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# PSYCHE

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715,

# PSYCHE

INDEX TO VOL. 65, 1958

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## INDEX TO AUTHORS

- Adams, P. A. The Relationship of the Protoperlaria and the Endopterygota. 115
- Blake, Doris H. Some New West Indian Eumolpid Beetles. 91
- Brown, W. L., Jr. A *Formica* Slave-maker Raiding the Nest of a Myrmicine Ant. 39
- The Indo-Australian Species of the Ant Genus *Strumigenys* Fr. Smith: Group of *S. godeffroyi* in Borneo. 81
- Carpenter, F. M. Mexican Snake-Flies (Neuroptera: Raphidioidea). 52
- Christiansen, K. The Collembola of Lebanon and Western Syria. Part III. Family Isotomidae. 59
- Deichmann, Elisabeth. Elizabeth Bangs Bryant. 1
- Parsons, Margaret C. Cephalic Glands in *Gelastocoris* (Hemiptera: Heteroptera). 99
- Wilson, E. O. A Chemical Releaser of Alarm and Digging Behavior in the Ant *Pogonomyrmex badius* (Latreille). 41
- Patchy Distributions of Ant Species in New Guinea Rain Forests. 26
- Wilson, E. O., N. I. Durlach and L. M. Roth. Chemical Releasers of Necrophoric Behavior in Ants. 108
- Woodland, J. T. Oogenesis and Fertilization in *Thermobia domestica* (Packard). 11





## INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

- Ants, 26, 39, 41, 81, 108  
*Anurophorus* ASFOURI, 60  
*Anurophorus* COIFFAITI, 59  
*Aphaenogaster* rudis, 39  
*Ballistura* LEVANTINA, 70  
*Ballistura* schöttli, 70  
 Cephalic Glands in *Gelastocoris*  
 (Hemiptera-Heteroptera), 99  
*Chalcosicya* ALAYOI, 91  
 Chemical Releaser of Alarm and  
 Digging Behavior in the Ant  
*Pogonomyrmex badius* (Latreille),  
 41  
 Chemical Releasers of Necrophoric  
 Behavior in Ants, 108  
 Collembola of Lebanon and Western  
 Syria. Part III. Family Isoto-  
 midae, 59  
 Distribution of Ant Species in New  
 Guinea Rain Forests, 26  
 Elizabeth Bangs Bryant, 1  
 Endopterygota, 115  
 Eumolpidae, 91  
 Fertilization in *Thermobia domes-*  
*tica*, 16  
*Folsomia*, 63, 69  
*Folsomia* candida, 68  
*Folsomia* cavicola, 69  
*Folsomia* penicula, 65  
*Folsomia* quadrioculata, 63  
*Folsomides* americanus, 63  
*Formica* Slave-maker Raiding the  
 Nest of a Myrmicine Ant, 39  
*Formica* subintegra, 39  
 Indo-Australian Species of the Ant  
*Strumigenys* Fr. Smith; Group of  
*S. godeffroyi* in Borneo, 81  
*Inocellia* PILICORNIS, 56  
 Inocelliidae, 56  
*Isotoma* notabilis, 78  
*Isotoma* viridis, 78  
 Isotomidae, 59  
*Isotomina* bituberculata, 71  
*Isotomina* pontica, 71  
*Isotomina* SALAYMEHI, 72  
*Isotomuris* palustris, 79  
 Lepismatids, 20  
*Metachroma* BREDENI, 94  
*Metachroma* CORNUTUM, 93  
*Metachroma* GRANDE, 98  
*Metachroma* MULIPUNCTATUM, 96  
*Metachroma* NANUM, 96  
*Metachroma* ZAYASI, 92  
 Mexican Snake-Flies (Neuroptera:  
 Raphidiodea), 52  
 Oogenesis and Fertilization in  
*Thermobia domestica* (Packard),  
 11  
 Patchy Distributions of Ant Species  
 in New Guinea Rain Forests, 26  
*Pogonomyrmex badius*, 41, 108  
*Proisotoma* minima, 70  
*Proistoma* minuta, 69  
 Protoperlaria, 115  
*Pseudisotoma* ANAMOLA, 76  
 Rain Forests, 26  
*Raphidia* AMERICANA, 54  
 Raphidiidae, 52  
 Relationship of the Protoperlaria  
 and the Endopterygota, 115  
 Snake-Flies, 52  
 Some New West Indian Eumolpid  
 Beetles, 91  
*Strumigenys* DYAK, 81  
*Strumigenys* FORFICATA, 86  
*Strumigenys* indagatrix, 86  
*Strumigenys* MJOEBERGI, 83  
*Strumigenys* SUBLAMINATA, 84  
*Tetracanthella* pilosa, 63  
*Thermobia domestica*, 11  
*Vertagopus* aborea, 74  
*Vertagopus* CILIATUS, 75





# PSYCHE

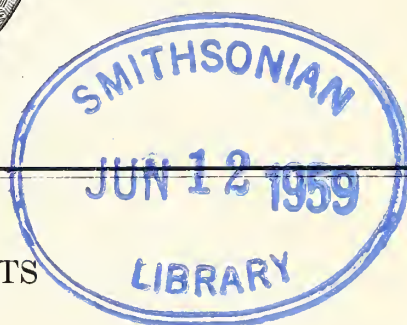
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Vol. 65

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## TABLE OF CONTENTS

Elizabeth Bangs Bryant. <i>Elisabeth Deichmann</i> . . . . .	1
Oogenesis and Fertilization in <i>Thermobia domestica</i> (Packard). <i>J. T. Woodland</i> . . . . .	11
Patchy Distributions of Ant Species in New Guinea Rain Forests. <i>E. O. Wilson</i> . . . . .	26
A <i>Formica</i> Slave-maker Raiding the Nest of a Myrmicine Ant. <i>W. L. Brown, Jr.</i> . . . . .	39

DIY 113  
U.S. MAIL 1958

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ELIZABETH BANGS BRYANT

April 7, 1875 — January 6, 1953

# PSYCHE

Vol. 65

March, 1958

No. 1

ELIZABETH BANGS BRYANT

BY ELISABETH DEICHMANN

Museum of Comparative Zoology

It was some years after I had come to Cambridge that I first met Miss Bryant. At that time (1926) the entomologists had their own entrance, and simply going around and making calls was not encouraged. But after Thomas Barbour became director (1928) and after the Biology Department had moved across the street, she and I became neighbors on the fourth floor. She discovered that I made tea for my lunch and suggested that I come in and drink tea with her, and for more than 15 years I usually had lunch with her about three times a week. She must have been about sixty when we first met and she seemed to change very little with the years. She was of medium height, fairly stout, with regal carriage. She had unwrinkled skin, clear blue eyes and white hair. In some quarters of the museum she was referred to, not unkindly, as "Queen Victoria" and although much taller and with a decidedly retroussé nose, her black dress, snow-white hair and somewhat pendulous cheeks gave her a certain resemblance to that lady. She is the only person I have known who used the word "twaddle", and that with as much emphasis as I imagine Queen Victoria did. Behind her sedate exterior she kept a rather youthful spirit. She was extremely well read with a rich vocabulary of old Yankee expressions and after she had used one of these she would suddenly pretend that she was embarrassed: "Oh, Miss Deichmann, I really should not teach you such language!"

It is perhaps quite characteristic that I never had the slightest idea of what her father had been, while I was



extremely well acquainted with the famous cat of her childhood, so dignified that she and her brother always referred to it as *Mister Verdant Green*. She belonged to a good substantial Boston family and seemed to be related to a large number of prominent persons, which did not prevent her from expressing her, not always high, opinion of these relatives. She had evidently had an extremely happy childhood and a youth filled with trips to Europe and the typical Bostonian's cultural interests. The family had even been so progressive that they had allowed her to go to Radcliffe, which definitely was the great adventure of her life, as for all women of her generation who suddenly were allowed to get the same education as their brothers. She belonged to the class of 1897 but she did not graduate. There may have been illness in her family, or it may have been just at that time that her family, as well as many other substantial Bostonians, were rather hard hit financially. Her interests were with natural history and she became early acquainted with the men in the Boston Natural History Museum and those connected with the Agassiz Museum, and in the latter institute she was soon given the little division of spiders to take care of. In her younger days she was an eager field worker: there was a widespread interest in nature study in Boston and she took part in many botanical and zoological excursions and built up quite a collection of New England spiders. Her father died rather early and after that time she took care of her mother for many years, while she regularly appeared in the Agassiz Museum three times a week, but her outdoor activities became quite naturally restricted and her circle of acquaintances limited to men much older than herself, Mr. Samuel Henshaw, Mr. Faxon and especially Mr. J. H. Emerton, who was delighted to see a younger person take over in the spider field.

In the museum she had been fortunate to be allotted a small division. With the myriapods and mites in two neighboring rooms, she was able to have all the spiders around her. She learned to type and besides she wrote hundreds of cards and labels in her precise, clear hand. Her reprint collection was well cared for, with binders which

she bought herself. Her first paper came in 1908; it was merely a list of local species, but it had probably taken some persuasion from her good friend, Mr. Emerton, to let her to allow her name to appear in print. It was 15 years later that her Barbados-Antigua report was published, and then, around 1930, she really began to be a regular contributor. Very likely it was the stimulus she received when Dr. Barbour saw to it that this volunteer worker of almost 30 years standing at last received a small salary. She steadfastly refused to be listed in *American Men of Science*, feeling that that was to intrude into the ranks of professionally trained, and no argument could change her position on that point. It was a great joy to her when other arachnologists visited her and she was always helpful to beginners who came to seek her advice. When somebody brought in a spider she would tell all about its habits and occurrence, and she never crushed the collector with a remark that it was one of the most common forms. "It is such a long time since I have had occasion to see a live specimen of this spider," — so the person went off feeling that his efforts had been fully appreciated.

Her main scientific work was not started until she was 55 years old, and continued to her death. Several large papers on West Indian spiders were illustrated by her clean pen drawings. She was handicapped in her work by an inadequate microscope and light (a modified automobile spotlight). She worked independently of all but a few colleagues in arachnology.

For several years her mother's health was failing and she looked after her with unswerving fidelity. After her mother's death she moved from the house in Allston to a pleasant top floor apartment in Brookline. It looked as if she was going to have more freedom and our long planned trip to St. Lucia in the West Indies, the type locality for so many of the West Indian spiders, seemed near to becoming reality, when the old housekeeper's health gave out and Miss Bryant undertook to care for her, most scornful of the idea that the housekeeper should be put in a Nursing Home.

There was one unusual activity in which Miss Bryant



indulged, and that was taking care of her investments. After her father's death, her mother, mindful of the debacle of some years before, made arrangements, so that she got a fixed income and divided the family fortune between the two children. That was in the happy days before the income tax had been invented. The usual course would have been that Miss Bryant's share be put in a trust fund, but here her old friend, Mr. Henshaw, intervened. She took, as always, his advice and developed into an extremely shrewd and careful investor. Through her interest in her investments, by reading newspapers and magazines, she acquired an unusual understanding of what was going on in the United States and in the world as a whole, and her down to earth realism and a total lack of sentimentality made conversations with her extremely interesting.

In addition to her indisputable business ability, which would have made her a gift to a brokerage firm, she possessed also the virtue, thrift. She saw to it that nothing was wasted in her house, got the utmost wear out of her few garments and she kept all unnecessary expenditures down to zero. She subscribed to a few magazines which she knew she could manage to read, and the back numbers were quickly passed on to some other person for whom she was happy to save the cost of a subscription. While despising people who made themselves miserable by being "penurious" she enjoyed her own little pet economies. For years she would happily trot down a few blocks so that she could get home on the 5 cent fare, and until her last illness it was our monthly joke when she handed me her check for the Faculty Club and asked me to take it over to Harvard Square when I was paying my own bill, adding with mock seriousness: "I just can't *bear* spending 3 cents on such a short distance, and the bus no longer sets me off in Harvard Square."

She felt her responsibility toward the needy, particularly children and old people, and she insisted on knowing where the money went. She saw to it that nothing was lost between her hand and that of the recipient. She lived for years in a rather poor district where as she once expressed it: "They are counting on my contribution" — and they got it. At



one time an over eager Community Chest agent tried to persuade her to give her large contribution through the Museum instead of just the token which she usually gave. But she was adamant, her contribution was going to where it had been going for years, long before the Community Chest had been established. The argument became rather heated: "It was her duty toward the Museum." Then Miss Bryant got up: "My resignation shall be on the Director's desk this afternoon!" The subject was quickly dropped.

When she had been fifty years out of college she received an honorary Phi Beta Kappa membership from Radcliffe as the one of her class who had made the most out of her education, and this was a great pleasure to her. But she appreciated it even more when, at about the same time, she was taken into the Radcliffe Sigma Xi, for this enabled her to get into contact with young people, a pleasure which her duties toward her mother had prevented for years. Contrary to her custom of never going out in the evening, she would attend all their evening meetings.

She continued working after her retirement in 1950, it seemed almost with even greater vigor than before. Several years before that time the difficulties the museum had, and still would have for years, regarding decent pay to the curators were clearly seen by us all; she had also seen how the Boston Natural History Museum had packed several collections aside and had given others away to where they could be used, and she realized that a similar fate might well befall the collections which she was in charge of. Suddenly she realized that she was able to act so that this should not happen. It was with deep emotion that she one day came to me and told me that she had radically altered her will so that the work could go on after her death and she was a changed person from that moment. Her plans for her work became bolder and she decided to get a new and better microscope even at this late time of her life.

It was when I came home from a trip in the fall of 1952 that she informed me that she was not feeling well and that an operation was necessary because of stomach cancer. After the operation I saw her two or three times a week at her home and our conversations went on almost as if she

were still in her office in the Museum. She admitted she was feeling oddly "lighthearted" and there were a few moments when she almost believed that she might get well enough to come back for a short time and do a little work. But when her new microscope at last arrived she sent it straight back to the Museum. At first she was well enough to get up and come out and wave goodby to me on the stair case, later she asked to be excused. The end came on January 6, 1953.

Her will was a model of careful consideration of the needy in the community and her family. Two of the larger bequests, of equal amounts, went to Radcliffe College, which had given her her education, and to the Museum, where she had been able to make use of it. With her usual reticence she had in the latter case succeeded in keeping her name hidden. The bequest was simply named the "Emerton Fund" in honor of the old arachnologist who had taught her to draw and encouraged her in her work.

There were also two small bequests each of 500 dollars to the two Radcliffe Honor societies. In the case of Phi Beta Kappa the money helped to hasten the completion of the \$10,000 Scholarship Fund which this old and fairly wealthy chapter had been working on, and her name was duly added to the Memorial Roll. In the case of the much younger, smaller, and anything but wealthy Chapter of Sigma Xi, the sum, with interest and smaller gifts added, was some years later voted to be used as the nucleus of a much needed loan for Radcliffe science students, and was named the "Elizabeth Bangs Bryant Loan Fund of Sigma Xi."

The following is the known list of her publications:

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OOGENESIS AND FERTILIZATION  
IN *THERMOBIA DOMESTICA* (PACKARD)<sup>1</sup>

BY JOHN T. WOODLAND

State Teachers College, Salem, Massachusetts

The materials and methods used in this study were the same as those described in an earlier paper (Woodland, 1957).

*Oogenesis*

The primary oocytes in the vitellarium reach a length of about 420 microns just before yolk accumulation begins. They measure only about 45 microns wide. Each has a large central nucleus about 40 microns in diameter. It is a typical vesicular oocyte nucleus and usually has a visible nuclear membrane. A fine network is visible throughout the nucleus and there is a large, eccentric, irregular, granular nucleolus which may be as long as 20 microns. Neither network nor nucleolus is Feulgen-positive. The finely-divided chromatin is so scattered throughout the large nucleus that it is barely visible. The cytoplasm appears very finely granular and contains a few inclusions. These are 10 to 15 microns in diameter and consist of a dozen or less clumped globules.

When each of the vitellaria contains four or five of these oocytes, yolk accumulation begins. It starts peripherally in all of the oocytes simultaneously and gradually proceeds toward the center. There appear scattered through the peripheral cytoplasm tiny globules which stain bright orange-red with Mallory's triple stain. They greatly resemble the globules of protein reserves scattered through the fat body surrounding the ovarioles, but are usually a little smaller. The negative images of small fat droplets also occur in the peripheral cytoplasm. The fat droplets and proteinaceous globules increase in size, forcing the diminishing cytoplasm into a network around them. By

<sup>1</sup>The research was carried out at the Harvard Biological Laboratories, Cambridge, Massachusetts, in partial fulfillment of the degree of Doctor of Philosophy.

the time that small fat droplets begin to appear in the center of the oocyte, the peripheral droplets and proteinaceous globules have greatly enlarged (3 to 7 microns in diameter) and are present in about equal numbers. The diminishing central layer of cytoplasm around the nucleus is connected by the fine network between the yolk globules to a thin peripheral cytoplasmic layer, the periplasm. By the time the perinuclear cytoplasm has become very thin, the fat droplets appear to have coalesced, for the visible proteinaceous yolk globules, some of which are now as large as 11 microns in diameter, stand out in fixed preparations against a clear background.

The oocyte has been growing only slightly meanwhile, and is still very narrow in proportion to its length. Before oviposition the maximum length of the egg increases by about two and one-half times, and its maximum width increases about eighteen times. Growth is accomplished chiefly by an increase in the proteinaceous yolk. Just before oviposition the egg contains relatively little fatty yolk.

At the start of the growth period the nucleus moves to the periphery. The nuclear network condenses at the periphery of the nucleus and the chromatin becomes distinctly visible with the Feulgen technique. Evidence of tetrads is seen. The interior of the large nucleus now appears homogeneous and has little affinity for the stains used. Before oviposition there occur both a marked decrease in nuclear volume and further condensation of the chromatin into small compact chromosomes.

The follicle cells start to secrete the endochorion at the time when yolk accumulation first begins. The process is best studied in preparations stained with phosphotungstic hematoxylin. Just before secretion of the endochorion starts, the brown-staining connective tissue sheath surrounding the ovariole becomes greatly thickened. It appears that the follicle cells withdraw material from the sheath and secrete it to form the endochorion. Comparison with the accompanying process of yolk accumulation indicates that the sheath is reduced to its former size within a relatively short time. The secretion of the exochorion, which occurs much later, is mentioned below.



The external appearance of the newly laid egg of the firebrat has been described by Adams (1933), Sweetman (1938), and Remington (1948). The present study reveals that the endochorion (Fig. 5, EN) is about 2 microns thick. Its thickness does not vary appreciably over the whole egg. There adheres to its outer surface a single layer of spherical droplets, each about 11 microns in diameter immediately after oviposition. The droplets are rather irregularly placed, but tend to be in groups with large intervening spaces. In the spaces are droplets many times smaller than the large ones. Within a few hours a change occurs. The large droplets break up into rather evenly spaced ones about 3 microns in diameter (Fig. 5, CD). Usually a space of 2 microns now occurs between droplets, although pairs of contiguous droplets are sometimes seen. The very minute droplets are still scattered among the larger ones. The appearance of the droplets is essentially the same on shed chorions long after the nymphs have left them. Possibly the droplets are present as a thin continuous film before oviposition.

The droplets adhere firmly to the exochorion. A few individual droplets are separated from it by sectioning, but the other procedures to which the eggs have been subjected practically never dislodge them. In contrast, the exochorion is loosened from the endochorion when the egg contents shrink during fixation, owing to dissolution of the fatty elements. Moreover, the exochorion is normally loosened from the endochorion during development, as the volume of the egg contents is diminished slightly. The surface of the endochorion is then seen to be reticulated into hundreds of small polygonal areas. Most of these polygons are fairly regular hexagons with diagonals usually between 55 and 85 microns long. The wall separating adjacent areas is 5 microns thick.

Sweetman (1938) supposed this hexagonal reticulation to be produced by the cells of the embryonic tissues, but the present study showed it to be produced by the follicular cells that secreted the endochorion. The large size of the hexagons emphasizes the amount the egg has grown since the endochorion was secreted.

The endochorion is hardly ever loosened at all from the yolk and no vitelline membrane has been found between them. Heymons (1897) reported a vitelline membrane in *Lepisma saccharina*, but Uzel (1898), who studied the eggs of the same lepismatid, did not mention it.

Between the exochorion and the endochorion at the anterior end of the egg is the micropylar area, a circular thickening about 280 microns in diameter (Fig. 5). The thickening consists of as many as twenty or more concentric lamellae, each about as thick as the exochorion, with which the thickening is identical in staining reactions and to which it adheres if the latter becomes loosened from the endochorion. The thickening is thinner peripherally than centrally, since not all of the lamellae extend to the margin of the area.

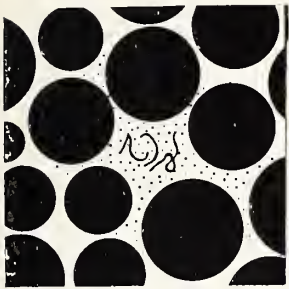
In the micropylar area are found three small infundibular depressions which, if connected, would form the corners of an equilateral triangle. Two of the depressions are shown in figure 5 (DP). The depressions, which can rarely be demonstrated to penetrate the micropylar thickening completely, are filled with folds of the exochorion and with the chorionic droplets described above. There sometimes ap-

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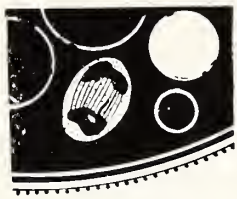
#### EXPLANATION OF PLATE 2

All figures represent portions of sections. Fixative: Maximow's. Stain: Feulgen's all figs. except 2 and 5; Mallory's triple, figs. 2 and 5. Magnifications approximate. Fig. 1. 20 minute old egg, showing sperm head accumulating cytoplasm, 400 x. Fig. 2. 30 minute old egg, showing egg nucleus in anaphase of first maturation division, 500 x. Fig. 3. 2½ hour old egg, showing egg nucleus in anaphase of second maturation division, 500 x. Fig. 4. 75 minute old egg, showing late telophase of first maturation division; secondary oocyte nucleus forming in upper left, first polar body in lower right; 500 x. Fig. 5. Longitudinal section through micropylar (anterior) end of 2 hour old egg, 160 x; CD, chorionic droplet; DP, depression; EN, endochorion; EX, exochorion; EXT, exochorionic thickening. Fig. 6. 90 minute old egg, showing late stage in the contraction of the sperm head, 1250 x. Fig. 7. Egg about 2 hours old, showing male pronucleus during its growth period; 1875 x. Figs. 8-11. 3 to 4 hour old eggs, 1250 x. Fig. 8. Early stage of union of male and female pronuclei. Fig. 9. Female pronucleus shown near top just entering the sperm plasm; male pronucleus (below). Fig. 10. Female pronucleus (below) and male pronucleus (above) about to unite. Fig. 11. Late stage of union of male and female pronuclei.

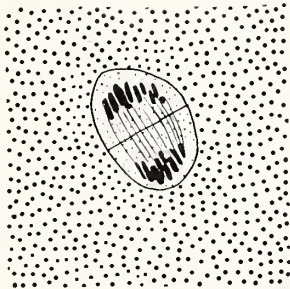




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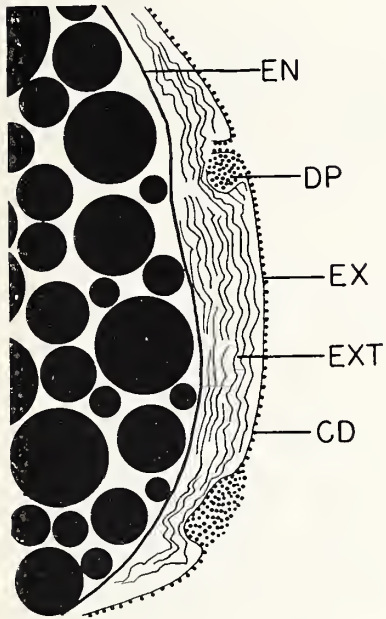
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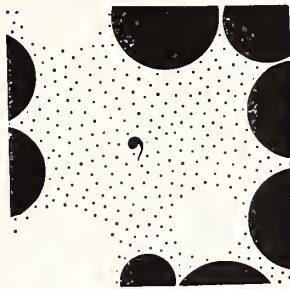
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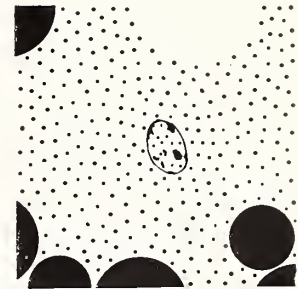
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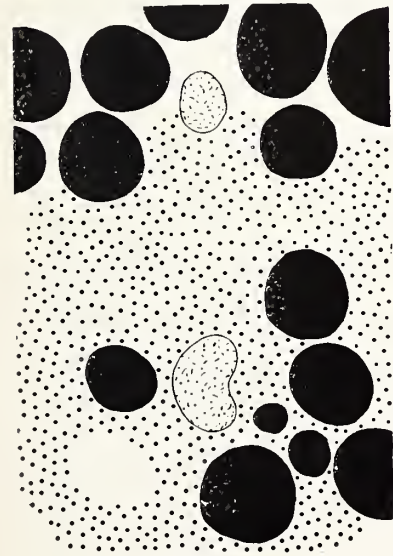
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8



11



pears to be an opening through the exochorion where it dips into a depression (Fig. 5), but no opening through the endochorion was found. Other evidence suggests that there is none. Eggs completely immersed in tap water at 37.5° C. for a period of 3 or 4 days during incubation hatch into healthy nymphs in about the normal time. (Hatching itself occurs under water, but the nymphs cannot get their abdomens out of the shell. This is because they cannot get traction and also occurs in a small percentage of eggs hatching in an empty glass container.) If openings completely penetrated the chorion, then water should be expected to enter the egg by osmotic pressure and cause it to burst. If eggs are kept in tap water for as long as seven days, the incubation period is prolonged by several days and only about half of the eggs hatch at all. Those not hatching do not burst nor are they turgid. Presumably they die from oxygen lack, as the water was not mechanically oxygenated.

The follicle cells appear to become a syncytium during the enlargement of the oocyte. This syncytium probably secretes the micropylar thickening and the thin structureless exochorion just before the oocyte leaves the ovariole. The chorionic droplets are believed to be added as the egg passes through the lateral oviduct, for droplets of similar appearance have been seen in the cells of the oviducal epithelium of females with large oocytes in the ovarioles.

#### *Fertilization*

After the oocyte leaves the gonopore but before it proceeds down the ovipositor, it is undoubtedly held at the base of the ovipositor for a few moments while sperms are discharged onto it by the spermatheca. The sperms presumably enter the probable openings in the exochorion over the depressions in the micropylar thickening. They can apparently penetrate the endochorion directly. They would not have to penetrate the endochorion directly under the micropylar thickening, but could pass between the lamellae of the thickening and enter nearer the equator of the egg. Whether the entire sperm penetrates the egg was not determined. Within the freshly laid egg, however, may usually be identified from one to six of the very long sperm heads,

each of which is bent and coiled upon itself many times.

The contents of the living, freshly laid egg appear to consist of colorless yolk spheres in a colorless liquid of low viscosity. The spheres are about 10 to 15 microns in diameter. In sections of eggs fixed with Maximow's fluid the negative images of the fat spheres measure 9 or 10 microns in diameter. Most of the more numerous, visible, proteinaceous yolk globules are 14 or 15 microns in diameter. Some of these globules appear structureless, while others appear finely granular. The globules appear only very slightly flattened at the poles with Maximow's fixative. The other fixatives used always badly distorted the yolk of young eggs. The yolk spheres and liquid fill the entire egg. Cytoplasm was not identified.

Perrot (1933) stated that the first maturation division occurs while the oocyte is still in the ovariole. He was not able to find any trace of the prophase of the division. He reported that the mitotic figure occupies a very small space at the periphery of the oocyte and figured the anaphase of the division. He stated further that after this first maturation division the nucleus enters a resting stage which he figured from a freshly laid egg. The present study did not confirm this part of Perrot's work. The only mitotic figures ever found in sections through the vitellarium were those of the follicle cells. The anaphase of such follicular mitoses often resembles that shown in the first of Perrot's figures just mentioned. Eggs fixed immediately after oviposition show the nucleus to be in the metaphase of the first maturation division. No nucleus resembling both in appearance and position that shown in the second of Perrot's figures was found until the beginning of the formation of the primary epithelium.

The anastral type of meiosis occurs. The mitotic figure is located more or less equidistant from the two poles of the egg, usually from 1 to 10 microns from the surface. The spindle axis is usually oblique to the egg surface, but is occasionally parallel to it. The distance between the two poles of the mitotic figure in metaphase and in anaphase (Fig. 2) is about 20 microns. The metaphase plate is about 8 microns in diameter. The chromosomes are very small



and close together. During telophase the mitotic figure is no longer fusiform, but is a spheroid with long axis about 14 microns long and short axis about 10 microns long. In presumably slightly older eggs a very distinct equatorial constriction is evident. The two groups of chromosomes separate to a distance of almost 30 microns. In favorably sectioned eggs most of the eighteen dyads in each group can be distinguished (Fig. 4). Many of the chromosomes are very short and V-shaped, so that the dyads look superficially like tetrads.

The first polar body is not extruded from the egg and does not divide. Its chromosomes never become surrounded by a nuclear membrane as do those of the secondary oocyte. The dyads gradually change into an irregular mass, which remains close to the surface of the egg and disappears relatively quickly. No certain trace of the first polar body was found later than the anaphase of the second maturation division.

The egg nucleus was never found in a resting stage between the maturation divisions. The spheroidal prophase nucleus, with its still distinguishable dyads, is believed to increase in size, since a series has been found with long axis varying from 8 to 15 microns in length. The second maturation division resembles the first in size and orientation, but its chromosomes are slightly more easily distinguishable (Fig. 3). The second polar body degenerates as does the first and has not been seen with certainty later than the four-celled cleavage stage. The chromosomes of the female pronucleus enter a resting stage with distinct nuclear membrane. The nucleus is a spheroid with long and short diameters of 9 microns and 5 microns respectively. It shows hardly any variation from egg to egg.

In the majority of freshly laid eggs, cytoplasm is seen starting to accumulate around one of the sperm heads (Fig. 1). This sperm and its sperm plasm are typically found on the longitudinal axis of the egg, about one-third of the way from the posterior pole to the anterior pole. The distance from the maturation spindle is roughly 400 microns. If several sperms are present in the egg, cytoplasm may or may not accumulate around more than one. In cases where



cytoplasm accumulates around from two to six sperms, their distribution is such that they are about equidistant from each other and from the surface of the egg. Just as much cytoplasm accumulates around a sperm whether it is the only one accumulating cytoplasm or whether five others are doing likewise. Accumulation of the sperm plasm ceases at about the time the oocyte nucleus has completed its first maturation division. By that time the sphere of sperm plasm is about 45 microns in diameter.

As cytoplasm accumulates around a sperm head, the latter undergoes a gradual decrease in length, with accompanying uncoiling and moderate increase in breadth. The Feulgen reaction indicates a simultaneous concentration of desoxyribonucleic acid toward the anterior end of the shortening sperm head (Fig. 6). Shortening continues until all that is visible within the sperm plasm is a minute nucleus about  $1\frac{1}{2}$  microns long. This male pronucleus is formed at about the time that accumulation of sperm plasm ceases. While the egg nucleus is undergoing the second maturation division, the male pronucleus gradually enlarges (Fig. 7) until it is about 8 or 10 microns in diameter (Fig. 9).

The female pronucleus then migrates from its peripheral position to the sperm plasm (Fig. 9). When fixed before it reaches the sperm plasm, it is found to be rather irregularly elongated in the direction in which it was presumably travelling. Cytoplasm has never been identified around it. Both male and female pronuclei are approximately the same size and their finely divided chromatin appears very similar. Fortunately they can easily be distinguished when the Feulgen reaction is followed by light green counterstain. The nuclear sap of the male pronucleus shows great affinity for light green, while that of the female pronucleus shows practically none at all. It appears further that the movement of each nucleus within the sperm plasm just prior to fixation can be detected. For adjoining each nucleus fixed at this stage is a palely-staining streak which is interpreted to indicate the path over which the nucleus has just passed (Fig. 10).

As the female pronucleus enters the sperm plasm the sperm nucleus starts to move toward it. The two pronuclei

come together and their nuclear membranes break down where they are in contact with each other (Fig. 8). At the same time the chromatin of each condenses into a fine spireme. The nuclear sap of the female pronucleus simultaneously develops an affinity for light green, so that the two pronuclei can no longer be distinguished. The spiremes of the two nuclei become coarser and intermingle before any distinct chromosomes are visible (Fig. 11). The maturation divisions occupy about one and one-half hours each. Union of the pronuclei occurs during the fourth hour after oviposition.

#### *Affinities of Lepismatids*

The lepismatids for which both embryological and morphological data are available are *Lepisma saccharina* L. (Heymons, 1896, 1897; Uzel, 1897, 1898), *Thermobia domestica* (Packard) (Woodland, 1952, 1957; Sahrhage, 1953; Wellhouse, 1953), and *Ctenolepisma lineata* Fabricius (Woodland, 1957). All three belong to Subfamily Lepismatinae. The data indicate that *Thermobia domestica* and *Ctenolepisma lineata* are very closely related to each other and less closely related to *Lepisma saccharina*, which is more primitive than they.

*Thermobia domestica* and *Ctenolepisma lineata* differ embryologically from *Lepisma saccharina* in that in them the germ disk is formed at the extreme posterior end of the egg, radial symmetry is maintained until the germ disk starts to elongate, the embryo does not sink bodily into the yolk, the amniotic pore is not closed by a chitinous plug, and spiracleanlagen are not found on the ninth and tenth abdominal segments. Adults of *Thermobia domestica* and *Ctenolepisma lineata* differ from those of *Lepisma saccharina* by lacking parameres and by possessing ventricular caecae, an anterior projection of the vas deferens beyond where the most anterior pair of vasa efferentia empties into it, and often a third pair of styli. In the former two species the vasa efferentia of the members of a pair of sperm tubes do not unite before joining the vas deferens and the free end of one member of each pair of sperm tubes is directed mediad, while the free end of the other member is directed laterad. In addition, the lateral oviducts are relatively



shorter than in *Lepisma saccharina*. The author considers all of these characters to be secondary or specialized ones. Remington (personal communication, 1949) has noted several taxonomic characters as evidence for considering *Lepisma saccharina* more primitive than the other two species: the cephalic hairs of the former occur singly and do not bear secondary hairs, while those of the latter occur in groups and bear secondary hairs; also, the former has a less well developed ovipositor.

In spite of the close relationship between *Thermobia domestica* and *Ctenolepisma lineata*, each has a few specialized characters not shared by the other. In *Ctenolepisma lineata* a modified morula stage is absent, synchrony of cleavage is maintained longer, and intravitelline separation occurs late. In *Thermobia domestica* the amnio-serosal folds develop only weakly and there is a transverse division of the distal segment of the maxillary palpus.

Although the embryology of lepismatids and symphylans appears superficially very different, owing to the difference in relative amounts of yolk in the eggs of the two groups, actually a great deal of embryological affinity exists between them. Some of the characters shared by *Thermobia domestica* and the symphylan *Hanseniella agilis* (Tiegs, 1940) are of particular interest: (1) The polar bodies are not extruded from the egg and degenerate rapidly. (2) A vitelline membrane is not apparent. (3) Periplasm has not been identified in freshly laid eggs. (4) The inner layer is entirely mesodermal and is produced without the formation of a ventral groove. (5) The time and manner of segregation of the germ cells are similar. (6) The surface cells secrete a cuticle, in *Hanseniella* before germ band formation, in *Thermobia* after germ disk formation. (7) The midgut epithelium is derived from yolk cells. (8) The neuropile of the nerve cord is not covered dorsally by nerve cells. (9) Fourteen post-cephalic segments occur in the adult. Anamorphosis occurs in *Hanseniella* but not, of course, in *Thermobia*. It may be noted, however, that *Hanseniella* hatches with 8 post-cephalic segments followed by a pre-anal and an anal segment. During anamorphosis 4 more segments differentiate in front of the pre-anal seg-



ment. In *Thermobia* a distinct pause occurs after differentiation of the first 5 abdominal (first 8 post-cephalic) segments. The cercus-bearing (pre-anal) and anal segments are prominent during the interval before the remaining abdominal segments are differentiated in front of them.

The characters in which *Hanseniella* differs from *Thermobia* may be grouped into several categories. Examples of characters with homologs in some primitive or generalized insects, but not in *Thermobia*, are: (1) Paired arteries arise from the aorta. (2) The presence of eversible sacs and coxal styli. Homologs of both of these structures are present in *Machilis*. In *Hanseniella* the two halves of the nerve cord arise laterally from the floor of the germ band rather than medially as in *Thermobia*. In *Hanseniella* the medial position is occupied by the "ventral organs" from which the eversible sacs arise. Examples of characters more primitive than those found in primitive insects are: (1) The adult has abdominal legs. (2) Only one pair of Malpighian tubules is present. (3) The labial segment is at first not part of the head. A few of the characters of *Hanseniella*, such as the secondarily acquired progoneate condition and the development of fat body from yolk cells, seem to express affinity with diplopods or as the incorporation of a pre-antennary ganglion into the brain, with chilopods. Other characters of *Hanseniella*, as the absence of eyes and the presence of only a single pair of tracheae (cephalic), are specializations which are probably adaptations to its environment of decaying foliage and rotting logs.

The following embryological differences between *Hanseniella* and lepismatids are considered by the author to be the result largely of the difference in relative volume of yolk in their eggs. In *Hanseniella*: (1) Cleavage is total. (2) The germ band is long and from the beginning represents thoracic and abdominal as well as cephalic material. (3) Absence of embryonic membranes; the germ band does not sink into the yolk. (4) Early eclosion, with subsequent anamorphosis. Actually nutritive value of the yolk rather than volume is concerned here. Information is not available on this subject in insects.

Tiegs (1940), however, deems it erroneous to consider the type of cleavage as simply the mechanical result of the quantity of yolk within the egg. In support of this contention he says that the eggs of symphylans are not unusually small, though cleavage is total. But consider the following comparison. The egg of *Hanseniella* is spherical, averaging 0.37 mm. in diameter; the long diameter of the ellipsoidal egg of *Thermobia* averages 1.00 mm., the short diameter 0.80 mm. At hatching, *Thermobia* measures 1.5 mm. long, exclusive of appendages. We deduce that *Hanseniella* also measures close to 1.5 mm. long at hatching, for the following reason. The circumference of a sphere 0.37 mm. in diameter is 1.2 mm. The body of the embryo is curved in a circle around the entire circumference of the egg, but is a little longer than the circumference since the bent head is directed inward. We therefore conclude that the egg of *Thermobia* contains a relatively much larger percentage of yolk than does the egg of *Hanseniella*.

Tiegs further supports his statement by noting that some tiny, yolkless insect eggs have superficial cleavage (Fernando, 1934). But there is no reason to suppose that superficial cleavage, once established, would not be as satisfactory for yolkless as for yolk-rich eggs. We do not consider, however, that this fact invalidates the theory that superficial cleavage was originally developed as an adaptation to large, yolk-rich eggs.

Although only one species of perlarian has been thoroughly studied embryologically, Miller's detailed account (1939, 1940) of *Pteronarcys proteus* reveals a number of similarities between the embryology of this perlarian and that of lepismatids: (1) Practically no cytoplasm is present in freshly laid eggs. (2) The embryonic rudiment represents chiefly cephalic material. (3) The germ band is of the immersed type. (4) The inner layer represents mesoderm only and is produced without the formation of a ventral furrow. (5) The mesoderm of the eleventh abdominal segment shows no coelomic sacs. (6) Transitory appendages appear on the intercalary segment and on abdominal segments two to ten.

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# PATCHY DISTRIBUTIONS OF ANT SPECIES IN NEW GUINEA RAIN FORESTS

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While recently engaged in field work in New Guinea the author had several excellent opportunities to study local areal distribution of rain forest ants. During one three-week period in April, 1955, a walk was made from Finschhafen, on the eastern tip of the Huon Peninsula, west for a distance of 45 kilometers through the midmountain rain forests of the Dedua-Hube regions to Tumnang and Laulaunung, thence south for thirty kilometers to Butala on the southern coast. In the vicinity of Lae intensive collecting was conducted over a distance of twelve kilometers in recently continuous lowland rain forest within the triangle formed by Didiman Creek, Bubia, and the section between the Busu and Bupu Rivers.

Areal distributions of individual species were found to be almost universally patchy, despite the external appearance of uniformity of the rain forest environment. Furthermore, in the cases of species abundant enough to be studied in some detail, the patchiness seemed to obtain at two levels of distribution, which for purposes of description here will be referred to as "microgeographic" and "geographic".

*Microgeographic patchiness.* The species common enough to be studied in detail are also relatively adaptable, occurring usually in spots of variable canopy density (see below) and sometimes in more than one major forest type (e.g., *Leptogenys diminuta* (Fr. Smith), which ranges from medium lowland rain forest to dry, monsoon forest). In this respect, at least, they seem to be no more specialized than the majority of temperate ant species. At the same time, they show definite preferences for certain local environmental con-

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## EXPLANATION OF PLATE 3

Plate 3. Primary medium-aspect rain forest near the lower Busu River, Northeast New Guinea. A bulldozer trail cuts through the lower left hand corner of the picture.





WILSON — NEW GUINEA RAIN FOREST



ditions. At the Busu River and in other lowland rain forest sites investigated, ant species tended to be segregated into local areas, sometimes a hectare in extent or less, which could be distinguished from adjacent areas by their specific canopy densities. When the total range of possible canopy densities at the Busu River, from the open aspect that fringes savanna areas, to the most closed aspect, ordinarily found covering sloughs, was arbitrarily divided into three divisions (open, medium, dense) and their faunas studied, the following microgeographic segregation of ant species was noted.

“Open rain forest”. (Plate 5) Broken canopy; considerable ground insolation; leaf litter 2 to 15 cm. thick; leaf mold present but thin and relatively dry; soil loose, well aerated, and relatively dry; moss scarce on both ground and tree trunks; A-stratum trees generally less than thirty meters high; lianes and plank buttresses much less common than in other two divisions; recumbent vines common on ground; soil and rotting logs generally thoroughly penetrated with dense root and rhizome growth; undergrowth relatively dense; sufficient to make human progress across the forest floor difficult. This is the aspect of old second-growth forest and may be created naturally by the fall of large forest trees or, in mountainous areas, by rockslides. It is also a more or less permanent feature of the fringe of forest, generally one to two hundred meters wide, that borders savanna areas. Occasional spots deep within rain forest approach the open aspect even though an immediate cause, such as a large fallen tree, is not in evidence. Ant species that appear to reach their maximum density in open rain forest at the Busu River included *Platythyrea parallela* (Fr. Smith), *Diacamma rugosum* (Le Guillou), *Odontomachus simillimus* (Fr. Smith), and *Cardiocondyla paradoxa* (Emery). In the canopy of the open forest, species of *Crematogaster*, especially subgenus *Xiphocrema*, and of *Technomyrmex* increased generally, while those of *Iridomyrmex* decreased.

“Medium rain forest”. (Plates 3, 4). By far the largest lowland area in the Lae area is covered by forest of the following aspect: closed canopy; ground insolation slight;

leaf litter as in open aspect; underlying leaf mold rich and moist; soil loose, well aerated and drained and relatively moist; moss common on the surface of the ground, on rotting wood lying on the ground and on tree trunks; A-stratum trees average 40 meters or more in height; plank buttresses common; lianes and epiphytes abundant; undergrowth sparse, making human progress across the forest floor easy. The majority of endemic ant species are concentrated in this division. Examples of genera that reached maximum density (in 1955) on the floor of the Busu forest included *Ponera*, *Myopias*, *Ectomomyrmex*, *Pheidole*, *Strumigenys*, *Rhopalothrix*, *Myrmecina*, and *Pristomyrmex*. In the canopy *Iridomyrmex* heavily predominated.

“Dense rain forest”. Closed canopy; little or no ground insolation; leaf litter thin, with one-quarter or more of the ground surface completely bare; leaf mold very poorly developed; soil dense, less well drained and moister than in medium forest; parts of the ground surface occasionally holding shallow pools of water after heavy rains; moss abundant, especially on larger rotting logs; A-stratum trees as tall as in medium forest; plank buttresses common; lianes and epiphytes abundant; undergrowth very sparse, even more so than in medium forest. Ants reaching maximum density in various strata of this division at the Busu River included some species of *Pheidologeton*, *Tetramorium*, *Leptomyrmex* and *Iridomyrmex*.

Careful analysis would probably reveal many finer details of microgeographic segregation than those indicated here, for the rain forest is an extraordinarily complex mosaic of local habitats, exhibiting seemingly endless nuances and combinations of erosion states, growth and death of vegetation, composition of leaf mold, and other environmental features. Ant species did not appear to be limited to any of these particular divisions within the rain forest proper. At most, the divisions probably serve as density foci, from which the species are constantly pressing out into adjacent, less favorable habitats,

*Geographic patchiness.* Ant species apparently show extensive and unpredictable variation in population density over short geographic distances above and beyond that already



noted with respect to microgeographic habitat segregation. This phenomenon was first observed in the Hube area of the Huon Peninsula, where, through a few kilometers distance in seemingly uniform mid-mountain forest, dominant species of the genera *Aphaenogaster* (*Planimyрма*), *Melanoplus*, and *Leptomyrmea* showed conspicuously irregular density patterns. The impression was gained that even within the most favored habitats these species showed irregular density patterns. This type of discontinuous distribution is superimposed on the mosaic, habitat-correlated microgeographic patchiness, and the two conditions probably grade into each other. It can be predicted that superimposition of the two levels of patchiness will result in very irregular and complex individual species distributions, which in turn will have a profound effect on the differentiation of local faunas at localities separated by as little as a few kilometers distance. Such an effect was in fact observed in the lowland rain forests of the Lae area, as described below

*Differentiation of local faunas in the Lae area.* In 1955 most of the area to the north of Lae and east of the nearby Busu River was covered with a mixture of primary and secondary rain forest, with occasional savanna enclaves. Native villages were not numerous, and native agriculture had not made serious inroads into the forest. In the vicinity of Bubia, to the northwest of Lae, extensive land was under cultivation, partly by the Government Agricultural Experiment Station, but even here the forest was still partly intact, and primary tracts were still accessible<sup>1</sup>.

<sup>1</sup> According to both Mr. Henry G. Eckhoff and Mr. Carl M. Jacobson (pers. commun.), who were among the first European settlers of the Lae district, extensive clearing of the forests of this area is a comparatively recent event. Prior to 1925 the only European settlement was the mission station at Malahang, on the coast near Lae. In 1925 a small amount of ground was cleared at Didiman Creek to establish the Government Agricultural Experimental Station. Between 1925 and 1930, further clearing proceeded in the vicinity but was still restricted to the present town limits of Lae. Mr. Eckhoff, who arrived in 1928, states that in 1929-30, "My wife and I were the only residents of Lae other than the air freighting companies. There were no other agricultural activities". The next principal development was the establishment of a poultry farm just outside the Lae township by Mr. Jacobson. During the Second World War a road was built from Lae through Bubia to the airfield at Nadzab. Since 1945 clearing for agricultural purposes has proceeded to a limited extent of either side of this road.



Three localities within this forested area were chosen as sites of intensive collecting (see figure 1). The Busu-Bupu forest was the least disturbed of the three; lumbering operations had commenced in the collecting area only the year before, and most of the forest seemed in primary condition. The Didiman Creek site contained a tract of forest, at least partly second-growth in nature, that had been preserved within the Government Agricultural Experimental Station on the northern edge of Lae. At Bubia, extensive forest tracts, primary at least in part, extended to the east of the Jacobson Plantation. The forest tracts at these three localities represent relict segments of what can reasonably be assumed to have been continuous, predominantly primary lowland forest as recently as thirty years ago. Bubia and

TABLE I.

	BUBIA	DIDIMAN CR.	BUSU R.
<i>Cardiocondyla paradoxa</i> Emery	X	XX	XX
<i>Crematogaster (Acrocoelia)</i>	X	XXX	—
<i>irritabilis</i> (Fr. Smith)			
<i>Crematogaster (Rhachiocrema)</i>	—	XX	—
sp. nov.			
<i>Tetramorium validiusculum</i>	XXX	X	XX
Emery			
<i>Tetramorium ornatum</i> Emery	—	XX	XX
<i>Triglyphothrix fulviceps</i>	—	XX	XX
Emery			
<i>Aphaenogaster dromedarius</i>	—	—	XX
Emery			
<i>Meranoplus hirsutus</i> (Fr. Smith)	X	—	XX
<i>Leptomyrmex fragilis</i>	XX	—	XX
(Fr. Smith)			
<i>Pseudolasius breviceps</i> Emery	XXX	XX	X

Subjective estimates of relative abundance of some dominant ant species at three neighboring localities in New Guinea. A dashed line means absent, or at least never observed; a single X, present but collected only once or twice; double-X moderately abundant; triple-X among the two or three most abundant species at the locality. Since collecting trips were wide-ranging, these estimates reflect most closely the relative abundance of colonies, rather than number of workers or biomass. Further explanation in text.

Busu-Bupu regions were almost connected by continuous forest even as late as 1955. There is no reason to believe

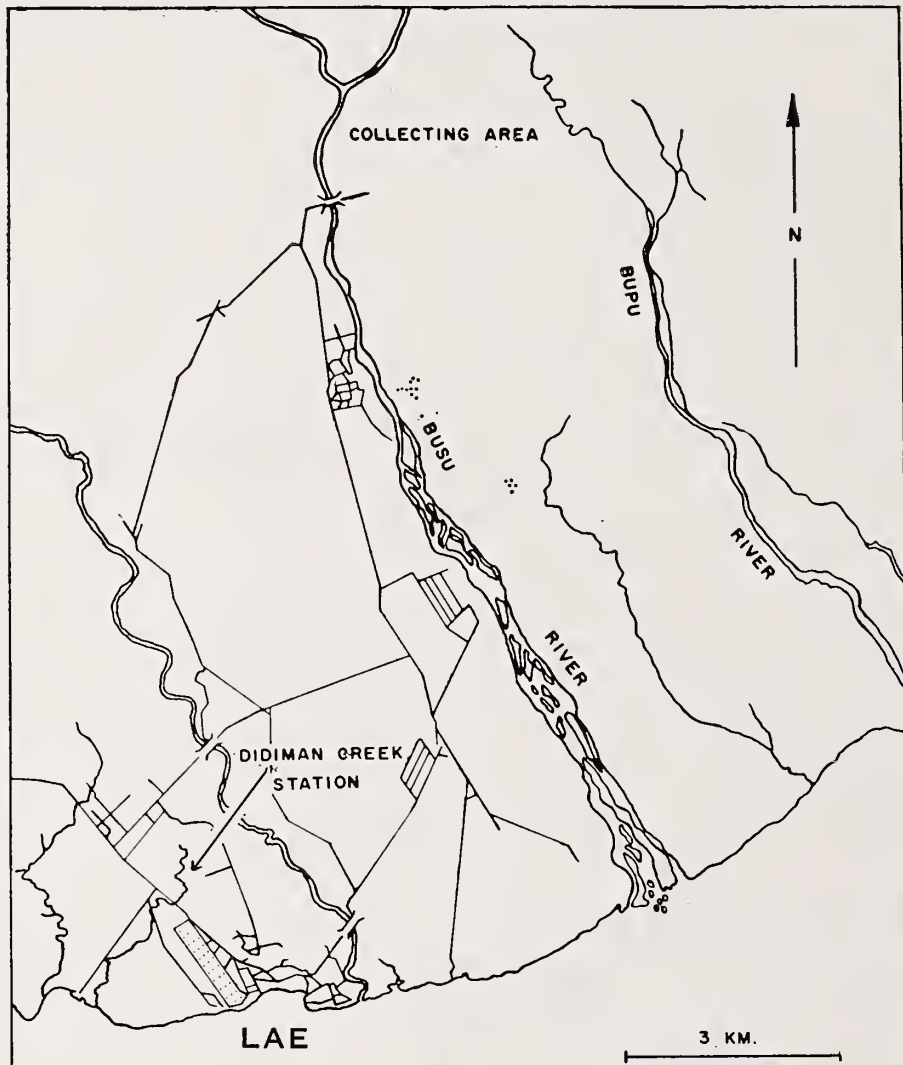


Figure 1. Map of the Lae area in 1955, showing Didiman Creek and the Busu-Bupu area, two of the collecting stations studied with respect to local distribution of species. The third station, Bubia, is located 12.5 kilometers to the northwest of the town of Lae.

#### EXPLANATION OF PLATE 4

Plate 4. Floor of primary medium-aspect rain forest near lower Busu River. An overhead tree has just been felled to allow in an unusual amount of sunlight. The exposed portion of the machete is approximately 20 inches, or 50 centimeters, in length. The greatest concentration of species and individual colonies to be found anywhere in New Guinea nest in small pieces of rotting wood in this situation.





PSYCHE, 1958

WILSON — NEW GUINEA RAIN FOREST

VOL. 65, PLATE 4



that the forests at the three localities, or the ant faunas in them, had been seriously disturbed by man. All three localities contained rich endemic Papuan faunas, with virtually no infiltration of introduced species.

Subjective impressions of the relative abundance of several of the dominant ant species are presented in Table 1. In each of the three localities, all of the major microgeographic areal divisions were studied. Each locality was visited at least twice during the author's two month stay in the Lae area, and a minimum of four days devoted to intensive collecting. Under these conditions, only the commonest species could be compared, but differences in local abundance of these were so striking that it seems safe to predict that similar patchy distributions are exhibited by other, less dominant members of the fauna.

#### DISCUSSION: THE EVOLUTIONARY IMPLICATIONS OF PATCHINESS

In any appraisal of comparative ecology, the New Guinea ant fauna is to be characterized first of all by the exceptional richness of its species and the great size of its biomass. The present study has shown that in addition to sheer size, an additional factor adds greatly to the total faunal complexity. This is the discordant patchy distribution of individual species. The fractioning of species into small subpopulations that are partially isolated from one another probably results in relatively high rates of evolution, whether through random drift or differential selective pressures or both (see for instance Kimura, 1955, and Ford, 1955). Moreover, as a result of discordant patchiness, no two localities harbor exactly the same fauna. Considering that several hundreds of species are thus involved, it is clear that the spatio-temporal structure of the entire New Guinea fauna must present the appearance of a great kaleidoscope. The effects of such a structure on the evolution of individual species of

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#### EXPLANATION OF PLATE 5

Plate 5. Floor of primary open-aspect rain forest near the lower Busu River. The undergrowth at this spot is made up preponderantly of an unidentified species of *Selaginella*.





PSYCHE, 1958

WILSON — NEW GUINEA RAIN FOREST

VOL. 65, PLATE 5



ants, as well as of other kinds of animals, must be considerable. It very possibly hastens the genetic divergence of local populations and plays an important role in the "exuberance" and amplitude that characterizes evolution in the tropics. Probably as the fauna increases in size, in passing from temperate to tropical areas or from small islands to large ones, the diversifying effects of a kaleidoscopic population structure increase exponentially.

There is abundant evidence that similar features of population structure occur in other groups of organisms in tropical forests. Aubreville (1938), in his "mosaic" or "cyclical" theory of regeneration, has described a kaleidoscope pattern in forest trees of the Ivory Coast. Richards (1952) doubts whether the mosaic theory holds for all rain forest associations, but accepts its validity in special cases where certain conditions have been met.

"The poor regeneration of the dominant species in African Forests seems in all probability to indicate that the composition of the community is changing. If the forest is in fact 'untouched and primitive', as Aubreville claims . . . . the changes must be cyclical as the Mosaic theory implies. On the other hand, if the community has undergone disturbance in the past, the present combination of species [in a given sample plot] may be a seral stage and the changes part of a normal (not cyclical) process of development toward a stable climax".

Moreau (1948) finds patchiness a common feature in the distribution of rain forest birds in Tanganyika. Where a species is absent from a locality, it is usually replaced by a related species (from the same family), but not always, leaving some inexplicable gaps. The following example is typical:

"Nearly all the montane forests of eastern Africa from Kenya southward are occupied by one or both of the little barbets, *Pogoniulus bilineatus* and *Viridobucco leucomystax*. On Hanang Mountain, where both these species are missing, *Pogoniulus pusillus*, normally a bird of deciduous trees at lower altitudes, appears in the mountain forests



(Fuggles-Couchman, unpublished). But this does not happen in the neighboring forests of the Mbulu District, where the fruit-eating barbets are not represented at all.”

Additional examples from other animal groups and other parts of the tropics (as well as the temperate zones) could be cited to show that patchiness is a widespread phenomenon, on both a very local (microgeographic) and broader (geographic) scale. To all such cases Richards' conditions must be applied, i.e., it must be asked whether patchiness has not arisen exclusively as a result of man-made disturbances. But patchiness as a result of natural disturbances, such as tree falls and stream erosion, is a good possibility also, and should be considered in the future. In the author's present opinion, much of the patchiness observed in New Guinea ant populations has actually arisen through natural disturbances, since enclaves of second-growth vegetation are a normal feature of remote, undisturbed forest. This argument has been taken up in somewhat more detail elsewhere (Wilson, 1959).

#### SUMMARY

The population structure of individual Papuan ant species is shown to be generally irregular. Patchiness exists at both a local, clearly ecological level, and a broader, "geographic" level not easily correlated with environmental influences. The combined irregularities in the distributions of multiple species result in distinct shifts of faunal composition and relative abundance over distances of only a few kilometers even in relatively continuous, homogeneous rain forest. The theoretical implications of discordant patchiness with respect to rapid evolution are discussed.

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A *FORMICA* SLAVE-MAKER RAIDING THE NEST  
OF A MYRMICINE ANT

BY W. L. BROWN, JR.

Museum of Comparative Zoology

Slave-making *Formica* of the *sanguinea* group normally raid the nests of *Formica* of the *fusca*, *pallidefulva* or *neogagates* groups to obtain pupae to be reared into slavery.

Occasionally, *F. sanguinea* group species have been seen to raid other formicine genera, especially *Lasius*, and Wheeler (1905, Bull. Amer. Mus. Nat. Hist. 21: 11) even recorded a raid on a nest of *Myrmica* (subfamily *Myrmicinae*) species that he watched in Connecticut. Raids by *Formica* on myrmicines apparently are rare occurrences, so the circumstances of such a raid are worth reporting.

On August 22, 1958, at Brown County State Park, Indiana, I witnessed a raid by *Formica subintegra* Emery on a nest of the much smaller myrmicine ant *Aphaenogaster rudis* Emery. The nest entrances of the raiders and the victims were simple holes situated only about one meter apart in the bare clay soil of a hilltop campground, shaded by hickories and a few oaks. The raid was first noticed at about 3 P. M., about 3 hours after a heavy rain had ceased. The sky was partly cloudy, and the air temperature stood at about 70°F.

Most of the visible activity occurred in and around the entrance to the *A. rudis* nest. Six dead or badly maimed *rudis* workers lay near the entrance, accompanied by one crippled *F. subintegra* worker. One *subintegra* worker grappled with a *rudis* worker and put it out of action while I watched. At irregular intervals, *subintegra* workers emerged, most of them carrying a pupa or a dead or struggling worker of *A. rudis*, with which they returned directly to their own nest and entered there. Two *subintegra* workers carried folded-up workers of their own species; when disturbed, these workers dropped their burdens, which proved to be active and apparently unhurt.

Around their nest entrance, at some distance, circled a few *Aphaenogaster* workers, mostly each carrying one of their own larvae or pupae. Their behavior resembled that of *Formica* slave species when being raided by *F. subintegra*.

Also running in the general vicinity of both nests, but not seen to participate directly in the raid, were a few workers of *Formica fusca* (*s. lat.*), all of them slave members of the *F. subintegra* colony.

The raid was under observation for about one hour, and my impression was that it had been in progress for some time before I first saw it. It compared with the terminal stages of other raids I have seen *F. subintegra* make on other *Formica* species. The raid was terminated by heavy rain in the early evening, and was not continued on the next day.

On partial excavation, pupae and dead or injured workers of *A. rudis* were found in the *subintegra* nest, but there were no *Aphaenogaster* workers present and intact that seemed to be acting as slaves. Therefore, I concluded that the raid would probably not be successful in introducing the *Aphaenogaster* into adult slavery.

In the present observation, it is not known whether the captured pupae or adult *Aphaenogaster* workers were eaten by the *Formica* raiders. But even if they were, such behavior is not necessarily of more than routine significance, since ants will eat their own pupae under various circumstances.

My own interpretation of the raid is based on the apparent lack of nests of suitable slave species of *Formica* in the campground, and the abnormally exposed nature of the *Aphaenogaster* nest. Since *F. subintegra* workers had been seen foraging singly over the area for several days previous to the raid described, I suspect that these represented scouts that were unsuccessful in locating suitable *Formica* spp. nests to plunder. Under such conditions, the pressure for the release of raiding activity may have been high, so that eventually even such a poor target as the *Aphaenogaster* nest came to represent a stimulus sufficient to start and maintain a raid.









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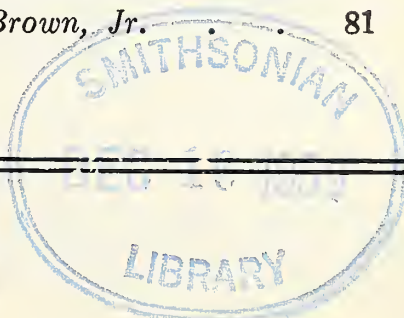
June-September, 1958

Nos. 2-3



## TABLE OF CONTENTS

A Chemical Releaser of Alarm and Digging Behavior in the Ant <i>Pogonomyrmex badius</i> (Latreille). Edward O. Wilson . . . . .	41
Mexican Snakeflies (Neuroptera: Raphidioidea). <i>F. M. Carpenter</i> . . . . .	52
The Collembola of Lebanon and Western Syria. Part III: Family Isotomidae. K. Christiansen . . . . .	59
The Indo-Australian Species of the Ant Genus <i>Strumigenys</i> : Fr. Smith: Group of <i>S. godeffroyi</i> in Borneo. W. L. Brown, Jr. . . . .	81



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## A CHEMICAL RELEASER OF ALARM AND DIGGING BEHAVIOR IN THE ANT *POGONOMYRMEX BADIUS* (LATREILLE)

BY EDWARD O. WILSON

Biological Laboratories, Harvard University

### INTRODUCTION

The complex social behavior of ants appears to be mediated in large part by chemoreceptors. If it can be assumed that "instinctive" behavior of these insects is organized in a fashion similar to that demonstrated for the better known invertebrates, a useful hypothesis would seem to be that there exists a series of behavioral "releasers", in this case chemical substances voided by individual ants that evoke specific responses in other members of the same species. It is further useful for purposes of investigation to suppose that the releasers are produced at least in part as glandular secretions and tend to be accumulated and stored in glandular reservoirs. In support of this hypothesis one such releaser, the trail substance of fire ants, has been described elsewhere (Wilson, 1959). This agent effects short-range exploratory behavior and also serves as the chief orienting stimulus. Goetsch (1952) has suggested the existence of another class of chemical releasers in ants, the *Fernalarm* substances, which are said to be released by excited workers to communicate a state of excitement within the colony. According to this author, workers of certain deserticolous species of the dolichoderine and formicine genera *Forelius*, *Tapinoma*, *Iridomyrmex*, *Dorymyrmex*, and *Camponotus* apparently can discharge abdominal secretions that create this effect among other workers through the air over short distances. Goetsch's interesting observation has not yet received experimental verification. The purpose of the present paper is to report



on yet another chemical releaser, a secretion of the mandibular glands of the harvesting ant *Pogonomyrmex badius*. This agent is especially interesting, because it operates to release two seemingly unrelated complex behavior patterns, general alarm behavior and digging.

#### MATERIALS

Observations were made chiefly on colonies collected at Ocean Drive Beach, South Carolina, and Gulf Shores, Alabama, and maintained in artificial nests in the laboratory. Since the mother queens of *Pogonomyrmex* colonies are notoriously difficult to find in the field, a note on the collecting method employed would seem to be in order. The best results were obtained by excavating small nests during the early morning, preferably following rainfall. The upper portions of the nests were simply dug out with a spade and scattered over a ground-cloth until the queen was sighted. Under such conditions, roughly half the nests opened yielded queens during the first ten minutes of search. Other methods tried, including deep lateral excavations and the use of sieves, proved relatively inefficient.

The colonies were housed in the laboratory in vertical, multistoried, plexiglas nests. The horizontal galleries were fitted with sliding plexiglas walls that could be moved to allow cleaning and to give access to the interior of the nest. The floors of the galleries were made of softwood strips. Curved plastic tubes led from the outside to the ends of the wooden floors to allow periodic watering of the nest interior. A single opening led from the bottom gallery outside to a walled foraging arena. The ants had been gradually habituated to strong light, so that it was possible at all times to keep the nest interior brightly illuminated. The foraging arena was illuminated during twelve hours of each day by fluorescent lamps turned on and off by an automatic timing device. A more detailed description of this type of artificial nest, which has proven successful in the pursuit of a variety of behavioral problems, is planned in a later report. During the present study, the adult population of the captive colonies ranged between 63 and 124, which is smaller than that of large juvenile and adult colonies in the wild.



## DESCRIPTION OF ALARM BEHAVIOR

When workers of *Pogonomyrex badius* are disturbed by alien mechanical or chemical stimuli, they show the following characteristic alarm response. *Low intensity*: rate of locomotion increases, with the ant moving in wide, poorly defined loops and circles; the head and antennae are periodically lifted high and the antennae waved about; the gaster may be periodically lowered so that its long axis is approximately perpendicular to the ground surface. *High intensity*: rate of locomotion increases still more, with the ant tending to move in tighter and more geometrical circling patterns; the head and antennae are periodically raised a moderate distance, but not as high as during lower intensity alarm; the mandibles are held partly open; the gaster may be periodically bent downward.

These two states of activity are not discontinuous but merely represent points on a gradient of intensity that is a function of the magnitude of the stimulus applied. Essentially the same pattern of behavior is exhibited both inside the artificial nest and outside it in the near vicinity of the nest entrance. Under laboratory conditions, the intensity of response outside the nest is inversely related to the distance of the locus of stimulation from the nest entrance. At the outer limits of the foraging arena, approximately one meter from the nest entrance, high-intensity responses have been difficult to induce, and workers have frequently shown instead a simple escape reaction.

A highly excited worker is a potential cause of a wave of alarm behavior among other workers. Under natural conditions a single worker exhibiting high-intensity alarm just outside the nest entrance can initiate general excitement that spreads centrifugally over the entire surface of the nest crater, along a radius of fifty centimeters or more. As the first worker commences a circling movement, it encounters other workers, which are stimulated to take up similar movement, in turn exciting other workers, and so forth. The wave of excitement seems to diminish in intensity away from the original stimulus in a roughly logarithmic fashion.

These results can be closely duplicated in laboratory

colonies. When waves of excitement caused by a continuing stimulus at a single locus inside the nest are measured, a pattern of alternating expansion and contraction through the linear galleries is noted. The maximum range of the wave expansions is a function of the magnitude of the stimulus. During the first several minutes the maximum range achieved by successive waves tends to be stable. This is evidently due to the fact that expansions are ordinarily led by no more than one or two workers that break away momentarily from the zone of continuous excitement close to the stimulus; these individuals run outward, creating lesser, shorter-lived excitement among workers they pass, then turn back in the inevitable looping pattern that characterizes alarm behavior. After several minutes the workers in the zone of continuous excitement begin to adapt

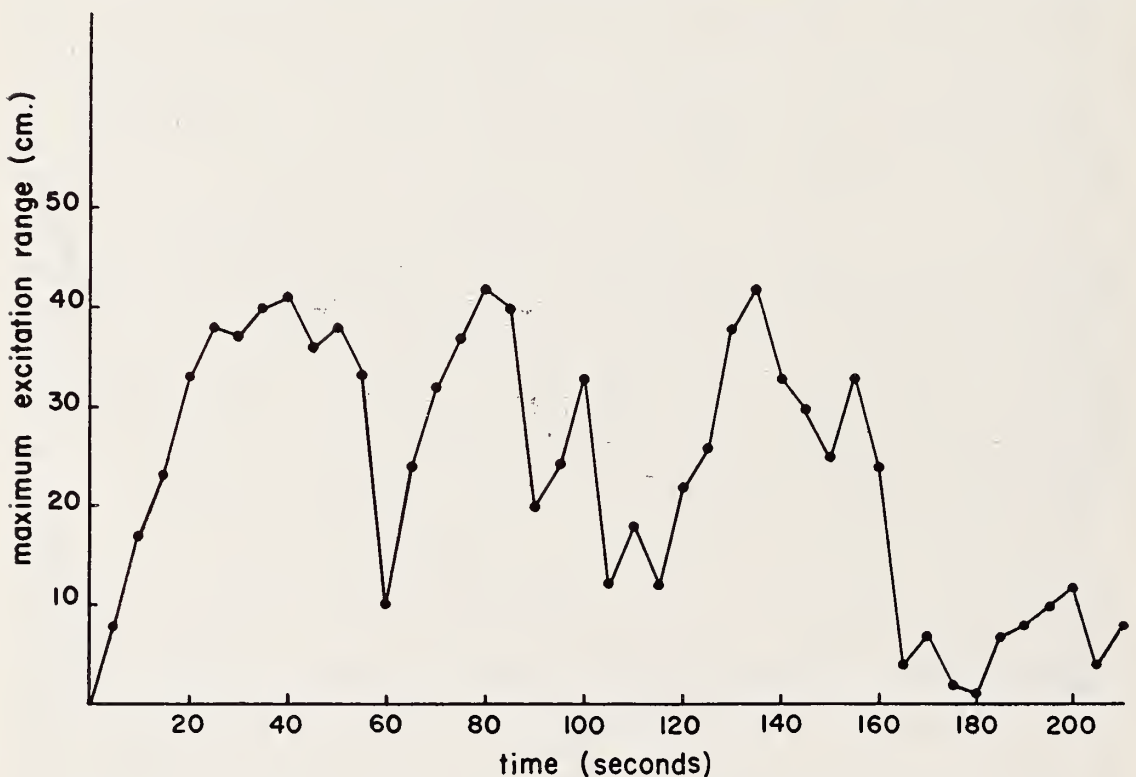


Figure 1. Spread of excitation through a laboratory colony of *Pogonomyrmex badius*. The continuing stimulus in this instance was an injured, immobile *Camponotus pennsylvanicus* (DeGeer) worker pinned to one spot in the nest interior. The maximum range of excitation was measured at five-second intervals in one direction only outward from the stimulus through the linear galleries of the artificial nest. Nest temperature:  $30^{\circ} \pm 2^{\circ}$  C. Further explanation in the text.

to the stimulus, the alarm behavior grows generally less intense, and the waves of expansion grow ever shorter (See figure 1).

#### THE RELEASE OF ALARM BEHAVIOR

##### BY THE MANDIBULAR GLAND SECRETION

It has been noted repeatedly that purely mechanical stimulation of one worker by another is not ordinarily adequate to effect alarm behavior of significant intensity. Workers falling accidentally from the nest walls have been observed to push heavily against other workers without creating noticeable excitement. The same is true when injured workers occasionally manifest abnormally high locomotory activity for sustained periods and repeatedly bump against nestmates. Workers within the nest can also be pushed about lightly with clean glass rods, providing the ants are allowed to adapt to the immobile rods for a short time beforehand. Two other kinds of stimuli have proven most effective in eliciting alarm behavior: sound, especially that transmitted through the solid medium of the nest walls, and alien chemical substances.

The presence of a chemical releaser of alarm behavior was suspected when it was noted that greatly excited *Pogonomyrmex badius* workers discharge a highly volatile, pungently odorous substance. When workers of another species, *Solenopsis saevissima* (Fr. Smith), were allowed to invade a *badius* nest, the substance was discharged continuously for several hours and was associated with a state of high excitement among the *badius* workers.

Dissections of anesthetized workers revealed that the substance is concentrated, perhaps exclusively, in the reservoir of the mandibular gland of the head.<sup>1</sup>

In a majority of workers that have been removed care-

<sup>1</sup>The morphology of the mandibular gland of ants has been described by Janet (1898) and more recently by Whelden (1957a, 1957b). As shown by these authors, the gland reservoir lacks constrictor muscles, and it seems likely that contraction is achieved through an increase in the surrounding hemolymph pressure. The gland and its reservoir are best exposed by splitting the head sagittally and removing the pharynx and associated tissues. Direct removal of the mandible by extraction almost always results in the collapse of the gland reservoir and loss of its contents.



fully from the nest, anesthetized, and dissected, the gland reservoirs have been partly or completely filled with a colorless fluid. When the reservoir walls are ruptured this fluid evaporates within several seconds and the characteristic pungent odor can be perceived by the human observer over a distance of 50 centimeters or more.

The releaser effect of the mandibular gland secretion was demonstrated in the following way. When workers were seized with forceps and held about two centimeters above groups of resting workers just outside the nest entrance, alarm behavior was induced in the resting workers after an interval of several seconds. The captive workers were not stridulating, thus eliminating the possible complication of this additional stimulus, but they were releasing sufficient quantities of mandibular gland secretion to be discernible to a human observer a short distance away. Freshly killed workers, which were not producing discernible amounts of the secretion, elicited no response when held above resting workers.

When workers were crushed between two pieces of glass above groups of resting workers, large quantities of the mandibular gland secretion were released, and high-intensity alarm behavior was elicited. That the effect was in fact produced by the mandibular gland substance and not by other substances released by crushing was tested in the following experiment. In separate trials various parts of an anesthetized worker were isolated and crushed above groups of workers in the manner described. Each body part was tested from a total of ten workers. The sequence of presentation was randomized to eliminate possible special sequential effects. Also, the trials were spread over a period of several days to reduce the decline of response due to adaptation. The results, presented in Table 1, show that the relatively minute mandibular gland produces more effect than any other part of the body, no matter how large. No attempt has been made to determine the extreme distance over which the contents of a single gland can act; the experiments described here suggest that it is not less than five centimeters at room temperature (26° C).

TABLE 1

## LOCATION OF OLFACTORY ALARM RELEASERS IN

*Pogonomyrmex badius* WORKER

Body part	Percentage of positive responses	Intensity of effect	Delay in onset of effect (range in secs.)	Duration of effect (range in secs.)	Duration of effect (M ± s.e.)
entire head	100%	moderate to high	3-13	15-150	50.7 ± 17.6
entire body minus head	30%	very low	4-8	10-15	13.3 ± 1.4
mandible plus mandibular gland	100%	moderate	4-9	10-40	28.0 ± 2.3
mandible alone	0	—	—	—	—
lateral half of head minus mandible and mandibular gland	0	—	—	—	—

Table 1. The effect on resting groups of workers of volatile substances artificially released from various body parts by crushing. Each selected part was separately crushed between two pieces of glass and then quickly exposed at a point four to five centimeters above groups of resting workers collected just outside the nest entrance. The results given in this table come from ten replications of the experiment. The lag in onset of behavior was measured to the nearest second, the duration of effect to the nearest five seconds. In the case of a negative response, the crushed material was held in position one minute before being withdrawn. In the course of dissection it was found expedient to leave the mandibular gland attached to the mandible in order to preserve the contents of the reservoir intact. Further explanation in text.

The above observations show that the mandibular gland secretion from a single worker is adequate of itself to release alarm behavior. The social excitation waves characterizing alarm behavior in *Pogonomyrmex badius* are evidently propagated by means of excited workers exposing other workers to the secretion as they dash outward in their looping movements. Since the active component of the secretion is highly volatile, mass excitation tends quickly to die down when the primary external stimulus is removed. Finally, it is interesting to note that workers suddenly killed by predators under natural conditions are still capable of producing the alarm effect, since their secretion will be released when the head is crushed. One is reminded of the observation made commonly by students of ants (e.g., Carthy, 1951; Sudd, 1957) that crushed workers induce alarm or avoidance behavior in their nest-mates. In the case of *Pogonomyrmex badius*, this effect can be ascribed specifically to the mandibular gland secretion.

THE RELEASE OF DIGGING BEHAVIOR  
BY THE MANDIBULAR GLAND SECRETION

During the experiments described in the preceding section, it was discovered that workers exposed several times in rapid succession to mandibular gland secretion frequently began to show digging behavior. The complex motor activity involved appeared to be identical in all respects to normal digging behavior observed during "nest work", except that it tended to be undirected, i.e., unrelated to any particular topographic feature, and hence inconsequential in results. Excavation started in this fashion furthermore involved little interaction among workers, it ceased when the exposure to the secretion ceased, and it was not followed up by later nest work. No attempt was made to determine the primary causation of the behavior. At least two explanations seem possible: (1) prolonged exposure to the secretion induced the behavior directly, (2) the behavior was a physiological by-product of a prolonged state of excitement caused by exposure.

One is tempted to refer to the seemingly functionless digging behavior as a "displacement activity", in the sense



employed by vertebrate ethologists (Tinbergen, 1951). It arises out of what can properly be called a conflict situation, during which workers become highly excited but encounter no object against which aggressiveness can be released. However, it should be noted that such behavior may well be functional under certain conditions. Experiments with substitute chemical agents, described in the next section, show that the digging becomes directional when the stimulus is confined to a single locus. It is probable that a worker buried by a cave-in will release mandibular-gland secretion; this becomes virtually certain if the cave-in is caused by the intrusion of some larger animal. As a result, it can be predicted that excavation following a major disturbance of the nest will tend to be directed toward those parts of the nest where workers are trapped. This hypothesis remains to be proven experimentally.

#### THE EFFECTS OF ALIEN CHEMICAL STIMULI

Apparently a wide variety of relatively volatile chemical agents are capable of inducing behavior patterns similar or identical to those released by the mandibular gland secretion. When groups of workers were allowed to come into direct contact with small amounts of formic acid, ethylamine, *n*-butyric acid or *n*-caproic acid absorbed in one-centimeter-square pieces of filter paper, they responded immediately with alarm behavior and in time with digging behavior. Further, the digging was concentrated around the paper squares. The ants made no attempt to remove the squares but instead tended to dig shallow trenches around them. When triethanolamine, ammonium sulfide, phenol, and oleic acid were tested in the same way, the ants either showed no reaction or (in the case of oleic acid) removed the paper square to the refuse pile of the foraging arena. When ethylamine and *n*-butyric acid were allowed to evaporate in the near vicinity of resting ants, so that these substances could be detected only by olfaction, the ants again responded with alarm and digging behavior. But in this case the intensity of the behavior was distinctly less than that following direct contact with the absorbed chemicals. It was also significantly less than

that following exposure to comparable amounts of the evaporated mandibular-gland secretion.

#### SUMMARY

The secretion of the mandibular gland of the myrmicine ant *Pogonomyrmex badius* (Latreille) contains an unidentified component that acts as a releaser of both alarm and digging behavior. This substance is highly volatile, so that the contents of a single mandibular gland reservoir can act through the air over at least five centimeters; at 26° C alarm behavior was effected over this distance within four to nine seconds under the experimental conditions used. Highly excited workers discharge the secretion during the characteristic looping movements of alarm behavior and in so doing tend to set up waves of excitement that spread among other workers through the nest galleries and over the nest surface. Prolonged exposure to the secretion induces characteristic digging behavior, which may be directional if the stimulus is confined to a single locus. The hypothesis is advanced that directional digging thus induced functions at least in part to expedite "rescue" work following nest cave-ins. Similar alarm and digging behavior can be induced through the air by some other relatively volatile agents, e.g., formic acid, *n*-butyric acid, and ethylamine.

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MEXICAN SNAKE-FLIES  
(NEUROPTERA: RAPHIDIODEA)<sup>1</sup>

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The geographical distribution of the genera of snake-flies has been discussed in two previous papers (Carpenter, 1936, 1956). Up to the present time, only two (*Agulla*, *Inocellia*) of the four genera in the order have been found in the New World, although the other two (*Raphidia*, *Fibla*) are represented in Miocene deposits of Colorado.

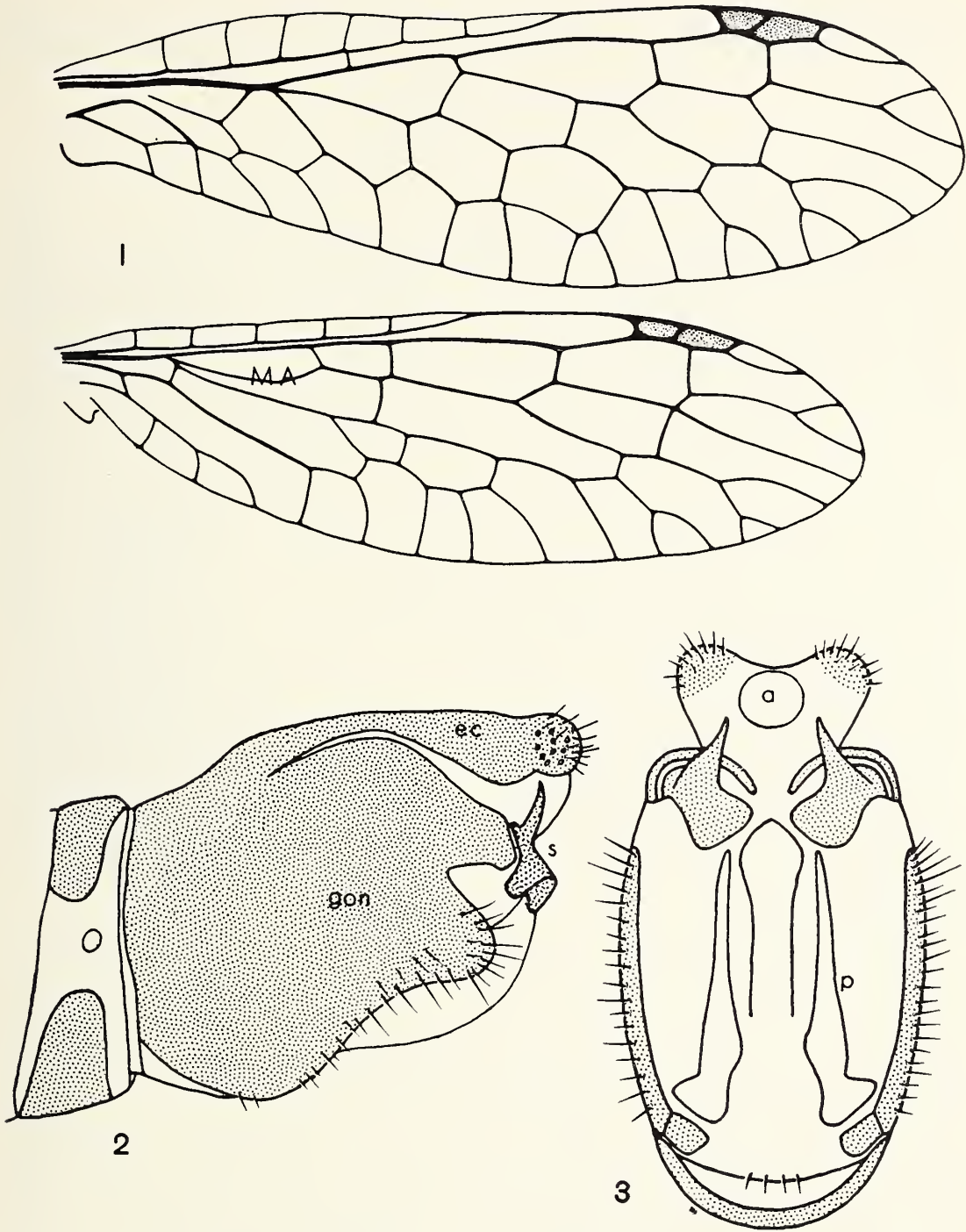
The present paper is concerned with several specimens of snake-flies obtained from Dr. William W. Gibson of the Rockefeller Foundation, Jean Mathieu of the Instituto Tecnológico y de Estudios Superiores de Monterrey, Mexico, and Dr. Henry E. Howden of the Canada Department of Agriculture, Science Service. The two species represented are of unusual interest: one belongs to *Raphidia* and is, therefore, the first living species of this genus to be found in the New World; the other is an *Inocellia* possessing strongly pilose antennae — a feature not otherwise known in the suborder Raphidiodea.

Family Raphidiidae

This family has previously been represented in the New World only by the genus *Agulla*. In addition to sixteen species occurring in parts of western United States and Canada, one species (*herbsti* Esben-Petersen) has been described from central Chile and two species have been described from Mexico. One of the latter (*australis* Banks) is known from San Lazaro in Baja California;<sup>2</sup> the other in southern Mexico. Specimens of the new species of (*caudata* Navas) was collected in the state of Guerrero

<sup>1</sup> Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

<sup>2</sup> The locality given in the published account (Banks, 1895) is "San Lazaro, Baja California," but the labels on the two cotypes (M.C.Z.) of *australis* read "San Lorenzo, Baja California."



*Raphidia americana* n. sp. All drawings based on holotype. Fig. 1. Fore and hind wings. Fig. 2 Terminal abdominal segments, lateral view. Fig. 3. Same, posterior view. Lettering: MA, stem of anterior media; gon, gonocoxite; s, stylus; ec, ectoproct; a, anus; p, paramere.

*Raphidia* were collected in southern Mexico, a little north-east of the *caudata* locality.

***Raphidia americana*, n. sp.**

Plate 6, figures 1-3

Male (holotype): length of fore wing, 6.4 mm.; width 2 mm.; length of hind wing, 6 mm.; width, 1.7 mm. Pterostigma about two and one-half times as long as wide. The general coloration and markings are typical of those of the genus; antennae, including first segment, yellow; head and prothorax black and reddish brown; thoracic tergites black, membranous areas of pleuron white; legs very light brown; abdominal tergites black, each with a white spot on the posterior margin near the outer edge of the sclerite; pleural membrane white; abdominal sternites brown, with a white patch posteriorly; wing veins nearly black; pterostigma yellowish, the proximal part somewhat darker than the distal. The terminal abdominal segments are shown in figures 2 and 3. The gonocoxites are firmly fused to the ninth sternite, forming a single, long, lateral plate; the styli are of moderate size, smaller than those of *notata*; the ectoproct is elongate, extending somewhat beyond the styli; the parameres are slender, weakly sclerotized plates closely pressed to the sides of the hypovalva.

Female (paratype): length of fore wing, 7.5 mm.; width, 2 mm.; ovipositor, 4 mm. The coloration and markings are similar to those of the males except for the antennae, the distal parts of which are dark brown (Antennal coloration is probably variable within the species).

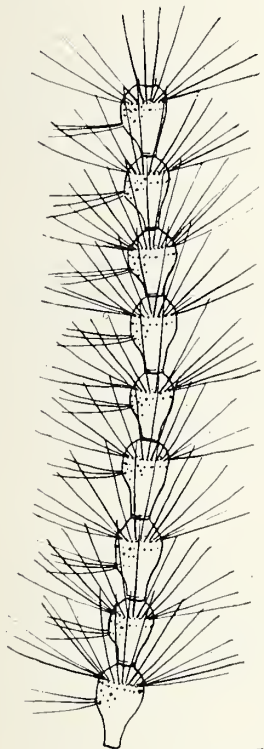
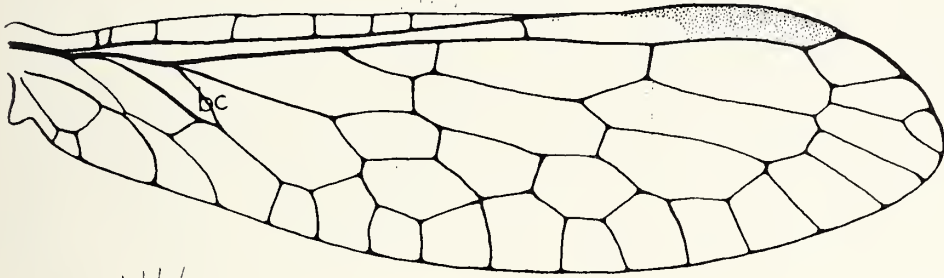
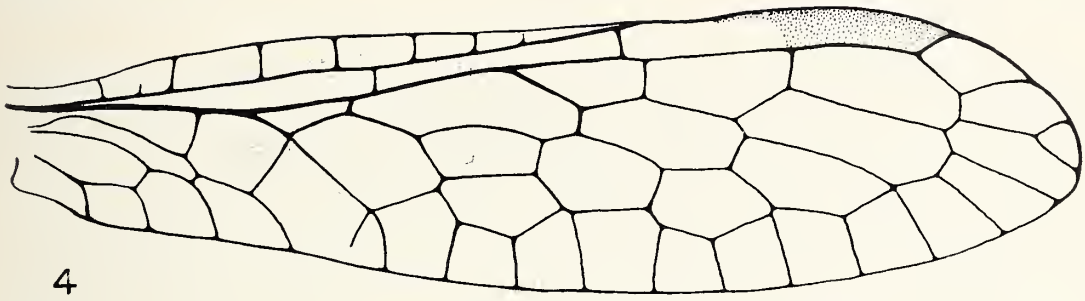
Holotype (♂): 5 miles north of Cuernavaco, Morelos, Mexico: 6000' elevation; beating pine; Aug. 28, 1958 (collected by H. E. Howden). In the Canadian National Collection Department of Agriculture, Ottawa, Canada.

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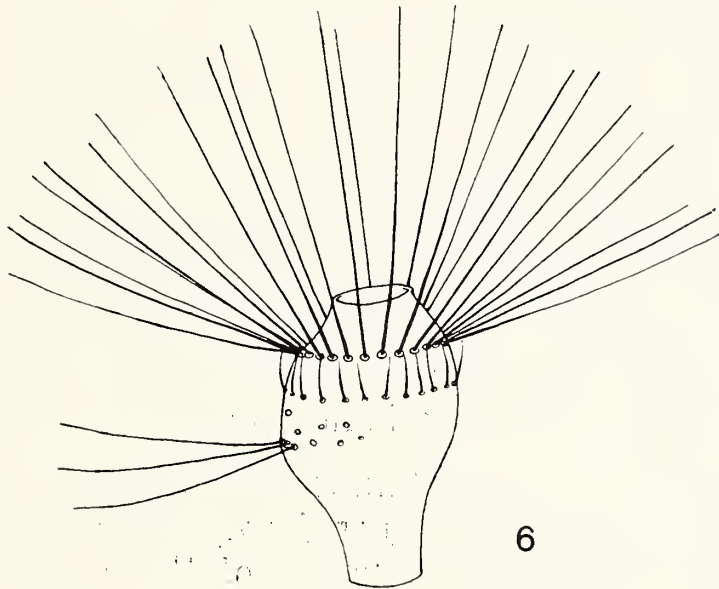
EXPLANATION OF PLATE 7

*Inocellia pilicornis* n. sp. All drawings based on holotype. Fig. 4. Fore and hind wings. Fig. 5. Part of an antenna. Fig. 6. A single antennal segment. Fig. 7. Terminal abdominal segments. Lettering: bc, basal crossvein.

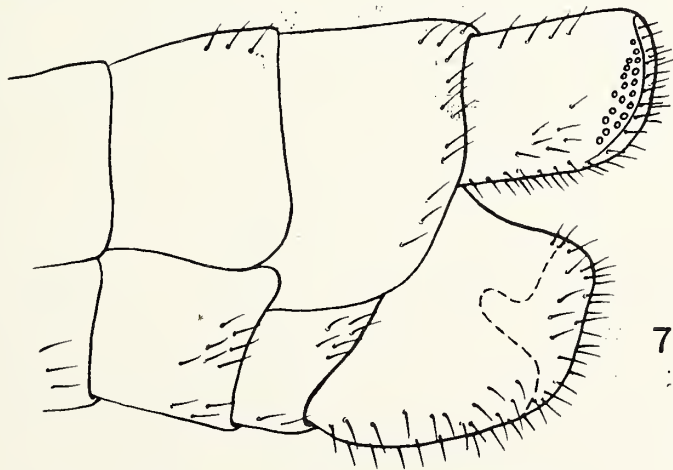




5



6



7

Paratype (♀): Y.M.C.A. Camp, Tepaztlan, Morelos, Mexico; beating cypress; Aug. 21, 1958 (collected by H. E. Howden). In the Canadian Collection, Ottawa.

This insect clearly possesses the long piece of MA in the hind wing, characteristic of *Raphidia*, as opposed to its absence in *Agulla*. The species is readily identified by the fusion of the ninth sternite and its coxopodite into a single plate on each side. In *R. notata* of Europe the ninth sternite and coxopodite are partially fused, but in most species of the genus they are distinctly separated by a membranous suture. It is interesting to note that a similar complete fusion occurs in some species of *Agulla* (e.g. *xanthostigma*), representing an independent and parallel development of this condition.

In other respects, *americana* is not notably different from other species of *Raphidia*. It differs from *notata* in having smaller styli and the absence of hooks on the gonocoxites of the ninth sternite.

As noted above, *americana* is the first known living species of *Raphidia* to be found in the New World, as that genus is now conceived (cf. Carpenter, 1936). In all probability it is a derivative of the original population of the genus that existed in the New World (at least in Colorado) in the middle Tertiary.

#### Family Inocelliidae

This family has previously been represented in the New World by two species of the genus *Inocellia*: *inflata* Hagen and *longicornis* Albarda, both of which occur in California, Oregon, Nevada, Washington, and British Columbia. The occurrence of the following new species in eastern Mexico is, therefore, of unusual interest.

#### *Inocellia pilicornis*, n. sp.

#### Plate 7, figures 4-7

Male: length of fore wing 8.7 mm.; width 2.3 mm.; length of hind wing, 7.5 mm.; width 2.2 mm. Pterostigma four times as long as wide. The veins and the pterostigma are light brown in the holotype, but are very dark brown or even black in the paratypes. The markings on the dorsal surface of the head are typical of those of species in the

genus: the anterior half dark brown or black, the posterior half lighter brown with four streaks of dark brown extending towards the posterior border. The antennae are light brown in the holotype but, except for the first two segments, are dark brown or black in the paratypes; the prothorax is brown to dark brown or black except for the anterior border, which is very light; the dark portion has the irregular dark and light brown markings characteristic of the genus. Mesonotum dark brown or black (paratypes) with a median, very light brown spot; mesoscutellum light brown; metanotum marked like mesonotum except that the median light brown spot extends to the anterior margin of the segment and includes some white. Abdominal tergites dark brown or black laterally, with a median light stripe extending continuously along all tergites; the light stripe is mostly light brown but includes some white at the anterior and posterior edges of the genus *Inocellia*. The antennae are 7 mm. long and consist of 60 to 61 moniliform segments; the individual segments (see figure 6) are asymmetrical: on one side (the surface toward the other antenna) there is a cluster of three (rarely, four) long setae arising from nearly the same spot; this side of the antenna segment has a somewhat flattened appearance. Each antennal segment has a ring of 25 long setae, arising on the distal half of the segment; slightly proximally, near the middle of the segment, is a ring of 14 to 16 short setae which project distally. A few other setal sockets can be observed near the base of the cluster of three setae mentioned above. The terminal antennal segment is about twice as long as the others and lacks the peculiarities of the other segments; it bears about thirty setae. The prothorax is somewhat shorter than the head; the ectoproct has rounded posterior margins, somewhat as in *I. longicornis*; the gonocoxites of the ninth segment have the distal margin folded inward forming a curved tooth, which is similar to that in *longicornis*.

The female is unknown.

Holotype (♂): near Hidalgo, Tamaulipas, Mexico; March 27, 1938 (collected by C. C. Plummer). In the Museum of Comparative Zoology.



Paratype (♂): Monterrey, Nuevo Leon, Mexico; Feb. 26, 1956 (collected by Philip S. Barker); to be deposited in the collection of the Rockefeller Foundation Agricultural Program, Mexico, but temporarily placed in the Museum of Comparative Zoology.

Paratype (♂): 5 miles south of Monterrey, Nuevo Leon, Mexico; Sept. 3, 1958; night beating, Acacia-cypress area (collected by H. F. Howden). In the Canadian National Collection, Ottawa, Canada.

This species is at once distinguished from all other described species of the genus by the pilose, moniliform antennae. It is also noticeably smaller than the other species of *Inocellia* known from the New World, having a wing expanse of 17 mm. as compared with an expanse of 24 mm. for *inflata* and *longicornis*.

The inocelliid affinities of the new species are shown by the absence of ocelli, the absence of the basal pterostigmal veinlet, the presence of a forked posterior cubitus, and the oblique position of the vein *bc* (figure 4) in the hind wing. The species has the normal venational pattern of *Inocella* (not that of *Fibla*, see Carpenter, 1936): in addition, the structure of the head, prothorax, and abdomen, including terminal segments, is typical of that of *Inocellia*. Hence, although the antennae (of the male, at least) are different from those of all other Raphidiodea, consisting of moniliform, pilose segments, I am assigning the species to *Inocellia*. Should the female turn out to have other characteristics which are equally peculiar, a separate genus will probably be needed for the insect.

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THE COLLEMBOLA OF LEBANON  
AND WESTERN SYRIA  
PART III FAMILY ISOTOMIDAE<sup>1</sup>

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The work herein described was done under N.S.F. Grant G 4563. I wish to gratefully acknowledge the work of my assistant, Jerry Tecklin, who did all of the preliminary sorting and most of the handling and mounting of the material here studied.

Relatively little has been known about the Isotomidae of the Syrian region. Until the work of Cassagnau and Delamare only a few of the more prominent epigeic forms had been described. With the above mentioned work the recorded species from the area were eight. In the present study four of these forms were recovered and two others were probably recovered. In addition 16 new records were established.

*Anurophorus coiffaiti* Cassagnau & Delamare

Plate 8, figures 6, 7

*Anurophorus coiffaiti* P. Cassagnau & Cl. Delamare, 1951 Biospeologica 75:377,378.

This species was the first of the genus to be described from Western Syria. The specimens at hand agree well with the illustrations and figures given by Delamare and Cassagnau. The P.A.O. (see figure 7) is characteristically oval with a definite indentation or indication of a listel at least on the forward margin. The abdominal thickenings characteristic of the species vary a great deal but some indication of these can be seen even in the youngest specimens. In some forms these fuse into a single large tubercle-like projection. The sense organ of the third antennal segment usually has only two short setae between the

<sup>1</sup> Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

guard rods instead of three as indicated in the describers' illustration.

The species appears in the moist regions, largely in the mountains. Type locality Antelias Lebanon, x 9-51. Other captures: LEBANON: Ain Zhalte Cedars, 177 M., XI '52; B'charra Cedars, 1900 M. v '52; between Dhour Schweir and Bikfaya, VIII '53; Nahr Array between B'kassine and Jezzine, 800 M.; Wadi Jahnam (N.W. Tripoli Prov.), VII 31 '52; Bikfaya VII '53. SYRIA: Latakia Oak Grove, just below Turkish border, VIII '53.

**Anurophorus asfourii, n. sp.**

Plate 8, figures 1-5

Body subcylindrical with deep constrictions between segments. Unpigmented prothorax much wrinkled and about  $\frac{1}{2}$  as long as mesonotum. Clothing of body of relatively uniform short smooth acuminate setae, mostly curved with slightly longer straight setae on last three abdominal segments. Intersegmental membranes clearly demarcated except for fifth and sixth abdominal segments, which are solidly fused. Pigment blue, in scattered scabrous patches over head, antennae, and tergites. Intersegmental membranes and legs pale. Eyes eight per side on a medially constricted eye patch. Antennal apex with a large bilobed bulb set in a deep pit. Fourth antennal segment clothed

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EXPLANATION OF PLATE 8

Figures 1-5: *Anurophorus asfourii* n. sp. 1. Habitus, paratype, seen from above and slightly to one side, setae omitted, 90X. 2. Tip of fourth antennal segment, paratype, 1000X. 3. Hind foot, paratype, 1000 X. 4. Third antennal segment "sense" organ, paratype, 1000 X. 5. Eyes and P.A.O. right side, paratype, 700 X. Figures 6 and 7: *A. coiffaiti*. 6. Tip fourth antennal segment, specimen from between Dhour Shweir and Bkfaya Lebanon, 1000 X. 7. Anterior portion eye and P.A.O. Same specimen as above, 1000 X. Figures 8-13: *Ballistura levantina* n. sp. 8. Habitus, setae and pigment omitted, paratype, 40X. 9. Hind foot, paratype, 1200X. 10. Inner margin of apex of fourth antennal segment, paratype, 1200X. 11. Inner part base of left dens showing dental projections, paratype, 1200 X. 12. Right mucro seen from above and slightly to one side, paratype, 1200X. 13. Left mucro, side view, holotype, 380X.





with a mixture of curved and straight acuminate setae, and a number of slightly curved blunt "sensory" setae. The latter type form about one third of the clothing of the apical half of the segment. Third segment clothed with a number of curved acuminate setae, and in addition six blunt setae as follows: on the dorsal surface two long rods enclose between them two short oval knobs (about one third as long as the rods); on the ventral surface there are two additional curved rods about one half as long as the dorsal ones. Second and first antennal segments each with a circlet of acuminate setae. P.A.O. broadly oval and more than twice as large as the largest eye. Eyes eight per side with eyes D, H, and E, being smaller than the remainder. Integument granulate save for the last two abdominal tergites which are finely reticulate. Legs with tibiotarsi subsegmented. Unguis without lateral teeth but with an extremely small inner tooth. Empodial appendage lanceolate, slightly less than half as long as unguis, and lacking any apical bristle. Unguis with three weakly clavate tenent hairs, the median being strikingly longer than the remainder.

The description of this form brings to four the number of species of *Anurophorus* having the fifth and sixth abdominal segments fused into a single mass. Although these species are generally similar they may be readily separated on the basis of the characteristics listed below:

SEPARATION OF SPECIES OF *Anurophorus* HAVING THE  
FIFTH AND SIXTH ABDOMINAL SEGMENTS FUSED

Species	P.A.O.	Organ	
		eyes/side	ungual tooth
<i>A. konseli</i>	broadly oval	4	-
<i>A. asfourii</i>	broadly oval	8	+
<i>A. oredonensis</i>	narrow, indented	5	-
<i>A. coiffaiti</i>	narrow, indented	8 (7)	-

In addition to these, special characteristics such as the abdominal thickenings of *A. coiffaiti* and the antennal chaetotaxy can be used for additional separation.

Type locality: Kammouha LEBANON (25 specimens), 1900 M., VII 19 '52; also taken from Latakia, SYRIA, oak grove just below Turkish border, VIII '53.

*Tetracanthella pilosa* Schött

*Tetracanthella pilosa* Schött, 1891. Ent. Tidskr. 12:191.

The specimens at hand agree with the descriptions and figures in Stach quite well. The only small difference noted was that the furcula was relatively longer. The species is quite rare in the region under consideration. It has been taken from: LEBANON: Ain Z'Halte Cedars, above forest, XI' 52; SYRIA: Pine Forest, Northern Latakia, VIII '53.

*Folsomides americanus* Denis

*Folsomides americanus* Denis 1931. Bul. Lab. Zool. Portici 26:69-170.

I have nothing to add to the comments of Cassagnau and Delamare (*op. cit.*) concerning this species except that comparison with North American material shows it to be identical with the specimens at hand. This material had previously been identified as *Folsomides parvus*. The species is widespread and abundant through the lowland and lower mountain regions of the area under consideration. Taken from LEBANON: Beirut, campus American University, many dates from 1951 through 1953; Souk el Gharb, VIII '53, between Kfardebiene & Bskinta, v '53; Beit ed Dine, XI '53; Saida, XI '51; 14 Km. South of Saida, XI '53; 2 km. East of Rayak, VII '52; Farayha, v '53. SYRIA Latakia, oak grove just below Turkish border, VIII '53.

*Folsomia*

This genus is the best represented Isotomid genus in the area. There are probably five species occurring in the area, and the nature of the population isolation and variation within several of the species concerned merits a great deal more study. Cassagnau and Delamare (*op. cit.*) describe one new species and mention the capture of three single specimens they determined as *Folsomia ksenemani*, I feel certain that these were in fact single-eyed specimens of the same species I have identified as *F. penicula* Bagnall. For this reason I have not included *ksenemani* in the list below. It is quite probable that larger series in each case would have shown the more typical four-eyed forms in each population.

*Folsomia quadrioculata* Tullberg

*Isotoma quadrioculata* Tullberg, 1871. Ofv. Kongl. Vet. Akadm. Forhandl. 27 (1):143-155.



A great deal has been written about the group of species related to the form named above. Out of this there has developed a welter of species: *brevicauda*, *quadrioculata*, *manolachei*, *nana*, *microchaeta*, *penicula* and *multiseta*. Further than this when we considered the excellent work of Agrell upon variation in eye number we can add to this group at least the one-eyed forms such as *regularis*, *diplophthalmia*, *agrelli*, *ksenemani*, *pseudodiplophthalma*, *similis*, and *monophthalma*. Most of these so-called species differ by very few characteristics, indeed often only by one. These are commonly chaetotaxy differences and there is not the slightest bit of evidence to deny the possibility that they represent single gene variations. Thus the differences seen could well represent in some cases balanced polymorphism, and in others ecotypical selection for a given gene. Further than this most of the species here mentioned have been studied at one time from a few relatively homogenous habitats and there is thus little opportunity to study the variation through a wide range of conditions. I wish to suggest that there is at present insufficient evidence to sort out accurately from the forms mentioned above more than a few forms and be able to say with any degree of assurance that they actually represent different species. The specimens studied below appear to be classifiable as two species, *F. quadrioculata* and *F. penicula*. If we accept this thesis, then it is possible to sort out the specimens at hand quite readily on the basis of the ventral manubrial chaetotaxy. If we sort them out thus, it appears that with few exceptions a given collection or sample is of one form or the other. If an attempt is made to sort out the populations on any other basis, this is not so and most samples are mixed. Further, in a statistical sense it is possible to sort out these two species upon about five additional characteristics; however, none of these shows very good correlation with the manubrial chaetotaxy. For purposes of illustrating the distribution of some of these characteristics through the population, a large number of specimens from twelve localities was sorted out to *quadrioculata* or *penicula* on a basis of the ventral manubrial setae. Fifteen specimens were chosen from each species and checked for a number of characteristics. The results are indicated below.

<i>Description of character</i>	% <i>quadrioculata</i> having	% <i>penicula</i> having
Eyes unequal in size	47	86
Largest setae posterior margin head twice smallest	33	100
Brush-like mass long setae (4-5 rows) at end abdomen	73	100
Gap of P.A.O. wider than lip	93	47
Dentes with median dorsal seta	47	93

Other differences examined (ex., angling P.A.O. dorsal chaetotaxy, occurrence one-eyed forms, shape of mucro) showed even less differentiation, or differences so fine as to be impractical. In many populations of both species an occasional one-eyed form is to be found, and a few populations consist of such forms exclusively, without differing in any other visible respect from the four-eyed populations.

The net result of this is to indicate that in the region studied there are two forms separable upon a basis of their manubrial chaetotaxy. It is convenient to consider them as two species but it must be understood that the real nature of their genetic relationship has yet to be established.

In the Western Syrian region *penicula* is widely distributed throughout the Lebanese mountains and the coastal plain, whereas *quadrioculata* is largely limited to the higher elevations of the Lebanon Mountains.

Distribution of *quadrioculata*: LEBANON: Ain Z'Halte Cedars, 1700 M. VII '52 & XI '52; between K'Fardebiene & Beskinta, 1900 M., VI '53; Hadeth Cedars, 1700 M., VII '53; B'Charra Cedars, 1900 M., v '53; Barouk Cedars, 1700 M., VI '53.

#### *Folsomia penicula* Bagnall

*Folsomia penicula* Bagnall 1939. Ent. Mo. Mag. 75:56-59.

*Folsomia tetrophthalma* Gisin 1946. Mitt. Schweiz. Ent. Ges. 20:219. (NEW SYNONYMY).

*Folsomia multiseta* Stach 1947. Acta Monographica Polska Akademia umiejtnosci 138:172-177. (NEW SYNONYMY).

*Penicula* was described for forms having two pairs of eyes with the posteriormost pair smaller than the fore pair and having a brush-like mass of setae at the end of the abdomen. In addition to this the members of the species are



characterized by having six or more ventral manubrial setae in adult animals. In 1946 Gisin pointed out that this species was probably identical with Kseneman's *F. diplophthalmia* var. *Tetrophthalmia*. Since Kseneman had indicated that in his opinion this was a matter of population variation and thus not subspecific in rank, this name would fall under the category of "infrasubspecific form" according to the rules "A name given to any infrasubspecific form if elevated to subspecific or specific rank by a subsequent reviser shall rank in its new status for purposes of priority as from the date on which it was so elevated, and shall be attributed to the author by whom it was so elevated." Thus *Folsomia tetrophthalmia* becomes a junior synonym of *F. penicula*.

The species is extremely common in Lebanon and Syria, and in a variety of habitats. The specimens at hand display characteristics which destroy the separation shown between this species and *multisetata* by Stach (1947). The table below indicates how this species violates both sets of limitations:

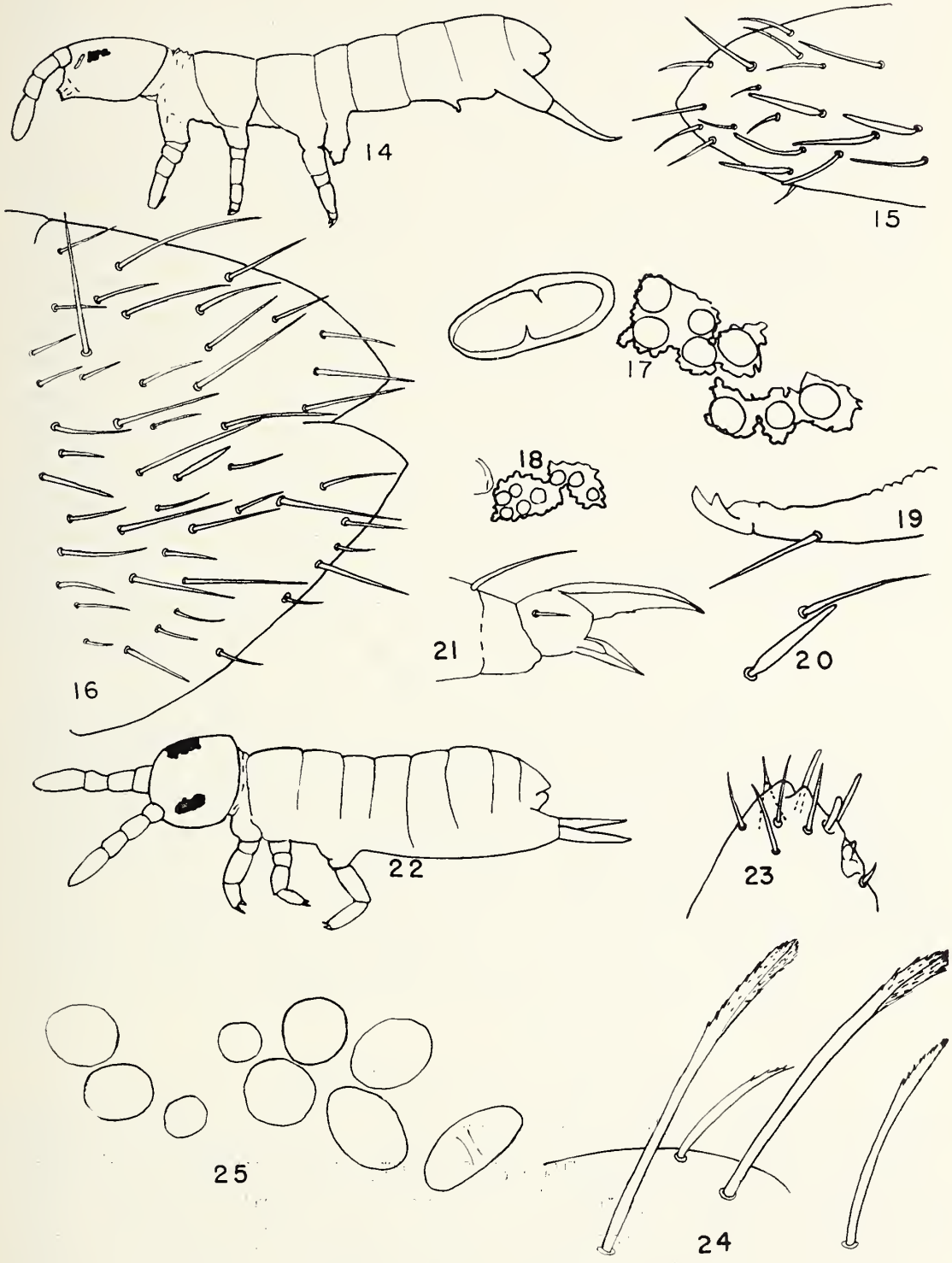
	penicula Stach	acc. multiseta Stach	acc. Leb. penicula
Ventral maubrial			
setae	12-13	14-17	11-16
P.A.O./ommatidium	3.5-4	4-5	3.5-6
ventral setae on dens	12	16-22	12-18

In view of this I feel best to consider *multisetata* a synonym of the locally variable *penicula*.

#### EXPLANATION OF PLATE 9

Figures 14-21: *Isotomina salaymehi* n. sp. 14. Habitus, specimen from Beirut, 90 ×. 15. Tip of fourth antennal segment, paratype, 1200 ×. 16. Chaetotaxy last two abdominal segments, side view, paratype, 600 ×. 17. Eyes and P.A.O. Unusual specimen with complete division eye patch, paratype, 1200 ×. 18. Eyes and edge P.A.O. showing normal condition, paratype, 600 ×. 19. Right mucro, paratype, 1100 ×. 20. Abdominal "sensory" seta with neighboring normal seta, paratype, 1100 ×. 21. Hind unguis, paratype, 1200 ×. Figure 22-25: *Vertagopus ciliatus* n. sp. 22. Habitus (slightly distorted by mounting) paratype, 90 ×. 23. Apex fourth antennal segment, holotype, 1200 ×. 24. Long ciliate setae of fifth and sixth abdominal segments, holotype, 1200 ×. 25. Eyes and P.A.O. left side paratype, 1200 ×.





One last point which must be discussed is the variation in the number of eyes. Agrell, Kseneman, Stach and a number of other investigators have accepted the fact that the number of eyes in at least some species of *Folsomia* is variable. Gisin in 1946 has stated that this condition has not been proven for any species of the genus. Among the specimens I have identified as *F. penicula* are occasional specimens with a single pair of eyes, and in one case a specimen lacking eyes entirely. Beyond this, an occasional (2) small sample may consist of all one-eye paired forms. In all cases, and particularly where the four-eyed and two-eyed forms occurred in the same population, a slow, careful comparison was made between the two-eyed and four-eyed forms and not the slightest difference other than the eyes could be found. To assume that these represent different species, particularly where the one-eyed paired forms represent two specimens in a sample of thousands, is to my view sheer folly. I feel therefore that I can state with authority that in the species I call *penicula* there are both two-eyed and four-eyed forms. The two-eyed forms are undoubtedly synonymous with those specimens identified by Cassagnau as *Ksenmani*. It is entirely possible that these two species are synonyms but before this can be ascertained the whole group must be thoroughly reviewed.

Distribution: LEBANON: Ain Z'Halte Cedars, many dates; B'Charra Cedars, v '53; Kammouha, VIII '52; Barouk Cedars, VI '53; Chamlane, XII '53; Vic. Beit ed Dine, XI '53; Beirut, American University campus, many dates. SYRIA: North Latakia pine forest, VII '53; Latakia, oak grove just below Turkish border, v '53.

#### *Folsomia candida* Willem

*Folsomia candida* Willem 1902. Ann. Soc. Ent. Belgique, 46:275-283.

The specimens at hand agree very well with the figures and descriptions given in Stach. The only notable difference was the absence of an inner tooth on the unguis. In this respect the present specimens are similar to Bagnall's *distincta*, but I agree with Stach that there is insufficient grounds for separating this species at the present time. The evidence of Delamare (1950) and this material point to a locally variable widespread form. The

present specimens are similar to the forms described and figured from Ardeche by Delamare in the absence of an inner tooth and the proportions of the dens, as well as in the existence of an occasional triangular P.A.O. However, in the chaetotaxy of the manubrial venter and the structure of the unguis, the present specimens are much more like those figured by Stach for *candida*.

Distribution: LEBANON: Beirut, campus American University, v '52; between Jezzine and B'Kassine, ix '52; Hermel, VII '52; Kammouha, VIII '52.

*Folsomia cavicola* Cassagnau & Delamare

*Folsomia cavicola* P. Cassagnau & Cl. Delamare Deboutteville *op. cit.* :381,382.

I have not recovered this species but it appears to be distinguished from *candida* in Lebanon by the absence of an apical filament on the unguis, presence of a large internal unguis tooth, and the blunt mucronal teeth. Also the apical tooth is strongly upcurved in contrast to the straight tooth of *candida*. Known only from Ghita cave.

*Folsomia* sp.

A single specimen taken (damaged) from the Nahr Array in Lebanon merits mention. The P.A.O. is divided by a prominent listel, and the last three abdominal segments are weakly fused. The furcula is short and the mucro three-toothed. The eyes appear to be eight/side but are hard to distinguish. While this is probably a new species of *Folsomia* the single damaged specimen is insufficient material for its description.

*Proisotoma minuta* Tullberg

*Isotoma minuta* Tullberg 1871. *op. cit.* :143-155.

The specimens at hand appear quite similar to those described and figured by Linnianemi, and Stach. There appears to be some variation in the setae on the tenaculum (most of the present forms have two setae) and in the eyes. In a number of specimens it appears that eyes G. and H are definitely smaller than the remainder. The size of the basalmost mucronal tooth is variable.

Distribution: LEBANON:Hermel, VII '52; 2 Km. N. of Saida, XI '53; Antilias, XI '52 Nahr Array, v '52; Beirut, American University campus. SYRIA: Latakia, below Turkish border. Oak Grove. VII '53: North Latakia pine forest.



*Proisotoma minima* (Absolon)

*Isotoma minima* Absolon 1901. Zool. Anz.24 (634): 32,33.

Only three specimens were recovered from one locality: LEBANON: Aaranita, VII '52.

*Ballistrura schötti* Dalla Torre

*Proisotoma schötti* (Dalla Torre) 1885, 46 Progr. St. Gymn. Innsbruck.

Handschin recorded this species from Palestine.

***Ballistura levantina*, n. sp.**

Plate 8, Figures 8-13

Facies *Hypogastrura*-like. Body and appendages thick. Uniformly blue-black in color except for slightly paler legs. Clothing of trunk and head of smooth, short curved setae of relatively uniform length. Sixth abdominal segment with a dozen longer setae about twice to three times as long as the shortest setae of the same segment. Antennae slightly but definitely longer than head. Fourth antennal segment without apical bulb, clothed with a variety of short, smooth setae. These are of three main types, straight to curved acuminate setae, straight truncate setae, and long mostly curved blunt "sensory" setae. In addition the dorsal surface bears a short triangular spine-like seta in a clear pit. Sense organ of third antennal segment of two oval central pegs, one of which is strongly curved. Remainder of antennae clothed with normal acuminate setae. P.A.O. elliptical, eyepatch. Tibiotarsus without subsegment. Tent hair not clavate and unguis untoothed. Empolial appendage with large inner basal lamella and clear apical filament. Manubrium without ventral setae and with numerous dorsal setae. Dentes thick but tapering. Mucro boat shaped with thick granulate central axis, and with toothed lateral lamellae. Mucro from side view very deep, more than  $\frac{1}{2}$  as deep as long. Tenaculum with four teeth and a single bristle. Corpus with an anterior projection much longer than the rami.

The species is similar to *B. crassicauda* in most respects. The differences between the two species are all small but in accumulation they indicate a real difference. Since previous abundant records of the group have shown little variation I feel the differences listed below merit specific separation.

Character	<i>crassicauda</i>	<i>levantina</i>
mucro	less than $\frac{1}{2}$ as deep as long	more than $\frac{1}{2}$ as deep as long
manubrium	with 4 ventral setae	without ventral setae
4th ant. seg.	without blunt "sensory" setae	with clear blunt "sensory" setae
3rd ant. seg. "sense organs"	peg-like, subcylindrical	oval
longest abdominal setae	$1.5 \times$ smallest	$2-3 \times$ smallest

There is some variation in the P.A.O. of the present species. In most specimens the margins are entire but a few show clear indentation in one or both margins. In most respects there is almost no variation in the large series seen.

Known only from type locality: LEBANON: Kadischa cave; moss near spray zone of waterfall near mouth, v '53 (30 specimens).

#### *Isotomina bituberculata* (Wahlgren)

Although the original description was not seen the specimens at hand agree very well with the available descriptions. The eye number is six per side. Some specimens have the eyes so heavily pigmented as to be difficult to count but observation during clearing with Potassium Hydroxide showed the actual number to six in every case examined. The posterior abdominal setae are unusually long in adults varying from .045 to .066 mm. This may very well be the same species described by Cassagnau and Delamare as *Isotomina pontica*. In some small specimens the median eyes are invisible until clearing is complete and this might account for the difference in identification. Distribution: LEBANON: 2 km. E. Rayak, VII '52; Hadeth, VII '53; below Bakich, v '53; 14 km. S. Saida, XI '53. SYRIA: Northern Latakia pine forest, VII '53.

#### *Isotomina pontica* Stach

*Isotomina pontica* Stach 1947. Acta Monog. Polska Akademia Umiejetnosci: 267.

Cassagnau and Delamare reported this from 3 localities:

Grotte d'Amchite, Roum, and Source de Hasbani. See the discussion above.

**Isotomina salaymehi, n. sp.**

Plate 9, figures 14-21

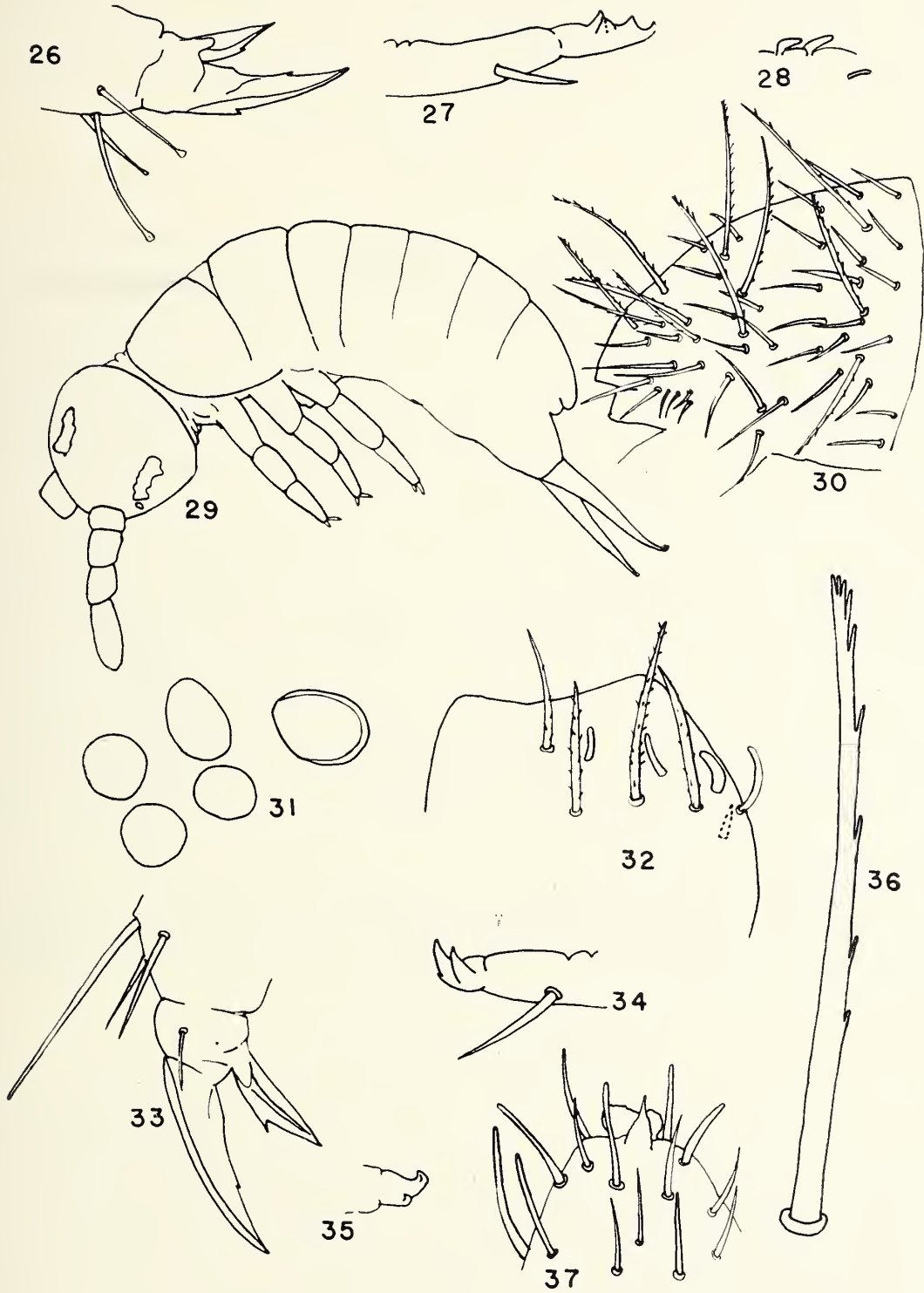
Body subcylindrical with last two segments solidly fused. Furcula reaching posterior border of second abdominal segment. Pigment gray, in the form of scattered granules. Eyepatches black and medially constricted. Fourth antennal segment clothed with numerous curved and straight acuminate setae. Six of these are basally slightly expanded and notably thicker than remainder. Third antennal segment with two short "sensory" oval knobs set by short stalks in separate pits. On either side a narrow rod. Remainder of antennae clothed with slightly curved to straight acuminate smooth setae. Thorax and first four abdominal segments clothed with short acuminate smooth setae, recumbent except for a single row of erect setae on the third and fourth abdominal segments. Fused fifth and sixth segments clothed with acuminate setae of various sizes, the longest 3 times as long as the shortest. In addition a single blunt "sensory" setae can be seen in the postero-lateral quadrant on each side. Eyes eight per side with eye D strikingly smaller than remainder. Legs unpigmented with incomplete but distinct subsegment on at least one pair of tibiotarsi. Unguis with minute inner tooth but without lateral teeth. Empodial appendage

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EXPLANATION OF PLATE 10

Figures 26-28: *Vertagopus ciliatus* n. sp. 26. Right fore foot, holotype, 1000 X. 27. Right mucro, holotype, 1000 X. 28. Third antennal segment "sense" organ, paratype, 1200 X. Figures 29-37: *Pseudisotoma (Isotomida) anamola* n. sp. 29. Habitus (slightly compressed in mounting) holotype, 90 X. 30. Fused fifth and sixth abdominal segments, paratype, 300 X. 31. Right P.A.O. and anterior four eyes, paratype, 1200 X. 32. Third antennal segment sense organ, paratype, 1200 X. 33. Right hind foot, paratype, 1200 X. 34. Mucro, side view, paratype, 1200 X. 35. Mucro seen from above, holotype, 1200 X. 36. Large ciliate seta from fig. 30 showing peculiar ciliation, 1200 X. 37. Tip fourth antennal segment, holotype, 1100 X.





acuminate, with striking central ridge, and basal part inner lamella expanded. Tenent hair acuminate. Tenaculum with four teeth and single large basal seta. Manubrium with one pair of ventral and 24 dorsal setae. Dens with a double row of ventral setae, and four dorsal setae. Mucro with two teeth and straight ventral margin.

### Discussion

This species can readily be separated from all described species of *Isotomina* by the well developed blunt "sensory" seta on the last abdominal segment. In other respects this species seems to be most closely related to *I. thermophila*, but it may also be separated from this species by the small eye D, by the presence of a tibiotarsal subsegment, and by the fact that the longest abdominal setae are three times as long as the shortest.

The present species shows a good deal of variation, particularly in respect to the eyes. The eye D is usually considerably smaller than the remainder but in a few specimens it is entirely absent. The eyepatch shows some tendency towards constriction in the middle, and in a few specimens it is actually divided into two patches. The clarity and presence of the tibiotarsal subsegment varies a great deal although most specimens show this on the third pair of legs.

Type locality: Antelias, Lebanon, XI '52. Other collections: LEBANON: Vic. Nabeth Safa, XI '53; Beirut, American University campus, v '52; Barouk Cedars, VI '53; 2 km. E. Rayak VII '52. SYRIA: S. Latakia.

### *Vertagopus aborea* Linne

*Podura arborea* Linne 1758. Systema naturae Edit. 10 Holmiae: 609.

The specimens at hand agree well with available descriptions and specimens except for two things: first, the color is not dark purple or purple blue but medium to pale gray-blue. Second, the fifth and sixth abdominal segments have setae twice as long as the shortest setae of these segments. As Stach points out, from the varied descriptions of this form it would appear that either a species complex or a geographically variable form is involved. In view of the general similarity of the present specimens with European

members of this species, I consider it best to place them in the same species. In the region it appears to be rare and only in the cedar forests. Distribution: LEBANON: B'Charra Cedars, v '53; Barouk Cedars, VI ,53; Hadeth Cedars, VII '53.

*Vertagopus ciliatus*, n. sp.

Plate 9, figures 22-25; plate 10, figures 26-28

Body subsylindrical, furcula reaching posterior border of second abdominal segment. Antennae clearly longer than head and slightly longer than furcula. Pigment dark blue in scabrous patches over antennae, head and body tergites. Legs, furcula, and venter light blue. Fourth antennal segment with two prominent apical humps and a single apical cone bearing a stout acuminate seta. Just below antennal apex a single stout curved rod and below this a distinct pit containing a spherical knob with a short curved conical seta on its basal margin. Outer margin of segment with two irregular rows of curved blunted setae. Third antennal segment "sense organ" of two strongly curved thickened knobs without clear protective setae. Remainder of antennae clothed with numerous curved and straight acuminate smooth setae. Fourth abdominal segment similar except for the posterior two rows of setae which are apically unilaterally ciliate. Fifth segment clothed with similar setae with the addition of a single row of long cylindrical setae, blunt and apically finely ciliate. Sixth segment with three rows of long setae, the anterior row similar to those of the fifth segment, the posterior two rows somewhat more acuminate. Tibiotarsus with three clubbed tenent hairs, the median strikingly longer than the others. Unguis narrow, with small internal and pronounced lateral teeth. Empodial appendage lanceolate with minute corner tooth. Eyepatch solid, eyes eight per side with eyes G and H smaller than remainder. P.A.O. oval, about as long as one large eye, with faint indication of transverse listel. Tena-culum with four teeth and five setae on corpus. Manubrium with fifteen ventral setae as follows: two transverse rows of three near apex and two converging longitudinal rows of four setae joined at a basal median seta. Dens with numerous stout acuminate ventral setae and four slender



dorsal ones. Mucro with four teeth, apical projecting forward and slightly smaller than remainder which are subequal.

### Discussion

This species appears to be most closely allied to *V. cinerea* but it may readily be separated from that species on the basis of the structure of the third antennal organ, the structure of the eyes and the peculiar abdominal setae. These setae occur on both adult males and female. These setae would appear to separate it readily from all described species of the genus. The P.A.O. usually shows some indication of a dividing listel but this may be entirely absent.

Known only from the type locality, Kammouha Spruce Forest, VIII '52,, LEBANON (8 specimens).

*Pseudisotoma* (*Istomidia*) *anamola*, n. sp.

Plate 10, Figures 29-37

Facies isotomine. Fourth antennal segment with apical bilobed bulb and striking conical projection bearing a stout acuminate seta. Apical half of segment with a number of slightly blunted curved setae somewhat larger than remaining setae which are acuminate, smooth, curved or straight. Remaining antennal segments clothed with slightly curved mostly sparsely ciliate acuminate setae of differing sizes. Third antennal segment organ of three thick short cylindrical pegs of varying diameter, the median being the largest. In addition there is a somewhat longer slender rod. All of these are situated in a straight line without protecting folds or pits. A small conical seta is located on the opposite surface of the segment. Head and body clothed with a variety of slightly curved to straight acuminate setae. The smaller ones are smooth but the larger setae on the thorax and abdomen are unilaterally sparsely ciliate. Eyes eight per side with the anterior two larger than remainder. P.A.O. broadly oval, about as long as one forward eye. Setae of legs acuminate smooth, those on femur sparsely striate. Unguis with minute median internal tooth and distinct lateral teeth. Empodial appendage lanceolate with a clear inner corner tooth. Tenent hairs acuminate. Tenaculum with four teeth, corpus without

setae. Fifth and sixth abdominal segments fused, remainder distinct. Manubrium slightly less than half as long as dens, dorsally with numerous setae, ventrally with a single pair of large setae near the base of the dens. Dens ventrally with numerous short acuminate setae, and dorsally with six slender short setae. Mucro short, with two large curved teeth and a minute apical tooth.

Only a few specimens of this unusual species were seen and all of these were apparently immature. The head body ratios and general condition of the animals would indicate that they were nearly adult and thus while significant change in some organs with growth cannot be ruled out (ex., manubrial chaetotaxy) it seems likely that the major characteristics described above will hold for the adult animals. The discovery of this species poses some interesting questions. If we accept the commonly used distinction between Proisotominae and Isotominae — i.e. two or less manubrial setae on venter — then this species would be in the Proisotominae and close to the genus *Isotomina* or *Proisotoma*. However, in all other structures the animal shows a clear relationship to the Isotominae, and has nothing in common with the genera mentioned above save the manubrial chaetotaxy. In the Isotominae it would appear to fall into Salmon's genus *Isotomidia*. This genus was created for species generally similar to *Pseudisotoma* except for the lack of clavate tenent hairs and the presence of papillae on the antennae. Stach, apparently feeling that this insufficient grounds for separation, placed this as a synonym of *Pseudisotoma*. The present species fits the criteria for *Isotomidia* except for the absence of the antennal papillae, and further differs from *Pseudistotoma* by the presence of an apical biloped bulb, and the single pair of ventral manubrial setae. In his description of *Isotomidia triseta* Salmon (1944) says "A few isolated setae occur on the manubrium . . ." and in his figures he shows what might be considered an apical bulb. In view of this and the differences between the two forms I have thought it best to consider *Isotomidia* a subgenus of *Pseudistotoma* until a thorough study of all the forms can be made.

The species has been taken from two localities in



LEBANON: Type locality: Wadi Jahnam (N.W. Tripoli province), VII '52 (2 specimens). Also taken from 2 km. E. Rayak, VII '52.

*Isotoma notabilis* Schaeffer

*Isotoma notabilis* Schaeffer 1896. Mitt. Naturh. Mus. Hamburg 13:187.

The specimens at hand agree well with available descriptions and specimens of the species. A few minor chaetotaxy differences could be seen, notably the absence of a pair of long setae on the second and third abdominal segments. A few specimens showed three eyes per side rather than the normal four. The species is widespread throughout Lebanon and Latakia but is oddly absent from the coastal plain area.

Distribution: LEBANON: Hadeth Cedars, VII '53; B'Charra Cedars, IV '53, Ain Z'Halte Cedars, VII '52 & XI '52; Kam-mouha, VII '52; Barouk Cedars, VI '53; below Bakich, V '53; Souk el Gharb, VIII '53; Vic. Beit ed Dine, XI '53; Bikfaya, VIII '53; 2 km. E. Rayak, VII '52; Antelias source, XI '52; Rahbeh B'kaa, IX '52. SYRIA: Latakia, oak grove below Turkish border.

*Isotoma viridis* Bourlet

*Isotoma viridis* Bourlet 1839. Mem. Soc. Roy. Sci. Agric. Arts Lille :401.

*Isotoma turkestanica* Stach 1947. *op. cit.* :355, 366. (NEW SYNONYMY).

The specimens agree on the whole very well with figures, descriptions and specimens previously identified as this species. Certain variations are worthy of note. First there are on most specimens clearly visible fine ciliate setae on the dens. In addition to this about half the specimens have the anteapical teeth not on a level. A last character of note is the P.A.O. In most, but not all, specimens this organ has a thickened margin of irregular shape. The pattern of the specimens is either of the type called *decorata* by Brown or in the form of stripes across the posterior margins of the segments.

The occurrence of the ciliated dental setae and the displaced anteapical tooth raises a serious question in connection with Stach's *I. turkestanica*. This form, briefly described in his key and without figures or further description in the text, differs from *viridis* by the occurrence of ciliated setae on the dens and the feet. In addition he



mentions the fact that the anteapical teeth are not on a level. In the specimens seen here the ciliate setae can be seen on the dens but not the legs while the teeth may or may not be level. In addition there is the variation in the structure of the P.A.O. not mentioned before. When we combine this with the well known local variability of the pattern in *viridis* I feel it best to consider *turkestanica* and the present form part of the locally variable widespread *I. viridis*.

In the region it has been found only from the Lebanon Mountains: LEBANON: B'Charra Cedars, v '53; Vic. Har-risa, XI '52; Ain Z'Halte Cedars, VII '52 & XI '52. Cassagnau & Delamare reported it from Chebaa and Handschin from several localities in Palestine.

*Isotomuris palustris* Muller

*Podura palustris* Muller 1776. Zoologicae Daniae Prodremus :184.

The specimens agree well with available descriptions of European forms identified as this species, A number of minor differences are seen: there are frequently no ciliate macrochaetae on the third abdominal segment, and the corner tooth on the last two pairs of empodial appendages is absent in about 85% of the animals. The patterns are varied. Distribution: LEBANON: 2 km. S. Saida, XI '53; Ain Z'Halte, XI '53; Ain Z'Halte Cedars, v '53; Kammoutha, VIII '52; Vic Quaaranita, VII '52; Wadi Jahanem (N.W. Tripoli province), VII '52; Vic. Beit ed Dine, XI '53; Harajel, XI '53; Chamlane, XII '53.

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THE INDO-AUSTRALIAN SPECIES OF THE ANT  
GENUS STRUMIGENYS FR. SMITH: GROUP OF  
*S. GODEFFROYI* IN BORNEO<sup>1</sup>

BY WILLIAM L. BROWN, JR.

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This paper is a further contribution in a series which, when complete, will cover the known species of the Indo-Australian portion of the dacetine ant genus *Strumigenys* Fr. Smith. For general background, explanations of abbreviations used in citing measurements and indices, and discussion of *S. godeffroyi* Mayr and related species, see Brown, 1949, *Mushi* 20: especially pp. 2 and 16-19. Previous parts of this series, the first two of which also include explanations of abbreviations for measurements, etc., are in *Psyche* 60: 85-89 (1953), 60: 160-166 (1954), 61: 68-73 (1954), 63: 113-118 (1956), and 64: 109-114 (1957). Figures of these species have been prepared, but are being saved for use in collective plates in connection with the eventual keys to all the Indo-Australian species of the genus.

I have seen a dealate female of *S. godeffroyi* Mayr from Long Navang, northern Borneo, E. Mjöberg leg. This species probably occurs at many coastal points and around settlements inland. It is widespread in the tropics of south-eastern Asia and the Pacific.

The following five species evidently are much more local and rare.

*Strumigenys dyak* sp. nov.

Holotype worker: TL 3.07, HL 0.80. ML 0.35, WL 0.80 mm.; CI 69, ML 44. Close to *S. solifontis* Brown, from Japan, but differing chiefly in the shorter and straighter mandibles, and in the long preapical tooth being set only a little more than half its own length away from the dorsal apical tooth. The size, proportions of the head, and shape of alitrunk are

<sup>1</sup> Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.



all as in *solifontis*, and even the pilosity of the two species is closely similar. The compound eyes of *dyak* are nearly twice the size of those of *solifontis*, and are more strongly convex and protruding laterally. Clypeus depressed and excised anteromedially.

Petiolar node as in *solifontis*, longer than broad and slightly longer than its peduncle; spongiform appendages well developed, but the lateral lobes not reaching the anterior nodal slope. Postpetiolar node smaller than that of *solifontis*, barely broader than long and only slightly broader than the petiole, its disc convex, smooth and shining, with a few short, weak longitudinal costulae along the anterior border. Unlike those of *solifontis*, the definitely smooth, shining areas on the sides of the alitrunk in *dyak* are restricted chiefly to the lower mesopleura. Basal gastric costulae somewhat spongiform, extending about  $1/5$  the length of the basal tergite.

Ground pilosity of head rather sparse, consisting of subreclinate to obliquely erect, short, fine truncate hairs, becoming feebly spatulate on the free clypeal margin. Scape hairs fine, directed apicad. Ground hairs of alitrunk rare, fine and inconspicuous, appressed to reclinate. About 6 longer, erect, fine truncate hairs bordering each occipital lobe laterally, posteriorly and medially; 3 pairs of the same on the alitrunk, the humeral pair being long and subflagellate, mesonotal pair long, pair on mid-pronotum not so long, inclined anteriorly. Sparse growth of long, fine erect hairs on petiole, postpetiole and gaster. Propodeal teeth acute and elevated, their infradental lamellae moderate in size, but expanded below and with a small growth of spongiform tissue laterally. Color ferruginous yellow (possibly faded); dorsum of head, except occipital lobes, faintly more pigmented. Mandibles and appendages light yellow, with red-brown teeth on the former.

Holotype a single worker from "head Camp, N. Borneo" (leg. E. Mjöberg, British North Borneo collecting tour), deposited in MCZ.

Paratype a single worker in MCZ, "foot of Mt. Murud," North Borneo (Mjöberg leg.). Size slightly smaller than in holotype, but proportions of head and mandibles identical.

TL 2.8, HL 0.73, WL 0.73 mm. Color a trifle darker than in holotype.

This species can be separated from *godeffroyi*, *indagatrix* and other similar forms occurring in Borneo by its larger size; sparse, fine, largely erect pilosity; and slender, constricted alitrunk.

*Strumigenys mjoebergi* sp. nov.

Holotype worker: TL 2.4, HL 0.65, ML 0.29, WL 0.60 mm.; CI 68, MI 45. Very similar to *S. godeffroyi*, but differing slightly in size and proportions, and more strongly in sculpture, pilosity and color. Mandibles very slightly more curved than in *godeffroyi*, the preapical tooth long and extremely close to the apical fork; insertions rather widely spaced apart and the shafts robust. Alitrunk form much as in *godeffroyi*. Propodeal teeth acute, only weakly elevated, their infradental lamellae weakly convex below, thin and nearly transparent, without spongiform masses on their lateral faces. Petiolar node a little longer than broad, much as in *godeffroyi*, but the posterior and lateral spongiform appendages scanty. Postpetiolar node distinctly broader than petiolar node, a bit less than half as wide as the gaster, strongly convex, the surface densely punctulate-striate, opaque; spongiform appendages well developed, but less strong than in *godeffroyi*; much of the sides of the node free, especially the anterolateral surfaces. Gastric costulae coarse, numerous, extending  $\frac{1}{3}$  or more the length of the basal gastric tergite; rest of gaster smooth. Alitrunk completely punctulate and opaque. Ground pilosity of head consisting of short decumbent hairs, narrowly spatulate or clavate, much heavier than in *godeffroyi*. Ground pilosity of alitrunk fine, sparse, very inconspicuous, reclinate. A few short, stubby, erect spatulate or clavate hairs on the occipital lobes, a pair on the center of the pronotum, another on the mesonotum, and a longer humeral pair; sparse complement of distinctly spatulate erect hairs on nodes and gastric dorsum. Color sordid ferruginous yellow, dorsum of head, except occipital lobes, faintly darkened; gaster darker, brownish; lower halves of sides of alitrunk deep reddish brown; mandibles, antennae and legs yellowish.

Holotype [MCZ] from Nata Ragong, North Borneo (E.



(Mjöberg leg.) without further data, but probably from rotten wood.

Paratype workers: 4 specimens with same data as for holotype [MCZ, USNM]. TL. 2.4-2.6, HL 0.68-0.71, ML. 0.29-0.30, WL. max. 0.68 mm.; CI 68-70, MI 43-44.

Paratype female: one dealate with same data as for holotype: TL 3.0, HL 0.74, ML 0.30, WL 0.78 mm.; CI 74, MI 41. Mesonotum evenly and densely punctulate throughout, without median sulcus or carina; bearing a few short, erect spatulate hairs. Scutellum convex, not strongly projecting. Anterior corner of mesanepisternum smooth and shining. Petiolar node broader than long. Sculpture of postpetiole and base of gaster stronger than in the worker, the latter extending half the length of the basigastric tergite in the middle. Other differences as usual for the caste; color like that of worker.

This species is distinguished from most *godeffroyi* group species by means of its striate, opaque postpetiolar disc. From the few forms with similar postpetiolar sculpture, *mjöbergi* differs in the position of the preapical tooth of the mandibles and in pilosity, other sculpture and color.

#### *Strumigenys sublaminate* sp. nov.

Holotype worker: TL 2.3, HL 0.61, ML 0.22, WL 0.61 mm.; CI 73, MI 36. A member of the *godeffroyi* group with rather short mandibles, similar to *S. jepsoni* Mann from the Fijis, but with more deeply excised posterior cephalic border and different sculpture and pilosity, etc.

Preocular laminae parallel, eyes convex, protruding laterally. Anterior clypeal border weakly concave in the middle. Mandibles stout, weakly arcuate and gently tapering toward apex. Teeth of apical fork subparallel, the ventral tooth a little more than half as long as the dorsal; two very indistinct intercalary denticles. Preapical tooth long and slender, about  $\frac{2}{3}$  the length of the dorsal apical tooth and set about half or a little more its own length distant from the dorsal apical tooth. Inner border proximad of preapical tooth very feebly concave and with a faint indication of subcultrate (lamine) margination.

Anterior half of alitrunk convex above, posterior half a little lower but forming a completely continuous, very nearly



straight (feebly convex) profile, without indication of metanotal groove. Propodeal teeth small, acute, subtended by ventrally broadened and convex lamellae without lateral spongiform facing. Petiolar node gently rounded above, longer than broad and slightly longer than its peduncle, its spongiform appendages limited to a moderate posterior rim and an anteriorly lobate midventral strip. Postpetiolar disc convex, about half again as broad as long and approximately half as broad as the gaster, with well developed appendages. Gaster narrow; basal costulae very short, somewhat spongiform in consistency. Postpetiolar disc, gastric dorsum, fore coxae, propodeal declivity and lower halves of sides of alitrunk nearly or quite smooth, strongly shining. Remainder of body densely punctulate, opaque; pronotum laterally with weak substriation.

Ground pilosity of head consisting of fairly conspicuous short, subreclinate spatulate hairs, anteriorly directed, forming regular fringes on anterior dorsal scrobe borders, anterior clypeal border and anterior borders of scapes, here directed toward scape apices. Promesonotum and dorsal surfaces of mandibles with similar hairs, but less conspicuous, directed mesad. Erect and inclined pilosity of short, stiff hairs with distinctly spatulate apices: 6 fringing posterior occipital margin, one on each lateral occipital margin, one pair on humeri and one pair on mesonotum, sparse rows of 4 each on petiole, postpetiole and gastric dorsum. Ventral side of head, and gaster near apex, with a few short fine hairs. Pilosity of appendages rather sparse, fine, subreclinate. Color rather uniform light ferruginous.

Holotype [MCZ] taken at 4000 feet altitude on Mt. Penrissen, Sarawak (Borneo) by E. Mjöberg, with no further data, but presumably from rotten wood. Seven paratype workers taken with the holotype [MCZ, USNM] show very little variation. TL 2.3-2.4, HL 0.61-0.63, ML 0.22, WL 0.61-0.62 mm.; CI 70-73, MI 35-36. Certain specimens show a slight effacement of the pronotal punctulation, giving this region a subopaque appearance somewhat like that of *S. godeffroyi*.

The dealate female paratype, taken with the holotype, has a very high-bulking thorax; mesonotum densely and finely

punctulate, without rugulation or median furrow, but with about 20 erect spatulate hairs. Petiolar node broader than long; otherwise, only the usual caste differences from the worker. TL 2.8, HL 0.65, ML 0.24, WL 0.72 mm.; CI 77, MI 37.

*Strumigenys indagatrix* Wheeler

*Strumigenys indagatrix* Wheeler, 1919, Bull. Mus. Comp. Zool. 63: 94, worker. Type loc.: Kuching, Sarawak, Borneo [MCZ]. Cotypes (syntypes) in M. C. Z.

Cotypes, 2 workers: TL 2.5, 2.5; HL 0.60, 0.60; ML 0.32, 0.32; WL 0.62, 0.63 mm.; CI 67, 67; MI 53, 53. This species is extremely close to *S. godeffroyi*, and may even be only an extreme variant of that species. So far as can be told from the cotypes, *indagatrix* differs only in its slightly longer mandibles, slightly less well developed eyes and dorsal alitruncal pilosity, and somewhat more complete alitruncal sculpture; punctulation on pronotal dorsum and sides of alitrunk covers these areas completely and uniformly, without noticeable effacement.

Wheeler's treatment of this species could scarcely be more misleading. He regarded *indagatrix* as similar to *S. mocsaryi*, but said that "the mandibles are decidedly shorter," actually the reverse of the true situation. He then compared the species to four of five *Strumigenys* species described by Forel from Java in a paper published in 1905, saying that *indagatrix* was "smaller than any of them," a statement that does not hold well in the case of two of the species (*signeae* and *ebbae*). It is curious that of the four 1905 Forel species, none is very close to *indagatrix*, while the fifth (*juliae*), which Wheeler does not mention at all, is exceedingly close to both *indagatrix* and *godeffroyi*, if indeed it is separable at all. Wheeler's comparisons are all the more puzzling when one realizes that his collection contained samples determined by himself as both *juliae* and *godeffroyi*. *S. indagatrix* remains known only from the types, and until more samples turn up, it must remain doubtfully distinct from *godeffroyi*.

*Strumigenys forficata* sp. nov.

Holotype worker: TL 2.79, HL 0.68, ML 0.23, WL 0.74



mm.; CI 73, MI 34. Maximum width across clypeus 0.27 mm.

Similar to *S. guttulata*, but the head narrower behind, with narrower occipital lobes. Mandibles stout and short, like those of *guttulata*, but the inner borders convex and bearing narrower convex, translucent lamellae that do not quite meet at full closure. Preapical tooth large, flattened, distinctly recurved, translucent in texture, much as in the lamella. Dorsal apical tooth straight, slender and quite acute, but only about 0.05-0.06 mm. long; ventral tooth stout, divergent, a little shorter than the dorsal tooth; 2 (possibly 3) intercalary denticles present. Antennal scrobes distinct, broad and deep, their dorsal borders distinctly produced laterally as slightly raised, anteriorly convex, thin but opaque lamellar borders. Center of head in region of vertex evenly convex; occipital lobes very feebly depressed. Posterior excision very broad, deep and semicircular, except that a broad, almost straight-edged translucent lamella fills its bottom, so that the excision appears broad and truncate in outline from dorsal view. Clypeus triangular, distinctly broader than long; posterior angle extended acutely, but narrowly rounded at the tip; anterior border very nearly straight, only very feebly depressed and concave medially. Eyes are small and situated at about the midlength of the head. Preocular laminae approximately straight and only feebly converging anteriorly.

Alitrunk rather narrow seen from above, only slightly wider across pronotum than through propodeum; anterior pronotal border narrowly rounded, with a projecting culate lamellar margin overhanging a deep transverse excavation in the dorsum of the cervix; anterodorsal margin of latter produced as a flange. Promesonotum in profile moderately convex; posterior mesonotum gently concave; metanotal groove obsolete; propodeal dorsum feebly convex. Propodeal teeth long, fine and spiniform, wholly enveloped in the thick, white opaque infradental lamellae, which are spongiform, broad but with irregular, feathery concave borders terminating in a higher ventral point. Since only the holotype is available, the feathery spongiform lamellar structure may possibly be an artifact, but there is nothing



definite to indicate that other than the natural condition prevails.

Petiolar node quite high, shorter than its peduncle, with a narrowly rounded anterior summit and a gently convex sloping posterodorsal face; anterolateral surfaces excavated and the two carinae of the anterior nodal slope fused into one median carina which mitigates the steepness of the slope as seen from lateral view. These modifications render the lower part of the anterior nodal slope rather narrow or "pinched" as seen from the front. Seen from above, free portion of posterodorsal face oval, slightly longer than broad and narrowed in front. Posterior collar broad (damaged on left side) with large posterolateral lobes of feathery spongiform material; midventral spongiform strip well developed. Dorsolateral and lateral surfaces of node with some reclinate, feathery spatulate hairs partly obscuring surface. Postpetiolar disc transverse-ellipsoidal, convex, moderate in size, but nearly twice as broad as long and twice as broad as the petiolar node, with very well developed spongiform masses; periphery of the disc with a few inconspicuous, reclinate feathery-spatulate hairs.

Gaster with a dense pad of fine hairs anteroventrally and a dense, broad anterodorsal margin of spongiform material meeting that of the postpetiole. A band of numerous short filiform costulae extending from the anterior spongiform margin a short distance onto the surface of the first gastric tergite, otherwise smooth and shining. Posterior surfaces of occipital lobes, alitrunk (except for dorsal surfaces of mesonotum and propodeum), most of petiolar node, postpetiolar disc, mandibles and fore coxae very nearly or quite smooth, shining. Clypeus subopaque. Most of head, entire mesonotum and dorsum of propodeum, scapes, most of legs and peduncle of petiole densely and finely punctulate, opaque or subopaque.

Entire dorsal pilosity consisting, with the few exceptions noted below, of moderately conspicuous appressed to decumbent spatulate or narrow cochlear hairs, those on the head abundant and uniform, directed anteriorly, diminishing on the occipital lobes toward the naked apices of the lobes; those on scape nearly appressed and directed apicad; those

on clypeus smaller and finer than on rest of cephalic dorsum, forming an inconspicuous fringe anteriorly; those on promesonotum few, somewhat feathery in consistency. Gaster with a few small, subreclinate, anteromedially inclined subspatulate hairs along the anterior margin. Sparse, small fine hairs, mostly appressed or decumbent, on underside of head, on mandibles, legs, propodeal dorsum, venter of gaster and apex of gaster.

Color medium ferruginous; mandibles, appendages, apices of occipital lobes, apex of gaster and both nodes lighter, yellowish. First gastric tergite medium reddish brown. Holotype a unique [MCZ] taken at Mt. Murud, North Borneo (E. Mjöberg leg.), no further data.









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No. 4



## TABLE OF CONTENTS

Some New West Indian Eumolpid Beetles. <i>Doris H. Blake</i> . . . . .	91
Cephalic Glands in <i>Gelastocoris</i> . <i>Margaret C. Parsons</i> . . . . .	99
Chemical Releasers of Necrophoric Behavior in Ants. <i>E. O. Wilson, N. I. Durlach, and L. M. Roth</i> . . . . .	108
The Relationship of the Protoperlaria and the Endopterygota. <i>Phillip A. Adams</i> . . . . .	115
Index to Authors . . . . .	131
Index to Subjects . . . . .	133



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# PSYCHE

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No. 4

## SOME NEW WEST INDIAN EUMOLPID BEETLES

By DORIS H. BLAKE

This paper is made up of the descriptions of six new species of *Metachroma* and a new species of *Chalcosicya*. Four of the seven new species were collected by Fernando de Zayas, who has been actively collecting insects in Cuba over many years. One of the other species was taken by Dr. J. F. G. Clarke on the Breden Smithsonian expedition in 1956 and the two others are from miscellaneous material in the National Museum collection.

### *Chalcosicya alayoi* new species

#### Figure 1

About 4 mm. in length, broadly oblong oval, shining, densely and coarsely punctate and with white pubescence not obscuring surface, black, except the brownish mouthparts, tibiae and tarsi.

Head with wide flat interocular space having a slight depression on vertex, densely and coarsely punctate and with long, closely appressed, white pubescence not concealing the shiny black surface below; mouthparts brownish. Antennae slender, not reaching the middle of the elytra, reddish brown. Prothorax convex, well rounded over head, sides arcuate, projecting in a sharp tooth beside eye, surface shiny, densely and coarsely punctate, and with long white pubescence. Scutellum rounded, shiny. Elytra broad, convex, a little prolonged at apex but not so conspicuously so as in many species of *Chalcosicya*, as *C. crotonis* Fabr. and *C. maestrensis* Blake; humeri well marked, a short depression within and another below basal callosity, surface very shiny and with coarse punctures, denser in basal depression, and rather sparse semi-erect white pubescence interspersed with finer pale brown erectish hairs. Body beneath shiny black, coarsely punctate, and with white

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pubescence. Anterior femora toothed. Length 4.3 mm.; width 2.6 mm.

*Type*, male, U.S.N.M. Type No. 64531, from Ciudadamar, Oriente Province, Cuba, collected in July 1953 by Fernando de Zayas and Pastor Alayo. One other specimen, a female, from Daiquiri, Oriente Province, collected in March 1955 by Zayas.

*Remarks.* — There are several species of *Chalcosicya* in Cuba, but this differs from *C. maestrensis*, *rotunda*, and *nana* by having the anterior femora toothed, from *C. parsoni* in being black, not green, from *ditrichota* in its more rounded form and differently shaped aedeagus. The second specimen from Daiquiri, in Zayas' collection, is a female, but I believe the same species.

#### **Metachroma zayasi** new species

#### Figure 2

About 4.5 mm. in length, broadly oblong oval, lustrous black with the antennae, tarsi and body beneath deep brown; the elytra with the striate punctation most developed in area about basal callosity and becoming faint at base and after the middle of the elytra.

Head with interocular space about one-third width of head, occiput finely punctate, a short median line down vertex and the usual groove about inner margin of eyes, lower front more densely and coarsely punctate; head shining above and becoming alutaceous in lower front, the mouthparts deep brown. Antennae not extending to the middle of the elytra, the outer joints slightly wider than the basal, deep brown. Prothorax nearly twice as wide as long at its widest with arcuate sides, convex, lustrous, finely punctate. Scutellum deep brown. Elytra lustrous black, the striate punctation not very distinct over basal callosity but becoming large in depression below and in intrahumeral sulcus, then becoming indistinct after the middle of the elytra. Body beneath shining deep brown or piceous with the tarsal joints paler brown. Length 4.5 mm.; width 2.5 mm.

*Type*, male, U.S.N.M. No. 64536, from Sierra del Cristal, Oriente Province, Cuba, collected in May 1955 by Fernando de Zayas.

*Remarks.* — This differs from *Metachroma schwarzi* Blake in being less coarsely punctate. In all the catalogues *Metachroma* is treated as a feminine noun and the specific names have the feminine ending, but in both Latin and Greek the word is neuter and the specific endings should be neuter.

***Metachroma cornutum* new species**

Figure 3

About 3.5 mm. in length, broadly oblong oval, shining, the elytra with a few short rows of striate punctures in basal half, reddish brown, the seven distal joints of antennae dark, lower front of head with a conspicuous outgrowth on each side forming two horns.

Head reddish brown, the interocular space about half its width; smooth over occiput and down front, with the usual groove about inner margin of eyes; at base of lower front above labrum on each side a small knob that projects outward when looked upon from above; jaws large and brown tipped. Antennae not reaching the middle of elytra, with the three basal joints pale yellowish brown, the rest gradually deepening in color. Prothorax about one-third wider than long with rounded sides and a small tooth at apical and basal angles; fairly convex, mirror smooth, entirely reddish brown. Scutellum reddish brown. Elytra short, broad and moderately convex with a distinct intrahumeral sulcus marked by a row of striate punctures vanishing before the middle, below the basal callosity four other short rows of punctures, a subsutural depressed line with punctures about the scutellum. Body beneath shining reddish brown with abdomen and legs a little paler. Middle and posterior tibiae emarginate near apex, claws long. Length 3.5 mm.; width 1.8 mm.

*Type*, male, U.S.N.M. Type No. 64532, collected by E. A. Schwarz October 5, at Cayamas, Cuba.

*Remarks.* — The very unusual development of the lower front of face with two hornlike excrescences marks this species. Unfortunately only one specimen is known.



**Metachroma bredeni** new species

## Figure 4

About 4 mm. in length, broadly oblong oval, shining, entirely yellowish brown, the prothorax alutaceous, the elytra distinctly striate punctate to below the middle.

Head with interocular space a little less than half width of head, occiput rounded, smoothly alutaceous with faint fine punctures, frontal tubercles outlined by a short median line down vertex, and a transverse line between eyes, the usual deep groove about inner margin of eyes; lower front alutaceous, not at all shiny, head entirely dull reddish brown with the jaws deep brown. Antennae extending nearly to the middle of elytra, the basal six joints paler and narrower than the outer joints. Prothorax not quite twice as broad as long with arcuate sides and a small sharp tooth at each angle, a short transverse depression over occiput, otherwise moderately convex, alutaceous and finely punctate, entirely pale yellowish brown. Scutellum pale. Elytra with a short intrahumeral sulcus and slight transverse depression below basal callosity; regular and well defined rows of punctures to beyond the middle of the elytra, the rows then becoming faint and indistinct on sides and apex; surface shiny, pale yellowish brown. Body beneath entirely pale, legs pale, femora obsolete punctate at apex, the usual emargination near apex of middle and posterior tibiae. Length 4 mm.: width 2.2 mm.

*Type*, female, U.S.N.M. Type No. 64533, collected by J. F. G. Clarke on the Breden Smithsonian expedition, March 21, 1956, at Castle Bruce Junction, Dominica, B.W.I.

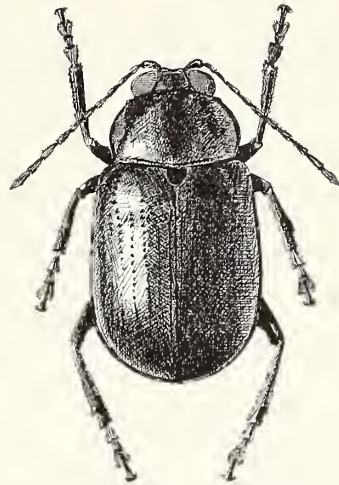
*Remarks.* — The entirely pale color and well marked striate punctation differentiate this from other pale West

## EXPLANATION OF PLATE 11

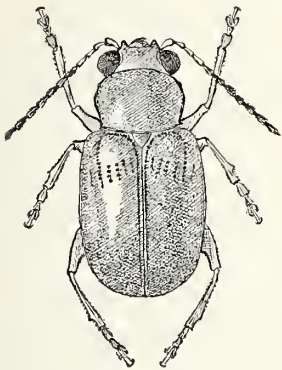
Figures 1-7. Fig. 1, *Chalcosicya alayoi*, Type, from Ciudadamar, Oriente Prov., Cuba. Fig. 2, *Metachroma zayasi*, Type, from Sierra del Cristal, Oriente Prov., Cuba. Fig. 3, *Metachroma cornutum*, Type, from Cayamas, Cuba. Fig. 4, *Metachroma bredeni*, Type, from Dominica, British West Indies. Fig. 5, *Metachroma nanum*, Type, from Puerto Rico. Fig. 6, *Metachroma multipunctatum*, Type, from Sierra del Cristal, Cuba. Fig. 7, *Metachroma grande*, Type, from Yunque, Oriente Prov., Cuba.



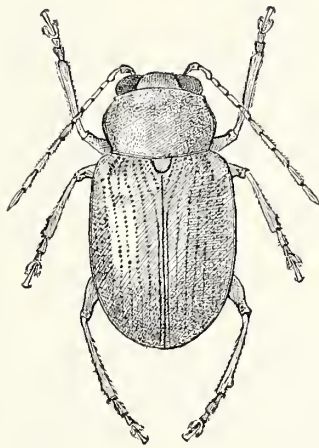
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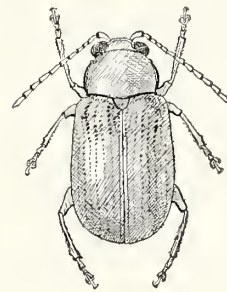
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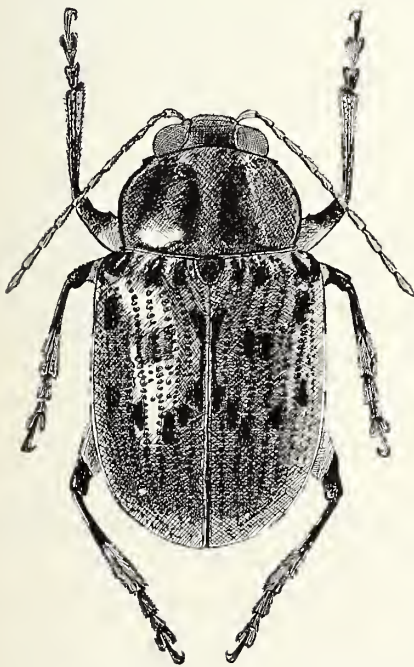
3. *Metachroma cornutum*



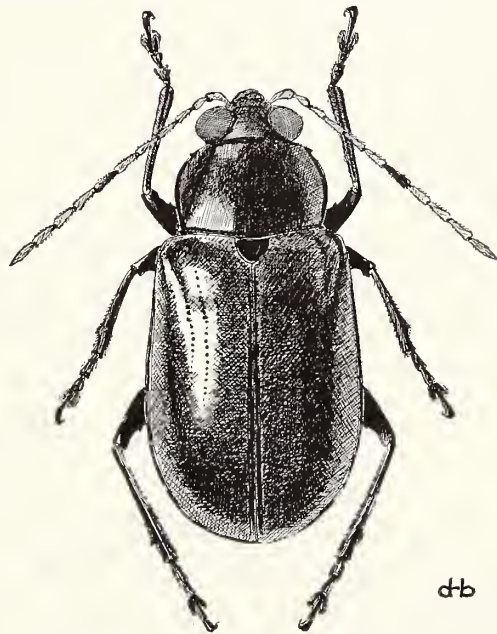
4. *Metachroma bredeni*



5. *Metachroma nanum*



6. *Metachroma multipunctatum*



7. *Metachroma grande*

db



Indian species. It is the first species of *Metachroma* to be described from Dominica. It resembles several North American species of *Metachroma* (such as *M. pallidum* Say) but has a less coarsely punctate head and prothorax, and in those species the prothorax is usually a deeper reddish brown in color.

***Metachroma nanum* new species**

Figure 5

About 3 mm. in length, oblong oval, shining, the elytra distinctly striate punctate, yellow brown without darker markings except brownish mouthparts.

Head with interocular space half its width, lightly but densely punctate over occiput, a groove about inner margin of eyes and a transverse line between antennal sockets; jaws large and deeper brown in color. Antennae entirely pale, not extending to the middle of the elytra. Prothorax moderately convex with arcuate sides, surface shining, very indistinctly punctate, entirely pale. Elytra with intra-humeral sulcus accentuated by row of punctures, and the depression below basal callosity having coarser punctures there, the striate punctation becoming gradually finer and evanescent at apex; surface very shiny, entirely pale yellow brown. Body and legs entirely pale, the usual emargination near apex of middle and hind tibiae. Length 3 mm.; width 1.6 mm.

*Type*, female, U.S.N.M. Type No. 64534, collected by Kline on guava (*Psidium guajava*), May 31, 1951, in Puerto Rico.

*Remarks*. — This is approximately the size of the Cuban species, *M. lituratum* Suffrian, but lacks the dark markings, and is also more distinctly punctate on the elytra.

***Metachroma multipunctatum* new species**

Figure 6

Between 5.5 and 6.5 mm. in length, broadly oblong oval, very shiny, the pronotum finely punctate, the elytra with large, closely set, striate punctures throughout; two of the four specimens deep chocolate brown with a large piceous spot on either side of pronotum and a row of three dark spots across the base of each elytron and one below the humerus and another in middle below that and an ir-



regular row of four below middle; suture in part dark; in the other two specimens the pronotum and elytra entirely dark; femora dark at apex, tibiae dark at base, entirely dark in dark specimens.

Head with interocular space about one-third width of head; coarsely and shallowly punctate, more densely so in lower front, a short median line and the usual deep groove along inner margin of eyes; deep brown or piceous. Antennae reddish brown, not reaching the middle of the elytra. Prothorax not quite twice as wide as long at widest point, with arcuate sides and small tooth at each angle, a transverse depression over occiput anteriorly; surface lustrous, finely and not densely punctate, in pale specimens a deep reddish brown with a large dark spot nearly covering each side, leaving only a small area anteriorly and at base and a median line pale, in dark specimens entirely dark. Scutellum piceous. Elytra broad and moderately convex with only a short intrahumeral sulcus, very coarsely striate punctate with some irregular punctures between the rows at the middle, punctation deep and distinct on the sides and at apex; very shiny, deep brown with darker spots consisting of three across the base of each elytron, one below humerus, another in middle and in a row of four below the middle, suture in part dark. In dark specimens the elytra entirely dark. Body beneath dark in all specimens, the femora in paler specimens pale with dark apex, the tibiae dark in basal half; in dark specimens the legs entirely dark; the usual emargination near apex of middle and hind tibiae. The front and hind femora with a small tooth. Length 5.5 to 6.5 mm.; width 3 to 3.7 mm.

*Type*, female, U.S.N.M. Type No. 64535, and three paratypes, all females, one of these in the collection of F. de Zayas, all collected in the Sierra del Cristal, Oriente Province, Cuba, May 1955, by F. de Zayas.

*Remarks*. — Although I have examined no males, I believe that these specimens represent two color forms, as in *M. longitarsum* Blake, one pale with spots, and the other entirely dark. The large, closely placed punctures serve to distinguish this species. The type is of the spotted form.

**Metachroma grande** new species

## Figure 7

About 6.5 mm. in length, broadly oblong oval, shining, the occiput and prothorax very lightly punctate, elytra with striate punctures also very light except in depression below basal callosity, entirely deep piceous black except the reddish brown antennae, tarsal joints and head.

Head with interocular space considerably less than half the width of head, eyes large, vertex with median line, as well as deep groove around the inner margin of eyes, surface finely and not densely punctate, lower front wrinkled; mouthparts paler reddish brown than the rest of head which is deeper brown. Antennae reddish brown, the 7th joint deeper brown, slender, not reaching middle of elytra. Prothorax not twice as broad as long, moderately convex, with rounded sides and small acute tooth at each angle, a slight transverse depression over head, surface very shiny and with fine, scarcely discernible punctures, entirely piceous. Scutellum piceous. Elytra with an intrahumeral sulcus and a depression below basal callosity with the striate punctures larger in depression and thence becoming finer and at sides and apex almost vanishing; surface lustrous piceous black. Body beneath and legs piceous, the tibiae at apex and tarsal joints deep reddish brown; the usual emargination near apex of middle and hind tibiae, and the front and hind femora with a small tooth. Length 6.5 mm.; width 3.2 mm.

*Type*, female, from Yunque, Oriente Province, Cuba, collected in July 1955 by F. de Zayas, and in his collection.

*Remarks*. — This is larger than either *M. zayasi* or *M. schwarzi* Blake and also less coarsely punctate on the elytra.

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CEPHALIC GLANDS IN *GELASTOCORIS*  
(HEMIPTERA-HETEROPTERA)

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In the literature on the anatomy of the aquatic Cryptocerata (Hemiptera-Heteroptera) there are many references to the "cephalic" or "maxillary" glands. These large cylindrical or sac-like structures, whose external openings lie at the base of the labium, are located on either side of the head in the Corixidae (Banks, 1939; Benwitz, 1956), Notonectidae (Bordas, 1905 a; Bugnion and Popoff, 1908), Naucoridae (Becker, 1929; Rawat, 1939), and Belostomatidae (Locy, 1884; Bugnion and Popoff, 1908). In the Nepidae, they may be partly (*Nepa*; Bordas, 1905 b) or entirely (*Ranatra*; Bugnion and Popoff, 1908; Neiswander, 1925) contained in the thorax, with ducts leading to the openings in the head. Previous investigations of these glands in the Cryptocerata have mentioned their presence only in the aquatic forms; they have never been reported in the shore-dwelling cryptocerates.

While studying the anatomy of the shore-dwelling cryptocerate *Gelastocoris oculatus oculatus* (Fabricius) (Gelastocoridae), the author noted two large, sac-like structures, one lying on either side of the ventral part of the head. Figure 1 indicates, in dotted lines, their approximate position, which is revealed by cutting away the exoskeleton from the entire ventral surface of the head. They lie immediately beneath this exoskeleton, extending anteriorly to the base of the labium and posteriorly a little beyond the antennal socket. Anteriorly they reach nearly to the

<sup>1</sup> This research was carried out during the tenure of the Ellen C. Sabin Fellowship, awarded by the American Association of University Women. Thanks are due to the members of the C. V. Riley Entomological Society, Columbia, Missouri, who collected the specimens of *Gelastocoris*.



midline, but diverge from each other posteriorly in the region of the subesophageal ganglion. They are bordered dorsally by the mandibular lever and the retractor muscles of the mandibular and maxillary stylets, and laterally by the sides of the head. The fact that these structures contain copious amounts of a milky secretion, and that their lumina open through definite orifices, suggests that they are glandular in nature. When the bug is disturbed, large quantities of this secretion are emitted from the large orifices, which are located on the ventral surface of the head just anterior to the antennal sockets (Fig. 1). In the following discussion, the term "orifice" will refer only to the hole in the exoskeleton, while the mouth of the gland, lying beneath the orifice, will be termed the "glandular opening."

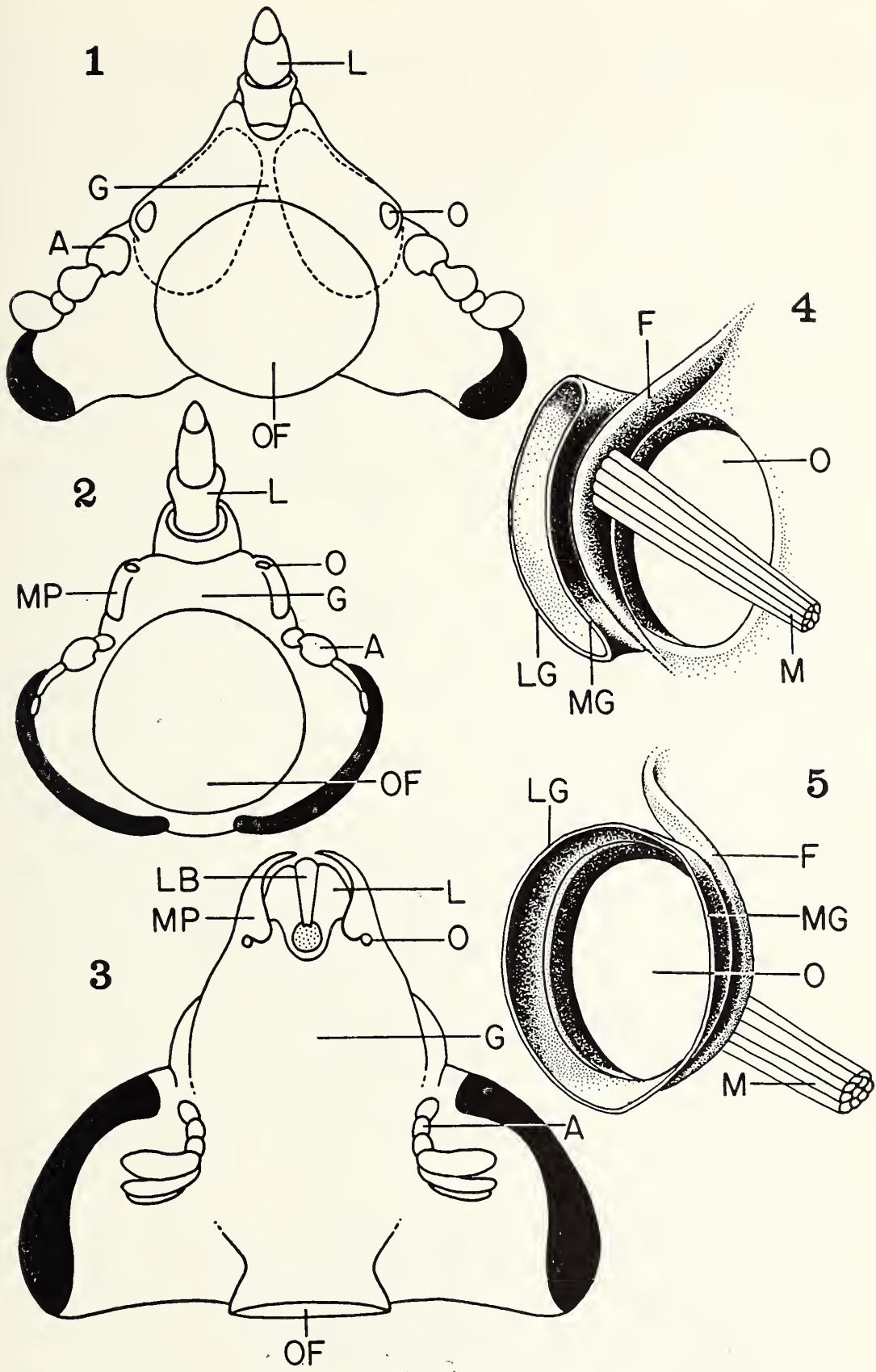
The opening mechanism of the gland is controlled by a slender muscle, which originates on the tip of the posterior wing of the hypopharynx and runs ventral to the gland to insert on a flap on the medial side of the glandular opening (Fig. 4). This flap is sclerotized and elastic; its two

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EXPLANATION OF PLATE 12

Figures 1-3. Ventral views of the heads of representative Cryptocerata, showing the positions of the orifices of the cephalic glands. The eyes are colored solid black. Figure 1. *Gelastocoris oculatus oculatus*. The dotted lines indicate the approximate position of the cephalic glands inside the head. 20 X. Figure 2. *Notonecta undulata*. 10 X. Figure 3. *Belostoma flumineum*. The labrum and labium have been cut off at the base of the second labial segment. 13 X. Figures 4 and 5. Views of the inner ventral surface of the head of *Gelastocoris*, showing the opening mechanism of the left cephalic gland. The anterior direction is to the top, the posterior direction to the bottom, the lateral direction to the left, and the medial direction to the right of the diagram. 375 X. Figure 4. The muscle is relaxed, and the glandular opening is shut off from the orifice in the exoskeleton. Figure 5. The muscle is contracted, and the glandular opening is pulled over beneath the orifice.

ABBREVIATIONS USED IN PLATE: A — antenna; F — sclerotized flap on medial side of glandular opening; G — gula; L — labium; LG — lateral wall of glandular opening; LB — labrum; M — muscle inserting on sclerotized flap; MG — medial wall of glandular opening; MP — maxillary plate; O — orifice in exoskeleton of head; OF — occipital foramen.



PARSONS — CRYPTOCERATA

ends are fused to the exoskeleton of the head on either side of the orifice, while its middle part is connected to the medial side of the glandular opening. When the muscle is relaxed, the flap lies just beneath the lateral edge of the orifice, and thus separates the orifice, which lies medial to it, from the glandular opening, which is lateral to it (Fig. 4). When the muscle contracts, the flap is pulled over to just beneath the medial side of the orifice; the glandular opening then lies immediately below the orifice, and the secretion can escape through the latter (Fig. 5).

The wall of the gland is very smooth and delicate, and appears silvery in freshly dissected specimens. Its histology was examined in serial sections through the heads of two fifth-instar nymphs and three adults of *Gelastocoris*; the material was fixed in Carnoy's or alcoholic Bouin's, prepared for sectioning by means of the Peterfi method, and stained in either Mallory's triple connective-tissue stain or in Delafield's hematoxylin and eosin. Text-figure 1 shows the general appearance of the glandular epithelium in an adult specimen. It is comprised of a simple layer of cells with no suggestion of an acinar arrangement. The most conspicuous elements are the large cells, which are usually flat in adult gelastocorids but appear more cuboidal or cylindrical in the nymphs. These cells probably produce the secretion. Their large nuclei are about 15  $\mu$  in diameter, and contain conspicuous nucleoli and many chromatin granules of various sizes. The cytoplasm is homogeneous and deeply staining in adults but appears more vacuolar in nymphs. An intracellular canaliculus with striated walls penetrates the cytoplasm of each large cell; it seems to run across the cell in an obliquely transverse direction, opening onto the lumen of the gland usually near the lateral boundary of the cell.

The lumen of the gland is lined by a delicate chitinous intima, which does not appear to penetrate into the canaliculi. Lying along the intima or between the intima and the large cells are small spindle-shaped nuclei, whose cytoplasm is either very sparse or absent; their greatest diameter ranges between 5 and 10  $\mu$ . In many parts of the epithelium the large cells are absent, and only the in-



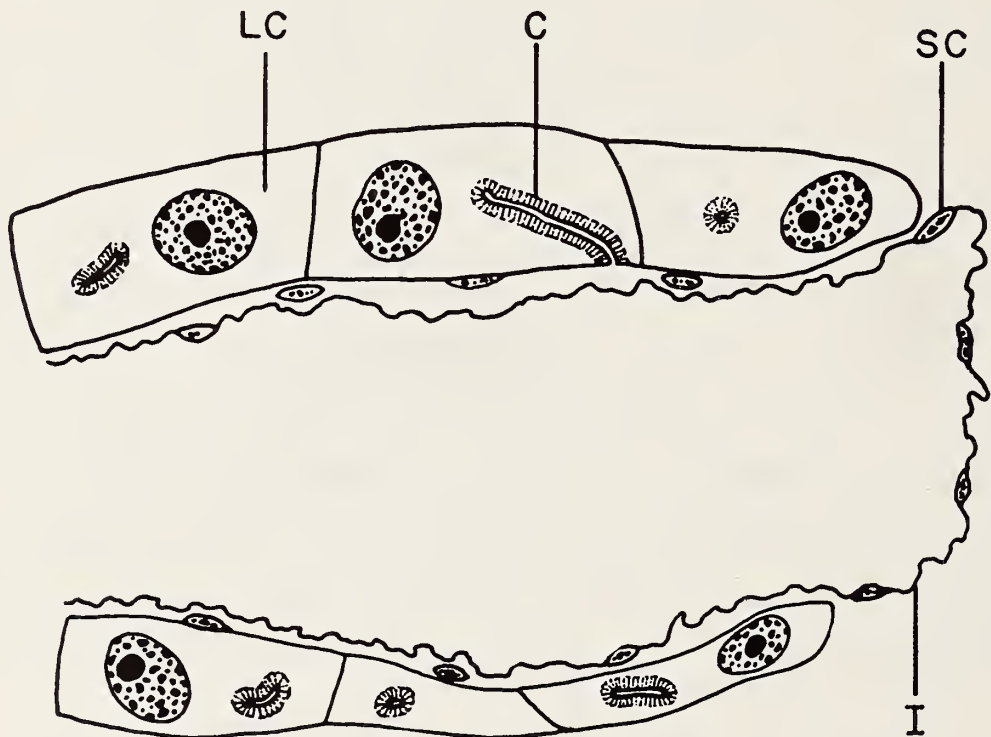
tima and the small nuclei remain. Such regions are not confined to any definite area of the gland, and their location varies from one individual to the next. The epithelium is never more than 15 or 20  $\mu$  thick, and the bulk of the gland consists merely of the very extensive lumen filled with a homogeneous, finely granular secretion which stains blue in Mallory's triple connective-tissue stain and pink in Delafield's hematoxylin and eosin.

These glands in the Gelastocoridae resemble in several ways the cephalic glands of aquatic Cryptocerata, and the similarities suggest that the former are homologous with the latter. Their paired ventral position in the head corresponds to that described by other authors for the cephalic glands of the Notonectidae, Naucoridae, Belostomatidae, and Corixidae (in the last family only the anterior part of the gland is ventral, the posterior part being dorsal to the brain). The simple sac-like shape of the gelastocorid glands is consistent with the previous descriptions of cephalic glands in aquatic bugs; to the author's knowledge, only the Naucoridae show a more complicated structure, having a lobed reservoir beside the glandular part of each gland (Becker, 1929; Rawat, 1939). A muscle controlling the opening mechanism of the gland has been described in *Corixa* and *Notonecta* (Benwitz, 1956) and in *Naucoris* (Becker, 1929); although in the former two genera this muscle originates on the wall of the head, in *Naucoris* it is attached, like that of *Gelastocoris*, to the tip of the posterior wing of the hypopharynx.

Histologically there are further resemblances. The three main components, the large cells, the smaller cells, and the chitinous intima, are mentioned in *Corixa* (Benwitz, 1956), *Naucoris* (Rawat, 1939), *Ranatra* (Bugnion and Popoff, 1908), and *Notonecta* (Bordas, 1905 a). The secretory epithelium is reported to be arranged into acini in *Naucoris* (Becker, 1929; Rawat, 1939) and *Notonecta* (Bugnion and Popoff, 1908), but no such arrangement is mentioned for the other forms. Locy (1884), Bugnion and Popoff (1908), and Benwitz (1956) report intracellular canaliculi within the large cells, similar to those seen in

*Gelastocoris*, and the last author describes the striations along these canaliculi.

The main difference between the glands of *Gelastocoris* and those of the aquatic Hemiptera is in the position of their external openings. Whereas in the aquatic Cryptocerata the orifices lie at or near the base of the labium, in *Gelastocoris* they are located much farther posteriorly on the head. A comparison of Figure 1 with Figures 2 and 3 points out this difference; *Notonecta undulata* and *Belostoma flumineum* are used as representatives of the aquatic forms.



Text-figure 1. Diagrammatic transverse or longitudinal section through the epithelium of the cephalic gland in an adult *Gelastocoris*. In this diagram the epithelium is folded double, so that the lumen appears much narrower than it actually is. The canaliculus of the upper middle large cell is shown opening onto the lumen of the gland; the other canaliculi are diagrammed in transverse or oblique section. 700 X.

Abbreviations used in figure: C — canaliculus; I — intima; LC — large cell; SC — small cell.

The function of the cephalic glands in the water bugs has not yet been satisfactorily established. Previous workers have suggested (1) that their secretion is used in sub-



duing prey, being somehow injected into or ingested by their victims, (2) that the secretion is defensive, serving to repel predators, or (3) that the glands function as excretory organs. The last theory was proposed by Becker (1929), but it was attacked by Rawat (1939) who found that carmine injected into the head of *Naucoris* was not taken up by the glands; the first two theories appear to be the most popular. In *Gelastocoris* it is unlikely that the secretion of the cephalic glands could be used for killing or paralyzing prey, since the orifice is a good distance from the beak. It seems most probable that it has a defensive function.

To the author's knowledge, cephalic glands have been reported in only three Gymnocerata. Macgill (1947) gave a brief description of two groups of glandular cells in the phytophagous bug *Dysdercus* (Pyrrhocoridae). These cells lie near the stylets and open onto the anterior part of the maxillary plate, at the base of the labium, by many small pores. Macgill considered their function to be the lubrication of the stylets; no histological details were given. Bugnion and Popoff (1911) figured maxillary glands in a section through the head of *Pyrrhocoris* (Pyrrhocoridae), but gave no histological description and did not mention the position of the external orifice. A brief account of maxillary glands in *Oncopeltus* (Lygaeidae) was given by Linder and Anderson (1955). It seems therefore that the cephalic glands are characteristic of the Cryptocerata but occur in the Gymnocerata. According to China (1955), the shore-dwelling families Gelastocoridae and Ochteridae are the most primitive of the Cryptocerata, having diverged from the ancestral line before it became aquatic. To date, however, the relationships between the aquatic and shore-dwelling Cryptocerata have been hypothesized mainly on the basis of external structural characters. The presence of cryptocerate-like cephalic glands in *Gelastocoris* offers some evidence from internal morphology that the Gelastocoridae are closely related to the aquatic Cryptocerata.

It might be proposed, on the basis of China's evolutionary theory, that the position of the orifice in *Gelastocoris* is the primitive condition, while that seen in the aquatic bugs is



a specialization, possibly accompanying a partial or total shift in glandular function from a defensive organ to a poison gland. Since, in all the aquatic bugs studied, the orifice is always near the base of the beak, bordering on the maxillary plate (Benwitz, 1956), any change to this location from that seen in *Gelastocoris* would have to have occurred just before the primitive line diverged into separate aquatic families. Against this theory, however, is Macgill's observation that the opening of the glands in the gymnocerate *Dysdercus* are at the base of the labium. This suggests that this location of the orifice is the primitive condition, and was found in the Proto-Heteroptera (to use the term of China, 1955) before the Gymnocerata and Cryptocerata diverged. If this theory is correct, the more posterior position of the orifice in *Gelastocoris* is a secondary acquisition. Why such a shift should take place is not clear, however, since the gelastocorids are predators, like their aquatic relatives, and orifices associated with the labium, which could allow the glands to serve as poison glands, would be advantageous to them. Although the second of these theories appears at this time to be the more commendable, more information on the presence or absence of cephalic glands in other Heteroptera, and on the location of their orifices, is needed to shed further light on this problem.

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# CHEMICAL RELEASERS OF NECROPHORIC BEHAVIOR IN ANTS

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## INTRODUCTION

One of the more conspicuous and stereotyped patterns of social behavior exhibited by ants is the transport of dead members of the colony from the nest to the refuse piles (McCook, 1882; Wheeler, 1926). Because of the obvious simplicity of this "necrophoric" response and the ease with which it can be experimentally elicited, it has proven to be one of the forms of ant behavior most amenable to physiological analysis. In the present paper are presented the results of a preliminary study of the response in the myrmicine ants *Pogonomyrmex badius* (Latreille) and *Solenopsis saevissima* (Fr. Smith), in which special attention has been paid to the releasing stimuli.

## DESCRIPTION OF THE BEHAVIOR

When the corpse of an adult *Pogonomyrmex badius* worker that has been allowed to decompose in the open air for a day or more is placed inside the nest or outside near the nest entrance, the first sister worker to encounter it ordinarily investigates it briefly by repeated antennal contact, then picks it up and carries it directly away from the nest toward the refuse piles. Under the conditions existing during the present study, most of the refuse piles of the captive colonies were located less than one meter from the nest entrance along the back wall of a closed foraging arena. This distance was evidently inadequate to allow the rapid consummation of the corpse removal response, for workers bearing corpses frequently wandered for many minutes

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back and forth along the back wall before dropping their burdens on the refuse piles. Others were seen to approach the back wall unburdened, to pick up corpses already on the piles, and to transport them in similarly restless fashion before re-depositing them.

It is a curious fact that in nature such "cemeteries" are rare or non-existent in the vicinity of *Pogonomyrmex badius* nests. During field studies conducted in northern Florida and southern Alabama, it was found that corpses removed from the nests are carried only a short distance beyond the rim of the nest crater before being dropped. Once abandoned, they are soon collected by scavenging workers of the dolichoderine species *Conomyrma pyramica* (Roger), one of the dominant ants occurring with *P. badius* in its native range. The swift *Conomyrma* workers patrol the vicinity of the *Pogonomyrmex* nests in large numbers during the day, and their activities apparently prevent the accumulation of *Pogonomyrmex* dead. It is not known whether other ant species assume this role outside the range of *Conomyrma*.

In the laboratory most injured and dying *Pogonomyrmex badius* workers leave the nest interior before succumbing. These individuals are usually found wandering through the foraging arena, unattended by sister workers. If similar behavior is exhibited in nature, it can safely be inferred that the removal of corpses is thus accomplished in large part by the dying ants themselves, as their last act as living workers. Under laboratory conditions queens and some larger major workers remain within the nest while dying. Several times it was observed that the bodies of these individuals remained in the nest for three days, during which they were frequently licked and moved about by the workers. After that time they were removed to the refuse piles.

#### EXPERIMENTS

*Assay of decomposition products.* The following experiment was designed to determine whether certain substances separated from the body of the corpse could by themselves elicit necrophoric behavior. A square of filter paper six

millimeters on the side was daubed with an acetone extract of *Pogonomyrmex badius* worker corpses and placed, in company with five untreated control squares, inside the foraging arena five centimeters from the nest entrance. In three separate trials, the treated squares were picked up within five minutes by the first workers to encounter them and transported directly to the refuse piles. In their reaction to the treated squares and in their locomotory patterns during transport, the workers appeared to behave in the same fashion as toward worker corpses. No immediate reaction to the control squares was noted, and they were not moved significantly from their original positions during the first several hours. In only one case was a control square transported in the direction of the refuse piles during the course of the first twenty-four hours.

A similar response was also evoked by objects other than paper squares. Seeds, for example, which ordinarily would be ignored or carried into the nest for storage, when daubed with the extract were carried to the refuse pile. The most dramatic example of the potency of this extract as a releaser occurred on three occasions when the objects chosen for experiment were live workers. Despite the fact that these ants were moving around under their own power and providing socially significant stimuli, they were treated by their sisters as corpses. However, unlike authentic corpses they would allow themselves to be carried to the refuse pile only to rise again and return to the nest! The cycle was observed to occur repeatedly during periods of one to two hours. During transport, the workers folded their appendages in the "pupal" posture usually taken by normal workers being carried to nest sites.

An attempt was next made to determine whether the chemical releasers could be removed from worker bodies by leaching so as to modify the response of living workers to the bodies. Three worker corpses were placed in bottles containing 50 cc. of acetone for periods of one to three weeks, then thoroughly dried and presented in succession to living workers in the manner described above. The behavior toward these treated bodies was markedly different from that shown toward untreated corpses. Instead



of transporting them away from the nests, the workers began to lick and chew them vigorously. One was carried quickly *into* the nest; the other two were dragged back and forth for short distances near the nest entrance. Several untreated corpses placed around the leached bodies were at the same time carried directly off to the refuse piles. One of the leached bodies was recovered several minutes after its introduction, daubed with corpse extract, and re-introduced. The same workers that had been licking it previously now carried it directly to the refuse piles. The other two leached bodies were left in position to observe their subsequent treatment. One was dismembered by the living workers; both were carried away from the nests only after forty minutes or longer.

The paper-square test described previously was next employed to test a few common fat and protein decomposition products and related compounds obtained as chemical reagents. The following substances produced no detectable response, either in saturated or dilute solutions: ammonium sulfide, di-alpha-amine. Weak to moderate alarm behavior, followed occasionally by digging behavior<sup>1</sup>, was evoked by the following substances: phenylethylamine, triethanolamine, phenol, n-valeric acid, n-caproic acid, n-caprylic acid, n-butyric acid, formic acid. The only substance tested that released the necrophoric response, or anything resembling it, was oleic acid. In repeated trials, oleic acid daubed onto paper squares and other small neutral objects invariably elicited a behavioral response from *P. badius* indistinguishable from that evoked by worker corpses.

On the assumption that oleic acid, or a related compound, is a principal natural releaser of the necrophoric response, an attempt was made to separate and analyze the long-chain fatty acids found in *Pogonomyrmex* worker corpses. Infrared spectra were prepared from a crude extract of about 200 dead bodies of *P. barbatus* (Fr. Smith). These spectra were made from a sample in CCl<sub>4</sub> and from a liquid film after the carbon tetrachloride was evaporated.

<sup>1</sup> A fuller account of alarm and digging behavior, and of the various stimuli that release these linked responses, has been presented elsewhere (Wilson, 1959).



The spectra indicated the presence in the crude extract of an ester (the principal compound) and a fatty acid. An attempt was made to separate the fatty acid from the mixture. The solvent of the original solution was evaporated and the residue dissolved in ether which was then washed with dilute  $\text{Na}_2\text{CO}_3$ . The alkaline wash containing the sodium salt of the fatty acid was separated from the ether solution containing the ester. The infrared spectrum of the ether solution compared well with the original crude material, indicating that the ester had been removed. The alkaline wash containing the Na salt of the fatty acid was acidified with dilute HCl and extracted with ether. The infrared spectrum of this ether extract indicated a fatty acid though the spectrum was not sufficiently distinctive to identify the compound specifically. In a series of tests using treated and untreated (control) paper squares, it was found that both the fatty acid and the ester evoked the necrophoric response. However, the fatty acid appeared to be the more effective of the two, in that it tended to release the response more quickly and to induce transport of the treated squares over greater distances. It was further observed that the acid-daubed squares were as a rule transported further away from the nest entrance during initial transport. Also, the ester-daubed squares frequently caused an initial mild alarm reaction that delayed the necrophoric response even more, whereas the acid-daubed squares were never observed to do so. It is possible that complete separation of the acid and ester was not obtained and that contamination of the ester fraction with the acid could account for the equivocal results.

*Use of another test species.* An attempt was next made to determine whether the fatty acid obtained from *Pogonomyrmex barbatus* would release necrophoric behavior in a phylogenetically remote ant species, *Solenopsis saevissima* (Fr. Smith). Four paper squares daubed with the acid were inserted, along with four control squares, into the brood chamber of an artificial nest containing a colony of *S. saevissima*. Within 25 minutes all four of the treated squares had been carried out and placed at the edge of the nest. Soon afterward the control squares were brought

out and dropped at the same place. Five hours later all of the treated squares had been moved to a position about twenty centimeters beyond the nest edge. A *saevissima* worker was later seen carrying a treated square back and forth in the restless fashion commonly seen in workers of this species carrying corpses.

*Assay of extract from another insect species.* To determine whether fatty extracts of corpses of another insect species causes the necrophoric response in *Pogonomyrmex badius*, extracts from meal worms (*Tenebrio molitor*) allowed to decompose in open air for two weeks were tested in the usual fashion. Treated paper squares were carried promptly to the refuse piles by the *Pogonomyrmex* workers, whereas control squares were left untouched for the first several hours. The behavior of the ants toward the treated squares seemed identical to that shown toward squares treated with the extract of *Pogonomyrmex* corpses.

### CONCLUSIONS

*Pogonomyrmex badius* workers utilize a relatively limited range of stimuli in "recognizing" insect corpses. Moreover, the stimuli appear to be exclusively chemical in nature. One of the principal chemical releasers is evidently the fatty acid that accumulates in the bodies of sister workers allowed to decompose in open air. An ester may also play a secondary role. Of several chemical compounds tested commonly found in insect corpses, oleic acid was the only substance which caused the ants to behave as they do toward dead insect bodies. Whether other substances present in ant corpses (and those of other animals) release the necrophoric response is not known. It may be suggestive that the common smaller molecular products of decomposition thus far tested have all produced neutral or alarm behavior without any element of necrophoresis. It is also noteworthy that long-chain fatty acids are chemically among the most stable and least volatile of fat and protein decomposition products and hence tend to accumulate disproportionately in insect corpses. As a result these substances have the potential to serve as efficient signals of the presence of aging corpses, as opposed to freshly

killed and edible insect prey. Finally, the fact that the fatty acid from *Pogonomyrmex barbatus* corpses induced typical necrophoric behavior in both *P. badius* and *Solenopsis saevissima* workers suggests that this behavior and its natural releasers may be widespread in the ants.

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# THE RELATIONSHIP OF THE PROTOPERLARIA AND THE ENDOPTERYGOTA

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The first worker to recognize that the Protoperlaria were a group distinct from the Protorthoptera, and probably ancestral to the Plecoptera, was Tillyard (1928a, b). The relationship of these orders has been discussed in more detail by Carpenter (1935). That the Protoperlaria might be of far greater phylogenetic significance has not generally been appreciated. Although the suggestion that the Protoperlaria were close to the ancestral form of the Endopterygota was made by Bradley (1939, 1942), this relationship has not previously been documented.

While a comparison was being made between the wings of the protoperlarian, *Lemmatophora*, and the neuropteran, *Sialis*, in an effort to determine the venational homologies of the latter, it became apparent that these insects exhibited a number of striking similarities. When the similarity of the wings was noticed, a comparison of other body structures seemed desirable. Since these could not be studied in the fossils, it was necessary to turn instead to the Plecoptera, in the hope that additional resemblances could be found. Such resemblances have been observed, particularly in the sternal region of the thorax, and in the wing articulation; these are discussed briefly below.

The Sialidae are extremely archaic insects; the venation has undergone but little change since the Permian. There are some specializations — fusion of MP and CuA in the fore wing, reduction of the anal fan, and lack of nygmata— but in structure and arrangement of the veins the wing remains primitive. No other living insect group shares with the Protoperlaria so many morphological features of

the wing. *Sialis mohri* Ross has been used in this study; the other genera of this family differ only slightly. *Neohermes californicus* (Walker) (Corydalidae) has been used in the study of wing articulation, since the wing base is larger and apparently less specialized than in *Sialis*.

Material of *Lemmatophora typa* examined includes the neotype, M. C. Z No. 3536, which is almost perfectly preserved, and upon which Figures 3 and 4 are largely based. Of a long series of impressions of hind wings which were studied, M. C. Z. No. 4425 was best. In none of these fossil specimens were the extreme bases of MP and CuA preserved.

I should like to acknowledge the kindness of F. M. Carpenter, who has made available the material used in this study, and who, together with W. L. Brown and E. O. Wilson, has contributed many helpful suggestions.

#### A. STRUCTURE OF THE VEINS.

In *Sialis*, the veins are not heavily sclerotized, most of them being formed as longitudinal folds in the membrane (Fig. 9b). As a consequence, these veins appear, viewed from one surface, as ridges, and from the other surface, as grooves.

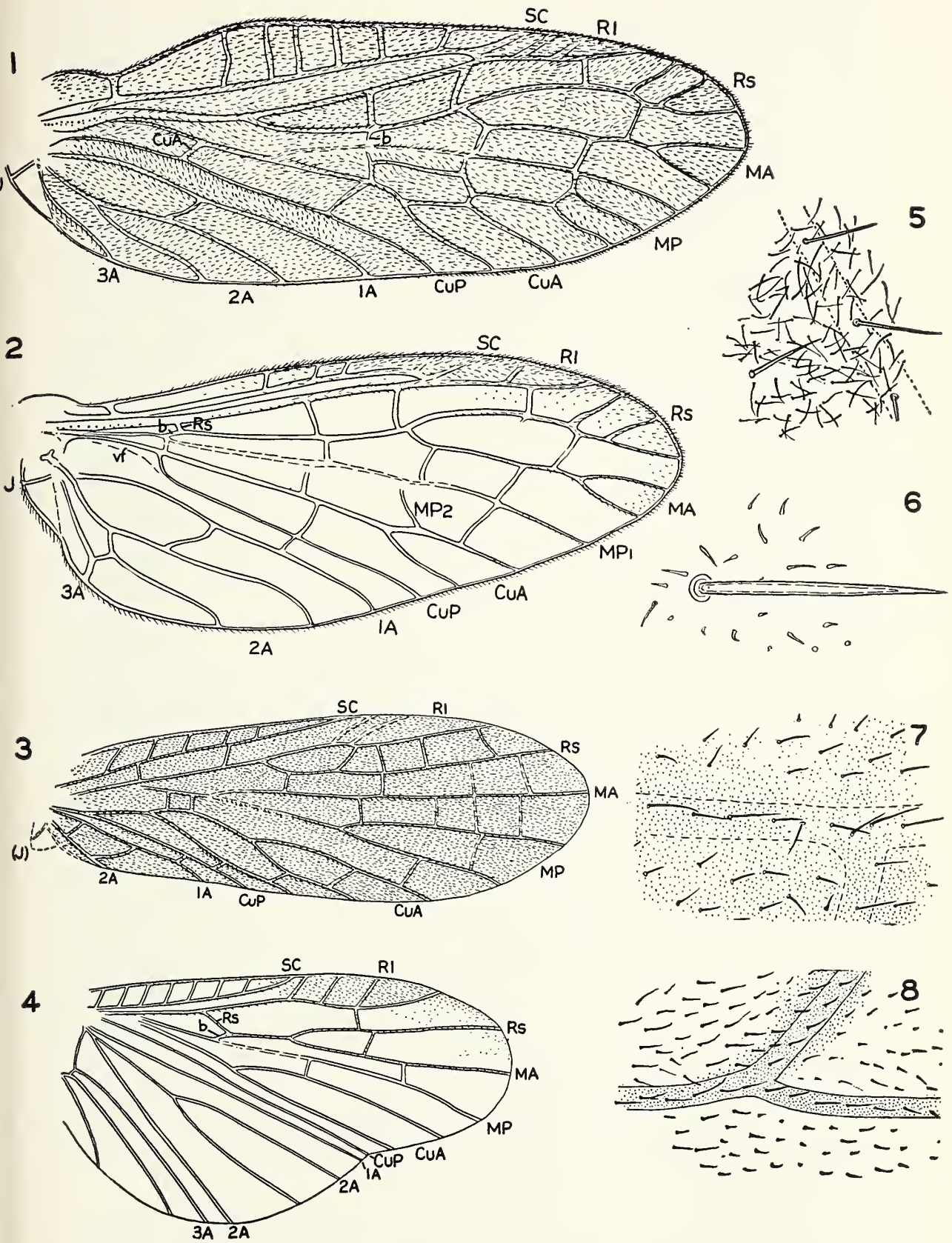
Since the fossil wings are molds of the upper and lower wing surfaces, it has been possible, by viewing under illumination nearly parallel to the surface, to reconstruct a cross-section of the hind wing of *Lemmatophora* (Fig. 9a). This is similar to that of *Sialis* in the general structure of the veins, and shares with it a remarkable peculiarity:

---

#### EXPLANATION OF PLATE 13

Figures 1, 2. *Sialis mohri* Ross. Anterior and posterior wings, showing venation and distribution of macrotrichia. Figures 3, 4. *Lemmatophora typa* Sellards. Anterior and posterior wings, showing venation and distribution of macrotrichia. Figure 5. *Pteronarcys californica* Newport. Portion of anal fan of posterior wing, showing macrotrichia on veins and membrane, and distribution of microtrichia. Figure 6. *Sialis mohri*. Structure of microtrichia and a macrotrichium. Figure 7. *Sialis mohri*. Portion of anterior wing, showing distribution of macrotrichia and microtrichia. (Microtrichia indicated by stippling.) Figure 8. *Lemmatophora typa*. Portion of anterior wing, showing distribution of macrotrichia and microtrichia. (Pigmentation indicated by stippling.)





ADAMS — PROTOPERLARIA AND ENDOPTERYGOTA



CuA is formed like a trough, appearing as a deep groove when viewed from above, and as a strong ridge, viewed from below. While in *Lemmatophora*, CuA is still found in its primitive position, lying on a weak convex fold of the wing, in *Sialis* this fold has been reversed, so that CuA lies at the bottom of a concave fold. CuA in the hind wing of all the other Exopterygota I have examined, with the possible exception of the Caloneurodea, is either indeterminate or on a more or less convex fold as in *Lemmatophora*. In all the neuropteroids where CuA is well developed in the hind wing, it is on a concave fold, as in *Sialis*.

Another peculiarity of the Protoperlaria is the structure of the stem of MP, which frequently is so weak as to be nearly indiscernible. There is little differentiation of the wing membrane along the course of this vein, except for the occurrence of a row of macrotrichia, and its being surrounded by a non-pigmented area. In both wings of *Sialis*, the stem of MP has a similar structure. This condition is a most unusual one, and its occurrence in *Sialis* is of considerable significance.

#### B. VENATIONAL PATTERN

The arrangement of veins is fundamentally the same in *Sialis* and in protoperlarians. In *Lemmatophora* Rs is simple, but is 2- or 3- branched in some other members of this order. Rs in sialids also is simple, but for a few marginal veinlets. Fusion of MA with Rs is of frequent occurrence among protoperlaria, but is subject to much variation. In *Lemmatophora*, coalescence of these two veins is clear in the posterior wing, as in the hind wing of *Sialis*. In the fore wing of *Lemmatophora*, coalescence does not take place. In *Sialis* it has, although the connection between MA and the base of MP is not clear as in the hind wing; here a weak crossvein may represent the basal piece of MA, or the basal piece may have moved toward the wing base and disappeared. The basal piece is, however, readily identifiable in the fore wings of most primitive Raphidiodea and Planipennia.

Fusion of CuA and MP in the fore wing, characteristic of Sialidae and Archisialidae, also occurs in some Proto-

perlaria (*Leucorium*, Artinska), but is not ordinarily found among the Planipennia.

Probably the most striking difference between the wings of *Lemmatophora* and *Sialis* lies in the shape, there being a well-developed anal fan in the protoperlarian, but none in *Sialis*. However, a functional fan is still present in the Corydalidae, and a reduced one in the Ithonidae and Poly-stoechotidae. Anal fans occur elsewhere in the Endopterygota, notably in the Trichoptera and Lepidoptera; one would therefore expect such a structure to be present in the ancestor of the Endopterygota. That its absence in *Sialis* is due to secondary reduction is indicated by the still relatively broad base of the hind wing. Reduction of the anal fan in *Sialis* is compatible with a general trend in the Neuroptera toward narrowing of the base of the hind wing.

#### C. TRICHIATION OF THE WINGS AND VEINS

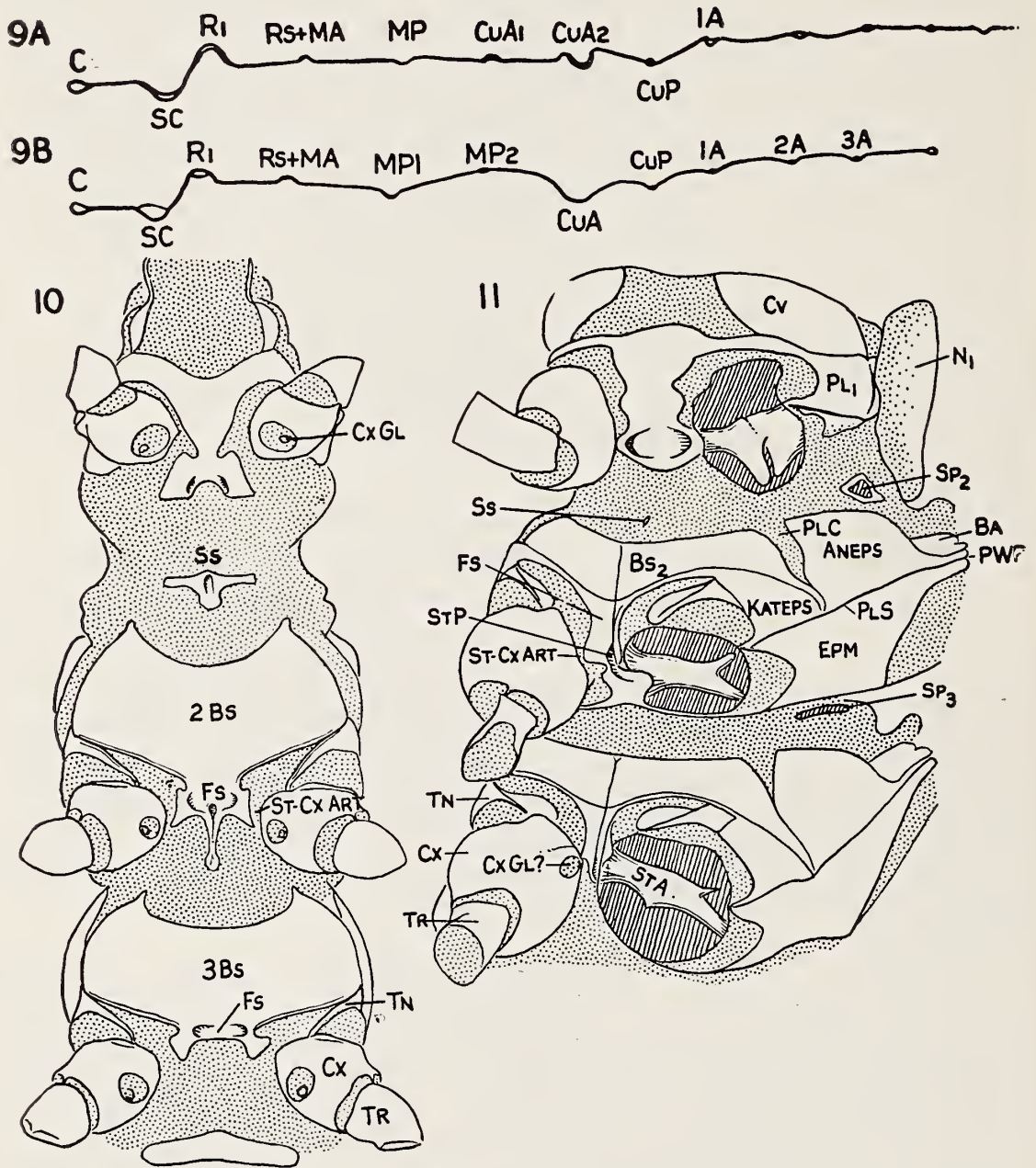
Tillyard (1918) has discussed the trichiation of the wings in the Panorpid Orders; he distinguishes two types of hairlike structures — *macrotrichia*, with articulated bases, equivalent to setae, and *microtrichia* which are simple outgrowths of the cuticle. Macrotrichia are found both on the veins and the wing membrane in many Endopterygota, but among the Exopterygota are largely restricted to the veins. Microtrichia occur in both groups, distributed uniformly over the surface of the wing, including the veins.

Tillyard (1928a) interpreted the fine hairs covering the wing membrane of *Protoperlaria* as microtrichia; he considered the macrotrichia to be restricted to the veins. This interpretation now appears to be open to question. A careful comparison of these "microtrichia" (Fig. 8) with the macrotrichia of *Sialis* (Fig. 7) discloses that these structures possess several features in common:

- a. Their size is approximately the same.
- b. In *Lemmatophora*, all the setae, whether on the veins or on the membrane, appear to have a definite basal socket, as do those of *Sialis*. These are distinguishable even in Tillyard's photograph of the wing surface (1928a, Fig. 7).



c. On the hind wing of both *Sialis* and *Lemmatophora*, these hairs are distributed similarly, on the apical part of the costal cell, the stigmatic area, the wing tip, and in rows along the anterior longitudinal



Figures 9-11.

Figure 9A. *Lemmatophora typa*. Reconstructed cross section of posterior wing. Figure 9B. *Sialis mohri*. Cross section of posterior wing. Figure 10. *Taeniopteryx* sp. Ventral view of thorax showing presence of weak sternocoxal articulations. Figure 11. *Sialis mohri*. Ventrolateral view of thorax, showing sternocoxal articulations, structure of internal skeleton, and general resemblance to *Taeniopteryx*.



veins only. There is a decrease in size toward the base of the wing.

In attempting to differentiate between the setae on the veins and those on the membrane, Tillyard greatly over-emphasized in his discussion the larger size of the setae on the costa and other veins. While it is true that the costal setae are very slightly larger than those of the membrane, much of the apparent size difference is illusory; in the fossil the setae of the wing membrane, seen against a colorless background, look brown, while those on the veins, seen against a brown background, look black, and therefore heavier.

Even though some size difference exists, this is not in itself sufficient reason for interpreting the hairs on the veins as macrotrichia, and those on the membrane as microtrichia, for in *Sialis* there is a similar size difference.

Furthermore, the microtrichia of *Sialis* (indicated by stippling in Figure 7, and shown in more detail in Figure 6) are very small, about the same size as the grain of the matrix in which are imbedded the fossils. Even were similar microtrichia present in *Lemmatophora*, as was almost certainly the case, they would therefore be obscured by the grain of the rock.

Tillyard's reluctance to recognize the macrotrichia on the wing membrane of *Lemmatophora* as such was probably due to an impression that macrotrichia do not occur in this location among the Exopterygota. While this is generally true, there is at least one exception. Since the Plecoptera are considered to be descended from the Protoperlaria, an examination was made of the wing surface of a representative of this order, *Pteronarcys californica* Newport. In this insect, prominent microtrichia are scattered over the entire wing. Small macrotrichia are sparsely distributed on the veins of the fore wing. But on the anal fan of the hind wing near the margin, large macrotrichia occur not only on the veins, but also on the wing membrane (Fig. 5).

From the above evidence, it seems reasonable to conclude that macrotrichia were present on both the veins and the

wing membrane of the Protoperlaria, in size and distribution almost identical to those of *Sialis*.

#### D. THE THORAX.

The sternum of the endopterygote thorax differs from that of the primitive Exopterygota in having a reduced furcasternum. The coxae of the Endopterygota have acquired a third point of articulation, on the furcasternum.

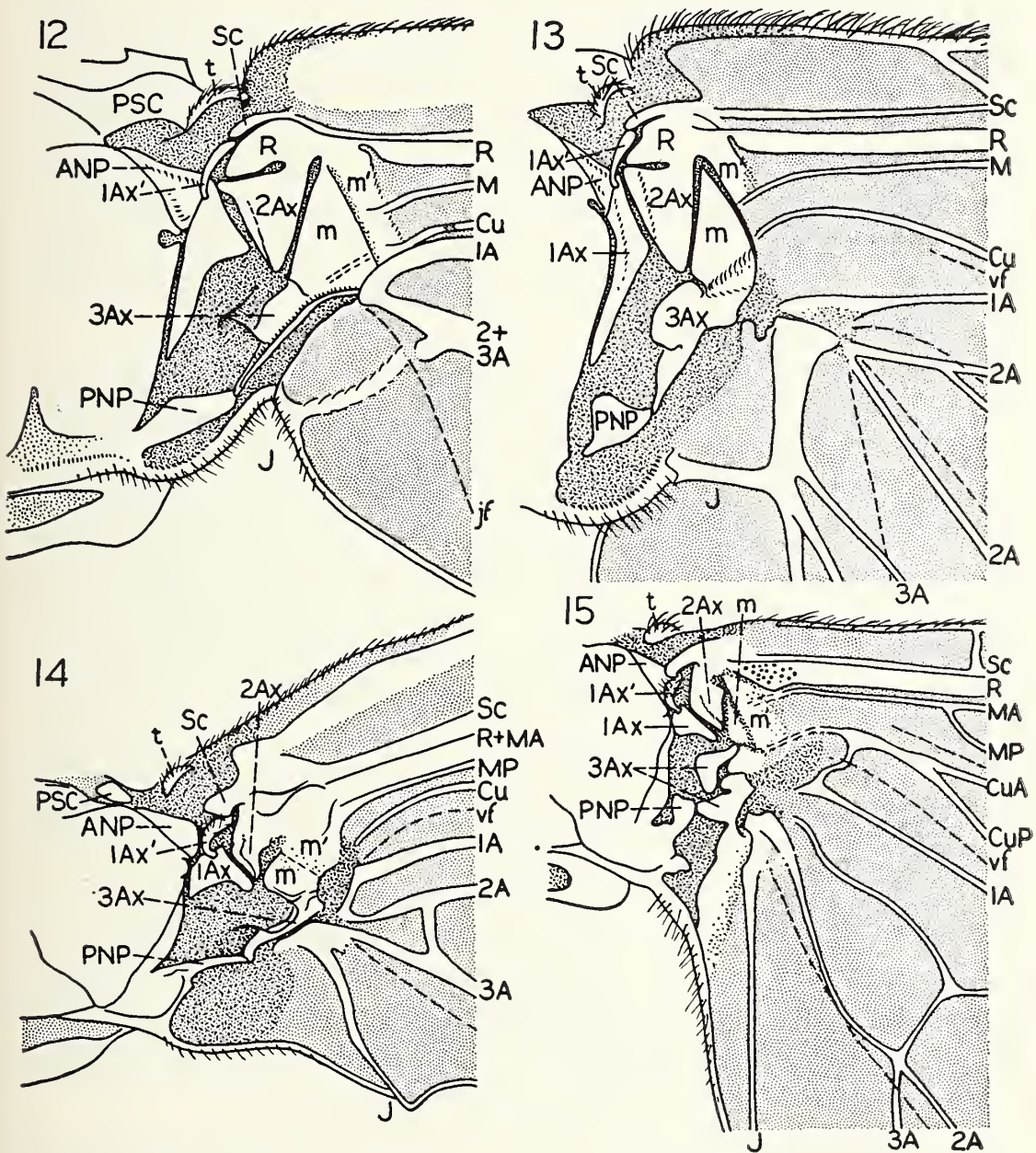
In the Plecoptera, the sternum is highly variable. Most studies of the thorax in this order have been made of *Pteronarcys*, or the large perlidae. In these stoneflies, the sternum is large and broad, and has slight resemblance to that of *Sialis*. But in some of the smaller stoneflies, such as *Taeniopteryx*, this is not the case.

The furcasternum (Fs) of *Taeniopteryx* (Fig. 10) is small, about the size as is that of *Sialis*. On both the mesothorax and metathorax, it bears on each side a process which extends close to the coxa; these have been termed *furcasternal arms* by Hanson (1946), who states "Although they are not articulated with the coxae, they appear to be adapted to offer them very strong support in the movement of the legs." The sternal coxal articulation (ST-CX ART) of the neuropteroid thorax is probably its most distinctive feature; one would expect this condition to have been derived from exactly such a stage as occurs in some stoneflies, by gradual strengthening of the association of the coxa and furcasternum. Once a sternal coxal articulation had become established, the thorax could be greatly strengthened by an infolding along the midline, reducing the exposed area of the furcasternum, so that the coxal bases become nearly contiguous. That such an infolding has taken place is indicated, not only by the structure of the furcasternum of neuropteroids, but also by the median longitudinal sutures on the basisterna (Fig. 11).

It is not necessarily to be inferred from the close resemblance of the thorax of *Taeniopteryx* to that of *Sialis*, that taeniopterygids are more primitive or more closely related to the Endopterygota than are other stoneflies. It is apparent, though, that these thoraces are constructed on the same general plan, and show remarkably similar capabilities for structural modification.



It is interesting to note, while reference is being made to the figure of the thoracic sterna of *Taeniopteryx*, the occurrence of openings of coxal glands (CxGl) on membranous areas of each coxa. Similar membranous areas occur on the hind coxae of *Sialis*, *Neohermes*, *Corydalus*, and *Chauliodes*, but in none of these insects has it been possi-



Figures 12-15.

Figure 12. *Pteronarcys californica* (Plecoptera). Base of right anterior wing. Figure 13. *P. californica*, Base of posterior wing. Figure 14. *Neohermes californicus* (Walk.) (Megaloptera). Base of anterior wing. Figure 15. *N. californicus*. Base of posterior wing.



ble to demonstrate by gross dissection any associated glandular structure. There is frequently, however, a small papilliform projection from one coxa interlocking with the membranous area of the other, apparently serving to restrict movement of the hind coxae.

#### E. WING ARTICULATION.

The axillary sclerites of Plecoptera (*Pteronarcys*, Figs. 12-13) and Megaloptera (*Neohermes*, Figs. 14-15) resemble each other in relatively large size, simple shape, and light degree of sclerotization. The wing base of *Pteronarcys* is the more generalized, while that of *Neohermes* appears to be modified for greater strength and flexibility. Only a few simple changes would be necessary to derive the more specialized wing base of *Neohermes* from that of *Pteronarcys*.

In *Neohermes*, the long posterior arm of the first axillary has been lost, and the anterior arm, which is connected to the basal process of Sc, is strengthened. The head of R has disappeared; this structure appears to be non-functional in *Pteronarcys*, and the articulation stronger without it. The third axillaries of the anterior wing are similar, but there has been a shift in the axis of articulation of the median plate with the second axillary, in *Neohermes*. In the anterior wing of both *Neohermes* and *Pteronarcys*, the third axillary articulates on a long, slender posterior notal wing process. In the posterior wing, however, the structures of third axillary and posterior notal wing process differ greatly. In *Neohermes* the third axillary is dissected, the median plate, flexor muscle attachment, and posterior articulating portion being separate. This condition, however, is not typical of all Neuroptera. It is also most unusual for the posterior wing process to remain attached to the metanotum; in nearly all other Neuroptera it is a separate sclerite, as in *Pteronarcys*.

The difference in articulation of the posterior wing may be due in large part to suppression of the anal fan in the Neuroptera. In *Neohermes*, although a functional fan is still present, the number of veins is small, and this region of the wing bears little resemblance to that of *Pteronarcys*.

## F. CONCLUSIONS.

Some evidence for a close relationship between the Protoperlaria and the Neuroptera has been discussed above. This evidence, summarized below, consists in part of distinctive wing characters which are shared by the archaic Sialidae and the Protoperlaria (a), and in part of some similarities between the Plecoptera (derivatives of the Protoperlaria) and the Neuroptera (b). To these may be added some general characters which would of necessity be expressed in any group ancestral to the Endopterygota (c).

a. Distinctive common features of the protoperlarian and sialid wing are:

1. The density and arrangement of veins and cross-veins is about the same; in particular, Rs has usually only one or two branches.
2. There is a strong tendency for coalescence of MA and Rs.
3. The stem of MP is weak.
4. CuA of the hind wing of Protoperlaria is structurally similar to that of *Sialis*, the upper surface being deeply grooved.
5. The distribution of macrotrichia on the membrane and veins is about the same.

b. Features shared by the Plecoptera and Neuroptera, indicative of relationship are:

6. Furcasternum with a coxal articulation.
7. Generally similar shape and arrangement of axillary sclerites.

c. Other features of the Protoperlaria which are not so distinctive, but which are consistent with their probable role as ancestors of the Endopterygota are:

8. A well-developed anal fan.
9. Cerci
10. Ovipositor.
11. Tibial spurs, present not only at the apex, but in a series along the length of the tibia.
12. Five-segmented tarsi.

In addition to the above morphological evidence, a close relationship of the Protoperlaria and the Neuroptera is in agreement with recent theoretical work on the origin of the larva, and the significance of the pupal stage. The nymphs of the Protoperlaria were described in detail by Carpenter (1935); they appear to have been similar to those of the Plecoptera. Presumably, there was a large number of nymphal instars, as is the case in the Plecoptera, some species of which have more than thirty.

Bradley (1942) recognized the significance of the Protoperlaria, suggesting them as possible ancestors of the Endopterygota because they are the most generalized known Neoptera, and because of some similarities in development of their close relatives, the Plecoptera, and of *Sialis*. More recently, Sharov (1953, 1957) has developed a theory of the origin of holometabolous development from an insect with a large number of immature stadia, including both larval and nymphal stages, and with several imaginal instars. Of the living Neoptera, the Plecoptera, with their large number of immature stages, approach closest to this condition.

The evidence described above appears sufficient to justify the statement that a close relationship probably exists between the Protoperlaria and the Neuroptera; moreover, there is no known feature of the Protoperlaria which would prevent their being considered directly ancestral to the Endopterygota.

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## LETTERING USED IN FIGURES

1A, 2A, 3A — first, second, and third anal veins.	MA — media anterior
ANEPS — anepisternum	MP — media posterior
ANP — anterior notal wing process	N1 — pronotum
1Ax' — anterior arm of first axillary sclerite	PLC — pleural cleft
b — basal piece of media anterior	PLS — pleural suture
BA — basalare	PNP — posterior notal wing process
C — costa	PSC — prescutum
CuA — cubitus anterior	PWP — posterior notal wing process
CuP — cubitus posterior	R1 — anterior branch of radius
Cx — coxa	Rs — radial sector
CxGl — membranous area bearing opening of coxal gland	SA — subalare
EPM — epimeron	SC — subcosta
EPS — episternum	SP — spiracle
Fs — furcasternum	Ss — spinasternum
J — jugal vein	STA — sternal apophysis
jf — jugal fold	ST-CX ART — sterno-coxal articulation
KATEPS — katepisternum	t — tegula
m.m' — medial plates	TN — trochantin
	TR — trochanter
	vf — vannal fold



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# PSYCHE

INDEX TO VOL. 66, 1959

---

## INDEX TO AUTHORS

- Bailey, N. S.* Additions to the Bioecology of the New England Tingidae and Piesmididae (Heteroptera). 63
- Brown, W. L., Jr.* The Neotropical Species of the Ant Genus *Strumigenys* Fr. Smith: Group of *gundlachi* (Rogers). 38  
The Release of Alarm and Attack Behavior in Some New World Army Ants. 25
- Carpenter, F. M.* Fossil Nemopteridae (Neuroptera). 20
- Creighton, W. S.* and *M. P.* The Habits of *Pheidole militicida* Wheeler (Hymenoptera: Formicidae). 1
- Johnston, D. E.* Some New Synonymy in the Haemogamasidae, Laelaptidae and Diplogyniidae Indicated by an Examination of Banks' Types of Mesostigmata (Acarina). 60
- Levi, H. W.* The Spider Genus *Styposis* (Araneae: Theridiidae). 13
- Werner, F. G.* *Carpophilus longiventris* in Saguaro Blossoms (Coleoptera: Nitidulidae). 25  
*Emelinus melsheimeri* (Lec.) in Arizona (Coleoptera: Ad-  
eridae). 36
- Wilson, E. O.* Communication by Tandem Running in the Ant Genus *Cardiocondyla*. 29
- William M. Mann. 55
- Wilson, E. O.* and *Mario Pavan.* Glandular Sources and Specificity of Some Chemical Releasers of Social Behavior in Dolichoderine Ants. 70



## INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

- Acarina, 60  
 Additions to the bioecology of the New England Tingidae and Piesmididae (Heteroptera), 63  
 Aderidae, 36  
*Androlaelaps frontalis*, 61  
 Ant Hill Odyssey, 55  
 Ants, 1, 25, 29, 37, 55, 70  
 Araneae, 13  
 Army ants, 25  
 Behavior in ants, 25, 70  
*Cardiocondyla*, 29  
*Cardiocondyla emeryi*, 29  
*Cardiocondyla venustula*, 29  
*Camponotus*, 33  
*Camponotus compressus*, 34  
*Camponotus paria*, 34  
*Camponotus sericeus*, 33  
*Carpophilus longiventris* in Saguaro blossoms, 35  
 Chemical releasers of social behavior 70  
 Coleoptera, 35, 36  
 Communication by tandem running in the ant genus *Cardiocondyla*, 29  
*Corythaica bellula*, 64  
*Corythucha bellula*, 65  
*Corythucha coryli*, 66  
*Corythucha caryae*, 65  
*Corythucha cydoniae*, 66  
*Corythucha marmorata*, 67  
*Corythucha mollicula*, 67  
*Corythucha pruni*, 67  
 Diplogyniidae, 60  
 Dolichoderine ants, 70  
*Emilinus melsheimeri* in Arizona, 36  
*Eulaelaps stabularis*, 61  
 Formicidae, 1, 25, 29, 37, 55, 70  
 Fossil Nemopteridae, 20  
*Galeatus peckhami*, 64  
*Gargaphia tiliae*, 64  
 Glandular sources and specificity of some chemical releasers of social behavior in Dolichoderine ants, 70  
 Habits of *Pheidole militicida*, 1  
 Haemogamasidae, 60  
*Haemogamasus longitarsus*, 60  
 Heteroptera, 63  
 Hymenoptera, 1, 25, 29, 37, 70  
 Laelaptidae, 60  
*Leptoypa mutica*, 63  
 Mann, W. M., bibliography, 51  
*Marquettia americana*, 21  
 Mesostigmata, 60  
 Nemopteridae, 20  
*Neolobogynium americana*, 61  
 Neotropical species of the ant genus *Strumigenys* group of *gundlachi*, 37  
 Neuroptera, 20  
 Nitidulidae, 35  
*Olivierina metzeli*, 20  
*Pheidole*, 1, 30  
*Pheidole militicida*, 1  
*Pogonomyrmex*, 9, 25  
*Piesma cinerea*, 63  
*Piesmidae*, 63  
 Release of alarm and attack behavior in some New World army ants, 25  
 Some new synonymy in the Haemogamasidae, Laelaptidae and Diplogyniidae indicated by an examination of Banks' types of mesostigmata (Acarina), 60  
 Spider genus *Styposis*, 13  
*Stephanitis globulifera*, 65  
*Stephanitis pyriodes*, 65  
*Stephanitis rhododendri*, 65  
*Strumigenys*, 37  
*Strumigenys denticulata*, 47  
*Strumigenys eggersi*, 46  
*Strumigenys gundlachi*, 40  
*Strumigenys jamaicensis*, 45  
*Strumigenys subdentata*, 48  
*Strumigenys* TRIECES, 50  
*Styposis*, 13  
*Styposis* AJO, 19  
*Styposis* CHICKERINGI, 15  
*Styposis* CLAUSIS, 15  
*Styposis flavescens*, 14  
*Styposis* NICARAGUENSIS, 15  
*Styposis* RANCHO, 18  
*Styposis* SCLEROPSIS, 18  
 Tandem running in ants, 29  
 Theridiidae, 13  
*Tingidae*, 63  
 William M. Mann, 55

Insects

8/1/59

# PSYCHE

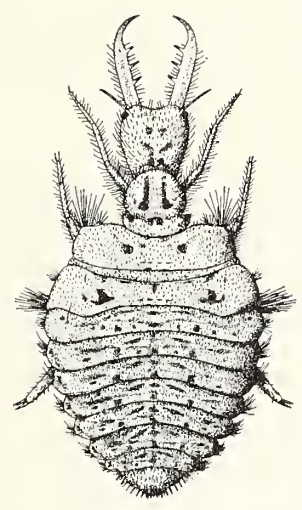
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Nos. 1-2



## CONTENTS

The Habits of *Pheidole militicida* Wheeler (Hymenoptera: Formicidae).  
*W. S. Creighton and M. P. Creighton* ..... 1

The Spider Genus *Styopsis* (Araneae: Theridiidae). *H. W. Levi* ..... 13

Fossil Nemopteridae (Neuroptera). *F. M. Carpenter* ..... 20

The Release of Alarm and Attack Behavior in Some New World Army  
 Ants. *W. L. Brown, Jr.* ..... 25



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## THE HABITS OF *PHEIDOLE MILITICIDA* WHEELER (HYMENOPTERA: FORMICIDAE)<sup>1</sup>

BY WM. S. CREIGHTON AND MARTHA P. CREIGHTON  
Department of Biology, City College, New York.

During the winter of 1959 the writers were able to study a number of nests of *Pheidole militicida* Wh. These were situated in an area along the eastern base of the Chiricahua Mountains, six to nine miles north of Portal, Arizona. Extended field studies were made on these colonies and samples taken from them were placed in small Janet nests and observed at the Southwestern Research Station. The need for such work will be clear to anyone familiar with W. M. Wheeler's remarkable views on the habits of *militicida*.

Wheeler's initial acquaintance with this ant was made on November 10th, 1910, at Benson, Arizona. A day or two later he found other colonies at Hereford. If Wheeler's hypothesis on the habits of this species is to be appreciated properly, it is important to understand exactly what information he secured from these colonies. Before he excavated them, Wheeler found the remains of numerous majors on some of the chaff piles. The material in the Wheeler Collection indicates that these remains consisted largely of head capsules which lacked all appendages. If Wheeler had found living majors in the nests that he excavated, these disarticulated remains would have received scant attention. Unfortunately, Wheeler did not find living majors in the colonies which he dug out. But it should be remembered that after Wheeler had examined the nests at Benson and Hereford, he knew surprisingly little about the ants that were living in them. He could not even be sure that the majors, whose remains he had discovered on the chaff piles, had come from the nests where he found them. All that Wheeler knew was that he had taken the minor of an undescribed species of *Pheidole* from these nests and that, after considerable digging, he had been unable to secure any accompanying majors.

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<sup>1</sup>Contribution from the Southwestern Research Station of the American Museum of Natural History.

The next factual data on *militicida* came to light a year or two later when W. M. Mann excavated nests near Benson in August and found both majors and minors living in them. These majors corresponded to the remains that Wheeler had taken earlier. With both major and minor castes available, Wheeler was in the position to describe *militicida* as a new species, which he did in 1915 (1). If Wheeler had been content to let the matter rest with the description of these two castes his action could have been defended not only as sound but also as conservative, for he had waited until the majors and minors had been certainly associated before presenting his description of them. But Wheeler was not content to limit his efforts to the description of *militicida*. He proceeded to develop a striking hypothesis as to its habits. This was so plausibly presented that one is apt to forget that this highly ingenious account is primarily compounded of supposition. Because Wheeler had found no majors in the Benson and Hereford colonies, he assumed that none were present. Because he had found the remains of majors on the chaff piles of these colonies, Wheeler assumed that all the majors in the colonies had been slaughtered by the minors. Having made these two assumptions Wheeler was forced to make others to support them, for this astonishing behavior on the part of the minor clearly demanded explanation. This Wheeler supplied as follows:

“It appears, therefore, that all the individuals of this caste (the majors) are regularly killed off by the workers on the approach of winter, probably after they have broken open all the hard seeds collected by the workers. Such a slaughter of the members of a large caste during the season when their activities are no longer required, when they would simply be a burden on the colony by consuming stored food and when fresh food cannot be collected, must have great advantages. Although I have never noticed this behavior in any other species of *Pheidole*, I believe that a study of the harvesting species with very large-headed soldiers in the deserts of the southwest may bring other similar cases to light.”

It is obvious that the most direct way to test Wheeler's theory would be to examine the nests of *militicida* during the winter months. If such examinations were properly carried out it would be possible to state with certainty whether or not majors are present in the nests at that time. But subsequent observations on *militicida* have all been made during the summer. The writers observed this ant at Safford, Arizona, in July 1950. In August, 1952 A. C. Cole studied colonies at Bayard and Deming, New Mexico, and in August 1956

he found others in the vicinity of Portal, Arizona. The information concerning the exact site of the latter colonies, which Dr. Cole obligingly furnished, was a notable help to this study and we wish to express our thanks for it.

While the observations just cited added to our knowledge of *militica*, none of them could furnish information on winter conditions in the nests of this species. Thus when Creighton and Gregg reviewed Wheeler's hypothesis in 1955 (2), they could do little more than point out the improbability of his explanation. Although it was clear that a number of southwestern species of *Pheidole*, which have majors with unusually large heads, showed none of the habits predicted by Wheeler, it was still possible that he might have been right in the case of *militica*. Positive proof that Wheeler's account of the habits of *militica* is incorrect was secured by the writers in the winter of 1959. During that winter we had fifteen colonies of *militica* under field observation on all but a few days. Living majors were taken from thirteen of these colonies during the period between January 8th and March 3rd. Our original attempts to secure majors were based upon the obvious method of digging out the colony. This proved to be the worst possible way to get them. Under ordinary conditions only two or three majors stay in the passages near the nest entrance. Since the major of *militica* is extraordinarily clumsy, it is seldom able to extricate itself if covered with soil. Hence, it is extremely likely to be missed when the nest is dug out, for the major will often remain perfectly quiet if only a thin layer of soil covers it. To be sure that the majors have not been missed, the soil must be sifted as the nest is excavated. With this in mind it is easy to understand why half the nests which Cole excavated in the summer of 1952 (3) appeared to contain no majors. During the first weeks of this study we faced a similar situation. Three of the eight nests excavated had yielded no majors. The remaining five had yielded a total of only fourteen majors, of which the greatest number taken from a single nest was five. Our results were, therefore, inconclusive for in no case had numerous majors been found in any nest.

Then the junior author hit upon a method of using bait to bring the majors out of the nests. The best bait was found to be various sorts of bread or scrambled eggs. Meat seemed decidedly less attractive. The bait was cut into pieces too large for the minors to move and these were placed close to the nest entrance. This baiting seldom failed to produce majors in quantity if continued long enough.



One colony which was baited for five successive days in February yielded a total of seventy-seven majors. Moreover, by using bait majors were secured from nests which had produced none when dug out. For, with one exception, the excavated nests reestablished themselves after a few weeks. This is clear evidence that these nests had not been fully exposed. The character of the *militicida* nest would make complete exposure difficult. All the nests that we have encountered have been built in light, friable soil between large stones. As these stones are removed the soil between them crumbles away and this obliterates any passages that were in it. As a result it is usually impossible to follow the passages to any depth and as excavation proceeds there is not the slightest indication of the direction it should take. In our opinion no nest of *militicida* has yet been completely excavated.

In areas where *militicida* is abundant there are often places where several nest entrances are close together. The distance between the entrances will vary from two to eight feet. It seems impossible at present to state whether each entrance represents a separate nest or whether they all belong to a single elongated nest. The total nest count given in this paper (15) is based upon the latter supposition. The total number of entrances found is five or six times greater. It was soon found that majors and minors from entrances a few feet apart could be mixed together without showing any signs of animosity. At first we accepted this as positive proof that the several entrances all belonged to one nest. But later the disconcerting fact came to light that the same result could be secured with specimens from nests a half a mile or more apart. The only explanation that would seem to fit this surprising behavior is that *militicida* is almost totally devoid of inter-colony animosity. The situation is made even more inexplicable by the strong animosity which *militicida* exhibits toward other species of ants.

We expected *militicida* to forage sporadically during the winter but it was a surprise to discover that it is one of the most consistent winter foragers in the area where it occurs. The only other ant which shows comparable activity is *Myrmecocystus mimicus* Wh. Except for one or two days when rain or snow fell, the minors of *militicida* were out every day during January, February and early March. As a rule the foraging did not begin until 3:00 P. M. By that time the surface temperature had reached 60°F. (16°C.) or better. Full foraging activity developed when the surface temperature reached 90°F. (31°C.). During January the surface temperature

drops rapidly towards sundown and foraging in that month ordinarily terminates soon after 5:00 P. M. This brief period of foraging is extended as the days lengthen and by the end of February the foraging lasts about three hours. During the winter months the seeds of two grasses are the principal ones collected. These are the fluff grass, *Tridens pulchellus* Hitch and the spike pappus grass, *Enneapogon desvauxii* Beauv.<sup>2</sup> Both these grasses fail to lose all their seeds at the end of the growing season, but the number of unshed seeds in the heads is low. Counts on five samples (30 cc. each) of fluff grass heads taken within foraging range of five *militicida* colonies gave an average of only 4.6 seeds per cubic centimeter. Nevertheless, these residual seeds furnish a steady, if meager, supply for, as the winter advances, the seeds or the spikelets containing them are gradually blown out of the heads and deposited in a thin layer on the surface of the soil wherever there is a windbreak. In the winter months the *militicida* minors collect their seeds entirely from this layer. During the many days that the foraging minors were observed, not one was seen to ascend a grass stem to get at the seeds. It is difficult to explain this reaction, for the percentage of seeds in the heads is several times as great as that in the layer on the ground. For this layer contains many spikelets that are devoid of seeds and the minors frequently bring these empty envelopes home. On several occasions we took numbers of the spikelets away from the workers as they reached the vicinity of the nest and found that not more than a third of these contained seeds.

Despite the short foraging period and the scant seed supply, the *militicida* minors bring in many seeds, for on warm days foraging is very active. Each nest entrance usually has a single foraging column but sometimes two or three columns may leave the same entrance. The columns are seldom more than fifteen feet long, an indication of the easy availability of the seed supply, regardless of its low yield. Since the rate of seed consumption in the captive colonies was very low, it seems probable that winter foraging augments the number of seeds stored in the nests. The *militicida* colony is thus provided with an abundant store of seeds which it can use with the arrival of spring. The spring months are the driest part of the year in the areas where *militicida* occurs. At Portal the total precipitation during April, May and June averages 1.52 inches, approximately 8.2% of the an-

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<sup>2</sup>We wish to thank Mr. Joseph Welch, who was working at the Station when this study was made, for his kindness in identifying these and other grasses as well as for helpful suggestions on the terminology of the spikelet.



nual total of 18.40 inches (4). In other stations where *militicida* occurs the percentage of spring precipitation is even lower. As the spring drought begins, the seed supply reaches its lowest ebb, for winter foraging has depleted the meager residue of seeds and no more seeds are likely to be set until after the summer rains. These unfavorable conditions often lead to a suppression of foraging in the spring, but this does not mean that the colony is inactive. For the sexual brood is brought to maturity at this time with the marriage flight following in early July. Thus the heaviest drain on the supply of seeds stored in the nests occurs during the spring months. It is at this time that the stored seeds are broken open and the food in them is made available to the rapidly developing brood.

Before taking up the feeding habits of *militicida* it is advisable to discuss certain features of the grass seeds which they use for food. At maturity a typical grass seed is enclosed in a complicated envelope of bracts. The outermost of these bracts are called glumes, the median ones lemmae and the innermost ones paleae. The lemmae often bear prominent projecting bristles called awns. These parts are attached, close above one another to a much-shortened stem called the rachilla. Collectively these parts make up a spikelet, which may contain one or more seeds. As a rule when a mature seed is shed, all of the spikelet except the glumes is shed with it. In some grasses this envelope fits the seed tightly, which makes its extraction difficult. In other grasses the envelope is loosely fitted around the seed and its extraction is comparatively easy. The spikelet of *E. desvauxii* shows the first condition, that of *T. pulchellus* the second. Since most of the seeds which the minors of *militicida* bring back to the nests are still in the spikelets, the seeds must be freed of these envelopes before they can be conveniently stored. Observations on the captive colonies showed that the seeds of *T. pulchellus* offer no particular problem because of their loose envelopes. The minors have little difficulty in pushing the lemmae aside and can often pull out the seeds without detaching the surrounding parts. Perhaps this is why the majors so seldom help when *pulchellus* spikelets are being handled. The spikelets of *E. desvauxii* are quite another matter. Each of the close-fitting lemmae has nine slender awns at its tip. These radiate outward at an angle of about 45 degrees and form a complete circle of bristles at the upper end of the spikelet. When attempting to free these seeds of the envelope both majors and minors will grasp the awns in their mandibles. When the major does so the awns are usually broken off, but the minor handles them more gently and when two minors grasp



the awns at opposite sides of the spikelet and pull in opposite directions they are usually able to break apart the lemmae and thus expose the inner parts of the spikelet. The seed then lies between two paleae but these do not completely enclose it and it is a simple operation for the minors to pick the exposed seed out. When the major extracts the seeds the lower end of the spikelet is grasped in the major's jaws. Pressure from these either breaks the lemmae apart or, if the seed has exactly the right position as the jaws close, it is forced outward between the lemmae and paleae, which spread enough to let the seed squeeze through. The envelope is often left intact when the seed has been extracted by this method. Whether intact or in fragments, the envelope is then ready to be placed on the chaff pile and the seed extracted from it may be cracked open and eaten or stored in one of the seed chambers.

There is abundant evidence that when the seeds are stored they are entire. The minors in our artificial nests spent many hours arranging and rearranging the seeds in groups. We take this to be the equivalent of the packing of the seed chambers in a free nest. No seed in these groups was ever damaged in any way until it was taken out and eaten. Moreover, there were usually a number of partially eaten seeds present in the nests, for the *pulchellus* seeds are seldom entirely consumed. Such opened seeds invariably shriveled after a day or two and usually moulded a few days later. That cracked or damaged seeds could be stored for months in the seed chambers seems thoroughly impossible.

We were surprised to discover that all the seeds opened in the artificial colonies were opened by the minors. The majors never made the slightest efforts to open the seeds and rarely paid any attention to them once their envelopes had been removed. In an effort to force the majors to crack open seeds, several nests containing only majors were set up. These were liberally supplied with seeds of *T. pulchellus*. Some of the majors in these nests lived for several weeks but they never made any attempt to open the seeds and ultimately all of them died, apparently from starvation, in the midst of the seeds which could have supplied them with food. The minors open the seeds of *pulchellus* and *desvauxii* by gnawing at the pointed end of the seed. Sometimes the seed is held by one minor and gnawed open by another, but a more common method involves only one minor, who places the blunt end of the seed on the floor of the nest and, with the seed held in a vertical position gnaws at its pointed end. The seeds of *desvauxii* are entirely consumed but, as noted above, those of *pulchellus*

are usually only half eaten. This may be due to the fact that in *pulchellus* the embryo is confined to the half of the seed which the ants eat, whereas in *desvauxii* the embryo extends more than three-quarters the length of the seed.

As will be seen from the previous paragraphs, the major of *militicida* has a very limited part in the harvesting operations and even this small part can be handled equally well by the minors. It seemed unlikely that the major would be limited to so small a share in the activities of the colony. The first hint that they might perform some unique activity essential to the colony was provided by the majors who came out of the nests during baiting. The junior author, who spent much time at this work, noticed that before the major emerged from the nest it would often stand for a considerable period just inside the nest entrance. When it did so it was a thorough nuisance to the minors, who had difficulty in getting past what amounted to a road block. When the major finally emerged from the nest it usually opened its jaws to their fullest extent and made short lunges in the direction of small pebbles and bits of grass as though it were trying to bite them. Later it was found that this same lunging and biting response could be elicited by throwing a small beam of light into the opening before the major left it. It was further clear that the primary reason why the major left the nest was not hunger. They almost never went directly to the bait, but wandered around in their clumsy fashion as though they were looking for something else. It was only after considerable patrol that some of them would go to the bait. These responses suggested that the function of the major might be to guard the nest entrance and, to test this, a nest was constructed which gave them the opportunity to do so.

This nest consisted of two chambers connected by a single, long passage which could be blocked or unblocked in the middle without disturbing the nest. The block consisted of a cotton plug which could be pushed into the connecting passage through a glass tube set at right angles to it. With the plug in place the nest was divided into two separate chambers; with the plug removed the two chambers communicated with each other through the single connecting passage. After the plug was in place majors and minors of *militicida* were placed in one chamber and their prospective intruders in the other. The nest was then set aside until both groups were accustomed to their surroundings. Usually it took no more than twelve hours for each group to become thoroughly tranquil and to demonstrate by this tranquility that it was unaware of the other group's presence nearby.



The ants selected as intruders were *Pogonomyrmex maricopa* Wh. and *Pogonomyrmex californicus* Buck. This choice was made because both species occur in close proximity to *militica* colonies in the field and the harvesting activities of all three species lead to frequent encounters outside the nests. The results secured from the experimental nest described above were highly interesting. On the removal of the blocking cotton plug both groups would begin to explore the communicating passage. They did so in an entirely different fashion. The *Pogonomyrmex* workers moved slowly into the passage but rapidly backed out of it when they became aware of the advancing *militica* workers. In most cases the *militica* minors first entered the passage. Some of them would usually be seized and killed by the *Pogonomyrmex* workers but others returned to the nest and alerted the majors. When these entered the passage they showed precisely the reactions that they had exhibited around their nest entrances. They advanced very cautiously, with the jaws wide open, and made frequent short lunges in the direction of the *Pogonomyrmex*

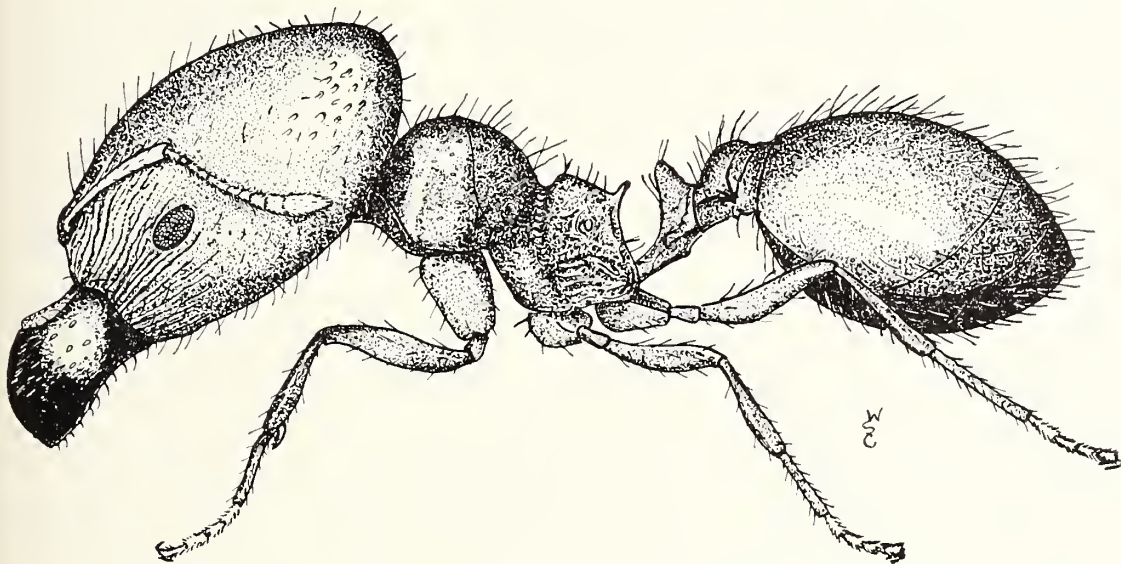


Fig. 1 — Major of *Pheidole militica* in the defensive posture.

workers. As the *militica* majors wedged themselves tightly into the passage, three or four ranks deep, the passage was completely blocked and the front face of this block was a highly dangerous area for the *Pogonomyrmex* workers for it consisted of the closely approximated heads and wide open jaws of the *militica* majors. As to what happened next depended on the *Pogonomyrmex* workers, who would charge up to the barrier and slash at the *militica* majors with their mandibles. These attacks were usually futile, for the only exposed parts of the *militica* major which could be damaged were



the antennae and these were held so closely against the head that the *Pogonomyrmex* workers were seldom able to grasp them. If these attacks were vigorously pressed the *militicida* major usually stood perfectly still and waited until the mandibles of its opponent were near its own. It then lunged forward, closed its jaws on the mandible of the *Pogonomyrmex* worker and attempted to break off the crushed mandible. The majors did not always succeed in doing so, particularly in the case of *maricopa*, whose heavy mandibles are hard to break, but they seldom failed to mangle the mandible so badly that it was useless. It may be added that this attack on the mandible is deliberate, for the *militicida* major will rarely strike at other parts when these are presented. We have repeatedly seen the *Pogonomyrmex* workers thrust their antennae or legs between the open jaws of the *militicida* major without causing the major to strike. They do not do so until there is a good chance that the mandible can be grasped and they rarely miss their target. After a number of *Pogonomyrmex* workers had been put out of action with useless mandibles, or sooner if the *Pogonomyrmex* workers did not press the attack vigorously, the *militicida* majors emerged from the passage and began a different sort of action. They no longer faced their opponents and struck at their mandibles but approached them from the rear and struck at the thorax or the petiolar nodes. As a result, most of the *Pogonomyrmex* workers were ultimately cut in two, either at the petiole or behind the pronotum. In this more open fighting it was also obvious that the petiolar nodes and the mesothoracic area were the principal targets. An examination of the *Pogonomyrmex* workers at the end of an engagement always showed much damage to mandibles, thorax and petiolar nodes and surprisingly little damage to legs and antennae. In short, there is nothing haphazard about the way in which the *militicida* majors deal with their opponents; they only strike at parts which will put their opponents out of action or kill them. It is clear that their method is highly effective for it was only occasionally that the *Pogonomyrmex* workers got the better of the engagement. Even when they outnumbered the *militicida* majors they often failed to kill a single one of them and when they did so it was usually a result of the *militicida* major having been stung. This incapacitates them but does not immediately kill them.

It should be clear that the activities just described are considerably more methodical than the ordinary scrimmages between fighting ants. In these activities the *militicida* major shows an efficiency that

is completely unlike its bumbling efforts elsewhere. This, plus the fact that these responses are repeated with surprising exactness time after time, and by majors from different nests, leads us to conclude that they are the normal guarding responses of the *militicida* major. If this is true the major of *militicida* is best regarded as a soldier. Its role in the harvesting activities of the colony is slight and it is not primarily a seed-crusher, as has been mistakenly supposed.

The defensive activities of the *militicida* major probably account for the mutilated remains which Wheeler found when he discovered this species, for the defending majors do not always dispatch the intruders without loss to themselves. This seems a more probable explanation than that proposed by Creighton and Gregg in 1955 (2), who suggested that the accumulation of dead majors discovered by Wheeler might have been a result of the high death rate of that caste during the peak of the harvest season. This now seems unlikely, for the death rate of the majors during the winter months has proved to be extremely low. Most of the fifteen colonies that we studied discarded no dead majors during the three months that they were under observation. Only four dead majors were placed on the chaff piles during this period. Each of these was carefully examined under a binocular microscope for signs of mutilation and each was found to be completely undamaged with not even a tarsal claw missing. This disposes of the last bit of evidence on which Wheeler based his hypothesis, for it is now clear that the minors of *militicida* neither kill the majors nor cut them to pieces after they have died. Thus Wheeler's views of the habits of *militicida* have proved to be at total variance with what these habits actually are.

In conclusion, it may be noted that *militicida* is a very difficult subject for investigations in artificial nests. This species is unusually sensitive both to temperature and humidity. Temperatures below freezing invariably kill the ants and they are almost as seriously affected by a heavy condensation of water on the glass of the nests. They seem unable to keep out of the water droplets and many of the minors die in them. They also die if the nest is too dry. This sensitivity made it difficult to maintain the captive colonies for any length of time. At the suggestion of Dr. Robert Chew, of the Department of Biology of the University of Southern California, the artificial nests were placed on a rack, in a covered aquarium, above a saturated solution of sodium chloride. In a closed system this should maintain a constant humidity of 78% of saturation regardless of temperature. The arrangement proved eminently satisfactory. It

not only reduced condensation but also largely eliminated the need for adding water to the individual nests. We wish to thank Dr. Chew for suggesting a method which not only benefited this study but which should be of value to anyone faced with the maintenance of a "fussy" species in the laboratory.

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THE SPIDER GENUS *STYPOSIS*  
(ARANEAE, THERIDIIDAE)<sup>1</sup>

BY HERBERT W. LEVI

Museum of Comparative Zoology, Harvard University

Theridiid spiders usually have eight eyes. Only recently the genus *Archerius* Levi (1957, Trans. Amer. Micros. Soc., 76: 114) was described from some California specimens having only six eyes. Since then an eight-eyed species from Japan was seen, a species having the anterior median eyes small. The number of eyes, then, may not be of generic importance.

Since the work on *Archerius*, another theridiid genus has been found in which the eye number is variable. In some species the anterior median eyes are present but small; other species lack them entirely. Judging by their similar appearance and by the genital structure, the species are closely related and belong to the genus *Styposis*.

A grant from the National Institutes of Health (E-1944) and a National Science Foundation grant (G-4317) made the completion of this paper possible. I would like to thank Dr. W. J. Gertsch and Dr. A. M. Chickering for specimens used and Professor M. Vachon for permitting me to examine *S. flavescens* in the Muséum National d'Histoire Naturelle in Paris.

*Styposis* Simon

*Styposis* Simon, 1894, Histoire Naturelle des Araignées, 1: 592. Type species by original designation and monotypy: *S. flavescens* Simon.

Small unpigmented spiders, less than 2 mm. total length. In some species carapace almost circular, weakly sclerotized, with six large eyes (except all eyes relatively small in *S. ajo*, Figure 27) arranged in two groups of three eyes touching each other (Figs. 1, 5, 10, 11). In other species (*S. flavescens*, *S. scleropsis*) carapace longer than wide, sclerotized, with raised reticulate pattern (Figs. 18, 24). In all species anterior median eyes absent or minute, their maximum diameter equal to radius of posterior medians. Chelicerae weak with one or two teeth on anterior margin (Fig 11), probably none on posterior. Legs fairly long; in some species patella and tibia 2.7 times carapace length (*S. clausis*), in others shorter 1.4 times carapace length (*S. ajo*, *S. flavescens*). Legs with many setae; comb on fourth tarsus greatly reduced, its setae almost smooth. Abdomen soft, sometimes wider than long, or high. Colulus two minute hairs slightly anterior of

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<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

usual position, difficult to discern and could not be found in some species.

Female genitalia with two seminal receptacles. Male palpus weakly sclerotized, parts translucent and difficult to delineate. Bulb twisted so that embolus faces the outside (and is partly hidden by the cymbium), and median apophysis faces ventrally (Figs. 6, 9, 16, 19). Median apophysis (M in Figs. 8, 14, 15, 20) a very large structure, functional, its end lying against the paracymbial hook (Fig. 14) at the distal end of the cymbium. Radix (R) present. The large structure supporting the embolus in *S. chickeringi* and *S. flavescens* probably is the radix (R in Figs. 14, 15, 20).

Six species are known from Central America and northern South America and one from the southwestern United States.

*Styposis* differs from *Archerius* by lacking the large colulus and by being less sclerotized. It differs from *Sphyrrotinus* by having the anterior median eyes reduced in size or absent and by the unusual position of the bulb in the palpal cymbium.

*Styposis flavescens* Simon

Figures 7, 18-22

*Styposis flavescens* Simon, 1894, *Histoire Naturelle des Araignées*, 1:592. Fig. 599. ♀ type from Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined.

*Description.* Carapace, sternum brown. Legs light brown. Abdomen whitish, without pigment. Carapace longer than wide. Cephalothorax heavily sclerotized; carapace and sternum with a net-like sclerotized pattern (Fig. 18). Diameter of anterior median eyes about equal to the radius of posterior medians. Anterior median eyes their radius apart, their radius from laterals. Posterior median eyes one-third diameter apart, two-thirds from laterals. Abdomen suboval in shape. Total length of female 1.4 mm. Carapace, 0.68 mm. long, 0.53 mm wide. First femur, 0.89 mm.; patella and tibia, 0.92 mm.; metatarsus 0.62 mm; tarsus, 0.41 mm. Second patella and tibia, 0.68 mm.; third, 0.47 mm.; fourth, 0.68 mm. Total length of male 1.5 mm. Carapace 0.75 mm. long, 0.56 mm. wide. First femur, 1.04 mm.; patella and tibia, 1.22 mm.; metatarsus, 0.81 mm.; tarsus, 0.47 mm. Second patella and tibia, 0.83 mm.; third, 0.59 mm.; fourth, 0.70 mm. The epigynum (Figs. 7, 22) has a slight median projection. The palpus (Figs. 19, 20) has a median apophysis with two projecting prongs, easily seen in lateral view. (Fig. 7 was made from the type, Figs. 18-22 from specimens collected in Nicaragua).

*Record.* Nicaragua. Musawas, Waspuc River, Oct. 10-31, 1955, ♀, ♂, Nov. 1-4, 1955, ♀, ♂ (B. Malkin).

***Styposis chickeringi*, new species**

Figures 10-17

*Types.* Male holotype and female paratypes from El Valle, Panama, July 1936 (A. M. Chickering), in the Museum of Comparative Zoology.

*Description.* Spider colorless, except for silvery eyes and spots of pigment where anterior median eyes usually are. Posterior median eyes one diameter apart, touching laterals. Chelicerae with one blunt tooth (Fig. 11). Abdomen wider than long (Fig. 10). Measurements of male holotype, total length 1.3 mm. Carapace, 0.77 mm. long, 0.72 mm. wide. First femur, 1.50 mm.; patella and tibia, 1.82 mm.; metatarsus, 1.32 mm.; tarsus, 0.44 mm. Second patella and tibia, 1.22 mm.; third, 0.75 mm.; fourth, 0.96 mm. Measurements of female paratype, total length 1.3 mm. Carapace, 0.60 mm. long, 0.55 mm. wide. First femur, 1.25 mm.; patella and tibia, 1.35 mm.; metatarsus, 0.96 mm.; tarsus, 0.36 mm. Second patella and tibia, 0.88 mm.; third, 0.52 mm.; fourth, 0.82 mm.

*Diagnosis.* The genitalia (Figs. 12, 13, 16, 17) as well as the eye distance separate this species from the others of this genus.

***Styposis nicaraguensis*, new species**

Figures 8-9

*Type.* Male type from Musawas, Waspuc River, Nicaragua, October 10, 31, 1955 (B. Malkin), in the American Museum of Natural History.

*Description.* Spider slightly yellowish. Anterior median eyes absent. Anterior eyes slightly more than their diameter apart. Posterior median eyes their radius apart, touching laterals. Chelicerae with two teeth on the anterior margin. Total length of male type 1.4 mm. Carapace 0.62 mm. long, 0.55 mm. wide. First femur, 1.46 mm.; patella and tibia, 1.55 mm.; metatarsus 1.03 mm.; tarsus, 0.47 mm. Second patella and tibia, 1.0 mm.; third, 0.56 mm.; fourth, 0.94 mm.

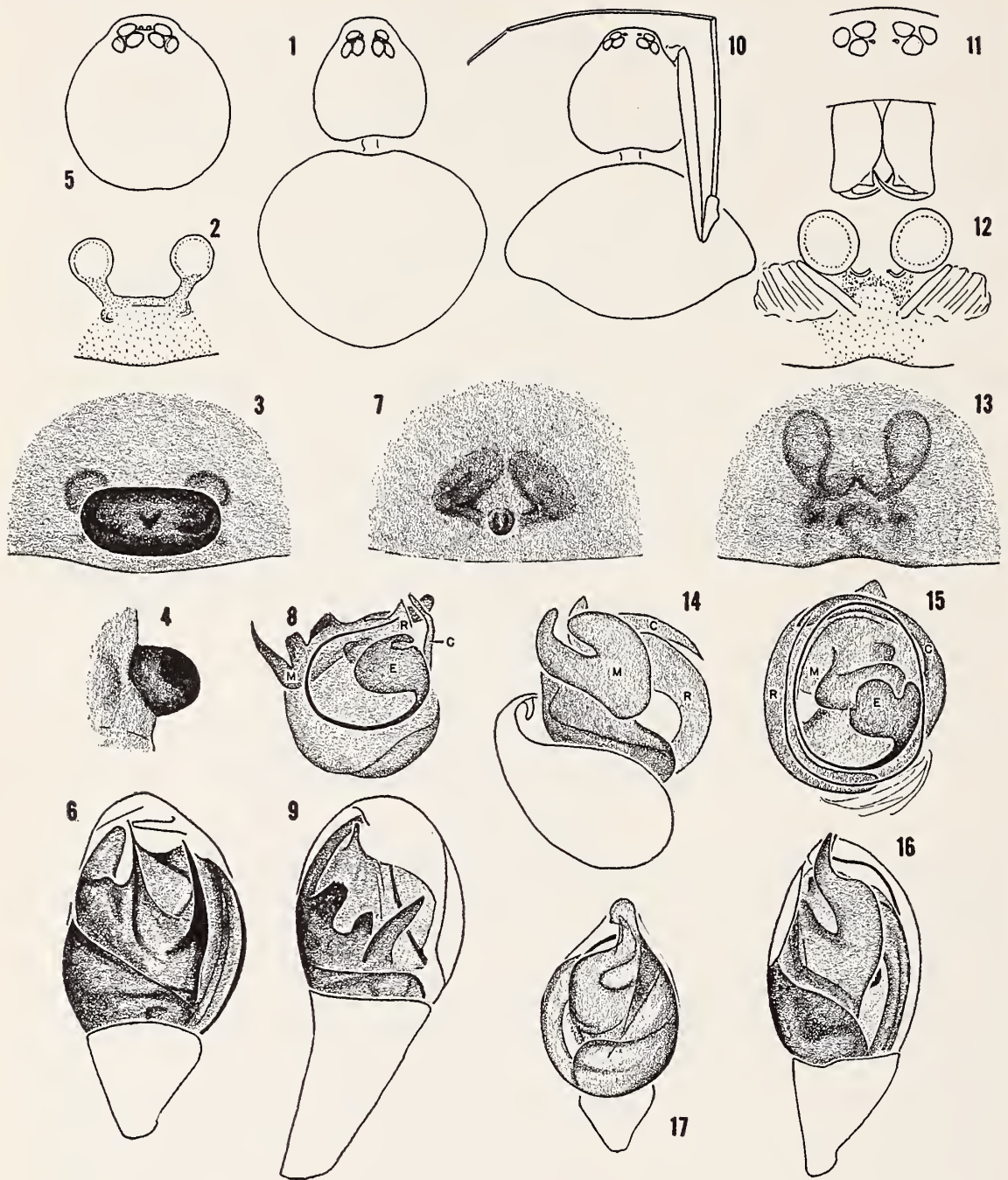
*Diagnosis.* The male palpus (Fig. 9) distinguishes this species.

***Styposis clausis*, new species**

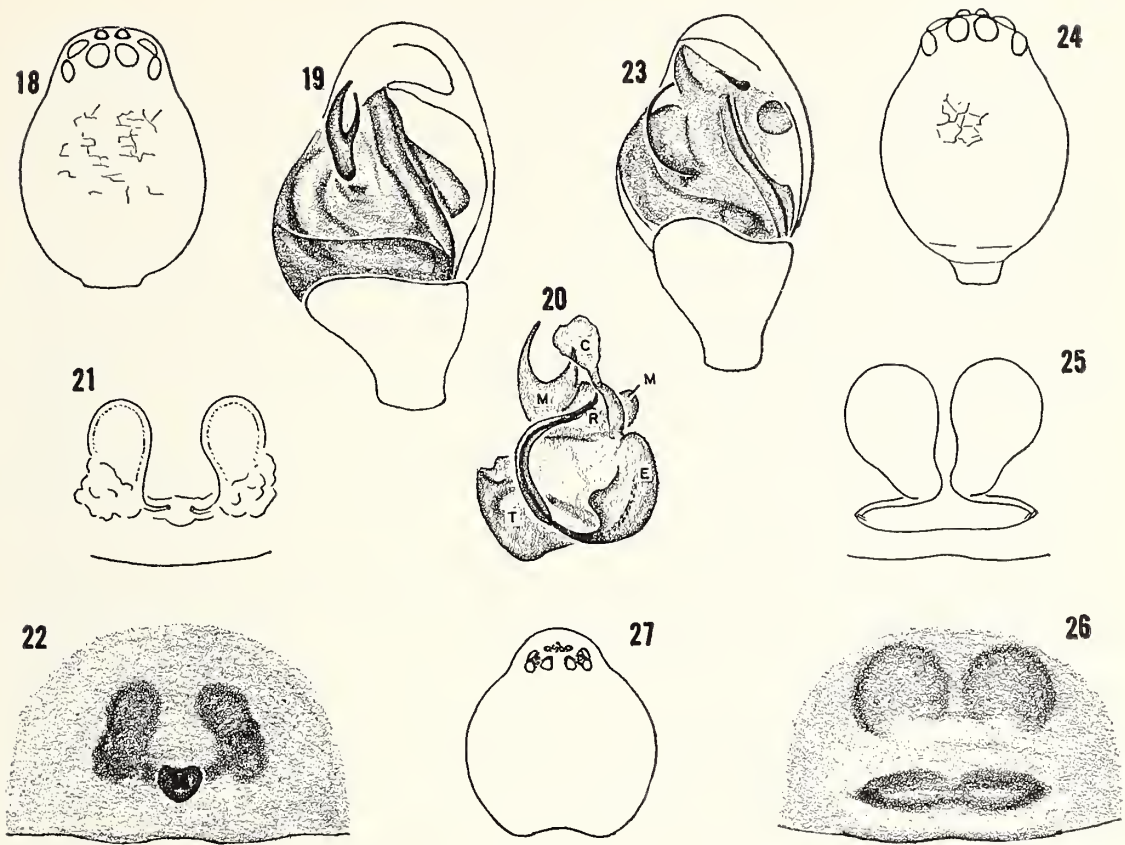
Figure 1-4

*Types.* Female holotype, female paratype from Forest Reserve, Canal Zone, July 4-6, 1939 (A. M. Chickering), in the Museum of Comparative Zoology.





Figs. 1-4. *Styposis clausis*, new species. 1. Female. 2. Female genitalia, dorsal view. 3. Epigynum. 4. Epigynum from side. Figs. 5-6. *S. rancho*, new species. 5. Carapace of male. 6. Left palp. Fig. 7. *S. flavescens* Simon, epigynum. Figs. 8-9. *S. nicaraguensis*, new species, palp. 8. Expanded, ectal view. 9. Ventral view. Figs. 10-17. *S. chickeringi*, new species. 10. Female. 11. Head of female. 12. Female genitalia, dorsal view. 13. Epigynum. 14. Palpus expanded, subventral view. 15. Palpus expanded, ectal view. 16. Palpus of type. 17. Right palp of paratype drawn at slightly different angle.



Figs. 18-22. *S. flavescens* Simon. 18. Carapace of female. 19-20. Left palpus. 19. Ventral view. 20. Ectal view, expanded. 21. Female genitalia, dorsal view. 22. Epigynum. Figs. 23-24. *S. scleropsis*, new species. 23. Palpus. 24. Carapace of male. Figs. 25-27. *S. ajo*, new species. 25. Female genitalia, dorsal view. 26. Epigynum. 27. Carapace of female. (Abbreviations: C, conductor; E, embolus; M, median apophysis; R, radix; T, tegulum).

*Description.* Carapace slightly yellowish, otherwise colorless. Six eyes. Anterior eyes one diameter apart. Posterior median eyes one-third diameter apart, almost touching laterals. Chelicerae with one blunt tooth on anterior margin. Abdomen wider than long when filled with eggs, otherwise longer than wide. It is not known whether the structure on the epigynum (Figs. 3, 4) is an epigynal plug or part of the epigynum. As the structures of the two specimens examined differ slightly, it probably is an epigynal plug. Total length 1.7 mm. Carapace, 0.73 mm. long, 0.69 mm. wide. First femur, 1.72 mm.; patella and tibia, 1.95 mm.; metatarsus, 1.33 mm.; tarsus, 0.52 mm. Second patella and tibia, 1.14 mm.; third, 0.73 mm.; fourth, 1.06 mm.

*Diagnosis.* The arrangement of the eyes (Fig. 1) and genitalia (Fig. 2) separate this species from others.



**Styposis rancho**, new species

Figures 5-6

*Type.* Male type from Rancho Grande, Venezuela, December 20, 1954 (A. M. Nadler), in the American Museum of Natural History.

*Description.* Carapace with a slightly dusky border. Abdomen with some white pigment on dorsum. Anterior median eyes minute. Anterior lateral eyes about one diameter apart. Posterior median eyes one-third of their diameter apart. Chelicerae with one tooth on the anterior margin. Abdomen probably wider than long, damaged in the type specimen. Total length 1.6 mm. Carapace 0.62 mm. long, 0.54 mm. wide. First femur, 0.96 mm.; patella and tibia, 1.02 mm.; metatarsus, 0.75 mm.; tarsus, 0.34 mm. Second patella and tibia, 0.77 mm.; third, 0.45 mm.; fourth, 0.65 mm.

*Diagnosis.* The eye arrangement (Fig. 5) and the palpus (Fig. 6) separate this species from others.

**Styposis scleropsis**, new species

Figures 23, 24

*Type.* Male from Summit, Panama Canal Zone, August 23-28, 1950 (A. M. Chickering), in the Museum of Comparative Zoology.

*Description.* Carapace, sternum, legs light brown. Abdomen grayish white. Carapace sclerotized, reticulate. Cephalothorax slightly elongated behind (Fig. 24). Anterior median eyes half the diameter of other eyes. Anterior median eyes their radius apart, two-thirds diameter from laterals. Posterior median eyes almost touching, their radius from laterals. Chelicerae heavy with a large tooth far removed from base of fang and a smaller tooth on base of larger one. Abdomen higher than long. Around the spinnerets a very lightly sclerotized ring, hardly different in color from less sclerotized portions. Colulus with two setae quite far anterior. Total length 1.2 mm. Carapace, 0.78 mm. long, 0.52 mm. wide. First femur, 1.00 mm.; patella and tibia, 1.18 mm.; metatarsus, 0.65 mm.; tarsus, 0.39 mm. Second patella and tibia, 0.76 mm.; third, 0.48 mm.; fourth, 0.66 mm.

*Diagnosis.* This species resembles *Cerocida* in the slightly elongated cephalothorax and the high abdomen. However, the small anterior median eyes and the palpal structure place it in *Styposis*. The shape of the carapace and the transparency of the palpal sclerites (Fig. 23) separate it from other species.



**Styposis ajo**, new species

Figures 25-27

*Type.* Female from 30 miles south of Ajo, Pima County, Arizona, January 4, 1941 (S. and D. Mulaik), in the American Museum of Natural History.

*Description.* Colorless except for pigment around eyes. Diameter of anterior median eyes less than half that of others. Anterior median eyes two and one-half diameters apart, one diameter from laterals. Posterior median eyes one diameter apart, their radius from laterals. Abdomen oval, longer than wide. Total length 1.6 mm. Carapace, 0.60 mm. long, 0.55 mm. wide. First femur, 0.78 mm.; patella and tibia, 0.88 mm.; metatarsus, 0.62 mm.; tarsus, 0.39 mm. Second patella and tibia, 0.67 mm.; third, 0.52 mm.; fourth, 0.83 mm.

*Diagnosis.* This species differs from others by the shape of the epigynum (Fig. 26). It is the only member of the genus from north of Central America.

## FOSSIL NEMOPTERIDAE (NEUROPTERA).<sup>1</sup>

BY F. M. CARPENTER

Harvard University

The living members of the neuropterous family Nemopteridae have a wide but irregular geographical distribution. Although they occur in southern Europe, Asia Minor, India, South America and Africa, they have not been found in North America. However, a fossil species, *Halter americana*, was described by Cockerell in 1907 from the Florissant shales in Colorado.<sup>2</sup> The published description of this fossil, unfortunately, was too brief and incomplete to be of use to specialists on Nemopteridae. Navas, who subsequently examined the type specimen in the British Museum (Natural History), published a new, but very inadequate, account of the fossil in 1913, erected a new genus, *Marquettia*, for it, and included a rough figure of the fore wing. The present paper is a more detailed description of the specimen, made in connection with my preparation of the insect part of the Treatise on Invertebrate Palaeontology.

I examined the type of *americana* in the British Museum in 1938, and Dr. R. Baker, of the Department of Palaeontology of the Museum, has recently sent me a series of excellent photographs of it. A second specimen of *americana*, contained in the Natural History Museum of the University of Colorado, has been loaned to me for study by the director of the Museum, Dr. Hugo Rodeck; it has added some significant features to our knowledge of the species. I have taken this occasion to discuss briefly the nemopterid *Olivierina metzeli*, which Pierce and Kirkby have recently described from an Oligocene deposit in Montana.

Unfortunately, the generic classification of the living Nemopteridae is far from satisfactory. Navas' two revisional studies were published nearly fifty years ago (1910, 1912), and the generic classification included there was mainly an arbitrary one. The genera were based almost entirely upon the shapes of the hind wings, without regard to the probably occurrence of convergence in several lines of evolution. The venation of the fore wing is surprisingly constant throughout the entire group with the exception of a very few species in which the

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<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

<sup>2</sup>This fossil naturally aroused much interest. It was selected by the editors of the Entomological News (19:34, 1908) as the most remarkable insect made known during the year 1907, and it was reproduced on the cover of the issues of the News for 1908.

pattern is much reduced. A satisfactory generic classification of the nemopterids will almost certainly not be achieved until the terminal abdominal segments of the males have been studied in detail for the majority of the species described from all parts of the world. The generic assignments of the fossils discussed below must, of course, be made mainly on the basis of the venation of the fore wing and the general shape of the hind wing, these being the characteristics which have been used in the classification of the living species up to the present time.

#### Genus *Marquettia* Navas

Navas, 1913, Mem. Real Acad. Cien. y Artes de Barcelona, 10:7

Head shaped much as in *Lertha*, the rostrum present but not elongate. Front wing broadly oval, with a venational pattern more or less characteristic of that found in the tribe Stenonemiini (Orfila, 1954). The radial sector is extensively branched, having ten main branches in addition to the anterior media.<sup>3</sup> The pterostigma is small and it was probably very light in color in the living insect, as in *Lertha*. The hind wing is slender, about the same as in *Kirbynia* in general form, except that it has a more rounded apex, like that of *Olivierina* and *Halterina*; it has two dilations, the dilated portion being nearly uniformly dark in color.

Type species: *Halter americana* Cockerell.

As pointed out above, this genus is related, so far as we can see from the known structure, to several stenonemiine genera, but it stands apart from all of these by the extensive development of the radial sector. In this respect, I consider the genus *Marquettia* to be the most primitive of the genera of the Nemopteridae known at the present time.

#### *Marquettia americana* (Cockerell)

Plate I and text figure 1.

*Halter americana* Cockerell, 1907, Science, 26:466

*Halter americana* Cockerell, 1908, Pop. Sci. Mo., 72: 125

*Marquettia americana* Navas, 1913, Mem. Real Acad. Cien. y Artes de Barcelona, 10:484, fig. 4.

Fore wing, length, 31 mm.; width, 10 mm. Length of hind wing, 44 mm.; length of body, 16 mm.; length of beak, 2.5 mm. The vena-

<sup>3</sup>I have used here the venational nomenclature proposed by Dr. P. A. Adams in his "Studies in the Neuroptera, with Special Reference to Wing Structure and Evolution in the Osmoidea" (unpublished doctoral thesis, Harvard University, June 1958).



tion is typical of that of the tribe Stenonemiini, as shown in text figure 1, with the exception of the presence of the numerous branches of the radial sector. The hind wing, which is about one and one-half times the length of the fore wing, has a slender petiole and terminates in two conspicuous dilations. The distal dilation appears to be at the termination of the wing; there does not seem to be a terminal extension, tapering more nearly to a point, as Navas indicated by dotted lines in his figure 4 (1913). The two dilations are almost certainly somewhat twisted as the fossil is preserved; this, of course, is what one would expect from the condition of the hind wing as it occurs in most living specimens of the family. The petiole of the wing is hyaline, but the two dilations are almost solidly dark in color, although there is an indication of a small hyaline area in the region of the twisting; this light area could, of course, be due to peculiarities of preservation, although the two light areas are in the same position in both of the hind wings.

**Holotype:** This consists of a nearly complete specimen with all four wings outstretched (plate 1), with the venation of the front wings very clear; collected in the Florissant shales, Colorado;<sup>4</sup> deposited in the Department of Palaeontology, British Museum (Natural History).

The species which Pierce and Kirkby described (1959) from Oligocene shales in Montana as *Olivierina metzeli* is apparently closely related to *americana* and may in fact be that species. The size of the insect is virtually identical with that of *americana*. Unfortunately, the specimen on which the *metzeli* is based is poorly preserved; the venation of the fore wing is not discernible, and the form of the hind wing is not clearly shown. The authors state that the dilated part of the hind wing narrows for a short distance and widens again to a narrow inflation. Mrs. Kirkby informs me that, though the apical portion is not complete in the type specimen, there is enough evidence preserved to show that the "paddle" widens again. Pierce and Kirkby apparently incorrectly interpreted Cockerell's description of his *americana* and they were unaware of Navas' published redescription of *americana* and of his establishment of the genus *Marquettia*. In his account of *americana*, Cockerell stated that the black area of

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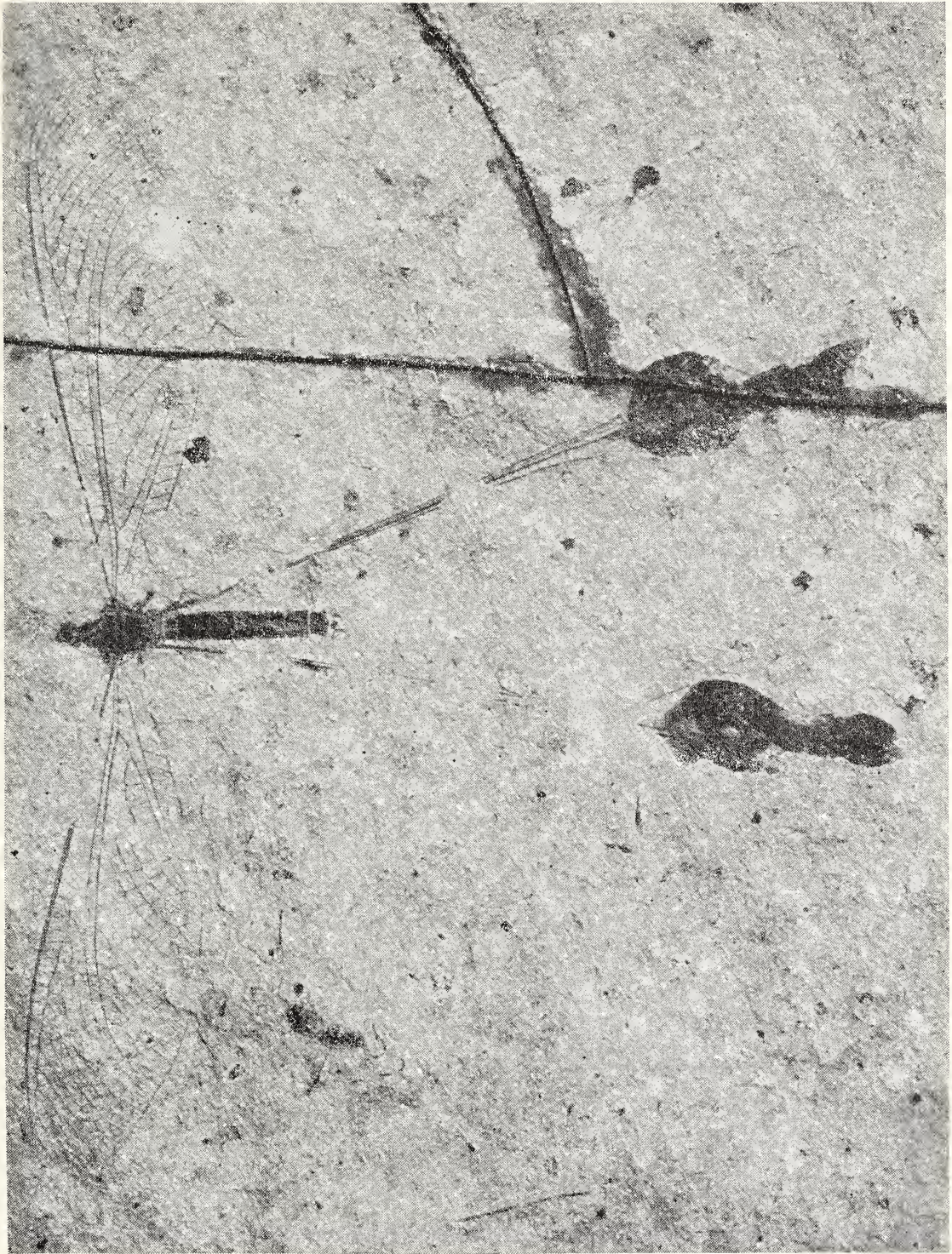
<sup>4</sup>Formerly thought to be of Miocene age but now usually considered Oligocene.

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#### EXPLANATION OF PLATE 1

*Marquettia americana* (Cock.). Photograph of holotype [Courtesy of British Museum (Natural History)].





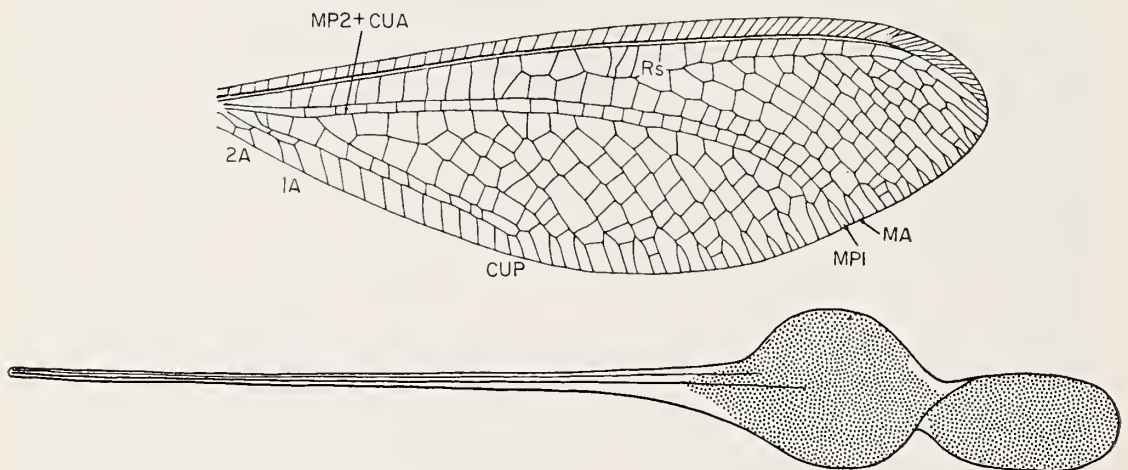
CARPENTER — FOSSIL NEMOPTERIDAE



the hind wing was solid and continuous, not broken into two as in the living *Halter extensa*. That he was referring to the interruption of the *black area* and not to the "paddle" is shown by his previous statement that the hind wing had an apical fiddle-shaped expansion, which was dark-colored. Pierce and Kirkby apparently concluded that *americana* had a single, undivided dilation. The two dilations are shown in Navas' figure of the type (1913).

Since *metzeli* has two dilations of the hind wing, as in *americana*, and resembles that species in all other known features, it may most reasonably be placed in the genus *Marquettia*, to which it is hereby assigned.

A generic revision of all known nemopterids may result in considerably generic synonymy, with *Marquettia* included. However, until such a revision is made, I believe *Marquettia* should be retained for these two fossil Nearctic species.



Text figure 1. Fore and hind wings of *Marquettia americana* (Cock.). Drawing based mainly on holotype, with additional details of specimen no. 4514, University of Colorado Museum.

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# THE RELEASE OF ALARM AND ATTACK BEHAVIOR IN SOME NEW WORLD ARMY ANTS

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The effect of odoriferous mandibular gland secretions (pheromones) as releasers of alarm behavior in *Pogonomyrmex* and some other ants has recently been investigated by Wilson (1959 and pers. commun.). It is not known how widely among the subfamilies of ants that the same or an homologous effect may occur, but Wilson, myself and others have been able to detect various pungent odors originating from the heads of worker ants in the subfamilies Myrmicinae (*Pogonomyrmex*, *Solenopsis*), Ponerinae (*Paraponera*, *Mesoponera*, *Leptogenys*), and Formicinae (*Acanthomyops*, *Lasius*). That these substances so often originate in the head is suggestive of a similar source and behavioral function, but in most cases experimental evidence of their function is lacking.<sup>1</sup>

A recent study trip to the Smithsonian Institution's Canal Zone Biological Area station on Barro Colorado Island<sup>2</sup> afforded a chance to study alarm behavior in the New World army ants (Dorylinae, tribe Ecitonini). Since the trip had other primary purposes, the army ant observations were rather limited, and some obvious tests that suggest themselves, such as trials of interspecific reactions, were not carried out. The results obtained, however, do indicate that the detailed study of army ant pheromones would be a rewarding one. Schneirla (1956 and earlier papers) has made intensive studies of the army ants of Barro Colorado, and has outlined many aspects of their biology, including the remarkably regular nomadic habits of the *Eciton* species. The first species I studied, *E. hamatum* (Fabricius), was also the one given the most attention by Schneirla and his colleagues; it is the most conspicuous army ant on the island.

A trunk trail of *E. hamatum* was found at midday running along the edge of a buttress root of a forest tree. The two-way stream of ants varied from two to six individuals in width, and the incoming ants bore much booty, mostly the pupae of the fungus-growing ant,

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<sup>1</sup>I have found that ants of the Australian formicine genus *Calomyrmex* produce a bright yellow or scarlet droplet at the base of each mandible when roughly disturbed, but it is not known whether this substance is odoriferous.

<sup>2</sup>The trip was supported by a grant from the Milton Fund of Harvard University.

*Atta*. A faint "meaty" odor was noticed as I brought my face close to the column; this odor increased markedly when I agitated a part of the column with my machete, and the ants savagely attacked the blade, biting and attempting to sting. (The meatlike odor of some New World army ants has been well known for years.) Selecting one of the large soldiers, with its conspicuous, shiny whitish head and long hooked jaws, I removed the head with forceps and placed it in the column, where it was at once vigorously attacked, bitten and stung by a mass of workers and soldiers that collected around it. The actively struggling body of this same soldier was then placed in the column at another point; the headless body, despite its considerable and highly irregular activity, attracted only momentary antennal play from passing nestmates.

Several more trials like this were made at different points along the column; it was found that soldier heads attracted more attackers than did the much smaller worker heads tried, and also that freshly crushed soldier heads drew a stronger attack than intact ones. To my nose, the strength of the meaty odor in each case appeared to be roughly proportional to the number and activity of the attackers, and I could detect none of this odor from the postcephalic part of the body after the heads had been removed. (Later, in the laboratory, crushed soldier heads of *E. hamatum* were sniffed by two colleagues and myself, and compared directly with the odor of beef and vegetable bouillon cubes, with the result that all of us found the odors close if not identical.)

Next, small dead twigs were broken in half, and one half rubbed against the crushed head of a worker. Such twigs when placed in the column were subjected to an attack as massive and vigorous as were the crushed heads alone. The untreated half of each twig, serving as a control placed at another point along the column, never received more than fleeting attention from passing soldiers and workers.

Similar results were consistently obtained with another column of *E. hamatum* found on a subsequent day.

The same kind of investigation was carried out briefly with a column of *Nomamyrmex esenbecki* (Westwood) found in the forest, utilizing the large and medium-sized workers for the decapitation test (this species lacks large soldiers). To my nose, crushed heads of this species have a different and weaker odor than do *E. hamatum* workers of the same size, but the alarm and attack reaction they provoked was similar to that of *hamatum* in intensity.

The test was also made with soldiers from a raiding swarm of

*Labidus praedator* (Fr. Smith) found in the Laboratory Clearing on Barro Colorado, and results were again similar to those of the first trials with *E. hamatum*. I could not be sure in this case that I detected any odor at all from the crushed soldier heads of *L. praedator*, but the intensity of attack on these heads indicated that an odor must have been readily detectable by the workers participating.

In summary, the detached heads of workers or soldiers of these army ants from three different genera were attacked by their nestmates when placed in the foraging column, while the remainder of the body evoked little or no response. Objects smeared with the substance from the crushed heads of soldiers drew intense attack, while untreated control objects did not. It seems likely that a pheromone originating in the head, and most likely specifically in the mandibular glands, occurs in the army ants as well as in *Pogonomyrmex*, and that its function is similar. Apparently, the ants will attack any strange object presented close to the center of concentration of the alarm odor.

The question arises as to how the individuals that are disturbed into producing the alarm odor are not themselves attacked in the normal course of events. Two of the most likely answers that suggest themselves to me are: (1) workers and soldiers, when normally disturbed, give off much lesser amounts of the alarm odor than is produced when a head is severed from the body or crushed, and the attack on severed heads or crushed heads represents a supernormal stimulus; (2) the postcephalic part of the ant's body bears some quality, probably again pheromonal in nature, that neutralizes attack behavior that might otherwise be released in nestmates. The second answer is favored as an hypothesis in the absence of further experiments. If a given soldier were protected by such a neutralizer or "identification pheromone," or by a "nest odor," it would presumably be able to indicate by means of alarm odor release the locality of an intruding disturbance without itself being subject to attack by its nestmates.

I should like to acknowledge helpful suggestions made by Prof. E. O. Wilson during the course of the work and the preparation of the manuscript.

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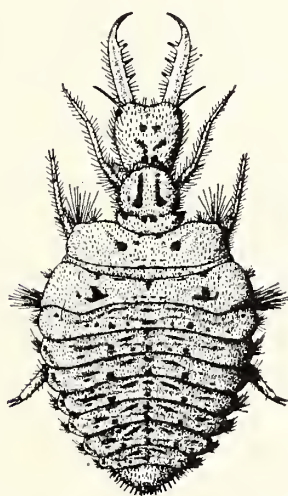
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## CONTENTS

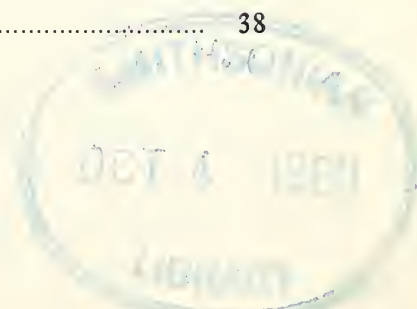
Communication by Tandem Running in the Ant Genus *Cardiocondyla*.  
 E. O. Wilson ..... 29

*Carpophilus longiventris* in Saguaro Blossoms (Coleoptera: Nitidulidae).  
 F. G. Werner ..... 35

*Emelinus melsheimeri* (Lec.) in Arizona (Coleoptera: Aderidae). F. G.  
 Werner ..... 36

The Neotropical Species of the Ant Genus *Strumigenys* Fr. Smith: Group  
 of *gundlachi* (Rogers). W. L. Brown, Jr. .... 38

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## COMMUNICATION BY TANDEM RUNNING IN THE ANT GENUS *CARDIOCONDYLA*<sup>1</sup>

BY EDWARD O. WILSON

Biological Laboratories, Harvard University

During field work in Puerto Rico in June, 1960, the author had the opportunity to study a hitherto little known form of communication among worker ants. This behavior, which for convenience might be called tandem running, involves the movement outward from the nest of closely coupled tandem pairs, and it apparently functions as a substitute for trail-laying to recruit fellow workers to food sources. On Puerto Rico, tandem running was studied more fully in the species *Cardiocondyla venustula* Wheeler but was also observed in a second member of the genus, *C. emeryi* Forel.

### Natural History of *C. venustula* on Puerto Rico

This species has been introduced by modern commerce into the West Indies and is probably native to some part of the Old World tropics. Wheeler (1908) in 1906 and the present author in 1960 found it abundant in the lowlands of Puerto Rico, especially in urban and other cultivated areas near the shore. The following generalizations are based on my 1960 observations, pertaining mostly to two colonies in urban Santurce.

As also noted by Wheeler, *venustula* colonies are small, in maturity containing probably no more than one or two hundred workers. Nests are built in open soil. Both Santurce nests were polydomous, with two or three entrances no farther than two meters apart. In each case most of the colony was concentrated in one of the subnests. Workers were often seen transporting brood and other adult workers between the subnests. In adult transport, the two ants face each other, and one grips the other by some part of the head (probably the mandibles) and swings it over its back; the transported worker as-

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<sup>1</sup>Based on research supported by a grant from the National Science Foundation.



sumes the "pupal" posture, with appendages tightly withdrawn. The nest entrances are circular or slit-shaped and large enough to accommodate only one or several ants at a time. Their appearance changes after each heavy rain, when excavation is renewed by the colony. Typically, the workers pile a circle of miscellaneous debris around the entrance holes. For example, the following particles were recorded around one chief entrance: dessicated fragments of *Pheidole* workers, small beetle elytron, unidentified piece of dry vegetable detritus, small tuft of cotton fibers. With each heavy rain the debris circle is washed away, but it is replaced within a few hours by the ants.

Foraging is most intense during the middle hours of the day, from late morning to middle afternoon. The workers seem to be most active in hot sunshine. As many as 23 were counted outside the larger of the two nests at peak activity. Workers hunt singly and range widely from the nest; a few were encountered as far as six meters away. Orientation is apparently visual; workers were frequently seen moving in nearly straight lines for considerable distances to and from the nests, and these could not be significantly disoriented by raking up soil in front of them. *Venustula* is principally, if not exclusively, a scavenger species. Following are records of food particles being brought to the nest by workers, made at random during a period of several hours: 8 pieces of unidentifiable material, probably insect in origin (see below); one fragment of insect unidentified to group; 4 body parts of another ant species, identified in 3 cases to *Pheidole*; 2 small beetles; one small spider; one cicadellid. In every case the insect material was either dried or, if fresh, crushed or mangled, obviously having been found in an inactive state by the *venustula* workers. No evidence of predation could be found. Workers were observed on many occasions to start away from the numerous small spiders, collembolans, cicadellids and other insects that swarmed in the nest vicinity. On the other hand, they readily accepted dead insects offered them. Insects too large to be carried back by a single worker were carved into manageable pieces by the foragers. The great majority of food particles brought to the nest ranged in size from slightly less than the volume of a *venustula* worker head to about three times this size. Workers also accepted sucrose solution readily.

#### Tandem Running in *C. venustula*

Workers of this species were never seen to lay or follow odor trails. Instead, a distinctive form of communication is employed during

foraging that involves, in most cases, only two workers at a time. The leader moves outward from the nest, with a single follower close behind. The communication is as follows: the leader remains perfectly still until touched on the abdomen by the follower ant. Then it runs forward for a distance of approximately 3 to 10 mm (or one to several times its own body length), only to come to a complete halt again. The follower ant is in a highly excited state, apparently stimulated by a secretion released by the leader; other workers approaching the leader become similarly excited, even when the latter is completely immobile at the time. After each contact and subsequent "drive" of the leader forward, the follower may press immediately behind and drive it again. More commonly, it circles widely about in a hurried movement that usually lasts for several seconds and may take it as far as a centimeter from the path set by the leader. In short time, however, the circling brings the follower once again into contact with the leader. If it touches the leader on the head or from the side, the latter does not move. In such cases the follower invariably moves around to the rear of the leader, touches it on the abdomen and starts it forward again.

On three occasions, the author removed the follower worker with a pair of forceps and lightly touched the leader on the abdomen with a fine vegetable fiber or human hair in an attempt to drive it artificially. The attempts were only partly successful, perhaps because the stimulus was too crude. In each case the leader moved forward, stopped, was touched again, moved forward, stopped, was touched a third time, and continued running thereafter. The runs between stimuli were somewhat longer than under natural conditions. The workers were successfully driven in this way only for distances of several centimeters before breaking away. In an attempt to induce following artificially, various body parts of workers were crushed on to the tips of strips of paper, which were then offered to workers around the nest entrance. Workers were both excited and mildly attracted, in contrast to a neutral or flight reaction to untreated strips, but they could not be induced to follow when the strips were drawn slowly over the ground.

In the great majority of cases, tandem running involved only two workers. Occasionally a third worker crowded in closely behind the leader worker but did not continue following for more than a few centimeters. Additional workers became excited by the leader only when they encountered it directly. There was no evidence of any kind of an odor trail.

A total of 16 tandem trips away from the larger *venustula* nest were followed to completion. Two of these were abortive, breaking off less than 15 centimeters from the nest. Seven led outward for distances of approximately one to two meters from the nest, in four cases to food baits set at this distance. The remaining seven led for three to five meters before breaking up or ending at a food source, a very considerable distance for so small an ant. All of the movements formed a nearly straight line, with only occasional, momentary doubling back. Eleven of the tandem runs ended without achieving any obvious goal. Five, however, ended at food sources, either dead insects occurring naturally or baits set by the author and both workers thereafter commenced feeding. Considering the greatly dispersed state of acceptable food, this seemed to be a highly significant proportion of "hits". Furthermore, almost all of the eleven fruitless runs were oriented in directions from which abundant food particles were being transported by other workers at the time.

The hypothesis was now considered, that tandem running is a means whereby newcomer ants are recruited to new food sources. This implies that the leader ant has visited the food source at least once and is now returning, bringing a sister worker in tow. The hypothesis could not be tested directly under field conditions, since workers were too small to mark with ink or paint and could not otherwise be traced when they re-entered the nest. However, the following indirect experimental evidence supports the hypothesis.

Baits were placed at varying distances from the nest and tandem pairs leaving the nest were followed during the next 30 or 60 minutes. In one experiment a small piece of moistened sugar was placed 10 cm. from the main nest entrance. Two tandem pairs left in the observation period; one arrived at the sugar, the other proceeded to a dead homopteran lying naturally at a position about 4 meters away. In two additional experiments, small, freshly killed moths were placed at positions 15 cm. and between one and two meters from the nest. Three tandem pairs arrived at these baits, while 5 moved in other directions. Thus in all three experiments five pairs arrived at targets and commenced feeding, while five went in other directions. Even if it is assumed that the five that missed were not heading for other, natural food sources, an unlikely proposition, the results are highly significant. Judging from the movements of individual workers approaching and passing baits in near-misses, the total angular sector through which individual (and tandem pairs) could move randomly outward and successfully hit the closest target was calculated as not



greater than  $30^\circ$  and probably less than  $20^\circ$ . This angle was less than  $1^\circ$  for the most remote targets. Thus the probability that pairs moving at random would hit one of the targets did not exceed 0.1 and was usually far less. The frequency of actual hits, 0.5, is highly significant. Furthermore, in each case of a hit, the pair at once broke apart and commenced feeding, indicating that recruitment was indeed the "goal" of their excursion.

Although tandem running is apparently devoted in part or entirely to the communication of food finds, it is employed only by a fraction of workers engaged in successful foraging. Less than 10% of workers running from the nest to food masses were coupled in tandem pairs. This is in contrast to the high degree of participation shown by trail-laying ant species such as *Solenopsis saevissima* (Fr. Smith), in which more than 90% of workers returning from rich food sources contribute material to the trail.

The nesting and foraging behavior of *C. emeryi* Forel appears to be very similar to that of *venustula*. On two occasions, at Santurce and Luquillo, Puerto Rico, pairs of *emeryi* workers were seen engaged in tandem running, apparently identical in form to that of *venustula*. This aspect of the behavior of *emeryi* has not been analyzed further.

#### Discussion

The first mention of tandem running in the literature is evidently that of Hingston (1928). This author gives the following description of foraging behavior in the Indian species *Camponotus (Orthonotomyrmex) sericeus* (Fabr.): "This ant nests on the ground and goes up trees in search of food. Its plan of communication is very simple, and, being so simple, is highly instructive. All that happens is that one ant leads another to the place where spoil has been found. One ant discovers spoil. It returns to the nest, finds a comrade and leads it to the required place. The two go off over the ground. The leader keeps in front; the led ant follows. Number two keeps in number one's footsteps, and repeatedly touches its tail. The leader moves particularly slowly in order not to lose connection with its follower. If number two happens to get out of touch, then the leader halts and waits until number two regains its place." In 1955, near Sydney, Australia, Mr. John Freeland showed me a pair of workers of an unidentified *Camponotus* engaged in tandem running quite similar to that in *Cardiocondyla*, although we did not guess the significance of the behavior at the time. Thus tandem running appears to be a wide-

spread form of communication in ants. Perhaps further directed observation will show it to be more common than the meager existing data have indicated.

It is valuable to speculate, as Hingston (1928) and later Sudd (1959) have done, that tandem running is a primitive communication form that can lead in evolution to trail laying. Hingston has described what appear to be excellent intermediate stages between tandem running and trail laying in the Indian species *Camponotus (Myrmosericus) paria* Emery and *C. (Tanaemyrmex) compressus* (Fabr.). In *paria* the leader ant does not halt and wait to be touched, while the follower often drops behind 2 or 3 inches and seems to be orienting at least in part by a rudimentary odor trail. The behavior of *compressus* resembles that of *paria* except that as many as ten or twenty workers follow in a single file behind the leader.

Nevertheless, it will have to be remembered that in *Cardiocondyla*, at least, tandem running is a highly evolved behavioral pattern in its own right. It can be fairly said to include more complex individual behavior than trail-laying and trail-following. In particular, the simultaneous release of a chemical stimulus and the drive behavior of the leader ant are quite elaborate in comparison with other known forms of ant communication. Even so, it would be most interesting to know whether any of the other species of *Cardiocondyla* show behavior patterns intermediate between tandem leading and trail-laying, as is apparently the case in *Camponotus*.

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*CARPOPHILUS LONGIVENTRIS*  
IN SAGUARO BLOSSOMS  
(COLEOPTERA: NITIDULIDAE)

BY F. G. WERNER  
University of Arizona, Tucson

The common Nitidulid in saguaro blossoms is not *Carpophilus pallipennis* (Say), as is the case with other common cacti in southern Arizona, but *C. longiventris* Sharp. Adults reach the flower early in the morning of the one day they are open and swarm over the inside of the perianth, at the base of the stamens. By noon, elongate (1.06-1.34 x 0.22-0.25 mm.) white eggs have been deposited just under the lining of the perianth, parallel to the surface. These must hatch within 24 hours, because small larvae can be found the next day. The perianth and style gradually wither and usually drop from the developing fruit within four or five days. By this time the larvae are mature. They change from white to pinkish-white and finally to tannish-white as they develop, probably partly because of the changing color of their food, pollen and probably other tissue, as decay progresses. The contents of the digestive tract show through the translucent body. Dead flowers on the ground rarely contain larvae, which must therefore leave soon after the flower has dropped, or even before, presumably to pupate in the ground. The larvae do not enter the developing fruit and so probably have no effect on them.

The adults are in most cases easily distinguishable from *pallipennis* by their dark elytra, but some small individuals have the elytra pale. In that case, they can be distinguished by the lack of small tubercles on the middle part of the hypopygidium, much sparser and less decumbent pubescence on the pygidium and by the secondary sexual characters given by Parsons (1943, Bull. M. C. Z., 92: 166-9). The large larvae are almost identical with those of *C. floralis* Er., as described and figured by Connell (1956, Delaware Agr. Exp. Sta. Bull., 318: 17-21). They appear to differ only as follows: prothoracic plates with about 10 setae around the edge and about 8 small pits alternating with them, plus 1-2 setae and 1-2 pits on the disc; caudal plate with indefinite margins, almost identical but with 2-3 small pits on each side; setae on caudal plate, and to a lesser extent on the dorsum of the thorax, slightly thickened apically, elsewhere tapering to a fine point. The differences are not great, and a comparison of specimens would be required to pick out those of diagnostic importance.



Parsons (*loc. cit.*) states that this species has been collected on *Yucca elata*. Saguaro (*Cereus giganteus*) is certainly the principal host plant in the Tucson area. We have never taken the species in other blossoms. *C. pallipennis* frequents saguaro blossoms only in small numbers.

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*EMELINUS MELSHEIMERI* (LEC.) IN ARIZONA (COLEOPTERA: ADERIDAE).—This species has not been recorded from west of Illinois and would be expected to occur only in the mesophytic portions of the Northeast and Midwest. Leng's record from Florida may refer to a misdetermined *E. ashmeadi*. A single male, collected at light by Anthony Ross, of the Department of Entomology, University of Arizona, in Pinery Canyon, W. slope Chiricahua Mts., July 11, 1958, agrees perfectly with the male from Illinois mentioned previously (Werner, 1956, *Psyche* 63: 32). This brings the total of described species known from Arizona to three. A small portion of the fauna of the Chiricahua Mts. appears to have been derived from that of the Midwest or at least from the same source. J. W. Green has recently identified a specimen of the lycid *Caenia dimidiata* (Fab.) from Pinery Canyon, July 9, 1955, Butler and Werner collectors. He expressed some surprise at its occurrence there, since it was previously known from only as far west as Arkansas. — F. G. WERNER, University of Arizona.

THE NEOTROPICAL SPECIES OF THE ANT GENUS  
*STRUMIGENYS* FR. SMITH:  
GROUP OF *GUNDLACHI* (ROGER)<sup>1</sup>

BY WILLIAM L. BROWN, JR.  
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This paper is a continuation of my series on the New World fauna of the dacetine ant genus *Strumigenys* Fr. Smith. Earlier parts, containing keys to the abbreviations for measurements and proportions, may be found in Jour. New York Ent. Soc. 61: 53-59, 101-110 (1953). In addition to these, other parts have been published or are being prepared. At the end of the series, an illustrated key to the New World members of the genus will be forthcoming.

Relationships of the *gundlachi* Group

The present section deals with a group approximately equivalent to what I called in my preliminary generic revision of the Dacetini (Brown, 1948, Trans. Amer. Ent. Soc., 74: 101-129) by the name *Strumigenys* subgenus *Pyramica*. At that time, the group seemed rather distinct from all the other *Strumigenys* species on the basis of the following characters:

1. Mandibular insertions more remote.
2. Apical fork of mandible with more or less reduced teeth.
3. Inner mandibular border with a series of three or more denticles, instead of two, one or no preapical teeth in *Strumigenys s. str.*
4. Antennal scapes shorter and broader.
5. Spongiform appendages of petiole and postpetiole reduced.
6. Labral lobes longer.
7. General habitus, especially head shape.

Since 1948, I have had the opportunity to study carefully the three species recently described by Kempf (1958, Rev. Brasil. Ent., 8: 59-68) as the *S. connectens* group, which bridges very nicely the gap between *Pyramica* and the more typical *Strumigenys* — in particular, the *S. louisianae* group. The steps from *Strumigenys* to *Pyramica* are so gradual that it is clear only an arbitrary distinction can now be drawn between the two groups. Under these circumstances, there is no need for a formal generic or subgeneric split, and the name *Pyramica* goes into the synonymy of *Strumigenys*. (The one other

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subgenus of *Strumigenys* is *Labidogenys* Roger, which also deserves synonymy from present evidence.) In the present paper, "*gundlachi* group" is used, instead of *Pyramica*, to include the species *gundlachi* (Roger), *eggersi* Emery, *subdentata* Mayr, *denticulata* Mayr, *jamaicensis* Brown and *trieces* n. sp. It should be emphasized, however, that the group is arbitrarily limited, and that *S. connectens* and its relatives could as well be included as not.

#### The Identity of *Pyramica gundlachi* Roger

Roger described *Pyramica gundlachi* in 1862, only two years after Frederick Smith had established *Strumigenys*. Roger based his species on worker and female specimens from Cuba. Roger himself quickly (1863) recognized that *gundlachi* was so close to *Strumigenys* that *Pyramica* would have to fall as a synonym of that genus. In 1890, Emery demonstrated that *gundlachi* was a composite species; the female was then named as *Strumigenys rogeri* Emery, a distinct species we now know to have been introduced into Cuba from Africa.

In the meantime Mayr (1887) had recharacterized *gundlachi* from a cotype worker that Roger had sent him earlier. Both Roger and Mayr described *gundlachi* as having the inner mandibular border unarmed before the apex and as having the ventral apical tooth divided. The remainder of the information available indicated to me that *gundlachi*, despite these characters and despite the fact that subsequent authors had described varieties in this complex as having unarmed preapical masticatory borders, belonged with a group including *eggersi*, *denticulata* and *subdentata* and their varieties and synonyms. Accordingly (without then knowing the *connectens* group) I revived *Pyramica* as a subgenus with *gundlachi* as the (monobasic) type species (Brown, 1948).

From 1887 until 1948, the true *gundlachi* was ignored by most authors, and its identity wrongly guessed by several others. Finally, through the kindness of the late Prof. Bruno Pittioni of the Vienna Museum, I was able to examine the critical syntype worker that Roger had sent to Mayr. The mandibles of this specimen turned out to be encrusted with ancient glue, and, since this was the only specimen in Mayr's collection, it seems clear that he merely followed Roger in describing the mandibles. The glue was carefully removed with Barber's fluid, revealing that the mandibles have a full complement of preapical denticles and a normal apical fork with two minute intercalary denticles. In short, the *gundlachi* syntype was found to be



identical with types of *S. eggersi infuscata* Weber and with many other samples from the Caribbean area in the MCZ. It became evident that most of the forms originally described as varieties of *S. eggersi* were in fact only variants of *gundlachi*. Later, Dr. E. M. Hering, of the Zoologisches Museum in Berlin, kindly confirmed the same points for the remaining *gundlachi* syntypes in the Roger Collection.

#### Relationship and Synonymy of *S. gundlachi* and *S. eggersi*

Early in the study, *S. denticulata* and *S. subedentata* (with its synonyms *clavata* and *tristani*) were recognized as distinct species. Later, the new species *jamaicensis* and *trieces* were discovered and set to one side. The large residue of samples available in the *gundlachi* group all appeared to fall into one complex of very similar but variable forms. On further study, this complex was resolved into two morphological species, one corresponding to the *gundlachi* type, and the other to syntypes of *eggersi* in the USNM, differentiated by the characters cited in the description below and shown in Figs. 7 and 8. There remained the task of determining the identity of the six subspecies and varieties assigned to *eggersi* by various authors: var. *vincentensis* Forel, var. *cubaensis* Mann, var. *banillensis* Santschi, var. *isthmica* Santschi, subsp. *infuscata* Weber and var. *berlesei* Weber. Of these, *vincentensis*, *cubaensis* and *banillensis* were all described as lacking preapical denticulation on the mandibles. The types of *cubaensis* were examined first; these are specimens of *Strumigenys louisianae* Roger, and have been synonymized accordingly (Brown, 1953, Amer. Midl. Nat., 50: 28-29.). A worker type of *banillensis* from the Santschi Collection proved to have partly broken but distinct preapical denticulation, and it agreed well otherwise with *gundlachi*. The unique type of *vincentensis* cannot be found in the British Museum or in the Forel Collection; it is almost certainly just another *gundlachi* specimen in which the denticulae were overlooked, judging from the description and locality. Types of *infuscata* and *berlesei* were compared with the *gundlachi* lectotype, and these names are judged to be straight synonyms. The description of *isthmica* agrees well with the types and Panamanian samples of *gundlachi*. All named variants of *eggersi* are thus accounted for. There is one more name: *S. bierigi* Santschi. The description of this form from Cuba fits the typical *gundlachi* so well that there seems no reason to doubt its synonymy; *gundlachi* is the most common

species of the group so far found on Cuba. The status of the names involved is summarized in list form:

Group of *S. gundlachi*

- gundlachi* (Roger)  
 = *eggersi* var. *vincentensis* Forel n. syn.  
 = *eggersi* var. *banillensis* Santschi n. syn.  
 = *bierigi* Santschi n. syn.  
 = *eggersi* var. *isthmica* Santschi n. syn.  
 = *eggersi* subsp. *infuscata* Weber n. syn.  
 = *eggersi* var. *berlesei* Weber n. syn.  
*eggersi* Emery  
*denticulata* Mayr  
*subedentata* Mayr  
 = *tristani* Menozzi n. syn.  
 = *clavata* Weber n. syn.  
*jamaicensis* Brown  
*trieces* n. sp.

*Strumigenys gundlachi* (Roger)

(Figures 1, 5)

- Pyramica gundlachi* Roger, 1862: 253, pl. 1, fig. 18a, worker nec female. Type loc.: Cuba. Lectotype, by present designation, the worker specimen in Naturhistorisches Museum, Vienna. Other syntypes in Zoologisches Museum der Humboldt Universität, Berlin. Lectotype examined.
- Strumigenys gundlachi*, Roger, 1863, Verz. Formic., p. 40. Mayr, 1887: 570, worker.
- Strumigenys eggersi* var. *vincentensis* Forel, 1893, Trans. Soc. Ent. London, p. 378, worker. Type loc.: Forest near Châteaubelaise, 1000 feet, St. Vincent, B. W. I. Location of type unknown, presumed lost. New synonymy.
- Strumigenys eggersi* var. *banillensis* Santschi, 1930: 80, worker. Type loc.: Sierra Banilla, near Habana, Cuba. Unique holotype in Santschi Coll., Basel; examined. New synonymy.
- Strumigenys bierigi* Santschi, 1930: 80, worker. Type locs.: (1) Marianao, Cuba; (2) La Habana, Cuba. Types in Santschi Coll., Basel; not seen. Santschi, 1931: 276, worker variation. New synonymy.
- Strumigenys (Strumigenys) eggersi* var. *isthmica* Santschi, 1931: 276, worker. Type loc.: France Field, Panama. Syntypes in Santschi Coll., Basel. New synonymy.
- Strumigenys (s. str.) eggersi* subsp. *infuscata* Weber, 1934: 35, worker, female. Type loc.: Limones Seboruco, Soledad, Cuba. Syntypes in MCZ, Coll. Weber. New synonymy.
- Strumigenys (s. str.) eggersi* var. *berlesei* Weber, 1934: 36, female. Type loc.: Harvard Botanical Gardens, Soledad, Cuba. Holotype in Coll. Weber, examined. New synonymy.
- Nec Strumigenys gundlachi* of Creighton (1930, Psyche, 38: 179, fig. 1 A), which is based upon a worker from what later became the type series of *S. caribbea* Weber. *S. caribbea* was formally synonymized with *S. silvestrii* Emery by Brown, 1959, Stud. Ent. (n. s.), 2: 25.

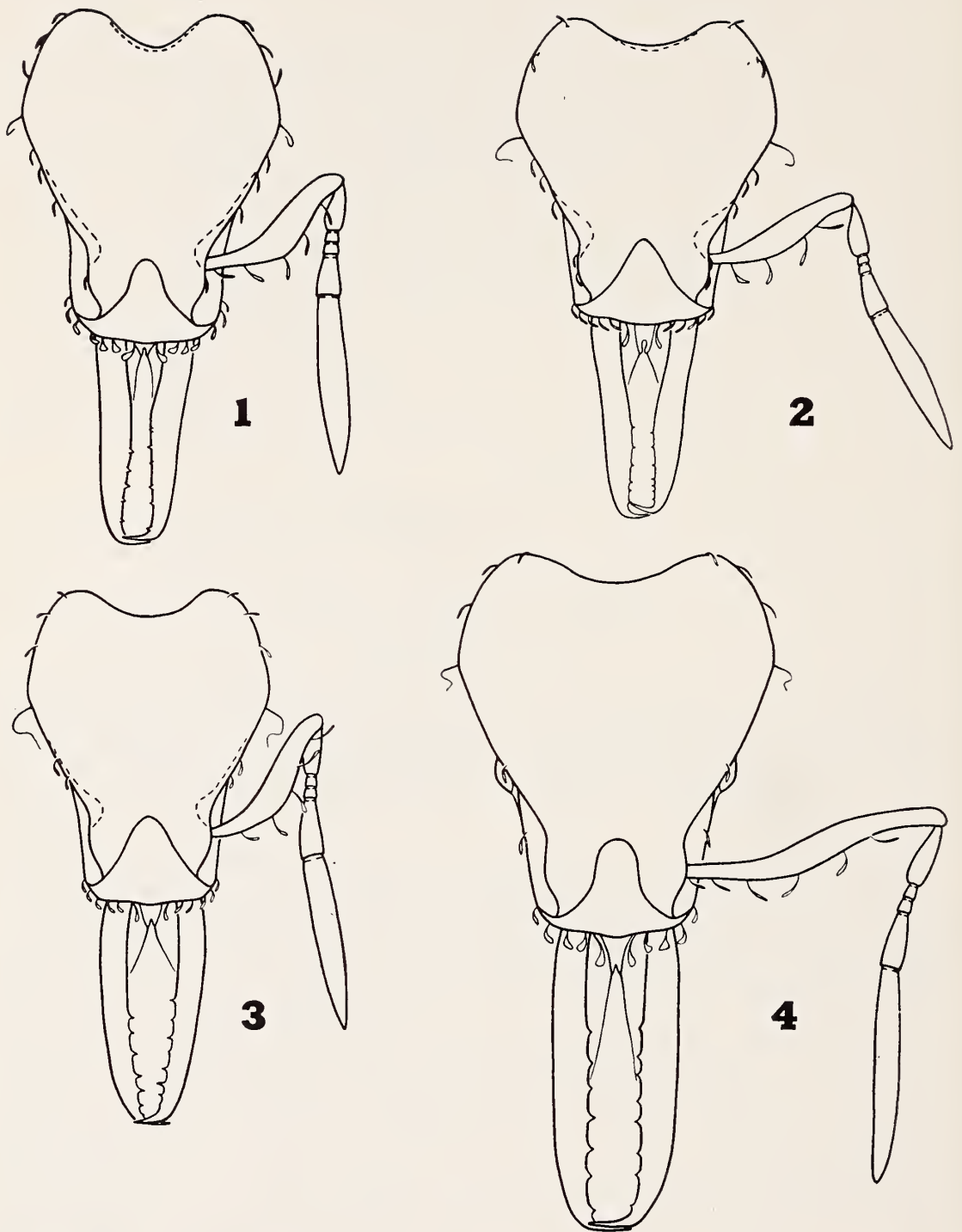
Worker: TL 1.7-2.1, HL 0.40-0.49, ML 0.24-0.32, WL 0.40-0.50 mm. CI 79-86, MI 59-66.

This variable species is small and rather slender, with convex head and alitrunk, the latter with a weak but readily discernible metanotal groove and acute, oblique propodeal teeth with concave, cariniform infradental lamellae. Mandibles straight, inner borders straight to weakly convex, with 4-9 preapical denticles along the apical half or more, which are very variable in size, shape and spacing in different samples, and are often very difficult to see except in dark silhouette against a bright background. The three most distal teeth are often larger than the rest, but sometimes all of them are extremely small. The dorsal tooth of the apical fork is short, but is longer than its ventral mate; between them are two minute intercalary denticles. Petiole and postpetiole shown in Figure 5; note the small but still distinct spongiform appendages.

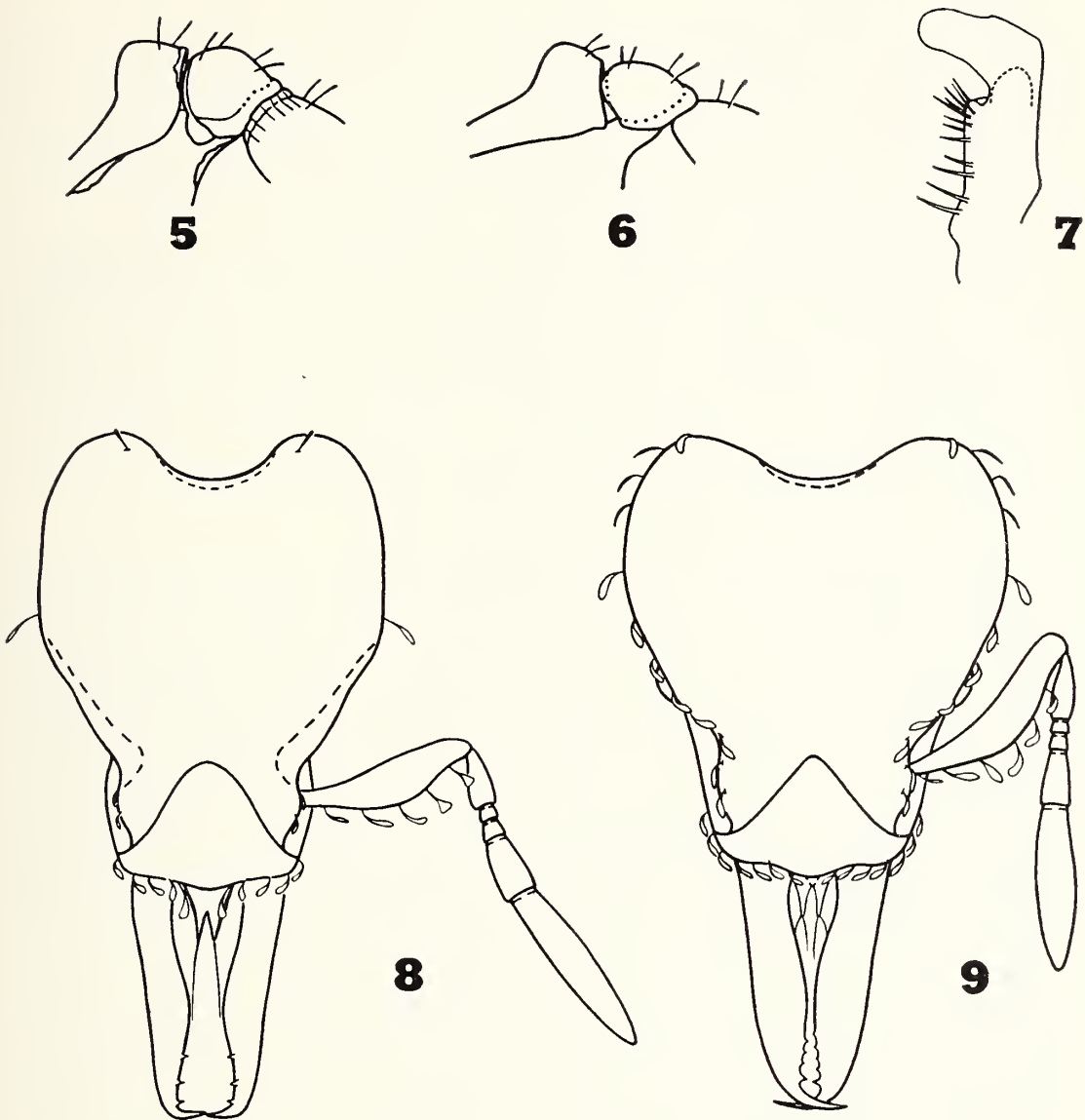
Body generally densely reticulate-punctulate, opaque, although in some examples the lower posterior sides of the alitrunk may have the sculpture partly effaced and shining. Gaster smooth and shining when clean, with distinct spaced longitudinal carinae taking up about the basal quarter or so of the first segment. Sometimes faint traces of shagreened sculpture also occur on the basal half of the gastric tergum, and some specimens are fouled with dirt or hardened secretion, so that it becomes difficult to tell them from *eggersi* workers in this respect.

Ground pilosity of head and promesonotum consisting of slender, curved, decumbent, linear-spatulate hairs, numerous on head but sparse on promesonotum. Fringing hairs of head shown in Figure 1. Mandibles with fine subappressed pointed hairs, and a row of short oblique pointed hairs along each inner mandibular border. Longer erect hairs are mostly slender, truncate to feebly remiform or clavate: one pair on vertex, one pair on occiput, one or two pairs on petiolar node, two or three pairs on postpetiole, and 30-45 hairs on gastric dorsum, arranged more or less in transverse rows. In addition, there are bilaterally paired erect hairs which may be either long and flagelliform or short and paddle-shaped (remiform). Apparently, remiform hairs are readily transformed into flagelliform ones by the detachment of the rim of the hair at one side, so that the hair frays out to a long, slender point. Flagelliform hairs are often seen reflexed or looped, like a furled coachwhip, and it is difficult to distinguish such hairs from the remiform ones. One of these hairs is to be found on each lateral occipital convexity (Figure 1), and there is a pair on the





Figures 1-4. *Strumigenys* of the *gundlachi* group, heads of workers, right antenna omitted; only the fringing pilosity is shown, and mandibular hairs are omitted. Figure 1, *S. gundlachi* (syntype of the synonymous *S. eggersi infuscata* from Cuba). Figure 2, *S. eggersi* from S. Teresa, Espiritu Santo, Brazil. Figure 3. *S. denticulata* from Trinidad. Figure 4. *S. jamaicensis*, paratype. Drawn to same scale.



Figures 5-9. *Strumigenys* of the *gundlachi* group. Figure 5, *S. gundlachi*, side view of pedicel to show spongiform appendages; same specimen as Figure 1. Figure 6, *S. eggersi*, side view of pedicel, same specimen as Figure 2. Figure 7, *S. subdentata* male, volsella of genitalia, Mixco, Guatemala. Figure 8, *Strumigenys trieces*, new species, holotype worker. Figure 9, *S. subdentata*, worker from Panama Canal Zone. Figures 5, 6, 8 and 9 are drawn to the same scale as Figures 1-4; Figures 8 and 9 carry the same conditions as 1-4.

humeri and a pair on the mesonotum. The pilosity varies in different samples, however, and specimens are frequently partly denuded. Color usually medium ferruginous, but some samples are much darker; a Jamaican series is blackish-brown.

The female is similar to the larger workers of the same nest series, apart from the usual caste differences, but the head averages a trifle broader (CI 83-89), and the gastric dorsum is more or less distinctly shagreened over the basal segment, but usually not so strongly sculptured as is the *eggersi* female. Male unknown.

Distribution: Occurs widely in countries bordering the Caribbean; actually reported from southern Mexico, Costa Rica and Panama; Central America may be the original home of the species. It is well established in Trinidad and Tobago, Cuba and Jamaica, and southern Florida, doubtless after introduction through human commerce, at least in some of these places, but it has not been found on the South American mainland.

Localities for material examined: Trinidad: Laboratory at Simla, 800 feet, 4 miles north of Arima (R. Foster leg.). Arima-Blanchisseuse Road (N. A. Weber leg.). Arima (Weber leg.). Macqueripe Bay (Weber leg.). St. Augustine (Weber leg.). Tobago Island: (R. Foster leg.). Jamaica: near Round Hill, Manchester Parish (H. B. Mills leg.). Southfield and Black River, St. Elizabeth Parish (Mills leg.). Cuba: various collections in and near Soledad, Las Villas Prov. (leg. M. Bates and G. Fairchild, E. O. Wilson, N. A. Weber), including types of *infuscata* and *berlesei*. Mina Carlota, Trinidad Mts. (Wilson leg.). Baragua, Camaguey (Bates and Fairchild leg.). Florida, U. S. A.: Royal Palm Ranger Station, Everglades National Park (L. J. Stannard leg.). Northern Key Largo (E. O. Wilson leg.). Mexico: Pueblo Nuevo, near Tetzonapa, Veracruz (Wilson leg.). Villa Hermosa, Tabasco (F. Bonet leg.). Finca el Real, Ocosingo Valley, Chiapas (Goodnights and Stannard leg.). Costa Rica: without further locality (leg. H. Schmidt, F. Nevermann). Panama Canal Zone: Barro Colorado Island, many collections by J. Zetek, E. S. McCluskey, W. L. Brown, Jr., and others.

Biology: E. O. Wilson (unpubl. notes) kept a colony of *gundlachi* for over a month in Cuba, during which time it captured and consumed entomobryoid and sminthurid collembolans, but ignored poduroids, a small cricket nymph, various mites and minute millipeds. Hunting is usually of the relatively immobile ambush type, which is to say that the ants approach the prey and, when close enough to de-



tect its position, freeze with mandibles held open toward it (at an angle of 60°-70° in this case). However, sometimes workers approach the prey and strike quickly and directly, without waiting. If prey is struck and continues to struggle, it is lifted off the ground and stung in the usual manner of *Strumigenys*.

McCluskey and I found this species in nearly every berlesate of upper soil and leaf litter that we examined on Barro Colorado Island; it is evidently there the most common dacetine species and one of the more frequent ant species of the forest floor. Wilson found *gundlachi* to be somewhat less abundant in Veracruz. Although it is abundant in tropical rain forest, it also lives in second-growth forest, thickets, and cacao plantations. Weber (1952) took a sample deep in a cave on Trinidad among manure and debris from the oil-birds (*Steatornis*) and bats living there.

*Strumigenys jamaicensis* Brown  
(Figure 4)

*Strumigenys jamaicensis* Brown, 1959, Brev. Mus. Comp. Zool., 108: 6, worker. Type loc.: Corn Puss Gap, 2000 ft., St. Thomas Parish, Jamaica. Holotype in Coll. Illinois State Natural History Survey, Urbana, Illinois; paratypes in MCZ.

Worker: TL 2.3-2.6, HL 0.52-0.56, ML 0.40-0.42, WL 0.55-0.57 mm. CI 81-82, MI 75-77.

Resembles *S. gundlachi*, but larger and with relatively much longer mandibles and antennae, particularly the scapes. Mandibles with gently convex outer borders and straight inner borders bearing 6-8 strong, acute denticles which occupy about the distal 2/3 of the border. Body in general relatively more slender than in *gundlachi*. Sculpture, pilosity and spongiform appendages as in *gundlachi*, although in *jamaicensis* the ground pilosity tends to be less conspicuous and the erect hairs larger; also, the gastric hairs are larger and fewer. Color blackish-brown. Female and male unknown.

In addition to the holotype nest series from Corn Puss Gap, I studied two additional (paratype) series from Hardwar Gap (about 4000 feet), Portland Parish, Jamaica. All of the specimens were taken by H. B. Mills by Berlese funnel from soil-leaf litter charges.

Distribution and relationships: So far as is known, this species is confined to the mountains of Jamaica. It appears to be a specialized descendant of an early immigrant population derived from the mainland *gundlachi* stock. Both *gundlachi* and *eggarsi* now also occur on Jamaica, probably as a result of accidental introduction by man, but

there is no evidence of intergradation between *jamaicensis* and either of these species.

*Strumigenys eggersi* Emery  
(Figures 2, 6)

*Strumigenys eggersi* Emery, 1890: 69, pl. 7, fig. 9, worker, female. Type loc.: St. Thomas, West Indies. Syntypes in Museo Civico di Storia Naturale, Genova, and in USNM, several examined.

*Strumigenys (Strumigenys) eggersi*, Santschi, 1931: 276 (records from Pinar del Rio Prov., Cuba, and key to "varieties.").

Worker: TL 1.6-2.0, HL 0.39-0.47, ML 0.22-0.27, WL 0.39-0.46 mm. CI 83-88, MI 56-64. Very similar to *S. gundlachi*, averaging a little smaller, with relatively shorter mandibles, although dimensions and proportions of the two species overlap broadly. Mandibles straight, with weakly convex inner borders, each bearing 4-8 minute denticles on its distal 1/3 to 1/2. Color yellowish ferruginous, lighter than usual for *gundlachi*. The two chief characters are these:

1. Spongiform appendages of petiole and postpetiole obsolete, the lateral postpetiolar lobes represented by a narrow lamellate margin (Figure 6).

2. First gastric tergum superficially reticulate-punctulate and opaque in front, becoming indefinitely shagreened and weakly shining behind.

The female differs from the workers in the same way that the *gundlachi* queen differs from its workers. Reticulate sculpture of gastric dorsum more distinct and more opaque than in worker. Male unknown.

Distribution: The home range is probably southern Brazil and Bolivia, though lack of collections from central and northern Brazil prevents us from knowing how far north this species extends. *S. eggersi* is also known from widely scattered localities in the West Indies, Florida and southern Mexico, sometimes sympatrically or nearly so with *S. gundlachi*, and it seems likely that it has been introduced by man at these points.

Localities for material examined: Bolivia: Espia Rio Bopi (W. M. Mann leg.). Brazil: Agudos, S. Paulo State (W. W. Kempf and C. Gilbert leg.). Rio de Janeiro (T. Borgmeier leg.). Santa Teresa, Espiritu Santo State (O. Conde leg.). West Indies: Trinidad (P. B. Whelpley leg.). Pitch Lake and Trinity Hills Forest Reserve, Trinidad (N. A. Weber leg.). Roseau, Dominica (Weber leg.). St. Thomas (Baron Eggers leg.), syntypes of *eggersi*, in USNM. Maya-

guëz, Puerto Rico (M. R. Smith leg.). Petit Goave and Fond Verrettes-Refuge, Haiti (H. B. Mills leg.). Jamaica: Spanish Town, St. Catherine Parish; Mt. Diablo, St. Ann Parish; Black River, St. Elizabeth Parish; Heron's Hill, Manchester Parish (all Mills leg.). Soledad, Las Villas Prov., and San Vicente, Pinar del Rio Prov., Cuba (E. O. Wilson leg.). Florida, U. S. A.: Fisher's Island (J. E. Porter leg.). Archbold Biological Station, Highlands County (H. S. Dybas leg.). Mexico: Palmillas, Tabasco (F. Bonet leg.). Chichen Itza, Yucatan (L. J. Stannard leg.).

Biology: Weber found specimens in a compost heap in the Botanical Garden at Roseau, Dominica, and in an island of vegetation growing in the Pitch Lake of Trinidad; also on Trinidad, he took a sample from low-growing epiphytes in second-growth forest. Kempf sifted specimens from humus in São Paulo. Indications are that this species can stand more dryness than many dacetines, and its presence in many culture areas suggests that it is spreading rapidly through nursery stock transport and other human commerce. The Floridian records for both this species and *gundlachi* are the first for the continental United States.

*Strumigenys denticulata* Mayr

(Figure 3)

*Strumigenys denticulata* Mayr, 1887: 576, worker. Type loc.: Blumenau, S. Catarina State, Brazil. Types in Naturhistorisches Museum, Vienna, and in MCZ; two workers examined. Emery, 1890: pl. 7, fig. 8, worker.

Worker: TL 1.8-2.2, HL 0.42-0.48, ML 0.31-0.39, WL 0.42-0.49 mm. CI 77-80, MI 74-83. Similar to *gundlachi* and *eggersi*, but more slender, and with very long, slender, slightly bowed mandibles, each bearing 5-9 denticles along the distal half or more of their inner borders. The antennae are also proportionately long and slender. Spongiform appendages obsolete, like those of *eggersi*. Sculpture as in *eggersi*, except that the gaster is predominantly smooth and shining, with only a weak basal shagreened band. Color yellowish-ferruginous to medium ferruginous.

Female with stronger and more extensive reticulation on gaster, covering nearly the entire dorsum of the first segment.

Distribution: Known from widely scattered localities in South America, reaching from northern Argentina to the Guianas and Trinidad. It probably ranges through much of central Brazil, whence no collections of ants are available from Berlese samples.

Localities for material examined: Argentina: Ing. Juarez, Formosa Prov. (N. Kusnezov leg.). Brazil: Blumenau, S. Catarina State



(Hetschko leg.), syntypes of *denticulata* in MCZ. Itapecirica, S. Paulo State (Kempf and Santos leg.). Agudos, S. Paulo State (C. Gilbert, W. W. Kempf leg.), several series. Belem, Pará State (C. R. Gonçalves). British Guiana: Kartabo Point, and Forest Settlement on the Mazaruni River (N. A. Weber leg.). Trinidad: Trinity Hills Forest Reserve (Weber leg.).

Biology: According to Weber (1952), this species occurs in both primary forest and second-growth, in leaf litter or in rotten twigs of low epiphytes. Kempf (1958) took it in humus, and Wasmann (1915) reports a sample taken in a nest of *Anoplotermes* in south-eastern Brazil.

*Strumigenys subedentata* Mayr

(Figures 7, 9)

*Strumigenys subedentata* Mayr, 1887: 570, 575, worker. Type loc.: "St. Catharina," Brazil. Syntypes in Naturhistorisches Museum, Vienna, and MCZ, two examined. Emery, 1890: pl. 7, fig. 11, worker.

*Strumigenys tristani* Menozzi, 1931, Boll. Lab. Zool. Portici, 25: 273, fig. 8, worker. Type loc.: Orijuaco, Costa Rica. Syntypes in MCZ and Coll. Consani (Bologna), several examined. New synonymy.

*Strumigenys* (*s. str.*) *clavata* Weber, 1934: 32, fig. 8, worker. Type loc.: Trece Aguas, Alta Vera Paz, Guatemala. Syntypes in MCZ, examined. New synonymy.

Worker: TL 2.0-2.4, HL 0.48-0.56, ML 0.26-0.30, WL 0.47-0.60 mm.; CI 82-86, MI 53-54. Larger and more robust than *gundlachi* and *eggersi* on the average. Mandibles thick, with distinctly convex inner margins; apical fork with a long dorsal and a short ventral teeth, plus two minute intercalary denticles. Close to the dorsal apical tooth is a small preapical tooth or denticle, followed closely proximad by 3-5 smaller denticles, confined to about the apical third of the inner margin.

Promesonotum convex, separated from propodeum by a distinct metanotal groove; humeral angles blunt. Propodeal teeth large, slightly raised, infradental lamellae reduced to carinae. Petiole with long peduncle and rounded node, spongiform appendages reduced to a cariniform posterodorsal collar. Postpetiole subreniform, distinctly wider than petiolar node, but less than half as wide as gaster; its spongiform appendages vestigial, approaching the state of those of the *eggersi* worker. Gaster without spongiform appendages.

Body and appendages densely reticulate-punctulate, opaque; gastric dorsum with a more or less distinct superimposed longitudinal striation. Underside of gaster, and sometimes also the posterior part of the gastric dorsum, with the sculpture more or less effaced and shining.

Pilosity conspicuous and abundant, particularly on head. Ground hairs spoon-shaped, subreclinate, curved forward and more or less mesad on dorsum of head; mandibular hairs pointed, dense, appressed, except for the row of large oblique hairs on each inner margin. A very few inconspicuous, narrowly spoon-shaped hairs on promesonotum. Larger, erect, remiform to clavate hairs: 2 pairs on head (Figure 9); one humeral and one median pair on pronotum; 3-5 pairs on mesonotum; 2 pairs on petiolar node; 3 pairs on postpetiole; about 6 rows of 6 hairs each on gastric dorsum.

Color medium ferruginous; a sample from Guatemala is more yellowish, but may be faded.

The female differs from the worker in the usual ways, and is only slightly larger.

Male (taken from nest series with workers, Mixco, Guatemala): TL 2.2, HL 0.43, WL 0.65, greatest diameter of compound eye 0.20, forewing L 1.9 mm. Mandibles vestigial, not opposable, with truncate apices. Notauli indistinct. Propodeal teeth well-developed and acute. Petiole slender, with a long, low node. Gaster and mesokatepisternum smooth and shining, body otherwise densely punctulate, opaque. Fine slender erect hairs corresponding in large part to the erect hairs of worker and female, but only some of those on the alitrunk are broadened at their apices. Head blackish-brown; body ferruginous brown; mouthparts and appendages brownish-yellow.

Venation of forewing as in *Smithistruma pergandei* (Emery), shown in Wheeler's "Ants," fig. 11D. Hind wing with 5 submedian hamuli. Volsella of genitalia shown in Figure 7.

Distribution: Known from southeastern and northeastern Brazil and Trinidad, so probably widespread also in the sparsely collected interior of South America. Common through Central America into southern Mexico. Except for Trinidad, unknown in the West Indies.

Localities for material examined: Brazil: Santa Catarina State, without further locality (Hetschko leg.), syntype of *subdentata* in MCZ. Agudos, S. Paulo State (W. W. Kempf leg.). Belém, Pará State (W. Beebe leg.). Trinidad: St. Augustine; Fyzabad; foothills north of Tunapuna; Arima-Blanchisseuse Road (all N. A. Weber leg.). Panama Canal Zone: Barro Colorado Island (leg. J. Zetek, N. A. Weber, E. C. Williams, Jr., E. S. McCluskey, W. L. Brown, Jr.), several collections, mostly from leaf litter and upper soil berlesates in forest. Costa Rica: Orijuaco (Tristan leg.), syntypes of *tristani* in MCZ. Turrucare (no collector cited). Guatemala: Trece Aguas, Alta Vera Paz (Schwarz and Barber leg.),

syntypes of *clavata* in MCZ. Mixco (W. M. Mann leg.). Mexico, Veracruz: Peñuela, ca. 700 m. (H. S. Dybas leg.). Tetzonapa (Dybas leg.). Pueblo Nuevo, near Tetzonapa (E. O. Wilson leg.). Las Hamacas, 17 km. north of Santiago Tuxtla (Wilson leg.).

Biology: *S. subedentata* is primarily a species of the leaf litter and upper soil layers in mesic tropical forest. Nests have been found on the underside of a small log buried in leaf litter, in a small pocket in the soil, and among rotting leaves and twigs. In life, the workers are active huntresses, resembling workers of *Strumigenys louisianae* Roger in general appearance and behavior. E. O. Wilson (unpubl. notes) kept a colony from Veracruz alive and gave them a variety of small arthropods, among which they accepted as prey entomobryoid collembola, while ignoring over two days small millipeds, *Reticulitermes* nymphs, a small isopod, and an undetermined soft-bodied mite. The colonies so far found have contained from about 20 to 90 workers and one or more queens. Wasmann (1915) records a sample taken in southeastern Brazil from a nest of the termite *Anoplotermes ater* (Hagen).

*Strumigenys trieces* new species  
(Figure 8)

Holotype worker: TL 2.3, HL 0.58, ML 0.28, WL 0.62 mm.; CI 78, MI 48. Similar to *S. subedentata*, but differing in the following characters:

1. Head proper relatively longer and narrower, and slightly more depressed.
2. Each inner mandibular margin with three small, acute, subequal teeth spaced out along its apical third.
3. Alitrunk, particularly promesonotum, depressed and only weakly convex; constriction at metanotum only slight as seen from above; metanotal groove obsolescent, marked by a broad, shallow dip in the dorsal profile as seen from the side.
4. Petiole and postpetiole more massive (broader) than in *subedentata*, the petiole with a shorter, thicker peduncle. Posterodorsal collar of petiole and ventral spongiform lobes of postpetiole a little larger than in *subedentata*.
5. Ground pilosity of head and alitrunk nearly or quite obsolete. Dorsum of head with three pairs of erect, slender remiform hairs, arranged as shown in Figure 8, except that the pair on the vertex is not shown in the figure. Similar slender, erect, remiform to truncate (or even bluntly pointed) hairs as follows: one pair on humeri; one



pair on mesonotum; one pair on petiolar node; 3 pairs on postpetiole; probably originally 6 rows of 6 hairs each on gastric dorsum (some apparently rubbed off). Large hairs fringing inner mandibular margins (not shown in Figure 8) linear-spatulate, with rounded ends, predominantly perpendicular to the shafts of the mandibles.

6. Punctulation denser and finer than in *subedentata*; gastric dorsum predominantly smooth and shining, with a few feeble longitudinal costulae occupying about the basal fifth of the first tergum. Color light ferruginous with slightly more brownish gaster.

Known only from the unique holotype worker (MCZ), labeled "Costa Rica/ F. Nevermann/ 18.VII.31."

Key to the Species of the *Strumigenys gundlachi* Group,  
Based on Workers and Females

1. Antennal scape 0.33 mm. or more long; large, dark-colored species with long mandibles (Fig. 4; Jamaica) ..... *jamaicensis* Brown
- Antennal scape < 0.33 mm. long ..... 2.
2. Mandibles short and thick (MI < 56); robust species, worker HL mostly > 0.48 mm. .... 3.
- Mandibles longer and slender (MI 56 or more); smaller species, worker HL mostly 0.48 mm. or less ..... 4.
3. Mandible very short in proportion to head (MI 48 in unique holotype), with exactly three small preapical teeth; ground pilosity of head nearly or quite obsolete; pronotum markedly flattened (Fig. 8; Costa Rica) ..... *trieces* Brown
- Mandible a little longer proportionate to head (MI 53-54), with more than three preapical denticles; ground pilosity abundant and conspicuous on head; promesonotum strongly rounded, not depressed (Fig. 9; s. Mexico to s. Brazil) ..... *subedentata* Mayr
4. Mandibles very long and slender (MI > 70), bowed outward (Fig. 3; Trinidad to n. Argentina) ..... *denticulata* Mayr
- Mandibles not so long (MI < 70), their shafts approximately straight ..... 5.
5. Spongiform appendages small but distinctly developed (Fig. 5); gastric dorsum of worker (when clean) predominantly smooth and shining, with a few basal costulae; female gaster commonly shagreened (Fig. 1; Caribbean countries) ..... *gundlachi* (Roger)
- Spongiform appendages obsolete (Fig. 6); gastric dorsum with distinct fine, mostly opaque reticulation (Fig. 2; Brazil, Bolivia, Caribbean countries) ..... *eggersi* Emery

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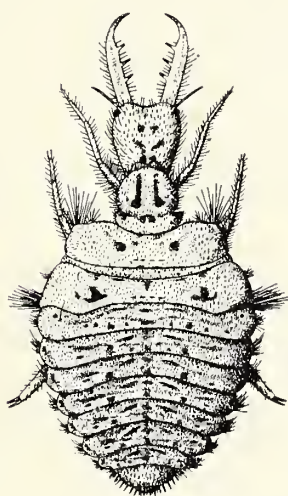
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Vol. 66

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## CONTENTS

William M. Mann. <i>E. O. Wilson</i> .....	55
Some New Synonymy in the Haemogamasidae, Laelaptidae and Diplogyniidae Indicated by an Examination of Banks' Types of Mesostigmata (Acarina). <i>D. E. Johnston</i> .....	60
Additions to the Bioecology of the New England Tingidae and Piesmidae (Heteroptera). <i>N. S. Bailey</i> .....	63
Glandular Sources and Specificity of Some Chemical Releasers of Social Behavior in Dolichoderine Ants. <i>E. O. Wilson</i> and <i>M. Pavan</i> .....	70
Author and Subject Index for Volume 66 .....	79



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WILLIAM M. MANN

1886-1960

From a photograph taken in October, 1956. Courtesy of the Smithsonian Institution and Mrs. Lucile Q. Mann.

# PSYCHE

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No. 4

WILLIAM M. MANN

*"Each day I would stroll along the beach to a new stream and follow it to a new part of the forest, in a continual state of exultation over the abundant and interesting specimens."*

ANT HILL ODYSSEY

The intense enthusiasm with which William Mann undertook the exploration of remote insect faunas was the dominant note in his unusual and distinguished scientific career. As a young man embarking on a series of extensive collecting trips to Brazil, Mexico, the West Indies, the Middle East, the South Pacific, and other parts of the world, he openly sought personal adventure as a major reward of scientific endeavor. The "Ant Hill Odyssey", as he later signified it in the title of his autobiography, was never allowed to stagnate in the physical confinement and routine that sometimes make scholarly enterprise falsely seem less than a great adventure. This spirit he was able to transmit to younger entomologists, and it was responsible for the beginning of the career of more than one young field biologist.

There would be little gain in attempting to recall here the events of Mann's crowded life already told so vividly in his autobiography. It may be noted that most of his entomological field work was conducted while he was a graduate student, and then a Sheldon Traveling Fellow, at Harvard University during 1911-17. As a student he served as Secretary of the Cambridge Entomological Club and Assistant Editor of *Psyche*. In 1917 he received a joint appointment in the United States Department of Agriculture and National Museum. In 1925 he fulfilled a life-long dream to become a zoo director when he succeeded Alexander Wetmore as head of the National Zoological Park. His autobiographical account ends with his 1917 appointment, but in fact the entomological odyssey never ended. As director of the national zoo, Mann made several major expeditions abroad to collect living animals and passed up no opportunity to gather insects, especially his beloved ants and ant-guests, on the side. Those privileged to know him in his later years could still sense the full ex-



citement of this continuing adventure in his wondrous after-dinner anecdotes of field trips around the world. A common story has it that Mann's faculty sponsor at Harvard, William Morton Wheeler, was at first keenly disappointed when he abandoned a full-time career as entomologist for zoo-keeping but soon became completely reconciled by his former student's obvious genius in the latter role. At the National Zoological Park, Mann was enormously successful. He developed humane, new techniques in zoo culture and was responsible for the introduction of many new animals to zoo life. He was renowned for the wit and eloquence with which he sought, and successfully obtained, the congressional appropriations needed to expand his zoo. His unfailing hospitality was extended to persons from all walks of life, and he had many close friends and an army of warm personal admirers. "Small in stature, puckish, bright-eyed and almost formally unkempt, Dr. Mann possessed a gentle wit which he used sparingly in public — lest it be considered unseemly in a scientist of his acknowledged standing. . . He became a familiar figure to thousands of Zoo patrons who brought away with them the charming memory of intimate little chats he was never too busy to hold with the least of his visitors."\* When he died in his Washington home on October 10, 1960, at the age of seventy-four, the Ant Hill Odyssey perhaps seemed to many of his friends no more than a remote chapter in a colorful past. Yet it should not be forgotten that his early work produced major contributions that have actually gained in value with the passage of time.

Mann's collections of ants and myrmecophiles, which are the most significant parts of his general collections, are divided chiefly between the Museum of Comparative Zoology and the U. S. National Museum. His entomological publications are based mostly on this material, a fact that gives them their exceptional value. Mann's collections, especially those of ants made in the West Indies and South Pacific, were unusually thorough. Few men have been able to write taxonomic papers on tropical insect faunas with such an intimate first-hand knowledge of the ecology and faunal relationships of his study material. As a result, his larger monographs have been little improved on by later work and will undoubtedly remain primary references for years to come. The following bibliography includes as complete a list of Mann's technical entomological publications as could be assembled at this time. References to his well-known popular article on ants in the National Geographic and to his autobiography are also included.

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\**The Washington Post*, October 11, 1960.

No attempt has been made to list his articles dealing with zoo culture, travel, and other popular topics.

E. O. Wilson

#### ENTOMOLOGICAL PUBLICATIONS OF WILLIAM M. MANN

##### 1911

Notes on the guests of some Californian ants. *Psyche*, 18(1):27-31.  
On some northwestern ants and their guests. *Psyche*, 18(3):102-109.

##### 1912

A third collection of Mallophaga from Alaskan birds. *Ent. News*, 23:12-17. (With V. L. Kellogg).

Mallophaga from islands off Lower California. *Ent. News*, 23:56-65. (With V. L. Kellogg).

Parabiosis in Brazilian ants. *Psyche*, 19(2):36-41.

Note on a guest of *Eciton hamatum* Fabr. *Psyche*, 19(3):98-100.

List of Histeridae and Buprestidae (Stanford Expedition to Brazil, 1911). *Psyche*, 19(4):118-121.

A protective adaptation in a Brazilian membracid. *Psyche*, 19(5):145-147.

Literature for 1911 on the behavior of ants and myrmecophiles. *J. Animal Behavior*, 2(6):400-420.

##### 1913

Literature for 1912 on the behavior of ants and myrmecophiles. *J. Animal Behavior*, 3(6):429-445.

Mallophaga from Brazilian birds. *Psyche*, 20(1):15-23. (With J. H. Paine).

##### 1914

Some myrmecophilous insects from Mexico. *Psyche*, 21(5):172-184.

The ants of Haiti. *Bull. Amer. Mus. Nat. Hist.*, 33(1):1-61. (With W. M. Wheeler).

1915

A new form of a southern ant from Naushon Island, Massachusetts. *Psyche*, 22(2):51.

A cursorial tick. *Psyche*, 22(2):60.

Some myrmecophilous insects from Hayti. *Psyche*, 22(5):161-166.

A gynandromorphous mutillid from Montana. *Psyche*, 22(5):178-180.

1916

The ants of Brazil (Stanford Expedition to Brazil, 1911). *Bull. Mus. Comp. Zool. Harv.*, 60(11):399-490, 7 plates.

The ants of the Phillips Expedition to Palestine during 1914. *Bull. Mus. Comp. Zool. Harv.*, 60(5):167-174. (with W. M. Wheeler).

1918

Myrmecophilous insects from Cuba. *Psyche*, 25(5):104-106.

1919

The ants of the British Solomon Islands. *Bull. Mus. Comp. Zool. Harv.*, 63(7):273-391, 2 plates.

1920

A proctotrypid inquiline with *Formica exsectoides* Forel (Hym.). *Proc. Ent. Soc. Wash.*, 22(3):59-60.

Ant guests from Fiji and the British Solomon Islands. *Ann. Ent. Soc. Amer.*, 13(1):60-69.

Additions to the ant fauna of the West Indies and Central America. *Bull. Amer. Mus. Nat. Hist.*, 42(8):403-439.

1921

The ants of the Fiji Islands. *Bull. Mus. Comp. Zool. Harv.*, 64(5):401-499.

A new genus of termite guest from Fiji. *Psyche*, 28(2):54-56.

Three new myrmecophilous beetles. *Proc. U. S. Nat. Mus.*, 59:547-552.

1922

Notes on a collection of West African myrmecophiles. *Bull. Amer. Mus. Nat. Hist.*, 45:623-630.

Ants from Honduras and Guatemala. *Proc. U. S. Nat. Mus.*, 61(13):1-54.

1923

New genera and species of termitophilous Coleoptera from northern South America. *Zoologica*, 3(17):323-366.



Two new ants from Bolivia. *Psyche*, 30(1) :13-18.

Two serphoid guests of *Eciton* (Hym.). *Proc. Ent. Soc. Wash.*, 25(9) :181-182.

A singular habit of sawfly larvae. *Psyche*, 30(1) :9-13. (With W. M. Wheeler).

## 1924

Myrmecophiles from the Western United States and Lower California. *Ann. Ent. Soc. Amer.*, 17(1) :87-95.

Notes on Cuban ants. *Psyche*, 31(1) :19-23.

## 1925

Ants collected by the University of Iowa Fiji-New Zealand Expedition. *Iowa Studies in Natural History*, 11(4) :5-6.

Guests of *Eciton hamatum* (Fabr.) collected by Professor W. M. Wheeler. *Psyche*, 32(3) :166-177.

New beetle guests of army ants. *J. Wash. Acad. Sci.*, 15(4) :73-77.

## 1926

Some new Neotropical ants. *Psyche*, 33(4-5) :97-107.

Three new termitophilous beetles from British Guiana. *Proc. Ent. Soc. Wash.*, 28(7) :151-155.

New Neotropical myrmecophiles. *J. Wash. Acad. Sci.*, 16(16) :448-455.

## 1928

A new *Microdon* from Panama. *Psyche*, 35(3) :168-170.

## 1929

Notes on Cuban ants of the genus *Macromischa* (Hymenoptera: Formicidae). *Proc. Ent. Soc. Wash.*, 31(8) :161-166.

## 1931

A new ant from Porto Rico. *J. Wash. Acad. Sci.*, 21(17) :440-441.

## 1934

Stalking ants, savage and civilized. *National Geographic Mag.*, 66(2) :171-192.

## 1935

Two new ants collected in quarantine. *Psyche*, 42(1) :35-37.

## 1948

*Ant Hill Odyssey*. Little, Brown. (Autobiography).

SOME NEW SYNONYMY IN THE HAEMOGAMASIDAE,  
LAELAPTIDAE AND DIPLOGYNIIDAE INDICATED  
BY AN EXAMINATION OF BANKS' TYPES OF  
MESOSTIGMATA (ACARINA)

BY DONALD E. JOHNSTON  
Institute of Acarology, Department of Zoology,  
University of Maryland

During the course of a study of certain of the Banks mite types in the collection of the Museum of Comparative Zoology at Harvard College some cases of obvious synonymy were found. Two of these cases sink Banks' names; the remainder result in the establishment of his names as senior synonyms. In addition to those of Banks, the types of Ewing's, Furman's and Hicks' species (all in U.S. National Museum) were examined in connection with this work. I am grateful to Drs. H. W. Levi and W. L. Brown for arranging for me to study the Harvard collection and for their many kindnesses during my visit.

The following lectotype designations are not as precise as one would wish. The Banks types in the Museum of Comparative Zoology are not numbered and most names are represented by cotypes. All of the suspected and certain type slides are arranged alphabetically according to species and kept as a unit in the Arachnida collection of the Museum. Thus the lectotypes designated herein will be found labeled as such in their proper place in the alphabetical filing scheme. It may also be noted here that some of Banks' species (none of those treated herein) are represented by cotypes in both the MCZ and the Acarina collection of the U.S. National Museum. The same is true of Jacot's material which has been divided evenly between these museums.

HAEMOGAMASIDAE

*Haemogamasus longitarsus* (Banks) Comb. Nov.

*Laelaps longitarsus* Banks, 1910. Proc. Ent. Soc. Wash. 12 (1):5. Ex mole's nest, Falls Church, Virginia. Lectotype in MCZ.

*Haemogamasus barberi* Ewing, 1925. Proc. Biol. Soc. Wash. 38:140. Ex nest of small mammal; Maryland shore of Potomac River, near Plummer Island. Type in U.S.N.M. NEW SYNONYMY.

*Haemogamasus microti* Ewing, 1925. Proc. Biol. Soc. Wash. 38:141. Ex *Microtus pennsylvanicus*, Bronxville, New York. Type in U.S.N.M. [= *barberi* according to Keegan, 1951:249]

Remarks: The type series of *Laelaps longitarsus* consisted of eight

specimens. These have been remounted individually and a female is here designated as lectotype (indicated on slide label).

*Eulaelaps stabularis* (Koch)

*Gamasus stabularis* Koch, 1836. Crust, Myr. Arachnid. Deutschlands, Fasc. 27, No. 1 Host unknown; Regensburg. Type unknown.

*Laelaps pedalis* Banks, 1909. Proc. Ent. Soc. Wash. 11 (3) :136. Ex chipmunk; Guelph, Ontario, Canada. Type in MCZ. NEW SYNONYMY.

*Laelaps propheticus* Banks, 1909. *Ibid*:136 Ex groundhog; Guelph, Ontario. Lectotype in MCZ. NEW SYNONYMY.

Remarks: The type slide of *L. propheticus* contained one female *E. stabularis* (here designated lectotype) and two *Haemolaelaps glasgowi* (Ewing). *Laelaps pedalis* is represented by a single female. The concept of *E. stabularis* with which Banks' names are synonymized is that of Strandtmann and Wharton (1958:127) and Bregatova (1956:100).

LAELAPTIDAE

*Androlaelaps frontalis* (Banks) Comb. Nov.

*Gamasus frontalis* Banks, 1910. Proc. Ent. Soc. Wash. 12 (3) :3. Ex *Perognathus*; Los Palms, 3500 feet, Santa Rosa Mountains, California. Lectotype in MCZ.

*Androlaelaps sinuosa* Furman, 1954. Pan-Pacific Ent. 30 (2) :120. Ex *Pergognathus* sp., probably *fallax fallax*, at Pigeon Pass, Riverside County, California. Type in U.S.N.M. NEW SYNONYMY.

Remarks: The type slide bore four females and two males of this striking laelaptid. These have been remounted individually and a female is here designated lectotype (indicated on slide label). Banks' placement of this species in *Gamasus* (presumably because of the large size and calcarate femora of legs II) is undoubtedly the reason for its having been overlooked by workers in the Laelaptidae.

DIPLOGYNIIDAE

*Neolobogynium americana* (Banks) Comb. Nov.

*Celaenopsis americana* Banks, 1906. Proc. Ent. Soc. Wash. 7: 137. Ex Histerid beetle (*Hololepta* sp.) at Indianapolis, Indiana. Lectotype in MCZ.

*Neolobogynium lateriseta* Hicks, 1957. Proc. Iowa Acad. Sci. 64: 616. Host unknown; Ames, Iowa. Type in U.S.N.M. NEW SYNONYMY.



Remarks: Banks' type slide contained 18 adults of both sexes of this common mite associate of *Hololepta* (Histeridae). These have been remounted and a female is here designated lectotype (indicated on slide label).

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ADDITIONS TO THE BIOECOLOGY  
OF THE  
NEW ENGLAND TINGIDAE AND  
PIESMIDAE (HETEROPTERA)<sup>1</sup>

BY NORMAN S. BAILEY  
Bradford Junior College, Bradford, Mass.

Intermittent summer collecting during the past ten years has added to my collection a considerable number of noteworthy records. These include additional stations for species previously reported from only a few localities within a particular state and for some of the less well-known species in New England, new records for the occurrence of six species previously unreported from one or more of the New England states, and a few new host plant records.

This is the first of a series of papers now in progress which will supplement my studies of the Tingidae of New England (1951). For ease of reference, therefore, it follows the pattern of that study in the sequence of genera and of species. (Bailey, 1951, page 5). All collections were made by the author unless otherwise specified.

FAMILY PIESMIDAE

*Piesma cinerea* (Say)

Shelton, Connecticut, August 2, 1951; Alna, Maine, August 15, 1954 and August 28, 1956. Found on a weedy *Amaranthus* (probably *retroflexus* L.) on each occasion.

In 1917 Professor Parshley reported this species from ocean drift at Beach Bluff, Massachusetts, and stated, "Not found heretofore north of Rhode Island". Since then it has become well-known from this state. The records from east-central Maine extend its range appreciably. Alna is a small town adjoining Wiscasset in the Sheepscot River Valley about fifty miles east-northeast of Portland.

Since published records for Connecticut are few, note is made of the Shelton collection.

FAMILY TINGIDAE

*Leptoypha mutica* (Say)

Windham, New Hampshire, August 11, 1958.

A large collection of adults, many teneral, a few nymphs, and some exuviae was made from suppressed ash (*Fraxinus*) and ash suckers

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<sup>1</sup>Acknowledgement is hereby gratefully made of a Sigma Xi — RESA Research Fund grant and Grant No. G5477 from the National Science Foundation, which make these studies possible.

growing on a dry, rocky hillside in a stand of young mixed hardwoods. This is, I believe, the third New Hampshire record for this small lace bug.

*Galeatus peckhami* (Ashmead)

Katahdin Trail, Maine, August 14, 1959; East Madison, New Hampshire, July 25, 1958.

Extended search was finally rewarded by these two collections from roadside asters (*Aster macrophyllus* L.) growing on dry, sunny banks. Though this host plant is common in northern New England, frequent search has provided only these two records. *Corythucha marmorata* (Uhler) is more commonly found on this aster.

*Gargaphia tiliae* (Walsh)

New Milford, Connecticut, August 2, 1951; Alna, Maine, August 29, 1956; Carroll, Maine, August 14, 1959; Petersham, Massachusetts, July 17, and 18, 1951; Conway, New Hampshire, July 25, 1958; Eaton, New Hampshire, July 25, 1958.

In general this arboreal species may be found on its host plant *Tilia*. Since few records have been published, those noted will extend our knowledge of its distribution. All the collections were made from *Tilia*.

*Corythaica bellula* Bueno

Alna, Maine, August 2, 1953, August 28, 1956, and September 9, 1958; Cedar Grove, Maine, July 11, 1953; Petersham (Harvard Forest), Massachusetts, July 16 and 17, 1951; Conway, New Hampshire, July 25, 1958 (sweeping); Eaton, New Hampshire, July 25, 1958.

Each collection was made by hand from *Panicum*, except in the instance noted. The Alna station was a wood road through a mature stand of *Pinus strobus* L. where the shade was almost constant but not intense and at a point where the road was beginning to rise at the base of a fairly sharp slope. This species was also seen, but not collected, on July 11, 1953, on *Panicum* growing on a little used, open drive within a stone's throw of the shore at Medomak, Maine. The Cedar Grove collection was from *Panicum* growing on a dry bluff overlooking the Kennebec River. These are the first Maine records.

In Bradford, Massachusetts, six collections of *C. bellula* Bueno were made from *Panicum* by hand and two by sweeping in 1957. Most of these were taken from an area of less than four square yards under a small red maple (*Acer rubrum* L.) where the *Panicum* was prominent and the total vegetation too sparse to cover the hard-packed



soil. These eight collections yielded 14 females, 4 males, and 8 nymphs. In 1958, six collections in the same area gave 6 females, 10 males, and 14 nymphs. The first specimens were taken on June 9th in 1957 and the last for the season on September 7th in 1958. Nymphs were taken as early as June 12th and as late as August 31st. Teneral adults occurred from as early as June 22nd until as late as August 17th. These data confirm the opinion that *C. bellula* Bueno should be found throughout New England in areas ecologically suitable.

*Stephanitis globulifera* (Matsumura)

West Hartford, Connecticut, August 25, 1958. They were abundant on *Pieris japonica* (Thunberg) Don used as foundation plants in front of a fairly new house in a recent development. This species first reported from North America in 1950 (Bailey) is apparently well-established in Connecticut, but I have yet to collect it elsewhere.

*Stephanitis pyrioides* (Scott)

West Newbury (Cherry Hill), Massachusetts, August 20, 1958. Nymphs and adults were found on young stock of several deciduous azalea species and hybrids growing in a lath house.

*Stephanitis rhododendri* Horvath

Petersham (Harvard Forest), Massachusetts, July 17 and 18, 1951.

The first collection was made from *Kalmia latifolia* L., a frequent host. The next day a few were found on *K. angustifolia* L. Although this is a very common shrub in eastern Massachusetts and Maine and, although it is on record as a host for this lace bug, this is my only collection from lambkill.

*Corythucha bellula* Gibson

Katahdin Trail, Maine, August 14, 1959; Gorham, New Hampshire, July 21, 1958.

This is the first record of the species from New Hampshire where it was found on roadside *Corylus*. Note below that *C. coryli* O. and D. also occurs in this state. The ecology of these two species in their contact zone should be a fruitful study since both utilize the same host. The Maine collection noted is a large one of particular interest since they were all taken from *Salix*.

*Corythucha caryae* Bailey

Scituate, Rhode Island, September 23, 1958.

This interesting range extension of a species previously collected only from a relatively limited area in eastern New Hampshire and

Massachusetts was the outstanding result of a one-day collecting trip into Rhode Island. They were found on *Carya* on the edge of a wooded area beside Route 14 and near the reservoir.

*Corythucha coryli* O. and D.

Monroe, Connecticut, August 2, 1951; Shelton, Connecticut, August 27, 1958; Epping, New Hampshire, September 20, 1958; Diamond Hill State Park, Rhode Island, September 23, 1958.

My collections now extend the range of this species into three more of the New England states for which there have been no published records. They were all taken from *Corylus* growing along the roadside.

*Corythucha cydoniae* (Fitch)

Newcastle, Maine, August 7, 1953; Haverhill (Ward Hill), Massachusetts, July 27, 1957 and August 23, 1960; Diamond Hill State Park, Rhode Island, September, 23, 1958.

This species can now be added to the faunal lists of two more New England states. Since it infests shrubs and small trees of several rosaceous genera that are widely distributed in the Northeast, the single reported occurrence north of Massachusetts suggested a wider distribution and also raised the question of limiting ecological factors. The wider range is now established but the ecological conditions controlling it surely deserve investigation. I have collected rather widely and, in a few areas, intensively in Maine with only the record cited above for this species. There it was feeding on native *Crataegus* in large numbers.

The single Rhode Island record, on the contrary, probably indicates lack of local interest in Tingids.

The Massachusetts records are given to report another host for *C. cydoniae*. *Cotoneaster hupehensis* Rehder and Wilson, used in a permanent shrub border in a local nursery was found to be heavily infested. About twenty yards away is a large clump of tall *Amelanchier*, also a part of the landscape arrangement, similarly infested. The lace bugs were breeding on both hosts.

The eighth edition of *Gray's Manual of Botany* (Fernald, 1950) considers *Pyracantha coccinea* Roemer (a previously reported host) a synonym for *Cotoneaster pyracantha* (L.) Spach while the 1949 revised edition of the *Manual of Cultivated Plants* (L.H. Bailey) maintains the distinctness of the genus *Pyracantha*. This leaves me with a question for the plant taxonomists to decide. If not another genus, we at least note another rosaceous species as a host for *C.*

*cydoniae* which thrives on many native and cultivated forms in this plant family.

*Corythucha marmorata* (Uhler)

Bradford, Massachusetts, July 6, 1957; Haverhill (Ward Hill), Massachusetts, July 27, 1957.

This species ranges throughout North America. In New England it feeds exclusively on a diversity of herbaceous composites. Apparently one of America's most successful Tingids in terms both of its wide distribution and of its local abundance, it is the only species of the fifteen in the genus occurring in New England that is neither arboreal nor thamnophilous. Its catholic preference for ubiquitous composites undoubtedly accounts in no small measure for its success.

Consequently, it was not surprising to find it thriving on two species previously unlisted. The Bradford observation was made on *Rudbeckia serotina* Nuttall, the common Black-eyed Susan or Yellow Daisy. On Ward Hill they were found on the cultivated Globe Thistle, *Echinops sphaerocephalus* L.

*Corythucha mollicula* O. and D.

Monroe, Connecticut, August 2, 1951; Newtown, Connecticut, August 2, 1951; Aurora, Maine (collected by Dr. A. G. Humes), July 13, 1950; Rockport, Maine, September 10, 1958; Sheepscot, Maine, August 6, 1953; Petersham (Harvard Forest), Massachusetts, July 18, 1951; Diamond Hill State Park, Rhode Island, September 23, 1958.

Probably again because of lack of collector interest, few records have been published for this species. Therefore, these, all from *Salix*, are cited.

*Corythucha pruni* O. and D.

Brookfield, Connecticut, August 2, 1951; Monroe, Connecticut, August 2, 1951; Shelton, Connecticut, August 27, 1958; Mattatuck, Connecticut, August 28, 1958; Alna, Maine, August 28, 1956 and September 9, 1958; Cedar Grove, Maine, September 15, 1957 and May 28, 1959; Dresden, Maine, June 22, 1957; Mexico, Maine (collected by Mr. J. J. B. Anderson), September 7, 1959; Newcastle, Maine, August 7, 1953; South Bristol, Maine, August 24, 1956; South Cushing, Maine, September 10, 1958; Epping, New Hampshire, September 20, 1958; Diamond Hill State Park, Rhode Island, September 23, 1958; Waterman, Rhode Island, September 23, 1958.



The Maine records cited establish the frequent occurrence of this species in the central coastal region and in other parts of that state. Another locality is added to the few published New Hampshire records. Rhode Island and Connecticut stations are given for the first time.

Of particular interest is the fact that the specimens from the two southernmost New England states suggest that typical *Corythucha pruni* O. and D. and typical *C. associata* O. and D. may represent extreme forms which have differentiated in the recent past from a common population. The latter has not yet been collected in Massachusetts nor further north. Until now, *C. pruni* had not been reported from southern New England. Both species restrict their feeding entirely to *Prunus serotina* Ehrhart. The collections noted above were all from this host. Two collections made in Connecticut in 1951 aroused my curiosity. In both, specimens of the two species were found on the same host plants. On recent critical examination of this material, I found that the Brookfield collections consisted of 26 specimens. Three of these were, on basis of hood size and form, definitely *C. pruni* (2 males and a female), 22 were *C. associata*, and one was questionably *C. associata* because the top of the hood was missing. Among the *associata* forms there was some variation in the height and width of the hood. The Monroe collection made the same day consisted of 38 that were surely *C. pruni* and a single female of *C. associata*. More recently a collection from Mattatuck produced 9 males of *C. pruni* and one female of *C. associata*. In Shelton one *C. pruni* male was found on a *Prunus* and another host plant in that town yielded 100 adults of *C. associata*.

Close study of these two species in Connecticut should answer some important questions. Except for the marked differences in their hood forms and, more significantly, the claspers of the males, they are very similar. In size and coloration they are almost identical. Frequent collections in several localities in this contact zone throughout one or two seasons would give valuable population information and specimens for careful comparison of structural details.

As previously mentioned, a similar situation involving the species *C. bellula* Gibson and *C. coryli* O. and D. whose primary host is *Corylus* may exist from central Maine and New Hampshire westward. Again we find two species of similar size with minor morphological distinctions. Similarly intriguing is the relationship between our two New England species whose host is commonly *Alnus*. Here, however, there are greater differences in size in addition to the

differences in structural details between the two and, consequently, their kinship is possibly more remote.

*Corythucha ulmi* O. and D.

Brookfield, Connecticut, August 2, 1951. Published Connecticut records are few. In my experience, this species is only rarely found even where elms are common.

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# GLANDULAR SOURCES AND SPECIFICITY OF SOME CHEMICAL RELEASERS OF SOCIAL BEHAVIOR IN DOLICHODERINE ANTS<sup>1</sup>

BY EDWARD O. WILSON<sup>2</sup> AND MARIO PAVAN<sup>3</sup>

## *Introduction*

Species of the ant subfamily Dolichoderinae are excellent subjects for the experimental analysis of chemical communication. The group is advanced evolutionarily, and large, complex societies are the rule. During foraging, workers of many species form long, conspicuous columns tightly bound to persistent odor trails. When disturbed they void volatile secretions that seem likely to function, at least in part, as olfactory releasers of alarm behavior. Furthermore, the dolichoderines have recently been the object of extensive biochemical research by Pavan, Cavill and their associates (cf. Pavan, 1950; Pavan and Ronchetti, 1955; Pavan and Trave, 1958; Cavill, Ford, and Locksley, 1956; Cavill and Locksley, 1957). Several terpenoids including the previously unknown iridomyrmecin, iso-iridomyrmecin, and irido-dial, have been identified as components of the anal gland secretion of various species. The availability of these substances in purified form has made possible for the first time the precise behavioral assay of natural secretory products in ants.

## *Trail Substances*

Applying the artificial trail technique used earlier by one of us (Wilson, 1959) in studies of the myrmicine *Solenopsis saevissima*, an attempt was made to determine the glandular source of the trail substance in workers of *Iridomyrmex humilis* Mayr. Groups of workers from laboratory colonies (grown from stocks originating from Baton Rouge, Louisiana) were attracted to drops of 1 M sucrose solution, about 6 mm in diameter, on glass feeding tables. Selected body parts of freshly killed workers were made into artificial trails directed at the feeding workers. The number of workers following the trails beyond the trail midpoint, i.e., 15 cm. from the sucrose bait, were recorded. When positive responses were obtained, the duration of biological activity was timed to the nearest half-minute. Preliminary experiments showed that the trail substance is limited to the abdomen,

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smears from other body parts proving consistently inactive. This result was not unexpected, since *humilis* workers can be clearly seen to drag the posterior portion of the abdomen over the ground while in the act of laying trails.

Five organs in the abdomen are capable of emptying glandular secretions to the outside: (1) the hind-gut; (2) the paired "true" poison glands, with a large reservoir, the poison vesicle; (3) Dufour's gland (also called the accessory gland); (4) the anal glands, opening just above the anus; (5) the glandular "ventral organ" recently discovered by Pavan (1955). In a series of experiments, the five organs were dissected out of freshly killed workers, washed in insect Ringer's solution, and bioassayed with artificial trail tests. The results, summarized in table 1, show that the bulk, and perhaps the entirety, of the trail substance resides in the ventral organ. The occasional weak

TABLE 1. Results of artificial trail assay of selected abdominal organs of *Iridomyrmex humilis* workers.

Organ	Number of tests	Number of positive responses*	Number of workers responding: range (with mean)	Duration of responses in minutes: range (with mean)
hind gut	6	0	0-2 (M<1)	0-1/2 (M<1/2)
true poison glands, plus reservoir	6	0	0-2 (M<1)	0-1/2 (M<1/2)
Dufour's gland	8	2	0-30 (M=8)	0-4 (M=1)
anal gland	5	1	0-15 (M=6)	0-1 (M=1)
ventral organ	7	7	65-339 (M=134)	2-9 (M=5)

\* Positive responses are defined, arbitrarily, as the crossing of the trail midpoint by 10 or more workers.

responses to the contents of the Dufour's and anal glands may not be biologically significant, i.e., may not indicate the presence of substances normally secreted into the trail, since responses of comparable magnitude have been obtained with pure methylheptenone, a substance not known to occur in *humilis* workers.

In a second series of experiments, the ventral organ and anal glands of *Iridomyrmex pruinosus* (Roger)<sup>4</sup> were assayed. As in *humilis*, the ventral organ smears caused strong trail following while re-

<sup>4</sup>Collected at Baton Rouge, Louisiana.

sponses to anal glands were negligible. Furthermore, artificial trails made with 2-heptenone, the anal gland secretion of *pruinus* (M. S. Blum, *in litt.* ), caused negligible responses.

In a third series of experiments, the hind-gut, poison apparatus, Dufour's gland, and ventral organ were assayed in a laboratory colony of the primitive dolichoderine *Monacis bispinosa* (Olivier).<sup>4</sup> The unusually restless and aggressive nature of the *Monacis* workers required the following modification in procedure. Straight trails 75 cm. in length were drawn down the middle of a clean glass plate. Three workers were then released, one at a time, and allowed to wander over the glass plate, crossing and re-crossing the trail. A positive response was recorded when the worker persistently followed the trail to its end. Of 18 workers thus exposed to trails made successively from 6 ventral organs, 17 gave positive responses. The responses of workers in triplicated control experiments using the other abdominal organs were all negative.

After the chief source of the odor trails in the three dolichoderine species had been located, bioassays were made across species, in order to determine the extent of species-specificity of the trail substances. As shown in table 2, each species appears to have a different substance.

TABLE 2. Intra- and interspecific trail-substance tests employed in the present study. Only intraspecific tests produced positive responses (+). The results of all interspecific tests employed were negative (-). Interspecific tests not attempted are indicated by a question mark.

Source	Recipient				
	<i>Monacis bispinosa</i>	<i>Liometopum occidentale</i>	<i>Iridomyrmex humilis</i>	<i>Iridomyrmex pruinosus</i>	<i>Tapinoma sessile</i>
<i>M. bispinosa</i>	+	?	-	?	-
<i>L. occidentale</i>	?	+	-	?	-
<i>I. humilis</i>	-	-	+	-	-
<i>I. pruinosus</i>	?	?	-	+	-
<i>T. sessile</i>	-	?	-	?	+

Further, the Dufour's glands and ventral organs of *Monacis bispinosa* were assayed with laboratory colonies of the myrmicine ants *Crematogaster lineolata* (Say), *Solenopsis geminata* (Fabr.), and *S. saevissima* (Fr. Smith). The ventral organ induced no detectable response in these species. The Dufour's gland caused no response in the *Crematogaster* but, quite unexpectedly, caused strong trail-following in *Solenopsis saevissima*! In fact, single *Monacis* glands consistently drew out approximately the same number of *S. saevissima* workers as single *saevissima* glands. It was also determined that a single *Monacis*

<sup>5</sup>Collected at Palmar, southern Costa Rica.

Dufour's gland caused a weaker response in *S. geminata*, well below the intensity caused by a *geminata* gland and approximately the same as that caused by a *saevisissima* gland (see Wilson, 1960). These results are interpreted as indicating the chemical identity, or near-identity, of the *Monacis bispinosa* and *Solenopsis saevisissima* Dufour's secretions. Curiously, the *Solenopsis* use the secretion as a trail substance, but the *Monacis* do not. The function of the secretion in *Monacis* remains unknown.

Some further comment is needed concerning the organ we are here referring to as the ventral organ. The gland was discovered in *Iridomyrmex humilis* by Pavan (1955) and described in greater detail by Pavan and Ronchetti (1955). It is a paddle-shaped organ resting on the ventral body wall just over abdominal sternite VI (sternite IV of gaster). It opens posteriorly via a neck-like constriction between the VI and VII abdominal sternites. The opening is fitted with an unusual beak-shaped deformation of the posterior border of sternite VI, a structure seemingly designed to guide the effluence of the gland contents. Until the present experimental work, the function of the gland remained unknown, although Pavan and his associates suggested that it produced either the trail substance or a secondary defensive secretion. Additional morphological studies by Miradoli Zatti and Pavan (1957) disclosed the presence of a closely similar gland in the primitive dolichoderine genera *Aneuretus* and *Leptomymex*. In the course of subsequent work we have noted its presence in *Monacis bispinosa* and *Hypoclinea doriae* Emery as well. The ventral organ appears to be peculiar to the Dolichoderinae and Aneuretinae and hence can serve as a valuable diagnostic character for these two closely allied groups. If it serves as the source of the trail substance in all of the dolichoderine tribes (and in the ancestral aneuretines), as the preliminary evidence suggests, it can be interpreted as a remarkable example of a "social organ" evolved *de novo* with the specific function of mediating worker communication.

#### *Alarm Substances*

When colonies of *Tapinoma sessile*, *Liometopum occidentale*, and *Monacis bispinosa* are disturbed by opening the nest, workers release considerable quantities of secretions from their anal glands which can be easily smelled by the human observer. When the anal glands are removed from freshly killed workers of these species and their contents released in the presence of groups of resting live workers, the latter are thrown instantly into a typical alarm frenzy, indistinguish-



able from that caused by direct mechanical disturbance. Other body parts tested in this manner do not induce the same reaction. Although the volatile components of the anal glands of each species produce a distinctly different smell to humans, there is evidently no species-specificity shown in the alarm response. Unlike the complete specificity shown in responses to trail substances, squashes of anal glands of each species produce approximately the same intensity of alarm curiosity in workers of the other two species as in its own. These results can be interpreted as indicating that either a common component exists in each of the anal secretions or else, as seems more likely, the secretions differ but the reactions are not species-specific.

In contrast, disturbed workers of *Iridomyrmex humilis* do not release quantities of volatile substances sufficient to be detected by the human observer. Moreover, they do not respond with more than mild excitement to single anal-gland squashes from sister workers or the other three dolichoderine species.

Pavan and Trave (1958) have shown that the volatile components of anal gland secretion of *Tapinoma nigerrimum* (Nylander) are methylheptenone ( $C_8H_{14}O$ ) and propyl-isobutyl-ketone ( $C_8H_{16}O$ ). Since our initial experiments suggested that the action of alarm substances is not species-specific, it was not surprising to find that small quantities of the two *nigerrimum* substances, manufactured synthetically and presented in separate tests, caused intense alarm behavior in *Tapinoma sessile*. No attempt has been made to map the full range of compounds that will induce the alarm frenzy in the dolichoderines that communicate alarm by anal secretions. However, the following preliminary study will show that not all volatile ant secretions have this effect. A simple olfactometer test designed to measure mass response in laboratory colonies of *Solenopsis saevissima* (cf. Wilson, 1960) was applied to a small (300-worker) colony of *Tapinoma sessile*. The tested compound was allowed to evaporate from a 15 mm<sup>2</sup> film into a nest inlet into which air was being gently drawn. The maximum increase, if any, of workers outside the nest was then measured during the ensuing five minutes. Each substance was tested three times. Tests were spaced at least two hours apart to reduce habituation, and substances were presented in irregular order to prevent special sequential effects. Formic acid, a common defensive abdominal secretion of formicine ants, caused either no visible response or very mild excitement in the nest, and increased the outside worker force by only 3-8. Concentrated Dufour's gland secretion of *Solenopsis saevissima*, which induced a mass exodus of *saevissima*

workers in similar tests, caused in *Tapinoma sessile* either no visible effect or mild excitement in the nest, and increased the outside worker force from minus-1 to 9. A mixture of nepetalactone (oil of catnip) and oil of peppermint caused mild excitement in the nest and an exodus of 2 to 24 workers. Propyl-isobutyl-ketone caused mild to intense excitement in the nest and an exodus of 12 to 23 workers; many of the workers were in maximum intensity of excitement and ranged widely over the foraging table. Methylheptenone caused mild to intense excitement in the nest, and an exodus of 4 to 69 workers, many of which were maximally excited and ranged widely over the foraging table. In one trial using methylheptenone, a queen, several callows, and other workers carrying brood also left the nest temporarily.

In two subsequent experiments, small *Tapinoma sessile* colonies were exposed in the manner just described to prolonged doses of methylheptenone. In both cases, excitement within the nest and individual worker exodus declined to about the normal level within 10 minutes. Shortly afterward, however, workers began mass movements along odor trails to secondary shelters away from the main nest. Within 90 minutes almost the entire colony had emigrated to the new nest sites, leaving behind only a few workers in the main nest.

#### Summary

In *Iridomyrmex humilis* Mayr, *I. pruinosus* (Roger), and *Monacis bispinosa* (Olivier), representing two genera phylogenetically far apart in the Dolichoderinae, the principal or exclusive source of the odor trail is the ventral organ, an exocrine gland opening behind abdominal sternite VI. Cross-species tests were made with the odor trails of these species and of *Liometopum occidentale* Emery and *Tapinoma sessile* Say. The trail-substances were found to be species-specific. The ventral organ is peculiar to the Dolichoderinae and the ancestral Aneuretinae, and it is interpreted as an example of a "social organ" that has been evolved *de novo* as part of the colonial communication system.

Volatile alarm substances are produced in the anal glands of each of the species except *Iridomyrmex humilis*. These releasers are not species-specific. The volatile anal secretions of *Tapinoma nigerrimum*, methylheptenone and propyl-isobutyl-ketone, when tested with workers of *Tapinoma sessile*, produced typical alarm behavior. Prolonged exposure induced colony emigration, which was then organized by the laying of odor trails.

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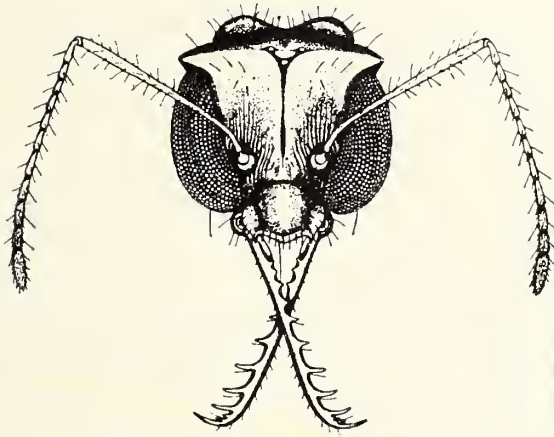
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Nos. 1-2



## CONTENTS

The Genus <i>Pseudosinella</i> (Collembola: Entomobryidae) in Caves of the United States. <i>K. Christiansen</i> .....	1
The Immature Stages of <i>Boriomyia fidelis</i> (Banks) with Taxonomic Notes on the Affinities of the Genus <i>Boriomyia</i> (Neuroptera: Hemerobiidae). <i>E. G. MacLeod</i> .....	26
The Female of <i>Inocellia pilicornis</i> Carp. (Neuroptera: Inocelliidae) <i>F. M. Carpenter</i> .....	41
A Note on the Prey and a Nesting Site of <i>Cerceris truncata</i> Cameron. (Hymenoptera: Sphecidae: Philanthinae). <i>F. G. Werner</i> .....	43
The Type Species of the Ant Genus <i>Eurhopaltrix</i> . <i>W. L. Brown, Jr.</i> and <i>W. W. Kempf</i> .....	44

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# PSYCHE

INDEX TO VOL. 67, 1960

---

## INDEX TO AUTHORS

- Brown, W. L., Jr.* and *W. W. Kempf*. The Type Species of the Ant Genus *Eurhopaltrix*. 44
- Carpenter, F. M.* A Triassic Odonate from Argentina. 71  
Studies on North American Carboniferous Insects. I. The  
Protodonata. 98  
The Female of *Inocellia pilicornis* Carp. (Neuroptera:  
Inocelliidae). 41
- Chickering, A. M.* A new *Acanthoctenus* (Araneae: Acanthoctenidae) from  
Jamaica, W. I. 81  
The Female of *Lucarachne beebei* Gertsch (Araneae:  
Symphytognathidae). 95
- Christiansen, K.* The Genus *Pseudosinella* (Collembola: Entomobryidae)  
in Caves of the United States. 1
- Crabill, R. E., Jr.* On the True Nature of the Azygethidae (Chilopoda:  
Geophilomorpha). 76
- Darlington, P. J., Jr.* Australian Carabid Beetles IV. List of Localities,  
1956-1958. 111
- Eisner, T.* Defense Mechanisms of Arthropods. II. The Chemical and  
Mechanical Weapons of an Earwig. 62
- Evans, H. E.* A Study of *Bembix u-scripta*, a Crepuscular Digger Wasp.  
45
- MacLeod, E. G.* The Immature Stages of *Boriomyia fidelis* (Banks) with  
Taxonomic Notes on the Affinities of the Genus *Boriomyia* (Neuroptera:  
Hemerobiidae). 26
- Werner, F. G.* A Note on the Prey and a Nesting Site of *Cerceris truncata*  
Cameron. (Hymenoptera: Sphecidae: Philanthinae). 43
- Wheeler, G. C.* and *J. Wheeler*. Techniques for the Study of Ant Larvae.  
87



## INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

- Acanthoectenidae, 81  
*Acanthoecten*, 81  
*Acanthoecten* REMOTUS, 81  
 Ant larvae, 87  
 Ants, 44, 87  
 Araneae, 81, 95  
 Arthropods, 62  
 Australian Carabid beetles IV. List of localities, 1956-1958, 111  
 Azygethidae, 76  
 Beetles, 111  
*Bembix u-scripta*, 45  
*Boriomyia*, 26  
*Boriomyia fidelis*, 26  
 Carabid beetles, 111  
 Carboniferous insects, 98  
*Cerceris truncata*, 43  
 Chilopoda, 76  
 Coleoptera, 111  
 Collembola, 1  
 Defense mechanisms of Arthropods.  
     11. The chemical and mechanical weapons of an earwig, 45  
 Digger wasps, 45  
 Earwig, 62  
 Entomobryidae, 1  
*Eurhopalothrix*, 44  
*Eurhopalothrix bolau*, 44  
 Female of *Inocellia pilicornis* Carp. (Neuroptera: Inocelliidae), 41  
 Female of *Lucarachne beebei* Gertsch (Araneae: Symphytognathidae), 95  
 Genus *Pseudosinella* (Collembola: Entomobryidae) in caves of the United States, 1  
 Geophilomorpha, 76  
 Hemerobiidae, 26  
 Hymenoptera, 43, 44, 45, 87  
 Immature stages of *Boriomyia fidelis* (Banks) with taxonomic notes on the affinities of the genus *Boriomyia* (Neuroptera: Hemerobiidae), 26  
*Inocellia pilicornis*, 41  
 Inocelliidae, 41  
*Lucarachne beebei*, 95  
 Neuroptera, 26, 41  
 New *Acanthoecten* (Araneae: Acanthoectenidae) from Jamaica, W.I., 81  
 North American Carboniferous insects, 98  
 Note on the prey and a nesting site of *Cerceris truncata* Cameron. (Hymenoptera: Sphecidae: Philanthinae), 43  
 Odonata, 71  
 On the true nature of the Azygethidae (Chilopoda: Geophilomorpha), 76  
*Palaeotherates pennsylvanicus*, 105  
 Paralogidae, 101  
*Paralogopsis longipes*, 103  
*Paralogus aeschnoides*, 102  
 Philanthinae, 43  
 Protodonata, 98  
*Pseudosinella*, 1  
*Pseudosinella alba*, 13  
*Pseudosinella argentea*, 15  
*Pseudosinella* BONETI, 24  
*Pseudosinella* DUBIA, 9  
*Pseudosinella duodecimpunctata*, 8  
*Pseudosinella* ESPANA, 19  
*Pseudosinella folsomi*, 18  
*Pseudosinella* GISINI, 14  
*Pseudosinella hirsuta*, 22  
*Pseudosinella* ORBA, 20  
*Pseudosinella petterseni*, 15  
*Pseudosinella sexoculata*, 12  
*Pseudosinella spinosa*, 23  
*Rhopalothrix*, 44  
*Rhopalothrix bolau*, 44  
 Sphecidae, 43  
 Studies on North American Carboniferous insects. I. The Protodonata, 98  
 Study of *Bembix u-scripta*, a crepuscular digger wasp, 45  
 Symphytognathidae, 95  
 Techniques for the study of ant larvae, 87  
 Triassic odonate from Argentina, 71  
 TRIASSOTHEMIS, 71  
 TRIASSOTHEMIS MENDOZENSIS, 71  
*Troglosinella*, 3  
*Troglosinella hirsuta*, 22  
*Troglosinella spinosa*, 23  
 Type species of the ant genus *Eurhopalothrix*, 44  
*Typus* DURHAMI, 98  
 Wasps, 45

# PSYCHE

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MARCH-JUNE, 1960

Nos. 1-2

---

## THE GENUS *PSEUDOSINELLA* (COLLEMBOLA, ENTOMOBRYIDAE) IN CAVES OF THE UNITED STATES<sup>1</sup>

BY K. CHRISTIANSEN

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In 1934 Bonet listed two troglophile species of the genus *Pseudosinella*, *P. decipiens* and *P. sexoculata*, from caves of the United States. In 1949 Delamare described two new troglobite species, *P. hirsuta* and *P. spinosa*, and placed them in a new genus *Troglosinella*. The present work is the result of the examination of more extensive collections from caves in the United States and has resulted in the addition of four more troglophile forms and the discovery of five new troglobite species. The work covered in this paper was made possible by a National Science Foundation Grant, No. G4563. Mr. Jerry Tecklin did much of the manual labor involved in preparation and he, Mr. James Hedges and Mr. George Darland, made a collecting trip through Missouri and northern Arkansas, recovering a good deal of critical material. Most of the remaining specimens were collected by Mr. and Mrs. Thomas Barr or Mr. Carl Krekeler. I wish to thank all of these people.

### Distribution

Collections are relatively complete only from the region immediately around Tennessee and Kentucky; however, we have a sufficient scattering of material from other regions to be able to discern the probable outline of the distribution of the group. The species of this genus are more widespread in caves than those of the genus *Sinella* previously reported, but the troglobite forms are still largely limited to the southeast quadrant of the country. In the troglophile forms the extensive invasion of the caves of Missouri and Arkansas is the most notable phenomenon. Generally speaking, the troglobite forms are severely restricted in distribution and, in cases of numerous collections, more or less continuous. The troglophile forms are much more wide-

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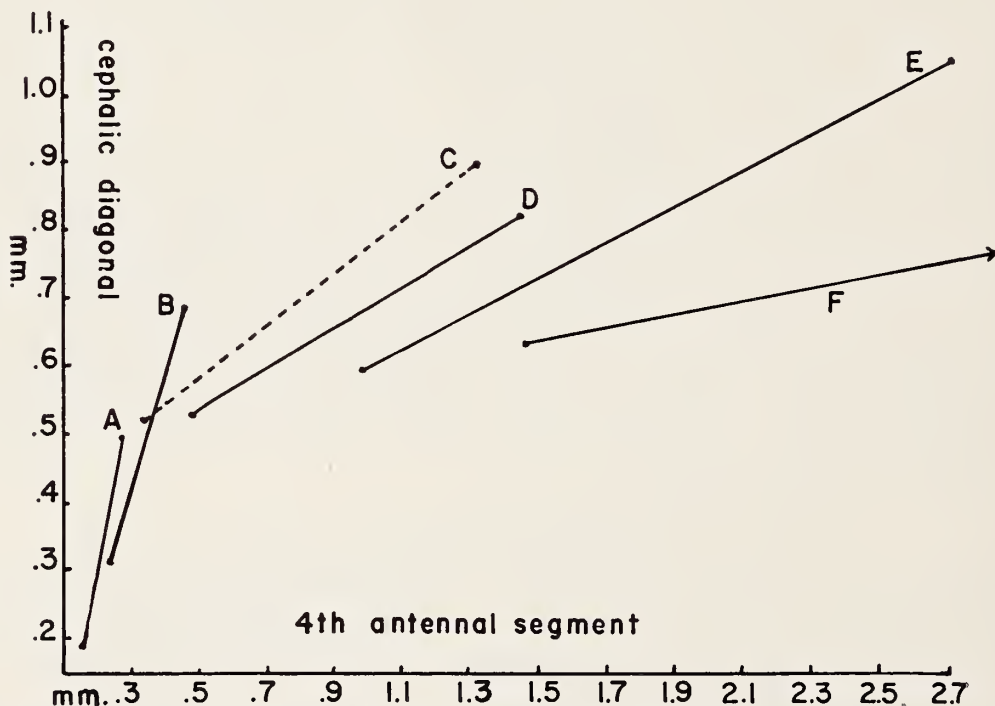
<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

spread and occur in widely disjunct populations. As was true in *Sinella*, the majority of the collections of troglophile forms falls outside of the areas occupied by the troglobite species.

### Biology

Little accurate, detailed information is available concerning the biology of the members of this genus. The visible gut contents indicate that fungal hyphae and spores make up the major portion of the diet of most members. The incompleteness of the data on and collections of both cave and epigeic forms of this genus makes it difficult to classify the habitat of the various species. On a basis of present data we can place the forms described here into four groups: 1) the definite troglo-

GRAPH I



Graph 1. Curves showing the differing ratios of the fourth antennal segment to the cephalic diagonal in the cave species of U. S. *Pseudosinella*. A includes: *P. argentea*, *P. folsomi*, *P. duodecimpunctata*, *P. alba*, and *P. sexoculata*; B: *P. dubia*; C (a probable average of several curves): *P. hirsuta*; D: *P. gisini*; E: *P. spinosa*; and F: *P. boneti*.

bites — including *P. spinosa*, *P. boneti*, *P. espana*, *P. hirsuta*, and *P. gisini*; 2) the doubtful troglobites — *P. dubia* and *P. orba*; 3) the doubtful troglophile — *P. argentea*; and 4) the definite troglophiles — *P. petterseni*, *P. alba*, *P. folsomi*, *P. duodecimpunctata*, and *P. sexoculata*.



## Systematic Account: General Discussion

The genus *Troglosinella* was created by Delamare for the species *hirsuta* and *spinosa*. Examination of much more extensive material encompassing several new species makes it clear that the generic limits set up by Delamare are impractical. Two of the most basic characteristics used to separate the genus (the ringing of the fourth antennal segment, and the small non-lamellate teeth) are present in some forms of *hirsuta* and absent in others. Beyond this the reduced tooth structure of the unguis appears in a number of separate epigeic forms. The spines of the dens, also used to separate the genus, are found in only one species (*P. spinosa*) and the "heavy hairs" found on the dorsum of the dens in *hirsuta* are found in large specimens throughout the whole of *Pseudosinella*. In view of this, and my failure to discover any other practical way to separate the genus from *Pseudosinella*, I consider *Troglosinella* Delamare to be a synonym of *Pseudosinella* Schäffer. It is regrettable that this is unavoidable, since the species clustered around *P. spinosa* do represent an evolutionary unit.

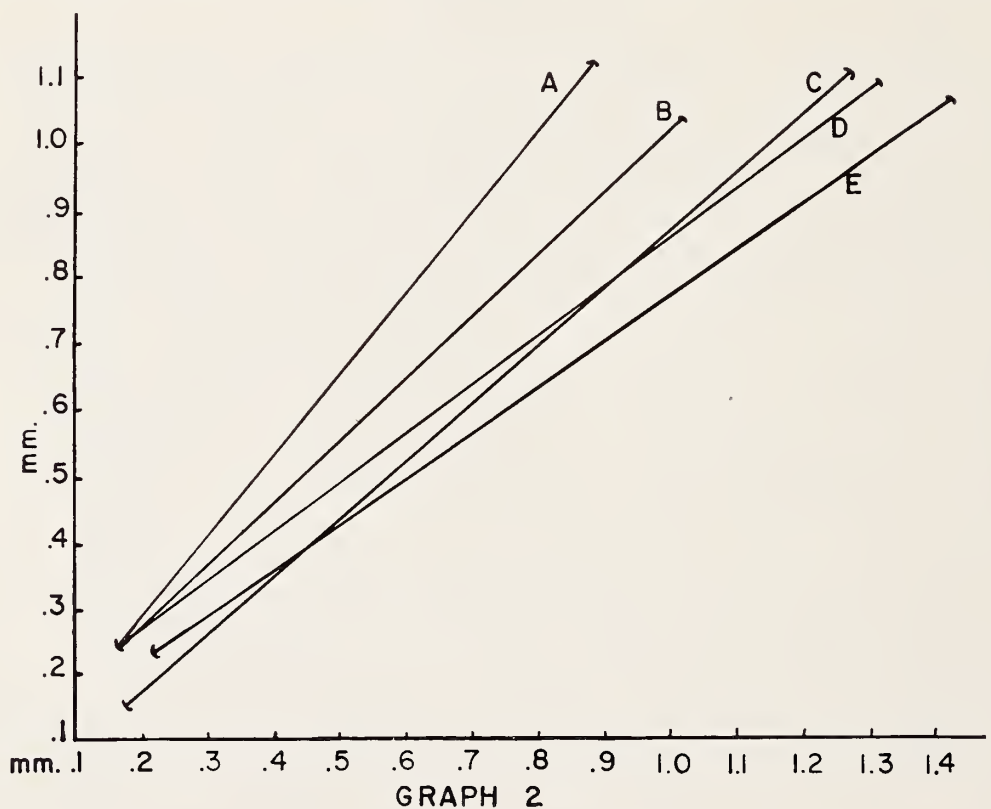
## Ratios and Size

As with almost all groups of Collembola, the size of the species varies considerably. It is extremely risky to determine the size of a particular species upon anything except large samples from a variety of localities. Time and again a whole sample will be made up of small individuals, or will consist exclusively of extra-large specimens. With all this in mind it is possible to break the cave species of *Pseudosinella* of the United States into three size ranges: small (averaging around 1 mm.) — *P. espana* (?), *P. alba*, *P. folsomi*, *P. duodecimpunctata*, and *P. sexoculata*; medium (averaging between 2-3 mm.) — *P. orba* (?), *P. boneti* (?), *P. dubia*, *P. gisini*, *P. argentea* and *P. hirsuta*; and finally the large (averaging around 4 mm.) — *P. spinosa*.

The ratios of the various organs vary, but if we consider all the species, almost any organ ratio can be expressed as a straight line, with one or two notable exceptions. The only striking exceptions involving several species concern the first and second abdominal segments and the length of the antennae. The latter is illustrated in graph 1, which shows the most sensitive segment, the fourth, plotted against the cephalic diagonal. It can be seen that the most highly evolved cave forms develop progressively longer antennae. For most of the other organs a single straight line can express the growth changes and encompass all species. Graph 2 shows a summary of such growth lines for organs of the various parts of the body. There are a few varia-

tions from the norm in several of these curves. The most striking is in connection with one population of *P. hirsuta* which has a longer fourth abdominal segment than is normal, and in all of the specimens examined of *P. duodecimpunctata* which have the manubrium, longer than is normal in the remaining species. It is quite probable that more exhaustive analysis will point out more such exceptions; however, it is apparent that there is little difference among the various species in most organ ratios.

The genus *Pseudosinella* under any definition is a patently polyphyletic group with characteristics largely determined by a particular ecology; it can be distinguished from its ancestral genus *Lepidocyrtus* upon only one basis — the reduction in the number of eyes. *Pseudosinella* usually shows additional characteristics in the loss of pigment and the modification of the unguis structure, either through great elongation and reduction in the size and number of inner teeth and/or through the enlargement of the basal inner unguis teeth. Within the North American cave forms there are three and possibly four separate evolutionary lines involved. Only one of these, the group including



Graph 2. Curves for five different organ ratios, each curve being a composite of all species. In the key below the ordinate is given first in each case. A: cephalic diagonal/second thoracic segment; B: cephalic diagonal/third tibiotarsus; C: manubrium/mucrodens; D: cephalic diagonal/mucrodens; E: cephalic diagonal/fourth abdominal segment.

*P. spinosa*, has gone through extensive evolution within the caves. In spite of the diverse origins of the species of this genus the forms are normally quite similar. The thorax has a somewhat enlarged second segment and the mucro is bidentate with a basal spine. The chaetotaxy is very uniform with macrochaetae on the head being commonly numerous only along the antennal bases, between the antennae, and on the anterior half of the ventral surface. The mesothorax has a series of rows along the anterior margin, and the lateral surface of the fourth segment and the last two segments have sparse coverings. Scattered macrochaetae and groupings of from two to four odd, short, feathered setae and one long filamentous ciliate seta occur on the third and fourth abdominal segments (See figure 11). The scales are hyaline, finely striate and apically rounded. On the whole we have an artificial but readily separated genus.

Key to the Cave Species of *Pseudosinella* of the United States

- |     |  |                                 |
|-----|--|---------------------------------|
| 1)  | Empodial appendage with a clear wing-like tooth at the end of a separate outer lamella .....     | 2                               |
| 1') | Empodial appendage with a small outer tooth or toothless .....                                   | 4                               |
| 2)  | Mucro without basal spine .....  | <i>P. espana</i> n. sp.         |
| 2') | Mucro with basal spine .....   | 3                               |
| 3)  | Unguis with median unpaired inner tooth .....  | <i>P. petterseni</i>            |
| 3') | Unguis without median unpaired inner tooth .....   | <i>P. folsomi</i>               |
| 4)  | Dens with spines .....   | <i>P. spinosa</i>               |
| 4') | Dens without spines .....  | 5                               |
| 5)  | With eyes .....  | 6                               |
| 5') | Eyeless .....  | 11                              |
| 6)  | Two or fewer eyes per side .....   | 7                               |
| 6') | Three or more eyes per side <sup>2</sup> .....   | 9                               |
| 7)  | All inner unguis teeth small .....   | 8                               |
| 7') | Basal, and sometimes all inner teeth large, two eyes per side .....                              | <i>P. alba</i>                  |
| 8)  | Tenant hair weakly clavate and/or median unpaired inner unguis tooth absent .....                | <i>P. gisini</i> n. sp.         |
| 8') | Tenant hair acuminate, median unpaired inner unguis tooth present .....                          | eyed forms of <i>P. hirsuta</i> |
| 9)  | Three eyes per side on two separate eyepatches ....  | <i>P. sexoculata</i>            |
| 9') | Some members of each population with more than three eyes per side, always on one eyepatch ..... | 10                              |
| 10) | All inner unguis teeth subequal, typically five eyes per side .....                              | <i>P. dubia</i> n. sp.          |

<sup>2</sup>Occasional members of a population with four or more eyes may be eyeless.



- 10') Basal inner unguual teeth clearly larger than others, typically six eyes per side ..... *P. duodecimpunctata*
- 11) Fourth antennal segment more than two times as long as cephalic diagonal ..... *P. boneti* n. sp.
- 11') Fourth antennal segment less than one and seven-tenths times as long as cephalic diagonal ..... 12
- 12) Distance from distal base of largest inner unguual tooth to base of unpaired inner tooth less than half that from unpaired tooth to apex of unguis (See figure 44), macrochaetae present in median field of dorsum of head ..... *P. orba* n. sp.
- 12') Distance from largest basal inner tooth to median unpaired tooth at least half as great as distance from apical tooth to apex of unguis, macrochaetae absent from median field of dorsum of head ..... 13
- 13) One or both basal inner unguual teeth large and prominent (See figure 31), ratio of fourth antennal segment to cephalic diagonal less than .8 ..... *P. argentea*
- 13') Both basal inner unguual teeth small (See figure 47), and/or ratio of fourth antennal segment to cephalic diagonal greater than .8 ..... eyeless forms of *P. hirsuta*

## EXPLANATION OF PLATE 1

Figures 1-5: *Pseudosinella duodecimpunctata*. 1. Habitus, specimen from New River Cave, Giles Co., Va.; setae and pigment omitted; 19 X. 2. Hind claw, same specimen; 900 X. 3. Mucro, same locality; 900 X. 4. Apical organs, third antennal segments two different specimens, same locality; 900 X. 5. Eyes and eye patch, same locality; 900 X.

Figures 6-11: *P. dubia* n. sp. 6. Habitus, specimen from Granny Dean Cave, Washington Co., Ark.; setae and pigment omitted; 18 X. 7. Apical organ, third antennal segment, same specimen; 900 X. 8. Eye patch right side, same specimen; 250 X. 9. Mucro, same specimen; 500 X. 10. Hind claw, same specimen; 500 X. 11. Typical setae association of fourth abdominal segment, paratype; 900 X.

Figures 12-16: *P. sexoculata*. 12. Habitus, specimen from Carlsbad Caverns, N. Mex., setae omitted, 30 X. 13. Mucro, same specimen, 900 X. 14. Apical organ third antennal segment, same specimen; 900 X. 15. Hind claw, same specimen; 900 X. 16. closeup of head, same specimen, A.-interantennal setae, B.-antennal base setae, C.-median field setae; 150 X.

Figures 17-21: *P. alba*. 17. Habitus, specimen from Niagra Cave, Fillmore Co., Minn.; 30 X. 18. Hind claw, same specimen; 900 X. 19. Apical organ, third antennal segment, same specimen; 900 X. 20. Mucro, same specimen; 900 X. 21. Right eye patch, specimen from Mystery Cave, Fillmore Co., Minn.; 300 X.

Figures 22-24: *P. folsomi*. 22. Apical organ, third antennal segment, specimen from Limberlost Valley Cave, Newton Co., Mo.; 900 X. 23. Hind claw, same specimen; 900 X. 24. Mucro, epigeic specimen from Harahan, La.; 500 X.



CHRISTIANSEN — PSEUDOSINELLA

## Descriptions of Species

*Pseudosinella duodecimpunctata* Denis

## Figures 1-5

*Pseudosinella duodecimpunctata* Dennis 1931, Mem. Soc. Ent. Ital. 10:82.

*P. (Pseudosinella) duodecimoculata* Bonet 1931, Mem. Soc. Esph. N.H. 14:324-6.

Facies typical of genus *Lepidocyrtus*. Background color yellowish white, with scattered blue pigment, particularly heavy along the sides of the thorax and head. Head broadly oval in shape with a clear V-shaped dorsal area marked off by pigment; six eyes per side on trapezoidal eye patches. Antennae 1.2-1.4 times as long as cephalic diagonal with third antennal segment in the form of a truncate cone clearly shorter than the second segment; apical organ of third segment with two irregular oval pegs in separate deep folds. Second thoracic slightly humped. Fourth abdominal segment about four times as long as third. Unguis with a clear external tooth and three inner teeth; basalmost of these usually salient and larger than remainder. Empodial appendage lanceolate, with one or more minute external teeth. Tenent hair curved and clearly clavate. Mucro with apical tooth weakly upturned and longer than anteapical, basal spine attaining the apex of the anteapical tooth. Anterior macrochaetae as follows: on dorsum of head a group of four interantennal setae near the anterior margin and a curved row of seven setae along each antennal base, the anterior three being distinctly smaller; ventral surface with a few scattered setae near the anterior margin of the median and lateral areas. Second thoracic segment has a double row along the anterior margin.

Type locality: Buco de Piombo, Italy. Distribution: widespread in southern Europe in caves and epigeic. In North America the species has been taken in Florida, Massachusetts, and North Carolina as an epigeic form. In caves of the United States it has been taken from New River Cave, Giles County, Virginia; Wind Cave, Jackson County, Kentucky; Old Spanish Cave, Stone County, Missouri; Panther Cave, Newton County Missouri; and Foster's Cave, Montgomery County, Tennessee.

## Discussion

The most striking variations seen in this troglophile species are in the number of eyes and amount of pigment. Most specimens have the twelve eyes characteristic of the species; but forms with ten eyes



are common; rarely, specimens appear with fewer, as can be seen in those from Tennessee which have from none to six per side. The tibiotarsus of this population is slightly longer than is normal for the species, but they are otherwise similar to forms seen elsewhere. This would appear to be an example of cave evolution proceeding within a population and would be worth additional study. Pigment may be uniformly distributed over the whole body or limited to the head region. The apical organ of the third segment varies from the condition described to two subcylindrical pegs.

The identity of this species with the European specimens is still in doubt as no comparisons could be made; however, there appears to be good agreement between the descriptions and the specimens at hand. This species may very well be the same as *P. collina*, which was described by Wray (1952) as having only two internal unguis teeth; but until this can be checked the two species must be considered separate.

*Pseudosinella dubia*, new species

Figures 6-11

Facies typical of genus. Background color white with an overall scattering of blue pigment, particularly dark on dorsum of head where it forms a diamond shaped mark between the eye patches. Head broadly oval; eyepatches elongate trapezoids, each bearing five eyes in two groups, an anterior group of three and a posterior group of two. Antennae about one and one half times as long as the cephalic diagonal; first three segments subcylindrical and fourth segment fusiform. Fourth segment dorsally with numerous blunted smooth setae of several different sizes and shapes; apical organ of third segment with two irregular flattened elliptical rods in a fold, and about fifteen additional blunt curved setae scattered over the inner ventral surface of the segment. Second thoracic segment markedly humped forcing the head into a slightly hypognathous position. Fourth abdominal segment about five times as long as third. Unguis with minute basal external tooth and three small internal teeth, with basal-most inner tooth on a level and frequently appearing as one under low magnification. Empodial appendage lanceolate, with a small but clear external teeth, exceeding the level of the unpaired internal unguis tooth. Tentent hair weakly clavate. Mucro with apical tooth about twice as long as subapical, and markedly upturned; basal spine exceeding the apex of subapical tooth. Anterior macrochaetae as follows: on dorsum of head four interantennal setae, the posterior pair closer together, and

a curved row of eleven setae around each antenna base; ventral surface with a few scattered setae on the anterior median portion.

Type locality: Devils Den Kitchen Cave, Washington County, Arkansas, IX-9-'59, Tecklin, Hedges and Darland coll. Also taken from Granny Dean and Devils Den Caves, Washington County, Arkansas.

#### Discussion

The number of eyes varies considerably, most specimens having five per side. However, many have four per side; in such cases it is the posteriormost eye of the anterior three which is missing, and the position of this eye is variable even when it is present. The tenent hair varies from acuminate to markedly clavate.

The taxonomic position, name and limits of this species are all moot. The species is clearly distinguished from the form called here *P. duodecimpunctata*. The antennae of *dubia* are longer, and the eye number typically different. The shape of the eye patch and distribution of the eyes are also different, as is the structure of both mucro and unguis. The question of the relationship between this form and Wray's *collina* or Guthrie's *Lepidocyrtus decemoculatus* is less easily settled. The present species appears to differ from *collina* in (1) the number of eyes (six vs. five per side typically); (2) the relative lengths of abdominal segments three and four (*collina* one: four, *dubia* one: five +); (3) antennal ratios; and (4) the comparison of lengths of the manubrium and dens. In addition, Wray's figures show the basal spine of the mucro not reaching the antepical tooth and the unguis

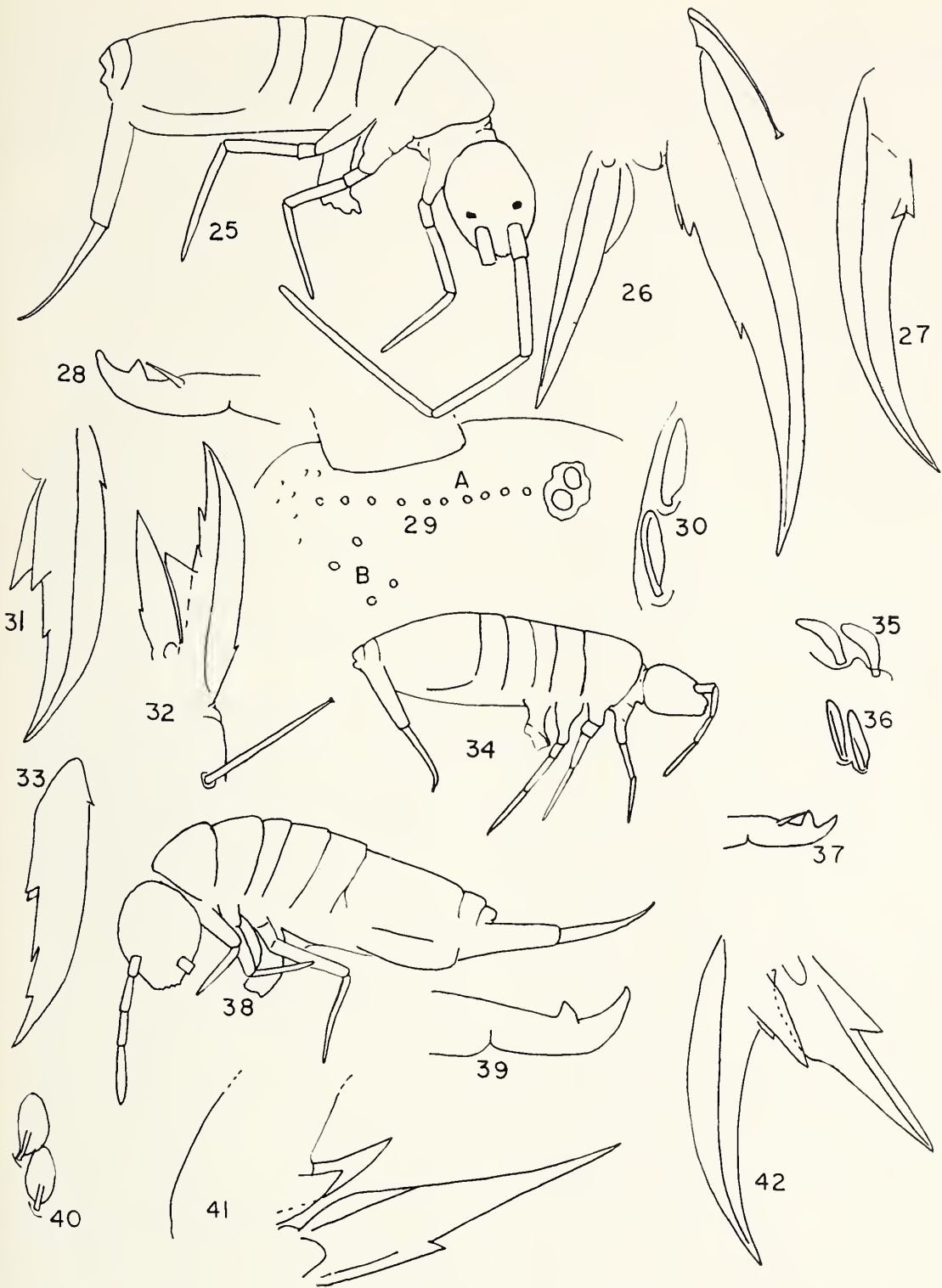
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#### EXPLANATION OF PLATE 2

Figures 25-30: *P. gisini* n. sp. 25. Habitus, specimen from Higgenbotham Cave, Greenbrier Co., W. Va., setae and pigment omitted; 12 X. 26. Hind claw, paratype; 350 X. 27. Hind unguis, specimen from McFerrin Cave, Greenbrier Co., W. Va.; 250 X. 28. Mucro, same specimen; 250 X. 29. Dorsal setae and eyes right side, paratype, Greenbrier Co., W. Va.; A.-inter-antennals, B.-antennal base setae; 120 X. 30. Apical organ, third antennal segment, specimen from McClung Cave, Greenbrier Co., W. Va.; 350 X.

Figures 31-37: *P. argentea*. 31. Typical hind unguis, specimen from Eli Reed Cave, Larue Co., Ky.; 350 X. 32. Hind claw showing unusually large basal tooth, specimen from Rankin Cave, Jefferson Co., Mo.; 350 X. 33. Hind unguis showing unusually small basal teeth, specimen from Crownover Saltpeter Cave, Franklin Co., Tenn.; 350 X. 34. Habitus, specimen from Mammoth Cave, Ky., setae omitted; 17 X. 35. Apical organ, third antennal segment, specimen from Rankin Cave, Jefferson Co., Mo.; 900 X. 36. Same organ, specimen from Sparkman Cave, White Co., Tenn.; 900 X. 37. Mucro, same specimen; 500 X.

Figures 38-42: paratypes of *P. espana* n. sp. 38. Habitus, setae omitted; 30 X. 39. Mucro; 900 X. 40. Apical organ, third antennal segment; 900 X. 41. Base of hind claw; 900 X. 42. Claw smaller specimen; 900 X.



CHRISTIANSEN — PSEUDOSINELLA



with two inner teeth. Both conditions differ in *dubia*. *Lepidocyrtus decemoculatus* is very poorly described, but every major described feature except the eye number would appear to indicate a separate species. The distribution of the eyes, the shape of the eyepatch, the hinted antennal ratios, and ratio of manubrium to dens all are different from those seen in *dubia*.

In any case, I feel that it is impossible to fit the present form into the descriptions of either species at this time. It is quite possible that close examination will show that this form is in fact synonymous with one or both of the species mentioned above.

*Pseudosinella sexoculata* Schött

Figures 12-16

*Pseudosinella sexoculata* Schött 1902, Bib. Kong. Sv. Vet.-Akad. Handl. 28: 34-5.

*Lepidocyrtus sexoculatus* Guthrie 1903, Publ. Geol. Nat. Hist. Survey Minn. Zool. Series 4: 86-7.

*P(seudosinella) sexoculata* Bonet 1934, Arch. Zool. Exp. Gen. 76: 370.

Facies typical of genus *Lepidocyrtus*. Background color dull yellow, pigment limited to eyepatches. Head circular, eyes three per side on two separate eye patches, two eyes in front and one behind. Antennae with fourth segment fusiform, second and third segments truncately conical and first segment subcylindrical; third segment strikingly shorter than the second and with an apical organ consisting of two basally constricted oval pegs in a deep fold. Second thoracic segment not strikingly humped, so that the head is prognathous. Fourth abdominal segment about three times as long as the third segment. Unguis without external teeth, the basal pair arising at different levels. Empodial appendage lanceolate with outer margin serrate. Tenent hair large and clearly clavate. Mucro with apical tooth slightly larger than antepical and markedly upturned at its apex; basal spine exceeding apex of antepical tooth. Anterior macrochaetae as follows: dorsum of head with a curved row of six setae along each antennal base and a single seta between the two eyepatches on either side; four interantennals, more posterior than normal; a medium pair of setae between and slightly in back of the two posterior eye patches; ventral surface of head with scattered setae along the anterior one-fourth. Second thoracic with a double row of setae along the anterior margin.

Type locality: epigeic greenhouses, Linköping, Sweden and Rosendal, Norway.

Distribution: a common epigeic form on the Pacific coast. Cave collections in the United States: Reids Cave, Fayette County, Kentucky; and Carlsbad Caverns, Eddy County, New Mexico.

#### Discussion

This form appears to be a rare troglophile in caves in the United States. Further exploration and collecting in western caves may show it to be more common than presently appears.

#### *Pseudosinella alba* (Packard)

Figures 17-21

*Lepidocyrtus albus* Packard 1873, Peabody Acad. Sci. 5th Ann. Rept: 37.

*Sira* (*Pseudosinella*) *alba* Schäffer 1900, Jahrb. Ver. Vaterl. Natur. 56: 269.

*Pseudosinella alba* Börner 1901, Zool. Anz. 24: 707.

Facies typical of genus *Lepidocyrtus*. Background color dull yellow white with scattered bluish or brownish pigment. Eyes two per side on square black pigment patches. Fourth antennal segment fusiform, third segment truncately conical and remainder subcylindrical; third segment noticeably shorter than second and with apical organ of two short subcylindrical pegs. Second thoracic segment slightly enlarged, with head prognathous. Fourth abdominal segment about four times as long as third. Unguis with three inner teeth with basal-most tooth being the largest. The empodial appendage is lanceolate with a small but clear external tooth. Tenent hair clavate. Mucro with apical tooth about twice as long as anteapical and not strikingly upturned; basal spine barely attaining apex of anteapical tooth. Anterior macrochaetae as follows: on the dorsum of head a group of four setae along the base of each antenna, and a group of four interantennal setae forming the corners of a narrow rectangle; in the center are four more setae marking the sides of a triangle which has its apex just anterior to the anterior pair. Ventral surface of head sparsely covered with setae over the anterior median portion. Anterior margin of second thoracic segment with a double row of setae.

Type locality: epigeic but uncertain, probably Massachusetts. A common epigeic form in the United States known from Mystery and Niagra Caves in Fillmore County, Minnesota and Christian Cave in Robertson County, Tennessee.

#### Discussion

I have examined and measured a considerable number of epigeic forms of this species and can find no significant differences between

these and the cave forms. The coloration is the most variable characteristic; some specimens are white save for the eyespots, while all others are almost totally blue.

*Pseudosinella gisini*, new species

Figures 25-30

Facies typical of genus. Color white with a scattering of blue pigment particularly clear upon the dorsum of the head. Head elongate oval with two eyes per side located upon a single dark eyepatch. Antennae about three and one half times as long as cephalic diagonal with all segments subcylindrical in shape; fourth antennal segment without apical cone and showing definite signs of ringing; third segment with apical organ of two curved, narrow, paddle-shaped setae with supporting rods along one margin. On the opposite side of the apex of third segment are five blunt finger-like setae. Second thoracic segment not humped. Fourth abdominal segment about four times as long as third. Unguis long and curved with external and lateral teeth minute and three inner teeth, basal pair small but clear and on a level, median unpaired tooth minute, visible only under highest magnification. Empodial appendage with slight basal internal swelling. Tenent hair finely clavate. Mucro with teeth subequal, apical tooth not sharply upturned, basal spine heavy, reaching apex of anteapical tooth. Anterior macrochaetae as follows: dorsum of head with four interantennal setae forming the corners of a rectangle, and a row of eight setae forming a straight line along each antenna base; ventral surface with scattered setae over the anterior half of the median and lateral surfaces. Second thoracic segment with two to three rows of setae along the anterior margin and a single row along the lateral margin.

Type locality: Foxhole Cave no. 1, Greenbrier County, West Virginia, VIII-19 '58. Barr coll. Also known from eight additional caves, all in Greenbrier County.

Discussion

The most prominent variation seen in the species concerns the median unpaired tooth of the unguis which may be entirely absent. In such forms the tenent hair is very weakly clavate so that this is visible only under highest magnification and with phase contrast. Although the typical form of this species is strikingly distinct from the typical form of *P. hirsuta* there are some specimens of the latter species which approach *gisini* in one or more characteristics (see discussion under *P. hirsuta*); however, the two can always be distinguished on a basis of the cephalic chaetotaxy and the tenent hair.



*Pseudosinella petterseni* Börner

*Pseudosinella petterseni* Börner 1901, Zool. Anz. 24: 707-8.

Facies typical of genus. Color silvery white without trace of pigment. Head circular and eyeless. Antennae with fourth segment fusiform, third segment truncately conical and remainder subcylindrical; apex of fourth segment rounded; apical organ of third segment with two subcylindrical pegs. Second thoracic segment not humped and the head prognathous at rest. Fourth abdominal segment about three and one half times as long as the third segment. Unguis with a small external tooth, and three well developed internal teeth; the basal pair not on a level and the basalmost one considerably larger than the remainder. Empodial appendage with a large outer wing tooth on a distinct lamella. Tenent hair strikingly clavate. Mucro with apical tooth twice as long as antepical; basal spine exceeding the apex of antepical tooth. Anterior macrochaetae as follows: dorsum of head with a row of six setae along each antenna base, the setae in each row being alternately large and small, the posteriormost seta of each row is displaced inward; interantennal setae are concentrated near the anterior margin of the head so that only two are clearly visible; ventral surface with scattered large setae on anterior one third of surface. Anterior margin of second thoracic segment with from two to four rows of setae.

Type locality: epigeic, Frauenberg bei Marburg, Germany.

Distribution: one of the commonest epigeic species in the United States; known in caves from Kendall and Burnett Counties, Texas, and Linn County, Iowa.

## Discussion

The specimens seen from the Texas caves differ slightly from the epigeic forms seen in most of the country; in the former the basal unguis tooth is smaller, the tenent hair clavate and the basal spine of the mucro shorter; however, these variations are probably geographical since epigeic specimens seen from New Mexico indicated similar modifications. Further collections from western caves will probably show this to be a much more common cave inhabitant than is presently indicated.

*Pseudosinella argentea* Folsom

Figures 31-37

*Pseudosinella argentea* Folsom 1902, Psyche 9: 366.

*P(seudosinella) decipiens* (?) Bonet 1934, Arch. Zool. Exp. Gen. 76: 370-3.

Facies typical of genus. Color white with scattered blue pigment particularly upon head. Head almost round when seen from above, often with traces of pigmentation on eyespot region; eyeless; antennae with third segment sub-conical in shape; fourth antennal segment much shorter than cephalic diagonal and with apex rounded, without apical cone. Apical organ of third segment of two strongly curved blunt pegs with an additional pointed peg off to one side. Thorax not humped and head prognathous. Fourth abdominal segment about four times as long as the third segment. Unguis with one or both basal teeth enlarged and a single median tooth prominent and projecting. Empodial appendage lanceolate with a very small external tooth. Tenent hair weakly clavate. Mucronal teeth subequal and basal spine attaining the apex of the median tooth. Anterior macrochaetae as follows: dorsum of head with four interantennal setae arranged in a narrow rectangle and with a small seta located in the center of this rectangle. Antennal bases with seven setae arranged 6-1 in a straight line along the base. Venter of head with a few scattered setae near the anterior margin. Second thoracic segment with three to four rows along the anterior margin and a single row of smaller setae along the lateral margin.

Type locality: a grave, Washington, D. C. Range: known from caves in Missouri, Central Tennessee, and single localities in Kentucky, Virginia, Arkansas, Georgia and Washington, D. C.

#### Discussion

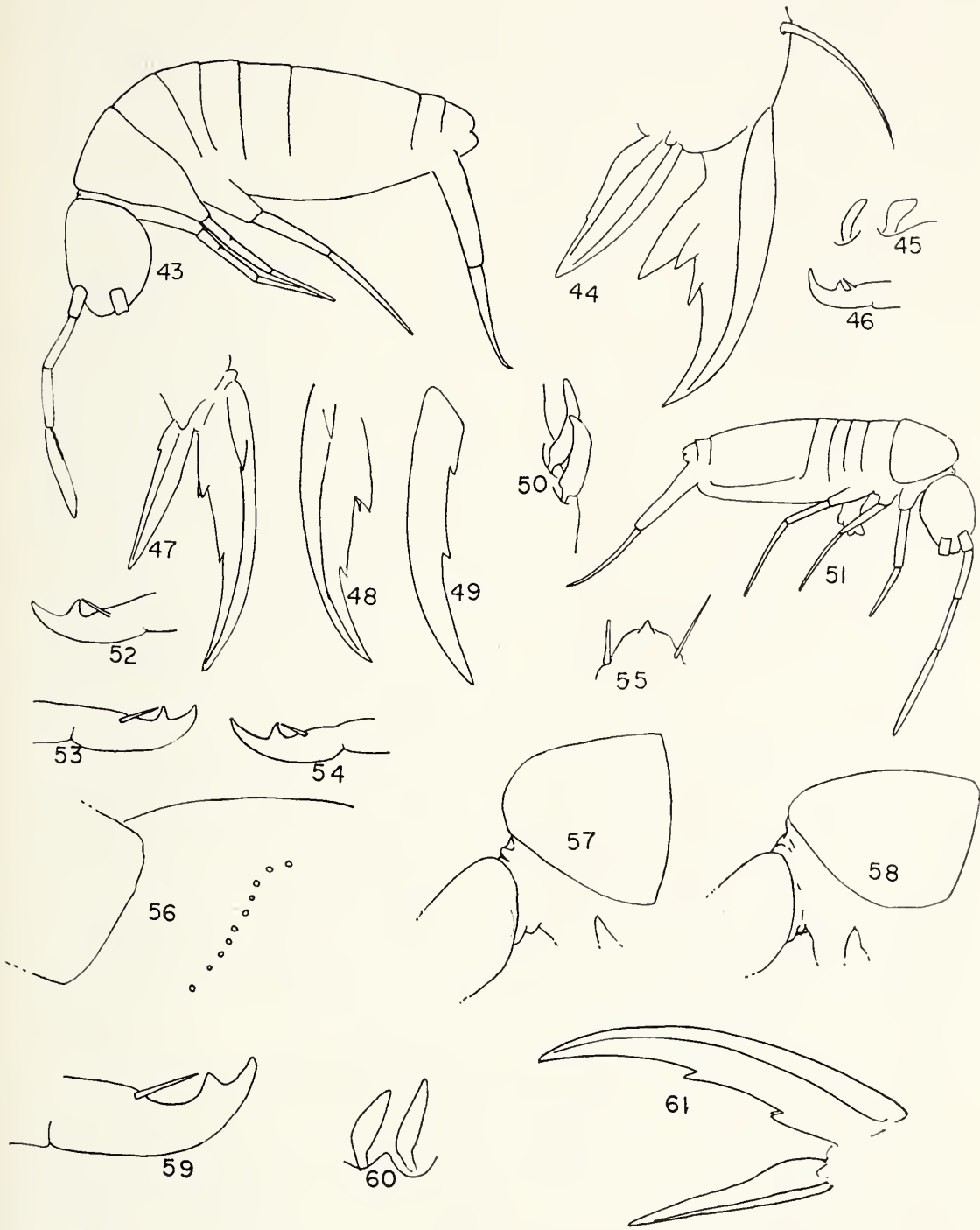
This species is almost as variable as *P. hirsuta* and in some forms the basic structure is very similar. The two species can always be sep-

#### EXPLANATION OF PLATE 3

Figures 43-46: holotype of *P. orba* n. sp. 43. Habitus, setae omitted; 30 X. 44. Hind claw; 500 X. 45. Apical organ, third antennal segment; 900 X. 46. Mucro; 500 X.

Figures 47-58: *P. hirsuta*. 47. Hind claw, specimen from Ward Cave, Bedford Co., Tenn.; 350 X. 48. Unguis, another specimen same locality; 350 X. 49. Hind unguis, specimen from Mill Creek Cave, Davidson Co., Tenn.; 250 X. 50. Apical organ, third antennal segment, same specimen as fig. 47; 900 X. 51. Habitus, topotype; 18 X. 52. Mucro, same specimen as fig. 47; 900 X. 53. Mucro, topotype; 900 X. 54. Mucro, same specimen as fig. 49; 900 X. 55. Apical cone fourth antennal segment, specimen from Piper Cave, Smith Co., Tenn.; 900 X. 56. Antennal base setae, same specimen; 250 X. 57. Thoracic profile, specimen from Gassaway Cave, Metcalfe Co., Ky.; 30 X. 58. Thoracic profile, specimen from Pratt Cave, Pickett Co., Tenn.; 30 X.

Figures 59-61: *P. spinosa*. 59. Mucro, specimen from Jared Hollow Cave, Putnam Co., Tenn.; 900 X. 60. Apical organ, third antennal segment, specimen from Payne Saltpeter Cave, Grundy Co., Tenn.; 900 X. 61. Hind claw, same specimen; 250 X.



CHRISTIANSEN — PSEUDOSINELLA



arated on a basis of the cephalic chaetotaxy and the apex of the antenna. The variations of the unguis structure are most striking. Typically the median tooth is large, but it may be small (see figures); also the basal teeth are normally staggered and of different sizes, but they may be of equal size and/or at the same level. The external tooth is usually present but may be folded and virtually invisible. A small apical tooth may be present. The tenent hair varies from strikingly clavate to acuminate. Some forms are totally without pigment while others are clearly colored. The cephalic diagonal, fourth antennal segment and head also vary considerably in size. The antennal base setae also vary with size (as is normal for the genus) but the huge majority of specimens examined had the number noted.

First examination of this material led to the belief that two or three species were involved; but, with larger series of specimens from many localities and careful analysis of the variation, it became apparent that no clear boundaries could be drawn within the whole group and that the combinations of characteristics were virtually at random. It appears that some of the variation is geographic in nature (example: large median tooth more common in northern populations) but an analysis of this must await further and more complete collections.

Specimens taken from caves in Virginia and identified by Bonet as *P. decipiens* (1934) are almost certainly *argentea*. It is quite possible that *P. argentea* is in fact synonymous with *P. decipiens*. The unguis in particular appears to have much the similar sort of variation in the European forms as in *argentea*. The figures for this species given by Denis, Bonet and Gisin would appear to indicate considerable variation; however, there are certain striking differences. First, in *argentea* a common form has both teeth arising at the same level, and this apparently is never true with *decipiens*. Second, Denis indicates the apical organ of the third antennal segment in *decipiens* as consisting of two cylindrical, straight pegs, whereas in *argentea* they consist of two basically constricted, strongly curved elliptical pegs. The fourth antennal segment is relatively longer in *argentea* than Bonet indicates for *decipiens*, and the fourth abdominal segment is from four to five times as long as the third rather than 3 to 3.5 times longer as indicated by Bonet for *decipiens*. In view of all of these I feel it wiser to maintain *argentea* until such time as a careful comparative study can be made between this form and *decipiens*.

*Pseudosinella folsomi* Denis

Figures 22-24

*Pseudosinella folsomi* Denis 1931, Mitt. Mus. Hamburg 44: 226-8.

Facies typical of genus. Color white without vestige of pigment. Head round, eyeless. All antennal segments subcylindrical; apex of fourth segment blunt; apical organ of third segment with two large elliptical pegs, constricted basally. Second thoracic segment slightly humped, head more or less prognathous. Fourth abdominal segment about three times as long as third. Unguis with only two strong basal internal teeth, arising at about same level and with one greatly enlarged. Empodial appendage with inner margin slightly truncate, and outer margin equipped with a prominent tooth on a distinct lamella. Tenent hair short and clavate. Mucro with apical tooth slightly longer than antepical; basal spine not attaining apex of antepical. Anterior macrochaetae as follows: dorsum of head with a group of five at each antenna base and four interantennals. Another pair of setae can be seen near the lateral margins of the middle of the dorsum; ventral surface with numerous scattered setae on the anterior third of the lateral and median portions. Anterior margin of the second thoracic segment with four to five rows of setae and a single row along the lateral margins.

Type locality: epigeic "Station No. 36," Massachusetts. Also recorded as an epigeic form from several places in the vicinity of Boston and New Orleans. Cave distribution: known only from Limberlost Valley Cave, Newton County, Missouri.

#### Discussion

Recent collections from South America would seem to indicate that this species is widespread in Chile at least. The fact that the epigeic collections in the United States have been limited to the vicinity of major ports makes it seem probable that this is an imported form here. Its one collection in a cave was in association with another troglophile species, *Sinella caeca*. Further collections will have to be made before anything can be said about the significance of this invasion.

#### ***Pseudosinella espana*, new species**

Figures 38-42

Facies typical of genus. Color white without trace of pigment. Head oval, eyeless. Antennae one and one half times as long as cephalic diagonal, with the first three segments subcylindrical and fourth segment ellipsoidal; apical organ of third segment with two paddle-shaped setae having central supporting rods. Second thoracic segment not strikingly humped. Fourth abdominal segment slightly more than three times as long as third. Unguis narrow and sickle-

shaped with only two large basal internal teeth. Empodial appendage with a basal internal swelling and a large external tooth upon a distinct lamella. Tenent hair small and acuminate. Mucro with apical tooth gradually curved and more than twice as long as anteapical; basal spine absent. Anterior macrochaetae as follows: dorsum of head with five interantennal setae and a row of six setae near each antenna base and a pair near the center of the dorsal field; a diagonal row of three and group of four setae near each latero-posterior margin of the dorsum; ventral surface with two mid-lateral patches of densely packed setae. Second thoracic segment with three to four rows of setae along the anterior margin and a single row along the lateral margins.

Type locality: Old Spanish Cave, Stone County, Missouri, VI '59, Tecklin, Darland, and Hedges coll. Also known from Coleman's Cave, Montgomery County, Tennessee. It is probably widespread but uncollected in caves between these two points.

#### Discussion

This species is the only Nearctic member of the genus to lack a basal spine. Except for this remarkable feature it is very similar to *P. folsomi* although it shows a number of cave adaptations not found in this last species.

#### ***Pseudosinella orba*, new species**

Figures 43-46

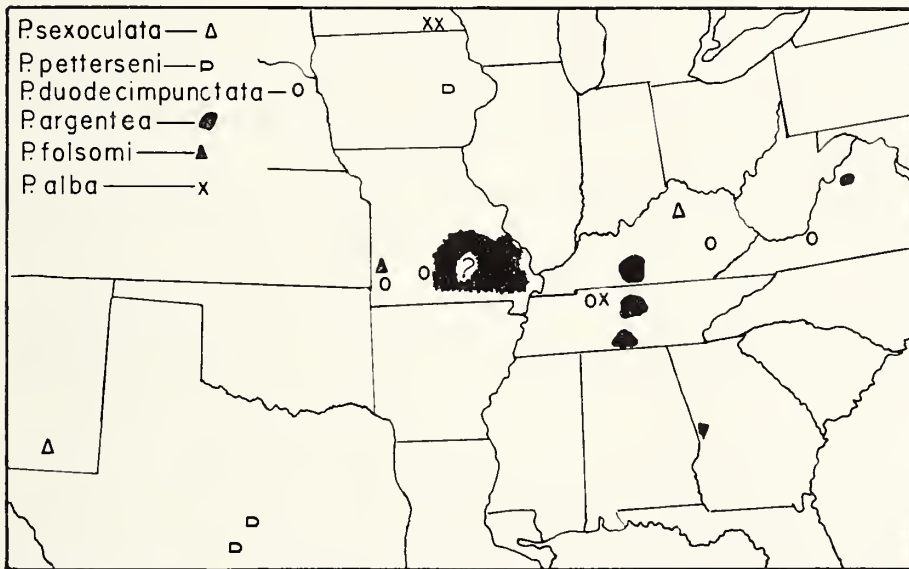
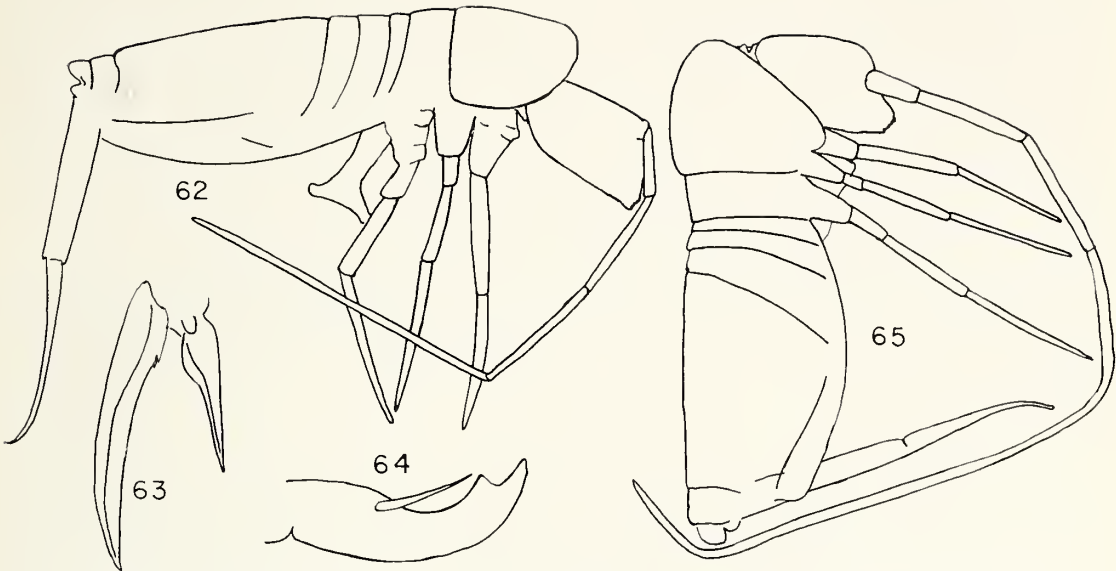
Facies typical of genus. Color white without trace of pigment. Head circular, eyeless. Antennae about twice as long as cephalic diagonal, all segments slightly ellipsoidal; second and third segments subequal in size; apical organ of third segment with two blunt oval pegs. Second thoracic segment slightly humped. Fourth abdominal segment about three times as long as third. Unguis broad, apically slightly hooked, basal internal teeth large, subequal, and arising well above the base of the claw; median unpaired tooth prominent and about at mid-level of unguis; a pair of small lateral teeth are near the base. Empodial appendage lanceolate, with external margin serrate and basally expanded. Tenent hair slender and acuminate.

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#### EXPLANATION OF PLATE 4

Figure 62: *P. spinosa*, Habitus, specimen from Payne Saltpeter Cave, Grundy Co., Tenn., setae omitted; 18 X. Figures 63-65: *P. boneti* n. sp. 63. Habitus, holotype; 18 X. 64. Mucro, holotype; 350 X. 65. Hind claw, paratype; 250 X. Figure 66: Map showing known cave locations of six troglophile species of *Pseudosinella* in the U. S. Figure 67: Map showing cave distribution of seven troglobite species of *Pseudosinella* in the U. S.





CHRISTIANSSEN — PSEUDOSINELLA

Mucro with apical tooth much larger than anteapical; basal spine slender but reaching the apex of the anteapical tooth. Anterior macrochaetae as follows: dorsum of head with an interantennal pair, and then in the anterior half of the median field six more arranged along the sides of a triangle with its apex near the interantennals; a straight row of eight setae along each antenna base; ventral surface with scattered setae along the anterior third. Second thoracic segment with two rows along the anterior margin and a transverse row of eight setae along the posterior margin.

Type locality: Morrill Cave, Sullivan County, Tennessee. X '56, T. Barr coll. Also taken from Hamilton Cave, Bland County, Virginia.

#### Discussion

This striking species is quite unique in the chaetotaxy of the head and the structure of the unguis. In both characteristics it appears to be related to *P. alba* and may well represent a cave derivative of this species. The fact that the modifications for cave life are relatively slight makes it entirely possible that this is in fact a troglophile form which is so far undescribed from epigeic habitats.

#### *Pseudosinella hirsuta* Delamare (new combination)

Figures 47-58

*Troglosinella hirsuta* Delamare 1949, Notes Biosp'e., 4: 121-2.

Facies typical of genus. Background color yellowish white with slight touches of blue or reddish (?) pigment, particularly in the region of the antennal bases. Head elliptical, normally without eyes. Antennae elongate with all segments subcylindrical; fourth segment usually showing signs of ringing with a definite small conical projection at the apex; apical organ of third segment with two curved elliptical paddles, constricted basally. Second thoracic segment slightly humped. Fourth abdominal segment about six times as long as the third. Unguis elongate with a small external and three small internal teeth, the basal pair being on the same level. Empodial appendage narrow and lanceolate with a small external tooth. Tenent hair small and acuminate. Mucro with apical tooth about twice as long as anteapical and weakly upturned at the apex; basal spine just reaching the apex of the anteapical tooth. Anterior macrochaetae as follows: dorsum of head with an interantennal group marking the corners of a narrow rectangle; a row of nine setae along each antenna base with the posterior one or two in each row displaced inward; ventral surface

with scattered setae along the anterior half. Two to three rows of setae along the anterior margin of the second thoracic segment.

Type locality: Tennessee caverns, Tennessee, H. Henrot coll. Distribution: major distribution in south-central Kentucky, central Tennessee and northeast Alabama; isolated populations in eastern Tennessee and Kentucky.

#### Discussion

This species is the most abundant and most variable troglobite form of the genus in North America. No single description can apply to all of the available specimens, but the characteristics listed above apply to about 60% of the specimens and with one or another major alteration would fit all save about 1% of the specimens seen. The variation is extensive and can be seen in virtually all characteristics so that some specimens resemble *P. argentea* while others are superficially similar to *P. gisini*; indeed single specimens are often hard to place. Analysis of the variable characteristics shows that they are definitely geographically determined; however, since there is no similarity among the distribution of the various characteristics, the subspecies concept is clearly not applicable.

In general there are six characteristics which vary strikingly and these and their limits of variation are listed below:

- A) Second thoracic segment, strongly humped to virtually flat.
- B) Unguis, condition seen in *argentea* to condition seen in *gisini*.
- C) Empodial appendage, lanceolate to clearly basally expanded.
- D) Ratio of fourth antennal segment to cephalic diagonal, 3:6-5:3.5.
- E) Mucro, antepical tooth middle to near apical tooth.
- F) Eyes, eyeless to two eyes per side.
- G) Pigment, totally white to head and thorax medium blue.

All in all the majority of the specimens are very similar to the form in the description and no one specimen carries very many of the variant characteristics.

#### *Pseudosinella spinosa* Delamare (new combination)

Figures 59-62

*Troglosinella spinosa* Delamare 1949, Notes Biosp'e., 4: 122-4.

Body elongate with attenuate appendages. Background color dull yellowish white with occasional flecks of reddish (?) pigment around the bases of the antennae. Head elliptical, strikingly longer than broad. Antennae with all segments subcylindrical, and fourth segment showing signs of ringing and subsegmentation; apex of antenna



with a small apical cone; apical organ of third segment with two flattened, fusiform, basally constricted paddles, in separate shallow folds. Second thoracic segment strongly humped forcing head into an opisthognathous position. Fourth abdominal segment about seven times as long as third. Unguis strikingly elongate, without external teeth but with three very small internal teeth, the basal pair being on a level and slightly smaller than the median unpaired tooth. Empodial appendage lanceolate, slender and with a striking internal basal expansion. Tenent hair small and acuminate. Mucro with anteapical tooth displaced toward apex; teeth subequal in size; basal spine not attaining level of anteapical tooth. Dens with one or two rows of heavy finely ciliate spines along anterior two thirds. Anterior macrochaetae as follows: dorsum of head with an interantennal group of five setae; a curved row of nine setae along each antennal base; ventral surface covered with numerous setae. Second thoracic segment with two to three rows of setae along anterior margin and a single row along the lateral margins.

Type locality: Alladin's Cave, Madison County, Alabama, H. Henrot coll. Distribution: limited to central Tennessee and north-east Alabama. Abundant within these limits.

#### Discussion

This is by far the most stable of the common troglobite species of this genus. The only striking variation is seen in the mucro, which has occasional populations with the anteapical tooth much more basal than is normal. Other variations are minor; for example, some forms are entirely white while others have a scattering of pigment over the whole body. The inner unguis teeth are often so minute as to be invisible under low magnifications. The dental spines are often difficult to observe.

#### ***Pseudosinella boneti*, new species**

Figures 63-65

Body elongate, appendages very attenuate. Color white without trace of pigmentation. Head oval without eyes. Antennae four or more times as long as head with all antennal segments subcylindrical; apical organ of third antennal segment with two paddle-shaped setae having the supporting rod along one margin. Second thoracic segment greatly enlarged, forcing the head into a hypognathous or opisthognathous position. First abdominal segment strikingly compressed; fourth abdominal segment almost seven times as long as third. Unguis extremely thin and elongate having only a single pair of in-

ternal basal teeth. Empodial appendage thin and basally swollen. Tenent hair minute and acuminate. Dens without spines. Mucro with apical and antepical teeth close together and near apex, subequal in size; basal spine not attaining level of antepical tooth. Anterior macrochaetae as follows: dorsum of head with seven interantennal setae and a row of eight setae along each antenna base; ventral surface with numerous densely packed setae along median and lateral area. Anterior margin of second thoracic segment with two to three rows of densely packed setae.

Type locality: Poms Cave, White County, Tennessee, III '57 T. Barr coll. Also taken from Dairyhouse Cave in the same county; Wolf Cave, Morgan County, Alabama; and Wind Cave, Pulaski County, Kentucky.

#### Discussion

This well marked species represents the apogee of cave evolution in the Nearctic *Pseudosinella*. The series available is limited and little variation has been seen. In some forms the unguis teeth are entirely absent, and in the specimens from Alabama and Kentucky the median tooth of the mucro is less apical than in the Tennessee specimens. The specimens from Kentucky sometimes have a very small median internal unguis tooth.

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THE IMMATURE STAGES OF *BORIOMYIA FIDELIS*  
(BANKS) WITH TAXONOMIC NOTES ON THE  
AFFINITIES OF THE GENUS *BORIOMYIA*  
(NEUROPTERA:HEMEROBIIDAE)

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Introduction

The genus *Boriomyia* Banks, 1904 (*sensu* Killington, 1937, Carpenter, 1940; *nec* Banks, 1905, Tjeder, 1941, *et seq.*) is known only from the Nearctic Region where it is represented by the type species *B. fidelis* (Banks) and by *B. speciosa* (Banks). To date the biology of the immature stages of neither of these species has been elucidated. *B. fidelis* has been taken with fair frequency in the middle Atlantic states and the author has made several attempts to rear this interesting hemerobiid; however, it has only been recently that this effort has met with any success. Although this study represents a portion of a more general investigation of the morphology and ecology of the immature stages of the Nearctic Neuroptera, it seems desirable to publish these notes at this time because of their bearing on the question of the relationship of *Boriomyia* to the other genera of the Hemerobiidae.

The writer wishes to express his gratitude to Mr. Ivan Huber of the Food and Drug Administration, Department of Health, Education and Welfare, who supplied the author with several living females, including the all-important specimens whose offspring form the basis for this account.

Methods

The immature stages which were utilized in this study were derived from three females collected in College Park and Greenbelt, Prince Georges Co., Md., in 1956 and 1958. After rearing and preservation, thirty-seven first instar larvae, ten second instar larvae, eighteen third instar larvae and two pupae were available for morphological investigations. Although this species can be identified from either sex of the adult with good reliability, the best taxonomic characters are found in the genitalia of the male. Accordingly, three pupae, the offspring of a single female, were allowed to transform and two of these produced males by which the initial identification of one of the original females was confirmed. These identifications were made by the writer utilizing the key of Carpenter (1940).



Past experience with numerous types of Neuroptera has indicated that when eggs can be obtained from field-collected females, these eggs are fertile. The usual procedure for inducing oviposition by such females has been to confine the insect in some suitable container. Thus Smith (1922) was quite successful in securing eggs from females of various Nearctic species of *Chrysopa* by placing them in lamp-chimney cages over growing, aphid-infested plants, the aphids serving as food for the female and possibly also as an oviposition stimulus. Killington (1937) utilized much the same procedure in obtaining eggs from many species of British hemerobiids.

Although this method was tried by the present writer, the inspection of so large a volume for the infrequent eggs supplied by the females of *B. fidelis* proved difficult. In addition, the broadly oval wings of this species with their numerous macrotrichiae render the insect somewhat clumsy and almost any confined space serves to trap the female, the leaf axils of the plants serving especially well in this respect.

A more satisfactory arrangement was found by confining the females individually in 75 x 25 mm. cotton-stoppered glass vials. Humidity was supplied from a small pledget of cotton, dampened with a solution of sucrose and water which was placed in the bottom of the vial. To obviate the possibility of the female becoming stuck to the wet cotton, a cardboard partition was placed between the damp cotton and the female and this was removed only for a short time each day to permit the female to drink. Small nymphs of the aphid *Macrosiphum liriodendri* (Monell) collected from nearby tulip trees (*Liriodendron tulipifera* (L.)) were supplied on a small piece of leaf daily.

Eggs, which were invariably laid on the cotton plug of the oviposition vial, were removed as soon as detected and placed singly in 40 x 13 mm. cotton-stoppered shell vials. Larvae were supplied each day with nymphs of the same aphid as was fed to the adults. This food was introduced into the vial on a piece of fresh leaf which probably served to maintain a reasonable humidity although no attempt was made to control or record this variable. Small wads of damp cotton were placed in the vials after the cocoons had been spun in order to prevent excessive dryness; however, these were not placed in vials with larvae in order to eliminate any possibility of the larvae becoming trapped and drowning. These rearings were carried out in a room open to the usual fluctuations in the summer temperatures

which occurred during the periods of this study (June 25-August 8, 1956, and June 19-July 18, 1958).

Color notes were made from microscopic observations of living larvae and these were supplemented by color photographs taken of freshly killed larvae. The drawings of Plates 5 and 6 were prepared by the author from these notes, from material fixed in Peterson's KAAD fluid (see Peterson, 1953, for details of preparation) and stored in alcohol, and from the examination of cleared specimens in temporary glycerine mounts with a binocular dissecting microscope and with a phase-contrast compound microscope. All measurements were made with an ocular micrometer calibrated with a stage micrometer. All indices of dispersion given in this paper are standard errors of the mean.

#### Description of The Developmental Stages

*Oviposition and embryonic development* — The three females used in this study were confined for periods of nine, fifteen and twenty-two days, during which times a total of ninety-four eggs was deposited. These were produced in a series of small lots which, with one exception, contained between one and eight eggs ( $\bar{x} = 3.53 \pm 0.53$  eggs/lot). In a single instance a freshly caught female, whose abdomen was noted to be tremendously swollen with eggs, laid twenty-seven eggs during her first twenty-four hours of confinement. Subsequent to this, however, the egg production of this female fell within the limits noted above. In all cases oviposition occurred at night and was never observed by the writer.

In addition to the ninety-four eggs produced by these females, the remains of an undetermined number of other eggs were noted which had, apparently, been partially consumed by the females. Six of the ninety-four eggs regarded as normal may also have been damaged by one of the females as these were slightly distorted in shape when first seen and none of them showed any signs of embryonic development. Three additional eggs although seemingly normal in all respects also failed to show any indication of development. Of the eighty-five eggs which showed apparent normal development, two failed to hatch.

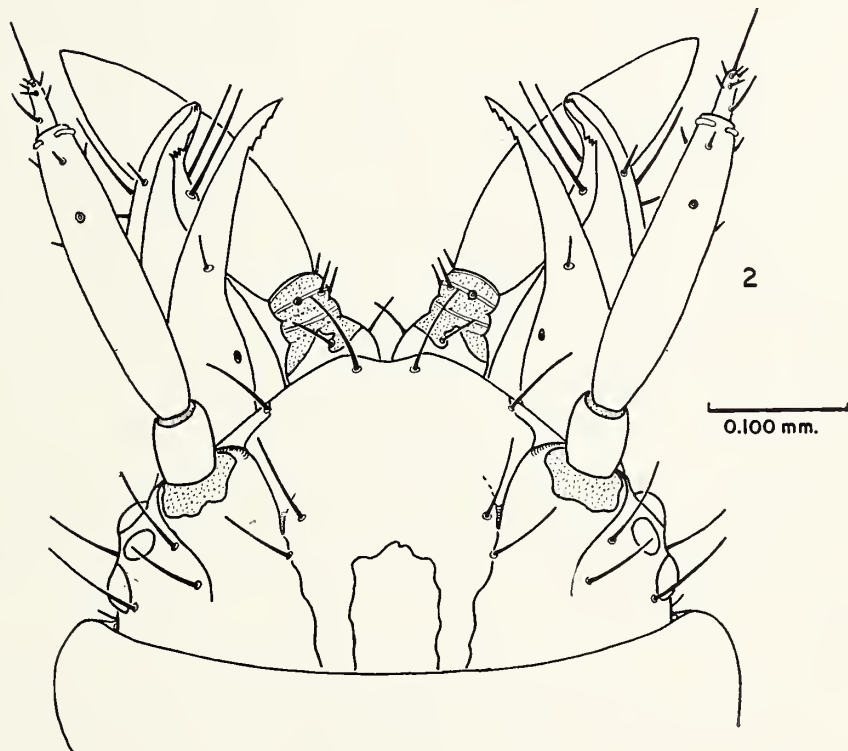
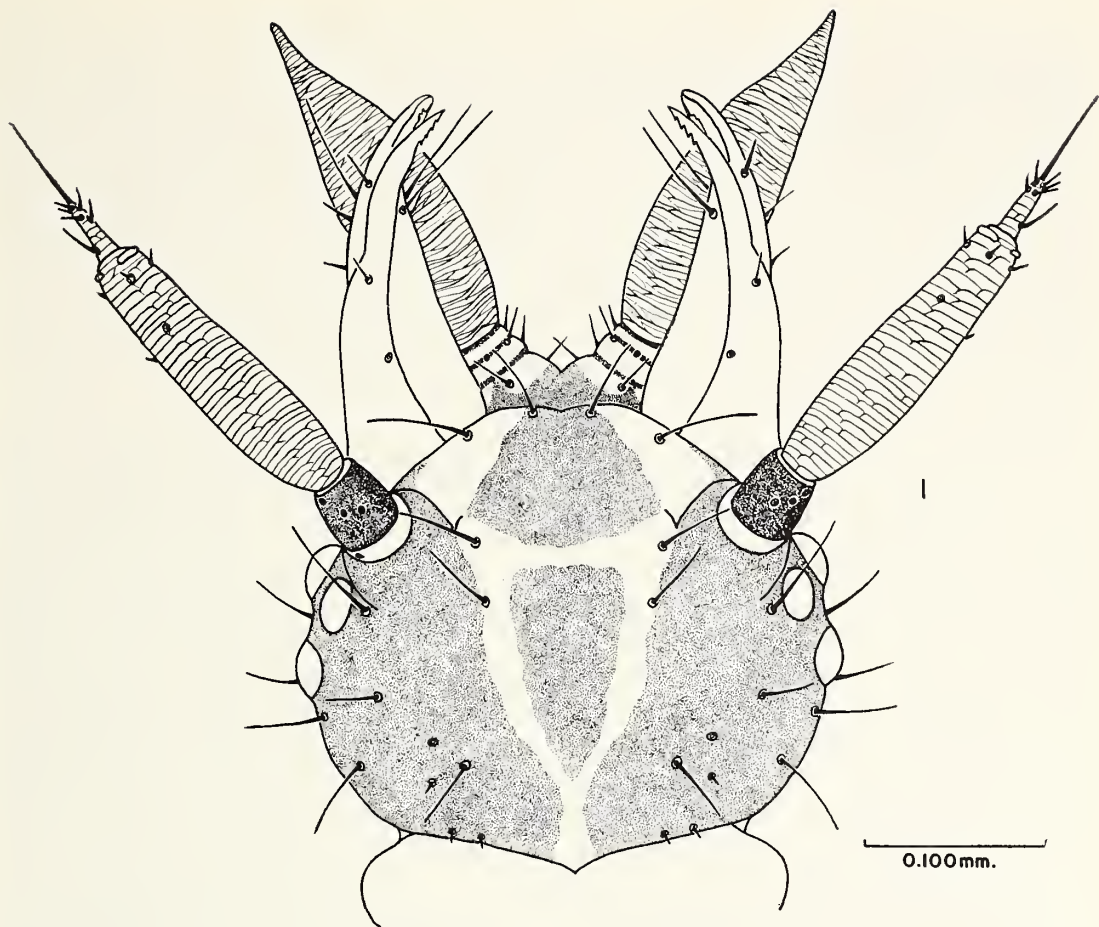
*Egg* — Approximately ellipsoid in shape, distinctly flattened on surface attached to substratum. Color, a pale greyish-yellow, becom-

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#### EXPLANATION OF PLATE 5

FIG. 1. Facies of head capsule of first instar larva, dorsal view.

FIG. 2. Head capsule and prothoracic "collar" of third instar larva, dorsal view.



MACLEOD — BORIOMYIA



ing greyish-brown as embryo develops. Micropyle sessile, flattened, chalk-white; a minute depression in center. Chorion, apparently smooth, but showing a minutely granulate texture at a magnification of 60X giving the impression of finely frosted glass. At higher magnifications an irregular imprinted pattern visible, attributed to the pressure of follicular cells of ovary by Killington (1946). Minute elevations and tubercles of chorion reported for several other hemerobiid genera by Killington (1936) lacking in *B. fidelis*. Size of a single unhatched egg: length — 0.7752 mm., greatest width — 0.3420 mm.

The eyes of the embryo become visible through the chorion after four days, while hatching takes place after about seven and one-half days of development ( $\bar{x} = 7.6 \pm 0.1$  days,  $N = 70$ ). As with other Neuroptera, emergence from the chorion is assisted by an egg-burster (figs. 5, 6) which forms a longitudinal ridge-like projection from the embryonic cuticle in the region of the clypeus. In a series of eggbursters derived from seven siblings which were studied in detail, the number of small teeth along the distal margin of the blade was found to vary between twenty-two and twenty-nine ( $\bar{x} = 25.0 \pm 0.9$ ). The two extremes are figured in figs. 5 and 6.

*First instar larva* (figs. 1, 3) — *Head capsule* ellipsoid, prominent, as wide as widest part of body; of a uniform grey color dorsally, this interrupted medially by a Y-shaped ecdysial cleavage line passing down to clypeal margins just medial to bases of jaws on either side; anterior, diverging arms of cleavage line cross connected by transverse area of pale cuticula at level of anterior tentorial pits delimiting a proximal frontal area and a distal clypeal area. Ocular area of head capsule antero-lateral, consisting of three, clear corneal swellings. Anterior two corneae each with one dark ommatidial element beneath; three additional ommatidia visible beneath posterior cornea. Latero-ventral surface of head capsule with usual pair of dark fuscous lines; the more dorsal, running between posterior tentorial pit and dorsal articulation of mandible, representing the subgenal sulcus, the more ventral, running from vicinity of posterior tentorial pit to maxillary component of jaw, representing cardo and stipes. Ventral surface of head capsule largely covered with shield-shaped mental region of labium.

*Antenna* three segmented, short, reaching only to tip of extended jaws. Basal segment dark, fuscous; short, only slightly longer than wide. Second segment comprising most of length of antenna, about five times as long as first segment. Third segment short, peg-like,

approximately of same length as basal segments; surmounted by a terminal seta slightly longer than segment itself. Distal two segments pale grey, showing usual irregular pattern of annular sclerotizations characteristic of antennae of hemerobiid larvae (fig. 1). *Jaws* slightly curved inwards; pale grey toward base, becoming dark brown for distal one-third of length. *Labial palpi* three segmented. Basal segment short, slightly wider than long; arising from largely fuscous, mound-like palpigeral swelling on antero-ventral surface of head capsule. Second segment of same shape as first segment. Both of basal two segments braced by a mid-segmental thin, dark, sclerotic ring. Distal segment of palpus elongate, inflated, reaching well beyond tips of jaws when extended forwards. Surface of distal palpal segment covered with same irregular pattern of annular sclerotizations found on distal two segments of antenna. Base of distal palpal segment braced by a thin fuscous ring.

*Thorax* — Prothorax with usual three subdivisions. Anterior subsegment short, transverse, forming a collar which overlaps posterior margin of head capsule only slightly. Posterior subsegment of prothorax with spiracle opening on lateral surface. Mesothorax with two subdivisions, metathorax consisting of leg-bearing portion only. Leg-bearing portions of thoracic segments with latero-dorsal sclerites reduced to mere vestiges, easily visible only upon examination of cleared specimens with phase microscope.

*Legs* largely pale except for thin fuscous sclerotizations partially encircling distal end of each coxa and each femur and proximal margin of each tibia. Pretarsus of all legs with usual clavate empodium extending from between the pretarsal claws.

*Abdomen* consisting of ten segments; first eight segments membranous, with a spiracle located laterally on each segment. Segment nine with a sclerite covering most of dorsal surface. Tenth abdominal segment largely covered with four small sclerites, one dorsally, one ventrally and one on each side. A pair of eversible pygopods contained within posterior portion of this segment.

Cuticle of thoracic and first eight abdominal segments of unfed larva a light pinkish-purple color through which color of body contents shows through as a light greenish-yellow background. Color of this background changing with the intake of food to an orange hue and then to a dark reddish-orange extending from middle of prothorax to second abdominal segment. Abdominal segments nine and ten pale grey throughout the first larval stadium with their sclerites just visible under a dissecting microscope. Aorta at first only

faintly visible between anterior prothorax and eighth abdominal segment, toward end of stadium becoming outlined by small isolated patches of developing fat body on either side of aorta. Fat body particularly well-developed in posterior subsegments of pro- and mesothorax.

Duration of first larval stadium —	3.4 ± 0.7 days (N = 33)
Length of unfed first instar larva (measured from clypeal margin of head capsule to posterior margin of dorsal sclerite of tenth abdominal segment) —	1.57 ± 0.12 mm. (N = 6)
Maximum width of head capsule (measured across ocular areas) —	0.3018 ± 0.0009 mm. (N = 7)

*Subsequent development of B. fidelis* — The head capsules of the second and third instar larvae (fig. 2) are quite similar to each other and differ from that of the first instar larva principally in being slightly wider in proportion to their lengths, which, combined with a lack of the curvature of the lateral margins of the head present in the first instar larva, gives the dorsal aspect of the head capsule a distinctly more quadrate appearance. In addition, the formerly fuscous regions of the clypeal area dorsally and the mental region of the labium ventrally of the first instar larva are pale in the subsequent larval instars so that only the frontal and parietal areas are darkened in these stages. The labial palpi are somewhat less inflated in appearance in the second and third instar larvae although they remain stouter than is usual in this family and reach well beyond the tips of the extended jaws.

The pretarsi of all legs of the second and third instar larvae lack the empodium present in the first instar larva, its place being taken by a delicate, fan-like arolium, arising from the dorsal surface of the pretarsus. Posteriorly, the tergal area of the ninth abdominal segment is no longer covered by a distinct sclerite in the second and third instar larva.

The body form of the second and particularly the third instar larva (fig. 4) becomes progressively swollen and grub-like with the development of a complex series of projecting lobes on the original segments of the body. The anterior subsegment of the prothorax remains short and collar-like and the head capsule becomes increasingly retracted within this portion of the body, so that although the head can be extended, the usual condition in which to find a living larva is with the



head withdrawn within the prothorax as far anteriorly as the bases of the antennae.

The body pattern visible to the eye is the result of the interplay between three somewhat variable features. The integument is lightly pigmented by a mottled pattern of a diffuse, purple color which overlies a much darker reddish-purple color due to the gut contents and hemolymph. Between these regions, the rapidly developing fat body creates an intricate series of patches which are nearly pure white in regions where the cuticle is faintly pigmented and which show as darker purple areas where the cuticle is more darkly pigmented. The exact pattern which the larva presents depends largely on the extent of the development of the fat body which gradually fills most of the available space of the hemocoel. One constant feature of this pattern is the presence of two white transverse bands across the body on the posterior subsegments of the prothorax and mesothorax due to the near lack of cuticular pigment in these regions. Ventrally the palpigera consistently include a small portion of the fat body within them which shows through the clear cuticle as a snow-white patch. In a dorsal view of a fully mature third instar larva (fig. 4) the fat body will be seen to have ramified throughout the body leaving only paired lateral "windows", from the posterior margin of the prothorax through the sixth abdominal segment, and the aorta in the dorsal midline through which the darker color of the hemolymph shows through.

A typically hemerobiid cocoon is spun by the third instar larva. This consists of a loose network of silk strands within which is located a more-compact inner cocoon which is, nevertheless, open enough to permit easy observation of the final stages of development. Pupation, metamorphosis and the eclosion of the adult all occur without any apparent cessation of development. The pupa is typical of that of many hemerobiids studied by the writer and, so far as can be ascertained, possesses no prominent features peculiar to *Boriomyia*. Post first instar development may be summarized as follows:

#### Measurements

##### Length

mature second instar larva —  $3.32 \pm 0.43$  mm. (N = 5)

mature third instar larva —  $4.53 \pm 1.05$  mm. (N = 5)

##### Maximum width of head capsule

second instar larva —  $0.3426 \pm 0.0063$  mm. (N = 4)

third instar larva —  $0.4073 \pm 0.0087$  mm. (N = 3)

##### Developmental times

second instar larva —  $3.5 \pm 0.7$  days (N = 20)

third instar larva —	
prior to spinning cocoon —	4.5 ± 0.1 days (N = 4)
post spinning —	6.9 ± 0.4 days (N = 4)
pupa —	10.7 ± 0.4 days (N = 3)

*Behavioral and ecological notes* — The young first instar larva is the only stage which is really active in the sense of seeking out prey. The older first instar larva and particularly the second and third instar larvae tend to remain immobile in some corner of the vial, a favored site for this position being between the cotton plug and the side of the vial. Aphids which move too close to the larvae are seized by a quick upward thrust of the jaws from below. The prey does not seem to be sucked as thoroughly as has been observed to occur with various species of *Hemerobius* and *Micromus* with which the author has worked. In these genera the prey is manipulated by the larva until the jaws have probed into every available corner of the body. The larvae of *B. fidelis* seem to simply suck the immediately available fluids of the prey with only incidental movement of the aphid.

One behavioral trait of the adult deserves some comment because of its bearing on the question of the affinities of *Boriomyia* discussed below. When at rest, the adult consistently assumes a distinctive position by placing the anterior surface of the head flat against the substratum with the antennae directed posteriorly between the legs and neatly clasped by both pairs of palpi. In many respects this position is reminiscent of the death-feigning position which many Neuroptera will assume if startled suddenly by a sharp vibration, although in this case the insect drops to the ground and lies on its side and even though the antennae are directed posteriorly beneath the body, they are not clasped by the palpi.

The natural ecology of this insect remains almost completely unknown as the writer has yet to locate any of the immature stages in the field. Of possible interest in terms of the habitat of this species is a collection of three males and two females taken in a short time in an open pine woods near Charleston, S. C. These were captured on April 20, 1957, and I am informed by the collectors, Messers. Ivan

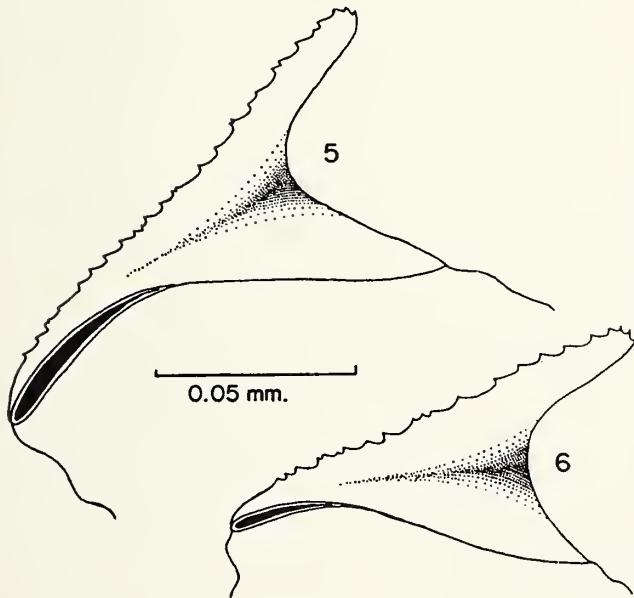
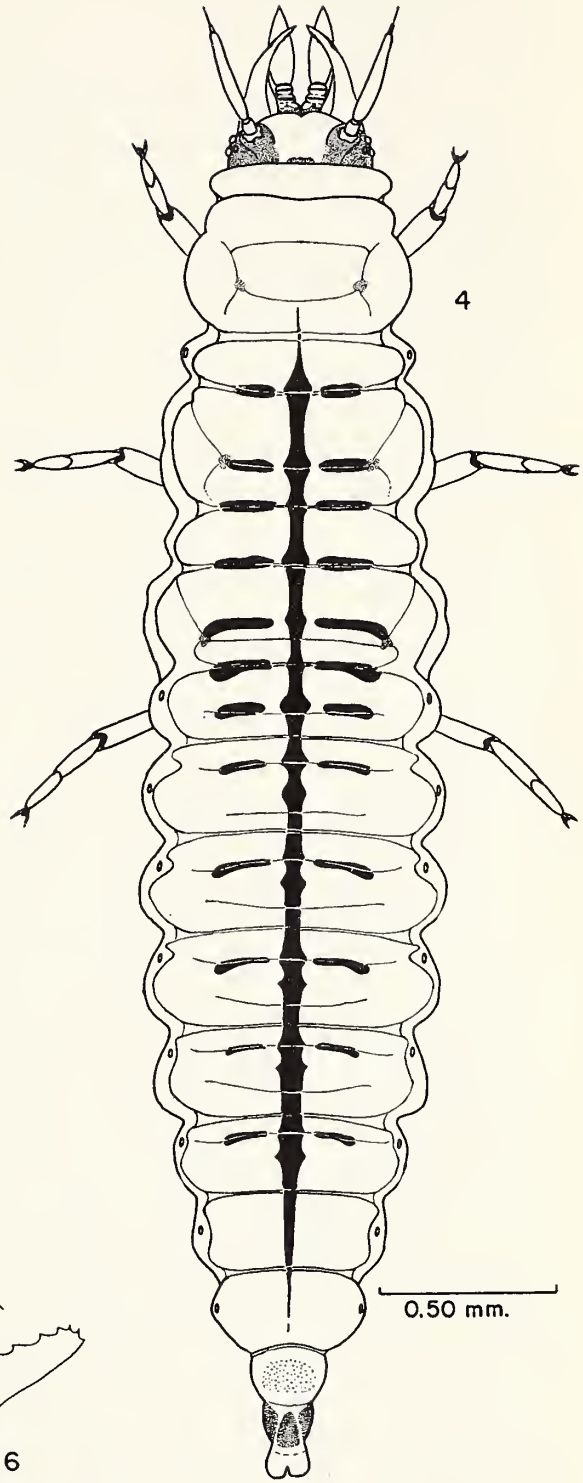
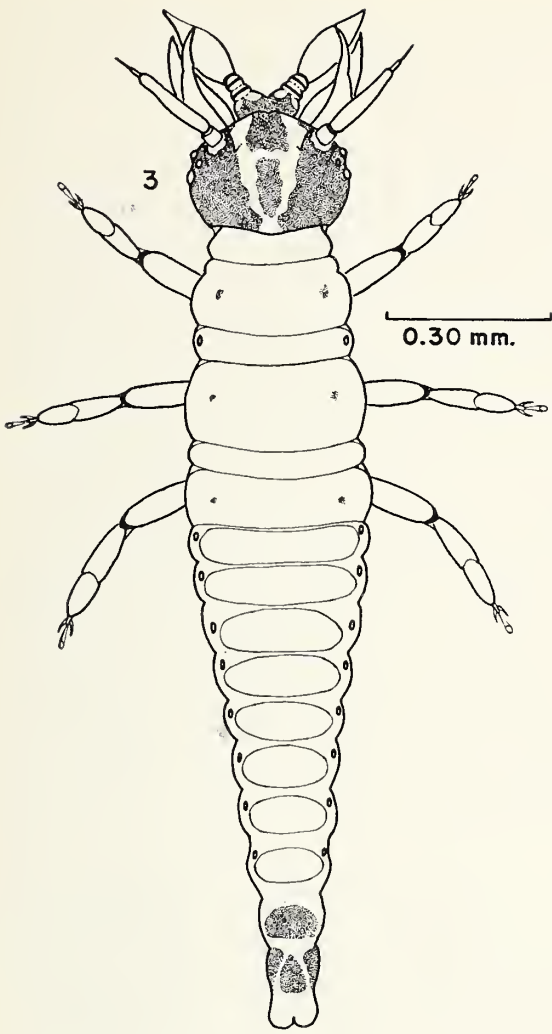
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EXPLANATION OF PLATE 6

FIG. 3. First instar larva, dorsal view.

FIG. 4. Mature third instar larva, dorsal view. The latero-dorsal sclerites of the larvae shown in figs. 4 and 5 are depicted as seen by the microscopic examination of cleared specimens. In life these sclerites are nearly invisible.

FIGS. 5 and 6. Egg bursters, showing extremes in the number of teeth, lateral view.



MACLEOD — BORIOMYIA



Huber and Paul E. Spiegler, that the insects seemed to be associated with piles of dead branches of yellow pine (*Pinus australis* Michx.) on the ground.

#### The Taxonomic Status of *Boriomyia*

A series of nomenclatorial mistakes combined with several taxonomic errors in evaluating published descriptions have obscured the true relationships of this genus within the Hemerobiidae. The name *Boriomyia* appeared for the first time in 1904 when Banks included his previously described species *Hemerobius fidelis* and *H. speciosus* under this generic name. A formal description of *Boriomyia* as a new taxon appeared in 1905 in Banks' Revision of the Nearctic Hemerobiidae. In this work, six Nearctic species were included in this genus in addition to *B. fidelis* and *B. speciosa*, one of these, *H. disjunctus* Banks, being designated as the type species. Subsequently additional Nearctic and numerous exotic species were referred to *Boriomyia* by various workers. In 1930 Banks, recognizing that *B. fidelis* and *B. speciosa* did not form a homogeneous group with the remainder of the species placed in *Boriomyia*, erected a new subgenus, *Allotomyia*, for these two species and subsequently (1935) treated this group as a full genus.

Killington (1937) agreed that the two groups of species recognized by Banks should be separated generically, but pointed out that since the name *Boriomyia* had been validated in 1904 when it was used in combination with two already-described species, Banks' 1905 designation of *H. disjunctus* as the type of *Boriomyia* was in violation of the Rules since this species was not included in *Boriomyia* when this name was originally validated. Designating *H. fidelis* as the type species of *Boriomyia*, Killington proposed the name *Kimminsia* for the British species formerly included in *Boriomyia*, the remaining non-British species of the former *Boriomyia* (other than *B. speciosa*) presumably being also referable to this genus. A Palearctic species, *H. betulina* Strøm was selected as the type of *Kimminsia*. These two genera were considered to be separated by venational features which had already been noted by Banks. These views were reiterated by Killington in 1937b. Tjeder (1941) in a critique of Killington's work and without specimens of *B. fidelis* to study felt that the venational distinctions which had been drawn between *Boriomyia* and *Kimminsia* were not sufficient to warrant generic separation. Subsequently in a long series of papers (1943a, 1943b, 1944, 1945, 1951, 1953a, 1953b, 1954, 1955, 1960), he has continued to use the name *Boriomyia* to cover the *Kimminsia* group of species.

Circumstances have thus conspired to make it seem that *Kimminsia* is a taxonomic segregate from the closely allied genus *Boriomyia* and that the question of whether to recognize one genus or two simply depends on the emphasis which one places on the differences in the venation of these two groups. Actually this is misleading, for as long ago as 1940 Carpenter pointed out that the differences between these two genera are much more far-reaching than had been suspected, involving not only consistent differences in venation, but fundamental differences in the basic organization of the genitalia of both sexes. Indeed, it was Carpenter's contention that the true affinities of *Boriomyia* lie not with *Kimminsia* at all, but rather with the genus *Megalomus*.

The findings of the present study lend complete support to this view. Details of the biology of the Palaearctic *Megalomus hirtus* (Linné) including several excellent figures of the larvae have been published by Killington (1934, 1937a), while the present author has reared the immature stages of an unidentified species of *Megalomus* from Mexico. In addition, modern figures and descriptions of larvae of species of *Kimminsia*, *Wesmaelius*, *Psectra*, *Symphorobius*, *Hemerobius*, *Micromus*, and *Drepanepteryx* have also been provided by Smith (1923, 1934), Killington (1936, 1937a, 1946) and Fulmek (1941) and as the writer has been able to rear or study larvae of species of the last four of these genera, detailed comparisons of a variety of larval types of the Hemerobiidae have been possible.

Only in very general features shared by the larvae of all known hemerobiids do those larvae of *Micromus*, *Hemerobius*, *Wesmaelius* and *Kimminsia* which are known bear any close structural resemblance to the larvae of the remaining groups and they will not be discussed further. A series of striking similarities is to be found in the larvae of *Boriomyia* and *Megalomus* involving the shape of the labial palpi, the form of the terminal segment of the antenna and in the appearance of the mature larva. The swollen, inflated shape of the labial palpi, particularly striking in the first instar larvae, but noticeable in the later two instars as well, is present only in *Symphorobius* and *Psectra* in addition to *Megalomus* and *Boriomyia* although it has never been observed to reach the extreme degree in the first two of these genera that it does in the latter two. The extremely shortened terminal segment of the antenna, surmounted by an apical seta nearly as long as or longer than this segment, is known to the writer only in *Boriomyia* and *Megalomus*. A much less drastic reduction in the terminal segment occurs in *Symphorobius*, but here the segment is somewhat flask-



shaped as it is dilated basally and the terminal seta is much shorter than the length of the segment. The swollen, physogastric appearance of the mature larva has probably been produced several times independently in the Hemerobiidae in correlation with a more sessile mode of larval life. The condition has been approached in *Symphorobius*, *Psectra* and *Drepanepteryx* although in no species of these groups known to the writer does it reach the extreme which has been produced in *Boriomyia* and *Megalomus*. Associated with this inflated, sessile larva is the habit of carrying the head deeply retracted within the prothorax, developed to an extreme degree in *Boriomyia*, *Megalomus*, and *Drepanepteryx*, and the suppression of the latero-dorsal sclerites of the thoracic segments. In *Symphorobius*, *Psectra* and *Drepanepteryx* these sclerites have been strongly reduced on the meso- and metathorax, but those of the prothorax have remained relatively large and prominent. In *Boriomyia* and *Megalomus* alone have the prothoracic latero-dorsal sclerites been reduced to the point where they are difficult to demonstrate. Killington states that these sclerites are lacking on the prothorax of *M. hirtus* although it seems possible that close scrutiny might reveal their presence since their remnants can just be detected in *B. fidelis* as well as the Mexican species of *Megalomus* studied by the writer. One additional point of resemblance between members of *Boriomyia* and *Megalomus* is to be found in the peculiar rest position of the adult noted above for *B. fidelis*, which was observed by the writer in adults of the Mexican species of *Megalomus* studied, and noted by Killington (1937a) in *M. hirtus*.

The writer has presented the evidence for the relationship of *Boriomyia* and *Megalomus* to Mr. Tjeder who, it has been noted, previously felt that there were insufficient characters to separate *Kimminsia* from *Boriomyia*. In addition, specimens of *B. fidelis* were supplied for his study. Mr. Tjeder has informed the writer (*in litt.*) that he is now in full agreement with the placement of *B. fidelis* near *Megalomus* (indeed, he feels that this species must be placed in *Megalomus*). He has, however, continued to use the name *Boriomyia* for the *Kimminsia* species (Tjeder, 1960), arguing (*in litt.*) that Banks' genotype designation for *Boriomyia* in 1905 must be considered valid. The writer is of the opinion that the Rules are perfectly clear on this point and that the validation of Banks' designation would require an action of the International Commission to set aside the Rules. It should be noted that in addition to Killington (1937a, 1937b) and Carpenter (1940), Fraser (1940, 1942, 1959), Friedrich (1953),



Nakahara (1956, 1960) and Parfin (1956) have used the names *Boriomyia* and *Kimminsia* in the sense adopted in the present paper.

Concerning the question of the validity of *Boriomyia* as a genus distinct from *Megalomus*, this must await a study of the type species of *Megalomus*, the Palearctic *M. tortricoides* Rambur, as well as a wider variety of species of this genus than has been available to the present writer. Carpenter (1940) was able to separate these genera on the basis of the position of the radial cross vein with reference to the point of origin of R5 in the hindwing, although he felt that species which were intermediate in this character would probably be found. Recently Nakahara (1960) has observed that *B. fidelis* possesses a median lobe of the fused parameres of the male genitalia (present also in *B. speciosa*) which is said to be lacking in species of *Megalomus*. A second character of *B. fidelis* considered by Nakahara to be of generic importance, the basally fused and apically bifucrate "aedeagus", is present also in at least the Nearctic species *M. minor* Banks which is a *Megalomus* by the criterion of a lack of the median lobe of the fused parameres.

It is the opinion of the present writer that stable generic limits in the Hemerobiidae usually involve greater differences in the basic ground plan of the male genitalia than those aduced by Nakahara, and frequently correlate with differences in the structure of one or more of the immature stages and in constant venational features as well. In these respects, *Boriomyia* seems poorly distinct from *Megalomus* and will probably fall as a synonym of this genus.

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THE FEMALE OF *INOCELLIA PILICORNIS* CARP.  
(NEUROPTERA: INOCELLIIDAE).<sup>1</sup>

BY F. M. CARPENTER  
Harvard University

The snakefly, *Inocellia pilicornis* Carpenter, was described in 1959 (*Psyche*, 65:56-58) from three males collected in the states of Nuevo Leon and Tamaulipas, Mexico. These males were unique among known Raphidiodea in possessing moniliform antennae, their segments bearing long radiating setae, arranged in a definite pattern. In July, 1960, Dr. H. F. Howden, who collected one of the males of the original set, found the first known female of this species, along with another male, very near the type locality. It now turns out that the female also has moniliform antennae, but the hair covering of the antennae, although distinctly different from that of other species, is not as similar to that of the male of *pilicornis* as might be expected.

The color markings of the female are like those of the male type, except that the median white marks on the meso- and metanotum and the abdominal tergites are in the form of patches instead of a continuous stripe. The forewing is 6.8 mm. long and 1.8 mm. wide; the

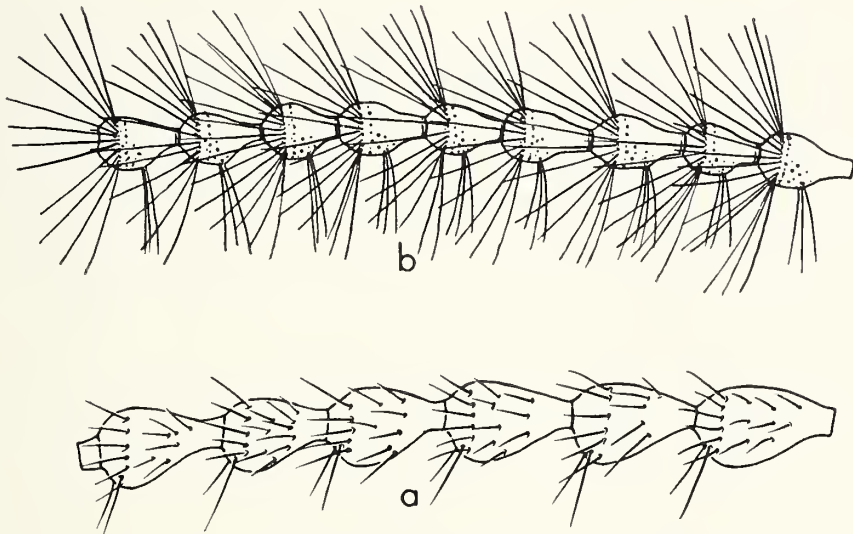


FIGURE 1. Portions of antennae of *Inocellia pilicornis* Carp. a, female, x 140 (specimen from Chipinguy Mesa); b, male, x 55 (holotype).

pterostigma, having a maximum length of 1 mm. and a width of a little less than .5 mm., is relatively shorter than in the male. The wing venation is like that of the holotype, illustrated in my account

<sup>1</sup> Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.



of the species. The antennae of the female are 3.7 mm. long. Each consists of 42 segments, instead of 60 as in the male, and the individual segments are smaller than in the male. The hairs on the antennal segments are shorter than those of the male and form a different pattern (figure 1). A ring of twelve conspicuous setae is located near the distal end of each segment and two prominent hairs occur on one side of each segment, slightly distal of the ring just mentioned; these two hairs are a little longer than the hairs comprising the ring and they almost always project in the same direction, as shown in figure 1a. The more proximal part of each antennal segment includes about 20 short hairs which are arranged somewhat irregularly and which do not form a second ring, as in the male. The ovipositor of the female is like that of other *Inocellia*; in the specimen at hand it is 5.5 mm. long. The body length of the female, exclusive of the antennae and ovipositor, is 6 mm.

It seems virtually certain that this new female, which was collected at Chipinguy Mesa, near Monterrey, Nuevo Leon, Mexico, July 28, 1960, belongs to *pilicornis*. A male, collected by Dr. Howden at the same time, is like the holotype, except that the white markings on the abdominal tergites are somewhat smaller.

Although the female turns out to have antennal characteristics as distinctive as those of the male, I do not believe that a new genus is necessary for this species. Other features, including the abdominal structures of the male and female, are similar to those of other species of *Inocellia*.

A NOTE ON THE PREY AND A NESTING SITE OF  
*CERCERIS TRUNCATA* CAMERON (HYMENOPTERA:  
SPHECIDAE: PHILANTHINAE)

BY F. G. WERNER

Department of Entomology, University of Arizona

This species seems to be very rare or extremely local in southern Arizona; Dr. H. A. Scullen, who has kindly provided the identification, held it as undescribed until he discovered that it had been described from Mexico by Cameron. However, there is a rather extensive nesting site in my own yard, at 1247 N. Warren Ave., Tucson. During the past four years I have been able to observe the habits of the species regularly and have found that the females store only beetles of the family Bruchidae (Mylabridae). The species stored at this site are all of medium size, and probably all come from leguminous trees and shrubs in the neighborhood. In order of abundance the bruchids gathered are: *Algarobius prosopis* (Lec.), *Mimosestes protractus* (Horn), *Mimosestes amicus* (Horn) and *Neltumius arizonensis* (Schffr.); this is roughly the relative abundance of these species when they are taken in general collecting. The most abundant source tree in the neighborhood is the so-called Mexican palo verde, *Parkinsonia*, which is planted extensively, blooms in the spring and has mature pods by mid-July, when the wasps become active.

The site occupied is on flat ground in the southwestern corner of the lot, about 10' x 10', shielded on south and west by a five-foot wall and partly shaded by large oleander bushes; the soil is bare and consists of well-packed fill about eight inches deep over caliche; almost all of the water that reaches it comes from rainfall. Activity of the wasps was checked weekly in 1958, when the first swarms of males and starts of nests were observed on July 20 and could not have started more than a week before this date. The males fly continually during the day, just over the oleander bushes and nearby vegetation, stopping occasionally to rest. Hundreds of individuals are involved in these flights. Smaller numbers, usually about twenty, patrol the nesting site, flying about four inches above the ground, and attempt copulation with females flying in the area or returning to their nests with prey. I could not discover where the males went at night. The females dig small holes, either bare or with a low mound up to 1½" in diameter. Most of their flying and provisioning activity occurs in the morning but even then the principal activity seems to consist of sitting in the nest entrance with only the front of the head exposed. By noon all

is quiet and most of the nest entrances are loosely plugged, only the occasional pushing up of dirt in some of the nests indicating that digging may be in progress. Marked nests were open for two or three days, except when they were plugged with loose dirt in the afternoon, and one nest was open at least five days. The nests were hard to keep track of during the period of observation because of frequent rains. By July 27 there were 55 nests in a marked area 4' x 4' and there were at least this many active during the rest of the summer. *Solenopsis* ants raided part of the site but there was no sign of social or other parasites.

Individual nests were dug up but none could be excavated completely. The holes could be followed down to about 4", where they seemed to end in loose dirt; below some of them, at 5" to 6", a cluster of up to ten bruchids, with an egg or larva, indicated where the cell must have been. The cells must be of very loose construction. Nesting activity and male swarming continued from mid-July well into September in 1958, gradually diminishing during the latter month. A similar schedule has been maintained in the two succeeding years. No adults have been seen until July, the normal starting time of the summer monsoon season.

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THE TYPE SPECIES OF THE ANT GENUS *EURHOPALOTHRIX*. — In our paper, "A world revision of the ant tribe Basicerotini," *Studia Entomologica*, Petrópolis, Brazil, 3: 202, 1960, we erected a new genus *Eurhopalothrix* to receive certain species formerly placed in *Rhopalothrix* Mayr, along with some new species. Through inadvertance, no type species was cited for the new genus, and we therefore here designate *Eurhopalothrix bolaii* (= *Rhopalothrix bolaii* Mayr, 1870) as type species of the genus *Eurhopalothrix* Brown and Kempf. — W. L. BROWN, JR., Department of Entomology, Cornell University, Ithaca, N. Y., and W. W. KEMPF, O. F. M., São Paulo, Brazil.



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The illustration on the front cover of this issue of *Psyche* shows the head of the worker of *Myrmoteras karnyi* Gregg. The original, drawn by Dr. R. E. Gregg, was published in *Psyche*, Volume 61, p. 21, 1954.

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# PSYCHE

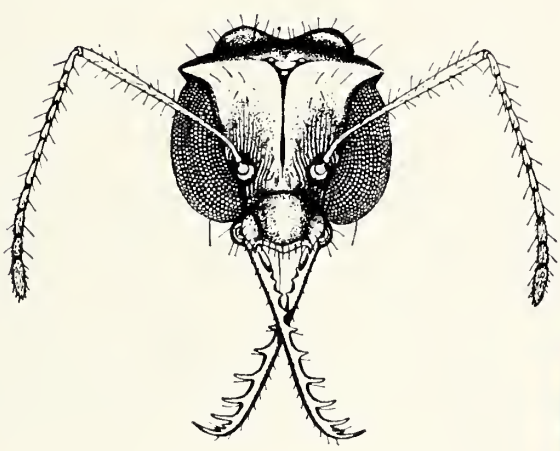
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## CONTENTS

A Study of <i>Bembix u-scripta</i> , a Crepuscular Digger Wasp. <i>H. E. Evans</i> .....	45
Defense Mechanisms of Arthropods. II. The Chemical and Mechanical Weapons of an Earwig. <i>T. Eisner</i> .....	62
A Triassic Odonate from Argentina. <i>F. M. Carpenter</i> .....	71
On the True Nature of the Azygethidae (Chilopoda: Geophilomorpha). <i>R. E. Crabill, jr.</i> .....	76



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# PSYCHE

Vol. 67

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No. 3

## A STUDY OF *BEMBIX U-SCRIPTA*, A CREPUSCULAR DIGGER WASP

BY HOWARD E. EVANS  
Museum of Comparative Zoology

One of the most characteristic features of the digger wasp genus *Bembix* is the almost complete obliteration of the ocelli. Two North American species, *arcuata* and *u-scripta*, provide the only important exceptions to this, and these species also possess several other structural features which set them aside from all other species of *Bembix*. A few years ago I presented some very incomplete data on a colony of *u-scripta* in southern Texas, suggesting at the same time that the behavior of the species ought to prove of unusual interest because of its apparently primitive structural features (Evans 1957). I have recently made further studies of this same colony and also of another small colony in southwestern New Mexico, thus providing an unusual opportunity to compare the behavior of two widely separate colonies of an uncommon species of distinctly localized distribution. These studies also demonstrate that *u-scripta* has one very remarkable feature in its behavior: the females hunt and provision only in the dusk, around and after sunset. Throughout the higher Hymenoptera, large ocelli are distinctly correlated with nocturnal flight. It seems very probable that the preservation of functional ocelli in this species represents an adaptation for flying in the twilight.

A second problem concerns the identity of *Bembix arcuata*: is this in fact a distinct species from *u-scripta*? The Texas colony was located not too far from the type locality of *arcuata*, the New Mexico colony not far from that of *u-scripta*. The New Mexico wasps had a much more extensively yellow color pattern (more like *u-scripta*), but there was considerable color variation in wasps from both localities. In fact, on the basis of the Texas locality alone, I have already tentatively placed *arcuata* in the synonymy of *u-scripta* (Evans 1959). Clearly it will be of interest to see what light behavior sheds on this matter.

In this paper I shall first consider the structural peculiarities of *Bembix u-scripta* and also the differences which are supposed to sepa-

rate *u-scripta* and *arcuata*, since this information lends more significance to the behavioral studies. There follows a discussion of the ethology of the two colonies studied and finally a brief statement of conclusions. The studies of the Texas colony were made with the assistance of a grant from the National Science Foundation, while those of the New Mexico colony were made during tenure of a fellowship from the John Simon Guggenheim Memorial Foundation. I am indebted to Dr. M. A. Cazier, Director of the Southwestern Research Station of the American Museum of Natural History, for making available the facilities of that station during the summer of 1959. I am also indebted to Drs. Cheng Shan Lin and Oliver S. Flint for assisting me in the field work on the Texas colony. The dipterous prey of the *Bembix* have been identified by the following specialists, to all of whom I am much indebted: W. L. Downes, R. H. Foote, M. T. James, C. Martin, R. H. Painter, L. L. Pechuman, H. J. Reinhard, C. W. Sabrosky, Y. Sedman, H. V. Weems, and W. W. Wirth.

#### MORPHOLOGICAL CONSIDERATIONS

The important structural features of *Bembix u-scripta* and *arcuata* are given as follows by Parker (1917, 1929):

1. Ocelli unusually well developed and apparently functional (posterior ocelli with lenses clear, convex, circular except truncated laterally; anterior ocellus in form of a fairly wide transverse band).
  2. Second transverse cubital vein of front wing only slightly curved (in other species of *Bembix* it is sharply bent).
  3. Male with basal segment of middle tarsus distinctly curved, its inner surface beset with several stout spines; middle femora of male dentate, middle tibiae ending in a spine-like process.
  4. Male with abdominal sternites devoid of processes, but seventh with a pair of carinae which diverge basally.
  5. Labrum with a small median elevation (both sexes).
  6. Basal segment of front tarsus with an unusually large number of comb-spines (8-10) (both sexes).
  7. Scape of male much thickened.
  8. Pygidium of female slightly rugose and with strong lateral ridges.
  9. Pattern of yellow maculations unusually strongly developed.
- To these nine characters should be added another:
10. Apical tergite of male with deep longitudinal lateral incisions which cut off a pair of appendages which much resemble the parameres of the genitalia.



All of these features are unique or shared with only a very few other species of *Bembix*. Some of them, though unique in *Bembix*, are shared (at least in some measure) with species of the more primitive bembicine genus *Stictiella*; these include characters 1, 2, and 3 above. Lohrmann (1948) has studied coloration in *Bembix* at some length, and has concluded that reduction in color pattern (i.e., less yellow) is correlated with structural advance; thus, on these grounds, character 9 should also be regarded as primitive. The remaining six characters should be regarded as specializations within the genus. However, those which involve the female (5, 6, 8) are not absolutely unique and the remainder (4, 7, 10) involve male secondary sexual characters, which are remarkably plastic in the bembicine wasps. The more striking features thus suggest that these wasps do, in fact, retain several features which may have been characteristic of the ancestral *Bembix*, though obviously an assortment of specializations of a less striking sort have been acquired.

In describing *Bembix arcuata*, Parker (1917) listed the following characters by which it differed from *u-scripta* (Fox 1895):

1. The nature of the male "genital stipes" (i.e., parameres), which are much more slender and attenuate than in *u-scripta*.
2. Mesosternum marked with black (yellow in *u-scripta*).
3. Abdominal sternites 2-4 with small lateral yellow spots (in *u-scripta* these are more extensively yellow and there is some yellow on the sternites behind these).
4. Apical sternite black (yellow in *u-scripta*).

Since the first of these characters involves an important structural distinction, it should be considered first. Parker based his interpretation of *u-scripta* on the type specimen, one other male, and four females. I have examined these two males and find that it is true that the parameres are less attenuate than in the type of *arcuata* — or in males from both colonies studied. However, the difference is slight and relative, and I cannot agree with Parker that the genitalia "differ widely". Parker's figures tend to exaggerate the differences between the two: yet the differences cannot be entirely reasoned away.

Study of the color characters supposed to separate these species reveals that while they may apply to the type specimens, they are by no means absolute when additional specimens are considered. The type of *u-scripta* is almost wholly yellow, that of *arcuata* predominantly black. Specimens from the Texas colony which I studied are close to *arcuata*, but exhibit enough variation to cause confusion in using Parker's key.

Specimens from the New Mexico colony are close to *u-scripta*, but again they do not agree perfectly and there is much variation to be considered. When specimens from other localities are considered also, it becomes obvious that the extent of maculation varies in a complete spectrum all the way from "*arcuata*" to "*u-scripta*". I have tabulated the variation in two color characters (Tables I and II), selecting these two merely because Parker emphasized them. I have also studied other characters, such as the very noticeable variation in the development of the U-shaped markings on the mesoscutum, with very similar results. This species has not been collected in enough localities to enable one to be certain of the relation of geography to color pattern, but the available evidence suggests a northwest to southeast cline.

TABLE I. COLOR OF APICAL STERNITE OF FEMALE

Locality	Number of Specimens		
	Largely yellow apically	Tip yellow all across	Tip yellow on sides
California <sup>1</sup>	2		
Wellton, Ariz.	1		
Rodeo, N. Mexico	2	7	
Lordsburg, N. Mexico		4	
Albuquerque, N. Mexico	1		
Mexcala, Guerrero		2	
Pt. Isabel, Texas		1	42

TABLE II. COLOR OF MESOSTERNUM OF MALE

Locality	Number of specimens			
	Almost wholly yellow	Black spots posteriorly	Posterior .6-.8 black, some on pleura	Sternum and pleura black except anterior border
Tucson, Ariz. <sup>2</sup>	2			
Rodeo, N. Mex.		9		
Lordsburg, N. Mex.		1		
Mesilla, N. Mex. <sup>3</sup>		1		
Pt. Isabel, Tex.		9	24	5
Cotulla, Tex <sup>4</sup>			2	1

<sup>1</sup> Paratypes of *u-scripta*, bearing no further locality data. These specimens otherwise have the yellow maculations generally reduced as compared to Arizona specimens, and also have a large black spot on the clypeus.

<sup>2</sup> Types of *u-scripta*

<sup>3</sup> Paratype of *arcuata*

<sup>4</sup> Type and paratypes of *arcuata*

## OBSERVATIONS ON COLONY AT PORT ISABEL, TEXAS

This colony was first discovered June 23-25, 1956, but at this time it was evident that the wasps had nearly completed their activities for

the season. Only a few females with badly worn wings and mandibles were still active, and even these ceased activity after June 25 (Evans 1957). I returned to the area May 8-11, 1958, and found the wasps at the peak of their activity. C. S. Lin revisited the area June 3-7 of the same year and found that the males had disappeared and that nesting of the females was more advanced. Thus in this area the wasps first become active in early May (probably in late April) and the females remain active for six to eight weeks. The species is certainly univoltine, as cocoons collected June 23, 1956, gave rise to adult males and females in late March, 1957 (they were overwintered at room temperature at Ithaca, N. Y.).

The colony was located on the protected beach of Laguna Madre about five miles west of Port Isabel. The soil here is a rather heavy, dark sand containing pieces of shells and bits of organic matter (chiefly bits of decayed seaweed and beach halophytes). This beach is occasionally swept by waves from Laguna Madre (which is salt), especially during the fall and winter, but there is little tide action. On certain parts of the beach there are extensive patches of low vegetation, chiefly *Salicornia*, certain composites, and various grasses. The wasps occurred only in bare places on the middle of the beach, that is, from about 8 to 15 meters above the high water mark but below the banks at the upper edge of the beach.

*Behavior of males.* — Males were observed only during early May, 1958, but at that time they were very abundant. Each morning we entered the area about 0800, and at this time the males were already engaged in their "sun dance". Each male flew rapidly in loops, figure eights, and irregular patterns only 2-6 cm. above the sand surface, much as in *Bembix cinerea* (Evans 1957). By 1030 some reduction of males could be noted, and by 1115 each day the last male had disappeared. By 1500 a few males were once again active, and from 1600-1900 each day there was a second though somewhat less populous sun dance. The greater part of this sun dance occurred in a small area somewhat apart from the major nesting area of the females, although males often flew briefly over various parts of the beach before rejoining the sun dance.

During the middle of the day, and also at night, the males enter short, oblique burrows in the sand and throw up a small barrier of sand behind them. These burrows tend to be grouped in small clusters. They are dug by the males, but the males usually re-enter an old burrow rather than digging a new one each day.



During the sun dance the males fly, at least some of the time, with their middle and hind legs hanging down. When they approach a female they attempt to descend upon her from above and grasp her with the legs. During this time the pair rise a meter or two in the air, then, if the female is receptive, descend to the ground, where copulation occurs. During mating, the male rests on top of the female, often buzzing his wings (perhaps to maintain balance), while the female remains completely motionless, her wings being clamped in place by the middle legs of the male. The spines of the middle femora of the male apparently fit over the wing-bases of the female, while the arcuate middle tarsi of the male appear to fit over the coxae of the female. The front legs of the male extend rigidly forward and the hind legs rigidly backward during copulation; neither pair is in contact with the female or the substrate. The male genitalia are of course extruded and work up and down rhythmically until they gain entry into the genital chamber of the female. The longest copulation observed lasted two minutes.

*Nesting behavior of females.* — Most of the females were concentrated in one large bare area on the beach. In this area there were at least 100 nests, many of them only a few centimeters apart. Nests on the periphery of the colony tended to be more widely separated. Here and there along the beach there were other smaller groups of nests, so that the total may have approximated 200.

Most new nests appear to be started in the morning (0900-1030). The female is able to dig about 10 cm. an hour, but because of frequent periods of inactivity, especially at midday, the greater part of a day is generally required to complete a nest. Much use is made of the mandibles in loosening the soil, and this results in much wear of the mandibles as the season progresses. The soil which is loosened is scraped back with the front legs in the usual manner of wasps of this genus. When the burrow is a few centimeters deep, the wasp allows the soil to clog the entrance, sometimes for long periods, before finally coming out and scraping it back from the entrance. The digging movements appear rather slow as compared to other species of the genus.

As digging progresses, a large mound of sand accumulates behind the entrance. This mound measures, on the average, about 18 cm. long, 10 cm. wide, and 1.5 cm. high. When the nest is completed, some individuals level this mound. The leveling movements are very characteristic and unlike those of any other known *Bembix*. The fe-

male (without closing the nest entrance) backs out to the middle of the mound of sand, then walks forward in a straight line scraping sand backward. When she arrives at the nest entrance, she turns to one side at a  $45-90^{\circ}$  angle and continues for another 1-3 centimeters, still scraping sand, which now falls over or slightly beyond the nest entrance. She then flies back to the center of the mound and repeats

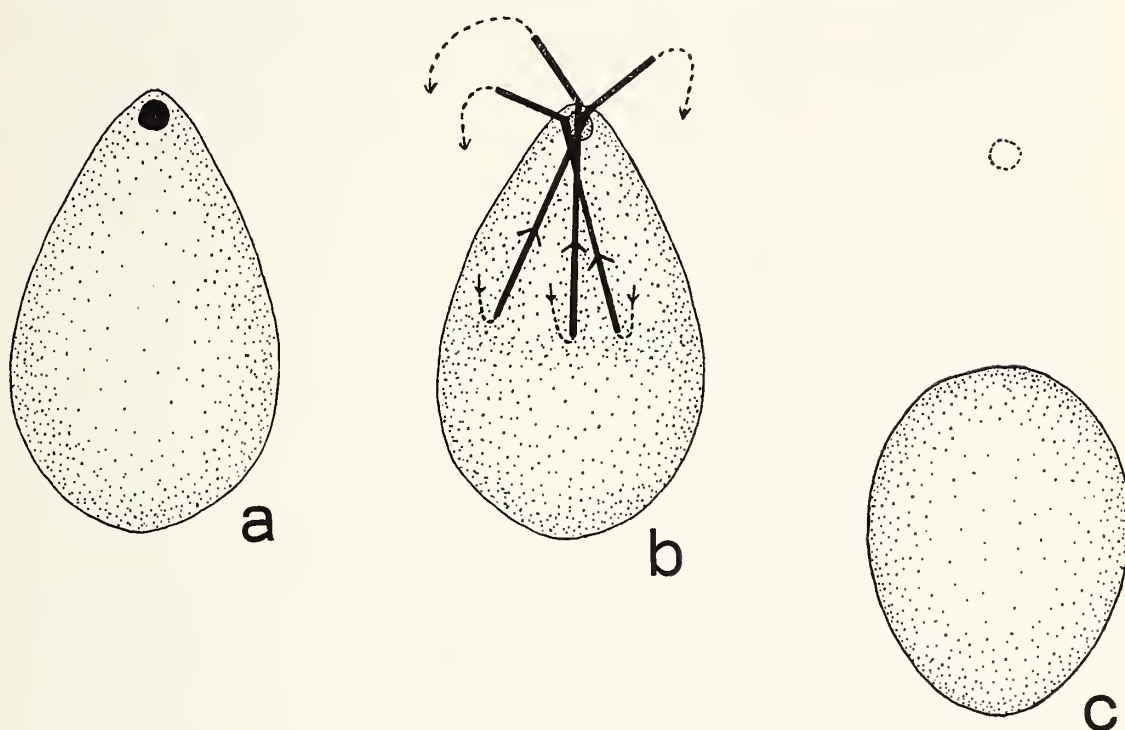


Fig. 1—Diagram of leveling movements of *Bembix u-scripta*. In *a* is shown the completed mound of earth with the open (blackened) nest entrance at one end. In *b* three typical routes of a female leveling the mound are shown; dashed lines indicate movement by flight. In *c* is shown the final product, with the nest entrance covered (indicated by dashed line) and mound well removed from entrance.

the performance. After a time this results in the soil immediately in front of and around the nest entrance being well scattered and flattened. However, the extremity of the mound of soil has not been touched and has in fact been added to. Thus the net result of the leveling movements is to move the bulk of the accumulated soil from the nest entrance to a position well removed from it (by about 8-12 cm.) (fig. 1).

In this colony relatively few individuals leveled the mound. We estimated that about 25% leveled, while some others exhibited weak and indefinite leveling movements. The remaining members of the colony left the mound of earth completely intact. As additional cells are added to the nests, some additional soil is added to the mound;

as a result nests containing several cells often have a very large mound of earth (as much as 3 cm. high). It was our impression that individuals that level following completion of the initial cell also level after each additional cell, but our data on this point are weak.

When the nest or new cell is completed, and leveling is completed if this is to occur, the female flies off to obtain her first fly, on which the egg is laid. This invariably occurs in the late afternoon or early evening, and after oviposition the female closes the nest from the inside for the night. Thereafter the nest entrance is left closed from the inside when the female is inside for long periods of time (at night and during much of the day). During these periods the cell is also closed off from the burrow by a small barrier of sand. The female remains in the bottom of the burrow just outside this barrier or "inner closure". During periods of provisioning, however, both inner and outer closures are removed. Nest entrances are occasionally found to be open for brief periods in the morning, probably while the female is out taking nectar from flowers. In this area no wasps were actually observed visiting flowers. Final closure of the nest is not especially distinctive and has already been described (Evans 1957).

*Description of nest.* — The burrow measures about 15 mm. in diameter, generally slightly more than this near the entrance. It enters the soil at a 45-70° angle with the horizontal but tends to level off as it approaches the horizontal cell. The burrow is often straight but may have a weak to strong lateral curve part way down. Measurements of 36 nests showed the burrow length to vary from 19 to 40 cm., with a mean of 30 cm. Depth of the bottom of the cell, measured vertically from the soil surface, varied from 10 to 22 cm., with a mean of 15 cm. Cells measured about 18 mm. in diameter and from 30 to 40 mm. in length.

Of 16 nests dug out May 8-11, 1958, 14 contained one cell and two contained two cells; none of these nests had yet received the final closure and hence all might have eventually had additional cells. Of 20 nests dug out by C. S. Lin June 4-7 of the same year, 11 contained one cell, 8 contained two, and one contained three. Only a few of these (including the three-celled nest) had received the final closure. The several nests dug out in late June, 1956, were nearly all multicellular (Evans 1957). Two nests were tricellular; one of these was still active while the other was receiving the final closure when dug out. Two other nests appeared to have four cells and another five. However, in these cases all the cells contained cocoons and the burrows



leading to them had been filled and hence could not be traced accurately. Because of the close proximity of nests in this colony, it is impossible to be certain that all of these cells belonged to the nest in question. The evidence now seems strong that the nest is usually closed after the completion of only two or three cells. It is not improbable that one-celled nests also occur, perhaps also four or five-celled nests rarely. Two or three-celled nests are characteristic of *Bembix nubilipennis* (unpublished observations), while *B. cinerea* and *B. belfragei* characteristically make one or two-celled nests (Evans 1957).

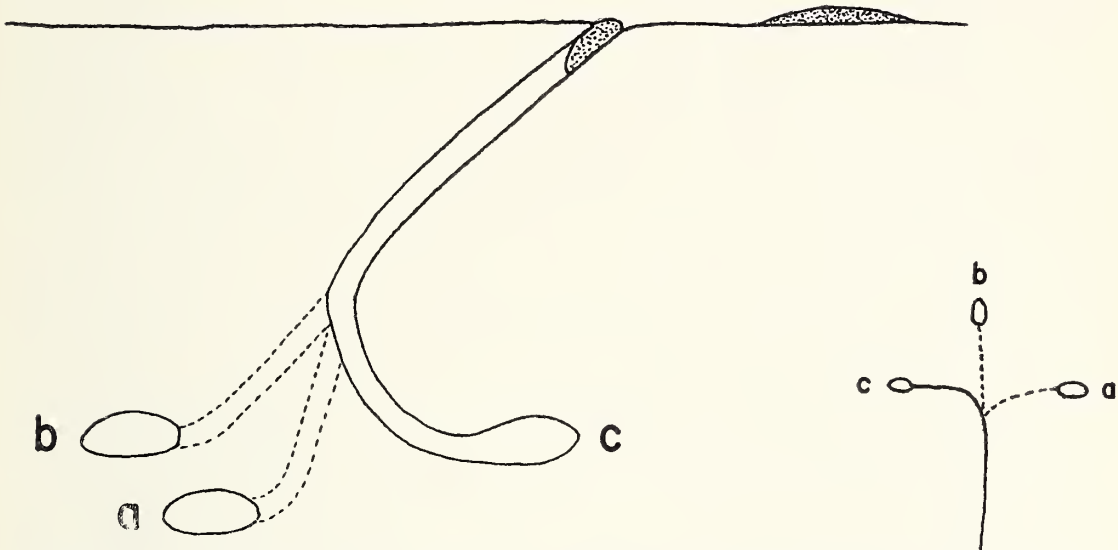


Fig. 2. — Typical three-celled nest of *Bembix u-scripta* (our field note no. 1635, Rodeo, N. Mex.). Cell *a* contained a completed and hardened cocoon, so was obviously the first cell of the nest. Cell *b* contained a fresh, still soft cocoon; cell *c* was a new cell which was empty when the nest was dug out. The figure on the left shows the nest in lateral view, compressed to a single plane, while the sketch on the right shows the proper relationship of the cells in a horizontal plane.

The cells of a given nest are normally separated by several centimeters of soil. After the first cell is fully provisioned, the bottom .3 to .5 of the burrow is packed tightly with sand. The wasp then constructs another section of burrow of about equal length at roughly a 90° angle with the main burrow and builds the second cell at the end of it. The third cell-burrow and cell are normally constructed from the opposite side of the main burrow (fig. 2).

*Provisioning.* — During the first two days of study, we were unable to find females provisioning their nests even though the nests which we dug out usually contained fresh flies. We left the area on these days at 1600-1700, a time when most digger wasps have completed

their activities for the day. On the third day we noted a few females provisioning their nests about 1600, and remained in the area until 1915. We discovered that there was a great emergence of females from their nests just before sunset. During the two-day period of observation, the first female carrying prey was seen at 1520, the last at 1905, with the great bulk of the provisioning occurring between 1700 and 1900. Sunset was at about 1830. Some females and males were still active at 1915, when it was too dark for us to see them well, but apparently these individuals were merely digging in for the night.

In order to determine what types of flies the wasps were taking at this unusual hour, we took 97 flies from females or from the nests. These flies represented 33 species of nine families; that is, there was an average of only three flies of any one kind. The most numerous flies were those of the genus *Acrosticta* (Otitidae) (26 examples). Bombyliidae, Asilidae, and Tachinidae were represented in roughly equal numbers, each family by several species. A complete list is presented in Table III. Although many species of *Bembix* are relatively unselective of their flies, I have never encountered a more remarkable diversity of prey in any one locality. Most of the flies used were relatively small, and a great many of them were used per cell (about 40). However, some relatively large flies were found in some nests.

It required very little study to determine that virtually all Diptera had ceased activity by the time the *Bembix* began to provision in numbers. Some of the flies (e.g., the otitids, and some of the bombyliids and sarcophagids) were seen commonly on the beach during the middle of the day, but in the evening they had disappeared. The *Bembix* apparently hunt widely in the vegetation and take virtually any "sleeping" flies within a certain size range which they encounter there.

Females carrying flies enter the nesting area with a rather loud buzzing only 10-20 centimeters high. They plunge quickly into the nest entrance which, as noted above, is never closed during provisioning. In less than a minute, they re-emerge from the burrow and quickly take wing. Several instances were observed of females attempting to steal flies from one another.

*Oviposition and development.* — The first fly is placed deep in the cell on its back, head-in, with one wing somewhat extended. The egg is laid erect, glued to the side of the fly near the base of the extended wing, or actually glued to the wing-base. One instance of abnormal oviposition was observed. In this case the fly (*Acrosticta* sp.) was actually smaller than the egg and was dorsum-up, with the egg of the wasp glued to the base of the abdomen and extending obliquely for-

ward. The egg of *u-scripta* measures about 4.5 mm. long.

The egg hatches in about two days and the small larva remains attached to the fly pedestal by a glutinous thread for several days. Provisioning is fully progressive; that is, flies are provided each day up until the larva is full-grown and nearly ready to spin its cocoon. The wasp does not clear the fly remains from the cell, and they merely accumulate in a mat on the bottom of the cell. Apparently about a week is required for completion of larval development.

TABLE III. PREY OF *BEMBIX U-SCRIPTA* AT PORT ISABEL, TEXAS

<i>Family and species of fly</i>	<i>Number taken</i>
STRATIOMYIDAE	
<i>Hermetia aurata</i> Bell	1
TABANIDAE	
<i>Tabanus texanus</i> Hine	1
BOMBYLIIDAE	
<i>Aphoebantus</i> sp. nr. <i>hirsutus</i> Coq.	6
<i>Lordotus gibbus gibbus</i> Lw.	5
<i>L. gibbus striatus</i> Painter	3
<i>Phthiria</i> sp.	1
<i>Poecilanthrax lucifera</i> Fabr.	3
<i>Villa parvicornis</i> Lw.	2
ASILIDAE	
<i>Erax cressoni</i> Hine	2
<i>E. tuberculatus</i> Coq.	4
<i>Pleisosomma unicolor</i> Lw.	1
<i>Psilocurus modestus</i> Will.	2
<i>P. puellus</i> Bromley	2
<i>Stenopogon ebyi</i> Bromley	6
SYRPHIDAE	
<i>Volucella fraudulenta</i> Will.	1
<i>V. unipunctata</i> Curran	3
<i>V.</i> sp.	1
OTITIDAE	
<i>Acrosticta mexicana</i> Cole	15
<i>A.</i> sp.	11
MUSCIDAE	
<i>Limnophora</i> sp.	1
<i>Mydaea</i> sp.	1
<i>Phyllogaster cordyluroides</i> Stein	5
SARCOPHAGIDAE	
<i>Sarcophaga johnsoni</i> Ald.	4
<i>S.</i> sp.	1
<i>Senotainia kansensis</i> Tns.	1
TACHINIDAE	
<i>Archytas marmoratus</i> Tns.	1
<i>Chaetogaedia</i> sp. nr. <i>analisis</i> Wulp	1
<i>Goniochaeta plagioides</i> Tns.	1
<i>Opelousia obscura</i> Tns.	1
<i>Phorocera tachinomoides</i> Tns.	1
<i>Promasiphya confusa</i> Ald.	1
<i>Tachinophyto</i> sp. nr. <i>vanderwulpi</i> Tns.	3
<i>Xenoppia monela</i> Rnh.	7



## OBSERVATIONS ON COLONY AT RODEO, NEW MEXICO

This small colony of *Bembix u-scripta* was discovered on August 28, 1959, in open desert at about 4000 feet elevation one mile north of the town of Rodeo, in extreme southwestern New Mexico. The area in question has only a few shrubs and small trees (chiefly mesquites and yuccas), but following the summer rains it is densely covered with composites and other flowering annuals, Russian thistle, and grasses. Here and there are small places devoid of vegetation. In some of these the ground is flat and the soil rather compacted, while in others the soil is loose, sandy, and somewhat blown-out or piled up in small dunes no more than a meter or two high. One of these small dunes contained about six nests of *Bembix u-scripta*, while two other nests were found in similar places not far distant. A colony of *Aphilanthops haigi* was located in the same dune with most of the *Bembix* nests, the nests of the two wasps intermingled. A few specimens of *Bembix sayi* and *B. Similans* also nested within the total area inhabited by *B. u-scripta*.

Many things about this situation were strikingly different from the Port Isabel location. The season was of course different, though August is properly considered "spring" in this area, as the summer rains occur in July and August and result in a great flowering of the desert and in the appearance of many Hymenoptera. The soil here was of finer texture, more friable, and apparently drier, although occasionally moistened temporarily by showers. No tests were made to determine whether the soil was of comparable salinity, but surely it was not, as this is not an area of notable internal drainage such as occur in some parts of the Southwest.

The total population of *Bembix u-scripta* in this area may have been no more than 30 to 40 individuals of both sexes. Consequently, in spite of the longer period of study (August 28- September 12), my data are more fragmentary. However, I was especially alert for resemblances to and differences from the Texas colony, and the following account stresses these.

*Behavior of males.* — The first males were observed August 21 flying over certain bare, sandy patches, although no females were discovered until a week later. The flight of the males was extremely rapid and the pattern of flight very irregular; it was only after many failures that I succeeded in taking one for identification. There were scarcely enough males for a typical "sun dance", though now and then two or three would fly about the same small area and make contact

with one another in flight briefly. Males were generally active 0800-1130 and again, in lesser numbers, 1600-1800. Several were seen visiting the flowers of *Gaillardia pulchella* for nectar, as were several females. At 1630 on September 8 a pair was seen in copula on these flowers. They remained together for two minutes, then separated briefly and once again came together. The details of copulation were essentially as described for the Texas colony.

*Nesting behavior of females.* — The nests in this area tended to be well separated, the closest nests being about half a meter apart. New nests were started in the morning and completed in the late afternoon; during much of the day the entrance to such a nest would be closed with a plug of sand thrown up from the inside, where the female was presumably resting or digging only intermittently. During the more active periods of digging the wasp now and then comes out and clears the sand from the entrance. Eventually a fairly large mound of sand accumulates outside the entrance. When the nest is completed, the female comes out (without closing the entrance behind her) and commences to level this mound of sand. The leveling movements were found to be precisely the same as in the Texas colony (fig. 1). They result in the mound being not so much leveled as spread out and moved slightly farther from the nest entrance. Following leveling, the 10 cm. directly in front of the entrance are typically smooth, with beyond this the mound, measuring about 20 cm. long by 18 cm. wide. Leveling was observed several times and little variation was noted; always it occurred in late afternoon and required 15-25 minutes. Following completion of a new cell in an old nest, little additional sand is usually thrown out, but such sand as accumulates is treated in the same manner. Also, when a female emerges from her nest in the late afternoon and is about to begin bringing in prey, she clears the entrance of sand and proceeds to level this sand briefly in the same manner. All individuals observed exhibited these leveling movements.

The general structure of the nests in this area was very much as described for the Texas colony. However, they were slightly deeper. In the eight nests which were dug out, burrow length varied from 30 to 42 cm. (mean 35 cm.), cell depth from 16 to 23 cm. (mean 18 cm.). Five of the eight nests had but one cell, while two had two and one had three (fig. 2). None of these nests had received the final closure when I dug them out, so all might eventually have had more cells. However, since I saw several females digging new nests toward

the end of the period of observation, I doubt if the number of cells per nest is normally more than two or three.

Nests dug out when the female was not provisioning were invariably found to have two closures, one at the entrance and one just outside the cell, with the female remaining just outside the inner closure. During provisioning, and also when the female is out taking nectar from flowers, the outer closure is not maintained, though the inner closure is normally maintained if the cell contains an egg or small larva.

*Provisioning.* — All provisioning occurred in the late afternoon and early evening, as in the Texas colony. During the period of observation, sunset occurred at about 1820-1830. However, the area in question was located directly east of the Chiricahua Mountains; the sun disappeared behind these shortly after 1800, leaving the area in deep shadow. The first female carrying prey was observed at 1600, the last at 1842, with the bulk of the provisioning occurring between 1730 and 1830. September 10 was a cloudy day, and several females were out of the nests earlier than usual (by 1430); however, none were seen with prey until about 1700.

Several females were observed hunting flies. They would fly about tall herbs (especially Russian thistle, *Salsola kali tenuifolia*) and actually fly in amongst the branches. Evidently they were searching for flies resting on the vegetation, for at this hour no flies were active. I was able to obtain only a few records of prey (Table IV). The wasps normally provide only a few fresh flies each evening, and nests dug out in the morning usually have few intact flies if any. It appeared that Bombyliidae provided the major prey in this area. Females provision very rapidly, entering the nests quickly and remaining inside only 15-30 seconds each time. One female was observed to bring in eleven flies in one hour (1720-1820).

TABLE IV. PREY OF *BEMBIX U-SCRIPTA* AT RODEO, NEW MEXICO

<i>Family and species of fly</i>	<i>Number taken</i>
THEREVIDAE	
<i>Chromolepida pruinosa</i> (Coq.)	1
BOMBYLIIDAE	
<i>Phthiria sulphurea</i> Loew	2
<i>Villa (Chrysanthrax)</i> sp.	1
<i>V. (Villa) salebrosus</i> Painter	1
SARCOPHAGIDAE	
<i>Sarcophaga</i> sp.	1
TACHINIDAE	
<i>Olenochaeta kansensis</i> Tns.	1
<i>Phorocera</i> sp.	1



Oviposition and development are as described for the Texas colony. Invariably provisioning occurs until the larva is nearly ready to spin its cocoon.

#### SUMMARY AND DISCUSSION

Despite the difference in season and ecological situation, the members of the two colonies studied exhibited striking resemblances in nesting behavior. The slightly deeper nests of the New Mexico colony were doubtless correlated with the lighter texture of the soil. As a general rule, with reference to populations of a single species or closely related species, wasps nesting in looser soil tend to make deeper nests. In this instance the difference in nest depth is slight, and it would be rash to claim that it is genetically determined. The fact that the New Mexico colony was much smaller and had the nests much more widely scattered may merely mean that this area was ecologically marginal for the species or that this population had undergone a decline because of unknown physical or biological factors.

The one difference which is more difficult to reason away pertains to the numbers of individuals exhibiting leveling movements. In the New Mexico colony, although the number of individuals observed was not large, all appeared to level the mound at the nest entrance in the manner characteristic of the species. In the Texas colony the majority did not, but roughly 25% of the individuals leveled in exactly the same way as the members of the New Mexico colony. It would be most interesting to study colonies from other parts of the range in this regard. It is conceivable that this percentage may be found to reflect a difference in gene frequency which varies clinally somewhat as color pattern appears to do in this species. On the other hand, one cannot be certain that even this difference is genetic; it is possible that the movements are innate but subject to threshold factors which were dependent upon the differing ecology of the two areas.

On the whole one cannot help but be much impressed by the similarity in the nesting behavior of these two widely separated colonies as well as the several unique features in the behavior of the species. In the following paragraphs some of the more significant features of the behavior are discussed one by one.

(1) The species is crepuscular, at least with respect to hunting and provisioning. Some females begin hunting 2.5-3 hours before sunset, but the majority do not become active until about an hour before sunset. From then on until about half an hour after sunset most females leave the nest entrance open and are actively provisioning. The

last females close the nest at about the time it becomes difficult for a human to observe them without artificial illumination. So far as I know this is unique among digger wasps.

(2) The females hunt flies which are at rest in herbaceous vegetation. The wasps fly in amongst the plants and presumably snatch the flies from the leaves and branches. This is in marked contrast to other *Bembix*, which pursue flies visiting flowers or flying about animals, dung, etc. The flies taken by *u-scripta* are exceedingly diverse and generally rather small for the size of the wasp.

(3) The mound of earth at the nest entrance is leveled in a manner unlike that of any other North American *Bembix*, though bearing some resemblance to that of *spinolae* and several other species.

(4) The nest is multicellular (apparently usually bicellular or tricellular), much like that of *nubilipennis*.

(5) The nest entrance is left open during provisioning but is at all other times closed from the inside (somewhat as in *sayi*).

(6) The egg is laid on the first fly (as in all but a few of the more specialized species of *Bembix*.)

(7) The cell is of simple structure and is not cleaned by the female.

Of these seven characteristics, the first three are unique, the fourth and fifth unusual although not unique, the last two common to all the more generalized species of *Bembix* (several more characters of this nature could easily be tabulated). Thus the total picture is not unlike that obtained from a study of structure: several unusual features built into a basically primitive *Bembix*. The most interesting of these features pertain to the unusual time of flight of provisioning females and the fact that they take Diptera which are at rest in vegetation. The well developed ocelli probably represent part of the morphological component of this adaptive complex. Since the ancestral *Bembix* doubtless had ocelli of nearly normal sphecoid type, it seems probable that *u-scripta* split off from this stock at a very early date, before the loss of ocelli became complete. This would also account for the fact that certain features of wing venation and male secondary sexual characters are more *Stictiella*-like than *Bembix*-like. The crepuscular provisioning behavior of *u-scripta* clearly enables the species to exploit a slightly different source of food from that of other species of the genus: a miscellany of mostly rather small flies which are snatched from their resting positions in vegetation. So far as can be judged at present, *u-scripta* is not strongly restricted ecologically; perhaps the

species is able to live side-by-side with other *Bembix* by virtue of its unusual provisioning behavior. Since *u-scripta* is one of the rarest of North American *Bembix*, I would hesitate to say that its unusual adaptations have proved outstandingly successful.

A final word on the second problem, that of the specific status of *arcuata* and *u-scripta*. I find it hard to believe that the wasps which I studied at Port Isabel, Texas, and Rodeo, New Mexico, represent different species. As indicated earlier, the Texas wasps were colored much like the type of *arcuata*, the New Mexico wasps much like the type of *u-scripta*. However, they were not colored precisely like the type of *u-scripta* and the parameres of male genitalia were more slender and attenuate than they appear to be in the type of that species. The final solution must come from studies farther west, from in and around Tucson, Arizona, the type locality of *u-scripta*. In the meantime I see no reason to abandon my former belief that the two names should tentatively be regarded as synonyms.

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DEFENSE MECHANISMS OF ARTHROPODS.  
II. THE CHEMICAL AND MECHANICAL WEAPONS  
OF AN EARWIG.<sup>1</sup>

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The European earwig, *Forficula auricularia* Linn., possesses two pairs of small sac-like glands (Vosseler, 1890) situated dorsally in the abdomen, and opening on the posterior margins of the third and fourth abdominal tergites (text fig. 1). The principal active components of their secretion have recently been identified as 2-methyl, and 2-ethyl-*p*-benzoquinone (Schildknecht and Weis, 1960). The glands have always been suspected to serve in defense against predators, and this suggestion, although advanced originally in lack of evidence, appears recently to have received at least indirect support, since it is now known that the quinone-containing secretion of certain other insects are, in fact, extraordinarily effective repellents (Eisner 1958a, 1958b).

In addition to the glands, *Forficula* possesses the typical dermapteran pincers, and these too have been claimed to play a defensive role (in addition to other roles, including prey capture), although the evidence is here again circumstantial at best (Burr, 1910; Gadeau de Kerville, 1905; Rau, 1933).

The purpose of this note is to present the results of some experiments designed to test whether the glands and pincers are really the effective defensive devices they were presumed to be.<sup>2</sup>

*The Pincers*

In order to facilitate close-range observation of the earwigs, they were attached to rods (by a technique used previously and already described in detail: Eisner 1958a, 1958b; Eisner et al., 1959), and adjusted to a normal stance on the substrate as shown in Plate 7, figure 1. In this way they were prevented from scurrying about, while at the same time retaining full mobility of head, abdomen, and legs.

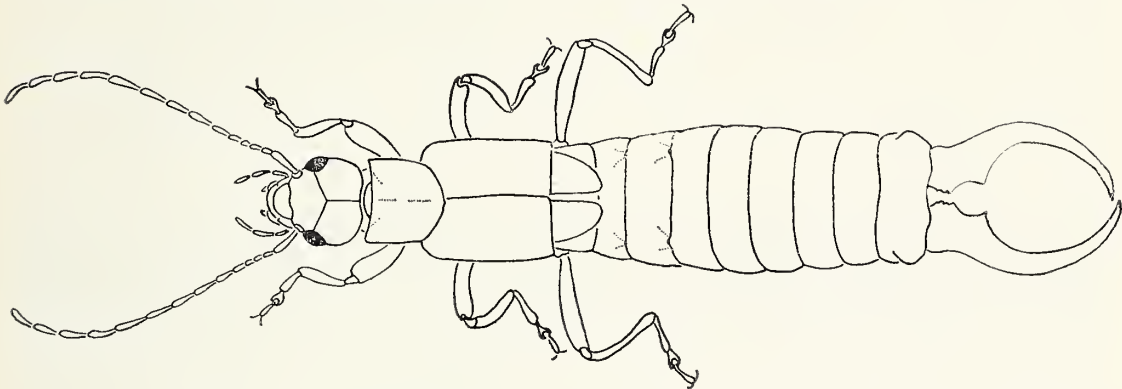
By subjecting such animals to mild traumatic stimuli, applied locally to the body or to individual appendages by pinching with fine forceps or touching with a warm needle, it was possible to witness very clearly the way in which the pincers are put to a defensive use.

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<sup>1</sup>This study was supported by Grant E-2908 of the U. S. Public Health Service.

<sup>2</sup>*Forficula auricularia* is established in the U. S. A. The specimens used were taken in Lexington, Mass.

No sooner had a stimulus been applied than the animals responded by revolving their abdomen, bringing the pincers to bear upon the region traumatized. They usually succeeded in grasping the instrument used for stimulation (Plate 7, figs. 2, 3) and, by pulling and tugging, attempted to free themselves from it. They sometimes released their grip momentarily, but as a rule persisted tenaciously for as long as the stimulus was maintained. The abdomen is remarkably maneuverable, being capable of bending and twisting to such an



Text Figure 1. *Forficula auricularia* Linn. showing the four glandular openings and the cuticular sculpturing around them on the third and fourth abdominal tergites.

extent that virtually no body part other than the abdomen itself is inaccessible to the pincers. Since the abdomen responds rapidly and with precision, the pincers can be shifted accurately and without delay from one region to another. This became quite clear when the animals were subjected to a rapid sequence of stimuli applied to different parts of their body.

The pressure that the animals can exert with the pincers is considerable. From personal experience, I can attest to the claim (cited by Burr, 1910) that the sharp prongs can pierce human skin (the prongs of the male are larger and somewhat more effective than those of the female).

#### *The Glands*

Adult earwigs, affixed to rods as before, were again subjected to localized stimulation, but this time they were placed on sheets of filter paper impregnated with an acidulated KI-starch solution. This paper discolours to an intense blue-black in the presence of quinones, and can therefore be used as an appropriate indicator for the detection of glandular discharges.

In Plate 8 are shown the types of pattern produced by the secretion. Evidently, the gland contents do not merely ooze out, — as

they do in certain millipedes and tenebrionid beetles that also discharge quinones (Eisner, 1961) — but rather are ejected forcibly as a spray. It is also apparent from the figures that the spray is not ejected in a fixed direction, but is actually aimed with considerable precision toward the particular region of the body subjected to stimulation. This finding, although new for earwigs, is by no means novel as it applies to arthropods in general: bombardier beetles, certain cockroaches, whipscorpions, and a variety of others, are all known to aim their spray (Eisner, 1958a, 1958b, 1961; Eisner et al., 1959; Eisner et al., 1961).

The mechanism by which the earwigs aim is intimately linked with the defensive use of their pincers, since by revolving the abdomen at its base while bringing the pincers toward the stimulus, the gland openings are automatically pointed in the proper direction. It is interesting in this context that the forceps seem to be used in precedence to the glands. When a stimulus is applied, a secretory discharge usually does not follow at once. As a rule, the pincers are brought into action first, and then, only after their persistent use for several seconds has proven futile, is the spray finally ejected. When the stimulus applied is a more violent one, however, such as when the head or abdomen is pinched with hot broad-tipped forceps, or the animal simply seized between the fingers, the discharge may follow with little or no delay. In other arthropods with similar defensive glands, but lacking such auxiliary mechanical devices as the earwig's pincers, even a slight traumatic disturbance usually elicits a prompt discharge (Eisner 1958a, 1958b; Eisner et al., 1959; Eisner et al., 1961).

Up to six consecutive discharges could be evoked from a single earwig, but usually they produced no more than four. The amount of secretion ejected decreases progressively, until finally there are produced on the paper no more than a few spots at close range.

The earliest that an earwig with depleted glands was ever tested to check on the restoration of its secretory supply was after a period of five days: by this time it was again able to discharge three times.

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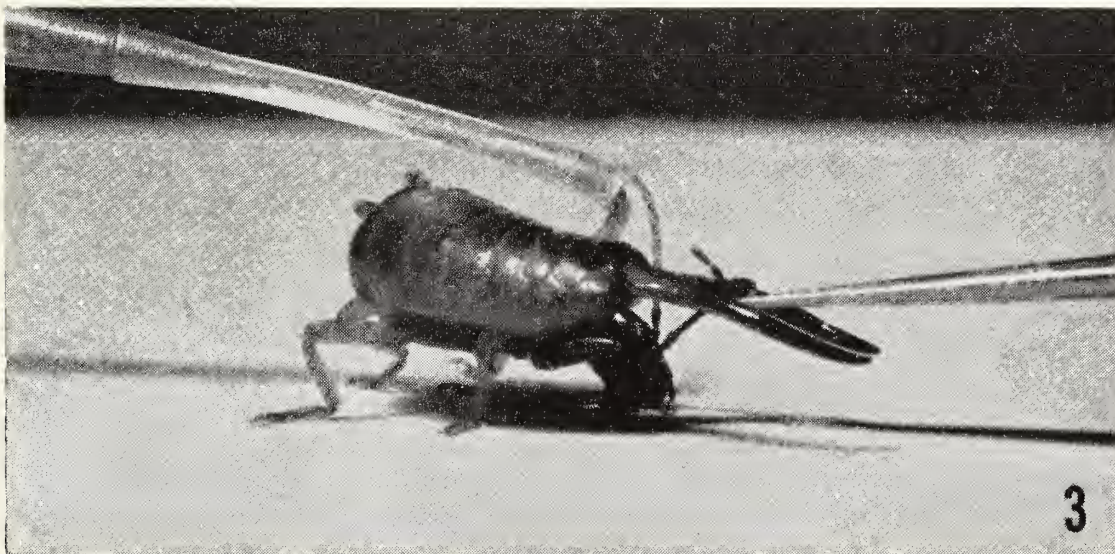
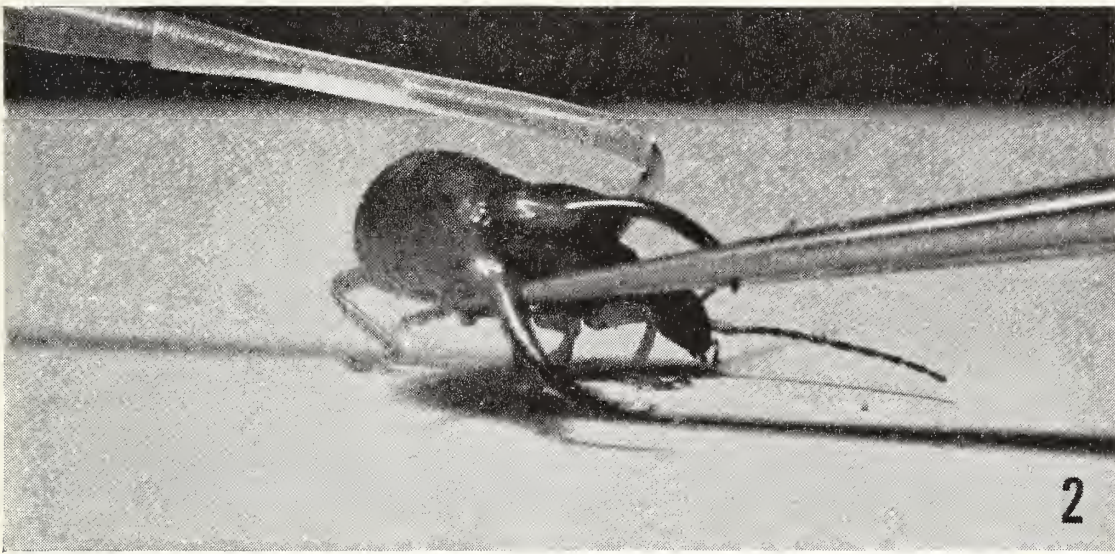
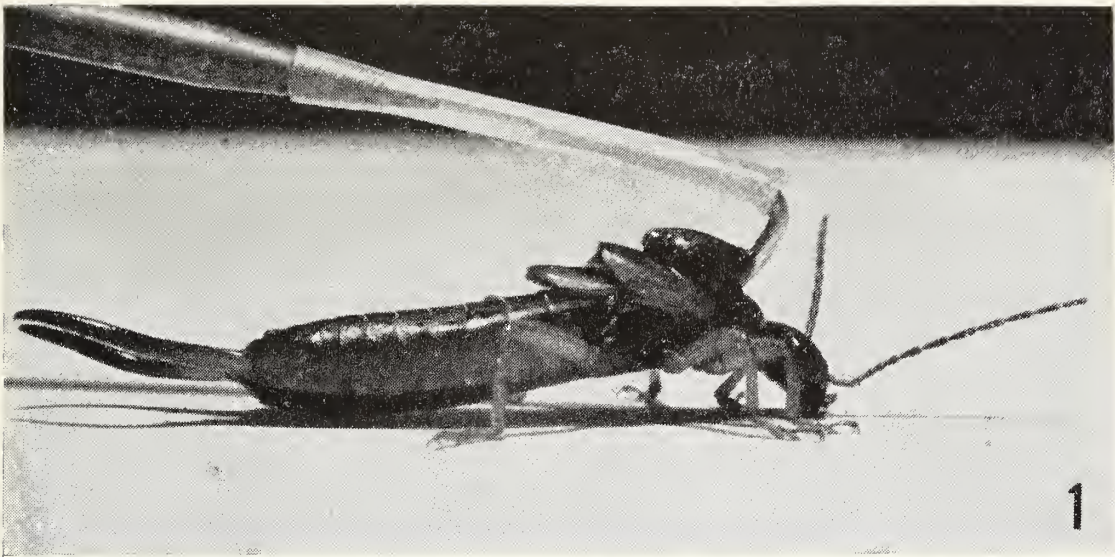
#### EXPLANATION OF PLATE 7

*Figure 1.* Earwig fastened to hook, in normal stance.

*Figure 2.* Earwig having its right metathoracic leg pinched with forceps, responding by bringing its pincers to bear upon the forceps.

*Figure 3.* Same as preceding, but the stimulus is applied to the right antenna.





EISNER — DEFENSE MECHANISMS



*Encounters with Predators*ANTS [*Pogonomyrmex badius* (Latreille)]

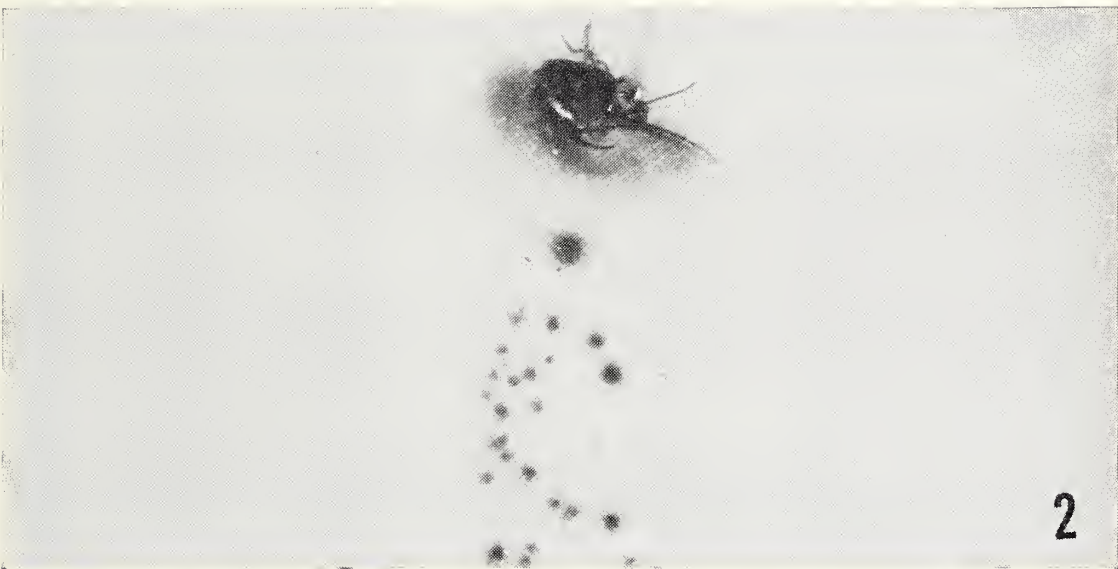
The experiments were carried out under the same conditions as prevailed in previous comparable studies (Eisner 1958a, 1958b), the earwigs being affixed to rods and placed individually close to the nest entrance of a laboratory colony of the ant. Sheets of KI-starch paper were placed under the earwigs.

The ants at first attacked singly or in groups of two or three. No sooner had one of them grasped the earwig with its mandibles (often mere contact seemed to suffice), than the earwig responded by attempting to catch the assailant with its pincers. Typically, the ant was seized and promptly removed from its hold, being released only after the abdomen had uncoiled and straightened out. The uncoiling of the abdomen is a rapid spring-like action, with the result that the ant is sometimes flipped several centimeters away.

No discharges were produced during these first attacks, all ants being successfully fought off by the use of the pincers alone. Gradually, however, the activity of the ants around the nest entrance became considerably intensified (perhaps in response to the release of the ant's own alarm substance; see Wilson, 1958), and within minutes the earwig was surrounded by a swarm of workers, some attempting to bite and sting it, others merely scurrying over its body. It was then that a discharge was finally produced. The result was an instantaneous dispersal of the entire swarm. For a few seconds thereafter none of the ants ventured within the immediate vicinity of the earwig. Many showed typical grooming activities, others underwent the conspicuous dragging behavior already noticed in this ant and the related *P. occidentalis* (Cresson) under similar circumstances involving insects which spray (Eisner 1958a, 1958b; Eisner et al., 1961). The swarm soon closed in again, but for yet another several seconds there occurred no real attacks, the ants turning and fleeing the moment they made contact with the earwig. That this avoidance behavior may have been attributable to residual secretion remaining on the earwig's body was suggested by the fact that a small strip of indicator paper held within millimeters from the earwig rapidly became discolored.

## EXPLANATION OF PLATE 8

*Figures 1, 2, 3.* Three different discharges elicited by pinching respectively the end of the abdomen (figure 1), the right mesothoracic leg (figure 2), and an antenna (figure 3). (The pictures were taken shortly after discharge, and the abdomens were therefore no longer in the exact positions they had assumed at the time of spraying).



EISNER — DEFENSE MECHANISMS



Eventually, within less than a minute, the earwig was again under assault. The attacks were at first countered by the pincers alone, but soon the swarm was dispersed as before by another discharge.

Several earwigs were tested in this way, the results being similar in all cases.

One earwig was left with the ants until well after all its secretion had become depleted. It was soon overrun by a swarm, and was by now entirely dependent on its pincers for defense. Under these conditions it became particularly clear how effective the pincers really are. During a period of 20 seconds that was timed, the earwig seized and successfully removed from its body a total of 19 attacking workers. This was, of course, a mere fraction of the total swarm, and the earwig was eventually bitten and stung repeatedly, and finally killed.

During none of these encounters did any of the ants receive lasting noticeable injury. Neither did the earwigs — not, at least, for as long as their secretion lasted.

PRAYING MANTIDS [*Hierodula patellifera* (Serville)]

The fifteen earwigs that were given to the three adult female mantids that were tested, were all caught and eaten in rapid succession, the mantids showing no signs of being affected by either the secretion or the pincers.

The same species of mantid also accepts the quinone-secreting cockroach *Diploptera punctata* Eschscholtz (Roth and Stay, 1958; Eisner 1958b), but it rejects the bombardier beetle *Brachynus ballistarius* Leconte (Eisner 1958a), the secretion of which is likely to be quinonoid like that of its congeners (Schildknecht, 1957). The reason for these inconsistencies in acceptability may be due to the fact that the various secretions do not contain precisely identical quinones, but also may have something to do with the special properties of the *Brachynus* spray, which differs from that of the others in that it is hot, and is discharged with a clearly audible detonation. [At the time I wrote on *Brachynus* (Eisner, 1958a), I was unaware of the thermal properties of its spray].

#### VERTEBRATES

The animals tested were two small toads (*Hyla versicolor* Le Conte), one bird [*Cyanocitta cristata* (Linn.)], and one mouse (*Mus musculus* Linn.).

Both bird and mouse ate readily every one of the several earwigs that was offered to them (within a period of a few hours), betraying no abnormalities during the meal, or ill effects thereafter. It would be well to bear in mind, however, that before ruling out the repug-

natorial effectiveness of an arthropod's secretion against a vertebrate, long-term feeding experiments should be made, to test for any discriminatory tendencies that might eventually develop after a greater number of encounters, and particularly in situations where the predator is also given palatable insects as an alternative choice.

With *Hyla* the results were different. Five of the eleven earwigs offered (over a period of a few hours) were caught and swallowed, but the rest were promptly spat out (there was no apparent order in the sequence in which the earwigs were either taken or rejected). Whether rejection was on the basis of the secretion alone, or was also attributable to trauma induced by the pincers, could not be determined. That the secretion may in itself be repellent is suggested by the fact that benzoquinones are strongly irritating when applied topically to an amphibian: a mere sprinkling of a few crystals of *p*-benzoquinone on *Hyla* invariably elicits a prompt scratch reflex. The pincers may also be of importance, however. In one instance a frog had difficulty rejecting an earwig, which was seen to have become firmly clamped to its tongue, and which was not removed until the frog used its forelegs to brush it away.

*Acknowledgements:* I am indebted to Professor Carrol M. Williams of Harvard University, and also to his family, for having collected the earwigs for me, and to Professor Edward O. Wilson for use of his *Pogonomyrmex* colonies at Harvard. Thanks are also due Professor Kenneth D. Roeder, Tufts University, who made the mantids available at his laboratory, and Dr. J. A. G. Rehn who identified them. Dr. Hermann Schildknecht, University of Erlangen, Germany, was kind enough to let me see his manuscript (Schildknecht and Weis, 1960) before its appearance in print.

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## A TRIASSIC ODONATE FROM ARGENTINA

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The fossil insect described in this paper was collected in 1958 in the precordilleran region of Mendoza in Argentina by the joint expedition of the Museum of Comparative Zoology and the Museo Argentino de Ciencias Naturales of Buenos Aires. The specimen was turned over to me for study by a member of the expedition, Professor Bryan Patterson.

The rock containing the insect is a nearly white shale, with definite bedding and numerous plant fragments. The insect consists of the distal part of a wing, very clearly preserved. About 6 cm. away from this wing there is another specimen, consisting of a small, distal fragment of a wing. The larger specimen is clearly odonate but certain structural details eliminate it from all described families of the order; because of our lack of knowledge of the proximal part of the wing, including the arculus region, I am placing this species in *Incertae Sedis*, in preference to establishing a new family on so few details. The smaller wing fragment can be interpreted best by comparison with the larger specimen, as will be noted below.

### ORDER ODONATA

Family: *Incertae Sedis*

Genus *Triassothemis*, new genus

Pterostigma well formed, elongate; nodus incomplete, without a costal indentation at the junction of the subcosta; nodus remote from the base of the wing: about 6 postnodals between nodus and pterostigma. The genus appears to be related to the suborder Archizygoptera, which has been found in the Triassic of Australia and Jurassic of Europe and Asia (Turkestan).

Type species: *Triassothemis mendozensis*, new species

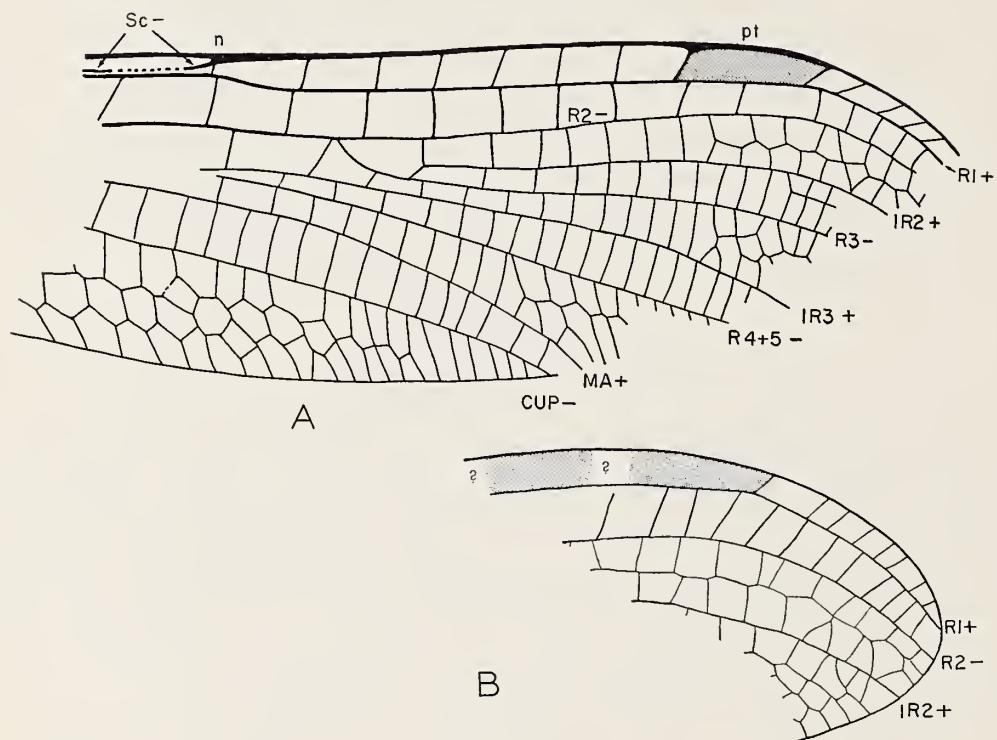
*Triassothemis mendozensis*, n. sp.

Text figure 1 A, plate 9.

Wing: length (as preserved), 25 mm.; width, 8.5 mm. Pterostigma about four times as long as wide, distinctly pigmented; costal border along the pterostigma somewhat thickened. Nodus incipient; subcosta distinctly thickened as it meets the costa; a short cross-vein between the end of the subcosta and R<sub>1</sub>, this cross-vein being almost aligned with the cross-vein below it (extending from R<sub>1</sub> to R<sub>2</sub>). R<sub>3</sub> separating from R<sub>2</sub> at a point not much distal of the nodus; R<sub>2</sub> and

R3 widely divergent distally, with four rows of cells between them. The origin of R4 + 5 from R2 + 3 is not shown in the specimen but it is clearly proximal of the level of the nodus. MA and R4 + 5 are markedly divergent distally. IA is not recognizable in the part of the wing that is preserved. Cross-veins are numerous and are distributed as shown in figure 1A.

Holotype: No.18040, in Museo Argentino de Ciencias Naturales, Buenos Aires; collected in the Estratos de Potrerillos, near Agua de las Avispas, along the south slope of Cerro Cacheuta, Argentina. The formation is of Triassic age (see Romer, 1960, for additional geological data). The preserved portion of the wing is very clear (see plate 9) and the venational convexities and concavities are distinct.



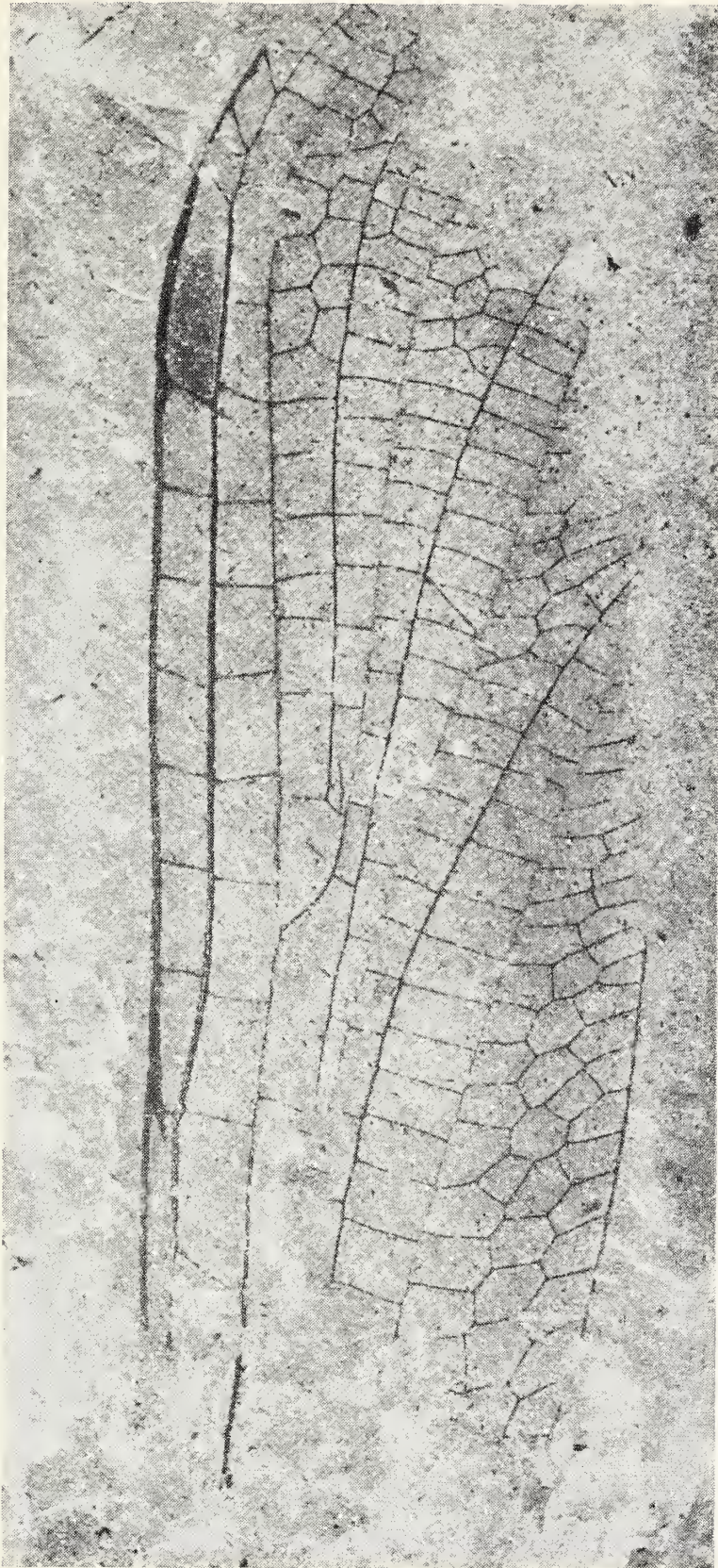
Text-figure 1A. Drawing of *Triassothemis mendozensis*, n. sp., from the Triassic of Argentina (holotype).

Text-figure 1B. Drawing of wing fragment associated with above specimen.

Sc, subcosta; n, nodus; R1, radius; IR2, R2, R3, IR3, R4 + 5, branches of radial sector; MA, anterior media; CuP, posterior cubitus; —, concave veins; +, convex veins; pt, pterostigma.

The most striking feature of this wing is the nature and location of the nodus. In its form, the nodus is like that of the Archizygoptera





Photograph of holotype of *Triassothemis mendozensis*, n. sp.  $\times 5$



but its position is very different. In the Archizygoptera the nodus is very remote from the pterostigma and close to the base of the wing, the subcosta being very short. In *Triassothemis*, the nodus is close to the pterostigma and probably at about the middle of the complete wing. The nodal area is so clearly preserved in the specimen of *Triassothemis* that there can be no doubt about its structure; although the subcosta has been broken away just before its termination, it is present on each side of this missing section. The distal location of the nodus apparently eliminates *Triassothemis* from the Archizygoptera, as the suborder is presently understood. Another peculiarity of the wing of *Triassothemis* is the widening of the area between R<sub>1</sub> and the costal margin of the wing, just beyond the nodus. That this is not a distortion is shown by the normal location and distribution of the cross-veins and the other veins in the anterior part of the wing. The pterostigma is like that of the Archizygoptera and the several branches of the radial sector have the divergent arrangements characteristic of that suborder, although the divergences are not quite so marked. The absence of a distinct anal vein (at least in the part of the wing which is preserved) is also suggestive of the Archizygoptera. In most respects, therefore, *Triassothemis* possesses many of the characteristics which we find in the wings of the Archizygoptera but the location of the nodus is very different from that of all of the genera of this suborder so far known.

The small apical fragment of a wing, which is located on the same piece of the rock as *Triassothemis*, resembles the latter in so far as the known parts of the venation are concerned (Figure 1B). R<sub>1</sub>, R<sub>2</sub>, IR<sub>2</sub> are arranged about as in *mendozensis* but there is a clear indication that the next vein, R<sub>3</sub>, would be somewhat more remote from IR<sub>2</sub> than it is in the specimen of *mendozensis*. The pterostigma is like that of *mendozensis* so far as its distal part is concerned, but it appears to extend proximally the full length of the preserved part of the wing, as shown in figure 1B. It seems very likely that this small wing fragment represents an odonate closely related to *Triassothemis mendozensis*; in fact, since we do not know anything about the differences between the fore and hind wings of the Archizygoptera, it is possible that the fragment is part of another wing of the type of *mendozensis*.

The discovery of this piece of Triassic rock containing two fossil insects, even though they are in fragmentary condition, points up the possible significance of Triassic strata in the Mendoza region of Argentina as a source of extensive collections of insects. Wieland

1925, 1926) has described two other Triassic insects collected in a Triassic deposit very near Cerro Cacheuta, one of these being a homopteron (*Tipuloidea rhaetica*) and the other a possible trichopteron (*Necrotaulius* (?) *affinis*). Both of the specimens on which these species were based are preserved on one piece of rock. In addition, Kurtz in his atlas of fossil plants from Argentina (1921) includes three sketches of insects which were found in the Triassic beds of the Mendoza area; these are stated in the caption of his plate 7 to be hymenopterous wings, although they are most certainly not representatives of that order. Also, one of the Triassic specimens which Kurtz identified as a plant (*Beira argentina*) and figured on his plate 22, fig. 336, is actually part of a wing of an insect, subsequently designated by Cockerell (in Wieland, 1926) as *Elcana* (?) *argentina*. It seems clear from this casual collecting of insects in the Triassic deposits of the Mendoza area that further exploration of these strata for insects is very desirable.

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ON THE TRUE NATURE OF THE AZYGETHIDAE  
(CHILOPODA: GEOPHILOMORPHA)\*

BY R. E. CRABILL, JR.

Smithsonian Institution, U. S. National Museum, Washington D. C.

The family Azygethidae was proposed for the reception of a single genus and species, *Azygethus atopus*, by R. V. Chamberlin in his 1920 study<sup>1</sup> of the Australian region's myriopod fauna. The new group's suprageneric rank was defended really on two grounds. The ultimate pedal segment reportedly had normal pleural sclerites, but even more remarkably this segment was said to bear a pair of spiracles. If the members of the genus did indeed all *normally* possess ultimate pedal segment spiracles, then their allocation to a new family would surely be justified, for they would thereby differ, not only from all other Geophilomorpha, but even from all other centipedes.

This character was so extraordinary that, sixteen years later, Attems expressed reservations as to its authenticity, and, regretting the total lack of figures, he urged that the specimen be re-examined. Nevertheless, in 1926<sup>2</sup> he did include Azygethidae in his treatment clearly implying his suspicion that the critical character might have been misrepresented originally.

And there the matter has remained until the present. No subsequent specimens of *atopus* have ever been discussed. No new species have ever been referred to the family. The original types have never been re-examined. In short, no corroborative evidence has ever been adduced in support of Chamberlin's original interpretation.

Furthermore, if we were to discount, for the moment, the spiracles and pleurites of the ultimate pedal segment and then attempt to imagine to what *other* family and genus the species could belong, our endeavor would prove fruitless. There are so many critical errors in the original description to lead one astray, that even a man of At-

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\*This study was undertaken with the aid of a grant from the National Science Foundation and is published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

<sup>1</sup>The Myriopoda of the Australian Region, Bull. Mus. Comp. Zool. Harvard, 64(1): 32, (1920).

<sup>2</sup>Handbuch der Zoologie, Kükenthal and Krumbach, Bd. 4: 366, (1926).  
of families. Two years later he failed even to mention the name<sup>3</sup>, but

<sup>3</sup>The Myriopoda of South Africa, Ann. South African Museum, 26, (1928).  
in his great monograph of 1929<sup>4</sup> he referred to the family again,

<sup>4</sup>Geophilomorpha, in Das Tierreich, Lief. 52: 347, (1929).



tems' broad experience and at times almost clairvoyant insight could not possibly have guessed to which of the existing genera and families *atopus* might be referable.

Thanks to the hospitality of Dr. Herbert W. Levi, who is in charge of the Arachnida and Myriapoda at Harvard's Museum of Comparative Zoology, I have been able to study the holotype and paratype. Both are females that were collected by W. M. Mann at Levuka on Fiji. Without the slightest doubt in my mind, both are referable to the oryid *Orphnaeus brevilabiatus* (Newport), which is probably the most widespread and common geophilomorph of the world's tropics.

Let us examine certain parts of the original description in light of what the type specimens themselves disclose. I shall not discuss those features that are accurately, or essentially accurately, described therein.

The mandible is said to have "a single pectinate lamella". At lower magnifications this appears superficially to be the case; however, optimal preparation and observation reveal the mandibles unquestionably to be those of an oryid; they are not geophiliform. The pectinate lamellae are simply pressed tightly against the distal end of the mandible, giving it, at first sight, a geophiliform appearance.

The "coxae", i. e. the coxosternal sides, of the first maxillae are reportedly "wholly discrete", that is, totally separated. If the reader will examine figure 1, plate 10, he will see that the coxosternum is continuous and that there is not the slightest division at point E. The two medial processes or lobes, D, are of course discrete, as they always are. Perhaps Dr. Chamberlin confused the two in preparing his original analysis.

Ventral pores are said to be absent, but ventral pores are present and, in aggregate, form the patterns that are so distinctive of *brevilabiatus*.

"Last pediferous segment with coxae distinct from the pleurae. . ." . Precisely what Chamberlin meant here is unclear; however, his use of the word pleurae, which is plural, implies a reference to pleural sclerites rather than to lateral body wall or membrane. In fact, between the leg base and tergite there is a weakly sclerotized plate-like protuberance which appears to be an out-folding of the lateral body wall (plate 10, fig. 2, F). This same structure is to be seen in specimens of *O. brevilabiatus*; it is more pronounced in some than others. Probably it represents an abortive paratergite, a serial homologue of the more anterior, typical paratergites. In any event, the statement

on p. 32, that "the pleural plates of the segment [are] normal" is quite misleading.

Finally, the ultimate pedal segment was reported to have a pair of spiracles, and in fact it has such spiracles (fig. 2, F). At the same time, there are mitigating circumstances. First, these spiracles occur only on the holotype: the paratype, otherwise identical with it, lacks them altogether. Secondly, the nature of the holotype's spiracles clearly suggests them to be anomalous, in this case probably ontogenetic freaks. Both are abortive, the left one more so than the right, and there is no evidence that either was ever functional. Both evidently lack a connection with the tracheal chain linking the more anterior, normal spiracles.

Such spiracular anomalies are not unknown. Indeed, I have reported having found one in a cryptopid centipede, *Scolopocryptops sexspinosa* (Say)<sup>5</sup>. In this case anomalous spiracles were discovered on the 7th pedal segment, which normally lacks them, although in a related genus, *Dinocryptops*, the 7th segment normally has them.

Thereby the old mystery surrounding the apocryphal family Azygethidae appears to be resolved. *Azygethus atopus* Chamberlin is a junior synonym of *Orphnaeus brevilabiatus* (Newport), and Azygethidae falls as a junior synonym of Oryidae. In closing I cannot help but wonder what other chilopod names owe their *raison d'être* to nothing more than to such sporadic, anomalous characters, and how long they will continue to obscure the real fabric of the system before their paroles are terminated.

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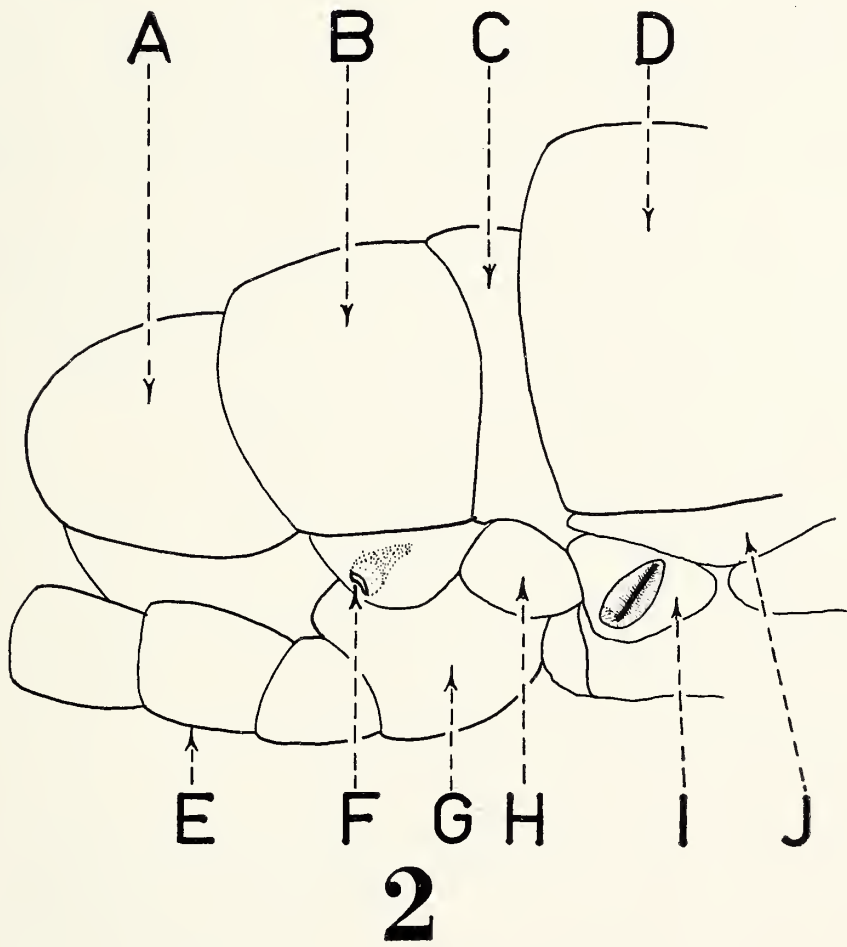
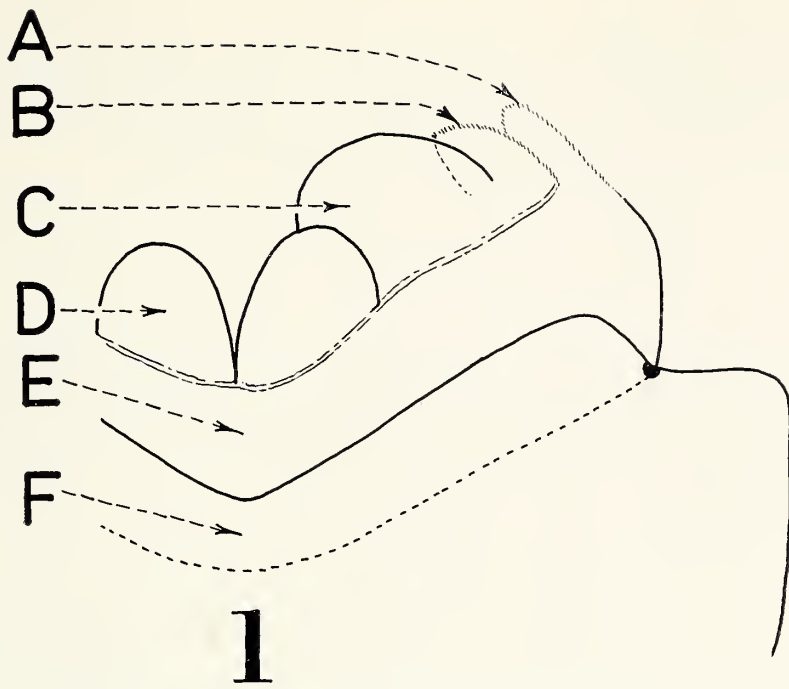
<sup>5</sup>On the reappearance of a possible ancestral characteristic in a modern chilopod, Bull. Brooklyn Ent. Soc., 50(5): 133-136, (1955).

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EXPLANATION OF PLATE 10  
*Azygethus atopus* Chamberlin

*Figure 1.* Paratype. First maxillae: left two-thirds, with adjacent second maxillae, the setae deleted. A=lappet of coxosternum. B=lappet of telopodite. C=telopodite. D=right medial lobe. E=coxosternum. F=hidden continuation of coxosternum concealed beneath anterior edge of second maxillary coxosternum.

*Figure 2.* Holotype. Posterior-most body segments: right side tilted slightly downward, setae deleted. A=tergum covering the postpedal segments. B=tergite of ultimate pedal segment. C=Pretergite of ultimate pedal segment. D=Tergite of penultimate pedal segment. E=right ultimate leg. F=Spiracle and plate-like bulge of ultimate pedal segment. G=Coxopleuron. H=Parapretergite. I=Stigmopleurite of penultimate pedal segment. J=Paratergite of penultimate pedal segment.



CRABILL — AZYGETHIDAE



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The illustration on the front cover of this issue of *Psyche* shows the head of the worker of *Myrmoteras karnyi* Gregg. The original, drawn by Dr. R. E. Gregg, was published in *Psyche*, Volume 61, p. 21, 1954.

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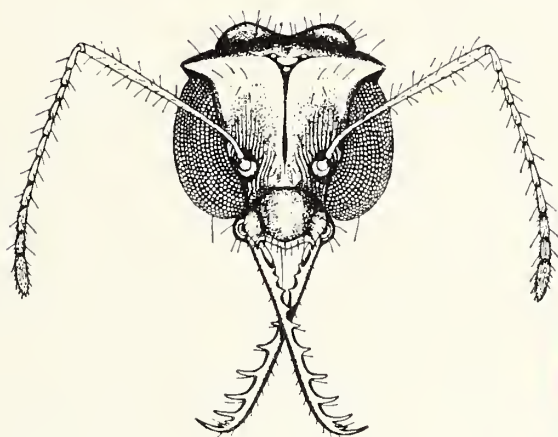
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No. 4



## CONTENTS

A New <i>Acanthoctenus</i> (Araneae: Acanthoctenidae) from Jamaica, W. I. <i>A. M. Chickering</i> .....	81
Techniques for the Study of Ant Larvae. <i>G. C. Wheeler</i> and <i>J. Wheeler</i> .....	87
The Female of <i>Lucarachne beebei</i> Gertsch (Araneae: Symphytognathi- dae) <i>A. M. Chickering</i> .....	95
Studies on North American Carboniferous Insects. I. The Protodonata <i>F. M. Carpenter</i> .....	98
Australian Carabid Beetles IV. List of Localities, 1956-1958. <i>P. J. Darlington, Jr.</i> .....	111
Author and Subject Index for Volume 67 .....	129

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# PSYCHE

Vol. 67

DECEMBER, 1960

No. 4

A NEW *ACANTHOCTENUS*  
(ARANEAE: ACANTHOCTENIDAE)  
FROM JAMAICA, W. I.<sup>1</sup>

BY ARTHUR M. CHICKERING  
Albion College, Albion, Michigan

About twenty-five species are known in this family and all have been assigned to the Genus *Acanthoctenus* Keyserling, 1876. These have been reported all the way from Mexico to Argentina. So far as I have been able to learn, however, no representative has ever been recorded from the West Indies. It is, therefore, of considerable interest to be able to report that both sexes of what I am compelled to regard as a new species have been collected in several localities in Jamaica, W. I. A holotype male and an allotype female have been selected and are described in accord with my usual formula in this brief paper. These types are being deposited in the Museum of Comparative Zoölogy at Harvard College, Cambridge, Mass.

Genus *Acanthoctenus* Keyserling, 1876  
***Acanthoctenus remotus* sp. nov.**  
(Figures 1-6)

*Holotype male.* Total length 11 mm. (somewhat exaggerated because of softened and stretched condition of the specimen in the region of the pedicel). Carapace 5.59 mm. long; 4.55 mm. wide opposite second coxae where it is widest; well rounded from opposite posterior eyes to posterior border; median longitudinal thoracic groove deep and long.

*Eyes.* Eight in three rows, two, four, two; essentially as in the Ctenidae (Fig. 1). Viewed from above, both rows recurved; viewed

<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoölogy at Harvard College.



from in front, anterior row strongly recurved, posterior row moderately recurved in order to produce the characteristic placement. Ratio of eyes  $AME:ALE::PME:PLE = 14:10::22:22$  (measurements taken from borders of the corneas). AME separated from one another by about one third of their diameter, from ALE by slightly more than their diameter. PME separated from one another by about one third of their diameter, from PLE by a little less than their diameter. LE separated from one another by about twice the diameter of ALE (the corneas of these eyes are extended much further than usual). Central ocular quadrangle wider behind than in front in ratio of 10:7, wider behind than long in ratio of 25:22. AME separated from PME by a little more than one third of their diameter. Height of clypeus equal to about the diameter of AME. The clypeus bears 17-18 long slender spines with one isolated on each side dorsal to the base of the cheliceral boss.

*Chelicerae.* Nearly perpendicular, slightly divergent, moderately robust. Basal segment 2.275 mm. long. With many long slender spinules extending forward from promargin and many long, curved, light colored hairs at distal end. Basal boss well developed. Fang moderately robust, fairly evenly curved; with three promarginal teeth, the middle one the largest; with three retromarginal teeth of moderate size and gradually diminishing in size from near base of fang distally.

*Maxillae.* Nearly parallel, moderately robust, only slightly concave in distal half along lateral border. Only slightly more than twice as long as broad. With well developed scopula along medial border to distal tip. Serrula only moderately well developed along distal lateral corner. With many long slender and stiff bristles especially along lateral border.

*Lip.* Only a little longer than wide in middle; slightly concave along distal border; reaches only slightly beyond middle of maxillae. Sternal suture slightly procurved.

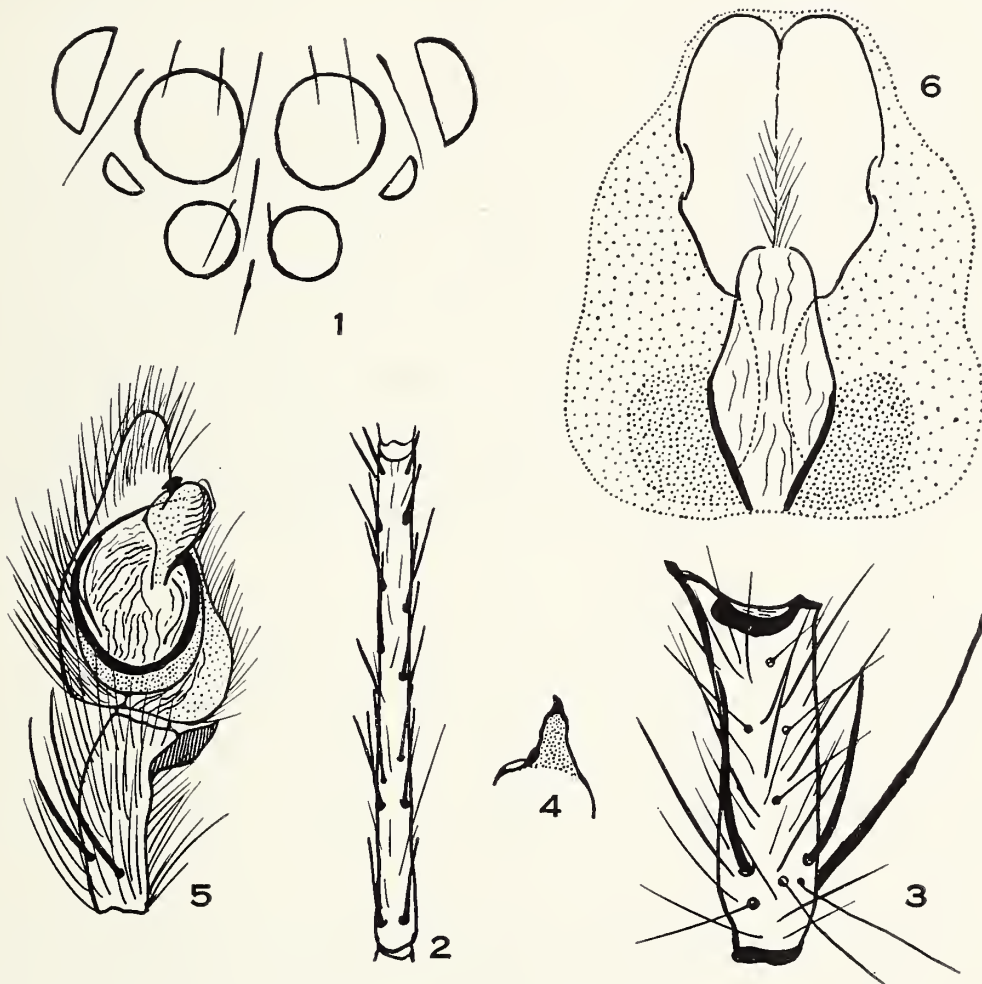
*Sternum.* Subrotund; as wide as long; slightly pointed at posterior end which is not extended between fourth coxae which are separated by about one fifth of their width. Only slightly scalloped opposite the coxae. Moderately well supplied with slender stiff bristles.

*Legs.* 1423. Width of the first patella at "knee" .845 mm., tibial index of first leg 6. Width of fourth patella at "knee" .780 mm., tibial index of fourth leg 8.

*Femora Patellae Tibiae Metatarsi Tarsi Totals*  
(All measurements in millimeters)

1.	8.450	2.795	10.400	9.425	3.250	34.320
2.	7.475	2.600	7.280	7.930	2.795	28.080
3.	5.590	1.820	4.940	6.630	2.405	21.385
4.	8.190	2.275	7.150	9.230	3.315	30.160
<i>Palp</i>	3.120	1.300	1.625	—	2.015	8.160

All trochanters slightly notched ventrally at distal border. Tarsi with two claws, each pectinate in a single row. Trichobothria observed on femora, tibiae, metatarsi, tarsi and on palps. The distribution appears to be irregular, but this has not been carefully enough studied to warrant a precise statement.



Figures 1-6. External Anatomy of *Acanthoctenus remotus*. Fig. 1. Eye group of male; seen from in front. Fig. 2. First tibia; ventral view. Fig. 3. Left palpal tibia; nearly dorsal view. Fig. 4. Left palpal tibial apophysis; lateral view. Fig. 5. Left palpal tibia and tarsus; nearly ventral view. Fig. 6. Ventral view of epigynum.

*Spines.* There are many prominent spines on the legs but those which seem to be the most distinctive are: First tibia with seven pairs of long, fairly robust, ventral spines (Fig. 2); first metatarsus with ventral spines 0-2-2-2-lr-lr-lp. Second tibia with ventral spines essentially as in first but with more irregularity; second metatarsus with spines essentially as in first but also with more irregularity. Third tibia with three pairs of these robust spines; third metatarsus with ventral spines 0-2-2-2. Fourth tibia with ventral spines 2-2-2; fourth metatarsus with four pairs of ventral spines very irregularly placed. Prolateral and retrolateral robust spines easily confused with ventral spines. Calamistrum apparently absent. Tarsal scopulae well developed on tarsi one and two but less well developed on tarsi three and four. Metatarsal scopulae moderately well developed on metatarsi one and two but absent from three and four. All tarsi with well developed claw tufts.

*Palp.* Relatively simple; closely similar to that of *A. spinigerus* Kersevald from Central America. Details best shown in Figures 3-5. Tibia with robust distal retrolateral apophysis; with two long slender dorsal spines near proximal end and a similar prolateral spine near proximal end. Patella with dorsal spines as follows: 2-0-1 (extremely long and slender). Hairs on tibia extremely long and stiff.

*Abdomen.* Somewhat ovate with widest part about one third of its length from posterior end; 5.85 mm. long and 3.575 mm. wide at widest part. With a pair of dorsal depressions a little behind the middle. With three pairs of spinnerets, all short but with anterior pair the largest and the middle pair the smallest. With cribellum obscure and poorly developed.

*Color in alcohol.* Carapace with a broad, median, nearly uniformly light stripe. On each side of the posterior half of the median thoracic groove there is an elongated dark spot. The whole area lateral to the median light stripe is brownish. Between the PLE there are four narrow stripes formed by light grayish hairs. The chelicerae are irregularly striped with brownish; in front at the outer proximal corner there is a narrow stripe of grayish hairs. Abdomen: the dorsum is brownish, much lighter in the middle in the dorsal half. There is also a group of four light colored tufts of long hairs in the posterior quarter. The whole ventral area, sternum, and venter is uniformly yellowish. The legs are generally brownish dorsally and yellowish ventrally.



*Female allotype.* Total length 15.08 mm., including the somewhat swollen bases of chelicerae; without the latter 14.625 mm. long. Carapace 6.11 mm. long, 5.20 mm. wide at interval between second and third coxae where it is widest; only slightly sloping from between PLE to about the middle of the well developed longitudinal median thoracic groove from which position it descends steeply to posterior border.

*Eyes.* Arrangement as in male. Ratio of eyes AME:ALE::PME:PLE = 14:12::20:23 (measurements taken from borders of corneal hypodermis). AME separated from one another by about five sevenths of their diameter, from ALE by about 9/7 of their diameter. PME separated from one another by about their radius, from PLE by about their diameter. Laterals separated from one another by about the long diameter of ALE. AME separated from PME by the radius of the former. Central ocular quadrangle wider behind than in front in ratio of about 5:3.5; wider behind than long in ratio of about 5:4.5. Height of clypeus equal to about 17/14 of the diameter of AME. Clypeus with about 12 long slender spines.

*Chelicerae.* Nearly perpendicular; parallel, robust, moderately gibbous in front; basal segment 2.6 mm. long. Basal boss well developed. With many stiff bristles in front. Fang and teeth along fang groove essentially as in male.

*Maxillae, Lip, and Sternum.* Essentially as in male.

*Legs.* 1423. Width of first patella at "knee" .975 mm., tibial index of first leg 9. Width of fourth patella at "knee" .910 mm., tibial index of fourth leg 11.

	<i>Femora</i>	<i>Patellae</i>	<i>Tibiae</i>	<i>Metatarsi</i>	<i>Tarsi</i>	<i>Totals</i>
	(All measurements in millimeters)					
1.	6.500	3.120	7.410	6.305	2.210	25.545
2.	6.125	2.795	6.110	5.655	1.820	22.505
3.	5.525	2.275	4.485	5.200	1.885	19.370
4.	6.825	2.275	5.850	8.190	2.340	25.480

Trichobothria observed on many segments of legs and palps but their exact distribution has not been determined. Calamistrum short and near proximal end of fourth metatarsus.

*Spines.* First leg: femur dorsal 0-1-1-1, prolateral 0-1-1-0, retro-lateral 0-1-1-0-1-1-1-0, ventral with numerous spines irregularly placed and difficult to describe significantly; first tibia with nine pairs

of ventral spines; first metatarsus with five pairs of what may be termed ventral spines but most of them are moved into a somewhat lateral position. The second tibia has seven pairs of spines and the second metatarsus five pairs, all similar to those on first leg. All legs are provided with numerous stout spines. The palpal claw is simple with four moderately robust teeth.

*Abdomen.* Regularly ovate; cribellum moderately well developed; clearly divided. Otherwise essentially as in male.

*Epigynum.* Essentials as shown in Figure 6.

*Color in alcohol.* Essentially as in male except as herein noted. Carapace more clearly striped than in male; on each side of the median light stripe there is a broad darker stripe and on each an additional light marginal stripe thus making five broad stripes on the carapace.

*Type locality.* Holotype male from St. Andrew, Upper Mountain View, January 15, 1950 (C. B. Lewis). Allotype female from St. Andrew, Cross Roads, December 3, 1950 (R. P. Bengry). The following specimens are also in the collection: One paratype male from St. Andrew, Upper Mountain View, May 15, 1950 (C. B. Lewis); one paratype female taken with holotype male; another female from St. Andrew, Upper Mountain View, February, 1951 (C. B. Lewis) and two females from St. Andrew, Half-Way Tree, October 18, 1950 (R. P. Bengry). The author of this paper took one immature female in Hope Gardens, near Kingston, June, 1954.

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## TECHNIQUES FOR THE STUDY OF ANT LARVAE

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Our studies on ant larvae have been published in 30 separate articles scattered in eight periodicals, appearing over a period of 33 years. Several entomologists have expressed regret that the studies have not been combined into a monograph. We regret this too, but no foundation has been willing to publish so long a treatise with so many illustrations and without economic or popular appeal, and no journal has been willing to accept it on the installment plan. The exigency of finance, then, has forced us to publish the body of the "monograph" piecemeal. This present article can be regarded as a part of the introduction. We are prompted to publish it at this time by requests for information concerning our techniques.

### *Living Material*

When living larvae are available, we observe and record as much as possible of their external anatomy. If the larvae are active the changeability of form is noted.

### *Preservation*

Any preservative may be used for ant larvae if only the external anatomy is to be studied. We prefer 85% ethyl alcohol. No special preparation is necessary; the larvae are simply dropped into the preservative. If the alcohol is too dilute or if the container has been overcrowded internal structures may be inadequately preserved, but the integument will still be usable for external anatomy. If large larvae are jostled the hairs may get broken.

Naturally if one plans to investigate also internal anatomy or histology, appropriate killing and fixing reagents are necessary.

If we have only one larva (or very few) of a species we make notes and drawings before subjecting it to any additional techniques. This is simply good insurance.

### *Relaxation*

Even dried larvae may be used for the study of external anatomy. Either of two methods of relaxing is recommended:



1. Two days in a 0.5% solution of trisodium phosphate. Transfer to 85% alcohol.

2. Two days (or less) in the following — 95% ethyl alcohol 280 ml; distilled water 230 ml; benzol 35 ml; ethyl acetate 95 ml.

Dried larvae are handled with extreme care, since hairs are more likely to get broken in this condition.

#### *Handling*

The most convenient receptacle for the treatment of larvae is a staining dish (= embryological cup) 41 x 41 x 18 mm in outside dimensions. Minute specimens, however, are best treated in culture slides (= hanging-drop slides). Small specimens are transferred with a pipette, larger specimens between the points of forceps (but without compression). Or, if one prefers, the larvae may be left in the same dish or culture slide; the old reagent is drawn off with a pipette and then replaced with the next reagent.

#### *Cleaning*

The best cleaning reagent is potassium hydroxide solution (10 gm KOH in 90 ml water). While still in preservative the larvae are punctured with a dissecting needle or minute insect pin on the right side to permit the ready penetration of the cleaning solution. The number and locations of the punctures and the size of the needle depend upon the size of the larva. The specimen is left in the cleaning solution until all the internal tissues are dissolved and only a transparent exoskeleton remains.

If cleaning is not complete by the end of two days, the following procedure may prove effective: transfer to 1% hydrochloric acid and leave 15 minutes; 15 minutes in 95% alcohol; then leave in KOH until clean. Some larvae contain droplets of opaque substances which are insoluble in KOH; these usually disappear later in alcohol or xylol.

#### *Staining*

The exoskeletons of ant larvae are stained in a very dilute solution of acid fuchsin. We use the following formula as a stock solution: acid fuchsin 0.1 gm, concentrated hydrochloric acid 1 ml, distilled water 1 liter; a few thymol crystals are added to prevent mold. The cleaned exoskeletons are washed in water for 15 minutes and transferred to 2 ml of 1% HCL in a staining dish; five drops of the stock solution of acid fuchsin are added. The integuments are left in the stain for 12 hours. We have experimented with stronger solutions of stain for shorter periods but have not been satisfied with the results.

If overstained the integument can be completely decolorized by leaving it in a 1% solution of potassium hydroxide for several hours. It can then be washed and restained.

#### *Dehydration*

After staining, the exoskeletons are transferred to 95% alcohol (about 3 ml), in which they remain for about an hour. At the end of this period eight drops of carbolxylol (= 3 parts xylol and 1 part melted phenol crystals) are added every five or ten minutes until 48 drops have been added to the alcohol. If the carbolxylol is added too rapidly the exoskeletons may collapse and become distorted; they can be restored by transfer to 95% alcohol. If oil droplets separate from the alcohol, too much water has been carried over from the stain; the integuments are transferred to fresh 95% alcohol.

#### *Clearing*

From the mixture of carbolxylol and alcohol the integuments are transferred to pure carbolxylol and left for 15 to 60 minutes; then to xylol in a culture slide (or if large, in a staining dish). Add a drop of thin Canada balsam every 15 minutes, allowing the xylol to evaporate meanwhile.

#### *Mounting*

When the balsam in the culture slide attains the same consistency as that which is being added, a large drop of the latter is placed on a slide and the exoskeleton is transferred to it. At this time medium to large specimens are surrounded — or at least flanked — by supports of some sort. We use fragments of broken slides which are of about the same thickness as the depth of the specimen. If it is obvious that the exoskeleton will not remain in the desired position, supports (such as a fine glass rod or fragments of cover slip) may be placed under the low part.

#### *Positioning*

With needles *dipped in xylol* the integument is now arranged in the proper position for drawing (discussed below). Since the balsam must be soft at this stage, the specimen will rarely remain in precisely the desired position; hence the slide is allowed to rest flat in a covered container (e.g., a petri dish) for 24 hours.

If the specimen then needs rearranging, this is done under a stereomicroscope with needles *dipped in xylol*. If the balsam is too firm a drop of xylol is put on it and let stand a few minutes before using needles. If it is apparent that the specimen will not remain in the

desired position, supports (fine glass rods or fragments of cover slip) may be inserted at this time. If supports were placed earlier, they may need readjustment. Shifting the retaining walls will sometimes correct the position of a specimen. After the rearrangement is completed more balsam is added if necessary to cover the specimen.

It is sometimes necessary to rearrange a specimen on half a dozen successive days. Once a specimen has remained in the desired position for 48 hours and is completely covered with balsam, the technique is considered finished.

If material is abundant we regularly make two kinds of mounts of each size and caste of each species: (1) an entire exoskeleton in side view; (2) detached head in full-face view, with the remainder of the exoskeleton ventral side up (or, if the head is applied to the ventral surface, the whole exoskeleton ventral side up). Other kinds of mounts are made whenever necessary.

For a side view an entire exoskeleton with the left side up and in strict profile, i.e., the middorsal line, the midventral line, the middle of the anus and the middle of the labium are all in the same plane. A good check is to be sure that the left spiracle of each somite is directly above the right spiracle of the same somite. It is conventional to show the entire larva viewed from the left side. Actually it doesn't matter which side is up. If for any reason (e.g., damaged left side) an integument is mounted with the right side up, it is a simple matter to reverse the original drawing.

The exoskeleton of the head is mounted in full-face (i.e., anterior) view. To accomplish this the uppermost line (imaginary) of the occipital border is set in the same plane as the lowermost part of the ventral surface of the labium.

When the head is applied to the ventral surface of the body (i.e., no neck), it is often possible to get it in the correct position by mounting an entire integument ventral side up. In most genera, however, it is necessary to cut off the head (either alone or with a portion of the prothorax) and mount it separately.

It is often necessary to prop up the ventral part of the head on fragments of cover slip, but only very large heads require retaining walls.

After the head is removed, the remainder of the integument is mounted with the ventral side up by following the procedure for the entire integument (see above).



### *Covering*

It is not, however, necessary to cover a mount if it is to be studied at low magnifications. In fact, covering is avoided whenever possible; if the balsam is soft (and it may take years for the interior of a thick mount to harden), the weight of the cover slip will set up currents which are likely to move the specimen out of the desired position.

If, however, the specimen must be studied under the high power objective (X440) of a microscope, a cover slip is essential. For study under an oil immersion objective (X970) the part of the integument is detached, flattened and covered.

If a cover slip is required on a thick mount, it may be added at any time after the surface of the balsam is hard. A drop of xylol is put on the surface and a large drop of thin balsam is put on a cover slip. The cover slip is inverted and one edge is rested on the balsam mount; the opposite edge is supported by a dissecting needle while it is slowly lowered into position. The cover slip is then adjusted by needles dipped in xylol.

If material is scarce — and especially if there is only a single larva — low-power studies are completed before the mount is covered. When material is abundant both covered and uncovered mounts are prepared.

### *Reversibility*

It is reassuring to realize that, *after the integument has been cleaned*, every step is reversible. The same may be said of any series of steps and even of the entire technique from cleaned exoskeleton to covered slide mount. Only one precaution is necessary: hydration (i.e., from 95% alcohol to stain) must be gradual.

### *Perfectionism*

The most important advice we can give to beginners is to avoid perfectionism in making mounts of ant larvae. Not only is perfectionism harmful to the technician (frustration, waste of time), but it can be very damaging to the material. Whenever the conscientious worker has an almost-good-enough preparation, there is always the temptation to try to adjust it a little bit more. Since the balsam must be a little thicker than usual to hold the specimen in the new position, the risk of damage is therefore proportionately increased and the damage may well be irreparable.

It is far better to stop short of perfection in mounting and resort to correction of the position of the slide. Before drawing we make

any slight correction that may be necessary by propping up an edge or a corner or an end of the slide on a small lump of plasticine.

### *Storage*

Prepared slides of ant larvae are always stored flat in the horizontal position. To store on edge is to risk displacement of the specimen, since the interior of a thick balsam mount requires years to harden. Thin mounts may, of course, be stored in any position as soon as the edges of the cover slip are sealed.

Preserved larvae may be stored indefinitely in 85% alcohol. The only precaution required is to prevent drying by evaporation through a faulty seal. (Dried larvae may be relaxed by methods given above.)

### *Summary of Technique*

- |  |   |
|--|---|
| 1. Puncture integument                         | 8. Carbolxylol 15-60 minutes  |
| 2. 10% KOH until clean                         | 9. Xylol  |
| 3. Distilled water — 15 minutes                | 10. Add thin balsam gradually   |
| 4. Transfer to 1% HCL                          | 11. Transfer to balsam on slide   |
| 5. Add 5 drops acid fuchsin; leave<br>12 hours | 12. Arrange in desired position   |
| 6. 95% alcohol for an hour                     | 13. Examine daily; rearrange as often<br>as necessary until desired position<br>has been maintained for<br>48 hours |
| 7. Add carbolxylol gradually                   |   |

### *Descriptions*

We have generally followed this plan in writing our specific descriptions of ant larvae: body shape; leg vestiges; spiracles; integument; body hairs; head shape; antennae; head hairs; labrum; mandibles; maxillae; maxillary palp; galea; labium; labial palp; opening of sericteries; hypopharynx. To facilitate taking notes we have prepared and used a mimeographed form with a blank space under each of the above headings.

When a larva is to be described the prepared slides are studied under a stereomicroscope for low magnifications and a microscope for high magnifications.

Measurements are made by comparison with the squares of an eyepiece reticule (= net micrometer) which has been calibrated with a stage micrometer.

### *Drawings*

All our drawings of ant larvae are made with the aid of a microscope. A reticule (= net micrometer) is placed in the eyepiece. This superimposes a grid of squares on the image of the object. The drawing of the object is made on coordinate paper. The size of squares used is determined by the desired enlargement of the drawing. If

coordinate paper is not available or if the squares are not of the desired size, it is not difficult to construct a coordinate grid on plain paper.

When the eyepiece grid is properly placed with reference to the image and the coordinate system is established on the paper, we are ready to start drawing.

The dimensions and proportions of the drawing are established by short marks across the lines of the coordinate system in the appropriate places. The main outline is constructed by joining these intersections with freehand lines. Structures inside or outside the main outline are treated in approximately the same way, but more freehand drawing is required because fewer squares are involved and smaller parts are likely to be wholly inside a single square. It is not necessary to complete all fine details at this stage.

The drawing is placed on a tracing table, a sheet of thin drawing paper (e.g., Ledger Linen) is laid on it; the drawing is copied onto the drawing paper in India ink with curve-pen (Keuffel and Esser). Finer details are drawn with a Hunt Mapping Pen No. 104.

In the case of bilaterally symmetrical structures (e.g., head in anterior view) only one half is drawn, with a vertical matching line down the middle. After this half (but not the matching line) has been inked the pencil drawing is turned over on the tracing table, matched up to the first half and then inked.

Most of our drawings are orthographic projections of opaque objects (even though the integuments studied are actually transparent). Only structures on the near side of the plane of the outline are drawn. For example, in a side view of a larva the outline represents the imaginary middorsal and midventral lines; hairs and other parts attached beyond (= below, in the field of the microscope) the plane of these two lines are not shown. To our rule of assumed opacity a few exceptions are made, e.g. dark-colored structures overlaid by translucent tissues.

We have found 120 mm to be a convenient length for a drawing of the entire larva. The plane of projection includes the middorsal line (imaginary), the midventral line (imaginary), the middle of the anus and the middle of the bottom of the labium. It is conventional to view the larva from the left. But if for any reason it has been drawn from the right, the original drawing (on co-ordinate paper) can be turned over on the tracing table before inking.

The head is drawn in full-face (i.e., anterior) view. The plane of projection passes through the uppermost line (imaginary) of the



occipital border and the lowermost part of the ventral surface of the labium. A convenient width (at the widest place) is 75 mm.

The mandible is also drawn in anterior view. The plane of projection passes through the apex, the inner (= medial) condyle and the outer (= lateral) condyle. If the mandible is drawn from a head mounted for full-face view, it is usually necessary to prop up an edge of the slide to bring these three points into the same horizontal plane. A convenient length for the mandible drawing is 65 mm.

THE FEMALE OF *LUCARACHNE BEEBEI* GERTSCH  
(ARANEAE: SYMPHYTOGNATHIDAE)<sup>1</sup>

BY ARTHUR M. CHICKERING  
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Miss Elizabeth B. Bryant established the genus *Lucarachne* in 1940 on the basis of both males and females taken in Oriente Province, Cuba, at 1500 feet elevation. She placed the genus, with some hesitation, among the Metinae of the Argiopidae and noted that it appeared to be closely related to *Theridion cidrelicola* Simon from Venezuela, the male of which is now considered to belong to the genus *Lucarachne* and is included in the Family Symphytognathidae. When Dr. Gertsch (1960) described *L. beebei* from males alone he noted that four species of the genus *Lucarachne* are now known as follows: *L. tibialis* Bryant from Cuba; *L. cidrelicola* (Simon) from Venezuela; *L. beebei* Gertsch from Trinidad; *L. palpalis* Kraus from Honduras and Mexico. Dr. Gertsch has recently identified a male *L. beebei* Gertsch from my Panamanian collection of 1936 taken in El Valle. In my collection made in Panama in 1958 numerous specimens of both males and females of this last-named species were found also near El Valle. One of the females has been selected and is described below in accord with my usual procedure.

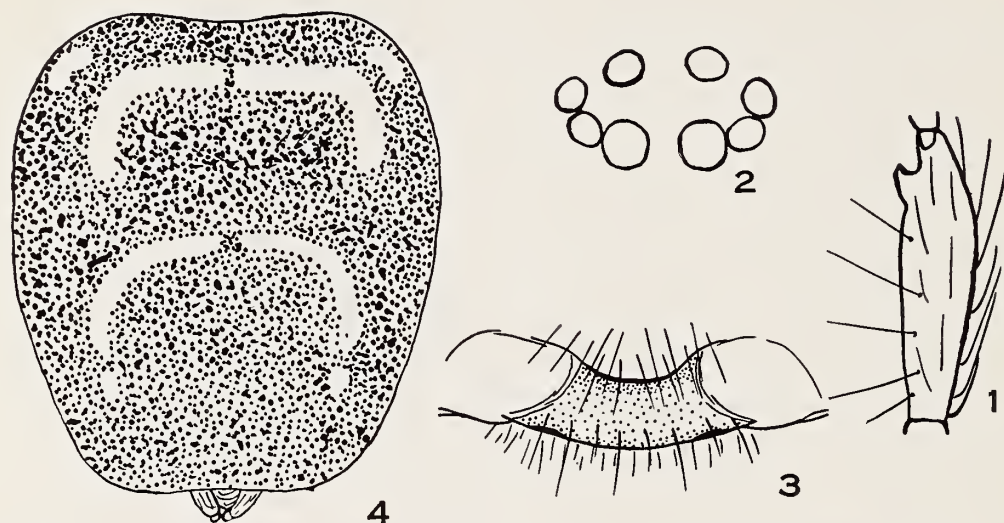
Genus *Lucarachne* Bryant, 1940  
*Lucarachne beebei* Gertsch

*Female.* Total length 2.05 mm. Carapace 1.012 mm. long, .85 mm. wide opposite interval between second and third coxae where it is widest; well rounded along margin from opposite posterior eyes to posterior border; gently arched from PE to near posterior border with highest part shortly behind those eyes; with few bristles or hairs.

*Eyes.* Eight in two rows. Region of AME considerably raised into a low blunt tubercle. Seen from above, posterior row nearly straight, anterior row strongly recurved; seen from in front, anterior row slightly procurved, posterior row strongly so, all measured by centers.

<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

Ratio of eyes AME:ALE::PME:PLE = 10:6::6:7. AME separated from one another by about three fifths of their diameter, from ALE by only a line. PME separated from one another by about five sixths of their diameter, from PLE by about the same distance. LE almost in contact. Central ocular quadrangle wider in front than behind in ratio of about 6:5; nearly as long as wide in front. Clypeus very high; height equal to nearly three times the diameter of AME.



Figures 1-4. External Anatomy of the Female of *Lucarachne beebei* Gertsch. Fig. 1. Left first femur; nearly ventral view. Fig. 2. Eye group of female; somewhat obliquely from above. Fig. 3. Epigynum, from below. Fig. 4. Abdomen; posterior surface.

*Chelicerae.* Moderately robust, vertical, parallel; fang regularly curved; promargin of fang groove apparently with three teeth the first of which is only a denticle while the other two are fairly robust; retromargin with only one rather small tooth.

*Maxillae.* Robust; slightly convergent.

*Lip.* Reaches about two thirds the length of the maxillae. Sternal suture only slightly procurved.

*Sternum.* Scutiform in general; quite convex; only slightly longer than wide; widest opposite interval between first and second coxae; extends between fourth coxae and terminates in a blunt truncature; fourth coxae separated by nine tenths of their width; posterior end with a cluster of stiff bristles.

*Legs.* 1243. Width of first patella at "knee" .132 mm., tibial index of first leg 9. Width of fourth patella at "knee" .110 mm., tibial index of fourth leg 10.



	<i>Femora</i>	<i>Patellae</i>	<i>Tibiae</i>	<i>Metatarsi</i>	<i>Tarsi</i>	<i>Totals</i>
	(All measurements in millimeters)					
1.	1.275	.422	1.000	.715	.620	4.032
2.	1.150	.390	.785	.715	.520	3.560
3.	.910	.325	.585	.484	.484	2.788
4.	.970	.340	.715	.715	.585	3.325

Legs with many long slender stiff bristles and few definite long slender spines the most significant of which appear to be the following: each patella with two of these dorsally placed, one near each end of the segment; each tibia has one of these on the dorsal surface near the proximal end; numerous extremely slender spines occur more or less in rows on the ventral surfaces of the femora. The first femur has a distinctive ventral apophysis near the distal end (Fig. 1). Trichobothria are present on the tibiae and metatarsi but the exact numbers and distribution have not been determined.

*Abdomen.* Ovoid; carried in nearly a perpendicular position; overlaps the carapace considerably; similar to that of *L. palpalis* Kraus (Fig. 4).

*Epigynum.* Simple; details best shown in Figure 3.

*Color in alcohol.* Essentially as described for the male by the author of the species; exposed posterodorsal surface essentially as shown in Figure 4.

*Collection records.* Dr. Gertsch had the male holotype and one male paratype from Trinidad. Collection records in Panama are as follows: a single male from El Valle from my collection of July, 1936, recently identified by Dr. Gertsch; several specimens of both sexes are included in my collection of 1958; these were taken about five miles south of El Valle in January.

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# STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS 1. THE PROTODONATA<sup>1</sup>

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## *Introduction*

This is the first of a series of papers based upon insects from Carboniferous strata in North America. The studies will be concerned in the main with previously described specimens (mostly types) in the Museum of Comparative Zoology, the U. S. National Museum and the Peabody Museum at Yale University, but will include new material whenever it is available.

## *Order Protodonata*

Up to the present time only three species of Protodonata have been described from North American deposits of Carboniferous age. The present paper includes the description of a fourth species and an account of the previously described ones. In addition, I have included a discussion of the status of the ordinal name Protodonata.

One of these protodonates belongs to the family Meganeuridae and another to the Paralogidae. The remaining two are best referred to *Incertae Sedis* for family designation, although their protodonate affinities are unquestionable.

## Family Meganeuridae

**Typus durhami**, n. sp.

Plate 11; text figure 1.

Forewing: greatest length of preserved part, 88 mm.; estimated complete length, 175 mm.; maximum width of preserved part, 27 mm. The venational details of both fore and hind wings, so far as preserved, are shown in text figure 1. The general venational pattern is close to that of *permianus* and other known species of the genus. The cells of the wings are larger than those of *permianus*, especially in the area between MA and CuP; R<sub>2</sub>+3 and R<sub>4</sub>+5 seem to diverge even more gradually in *durhami* than in *permianus*. The basal origin of

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<sup>1</sup>This research was supported by National Science Foundation Grant No. NSF G 14099, and the article is published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

R<sub>3</sub> is not preserved in the fore wing but in the hind wing it is clearly visible and is associated with the oblique cross-vein (Sn) characteristic of most Meganeuridae (Carpenter, 1947, p. 47); the cross-vein is not so pronounced as it is in *permanus*, however. The differences between the fore and hind wings in the proximal region are like those in other species of *Typus*.

Holotype: U. S. National Museum, Washington, D. C.<sup>2</sup> The specimen (field number 8758) was collected in May, 1939, by Mr. Charles B. Read at Durham, Georgia, the locality data being "Catoosa (TVA. Durham Quad.), Williams Coal Company Mine in No. 4 Coal. Plants from roof shale." According to Butts' account of the stratigraphy of the Paleozoic area in northwest Georgia (Butts and Gildersleeve, 1948, pp. 54-56), the coal mines at Durham are in the Walden sandstone part of the Pottsville Series. Butts states that "according to the best knowledge, the Pottsville Series of Georgia is of Lower Pottsville age and falls within the limits of the Lee Conglomerate of Tennessee and Virginia and corresponds approximately to the lower part of the Pottsville of the anthracite coal fields of Pennsylvania which carry the Lykens number 4 and 5 and the Lykens Valley coals." A brief discussion of the nature of the no. 4 coal at Durham is contained in Gildersleeve's account (*ibid.*, 1948, p. 104) of the mineral resources of the Paleozoic area in northwest Georgia.

As can be seen from the photograph (Plate 11), the specimen consists of the apical portions of the fore and hind wings; although the remainder of the insect, which was presumably originally preserved, is broken away, the preserved portions are very clear. I have assigned this species to the genus *Typus* but it might conceivably belong to *Megatypus* or *Boltonites*; the absence of the basal part of the wing containing the regions of the anal crossing and the second anal vein prevents a more definite generic assignment.

The interest attached to this species is in the evidence which it provides for the existence of the Meganeuridae in North America during the Carboniferous. It is the first such fossil that can be definitely assigned to the family. Furthermore, *Typus durhami*, occurring in the Lower Pottsville Series (corresponding approximately to Westphalian A), is among the oldest fossil insects known from North America.

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<sup>2</sup>I am indebted to Dr. S. H. Mamay of the United States Geological Survey for sending me this specimen for study.



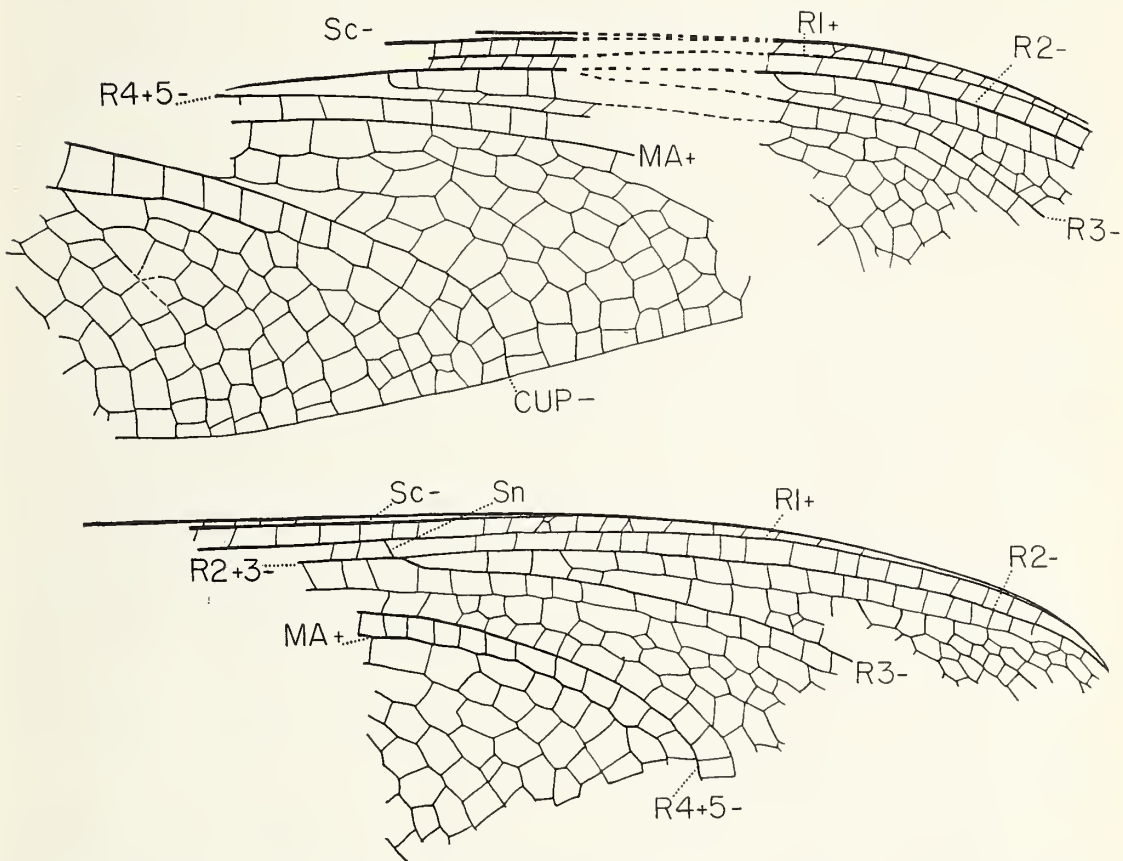


CARPENTER — PROTODONATA



## Family Paralogidae

The distinctive features of this family are the short subcosta, which terminates just beyond the middle of the wing; and the widely divergent branches of Rs ( $R_2 + 3$  and  $R_4 + 5$ ). The complete absence of the apparent vestige of CuA may also be a family trait. *Paralogus* is the only Carboniferous genus that clearly belongs here but in my opinion the Permian genus *Oligotypus* Carp. does also. Fraser (1957) considered *Oligotypus* to be a meganeurid, but, as shown below, his concept of the Paralogidae has not been entirely correct. *Oligotypus*



Text figure 1. Drawing of *Typus durhami*, n. sp. (holotype), fore and hind wings. Sc, subcosta; Rs, radius;  $R_2$ ,  $R_3$ ,  $R_4 + 5$ , branches of radial sector; MA, anterior media; CuP, posterior cubitus; Sn, subnodal vein.

differs from *Paralogus* only in minor details: the wing is somewhat more slender, and the branches of MA and 1A arise as a series of irregular veinlets, instead of distinct branches as in *Paralogus*. The following review of the structure of *Paralogus* strengthens my conviction that it and *Oligotypus* belong to the same family.

## EXPLANATION OF PLATE 11

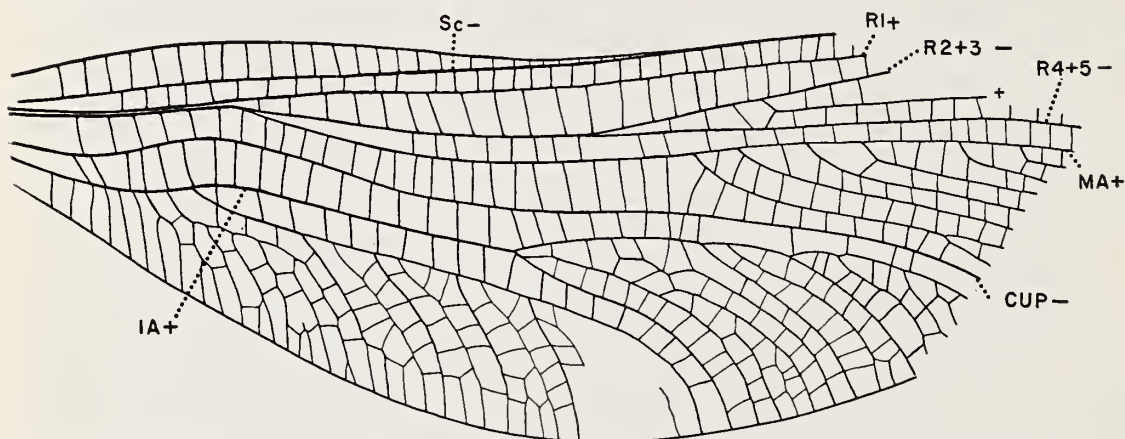
Photograph of *Typus durhami*, n. sp. (holotype)  $\times 11/10$ .

*Paralogus aeschnoides* Scudder

## Text figure 2.

*Paralogus aeschnoides* Scudder, 1893, U. S. Geol. Surv., Bull. 101: 21; pl. 1, fig. a.

The unique specimen on which this species was based was collected by Mr. F. P. Gorham (1889) in Upper Carboniferous rocks at Silver Spring, East Providence, Rhode Island, and was donated to the Museum of Comparative Zoology by Professor Gorham in 1932. It consists of a well-preserved wing, about two-thirds complete. Scudder's drawing of the fossil is good and even shows by means of shading the convexity and concavity of the veins. I have included here a new description and an original illustration of the fossil, in part because a few details of phylogenetic significance were not clearly indicated by Scudder and in part because Dr. Fraser's recent illustration of the fossil (presumably based on Scudder's drawing) is misleading in several important respects.



Text figure 2. Drawing of *Paralogus aeschnoides* Scudder (holotype). Lettering as in text figure 1.

The wing fragment, as preserved, is 54 mm. long, and has a maximum width of 19 mm.; the complete wing was probably about 80 mm. long. The subcosta terminates a short distance beyond the middle of the wing and beyond the point of separation of  $R_2 + 3$  and  $R_4 + 5$ . The two latter veins diverge widely after their origin; MA has a series of pectinate branches beginning just beyond the divergence of  $R_2 + 3$  and  $R_4 + 5$ ; just before the level of this divergence, 1A separates into a divergent fork and sends a series of additional branches towards the distal part of the wing.

The wing itself is broad for a protodonate and has a strongly curved posterior margin. However, on the basis of our knowledge of the differences between the fore and hind wings of Meganeuridae, I



believe that the specimen of *aeschnoides* is a fore wing. At any rate, the distance between the posterior margin of the wing and the first anal is like that of other protodonate fore wings, not hind wings.

As can be seen from Scudder's illustration, the wing was subjected to some distortion in the process of preservation; it rests on a very uneven surface of the rock, so that the contour of the anterior margin of the wing is difficult to follow exactly. This is made worse by the presence of a slight "fault" extending obliquely across the wing, so that the veins in the anterior part of the wing are not quite aligned on the two sides of the fault. The result of the faulting and of the irregularity of the surface of the rock is to cause a more pronounced curvature of the anterior margin of the wing than would presumably otherwise have been present. The drawing in text figure 2 has been made without any attempt to restore the presumed original shape of the wing, apart from aligning the veins across the fault.

Scudder's representation of the shape of the wing is correct, the proportions of his drawing being approximately the same as those in the fossil. On the other hand, Fraser's drawing (1957, figure 11), showing a markedly broad wing and strongly curved posterior margin, is apparently incorrect. At any rate, I do not know of any evidence which supports this conception of the wing. Two other, more minor, corrections in Fraser's figure should be noted. The vein which he has labelled R<sub>3</sub> is a convex intercalary vein; R<sub>2</sub> and R<sub>3</sub> presumably separate much further along the wing. Also, the subcosta terminates gradually somewhat beyond the level of the separation of R<sub>2</sub> + 3 and R<sub>4</sub> + 5, not abruptly before this level as shown in Fraser's drawing. The short basal vein, termed CuA, which is consistently present in the meganeurids, is not discernible in the specimen of *aeschnoides* although Dr. Fraser has shown it in his drawing. The absence of this vein appears to be another characteristic shared by *Paralogus* and *Oligotypus*.

The deposit in which the specimen of *aeschnoides* was found is usually referred to the Allegheny or Conemaugh Series, about equivalent to the Upper Westphalian of Europe.

Family: Incertae Sedis

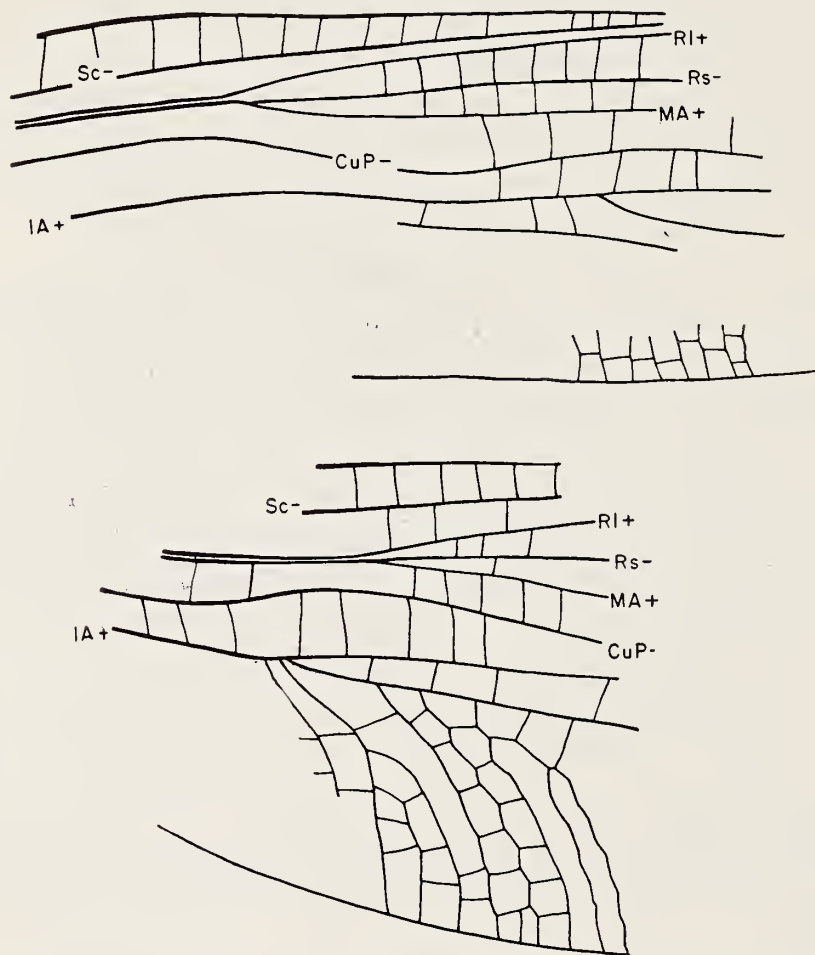
*Paralogopsis longipes* Handl.

Text figure 3.

*Paralogopsis longipes* Handl., 1911, Amer. Journ. Sci., (4) 31: 374, fig. 58.

The specimen on which this species was based is contained in an ironstone nodule from the vicinity of Mazon Creek, Illinois; the type

is in the Peabody Museum at Yale University, where I examined it several years ago. Although Handlirsch figured only the hind wing (so far as it was preserved), a portion of the fore wing is also present; this is clearly narrow, more like that of the Meganeuridae than of the Paralogidae, where *Paralogopsis* has previously been placed (Fraser, 1957). However, since the key parts of the wings (such as the forking of Rs) are not included in the preserved portion, the family relationships remain obscure.



Text figure 3. Drawing of *Paralogopsis longipes* Handl. (holotype). Lettering as in text figure 1.

The significance of this fossil is that it provides the only record of the Protodonata in the Carboniferous strata of the Eastern Interior Region of North America. The Frances Creek shales, which yield these ironstone nodules, are considered part of the Carbondale Formation; this is regarded as about equivalent to the middle or late Westphalian stage (late C or early D) of Europe.

*Palaeotherates pennsylvanicus* Handl.

## Text figure 4.

*Palaeotherates pennsylvanicus* Handlirsch, 1906, Proc. U. S. Nat. Mus., 29: 690, fig. 17.

*Palaeotherates pensilvanicus* [sic] Handlirsch, 1906, Fossilen Insekten: 311; pl. 32, fig. 5.

The fossil on which this species was established consists of a wing fragment preserved in black shale; it was collected in 1887 in interconglomerates, at Coxtton, one mile north of Pittston, Pennsylvania. The type specimen, which is in the U. S. National Museum (No. 38787), was kindly loaned to me for study through the courtesy of Dr. G. A. Cooper.

Handlirsch's drawing of the fossil, although correctly representing the general venational features, omitted two significant details, — the subnodal vein and the costa. He recognized that the "second vein" must be the radius (R1), but since he could detect no anterior vein, other than a marginal one, he concluded that the subcosta had fused with the costa in the area of the wing preserved. However, the clear preservation of the subnodus (Sn), which Handlirsch did not figure, shows that the part of the wing represented was too near the middle of the wing for the termination of the subcosta to have taken place. Furthermore, careful study of the fossil shows that the anterior margin of the wing (costa) is actually present as distinct from the subcosta in the distal part of the fossil, although it is broken away along the rest of the wing fragment. It now becomes clear that the fossil represents a fragment of the wing just beyond the middle; it includes the point of separation of R2 and R3, but not the separation of R2 + 3 and R4 + 5. Handlirsch's naming of the veins is incorrect; the convexities and concavities, which are clearly preserved in the fossil, show that R4 + 5 was included in the complex which he termed the media.

The original insect was probably about the size of most species of *Typus*, not "very large" as estimated by Handlirsch. The wing fragment is 45 mm. long, and on the basis of comparisons with other protodonates, it probably represents about one-third of the complete wing. Since the width of the wing of *pennsylvanicus* is 18 mm., its original dimensions were probably close to those of *Typus gracilis* Carp. (Permian), which is 145 mm. long and 26 mm. wide.

The drawing of the fossil shown in text figure 4 is based on the type specimen. The venational pattern, so far as it is known, is like

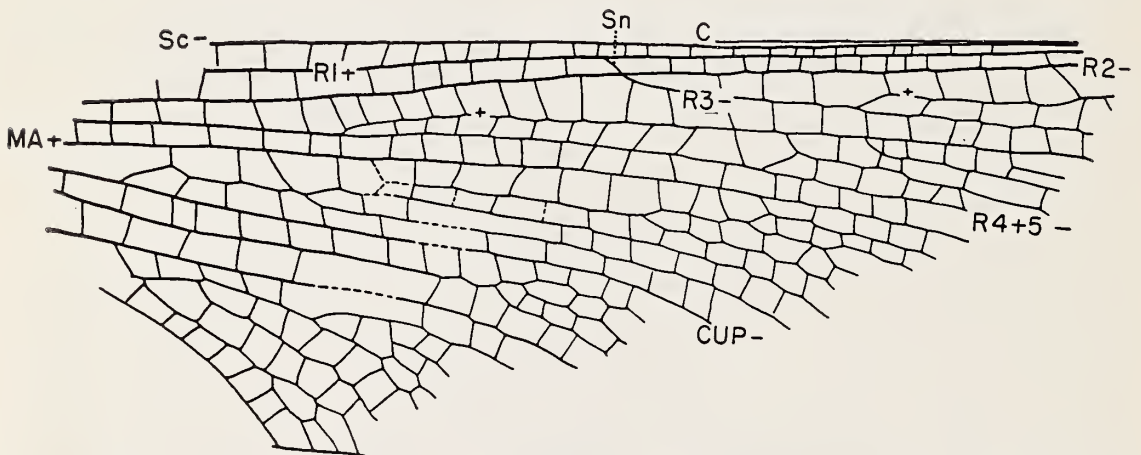


that of the meganeurids, but, since the proximal half of the wing is unknown, I consider the family position uncertain. It is clearly not a member of the Paralogidae, where it was placed by Fraser (1957).

The deposit in which this fossil was collected appears to be of upper Pottsville age corresponding to Westphalian C of the European classification.

#### *Status of the Ordinal Name Protodonata*

I take this opportunity to discuss the status of the ordinal name Protodonata, in an attempt to clear up some of the confusion which has appeared in the literature in recent years. Handlirsch (1906b) first defined this group as an order in 1906<sup>3</sup> and he placed here three new



Text figure 4. Drawing of *Palaeotherates pennsylvanicus* Handl. (holotype). Lettering as in text figure 1.

<sup>3</sup>Much confusion has resulted from two, almost simultaneously published works by Handlirsch, both appearing in 1906. His *Revision of American Paleozoic Insects* (Proceedings of the U. S. National Museum, Vol. 29, pp. 661-820) is an English translation of a specially prepared account of the Paleozoic insects then known from North American deposits. New species, genera and higher taxa were described and illustrated. His *Die Fossilen Insekten* was published by Englemann in Leipzig in parts over a period of two years. The first part, consisting of pages 1-640, was published in 1906 (See *Fossilium Catalogus*, (I), Pars 16, 1922, p. 10). This part dealt with the Paleozoic insects and included, among the others, descriptions and figures of the North American fossils. That this work was published *after* the English account is shown by the references in *Die Fossilen Insekten* to specific pages in the Proceedings article. Unfortunately, many (but not all) of the species, genera and higher taxa already described in the Proceedings account were described again and designated as new in the larger, German treatise.

In reality, the first designation of the Protodonata as an *order* was made in the Proceedings article mentioned above. The discussion of the characteristics of the order was essentially that given later in *Die Fossilen Insekten*, but only two genera, *Paralogus* and *Palaeotherates*, were actually mentioned as included in the order.

families: Protagrionidae Handl., Meganeuridae Handl., and Paralogiidae Handl. The Protagrionidae<sup>4</sup> were known only from a single wing (*Protagrion audouini*), but the Meganeuridae were known from many specimens, some of which included the body structures. Handlirsch's definition of the order was accordingly based on the meganeurids and the order itself was considered by him to be related to both the Paleodictyoptera and the Odonata. In the course of several years, as more meganeurids and Paleodictyoptera were found, it became increasingly evident that the Protagrionidae were not at all closely related to the Meganeuridae or to the Odonata. In 1932, Martynov (1932a), after pointing out the differences between these two groups, removed the Meganeuridae and Paralogiidae from the Order Protodonata and placed them in a new order which he erected for them, the Meganisoptera. The Order Protodonata was therefore left with the family Protagrionidae, which was then recognized as having no odonate affinities.

In 1943, after a detailed study of the original specimen of *Protagrion audouini* (preserved in the Paris Museum), I published an account of this fossil and transferred the family Protagrionidae to the Paleodictyoptera, where it clearly belongs, in association with several related families; at the same time I restored the Meganeuridae and Paralogiidae to the Order Protodonata, as they were originally placed by Handlirsch.

In 1957, in his account of the classification of the Odonata (p. 21), Fraser agreed to the separation of the Protagrionidae from the Meganeuridae and Paralogiidae, but he insisted that the name Protodonata must be associated with *Protagrion*, and contended that I was in error in placing the Meganeuridae in the Order Protodonata. His reason for these assertions was that "Brongniart established his family Protagriidae [Protagrionidae] on a single genus *Protagrion* (1885); the family was therefore a monotypic one and by the International Rules of Nomenclature it matters not whether the family afterwards assumed ordinal rank or that further genera or families were added to it, it must take the characters from *Protagrion*, that is, from the original type."

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<sup>4</sup>Throughout this article I am using the name Protagrionidae, instead of Protagriidae, for the family based upon the genus *Protagrion*. This is in accordance with the information provided by Professor Joshua Whatmough of Harvard University and published in B. E. Montgomery's article on this subject (*Annals Ent. Soc. Amer.*, 47: 473-474, 1954).

It is clear from this quoted passage that Fraser's conclusions are based on his belief that *Protagrion* was designated by Brongniart as the type genus of the Order Protodonata and that the Rules of Nomenclature consequently require us to use that conception of the order. I believe it is Dr. Fraser who is in error here. The Rules of Nomenclature have not been applied by the Commission on Nomenclature to orders and higher taxa. The accepted policy regarding these higher categories has been well summarized by Simpson in his recent discussion of the principles of taxonomy (1961, p. 30): "Proposals have been made to extend the type system (and priority) to names of still higher taxa, above superfamilies, but this provision is not now embodied in the Rules or in general usage. At present the names of those higher taxa, of course much less numerous than names of genera or species, are determined only by consensus and acceptance of authority, and at these levels that informal system seems to work at least as well as the Rules do at lower levels."

Since the term Protodonata was first used in an ordinal capacity by Handlirsch (1906b), as I have stated above, and since his definition of the order was based mainly on the Meganeuridae, I prefer to use the name Protodonata for the order containing the Meganeuridae.

Moreover, if the Rules of Nomenclature are applied to the ordinal name here, I contend that *Protagrion* has no standing as the type genus of the Protodonata and that, in fact, the genus *Meganeura* more logically and appropriately stands as the type genus. In this connection it is necessary to correct Fraser's statement quoted above, that "Brongniart established his family Protagriidae on a single genus *Protagrion* (1885)". At no time did Brongniart ever use the family name Protagriidae [Protagrionidae]; it was first used by Handlirsch in 1906 (1906b). Consequently, this statement by Fraser has no meaning or application whatsoever to the term Protodonata. The name Protodonata was first used by Brongniart in 1885 (p. 55). In this paper Brongniart discussed a series of orders, one of these being the "Neurorthopteres" and another the "Pseudoneuroptera". In this latter order he placed, among others, two families, one which he called Megasecopterida and another which he designated Protodonata. His precise statement about the "family Protodonata" is as follows: "Je rangerai à côté de ces Megasecopterida un type ancestral des Libellules; la création de la famille des Protodonata . . . et du genre *Protagrion* . . . me semble nécessaire. Une aile seulement a été trouvée jusqu'ici à Commentry; elles [sic] mesure 10 centimètres de



long et 2 centimètres de large. Sa forme, sa nervation et sa réticulation rappellent beaucoup celle des Odonates actuels. Il y a cependant d'assez notables différences."

Since this was the first mention of the genus *Protagrion* in the literature anywhere and since there was no mention of any species in the genus, the name *Protagrion* was a *nomen nudum*. This use of the term Protodonata did not, therefore, establish a precedent or policy with respect to use of the name. The next use of the term Protodonata, again for a family, was by Brongniart in 1894 (p. 394). At the beginning of Chapter V, entitled "Protodonata", there was a discussion of the characteristics of the Protodonata based almost entirely on *Meganeura*; the genus *Protagrion* was not even mentioned there. In the descriptive part of the work, the first genus considered was *Meganeura*, which was fully described, along with two species in the genus, *monyi* and *selysii*. The other genera also assigned in the "family Protodonata" in chronological order were: *Paralogus*, *Titanophasma*, *Protagrion*, *Campyloptera*, and *Brodia*. *Protagrion* was, therefore, fourth in the series of genera placed in the "family Protodonata". From this I think it is clear that there is no basis for Dr. Fraser's statement that the Order Protodonata "must take the characters of *Protagrion*".

Since the first definition of the Protodonata as an order (Handlirsch, 1906b) was based mainly on the Meganeuridae, and since Brongniart's first valid use (1894) of the term Protodonata for a "family" was based almost exclusively on *Meganeura*, I do not accept the removal of the Meganeuridae from the Protodonata and the erection of another order (Meganisoptera) for that family. In my opinion the Order Meganisoptera is identical with the Order Protodonata.

Whether the Protodonata should be considered a separate order or a suborder of the Odonata is largely a matter of personal choice. Fraser (1957, p. 24) considers the group (Meganisoptera) to be a suborder, whereas Martynov (1932b, p. 43; 1938, p. 62) treated it as a distinct order. I strongly support its ordinal rank; the absence of a nodus, a pterostigma and a true arculus places these insects outside the phylogenetic complex of the Odonata.

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AUSTRALIAN CARABID BEETLES IV. LIST OF  
LOCALITIES, 1956-1958<sup>1</sup>

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Museum of Comparative Zoology, Cambridge, Mass.

This is a brief account, with list of localities, of a collecting trip that I made to Australia from December 1956 to June 1958. My wife and fourteen year old son accompanied me. My own travel expenses were paid in part by a fellowship of the John Simon Guggenheim Memorial Foundation. My purpose was to collect carabid beetles in the wetter forests of the whole eastern edge of Australia, from southern Tasmania to northern Cape York. The present paper summarizes our itinerary and then lists the localities at which Carabidae were obtained. I had collected at some of these localities previously, in 1931-1932, as a member of the Harvard Australian Expedition.

We reached Sydney December 2, 1956, and proceeded to Tasmania December 7. We bought a used (and abused) Volkswagen pickup truck in Hobart and traveled and lived in it most of the time thereafter.

We stayed in Tasmania until April 5, 1957. Collecting was done mostly in the wetter forests there; first into the accessible edges of the almost impenetrable southwestern forest (Arve River, Hartz Mountain, Mt. Field, Florentine River, Zeehan, etc., and later Corinna); then in mountainous north-central Tasmania (Lake St. Clair, Waldheim and Cradle Mt., Great Lake, Waratah, etc.); and finally on isolated mountains and plateaus in the northeast (Mt. Ben Lomond, Blue Tier, Mt. Barrow, etc.). Although the most extensive wet forests are in the south and west, we found some of the finest stands of *Nothofagus* (southern beech) on and near the Blue Tier in northeastern Tasmania. Lake St. Clair was the best (most diverse and richest) Tasmanian locality visited. The most southern locality reached was Cockle Creek, about 5 miles from the southernmost tip of land.

On the mainland of Australia, beginning in April, 1957, we worked the Otway Ranges southwest of Melbourne, then crossed the mountains via Mt. Hotham and Omeo to Canberra, which we reached May 1, and where we made winter quarters in a rented house.

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<sup>1</sup>Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.



At Canberra I studied the types of Australian Carabidae in the Sloane Collection, now in care of the Commonwealth Scientific and Industrial Research Organization. During this time we collected repeatedly on the Brindabella Range west of Canberra, briefly on the lower slopes of Mt. Kosciusco, and at other places within reach.

From Canberra, starting September 1, 1957, we crossed by the Sturt Highway to Adelaide, where I examined Sloane's and Lea's Tasmanian carabid types. We then followed the coast south, east, and north, via Melbourne, to Sydney, making side trips to collect on Mt. Baw Baw, Wilsons Promontory, etc.

From Sydney, October 15, 1957, we started a long zig-zag through northern New South Wales, going west almost to Nyngan, back to the Mt. Royal Range (incl. Barrington Tops), and north via the Comboyne, the Dorrigo-Ebor plateau (including New England National Park and Point Lookout, a magnificent, mile-high collecting place), Armidale, and a series of localities across extreme northern New South Wales, to Brisbane in Queensland.

We reached Brisbane November 12, 1957, and left on the 16th for North Queensland. Going north, we worked (among other places) the Eungella Range (an important, isolated rain forest locality inland from Mackay), and Mt. Spec, Mt. Fox, and the Kirrama Range. We reached Cairns December 6.

From Cairns, we began work on the Atherton Tableland, in the largest and richest tropical rain forest area in Australia. We found the ground at Kuranda too dry, so moved our headquarters to Atherton and collected thereabouts, especially on the Dividing Range south and west of the town. December 13-16, 1957, we camped and collected on Mt. Bartle Frere. December 20, we returned to Cairns, and in the next few days did Thornton Peak (Mt. Alexandra) northeast of Daintree and Mt. Lewis southwest of Mossman. From December 31, 1957 to January 3, 1958, I collected alone on Mt. Bellenden Ker.

On January 7, 1958, we flew to Thursday Island and crossed to the tip-of-peninsular forests of Cape York, collecting at Bamaga and Lockerbie until the 20th. From Lockerbie we worked to within 10 miles of the northern tip of continental Australia. My son and I interrupted the return flight at Iron Range for a week's collecting, including a side trip on foot to Tozer Gap.

We spent most of February, 1958, on the Atherton Tableland, where, however, collecting was hampered by continual heavy rain.

From late February until March 13 we were moving south, re-visiting the Kirrama Range and Mt. Spec, and reaching two additional, important localities: the isolated rain forest on the Elliot Range southeast of Townsville, and Mt. Jacob near Many Peaks, where is the northernmost rain forest (or semi-rain forest) of the South Queensland forest system.

From Brisbane, March 19 to April 12, 1958, we made a loop south to Victoria, to collect on high mountains that had been snow covered before. We reached highest altitudes on Mt. Kosciusco, then drove south on the Bonang Highway into Victoria (this road cuts some fine and apparently unworked collecting areas), then collected on the summit ridge of Mt. Baw Baw, on Mt. Buller briefly, on Mt. Hotham again, and at Pretty Valley on Mt. Bogong. Returning north we touched Exeter and Ourimbah (type localities) in south-central New South Wales, Bellangry Forest northwest of Wauchope, Point Lookout again, and localities in the extreme north of New South Wales.

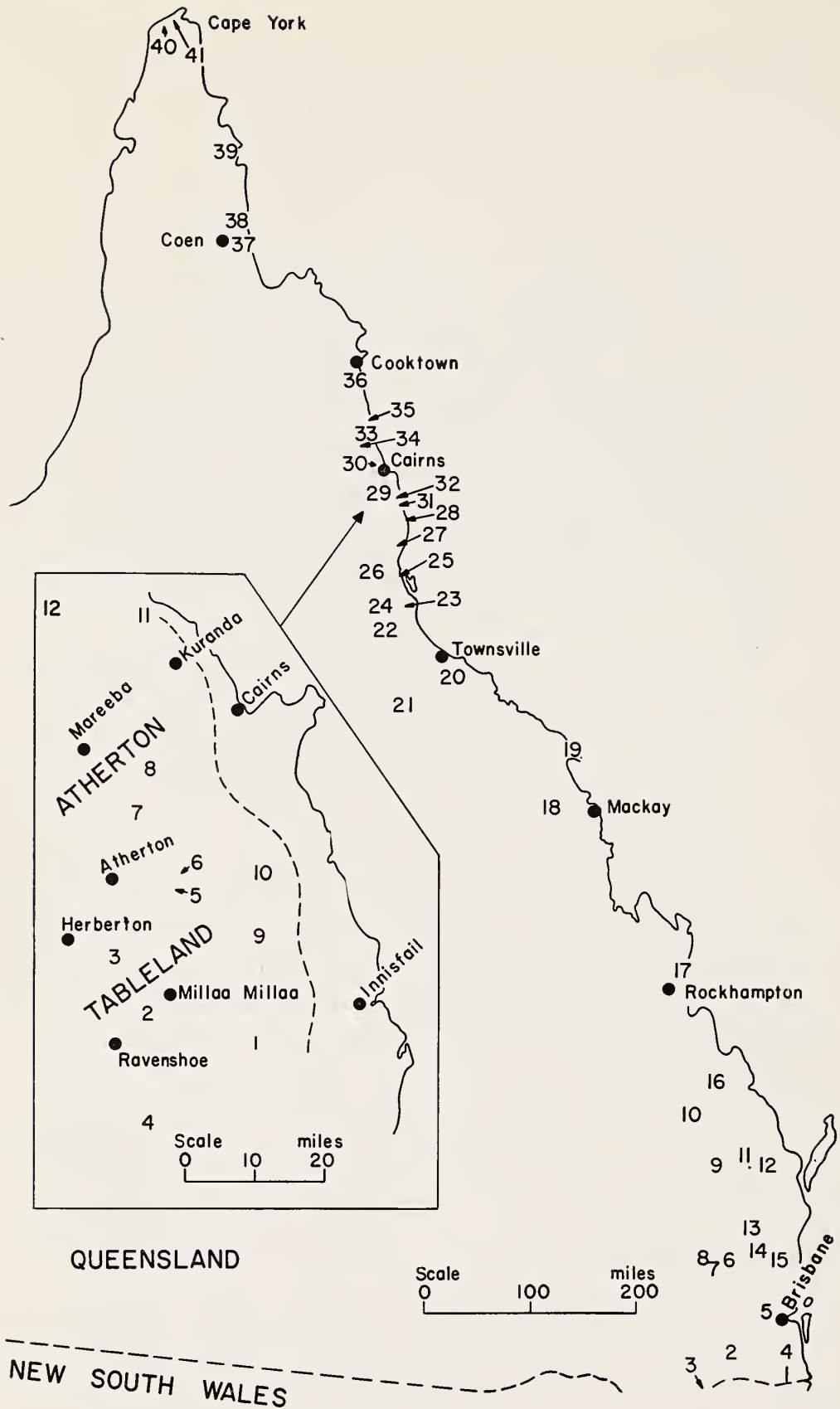
On April 19, 1958, we started another loop, through South Queensland, working rain forest areas, the most important being on the Bunya and Blackall Ranges. Then, beginning May 6, we spent a week at Binna Burra on the McPherson Range on the Queensland-New South Wales border.

Beginning May 23, 1958, we flew back to Cairns, collected along the Black Mt. road north of Kuranda, flew halfway up the Cape York Peninsula to Coen, and from there were taken by Lea Wassell to Silver Plains and the Rocky Scrub (rain forest) on the east side of the peninsula. Returning from this trip, we stopped for nearly a week at Shiptons Flat and Mt. Finnigan, about 25 miles south of Cooktown.

We were back in Sydney June 17, 1958, and from there circled through the southern Blue Mts. (Springwood), the Burragorang Valley, Burrawang, etc.

We started the flight home from Sydney June 25, reaching Boston the afternoon of June 29, 1958.

All specimens collected reached Boston safely, and have been mounted and labeled and are ready for study. We got little except Carabidae and a useful series of ants collected by my son. We had neither time nor strength for general collecting.



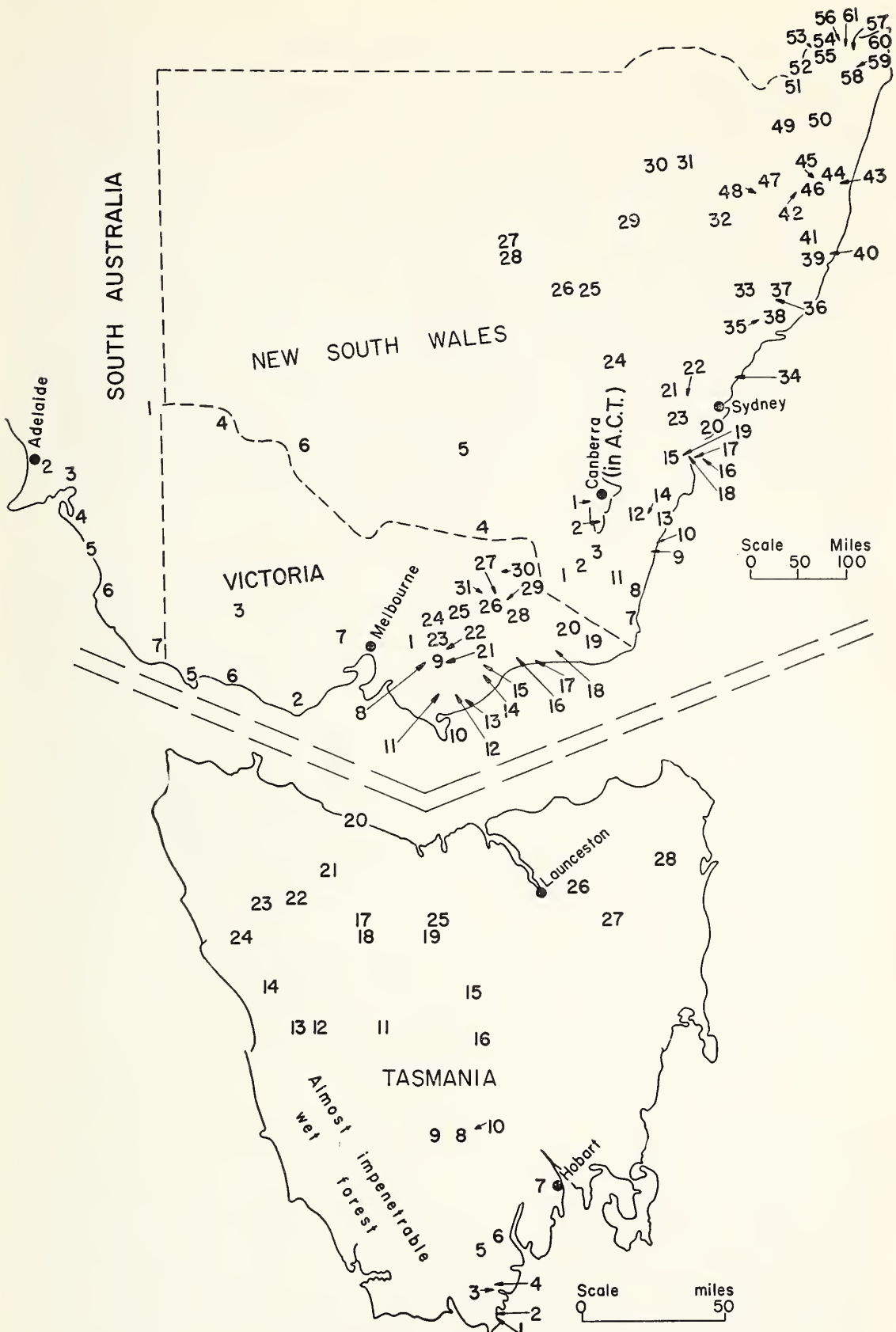
QUEENSLAND

Scale 0 100 200 miles

NEW SOUTH WALES

MAP OF QUEENSLAND WITH INSET OF ATHERTON TABLELAND





MAPS OF NEW SOUTH WALES, VICTORIA, AND EASTERN SOUTH AUSTRALIA AND OF TASMANIA.

## LIST OF LOCALITIES

Localities are listed approximately from north to south, because faunal transitions are best treated in that direction, although our collecting (and the numbering of our maps) was in general in the other direction. Letters and numbers following the names refer to the accompanying maps (Q=Queensland map, etc), on which the approximate position of localities is shown by number. One number is sometimes used to include two or more adjacent localities. Names are spelled according to Gazetteer No. 40, AUSTRALIA, prepared by the United States Office of Geography, Dept. of Interior (1957), with my original spelling indicated in parentheses if different. Latitudes and longitudes of most localities can be obtained from this gazetteer. Topography of each locality is indicated by "low" (lowlands, incl. interior plains with lowland topography even if at moderate altitudes), "plat" (plateaus rising from lowlands), "mts" (mountains), and "rge" (mountain range). Altitudes given are usually the approximate or prob(able) altitudes at which collecting was done rather than exact altitudes of fixed points. Types of forests chiefly collected in are indicated as savannah w(oodland), sclerophyll f(orest), and rain f(orest). This is the primary classification of forests in the wetter parts of eastern Australia (see "The Australian Environment," Commonwealth Scientific and Industrial Research Organization, Melbourne, second ed., 1950, p. 78). Savannah woodland has trees (usually eucalypts) widely spaced, and ground covered with grass or herbs. Sclerophyll forest has trees closer, and dense undergrowth of shrubs. Rain forest has trees close, often many vines, but scanty undergrowth. Of course there is variation and transition within this main classification. Savannah woodland varies in height and spacing of trees and (in Tasmania and southern Australia) sometimes merges with sclerophyll forest. Sclerophyll forest may be dry or wet, and wet sclerophyll is sometimes difficult to distinguish from poor rain forest. Tropical rain forest (often with giant fig trees etc.) and south temperate rain forest (often with antarctic beeches of the genus *Nothofagus*) are very different botanically, and entomologically. And tropical rain forest varies considerably and (as here used) sometimes grades into seasonally dry monsoon forest. My classification of forests in the following list is somewhat arbitrary and is based on general impressions rather than exact data. Dates are those of my collecting. Previous collecting done at the same localities in 1931-1932 is indicated in parentheses. Single words or phrases are used

to indicate *principal* collecting methods used at each locality. "Logs" means under logs on the ground, or in rotting logs. "Stones" means under stones. "Waterside" means beside, or in vegetation in, standing or running water. "Drowning" means throwing large quantities of loose soil, leaf litter, or debris into water and catching the Carabidae that come to the surface of the wet materials. This is a little known but very effective collecting method. "Bark" means collecting under loose slabs and flakes of bark on trunks of living trees, usually eucalyptus. A whole special insect fauna lives in this habitat in Australia. "Arboreal" means beating and sweeping. And "light" means collecting insects attracted to artificial light at night. "Usual ground m(ethods)" means first four methods listed above. "All usual m(ethods)" means all methods listed except light, which is separately specified.

- LOCKERBIE, Q41; low; light rain f, savannah w; Jan. 11-15, 58; all usual m, light.
- BAMAGA, Q40; low; savannah w, light rain f; Jan. 7-11. 15-20, 58; all usual m, light.
- IRON RANGE, Q39; low; rain f, savannah w; Jan. 21-28, 58; all usual m.
- TOZER GAP, Q39; mts to over 1000 ft.; rain f, savannah w; Jan. 25-26, 58; logs, stones.
- COEN, named on Q map; low; savannah w, gallery f; May 27, June 4-5, 58 (also 1932); all usual m.
- ROCKY RIVER (Rocky Scrub), Q38; low to mts *c.* 2000 ft.; rain f., savannah w; May 30-June 2, 58 (also west side this "scrub" in 1932); all usual m incl. much drowning of ground debris from upper banks of river in rain f.
- SILVER PLAINS, Q37; low; savannah w; May 27-June 4, 58; logs, waterside, light.
- COOKTOWN, named on Q map; low; poor rain f, savannah w (much cleared); June 5, 10-12, 58; little collecting.
- SHIPTONS FLAT, Q36; *c.* 1000 ft.; good savannah w to gallery rain f, with transitions; June 5-10, 58; all usual m.
- MT. FINNIGAN, Q36; 1000 to over 3000 ft.; rain f, savannah w, transitions; June 5-10, 58; all usual m (collected up to and in edge elfin f, but catch inexplicably poor).
- THORNTON('s) PEAK (or Mt. Alexandra), Q35; *c.* 1000 to *c.* 4500 ft.; rain f, elfin f near summit; Dec. 21-22, 57; stones, logs (collecting cut short by bad weather).
- MOSSMAN-DAINTREE AREA, Q33; low; diverse vegetation (much altered); Dec. 20-27, 57; little collecting except on Thornton Peak (see above) and Mt. Lewis (see below).
- MT. LEWIS, Q34; to *c.* 4000 ft.; rain f; Dec. 25-27, 57; stones, logs.
- CAIRNS, named on Q map; low; diverse vegetation (much altered) incl. remnants rain f; various dates Dec. 57-Feb. 58, May-June 58; all usual m, light.
- KURANDA, Q30, and named on Atherton Tab map; on plat *c.* 1000 ft.; rain f, some savannah w; various dates Dec. 57 to May 58; all usual m.



- ATHERTON TABLELAND, Q29, and inset on Q map; plat *c.* 2000-3000 ft., with mts to 4000 (attached Mts. Bartle Frere, Bellenden Ker over 5000); many tracts rain f, good savannah w; several visits, Dec. 57 to May 58 (also 1932); intensive collecting at various points, all usual m.
- MT. MOLLOY (town), Atherton Tab map 12 (but town not on the tableland); low; dry savannah w; Dec. 27, 57; little collecting.
- MAREEBA, named on Atherton Tab map; low; savannah w; several brief visits, but collected especially some miles north, Feb. 58; collecting especially on margins shallow, flooded ponds (flood collecting).
- DAVIES CREEK ROAD, Atherton Tab 8; mts to *c.* 3000 ft.; good savannah w to good rain f; Dec. 27-29, 57, May 25, 58; logs, stones.
- MOUNTAINS NORTH OF KAIRI, Atherton Tab 7; to 4000 ft.; rain f; Dec. 19, 57; logs, stones.
- ATHERTON (named on Atherton Tab map); on plat prob. *c.* 3000 ft. (mountains south and west to 4000 ft.), good savannah w, patches rain f on flat tableland near town, much rain f on mts.; Dec. 10-20, 57, Feb. 3-11, 58; all usual m.
- LAKE BARRINE, Atherton Tab 6; on plat prob. *c.* 2000 ft.; rain f; no collecting this trip (much in 1932).
- LAKE EACHAM, Atherton Tab 5; on plat prob. *c.* 2000 ft.; rain f; Feb. 58; stones, waterside.
- HERBERTON, named on Atherton Tab map; prob. *c.* 2000 ft.; savannah w (prob. some rain f to east, not visited by us); Feb. 58; collecting chiefly in piles of dead leaves under small fallen eucalypts.
- LONGLANDS Gap, Atherton Tab 3; mts prob. *c.* 3000 ft.; rain f; Dec. 18, 57, Feb. 11, 58; all usual m.
- THE CRATER, Atherton Tab 3; prob. over 2000 ft.; rain f; Dec. 18, 57; logs, stones.
- MT. BELLENDEN KER, Q32, Atherton Tab 10; to *c.* 5000 ft.; mostly rain f; Dec. 31, 57-Jan. 3, 58; stones, logs.
- MT. BARTLE FRERE, Q31, Atherton Tab 9; to *c.* 5000 ft.; mostly rain f; Dec. 13-16, 57; stones, logs.
- MILLAA MILLAA, named on Atherton Tab map; on plat prob. *c.* 2500 ft.; rain f; Dec. 18, 57 (also 1932); stones, logs.
- MT. FISHER, Atherton Tab 2; to *c.* 4000 ft.; rain f; Feb. 12, 58; stones, logs.
- RAVENSHOE, named on Atherton Tab map; on plat prob. *c.* 3000 ft.; good savannah w, rain f south and east; Feb. 11-13, 20-21, 58; logs, stones, and special collecting by edges of rain pools west of town, washing leaf debris from under thickets etc., and treading heavy aquatic vegetation over deep water in pool of river visible from road 2 or 3 miles west of town.
- CRAWFORDS LOOKOUT, Atherton Tab 1; prob. *c.* 1000 ft.; rain f, savannah w; Feb. 21-22, 58; little collecting.
- INNISFAIL, Q28, and named on Atherton Tab map; low; mixed vegetation (much altered); Feb. 22, 58; no collecting in town, but some in rain f, along Millaa Millaa-Innisfail road; logs, stones.
- TULLY FALLS, Atherton Tab 4; prob. 2000-3000 ft. (above falls); some rain f; Feb. 58; little collecting.
- TULLY, Q27; low; various vegetations; passed Dec. 57, Feb. 58; little collecting.
- CARDWELL, Q25; low; various vegetations; passed Dec. 57, Feb. 58; little collecting.
- KIRRAMA RANGE, Q26, to *c.* 3000 ft., rain f, savannah w; Dec. 4-6, 57, Feb. 22-23, 58; usual ground m.

- INGHAM, Q23; low; mixed vegetation; passed Dec. 57, Feb. 58; little collecting.
- MT. FOX PLATEAU, Q24; *c.* 2000 ft.; savannah w, some rain f; Dec. 3, 57; poor collecting.
- MT. SPEC PLATEAU (incl. Paluma Range), Q22; to *c.* 3000 ft.; rain f, savannah w to west; Nov. 30-Dec. 2, 57, Feb. 23-27, 58; stones, logs.
- TOWNSVILLE, named on Q map; low; dry savannah w (much altered by man); Nov. 29-30, 57, Feb. 27-Mar. 1, 58; little collecting near town, except some at lights in outskirts.
- ELLIOT RANGE, Q20; to over 3000 ft.; savannah w on slopes, rain f on high ridge; Mar. 2, 58; logs, stones in rain f on "Sharp Elliot".
- CHARTERS TOWERS, Q21; low; dry savannah w; Mar. 3, 58; a little river-bank collecting where Townsville road crosses Burdekin R.
- PROSERPINE, Q19; under 1000 ft.; mixed vegetation (much altered by man) incl. palm f toward Repulse Bay; Nov. 28, 57; very poor collecting (too dry), in palm f.
- MACKAY, named on Q map; low; mixed vegetation (altered by man); Nov. 21-22, 27-28, 57, Mar. 5-6, 58; little collecting near town, but some along road toward Rockhampton.
- EUNGELLA RANGE, Q18; to *c.* 4000 ft.; rain f, good savannah w to west; Nov. 22-27, 57; all usual m.
- BYFIELD, Q17; low; mixed vegetation (largely altered by man) incl. remnants approaching rain f; Nov. 18-19, 57; logs, stones, drowning along small brook in palm f.
- ROCKHAMPTON, named on Q map; low; dry savannah w, swamps, dense dry sclerophyll *c.* 50 miles west; passed Nov. 17-20, 57, Mar. 58; little collecting near the town, mostly around swamps, but some at stated distances in various directions.
- MANY PEAKS, Q16; low; savannah w; Mar. 11, 58; no collecting at town but some along road north.
- MT. JACOB, Q16; *rge c.* 2000 ft.; rain f (or something like it), savannah w; Mar. 11-12, 58; logs, stones.
- MONTO, Q10; low; savannah w, tract of dense dry sclerophyll f; Apr. 23-25, 57; logs, stones esp. in sclerophyll f.
- GAYNDAH, Q9; low; savannah w, formerly rain f but latter cleared; Apr. 22-25, 57; little collecting, mostly bark, river margins.
- BIGGENDEN, Q11; low, hills; savannah w, something like rain f to southwest; Apr. 30, 58; little collecting, in rain f.
- GOODNIGHT FOREST, Q12; low; thick dry sclerophyll; May 1, 58; poor collecting, but a few small carabs by water holes.
- GALLANGOWAN FOREST, *v.* Manumbar, Q13; *rge c.* 2000 ft.; rain f, good savannah w or open sclerophyll f; Apr. 26-27, 58; logs, stones.
- JIMNA, Q14; moderate altitude; mixed vegetation; Apr. 27, 58; little collecting.
- BLACKALL RANGE, incl. Mapleton, Montville, Maleny, Q15; to *c.* 2000 ft.; rain f, good savannah w or open sclerophyll f; Apr. 27-28, May 3-5, 58; logs, stones, mostly in rain f.
- KENILWORTH, Q15; low; mixed vegetation incl. rain f; May 2, 58; logs, stones.
- BUNYA MTS., Q8; to over 3000 ft.; rain f, good savannah w or open sclerophyll f; Apr. 20-21, 58; stones, logs.
- COOYAR CREEK, Q7; low; savannah w; Apr. 19-20, 58; logs.
- BENARKIN, Q6; low; woods approximating rain f; Apr. 19, 58; little collecting.

- YARRAMAN, Q6; low; savannah w, woods approximating rain f; Apr. 19, 58; logs.
- BRISBANE, named on Q map; low; savannah w; various visits Nov. 57 to June 58 (also 1932, 1943); little collecting near city (specimens from nearest rain f, on Mt. Glorious & Mt. Tamborine, labelled from these places).
- MT. GLORIOUS, Q5; prob. *c.* 1000 ft.; rain f, good savannah w; mid-May 58; little collecting (more in Nov. 43), stones, logs, mostly in rain f.
- MT. TAMBORINE, Q4; plat *c.* 2000 ft.; rain f; not visited 1957-58 but collected Nov. 1943; logs, stones, drowning debris in rain f.
- CUNNINGHAMS GAP, Q2; mts *c.* 2000-4000 ft.; rain f; May 13-14, 58; logs, stones (most specimens taken in gap proper, but we collected from there nearly to summit Mt. Cordeaux, *c.* 4000 ft.).
- MCPHERSON RANGE (Q. Nat. Park), Q1; to *c.* 4000 ft.; mountain rain f, some savannah w, small areas almost pure *Nothofagus* f on highest points; May 58 (see Binna Burra, below) (collected on McPherson Range also 1932).
- BINNA BURRA (Binnaburra), Q1; on rge *c.* 3000 ft. and over; mountain rain f, some savannah w; May 6-10, 58; usual ground m.
- BEECHMONT, Q1; on rge *c.* 3000 ft.; rain f, savannah w; passed repeatedly 1957-1958 but collected only 1943, in rain f probably now cleared.
- SPRINGBROOK, Q1; on rge *c.* 2000 ft.; mixed vegetations incl. rain f; May 10-11, 58; little collecting, logs, stones.
- STANTHROPE, Q3; to prob. *c.* 5000 ft.; savannah w etc. (no rain f); passed repeatedly 1958; no personal collecting, but obtained specimens from Mr. E. Sutton.
- WYBERBA, Q3; to over 5000 ft.; savannah w and/or good sclerophyll f, rocky and bushy country; May 16, 58; poor collecting (dry year) but good locality, specimens obtained from Mr. Sutton.
- WOODENBONG, NSW56; moderate alt.; good savannah w; May 17, 58, and other dates; poor collecting (dry year), logs.
- UNUMGAR FOREST (Cox's Road), NSW61; mts *c.* 2000 ft.; mostly rain f; May 17-18, 58; logs, stones.
- WIANGAREE, NSW57; low; savannah w; Nov. 9, 57; waterside.
- MURWILLUMBAH, NSW60; low to *c.* 1000 ft.; mixed vegetation incl. rain f *c.* 10 miles westsouthwest (at Byrill Ck.); Nov. 10-11, 57; stones, logs, in rain f.
- DUNOON, NSW59; moderate altitude; mixed vegetation including rain f at rather low altitude (also rain f at prob. *c.* 2000 ft. up forestry road to Whian Whian Forest); Nov. 10, 57, Apr. 12, 58; logs, stones in rain f.
- LISMORE, NSW58; low; mixed vegetation incl. small piece rain f preserved in town, larger piece *c.* 4 miles northeast; several dates especially Apr. 11, 58; logs, stones, mostly in rain forest 4 miles northeast.
- ACACIA PLATEAU, NSW54; *c.* 2000 ft.; rain f; Nov. 7-8, 57; logs, stones.
- ACACIA CREEK, NSW53; low; mixed vegetation, now no real rain f; Nov. 7, 57; little collecting.
- TOOLOOM RANGE, NSW55; to *c.* 2000 ft.; rain f south slope, also savannah w; Nov. 8-9, 57, May 16-17, 58; usual ground m incl. drowning debris from beside small temporary pond in opening in rain f.
- WILSONS DOWNFALL, NSW52; moderate altitude; savannah w; Nov. 7, 57; little collecting.
- TENTERFIELD, NSW51; moderate to rather high altitude; savannah w; Nov. 7, 57; collecting at stated distances in various directions, logs, stones.



- GLEN INNES, NSW49; various altitudes; savannah w; Nov. 5, 7, 57, and other times briefly; collecting at stated distances in various directions, logs, stones.
- c. 40 miles eastnortheast (ENE) Glen Innes, NSW50; moderate altitude; savannah w, heathy f, patches rain f; Nov. 6, 57; usual ground m.
- ARMIDALE, NSW47; moderate altitude; savannah w; Nov. 2-5, 57, and other brief visits; little collecting.
- URALLA, NSW48; moderate altitude; savannah w; Nov. 3, 57; logs.
- EBOR, NSW45; to c. 5000 ft.; savannah w; Oct. 31-Nov. 1, 57, Apr. 9, 58; logs, stones.
- NEW ENGLAND NATIONAL PARK (Point Lookout), NSW46; to over 5000 ft.; rain f incl. *Nothofagus*, some savannah w; Nov. 1-2, 57, Apr. 9, 58; usual ground m.
- DORRIGO, NSW44; plat c. 2000-3000 ft. (and same plateau west rises to c. 5000 ft. at Ebor etc.); rain f, savannah w; Oct. 31, 57 (also 1932); stones, logs.
- BELLINGEN, NSW43; low; mixed vegetation incl. remnants of something like rain f; Oct. 30-31, 57; logs, stones.
- THE BIG HILL (Kempsey-Ebor road), NSW42; up to Ebor plat; semi-rain f; Apr. 8, 58; logs, stones.
- BELLANGRY FOREST (northwest of Wauchope), NSW41; mts to prob. c. 3000 ft.; rain f, said to include *Nothofagus*; Apr. 6-7, 58; logs, stones.
- THE COMBOYNE, NSW39; plat to c. 2800 ft.; mixed f incl. remnants rain f in gullies; Oct. 28-29, 57; logs, stones, especially near Mt. Gibraltar and in gully northeast.
- PORT MACQUARIE, NSW40; low; mixed f incl. small tract something like rain f; Oct. 29-30, 57; logs.
- MT. ROYAL RANGE, NSW33; plat to c. 5000 ft.; savannah w on slopes, savannah w and rain f incl. *Nothofagus* on plat; Oct. 23-27, 57; usual ground m (see 3 following localities).
- BARRINGTON HOUSE, NSW33; low at southeast foot Mt. Royal Range; gallery rain f along river; Oct. 25-26, 57; usual ground m.
- BARRINGTON TOPS, NSW33; plat on southeast end Mt. Royal Range, which see (above); Oct. 27, 57 (also 1932); usual ground m.
- TOMALLA TOPS, NSW33; plat on northwest end Mt. Royal Range, which see (above); Oct. 23-25, 57; usual ground m.
- GLOUCESTER, NSW37; low; savannah w; Oct. 28, 57; logs.
- PATERSON, NSW35; low; savannah w; Oct. 25, 57; logs.
- STRATFORD, NSW36; low; savannah w; Oct. 28, 57; logs.
- BOORAL (10 miles east of), NSW38; low; savannah w, thicker in stream gully; Apr. 6, 58; logs.
- OURIMBAH, NSW34; low; savannah w, formerly semi-rain f (we did not find latter); Apr. 5, 58; poor collecting.
- TAMWORTH, NSW32; low; savannah w; Oct. 22, 57; chiefly waterside.
- MT. KAPUTAR, NSW31; to c. 4000 ft.; savannah w with underbrush in places; Oct. 20, 57; logs, stones, chiefly near summit.
- NARRABRI, NSW30; low; savannah w and/or rather dry sclerophyll f; Oct. 19, 57; little collecting.
- COONABARABRAN (north of), NSW29; low; savannah w and/or dry sclerophyll f; Oct. 19, 57; logs, stones.
- NYNGAN, NSW27; low; originally dry savannah w or sclerophyll f, now mostly cleared for sheep; in vicinity Oct. 17-19, 57; poor collecting (dry year) at stated distances south and east.

- BOGAN RIVER, NSW28; low; originally dry savannah w or sclerophyll f, now mostly cleared for sheep; Oct. 18-19, 57; poor collecting (dry year) except by edges pools in bed of Bogan R., but specimens obtained from Mr. J. W. T. Armstrong.
- NARROMINE, NSW26; low; savannah w and/or rather dry sclerophyll f; Oct. 17, 57; little collecting.
- DUBBO, NSW25; low; savannah w or rather dry sclerophyll f; Oct. 17, 57; little collecting.
- ORANGE, NSW24; low; originally savannah w or rather dry sclerophyll f; Oct. 16, 57; little collecting.
- MT. CANOBOLAS, NSW24; to *c.* 4500 ft.; savannah w; Oct. 16-17, 57; stones, logs near summit and especially near camp site at base (specimens taken at base are so labeled).
- BLUE MTS., NSW21; mts to over 3000 ft.; various vegetations incl. bushy heath, sclerophyll f, savannah w, wetter f in ravines; collected only at Springwood (see below) in 1957-58 (but at several localities in 1932).
- SPRINGWOOD, NSW22, prob. *c.* 1000 ft.; savannah w, wetter f in ravine to south; June 58; logs, stones, especially in wet ravine.
- BURRAGORANG VALLEY, NSW23; low; savannah w; June 58; logs.
- SYDNEY, named on NSW map; low; originally savannah w, dry sclerophyll, etc., but now much altered by man; in vicinity various dates 1956-1958 (also 1931-1932, 1943); little collecting near city.
- NATIONAL PARK, NSW20; low; sclerophyll f etc.; Oct. 9-10, 57 (also 1931); little collecting.
- EXETER, NSW15; low; savannah w; Apr. 4, 58; logs.
- BURRAWANG, NSW19; low; savannah w; June 58; logs, stones.
- MACQUARIE PASS, NSW18; edge plat; savannah w and thickets; June 58; drowning ground debris.
- JAMBEROO, NSW17; low; savannah w and wetter thicker f in ravine; June 58; stones, logs in wetter f.
- KIAMA, NSW16; low but Saddleback Mt. to prob. *c.* 2000 ft.; savannah w much cleared, but remnants of good woods still on Saddleback; Oct. 8-9, 57; logs, stones in f on Saddleback.
- SADDLEBACK MT., see Kiama, above.
- TERMEIL (Batemans Bay), NSW13; low, but worked into hills northwest nearly to Pigeon House; savannah w; Oct. 5-7, 57; logs, stones, and by pools intermittent brook in hills toward Pigeon House.
- BATEMANS BAY, see Termeil (above).
- PIGEON HOUSE, see Termeil (above).
- CLYDE MT., NSW14; prob. *c.* 2000 ft. (edge plat); good mixed forest with considerable underbrush; several visits from Canberra May-Aug. 57; logs, stones.
- BRAIDWOOD, NSW12; low (but on plat); savannah w (mostly cleared); July 11, 57; flood collecting along river and streams.
- MORUYA, NSW10; low; savannah w (mostly cleared); July 11, 57; flood collecting.
- BODALLA, NSW9; low; savannah w (mostly cleared); July 11, 57; collecting esp. by standing flood water in woods.
- BROWN MT., NSW11; prob. *c.* 2000 ft. (edge plat); good woods with considerable underbrush; Oct. 4, 57; logs, stones.
- BEGA, NSW8; low; savannah w (partly cleared); Oct. 4, 57; logs, stones.
- EDEN, NSW7; low; savannah w (much cleared); Oct. 4, 57; collecting at stated distances north and west, logs, stones.
- COOMA, NSW3; on plat; savannah w; passed several times; little collecting.

- ADAMINARY DAM, NSW2; on plat; savannah w; Aug. 3, 57; attempted flood collecting as dam filled, but unsuccessful.
- MT. KOSCIUSCO, NSW1; to over 7000 ft. (highest mt in Australia); good sclerophyll f on slopes, open snow gum w higher, mountain moors still higher; Aug. 3, 57, Mar. 22-23, 58 (also 1931); usual ground m, bark.
- ALBURY, NSW4; low; savannah w etc. (mostly cleared); passed on various occasions; little collecting.
- BALRANALD, NSW6; low; various dry w; Sept 2-3, 57; little collecting.
- NARRANDERA, NSW5; low; various more or less dry w; Sept. 1-2, 57; little collecting, mostly by drowning broken earth
- CANBERRA, Australian Capital Territory, named on NSW map; in wide valley on plat; savannah w; May through Aug., 57; usual ground m, bark, but collecting poor (dry year).
- BRINDABELLA RANGE (incl. Mt. Franklin and Mt. Gingera), ACT1 on NSW map; to over 6000 ft.; savannah w, sclerophyll f, open snow gum forest (in order with increasing altitude); May, June, 57; usual ground m.
- GUDGENBY RIVER, ACT2 on NSW map; in valley on plat; savannah w; June 9, 57; logs, stones, bark.
- MITTA MITTA, V30; low; sclerophyll f; Apr. 30-May 1, 57; little collecting.
- GLEN WILLS, V29; moderate altitude; sclerophyll f; Apr. 30, 57; bark.
- OMEQ, V28; low; sclerophyll f; Apr. 25-30, 57; logs, stones, bark, especially along road toward Mt. Hotham.
- MT. BOGONG incl. Pretty Valley, V27; plat to c. 6000 ft.; sclerophyll f on slopes, open snow gum w and moors higher; Apr. 2, 58; logs, stones.
- PRETTY VALLEY, see Mt. Bogong.
- MT. HOTHAM, V26; to c. 6000 ft.; sclerophyll f on slopes, open snow gum w and moors higher; Apr. 24-28, 57, Mar. 29-31, 58; usual ground m, bark.
- BRIGHT, V31; low; sclerophyll f; Apr. 23-24, 57, Mar. 29, Apr. 1, 3 (toward Mt. Buffalo on latter day), 58; logs, stones, bark.
- MT. BULLER, V25; to over 5000 ft.; savannah w, sclerophyll f on lower slopes, open snow gum w higher; Mar. 28, 58; logs, stones, drowning debris from under clumps of snow gums.
- JAMIESON, V24; moderate altitude; sclerophyll f; Mar. 27, 58; little collecting.
- WOODS POINT, V23; moderate altitude; sclerophyll f; Mar. 27, 58; little collecting.
- ABERFELDY, V22; moderate altitude; savannah w and/or sclerophyll f; Mar. 27, 58; logs, stones.
- WALHALLA, V21; moderate altitude; sclerophyll f and/or savannah w; Mar. 27, 58; little collecting.
- MT. BAW BAW, V9; to c. 5000 ft.; sclerophyll f on slopes, open snow gum w higher, vestiges rain f incl. *Nothofagus* in gullies c. 4000 ft.; Sept. 27-28, 57, Mar. 25-27, 58; logs, stones on wooded slopes (1957), and in high snow gum w (1958), and drowning debris from *Nothofagus* gully (1958) (all "*Trechus*" by last method).
- MT. DONNA BUANG, V1; to c. 4000 ft.; sclerophyll f, approaching temperate rain f in gullies; several visits Apr. 57 (also 1931); logs, stones, drowning, especially near summit and at Cement Creek.
- CEMENT CREEK, see Mt. Donna Buang.
- BONANG HIGHWAY, V20; moderate altitudes (from plat south to low); sclerophyll f approaching temperate rain f in gullies; Mar. 24, 58; logs, stones, drowning.
- MT. DRUMMER, V19; prob. to c. 2000 ft.; savannah w, sclerophyll f; Oct. 3, 58; logs, stones, especially in gully north of road on east slope.



- ORBOST, V18; low; savannah w and/or sclerophyll f; Oct. 2-3, 57; little collecting.
- LAKES ENTRANCE, V17; low; savannah w and/or sclerophyll f; Oct. 2, 57; little collecting.
- BAIRNSDALE, V16; low; savannah w and/or sclerophyll f; Oct. 2, 57; little collecting.
- STRATFORD, V15; low; savannah w and/or sclerophyll f; Oct. 2, 57; little collecting.
- SALE, V14; low; savannah w; Oct. 1-2, 57; flood collecting.
- YARRAM, V13; low; savannah w and/or sclerophyll f; Oct. 1, 57; little collecting.
- TARRA VALLEY, V12, on rge prob. *c.* 1000 ft.; sclerophyll f approaching temperate rain f in wet gullies; Sep. 30-Oct. 1, 57; logs, stones.
- GUNYAH, V11; on rge prob. *c.* 1000 ft.; sclerophyll f approaching temperate rain f in wet gullies; Sept. 30, 58; logs, stones.
- WILSONS PROMONTORY (most southern point of continental Australia), V10; low; sclerophyll f, heath, moors, dunes; Sept. 28-30, 57; poor collecting, tried especially in forest at Lilly Pilly Gully.
- NOOJEE, V8; moderate altitude; savannah w to sclerophyll f; Sept. 26, 57, Mar. 25, 58; logs in woods by Neerim-Noojee road.
- MELBOURNE, named on V map; low; savannah w (mostly cleared); Apr. & Sept., 57; little collecting near city.
- WERRIBEE GORGE, near Bacchus Marsh, V7; low; savannah w; Sept. 19, 21, 57; logs, stones, waterside (beautiful locality, but dry year).
- BEECH FOREST, see Otway Ranges.
- OTWAY RANGES incl. Beech Forest, V2; plat *c.* 2000 ft.; sclerophyll f approaching rain f in ravines, some *Nothofagus*; Apr. 12-13, Sept. 17-18, 57; logs, stones drowning, especially at Tanybryn Junction and Crowes.
- PORT FAIRY, V6; low; various vegetations; Sept. 17, 57; little collecting.
- PORTLAND, V5; low; various vegetations; Sept. 17, 57; little collecting.
- THE GRAMPIANS, V3; mts prob. to over 2000 ft., dry sclerophyll w, heath; Apr. 14-15, 57; stones, logs (poor collecting, dry year).
- MILDURA, V4; low; dry woods etc.; Sept. 3, 57; little collecting.
- RENMARK, SA1; low; dry woodland etc., much cleared; Sept. 4, 57; little collecting.
- ADELAIDE, named on SA map; low; savannah w (much cleared); Sept. 6-14, 57 (also 1931); little collecting near city.
- MT. LOFTY RANGE, SA2; plat to *c.* 2000 ft.; savannah w etc.; Sept. 9, 14, 57; stones, logs.
- MURRAY BRIDGE, SA3; low; various vegetations; Sept. 15, 57; collecting mostly along road south toward Meningie.
- MENINGIE, SA4; low; various dry vegetations; Sept. 15, 57; collecting mostly along roads north and east.
- THE COORONG, SA5; lagoon connected with ocean; various dry vegetations, sand; Sept. 15, 57; little collecting.
- KINGSTON, SA6; low; various dry vegetations; Sept. 16, 57; little collecting.
- PRINCES HIGHWAY at South Australia-Victoria line; V7; low; good savannah w; Sept. 16, 57; logs, digging (carenums and *Teropha*).
- LAUNCESTON, named on T map; low; savannah w etc.; based here Feb. 24-Apr. 5, 57; little collecting near city.
- MT. BARROW, T26; to *c.* 4000 ft.; sclerophyll f on slope, *Nothofagus* thickets near tree line, open summit; Apr. 2, 57; stones near summit, drowning debris from *Nothofagus* thickets, logs, stones in f near base.

- MT. BEN LOMOND, T27; to *c.* 5000 ft.; savannah w near base, sclerophyll f on slopes (no rain f but ti tree flats and wet gullies in sclerophyll area), moors etc. above *c.* 4000 ft.; Mar. 5-10, 57; usual ground m, bark.
- BLUE TIER (plat), T28; plat *c.* 2000 ft.; temperate rain f incl. *Nothofagus* (partly cleared); Mar. 26-Apr. 1, 57; usual ground m incl. much drowning of debris from rain f. Included in collection from this locality are specimens taken in *Nothofagus* f (big trees) beside road between Goshen and Weldborough.
- LOTTAH, T28; probably *c.* 1000 ft. (foot of Blue Tier); probably formerly sclerophyll f; Mar. 26, Apr. 1, 57, little collecting. This is an old type locality, but the vegetation has been much altered, and the old collections may have been made many miles from the town of Lottah, perhaps on the Blue Tier.
- GOULDS COUNTRY, T28; moderate altitude; wet sclerophyll f; Apr. 1, 57; logs, stones, drowning debris from under thickets.
- MOLE CREEK, T25; low; savannah w; Apr. 3, 57; bark, and unsuccessful attempted cave collecting.
- MERSEY RIVER, T19; deep river valley; sclerophyll f; Mar. 2-3, 57; poor collecting, mostly washing river banks.
- WALDHEIM, *v.* Cradle Mt., T17; mts *c.* 4000 ft.; temperate rain f incl. *Nothofagus*, open snow gum w, moors; Feb. 23-Mar. 1, 57; usual ground m incl. much drowning of debris from rain f and from under clumps of snow gums.
- CRADLE MT., T18; *c.* 5000 ft.; moors, bushy heath, rocks, mountain lakes; Feb. 26, 57; stones to *c.* 4500 ft., a little drowning.
- BURNIE, T20; low; savannah w; Mar. 13, 23, 57; little collecting.
- HIGH LAND SOUTH OF BURNIE, T21; prob. *c.* 1000-2000 ft., wet sclerophyll f, temperate rain f incl. *Nothofagus*; Mar. 20-23, 57; usual ground m.
- WARATAH, T22; prob. *c.* 2000 ft.; temperate rain f incl. *Nothofagus*, wet sclerophyll f; Mar. 13-14, 18-20, 57; usual ground m incl. much drowning of debris from rain f. This is a famous old type locality. For practical purposes it includes Magnet (not visited by us), which is nearby.
- MAGNET, T22, see Waratah, above.
- WHYTE RIVER, T23; low; sclerophyll f, temperate rain f incl. *Nothofagus*; Mar. 17-18, 57; usual ground m.
- CORINNA, T24; low; temperate rain f incl. *Nothofagus*; Mar. 14-17, 57; usual ground m.
- ZEEHAN, T14; low; wet sclerophyll f, rain f in places (but much cleared); Jan. 17-19, 57; usual ground m, mostly *c.* 8 miles north, and along Rosebery Road.
- QUEENSTOWN, T13; low; vegetation stripped; Jan. 17, 19, 57; little collecting except along road toward Lake St. Clair.
- (THE) KING RIVER, T12; low; original f stripped, now ti tree thickets etc.; Jan. 17, 19, 57; mostly washing river bars.
- LAKE ST. CLAIR, T11; plat and mts *c.* 2400 ft. and over; savannah w (to south), wet sclerophyll f, heavy temperate rain f incl. much *Nothofagus*; Jan. 11-17, 19, 57; usual ground m, and waterside near lake, treading wet moor toward Mt. Rufus.
- GREAT LAKE, T15; on plat *c.* 3500 ft.; savannah or snow gum w, open (stripped?) country, moors; Jan. 20 (south end of lake), Mar. 4 (north end), 57; stones, logs at south end, drowning debris from under pencil pines above north end of lake.
- OUSE VALLEY, T16; deep valley; savannah w; Jan. 20, 57; logs etc., bark.

- TARRALEAH, c. 20 miles southeast L. St. Clair (T11); moderate altitude; sclerophyll f (also rain f?); Jan. 11, 57; little collecting (but specimens received from Prof. V. V. Hickman).
- ELLENDALE, T10; low; savannah w and/or sclerophyll f; Jan. 11, 57; water-side (by pond in open).
- MT. FIELD, T8; to c. 4000 ft.; wet sclerophyll f, temperate rain f on slopes, open snow gum w, moors above, mountain lakes; Jan. 2-7, 57; usual ground m especially logs, stones toward Mt. Field West, drowning debris from under pencil pines near Lake Dobson, drowning in temperate rain f c. half way up road, logs, bark at base.
- FLORENTINE VALLEY, T9; low; wet sclerophyll f with gigantic eucalypts, strips of rain f with *Nothofagus*; Jan. 25-27, 57; usual ground m.
- HOBART, named on T map; low; savannah w etc.; based here Dec. 7, 56 to Feb. 23, 57; specimens labeled "v. Hobart" are from v. city south to v. Kingston, by usual ground m, bark.
- MT. WELLINGTON, T7; to c. 4000 ft.; sclerophyll f approaching rain f in gullies (but altered by burning), open grass near summit; several visits Dec. 56 to Feb. 57; usual ground m (collecting poorer than formerly, probably because of fires in last few decades).
- ARVE RIVER, T6; low; wet sclerophyll f with gigantic eucalypts, rain f with *Nothofagus*; Dec. 20-26, 56; usual ground m, especially drowning debris from ground around bases of big trees in forest.
- HARTZ MT., T5; to c. 4000 ft.; wet sclerophyll f and heavy rain f (fine *Nothofagus*) on slopes, moors and stone above c. 3000 ft.; Feb. 8-10, 57; usual ground m.
- HASTINGS, T4; low; sclerophyll f; Dec. 26, 56, Feb. 10-12, 57; little collecting, but good things under logs, boards in second growth along old logging road.
- IDA BAY CAVE, T3; low; wet cave, opening in sclerophyll f; Dec. 27, 56, Feb. 13, 57; cave collecting, and logs, streamside near cave mouth.
- CATAMARAN, T2; low; wet sclerophyll f; Dec. 28-29, 56; logs etc.
- COCKLE CREEK, T1; low; wet sclerophyll f; Dec. 28, 56; logs, stones, treading small swampy pond.



## CAMBRIDGE ENTOMOLOGICAL CLUB

A regular meeting of the Club is held on the second Tuesday of each month October through May at 8:00 p. m. in Room B-455, Biological Laboratories, Divinity Ave., Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

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The illustration on the front cover of this issue of *Psyche* shows the head of the worker of *Myrmoteras karnyi* Gregg. The original, drawn by Dr. R. E. Gregg, was published in *Psyche*, Volume 61, p. 21, 1954.

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