species.

According to Brause, *O. Schlechteri* was collected in the humus of a virgin forest in association with species of *Sciaphila*, *Gymnosiphon*, and *Cotylanthra*.

21. OPHIOGLOSSUM OPACUM Carmichael

> *Ophioglossum opacum* D. Carmichael, in Trans. Linn. Soc. **12:** 509. 1818. Based on material collected from the top of the dome of the mountain, island of Tristan da Cunha. The species is illustrated by Hooker and Greville in Icones Filicum. 1: pl. 40B. 1831.

Since the writer, like Prantl, has had opportunity only to study the description and illustration furnished by Hooker and Greville, and Carmichael's description, the original diagnosis is here reproduced. "*Ophioglossum opacum*, spica caulina, fronde cordata opaca; venis inconspicuis, radice bulbosa."

Hooker and Greville state that this species is very nearly allied to *O. reticulatum*, but Prantl classifies it with *O. crotalophoroides*, from which it seems to differ chiefly in the shorter fertile segment, which apparently barely equals the opaque blade.

The species has also been collected in St. Helena (A. Br. in Kuhn, Fil. Afr. p. 178. 1868).

Since preparing the above, the writer has had opportunity to study a collection of *O. opacum*, loaned from the British Museum, gathered by Mr. Robertson on the island of St. Helena, June, 1773. These specimens have the globose rootstock not nearly as thick as in *O. crotalophoroides*, 3–6 mm. in diameter, while the fertile segment either equals or somewhat exceeds the sterile.

22. Ophioglossum crotalophoroides Walter. *Figure 26.*

Ophioglossum crotalophoroides Walter, Flora Caroliniana. p. 256. 1788. Based on material from Carolina. Described as "frondibus subcordatis, scapo frondibus tertius longiori."

Ophioglossum bulbosum Michaux, Fl. Bor. Am. **2**: 276. 1803. Nomen nudum.

Ophioglossum pusillum Michaux, Fl. Bor. Am. **2**: 276. 1803. Based on plants growing in sand in South Carolina.

?"*Ophioglossum pusillum* Raf., in Desv. Journ. de Bot. **4**: 273. 1814."

Ophioglossum pusillum Nuttall, Genera of North American Plants **2**: 248. 1818. Based on specimens growing on the margins of ponds in South Carolina and described as having cordate blades. The type, in the herbarium of the Philadelphia Academy of Natural Sciences, consists of small material without the base. There are four blades, one separate and three together; two with fertile spikes and one with the sporangia bearing portion broken off. The blades are subtruncate, ovate, and apiculate. This is questionable material which only doubtfully is to be referred here.

"*Ophioglossum tuberosum* Hooker and Arnott, Bot. Beech. Voy. p. 53. 1832."

Ophioglossum stipatum Colla, in Mem. Ac. Torino. **39**: 52. pl. 75, f. 1. 1836. Based on material sent from Chile. One plant is illustrated in the figure.

Ophioglossum vulgatum var. *crotalophoroides* (Walt.) D. C. Eaton, in Chapm., Fl. So. U. S. p. 599. 1860.

Plant 2–11 cm. high, with large globose-bulbous rootstock, 4–10 mm. in diameter, bearing several fibrous roots and usually several leaves during a single growing season; common stalk 0.7–2.5 cm. long; blade cordate, ovate, or rarely elliptical, abruptly contracted to a short (1 mm.) petiolate base, obtuse or rounded at apex, 1–1.5 cm. long, 0.8–1.2 cm. wide, usually borne horizontally; venation lax, often difficult to make out because of the rather thick texture of the blade; fertile stalk 1–7 cm. long; fruiting spike 3–11 mm. long; sporangia 0.6–1.2 mm. in diameter. Gametophyte unknown.

This is a very distinct species, at once characterized by the large globose-bulbous rootstock, the usually cordate blade which is borne horizontally, and the slender fertile segment which much exceeds the lamina. The only closely related species is *O. opacum*, in which the fertile segment merely equals the blade. That is only doubtfully specifically distinct from the present species.

O. crotalophoroides is a plant of damp pastures, old fields, grassy glades, open pine woods, and rarely rocky slopes. It ranges from South Carolina and Florida west through Alabama, Mississippi, and Louisiana to Texas, and south to Mexico, Guatemala, Colombia, Venezuela, Peru, Chile, Bolivia, Argentina, and Uruguay.

SOUTH CAROLINA. *T. Nuttall* (Ph). *H. W. Ravenel* (Ph).

FLORIDA. Citrus, Duval, Franklin, Manatee, Nassau, and Putnam Counties.

ALABAMA. Lee, Mobile, and Tuscaloosa Counties.

MISSISSIPPI. Clarke, Harrison, and Jackson Counties.

LOUISIANA. Orleans and Rapides Counties.

TEXAS. Harris and Hunt Counties.

MEXICO. States of Mexico and Michoacan.

GUATEMALA. Chimaltenango: Chichavac, *A. F. Skutch 604* (U); also *418* (U).

HONDURAS. Comayagua: El Achote, *T. G. Yuncker, R. F. Dawson* & *H. R. Youse 6357* (U).

COLOMBIA. Santander: edge of Paramo de las Vegas, 3300–3700 m.; *E. P. Killip* and *A. C. Smith 15611* (G, NY, U). Herbarium Lehmanniarum *5575* (U).

VENEZUELA. Los Andes: Tovar, *A. Fendler 342* (G, Ph).

PERU. Cuzco, Apurimac Valley, *F. L. Herrera 3076* (U).

CHILE. Valparaiso. *D. Bertero 1195* (G, NY, U); also *Capt. King 1364* (G). *Dr. Styles* (Ph).

BOLIVIA. Larecaja: Soratora, *G. Mandon 1601* (G, NY). *E. Asplund 4840* (U). *O. Buchtien 443* (U).

ARGENTINA. Buenos Aires: Tapiales, *A. Burkart 2205* (G).

URUGUAY Montevideo: Punta Gorda, *G. Herter 12* (G, H); also *71213* (NY); Punta Brava, *Corn. Osten 5273* (U).

23. OPHIOGLOSSUM LANCIFOLIUM Presl

Ophioglossum lancifolium Presl, Suppl. Tent. Pterid. p. 50. 1845. Based on material from the island of Mauritius.

Plant slender, 6–13 cm. high, with short cylindrical rootstock bearing several fibrous roots and usually one leaf during a single growing season; common stalk 2.5–5 cm. long; blade membranous, elliptic-lanceolate, 1.8–4.5 cm. long, 3–8 mm. wide; veins forming long slender areoles, particularly below; fertile stalk 2.5–7.3 cm. long; fruiting spike 1–2.8 cm. long; sporangia 0.4–1.0 mm. in diameter.

This species was described from the island of Mauritius by Presl. Later students have also reported it from Madagascar, where Christensen (1932) suggests that it may intergrade with forms of *O. nudicaule*. It is distinguished from that species by the long common stalk and by the long narrow sterile blade.

The writer has seen specimens only from the Philippines. These seem to agree in all respects with Presl's original description.

PHILIPPINES. Island of Mindanao. Davao: Todaya (Mt. Apo). *A. D. E. Elmer 11050* (U). Rio Lanati, *A. Loher 853* (M, U).

Since writing the above, the writer has had opportunity to study two collections loaned from the British Museum: *W. J. Eggeling 2081,* from marshy Imperata Swamp, near Budongo, Uganda; and *J. M. Hildebrandt 3850,* Imerina, central Madagascar.

24. Ophioglossum lusitanicum L. *Figure 28.*

Plant 2–12 cm. high, with cylindrical rootstock surrounded by a sheath formed by the remains of the persistent bases of the leaf stalks of previous seasons; common stalk 0.5–3.5 cm. long; blade rather fleshy, cuneate or rarely subtruncate at base, linear, linear-lanceolate, elliptical, or ovate-lanceolate, obtuse or acute at apex, 0.5–5 cm. long by 0.1–1.0 cm. wide; veins several forming small areoles; fertile stalk 1–7 cm. long; fruiting spike 0.4–1.7 cm. long; sporangia 0.4–1.2 mm. in diameter. Gametophyte unknown.

O. lusitanicum may be distinguished from related forms by the rather fleshy lamina, the short fertile segment which does not far surpass the blade, and the brown sheath about the rootstock. The species is divisible into three subspecies. These are separated in the following key:

A. Sterile blade very narrow, 1–5 (–7) mm. broad, usually widest above middle and tending to be obtuse or blunt at apex; meshes of veins few. Plants of southern Europe, Asia, and Africa. 23a. *O. lusitanicum* ssp. *typicum*

A. Sterile blade broader, 3–10 mm. wide, usually broadest at or below middle and tending to be acutish at apex; meshes of veins more numerous. B

  B. Sterile blade large, 1–5 cm. long by 0.5–1.0 cm. wide, short attenuate at base. Plants of California and Mexico. 23b. *O. lusitanicum* ssp. *californicum*

  B. Sterile blade smaller, 1–3 cm. long by 0.3–0.8 cm. wide, longer attenuate at base. Plants of southern South America, New Zealand, and Australia. 23c. *O. lusitanicum* ssp. *coriaceum*

24a. Ophioglossum lusitanicum L., ssp. typicum

Ophioglossum lusitanicum L., Sp. pl. **2:** 1063. 1753. Based on material from Portugal.

Ophioglossum Loureirianum Presl, Suppl. Tent. Pterid. p. 55. 1845. Based on material from Cochin-China which Loureiro (Fl. Coch. **2:** 825. 1790) listed as *O. lusitanicum*. The writer has not seen the type.

Ophioglossum lusitanicum L., var. *britannicum* Le Grand, in Bull. Soc. Bot. France **44:** 219. fig. 1897. Based on a single specimen found in the midst of a large colony of normal *O. lusitanicum* at Lanveoc near Brest. This probably should be referred here.

Ophioglossum alpinum Rouy, in Bull. Soc. Bot. France **44:** 437. 1897. Based on specimens from dry swards of the Bourget-au-dessus of Briancon, Hautes-Alpes, France. The description indicates material intermediate between *O. lusitanicum* and *O. vulgatum*, which only doubtfully belongs here.

Ophioglossum Braunii Prantl, in Ber. deutsch. bot. Ges. **1:** 351. 1883. Based on specimens from the Cape Verde Islands.

Plant 2–10 cm. high, with sterile blade fleshy, linear, elliptic-lanceolate, or oblanceolate, usually widest above middle and tending to be obtuse or blunt at apex, 0.8–1.7 cm. long, 0.1–0.7 mm. wide; venation lax, with few parallel veins forming large areoles.

O. lusitanicum ssp. *typicum* is a plant of open sandy or grassy places, pastures, and glades. It occurs in Iceland, France, Portugal, Italy, Azores, Madeira, Algeria, and Afghanistan, also elsewhere in Asia and Africa.

ICELAND. Crater of Volcano near Reykjahlid, Myvatu, *Miss E. Taylor* (G, Ph, U).

FRANCE. Basses Pyrénees: Pau, *B. de Brutelette* (G, M). Channel Islands: Guernsey *W. Luff* (NY). Corsica: Bonifacio, *E. Reverchon 10* (M): Bastia, *C. Mob* (M). Finistère: Brest, *R. Lenormand* (M). Var: Hyères, *C. Lory* (M). Cap Ferret, Herb. J. Gay (G).

ITALY. Campania: Naples, *R. C. Alexander* (Ph, U). Sardinia: Sta. Teresa, *E. Reverchon* (G, U). Sicily: Messina, *H. Ross 300* (G, U); Pantelleria, *H. Ross* (G, NY). Tuscany: Pisa, *J. Ball* (G). Venezia Gulia E. Zara: Ravigno, *Tommasini* (NY); Torre d'Orlando, Pola, *Tommasini 1584* (M). Granabello, *N. A. Pedicino 1869* (M).

AUSTRIA. *K. Hulch* (U).

GERMANY. ———, *G. K. Merrill* (G).

PORTUGAL. "Lingua de Cobra menor, in pinetis sabulosis trans Tagum in valle de Zebro rarissimum, Feb. 1840," *Welwitsch 316* (M).

AZORES. San Miguel, *Sophie Brown* (M).

MADEIRA. ———, *H. Falkenan* (C). ———, *R. T. Lowe* (G).

ALGERIA. Boujareah, *L. Durando 1586* (M). Mostagenem, *B. Balansa* (G).

AFGHANISTAN. ———, *J. C. G. Aitcheson 437* (Ph).

INDIA. Reported (cf. Kew Bull. p. 278. 1936) from east coast, Chingleput District, near Vandalur, amongst grass in open places and in scrub jungle, 200 ft., E. Barnes 298.

24b. **Ophioglossum lusitanicum** ssp. **californicum** (Prantl), n. comb.

Ophioglossum vulgatum Cleveland (not L.), in Bull. Torr. Club **9**: 55. 1882. Referred to plants from Arizona and California.

Ophioglossum californicum Prantl, in Ber. deut. bot. Ges. **1**: 351. 1883. Based on specimens collected in April, 1882, by Cleveland at San Diego, Calif. Cotypic material at the Gray Herbarium and the Herbarium of the New York Botanical Garden has been examined by the writer.

Plant 3–13 cm. high, with sterile blade of firm texture or somewhat fleshy, elliptical or lanceolate, widest at or below the middle and tending to be acute at apex, 1–5 cm. long, 0.5–1.0 cm. wide; venation rather diffuse, with many parallel veins (6+) forming numerous small areoles.

This is a plant of moist mesas in California, Lower California, and parts of central Mexico. While most of the plants belonging to this subspecies are quite distinct, some individuals closely approach forms of ssp. *typicum* and *coriaceum*, from which they can scarcely be separated, except as the place of collection is taken into consideration.

CALIFORNIA. Amador: Ione, *E. Braunton 1255* (G, M, NY, U). Monterey: Monterey, *E. K. Abbott* (G, NY). San Diego: San Diego, *D. Cleveland* (G, NY).

MEXICO. Baja California: near Encenada, *M. E. Jones 3750* (NY, U, Herb. I. W. Clokey); ———, *C. G. Pringle* (G, M, NY, U). Mexico: Nevado de Toluca, *J. N. Rose & J. H. Painter 7875* (G, M); ?Ajusco, *C. R. Orcutt 3733* (M, U).

24c. **Ophioglossum lusitanicum** ssp. **coriaceum** (Cunn.), n. comb.

Ophioglossum gramineum R. Brown (non Willd.), Prod. Fl. Nov. Holl. p. 163. 1810. Based on material from Australia which, from the short description and according to Prantl, should be referred here.

Ophioglossum coriaceum A. Cunningham, in Hooker's Companion to the Botanical Magazine **2**: 361. 1836. Based on specimens from Matauri, New Zealand.

Ophioglossum vulgatum var. ε *minimum*, var. β *costatum*, var. γ *gramineum*, and var. δ *lusitanicum* J. D. Hooker, Fl. Nov. Zeal. **2** (2): 50. 1855. These four varieties represent minor forms which Hooker states are common in grassy places throughout the Northern and Middle Islands.

Ophioglossum minimum (Hk. fil.) Armstrong, in Trans. N. Zeal. Inst. **13**: 342. 1881. Based on specimens collected on the Canterbury Plains near Christchurch.

Plant 3–9 cm. high, with sterile blade rather fleshy, narrowly elliptical, linear, or linear-lanceolate, widest towards the middle, acute or obtuse at apex, 1–3 cm. long, 0.3–0.8 cm. wide; venation intermediate between that in ssps. *typicum* and *californicum*.

The subspecies *coriaceum* is only doubtfully distinct from ssp. *californicum*, while many individuals occur which are almost indistinguishable from ssp. *typicum*. This population definitely does not merit specific recognition, even though most modern authors have so maintained it.

O. lusitanicum ssp. *coriaceum* is a plant of grassy open places in Bolivia, Chile, New Caledonia, Australia, and New Zealand.

Bolivia. Cochabamba: Cochabamba, *A. M. Bang 946* (M, NY, U). Larecaja: Sorata, *G. Mandon 1600* (G, NY). Challopata, *E. Asplund 4839* (U).

Chile. Aconcagua: Lamache, *G. Looser 2565* (NY, U); also *1997* (G).

Isle of Pascua. Mt. Katiki, *C. & I. Skottsberg 651* (G, NY, U).

New Caledonia. ———, *I. Franc 487* (NY).

Australia. New South Wales: Coolabok, *J. G. Smith* (M); Hunter River, ———, (NY). Victoria: Melbourne, ——— (NY); by the Yarra, ——— (NY).

Tasmania. Near Perth, ——— (NY).

New Zealand.

North Island. Auckland: Kapiti, *J. W. Brame* (U); Little Barrier Island, *T. Kirk* (G, M). Wellington: Cape Terawhiti, *T. Kirk 840* (U). Pohue, *T. Kirk* (M).

South Island. Canterbury: Waimakariri, *T. Kirk* (G). Marlborough: Marlborough, ——— (C). Mt. Tulesse, *T. Kirk* (M).

25. Ophioglossum gramineum Willd.

"*Ophioglossum gramineum* Willd., Schrift. Ak. Erfurt. 1802. 18. t. 1, f. 1."

Ophioglossum costatum R. Brown, Prod. Fl. Nov. Holl., p. 163. 1810. Since the writer has not seen the type specimen, he, like Prantl (1884), is in doubt whether this should be referred here.

Ophioglossum gracillimum Welwitsch, in Hooker and Baker, Synopsis Filicum, p. 445. 1868. Based on material from Angola with a truly linear, very narrow sterile blade.

Ophioglossum lusitanicum var. *gracillimum* A. Braun; in Kuhn. Fil. Afr. p. 177. 1868. Based on plants collected in 1857 by Welwitsch, no. 36. near Catete, district of Pungo Andongo, Angola.

Ophioglossum vulgatum var. *lanceolatum* Luerssen, in Journ. Mus. Godeffr. **8**: 247c. pl. 12. 1875. Based on material from Queensland, Australia. The writer has decided, as a result of studying Luerssen's figures, that this should be referred here.

Ophioglossum lusoafricanum Welw., Prantl, in Ber. deutsch. bot. Ges. **1**: 351. 1883. Based on plants collected in 1857 by Welwitsch, no. 34, on the heights of Pedra Cazella, district of Pungo Andongo, Angola. Apparently this differs from the preceding only in the larger spores, which would scarcely seem a sufficient distinction for specific segregation in this highly variable genus.

Ophioglossum Dietrichiae Prantl, in Ber. deutsch. bot. Ges. **1**: 352. 1883. Based on the collection of A. Dietrich from Rockhampton, Queensland, Australia. The writer does not consider the venation characters, as described by Prantl, of sufficient value to separate this from *O. gramineum* Willd.

Ophioglossum lanceolatum (Luerss.) Prantl, in Ber. deutsch. bot. Ges. **1**: 352 1883.

Ophioglossum moluccanum f. *inconspicuum* Raciborski, in Nat. Tijdschr. Ned. Ind. **59**: 237. pl. 2, f. 5. 1900. Based on specimens from Java.

Ophioglossum Prantlii C. Christensen, Index Filicum, p. 471. 1906. This is a renaming of *O. lanceolatum* because of the earlier homonym of Watelet, which probably equals a form of *O. vulgatum* L.

Ophioglossum inconspicuum (Rac.) van Alderwerelt van Rosenburgh, in Bull. Dept. Agric. Ind. Neerl. **21**: 9. 1908. Based on the collection of Versteegh, no. 1942, from New Guinea. Said to differ from the type in being two or more times as large and in having the fronds more numerous, even to 12–15, and tufted.

Ophioglossum gregarium Christ, in Nova Guinea. Botanique 1. **8**: 164. 1909. Based on *O. inconspicuum* var. *majus*.

Although the writer has not had the opportunity to examine authentic material of any of the above listed names, he is venturing to place them together as synonyms of *O. gramineum*, since, from a study of the original descriptions and discussions in the literature, he has been unable to discover fundamental characters to justify these various segregations. Abundant material and careful study is necessary to determine the relationships and limits of this species group. In the absence of material, no satisfactory conclusion can be reached.

The following brief generalized description has been compiled from the literature: Plant slender, 5–15 cm. high, with cylindrical rhizome bearing one or several leaves; sterile blade linear or linear-lanceolate, acute, 1–5 cm. long and 1–2 (–3) mm. broad, with only 2 or 3 parallel veins.

As here considered this aggregate species occurs in Africa, India, the East Indies, and Australia.

Since writing the above, the writer has had opportunity to examine a sheet, loaned from the British Museum, representing the collection of *R. G. N. Young 854*, from Malange, Angola.

26. OPHIOGLOSSUM LINEARE Schlechter and Brause

Ophioglossum lineare Schlechter & Brause, in Engl. Jahrb. **49**: 59. fig. 3F. 1912. Based on specimens collected in July, 1902, by Schlechter, no. 14634, in the virgin forest at Punam, 600 m., Neu-Mecklenburg, Bismarck-Archipelago.

Since no material of this species has been available for study, the original description is here reproduced. "*Ophioglossum lineare* Schlechter et Brause n. sp.—Rhizoma cylindricum. Folia singula, usque ad 5,5 cm. longa, laminam sterilem non formantia. Petiolus (simul pedunculus) 5 cm. longus, 1–1,5 mm. latus, sublinearis, in apicem obtusiusculum desinens, pellucidus; nervo mediano validiore, substricto, usque ad folii apicem conspicuo, utrinque singulos vel binos nervos laterales interdum anastomosantes emittente. Sporangia usque ad 12-juga, cr. 0,5 mm. lata."

Brause states that *O. lineare* is like *O. simplex* Ridley of Sumatra, with no sterile blade, but that species is much larger, being 10–15 cm. high and 3 mm. broad instead of 5 cm. high and 1–1.5 mm. broad as in *O. lineare*. Since no anatomical study has been made of this species, it is doubtful whether it is truly a member of the subgenus *Ophioderma* to which *O. simplex* belongs or whether it represents a reduced state of *Euophioglossum*.

According to Dr. Schlechter, this small species grows in the humus of the virgin forest in association with *Burmannia neohiberna*, *Sciaphila*, and *Epirhizanthes*.

D. Subgenus **Rhizoglossum** (Presl) Clausen, n. stat.

Rhizoglossum Presl, Suppl. Tent. Pterid. p. 48. 1845.

This subgenus is characterized by having the fertile and sterile segments separate to the base. The fertile segments are borne from the center of the erect rootstock, surrounded by the several linear sterile blades. The roots are numerous and borne in a fascicle. Only one species is known.

27. OPHIOGLOSSUM BERGIANUM Schlechtendal

Ophioglossum Bergianum Schlechtendal, Adumbratio Fil. in Promontorio Bonae Spei Prov. p. 10. 1825. Based on specimens collected in June on the west side of Mt. Leuweberg, Cape of Good Hope, Africa.

Rhizoglossum Bergianum (Schlecht.) Presl, Suppl. Tent. Pterid. p. 48. 1845.

Plant 2–6 cm. high, with short erect rhizome bearing numerous roots in a fascicle and several leaves with the fertile and sterile segments separate to the base; rootstock surrounded by a brown sheath formed by the persistent bases of the old leaf stalks; sterile blades 3–4, 1.6–2.5 cm. long, 0.5–1 mm. wide, linear, surpassed by the fertile segments; the latter 3–4, 1–5 cm. long and 0.3–1 mm. wide, with the stalk 0.5–3 cm. long, fruiting spike 2–5 mm. long, sterile tip linear acuminate, 1.8–4 mm. long; sporangia in about 5–6 pairs, 0.3 mm. in diameter. Gametophyte unknown.

This interesting and striking little plant is known only from Cape Colony, where it has been collected at several places on the plains and mountain sides.

Cape of Good Hope. Lammkrall, *R. Schlechter 10843* (M, NY, Ph, U). Wynberg, *R. Schlechter 1400* (G). *Rawson 1580* (M).

The writer has also recently examined some specimens, loaned from the British Museum, from Table Mountain, Cape Town, and the Stellenbosch Flats. In some of these the sterile blades are linear-oblong and attain a length of 5 cm. and a width of 4 mm.

E. Dubious and Rejected Names

Hemionitis falcata Willd., Sp. pl. **5**: 126. 1810. Mr. C. A. Weatherby has kindly loaned to the writer a photograph of the type, preserved in the herbarium at Berlin. This consists of a portion of a sterile lamina which has been identified by both Mettenius and Hieronymus as *Ophioglossum pendulum.* Without study of the type itself, however, this name can not be definitely placed. Should the specimen prove to be *O. pendulum*, then *Antrophyum zosteraefolium* Fee, which was founded on it, also becomes a synonym of that species.

Ophioglossum Alleni Lesquereux, in U. S. Geol. Surv. Terr., Sixth Ann. Rept. 1872: 371. 1873. Described from the Miocene Tertiary Shales of Florissant, Colorado. Hollick (1923) has demonstrated that this is neither an *Ophioglossum* nor any other kind of a pteridophyte, but that it probably represents a carpellary structure of a spermatophyte.

Ophioglossum binervatum Diels & Schltn. Apparently never published. Specimens distributed under this name are to be referred to *Ophioglossum nudicaule* L. fil.

Ophioglossum decipiens G. Poirault, in Ann. Sc. Nat. Series 7. **18**: 146. 1893. Based on material collected in Sept., 1866, by Bourgeau (Herbier de la commission scientifique du Mexique no. 3073) at "Borrego, région d'Orizaba." Since the writer has not had opportunity to study the type, he has been unable satisfactorily to dispose of this name. The original description somewhat suggests *O. Engelmanni.*

Ophioglossum hastatiforme Cockerell, in Torreya **24**: 10. 1924. Based on two specimens from the Wind River or Bridger formation, Eocene Tertiary, Tipperary, Wyoming. These specimens were subsequently declared by Berry (1924) to be *Danaea canadensis* Knowlton. Upon further study, Cockerell (1926) rejected this suggestion and stated that *O. hastatiforme* not only was not a *Danaea*, but also that it was probably not even a pteridophyte. He then suggested that it might represent some kind of fossil alga. He further stated that L. Ward had described a similar fossil, *Xantholithes propheticus*, from Laramie, near Glendive, Montana. Since this seemed to him to be congeneric with *O. hastatiforme*, Cockerell renamed his plant *Xantholithes hastatiformis.*

"*Ophioglossum pubescens* Rafinesque, in Journ. de Bot. **4**: 273. 1814." The writer has not found the description of this species in the volumes of the Journal de Botanique which he has examined.

Ophioglossum Usterianum Christ, in A. Usteri, Fl. Sao Paulo. p. 137. 1911. Based on material collected in a very dry field near Santa Anna, Sao Paulo, Brazil. In the absence of specimens, the writer has been unable properly to locate this name. The description suggests that it may represent a form of *O. reticulatum* or perhaps of *O. petiolatum.*

Ophioglossum valdivianum R. A. Philippi, in Linnaea. **33**: 306. 1865. Based on material from the Province of Valdivia, Chile. Without seeing specimens, the writer does not know how to treat this name.

PHYTOGEOGRAPHIC CONSIDERATIONS

The *Ophioglossaceae* are of world wide distribution. One or more of the fifty-two species here recognized occurs on every major land mass of the earth's surface, except at the two poles, where conditions are unsuitable for vascular plant life.

No fossils, either of extinct or living species, are known. This is probably because herbaceous plants of this type, consisting usually only of a single leaf and a short rhizome, would not be likely to be preserved in the rock strata. Despite the lack of fossil evidence, however, there can be no question that the *Ophioglossaceae* are among the most primitive of the true ferns. The wide ranges of many of the species, the extreme variability of the forms within the genera, the relatively simple morphological structure, all indicate a decidedly primitive group.

Of the vascular plants, we find wide and broken ranges similar to those exhibited by certain species of *Botrychium* and *Ophioglossum*, only among some of the *Lycopsida: Lycopodium, Isoetes,* and *Equisetum*, in which the same species may occur in an identical form in such widely separated regions as the southeastern United States, Madagascar, and the East Indies. In *Ophioglossum*, species like *O. reticulatum*, *O. petiolatum*, *O. nudicaule*, and *O. palmatum* are of just such very wide distribution throughout tropical and subtropical regions, although the last is known only from isolated and widely separated stations. These wide ranges may indicate one of two things. Either the wind blown spores of the *Ophioglossaceae* are admirably suited for wide dissemination and are carried long distances where they germinate and start new colonies, in which case the wide ranges may have been developed in a very short period during modern times; or these plants were at one time much more widespread than at present and now exist only in isolated regions as remnants or relics. For the first three species of *Ophioglossum* cited above, the former argument would seem to hold, while for *O. palmatum*, certain of the widespread Botrychia with broken ranges, like *B. Lunaria*, as well as several other Ophioglossa, the latter argument would seem more appropriate.

The writer would conclude from the behavior of those species which he has been able to study in the field in the northeastern United States, that most of the forms possess the ability to move about, producing new colonies and adapting themselves readily to varying conditions. Thus, while the family is an old one, the present day species exhibit certain of the characteristics of a modern group.

Before we can properly derive much significance from the distribution of these plants, much more collecting must be done. Even for the more intensively botanized regions, only an incomplete picture of the detailed distribution of the various species is available, while from many vast areas, like most of South America, Africa, and Australia, as well as much of Central America, almost nothing is known, if we consider the scant collections that are now available in the light of the size of these great land areas.

CONCLUSIONS

In this paper the writer has discussed 52 species. These are arranged in three genera:

Botrychium	23 species
Helminthostachys	1 species
Ophioglossum	28 species

Botrychium and *Ophioglossum* have been divided respectively into three and four subgenera. The species have been arranged in these subgenera according to what the writer considers to be a natural series.

Many species have been redefined, their ranges more fully stated, and their relationships developed so far as our present knowledge permits. Where divisions of species are correlated with geographical range, these have been treated as subspecies, while minor divisions of species not correlated with range have been treated as varieties. One subspecies of *Botrychium matricariaefolium*, one variety of *Botrychium simplex*, two species of *Ophioglossum*, and three varieties of *Ophioglossum nudicaule* are described as new.

Only two new species are described. The writer has not been surprised to find no more than two new species in this group, because it has been a popular one with fern students, both amateur and professional, for a long period. Whenever a form has been found that is even slightly different from the usual, it has been quickly described as new. Hence, there is an available name, or rather there are usually several available names, for every minor variation, and, as a result, this monograph has been a work of synonymy.

The classification here set forth is one based on the general gross morphology of the plants. Since technical characters based on venation or on spores have seemed neither reliable nor practical, they have been used less in this monograph than in previous papers. There will be criticism of the present treatment for this reason, but the writer feels that a frank admission of the unsatisfactory nature of certain of these characters, and the use of only those characters which can be easily understood and clearly interpreted by general students, may represent a much more helpful contribution, than an attempt to be highly technical and to use characters which can neither be clearly checked nor understood by others than specialists in the group, particularly when those technical characters are found to be entirely unsatisfactory for taxonomic purposes.

In this paper, most of the essential taxonomic data relating to the *Ophioglossaceae* and available up to the present time, have been brought together. With these data now organized, the way is open for serious work within the family.

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Literature cited

Alderwerelt van Rosenburgh, C. R. W. K. van. 1909. Malayan Ferns.

————. 1911. New or interesting Malayan ferns. 3. Series 2, no. 1, p. 1–29.

————. 1913. New or interesting Malayan ferns. 5. Series 2, no. 11, p. 1–38.

————. 1916. Malayan ferns and fern allies. Supplement 1. p. 453–455.

Almeida, J. D. d'. 1922. The Indian Ophioglossums. Journ. Ind. Bot. Soc. **3**: 58–65.

Angström, J. 1854. Anmärkingar om de skandinaviska arterna af slägtet *Botrychium*. Bot. Not. Nos. 5 & 6: 65–72.

Baas-Becking, L. G. M. 1920. Origin of the vascular structure in the genus *Botrychium*, with notes on the general anatomy. Rec. Trav. Bot. Nieuwl. **18**: 333–375.

Baker, J. F. 1891. A summary of the new ferns which have been discovered or described since 1874. Ann. Bot. **5**: 181–221, 301–332, 455–500.

Ballard, A. F. 1934. *Botrychium chamaeconium*. Bitter & Hier. In Hooker's Icones Plantarum **33**: pl. 3255. p. 1–2.

Bauhin, Caspar. 1620. *Ophioglossum* and *Lunaria*. In Prodromus theatri botanici. p. 354–355.

Bauhin, J. and Cherlero, J. H. 1651. *Ophioglossum* and *Lunaria*. In Historia plantarum universalis. **3**: 708–712.

Beer, R. 1906. On the development of the spores of *Helminthostachys zeylanica*. Ann. Bot. **20**: 177–186. pl. 11 & 12.

Benedict, R. C. 1908. Studies in the *Ophioglossaceae*. II. A descriptive key to *Botrychium* in North America. Group of *B. lanceolatum*. Torreya **8**: 100–103.

————. 1909. Studies in the *Ophioglossaceae*. III. Key to *Botrychium* in North America: Group of *B. ternatum*. Torreya **9**: 197–200.

Berry, E. W. 1924. *Ophioglossum hastatiforme* Ckl., not an *Ophioglossum*. Torreya **24**: 49–50.

Bitter, G. 1902. *Ophioglossales*. *In* Die Natürlichen Pflanzenfamilien, begr. von A. Engler und K. Prantl. Leipzig. p. 449–472, 799–800. fig. 258–263.

Bower, F. O. 1894. A theory of the strobilus in archegoniate plants. Ann. Bot. **8**: 343–365.

———. 1896. Studies in the morphology of spore-producing members. II. *Ophioglossaceae.* London, Dulau and Co. p. 1–87. pl. 1–9.

———. 1903. Studies in the morphology of spore-producing members. V. General comparisons and conclusions. Phil. Trans. Roy. Soc. London. **196B**: 191–257.

———. 1907. *Ophioglossum simplex* Ridley. Ann. Bot. **18**: 205–216. pl. 15.

———. 1926. *Ophioglossaceae. In* The ferns. **2**: 42–94. illus.

Britton, E. G. 1897. A revision of the North American species of *Ophioglossum.* Bull. Torr. Club **24**: 545–559. pl. 318–319.

Bruchmann, H. 1904. Ueber das Prothallium und die Keimpflanze von *Ophioglossum vulgatum* L. Bot. Ztg. **62**: 227–247.

———. 1906. Ueber das Prothallium und die Sporenpflanze von *Botrychium Lunaria* Sw. Flora **96**: 203–230. pl. 1–2.

Butters, F. K. 1917. *Botrychium virginianum* and its American varieties. Rhodora **19**: 207–216. fig. 6.

Campbell, D. H. 1886. The development of the root in *Botrychium ternatum.* Bot. Gaz. **11**: 49–53. pl. 4.

———. 1895. The structure and development of the mosses and ferns (Archegoniatae). London, Macmillan & Co., 1895. p. i–viii, 1–544. ill.

———. 1904. The affinities of the *Ophioglossaceae* and *Marsileaceae.* Am. Nat. **38**: 761–775.

———. 1907. Studies on the *Ophioglossaceae.* Am. Nat. **41**: 139–159.

———. 1911. The Eusporangiatae. *Ophioglossales.* Carneg. Inst. Wash. Pub. 140. p. 5–116.

———. 1920. The genus *Botrychium* and its relationships. Proc. Nat. Acad. Sc. (U. S.) **6**: 502–503.

———. 1921. The gametophyte and embryo of *Botrychium obliquum,* Muhl. Ann. Bot. **35**: 141–158. pl. 8, fig. 1–11.

———. 1922. The gametophyte and embryo of *Botrychium simplex,* Hitchcock. Ann. Bot. **36**: 441–455. pl. 16, f. 1–10.

Cheeseman, T. F. 1925. *Botrychium australe.* In Manual of the New Zealand Flora. p. 94.

Christensen, C. 1906. Index filicum. i–lix, 1–744. Hafniae, H. Hagerup. Also Supplements 1, 1913, p. 1–131; 2, 1917, p. 1–60; and 3, 1934, 1–219.

———. 1932. *Ophioglossaceae in* The Pteridophyta of Madagascar. Dansk Bot. Ark. **7**: 183–186. pl. 74.

Chrysler, M. A. 1910. The nature of the fertile spike in *Ophioglossaceae.* Ann. Bot. **24**: 1–18. pl. 1–2, fig. 1–16.

———. 1925. *Botrychium lanuginosum* and its relation to the problem of the fertile spike. Bull. Torrey Club **52**: 127–132. pl. 4.

———. 1926. Abnormalities in *Botrychium* and certain other ferns. Bull. Torrey Club **53**: 279–288. pl. 9, fig. 1–5.

Clausen, R. T. 1934. Studies in the genus *Botrychium* in northeastern North America. Manuscript thesis. p. 1–106. pl. 1–19.

———, **and Edwards, J. L.** 1937a. The *Ophioglossaceae* of New Jersey, a study in local distribution. Bull. Torrey Club **64**: 269–285. *pl.* 7.

———. 1937b. A monograph of the *Ophioglossaceae*. Manuscript thesis. p. 1–278. figs. 1–44.

———. 1938. *Ophioglossum petiolatum* Hooker. Am. Fern Journ. **28**: 1–11 pl. 1–3.

Cockerell, T. D. A. 1926. The supposed fossil *Ophioglossum*. Torreya **26**: 10–11.

Copeland, E. B. 1909. The ferns of the Malay-Asiatic region. Part 1. Phil. Journ. of Science **4**: 1–65. pls. 1–21.

Couch, G. C. 1937. Unusual fall growth of *Ophioglossum Engelmanni*. Proc. Okla. Acad. Sci. **17**: 58.

Davenport, G. E. 1877. Notes on *Botrychium simplex*. Salem, Mass., John H. Choate. p. 5–22. pl. 2.

————. 1878. Vernation in Botrychia. Bull. Torrey Club **6**: 193–199. pl.

———. 1881. Vernation in Botrychia. Bull. Torrey Club **8**: 100–101.

————. 1897. *Botrychium ternatum* Sw., and its varieties. Fern Bull. **5**: 40–43.

Du Rietz, G. E. 1930. The fundamental units of biological taxonomy. Svensk. Botanisk Tidskrift. **24** (H.3): 333–428.

Eames, A. J. 1936. *Ophioglossaceae*. *In* Morphology of vascular plants. p. 117–143. fig. 78–90.

Eaton, D. C. 1878. The ferns of North America. v. **1**. illus.

————. 1881. *Botrychium matricariaefolium* A. Br. Bull. Torrey Club **8**: 100.

Ewart, A. J. 1930. Flora of Victoria. p. 1–1257.

Farwell, O. A. 1916. Fern notes. Rept. Mich. Acad. Sci. **18**: 78–94.

————. 1924. *Botrychium*. *In* Michigan. Papers Mich. Acad. Sci. Arts and Letters. **3**: 89–90.

Farmer, J. B. & Freeman, W. G. 1899. On the structure and affinities of *Helminthostachys zeylanica*. Ann. of Bot. **13**: 421–444. pls. 21–23.

Fernald, M. L. 1915. *B. angustisegmentum* (Pease and Moore) n. comb. Rhodora **17**: 87.

————. 1936. Minor forms and transfers. Contr. Gray Herb. **113**: 233–236.

Fuchs, L. 1542. *Lunaria minor*. *In* De Historia stirpium. p. 481–482.

Gmelin, S. G. 1768. *Osmunda lanceolata* and *Osmunda multifida*. Nov. Comment. Acad. Petrop. **12**: 517–518. pl. 11.

Graves, E. W. 1931. Botrychiums of the Central States. Am. Fern Journ. **21**: 125–132. pl. 11.

————. 1932. The Botrychiums of Indiana. Am. Fern Journ. **22**: 48–52.

————. 1935. Describing Botrychiums. Am. Fern Journ. **25**: 109–120. pl. 9–11.

Gray, S. F. 1821. A natural arrangement of British plants. **2**: 19.

Hofmeister, W. 1855. Keimung des *Botrychium Lunaria*, Sw. Bonplandia **3**: 331–335. pl. 3.

————. 1857. Keimung und Entwickelung des *Botrychium Lunaria*. Entwickelung der Vegetationsorgane von *Ophioglossum vulgatum* L. Abh. der k. Sächs. Gesell. der Wissen. Leipzig. Bd. 5. Abh. der math.-phys. classe **3**: 657–664. pl. 12.

Holle, H. G. 1875. Ueber Bau und Entwickelung der Vegetationsorgane der Ophioglosseen. Bot. Zeit. **33**: col. 241–254, 265–276, 281–289, 297—302, 313–322. pl. 3 & 4.

Hollick, A. 1923. Taxonomic and morphologic status of *Ophioglossum Alleni* Lesquereux. Bull. Torrey Club **50**: 207–213.

Holmberg, O. R. 1922. *Botrychium intermedium.* *In* Hartman's Handok i Skandinaviens Flora Häfte **1**: 33.

Hooker, W. J. and **Baker J. G.** 1868. Synopsis filicum. p. 1–482. pl. 1–9.

Hultén, E. 1928. *Ophioglossaceae,* in Flora of Kamtchatka and the adjacent islands. Kungl. Sv. Vet. Akademiens Handlingar **5**(1): 45–50.

Jeffrey, E. C. 1897. The gametophyte of *Botrychium virginianum.* Ann. Bot. **11**: 481–426.

————. 1898. The gametophyte of *Botrychium virginianum.* Univ. of Toronto Studies. Biological Series. No. 1: 3–32. pl. i–iv.

Lang, W. H. 1902. On the prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica.* Ann. Bot. **16**: 23–56. 1902.

————. 1913. Branching of *B. Lunaria.* Ann. Bot. **27**: 203–242. pl. 20–21, fig. 1–14.

Lasch, W. 1856. Ueber *Botrychium Kannenbergii.* Bot. Zeit. **14** (no. 35): 606–608.

Linnaeus, C. 1753. *Ophioglossum* and *Osmunda.* *In* Species plantarum. Ed. 1. 2: 1062–1064.

Litardiere, R. de 1921. Recherches sur l'élément chromosomique dans la caryocinèse somatique des Filicinées. La Cellule **31**: 255–473. pl. 1–9.

————. 1927. Le *Botrychium simplex* Hitch. en Corse. Bull. Soc. Bot. de France. **74** (ser. 3): 729–734. pl. 1.

Luerssen, C. 1889. *Botrychium.* *In* Die Farnpflanzen oder Gefässbundelkryptogamen (Pteridophyta). p. 551–593. pl. 182. fig.

Lyon, H. L. 1905. A new genus of *Ophioglossaceae.* Bot. Gaz. **40**: 455–458. fig. 1.

Milde, J. 1858a. Die Gefässkryptogamen in Schlesien; und Ueber *Botrychium crassinervium* Rupr. und seine Verwandten. Nov. Act. Acad. Caes. Leop. Nat. Cur. **26**: 371–753, 757–767. pl. 31–54, 55.

————. 1858b. Ueber *Botrychium lanceolatum* Angstr. Bot. Zeit. **16**: 69–70 .

————. 1864. Ueber Botrychien, deren Eintheilung und Unterscheidung. Bot. Zeit. **22**: 101–107.

————. 1868. Index Botrychiorum. Verh. k. k. Zool. Bot. Ges. Wien. **18**: 507–516.

————. 1869. Botrychiorum Monographia. Verh. k. k. Zool. Bot. Ges. Wien. **19**: 55–190. pl. 7 & 8.

Nakai, T. 1925. Notes on Japanese ferns. Bot. Mag. Tokyo. **39**: 192–194.

————. 1926. Notes on Japanese Ferns. Bot. Mag. Tokyo. **40**: 371–396.

Palmer, E. J. 1932. Notes on *Ophioglossum Engelmanni.* Am. Fern Journ. **22**: 43–47.

Petry, L. C. 1914. The anatomy of *Ophioglossum pendulum.* Bot. Ges. **59**: 345–365. pl. 20–21.

————. 1915. Branching in the Ophioglossaceae. Bot. Gaz. **59**: 345–365. pl. 20–21.

Prantl, K. 1883. Systematische Uebersicht der Ophioglosseen. Ber. deutsch. bot. Ges. **1**: 348–353.

————. 1884. Beiträge zur Systematik der Ophioglosseen. Jahrb. Bot. Gart. Berlin. **3**: 297–350. pl. 7 and 8.

Presl, K. B. 1845. *Ophioglossaceae* in Supplementum Tentamis Pteridophyta. Abh. Böhm. Ges. Wiss. v. **4**: 301–320.

————. 1847. *Ophioglossaceae* in Die Gefässbundel im Stipes der Farrn. Abh. Böhm. Ges. Wiss. V. **5**: 322–324. pl. 2.

Roeper, J. 1859. Zur Systematik und Naturgeschichte der *Ophioglosseae*. Bot. Zeit. **17**: 1–2, 9–17, 241–246, 249–254, 257–262, 265–268. pl. 12.

Ruprecht, F. J. 1845. *Ophioglossaceae*, in Distributio Cryptogamarum vascularium in Imperio Rossico. Beitr. Pflanzenk. Russ. Reich. **3**: 32–34.

————. 1859. Bemerkungen ueber einige Arten der Gattung *Botrychium*. Beitr. Pflanzenk. Russ. Reich. **11**: 31–43.

Stengel, K. G. 1858. Untersuchungen ueber Bau und Wachsthum der Farne. I. Stamm und Wurzel von *Ophioglossum vulgatum*. Nov. Act. Acad. Caes. Leop. -Carol. Nat. Cur. **26**(2): 771–780. pl. 56 & 57.

Swartz, O. 1800. Genera et species filicum. Journ. für die Botanik. **2**: 3–120.

Tidestrom, Ivar. 1905. Notes on *Botrychium virginianum* (L.) Sw. Torreya **5**: 160–162.

Trew, C. J. 1757. Nov. Act. Phys. -Med. Acad. Caes. Nat. Cur. **1**: 56. pl. 2.

Underwood, L. M. 1898. American ferns—I: The ternate species of *Botrychium*. Bull. Torrey Club **25**: 521–541.

————˙ 1903. An index to the described species of *Botrychium*. Bull. Torrey Club **30**: 42–55. f. 1–7.

————, **and Benedict, R. C.** 1909. Ophioglossaceae. *In* North American Flora. **16** (part 1): 3–13.

Victorin, Frère Marie-. 1927. Sur un *Botrychium* nouveau de la flore americaine et ses rapports avec le *B. Lunaria* et le *B. simplex*. Contr. Lab. Bot. Univ. Mont. **11**: 319–340. pl. 1–3.

————. 1932. La validité du *Botrychium minganense* Vict. Contr. Lab. Bot. Univ. Mont. **21**: 4–7.

Weatherby, C. A. 1935. List of varieties and forms of ferns of eastern North America. *Botrychium virginianum*. Am. Fern. Journ. **25**: 96–97.

Wherry, E. T. 1935. *Ophioglossum Engelmanni* Prantl. Claytonia **1**: 39–41.

Whitwell, W. 1898. *Botrychium matricariaefolium* A. Br. and *B. lanceolatum* Angst. in Britain. Journ. of Botany **36**: 291–297. pl. 388 B & C.

Willis, J. C. 1922. Age and area, a study in geographical distribution and origin of species. Cambridge. pl. 1–258.

————. 1923. Age and Area: a reply to criticism, with further evidence. Ann. Bot. **37**: 193–215.

Woynar, H. 1913. Bemerkungen ueber Farnpflanzen Steiermarks. Mitteil. Naturwiss. Ver. Steiermark **49**: 120–200.

ADDITIONS AND CORRECTIONS

Page 47. Botrychium alabamense.

Under Georgia, add Hall County.

Page 54. Botrychium dissectum var. tenuifolium.

The writer recently has examined specimens in the herbarium of the University of Georgia from the following additional counties in Georgia: Burke, Clarke, Columbia, Dawson, DeKalb, Fulton, Jenkins, Macon, Randolph, Taylor, and Winterville.

Page 57. Botrychium dissectum var. typicum.

Add Georgia. Cobb Co.: Marietta, *Adell Hamlin* (Herb. Univ. Ga.).

Page 100. Botrychium virginianum ssp. typicum.

Under North Carolina, add Randolph County. Under Georgia, add Bulloch, Clarke, Dawson, DeKalb, Greene, and Rabun Counties.

Page 134. Ophioglossum petiolatum.

The writer and Mr. Harold Trapido have recently had opportunity to visit in Florida the Messrs. E. P. and R. P. St. John who have kindly revealed and provided guidance to various of their stations for this species, thereby affording opportunity for intimate study of living material and observation of the habitats. Result of this experience indicates that the description of the species should be modified somewhat to read: "blade rather fleshy in texture,"—"acute or blunt at apex, occasionally rounded in diseased specimens." Plants growing in the open usually had the blade sessile and rather small, while those growing beside limestone rocks or among tall grasses, where they were partially shaded, were more slender, with a considerable haft often developed. Since all of the habitats observed seemed artificial, roadside ditches and excavations from which rock had been removed, one might well wonder whether this species is perhaps of recent introduction in Florida, since none of the earlier collectors seem to have found it, although they did find the much less conspicuous *Ophioglossum nudicaule* and *O. crotalophoroides*.

Dr. H. L. Lyon has now sent specimens of *O. petiolatum* from Kaimoki, Honolulu, Hawaiian Islands. These plants are rather typical of the species, although, like many of the Florida plants, they are not acute at the apex, but are decidedly blunt. Dr. Lyon writes that the species "is easily obtained in Honolulu," and that "it frequently appears as a weed in the soil about potted plants in our nursery."

Page 143. Ophioglossum nudicaule.

Dr. E. P. St. John has kindly shown to the writer various colonies of plants of this species which he is describing or considering for naming in future publications. Although the writer much regrets that he must do so, it seems his ungracious duty to state that he has been unable to segregate any species from the Florida population of *O. nudicaule* and that his field experience now leads him to the conclusion that the varieties *typicum*, *tenerum*, and *minus* are perhaps not worthy of any nomenclatorial distinction.

INDEX TO SCIENTIFIC NAMES

New names and the final members of new combinations are in **bold face type.** Numbers in **bold face type** indicate the principal references to the groups designated. Names in *italic type* are synonyms.

Memoirs

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R. P. Wodehouse

Studies in The Cichorieae

Dubyaea and Soroseris, Endemics of the Sino-Himalayan Region

By

G. LEDYARD STEBBINS, JR.

Published for the Club by
George Banta Publishing Company
Menasha, Wisconsin

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Table of Contents

Studies in the Cichorieae: Dubyaea and Soroseris, Endemics of the Sino-Himalayan Region

G. LEDYARD STEBBINS, JR.

I. INTRODUCTION

The fruitful results of the combined cytogenetic and systematic studies which Professor E. B. Babcock has conducted for the last twenty years on the genus *Crepis* have amply demonstrated the excellence of this material for this work. In order to provide a background for these studies, and to understand what relation the evolutionary processes in *Crepis* bear to the broader problems of the evolution of the larger plant groups, an examination is necessary of the relatives of this genus, particularly those which might represent or be related to its actual ancestors. A preliminary effort in this direction was made by Babcock (1936) in connection with a survey of phylogenetic trends in *Crepis* itself. He suggested that the most probable center of origin for the genus was south central Asia, and cited as the nearest living relative of its ancestors a species of the northwestern Himalaya, which was then known as *Paleya oligocephala*. He also pointed out the significance of the occurrence in this region of a small group of species, usually treated as the Section GLOMERATAE of *Crepis*, which appeared to show affinities to both *Crepis* and *Prenanthes*.

As a continuation of this work, the present author is making a survey of the genera of the Compositae, tribe Cichorieae related to *Crepis*, and has given particular attention to the groups centering about or near the hypothetical center of origin for *Crepis*, Central Asia. Early in the progress of this survey the existence of a genus related to *Crepis* and endemic to the Sino-Himalayan mountain region was postulated (Stebbins 1937). This genus, which is a redefinition of DeCandolle's genus *Dubyaea*, was found to include the two primitive relatives of *Crepis*, *D. hispida* (*Lactuca* or *Crepis Dubyaea*) and *D.* (*Paleya*) *oligocephala*, and in addition four species previously referred to *Lactuca*. Further studies of *Dubyaea* have amply justified its claim to generic rank, and have added three species to the number recognized. In addition the opinion of Babcock (1936), that the anomalous group of the GLOMERATAE do not belong in *Crepis* has been fully verified, but their retention in *Prenanthes* has proved equally untenable. Instead they constitute a genus by themselves, endemic to the Sino-Himalayan region and Tibet, which is most closely related to *Dubyaea*. The present work is a systematic monograph of these two genera, together with a consideration of their position in the tribe Cichorieae. A third group, consisting of three anomalous species of *Lactuca*, has been confused by previous botanists with the GLOMERATAE, and is therefore included in the systematic treatment.

This study has brought to light much evidence concerning the origin not only of *Crepis*, but in addition of four or five other genera of the Cichorieae: *Prenanthes*, *Lactuca*, *Youngia*, *Ixeris*, and perhaps *Hieracium*. For this reason, some general discussion of the relationships of these genera has been made. In addition, the distribution of the species of these genera has provided additional evidence on some of the interesting phytogeographic problems connected with this region, a part of which has been aptly termed "one of the botanical treasure houses of the world" (Ward 1935, p. 263). These problems, therefore are given special attention in the section on distribution.

This study was based on the specimens in the Herbarium of the University of California (UC) and in the following herbaria, loaned to the author through the generosity of their curators: Botanical Museum and Gardens, Berlin (B); Forest Research Institute, Dehra Dun, India (DD); Royal Botanic Garden, Edinburgh (E); Gray Herbarium, Harvard University (G); Royal Botanic Gardens, Kew (K); Natural History Museum, Vienna (V); New York Botanical Garden (NY); Smithsonian Institution, Washington (US). The author gratefully acknowledges with many thanks the privilege of borrowing these specimens. He is particularly indebted to Professor E. B. Babcock for his advice and criticism throughout the work. Helpful suggestions have also been received from Dr. H. Handel-Mazzetti. The author, however, assumes full responsibility for both the systematic treatment adopted and the conclusions reached in the general sections. The drawings were prepared by Mrs. Katherine D. Jenkins, except for portions of Figures 2 and 3, which are the work of Miss Anna Hamilton. The author is much indebted for their painstaking care in the work. Grateful acknowledgment is also made for the partial support of this investigation from the following institutions: Rockefeller Foundation; Carnegie Institution of Washington; Board of Research of the University of California; American Philosophical Society.

II. KEY TO THE SINO-HIMALAYAN GENERA OF CICHORIEAE

In order to orient the reader on the interrelationships of the tribe Cichorieae in this region as conceived by the present author, and to provide a ready means of identifying plants as belonging to the groups to be considered, an artificial key to these genera as they occur in the Sino-Himalayan region is presented. It should be noted that the generic characters as used in this key do not necessarily apply to species which are not found in the region under consideration. The genus *Faberia* is not included in the key since, in the opinion of the author, it is not generically distinct from *Prenanthes*. A discussion of this group will be made in a later publication.

A. Pappus none or rarely uncinate . . . . *Lapsana*

A. Pappus present, setose.

B. Pappus setae plumose.

C. Plants glabrate or floccose-tomentose; plumes of pappus setae long, interlaced . . . . *Scorzonera*

C. Plants setose-hispid; plumes of pappus setae not interlaced . . . . *Picris*

B. Pappus setae not plumose.

D. Achenes tuberculate or muricate on the surface, at least on the upper portion.

E. Plants with well-developed, branched stems . . . . *Chondrilla*

E. Plants acaulescent, the heads borne on hollow scapes . . . . . *Taraxacum*

D. Achenes smooth, scabrous, spiculate, or rugose.

E. Achenes strongly obcompressed, with 2–4 principal ribs; ovary with 2–4 principal vascular bundles; at least some of the pappus setae only 2- or 4-celled in cross section at the base.

F. Involucres with 80 or more florets; pappus setae of two very dissimilar types, some relatively coarse and straight, others very fine and flexuous, 2–4-celled in cross section, causing the pappus to adhere to clothing, etc. . . . . *Sonchus*

F. Involucres with 3–30 or rarely up to 50 florets; pappus setae relatively uniform, all more or less straight, often brittle . . . . *Lactuca*

E. Achenes terete or slightly obcompressed, with 5–10 principal ribs; ovary with 5–20 vascular bundles.

G. At least some of the pappus setae only 4-celled in cross section at the base; corollas small and delicate, the tube elongate, distinctly exceeding the ligule; stigmatic branches slender and pale . . . . *Lactuca* spp.

G. All of the pappus setae more than 4-celled in cross section at the base (except in a few species of *Launaea* and *Crepis*); corolla tube sometimes slightly exceeding, but mostly equalling or shorter than the ligule.

H. Involucral bracts more or less evenly imbricated, the outer passing gradually into the inner.

I. Heads with 8–12 florets; achenes pale buff or somewhat greenish, the principal ribs thick and corky . . . . *Launaea*

I. Heads with 10 or more, mostly very many florets; achenes yellowish, reddish, or blackish, the ribs relatively slender and closely spaced.

J. Stigmatic branches terete, 0.1–0.14 mm. broad, achenes terete, with 10–15 equal ribs, truncate at the apex . . *Hieracium*

J. Stigmatic branches somewhat flattened, 0.16–0.3 mm broad; achenes slightly obcompressed, unequally ribbed, or with 5 widely spaced, slender ribs, more or less attenuate at the apex or with a short, thick beak . . . . *Dubyaea*

H. Involucral bracts consisting of a distinct inner and outer series.

K. Tufted alpine plants, the heads crowded in a glomerate inflorescence; outer involucral bracts narrowly linear, slightly shorter than to exceeding the inner; inner involucral bracts coalescent at the base; receptacle concave . *Soroseris*

K. Plants of various habit; outer involucral bracts deltoid or lanceolate, mostly $\frac{1}{5}$ to $\frac{1}{2}$ as long as the inner; inner bracts distinct from each other; receptacle flat or convex.
  L. Mostly tall or climbing plants of mesophytic situations; flowers purplish, bluish or whitish, never yellow; corolla tube about equalling or somewhat exceeding the ligule; stigmatic branches blackish, somewhat flattened, 0.16–0.26 mm broad; achenes truncate or rarely attenuate at the apex.................. *Prenanthes* (incl. *Faberia*)
  L. Flowers yellow or whitish (except in some species of *Ixeris*, which have long-beaked achenes); corolla tube distinctly shorter than the ligule; stigmatic branches yellowish, terete, 0.14 mm or less in diameter (blackish and flattened only in *Youngia* sect. *Desiphylum*, a group of dwarf alpines); achenes attenuate at the apex or beaked.
    M. Achenes terete, equally ribbed......... *Crepis*
    M. Achenes somewhat obcompressed.
      N. Achenes unequally ribbed, the ribs obtuse, usually not beaked................... *Youngia*
      N. Achenes equally ribbed, the ribs often acute or alate, distinctly beaked............. *Ixeris*

III. THE GENUS DUBYAEA

HISTORY OF THE GENUS

The genus *Dubyaea* was first constituted by De Candolle (Prodr. 7: 247) to include three species; *D. cristulata* of New Holland, *D. hispida* of the Himalaya, and *D. sonchoidea* of Armenia. It was named in honor of J. E. Duby, a contemporary French botanist who prepared the monograph of *Primula* for the Prodromus. I have not seen any specimens of *D. cristulata*, and, so far as I am aware, this species has not been mentioned in any subsequent publications. It is presumably a species of *Sonchus*, and perhaps *S. grandifolius* Hook. f. *D. sonchoidea*, based on *Lasiopus sonchoides* Don, is *Taraxacum montanum* DC. The third species, *D. hispida*, was based on *Hieracium hispidum* Wall. This species was transferred by C. B. Clarke (Comp. Ind. 271) to *Lactuca*, as *L. Dubyaea*. Clarke was apparently influenced by the presence of compressed (or obcompressed) achenes, and the resemblance between the involucres of this species and those of *L. Lessertiana* (Wall.) Clarke. Hooker (Fl. Brit. India 3: 409) erected for the species the section Dubyaea of *Lactuca*. This treatment was followed by all later writers on the Sino-Himalayan flora until recent years, as well as by Hoffmann in "Die Natürlichen Pflanzenfamilien" (vol. 4, pt. 5: 372). Franchet in 1895 (Jour. de Bot. 60: 294) and W. W. Smith in 1920 (Notes Bot. Gard. Edinb. 12: 211) each added a species to this section. In 1916 Hutchinson (Kew Bull. 189) described *Crepis* *bhotanica*, the type of which is unquestionably *D. hispida*, while in 1929 Marquand and Shaw (Jour. Linn. Soc. 48: 194) transferred the same species to *Crepis* as *C. Dubyaea*, without comment. Their disposition of the species was generally accepted by later writers. Handel-Mazzetti described in 1924 (Sitzganz. Akad. Wiss. Wien 61: 23) a new section of *Lactuca*, Sect. AMOENAE, which on the basis of its involucral and floral characteristics he placed next to the sect. DUBYAEA, but which differed strikingly from that section in habit and in the shape of the heads. In 1936 (Symb. Sin. 7(4): 1182) he retained this section as well as Franchet's species of the section DUBYAEA, *L. atropurpurea*, in *Lactuca*, but placed *Dubyaea hispida* (*L. Dubyaea*) in *Crepis*. He did not give any reason for segregating the species of the Sect. DUBYAEA, *D. hispida* and *D. atropurpurea*, into two different genera, but suggested an affinity of Sect. AMOENAE to *Lactuca atropurpurea*. In 1937 (Jour. Bot., 75 p. 17) the writer pointed out the difficulty of referring all of these obviously interrelated species either to *Lactuca* or to *Crepis*, and suggested that De Candolle's genus be reconstituted for them.

REVISED GENERIC DESCRIPTION

Dubyaea DC., Prodr. 7: 247, 1838. (Compositae-Cichorieae). Herbaceous perennials with milky juice; leafy stemmed or acaulescent; leaves various in size and shape; inflorescence cymose or racemose, of few heads, or heads solitary; involucres large, broadly or narrowly campanulate, 10–80 flowered; involucral bracts numerous, rather evenly imbricated, not at all thickened at maturity; corollas large, completely glabrous, the tube shorter than the ligule; anthers short-caudate, blackish or yellowish; style with numerous and conspicuous barbs ("collecting hairs") below the branches of the stigma; stigmatic branches linear, flattened, 1–3 mm long, 0.16–0.3 mm broad, covered with barbs on the outer surface, evenly papillate on the inner surface, style and stigmas mostly blackish or greenish on the upper portion; achenes fusiform, in some species short-rostrate, in others nearly truncate at the apex, slightly obcompressed, with 5–10 prominent ribs and usually 1–6 lesser ones; pappus setae coarse, rigid; receptacle plane or somewhat convex, shallowly or deeply pitted, the margins of the pits plane or erose, not ciliate; receptacular paleae absent. Basic chromosome number probably $x=8$.

Nine species, natives of western China and the Himalaya Mountains, mostly in alpine or subalpine situations. Type species *Dubyaea hispida* (Don) DC. (*Hieracium hispidum* Don).

RELATIONSHIPS OF DUBYAEA

The genus *Dubyaea* shows a definite relationship to most of the larger genera of the tribe Cichorieae which have a capillary pappus (subtribe

Crepidinae of Hoffmann, Planzenfamilien 5(4): 366). To *Lactuca*, with which genus *Dubyaea* has been united by most authors, the resemblance is chiefly in habit. *D. atropurpurea* (Franch.) Stebbins is very similar in general appearance to *Lactuca atropurpurea* Franch. (*L. grandiflora* Fr.), as well as to *L. macrantha* Clarke. *Dubyaea* differs from *Lactuca*, however, in having only slightly flattened achenes, which contain five main vascular bundles and a number of lesser ones, and in its much coarser pappus setae, most of which are more than four cells in cross section for practically their entire length, and may therefore be said to lack terminal trichomes (Babcock and Stebbins 1937, p. 7) (cf. Figure 1). *Lactuca atropurpurea* and *L. macrantha*, have strongly flattened achenes with 2–4 main vascular bundles and the relatively weak pappus bristles characteristic of *Lactuca* (Stebbins 1937, pp. 13–14). The bulk of the species of *Lactuca*, furthermore, differ widely from *Dubyaea* in their relatively small and numerous heads, their smaller and more delicate corollas, their slender, terete, and pale stigmatic branches, and their much more strongly flattened achenes.

Between *Crepis* and *Dubyaea* there is an equally close connection. *Dubyaea hispida* (Don) DC. and *D. oligocephala* (Sch. Bip.) Stebbins are similar in habit respectively to *Crepis kashmirica* Babcock and *C. sibirica* L. These species of *Crepis* also have the coarse pappus bristles and the floral anatomy characteristic of *Dubyaea*. They differ, however, in possessing the slender, terete, and yellow stigmatic branches (Figures 7, 8) as well as the terete, evenly ribbed achenes characteristic of *Crepis*. From the bulk of *Crepis* species, *Dubyaea* differs also in its larger heads with more numerous, evenly imbricated involucral bracts, in its larger florets and achenes, and coarser pappus setae.

The connection between *Dubyaea* and *Youngia* has already been pointed out (Babcock and Stebbins 1937, pp. 15–16). *Youngia* differs from *Dubyaea* in its smaller, narrower involucres, of which the bracts are divided into a distinct outer and inner series, the former being much shorter and deltoid. Furthermore all of the sections of *Youngia* except Sect. DESIPHYLUM have, like most *Lactuca* and *Crepis* species, much smaller florets and achenes, and less coarse pappus bristles then *Dubyaea*. The genus *Ixeris*, a close relative of *Youngia*, shows a similar relationship to *Dubyaea*. *D. chimiliensis* (W. W. Smith) Stebbins, in particular, resembles *Ixeris* in its glabrous habit, lanceolate, entire leaves, and in the color and beaked character of its achenes. The species of *Ixeris* most nearly related to *Dubyaea* is *I. alpicola* Nakai of Japan, but there is also a connection between *Dubyaea chimiliensis* and *Ixeris laevigata* (DC.) Stebbins through the anomalous *Youngia silhetensis* (DC.) Babcock and Stebbins. The generic position of the latter species is still in doubt; morphologically it stands midway be-

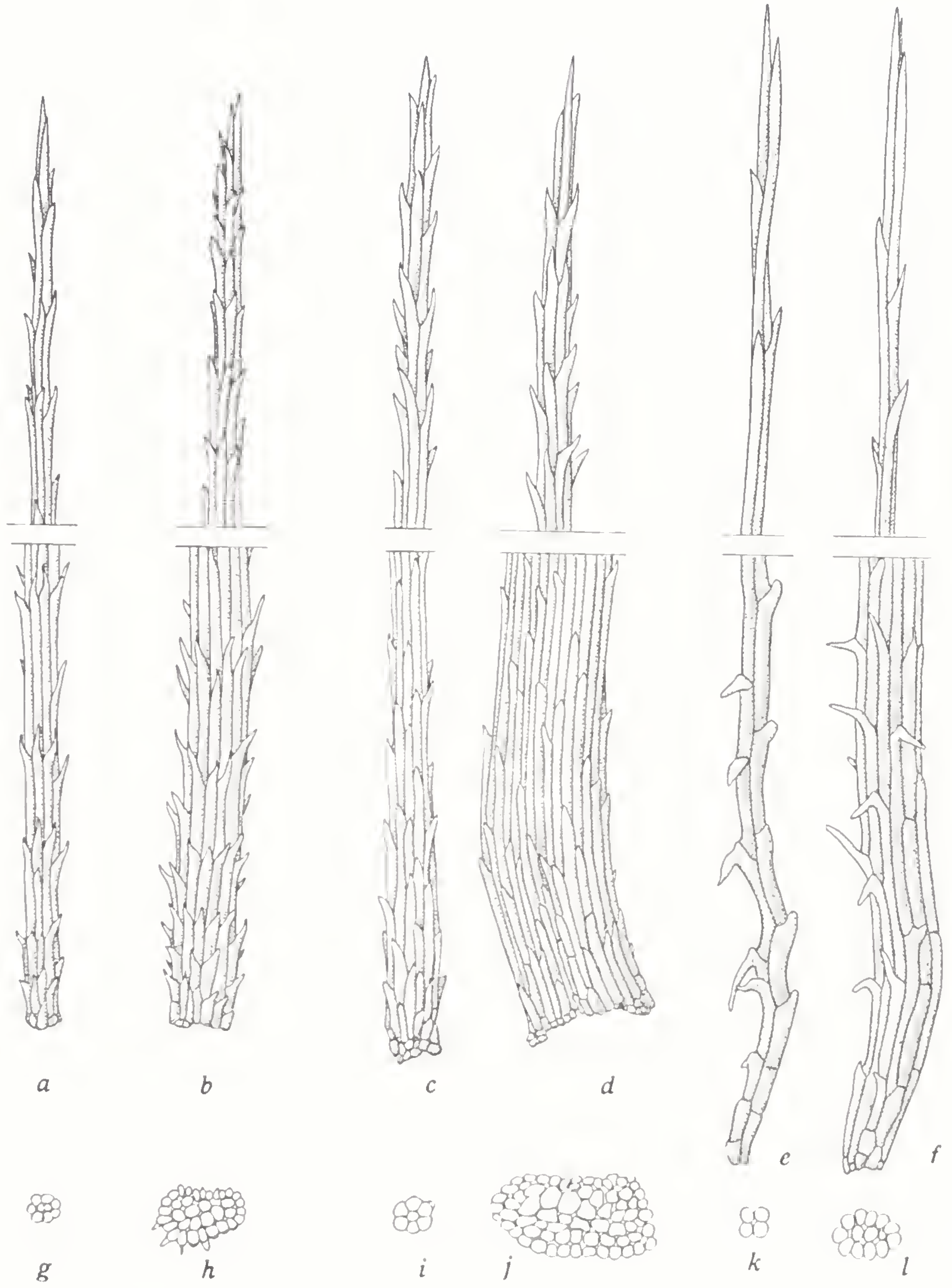

Fig. 1. *a–f*. Side views of the basal and apical portions of the weakest and strongest pappus setae of: *a*, *b*, *Dubyaea chimiliensis*; *c*, *d*, *Soroseris rosularis*; *e*, *f*, *Lactuca disciformis*. *g–l*, cross sections at the base of the weakest and strongest pappus setae of: *g*, *h*, *Dubyaea atropurpurea*; *i*, *j*, *Soroseris Deasyi*; *k*, *l*, *Lactuca disciformis*. All ×100.

tween *Dubyaea chimiliensis* and *Ixeris laevigata*. It resembles the former in its coarse pappus setae and unequally ribbed achenes, and the latter in habit, as well as its small, narrow involucres whose bracts are in two series. Its diagnostic characters place it in *Youngia*, and emphasize further the close connection between *Youngia* and *Ixeris*.

Another genus which shows a close affinity to *Dubyaea* is *Prenanthes*. These two genera are similar in the character of their corollas, styles, and stigmas, in their slightly flattened achenes, in the vascular anatomy of their ovaries, and in their coarse pappus setae. *Prenanthes*, however, has more numerous, smaller and mostly fewer flowered involucres, of which the bracts are sharply differentiated into two series, while its achenes are in most species cylindric and truncate at the apex, rather than fusiform. The species of *Prenanthes* nearest to *Dubyaea* both in habit and in the size of the involucres is *P. crepidinea* Michx. of the eastern United States, but *P. ochroleuca* (Maxim.) Hemsl. and *P. acerifolia* (Maxim.) Matsumura, both of Japan, also show some resemblances to *Dubyaea*. It is an interesting fact that *Prenanthes*, which is closer to *Dubyaea* in floral characteristics than is any other genus, nevertheless deviates more from it in habit than do certain species of *Lactuca*, *Crepis*, and *Youngia*.

Dubyaea also shows a definite relationship to *Hieracium*. *D. glaucescens* Stebbins resembles *Hieracium* in its yellow, uniseriate pappus and more or less truncate achenes, while the deltoid, evenly imbricated involucral bracts are not unlike those of some species of *Hieracium* sub. *Archieracium*. *D. glaucescens* however, has purple flowers, which are not known in *Hieracium;* its stigmas are broader, and its achenes are typical of *Dubyaea* in being unequally ribbed, while those of *Hieracium* are terete and equally ribbed. *Dubyaea tsarongensis* (W. W. Smith) Stebbins, furthermore, shows a resemblance both in habit and in the character of its corollas, achenes and pappus to *Hieracium Krameri* Franch. & Sav. of Japan, and *H. Nakaii* Kitagawa of Korea. These two species are somewhat anomalous in *Hieracium*, but are connected with the rest of the genus through *H. hololeion* Maxim. *Hieracium*, however, is definitely more remote from *Dubyaea* than are the other genera mentioned.

Dubyaea somewhat resembles *Sonchus* in habit, and in the size and character of its involucres, but in other characteristics the two genera are rather remote from each other. There is also a habital resemblance between *Dubyaea* and certain species of *Hypochaeris*, such as *H. grandiflora* Ledeb., which has in addition achenes similar in shape and ribbing to those of *Dubyaea*. This may signify a real relationship, although the paleae on the receptacle and the character of the pappus, as well as the slender, yellow stigmatic branches contrast sharply with the characteristics of

Dubyaea. The close connection between *Dubyaea* and another Cichoriaceous genus endemic to the Sino-Himalayan region will be discussed below.

Dubyaea, therefore, shows affinities to a number of the well known, widespread genera of the Cichorieae. The phylogenetic significance of these relationships will be discussed in a later section of this paper.

DIAGNOSIS OF SECTIONS

SECTION 1. **Eudubyaea,** sec. nov.—Stout, leafy stemmed perennials, hirsute or glabrous; leaves mostly lyrate, runcinate, or sinuate pinnatifid, or at least strongly dentate; involucres large, broadly campanulate, with 40–80 florets; involucral bracts numerous, deltoid or lanceolate; flower color various; pappus setae yellowish, cream color, or white. Type species, *D. hispida* (Don) DC.

SECTION 2. **Ixeridopsis,** sect. nov.—Slender perennials, leafy-stemmed or scapose, glabrous; leaves lanceolate or oblanceolate, the margins entire; involucres broadly campanulate, with 20–35 florets; involucral bracts loosely imbricated, broadly oblanceolate or narrowly elliptic; flowers bright yellow; pappus yellowish. Type species, *D. tsarongensis* (W. W. Smith) Stebbins.

SECTION 3. **Amoenae** (Hand.-Mazz.) comb. nov.—Acaulescent perennials, hirsute or glabrous, the leaves all basal, pinnatifid or entire; scapes naked or bracteate; involucres narrowly cylindric-campanulate, with 10–17 florets; involucral bracts deltoid or lanceolate; flowers blue or bluish purple; pappus setae rufous. (*Lactuca* Sect. AMOENAE Hand.-Mazz. Sitzganz. Akad. Wiss. Wien. Math. Nat. 61: 23, 1924; Symb. Sin. 7: 1182, 1936). Type species, *D. amoena* (Hand.-Mazz.) Stebbins.

ARTIFICIAL KEY TO THE SPECIES OF DUBYAEA

A. Stems 1–7 dm tall, leafy (except sometimes in no. 7); involucres broadly campanulate, 20–80-flowered.

B. Plants hirsute or glabrous; basal leaves relatively large, mostly 15–30 cm long and 2–8 cm broad, dentate or pinnatifid.

C. Flowers blackish purple, dull brownish yellow, or bluish; achenes not at all rostrate; pappus setae yellow or tawny.

D. Plants glandular-hispid; leaves lyrate-pinnatifid with a large terminal lobe; flowers blackish purple or dull brownish yellow; achenes 6.5–8 mm long. . 1. *D. atropurpurea*

D. Plants glabrous and glaucous; leaves sinuate-pinnatifid; flowers purple or bluish purple; achenes about 3.5 mm long. . . . . 2. *D. glaucescens*

C. Flowers bright yellow, orange yellow, or pinkish crimson; achenes more or less rostrate or subrostrate; pappus setae white or cream colored.

E. Heads nodding; outer involucral bracts relatively few; body of achene dark (at least in no. 4).

F. Basal and lower cauline leaves on distinct, slender petioles; flowers pinkish crimson. . . . . 3. *D. rubra*

F. Basal and lower cauline leaves sessile or cordate-clasping; flowers yellow . . . . 4. *D. hispida*

E. Heads erect; involucral bracts numerous and evenly imbricated; achenes stramineous throughout . . . . 5. *D. oligocephala*

B. Plants completely glabrous; basal leaves smaller, 4–16 cm long and 0.6–2.2 cm broad, the margins entire.

G. Stems 2–4.5 dm tall; lower cauline leaves as large as the basal; heads 2–6 in an inflorescence; involucres 22–30 mm long; achenes 8.5–10 mm long, with a short, thick beak ....6. *D. chimiliensis*

G. Stems 0.9–2 dm tall, cauline leaves all reduced, mostly linear and bract like; heads solitary or rarely 2; involucres 12–16 mm long; achenes 4–5.5 mm long, not beaked ....7. *D. tsarongensis*

A. Plants acaulescent, the flowering scapes 1.5–7 cm long, naked or with a few linear bracts; involucres narrowly cylindric, 10–17-flowered.

H. Plants more or less glandular-hispid; leaves mostly pinnatifid; scapes 3–6..8. *D. amoena*

H. Plants glabrous throughout; leaves entire or remotely and minutely denticulate; scapes solitary.......................9. *D. gombalana*

SECTION I. EUDUBYAEA

1. **Dubyaea atropurpurea** (Franch.) Stebbins, Jour. Bot. 75 (1937): 51. (Fig. 2, *a–d*).

Perennial from a stout taproot; stems 3–7 dm tall, stout, angulate or striate, hirsute, leaves mostly cauline, the lower large, lyrate-pinnatifid, sessile, the blade glabrous above, sparsely short hirsute along the veins below; upper leaves elliptic, sinuate-dentate, usually cordate-clasping at the base; heads 3–8, nodding on elongate, densely blackish-hirsute peduncles; involucres large, broadly campanulate, about 60–70-flowered, 18–22 mm long, the bracts in several series, the outer narrowly lanceolate or linear, attenuate at the apex, the inner broadly lanceolate, 4–5.5 mm broad, all lead-color and blackish-hirsute at least along the midrib; corollas blackish violet, brown, or deep dull yellow, 15–18 mm long, the tube 3.5–4.5 mm long, $\frac{1}{5}$–$\frac{1}{3}$ as long as the ligule; anthers yellowish, 4–5.5 mm long; stigmatic branches 1.7–2.5 mm long, 0.3 mm broad; achenes 6.5–8 mm long, stramineous, oblong or somewhat fusiform, with about 10 strong ribs, and a few indistinct ones between them; pappus bristles 1–2-seriate, coarse, yellowish or rufescent, 8–10 mm long. (*Lactuca atropurpurea* Franch. in Morot, Journ. de Bot. 9: 294, 1895.)

Southwestern China and adjacent Burma, in subalpine and alpine meadows at 3000–4000 m. The following are typical:

China: Yunnan Prov., eastern slopes of Lichiang Range, alt. 3640 m, *Forrest 6218* (E,B), *Rock 5373* (B,US); Tali Range, alt. 3330–3640 m, *Forrest 4060* (E); western flank of Shweli-Salween divide, alt. 3030 m, *Forrest 9025* (E); Tsangshan Range, *Rock 6349* (B); Mt. Habashan, *Rock 9707* (B); Fuchuan Range, alt. 3790 m, *Rock 23290* (UC); west of Hsiao-Chung-tien, *Rock 24626* (UC); Pi-lo-shan, Che-tse-lo, alt. 4000 m, *Tsai 58629* (UC, G). Burma: Northeast upper Burma, N'Maikha-Salween divide, *Forrest 27299* (US,K).

This is unquestionably the most primitive species of *Dubyaea*. Its nearest relationship is with *D. hispida*, but the two species are nevertheless

Fig. 2. *a–d. Dubyaea atropurpurea; a–c*, from *Rock 24626* (UC), *d*, from *Forrest 9025* (E); *a*, habit ×$\frac{1}{4}$; *b*, involucre, ×2; *c*, corolla, ×4; *d*, achene, ×8. *e–h*, *D. glaucescens*, from cotypes (B, K); *e*, leaf, ×$\frac{1}{4}$; *f*, involucre, ×2; *g*, corolla, ×4; *h*, achene, ×8.

very distinct from each other in a number of characteristics. Judging from the number of collections seen, it must be rather common within its range. The nomenclatural problem connected with this species has been discussed elsewhere (Stebbins, loc. cit.).

2. **Dubyaea glaucescens** sp. nov. (Fig. 2, *e–h*).—Caulis 40–50 cm altus, striatus, glaber; folia basalia sessilia anguste obovata, ca. 20 cm longa, 6 cm lata, sinuato-dentata vel pinnatifida, apice acuta vel acuminata, margine remote denticulata, glaberrima, glaucescentia, subtus pallida; folia caulina inferiora basalibus similia, basi amplexicaulia; folia superiora minora, elliptica vel ovata, cordato-amplexicaulia; capitula 3–4, longissime pedunculata, cernua, pedunculis 8–17 cm longis glaberrimis striatis; involucra 18–20 mm longa, late campanulata, multiflora, phyllis imbricatis glaberrimis, exterioribus deltoideis vel ovatis, acutsi, interioribus lanceolatis acutis, corollae purpureae (ex nota collectoris), 17 mm longae; antherae pallidae, 6–6.5 mm longae; rami stigmati 2 mm longi, pallidi; achaenia oblonga, 3.5 mm longa, apice truncata vel paullo contracta, inaequaliter ca. 12-costata, pallide fusca; pappi setae uniseriatae, sordide flavescentes, rigidae, 9–10 mm longae; receptaculum profunde foveolatum; foveolis margine valde erosis.

Perennial from a taproot, glabrous throughout; stem 40–50 cm tall, striate, glabrous; basal leaves sessile, narrowly obovate, about 20 cm long and 6 cm broad, sinuate-dentate or shallowly pinnatifid, acute or acuminate at the apex, the margin remotely denticulate, completely glabrous, glaucescent, paler below; lower cauline leaves similar to the basal, auriculate-clasping at the base, upper leaves smaller elliptic or ovate, cordate-clasping at the base; heads 3–4 per plant, nodding, solitary on the ends of elongate, stout, striate, glabrous peduncles, these 8–17 cm long; involucres 18–20 mm long, broadly campanulate, many-flowered, the bracts rather evenly imbricated, completely smooth and glabrous, lead-color, the outer deltoid or ovate, acute, the inner lanceolate, acute; corollas "purple" (collector's note), 17 mm long, the tube 5 mm, the ligule 12 mm long; anthers pale, yellowish or bluish, 6–6.5 mm long; branches of the stigma about 2 mm long and 0.2 mm broad, pale; achenes oblong, 3.5 mm long, truncate or slightly contracted at the apex, unequally about 12-costate, pale brownish; pappus bristles uniseriate, dull yellowish, coarse and stiff, 9–10 mm long; receptacle deeply pitted, the margins of the pits strongly erose.

Known only from the type collection: CHINA: Szechuan Prov., Omei Hsien, cliff, alt. 910–1210 m, *Wilson 2493* (G type, B, K, US).

This species is closest to *D. atropurpurea*, but is strikingly different from it, as well as from all other species of the genus. Its completely glabrous and glaucous habit, as well as its broad outer involucral bracts, set it off sharply from any other species of this section, and recall *D. tsarongensis* of the section *Ixeridopsis*. *D. glaucescens*, however, is totally different from *D. tsarongensis* in other respects. The oblong, almost columnar achenes and yellow, uniseriate pappus of *D. glaucescens* suggest those of *Prenanthes* subg. *Nabalus* and *Hieracium*, but it does not approach these genera in other respects. The pollen grains are very large, 38–40μ in diameter, and are nearly all 4-pored. Since all species of Cichorieae with 4-pored pollen grains of which the chromosome number is known are cytologically polyploids, this suggests that *D. glaucescens* is also a polyploid.

The habitat of *D. glaucescens* differs from that of all other species of *Dubyaea*, since it occurs at low altitudes, in a zone characterized by a warm temperate climate and by the presence of a mixed deciduous forest containing a great wealth of genera and species of woody plants.

3. **Dubyaea rubra** sp. nov. (Fig. 3, *e–f*)—Herba perennis; caulis 4.5–6 dm altus, ad basim glaber, ad apicem hirsutus pilis glandulosis; folia basalia petiolata, sagittata, 3.5–7 cm longa, 2.5–4.5 cm lata, margine remote denticulata vel dentata; folia caulina elliptica, inferiora petiolata, superiora sessilia, nec cordata nec amplexicaulia; capitula 4–6 pro planta, longe pedunculata, cernua, multiflora; involucra 15–17 mm longa, phyllis imbricatis, linearis vel lanceolatis, dense nigro-hirsutis, acutis vel acuminatis; corollae roseo-rubescentes, 17–18 mm longae; antherae 5 mm longae, nigrescentae; achaenia ignota; pappi setae multiseriatae, albae vel lacteae, 9–10 mm longae.

Perennial herb; stem 4.5–6 dm high, glabrous toward the base, hirsute toward the apex with glandular hairs; basal leaves petiolate, sagittate, 3.5–7 cm long, 2.5–4.5 cm broad, remotely denticulate or dentate on the margin; cauline leaves elliptic, acute, the lower petioled, the upper sessile but not cordate-clasping; heads 4–6 in a corymbose inflorescence, nodding on elongate peduncles; involucres campanulate, about 50–60-flowered, 15–17 mm long, the bracts inbricated in several series, the outer shorter, all linear or lanceolate, densely blackish-hirsute, acute or acuminate; corollas "pinkish crimson" (collector's note), 18–19 mm long, the tube 8 mm, the ligule 10–11 mm long, 1.8–2 mm broad; anthers 5 mm long, greenish or blackish; branches of the stigma 1.8–2 mm long; pappus setae multiseriate, white or cream color, 9–10 long; achenes not seen.

Known only from the type. CHINA: Szechuan Prov., Muli, alt. 3940 m, *Ward 4836* (E).

This species is very close to *D. hispida*, from which it differs chiefly in the shape of its basal leaves, the lower cauline leaves petioled, the upper cauline leaves not at all cordate-clasping, and in its smaller, pinkish-crimson corollas and dark anther tubes. It is taller than most of the *D. hispida* seen from China, but is equalled in height by specimens of that species from the western Himalaya.

Fig. 3. *a–d*, *Dubyaea hispida; a–b* from *Handel-Mazzetti 9988* (UC), *c*, from *Bees 3533* (K), *d*, from *Hort. Calif. Genet. 3245; a*, habit, ×$\frac{1}{2}$; *b*, involucre, ×2; *c*, corolla, ×4; *d*, achene, ×8. *e–f Dubyaea rubra*, from type (E); *e*, habit, ×$\frac{1}{2}$; *f*, corolla, ×4.

4. **Dubyaea hispida** (Don) DC., Prod. 7: 247, 1838. (Fig. 3, *a–d*)—Stems from a creeping rhizome, 1.2–6 dm tall; basal leaves sinuate-dentate to lyrate-pinnatifid, the blade sparsely brownish-hirsute on both surfaces or glabrate above; cauline leaves 2–8, the lower similar to the basal, the upper gradually reduced, elliptic or ovate, mostly cordate-clasping at the base; heads 2–16 in a corymbose inflorescence, nodding, on elongate, blackish-hirsute peduncles; involucres campanulate, 15–20 mm long, the outer bracts acute or acuminate, narrowly lanceolate or the outermost linear, the longest $\frac{2}{3}$–$\frac{4}{5}$ the length of the inner; inner bracts about 18–20, lanceolate, acute, 2–3 mm broad, blackish-hirsute at least along the midrib; florets about 40–50 per involucre; corollas yellow, 20–25 mm long, the tube glabrous, 6–10 mm long, shorter than the ligule; anthers yellow, 4–5.5 mm long; stigmatic branches blackish, 2–2.5 mm long; achenes fusiform, somewhat obcompressed, 6.5–9 mm long, the body brownish or blackish, the apex pale, stramineous, subrostrate; pappus setae multiseriate, cream color, 10–12 mm long. (*Hieracium hispidum* Don, Prod. Fl. Nepal, 165, 1825, non Forsk.; *H. heteranthum* Wall. cat. n. 3253; *Lactuca Dubyaea* C. B. Clarke, Comp. Ind. 271, 1876; Hook. f., Fl. Brit. Ind. 3: 409, 1882; *Crepis bhotanica* Hutchinson, Kew Bull. 1916: 189; *Crepis Dubyaea* Marq. et Shaw, Jour. Linn. Soc. 48: 194, 1929.)

Western Himalaya in Kumaon and Garwhal Provinces, east to western China, Szechuan Province, in meadows or open alpine slopes at 3000–4500 m altitude. The following, selected from a considerable series, are tyical: India: Kumaon Province, near Ralaim, alt. 3330–3635 m, *Duthie 3093* (B, DD); Sikkim Prov., Megu, alt. 4090 m, *Ghose* in 1932 (UC). Bhutan: without locality, *Bees 3533* (type of *C. bhotanica* Hutchinson, K). Burma: Semhku Valley, alt. 3330–3635 m, *Ward 7538* (K). Tibet: Tomo La, alt. 4240 m, *Ward 6188* (K). China: Yunnan Prov., Mekong-Salwin divide, alt. 4240 m, *Forrest 20730* (B, K); Szechuan Prov., Mt. Konka, alt. 4480 m, *Rock 16883* (B).

This is much the most widespread and best known of the species of *Dubyaea*. It is remarkably uniform throughout its range, the variation found being chiefly in the height and luxuriance of the plant, and to a lesser extent the shape of the leaves. The chromosome number has been already reported as 2n = 16 (Babcock, Stebbins and Jenkins 1937).

5. **Dubyaea oligocephala** (Sch. Bip.) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 4)—Stems from a taproot, 1.5–4.5 dm tall, hirsute or nearly glabrous below, glabrous or hirsute above; basal leaves oblanceolate to obovate in outline, lyrate pinnatifid or merely dentate, the apex acuminate, glabrous or pubescent; cauline leaves 2–6, the lowermost similar to the basal, the upper reduced, lanceolate, cordate-clasping at the base; heads 2–6 in a cymose inflorescence, erect on divergent peduncles 2–14 cm long; involucres campanulate, 14–20 mm long, the bracts numerous, evenly imbricated in several series, narrowly deltoid to lanceolate, obtuse or somewhat acute at the apex, glabrous or tomentulose on the outer surface, the outer ones strongly ciliate along the margins; florets about 70–80 per involucre; corollas yellow, 18–25 mm long,

the tube glabrous, shorter than the ligule; anthers yellow, 4.5–5.5 mm long; stigmatic branches blackish, 2.5–3 mm long; achenes stramineous, fusiform, somewhat obcompressed, total length 7–12 mm tapering upward into a stout beak $\frac{1}{5}$–$\frac{1}{3}$ as long as the body, unequally about 12-ribbed; pappus setae white, less coarse than other species of *Dubyaea,* 7–9 mm long, more or less deciduous at maturity. (*Crepis sibirica* Clarke, Comp. Ind.: 252, 1876; Hook. f., Fl. Brit. Ind. III: 394, 1882, *non* L.)

Western Himalaya Mountains, in Kashmir and adjacent Punjab, in open, rocky or gravelly places at altitudes of 2250–3000 m.

Clarke, (loc. cit.) identified this species with the northern Asiatic *Crepis sibirica* L., which it resembles superficially. *D. oligocephala,* however, has the involucral bracts much more numerous and evenly imbricated than *C. sibirica;* its stigmatic branches are blackish and somewhat flattened, as in other species of *Dubyaea,* while those of *C. sibirica* are yellow, more slender, and nearly terete, as is typical of *Crepis;* and finally D. *oligocephala* has the obcompressed, unequally ribbed achenes of *Dubyaea,* while those of *C. sibirica* are typical of *Crepis* in being terete and equally ribbed. Hooker (loc. cit.) noted that the achenes of the specimens of "*Crepis sibirica*" (*D. oligocephala*) seen by him were "quite smooth," and added the comment: "I have *not* quoted Boisser who describes the achenes (of *C. sibirica*) as 20–30-ribbed, the ribs transversely rugulose and scaberulous." Boissier described the achenes of true *C. sibirica* quite correctly, while Hooker's description is equally correct for *D. oligocephala.* Apparently neither Hooker nor Clarke compared mature achenes of the Indian plant with those of true *Crepis sibirica.*

Dubyaea oligocephala occupies the western limit of the range of the genus. It is most closely related to *D. hispida,* which it also approaches geographically. There is, however, a gap of about 240 km (150 miles) in the western Himalaya between the known ranges of *D. hispida* and *D. oligocephala,* in which area no species of *Dubyaea* is known to occur. *D. oligocephala,* moreover, occupies a somewhat different habitat from that of *D. hispida,* occurring at lower elevations, and apparently in drier situations.

Two subspecies of *D. oligocephala* may be recognized, and are distinguished as follows:

Basal leaves 1.5–5 cm broad; broadest involucral bracts 3–4 mm broad, outermost bracts not usually squarrose; mature achenes 9–12 mm long............................a. *typica*

Basal leaves 4.5–8 cm broad; broadest involucral bracts 2.2–2.8 mm broad, the outer ones squarrose; mature achenes 7–8.5 mm long..............................b. *latifolia*

5a. **Dubyaea oligocephala typica** nom. nov. (Fig. 4, *a–f*)—Basal leaves lanceolate, 12–28 cm long, 1.5–5 cm broad, their lobes deltoid, acute at the

Fig. 4. *Dubyaea oligocephala*. *a–f*, subsp. *typica*; *a*, *c*, *d*, from type and cotype; *b*, *e*, from *Clarke 31335* (Calcutta); *f*, from *Stewart 12381* (UC). *a*, habit, ×½; *b*, involucre, ×2; *c*, *d*, outer and inner involucral bracts, ×4; *e*, corolla, ×4; *f*, achene, ×8. *g–j*, subsp. *latifolia*, from type (K); *g*, leaf, ×½; *h*, *i*, involucral bracts, ×4; *j*, achene, ×8.

apex; plants hispid or nearly glabrous; involucral bracts rather broad, mostly 2–4 mm broad at the widest part; achenes slender and with well developed beaks, 9–12 mm long, including the beak. (*Paleya oligocephala* Sch. Bip., Pollichia 2: 320, 1866.)

The following are typical: INDIA: Kashmir Prov. without definite locality, *Jacquemont 1205* (P type, K, photo and fragments in UC); without locality, *Falconer 613* (K); Marbul Pass, 3030 m, *Clarke 31335D* (K); Laka, *Edgeworth 5048* (K); Sonamarg, *Stewart 12381* (UC, K, NY, G); Punjab Prov., Murree, *Saunders* in 1914 (K).

Subsp. *typica* is somewhat variable in size and pubescence, but is otherwise very constant.

5b. **Dubyaea oligocephala latifolia** subsp. nov. (Fig. 4, *g–j*)—A subsp. typica differt foliis latioribus, 4.5–8 cm latis; segmentis obtusis vel rotundatis; phyllis involucri pluribus, angustioribus, 1.2–2.8 mm latis; achaeniis brevioribus, 7–8.5 mm longis.

Stems densely hispid below; basal leaves short-pubescent on the upper surface, hispid along the veins below, narrowly obovate, 14–28 cm long, 4.5–8 cm broad, the apex acute or obtuse, the lobes obtuse or rounded; involucral bracts more numerous than in subsp. *typica*, narrow, 1.2–2.8 mm broad (at least in each head 2.2–2.8 mm broad); achenes 7–8.5 mm long, the beak often nearly absent.

Western Himalaya, east of the range of subsp. *typica*. The following have been seen:

INDIA: Punjab Prov., Dharmsala, alt. 2730 m, *Clarke 24012* (K *type*); near Dalhousie, alt. 2270 m, *Drummond 983* (K); Dalhousie, *Clarke 22439* (K).

In its broader leaves, as well as in its hispid character, relatively narrow involucral bracts, and shorter achenes, subsp. *latifolia* is somewhat transitional from *D. oligocephala* toward *D. hispida*. This is interesting in view of the fact that subsp. *latifolia* occupies a range adjoining that of *D. hispida*, and about equidistant between the known western limits of the latter species, and the eastern limits of the known range of *D. oligocephala* subsp. *typica*.

SECTION 2. IXERIDOPSIS

6. **Dubyaea chimiliensis** (W. W. Smith) comb. nov. (Fig. 5, *a–c*)—Plant glabrous throughout; stems from a taproot, 2–4.5 dm tall; larger basal leaves oblanceolate, 8–18 cm long, 1.5–2.2 cm broad, obtuse or apiculate at the apex; cauline leaves 2–4, sessile, similar to the basal, the lower 6–14 cm long, the upper gradually reduced; heads 2–6 on a stem, nodding, on slender peduncles, the lower of which arise from the upper leaves; involucres 22–30 mm long, broadly campanulate, about 30–35-flowered, the bracts oblanceolate to narrowly elliptic, acute, loosely imbricated, 5–8 mm broad at the widest part;

Fig. 5. *a–c*, *Dubyaea chimiliensis*, from *Forrest 25021* (US, E); *a*, habit, ×½; *b*, corolla, ×4; *c*, achene, ×8. *d–g*, *Dubyaea tsarongensis*, *d–f*, from cotype (E); *g*, from *Rock 22545* (UC); *d*, habit, ×½; *e*, involucre, ×2; *f*, corolla, ×4; *g*, achene, ×8.

corollas golden yellow, 18–23 mm long, the tube 3.5–4.5 mm, the ligule 15–18 mm long, sharply contracted at the base; anther tube yellow, 5.5–6 mm long; stigmatic branches blackish, flattened, 1.6–2 mm long; achenes 8.5–10 mm long, fusiform, tapering to a short, thick beak; pappus setae yellow, fragile, deciduous, 7.5–8.5 mm long. (*Lactuca tsarongensis* f. *chimiliensis* W. W. Smith, Notes Bot. Gard. Edinb. 12: 211, 1920; *Crepis tsarongensis* var. *chimiliensis* Anthony, op. cit. 18: 194, 1934; *Dubyaea tsarongensis* subsp. *chimiliensis* Stebbins, Jour. Bot. 75 (1937): 18.)

Chimili Mountains, Northeast Upper Burma, in alpine meadows. The following have been seen:

Burma: west flank of Chimili, alt. 3330–4240 m, *Forrest 24936* (E, NY, US); *25021* (E, K, NY, US), *26947* (E, K, NY, US); *27254* (K); *27306* (K, B, US).

The recognition of *D. chimiliensis* as a species is, in the opinion of the writer, justified by the definite differences between it and *D. tsarongensis*, not only in habit, but in floral characteristics as well. The involucres of *D. chimiliensis* are much larger and their bracts are broader. The corollas are quite different in shape (Fig. 5b), being markedly contracted at the base of the ligule in *D. chimiliensis*. Furthermore, the achenes of *D. chimiliensis* appear to be considerably larger than are those of *D. tsarongensis*, and are definitely rostrate, while the only ones of *D. tsarongensis* which have been seen, although they are immature, do not look as if they would develop any beak. There is no overlapping between the two species in any of these characteristics. In fact, no intermediate forms between them would be expected, since they occupy different mountain ranges, 160 km apart from each other.

7. Dubyaea tsarongensis (W. W. Smith) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 5, *d–g*)—Plant with the general habit of *D. chimiliensis*, but smaller throughout; stems 0.9–2 dm tall; basal leaves 4–10 cm long, 6–15 mm broad; cauline leaves much reduced, often linear and bract-like; heads solitary or rarely 2 on the stem; involucres 12–16 mm long, about 20–25-flowered; broadest inner bracts 3–5 mm broad; corollas 18.5–22 mm long, the tube 3.5–5, the ligule 15–18 mm long, gradually tapering toward the base; anther tube 3.5–5.5 mm long; achenes (immature) 4–5.5 mm long, truncate or slightly tapering toward the apex, but not at all beaked; pappus setae 6–7 mm long. (*Lactuca tsarongensis* W. W. Smith, Notes Bot. Gard. Edinb. 12: 211, 1920; *Crepis tsarongensis* Anthony, op. cit. 18: 194, 1934.)

Southeastern Tibet and adjacent Upper Burma, in alpine meadows. The following have been seen:

Tibet: Doker-La, Tsarong Prov., alt. 3330 m, *Forrest 16871* (E *type*, K); Mt. Kenichunpo, north of Sikitung, alt. 4090 m, *Rock 22148*, *22545* (UC); Upper Burma: Imaro Bum, *Ward 3585* (E).

In habit, size of heads, and shape of achenes, *D. tsarongensis* is nearer to *D. amoena* and *D. gombalana* than to *D. chimiliensis*, which it is in other respects much more closely related. In fact, *D. chimiliensis* and *D. tsarongensis* are in a way connecting links between the sect. *Eudubyaea* and the sect. *Amoenae*.

SECTION 3. AMOENAE

8. Dubyaea amoena (Hand.-Mazz) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 6, *a–c*)—Dwarf acaulescent perennial from a fusiform taproot; basal leaves 4–12 cm long, repand-dentate or pinnatifid, the lobes triangular-lanceolate, glabrous or sparingly glandular-hirsute on the midrib above; scapes 3–6, 2–7 cm long, glandular-hirsute, naked or with 1–2 linear bracts; involucres 15–18 mm long, narrowly campanulate, the bracts relatively few, evenly imbricated, lanceolate, blackish, glandular-hirsute; florets 10–16 per involucre; corollas blue or bluish purple, 20–27 mm long, the tube 6–9 mm long; anther tube blackish-blue (in sicc.), 3.5–4 mm long; mature achenes stramineous or somewhat reddish, 5.5–6.5 mm long, somewhat obcompressed, with 5 distinct nerves, otherwise smooth; papus setae 11–12 mm long, persistent, multiseriate, stiff and coarse, rufescent. (*Lactuca amoena* Hand.-Mazz., Sitzganz. Akad. Wiss. Wien. Math-Nat. 61: 23, 1924; Symb. Sin. 7: 1183, t. 17, fig. 12, 1936.)

Northwestern Yunnan and adjacent Tibet, in rocky alpine slopes and pastures. The following have been seen:

China: Yunnan Prov., Salwin-Irrawady divide above Chamutong, alt. 3825 m, *Handel-Mazzetti 9913* (V *type*, B); Tibet: Tsarong Prov., Salwin-Kiu Chiang (Irrawady) divide, alt. 4390 m, Forrest *18889* (B), *20331* (B, US), *22936* (B, US); Mt. Kenichunpo, alt. 4090–4240 m, *Rock 21975*, *22518* (UC).

The stiff, coarse pappus bristles and flattened stigmatic branches as well as the shape and ribbing of the achenes, serve to place this species in *Dubyaea* rather than *Lactuca*. The mature achenes resemble those of *D. atropurpurea*, except that they have fewer ribs.

9. Dubyaea gombalana (Hand.-Mazz.) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 6, *d–e*)—In habit similar to *D. amoena;* basal leaves 3–9 cm long, narrowly lanceolate, acute or apiculate, entire or minutely and remotely denticulate; scapes solitary, 1.5–5 cm long, glabrous; involucres narrowly campanulate, 13–17 mm long, the bracts evenly imbricated, glabrous; florets 10–17, corollas about as in *D. amoena;* anther tube pale, 4–4.5 mm long; mature achenes not seen, but presumably like those of *D. amoena;* pappus setae as in *D. amoena*. (*Lactuca gombalana* Hand.-Mazz., Sitzganz. Akad. Wiss. Wien, Math-Nat. 61: 23, 1924; Symb. Sin. 7: 1183, t. 17, fig. 13, 1936.)

Northwestern Yunnan and adjacent Tibet. The following have been seen: Yunnan: Mt. Gomba-la, Salwin-Irrawady divide above Chamutong, alt. 3900 m, *Handel-Mazzetti 9889* (V *type* B); Tibet: Tsarong Prov., Salwin-Kiu-

Fig. 6. *a–c*, *Dubyaea amoena*, *a–b*, from type (V); c, from *Rock 22518* (UC); *a*, habit, ×½; *b*, involucre, ×2; *c*, achene, ×8. *d–e Dubyaea gombalana*, from type (V); *d*, habit, ×½; *e*, involucre, ×2.

Chang divide, alt. 4240–4545 m, *Forrest 20257* (B, US); Mt. Kenichunpo, north of Sikitung, alt. 4240 m, *Rock 22160* (UC, US).

This species is close to *D. amoena*, but differs in its solitary scapes, the shape of its leaves, and in being glabrous throughout. In all of these respects it is transitional toward *D. tsarongensis*. The three species, *D. tsarongensis*, *D. amoena*, and *D. gombalana*, all found on the same mountain range and all except *D. tsarongensis* known only from this range, form the most striking case of endemism in the whole tribe of Cichorieae in Eastern Asia. They have no close relatives, except for the equally isolated *D. chimiliensis*, which occurs on a neighboring mountain range further south. The origin of these isolated endemics in post-Pleistocene time is difficult to imagine; they represent much more likely the last remnants of a group which was formerly more widespread.

SPECIES EXCLUSAE

Dubyaea cristulata DC., Prod. 7: 247. = Sonchus sp. (?)
Dubyaea ramosissima Hance ex Walp., Ann. 2: 1028 = *Ixeris denticulata* (Houtt.) Stebbins subsp. *ramosissima* (Benth.) Stebbins.
Dubyaea sonchoidea DC., Prod. 7: 247. = *Taraxacum montanum* DC.

IV. THE GENUS SOROSERIS

GENERIC DESCRIPTION

Soroseris, gen. nov. (Compositae-Cichorieae)—Herbae perennes pumilae laticiferae; caulis crassus, brevis, saepe cavus, ad basim saepissime cataphyllis ovatis vel lanceolatis vestitus, inflorescentia aggregata glomerata, capitulis numerosis, cymosa vel racemosa; flosculis 4–25 pro involucro; phylla involucri 2–3 seriata, extima 2 vel rarius 3–4, linearia, interiora subaequalia, lanceolata, ovata, vel anguste elliptica, ad basim coalescentia; corollae ligulatae, ligulis luteis vel albidis; antherae breviter caudatae, lutescentia vel nigrovirescentia; rami stigmati nigrescentes vel virescentes, leviter compressi, 1–3.5 mm longi, 0.2–0.35 mm lati; achaenia oblonga ad basim attenuata, ad apicem parce vel abrupte contracta, leviter obcompressa, multistriata; pappus setosus, setis simplicibus, numerosissimis, multiseriatis, crassis, rigidis, maturitate deciduis; receptaculum concavum, nec ciliatum nec paleaceum.

Dwarf alpine perennials with milky juice; stems thick, often hollow, usually short and partly or wholly subterranean: lowermost leaves usually replaced by bladeless petiolar cataphylls; upper leaves various; aggregate inflorescence glomerate, the heads numerous and closely crowded, cymose or somewhat racemose; involucres 4–25-flowered; involucral bracts in 2–3 series, the outermost usually 2, sometimes 3 or 4, narrowly linear, shorter than or exceeding the inner ones; inner bracts subequal, lanceolate, ovate, or narrowly elliptic, somewhat coalescent at the base; flowers perfect, bisexual; corollas ligulate, yellow or white, often blackish at the base of the ligule; anthers shortly caudate, yellowish, greenish, or blackish; pollen grains subechinolophate or merely echinate, the spines large; stigmatic branches blackish or greenish, somewhat flattened, 1–3.5 mm long, 0.2–0.3 mm broad, the barbs on their outer surface numerous, acute, deltoid in outline, those on the style below the stigma few, not enlarged; achenes oblong, somewhat attenuate at the base and slightly but abruptly contracted at the apex; slightly obcompressed, convex on the outer, angulate on the inner surface, many striate; pappus setose, the setae very numerous, multiseriate, simple, coarse and stiff, deciduous from the mature achene; receptacle concave, slightly pitted, not paleaceous or fibrillate. Type species: *Soroseris glomerata* (Decne.), = *Prenanthes glomerata* Decne. Basic chromosome number, $x = 8$. The generic name is compounded from the two Greek words σωρός, a heap, and σέρις, an ancient name for a Cichoriaceous plant. It refers to the unusual habit of these plants.

RELATIONSHIPS OF SOROSERIS

In most of its floral characteristics, that is the character of the corollas, style and stigmas, the pappus, and the vascular anatomy of the florets, *Soroseris* is similar to *Dubyaea*, *Youngia* Sect. *Desiphylum*, and *Prenanthes*, subg. *Nabalus*. The bulk of its species, however, those belonging to the section EUSOROSERIS, are strikingly different from any of these three groups in the following characteristics. Their habit is quite different from that of any of these groups, but is approached by *Dubyaea* Sect. AMOENAE and by *Youngia* Sect. DESIPHYLUM. The sections of *Lactuca* and *Crepis* which approach *Soroseris* in habit are very different from it in floral characteristics, as will be explained below. The other distinctive characteristics possessed by Sect. EUSOROSERIS are the pair of elongate, linear outer involucral bracts, the predominance, except in *S. glomerata*, of four inner bracts and four florets per involucre (in *Prenanthes*, *Youngia*, and most other Cichoriaceous genera the number of florets, when greatly reduced, is usually 5 rather than 4); the concave receptacle with the involucral bracts more or less coalescent at the base; and the character of the styles and pollen grains. The styles of Sect. EUSOROSERIS are distinctive in having very few barbs below the forking of the stigmatic branches: they lack the "collecting hairs" so characteristic of most genera of the Cichorieae (Figure 7, b–c). The pollen grains of this section differ from those of most genera of the Cichorieae in being merely echinate, without a trace of the ridged or lophate pattern (Figure 7, d–g, compare Wodehouse 1928, 1935). The only species known among the relatives of *Soroseris* which has these distinctive types of stigma and pollen grain is *Pernanthes subpeltata* Stebbins, an isolated species of Africa, which is very different in habit and in other respects from *Soroseris* (Stebbins 1937c).

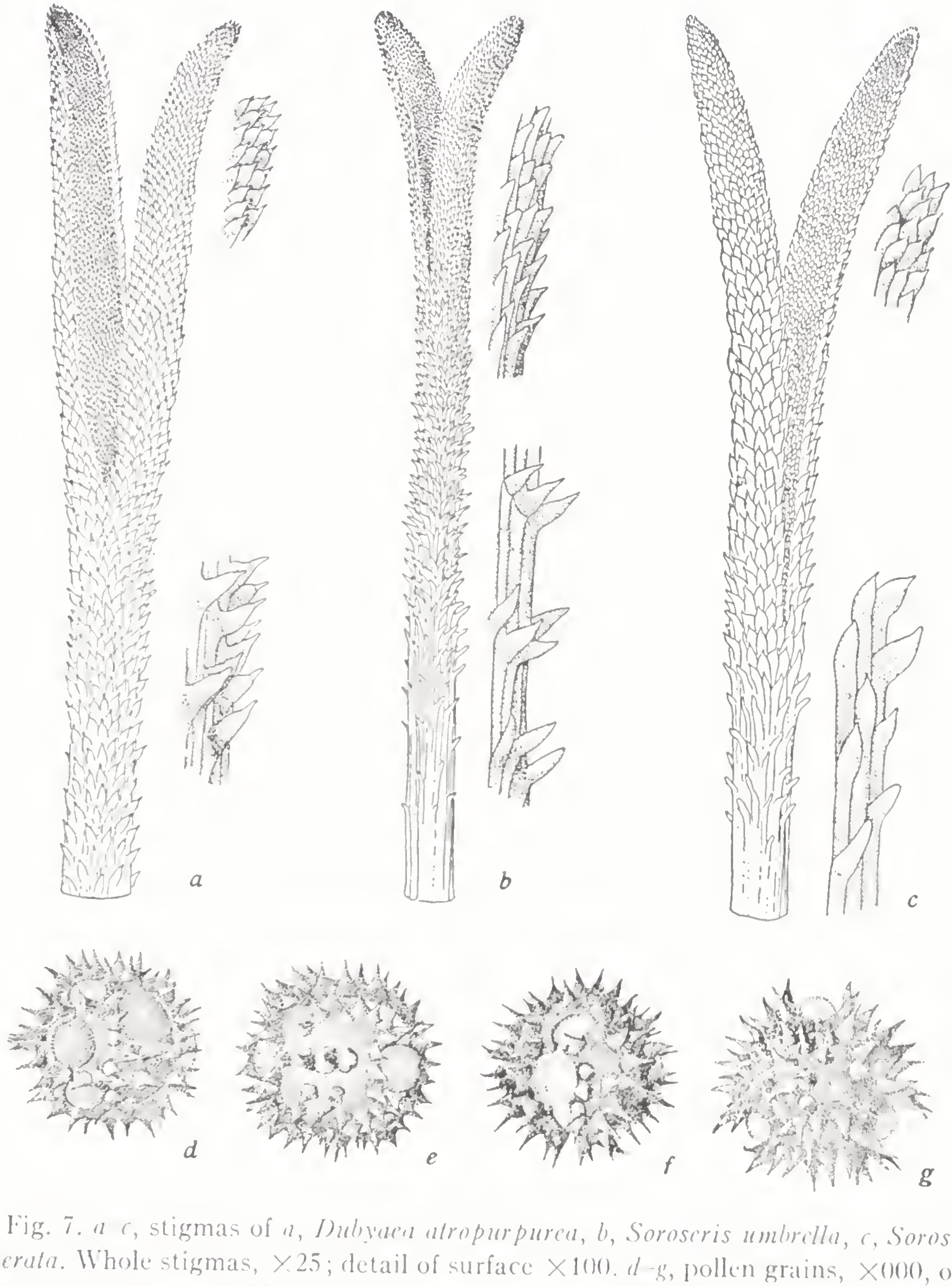

Fig. 7. *a–c*, stigmas of *a*, *Dubyaea atropurpurea*, *b*, *Soroseris umbrella*, *c*, *Soroseris glomerata*. Whole stigmas, ×25; detail of surface ×100. *d–g*, pollen grains, ×000, of *d*, *Dubyaea atropurpurea*, oblique poral view; *e*, *Soroseris umbrella*, equatorial view; *f*, *g*, *Soroseris glomerata*, *f*, oblique poral, *g*, polar view.

Fig. 8. *a–d* stigmas of *a*, *Prenanthes trifoliolata* (Cass.) Fernald, *b*, *Lactuca atropurpurea* Franch., *c*, *Crepis sibirica* L., *d*, *Crepis tectorum* L. *e–h*, pollen grains of *e*, *Prenanthes trifoliolata*, oblique poral view; *f*, *Lactuca atropurpurea*, polar view; *g*, *Crepis sibirica*, oblique poral view; *h*, *Crepis tectorum*, polar view. Magnification as in Fig. 7.

If the Sect. EUSOROSERIS were the only section of *Soroseris* extant, the genus would be a very much isolated one, whose affinities would be obscure. *S. umbrella*, however, of the Sect. DUBYAEOPSIS, is definitely a connecting link toward the genus *Dubyaea*. *S. umbrella* has the habit, the linear outer bracts, the concave receptacle, and coalescent inner bracts, the achene shape and the deciduous pappus setae characteristic of *Soroseris*, but in its large heads with numerous involucral bracts and florets, it resembles *Dubyaea*. Its styles and pollen grains are intermediate between these of Sect. EUSOROSERIS and those of *Dubyaea* (Fig. 7). There is another, but less obvious relationship between Sect. EUSOROSERIS and *Dubyaea* Sect. AMOENAE. The habit of these two sections is somewhat similar. Sect. EUSOROSERIS differs chiefly in having much more numerous and shorter peduncles. There is also some similarity between *S. Gillii* and *D. amoena* in leaf shape. The involucres, florets, and achenes of the two sections are. however, very different from each other. The glabrous habit and the leaf shape of *S. Gillii* subsp. *erysimoides* recall *Dubyaea* Sect. IXERIDOPSIS while the two sections also resemble each other in their relatively short corolla tubes. There are, therefore, one definite and two suggestive connections between *Dubyaea* and *Soroseris*. The relationship between *Soroseris* and *Youngia* is less evident, and is shown chiefly by the resemblance in habit, corollas, and pappus between *S. umbrella* and *Youngia depressa*. The short, deltoid outer bracts of *Youngia*, however, contrast sharply with the elongate, linear ones of *Soroseris*, while the achenes of the two genera are quite different. *Prenanthes* resembles *Soroseris* in its narrow, few-flowered involucres and in the shape of its achenes, but the limit of reduction in floret number is mostly five in *Prenanthes* and four in *Soroseris*, while the shape of the outer involucral bracts is quite different in the two genera. Furthermore, the two genera differ widely from each other in habit, and no species is known which suggests any direct connection between them. For this reason the writer believes that the similarities between *Soroseris*, *Youngia*, and *Prenanthes* are due merely to their common relationship with *Dubyaea*.

The connection between *Soroseris* and *Crepis* is still more remote. The differences between *Dubyaea* and *Crepis* in stigmas and achenes has already been mentioned; *Soroseris* is even more different from *Crepis* in these respects than is *Dubyaea*. In the shape of its involucres, as well as in the character of its styles, stigmas, pappus setae, and achenes, *Soroseris* is nearer to *Prenanthes* than to *Crepis*. The habital resemblance between *Crepis nana* Richards. and *Soroseris* is, in the opinion of the writer, merely a case of parallel evolution, in response to a similar ecological habitat.

C. nana has the short outer bracts, small corollas, slender, pale stigmatic branches, weak pappus bristles, slender, terete achenes, and the reduced floral anatomy most characteristic of *Crepis;* in all of these respects it differs more widely from *Soroseris* than do such *Crepis* species as *C. sibirica* and *C. kashmirica*, which in their habit show no resemblance whatever to *Soroseris*.

DIAGNOSIS OF SECTIONS OF SOROSERIS

Section 1. **Dubyaeopsis** sect. nov.—Leaves large, lyrate-pinnatifid with the lateral lobes much reduced, or merely elliptic to orbicular; involucres large with 10–15 inner bracts and 15–25 florets; inner bracts not thickened at maturity.

Section 2. **Eusoroseris** sect. nov.—Leaves small, entire or pinnatifid; involucres narrow, with 4–5 inner bracts and florets; inner bracts spongy-thickened at maturity.

ARTIFICIAL KEY TO THE SPECIES OF SOROSERIS

A. Leaves large, the blade mostly 3–6 cm broad; involucres with 10–15 inner bracts and 15–25 florets; inner bracts not thickened at maturity . . . . 1. *S. umbrella*

A. Leaves less than 2 cm broad; involucres with 4–5 inner bracts and 4–5 florets; the inner bracts spongy thickened at the base at maturity.

  B. Cataphylls numerous on the lower part of the stem; leaf blades elliptic or spatulate; ligule of corollas mostly equalling or shorter than the tube.

    C. At least some heads of the inflorescence with 5 inner bracts and 5 florets; all of the inner bracts essentially similar, and with scarious margins . . . . 2. *S. glomerata*

    C. All of the heads with 4 inner bracts and 4 florets; inner bracts in two dissimilar pairs, the outer (lower) pair lanceolate and without scarious margins, the inner (uppermost) broader, often ovate or elliptic, and with more or less distinct scarious margins.

      D. Leaf margins entire or remotely denticulate; involucres 10–15 mm long; ligule of corollas gradually contracted at the base, shallowly and evenly 5-dentate at the apex; anthers 3.5–5 mm long, yellowish.

        E. Leaves on slender petioles, these 0.5–1.5 mm in diameter at the apex; involucres 10–13 mm long; lower pair of inner involucral bracts 1.5–2.5 mm broad, acute at the apex; western Himalaya and western Turkestan . . . . 3. *S. Deasyi*

        E. Petioles of leaves 2–4 mm broad at the base of the blade; western China and adjacent Tibet.

          F. Involucres 11–13 mm long; lower pair of inner involucral bracts 2.9–3.2 mm broad, obtuse or acute at the apex . . . . 4. *S. rosularis*

          F. Involucres 12–19 mm long; lower pair of inner involucral bracts 1.5–2.5 mm broad, acute at the apex . . . . 5. *S. bellidifolia*

      D. Leaf margins coarsely dentate; involucres 7–9 mm long; ligules of corollas abruptly contracted at the base, deeply and unevenly 5-dentate at the apex; anthers 2.5–3.5 mm long, blackish or greenish . . . . 6. *S. pumila*

  B. Cataphylls few or none; leaf blades lanceolate or oblanceolate; ligules distinctly exceeding the tube of the corolla; anthers blackish or greenish.

          G. Involucres 11–16 mm long; upper (innermost) pair of involucral bracts 3.2–4.5 mm broad; corolla tube 5.5–10.5 mm long; pappus setae 10–16 mm long . . . . 7. *S. Gillii*

          G. Involucres 7–12 mm long; uppermost pair of inner bracts 2–3.5 mm broad; corolla tube 3–6 mm long; pappus setae 6.5–11 mm long . . . . 8. *S. Hookeriana*

1. **Soroseris umbrella** (Franch.) comb. nov. (Fig. 9, *a–e*).—Stems 5–18 cm long, mostly subterranean and rhizomatous; cataphylls numerous, the lower ovate, the upper lanceolate or linear; leaves on petioles 3–12 cm long, these sparsely hirsute, the blade glabrous or closely tomentulose, orbicular or lyrate-pinnatifid with a few small lobes below the large terminal one, 2–8 cm long, 1.5–6 cm broad; inflorescence densely cymose, peduncles 1.5–8 cm long, thick, simple or branched, bearing 1–4 small leaves or lanceolate bracts; involucres 14–20 mm high; outer bracts 2–4, broadly linear, equalling or somewhat shorter than the inner; inner bracts 10–15, lanceolate, acute, sparsely hirsute or glabrous, not thickened at maturity, coalescent at the base; florets 15–25; corollas yellow, 12–20 mm long, the tube slightly shorter than the ligule; anthers 3–5.5 mm long; achenes 3–6 mm long, narrowly oblong, slightly contracted at the apex, prismatic in cross section, stramineous, fuscous or olive green, smooth or lightly striate; pappus setae white, 9–11 mm long, deciduous at maturity. (*Crepis umbrella* Franch., Jour. de Bot. 9: 255, 1905.)

Western China and eastern Tibet, in alpine situations. The following are typical: CHINA: Szechuan Prov., Mt. Konka, alt. 5140 m, *Rock 16822* (B); Yunnan Prov., Likiang Snow Range, *Forrest 3004* (B, K); *Rock 5303* (B), 9846, 9926 (K), 25320 (UC); Mekong-Yangtze divide, alt. 3640–3940 m, *Forrest 20373* (K); Mountains of Hung-Po, alt. 4550 m, *Rock 23402* (UC). TIBET: Pa La, alt. 3333 m, *Ward* in 1924 (K).

The last named specimen differs from the typical Chinese *S. umbrella* in its coarsely dentate leaves, shorter anthers, and somewhat smaller achenes. It may represent a distinct subspecies. Another specimen from Tibet (Chumbi, *King's collector 586*, B) is in general similar to *S. umbrella*, but has much smaller involucres (10–12 mm long) more acute inner bracts and black achenes 3 mm long. It may represent a distinct species, but the material available is not sufficient for description.

Soroseris umbrella is a most distinctive species, and forms a connecting link between the other species and *Dubyaea* and *Youngia*. Its habit and leaves recall those of *S. Deasyi* and *S. rosularis*, except for size, so that these two species are perhaps the nearest relatives of *S. umbrella*.

2. **Sorosis glomerata** (Decne.) comb. nov. (Fig. 9, *f–g*)—Stems always short, chiefly subterranean and rhizomatous, 3–6 cm long; cataphylls numerous, broadly lanceolate to ovate; leaves mostly spatulate or obovate, on broadly winged petioles, the blade 6–10 mm long, 4–7 mm broad, 3-nerved, glabrous or slightly hirsute; inflorescence flat, cymose; heads on peduncles 0.5–6 mm long; involucres 10–12 mm long; outer bracts 2, linear, hirsute, slightly shorter than the inner; inner bracts 4 or 5, all with scarious margins, 1.5–3 mm broad, obtuse or acute at the apex, hirsute throughout with whitish, crisped trichomes or glabrate toward the base; florets 5; corollas white or perhaps sometimes yellow; 12.5–15 mm long, the tube 7–9 mm, the ligule 5.5–6 mm long; anther tube 3–4 mm long, greenish; style black, the branches of the

Fig. 9. *a–e*, *Soroseris umbrella*, *a–c* from *Forrest 10952* (UC); *d–e*, from *Rock 25320* (UC): *a*, habit, ×$\frac{1}{2}$; *b*, involucre, ×2; *c*, corolla, ×4; *d*, achene, ×8; *e*, pappus seta, ×8. *f–g*, *Soroseris glomerata*, from *Champion 52* (DD): *f*, leaf, ×1; *g*, involucre, ×2.

stigma 2.8–3 mm long; achenes 5–6 mm long, grayish brown, somewhat attenuate at the base, slightly contracted at the apex; pappus setae 6.5–7.5 mm long, silvery gray, somewhat paler toward the base. (*Prenanthes glomerata* Decne. ex Jacquem., Voy. Ind. 99, t. 107, 1834; *Crepis glomerata* Benth. et Hook. f., Gen. Pl. 2(1): 515, 1873; Hook. f., Fl. Brit. India 2: 398, 1882, in part; *Crepis sorocephala* Hemsl., Jour. Linn. Soc. 30: 116, t. 4, figs. 1–4, 1894.)

Central Himalaya in Garwhal and Almora provinces and Tibet, in stony or rocky situations at altitudes of 3800–5400 m. Only the following have been seen:

INDIA: Sumna, Almora Prov., alt. 4436 m, *Champion 52* (DD). TIBET: Chaldu, north of Antadhura Pass (Almora Province) alt. 4700 m, *Champion 51* (DD).

The plants of these two collections agree well with the description and illustration of *Prenanthes glomerata* Decne. (loc. cit.), as well as those of *Crepis sorocephala*. Hemsley (loc. cit.) listed three differences between his *C. sorocephala* and *S. glomerata:* "foliis carnosis, floribus albis, achaeniis oblongo-obovoideis." The original description of *P. glomerata* Decne. (loc. cit.) also characterizes its leaves as "carnosa" and the achene as "inferne subattenuatus," but makes no mention of the color of the flowers. The corollas on the specimens seen by the writer, which were collected in the same general region as Jacquemont's type, are pale, and were very likely white or cream color when fresh. Hence none of the differences listed by Hemsley may be said to hold.

True *Soroseris glomerata* has been very rarely collected, but may have a very wide range in Tibet. The two localities cited by Decaisne (loc. cit.) are "supra Ghauti" and "Kioubrang Ghauti." The former could not be accurately located on Jacquemont's map, but the latter is a pass east of the Sutlej River, and just north of the sources of the Ganges and Jumna Rivers (cf. Jacquemont, Voy, Ind., atlas). This would place it about on the border between what is now the province of Tehri Garwhal and Tibet. The two localities of Champion listed above are about 240 km east of this, while the type locality of *Crepis sorocephala* Hemsl. (Jour. Linn. Soc. 30: p. 102) is probably "west and north of Lhassa," about 1100 km east of the type locality of *S. glomerata*. The intervening region is almost or completely unknown botanically. No specimens of true *S. glomerata* have been seen from elsewhere in the Himalaya. Those from Kashmir are all *S. Deasyi* (v. infra), while the only species known from Sikkim are *S. Hookeriana* and *S. pumila*. The citation of the locality of *C. glomerata* by Franchet (Jour. de Bot. 9: 256) as "Kaschmir (Jacquemon)" is erroneous, as is evident from the previous discussion.

3. **Soroseris Deasyi** (S. Moore) comb. nov. (Fig. 10, *e–f*)—Stems short, 3–13, mostly 5–6 cm long, chiefly subterranean and rhizomatous; cataphylls numerous, lanceolate or linear, or the lowermost ovate; leaves on elongate, slender petioles, these mostly 0.5–1.5 mm in diameter at the apex (*in sicc.*), blades elliptic, obovate, or spatulate, 1–1.8 cm long, 0.5–1.5 cm broad, more or less definitely 3-nerved, their margins entire or denticulate, their apex rounded; inflorescence flat, cymose, the heads on peduncles 1–20 mm, mostly 5–6 mm long; involucres 10–13 mm long; outer bracts 2, linear, shorter than or exceeding the inner; inner bracts 4, hirsute, the lower (outer) pair 1.5–2.5 mm broad, acute at the apex, without scarious margins; the upper (inner) pair 2.5–4 mm broad, acute or obtuse at the apex, with broad scarious margins; florets 4; corollas yellow, the ligules blackish at the base, length of corolla 13–17 mm, the tube 7–9 mm, the ligule 6–8 mm long; anther tube 3.5–4.5 mm long, dark yellow or somewhat reddish (*in sicc.*); style greenish or blackish, the stigmatic branches 2–2.8 mm long; achenes yellowish or reddish, 5–6 mm long, somewhat attenuate at the base and slightly contracted at the apex; pappus setae dirty white to pale rufous, 9–11 mm long. (*Crepis glomerata* Hook. f., Fl. Brit. Ind. 3: 398, 1882, in part, not *Prenanthes glomerata* Decne.; *Lactuca Deasyi* S. Moore, Journ. Bot. 38: 428, 1900.)

Western Himalaya in Kashmir and Punjab, north to Chinese Turkestan (Sinkiang). Rocky talus slopes and gravel slides at 4000–5000 m. The following have been seen (all but the last identified as *Crepis glomerata*):

INDIA: Kashmir Prov., Har Nag, Upper Lidar Valley, alt. 4212 m, *Stewart 12389* (UC, K, B, G, NY); Mt. Kolahai, alt. 4212 m, *Stewart 9420* (K); Dessai Baltistan, alt. 4212 m, *Meebold 980* (B); Pir Panjal, *Duthie 25659* (K); Lahul, *Edgeworth 5040* (K); Zoypal, alt. 4090 m, *Coventry 928* (K); Punjab Prov., without locality, *Drummond 25561* (K). CHINESE TURKESTAN (Sinkiang): Aksu, alt. 5000 m, *Deasy 95* (type of *Lactuca Deasyi* S. Moore, in herb. British Museum, photo and fragments UC).

S. Deasyi is the species of Kashmir which has generally passed as *Crepis glomerata*. A photograph and fragments of the type specimen of *Lactuca Deasyi* show beyond any doubt that it belongs in the same genus with *Soroseris glomerata*. It matches fairly well a considerable series of specimens from Kashmir, which differ from true *S. glomerata* in their larger leaves, larger heads, involucres with four inner bracts, the lower pair of which have no scarious margins, in the length and color of the pappus setae and other details. In fact, the affinity of *S. Deasyi* is much closer to *S. rosularis* of Yunnan and *S. bellidifolia* of northwestern China than to *S. glomerata*.

4. **Soroseris rosularis** (Diels) comb. nov. (Fig. 10, *a–d*)—Stems short, 2–10 cm long, chiefly subterranean and rhizomatous; cataphylls numerous, ovate or lanceolate; leaves on broad, elongate petioles, 1.5–7 cm long, 2–4

mm broad at the base of the blade; blades spatulate, obovate, or elliptic, 1–2 cm long, 0.5 cm broad, obtuse or rounded at the apex, inconspicuously 3-nerved, the margins entire or remotely denticulate; the margins and upper part of the petiole hirsute, becoming glabrate in age; inflorescence flat, cymose, peduncles 2–6 mm long; involucres 11–13 mm long; inner bracts 4, lightly hirsute, the lower pair obtuse or acute at the apex, 2.8–3.2 mm broad, without scarious margins, the upper pair rounded at the apex, 4.5–5.5 mm broad when fully spread out; florets 4; corollas yellow, the base of the ligule and upper part of the tube black, 12.5–15.5 mm long, the tube 6–8.5, the ligule 6–7 mm long; anthers yellowish, 3.5–4 mm long; style blackish, the stigmatic branches 2–2.8 mm long; achenes not seen; pappus setae 8.5–10.5 mm long, stramineous or pale rufescent. (*Crepis rosularis* Diels, Notes Roy. Bot. Gard. Edinb. 25: 201, 1912.)

Yunnan Province, China, in limestone rocks at 3300–4000 m. The following have been seen:

CHINA: Yunnan, eastern flank of Lichiang Range, Lat. 27° 30′ N, alt. 3333–3636 m, *Forrest 6093* (UC, K, B), *10461* (UC, B); same locality, *Rock 4479, 5474* (B); same locality, *Schneider 2065* (B).

This species is so close to *S. Deasyi* that, were it not for the great separation in the range of the two, they might be considered subspecies of the same species. *S. rosularis*, however, has consistently broader petioles and involucral bracts than *S. Deasyi*, while the leaves are less conspicuously 3-nerved. As described by Franchet (Jour. de Bot. 9: 256, 1895), the lateral nerves of the leaves of *S. glomerata* and *S. Deasyi* diverge from the median one at or near the base of the blade, while in *S. rosularis* the laterals run parallel to the median nerve for ⅓ to ½ of the distance from base to apex of the blade, so that the blade appears 1-nerved, at least in its lower half. There is, however, considerable variation in this characteristic, even among the different leaves on the same plant, and the distinction between *S. Deasyi* and *S. rosularis* in this respect is not sharp. As described by Franchet (loc. cit.), this apparently one-nerved condition of the leaves is more pronounced in *S. Hookeriana* and *S. Gillii* (= "*C. trichocarpa*").

5. **Soroseris bellidifolia** (Hand.-Mazz.) comb. nov. (Fig. 10, *g–i*)—In habit like the last two, but more robust; stems 8–11 mm long; cataphylls numerous, ovate or lanceolate; leaves on petioles 5–8 cm long and 2–4 mm broad; the blade obovate or elliptic, 1.5–2.5 cm long, 0.8–1.5 cm broad, its apex obtuse or rounded, its margin entire or remotely denticulate; inflorescence flat, cymose; involucres 12–15 mm long; outer bracts 13–20 mm long; inner bracts 4, conspicuously hirsute, the lower pair acute, 1.5–2.5 mm broad, the upper pair acute or obtuse, 4.5–5.5 mm broad, narrowly elliptic in outline, tapering conspicuously toward the apex; florets 4; corollas 20 mm long, yellow, the base of the ligule and apex of the tube black, the tube 10 mm, the

ligule 10 mm long; anthers yellowish (or blackish?), 5 mm long; achenes reddish brown, tapering toward the base and slightly contracted at the apex, 8 mm long; pappus setae deep yellow or somewhat rufous at the base, grayish at the apex, 10–11 mm long. (*Crepis Gillii* var. *bellidifolia* Hand. Mazz., Acta Horto Goth. 12: 355, 1938.)

Western China, from Kansu to Yunnan Provinces. The following is the only typical specimen seen:

China: Southwestern Kansu Prov., Minshan, west of Shimen range, 4100 m, *Rock 13025* (UC, B, K).

The writer has not been able to see the type of *Crepis Gillii* var. *bellidifolia*, so that the present description is based on the Rock collection also cited by Handel-Mazzetti, and from the same general region.The specimens of this collection are obviously more closely related to S. *rosularis* and *S. Deasyi* than to *S. Hookeriana* and *S. Gillii*. They have the numerous cataphylls characteristic of the two former (although these are not clearly visible on any except the UC specimen, which is the only one that is mounted with the outside of the stem up), and agree with them in leaf shape and in the long corolla tube.

S. bellidifolia resembles *S. rosularis* in its broad petioles and *S. Deasyi* in its narrow, more or less acute involucral bracts, but differs from both of these species in its more robust habit, somewhat longer involucres, larger corollas, larger achenes, and in the color of its pappus. One collection from Yunnan, on the Mekong-Yangtze divide, east of Yeh-chih, alt. 3940–4240 m, *Forrest 20367* (part, UC, B), contains specimens which agree with *S. bellidifolia* in their general appearance and the color of the pappus, but which in the shape of the involucral bracts, the relative length of the corolla tube and ligule, and to some extent the leaf shape, are transitional toward *S. Hookeriana* subsp. *erysimoides* and *S. Gillii* subsp. *hirsuta*. Since a specimen of the latter subspecies is on the Berlin sheet of the same collection, the transitional forms may be the result of hybridization between *S. bellidifolia* and *S. Gillii*. Their pollen is somewhat more irregular than that of *S. rosularis*, and contains about 20% of obviously defective grains. No pollen of *S. bellidifolia* was available. If many more localities are found in which transitional forms like this occur, the different species here recognized may have to be combined, but the wisest course at present is to keep them separate, even though they are not sharply differentiated from each other.

6. **Soroseris pumila** sp. nov. (Fig. 10, *j–q*)—Radix tenuis, ad apicem 3–7 mm crassa; caulis rhizomatus, tenuis, 2.5–10 cm longus, ad mediam 2–8 mm crassus, ad apicem in inflorescentiam expansus, cataphyllis pluribus obsita,

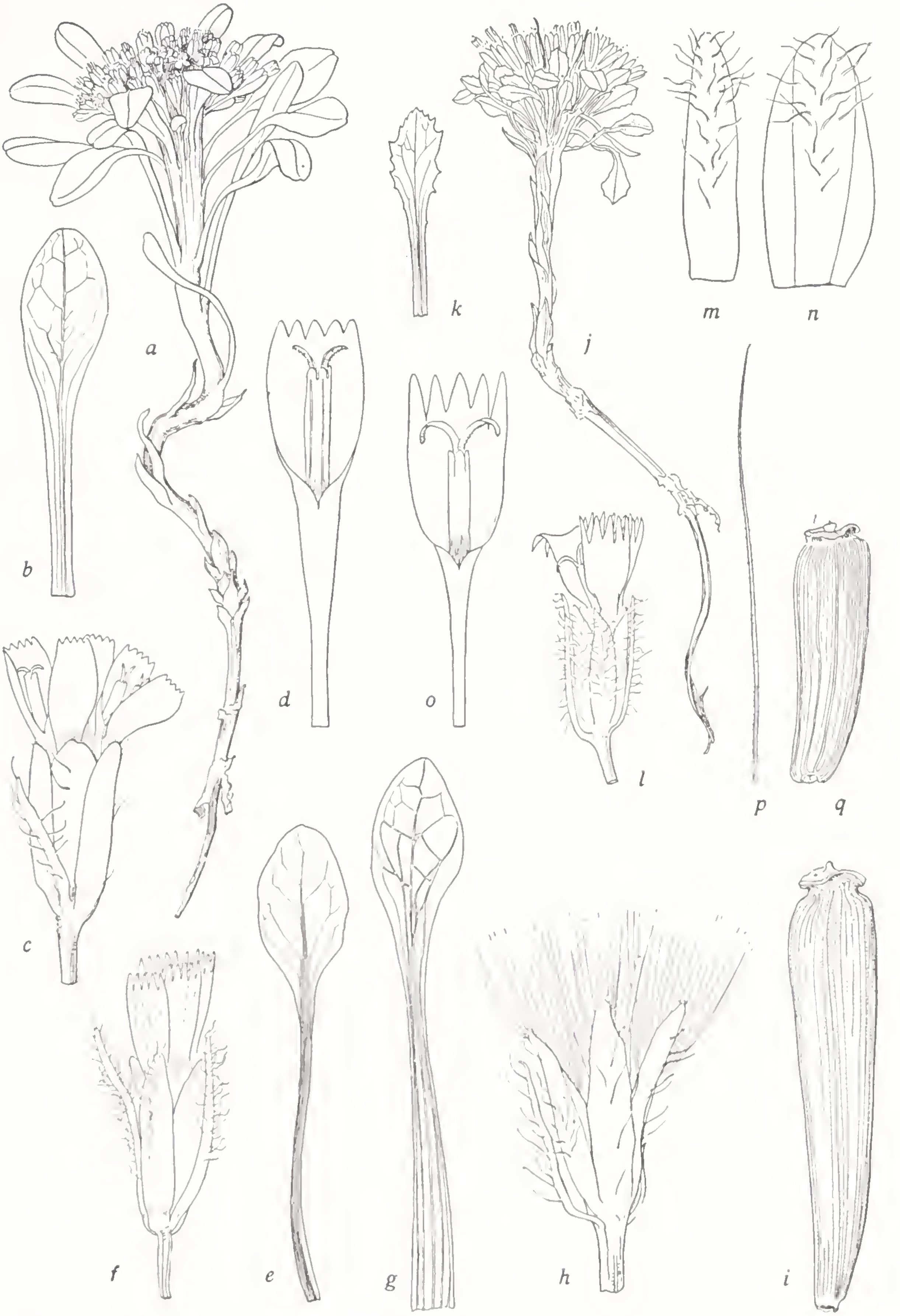

Fig. 10. *a–d*, *Soroseris rosularis*, from *Forrest 1046* (UC): *a*, habit, ×½; *b*, leaf ×1; *c*, involucre, ×2; *d*, corolla, ×4. *e–f*, *Soroseris Deasyi*, from *Stewart 12389* (UC). *e*, leaf, ×1; *f*, involucre, ×2. *g–i*, *Soroseris bellidifolia*, from *Rock 13025* (UC): *g*, leaf, ×1; *h*, involucre, ×2; *i*, achene, ×8. *j–q*, *Soroseris pumila*: *j–o*, from type, *p–q*, from *Hooker* s.n.; *j*, habit, ×½; *k*, leaf, ×1; *l*, involucre, ×2; *m*, *n*, inner bracts, ×4; *o*, corolla, ×4; *p*, pappus seta, ×8; *q*, achene, ×8.

infimis ovatis, superioribus lanceolatis vel linearibus, acutis; folia spatulata vel oblanceolata, petiolis tenuis 1–5 cm longis, lamina 5–20 mm longa, 3–9 mm lata, valde dentata vel ad basim subpinnatifida, apice obtusa vel rotundata, folia inferiora sparse, folia superiora dense hirsuta; inflorescentia discum formans, capitulis numerosis, pedunculis 2–5 mm longis; involcura 7–9 mm longa, phyllis exterioribus 2, 9–12 mm longis, linearibus, hirsutis, phyllis interioribus 4, hirsutis, apice obtusis, intimis ovatis vel ellipticis, 3–4 mm latis margine scariosis; floscula 4; corollae 7.5–11 mm longae, tubo 3–5 mm longo, ligule 4.5–6 mm longa, ad basim abrupte contracta, apice profunde et irregulariter 5-dentata; antheris 2.5–3.5 mm longis, nigrescentibus (in sicc.); achaenia 3.5–4.2 mm longa ad basim attenuata, ad apicem paullo sed abrupte contracta; pappi setae 7–8 mm longae argenteae, griseae, vel rarius lutescentiae.

Root slender, elongate, 3–7 mm thick at the apex; stem subterranean and rhizomatous, slender, 2.5–10 cm long, 2–8 mm thick at the middle, expanded at the apex into the inflorescence; cataphylls several and conspicuous, the lowermost ovate, the middle and upper ones lanceolate or linear, acute; leaves spatulate or oblanceolate, probably purplish-green when fresh, the petioles slender, 1–5 cm long, the blade 5–20 mm long, 3–9 mm broad, coarsely and closely dentate or subpinnatifid at the base, obtuse or rounded at the apex, the lower sparsely, the upper densely hirsute; inflorescence flat, corymbose, the heads numerous, peduncles 2–5 mm long; involucres 7–9 mm long, the outer bracts 2, 9–12 mm long, linear, hirsute, inner bracts 4, hirsute, in two pairs, the lower (outer) pair 1.5–2 mm broad, obtuse or somewhat acute at the apex, without scarious margins, the upper (innermost) pair 3–4 mm broad, elliptic, 3–4 mm broad, with broad scarious margins; florets 4; corollas 7.5–11 mm long, the tube 3–5 mm, the ligule 4.5–6 mm long, abruptly contracted at the base and rather broad for its length, deeply and irregularly 5-dentate at the apex; anthers 2.5–3.5 mm long, blackish (*in sicc.*); achenes 3.5–4.2 mm long, attenuate toward the base, slightly but abruptly contracted at the apex; pappus setae 7–8 mm long, silvery gray or rarely yellowish. (*Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, 1882 in part, not *Prenanthes glomerata* Decne.)

Eastern Himalaya Mountains, in Sikkim and adjacent Tibet, at altitudes of 3940–5150 m, probably on rocky talus slopes. The following have been seen:

TIBET: Chumolari, alt. 4850 m, *Lepcha 527* (type, K). INDIA: Sikkim Prov., Kinchin jharo (?) alt. 4850 m, *Hooker* s.n. (part, K. B); Sikkim, *Elwes* in 1877 (K); Mizarpohri, *King's collector* in 1887 (DD); Guiche La, alt. 4390 m, *Ghose* in 1932 (UC).

This species is distinguished from all others of the genus by the small size, both of its vegetative and floral parts, as well as by the shape and peculiar dentation of its leaves. Furthermore the ligules of the corollas are remarkably broad for their length and, in the specimens examined, are more deeply and irregularly toothed at the apex than are those of any other species of *Soroseris*. On the basis of its habit, its numerous cataphylls, the shape of its leaves, and the relative length of corolla tube and ligule, *S. pumila* is closest to *S. Deasyi* and *S. rosularis*, from both of which it differs in its blackish anther tubes, as well as in the characters mentioned above. Phylogenetically it may be considered the most reduced and specialized species of the genus, and is probably an offshoot from the complex of *S. Deasyi* and *S. rosularis*.

7. **Soroseris Gillii** (S. Moore) comb. nov. (Fig. 11, *a–h*)—Stems mostly short, 2–12 cm tall; cataphylls few or none; leaves lanceolate, pinnatifid or dentate; inflorescence flat, cymose, often very broad; involucres 11–16 mm long, inner bracts 4, glabrous or hirsute, acute or obtuse at the apex, the lower pair 1.6–2.5 mm broad, without scarious margins, the upper pair 3.2–4.5 mm broad, with scarious margins; florets 4; corollas yellow, the base of the ligule and apex of the tube blackish, 14.5–21.5 mm long, the ligule equalling or somewhat longer than the tube; anthers blackish (*in sicc.*), 4–6 mm long; branches of the stigma 2–3 mm long; achenes 3–6 mm long, blackish when mature, obovoid, the lower pair definitely obcompressed, the upper pair subterete; pappus setae rufous, stramineous, or grayish at the summit, 10–16 mm long.

Western China to the Western Himalaya, in meadows, gravelly places and talus slopes (screes) at 3700–5000 m altitude.

The distinction between *S. Gillii* and *S. Hookeriana* is chiefly in the size of the floral parts, *S. Gillii* being larger throughout. There is little or no overlapping in at least some characteristics, such as the length of the corolla tube and the breadth of the innermost involucral bracts, while there is an accompanying difference in habit, since *S. Hookeriana* generally has well developed stems, while *S. Gillii* rarely has. Furthermore, both *S. Gillii* subsp. *typica* and *S. Hookeriana* subsp. *erysimoides* have been collected in the vicinity of Tatsienlu, western Szechuan, but the specimens show no sign of intergradation between the two. Further collections, particularly from the critical region of southwestern Szechuan and northwestern Yunnan, may make necessary the uniting of *S. Gillii* under *S. Hookeriana*, but at present the writer feels justified in maintaining them as separate species.

Four subspecies may be recognized under *S. Gillii*, as follows:

A. Inner involucral bracts mostly obtuse or rounded at the apex, dark green or blackish in color, glabrous, short pubescent, or sparsely hirsute; pappus rufous or stramineous.
    B. Involucres 13–16 mm long; the inner bracts glabrous or short-pubescent; anthers 5–6 mm long; pappus setae 12–15 mm long. . . . . a. subsp. *typica*
    B. Involucres 11–12 mm long, the inner bracts sparsely hirsute along the midrib; anthers 4 mm long; pappus setae 10–10.5 mm long. . . . . b. subsp. *Handelii*

A. Inner involucral bracts mostly acute at the apex, greenish or yellowish, sparsely to strongly hirsute; pappus setae grayish at least at the apex.
  C. Leaves runcinate-pinnatifid; inner bracts densely hirsute; pappus setae 12–14 mm long; Yunnan and adjacent Tibet............................c. subsp. *hirsuta*
  C. Leaves sinuate-pinnatifid, sinuate-dentate, or merely denticulate; inner bracts sparsely to moderately hirsute; pappus setae 10–15 mm long; western Himalaya...d. subsp. *occidentalis*

7-a. **Soroseris Gillii typica** nom. nov. (Fig. 11, *a–b*)—Leaves runcinate-pinnatifid, the blade 3–8 cm long, 0.7–1.8 cm broad; inflorescence flat, cymose, the heads very numerous, on peduncles 2–12 mm long; involucres 13–17 mm long, the inner bracts glabrous or rarely short-pubescent, dark green or blackish at least toward the apex, the apex obtuse or rounded; corolla tube 8–10.5 mm long, the ligule 9–12 mm long; anthers 5–6 mm long; achenes 3–6 mm long; pappus setae 13–16 mm long, rufous. Chromosome number, 2n = 16. (*Crepis trichocarpa* Franch., Jour. de Bot. 9: 257, 1895 (?); *Crepis Gillii* S. Moore, Jour. Bot. 47 (1899): 170; Hand.-Mazz. Acta Horto. Goth. 12: 355, 1938, pro parte, vars. *erysimoides* et *bellidifolia* exclusae).

Western China and adjacent Tibet. The following have been seen:

CHINA: Szechuan Prov.; near Tachienlu, *Pratt 456, 482, 875* (K); Tatsienlu, *Soulié 2160* (B); Tongolo, *Soulié 2663, 2664* (B); Baurong to Tachienlu via Hadjaha, *Stevens 178, 379* (B); Mt. Mitzuga, west of Muli Gomba, alt. 3050–4875 m, *Rock 16242* (B); north of Chiu-Lung-Hsien, Minya Country, alt. 5000 m, *Rock 17449* (B); between Litang and Yalung Rivers, alt. 4400 m, *Rock 16630* (B); between Litang and Shou-Chu Rivers, alt. 4510 m, *Rock 16756* (B); Kaushu shan, Leirong, alt. 4090 m, *Rock 24094, 24502* (UC). TIBET: between Labrang and Yellow River, alt. 3700 m, *Rock 14529* (UC, B, K). The last specimen transitional toward subsp. *occidentalis*.

Handel-Mazetti (loc. cit.) rejected Franchet's *Crepis trichocarpa* on the grounds that the type specimen did not possess pubescent achenes as described and emphasized by Franchet. The writer has not seen this type, but since pubescent achenes have not been seen on any species of this genus, the opinion of Handel-Mazzetti, that Franchet's description is based on a *planta composita*, is probably correct.

7-b. **Soroseris Gillii Handelii** subsp. nov. (Fig. 11, *c–d*)—A subsp. typica differt involucris 11–12 mm longis, phyllis interioribus ad apicem sparse hirsutis; corollis 15–16 mm longis, tubo 7–8 mm, ligula 8.5–9 mm longa; antheris 4 mm longis; pappi setis 10–10.5 mm longis.

Leaves runcinate-pinnatifid or sinuate-dentate, the blade 2–4 cm long, 0.5–1.3 cm broad; involucres 11–12 mm long, the inner bracts dark green or blackish, sparsely hirsute toward the apex, the apex obtuse or rounded; corolla tube 7–8 mm, the ligule 8.5–9 mm long; anthers 4 mm long; pappus setae stramineous or rufous, 10–10.5 mm long.

Southwestern China. The following have been seen:

CHINA: southwestern Szechuan, Döko range, above Muli monastery, alt. 4350 m, *Handel-Mazzetti 7417* (type, B); Yunnan, Che-tse-lo, top of Pi-lo-shan. alt. 4000 m, *Tsai 58037, 58192* (UC, G).

Fig. 11. *a–h*, *Soroseris Gillii*: *a–b*, subsp. *typica*, from *Rock 16630* (UC): *a*, leaf, ×1; *b*, involucre, ×2; *c–d*, subsp. *Handelii*, from type (B); *c*, leaf, ×1; *d*, involucre, ×2; *e*, *f*, subsp. *hirsuta*, from *Forrest 19054* (B): *e*, leaf ×1; *f*, involucre, ×2; *g*, *h*, subsp. *occidentalis*, from type (K): *g*, leaf, ×1; *h*, involucre, ×2. *i–n*, *Soroseris Hookeriana*: *i–l*, subsp. *erysimoides*, from *Rock 12645* (UC, G): *i*, habit, $\times\frac{1}{2}$; *j*, leaf, ×1; *k*, involucre, ×2; *l*, corolla, ×4; *m–n*, subsp. *typica*, from *Hooker*, s.n. (K).

This subspecies differs from subsp. *typica* chiefly in its smaller heads and florets. The former is very constant in the size of the floral parts, however, while the two specimens cited under subsp. *Handelii*, both of them collected south of the range of subsp. *typica* are also closely similar in this respect. Subsp. *Handelii* forms a morphological transition from subsp. *typica* to subsp. *occidentalis*, resembling the latter as much as the former.

7-c. **Soroseris Gillii hirsuta** (Anthony) comb. nov. (Fig. 11, *e–f*)—Leaves, inflorescence, and involucral bracts conspicuously hirsute; leaves runcinate pinnatifid, the blade 2–4.5 cm long, 0.5–1.3 cm broad; involucres 12–15 mm long, the inner bracts acute at the apex, yellowish-green in color, densely hirsute with long, whitish trichomes; corollas 15–19 mm long, the tube 5.5–6.5, the ligule 9–12 mm long; anthers 4.8–5 mm long; pappus setae 12–14 mm long, stramineous but grayish toward the apex. (*Crepis Gillii* var. *hirsuta* Anthony, Notes Bot. Gard. Edinb. 18: 193. 1934.)

Northwestern Yunnan and southeastern Tibet. The following have been seen:

China: Yunnan Prov., Bei-ma Shan, alt. 4240 m, *Forrest 14500* (B); northeast of Atuntze, alt. 4240–4540 m, *Forrest 20059* (UC, B); Mekong-Salwin divide, alt. 4090–4240 m, *Forrest 20088* (B); Mekong-Yangtze divide, east of Yeh-chih, alt. 4090–4240 m, *Forrest 20367* (part, B). Tibet: Salwin-Kiu-chiang divide, Tsarong, *Forrest 19054* (B).

This subspecies differs from subsp. *typica* only in the pubescence of the plant, the shape and color of the inner bracts, and the color of the pappus, but each subspecies is quite constant in these respects within its range.

7-d. **Soroseris Gillii occidentalis** subsp. nov. (Fig. 11, *g–h*)—Folia lanceolata, 2–4 cm longa, 0.5–1 cm lata, apice acuta, runcinato-pinnatifida, dentata, vel integra; involucra 11–14 mm longa, phyllis interioribus hirsutis; achaenia 5–6.5 mm longa; pappi setae 11–12.5 mm longae, ad apicem griseae, ad basim stramineae.

Leaves on slender petioles, the blade lanceolate, 2–4 cm long, 0.5–1 cm broad, acute at the apex, shallowly runcinate-pinnatifid, coarsely dentate, or sometimes merely denticulate; involucres 11–14 mm long, rather lightly hirsute or occasionally glabrate; achenes 5–8.5 mm long, reddish brown; pappus setae 11–12.5 mm long, gray at the apex, stramineous toward the base. (*Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, in part, not *Prenanthes glomerata* Decne.)

Western Himalaya in Kumaon, Garwhal, and adjacent Tibet. The following have been seen:

India: Garwhal Province (Tehri) Gangotri, alt. 4240–4550 m, *Keshavanand 31* (K, *type;* DD); Dudu Gadh, alt. 4550–4700 m, *Duthie 824* (K,DD); Kalajowar, *Strachey and Winterbottom 2* (G); Kumaon Province, Ralam Valley, *Duthie 24526* (K, DD); Barji Kang, *Strachey and Winterbottom 2* (K). Tibet: Meyin Madden, *Strachey and Winterbottom 2* (K).

This subspecies is very close to subsp. *hirsuta*, a surprising fact considering the distance that separates them. The exact relationships between these two subspecies, as well as between subsp. *occidentalis* and *C. Hookeriana* subsp. *typica*, will be clearer when more is known about the *Soroseris* flora of Nepal and southeastern Tibet.

8. **Soroseris Hookeriana** (C. B. Clarke) comb. nov. (Fig. 11, *i–n*)—Stems sometimes short, but more often well developed, 4–35 cm tall; cataphylls few or none; leaves lanceolate or oblanceolate, runcinate-pinnatifid, dentate, denticulate, or entire; inflorescence flat, hemispherical or ovoid; involucres 7–12 mm long; inner bracts 4, olive or blackish green, sometimes paler below, glabrous, hirsute toward the base, or rarely hirsute throughout, the lower pair 1.2–2 mm broad, usually acute at the apex, the upper pair 2–3.5 mm broad, with broad, scarious margins, acute, obtuse, or sometimes rounded at the apex; florets 4; corollas 10–17 mm long, the tube 3–6 mm, the ligule 6.5–12 mm long; anthers blackish or greenish, 3.5–5.5 mm long; mature achenes columnar, obovoid, or occasionally fusiform, all nearly terete, 3.5–6.5 mm long; pappus setae gray or stramineous toward the base, 6.5–11 mm long.

Eastern Himalaya north to northwestern China, in meadows, stony pastures, and talus slopes (screes), at altitudes of 3300–5100 m.

This is the most widespread and the most frequently collected species of *Soroseris*. It is the only one in which well developed, hollow stems are usually found. Its range is in general similar to that of *S. Gillii*, but in Western China *S. Gillii* is confined to the southern part (Yunnan, southwestern Szechuan), while *S. Hookeriana* occurs principally farther north (Kansu, Shansi) and extends southward through Tibet to the Sikkim Himalaya. Two subspecies of *S. Hookeriana* may be recognized and distinguished by the following key:

Leaves pinnatifid, acute at the apex; upper leaves, bracts of the inflorescence and peduncles strongly hirsute; pappus setae 7–9 mm long . . . . a. subsp. *typica*

Leaves entire or denticulate, obtuse at the apex; upper leaves, bracts of the inflorescence and peduncles glabrous or sparingly hirsute . . . . b. subsp. *erysimoides*

8-a. **Soroseris Hookeriana typica** nom. nov. (Fig. 11, *m–n*)—Stems 4–20 cm tall, hollow; leaves lanceolate, the blade 2–7 cm long, 0.3–1.5 cm broad, pinnatifid, the lobes and apex acute; upper leaves, bracts of the inflorescence, peduncles, and outer involucral bracts densely hirsute with long, yellowish trichomes; involucres 8.5–10 mm long; inner bracts glabrous, hirsute at the base, or occasionally hirsute throughout; pappus setae 7–9 mm long, grayish at the summit, dirty white, stramineous or yellowish on the lower part. (*Crepis Hookeriana* C. B. Clarke, Comp. Ind. 255, 1876, non Bal.; *Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, 188, in part, not *Prenanthes glomerata* Decne.).

Eastern Himalaya, in Sikkim and adjacent Tibet. The following have been seen:

INDIA: Sikkim Prov., 4240–4850 m, Ghora la (?), Karkole (?), Hooker s.n. (in part) (K, B, G, NY); Tankra Mt., alt. 4090 m, *Gammie 421* (K); Ghora La, alt. 4850 m, *Bibu and Rhomoo 5173* (K); Boktu, alt. 4090 m, *Ghose* in 1932 (UC); Tango (?), alt. 4240 m, *Smith and Cave 2500* (B); Le lap la, *King* in 1877 (DD); Lugnak la, *Wager 269* (K). TIBET: Yatung, *Hobson* in 1897 (K); Chumolari, alt. 4850 m, *Lepcha 519* (K); Lonok, *Younghusband 217* (B); Tang la, eastern Himalaya, *Ward 5946* (K). The last specimen is transitional toward subsp. *erysimoides.*

The specific name *Hookeriana*, though invalid in *Crepis* for this species, can be used in *Soroseris*, since no other specific name exists for the species as here recognized. The case is quite parallel to that of *Dubyaea atropurpurea* (Stebbins Jour. Bot. 1937:51).

The collections of Hooker from Sikkim, all of them identified by him as *Crepis glomerata*, include three different forms. That described above is represented by one full sheet in the Kew Herbarium, which is probably the type sheet of Clarke's *C. Hookeriana.* It agrees very well with the description of Clarke (loc. cit.). Three plants of subsp. *typica* are on the sheet in the Berlin Herbarium, two on that in the Gray Herbarium, and one in the New York Botanical Garden sheet. The second sheet in the Kew Herbarium contains mostly plants of *S. pumila*, but in addition two of *C. Hookeriana* subsp. *erysimoides.* The latter subspecies also appears (though not always in its typical form) on all of the other sheets. The three forms were evidently collected in different localities, judging from the rough labels on the Kew sheets. The writing on these labels is almost illegible to the present author, but the best possible interpretations of these localities are given with the citations.

8-b. **Soroseris Hookeriana erysimoides** (Hand.-Mazz.) comb. nov. (Fig. 11, *i–l*)—Plants mostly glabrous throughout; stems 4–25 cm tall, hollow; leaves numerous, oblanceolate, lanceolate, or linear, the blade 2–7 cm long, 1.5–11 mm broad, its margin entire, undulate, or minutely and remotely denticulate, its apex obtuse or rounded; involucres 7–12 mm long, the inner bracts glabrous or sparingly hirsute; pappus setae 7–9 mm (rarely 11 mm) long, grayish, or whitish below, rarely stramineous. (*Crepis Gillii* var. *erysimoides* Hand.-Mazz., Acta Horto Goth. XII: 355. 1938.)

Eastern Himalaya, where it passes into subsp. *typica*, north through eastern Tibet to western and northwestern China. The following have been seen:

INDIA: Sikkim Prov., Zemutory (?), alt. 3940–5150 m, *Hooker*, s.n. (in part, K, G, NY, B). BHUTAN: Do-tha, *Dungboo 265* (K). TIBET: Sham Man (?) Chumbi and Phari, *Dungboo* in 1879 (B); Chumighata, eastern Himalaya, alt. 4850 m, *Lepcha 77* (K); Dzomo La, between Radja and Jupar Range, alt. 4060 m, *Rock 14386* (UC, B); Wanchen nira, between Labrang and Yellow

River, alt. 4060 m, *Rock 14517* (UC, B); Amnyi Machen Range, *Rock 14442* (UC, B). China: Shensi Prov., Tai pa shan, *Leason* in 1910 (K); *Giraldi 309, 3049, 3052* (B); Miao-wang-shan, *Giraldi 3051* (B); Tsin Ling Shan, alt. 3350 m, *Limpricht 2747* (B); Kansu Prov., Tangut region, *Przewalski* in 1872 (B); Sin hong shan and Ma ho shan, *Licent 4408* (K); west of Adjuan, alt. 3640 m, *Rock 12645* (UC, B); Szechuan Prov., Sungpan Hsien, *Fang 4027* (K, B, G); Ta Tsien Lu, *Soulie* 2159 (B); Tongolo, *Soulie 836* (K); Yunnan Prov., Bei Ma Shan, alt. 4240–4540 m, *Forrest 14516* (K, B), *20943* (UC, B); same locality, *Rock 9993* (B); Mekong-Salween divide, alt. 3940–4240 m, *Forrest 19712* (K). (The last specimen transitional toward *S. Gillii.*)

Subsp. *erysimoides* is the more distinctive and widespread of the two subspecies of *S. Hookeriana*. It is very constant throughout the center of its range. In the eastern Himalaya it appears to pass gradually into subsp. *typica*, which subspecies may be regarded as intermediate between subsp. *erysimoides* and *S. Gillii* subsp. *occidentalis*. As mentioned above, one of the main reasons for maintaining *S. Hookeriana* and *S. Gillii* as distinct species is the striking morphological discontinuity between *S. Gillii* subsp. *typica* and *S. Hookeriana* subsp. *erysimoides* in western China, where the ranges of the two overlap. If, however, further exploration of the eastern and central Himalaya shows that *C. Gillii* subsp. *occidentalis* intergrades with *C. Hookeriana* subsp. *typica*, the two species will have to be merged. Some of the specimens from Northern China (*Giraldi* nos. 3049, 3051, 3052) are transitional toward *C. Gillii* also. When more material is available from this region, these may be found to constitute a distinct subspecies, characterized by larger involucres, hirsute bracts, and stramineous pappus.

V. LACTUCA, SECTION AGGREGATAE

Lactuca, Sect. Aggregatae Franch. Jour. de Bot. 9: 257, 1895. Plants with the habit of *Soroseris;* stems very short, expanded at the apex, the heads closely crowded and sessile or subsessile at its summit; involucres with 4–6 bracts, all of which are similar in length and in general outline; achenes slightly or strongly obcompressed, strongly contracted at the apex, 3–5 ribbed. Three species known, natives of Tibet and the mountains of western China.

The species of this section resemble superficially those of *Soroseris*, but there are definite differences between the two, even in habit. The larger leaves in Sect. Aggregatae have petioles which are sharply dilated into a sheathing base, while in *Soroseris* the petioles are uniform in breadth. The heads of these *Lactuca* species are sessile or on very short peduncles less than 2 mm long, while in *Soroseris* the peduncles are always well developed. Finally, the involucres of the species of *Soroseris* all have two or more narrowly linear or filiform outer bracts subtending the main series of broadly linear, lanceolate or elliptic inner ones, while in the Sect. Aggregatae these are altogether lacking.

In floral characteristics, the two groups are still more different. The corollas of these *Lactuca* species are purple or blue, colors not found in *Soroseris*, while the corolla tube is very long and slender, a characteristic feature of many *Lactuca* species, but not of *Soroseris*. The pollen grains have the echinolophate pattern characteristic of *Lactuca* and other Cichorieae but not of *Soroseris* (cf. Figure 8). The achenes are more abruptly contracted at the apex than are those of *Soroseris*, and have fewer ribs. *L. porphyrea* and *L. disciformis* have ovaries with 5 vascular bundles, a condition anomalous in *Lactuca*, but found in some other Asiatic species, such as *L. melanantha* Franch. and *L. chungkingensis* Stebbins (Stebbins 1937a). The supernumerary vascular bundles of the ovary so characteristic of *Soroseris* (p. 000) are, however, lacking, as in all other species of *Lactuca*. Finally, the pappus setae of Sect. AGGREGATAE are typical of *Lactuca* in being slender, fragile, and some are only 4-celled in cross section at the base (Fig. 1, e, f). They contrast sharply with the thick, coarse pappus setae of *Soroseris* (Fig. 1, c, d). On the basis of these differences the writer believes that this section of *Lactuca* has no particular relationship with *Soroseris*, but has acquired a similar habit through parallel evolution, in response to a similar environment.

The affinities of Sect. AGGREGATAE to other species of *Lactuca* are somewhat obscure. *L. macrorhiza* Hook. f. resembles *L. Souliei* Franch., the best known species of Sect. AGGREGATAE, in leaf shape, flower color, the character of the stigmas and to some extent the involucral bracts. The involucres of *L. macrorhiza*, however, have many more bracts and florets, while its involucral bracts are in several series, and more or less evenly imbricated. The corollas of *L. macrorhiza* and its relatives have short tubes and long ligules, while the achenes are either longer beaked or are not so abruptly contracted at the apex, and are more striate. In their heads with few florets and long corolla tubes the species of Sect. AGGREGATAE, approach those of Sect. SORORIA, but these two sections are very different in habit and in their achenes. The present section is therefore an isolated one, but has its nearest relatives among characteristic Sino-Himalayan species.

The three species may be identified by the following key:

A. Leaves lyrate-pinnatifid; achenes strongly obcompressed, 1-nerved on each face . 2. *L. Souliei*

A. Leaves merely dentate; achenes moderately obcompressed, 5-ribbed; ovary with 5 vascular bundles.

  B. Leaves on slender, wingless petioles, closely sinuate dentate; corolla 16–19 mm long; anther tube 5–5.5 mm long; pappus setae 10–12 mm .... 1. *L. porphyrea*

  B. Leaves on short, alate petioles, remotely repand-dentate; corollas 8–9 mm long; anther tube 2–2.5 mm long; pappus setae 7–10 mm .... 3. *L. disciformis*

1. **Lactuca porphyrea** (Marq. & Shaw) comb. nov. (Fig. 12, *e–f*)—Stems from a slender root, 5–6 cm long, expanded toward the apex; leaves purplish red, glabrous, on slender petioles which are expanded at the base to a triangular sheath, the blade elliptic to obovate or spatulate, closely sinuate-dentate; involucres 11–13 mm long; their bracts uniseriate, 4–5 in number; corollas purple, 16–19 mm long, the tube slender, 9–10 mm long; branches of the stigma pale, 2 mm long, 0.27 mm broad; achenes unknown; pappus setae 10–11 mm long. (*Crepis glomerata* var. *porphyrea* Marq. et Shaw, Jour. Linn. Soc. Bot. 48: 194, 1929.)

Fig. 12. *a–d*, *Lactuca disciformis*, from type (B): *a*, habit, ×1; *b*, leaf, ×1; *c*, involucre, ×2; *d*, corolla, ×4. *e–f*, *Lactuca porphyrea*, from type: *e*, leaf, ×1; *f*, corolla, ×4. *g*, *h*, *Lactuca Souliei*, from Schneider 3136 (US): *g*, leaf, ×1; *h*, corolla, ×4.

Known only from the type: TIBET: On bare stony chutes and screes, above Pasum Lake, alt. 3400–3600 m, *Ward 6113* (K, type). Also seen by the same collector above Atsa, 4850–5150 m (note on label of type specimen).

The distinctions between this species and *Soroseris glomerata* have already been mentioned in the discussion of the Sect. AGGREGATAE. The two species, although superficially similar in habit, are not related to each other. The collector of *L. porphyrea*, Capt. F. Kingdon Ward, identified correctly the genus of this plant, since the original label bears the legend "Lactuca sp." Furthermore, his keen eye for plants in the field was able to judge its true relationships. In describing the flora of Pasum Lake (Gard.

Chron. 78: 130–131, 1925) he says that he found "on some gravel screes, a fine, purple-flowered *Lactuca*—not the one which is so common in western China (presumably *L. Souliei*), but a much larger flowered species."

2. Lactuca Souliei Franch. Jour. de Bot. 9: 257. 1895. (Fig. 12, *g–h*)—Leaves purplish or green, lyrate-pinnatifid, the lobes angulate-dentate; involucres 11–13 mm long, similar to those of *L. porphyrea;* corollas blue, 14–15 mm long, the tube 8–9, the ligule 6–7 mm long; anther tube blue, 4–4.5 mm long; stigma branches 1.5–1.8 mm long; achenes 4–4.5 mm long, reddish, strongly flattened, with 1 nerve on each face; pappus setae 8–9 mm long. Western China and adjacent Tibet, on stony talus slopes (screes) at 3300–4400 m altitude. The following have been seen:

China: Yunnan prov., near Lichiang, alt. 4000 m, *Schneider 3136* (US); Likiang snow range, alt. 4400 m, *Rock 24886* (UC, K); near Chungtien, alt. 4000 m, *Schneider 3001* (US); northeast of Atuntze, alt. 4000–4250 m, *Forrest 20289* (US); Chien-chuan-Mekong divide, alt. 4200 m, *Forrest 23126* (US).

3. Lactuca disciformis (Mattf.) comb. nov. (Fig. 12, *a–d*)—Similar to the last two in habit, but smaller; leaves reddish-purple to greenish, spatulate to obovate, remotely and coarsely repand-dentate; involucres 9–11 mm long (excluding the pappus); corollas purple (collector's note), 8–9 mm long, the tube 5.5–6 mm, the ligule 2.5–3 mm long; anther tube bluish or purplish, 2–2.5 mm long; stigmatic branches 0.6 mm long; immature achenes reddish, similar in shape to those of *L. Souliei*, but with 5 prominent ridges; pappus setae 7–10 mm long. (*Crepis disciformis* Mattf., Notizbl. Bot. Gard. Berlin-Dahlem, 1935, p. 46.)

Southwestern Kansu and northwestern Szechuan, in rocky places and alpine meadows, at 4000–5100 m altitude. Only the following has been seen.

China: Kansu Prov., Mt. Kwang Kei, west Tebbu Land, alt. 4000 m, *Rock 13729* (B type, US).

This species is in the reduced size and the proportions of its corollas farther removed from *Soroseris* than are the other two species of the section Aggregatae. In every important diagnostic characteristic except the 5-costate achenes it resembles *L. Souliei.*

VI. DISTRIBUTION OF THE SPECIES

A. DUBYAEA

According to our present knowledge, the species of *Dubyaea* show a remarkably high degree of endemism. The genus itself is endemic to the Sino-Himalayan region, while six of its nine species are highly localized, even within that area. Seven species are endemic to western China or southeastern Tibet, one to the northwestern Himalaya, while one, *D. hispida*, occurs in both the Chinese mountains and the Himalaya (Fig. 13).

There are no endemic species of *Dubyaea* known from the eastern Himalaya. Another remarkable fact is that three species, *D. chimiliensis*, *D. gombalana*, and *D. amoena*, are known only from a single series of mountain ranges, those forming the divide between the Salween and Irrawady river systems, while a fourth, *D. tsarongensis*, is nearly confined to these ranges. In addition, it is interesting to note that the only two species which are not alpine or subalpine in their distribution, *D. oligocephala* and *D. glaucescens*, occur at opposite ends of the range of the genus, the former in the northwestern Himalaya, the latter in Szechuan.

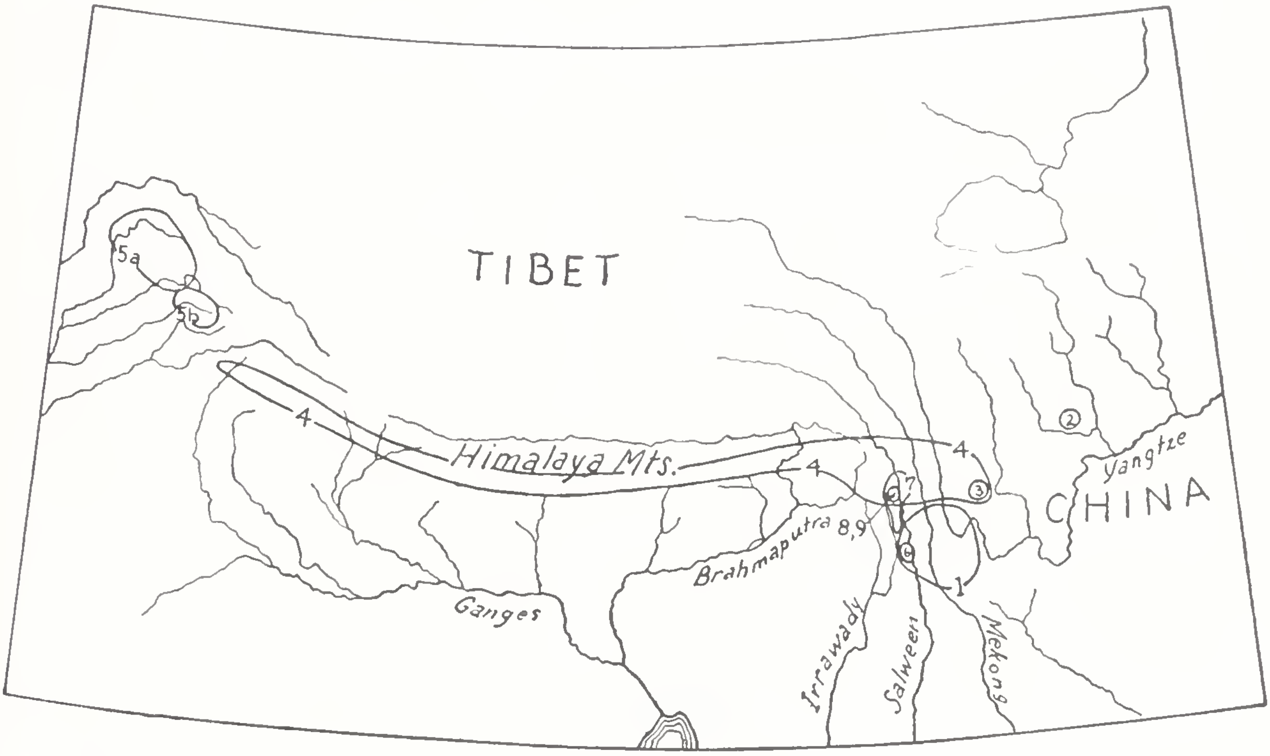

Fig. 13. The distribution, generalized, of the species of *Dubyaea:* 1, *D. atropurpurea;* 2, *D. glaucescens;* 3, *D. rubra;* 4, *D. hispida;* 5a, *D. oligocephala* subsp. *typica;* 5b, *D. oligocephala* subsp. *latifolia;* 6, *D. chimiliensis;* 7, *D. tsarongensis;* 8, 9, *D. amoena* and *D. gombalana.*

The above facts, coupled with our knowledge of the primitiveness of the species have a definite bearing on the interrelationships of the floras of which the species of *Dubyaea* form a part. Two hypotheses have been advanced as to the origin of the Sino-Himalayan flora. Diels (1913) has suggested that the alpine flora of China, like its temperate flora, is a very ancient one, and that the flora of the Himalaya is largely tributary to it. Ward (1935), on the other hand, believes that the Tertiary alpine flora of southeastern Asia was completely exterminated during the Pleistocene ice age, and that the present flora, including the various endemic genera, has originated in southeastern Tibet in post-Pleistocene time. The explanation of Diels obviously is much more in accord with the evidence from

Dubyaea. At least some of its species, *D. atropurpurea*, *D. hispida*, *D. oligocephala*, and *D. chimiliensis*, are clearly more primitive than, and probably older than the species of such widespread genera, as *Prenanthes*, *Lactuca*, and *Crepis*, which are themselves most certainly of Tertiary age (see below). Furthermore, most of the species of *Dubyaea* are very distinct from each other; if they had originated in recent times their phylogenetic interrelationships should be much clearer. Two of them could, perhaps, be of recent origin. *D. tsarongensis* is closely related to *D. chimiliensis*, and may have originated from it relatively recently, while *D. rubra* shows a similar relationship to *D. hispida*. The other species, however, appear to be relict types, whose Tertiary ancestors were much more numerous and widespread. Ward (1935) has produced convincing evidence that the alpine regions of southeastern Tibet were heavily glaciated in Pleistocene time. This glaciation may well have been the final catastrophe which destroyed or greatly restricted the species of a genus which had already passed its prime when the glaciation began. Of the few survivors, only *D. hispida* was able to spread extensively into the glaciated territory. *D. chimiliensis*, *D. amoena* and *D. atropurpurea* are, therefore, relict endemics similar to those found in the unglaciated nunatak areas of northeastern North America, Alaska, the Alps, and probably most of the mountain systems of the Northern Hemisphere. *D. glaucescens*, one of the two species found at lower altitudes, belongs to the warm temperate forest flora of western China, a flora characterized by "nine-tenths of the monotypic genera of trees that are so prominent a feature of the Chinese flora" (Wilson, 1929, p. 283). These genera, including such isolated types as *Davidia*, *Eucommia*, *Tapiscia*, *Carrieria*, *Itoa*, and *Idesia*, as well as the numerous genera in the same flora which have the well known distribution of Eastern Asia—Eastern North America (Wilson, 1929, p. 289), are certainly ancient, relict types, and probably represent the remnants of a flora which was widespread in Mesozoic and early Cenozoic time (Fernald 1931, p. 62). The presence of *D. glaucescens* in this assemblage, together with its isolated position both systematically and ecologically, suggests that its ancestors were also widespread at that remote period, and have since been superseded by their younger relatives in *Prenanthes*, *Lactuca*, *Crepis*, and *Hieracium*.

D. oligocephala also occupies an isolated range with respect to the other species of *Dubyaea*. It is interesting to note that the flora of the Northwestern Himalaya, where *D. oligocephala* is found, contains many European and Western Asiatic types not found elsewhere in the Sino-Himalayan region (Hooker 1909). That this is true of the tribe Cichorieae is evidenced by the presence in that region of five species of *Hieracium* and of *Chondrilla*. Both of these are typically European and western Asiatic genera which are sparingly or not at all represented farther east. In view of this geographic affinity, the fact that *D. oligocephala* is more closely related than is any other species of *Dubyaea* to the predominantly European and western Asiatic genus *Crepis* has some significance. *D. oligocephala* may easily be the remnant of a group of species which was formerly widespread in Western Asia and Europe, and which figured in the ancestry of *Crepis*.

The distribution of *Dubyaea* agrees in general with that of another Composite genus, *Cremanthodium*. Good (1929) has given us a very thorough account of the distribution of this genus in relation to the climatic and physiographic features of the Sino-Himalayan region, and his account of the latter features serves very well as a guide to the distribution of *Dubyaea*. There is in both genera a concentration of species in the river gorge area of southeastern Tibet, northwestern Yunnan, and southwestern Szechuan. In both genera the number of endemics in the Himalaya is small. The same arguments, therefore, which are used by Good to indicate the origin of *Cremanthodium* prior to the Himalayan uplift hold also for *Dubyaea*. In addition, it is interesting to note that the eastern continuation of the Himalaya, the importance of which as a rain screen and consequently as a barrier to plant migration has been emphasized by Ward (1935), appears to have been important in limiting the range of three species. *Dubyaea atropurpurea* and *D. chimiliensis* occur only south of this barrier, while *D. hispida* has been found in this region only to the north of it. The fact that *D. atropurpurea* and *D. chimiliensis* are in their floral anatomy among the most primitive species of the genus (see below), and are furthermore unspecialized in habit, suggests that they are also the oldest, while *D. hispida* in these respects suggests a more recent origin. The fact that the two presumably older species are confined to the moist side of the rain screen is in accord with the suggestion of Good (1929, p. 314), that "before the Himalayan uplift . . . the western Chinese mountains were, except in the southwest, much wetter than now." Presumably *D. atropurpurea* and *D. chimiliensis* were more widespread at this early period than now, but were already so fixed that they could not adjust themselves to a changing environment, and so became confined to regions of which the climate was relatively little affected by the Himalayan uplift. *D. hispida*, on the other hand, probably originated since the beginning of the Himalayan uplift, and has apparently been increasing its range in relatively recent times.

B. SOROSERIS

The genus *Soroseris* is endemic to the same general region as the related genus *Dubyaea*, but the distribution of the species within this region is quite different. The eight species, as recognized in the present treatment, are distributed as follows (Fig. 14). Two, *S. rosularis* and *S. bellidifolia*, are known only from western China; one, *S. Deasyi*, occurs in the northwestern Himalaya and adjacent western Tibet; one, *S. glomerata*, in south central Tibet and the west central Himalaya, and one, *S. pumila*, in the eastern Himalaya. The three more widespread species are all found in southeastern Tibet. One of these, *S. umbrella*, extends eastward to the mountains of Szechuan and Yunnan, and west to the eastern Himalaya. Another, *S. Gillii*, also extends eastward to Szechuan and Yunnan, where it is more common than *S. umbrella*, but skips the eastern Himalaya, recurring in Kumaon and Garwhal, in the west-central Himalaya. The third, *S. Hookeriana*, is the most widespread species of all. It also extends to the mountains of China, but has a more northerly range there than *S. umbrella* and *S. Gillii*, and is in addition the most common species of *Soroseris* in the eastern Himalaya.

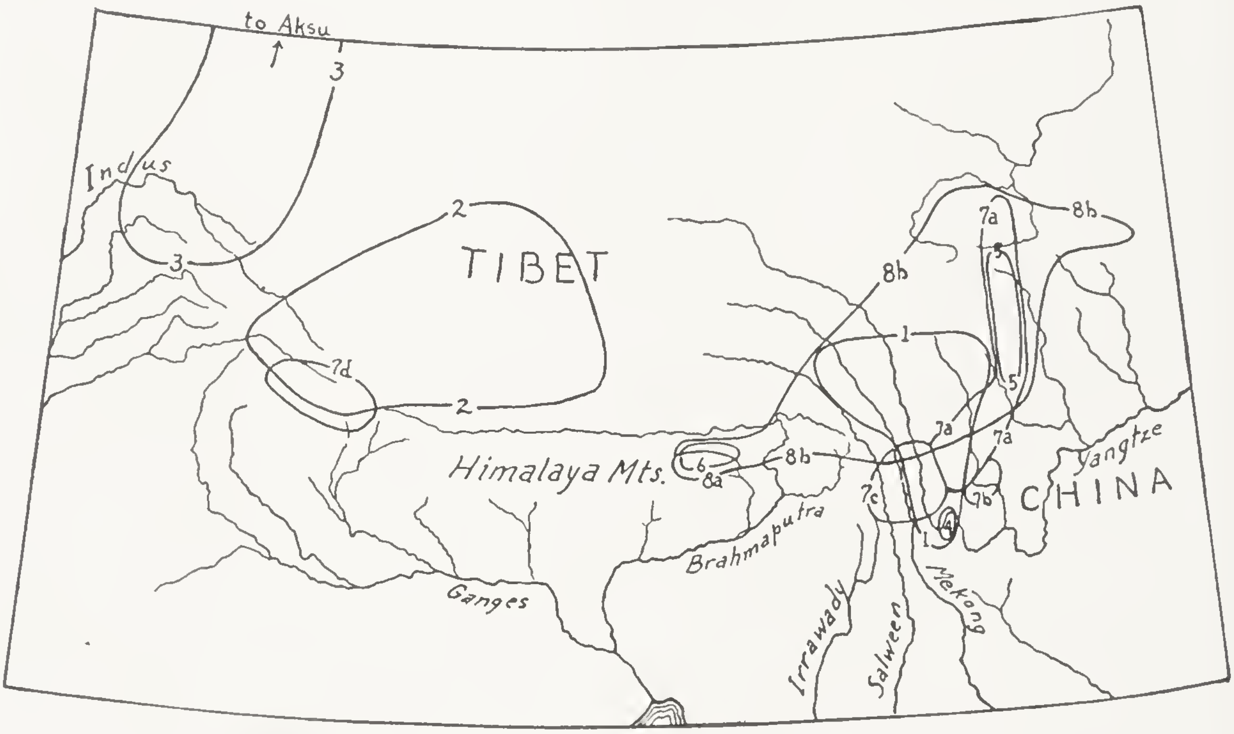

Fig. 14. The distribution, generalized, of the species of *Soroseris:* 1, *S. umbrella;* 2, *S. glomerata;* 3, *S. Deasyi;* 4, *S. rosularis;* 5, *S. bellidifolia;* 6, *S. pumila;* 7a, *S. Gillii* subsp. *typica;* 7b, subsp. *Handelii;* 7c, subsp. *hirsuta;* 7d, subsp. *occidentalis;* 8a, *S. Hookeriana* subsp. *typica;* 8b, subsp. *erysimoides.*

When this distribution is compared with that of *Dubyaea*, two striking differences are evident. In the first place, the species of *Soroseris* have, in general, a much wider distribution than those of *Dubyaea*. The only two species whose known range is relatively restricted are *S. rosularis* and *S. pumila*. *S. rosularis*, moreover, is doubtfully distinct from *S. bellidifolia* and *S. Deasyi*. The remaining six species all have as broad or broader ranges than any species of *Dubyaea* except *D. hispida*. The second difference is that the species of *Soroseris* are not concentrated in the Chinese mountains as are those of *Dubyaea*. The only two species not known west of longitude 98° are *S. bellidifolia* and *S. rosularis*. As is stated in the systematic section of this paper, these two species are doubtfully distinct from each other and from *S. Deasyi*, of Kashmir, western Tibet, and Turkestan. These three forms may, when further material has been seen, prove to be merely geographical segregates of one widespread species of which the center of distribution is in Tibet. If this proves to be true, then every species of *Soroseris* will be represented in the Tibetan flora. For this reason, the writer believes that the Tibetan plateau is the center of distribution of *Soroseris*. In contrast to this, the present center of *Dubyaea* is the mountains of southwestern China, and of the river gorge region in the southeastern corner of Tibet. The definite affinity between *Soroseris* and *Dubyaea* is in full agreement with the opinions of Hemsley and Pearson (1902), and Ward (1935), that the greatest affinity of the Tibetan flora is with that of the Sino-Himalayan region.

One of the interesting features of the distribution of *Soroseris* is the presence of two forms in the western Himalaya which have their closest relatives in the Chinese mountains but not in the eastern Himalaya. The affinity of the northwestern Himalayan *S. Deasyi* to *S. rosularis* of Yunnan has already been mentioned; *S. Gillii* subsp. *occidentalis* of Garwhal Kumaon, and adjacent Tibet is the second case. This affinity between the Chinese mountains and the western Himalaya has been shown by Diels (1913) to exist in a number of genera.

VII. FLORAL ANATOMY OF DUBYAEA AND SOROSERIS

A wealth of evidence obtained from many different groups has shown that the vascular anatomy of the flowers provides valuable clues to the interrelationships and phylogeny of families, genera and species of Angiosperms. *Dubyaea* and *Soroseris* have proved particularly interesting among the genera of the Cichorieae in this respect, and for this reason the floral anatomy of their species will be described in some detail. Since no preserved flowers of either *Dubyaea* or *Soroseris* were available, this study was of necessity based entirely on preparations obtained from herbarium specimens. They were made in two ways. Whole mounts of florets of all of the species were prepared according to the bleaching and clearing method devised by the author (Stebbins 1938). In addition, material of the more critical species was boiled in water for 20 minutes, then soaked in hot water in a double boiler for 2–3 hours, after which it was transferred first to 95% ethyl alcohol, then to butyl alcohol. It could then be embedded in paraffin, sectioned, and stained in gentian violet according to the usual schedule. The preparations thus obtained, though somewhat crushed in places, were well stained, and showed the position of the vascular bundles very clearly. For the sake of comparison, sections of florets, of *Prenanthes trifoliolata* (Cass.) Fernald, which in general resembles *Soroseris* in its floral anatomy, were also studied. The only advantage of these sections for anatomical study over those obtained of *Dubyaea* and *Soroseris* lay in their more reliable preservation of the more delicate tissues, such as the phloem. The author feels confident, therefore, that the description given below is quite accurate as to the general features which it includes, even though it is not based on the usual well preserved material.

The floral anatomy of several species of Compositae, including one species of the tribe Cichorieae, *Lapsana communis*, was thoroughly investigated by Koch (1930a, b). Although the species of *Dubyaea* and *Soroseris* agree in general with her descriptions, most of them have certain striking features not described by her. These features provide valuable evidence bearing not only on the position of these two genera in the tribe Cichorieae, but in addition on the broader relationships of the tribe and perhaps the Compositae as a whole. These features all involve the anatomy of the ovary, style, and stigma; the corollas of all of the species agree with the description given by Koch (1930a) of *Lapsana*, and which has been found by the present writer in practically every species of Cichorieae investigated. A slight exception is found in *Dubyaea atropurpurea*, in which the median bundles of the corolla lobes (cf. Koch 1930a) exist at its apex and extend down to about the base of the teeth, where they disappear.

The species of *Dubyaea* are remarkably diverse in the anatomy of their ovaries, since among the nine known members of this genus five different anatomical types are found. Three species, *D. atropurpurea*, *D. chimiliensis*, and *D. gombalana* are interesting enough to be described in detail.

D. atropurpurea (Fig. 15, *a–h*). At the base of the ovary of this species five large bundles pass out from the stele (Fig. 15*a*). Since these eventually form the supply to the corolla, stamens, and style, they are termed the principal bundles. Directly above this level the stele divides into a varying number of lesser bundles, leaving only a small remainder of vascular tissue in the center. These lesser or supernumerary bundles pass directly out between the principal bundles to the ovary wall (Fig. 15*b*). Some of them then form two or three branches, while others remain unbranched. All are much smaller than the principal bundles, and become differentiated at a later stage. They are best seen in ovaries from which the corolla has withered, and which have begun to grow into achenes. The remainder of the vascular tissue forms the ovule trace, which is at first rather broad and is embedded in a large mass of parenchyma. At the base of the cavity of the ovary, this parenchyma separates into two ribbon-shaped bands which pass toward the ovary wall on either side of the ovule trace and then turn upward, so that they appear crescent-shaped in cross section (Fig. 15*c*). They soon become narrower, and are differentiated into clearly recognizable, though relatively weakly staining, xylem and phloem elements. The differentiation of these two inner bundles takes place last in the development of the ovary; in all of the species examined they were not completely differentiated until well after flowering time. They are the conducting cords of other authors (Lavialle 1912). They continue on either side of the ovule until slightly above its summit, so that a cross section of the ovary at this level (Fig. 15*d*) shows an outer row consisting of the 5 principal and 7–10 or more supernumerary bundles, and an inner pair of relatively indistinct, flattened ones. The latter now disappear. At the apex of the ovary the central cavity becomes cruciform in outline, with the ends of two of the arms directly over the position of the inner pair of bundles (Fig. 15*e*).The principal bundles have become much broader, while most of the supernumerary bundles drop out at this point. Four of the principal bundles then give rise to bundles supplying the style (Fig. 15*f*). Two of these are relatively thick; they arise at a slightly lower point than the other two, and pass diagonally upward and inward along the long axis of the ovary. The other two more slender ones pass horizontally inward, or may even turn downward slightly. They reach the edge of the much reduced ovary cavity, which has now become elongated parallel to the short axis of the ovary, directly over the position of the two inner bundles, where they turn abruptly upward to enter the style. The stamen bundles diverge from those of the corolla at nearly the same level at which the stylar bundles branch inward from the principal ones. The four stylar bundles continue upward to the base of the stigmatic branches, where the two lesser ones divide, sending one branch to each of the two stigmas. Each stigmatic branch, therefore, contains three bundles; a strong central one and two smaller lateral ones (Fig. 15*h*).

D. chimiliensis (Fig. 15*g*). This species is similar to *D. atropurpurea* except for three differences. The supernumerary bundles are relatively few in number (3–5), are not branched, and sometimes end below the summit of the achene. The two inner bundles are connected with the summit

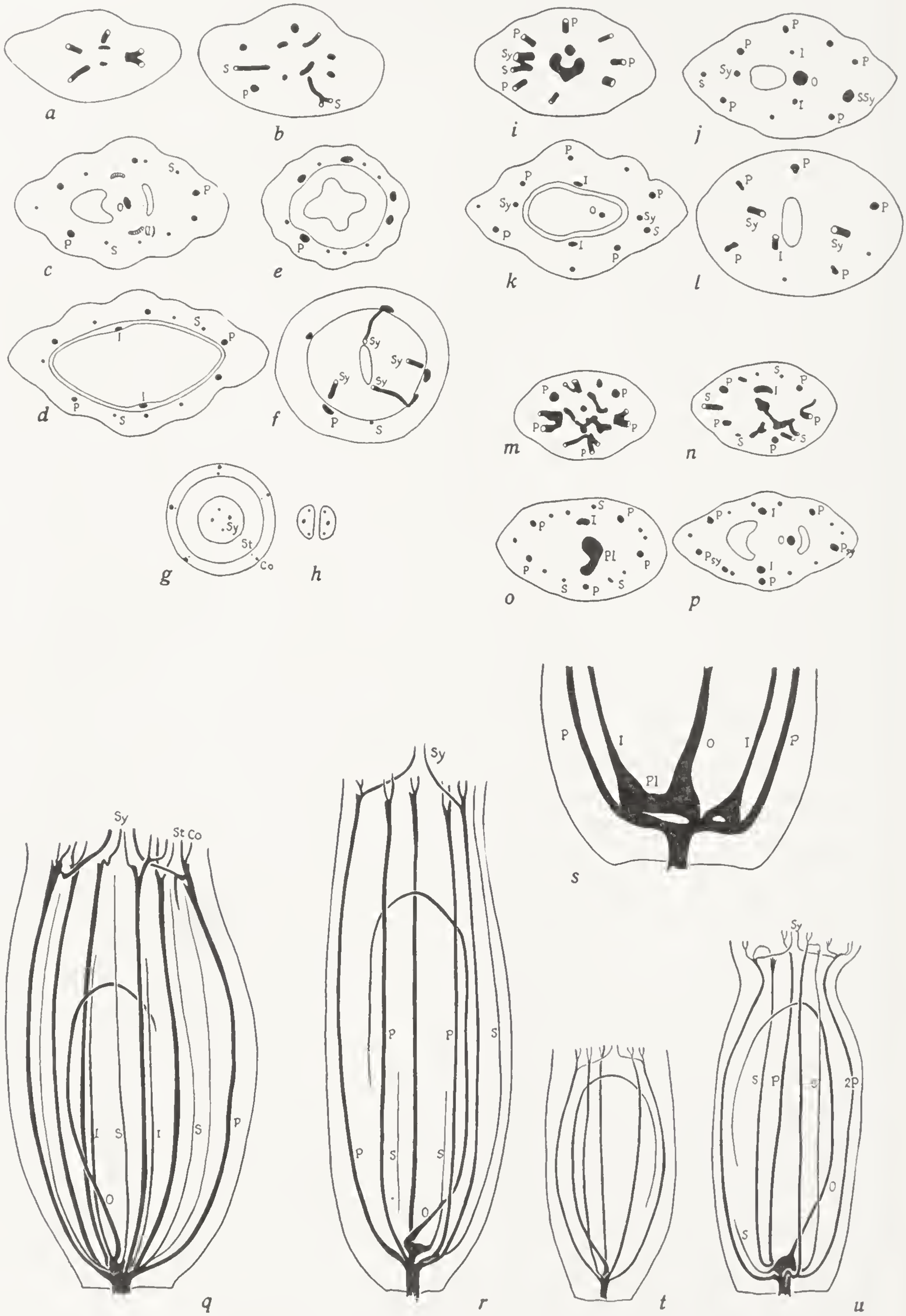

Fig. 15. *a–h*, Diagrams of cross sections at successive levels of the mature ovary of *Dubyaea atropurpurea*. *a*, base of ovary, showing principal bundles passing out from stele; *b*, slightly higher level, showing supernumerary bundles (S) passing out between the principal ones (P); *c*, base of ovary cavity, showing principals, supernumeraries,

of the stele, emerging on either side of the ovule trace, as described below for *D. gombalana*. Finally the two lesser stylar bundles end just below the base of the stigmas, so that the stigmatic branches themselves contain only one bundle each.

D. gombalana (Fig. 15, *i–l*). In this species the supernumerary bundles are as in *D. chimiliensis*, except that they pass out from the stele at practically the same level as the principal ones, and members of the two series are often fused for a short distance. The remainder of the stele exists for a short distance as a nearly continuous ring (Fig. 15*i*), then breaks up into the large ovular trace and the two inner bundles, one of which leaves the stele slightly before the other (Fig. 15*j*). These two inner bundles extend farther up the ovary than in *D. chimiliensis* or *D. atropurpurea*, and in the specimen illustrated one of them has persisted to the apex of the ovary (Fig. 15*e*), where it occupies a position comparable to that of the lesser stylar bundles in *D. atropurpurea* (cf. Fig. 15*f*). It ended at this point, however, and the style of *D. gombalana* has only two bundles, corresponding to the larger ones in *D. atropurpurea*. The course of these stylar bundles, however, differs strikingly from the situation in *D. atropurpurea* and *D. chimiliensis*. One or both of them are free from the principal bundles throughout almost their entire length. They branch off from one of the principal at about the level of the base of the ovary cavity, and continue upward near the inner edge of the ovary wall. The middle part of the

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ovular bundle (O), and parenchyma from which inner bundles arise (I); *d*, upper part of ovary, above apex of ovule, showing principals, supernumeraries, and inner bundles; *e*, near summit of ovary, showing expansion of principal bundles and cruciform shape of cavity; *f*, summit of ovary, showing stylar bundles (Sy) passing inwards; *g*, base of corolla, showing corolla (Co), stamen (St), and stylar (Sy) bundles; *h*, cross section of stigmatic branches showing three bundles in each branch. *i–l*, diagrams of cross sections of ovary of *Dubyaea gombalana*, *i*, base of ovary, showing principal and supernumerary bundles, and central mass of vascular tissue; *j*, base of cavity; one of the stylar bundles is free, the other still fused to a supernumerary bundle; the large ovular and the two inner bundles are evident; *k*, middle of ovary, showing principal, supernumerary, stylar, and inner bundles; *l*, summit of ovary; stylar bundles passing inward, one inner bundle still evident. *m–p*, *Soroseris Deasyi; m*, base of ovary; *n*, next section above, showing one inner bundle and irregular mass of vascular tissue in center; *o*, slightly higher section, showing placental platform (Pl); *p*, base of ovary cavity, showing ovular and enlarged inner bundles; Psy, the two principal bundles from which the stylar bundles will arise. *q*, *Dubyaea chimiliensis*, diagram of vascular system of ovary; P, principal; S, supernumerary; O, ovular; I, inner; Co, corolla; St, stamen; Sy, stylar bundles. *r*, *Dubyaea hispida*, vascular system of ovary. *s*, *Soroseris Gillii*, Diagram of median longitudinal section at base of ovary; *t*, *Crepis nana*, showing reduced vascular system of ovary most frequent in the Cichorieae; *u*, *Lactuca Lessertiana*, showing fusion of two principal bundles (2P).

ovary in cross section, therefore, shows an outer series of 7–9 and an inner one of 4 bundles (Fig. 15*k*).

D. oligocephala and *D. tsarongensis* are similar to *D. gombalana*, except that the inner bundles are less strongly developed, and one or both of the stylar bundles are adnate to the principal ones. *D. hispida*, *D. amoena*, and probably *D. rubra* are also similar, except that the stylar bundles are always both adnate to the principals (Fig. 15*r*). *D. glauscens* lacks the supernumerary bundles, so that its anatomy is essentially like that illustrated by Koch (1930a) for *Lapsana communis* and by the present author (Fig. 15*t*) for *Crepis nana*. Thus there exists within *Dubyaea* a complete series of anatomical types illustrating the reduction from the complex structure found in *D. atropurpurea*, *D. chimiliensis*, and *D. gombalana*, to the simple type which is probably the most common one in the Cichorieae as a whole.

The species of *Soroseris*, on the other hand, are much more uniform anatomically, and all conform to the pattern exemplified by *S. Deasyi* and *S. Gillii* subsp. *typica* (Fig. 15, *m–p*). In these the supernumerary bundles are relatively numerous, but pass out of the stele at practically the same level as the principal ones, the two series often being fused at the base (Fig. 15*m*). There remain in the center several irregular masses of vascular tissue, which quickly form themselves into two groups. One of these is the much broadened base of one of the two inner bundles, while the other is a large platform of vascular tissue, crescent-shaped in cross section (Fig. 15*o*). From one end of this platform there emerges the second inner bundle, while at the other, in the center of the ovary, is the ovule trace. This is much thickened at the base, and gradually tapers upward (Fig. 15*p*, *s*). The inner bundles become quickly weaker, and in the middle of the ovary are flattened, weakly staining strands like those of *Dubyaea atropurpurea*, which die out in its upper portion. The principal and supernumerary bundles continue to the summit of the ovary, where the former give rise to 2 stylar, 5 corolla, and 5 stamen bundles, and the latter end, as in *Dubyaea hispida*. The species of *Soroseris*, therefore, resemble *Dubyaea atropurpurea* in the number of their supernumerary bundles, but are more like *D. gombalana*, *D. hispida*, and many other species in the fusion of the bases of principals and supernumeraries, and in the number of stylar bundles, while they suggest *D. gombalana* in the strong development of the inner bundles. A striking feature of the anatomy of *Soroseris*, not found in any species of *Dubyaea*, is the large, thick platform of solid vascular tissue (mostly xylem elements) from which the ovule trace and one of the inner bundles arise (Fig. 15*p*, *s*).

Interpretation of Floral Anatomy

Due to the great degree of reduction, fusion, and adnation found in the Compositae, the interpretation of the homologies of the various vascular bundles described above is difficult. For this reason, they have been described as objectively as possible, without designating them by names which would imply their homologies. These homologies, however, can be inferred with some assurance on the basis of the whole series of forms investigated, together with the results obtained by other workers, principally Dr. Koch, and on the available knowledge of the situation in other families.

In the first place, the principal and supernumerary bundles apparently belong respectively to an outer and an inner whorl of perianth members, that is the calyx and corolla. This assumption can be reconciled with the fact that the outer, or principal series actually supplies the corolla when we remember that the only bundles persisting in the corolla of the Cichorieae are those leading to the sinuses between the lobes. These bundles as Koch has pointed out, represent the fused lateral bundles of two adjacent petals, and normally would be opposite the calyx lobes. With the adnation of calyx and corolla, therefore, these fused laterals would tend to fuse with the median sepal bundles directly opposite them. The principal bundles, therefore, probably represent the median sepal bundles, to which have been fused the lateral corolla as well as the stamen bundles. On this basis the supernumerary bundles, which apparently correspond to the "vestigial bundles" found by Koch (1930a) in *Solidago nemoralis*, must represent the median corolla bundle system, which persists only in that part of the corolla limb adnate to the ovary, and in *Dubyaea* and *Soroseris* never extends upward into the free, visible part of the corolla. This interpretation is strengthened by the evidence from *Senecio cruentus* DC. In this species the ovary of the disk florets has 5 primary and 3–5 supernumerary bundles. The latter arise much as they do in *Dubyaea glomerata* and *D. hispida*. In some cases they die out in the upper part of the ovary wall, as in the Cichorieae, while in others they continue into the corolla, and extend to the apex of a lobe, thus forming a median corolla bundle.

The two major bundles supplying the style in *Dubyaea atropurpurea* and *D. chimiliensis*, and the only two stylar bundles present in the other species, represent the dorsal carpellary bundles, as is generally true of Angiosperms. (Eames 1931, Hunt 1937). These are adnate to the composite median calyx-lateral corolla-stamen bundles except in *D. gombalana* and in some ovaries of *D. oligocephala* and *D. tsarongensis*. There remains the problem of the lesser stylar bundles and of the two inner bundles or conducting cords. Their homology presents a dliemma, since both of them give evidence of representing the ventral carpellary bundles. The lesser stylar bundles in *D. atropurpurea* form the lateral bundles of the stigmatic branches, conforming exactly to the diagram of Eames (1931, Fig. 29*c*), and agreeing with the interpretation of Hunt (1937) that the stigma or stigmatic branch, when it possesses three veins, represents the apex of a much contracted and narrowed, but primitively trilobate sporophyll, of which the lateral lobes are supplied by the ventral carpellary bundles, which bundles also supply the placentae. On the other hand, the close connection between the base of one or both of the inner bundles and the ovule trace in *Dubyaea gombalana*, *D. chimiliensis*, and the species of *Soroseris* suggests that these bundles are the placental ones, and therefore the ventral carpellary bundles. This interpretation seems particularly apt in the case of *Soroseris*, in which the ovule trace appears to arise from the much broadened and thickened base of one of these two bundles, while the other arises from a different part of the apex of the stele (Fig. 15*s*). Further evidence for it is the fact that both of the inner bundles, when well developed, are much broadened at the base, in marked contrast to the other bundles of the ovary. This broadening may very well represent a vestigial placental surface, from which, in the many-ovuled ancestors of the Cichorieae, additional ovule traces arose.

An hypothesis to explain this difficulty is suggested by the fact that the lesser stylar bundles, when present, always pass into the stigma at a point directly above the position of the two inner bundles. Perhaps, therefore, both sets of bundles represent portions of the ventral carpellaries, which in the ancestral form were continuous from the base of the ovary into the style, but which during the phylogenetic process of reduction have disappeared from the upper part of the ovary. Before this disappearance the upper portion of the ventral carpellary bundles was connected to a median lateral carpellary (Eames 1931, p. 156) by means of a short horizontal bundle, such as is usually found in well developed carpels as part of the netted venation of their walls. The fusion of the median lateral with a primary calyx-corolla bundle and the disappearance of the ventral in the upper part of the ovary resulted in the apparent fusion of the upper part of the ventral bundle to a principal. The secondary nature of the horizontal basal portion of the lesser stylar bundles is strongly suggested by their irregular course, and by the irregular shape of their tracheids. Furthermore, they always pass inward diagonally, so that the lesser stylar bundles are never opposite the principals to which they are connected.

If this hypothesis is correct, then some form should be found, either among the primitive Compositae or their relatives, in which ventral bundles situated like those of *Dubyaea* and *Soroseris* are continuous, and possess the horizontal connecting bundle at the summit of the ovary. This situation is approached in the specimen of *D. gombalana* illustrated in Figure 15*l*.

The type of ovary ancestral to that now found in the Cichorieae was therefore, probably bicarpellate but unilocular, with two parietal placentae formed by the fused ventral bundles of adjacent carpels corresponding to the diagram of Eames (1931, fig. 29). Furthermore, the lack of adnation, so far as the vascular system is concerned, between ovary and perianth in *D. gombalana* suggests that the Cichorieae are not very distantly related to ancestral forms possessing a superior ovary. Koch (1930a, b) did not report this condition in any of the species investigated by her. The writer has seen it as an occasional feature in the florets of *Senecio cruentus* DC., *Ligularia japonica* (Thunb.) Less., and *Cremanthodium Helianthus* Maxim., and a few other species of the *Senecioneae*, and in *Dinoseris salicifolia* Griseb. of the Mutisieae, but it is by no means common in the Compositae, and the writer knows of no species in which it is as regular a feature as in *Dubyaea gombalana*. A fuller discussion of these points in connection with the phylogeny of the Cichorieae as a whole will be presented in a later publication.

Comparison with other genera of Cichorieae

There are no other genera known to the writer in the Cichorieae which contain as many primitive anatomical features as *Dubyaea* and *Soroseris*. The nearest approach to the situation found here is in *Prenanthes*. In most of the species of this genus (*P. purpurea* L. and *P. yakoensis* Jeffr. are exceptions) supernumerary bundles are present. They may be few, as in *Dubyaea hispida*, or numerous, as in *Soroseris*. The latter situation is most characteristic of the American species of *Prenanthes* (*P. serpentaria* L., *P. alba*, L., *P. trifoliolata* (Cass.) Fernald, *P. altissima* L.) but occurs also in the Asiatic *P. acerifolia* (Maxim.) Matsum. In all of the species of *Prenanthes* there are only two stylar bundles, that is the dorsal carpellaries, but in *P. acerifolia* one or both of these may be free from the calyx-corolla, principal bundles. The "platform" of vascular tissue that is so conspicuous in *Soroseris* exists also in *Prenanthes*, although its shape is somewhat different in the latter genus, while the two inner, presumably ventral carpellary bundles occur regularly in the developing achenes.

Youngia, Sect. DESIPHYLUM, also approaches *Dubyaea* and *Soroseris* anatomically. *Y. depressa* (Hook. f.) Babcock & Stebbins and *Y. conjunctiva* Babcock & Stebbins, the two species of this section investigated, both have supernumerary bundles and well developed platforms. In *Y. con-*

junctiva four bundles are generally present in the style although in both species the stylar bundles are adnate to the principal calyx-corolla series. The material available was not old enough for the determination of the presence or absence of the inner "ventral" bundles. In the remaining sections of *Youngia* and in the related *Ixeris* the *Lapsana* type of anatomy is predominant. *Crepis*, also, has a more reduced floral anatomy than the more primitive species of *Dubyaea*. Supernumerary bundles occur in some species of the subgenus CATONIA and in a few of EUCREPIS, while in *C. aurea* (L.) Cass., *C. mollis* (Jacq.) Asch. and perhaps a few other species one of the dorsal carpellaries is occasionally free from the primaries. Three or four stylar bundles exist in *C. paludosa* (L.) Moench., *C. viscidula* Froel., and *C. geracioides* Haussk. The two "ventral" bundles have been seen in *C. occidentalis* Nutt. and probably occur in other species. The majority of *Crepis* species, however, have the simple *Lapsana* type of anatomy, as exemplified by *C. nana* Richards. (Fig. 15*t*). Only twelve species of *Hieracium* have as yet been examined, but all of these had the *Lapsana* type of anatomy except for *H. umbellatum* L. and *H. Nakaii* Kitagawa. In the former species one of the dorsal carpellaries was free in about one-half of the ovules of a specimen from Blankenburghe, Belgium, but no supernumerary bundles were found, while in *H. Nakaii* the dorsals are adnate but supernumeraries occur. The species of *Lactuca*, except for a few exceptional ones like *L. porphyrea* and *L. disciformis* (see above), have two or more of the principal bundles fused, so that the number of these bundles is reduced to four, three, or most often two (cf. Stebbins 1937). Supernumerary bundles are present in a few species, such as *L. Lessertiana* (Fig. 16*u*), but are usually lacking. *Lactuca*, therefore, has the most specialized floral anatomy of any of the genera under consideration.

VIII. SOME HISTOLOGICAL CHARACTERISTICS OF DUBYAEA AND SOROSERIS

Two histological characteristics are of value in determining the relationships of *Dubyaea* and *Soroseris*. These are the presence or absence of sclerenchymatous tissue at the summit of the ovary, and the form of the crystals found in the uppermost part of the ovary wall. Both of these can be determined from herbarium specimens. They are quite evident in the cleared mounts of ovaries which were used for anatomical study, and can be determined on any herbarium specimen by boiling ovaries first in water, then in concentrated ammonia on a slide, and then flattening them out under a cover glass.

The sclerenchymatous tissue, when present, usually covers the summit of the ovary, in the region inside of that occupied by the vascular bundles which supply the corolla (Fig. 16*c*). Its cells are large, thick-walled,

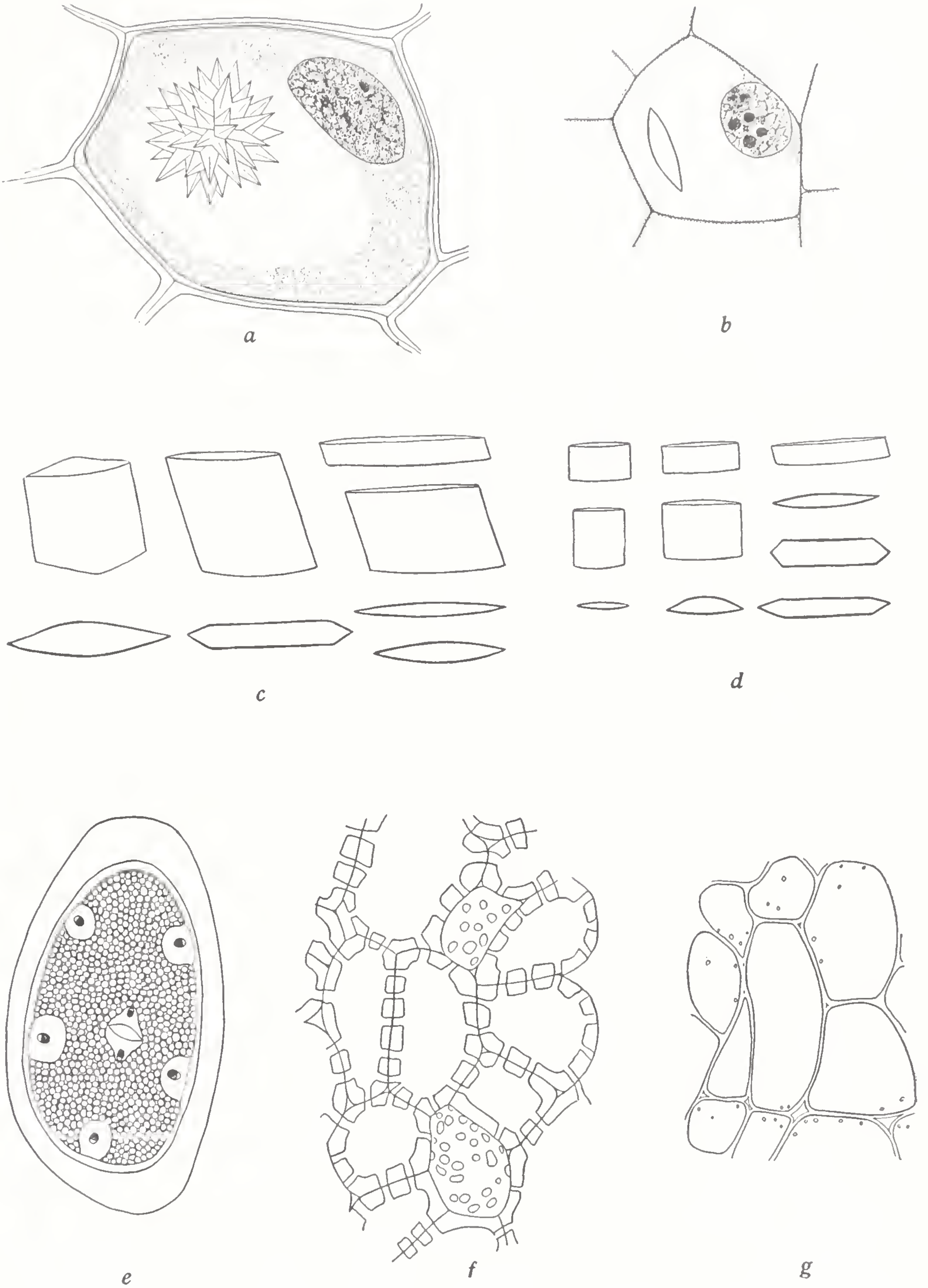

Fig. 16. *a–d*, Types of crystals: *a*, cell from ovary wall of *Crepis intermedia; b*, cell from ovule integument of the same; *c*, crystals from summit of ovary of *Dubyaea oligocephala; d*, from ovule integument of the same. All ×1250. *e*, Diagram of summit of ovary of *Soroseris Deasyi*, showing position of sclerenchyma (circles). *f*, sclerenchyma cells from *S. Deasyi; g*, parenchymatous cells from the corresponding region of *Dubyaea chimiliensis*.

prominently pitted, and stain the same color as the xylem strands (Fig. 16f). In contrast, the cells in the same region of such a species as *Dubyaea chimiliensis* are thin-walled and parenchymatous. Intermediate conditions are sometimes found, but the lignified sclerenchyma can always be recognized when present.

Crystals may occur in three regions in the ovary; the apex of the ovary wall, the base of the same, and the ovule integument. Those found at the base of the ovary are always the same as those at its summit, but the ones in the ovule integument are usually different in structure. Both types reacted positively to the usual tests for calcium oxalate (Ballard 1921). Figure 16*a* shows a cell from the summit of the ovary of *Crepis intermedia* Gray, containing an aggregate crystal, or druse, while Fig. 16*b* shows a cell from the ovule integument of the same floret containing a simple crystal, shown in end view. Both cells were drawn from a preparation fixed in a chrome-acetic formalin fixative, sectioned, and stained with a modification of Flemming's triple stain. The crystals found in the ovule integument of *Dubyaea oligocephala* are exactly like those in the corresponding tissue of *Crepis*, while in the ovary wall of *D. oligocephala* the same type of crystal is found (Figs. 16*c*, and *d*). These simple crystals are strongly flattened, being narrowly lenticular or prismatic in end view, and rectangular, rhomboidal, or occasionally pentagonal or hexagonal in side view.

The type of crystal found in any tissue is in these species apparently correlated with the condition of the cytoplasm at the time of crystallization. Both types are undoubtedly formed within the cytoplasm, and come to lie in the vacuole only after the cell has matured. In the cells which form aggregate crystals, the cytoplasm is relatively dense and evenly distributed while the crystal is forming, while the simple crystals are apparently formed in cells which have relatively thin cytoplasm, and in which vacuoles appear early. The structure of the crystals, therefore, is a significant indicator of certain physico-chemical properties of the cells in which they occur. The specificity of their occurrence both as to types of tissue and groups of organisms is clearly pointed out in Netolitzky's (1927) thorough review of the subject.

Table I shows the distribution of sclerenchyma and crystal types in the eight genera under consideration. In this table, the presence of sclerenchyma is indicated by a + sign; its absence by a − sign. The letter a denotes aggregate; s, simple crystals; −, the absence of crystals in that particular tissue. All of the species of *Dubyaea* and *Soroseris* were examined, except *D. rubra* and *S. bellidifolia*, of which little material was available, and which have close relatives among the other species. The number of species examined in the other genera is given after the name of the genus; in every case the species were selected from subgenera and sections representing as much of the total variation within the genus as possible. When a particular type is represented by only a few species of the genus, the symbol for that type is placed in parentheses.

Dubyaea contains four histological types in respect to these characteristics. In the first, represented by *D. atropurpurea* and the Sect. Amoenae, sclerenchyma is present, but crystals are absent from the ovary wall or nearly so. The second, represented only by *D. glaucescens*, is unique among the species investigated, since it combines the presence of sclerenchyma with that of aggregate crystals. In the third, represented by *D. hispida* and *D. oligocephala*, sclerenchyma is absent, but simple crystals occur in the ovary wall. In the fourth, the section Ixeridopsis, there are no sclerenchyma cells or crystals in the ovary wall.

Soroseris is more uniform. The bulk of the species conform to a type not known in *Dubyaea* in having both sclerenchyma and simple crystals. The crystals may be in the sclerenchyma cells, but are usually below or above this layer of tissue, in ordinary parenchyma cells. *S. Gillii* and *S.*

TABLE I

Distribution of sclerenchyma tissue and crystals in Dubyaea, Soroseris, and related genera.

SPECIES	SCLERENCHYMA	CRYSTALS	
		ovary wall	ovule integument
Dubyaea atropurpurea	+	−	s
D. glaucescens	+	a	s
D. hispida	−	s	s
D. oligocephala	−	s	s
D. chimiliensis	−	−	s
D. tsarongensis	−	−	s
D. amoena	+	−	s
D. gombalana	+	−	s
Soroseris umbrella	+	s	s
S. glomerata	+	s	s
S. Deasyi	+	s	s
S. rosularis	+	s	s
S. pumila	+	s	s
S. Gillii	+	s−	s
S. Hookeriana	+	−	s
Prenanthes, 13 spp.	+, (−)	s, (−)	s
Lactuca, 20 spp.	+, (−)	s, s+a	s, s+a, (a)
Crepis, 30 spp.	−	a, − a, (a+s) (s), (−)	s
Youngia, 5 spp.	−, (+)	s	s
Ixeris, 5 spp.	−	− (s)	s
Hieracium, 10 spp.	+, −	s, −	s

Hookeriana agree with *Dubyaea* Sect. AMOENAE; an interesting fact in view of the habital resemblance between these two groups of species.

Among the other genera investigated, *Prenanthes* and *Hieracium* are like *Soroseris*, *Youngia* is like *D. hispida*, and *Ixeris* is like *Dubyaea* Sect. IXERIDOPSIS. The bulk of *Crepis* species differ from any known species of *Dubyaea* or *Soroseris* in that they combine absence of sclerenchyma with aggregate crystals in the ovary wall. This is very conspicuous in *C. sibirica*, *C. kashmirica*, and other species of the subgenus Catonia which approach *Dubyaea* in habit. In all of them the aggregate crystals are particularly large and abundant, contrasting sharply with the equally conspicuous simple crystals of *D. oligocephala*. *Lactuca* is extremely variable in the distribution of both sclerenchyma and crystal types. An explanation of this variability is not yet available. Most of the Sino-Himalayan species, however, including *L. atropurpurea* and *L. Lessertiana*, the two most nearly related to *Dubyaea*, are either like *D. atropurpurea*, as is the case with these two, or are like *Soroseris* and *Prenanthes*. The available histological evidence, therefore, agrees well with that from other lines as to the relationships of the genera in question.

IX. CYTOLOGY OF THE SPECIES

Due to the difficulty of obtaining seed and of raising the plants, only a few of the species of *Dubyaea* and *Soroseris* are known cytologically. The somatic chromosome number $2n = 16$ was first reported by Babcock and Cameron (1934) for *Dubyaea hispida* (as *Crepis bhotanica*), while the root tip chromosomes of both this species and *D. oligocephala* were illustrated by Babcock, Stebbins and Jenkins (1937). In this paper the striking similarity between the chromosomes of these two species was pointed out, as well as their close resemblance to those of several species of *Prenanthes*. The hypothesis was put forward there that among primitive species of *Cichorieae* great changes in the phenotypic characteristics of the plant are accompanied by relatively slight changes in chromosome morphology and probably also chromosome structure, while in the more advanced species the reverse is often the case. This hypothesis is well borne out by the chromosomes of *Soroseris*, so far as they are known. Babcock and Cameron (1934) reported the number $2n = 16$ for a species of this genus, of which seed was received bearing the tentative identification *Crepis glomerata*. Later examination of the specimen collected with this seed (*Rock 24502*) has shown it to belong to *Soroseris Gillii* subsp. *typica*. A somatic metaphase plate of this species, from sections prepared according to the method previously described (Babcock, Stebbins, and Jenkins 1937) is illustrated in Figure 17. The only other *Soroseris* species of which it has been possible to obtain seedlings was one sent by S. L. Ghose & Co., Darjeeling, India, under the name *Crepis glomerata*, and collected in Sikkim. Since the particular seed collection from which germination was obtained did not have a specimen accompanying it, and since the specimens accompanying other collections sent by this firm included both *S. Hookeriana* subsp. *typica* and *S. pumila*, the identity of the seedlings grown is not certain. They all died as young seedlings. Judging from the appearance of the achenes, however, they were more likely *S. pumila*. The chromosome number of this species is also 2n = 16, and the size and morphology of the chromosomes are similar to that of *S. Gillii*, although no very satisfactory metaphase plates could be found.

Fig. 17. Somatic metaphase plate from root-tip of *Soroseris Gillii* subsp. *typica* (×2500).

As can be seen by comparing Figure 17 with the figures of *Dubyaea* previously published, the chromosomes of *Dubyaea* and *Soroseris* are very similar to each other in size and morphology as well as in number. In both genera the chromosomes have mostly median or submedian constrictions and there is little variation in size between the different members of the section. The size and morphology of the satellited chromosome pair is exactly comparable in the three species. As pointed out for *Dubyaea* (Babcock, Stebbins and Jenkins 1937) the karyotype of these species has all the characteristics of a primitive one, according to the criteria used by other workers. *Soroseris*, therefore, in spite of its specialized habit, has retained a primitive karyotype along with primitive floral characteristics, pollen grains, and ovary anatomy.

Since no further cytological information has been obtained on either *Dubyaea* or *Prenanthes*, the status of the hypothesis put forward earlier (Babcock, Stebbins, and Jenkins 1937), that the great morphological changes involved in the evolution of *Prenanthes* from *Dubyaea* have been accompanied by relatively few structural changes in the chromosomes, has not been altered. The somatic numbers of four additional Sino-Himalayan species of *Lactuca*, however, have been obtained. *L. Brunoniana* (Wall.)

Franch. (*Prenanthes Brunoniana* Wall.), *L. rapunculoides* Clarke, *L. macrantha* Clarke, and *L. Lessertiana* (DC.) Clarke all have the somatic number 2n = 16. The chromosomes resemble in size and morphology those of *L. bracteata* Hook. f. et Thoms., already illustrated (Babcock, Stebbins, and Jenkins 1937, Fig. 3e). They differ from those of *Dubyaea* and *Soroseris* in having mostly subterminal constrictions, and in the great difference in size between the members of a complement. As previously pointed out (Babcock, Stebbins, and Jenkins 1937) these are both relatively advanced characteristics, and are well correlated with the greater specialization in floral and fruit characteristics of *Lactuca*. *Dubyaea* and *Soroseris*, therefore, are cytologically nearest to *Prenanthes*. They are less similar to *Youngia* and *Lactuca*, although they have the same basic haploid number (x = 8) as most *Youngias* and many *Lactucas*. They are different from *Hieracium* in number, since this genus has the basic haploid number 9, but are rather similar to it in chromosome size and morphology. They are most different from *Crepis*, in which genus the basic haploid numbers 5 and 4 prevail, and the chromosomes have mostly subterminal constrictions (Babcock and Cameron 1934, Babcock 1936).

The stomata and pollen of all of the species of *Dubyaea* and *Soroseris* were examined since as has been noted previously (Babcock and Stebbins 1937, Sax and Sax 1937) these structures often provide evidence of polyploidy in a group, and have proved reliable in most groups of Cichorieae in which they have been tested. The only putative polyploid in *Dubyaea* is *D. glaucescens*, in which the pollen grains are nearly all 4-pored, and the average length of the guard cells is about 45μ, as compared with 28–36μ for the other species of *Dubyaea*. There are no species extant which either from the point of view of external morphology or of geographic distribution would serve as a likely diploid ancestor of *D. glaucescens*. *D. atropurpurea*, its nearest living relative, not only occupies an entirely different climatic province, separated by several intermediate phytogeographic regions from *D. glaucescens*, but in addition has larger heads, flowers and achenes, whereas the diploid ancestors of *D. glaucescens* would be expected to be smaller in these respects. The diploid ancestors of *D. glaucescens* are very likely extinct. This species may easily be the last remnant of a polyploid complex (cf. Babcock and Stebbins 1938) which was formerly more widespread and contained several species. The cytological evidence, therefore, points toward both the primitive and the relic nature of the genus *Dubyaea*.

The species and subspecies of *Soroseris* all have 3-pored pollen grains, and all compare closely in stomatal size with the known diploids, except for *S. Gillii* subsp. *hirsuta*. In this subspecies the average length of the guard cells is 42μ (specimen, *Forrest 19054*) as compared with 34μ for subsp. *typica*. If subsp. *hirsuta* is polyploid, it is very likely of recent origin, and it has no morphological characteristics not found at least to some degree in other subspecies of *S. Gillii*.

X. PHYLOGENETIC RELATIONSHIPS OF THE GENERA

A. DUBYAEA

In regard to *Dubyaea*, the following conclusions have been reached:

1. The genus shows definite relationships to several of the larger genera of the tribe Cichorieae.
2. Its species are sharply distinct from each other morphologically.
3. They are mostly narrowly endemic to regions noted for their large number of relict endemics.
4. They are the most primitive in floral anatomy of all the Cichorieae, and among the most primitive of the Compositae in this respect.
5. Those investigated are also primitive in chromosome morphology.

These conclusions all suggest the same hypothesis: that *Dubyaea* as known at present contains the last remnants of an ancient genus which was once much larger and more widespread, and which contained the direct ancestors of some or all of the present species of *Prenanthes*, *Lactuca*, *Crepis*, *Youngia*, *Ixeris*, and *Hieracium*. Three points remain to be considered. First, what is the age of *Dubyaea;* second, what is its origin; and third, has its center of distribution always been the Sino-Himalayan region, and is this the center from which the other genera radiated?

In regard to the age of *Dubyaea*, the following suggestion can be made. *Prenanthes* is in many ways more specialized than *Dubyaea*, and appears to be a younger derivative. The minimum age for *Prenanthes* is suggested by its distribution. It has two main centers; temperate eastern Asia and temperate eastern North America. Furthermore, the most primitive species in each center, *P. acerifolia* and *P. ochroleuca* in Asia, and *P. crepidinea* in North America, are restricted in range and rare in occurrence; they have every characteristic of ancient species. *Prenanthes*, therefore, apparently belongs to that ancient temperate flora about which much has been written, and whose characteristics have been so ably summed up by Fernald (1931). Its origin can hardly be placed at later than the early part of the Tertiary period. *Dubyaea*, since it is probably older, may very well date back to the Cretaceous period.

No evidence is available on the origin of the genus. As has been said previously, it is as primitive or more primitive than any other genus of the tribe. Its origin, therefore, would have to be sought either in some other tribe of the Compositae or in another family of plants. A preliminary survey has been made of the genera of the Mutisieae, Cynareae, Senecioneae, and Vernonieae which have been suggested as related to the Cichorieae, but none has been found which, when all of its characteristics are considered, suggests the ancestry of *Dubyaea*. Equally fruitless has been an examination of various Calyceraceae, Goodeniaceae, Lobeliaceae, Companulaceae, Rubiaceae, and Caprifoliaceae. A more detailed discussion of this problem will be made in a later publication, in which the affinities of the Cichorieae as a whole will be considered, but the writer believes at present that the tribe is so old and so isolated systematically that its ancestors are extinct, and that there are no living species or groups of species which connect it with any single other modern tribe or family.

The position of the original center or centers of distribution of *Dubyaea* is suggested by the distribution of its modern relatives. None of the six larger genera mentioned above agree exactly with *Dubyaea* in their centers of distribution. *Youngia* is the closest in this respect (Babcock and Stebbins 1937), but most of its species are found in temperate regions, and it has few representatives in the subalpine region of Yunnan and the River Gorge country which is such a conspicuous center for *Dubyaea*. *Prenanthes* and *Ixeris* both have their major centers of distribution in eastern Asia, but they have few or no alpine or subalpine representatives, and their most primitive species are found farther east, in Japan and Korea. *Lactuca* has two major centers of distribution, one in the Sino-Himalayan region and one in southwestern Asia and southeastern Europe. These two centers are about equal in size, and both contain an equal number of primitive types. This suggests a polyphyletic origin for *Lactuca*, a suggestion which is supported by other evidence. *Crepis* and *Hieracium* have their major Old World centers of distribution in southwestern Asia and Europe, and are represented in the Sino-Himalayan region by only a few outlying species. The distribution of these six genera, therefore, in no way supports the hypothesis that they radiated outward from the Sino-Himalayan region.

All the evidence suggests that the present region of concentration of *Dubyaea* species never has been a real center of distribution for the genus. More likely, it has acted as a haven for the preservation of these ancient types which elsewhere have been eliminated by changes in the environment, and by competition with their more aggressive descendants. The hypothesis of Matthew (1915, p. 180) that the primitive types of a group tend to be preserved near the edges of its range, is well supported by these genera of the Cichorieae. The Sino-Himalayan region is definitely on the edge of the range of the tribe as a whole. To the south and southeast of it the country is mostly tropical or subtropical, and is occupied by only a few scattered species of Cichorieae, while the altitudinal range of *Dubyaea* is higher than that of any other members of the tribe except for its derivative, *Soroseris,* and a few species of *Lactuca.*

Considered from this point of view, the present range of *Dubyaea* has little bearing on the place of origin of *Crepis* or of any other of the genera derived from this ancestral stock. If *Crepis* had originated in the Sino-Himalayan region, many species would have been preserved in this rich and varied flora. The actual number of *Crepis* species found is small, and they are not closely interrelated. They appear much more like migrants which from time to time have invaded the Sino-Himalayan region from elsewhere. The suggestion of Babcock (1936), that *Crepis* originated in south central Asia, is not supported by the present evidence. The suggestion of southwestern Asia, made in the same publication, is a more likely one.

In a relict genus like *Dubyaea,* the construction of anything like a phylogenetic tree is a hopeless task. As has been mentioned previously, representatives of all three sections have different primitive anatomical characteristics, and between EUDUBYAEA and IXERIDOPSIS there is nothing to choose as to primitiveness of habit and floral characteristics. EUDUBYAEA, however, has more relationships with other genera than has either IXERIDOPSIS or AMOENAE. The ancestral types of *Prenanthes, Lactuca, Crepis, Hieracium,* and some of *Youngia* would be associated with this first section. Species of this type, therefore, were probably widespread throughout Eurasia in early Tertiary time or earlier, and very likely had well developed distributional centers in both the western and the eastern end of the continent. IXERIDOPSIS resembles only *Ixeris* and some species of *Youngia,* so that it has probably always been confined to eastern Asia. The AMOENAE are related only to *Soroseris,* and that relationship is not very close. This anomalous section probably has always been endemic to the Sino-Himalayan region. It is perhaps the youngest of the three, and most likely dates from the uplift of the Himalaya in mid-Tertiary time. Within the sections, the interrelationships of the species are no longer clear. *D. atropurpurea, D. chimiliensis,* and *D. gombalana* are each the most primitive member of their section, but none is ancestral to the other species with which it is associated.

B. SOROSERIS

As has already been mentioned, *Soroseris* is most closely related to *Dubyaea,* and is most probably derived from that genus. The most obvious connection is from *Dubyaea hispida* through *Soroseris umbrella* to *S. glomerata, S. Deasyi, S. rosularis,* and *S. bellifidolia.* The assumption of this phylogenetic line involves two difficulties. In the first place, *D. hispida* has a more reduced ovary anatomy than has any species of *Soroseris*, and in that respect may be considered more advanced. Secondly, the echinate pollen grain pattern characteristic of Sect. EUSOROSERIS, since it is found in the majority of the genera of the Compositae, is probably a more generalized and, therefore, a more primitive type than the echinolophate pattern characteristic of the Cichorieae, and found in most species of *Dubyaea* (Wodehouse 1928). The only species of *Dubyaea* which has a more primitive floral anatomy than *Soroseris*, and whose pollen grains approach those of Sect. EUSOROSERIS, is *D. atropurpurea*. This species, however, is the farthest from *Soroseris* of all in habit, size of involucres, and most other characteristics. For this reason the best hypothesis is that the ancestors of *Soroseris* were a series of species of *Dubyaea* now extinct, some of which resembled *D. hispida*, but which possessed certain primitive features now lost by their modern counterpart. *S. umbrella* was an early offshoot from the main line, which developed a habit and involucres resembling those of the Sect. EUSOROSERIS, but with much less reduction, and in addition developed the subechinolophate type of pollen grain found in the modern species of *Dubyaea*. *S. glomerata*, *S. Deasyi*, *S. rosularis*, and *S. bellidifolia* are all about equally advanced phylogenetically, and are so closely interrelated that all could have been derived from one variable species through the "fixing" of certain distinctive characteristics through geographical isolation and consequent inbreeding. *S. glomerata* is less specialized than the other three in its involucres, but more so in habit. *S. pumila* may be considered as a more specialized offshoot from the common ancestor of the four species already mentioned. The remaining two species, *S. Gillii* and *S. Hookeriana*, are doubtfully distinct from each other, and may very well be segregates from a common ancestral stock. They possess certain habital characteristics, however, not found in the *S. glomerata* group, *S. umbrella*, or even *Dubyaea hispida*. As has already been mentioned, *S. Gillii* and *S. Hookeriana* have certain features of habit and leaf shape in common with *Dubyaea tsarongensis*, *D. amoena*, and *D. gombalana*. Since these three species approach *Soroseris* in habit more nearly than do any other species of *Dubyaea*, the supposition is not unlikely that their ancestors figured also in the ancestry of *S. Gillii* and *S. Hookeriana*. On this basis, *Soroseris* must be considered as somewhat polyphyletic, in that different though related ancestral forms of *Dubyaea* figured in the origin of its species. Their relative uniformity in general habit and in the characteristics of their involucres can be explained partly through their common exposure to the rigorous selective activity of the same extreme environment, and partly through interracial and interspecific crossing during the evolution of the genus.

The "cushion" habit, consisting of greatly expanded, apparently hollow stems and closely crowded heads, is more strongly developed in *Soroseris* than in any other of the Cichorieae. This is undoubtedly due to the extreme environment to which these plants are subjected. A similar habit is found in many other Tibetan species, notably in the genus *Saussurea* of the Cynareae (Hemsley and Pearson 1902, Ward 1935). As Hemsley and Ward have pointed out, the rigors of the Tibetan climate involve not only extreme temperatures, due to the great altitude of the plateau and the surrounding mountain ranges, but in addition drouth and very high winds. Since the Tibetan plateau is the center of distribution of the genus, and its species are particularly adapted to the conditions prevailing there, the origin of *Soroseris* is most likely contemporaneous with the origin of the plateau itself. In Mesozoic and earliest Tertiary times, Tibet was under a vast inland sea (Burrard and Hayden 1934). By the end of the Eocene period the uplift of the plateau and of the Himalaya mountains to the south of it had begun, and this uplift has been more or less continuous up to the present time, at least that of the Himalaya. There must have been some time during this uplift when Tibet had a temperate climate; at this time it could have been colonized by species of *Dubyaea*. As a result of further uplift and of the rise of the Himalaya to the south, which cut off the moist ocean winds, the climate of Tibet became drier and drier. The species of *Dubyaea* were largely exterminated from that area, and only those forms which evolved into *Soroseris* could survive. This change of climate and the consequent evolution of *Soroseris* probably took place during the middle or latter part of the Tertiary period. The species of *Soroseris* then spread to dry mountain slopes on the great ranges surrounding the plateau on all sides. Their ranges were probably somewhat reduced in extent by the Pleistocene glaciation, which covered the southeastern part of the plateau, but since most of Tibet proper was too dry to be extensively glaciated (Ward 1935), *Soroseris* must have suffered less from this catastrophe than *Dubyaea*. The glaciation, however, could have been a major factor in producing the isolation necessary for the differentiation of closely related species and subspecies, such as are now characteristic of the genus, so that the present forms of *Soroseris* are probably to a large extent of Pleistocene origin.

Literature Cited

Babcock, E. B., 1936. The origin of *Crepis* and related genera, with particular reference to distribution and chromosome relationship. *Univ. Calif. Publ. Bot.* Essays in Geobot. in honor of W. A. Setchell, pp. 9–53.

————, **and D. R. Cameron,** 1934. Chromosomes and phylogeny in *Crepis* II. The relationships of one hundred eight species. *Univ. Calif. Publ. Agr. Sci.* **6**: 287–324.

———, **and G. L. Stebbins, Jr.,** 1937. The Genus *Youngia*. *Carnegie Inst. Wash. Publ.* no. 484. 106 pp.

———, **and G. L. Stebbins, Jr.,** 1938. The American Species of Crepis; their interrelationships and distribution as affected by polyploidy and apomixis. *Carnegie Inst. Wash. Publ.* no. 504. 199 pp.

———, **G. L. Stebbins, Jr., and J. A. Jenkins,** 1937. Chromosomes and phylogeny in some genera of the Crepidinae. *Cytologia, Fijii Jubl. Vol.*: 188–210.

Ballard, C. W , 1921. The Elements of Vegetable Histology. 246 pp. John Wiley & Sons, New York.

Burrard, S. G., and H. H. Hayden, 1934. A sketch of the geography and geology of the Himalaya Mountains and Tibet. 360 pp.

Diels, L., 1913. Untersuchungen zur Pflanzengeographie von West China. *Beibl. Bot. Jahrb.* **109**: 55–88.

Eames, A. J., 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. Jour. Bot. **18**: 147–188.

Fernald, M. L., 1931. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33**: 25–63.

Good, R. D'O., 1929. The taxonomy and geography of the Sino-Himalayan genus *Cremanthodium*. Benth. *Jour. Linn. Soc.* **48**: 259–316.

Hemsley, W. B., and H. H. W. Pearson, 1902. The flora of Tibet or high Asia, . . . *Jour. Linn. Soc.* **35**: 124–265.

Hooker, J. D., 1909. Sketch of the flora of British India. *Imp. Gaz. Oxford.* vol. 1: 157–212.

Hunt, K. W., 1937. A study of the style and stigma, with reference to the nature of the carpel. *Am. Jour. Bot.* **24**: 288–295.

Koch, Minna F., 1930a. Studies in the anatomy and morphology of the Composite Flower I. The corolla. *Am. Jour. Bot.* **17**: 938–952.

———, 1930b. Ibid. II. The corollas of the Heliantheae and Mutisieae. *Am. Jour. Bot.* **17**: 995–1010.

Lavialle, P., 1912. Recherches sur le développement de l'ovaire en fruit chez les Composées. *Ann. d. Sci. Nat. Bot.* 9e sér., **15**: 39–152.

Matthew, W. D., 1915. Climate and Evolution. *Ann. New York Acad. Sci.* **24**: 171–318.

Netolitzky, F., 1929. Die Kieselkörper. Die Kalksalze als Zellinhaltskörper. *Hand. der Pflanzenanat.* **3**, pt. 1a.

Stebbins, G. L., Jr., 1937a. Critical notes on *Lactuca* and related genera. *Jour. Bot.* **75**: 12–18.

———, 1937b. Critical notes on the genus *Ixeris*. *Jour. Bot.* **75**: 43–51.

———, 1937c. The scandent species of *Prenanthes* and *Lactuca* in Africa. *Bull. Jard. Bot. de L'Etat*, Brussells, **14**: 333–352.

———, 1938. A bleaching and clearing method for plant tissues. *Science* **87**: 21–22.

Ward, F. L., 1935. A sketch of the geography and botany of Tibet, being materials for a flora of that country. *Jour. Linn. Soc.* **5**: 239–265.

Wilson, E. H., 1929. China—Mother of Gardens. 408 pp. Boston, Stratford Co.

Wodehouse, R. P., 1928. The phylogenetic value of pollen grain characters. *Ann. Bot.* **42**: 891–934.

———, 1935. Pollen Grains. 574 pp. New York, McGraw-Hill Co.

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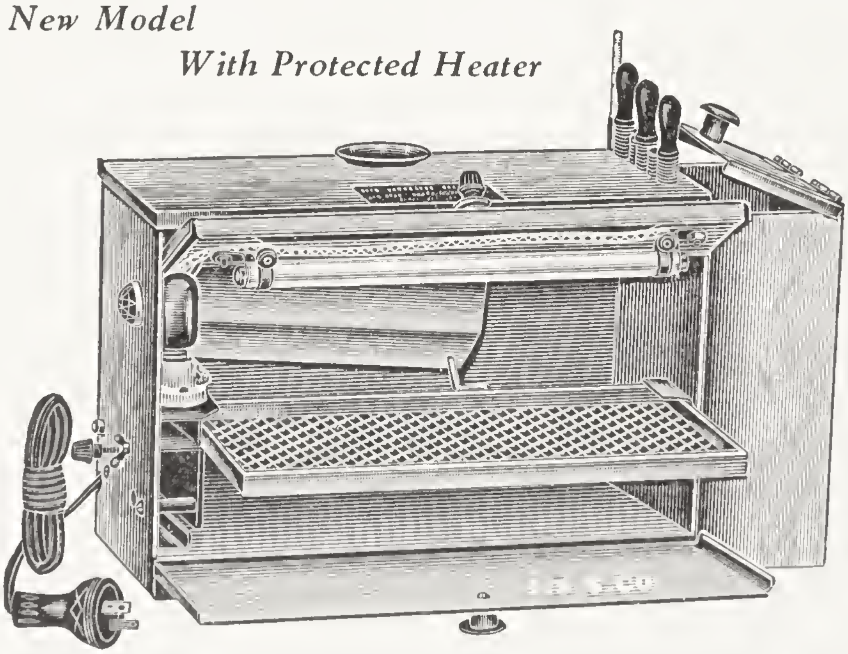

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MEMOIRS OF THE TORREY BOTANICAL CLUB

A Monograph on the Genus Downingia

By

ROGERS McVAUGH

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A Monograph on the Genus Downingia

Rogers McVaugh

(WITH SIXTEEN FIGURES AND ELEVEN MAPS)

INTRODUCTION

The genus *Downingia* (Campanulaceae—Lobelioideae) is a very natural and well-defined group, made up of about 13 species. All the species occur in western United States, with the greatest concentration of species in California. A single species, *D. pusilla*, occurs both in California and Chile. All the downingias are annuals of like appearance, the vegetative characters of the several species being so nearly identical that they are scarcely to be relied upon as means of identification. With some minor exceptions, the important taxonomic characters of the genus are localized in the flowers and fruits. The flowers are commonly blue or purplish, varying to white or pink in some individuals, and are similar in size, markings, and conformation in all the species, so that in a few cases only can gross morphological characters be used to distinguish single species. The fruit in all the species is an elongated capsule, sessile in the axil of a leafy bract and dehiscent at maturity by long slits on the sides.

The superficial resemblances found in all the species make it necessary for the taxonomist to treat the genus exactly as if it were a genus of grasses or of the Compositae, where the distinguishing features are often technical ones and equally often invisible to the unaided eye. In *Downingia*, even though a single flower may be as much as 3.5 centimeters in length, it is often necessary to examine a specimen with a magnification of 10 or 15 diameters before a positive identification can be made.

The corolla of *Downingia*, while in general essentially like that of the majority of the members of the Lobelioideae, has several specialized features which have been much relied upon as means of identification. The "lower lip," as in the flower of *Lobelia* and other genera, is three-lobed and flattened; it may be strongly reflexed or not at all so. At the base of the lip may be found one or more dark purplish spots, in combination with patches or blotches of white or yellow or both. Short horn-like processes are sometimes produced at the base of the lower lip. The sinuses between the "upper" and "lower" lips of the corolla are of different depths in the different species, and some stress has been placed upon the depth of these sinuses in relation to the plane of the reflexed lower lip. The two lobes of the corolla which form the "upper lip" are variously erect, recurved, crossed one upon another, or curled into a ring.

Features of the kind just mentioned are evident in the fresh flower, but are hard to distinguish in herbarium specimens, except after prolonged study. Flower-color is usually imperfectly or not at all preserved in the herbarium, while such features as the degree of flexion of the lip of the corolla or the direction of the lobes of the "upper lip" are often totally obscured in a pressed flower. The most recent student of the genus, Dr. Robert F. Hoover, has already pointed out[1] that collectors of these plants should study the fresh flowers and make ample notes on the color and conformation of the corollas.

Study of a large series of herbarium specimens, however, brings out the fact that certain morphological characters of these plants are not obscured by drying and are therefore ordinarily available to the student. It has proven quite feasible to separate the several species by means of characters which are discernible even in imperfectly prepared specimens. This does not in the slightest degree detract from the importance of information concerning the fresh flowers; all herbaria at present are suffering from a deplorable lack of just such information.

The genus *Downingia* was established by John Torrey in 1856, and dedicated by him to Andrew Jackson Downing, a horticulturist of Newburgh, New York. Torrey proposed this name to replace *Clintonia* of Lindley, which was antedated by *Clintonia* of Rafinesque. There were already three published names for the genus when Torrey proposed *Downingia*, and his name has been conserved by international agreement. Torrey was aware that *Wittia* had been proposed as a name by Kunth in 1850, but rejected it because he considered it unsuitable to dedicate more than one genus to a single man (De Witt Clinton). Two earlier names proposed by Rafinesque (*Bolelia*, 1832, and *Gynampsis*, 1833) were disregarded by Torrey and may have been unknown to him.

The first downingias made known to science were grown from seeds collected by David Douglas in what is now Oregon. The original species, *D. elegans*, was described by Lindley in 1829 (as *Clintonia elegans*), and a second species, *Clintonia pulchella*, was described by Lindley in 1836, from plants grown from seeds collected in California by Douglas in 1833. Until the year 1886 all collections of Californian or other North American downingias were referred to one of these two species.

In 1886 Asa Gray described a third North American species, and in the same year Edward Lee Greene, the first real student of these plants in the field, described a fourth species. Between 1886 and 1895 Greene proposed 8 new species of *Downingia*, all except one of which appear to be perfectly distinct species. Since Greene's time but one valid species has been discovered in California, and but two elsewhere.

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[1] A provisional key to the species of *Downingia* known in California. Leafl. West. Bot. **2**: 33–35. Au 1937.

The next student of the genus, Professor W. L. Jepson, published in 1922[2] a revision of the Californian species. He recognized 7 species, reducing *D. insignis* Greene to synonymy under *D. elegans*, *D. montana* to a variety of *D. bicornuta*, and *D. tricolor* to synonymy under *D. concolor*. Essentially the same treatment was employed in Jepson's California *Manual* published three years later.[3]

In 1937 Dr. Robert F. Hoover, one of Professor Jepson's students, published a key[4] to the species of *Downingia* known to him from the state of California. He included a total of 13 species. He was in agreement with Jepson on the status of *D. insignis* and *D. tricolor*, but accorded specific rank to *D. montana*. His list also included *D. laeta* Greene, which was not known to Jepson from the state, as well as *D. pallida* Hoover, *D. bella* Hoover, *D. immaculata* Munz & Johnston, and *D. mirabilis* J. T. Howell, all of which had been published after the preparation of Jepson's treatment.

The present monograph recognizes 13 species in the genus, all of which occur in California and 6 of which are apparently endemic to that state. The range of the genus as a whole is from southwestern Saskatchewan to west-central Washington, south to central Utah, western Nevada, and southern California, with a single species common to California and Chile. Specific limits as interpreted by the present writer agree fairly well with those of Jepson and Hoover; the principal exceptions are noted in the text below.

Morphological specialization in *Downingia* is considerable. Evidence from species of other genera of Lobelioideae, native to ancient or long-isolated areas like the West Indies, indicates that the method of dehiscence of the capsule is an advanced one for the family. That the genus *Downingia* is in a state of flux, from the point of view of evolution, is indicated by the presence of both unilocular and bilocular ovaries in the same genus. Other non-primitive characters of the genus are the annual duration of all the species, the reduced foliage leaves and the assumption of much of the photosynthetic activity by the bracts, the sessile ovary, and the lack of bracteoles of the pedicel. As noted above, the corolla in many of the species is highly evolved, both in color-pattern and in conformation. The seeds of *Downingia* are unique in being fusiform and apiculate; the seeds of many of the supposedly primitive members of the subfamily Lobelioideae are variously sculptured and pitted, and vary from globose to bluntly ellipsoid. Additional evidence of a recent development of the genus is fur-

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[2] Revision of the California species of the genus *Downingia* Torr. Madroño **1**: 98–102. 1922.

[3] A Manual of the Flowering Plants of California, Berkeley, 1923–1925.

[4] Leafl. West. Bot. **2**: 33–35. Au 1937.

nished by geographical distribution of some of the species, which are wholly confined to the great interior valley of California; this region has suffered submergence relatively recently, geologically speaking, so that the components of its flora must be recent introductions or recent developments. Such a species as *Downingia ornatissima*, which is seemingly wholly confined to the Great Valley, with no very evident connections inside the genus, and with a highly evolved corolla as well (even for *Downingia*, where such a corolla is the general rule), is apparently of relatively modern origin.

The corolla of *Downingia* resembles, in essentials, that of the other genera of the Lobelioideae. In certain species the corolla is almost indistinguishable from that of *Porterella carnosula* (which, indeed, is apparently identical with *Downingia* in vegetative and other characters except for its pedicellate, apically dehiscent capsule). So far as can be ascertained at the present time, the genus *Downingia* may be assumed to have arisen from an ancestor very similar to or identical with that of *Porterella*. *Porterella* in its turn has apparently been derived from a "*Laurentia*"-like ancestor, a complex which may have contributed to some of the small blue-flowered species which we now divide among several genera, including *Diastatea*, "*Laurentia*" (*Lobelia*, sect. *Isotoma*), and *Lobelia*.

The changes brought about by the evolutionary process are assumed to be roughly as follows:

1. Assumption of a semi-aquatic habitat.
2. Assumption of an annual duration by all species.
3. Reduction of vegetative (foliar) tissue to a minimum.
4. Disappearance of pedicel and accompanying bracteoles.
5. Lengthening of the ovary and change from apical to lateral dehiscence.
6. Development of fusiform, apiculate seeds.

Subsequent changes in certain of the species are thought to be as follows:

7. Development of a unilocular ovary through abortion.
8. Development of highly specialized patterns of color and conformation in the corolla.

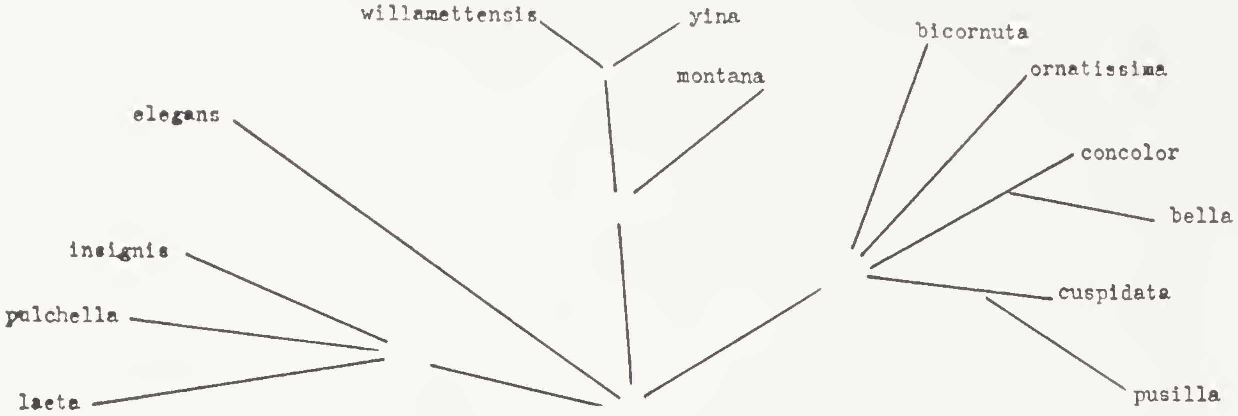
The process outlined above may, on the other hand, be far too simple. The most important single bit of evidence upon which the above assumptions are based is the strong resemblance between *Downingia* and *Porterella*, added to the technical similarities between *Porterella* and *Lobelia*, sect. *Isotoma*. Such resemblances, while highly useful to the taxonomist, must not to be leaned upon too heavily. The transition from apical to lateral dehiscence of the capsule appears in this case to be a considerable one. The valves in *Downingia* vary from 3 to 5 in number, while in the genera with apical dehiscence they are almost invariably two. Furthermore, the character of lateral dehiscence of the capsule is not peculiar to *Downingia*, but is shared with the monotypic genus *Cyphocarpus*, which is a Chilean endemic, and with certain Australian species now referred to *Lobelia*. *Cyphocarpus* is peculiar among plants of campanulaceous affinities in having a truly lobeliaceous corolla, a capsule essentially like that of *Downingia*, but stamens entirely free from each other. It has been thrown, for lack of a better place, into the "Cyphiaceae" by most authors. Its presence in Chile, along with that of a true species of *Downingia*, may be suggestive of some previously unsuspected connection between the two genera. The single Chilean species of *Downingia*, *D. pusilla*, is but one member of the puzzling group of species common to temperate North America and temperate South America; the presence of representatives of otherwise strictly North American genera in southern South America is unexplained as yet, although a widely recognized phenomenon. It is indeed possible that *Downingia* has developed from some ancestral type, quite unlike *Lobelia*, from which ancestor cyphioid genera like *Cyphocarpus* may have come as well.

Whatever the source of the immediate forerunner of the modern genus *Downingia*, the putative characteristics of such a primitive *Downingia* are as follows:

1. A bilocular capsule with tough walls, these tardily dehiscent even at maturity.
2. A corolla very like that of *Downingia montana*, with relatively long and slender tube, reflexed lower lip and pronounced inequality between the lobes of the upper and lower lips. This corolla is assumed to have been almost without the peculiar folds and protuberances so noticeable in some of the present species. The purple coloration at the base of the lower lip is assumed to be a primitive character in the genus, since it is persistent in most of the species.
3. Seeds untwisted, with faint lines.

A plant like that described above appears to be most closely akin to the genus *Lobelia*, and presumably subsequent evolution of *Downingia* has been away from this type. A few species have developed the unilocular condition, while others have lost the purple coloration of the corolla-lip, and have developed peculiar features of the corolla not found elsewhere. The capsule in some species has apparently become progressively more delicate and hyaline divisions have been developed between the valves, the valves then separating at maturity. In a few species the upper lobes of the corolla have become almost as large as the lower. Additional changes are found in the seeds, which in most species have lost the surface markings and become perfectly smooth and shining; in two species the seeds are characteristically twisted, with the surface markings oblique; this is apparently an evolutionary advance.

The accompanying scheme shows graphically the supposed interrelationships of the species.



METHODS

The conclusions reached by the writer in the present paper are based upon herbarium study of approximately 1500 specimens of *Downingia*, comprising roughly 700 different collections. A record was kept for each specimen examined, the following data being recorded:

Height of plant (range of variation if possible).
Length of inflorescence, measured from lowest flower-bract to top of plant.
Number of flowers (range of variation, if possible).
Size of leaves (if present).
Presence and extent of pubescence.
Size of flower-bracts (length, and breadth at widest part).
Diameter and length of mature capsule, if available.
Character of capsule-wall (tough, fragile with hyaline divisions, etc.).
Length of calyx-lobes (including range of variation).
Length of corolla when straightened out (often estimated, owing to the imperfect preservation of the corolla when pressed).
Dimensions of corolla-lobes.
Length of corolla-tube, measured (1) from summit of hypanthium to the lowest point of the lateral sinus and (2) from summit of hypanthium to lowest point of dorsal sinus.
Length of the filament-tube, measured from the summit of the corolla-tube to the base of the anther-tube.
Length of the anther-tube.
Additional features have been noted for certain species, as, for example, the length of the twisted appendage of the anther-tube in *D. bicornuta*.

It was not practicable to secure all the above data for every specimen examined; a plant with immature fruits, for example, furnishes no information about the capsule or the seeds. A very old fruiting specimen may be wholly without remains of the corolla; again, a scanty herbarium specimen may bear so few flowers that it is difficult to make dissections without damaging the specimen. As in all the members of the Lobelioideae, however, pressed specimens of *Downingia* usually have all the above parts well-preserved except the corolla-lobes. In almost any specimen, no matter how poorly prepared, it is possible to measure the corolla-tube, the filament-tube, and the anther-tube with very little error. The corolla-lobes, on the other hand, are not available for study on more than about 25 per cent of the flowers.

The measurements given below, in the descriptions of the several species, are derived from those obtained as described above. Where a measurement is given as "(2.5) 4.0—6.0 (7.5)" it indicates that the principal range of variation is from 4 to 6, with rather an abrupt change of frequency of occurrence at those points, but with occasional extreme individuals varying as far as 2.5 or 7.5. The stated limits of variation of each character are derived from the measurements of roughly 90 per cent of the whole number of specimens examined, with the exception of the corolla-lobes, as stated above, the capsule, which is present in roughly half the plants seen, and the leaves, which are often absent at flowering time.

The specimens were examined with the aid of a binocular dissecting microscope, with available magnification of 7, 15, and 20 diameters.

Examination of any series of measurements similar to the above usually shows, sometimes in very startling fashion, simple and positive ways of separating species which have previously been confused. It is, or should be, axiomatic that while any two unrelated species may appear to be alike in any single character, the probability of such similarity decreases very rapidly when one increases the number of characters under consideration. To state this simply in another way, we may assume that any two species, if actually distinct, will differ from each other not in a single character, but in many characters, except in the relatively rare cases where the difference between species lies in a single gene. We may, accordingly, expect to find certain sets of characters, even in related species, where there is no overlapping of measurements and little possibility of confusion of different species.

The large-flowered species, *Downingia insignis* Greene, may be used as a case in point. The flowers are superficially very similar to those of *D. elegans*, both species having a long-exserted and strongly recurved anther-tube and a broad campanulate corolla-tube without a reflexed lower lip. On the basis of this superficial similarity, *D. insignis* has been merged with *D. elegans* by almost all Californian botanists. When the measurements of all the supposed *D. elegans* are plotted graphically some discrepancies are at once apparent. The curve for length of corolla-tube, for example, is plainly bimodal, with one region of greatest frequency between 3.5 and

5.0 mm., and a second between 2.0 and 3.2 mm. When all the specimens having the longer corolla-tube are segregated from the others, they are found to constitute a perfectly distinct group, differing from *Downingia elegans* in geographical range, time of flowering, number of loculi in the ovary and method of placentation, size and toughness of capsule, shape and surface-markings of anthers, color-pattern of corolla, and general aspect of plant-body. The single character of length of corolla-tube having served as a clue to the identity of *D. insignis*, the species was then easily shown to be abundantly distinct.

The above arguments may be taken to apply equally well to qualitative data as to quantitative. In certain groups of plants it is often impossible to obtain enough material of flowers and fruits to enable the taxonomist to carry out a program like that outlined above. When abundant flowering and fruiting material is available, however, such a course seems to be the logical one. The principal difficulty is the determination of the most dependable characters in a given group; that is, the characters with a relatively small range of variation. In the Campanulaceae, for example, little importance may be attached to the size of the plant itself; *Specularia perfoliata* or *Lobelia inflata* may produce perfect flowers and fruit when growing under adverse conditions so that the plants are not more than one or two centimeters in height, while the same species under favorable conditions may attain many times this height. As in most other plant-families, the principal diagnostic characters of the Campanulaceae are to be found in the flowers and fruits, but some characters of flower and fruit are much more dependable than others. In general too much stress should not be placed upon the size and shape of the corolla-lobes, as these appear to vary considerably with differences in habitat of the plant. Length of the corolla-tube, at least in the Lobelioideae, appears to vary within quite definite limits, as does that of the filament-tube and that of the anther-tube.

DELIMITATION OF SPECIES

Specific limits, according to the writer's concept, are determined through consideration of the following:

1. *Morphology.* As has been stated above, each true species may be expected to differ from all others by several or many characters; the apparent absence of such distinctive features is often due to inadequate examination of the available material. Logically the writer would consider a difference of but few genetic characters sufficient to establish the identity of a species. In practice, however, such a case is rarely found, or, if present, usually goes undetected. Ordinarily, in nature, a species may be defined as that population which, while perhaps indistinguishable from other populations

in many of its features, differs significantly from them, without intermediate states, in several ways.

Subspecific limits are determined in a similar fashion. The terms employed here, namely "variety" and "form," are used as follows:

A variety is defined as that population within a species which differs in one or more ways from the remainder of the species, the differences being more or less strongly linked with differences in geographical distribution. The writer has never studied a variety which was not partially segregated geographically from the other varieties of the species. A variety is connected by intermediates, these usually numerous, to the other variety or varieties, and their ranges are ordinarily adjoining or overlapping.

A form is defined as a variant differing from the rest of the species by (usually) a single trivial character. A form is understood to be without geographical significance.

2. *Areal distribution.* Wholly disjunct ranges of two supposed entities, while strongly indicative of specific differences between the two, are nevertheless not conclusive, and evidence from distribution must be used in conjunction with that from morphology.

SYSTEMATIC TREATMENT

DOWNINGIA Torrey, Pacific Rail. Rep. **4**^{5}**:** 116. 1856, nomen conservandum.

Clintonia Dougl., ex Lindl., Bot. Reg. **15:** t.1241. 1829, non *Clintonia* Raf., 1818.

Bolelia Raf., Atl. Jour. 120. 1832.

Gynampsis Raf., Herb. Raf. 48. 1833; Fl. Tellur. **3:** 5. 1837.

Wittia Kunth, Abh. Akad. Berlin **1848:** 32. 1850.

Soft-stemmed annual herbs, simple or somewhat branched, erect or decumbent, sometimes rooting at the lower nodes, often corky-parenchymatous below. Vegetative parts wholly glabrous, or rarely the upper part of the stem or the calyx-lobes scabrous-ciliate; ovary and capsule often minutely scabrous. Leaves cauline, numerous, much smaller than the flower-bracts, soon deciduous and often not functional at flowering time, lanceolate to subulate or the uppermost broader, sessile, entire or rarely with a few minute teeth, the upper usually obtuse, the lower acute to acuminate or awn-pointed.

Inflorescence a simple raceme, the terminal flowers often aborting and overtopped by the earlier developing ones. Flowers perfect, 5-merous (except for the gynoecium, in which the placentae are 2, the loculi one or 2 and the valves 3–5), sessile in the axils of foliaceous bracts but appearing long-stalked because of the great elongation of the ovary. Flowers inverted in anthesis by the twisting of the capsule, the (apparently) lower lip of the corolla being morphologically the upper one, and the (apparently) upper lip being actually the lower. Corolla blue, occasionally varying to pink or white, usually with a symmetrical white or yellow blotch on the lower lip. Corolla-tube entire, neither fenestrate nor cleft to the base between the two smaller corolla-lobes. Limb more or less strongly bilabiate, the 2 lobes of the one lip (the "upper") mostly smaller and narrower than the 3 prominently fused lobes of the other; lower lip often furnished with folds and ridges or nipples at the basal angle.

Stamens syngenesious and monadelphous, with the general characters of the subfamily. Two smaller anthers each with a terminal tuft of bristles and usually with a terminal hornlike process as well. Ovary wholly inferior, topped by the free calyx-lobes. Calyx lobes normally entire except for a minute tooth on each edge near base; three upper lobes (those alternating with the two narrower lobes of the corolla) usually longer than the other two. Ovary linear to fusiform, 10—75 times as long as wide when mature, opening elastically by 3—5 longitudinal slits in the wall, the slits extending nearly the entire length of the capsule. Ovary and capsule unilocular, with 2 parietal placentae extending the length of the loculus, or bilocular, with the 2 placentae extending the length of the two faces of the delicate longitudinal central septum. Ovules and seeds many, the mature seeds fusiform, apiculate, light brown with darker tips, smooth and polished or with faint longitudinal cellular lines and but slightly lustrous.

TYPE SPECIES: *Downingia elegans* (Dougl. ex Lindl.) Torr.[5]

The collections in herbaria have been made available to the writer through the generous cooperation of the persons in charge. It is a pleasure to acknowledge the kindness of these botanical friends, without whose aid the completion of this study would have been impossible. In citing specimens from the several herbaria, the following abbreviations are used: The Academy of Natural Sciences of Philadelphia (ANS); the California Academy of Sciences (CalAc); Catholic University of America (Cath); Herbarium of E. L. Greene, University of Notre Dame (ELG); Field Museum of Natural History (F); Forest Service, United States Department of Agriculture (FS); Gray Herbarium, Harvard University (G); University of Idaho, Pocatello (Id); Montana State University (Mont); The National Arboretum, Washington, D. C. (USNA); New York Botanical Garden (NB); National Museum of Canada (O); University of Oregon (Ore); Pomona College (P); Rocky Mountain Herbarium, University of Wyoming (R); Stanford University (S); University of California at Berkeley (UC); United States National Herbarium (US); Willamette University (WU).

In the following discussion, certain special terms are used as follows:

Lower lip: The three-lobed lip of the corolla, actually originating next to the inflorescence-axis but twisted away from the axis in anthesis so that the rest of the corolla is between it and the stem.

Upper lip: The two-lobed lip of the corolla, actually the lower or outer

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[5] Some authors have regarded *Downingia pulchella* as the type species of the genus, but such a course appears illogical. Torrey proposed *Downingia* as a name to replace the illegitimate *Clintonia* of Lindley, and at the same time (1856) transferred *Clintonia pulchella* to *Downingia*. *Clintonia elegans* was not transferred to *Downingia* until 1874, but it was the original species of Lindley's genus *Clintonia*, antedating *C. pulchella* by 7 years, and must therefore be regarded as the type species of *Downingia*.

lip but through inversion of the flower becoming apparently the upper or inner one.

Filament-tube: The united filaments, measured from the summit of the ovary (the base of the calyx-lobes) to the base of the anther-tube.

Corolla: Measurements of corolla apply to length from base (at summit of ovary) to tip of the longest lobes.

Corolla-tube: the sympetalous part of the corolla, its length measured either to the *lateral sinuses* (from the summit of the ovary to the deepest point of the sinus between the upper and lower lips) or to the *dorsal sinus* (from the summit of the ovary to the deepest point of the sinus between the two narrow lobes of the corolla, that is, those of the upper lip).

ANALYTICAL KEY TO THE SPECIES

1. Corolla 2.0—7.0 mm. long, not at all or scarcely exceeding the calyx-lobes; lower lip ascending, never sharply reflexed; filament-tube 1.0—2.8 mm. long; anther-tube not incurved, its long axis nearly or quite parallel with that of the filament-tube (see figures 7–9, p. 17) 2

  2. Corolla 2.0—4.0 mm. long; filament-tube 1.0—1.8 mm. long; anther-tube 0.6—1.1 mm. long; seeds appearing as if twisted, the very fine cellular lines of the surface running obliquely to the long axis of the seed, at least in part . . . . *D. pusilla* (p. 35)

  2. Corolla 4.0—7.0 mm. long; filament-tube 1.8—2.8 mm. long; anther-tube 1.3—2.2 mm. long; seeds not appearing twisted . . . . *D. laeta* (p. 43)

1. Corolla 5.0—20.0 mm. long, usually much exceeding the calyx-lobes; lower lip of corolla sharply reflexed or the anther-tube sharply incurved and standing almost at right angles to the filament tube 3

  3. Anther tube strongly incurved, usually standing almost at right angles to the filament tube; lower lip of corolla not sharply reflexed nor forming a sharp angle with the corolla-tube; corolla-tube broadly funnel-form or campanulate, the lateral sinuses conspicuously deeper than the dorsal one so that the two upper corolla-lobes form a distinct cleft upper lip (see figures 1, 2) 4

    4. Ovary and capsule bilocular, the ovules attached to the two faces of a longitudinal septum;[6] anther-tube relatively short and thick, 2.4—3.5 mm. long, 1.0—1.3 mm. in diameter, nearly uniformly dirty-white in color; anthers minutely granular-roughened over the whole surface; flowering season from March to mid-June . . *D. insignis* (p. 40)

    4. Ovary and capsule unilocular, the ovules attached to the ovary wall along two longitudinal lines;[6] anther-tube relatively slender, 2.0—4.0 mm. long, 0.6—1.0 mm. in diameter, pale bluish-gray (when dry) with pale gray or white connectives forming longitudinal stripes; anthers smooth and glabrous or sparsely pilose, never granular-roughened, flowering season from June to September . . . . *D. elegans* (p. 50)

  3. Anther-tube not at all or very slightly incurved; lower lip of corolla reflexed, forming a sharp angle with the corolla-tube (see figures 3, 11) 5

    5. Pair of bristles at apex of anther-tube usually tightly twisted together, forming an appendage 0.6—2.7 mm. in length; corolla-tube prominently bearded within on lower side; base of lower lip with dark purple nipple-like projections (figures 4–6) . . . . *D. bicornuta* (p. 27)

    5. Pair of bristles at apex of anther-tube, if present, never twisted together; corolla-tube glabrous within or, in *D. ornatissima*, sparsely pilose; base of lower lip without purple

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[6] This is readily discernible, even in immature fruits, if the calyx and ovary-wall be slit longitudinally by the point of a needle, under a dissecting lens.

nipple-like projections.. 6

6. Anther-tube 2.6—3.5 mm. long, rarely less, usually gradually narrowed and pointed at tip; filament-tube exceeding the corolla-tube so that the anther-tube is prominently exserted (filament-tube usually 3.0—4.5 mm. long, mostly 1.5—2.0 times the length of the corolla-tube measured at the lateral sinuses); lower lip of corolla with three purple spots at base (figure 10)............................*D. pulchella* (p. 37)

6. Anther-tube 1.4—2.5 (rarely 3.0) mm. long, cylindric, the tip blunt or rounded, if pointed very abruptly so; filament-tube about equalling or somewhat exceeding the corolla-tube, never more than 1.5 times as long as the corolla tube measured at the lateral sinuses...7

  7. Dorsal sinus of the corolla produced backward and outward into a short hornlike process with upcurved tip (this may be small or absent in individual plants); corolla-tube sparsely pilose within; anther-tube wholly exserted, often for a distance of 1.0—2.0 mm., the filament-tube plainly exceeding the corolla-tube as measured on dorsal side (figure 3)..............................*D. ornatissima* (p. 22)

  7. Dorsal sinus of the corolla without projecting fold or horn; corolla glabrous within; base of the anther-tube normally included, the filament-tube equalling or shorter than the corolla-tube measured on dorsal side..............................8

    8. Ovary and capsule bilocular, the ovules attached to the two faces of a longitudinal septum...9

      9. Seeds not appearing as if twisted, the markings, if any, paralleling the long axis of the seed; lower lip of corolla with one or more purple spots at base......10

        10. Two upper corolla-lobes minutely ciliate-scabrous on margins near tip (this plainly visible when magnified about 15×); lower lip of corolla with large purple spot at base, the purple color covering the low ridges at basal angle of lip (figures 12, 13).............................*D. concolor* (p. 18)

        10. Two upper corolla-lobes smooth on margins; corolla with three or two purple spots at base of lower lip (at mouth of tube).............*D. bella* (p. 21)

      9. Seeds appearing as if twisted, the very fine cellular coat marked by minute lines running obliquely to the long axis of the seed; base of lower lip of corolla yellow, without purple areas (figure 16)...............*D. cuspidata* (p. 30)

    8. Ovary and capsule unilocular, the ovules attached to the ovary wall along two longitudinal lines...11

      11. Three larger anthers usually abundantly pilose near tip, with an additional tuft of minute bristles at the extreme tip; seeds dull or scarcely lustrous, with faint but plainly visible longitudinal lines (magnification ca. 15×); lower lip of corolla with three purple grooves alternating with three purple ridges at base; range from Shasta County, California, south along the Sierra Nevada to Tuolumne County (figures 11, 15)................*D. montana* (p. 45)

      11. Three larger anthers glabrous or sparsely pilose near tip, the bristle-like tufts at the extreme tips usually reduced to minute serrulations; seeds smooth, shining, with no lines visible on the surface (magnification 15×); range from Humboldt County, California, north to Washington..............12

        12. Valves of the capsule separated by hyaline lines extending the length of the capsule, these visible as impressed lines even before maturity; mature capsule terete, linear or fusiform, broadest about the middle, plants 10 cm. high or less, diffusely branched from the base; range from northern Siskiyou County, California, to Klamath County, Oregon.......*D. yina* (p. 47)

        12. Valves of the capsule usually invisible before splitting, with no impressed lines nor scarious divisions on calyx-tube; mature capsule subulate, broadest near base; plants up to 35 cm. high, usually erect; range from Humboldt County, California, north to Washington, mostly west of the Cascade Ranges...................................*D. willamettensis* (p. 48)

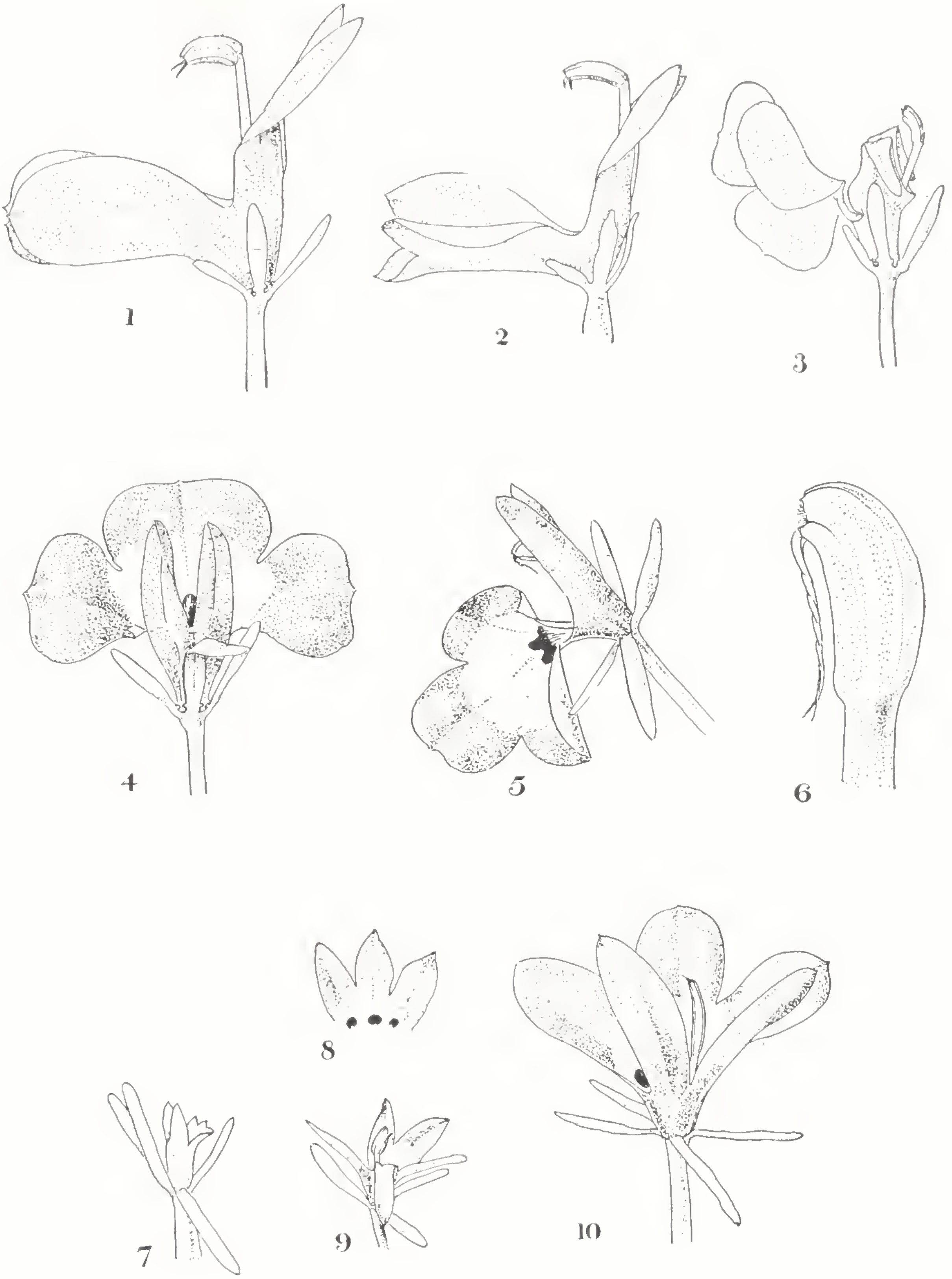
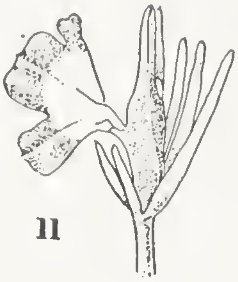


FIG. 1. Lateral view of flower of *Downingia insignis*, ×2.5 (CalAc 174146). FIG. 2. Lateral view of flower of *Downingia elegans* var. *elegans*, ×2.5 (*Bracelin 695*). FIG. 3. Lateral view of flower of *Downingia ornatissima* var. *ornatissima*, ×2.5 (*Eastwood 10185*).

FIG. 4. Dorsal view of flower of *Downingia bicornuta* var. *bicornuta*, ×2.5 (*Hoover 1099*). FIG. 5. Lateral view of flower of *Downingia bicornuta*, ×2.5 (*Stanford 937*). FIG. 6. Lateral view of anther-tube of *Downingia bicornuta* var. *picta*, ×12.5 (*Hoover 1083*).

FIG. 7. Lateral view of flower of *Downingia pusilla*, ×2.5 (*Heller & Brown 5362*). FIG. 8. Portion of lower lip of corolla of *Downingia laeta*, ×2.5. FIG. 9. Lateral view of flower of *Downingia laeta*, ×2.5 (*M. E. Jones*, June 24, 1897; P). FIG. 10. Dorso-lateral view of flower of *Downingia pulchella*, ×2.5 (*Jepson*, June 1896; G).



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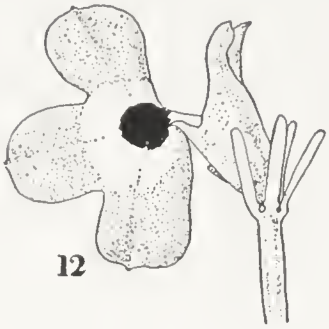

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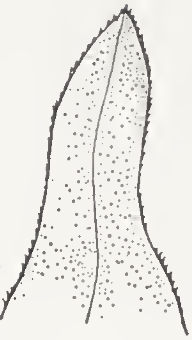

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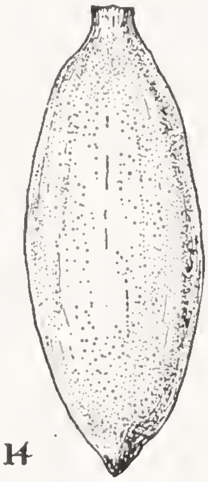

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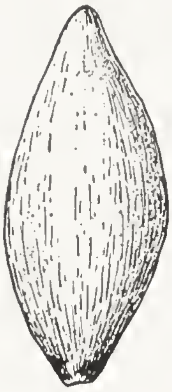

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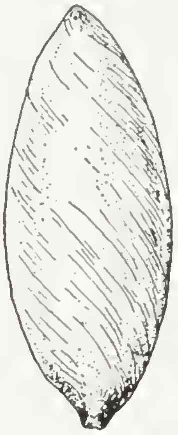

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Fig. 11. Lateral view of flower of *Downingia montana*, ×2.5 (*Hoover 1203*). Fig. 12. Lateral view of flower of *Downingia concolor* var. *tricolor* ×2.5 (*Heller & Brown 5631*). Fig. 13. Tip of upper lobe of corolla of *Downingia concolor*, ×10.

Figs. 14–16. Seeds of Downingia, ×50. Fig. 14. *Downingia elegans*. Fig. 15. *Downingia montana*. Fig. 16. *Downingia cuspidata*. No attempt is made to indicate color values, as seeds taken from dried material vary considerably in color. The color range is from a very dark brown to a light amber; the entire range may be seen in specimens of the same species. The reasons for the differences in pigmentation are not clear; apparently the stage of maturity of the seed is an important factor but not the only one.

The seed shown in figure 14 is the type found in most of the species. The surface is somewhat lustrous and practically unmarked. The body of the seed is terete, or very slightly angled; the ends are slightly constricted and darker in color than the body. The seed shown in figure 15 is very similar to that of figure 14 but the surface cells form a more distinct pattern which shows up as a series of faint but evident longitudinal lines. This pattern is best seen in *D. montana*, but a similar and less distinct pattern may sometimes be seen in the other species. The type of seed shown in figure 16 is peculiar to *D. cuspidata* and *D. pusilla*.

Thanks are due to Mr. B. Y. Morrison, of the Division of Plant Exploration and Introduction, who made the seed drawings reproduced above.

1. Downingia concolor Greene, Bull. Calif. Acad. **2**: 153. 1886.

Plants few—20 (33) cm. high, glabrous except for the hypanthium, which is mostly somewhat scabrous but sometimes glabrous. Leaves 0.4—2.0 mm. wide by 5—18 mm. long. Inflorescence few—15 cm. long, loosely few—15-flowered. Flower-bracts elliptic to ovate, usually obtuse or at least blunt-tipped, 1.0—3.0 (4.0) mm. wide by 5—16 mm. long, usually 3—6 (10) times as long as wide.

Ovary linear, in fruit unchanged in shape or becoming narrowly fusiform (rarely somewhat subulate); mature capsule 0.8—1.5 (2.0) mm. in diameter by (12) 30—50 (62) mm. long. Calyx-lobes elliptic to linear or oblanceolate, obtuse or subacute, ascending or rotately spreading, subequal or the two lower ones distinctly shorter, 3—8 mm. long.

Corolla 7—13 mm. long, glabrous except for the two upper lobes, which are ciliate-scabrous on the margins near tips and sometimes on the inner surface near the tips. Color blue (or "deep blue"), the lower lip with a quadrate or two-lobed purple or red-purple ("velvety purple" according to Jepson) spot at the base of the central white area; the white may be much reduced or lacking, leaving the whole lip blue except for the purple spot at base. Base of the lower lip with two low ridges or nipple-like processes arising in the purple spot.

Corolla-tube (2.5) 3.0—4.0 (5.5) mm. long, narrowly funnel-shaped ("turbinate" according to Greene), the lateral sinuses usually cut well below the plane of the lower lip (sometimes as much as 1 mm.); lateral sinuses about as deep as or slightly deeper than the dorsal one; corolla-tube measured to dorsal sinus 3.0—4.5 (5.5) mm. long. Two upper corolla-lobes lanceolate or shortly ovate, mostly recurved and often appressed to the corolla-tube but sometimes erect or only slightly recurved; tip acute; lobes mostly 0.8—1.2 mm. wide by (2.5) 3.5—5.0 mm. long. Lobes of the lower lip rounded to truncate, oblong to obovate, usually mucronate.

Filament-tube (2.0) 2.5—4.0 (5.0) mm. long, glabrous, the filaments united their whole length or nearly so; base of anther-tube usually covered by dorsal side of corolla-tube (whole anther-tube sometimes included); anther-tube 1.8–2.3 (2.6) mm. long, the anthers glabrous or somewhat pubescent on the backs; all anthers minutely tufted at tips, the two shorter ones prominently so and each bearing a short hornlike process as well.

Seeds not twisted, the fine cellular markings running longitudinally. Placentae axile.

KEY TO THE VARIETIES

1. Mature capsule tough, firm-papery, tardily dehiscent, lacking hyaline divisions between the valves, mostly 30—50 mm. long; range from Lake County to Monterey County, California . . . . var. *tricolor*

1. Mature capsule soon dehiscent, the valves separated by delicate hyaline lines of tissue; capsule mostly 12—25 mm. long; known only from vicinity of Cuyamaca Lake, San Diego County, California . . . . var. *brevior*

1a. DOWNINGIA CONCOLOR var. TRICOLOR (Greene) Jepson, Fl. W. Mid. Calif. ed. 2. 402. 1911. *D. concolor* Greene, l.c. *Type locality*: "Wheat field near the village of Suisun" (Solano County, California). TYPE: *E. L. Greene*, May 2, 1886, No. 16108 of the Greene Herbarium.

D. tricolor Greene, Pittonia **2**: 79. 1890. *Type locality*: "Fields of the lower Sacramento Valley near Elmira." TYPE: "Near Elmira," *E. L. Greene*, May 1890, No. 16111 of the Greene Herbarium.

Bolelia concolor Greene, Pittonia **2**: 127. 1890.

B. tricolor Greene, l.c.

B. concolor var. *tricolor* Jepson, Fl. W. Mid. Cal. ed. 1, 481. 1901.

Vernal pools, mud-flats, and margins of ponds; low elevations in the coastal regions of California from Lake County to Monterey County. Flower and fruit from April 1 to July 15; most collections have been made in May.

Specimens examined: CALIFORNIA: Near San Francisco, *Dr. A. Kellogg* in 1866 (US); Sacramento Valley, *E. L. Greene*, May 1890 (S,UC); road to Mt. Atlas, Napa Valley, *Belle R. Jackson*, May 29, 1938 (CalAc); without loc., *H. N. Bolander 3985* (G). LAKE: Near Lakeport, *C. F. Baker 3057* (ELG, F, G, NB, P, R, UC, US); Kelseyville, *M. S. Baker 5917* (CalAc), *5918* (UC), *7508* (CalAc); 3 miles n. of Middletown, *C. B. Wolf 1911* (S); 5 miles n.e. of Middletown, *L. R. Abrams 12314* (S); n. of Middletown, *Eastwood and Howell 5547* (CalAc). MONTEREY: Priest Valley, *A. Eastwood*, May 13, 1893 (CalAc); near Santa Rita, *E. K. Abbott*, May 1889 (CalAc). NAPA: Without loc., *Belle R. Jackson*, May 10, 1923 (CalAc). SAN BENITO: 2 miles n.e. of Hollister, *R. F. Hoover 3487* (UC). SANTA CLARA: Morgan Hill, *M. S. Clemens*, April 1921 (NB); *J. T. Howell 4750* (CalAc); between Gilroy and Morgan Hill, *L. R. Abrams 5664* (S); between Morgan Hill and San Martin, *R. Bacigalupi*, May 12, 1923 (S); near Gilroy, *M. E. Lang*, 5/6/22 (S); Gilroy, *J. T. Howell 5190* (CalAc, Cath, P); Mayfield, *S. H. Burnham*, May 22, 1895 (G); *W. R. Dudley*, May 2, 1893 (S) and May 3, 1896 (S); *L. R. Abrams*, May 1901 (P, S). SOLANO: Elmira, *C. F. Baker 2895* (CalAc, ELG, G, NB, P, R, UC, US); Vanden, *Mrs. Brandegee*, April 1893 (S); Suisun, *E. L. Greene*, May 2, 1886 (CalAc, ELG (TYPE), F, NB, O, UC, US); May 3, 1886 (G); May 1890 (NB, Ore, UC); May 2, 1890 (ELG, UC); May 5, 1890 (NB, US); Suisun, *A. Eastwood 10417* (CalAc); near Suisun, *Heller and Brown 5592* (F, G, NB, P, R, S, US); Elmira, *E. L. Greene*, May 4, 1890 (S); near Elmira, *A. A. Heller 14545* (US). SONOMA: Santa Rosa, *K. Brandegee*, without date (UC); *Heller & Brown 5631* (F, G, P, NB, S, US); *A. Eastwood*, April 24, 1921 (CalAc, G, R); Mark West, *H. N. Bolander 3895* (US); Elverano, *Michener & Bioletti*, May 30, 1892 (NB); Sebastopol, *J. T. Howell 13017* (CalAc); 2 miles n. of Windsor, *Eastwood & Howell 2508* (CalAc); near Windsor, *W. W. Carruth*, June 1901 (CalAc); near Healdsburg, *M. A. King*, May 1897 (UC); "Schellville," *Michener & Bioletti 174*, May 1891 (G); Shellville, *F. T. Bioletti*, May 1892 (ELG, UC); Sonoma, *F. T. Bioletti*, May 1891 (ELG, S, UC); "S(anta) R(osa)—Sebastopol Highway," *M. S. Baker 2161b* (S); "Laguna near Sta. Rosa Creek," *J. M. Bigelow*, May 1, 1854 (NB); without loc., *E. Samuels 140* (US). TULARE: Deer Creek, *J. W. Congdon*, March 1881 (S).

1b. DOWNINGIA CONCOLOR var. **brevior** McVaugh, var. nov. A var. *tricolore* capsula breviore capsula lineis hyalinis dehiscente differt.

Type locality: Cuyamaca Lake, San Diego County, California. TYPE: *L. R. Abrams 3851*, in the herbarium of the New York Botanical Garden.

Muddy places, San Diego County, California. Known surely only from the vicinity of Cuyamaca Lake, at an elevation of about 1400 meters. Collected in flower and fruit from May to July.

Specimens examined: CALIFORNIA—SAN DIEGO: "Cuyamanca," *T. S. Brandegee*, June 3, 1896 (P, UC); Cuyamaca Valley, *S.B. & W.F. Parish 394* (G); Cuyamaca Mt., *S. B. & W. F. Parish*, June 1880 (S); same loc., *S. B. & W. F. Parish 398* (F); Cuyamaca Lake, *T. S. Brandegee*, July 16, 1906 (F, NB); Cuyamaca Lake, *L. R. Abrams 3851* (CalAc, F, G, NB, P, S, UC, US);

Cuyamaca Lake, *P. A. Munz 9785* (G, P, S, UC); Cuyamaca Lake, *M. E. Jones*, June 11, 1932 (UC) and May 30, 1926 (P, S); "in flumen prope San Diego," *M. F. Spencer 1073*, April 16, 1919 (UC); "in pools on the mesas," *M. F. Spencer 1073*, May 25, 1920 (P).

As stated above, this variety has been collected a number of times in the vicinity of Cuyamaca Lake, but no other locality is known to the writer, and Munz[7] gives the single locality "Muddy shores of Cuyamaca Lake." The two Spencer collections just cited may have been collected elsewhere in San Diego County, but their exact origin is unknown.

The differences between var. *brevior* and the more widely distributed var. *tricolor* appear to be slight but constant. Vegetatively the two are indistinguishable, and the flowers of the two appear to be identical. The differences lie in the capsules, which in var. *tricolor* are ordinarily longer than those of var. *brevior* and much tougher when dry; they lack the evident hyaline lines, along which the capsules of var. *brevior* soon open.

2. DOWNINGIA BELLA Hoover, Leafl. West. Bot. **2**: 2. 1937.

Type locality: "Near San Joaquin River southwest of Modesto" (Stanislaus County, California). TYPE: *R. F. Hoover 837*, April 1, 1936, in the herbarium of W. L. Jepson, not seen. Isotypes in the Gray Herbarium and in the herbaria of Stanford University, the University of California, and the California Academy of Sciences.

Plants few—17 cm. high, entirely glabrous or the capsule somewhat scabrous; stems fistulous, according to Hoover. Leaves 1.0—1.5 mm. wide by 5—12 mm. long. Inflorescence 6—8 cm. long, loosely 3—7-flowered. Flower-bracts oblong to elliptic, acute, or obtuse, 1.0—2.5 mm. wide, 7.0—18.0 mm. long, mostly 4—9 times as long as wide.

Ovary linear, in fruit probably more or less unchanged in shape (mature fruit not seen); nearly mature capsule about 1 mm. in diameter by 35—50 mm. in length, the lateral walls tough and tardily dehiscent, the divisions between the valves obscurely or not at all marked. Calyx-lobes linear or elliptic, ascending or rotately spreading, blunt-tipped, (2.0) 3.0—6.0 mm. long.

Corolla 10—12 mm. long, glabrous. Color deep bright blue, the lower lip with "central white area with yellow center" (Hoover, l.c.). Base of lower lip with two yellow ridges or projections, these alternating with three small purple spots or the central purple spot absent. Tube about the same color as the limb, or lighter just below the lower lip.

Corolla-tube 3.0—4.0 mm. long, narrowly funnelform or nearly cylindrical, the lateral sinuses cut about as deeply as the dorsal one and cut slightly below the plane of the lower lip. Two upper lobes lanceolate or nearly ovate, 1.3—2.0 mm. wide, 3.0—4.5 mm. long, acute, erect or somewhat recurved, but parallel with each other and with the corolla-tube, never curving to the side. Lower lip plane or essentially so, the lobes divergent, rounded or truncate, mucronate.

Filament-tube 2.7—3.5 mm. long, glabrous, the filaments united their

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[7] A Manual of Southern California Botany, 503. 1935.

whole length or nearly so; base of anther-tube covered by dorsal side of corolla-tube; anther-tube 1.6—2.4 mm. long.

Mature seeds not seen; markings of seeds longitudinal, the seeds not twisted; placentae axile.

Vernal pools of alkaline plains of the Great Valley of California, from Colusa County to Tulare County. Flower from about March 20 to May 15.

Specimens examined: CALIFORNIA—COLUSA: 4 miles e. of Williams, *R. S. Ferris 499* (NB, S). MERCED: Merced, *J. T. Howell 4168* (CalAc); 6 miles s. of Merced, *R. F. Hoover 953* (CalAc); 2 miles s.e. of Athlone, *R. F. Hoover 1754* (G). STANISLAUS: Near San Joaquin R., s.w. of Modesto, *R. F. Hoover 563* (CalAc); *R. F. Hoover 837* (CalAc, G, S, UC); 10 miles w. of Modesto, *R. F. Hoover 386* (CalAc); *R. F. Hoover 3079* (UC). TULARE: Pixley, *A. Eastwood*, April 3, 1917 (CalAc); 4 miles n. of Visalia, *R. F. Hoover 921* (CalAc, UC); without loc. *T. J. Patterson*, May 28, 1886 (ELG).

The writer has seen but 11 collections of *Downingia bella*, all of which were made when the plants were in flower. In the absence of mature fruit and of more ample collections, it seems unwise to be dogmatic about the status of the plant in question, but it appears to be scarcely specifically distinct from *D. concolor*. In the material examined, the plants of *D. bella* average somewhat smaller than those of *D. concolor*, as do most of the flower-parts. These measurements are hardly significant, however, owing to the small amount of material examined. The only constant differences that the writer has been able to discover lie in the corolla; in *D. bella* the lower lip bears three purple spots instead of the one broad purple blotch of *D. concolor*. In addition, there is apparently no trace of ciliation on the upper corolla-lobes of *D. bella*. Hoover[8] stresses the point that the stem of *D. bella* is "fistulous," while that of *D. concolor* is not. This the writer has been unable to check. As may be seen by reference to the map (map 4), the ranges of the two species do not overlap, so far as is known.

Although the differences between the two plants are very minor ones, lying principally in color-pattern and ciliation of the corolla, the best course for the present seems to be to regard them as distinct species. The writer has seen no intermediates between them, and any change in the status of either may await further field study.

3. DOWNINGIA ORNATISSIMA Greene, Pittonia **2**: 80. 1890.

Plants few—20 (30) cm. high, entirely glabrous except for the hypanthium, which is usually scabrous. Leaves 0.5—2.0 mm. wide by 5.0—12.0 mm. long. Inflorescence few—12 (21) cm. long, loosely few—20-flowered. Flower-bracts lanceolate to elliptic or ovate, 1—4 (6) mm. wide by 6—12 (16) mm. long, usually 3—5 (10) times as long as wide, obtuse or acute.

Ovary linear, unchanged in fruit or becoming narrowly subulate, the ma-

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[8] Leafl. West. Bot. **2**: 33-35. Au 1937.

ture capsule 0.5—1.5 mm. in diameter by 25—65 mm. in length, the lateral walls tough and not easily ruptured even when dry, with no evidence of scarious valves. Calyx-lobes linear to broadly elliptic, widest at or near the middle, all subequal in length or the two lower shorter, rounded to blunt or acute at tip, 1.7—6.0 (9.0) mm. long, erect or somewhat rotately spreading.

Corolla (7.0) 8.0—13.0 mm. long, the tube sparsely pilose within on lower side; corolla glabrous without. Lower lip bright or dark blue to pale lilac or nearly white, with squarish white center bearing two yellow or yellowish-green spots which contract into folds at the angle of the throat. Tube blue or lighter-colored.

Corolla-tube 2.5—4.0 (5.0) mm. long, narrowest at base and gradually wider to the apex, the lateral sinuses cut so deeply that the lower lip often appears hinged; dorsal sinus cut about as deeply as the lateral ones. Cleft (sinus) between the two upper lobes projected backward so as to appear like a short horn with upcurved tip; this horn-like projection may be very small or lacking; similar but smaller projections sometimes occur at the lateral sinuses. Two upper corolla-lobes lanceolate or narrowly triangular, somewhat enlarged at base, 2.5—6.0 mm. long, divergent, with the tip of each curled backward and outward into a ring, horizontally spreading with recurved tips, or ascending and appressed and only very slightly divergent. Lower lip plane or somewhat concave, the folds at base sometimes prominent and nipple-like, the lobes oblong, rounded or truncate, mucronulate.

Filament-tube 3.0—4.5 (6.0) mm. long, the filaments pubescent near base, connate nearly their whole length. Anther-tube 1.7—2.5 mm. long, wholly exserted, the base surpassing the dorsal sinus of the corolla by an appreciable amount, the distance usually 0.5—1.0 mm. (sometimes 2.5 mm.); anther-tube often bent abruptly downward; anthers all white-tufted at tips, the two shorter ones prominently so, each with a sharp horn-like process in addition; anthers glabrous or pubescent on the backs, the pubescence often with bulbous tips.

Seeds not twisted, the very fine lines longitudinal; placentae axile.

KEY TO THE VARIETIES

1. Two upper corolla-lobes glabrous within, divergent, with the tip of each curled outward and backward into a ring or at least strongly recurved . . . . var. *ornatissima*
1. Two upper corolla-lobes minutely pubescent within near tips, divergent . . . . var. *eximia*

3a. DOWNINGIA ORNATISSIMA var. **ornatissima** McVaugh, nom. nov.

D. ornatissima Greene, l.c. *Type locality:* "Fields of the lower Sacramento Valley near Elmira" (Solano County, California). TYPE: "Near Elmira," *E. L. Greene*, May 1890, No. 16100 of the Greene Herbarium.

Bolelia ornatissima Greene, Pittonia **2**: 127. 1890.

Heavy clay soils, vernal pools and desiccating mud-flats, Sacramento Valley, California, south about to Merced County. Collected in flower from April 10 to May 30.

Specimens examined: CALIFORNIA: Knight's Ferry, Stanislaus, *J. M. Bigelow* (Whipple Exp., 1853–1854) (G); Stanislaus River, *J. M. Bigelow* (Whipple Exp., May 8, 1854) (NB); without loc., *J. M. Bigelow* (Whipple Exp., 1853–

1854) (US); without loc., *T. Hartweg 1822* (G, NB). AMADOR: Ione, *H. Edwards*, May 1878 (NB). BUTTE: Without loc., *M. M. Miles* in 1886 (NB); 4 miles e. of Chico, *Heller 13931* (US); near Butte City, *Heller & Brown 5442* (F, G, NB, S, US); 8 miles n. of Oroville, *A. A. Heller 11305* (CalAc, ELG, F, G, NB, S, UC, US); Berry Canon near Clear Creek, *Heller & Brown 5549* (F, G, NB, P, R, S, US); near Clear Creek, *H. E. Brown 188* (F, R, S, US); Butte Creek, *Mrs. R. M. Austin 1905*, Apr. 25, 1897 (NB, US); fields, *Mrs. C. C. Bruce 1905*, May 1898 (NB); Honcut, *L. S. Rose 33188* (CalAc); Durham, *Mrs. J. H. Morrison*, May 1, 1932 (CalAc); "adobe swales and in water," *Mrs. R. M. Austin 66* (UC). CALAVERAS: Near Jenny Lind, *E. E. Stanford 972* (P, S, US). COLUSA: Near Colusa, *A. A. Heller 13540* (F, NB, S, US). CONTRA COSTA: Near Antioch, *Mrs. Curran* in 1886 (ELG); 4 miles s. of Antioch, *Eastwood & Howell 2153* (CalAc). GLENN: Willows, *A. Eastwood 10185* (CalAc, G, US). MARIPOSA: 4.7 miles w.s.w. of Hill's Mine, *C. M. Belshaw 1843* (FS). MERCED: Merced, *A. Eastwood 4399* (CalAc, G, US); 8 miles n.e. of Merced, *J. T. Howell 4201* (CalAc, Cath, F, NB, P, US) and *4214* (CalAc, NB); 2 miles n.e. of Planada, *R. F. Hoover 2304* (UC); 7 miles s.e. of LeGrand, *R. F. Hoover 1084* (S); 3 miles n. of Snelling, *R. F. Hoover 961* (UC). PLACER: Auburn, *Mrs. Ames*, without date (F). SACRAMENTO: Rio Linda, *R. F. Hoover 2206* (UC); 5 miles n.w. of Thornton, *R. F. Hoover 2188* (S). SAN JOAQUIN: 7 miles s.w. of Stone Corral, Jackson Quad., *C. M. Belshaw 1965* (UC); near Lockford, *W. P. Steinbeck*, May 9, 1923 (CalAc.) SOLANO: Vallejo, *E. L. Greene*, May 1874 (NB); near Little Oak, *W. L. Jepson*, May 2–6, 1891 (UC, US); Hartley's, *C. F. Baker 2882* (CalAc, ELG, F, G, NB, O, P, R, UC, US); Vacaville, *C. F. Baker 2917* (ELG, F, G, NB, P, R, UC, US); between Elmira and Cannon, *Mrs. K. Brandegee 174* (F, G, NB, O, Ore, P, R, S, UC, US); Elmira, *C. F. Baker 2901* (ELG, F, G, NB, P, UC, US); near Elmira, *A. A. Heller 14547* (US); near Elmira, *W. L. Jepson*, May 30, 1891 (NB, UC, US); 1 mile n. of Elmira, *J. T. Howell 5206* (CalAc); Elmira, *E. L. Greene*, May, 1890 (ELG, O, UC); near Elmira, *E. L. Greene*, May 2, 1890 (NB) and May 5, 1890 (NB, Ore, US); near Elmira, *E. L. Greene*, May, 1889 (ELG); near Suisun, *E. L. Greene*, May, 1890 (ELG, US); SUTTER; Pleasant Grove, *R. F. Hoover 2221* (UC). TEHAMA: near Vina, *R. F. Hoover 2252* (UC). TUOLUMNE: Without loc., *J. S. Congdon*, without date (NB). YOLO: Near Madison, *Heller & Brown 5418* (F, G, NB, P, R, S, US); "By-Pass," *E. A. Wilkins*, April 28, 1932 (S, UC).

3b. *Downingia ornatissima* var. **eximia** (Hoover) McVaugh, comb. nov.

D. mirabilis J. T. Howell, Leafl. West. Bot. **1**: 221. 1936. *Type locality:* "5 miles northeast of Merced, Merced Co., Calif." TYPE: *J. T. Howell 4200*, April 25, 1929, No. 232457 of the herbarium of the California Academy of Sciences.

D. mirabilis var. *eximia* Hoover, Leafl. West. Bot. **2**: 6. 1937. *Type locality:* "3 miles west of Orange Cove, Fresno Co." (California). TYPE: *R. F. Hoover 1000*, April 28, 1936, in the herbarium of W. L. Jepson, not seen. Isotypes in the herbaria of the California Academy of Sciences, the University of California and Stanford University.

Habitat and flowering season of var. *ornatissima*. Range from Tulare

County, California, northward throughout the San Joaquin Valley and occasionally as far as Butte County.

Specimens examined: CALIFORNIA—CALAVERAS: Near Jenny Lind, *Constance & Morrison 2160* (R); CONTRA COSTA: 4 miles s. of Antioch, *Eastwood & Howell 2153* (F, NB). FRESNO: 3 miles w. of Orange Cove, *R. F. Hoover 1000* (CalAc, S, UC); near Pinedale, road to Friant, *R. F. Hoover 3459* (UC); 5 miles e. of Clovis, *R. F. Hoover 996* (CalAc). MADERA: Califa, *L. S. Rose 32205* (CalAc) and *32206* (Cath); 16 miles n. of Fresno (10 miles s. of Bates), *Keck & Stockwell 3336* (CalAc, S, UC); Berenda, *R. F. Hoover 906* (CalAc); 14 miles n.e. of Madera, *Eastwood & Howell 5341* (CalAc); Chowchilla, *J. T. Howell 13844* (CalAc); Daulton, *R. F. Hoover 3451* (UC); 6 miles e. of Madera, *A. G. Vestal*, April 24, 1927 (S); 6 miles n. of Madera, *L. R. Abrams 11638* (P, S); near Bellevue, *L. Constance 2197* (R). MERCED: 6 miles s.e. of LeGrand, *R. F. Hoover 1081* (CalAc, UC); Ryer, *R. F. Hoover 1074* (UC) and *2091* (G); 5 miles n.e. of Merced, *J. T. Howell 4200* (CalAc, Cath, F, NB, P, UC). SAN JOAQUIN: Peters, *E. E. Stanford 1029* (P); road to Stockton, 7 miles from Escalon, *J. T. Howell 4679* (CalAc, F); French Camp, *J. A. Sanford 155*, in 1890–91 (UC). STANISLAUS: 4 miles s. of Oakdale, *R. F. Hoover 488* (G); Turlock, *F. R. Fosberg*, April 6, 1927 (P); Turlock, *Miss Ellis*, May 1, 1886 (S); Turlock Reservoir, *L. S. Rose 37275* (CalAc, Cath, NB); Warnerville, *R. F. Hoover 1044* (CalAc, UC) and *1999* (UC); Hickman, *L. S. Rose 37271* (CalAc, F, US); 2 miles s. of Hickman, *R. F. Hoover 2085* (G, S, UC); Montpellier, *R. F. Hoover 585* (CalAc). TULARE: 1 mile e. of Orange Cove, *R. F. Hoover 1011* (G, UC); Woodlake, *R. F. Hoover 3481* (UC).

Downingia ornatissima, as here understood, is a distinct species not at all to be confused with any other in the genus. It forms a rather homogeneous unit ranging throughout the Great Valley of California at low altitudes. There is little variation within the species except in details of the conformation of the corolla. Individual plants in all parts of the range occasionally lack the tiny horn-like projection on the corolla-tube, and the two upper corolla-lobes vary in position to a considerable extent. Corolla-color is also variable, ranging from bright or dark blue to pale blue or nearly white. The two varieties proposed in this paper, while quite distinct in their most extreme forms, are scarcely separable in the lower San Joaquin Valley, and so must be regarded as rather formal varieties, and arbitrarily separated as such.

Downingia mirabilis was described by Howell from plants said to have "the upper frontal part of the corolla-tube rounded and dome-like, without that ridge and spur so prominent and distinctive in *D. ornatissima*," and "the folds and horn-like nipples in the angle of the throat . . . outward-curving and very much more elongate" (than in *D. ornatissima*). Examination of the type (*Howell 4200*) shows that while some of the plants have the corolla lacking the "spur," others are perfectly good specimens of *D. ornatissima*, including spur. Some of the corollas have the upper lobes recurved, while in other corollas they appear to have been erect and appressed. In the opinion of the present writer the variations discussed above are not of sufficient magnitude to warrant specific recognition for the plants in which they occur.

In the original description of *D. mirabilis* var. *eximia*, Hoover stated that the name applied solely to the plants with upper corolla-lobes erect and appressed, these having been found in the upper San Joaquin Valley. In establishing the plant of the entire San Joaquin Valley as a variety of *D. ornatissima* it becomes necessary to use Hoover's varietal name, while extending the morphological limits of the group of plants to which it applies.

There appear to be but two significant subspecific groups comprising the single species *D. ornatissima*. The one first described, that which occurs commonly in the Sacramento Valley, has the upper corolla-lobes glabrous within and almost invariably outwardly curled. At the other end of the range of the species, in the upper San Joaquin Valley, the upper corolla-lobes are plainly and often densely white-pubescent within, and, in addition, are more often erect and appressed or simply recurved. In the present treatment, segregation into varieties has depended for the most part upon the single character of the pubescence of the corolla-lobes; not only does the position of the corolla-lobes often become obscured in dried material, but also this character appears to be but slightly correlated with other features. As a result of such arbitrary segregation, a single collection will sometimes contain plants of both varieties; the writer has found this to be true to the greatest degree in collections from Merced and Stanislaus Counties.

Downingia ornatissima is rather difficult to separate from the other species of the genus by means of key-characters, especially when dry, as the flowers are of about the same size as those of several other species and flower-color is an unsatisfactory character for use except in fresh material. It is, however, one of the easiest species to recognize in the herbarium. The corolla-tube is almost invariably sparsely hairy within; the only other species with this feature is *D. bicornuta*, which may be distinguished at once by the twisted appendages at the apex of the anther-tube. *D. ornatissima* is, furthermore, easily recognized by means of the small conical projection at the summit of the corolla-tube; rarely indeed is a collection seen in which this feature is not found in any of the flowers. A third important diagnostic feature is the filament-tube, which is slightly curved backward and plainly longer than the dorsal side of the corolla-tube; such a filament-tube is not found in any species likely to be confused with *D. ornatissima*. Also peculiar to this species are the bulbous-tipped hairs found on the backs of the anthers; these hairs are apparently unique in the genus.

4. DOWNINGIA BICORNUTA A. Gray, Syn. Fl. N. Am. **2**[1] (suppl.): 395. 1886.

Plants few—25 (40) cm. high, entirely glabrous (hypanthium very rarely obscurely scabrous). Leaves 0.4—1.0 (2.0) mm. wide by (3.0) 6.0—15.0 (20.0) mm. long. Inflorescence few—12 (28) cm. long, loosely 1—10- (17-) flowered. Flower-bracts linear to broadly lanceolate, usually 5—10 times as long as wide, 1—3 (4) mm. wide, 5—15 (28) mm. long, obtuse or subacute.

Ovary linear, at maturity becoming linear to narrowly subulate, tapering very gradually from just above the base to the apex. Capsule with lateral walls thin but tough and not easily fractured; valves scarcely apparent even at maturity, or rarely conspicuous. Calyx-lobes linear or narrowly elliptic, rounded at tip or bluntly pointed, widest near the middle, usually plainly of two lengths, (2.5) 3.0—8.0 (13.0) mm. long, often rotate-spreading.

Corolla glabrous without, the tube densely white-bearded within on the lower side. Lower lip deep purplish-blue with a central area of white, yellow or yellowish-green, this central area marked with two yellow or green spots. Base of lower lip dark purple, with two ascending horns or nipples at the inner angle; lateral margins of the lower lip folded into two less prominent nipples, making four in all in a transverse line. Two upper lobes purplish-blue, slightly darker in color than the lower lip.

Corolla-tube broadly funnel-shaped, the lateral sinuses cut so deeply that the lower lip appears hinged; distance from summit of hypanthium to lateral sinuses slightly less than that to dorsal sinus. Two upper lobes ovate or triangular, acute, 1.0—1.3 mm. wide by 4.0—7.0 (8.5) mm. long. Lobes of the lower lip rounded or truncate, mucronulate. Filament-tube (2.3) 3.0—4.0 (4.8) mm. long; anther-tube (1.8) 2.0—2.5 (3.0) mm. long, usually partially included in the corolla-tube and often concealed by the two upper corolla-lobes.

Anthers minutely tufted at tip, smooth or sparsely bristly on the backs; two shorter anthers each with a recurved horn-like process from the apex, the processes tightly twisted together (rarely absent or not twisted).

Seeds not twisted, the markings very faint, longitudinal; placentation axile.

KEY TO THE VARIETIES

1. Twisted bristles at apex of anther-tube 0.6—1.5 mm. in length; corolla-tube (measured at lateral sinuses) 2.5—4.5 mm. long, blue, with purple veins . . . . var. *bicornuta*
1. Twisted bristles at apex of anther-tube 1.6—2.7 mm. in length; corolla-tube 1.5—2.6 mm. long, mostly with brownish-yellow spot on upper side . . . . var. *picta*

4a. DOWNINGIA BICORNUTA var. **bicornuta** McVaugh, nom. nov.

D. bicornuta A. Gray, l.c. *Type locality:* "Northern part of California." TYPE: Chico, Butte County, California, *Mrs. Bidwell* in 1879, in the Gray Herbarium.

Bolelia bicornuta Greene, Pittonia **2**: 127. 1890.

Downingia sikota Applegate, Contr. Dudley Herb. **1**: 97. 1929. *Type locality:* "Swan Lake, Klamath Co., Oregon." TYPE: *E. I. Applegate*, July 24, 1904, No. 163278 of the herbarium of Stanford University. This number

(163278) was cited by Applegate in his original description, where the collector's number was given as 3170. No collector's number appears on the type.

Corolla 9.0—19.0 mm. long, the tube blue, with darker veins, the lower side lighter-colored, with two white or yellow longitudinal spots or streaks. Corolla-tube (2.5) 3.0—4.0 (4.5) mm. long. Mature capsule 1.0—2.0 mm. in diameter by 35—65 (90) mm. long. Two upper corolla-lobes divergent, erect or recurved. Lower lip usually plane or nearly so. Horn-like processes of the apex of the anther-tube 0.6—1.5 mm. long.

Drying soil of vernal pools, muddy soil of roadside pools, low land recently under water, moist depressions in clay soil in fields or in grasslands, wet banks of lakes and ponds. Southeastern Oregon and southwestern Idaho, south to northern and western Nevada, and Nevada and Stanislaus Counties, California. Often occurs at elevations of from 1200 to 1800 meters, and at lower elevations in the Sacramento Valley; rare in the San Joaquin Valley. Collected in flower and fruit from late April to early August.

Specimens examined: CALIFORNIA: Near Summit, *V. Rattan 298*, 1860–67 (US); Slippery Ford to Pyramid Peak, 7000 ft., *W. H. Brewer 2132*, Aug. 20, 1863 (US); "Valley of the Sacramento," *Dr. Stillman*, without date (NB); "collected in Sierra Nevada in 1863 by State Survey," No. 2132 (UC); "Geological Survey of California," *W. H. Brewer* in 1863 (G); "California," *Rev. Mr. Fitch*, in 1850 (NB); "Grove of large trees (Sequoia gigantea)," *J. Torrey 279*, in 1865 (NB). BUTTE: Chico Creek, *A. Gray*, Apr. 28, 1885 (F); near Nelson, *Heller & Brown 5448* (F, G, NB, P, R, S, US); Nelson, *H. F. Copeland 873* (P); Chico, *Bidwell* in 1879 (G, TYPE); Chico, *E. B. Copeland 3176* (ELG, G, NB, P, R, UC, US), *3283* (ELG, P) *3284* (ELG, O, P, S, UC); near Chico, *Edw. Palmer 2083* (NB, P, UC, US); near Chico, *E. L. Greene*, June 1882 (ELG); June 1889 (UC); June 1890 (UC); Chico-Oroville road, *A. A. Heller 13935* (US); 5 miles from Chico on Oroville road, *A. A. Heller 11316* (CalAc, ELG, F, G, NB, S, UC, US); 9 miles north of Chico, *A. A. Heller 14363* (CalAc, Cath, F, G, NB, Ore, P, R, S, UC, US); Butte Creek, *Mrs. R. M. Austin 1905*, April 25, 1897 (NB); Butte, fields, *Mrs. C. C. Bruce 1905*, April 1897 (P); May 1898 (NB); without loc., *M. M. Miles*, in 1886 (NB). COLUSA: Near College City, *Heller & Brown 5434* (F; a single plant on a sheet of *D. pulchella*). LASSEN: 10—15 miles w. of Amedee, *M. E. Jones*, June 24, 1897 (P, S, US); Honeylake Valley, *J. B. Davy 3348* (UC); flat near Eagle Lake, *M. S. Baker*, July 21 (UC); Pine Creek, *M. S. Baker*, July 12 (UC). MODOC: Egg Lake, *M. S. Baker*, June 24, 1893 (UC); Rattlesnake Creek, near Alturas, *E. I. Applegate 3028* (S) NEVADA: Truckee, *J. W. Stacey 4* (CalAc). PLUMAS: Near Vinton, *Heller & Kennedy 8675* (F, G, NB, S, US); near Lassen Buttes, *H. E. Brown 615* (F, NB, R); 4¾ miles s.e. of East Butte, Sierra Co. (Sierraville Quad.), *E. Sawyer 98* (UC). SHASTA: Goose Valley, *A. Eastwood 745* (G, NB, US); *A. Eastwood 978* (CalAc); Burney, *Ellsworth Bettal*, June 12, 1923 (CalAc). SIERRA: Sierra Valley, *J. G. Lemmon*, in June (F). STANISLAUS: Gobin Ranch, 13 miles e. of Waterford, *R. F. Hoover 1099* (CalAc). SUTTER: Edge of tule land, *E. B. Copeland 3285* (G, NB, US). TEHAMA: 10 miles e. of Red Bluff, *D. K. Gillespie 9272* (S).

NEVADA—ELKO: Deeth, *A. A. Heller 10555* (NB; a single plant on a sheet with *D. laeta*). WASHOE: Between Washoe and Franktown, *A. A. Heller 10596* (CalAc, F, G, NB, P, S, UC, US); Washoe, *C. L. Brown*, July 28, 1907 (CalAc); Lake Washoe, west of Carson City, *I. Tidestrom 10454* (Cath); Lake Washoe, *J. Torrey 279*, in 1865 (G, NB, US); "Truckee Meadows near Glendale," *W. W. Bailey 728*, July 1867 (G, NB, US); "5 miles south (=north) of Carson City on the Reno Road, *D. R. Goddard 1040* (UC).

IDAHO—ADA: Owyhee, *M. E. Jones 25531* (P, S).

OREGON: Shirk, *J. B. Leiberg 2583* (F, G, NB, Ore, P, UC, US); "P ranch," *Griffiths & Hunter 312* (NB, US). HARNEY: 1 mile e. of Burns, *J. W. Thompson 11975* (CalAc, G, P, US); Stein's Mt., Blitzen Valley, *P. Train*, without date (NB). KLAMATH: Lone Pine Ranch, Swan Lake, *E. I. Applegate 3171* (S) and *3173* (S); Brookside Ranch, Swan Lake Valley, *E. I. Applegate 3561* (S); Swan Lake Valley, *F. A. Walpole 2230* (US); Barkley Spring, Klamath Lake, *E. I. Applegate 5134* (S); Barkley Spring, *E. I. Applegate 3615* (S); Sprague River, near mouth Whiskey Creek, *E. I. Applegate 5914* (WU). MALHEUR: 1 mile n. of Sheaville, *P. Train*, July 7 (US). LAKE: Guano Ranch, *F. V. Coville 605* (US); near Adel, *M. E. Peck 19469* (WU); near Adel, *R. C. Andrews 500* (Ore). WASCO: The Dalles, *Davidson* (M. E. Jones herb.) (P).

The following specimens of *D. bicornuta* may be cited as intermediate between var. *picta* and var. *bicornuta*:

CALIFORNIA—MERCED: Ryer, *R. F. Hoover 2092* (G, S, UC). The corolla-tube is longer than usual in var. *picta*, and the twisted bristles of the anther-tube are shorter than is usual in this variety. SAN JOAQUIN: Near Stockton, *E. E. Stanford 188* (G, P, S). Corolla like that of typical *D. bicornuta*, but the tube as short in some plants as in var. *picta*, and the twisted bristles short for the variety. SHASTA: Redding, *W. W. Jones 297* (G); corolla and corolla-tube very short for the species, but the twisted bristles less than 1.0 mm. long. STANISLAUS: 4 miles s. of Oakdale, *R. F. Hoover 486* (UC); corolla almost large enough for typical *bicornuta*, but the bristles as much as 1.7 mm. long. TEHAMA: 5 miles s. of Cottonwood, *Eastwood & Howell 1844* (CalAc, P); *L. S. Rose 34244* (Cath, NB). In these collections the corolla-tube is much shorter than is usual in the typical plant.

4b. DOWNINGIA BICORNUTA var. PICTA Hoover, Leafl. West. Bot. **2**: 4. 1937.
Type locality: "7 miles southeast of LeGrand, Merced Co." (California). TYPE: *R. F. Hoover 1083*, May 1, 1936, in the herbarium of W. L. Jepson, not seen. Isotypes in the Gray Herbarium and in the herbaria of the California Academy of Sciences, Stanford University and the University of California.

Flowers and fruit slightly smaller than in var. *bicornuta*. Corolla 7—10 mm. long. Corolla-tube (1.5) 2.0—2.6 mm. long. Mature capsule 0.5—1.5 mm. in diameter by 35—57 mm. long.

Corolla-tube with brownish-yellow spot on upper side; lower lip strongly concave; two upper lobes white or pale blue, often tipped with darker blue, not divergent but directed toward each other so that the tips cross, sharply reflexed and appressed to the corolla-tube. Horn-like processes of the anther-tube 1.6—2.7 mm. long, often longer than the tube itself.

Habitat the same as that of var. *bicornuta*. Ranges through the Sacramento and San Joaquin Valleys, at low elevations, from Shasta County to Fresno County, California. Collected in flower and fruit from April 13 to May 27.

Specimens examined: CALIFORNIA: Mokelumne R., *V. Rattan* in 1884 (G). FRESNO: Near Pinedale, road to Friant, *R. F. Hoover 3460* (UC). MERCED: Merced, *A. Eastwood 4399* (US); Oakdale Rd., near Merced, *J. T. Howell 2* (CalAc); 2 miles n. of Merced, *R. F. Hoover 2104* (G); 7 miles n. of Merced, *R. F. Hoover 2100* (G, UC); 6 miles n. of Merced, *J. T. Howell 4204* (CalAc, Cath, F, NB, P, UC, US); 2 miles n.w. of Merced, *J. T. Howell 4174* (CalAc, F, NB, P, US); 7 miles s.e. of LeGrand, *R. F. Hoover 1083* (CalAc, G, S, UC); 2 miles n.e. of Planada, *R. F. Hoover 2305* (UC); 6 miles s.w. of Hill's Mine, Indian Gulch Road, *H. S. Yates 5087* (UC). SACRAMENTO: Rio Linda, *R. F. Hoover 2200* (UC); Sacramento, *E. Hannibal*, April 28, 1918 (S); East Sacramento, *F. Ramaley 11173* (UC). SAN JOAQUIN: Near Stockton, *E. E. Stanford 937* (G, P, US); near Stockton, *W. P. Steinbeck*, April 1923 (CalAc); 2 miles s.s.w. of Wallace, *R. D. Roseberry 167* (FS); 4 miles s. of Galt, *D. K. and J. W. Gillespie 9234* (S, UC); 3 miles east of Clements, *J. T. Howell 4711* (CalAc, F, P); Linden, *F. W. Gunnison*, May 1896 (UC). SHASTA: Near Redding, *Mrs. C. A. Rose*, May 1930 (CalAc). STANISLAUS: Between Oakdale and Waterford, *C. Dudley* in 1935 (CalAc); Turlock Reservoir, *L. S. Rose 37274* (CalAc). SUTTER: Pleasant Grove, *R. F. Hoover 1142* (G).

The varieties of *Downingia bicornuta* are well marked. Var. *picta* is wholly confined to the Great Valley of California, while all material from the region of the Sierra Nevada and eastward and northward may safely be referred to var. *bicornuta*. The latter extends sparingly into the Sacramento Valley (the type came from Chico, Butte County), and occasional intermediates are found in the region where either variety may be expected to grow. The descriptions of flower-color in *D. bicornuta*, found in the present paper, have been taken in part from Hoover.[9] From his original description and from examination of herbarium material annotated by him, it would appear that the present interpretation of var. *picta* is a somewhat broader one than that originally intended. The present writer has been unable to check flower-color, except in especially well-prepared herbarium specimens; it may well transpire that the brownish-yellow spot on the corolla-tube, a character emphasized by Hoover for var. *picta*, is simply of local occurrence in the San Joaquin Valley. Whether or not this proves to be true, Hoover's name must be taken up for the variety of *D. bicornuta* with short corolla-tube and long twisted bristles.

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[9] New or imperfectly known Californian species of *Downingia*. Leafl. West. Bot. 2: 1–6. Ja 1937.

5. DOWNINGIA CUSPIDATA (Greene) Greene, ex Jepson, Fl. W. Mid. Calif., ed. 2. 403. 1911.

Bolelia cuspidata Greene, Erythea **3**: 101. 1895. *Type locality:* "Grain field west of Yountville, Napa Co., Calif. . . . also in more slender form, with smaller and paler flowers, in Los Guilucos Valley, Sonoma Co., . . . F. T. Bioletti." TYPE: The specimen cited first, that said to have been collected at Yountville, Napa County, has not been located. It cannot be found in the Greene Herbarium (September, 1939). The COTYPE, collected by *F. T. Bioletti*, June 10, 1893, has been seen in the Gray Herbarium and in the herbaria of Stanford University and of the University of California.

Downingia pulchella var. *arcana* Jepson, Madrono **1**: 100. 1922. *Type locality:* La Mesa, San Diego County, California. TYPE: *W. L. Jepson 6678*, presumably in the personal herbarium of Professor Jepson, not seen.

Downingia immaculata Munz & Johnston, Bull. Torrey Club **51**: 300. 1924. *Type locality:* "South of Lake Elsinore, Riverside County, California." TYPE: *P. A. Munz 5093*, April 29, 1922, No. 13766 of the herbarium of Pomona College.

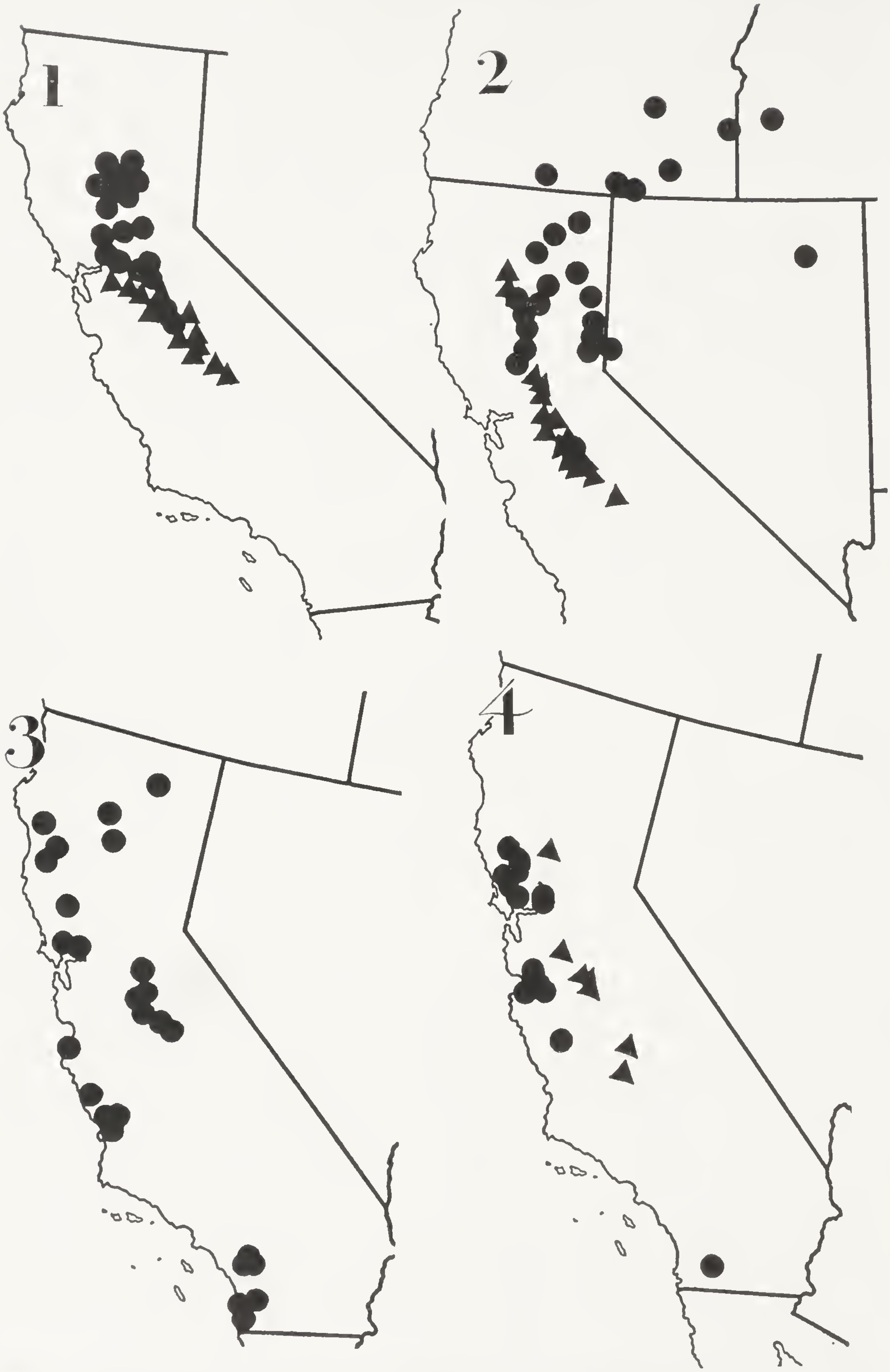
Downingia pallida Hoover, Leafl. West. Bot. **2**: 1. 1937. *Type locality:* "Warnerville, Stanislaus Co." (California). TYPE: *R. F. Hoover 1042*, April 29, 1936, in the herbarium of W. L. Jepson, not seen. Isotypes seen in the herbaria of the California Academy of Sciences, Stanford University, and the University of California.

Plants few—25 (30) cm. high, entirely glabrous or the hypanthium sparsely scabrous, especially when young. Leaves 0.2—2.0 mm. wide, 3.0—13.0 mm. long. Inflorescence few—10 (17) cm. long, loosely 1—15- (25-) flowered. Flower-bracts linear to broadly elliptic or less often lanceolate, obtuse or subacute, 1—3 (4) mm. wide by 4—10 (13) mm. long, mostly about 3—5 times as long as wide.

Ovary linear, in fruit becoming fusiform; mature capsule (0.6) 1.0—1.6 (2.0) mm. in diameter by (15) 20—40 (55) mm. in length, the lateral walls tough but the valves easily separated and marked by conspicuous impressed lines or distinct hyaline slits, the lines or slits evident even in the young condition. Calyx-lobes elliptic to oblanceolate, obtuse or rounded, ascending, subequal in length, about 1.0 mm. wide or less, (1.3) 3.0—8.0 (11.0) mm. in length.

Corolla 7.0—15 mm. long, glabrous. Color bright or pale blue or lavender, sometimes white; lower lip with central white area, this with central or basal yellow spot or two more or less confluent such spots. Tube pale below base of lower lip but sometimes darker at base; two upper lobes often darker and with purplish veins.

Corolla-tube (2.3) 3.0—4.0 (5.2) mm. long, almost cylindrical but slightly expanded distally, the lateral sinuses usually slightly deeper than the dorsal one and cut very slightly (0.5 mm. or less) below the plane of the lower lip; tube measured to dorsal sinus 3.0—4.5 (5.0) mm. long. Two upper corolla-lobes ovate, acute, slightly divergent or recurved and overlapping in age, 1.0—2.5 mm. wide by (2.5) 3.0—6.0 (7.0) mm. long. Lower lip plane or nearly so, with two low inconspicuous yellow ridges at base, the lobes broadly ovate or oblong, mucronate, rounded to retuse or even obcordate.



Map 1. Distribution of *Downingia ornatissima* var. *ornatissima* (circles) and var. *eximia* (triangles). Map 2. Distribution of *Downingia bicornuta* var. *bicornuta* (circles) and var. *picta* (triangles). Map 3. Distribution of *Downingia cuspidata*. Map 4. Distribution of *Downingia bella* (triangles) and *Downingia concolor* (circles).

Filament-tube (2.0) 2.5—4.0 (4.5) mm. long, glabrous, the filaments united their whole length or nearly so; summit of the tube mostly exceeded by the base of the dorsal sinus of the corolla, the base of the anther-tube thus included. Anther-tube 1.4—2.5 mm. long (the mean about 1.7 mm.); anthers smooth or sparsely pubescent on the backs, all minutely white-tufted at tip, the three shorter ones prominently so and each bearing a short horn-like process as well.

Seeds lustrous, twisted, the very fine cellular markings running obliquely to the long axis of the seed. Placentae axile; valves 4 or 5.

Wet or drying clay soil of vernal pools, mud-flats, stream-beds and grassy meadows, at elevations up to about 450 meters. Coast Ranges and central Sierra Nevada foothills, California. Collected in flower and fruit mostly from mid-April to mid-May; in the northern Coast Ranges collections have been made as late as mid-June, and in southern California flowering specimens have been collected as early as March 28.

Specimens examined: CALIFORNIA: Without loc., *V. Rattan* in 1884 (G); Sacramento Valley, *E. L. Greene* in 1895 (US). CALAVERAS: Mokelumne Hill, *F. E. Blaisdell*, without date (CalAc); 4.7 miles from San Andreas, road to Valley Spr., *J. T. Howell 4702* (CalAc, F); Salt Springs Valley, *J. P. Tracy 5649* (P). HUMBOLDT: Fort Seward, *J. P. Tracy 4468* (UC, US). LAKE: Jordan Park, road to Lower Lake, *M. S. Jussel*, May 1, 1932 (CalAc); 2 miles w. of Lower Lake, *L. S. Rose 36206* (CalAc); 4 miles s. of Kelseyville, *M. S. Baker 7507* (CalAc); Kelseyville, *J. W. Blankinship*, May 4, 1925 (CalAc) and June 16, 1926 (CalAc); midway between Kelseyville and Lower Lake, *M. S. Baker 7642* (CalAc). MADERA: 5 miles from Raymond, road to Coarse Gold, *Eastwood & Howell 5458*; San Joaquin Experimental Range, *H. H. Biswell 130* (FS, USNA, UC). MARIPOSA: Mariposa-Raymond Rd., near Oakvale School, *R. F. Hoover 3445* (UC). MENDOCINO: Without loc., *G. R. Vasey* in 1875 (F, US); Round Valley, *P. B. Westerman*, without date (UC); Round Valley (county?), *V. Rattan* in 1884 (S); Round Valley, *V. K. Chesnut 24* (US); Sherwood Valley, *J. B. Davy 5163* (UC). MERCED: 4 miles s. of Snelling, *R. F. Hoover 2068* (G, UC). MODOC: Egg Lake, *M. S. Baker*, June 18, 1893 (UC). MONTEREY: 1.3 miles s.e. of Jolon, *Keck & Stockwell 3224* (P, S, UC); 2.5 miles s.e. of Jolon, *B. O. Schreiber 2488* (FS); Pacific Grove, *Miss M. E. B. Norton*, without date (CalAc). NAPA: Napa, *Hilda Smyth* in 1899 (CalAc). RIVERSIDE: 1.5 miles s. of Lake Elsinore, *P. A. Munz 5093* (P, R, S, UC); Perris, collector unknown, May 1, 1922 (P); Menifee Valley, *Munz & Johnston 5380* (P); Menifee, *Etta McEven*, April 19, 1897 (S, UC); Winchester, *Lillian Dickson*, April 1896 (UC). SAN DIEGO: 4 miles north of San Diego, *L. R. Abrams 3445* (CalAc, F, G, NB, O, P, S, UC, US); mesas, San Diego, *T. S. Brandegee 1668* (ELG, G, NB, P, UC, US); "in paludibus prope San Diego," *M. F. Spencer 1073*, 5/6/1923 (G); "in pools, Camp Kearney road, San Diego," *M. F. Spencer 1073*, April 16, 1919 (CalAc, G, NB, P); Camp Kearney Mesa, *M. F. Spencer 141*, April 16, 1919 (F); Camp Kearney, *Purer 6890* (P); Camp Kearney mesa, *F. Youngberg 15* (P); Miramar-Kearney mesa, *F. F. Gander 1651* (CalAc); mesa, San Diego, *C. R. Orcutt*, May 1889 (NB); "mesas," *C. R. Orcutt*, May 19, 1884 (ELG, F, US); mesas back of San Diego, *H. M. Hall 3923* (NB, UC, US); 6

miles n. of San Diego, *F. W. Peirson 3394* (P); Ramona, *T. S. Brandegee* (C. F. Baker 3425) (ELG, O); Ramona, *T. S. Brandegee*, May 25, 1903 (CalAc, P, UC); s. of Ramona, *E. A. Purer 6949* (P). SAN LUIS OBISPO: Paso Robles, *Condit & White*, April 17, 1909 (UC); Paso Robles, *Benj. Cobb*, April 20, 1907 (S, UC); e. of Paso Robles, *C. Dudley*, April 1936 (CalAc); Estrella, *L. Jared*, without date (UC); near Estrella, *Eastwood & Howell 4190* (CalAc, F, NB, US); 3 miles e. of Templeton, *I. L. Wiggins 2072* (S). SHASTA: 3 miles e. of Redding, *R. F. Hoover 1204* (CalAc, G, S, UC). SONOMA: Without loc., *F. T. Bioletti* in 1894 (ELG); Los Guilucos Valley, *F. T. Bioletti*, June 10, 1893 (G, S, UC). STANISLAUS: Warnerville, *R. F. Hoover 1042* (CalAc, S, UC); *2046* (G, UC). TEHAMA: Coyote Cr. Bridge s. of Red Bluff, *R. F. Hoover 2289* (UC); 10 miles e. of Red Bluff, *D. K. Gillespie 9274* (S, UC). TUOLUMNE: 1 mile w. of Chinese Camp, *R. F. Hoover 1977* (G, S, UC); Sonora, *E. A. Greene*, April 25, 1925 (S).

The present writer has been unable to find a means by which one can separate *Downingia cuspidata* from *D. immaculata* and *D. pallida*, and feels that it is impossible to accord even varietal status to the two last-mentioned. *D. cuspidata* was originally described from the region north of San Francisco Bay and its existence elsewhere has not been suspected. Jepson[10] and Hoover[11] separate the species essentially as follows:

Corolla-tube longer than the calyx-lobes . . . . *D. cuspidata*
Corolla-tube equalling or shorter than the calyx-lobes . . . . *Downingia* spp.

In any of the species of *Downingia* that may be confused with *D. cuspidata*, the calyx-lobes are so variable in length that the above key-character is a very weak one. Flowers having calyx-lobes of the two sorts indicated may often be found on the same plant.

Examination of all the available material indicates that *D. cuspidata* is one of a group of five species having a bilocular ovary and a relatively long and narrow corolla-tube (see figures 11, 12, for indication of the general sort of corolla meant). *D. cuspidata* is unique, however, in having the following combination of characters:

Base of lower corolla-lip yellow, with no purple spots or blotches; two upper lobes of corolla not sharply recurved nor inrolled.

Capsule splitting at maturity, the valves separated by usually prominent hyaline lines, the tissue of which soon breaks up and allows the valves to separate.

Seeds appearing as if twisted; cellular markings of the seedcoat, at least on one side of the seed, strongly oblique to the long axis of the seed. *D. pusilla* is the only other species having this feature.

The species with which *D. cuspidata* may be confused are chiefly *D. concolor* and *D. bella*, either of which may be distinguished at once by the

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[10] Madroño **1**: 98–102. 1922. A Manual of the Flowering Plants of California, 1923–1925.
[11] Leafl. West. Bot. **2**: 33–35. Au 1937.

non-twisted seeds, the purple spots on the corolla-tube, or the much tougher capsule. *D. ornatissima* lacks the purple spot of the corolla, but its own corolla is so characteristic that it should not ordinarily be confused with *D. cuspidata*.

The series of plants from Riverside and San Diego Counties, designated by Munz and Johnston as *D. immaculata*, seems not to differ from typical *D. cuspidata* in any essential features. The corolla, and flower-parts in general, seem to average slightly larger than those of plants from the region north of Sacramento, but many individual plants are found which match exactly, feature for feature, material of *D. cuspidata* from the type region. The cotype material, from Sonoma County, is very slender, with short leaves and smallish flowers; it seems probable that this represents a form of ecological origin, since the plants of *Downingia* were mixed with those of a species of *Eleocharis* and other grass-like aquatics, and apparently came from a wet, swampy situation. Other material from the type region and northward is much stouter and taller, with longer leaves and larger flowers.

The second proposed species, here thrown into synonymy under *D. cuspidata*, is *D. pallida* Hoover. This was based largely upon a pale color-form occurring in the central Sierra Nevada foothills. This color-form is sometimes recognizable even in dried material, but the writer has been unable to detect additional differences between it and typical *D. cuspidata*. The color, furthermore, does not appear to be constantly related to range, for blue-flowered specimens, exactly matching material from the northern Coast Ranges, have been seen from Madera, Mariposa, and Tuolumne Counties.

6. DOWNINGIA PUSILLA (G. Don) Torrey, U. S. Expl. Exped. **17**: 375. 1874.

Clintonia pusilla G. Don, Gen. Syst. **3**: 718. 1834. (Based on *Lobelia pusilla* Poeppig ms., ex Cham. in Linnaea **8**: 217. 1833, nomen nudum). *Type locality:* Chile. TYPE: Not verified.

Bolelia humilis Greene, Pittonia **2**: 226. 1892. *Type locality:* "Moist plain, Sonoma County" (California). TYPE: *F. T. Bioletti* in 1892, No. 16097 of the Greene Herbarium.

Downingia humilis Greene, Leafl. Bot. Obs. & Crit. **2**: 45. 1910.

Plants 2—12 cm. high, entirely glabrous or the hypanthium minutely scabrous; stems relatively stout for their height, up to 1.5 mm. in diameter at base. Leaves 0.5—1.0 mm. wide by 4.0—7.0 mm. long. Inflorescence 2—5 cm. long, 1—7-flowered. Flower-bracts 1.0—1.5 mm. wide by 5—8 mm. long, 5—7 times as long as wide, elliptic or lanceolate, obtuse.

Ovary linear, in fruit becoming narrowly ellipsoid or subulate; mature capsule 1—1.2 mm. in diameter, 20—27 mm. long, the lateral walls firm and not easily ruptured, the valves appearing as impressed lines or as scarious divisions. Calyx-lobes elliptic to linear, blunt-tipped, widest at or near the middle, erect and often appressed, 3.0—8.0 mm. long, the two lower ones usually plainly shorter than the others.

Corolla 2.5—4.0 mm. long, glabrous. Two upper lobes deltoid-lanceolate, about 0.8 mm. wide by 1.2—1.5 mm. long (somewhat recurved ?); lower lip (more or less erect?), not sharply deflexed at base, the three deltoid lobes about 0.8 mm. wide by 1.2 mm. long. Color white or the lower lip blue-tipped, with white center and yellowish patch near base.

Corolla-tube 1.3—2.0 mm. long, narrowly funnel-shaped, the lateral sinuses cut about as deeply as the dorsal one.

Filament-tube 1.0—1.8 mm. long, glabrous, the filaments connate nearly their whole length. Anther-tube 0.6—1.1 mm. long, the anthers white-apiculate, the two shorter ones with a few bristles and a blunt horn-like process at the tips.

Seeds twisted, the cellular lines markedly oblique to the long axis of the seed; placentae axile.

Vernal pools at low elevations, Sacramento Valley and San Joaquin Valley, California. Collected in flower and fruit from March 27 to May 4. Also in Chile, where collected in January, according to available data. Reported from southern Argentina (Golfo de San Jorge) by Spegazzini (An. Soc. Cient. Arg. **53**: 70. 1902).

Specimens examined: CALIFORNIA—MERCED: 5 miles n. of Snelling, *R. F. Hoover 2063* (G, UC). NAPA: Near Napa, *Heller & Brown 5362* (F, G, NB, P, R, S, US). SOLANO: Vanden, *Mrs. Brandegee,* April 1893 (UC). SONOMA: Sonoma Co., *F. T. Bioletti* in 1892 (UC, US); Shellville, *Michener & Bioletti,* May 1, 1892 (UC); summit of Bennett Valley road from Glen Ellen to Santa Rosa, *J. T. Howell 11807* (CalAc). STANISLAUS: Near La Grange on Snelling Road, *R. F. Hoover 970* (CalAc); Warnerville, *R. F. Hoover 1992* (G, S, UC).

CHILE: Panguipulli, *F. Claude Joseph 2725* (US); Prov. Colchagua, *Bridges 169,* in 1862 (NB); Valle de Marga-Marga, Prov. Aconcagua, ca. lat. 33° 10′ S., *Jaffuel & Pirion 3136* (G) and *3137* (G); without locality or date, *Fielding* (G).

This species is regarded for the present as a derivative one, related to *D. cuspidata* by the twisted seeds and the corolla, which is unmarked by purple. If *D. pusilla* be actually a derivative species, of relatively recent origin as compared to the rest of the genus, its presence in Chile may be accounted for in one of two ways. It is possible that it arose at a time when a hypothetical ancestor existed both in North and South America, all traces of the ancestor having now been lost in the latter continent. The second and seemingly more plausible explanation is that the single species, *D. pusilla*, was transported accidentally, by birds or other agency, from California to Chile.

There are no apparent differences between North and South American material, so that the writer can see no justification for maintaining *D. humilis* (Greene) Greene as a distinct species. Material from South America is very scarce in North American herbaria, and it is possible that examination of more ample collections will demonstrate at least varietal differences between the Chilean plant and that of California.

D. pusilla is often associated with *D. laeta* in keys and synoptical treatments, largely because of the size of the flowers; the corolla is relatively small in both species, as compared to that of other species of the genus. There is, however, little actual affinity between the two. The present study indicates that *D. laeta* is a derivative species akin to the group having a broad funnel-shaped or campanulate corolla-tube, with three purple spots at the base of the lower lip.

7. DOWNINGIA PULCHELLA (Lindley) Torrey, Pacific Rail. Rep. **4**^{5}**:** 116. 1856.
Clintonia pulchella Lindl., Bot. Reg. **22:** t. 1909. 1836. *Type locality:* "California." TYPE: Not seen. A specimen labelled "Nova California," collected by David Douglas in 1833, now in the Gray Herbarium, is apparently an isotype.
Bolelia pulchella Greene, Pittonia **2:** 126. 1890.

Plants few—25 (40) cm. high, entirely glabrous or the hypanthium sparsely scabrous. Leaves 1—2 mm. wide by 4—12 mm. long. Inflorescence few—15 (20) cm. long, loosely few—15- (20-) flowered. Flower-bracts elliptic to lanceolate or ovate, usually obtuse, 2—7 mm. wide, 8—20 (25) mm. long, usually 3—6 times as long as wide.

Ovary linear, in fruit little changed in shape or becoming narrowly subulate or fusiform; mature capsule 1.0—1.5 (2.0) mm. in diameter by 30—75 mm. long, the lateral walls tough and ruptured with difficulty when dry, the valves never apparent. Calyx-lobes elliptic, obtuse or rounded at tip, usually rotately spreading in flower and fruit, subequal in length, 0.5—2.0 mm. wide, 3—7 (10) mm. long.

Corolla 8—13 mm. long, glabrous. Color "deep bright blue," less often pink or pure white; lower lip with central white area bearing two yellow spots which pass into low narrow yellow folds at the base of the lip; alternating with the folds, at the base of the lip, are three dark purple spots; tube purple.

Corolla-tube (1.5) 2.0—3.0 mm. long, funnel-shaped, with narrow base; lateral sinuses usually cut slightly deeper than the dorsal one; tube measured to dorsal sinus 2.0—3.0 (3.3)mm. in length. Two upper corolla-lobes elliptic or oblanceolate, strongly divergent and spreading, acute at tip, 2.0—3.0 (4.0) mm. wide by 6.0—8.0 mm. long. Lower lip reflexed, the lobes oblong, acute or mucronate, 3.5—5.0 mm. wide by 4.5—6.0 mm. long.

Filament-tube (2.5) 3.0—4.5 (5.0) mm. long, glabrous, the filaments united their whole length or nearly so; summit of the tube usually considerably exceeding the dorsal sinus of the corolla, the anther-tube thus prominently exserted. Anther-tube (2.2) 2.6—3.5 mm. long, attenuate and pointed at tip; anthers glabrous or minutely ciliate on the backs, the two shorter ones minutely white-tufted at tip and each with a slender horn-like process as well.

Seeds shining, not twisted; placentae axile.

Low moist soil; muddy borders of drying vernal pools, moist fields, salt-marshes. Low elevations, central California from Monterey and Merced Counties north to Colusa County; an isolated station in Lassen County. Collected in flower and fruit from April 15 to June 7 (Lassen Co. in Aug. ?).

Specimens examined: CALIFORNIA: "Nova California," *Douglas* in 1833 (G; ISOTYPE); "California," *Douglas* (Torrey Herb.) (NB; probably ISOTYPE); "Wallamet," *Tolmie* (G); "Cult. Hort. Cantab." (Torrey Herb.) July 1868 (NB); "upper Mojave," *Dr. J. G. Cooper*, 1860–1861 (G); without loc., *V. Rattan* in 1884 (G). ALAMEDA: Mt. Eden, *Mrs. T. S. Brandegee*, May 22, 1893 (G, NB, R, S, UC, US); *Evelina Cannon*, May 1893 (CalAc); Alvarado, *W. L. Jepson*, June 1896 (G); June 7, 1896 (UC); between Alvarado and Mt. Eden, *I. L. Wiggins 5860* (CalAc, Cath, P, S, UC); Haywards, collector unknown, May 1915 (CalAc); Haywards, *Lemmon herb.*, without date (P, UC); near Newark, *J. Burtt Davy 1106* (UC); Mt. Diablo base, w. 121°, *W. P. Gibbons 238* (NB). COLUSA: Near College City, *Heller & Brown 5434* (G, F, NB, P, S, US). LASSEN: Bieber, *W. C. Merrill*, Aug. 1892 (P; also a mixed collection, with *D. insignis*). MERCED: 10 miles w. of Merced, *R. F. Hoover 2105* (CalAc, G, UC). MONTEREY: Near Santa Rita, *E. K. Abbott*, May 1889 (CalAc). SACRAMENTO: Near DelPaso, *E. A. Wilkins*, April 28, 1932 (UC). SAN BENITO: Hollister, *W. A. Setchell*, April 14, 1897 (UC); near Hollister, *Eastwood & Howell 5304* (CalAc); 7 miles n.w. of Hollister, *J. T. Howell 11029* (CalAc, Cath, P). SAN JOAQUIN: Stockton, *E. L. Greene*, June 1889 (ELG); near Stockton, *J. A. Sanford*, May 1890 (ELG); Oxford Manor, Stockton, *C. R. Quick*, Apr. 22, 1929 (US); French Camp, *J. A. Sanford 155* (UC). SANTA CLARA: San Jose, *Miss M. E. B. Norton*, May 1879 (F); San Jose, *G. R. Kleeberger*, in 1879 (CalAc); "prope San Jose, Mrs. Atwater," June 1873 (US); East San Jose, *R. L. Pendleton 860* (P); east of San Jose, *V. Rattan*, June 1880 (S); Milpitas, *R. J. Smith*, April 1906 (R, S); Bolsa road near San Benito Co. line, *R. F. Hoover 3482* (UC); Santa Clara, *B. F. Leeds*, May 29, 1891 (F). SOLANO: Central Solano, *W. L. Jepson*, May 2–6, 1891 (NB, US); near Elmira, *E. L. Greene*, May 1890 (ELG); near Vacaville, *W. L. Jepson*, May 2–6, 1891 (S); Little Oak, *W. L. Jepson*, May 2–6, 1891 (ELG, UC); Suisun, *A. Eastwood 10423* (CalAc) and without no., Apr. 30, 1921 (CalAc); Suisun, *E. L. Greene*, May 4, 1890 (ELG). YOLO: Near Madison, *Heller and Brown 5421* (F, G, NB, S, UC, US); "By-Pass," *E. A. Wilkins*, April 28, 1932 (UC).

OREGON—MARION: Silverton, *Elihu Hall* in 1871 (US). The plants of this collection are mounted on a mixed sheet with specimens of *D. elegans*, and a mixing of labels may have occurred.

All collections of the genus *Downingia* made in California between 1836 and 1886 were either unidentified as to species, labelled *D. elegans*, or thrown indiscriminately into *D. pulchella*. This lack of discrimination accounts for much of the misinformation that has been published concerning a very clear and unmistakable species. In Gray's *Synoptical Flora* (1886) the range of *Downingia pulchella* is given as "California, nearly throughout the state, and in the borders of N. Nevada and Oregon." In 1924 Munz & Johnston[12] stated that it did not occur in southern California south of the

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[12] Bull. Torrey Club **51**: 300–301. 1924.

region of San Luis Obispo County, but in 1925 Jepson[13] gave the range as "South Coast Ranges; Sacramento Valley, Sierra Co.; n. to southern Ore." Essentially the latter range was repeated by Hoover.[14] The actual center of distribution for the species seems to be in the neighborhood of San Francisco Bay. From this center it extends southward to Merced and northern Monterey County and northward to Colusa County. The writer has seen collections from Lassen County, as well as from Ormsby County, Nevada, and Marion County, Oregon, in which specimens of *D. pulchella* had been mounted on the herbarium sheets with full collections of another species. It is probable that the Nevada and Oregon collections are not authentic, so far as concerns the occurrence of *D. pulchella* at the stated localities. The occurrence of the species in Lassen County, California, is also open to doubt but is entirely possible, since *D. insignis*, a related species with similar range, has been found both in Lassen and in Modoc Counties.

There is in the Gray Herbarium a specimen of *Downingia pulchella*, collected by Dr. J. G. Cooper during the spring of 1861, labelled "upper Mojave." There is also a specimen of *D. laeta*, collected by Dr. Cooper on June 6, 1861, now in the United States National Herbarium and labelled "Upper Mojave River." The locality on the former appears to have been written by Asa Gray. Dr. Cooper is known to have passed over the trail from Fort Mohave to Cajon Pass in the spring of 1861, and to have travelled along the Mohave River, above Soda Lake, in May of that year. It is scarcely credible, however, that he should have collected there both *Downingia pulchella* and *D. laeta*, neither of which is known otherwise from this part of California. The origin of his specimens is accordingly unknown; it is not unlikely that these specimens were mixed with a series of other plants from southern California.

Like *Downingia ornatissima*, *D. pulchella* is a species which is exceedingly easy to recognize and not closely related to any other species, but which is difficult to set off by the use of key characters. It differs from all other species in its long and narrow anther-tube which is narrowed and pointed at the apex, rather than obtuse or rounded as in the rest of the species. It is characterized further by the short and flaring corolla-tube, from which the filament-tube is conspicuously exserted. The three purple spots at the base of the lower lip of the corolla are usually visible, even in dried material.

The species most closely related to *D. pulchella* appears to be *D. insignis*. The two resemble each other strongly in capsule characters, in habit and in color-pattern of corolla.

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[13] A Manual of the Flowering Plants of California.

[14] Leafl. West. Bot. **2:** 33–35. Au 1937.

8. DOWNINGIA INSIGNIS Greene, Pittonia **2**: 80. 1890.
Type locality: "Fields of the lower Sacramento valley near Elmira" (Solano County, California). TYPE: "Near Elmira," E. L. Greene, May 2, 1890, No. 16107 of the Greene Herbarium.
Bolelia insignis Greene, Pittonia **2**: 126. 1890.

Plants slender, the stems attaining a maximum diameter of about 2 mm. at base, often somewhat zigzag, (6) 10—24 (30) cm. high, the whole plant glabrous or the capsule sometimes minutely scabrous. Leaves 1—2 mm. wide by 5—15 mm. long. Inflorescence 4—12 (20) cm. long, loosely 1—8- (16-) flowered (the mean about 5 flowers); inflorescence-axis often poorly defined and overtopped by the tips of the capsules even of the lower flowers. Flower-bracts 1—5 mm. wide by 6—20 mm. long, mostly about 2—6 times as long as wide, elliptic to ovate, obtuse, rounded or sometimes subacute.

Ovary linear, enlarged in fruit, the mature capsule terete or slightly angled, linear or narrowly subulate, usually strongly appressed, 0.8—1.5 (2.0) mm. in diameter by (25) 45—80 mm. in length; lateral walls tough when dry and ruptured with difficulty, with no evidence of impressed or scarious valves. Calyx-lobes elliptic, obtuse or rounded, ascending, 1—2 (3) mm. wide by 3—8 (12) mm. long, usually broadest about the middle.

Corolla 9—15 mm. long, glabrous. Color "sky-blue" (according to Greene), the veins darker; lower lip with central white area, this sometimes with two oblong parallel green spots; base of lower lip with two low golden-yellow folds in a field of dark violet-purple, or the latter reduced to three purple spots at the summit of the corolla-tube.

Corolla-tube (3.0) 3.5—5.0 mm. long, broadly funnelform ("campanulate," according to Greene), the lateral sinuses deeper than the dorsal one; length of tube measured at dorsal sinus 4.5—6.0 mm. Two upper lobes ascending and parallel, elliptic, acute, 2.0—3.0 mm. wide by 6.0—10.0 mm. long. Lower lip concave, usually exceeded in length by the two upper corolla-lobes, not reflexed, not forming an angle with the tube, the three lobes oblong to ovate, acute or mucronate, 2.5—7.0 mm. long.

Filament-tube (7.0) 9.0—10.5 (11.5) mm. long, glabrous, the filaments united very nearly their whole length. Anther-tube 2.4—3.0 (3.5) mm. long, 1.0—1.3 mm. in diameter, usually strongly incurved and standing about at right angles to the filament-tube. Anthers a dirty white in color, the cells hardly darker than the connectives, all the anthers minutely granular-roughened over the whole surface; two shorter anthers white-tufted at tip, each with a short horn-like process in addition.

Seeds not twisted; placentae axile.

Heavy clay soils of vernal pools and in low grassy places, Great Valley of California, at low elevations from Stanislaus County northward. Also extends to Lassen and Modoc Counties, California, and to Washoe County, Nevada. Collected in flower and fruit from March 3 to June 14; a single collection in August. Most of the collections have been made in May.

Specimens examined: CALIFORNIA—BUTTE: 6 miles n.w. of Chico, *A. A.*

Heller 11468 (CalAc, ELG, F, G, NB, S, UC, US). COLUSA: Near Princeton, *A. Eastwood 11201* (CalAc); near College City, *M. A. King* in 1905 (UC); Colusa, *A. A. Heller*, May 19, 1902 (CalAc, G, NB, UC, US); near Colusa, *Heller & Brown 5438* (F, G, NB, P, S, US). CONTRA COSTA: Near Byron, *E. L. Greene*, May 23, 1886 (ELG); Byron, *L. S. Rose 37225* (F, NB); ¼ mile s. of Byron, *I. L. Wiggins 4570* (P, S, UC); Byron Springs, *A. Eastwood 14444* (CalAc, P); 8 miles s. of Antioch, *L. S. Rose 36154* (CalAc, F, NB, UC, US). GLENN: "Glenn Co.," collector unknown, April 27, 1916 (CalAc); Willows, *A. Eastwood 10223* (CalAc). LASSEN: Susan R. at Litchfield, *L. Constance 2328* (USNA); Pete's Valley, *Jean Linsdale*, June 9, 1929 (CalAc); Bieber, *W. C. Merrill*, Aug. 1892 (P). MODOC: 2 miles e. of Alturas, *J. T. Howell 12202* (CalAc). PLUMAS: Prattville, collector unknown, July 4, 1892 (UC). SAN JOAQUIN: Without loc., *Tracy*, April 1892 (ELG); Stockton, *A. L. Grant*, March 3, 1916 (P), *J. A. Sanford 161* (UC), *J. A. Sanford*, May 10, 1890 (ELG); *V. Rattan*, without date (S); *E. E. Stanford 168* (G, P, S); 5 miles s.e. of Stockton, *R. F. Hoover 2078* (G, S); "Stockton, St. Joaquin Riv.", *Dr. Rich*, without date (NB); French Camp, *R. F. Hoover 2185* (UC); Lockeford, *W. P. Steinbeck*, May 9, 1923 (CalAc). SOLANO: Near Vanden, *J. T. Howell 5213* (CalAc, Cath, F, US); "north-western Solano," *W. L. Jepson*, May 2–6, 1891 (ELG, NB, UC, US); near Suisun, *E. L. Greene*, May 5, 1890 (NB); and May 1890 (UC); near Elmira, *E. L. Greene*, May 5, 1890 (US); Elmira, *Heller & Brown 5591* (F, G, NB, P, R, S, US); near Elmira, *A. A. Heller 14546* (US); Little Oak, *W. L. Jepson*, May 15, 1896 (G, UC). SONOMA: Near Sonoma, *F. T. Bioletti*, in 1892 (NB). STANISLAUS: 7 miles w. of Modesto, *R. F. Hoover 3077* (UC). SUTTER: "Edge of tule land," *E. B. Copeland 3285* (ELG, G, NB, P, US). YOLO: 4 miles n. of Zamora, *D. K. Kildale 5026* (S); between Woodland & Davis, *L. R. Abrams 12604* (S). YUBA: "Yuba Co.," without collector or date (CalAc).

NEVADA—WASHOE: 3.5 miles n. of Reno, *R. C. Wilson 640* (FS); 5 miles e. of Poeville, *D. Tillotson 156* (FS); Chas. Sheldon Antelope Refuge, *G. H. Greenway 139* (USNA).

OREGON—MALHEUR: Barren Valley, *W. C. Cusick 1261* (F). The Cusick specimens are typical *D. insignis*, but mixed with them on the sheet is a number of plants with the stamens of *D. elegans* and the longer corolla-tube of *D. insignis*. The ovary is unilocular, as in *D. elegans*, but none of the plants has mature fruit. These anomalous specimens may represent a hybrid between *D. elegans* and *D. insignis;* similar plants from what is apparently the same collection, are in the herbarium of the University of Oregon.

As discussed above (p. 11), this species is perfectly distinct from *D. elegans*. The two species seem to have arisen from a common stock, to judge by their very similar flowers, but at the present time, in the writer's opinion, *D. insignis* has much more in common with *D. pulchella* than with *D. elegans*. Some of the differences between *D. elegans* and *D. insignis* are brought out in the key (p. 15); additional differences worthy of note may be summarized as follows:

Map 5. Distribution of *Downingia laeta*. Map 6. Distribution of *Downingia montana*. Map 7. Distribution of *Downingia elegans* var. *elegans* (circles) and var. *brachypetala* (triangles). Map 8. Distribution of *Downingia willamettensis* (circles) and *Downingia yina* (triangles).

insignis	*elegans*
Capsule tough when dry, usually 45—80 mm. in length	Capsule papery when dry, usually 25—45 mm. in length
Corolla with purple spots at summit of tube	Corolla without purple spots at summit of tube
Corolla-tube mostly 3.5—5.0 mm. long	Corolla-tube mostly 2.0—3.2 mm. long
Range throughout Sacramento Valley, sparingly northward and eastward	Range from mountains of northern California northward

The range of *Downingia insignis* comprises the whole of the lower Sacramento Valley and extends southward into the lower part of the San Joaquin Valley. There are also records, apparently well authenticated, of the occurrence of the species at several localities in Lassen and Modoc Counties, California, and in Washoe County, Nevada. The Nevada records are unexpected ones, but specimens were collected at three localities by Forest Service collectors working independently, and there appears to be no doubt of the authenticity of the collections. Undoubted plants of *D. insignis* make up a part of the collection from "Barren Valley, Malheur Co., Oregon," *W. C. Cusick 1261*, in the Field Museum. As explained under the citation of specimens (p. 41), the remainder of the collection is made up of somewhat anomalous plants of *D. elegans;* it is quite possible that both species occur at this locality, and that it is the northernmost known locality for *D. insignis.*

9. DOWNINGIA LAETA (Greene) Greene, Leafl. Bot. Obs. & Crit. **2**: 45. 1910.

Bolelia laeta Greene, Erythea **1**: 238. 1893. *Type locality:* "Humboldt Wells, Nevada." TYPE: *E. L. Greene*, July 6, 1893, in the Greene Herbarium, without number.

Bolelia brachyantha Rydberg, Mem. N. Y. Bot. Gard. **1**: 483. 1900. *Type locality:* "Augusta, Montana." TYPE: *R. S. Williams 712*, July 30, 1887, in the herbarium of the New York Botanical Garden.

Downingia brachyantha (Rydb.) A. Nels. & Macbr., Bot. Gaz. **55**: 382. 1913.

Plants few—20 (30) cm. high, entirely glabrous. Leaves 0.5—2.0 mm. wide by 5—18 (25) mm. long. Inflorescence few—10 cm. long, rather closely 1—10-flowered. Flower-bracts elliptic to lanceolate or ovate, obtuse or subacute, 1—4 mm. wide by 7—22 mm. long, usually 3—6 (8) times as long as wide.

Ovary linear, in fruit becoming narrowly subulate or fusiform, terete, the mature capsule 1.0—2.0 mm. in diameter by 21—43 mm. in length; lateral walls thin but rather tough and tardily dehiscent, the valves inconspicuous, sometimes appearing as faintly impressed lines. Calyx-lobes elliptic, rounded to subacute at tip, 1.0—2.0 mm. wide, (2.5) 3.0—7.0 (9.0) mm. long, ascending.

Corolla 4—7 mm. long, glabrous. Color light blue or purplish; lower lip with central area white or yellow and with a transverse band of purple at base, this sometimes reduced to two or three purple spots. Tube yellow on lower side below the purple area.

Corolla-tube (1.0) 1.3—1.6 (2.0) mm. long, funnelform, the lateral sinuses cut about as deeply as the dorsal one or very slightly deeper; length of tube measured at dorsal sinus (1.1) 1.5—2.0 mm. Two upper lobes ascending (?), lanceolate or triangular, acute, 1—2 mm. wide, 2.0—4.5 mm. long; lower lip concave (?), not reflexed nor forming a sharp angle with the tube, the three lobes oblong, acute, 1.5—3.5 mm. long.

Filament-tube 1.8—2.5 (2.8) mm. long, glabrous, the filaments united their whole length or nearly so. Anther-tube 1.3—2.0 (2.2) mm. long, little or not at all incurved, its long axis nearly or quite parallel with that of the filament-tube; anthers glabrous or ciliate on the backs, the two shorter ones white-tufted at apex and each with a slender horn-like process as well.

Seeds not at all or very slightly twisted; placentae axile.

Wet muddy places in low fields, ditches, borders of sloughs, ponds, and streams, and in vernal pools, often at elevations of 1200—2000 meters. Southwestern Saskatchewan south to southwestern Wyoming, south-central Oregon, and western Nevada. Collected in flower and fruit from June 1 to August 23.

Specimens examined: CALIFORNIA: "Upper Mojave River," *Dr. J. G. Cooper*, June 6, 1861 (US). LASSEN: Honeylake Valley, *G. H. True 518* (CalAc); 10—15 miles w. of Amedee, *M. E. Jones*, June 24, 1897 (P); 10 miles s. of Amedee, *M. E. Jones*, June 22, 1897 (US). MODOC: Fort Bidwell, along Alkali Lake, *M. H. Manning 327* (US).

IDAHO—BEAR LAKE: Road from Paris to Montpelier, *L. F. Henderson*, August 1899 (NB); same loc., *L. F. Henderson 4821* (G, Ore, US). JEFFERSON: Roberts, *R. J. Davis 1059* (Id).

MONTANA—LEWIS & CLARK: Near Augusta, *R. S. Williams 712* (NB, US).

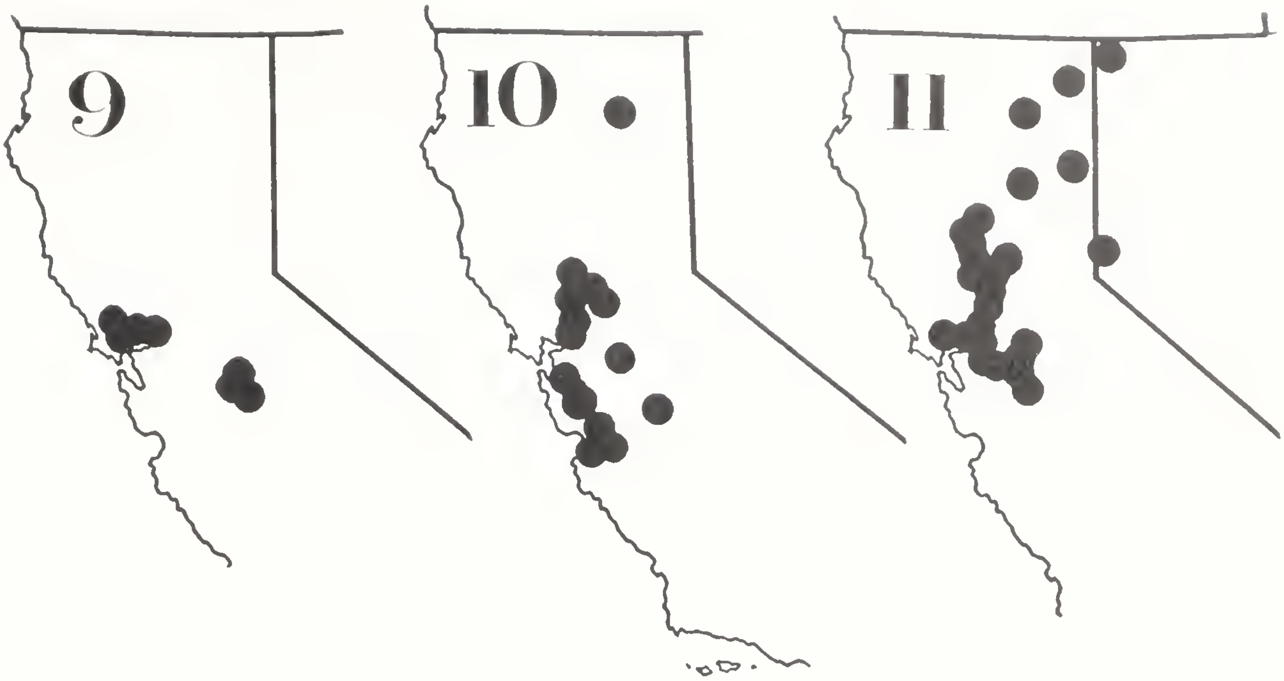
NEVADA—ELKO: Humboldt Wells, *E. L. Greene*, July 6, 1893 (ELG, UC); O'Neil, *Nelson & Macbride 2084* (G, NB, R, US); Deeth, *A. A. Heller 9039* (F, G, NB, S, US); Deeth, *A. A. Heller 10555* (CalAc, F, G, NB, S, UC, US); H. D. Ranch, 28 miles n. of Wells, *M. E. Jones*, July 25, 1901 (P). EUREKA: Palisade, *E. L. Greene*, July 24, 1896 (F, UC). NYE: Potts Ranger Station, Toiyabe Forest, *B. K. Crane 205* (FS). ORMSBY: Eagle Valley near Carson, *C. F. Baker 1051* (ELG); Eagle Valley, *C. F. Baker 1057* (G, NB, P, US). WASHOE: Near Sparks, *Heller & Kennedy 8653* (F, G, NB, S, US); Truckee Meadows, near Glendale, *W. W. Bailey 728* (NB, US); Glendale, *P. B. Kennedy 1571* (NB, US); 5 miles n. of Carson City, *D. R. Goddard 1041* (F, UC).

OREGON—HARNEY: Harney Valley, *W. C. Cusick 2602* (ELG, F, G, NB, Ore, P, R, UC, US); near Burns, *L. F. Henderson 8850* (CalAc, Ore); east of Burns, *J. W. Thompson 13286* (CalAc, NB, US, WU); 1 mile e. of Burns, *J. W. Thompson 11968* (NB, P, US); 4 miles s.e. of Burns, *M. E. Peck 18940* (WU); 5 miles s.e. of Burns, *M. E. Peck 13915* (S, WU). LAKE: Near Lakeview, *M. E. Peck 15284* (WU); Goose Lake Valley, near Lakeview, *M. E. Peck 15296* (S, WU); S. of Paisley, Chewaucan Marsh, *Constance 9681* (Ore).

UTAH—BOX ELDER: Brigham, collector unknown (USNA). CACHE: ½ mile w. of Logan airport, *B. Maguire 2444* (G, P, R, UC). DAVIS: Farmington, *W. W. Jones 133* (UC) and *295* (G). JUAB; Willow Spring, *M. E. Jones*, June 4, 1891 (G, P). UTAH: Mt. Nebo, *L. N. Goodding 1108* (G, R).

SASKATCHEWAN: "Crane Lake, Assiniboia," *J. Macoun*, June 11 and July 3, 1894 (herb. G. S. Can. 7532 and 7533) (ELG, O).

WYOMING—UINTA: 2 miles n. of Evanston, *L. Williams 7933* (R).



MAP 9. Distribution in North America of *Downingia pusilla*. MAP 10. Distribution of *Downingia pulchella*. MAP 11. Distribution of *Downingia insignis*.

10. DOWNINGIA MONTANA Greene, Pittonia **2**: 104. 1890. *Type locality:* Lake Eleanor, Tuolumne County, California. TYPE: "Lake Eleanor," *Elmer Drew*, June 1889, No. 16098 of the Greene Herbarium.
Bolelia montana Greene, Pittonia **2**: 127. 1890.
Downingia bicornuta var. *montana* Jepson, Madroño **1**: 102. 1922.

Plants few—15 cm. high, slender, entirely glabrous or the hypanthium minutely scabrous; upper part of the stem rarely minutely scabrous. Leaves linear to elliptic or subulate, sometimes few-toothed, 0.3—1.0 (1.5) mm. wide by (2.0) 5.0—13.0 (18.0) mm. long, acute to acuminate. Inflorescence 3—12 cm. long, loosely 1—10-flowered. Flower-bracts similar to the leaves but slightly larger, often toothed, 0.8—1.5 mm. wide by 8—16 mm. long, 8—13 times as long as wide.

Ovary linear, becoming narrowly subulate in fruit, the mature capsule 0.6—1.5 mm. in diameter by 15—35 (45) mm. long, the lateral walls firm, usually with evident hyaline valves, these apparent as impressed longitudinal lines at an early stage. Calyx-lobes linear-subulate or very narrowly elliptic, acute, sometimes scabrous-ciliate on the margins, the two lower ones usually conspicuously shorter than the others; all ascending, often appressed in anthesis, (2.0) 4.0—8.0 (11.0) mm. long.

Corolla 9—12 mm. long, glabrous. Lobes of the lower lip light blue or violet; central part of lip white; base dark bluish-purple, with two prominent purple folds at the angle; tube "blue becoming violet," the lower side within with two greenish yellow ridges alternating with three purple grooves. (Central part of lower lip usually appears bright yellow in dried material.)

Corolla-tube 3.3—5.0 mm. long, narrowly funnel-shaped, often nearly cylindrical below and expanded near the summit; lateral sinuses extending well below the angle of the lower lip, cut more deeply than the dorsal one by a distance of 0.5—1.0 mm. Two upper corolla-lobes narrowly triangular, erect, usually concealing the anther-tube (in dried material), 4.0—5.5 mm. long, sometimes minutely roughened on the margins near tips.

Filament-tube 3.0—4.0 (4.7) mm. long, its apex usually not surpassing the dorsal sinus of the corolla; filaments connate nearly their whole length, glabrous or very minutely pubescent on the margins at base. Anther-tube 1.7—2.2 mm. long; all 5 anthers prominently bearded at tip, the two shorter ones with stiff tufts of bristles and each with a short horn-like process as well.

Seeds not twisted, the surface scarcely lustrous, the fine longitudinal markings easily visible with a magnification of about 20×. Placentae parietal; valves 3.

Moist open grassy meadows in pine forests, mostly at elevations of 1000—1700 meters; western slope of the Sierra Nevada from Tuolumne County, California, northward to Shasta County. Collected in flower and fruit from May 22 to August 1.

Specimens examined: CALIFORNIA: Without loc., *D. C. Roberts*, Aug. 1905 (CalAc); *Kellogg & Harford 616*, in 1868—9 (CalAc, NB, US). BUTTE: Butte Meadows, *A. A. Heller 12843* (ANS, CalAc, F, G, NB, S, US); *A. A. Heller 14656* (NB, S, US). CALAVERAS: Avery Station, *R. F. Hoover 2350* (UC); Calaveras Ranger Station, Avery, *W. W. Eggleston 9178* (USNA, US); Big Trees, *Harry Edwards*, June 1874 (NB). ELDORADO: Sly Park, *H. M. Hall 11311* (CalAc). PLACER: Near Emigrant Gap, *H. M. Hall 8736* (UC, US); without loc., *Mrs. M. M. Hardy* in 1893 (ELG, UC, US). SHASTA: 3 miles e. of Redding, *R. F. Hoover 1203* (CalAc, G, UC); n. fork of Battle Creek, 4000 ft., *Hall & Babcock 4280* (UC). TUOLUMNE: Hog Ranch, Mather, *Keck & Heusi 285* (CalAc, G, Ore, P, S, UC); Mather, *D. D. Keck 1167* (CalAc); Mather, *P. A. Munz 7338* (P); vicinity of Hog Ranch, *Hall & Babcock 3311* (NB, P, R, S, UC, US); Ranger's Cabin, Hetch-Hetchy, *Adele L. Grant 852* (P); Dry Meadows, Big Trees Quadrangle, *R. D. Roseberry 280* (UC).

Downingia montana is one of the group of three species having an unilocular ovary, a long narrow corolla-tube and short stamens, with the anthers not strongly bent inward and the lower part of the anther-tube usually included. It is more difficult to decide upon specific limits in this group than anywhere else in the genus. *Downingia montana* is ordinarily easy to separate from the closely related *D. yina* and *D. willamettensis* by its very narrow, often linear or subulate leaves and its very unequal calyx-lobes, which are also linear-subulate for the most part. Individual plants, however, both of *D. yina* and *D. willamettensis* are not separable by vegetative characters from *D. montana*, so that it is impossible to construct a key to this group based upon such characters. The flowers of the three species are closely similar; the corolla of *D. montana* is prominently marked with purple at the base of the lower lip, with two purple ridges; the corollas of the other two species, however, are less prominently marked with purple. In *D. yina* there are no purple spots, so far as known to the writer, and in *D. willamettensis* there are ordinarily three purple spots at the base of the lower lip, these sometimes being reduced or absent. The characters of seeds and anthers, emphasized in the key (p. 16), prove to be the most dependable means for separating the species.

In the opinion of the writer, *Downingia montana* is to be regarded as a well-marked species, perfectly distinct from the other two species just discussed. It is restricted in range and habitat, and, although undoubtedly closely akin to *D. yina* and *D. willamettensis*, seems never to form intermediates with them. It differs markedly from them in seed and capsule characters, and probably should be regarded as slightly less highly evolved than either of them.

11. DOWNINGIA YINA Applegate, Contr. Dudley Herb. 1: 97. 1929.
Type locality: Four Mile Lake, Klamath County, Oregon. TYPE: *E. I. Applegate 4479*, July 29, 1925, No. 163277 of the herbarium of Stanford University.

Plants 3.0—10.0 cm. high, usually diffusely branched from the base, entirely glabrous or the hypanthium sparsely scabrous. Leaves up to 1.5 mm. wide by 8.0 mm. long. Inflorescence 5 cm. long or less, with 10 flowers or fewer. Flower-bracts narrowly elliptic or lanceolate, acute, up to 3.0 mm. wide by 13.0 mm. long.

Ovary in fruit becoming fusiform, terete, not conspicuously twisted, broadest about the middle, about 1.5 mm. in diameter by 20.0—25.0 mm. long; lateral walls thin and easily fractured, the three valves separated by thin hyaline divisions. Calyx-lobes elliptic to subulate, acute, up to about 1.0 mm. wide by 6.0 mm. long.

Corolla 8—10 mm. long, glabrous, resembling that of *D. willamettensis*. Color dark blue or purplish; lower lip with central yellow area and with two low yellow ridges at base.

Corolla-tube 3.5—4.5 mm. long. Two upper lobes "erect," according to Applegate. Filament-tube 2.5—3.5 mm. long; anther-tube 1.6—2.0 mm. long, the two smaller anthers white-tufted at tip and each with a short horn-like process as well, the three larger anthers sparsely ciliate on backs, scarcely tufted at tip.

Seeds dull or slightly lustrous, lacking lines, not twisted; placentae parietal, central septum none.

Boggy places about lakes and ponds, and beds of partially dried rain-pools; Cascade Mountains of southern Oregon and northern California, at altitudes up to at least 1650 meters. Collected in flower from July 1 to August 15. The only fruiting specimen seen by the writer (*Peck 14698*) was collected July 1, 1931.

Specimens examined: OREGON—KLAMATH: Lake of the Woods, *M. E. Peck 14698* (WU); Lake of the Woods, *M. W. Gorman*, August 14, 1896 (US); small pond, south side of Four Mile Lake, east base of Mt. Pitt, *E. I. Applegate 4479* (S, TYPE); Four Mile Lake, *M. E. Peck 16572* (WU).

California—siskiyou; Soda Creek, Siskiyou Mts., Sect. 30, T48N, R8W, *L. C. Wheeler 2870* (FS, USNA, P).

The following are referred doubtfully to this species:

California—siskiyou: Bray, *L. E. Smith,* July 1915 (CalAc). trinity: Big Flat, *J. T. Howell 13206* (CalAc); Preacher Meadow, *Eastwood and Howell 4931* (CalAc).

This species is intermediate in many respects between *D. montana* and *D. willamettensis,* and its exact status is uncertain. The writer has examined but five collections that may be referred here without hesitation. Further collections may demonstrate that *D. yina* and *D. willamettensis* are conspecific, in which case the former name, being the earlier, will have to be applied to the whole group. At the present time the writer prefers to uphold both as valid species, the name *Downingia yina* being restricted to a small diffuse plant of the high Cascades. The fruits of this species, in the single specimen seen, differ considerably from those of *D. willamettensis* in their fusiform rather than subulate shape, and in being terete and very thin-walled, with evident hyaline divisions. The flowers are, on the average, slightly smaller than those of *D. willamettensis,* and the plants themselves are small and usually diffuse, as contrasted to the larger and usually erect plants of the other species.

12. Downingia willamettensis M. E. Peck, Proc. Biol. Soc. Wash. **47:** 187. 1934.

Type locality: "2 miles east of Aumsville, Marion Co." (Oregon). type: *M. E. Peck 16291,* July 11, 1930, in the herbarium of Willamette University.

D. pulcherrima M. E. Peck, Proc. Biol. Soc. Wash. **50:** 94. 1937.

Type locality: Silver Creek Valley, 10 miles west of Riley, Harney County, Oregon. type: *M. E. Peck 18919,* June 19, 1936, in the herbarium of Willamette University.

Plants (few) 10—35 cm. high, glabrous except for the hypanthium which is usually plainly scabrous. Leaves 0.5—2.0 mm. wide by (3.0) 8—23 mm. long. Inflorescence few—15 (25) cm. long, loosely or closely (few) 10—20- (35-) flowered. Flower-bracts elliptic to ovate, usually acute, (1.0) 2—7 mm. wide by (6.0) 8—20 (27) mm. long, mostly 3—5 (8) times as long as broad.

Ovary linear, in fruit becoming subulate, usually somewhat angled, upcurved distally, usually prominently twisted near base; mature capsule 1.0—1.5 (2.0) mm. in diameter, 20—40 (50) mm. long, the lateral walls thin and papery, the three valves usually invisible before splitting, with no impressed lines nor hyaline divisions on the hypanthium. Calyx-lobes linear to narrowly elliptic, usually strongly ascending and acute, mostly of two distinct lengths, 1.5 mm. or less in width, (2.7) 4—7 (8) mm. in length.

Corolla 7—12 (16) mm. long, glabrous. Color lavender to deep bright blue; lower lip with central yellow area surrounded by white except at base, where the yellow is continued over two low ridges into the tube; alternating with these low ridges, which are parallel to the long axis of the tube, are three purplish patches which may be faint or entirely absent. Tube about the same color as the limb, or lighter-colored on the lower side.

Corolla-tube (3.2) 3.5—5.5 mm. long, nearly cylindrical but slightly dilated distally, the lateral sinuses usually slightly deeper than the dorsal one and cut very slightly below the plane of the lower lip; tube measured to dorsal sinus 4.0—6.5 mm. long. Two upper corolla-lobes acute, linear-lanceolate or linear-oblanceolate, rarely broader, slightly divergent, erect or slightly curving backward, 1.0—1.5 (2.2) mm. wide; (4.0) 5.0—7.0 mm. long. Lower lip plane or slightly concave, the lobes oblong to obovate, rounded and mucronate.

Filament-tube 2.0—4.0 (5.0) mm. long, glabrous, the filaments united their whole length or nearly so; base of anther-tube usually covered by dorsal side of corolla-tube; anther-tube (1.7) 2.0—2.5 (3.1) mm. long, the anthers somewhat pubescent on the backs; two shorter anthers prominently white-tufted at tips and each bearing a short horn-like process as well.

Seeds usually shining as if varnished, with no lines visible at a magnification of 20×, not twisted. Placentae truly parietal; central septum none.

Wet soil, usually in heavy clay, vernal pools, banks of sloughs, small ponds and streams, ditches and wet depressions in fields. Central and western Washington south to Humboldt County, California, mostly west of the Cascade Ranges. Collected in flower and fruit throughout the summer, mostly from June 1 to August 1.

Specimens examined: CALIFORNIA—HUMBOLDT: Alton, *J. P. Tracy 3781* (NB, US); near Fortuna, *A. A. Heller 13771* (F, NB, S); Hydesville, *V. Rattan* in 1878 (S); near Hydesville, *J. P. Tracy 3271* (G, UC, US); Rohnerville, *J. B. Feudge 108* (P). SISKIYOU: S. side Mt. Shasta, *H. E. Brown*, July 1897 (NB); n. side of Mt. Shasta, *H. E. Brown 480*, July 1–15, 1897 (NB, S, US) and *H. E. Brown 980* (F).

OREGON: Without loc., *E. Hall* in 1871 (G); Pelican Ranger Sta., Crater Forest, *Brown & Murray 121* (FS); Willamette Valley, *T. Howell 1678* (NB); COOS; Myrtle Point, *G. A. Holzinger 59* (US). CURRY: east of Lowery's, bluffs of Rogue R., *L. F. Henderson 11728* (Ore). DOUGLAS: Near Drain, *G. C. Kimber 59* (NB, S); n. of Yoncalla, *A. A. Heller 14707* (NB, US); near Sutherlin, *Eastwood & Howell 2831* (CalAc). HARNEY: 40 mi. s.e. of Burns, *J. W. Thompson 13280* (NB); Silver Creek Valley 10 miles w. of Riley, *M. E. Peck 18919* (WU). JACKSON: Desert of Sam's Valley, *Henderson 12407* (Ore); near Medford, *J. B. Leiberg 4117* (Ore, US); 30 miles e. of Medford, *J. H. Heckner*, June 1927 (S, WU); nr. Woodville, *M. E. Peck 3137* (WU); n. of Medford, *J. W. Thompson 10293* (NB, S). JOSEPHINE: Grant's Pass, *C. V. Piper 6141* (Cath, G, US). LANE: Florence, *W. S. Cooper 33–166* (UC); nr. Eugene, *Patterson*, without date (Ore); Noti Road, *Henderson 16608* (Ore); 9 mi. n.w. of Eugene, *L. F. Henderson 16360* (Ore). MARION: Salem, *E. Hall* in 1871 (F); 2 miles e. of Aumsville, *M. E. Peck 16291* (WU, TYPE); 1 mile east of Salem, *J. W. Thompson 2666* (S); Salem, *Mrs. L. Reynolds*, without date (WU); Salem, *M. E. Peck 3134* (WU). WASCO: Near Dalles City, *W. N. Suksdorf 1552* (F, G, NB, Ore, S, US).

WASHINGTON: "Yakima Region. Simcoe Mts. & Klickitat," *T. S. Brandegee* in 1882 (F, UC); "La Camas Meadows," *Gorman 5006* (Ore). CLARK: Lacamas Cr., *C. English, Jr. 422* (US). DOUGLAS: Wilson Creek, *Sandberg and Leiberg 6219*, June 1893 (NB); without collection no. (F, O, UC); near Wilson Creek, *Sandberg and Leiberg 287* (NB, Ore, US); junction of Crab and Wilson Creeks, *Sandberg and Leiberg 287* (CalAc, F, G, O, UC). KLICKITAT: Rockland, *W. N. Suksdorf 2763* (G). LEWIS: Chehalis, *J. M. Grant*, Aug. 1917 (NB, US); Centralia, *M. E. Jones*, June 21, 1902 (P); Lewis & Clark State Park, *J. T. Howell 7347* (CalAc). MASON: 20 miles s.w. of Shelton, *W. J. Eyerdam 1232* (F, UC).

This species has usually been confused with *D. elegans*, although the two are easily distinguished by the totally dissimilar corollas and stamens (see figures 2, 11). The ranges of the two species overlap to some extent in western California, Oregon, and Washington, and it is possible that some hybridization has taken place between them. This will be discussed under *D. elegans* var. *brachypetala*. The other species with which *D. willamettensis* might possibly be confused, in the southern part of its range, are *D. concolor* and *D. cuspidata*. If mature fruit is available, *D. willamettensis* is at once separable from the others; in the absence of fruit *D. concolor* may at once be eliminated by the ciliate upper lobes of the corolla and the large purple area at the base of the lower lip; *D. cuspidata* may be distinguished by the absence of purple coloration at the base of the lower lip, and by the seeds, which are twisted even when young.

13. DOWNINGIA ELEGANS (Dougl. ex Lindl.) Torrey, U. S. Expl. Exped. **17**: 375. 1874.

Plants mostly 10—40 (50) cm. high, glabrous except for the scabrous hypanthium; stems mostly stoutish, sometimes 4 mm. in diameter at base. Leaves 0.2—4.0 (6.0) mm. wide by 5—25 mm. long. Inflorescence few—20 (30) cm. long, loosely or closely few—25- (50-) flowered (the mean about 10 flowers); inflorescence-axis well-marked and straight, usually much overtopping the early flowers. Flower-bracts elliptic to lanceolate or ovate, (1.0) 2.0—9.0 mm. wide by (6.0) 8.0—26.0 mm. long, usually 3—6 times as long as wide.

Ovary linear, in fruit becoming subulate, the mature capsule broadest near the base, (1.0) 1.5—2.0 mm. in diameter by (15) 25—45 (55) mm. in length, terete or somewhat angled at maturity. Lateral walls papery and easily ruptured when dry, splitting along longitudinal lines but with no evidence of impressed or hyaline divisions. Calyx-lobes linear or elliptic, broadest about the middle, obtuse or subacute, 1.0—2.5 mm. broad by (3.0) 4.0—10.0 (14.0) mm. long, ascending.

Corolla glabrous, minutely roughened within at base. Color "blue," "wisteria blue," "deep navy blue," varying to "lavender-pink" or pure white; lower lip with central white spot, this marked near base by two low yellow ridges which are distinctly white-margined; corolla-tube lighter, with purple veins and often with three oblong purple blotches at very base on the lower side.

Corolla-tube broadly funnelform ("campanulate," according to Jepson), the lateral sinuses usually much deeper than the dorsal one. Two upper lobes ascending and somewhat divergent, acute, lanceolate or elliptic, 1.0—2.5 mm. wide by 3.5—13.0 mm. long. Lower lip concave, in length somewhat exceeded by the two upper lobes, not reflexed nor forming an angle with the tube, the three lobes parallel, in shape oblong, ovate, or deltoid, acute, 2—4 mm. long.

Filament-tube glabrous, the filaments united their whole length. Anther-tube 0.6—1.0 mm. in diameter, usually strongly incurved and often standing at right angles to the filament-tube; anthers bluish-gray with white connectives , these forming (usually) conspicuous longitudinal bands; anthers smooth and glabrous or few-ciliate, not scabrous nor granular-roughened, the two shorter anthers white-tufted at tip, each with a short, usually recurved, hornlike process as well.

Placentae truly parietal; central septum none. Seeds not twisted.

KEY TO THE VARIETIES

1. Filament-tube 4.5—10.5 mm. long; corolla 8.0—18.0 mm. long .... var. *elegans*
1. Filament-tube less than 4.5 mm. long; corolla 5.0—9.0 mm. long .... var. *brachypetala*

13a. DOWNINGIA ELEGANS var. **elegans** McVaugh, nom. nov.

Downingia elegans (Dougl. ex Lindl.) Torrey, l.c.

Clintonia elegans Dougl. ex Lindl., Bot. Reg. **15**: t. 1241. 1829. *Type locality:* "Plains of the Columbia, near Wallawallah R., and near the head springs of the Multnomah." TYPE: Not seen.

Gynampsis flexuosa Raf., Herb. Raf. 48. 1833, nomen nudum. *Type locality:* "Oregon Mts." TYPE: Not seen.

Clintonia corymbosa A.DC., DC. Prodr. **7**: 347. 1839. *Type locality:* "In America bor. occid." TYPE: Columbia River, *David Douglas* in 1830, in the DeCandolle Herbarium, Geneva, Switzerland, not seen. Photograph of type in the herbarium of the National Arboretum, Washington, D. C.

Bolelia elegans Greene, Pittonia **2**: 126. 1890.

Downingia corymbosa (A.DC.) A. Nels. & Macbr., Bot. Gaz. **55**: 382. 1913.

Corolla 8—13 (18) mm. long; corolla-tube (1.5) 2.0—3.2 (4.3) mm. long (measured to lateral sinuses) and (3.3) 4.0—5.5 mm. long (measured to dorsal sinus). Filament-tube (4.5) 6.0—8.0 (10.5) mm. long; anther-tube (2.2) 2.5—3.5 (4.0) mm. long.

Vernal pools, mud flats, muddy borders of ponds, grassy meadows, wet roadside ditches, sometimes partially immersed; at middle altitudes, the maximum being about 2000 meters. Northern Idaho and northeastern Washington south in mountain ranges to Elko County, Nevada, and Plumas and Humboldt Counties, California. Flower throughout the summer, from June 1 to September 1; an occasional collection in late May or in early October.

Included in this variety is *D. elegans* forma *rosea* St. John, Res. Stud.

St. Coll. Wash. 1:105. 1929. The TYPE was collected 3 miles east of Princeton, Latah County, Idaho (*H. St. John 9627*). The writer has seen isotypic material of this form, the flowers of which are stated to be "lavender-pink" instead of the usual blue.

Specimens examined: Locality unknown: "Rocky Mts.," *Geyer 665*, in 1845 (NB); "Oregon and northern California," *Wilkes exp. 532 bis* (US); "U.S. Exploring Expedition, under Command of Capt. Wilkes," without date (NB); "Cult., Hort. Cantab.," July 1868 (Torrey Herb.) (NB); "Morelia, Michoacan," *Bro. Arsene*, Feb. 1911 (F).

California: Without loc., *Mrs. R. M. Austin* (ELG, NB); without loc., *J. G. Lemmon 174* (F, NB); Upper Sacramento, *F. W. Morse* in 1886 (ELG); Sierra Nev. Mts., *J. G. Lemmon* in 1875 (US); Sacramento River, upper Sacramento Valley, *Hall & Babcock 4023* (NB, R, UC, US); Indian Valley, *A. W. Roberts*, May 10, 1872 (NB); Haywards, *Lemmon herb.*, without date P, US); ⅛ mile below McCullom's Mill on Klamath River, *M. S. Baker 8290* (CalAc); Lake Tahoe, *Harry Edwards 545* (NB). DEL NORTE: 2 miles e. of Gasquet, *Parks & Tracy 11327* (UC); Gasquet, *F. W. Peirson*, July 13, 1923 (P). HUMBOLDT: Without loc., *Chesnut & Drew*, Aug. 1888 (UC); near Jarnigan's, *Chesnut & Drew*, July 10, 1888 (UC); 6 miles n. of Garbersville, *F. W. Peirson 3871* (P); Miranda, s. fork Eel River, *D. K. Kildale 5231* (S). LASSEN: Hall's Flat, Sec. 20 T33N, R7E, *G. A. Fischer 34* (FS). MENDOCINO: Without loc., *H. N. Bolander 6570* (F, US); Mendocino Creek, *State Survey 6570* (UC). MODOC: Rim Rock Valley Reservoir, Devil's Garden, *L. C. Wheeler 3916* (G, NB); Willow Creek Valley, *Mrs. R. M. Austin*, June 1894 (NB, UC); Willow Creek, Devil's Garden, *Mrs. R. M. Austin 119*, July 1895 (P, US); Goose Lake Valley, *Mrs. R. M. Austin 277*, July 1894 (UC) and August 1894 (NB, S); Goose Lake, *Mrs. C. C. Bruce*, July 1899 (S); Egg Lake, *M. S. Baker*, July 25, 1893 (G, NB, UC); Egg Lake, *L. S. Smith 1368* (FS); Little Hot Spring Valley, *M. S. Baker*, June 15, (UC); Mt. flats, 6500 feet, *M. F. Gilman 644* (UC); Forestdale, *F. P. Nutting*, in August (P); Sibley Draw, Modoc N. F., *Ivar Tidestrom 3660* (Cath). NEVADA: Near Truckee, *E. L. Greene*, July 25, 1895 (ELG, O); Master Valley near Truckee, *C. F. Sonne*, July 25, 1895 (NB); w. of Sardine Valley, *C. F. Sonne*, July 18, 1884 (F, S); near Russell Valley, road to Sardine Valley, *C. F. Sonne*, July 18, 1885 (P); Truckee River at Malheur Dam, *C. F. Sonne*, Sept. 20, 1885 (P). PLUMAS: Greenville, *M. S. Clemens*, June 8, 1920 (CalAc, NB); 7 miles s. of Chester, *Mrs. H. P. Bracelin 695* (CalAc, Cath, F, NB, Ore, P, R, S, UC, US); between Vinton and Beckwith, *Heller & Kennedy 8677* (CalAc, F, G, NB, P, S, US); Charlie's Valley, Sec. 26, *Sawyer 159* (FS); Blairsden, *A. J. Rosenberg*, July 20, 1917 (CalAc, US); Taylorsville, *M. S. Clemens*, June 12, 1920 (CalAc); Gray Eagle Canyon, *Mrs. Chas. Durbrow*, July 1918 (CalAc); Prattville, *M. E. Jones*, July 3, 1897 (NB, P, R, US); Prattville, *Mrs. A. L. Coombs*, July 7, 1902 (NB, R, S, UC, US) and summer 1906 (CalAc); Prattville, collector unknown, July 4, 1892 (UC); between Prattville and Chester, *D. D. Keck 1716* (CalAc, P, S); Lake Almanor, near Prattville, *J. T. Howell 2166* (CalAc); near Lake Almanor, *F. W. Peirson 6802* (P); Big Meadows, *Mrs. R. M. Austin* in 1880 (UC); *Mrs. R. M. Austin & Bruce*, July 1897 (G), *Mrs. A. L. Coombs*, Sept. 1912

(CalAc, G, US); without loc., *J. M. Coulter* in 1876 (F); *Mrs. Austin* in 1879 (F, O) and in 1876 (US); *Mrs. Ames* in 1873 (G, NB). SHASTA: Goose Valley, *Eastwood 745* (CalAc) and *978* (G, NB, US); Anderson, *W. W. Jones 296* (G); Fall River Springs, *Hall and Babcock 4197* (P, UC). SIERRA: Loyalton, *A. Eastwood 7834* (CalAc); Campbell's Hot Springs, *J. A. DeCou 460* (UC); Sierra Valley, *Hall & Babcock 4464* (UC); Sierra Valley, Hot Springs, *W. R. Dudley*, Aug. 26, 1909 (S); Sierra Valley, *J. G. Lemmon*, without date (G); without loc., *Lemmon 136* (G). SISKIYOU: Weed, *L. E. Smith 386* (CalAc, G, US). TRINITY: Without loc., *V. Rattan*, June 1883 (G); Hyampom, *V. Rattan*, June 1883 (S); Hyampom, *Bolander*, without date (S).

IDAHO: Priest River Forest Reserve, *J. B. Leiberg 2862* (Ore, US) and *J. B. Leiberg 162* (US); Middle St. Joseph's River, Coeur d'Alene Mts., *J. B. Leiberg 1275* (G, NB, Ore, UC, US); Thatuna Hills, *Epling & Hauck 9701* (US); "Palouse country and about Lake Coeur d'Alene," *G. B. Aiton*, June–July 1892 (G, S, US); "Pend Oreille river banks," *Dr. Lyall* in 1861 (Oregon Boundary Comm., Ft. Colville to Rocky Mts.) (G); Chacolet Lake, *R. C. Stillinger 15* (US). BENEWAH: St. Maries, *C. C. Epling 8052* (F). BONNER: N. shore of Lake Pend Oreille, *J. B. Leiberg*, July 15, 1888 (ELG, NB); Lake Pend Oreille, *E. L. Greene*, Aug. 9, 1889 (ELG, S); Lake Pend Oreille, *B. W. Everman*, Aug. 7, 1893 (F); Sand Point, *L. M. Umbach 431*, Aug. 24, 1901 (NB); without number, Aug. 24, 1901 (F, S, US); Hope, *D. T. McDougal 942* (F, G, NB); Hope, *A. A. Heller* (No. 942, same collection as that of McDougal, just preceding) (F, S); valley of Lake Pend Oreille, *J. H. Sandberg et al. 942* (CalAc, ELG, F, G, NB, P, S, US). CLEARWATER: 5 miles w. of Weippe, *L. Constance 2025* (R, UC, US). KOOTENAI: "Coeur d'Aleine Lake," *Geyer*, without date (G); "shore of Coeur d'Alene Lake," *S. Watson 247* (G); Farmington Landing, Lake Coeur d'Alene, *J. H. Sandberg et al. 536* (CalAc, ELG, F, G, NB, P, S, US); Lake Coeur d'Alene, *L. Benson 2458* (G, NB, S, US); Lake Coeur d'Alene, *H. J. Rust 406* (US); without loc., *J. H. Sandberg 6467* (UC) and without number, July 1888 (F); without loc., *J. B. Leiberg*, July 1892 (F). LATAH: Moscow, *L. R. Abrams 741* (NB, S, UC); 3 miles e. of Princeton, *H. St. John 9626* (G, NB, Ore, P, R, S) and *9627* (G, NB); Moscow, *L. F. Henderson 4878* (G); Moscow, *Henderson* in 1894 (US). SHOSHONE: Kellogg to Mullan Pass, *Wiegand et al. 2398* (NB).

NEVADA—ELKO: Owyhee, Duck Valley Res., *Nelson & Macbride 2216* (G, NB, R, US).

OREGON: Without loc., *W. C. Cusick 108* (F); without loc., *Rev. Mr. Spalding*, July 31 (G); Elk Creek, 600 m., *J. B. Leiberg 4170* (US); "eastern Oregon," *W. C. Cusick 1753* (ELG, S, UC, US); "Oregon & Washington Terr.," *Wilkes Exped. 5532 bis*, in 1838–42 (NB); Clear Water, *Rev. Mr. Spalding*, without date (G); Barren Valley (Malheur Co.), *Cusick 1261* (G, US); Wallamet, *Tolmie*, without date (G); Blue Mts., *R. D. Nevius* in 1874 (G); Silver Lake to Fort Klamath, *H. W. Furlong et al.*, June 15–July 15, 1901 (UC); Lower Williamson River, *J. B. Leiberg 728* (G, NB, Ore, P, R, S, US); "Big Valley," *Mrs. R. M. Austin & Bruce 2151* (NB, S, UC); "Clark's Creek 3 miles above mouth," *Sheldon 8864* (NB, US); Willamette Valley, *Th. Howell 1678* (NB); Elk Creek, *Leiberg 4170* (Ore). BENTON: Corvallis, *M. Craig 5076* (NB); near Corvallis, *W. E. Lawrence 2027* (S, US); near Corvallis, *E. S. Spalding*, Aug. 24, 1923 (P); 8 miles s. of Corvallis, *J. W. Thompson 4368* (S, US); Jct. City to Corvallis, *L. R. Abrams 8732* (S); Monroe, *P. A. Munz 9899* (P, S); Monroe, *Eastwood & Howell 2860* (CalAc). CLACKAMAS: Gladstone, *C. V. Piper 6191* (G, US); *Th. Howell*, July 1898 (Ore). HARNEY: Near Burns, *L. F. Henderson 8851* (CalAc); Silver Creek Valley, *M. E. Peck 18923* (WU); 5 miles s.w. of Riley, *Mrs. R. D. Cooper*, May, 1914 (WU). JACKSON: Wimer, *E. W. Hammond 251* (NB, US); near Prospect, *A. A. Heller 13483* (F, NB, S, US); Fall Creek, *E. B. Copeland 3471* (CalAc, ELG, G, NB, P, R, UC, US); Butte Falls, *L. E. Smith*, Aug. 1912 (CalAc); lower part of Antelope Cr., *E. I. Applegate 2378* (US); near Woodville, *M. E. Peck 3135* and *3137* (WU); 4 miles s. of Medford, *P. B. Kennedy*, June 11, 1935 (CalAc); High Cascades 30 miles e. of Medford, *J. H. Heckner*, June 1927 (WU); Big Butte Creek, *E. I. Applegate 2524* (US). JOSEPHINE: Grant's Pass, *H. S. Prescott*, June 4, 1912 (F); 5 miles s.w. of Grant's Pass, *F. W. Peirson 3872* (P); 1 mile s.w. of Obriens, *H. S. Yates 5791* (UC); 5 miles w. of Cave City, *Maguire et al. 15290* (R); Takilma, *D. K. Kildale 10163* (S); w. fork Illinois River, near Floyd School, *L. R. Abrams 8631* (P, S); 4 miles e. of Applegate River on Crescent City road, *D. K. Kildale 8223* (S); near Kerby, *J. W. Thompson 12937* (CalAc, NB); 10 miles w. of Kerby, *D. K. Kildale 8148* (S); near Waldo, *W. C. Cusick 2934* (F, G, NB, Ore, P, UC, US); Waldo, *A. A. Heller 14633* (NB, S, US); near Waldo, *J. W. Thompson 4681* (Cath, G, S, US); Waldo, *P. A. Munz 9896* (G, P); 3.5 miles w. of Waldo, *J. T. Howell 6743* (CalAc); Waldo, *A. Eastwood 2118* (CalAc). KLAMATH: 10 miles w. of Beattie, *J. W. Thompson 13192* (CalAc, NB, US, WU); Keno, *M. E. Peck 16771* (S); 15 miles s.w. of Lake of the Woods, *M. E. Peck 16704* (S, WU); Klamath Valley, *Dr. H. M. Cronkhite 47* (G, UC, US); Swan Lake Valley, *F. A. Walpole 2231* (US) and *2239* (US); Swan Lake Valley, *E. I. Applegate 251* (G, US); w. of Klamath Lakes, *K. M. Wiegand et al. 2400* (F). LANE: Eugene City, *Mrs. S. A. Collier*, Sept. 1880 (G); Eugene City, *E. L. Greene*, Aug. 1889 (ELG, NB); 5 miles s.w. of Eugene, *L. Constance 947* (F, G, NB, P, R, S, US); Mackenzie River, *Mrs. A. L. Coombs*, without date (CalAc). LINN: Near Brownsville, *L. F. Henderson 13638* (Ore). MARION: ½ mile n.w. of Detroit, *D. C. Ingram 1371* (FS); Salem, *Drake & Dickson*, July 1887 (F); Salem, *J. C. Nelson 254* (S) and *1629* (G); Salem, *Mrs. L. Reynolds*, without date (WU); Salem, *L. F. Henderson 593* (S, UC); Silverton & Salem, *Elihu Hall 330* (F, G, NB); Silverton, *Elihu Hall* in 1871 (US); near Aumsville, *M. E. Peck 16280* (WU). SHERMAN: Kent, *M. E. Peck 9969* (NB, S, WU). UNION: Without loc., *W. C. Cusick 108* (G); La Grande, *M. E. Peck 3136* (WU); near Island City, *Eastwood & Howell 3464* (CalAc, US). WASCO: Mayers State Park, *Eastwood & Howell 3536* (CalAc); near The Dalles, *J. W. Thompson 11875* (CalAc, G, P, US); near The Dalles, *G. N. Jones 4195* (CalAc). WASHINGTON: Farmington, *J. E. Kirkwood 211* (NB); Gaston, *M. E. Peck 16191* (WU); "Tualitin Plains," *J. Howell*, July 1877 (F); Hillsboro, *T. J. Howell*, July 1881 (F); near Hillsboro, *J. T. Howell 7327* (CalAc).

WASHINGTON: Without loc., *G. R. Vasey 388* (G, NB, US); Topnish Creek, *T. S. Brandegee* in 1882 (UC). CLARKE: Manor, *C. V. Piper*, July 14, 1899 (NB). KITTITAS: Ellensburg, *F. D. Kelsey* in 1888 (ELG); Ellensburg, *K. Whited 569* (US). SPOKANE: Near Spangle, *W. N. Suksdorf 1551* (G, S); 12

miles w. of Spokane, *Sister Mary Milburge 630* (S); Medical Lake, *G. W. Turesson*, July 13, 1913 (R); without loc., *W. N. Suksdorf 146* (NB). STEVENS: Calispell Lake, *F. O. Kreager 316* (G, NB, US); "Fort Colville," *S. Watson*, Oct. 2, 1880 (G). WHITMAN: 2 miles n. of Garfield, *H. St. John 7613* (G, NB, P, R, S); between Moscow and Pullman, *A. Eastwood 13394* (CalAc); Pullman, *C. V. Piper 1728* (F, G, R, S) and without number, July 15, 1901 (P); Pullman, *A. D. E. Elmer 131* (NB, P, US); Pullman, *W. R. Hull 454* (G).

13b. DOWNINGIA ELEGANS var. **brachypetala** (Gandoger) McVaugh, comb nov.

Downingia brachypetala Gandg., Bull. Soc. Bot. France **65**: 55. 1918. *Type locality:* Falcon Valley, Klickitat County, Washington. TYPE: *W. N. Suksdorf 2762*, June 22, 1897, not seen. Isotypes seen in the Gray Herbarium and in the herbaria of Stanford University and of the University of Oregon.

Corolla 5.0—9.0 mm. long; tube 1.5—2.5 (3.5) mm. long, the length when measured to dorsal sinus 3.6—4.0 mm. Filaments 3.0—4.0 mm. long; anther-tube 2.0—2.5 mm. long. Capsule apparently slightly broader in proportion to its length than in var. *elegans*.

Habitat the same as that of var. *elegans*. Range somewhat more restricted than that of var. *elegans;* var. *brachypetala* is the principal representative of the species in Lake and Mendocino Counties, California, whence it extends northward along the Cascade Ranges to southern Washington. A few collections of this variety have been made in northeastern California and in northern Idaho. Flowering season the same as that of var. *elegans*.

Specimens examined: CALIFORNIA—LAKE: Snow Mountain, *T. S. Brandegee*, June 1892 (CalAc); Snow Mt., *Mrs. Brandegee*, Aug. 1892 (CalAc); w. slope of Snow Mt., just beyond Cedar Creek, *M. S. Baker 3478b* (S); Snow Mt. House, *M. S. Baker 3099a* (UC). LASSEN: 10 miles s. of Amedee, *M. E. Jones*, June 22, 1897 (Ore, P, R, US); 10-15 miles w. of Amedee, *M. E. Jones*, June 24, 1897 (NB). MENDOCINO: Sherwood Valley, *W. R. Dudley*, June 17, 1899 (S); Little Lake, *V. Rattan*, June 1882 (S); Willits, *L. R. Abrams 7527*. (S); 1 mile n. of Willits, *D. K. Kildale 5670* (S); middle fork of Eel River, *J. W. Blankinship*, June 8, 1893 (CalAc); Potter Valley, *J. W. Blankinship*, June 5, 1893 (CalAc); Potter Valley, *A. Eastwood 12639* (CalAc); Laytonville, *A. Eastwood*, Aug. 3, 1902 (CalAc). TRINITY: Van Duzen River near Cobb, *L. B. Kildale 10439* (S).

IDAHO—BONNER: Lake Pend d'Oreille, *J. B. Leiberg*, July 15, 1888 (NB). KOOTENAI: Without loc., *J. H. Sandberg*, July 1887 (F).

OREGON—CLACKAMAS: Clackamas, *J. Lunell*, July 8, 1903 (R, US). HOOD RIVER: Hood River, *L. F. Henderson*, July 6, 1880 (Ore), June 30, 1882 (S); near Hood River, *L. F. Henderson 814*, June 7, 1924 (G). JOSEPHINE: Old road to Waldo between Rough & Ready and Dew Creeks, *D. K. Kildale 5831* (S). KLAMATH: Klamath Lake, *Constance 9682* (Ore). MARION: Salem, *L. F. Henderson 593* (F); Salem (locality not certain), *Elihu Hall 330* (NB); Silverton, *Elihu Hall 330* (US). MULTNOMAH: Mt. Scott, *E. P. Sheldon 11166* (F, G, NB, Ore, P, S, US). WASCO: Near The Dalles, *M. E. Jones*, July 29, 1897 (P, US); The Dalles, *Mr. C. Davidson*, June 1886 (P); The Dalles, *T. S. Brandegee* in 1882 (UC); The Dalles, *J. W. Thompson 2818* (S, WU); near The Dalles, *J. W. Thompson 11875* (NB, P); Dalles, *Harford and Dunn*, June 10, 1869 (NB; the label on this sheet is accompanied by that of the widely distributed collection, *Kellogg and Harford 617*, with the simple locality "Oregon"; it is possible that the two collections are in reality one and the same); Dalles of Oregon, *Kellogg & Harford 617*, June 1869 (US). WASHINGTON: Forest Grove, *F. E. Lloyd*, July 6, 1894 (NB); Forest Grove, *C. P. Smith 3692* (S); Tualatin, *M. W. Gorman 5059* (S); north of Gaston, *J. W. Thompson 821* (S) and *2969* (WU).

WASHINGTON—KLICKITAT: Falcon Valley, *W. N. Suksdorf 2762* (G, Ore, S); "western Klickitat County," *W. N. Suksdorf*, Sept. 4, 1881 (F, O); North Dalles, *J. W. Thompson 11124* (CalAc, Cath, G, NB, P, US); Trout Lake near Mt. Adams, *F. E. Lloyd*, Aug. 22, 1894 (NB).

The flowers of *Downingia elegans* are extremely variable in size, both the corolla and the stamens being involved. The filament-tube, usually a flower-part of limited variability in this genus, ranges from 3.0 to 10.5 mm. in length. Measurements were obtained from the plants of 267 collections of this species and these were tabulated as follows:

Length of filament-tube (mm.)	*Number of collections*
3.0	3
3.5	24
4.0	16
4.5	8
5.0	18
5.5	13
6.0	41
6.5	31
7.0	42
7.5	23
8.0	30
8.5	5
9.0	7
9.5	1
10.0	3
10.5	2

The critical point for the upper limit of variability seems here to be at the 8 mm. level. In the other direction, there appears to be a break between 4.0 and 5.0 mm. When the measurements for corolla and anthers, obtained from the same series of specimens, were plotted in like manner, a similar but less sharply defined break was observed in the series. A maximum length of 4.5 mm. for the filament-tube appears to correspond roughly to a maximum length of 9.0 mm. for the corolla and 2.5 mm. for the anther-tube.

The "variety" thus obtained is apparently an arbitrary one, not sharply set off from var. *elegans* either by geographical range or by morphology. Its range is seemingly much more restricted than that of var. *elegans*, the latter being common in northeastern California and northward into Idaho and eastern Washington, while but three undoubted collections of var. *brachypetala* have been seen from the same region.

Most of the material of var. *brachypetala* is an exact match for var. *elegans* in all respects except size of flower. Occasional specimens, however, particularly those from certain regions, have a much longer and narrower corolla-tube, in relation to the rest of the corolla, than is usual in this species. All the collections cited from Snow Mountain, Lake County, California, have flowers of this type, as does the widely distributed collection from Mt. Scott, Multnomah County, Oregon, *E. P. Sheldon 11166*. These plants resemble individuals of *Downingia willamettensis* in which the corollas have become deformed; they are, indeed, sometimes to be distinguished from *D. willamettensis* solely by means of the incurved anther-tube. The capsule of *D. elegans*, when mature, is almost identical with that of *D. willamettensis*. For the present, at least, the writer is unable to make any disposition of these puzzling specimens other than that of lumping them, with the usual small-flowered but otherwise typical *D. elegans*, in var. *brachypetala*. It is noteworthy that the range of *D. elegans* var. *brachypetala* coincides approximately with the area in which typical *D. elegans* and *D. willamettensis* grow together. The two latter species are often closely associated; they are occasionally collected together at the same locality and mounted on the same herbarium sheet for the same species. It is not impossible that var. *brachypetala* may be of hybrid origin.

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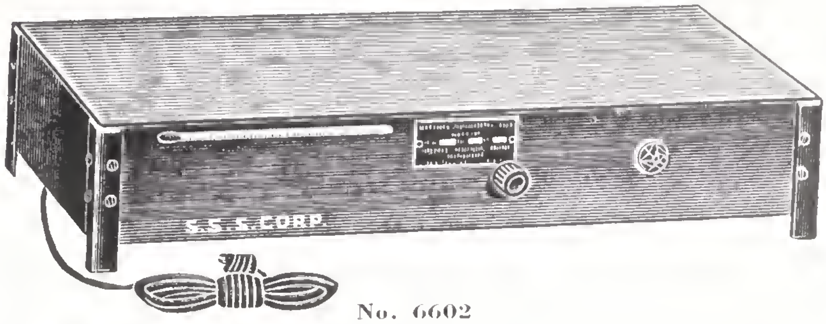

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