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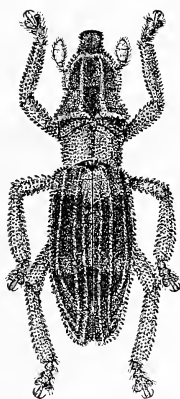
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PSYCHE

Vol. 68

MARCH, 1961

No. 1

AUSTRALIAN CARABID BEETLES V.¹ TRANSITION OF WET FOREST FAUNAS FROM NEW GUINEA TO TASMANIA

BY P. J. DARLINGTON, JR.

Museum of Comparative Zoology, Cambridge, Mass.

Introduction

Beetles of the family Carabidae (predaceous ground beetles) are numerous in tropical rain forest in New Guinea and numerous also (but less diverse) in cool south temperate rain forest in Tasmania, but no species and hardly any genus is common to the two faunas, and even the dominant tribes are different. However there is no single boundary between the New Guinean and Tasmanian faunas, but a broad and complex transition, which I shall try to describe.

My interest in this part of the world began with the Harvard Australian Expedition of 1931-1932, when I collected Carabidae in eastern Australia north to part of the Cape York Peninsula, as well as in southwestern Australia. In 1943-1944 I spent eleven months in New Guinea as an army entomologist, and was able to collect Carabidae especially in lowland rain forest at Dobodura, Papua, while hospitalized there, and in mountain forest on the Bismarck Range, Northeast New Guinea, in lieu of leave. I have sorted and arranged my own and much borrowed material and am now more than half way through writing "The Carabid Beetles of New Guinea" (see Darlington 1952), so that I have a good knowledge of New Guinean Carabidae. Recently, from December 1956 to June 1958, I have been again in eastern Australia, traveling and living in a small truck with my wife and fourteen-year-old son, and collecting Carabidae in practically every important piece of wet forest from the northern tip of Cape

¹Earlier parts of this series are listed in the reference list at the end of this paper.

York to the southern tip of Tasmania.² A brief itinerary with maps and list of localities has been published (1961). Information and collections obtained during this trip have enabled me to correlate other information and write the present paper. New genera and species referred to now (but not by name) will be described in forthcoming numbers of *Psyche* and *Breviora*.

The Forests

My "wet forests" are rain forests as classified in "The Australian Environment" (CSIRO 1950, 77-96). That is, they are dense, ever-green (non-deciduous) forests with closed canopies, often (in tropical rain forest) with many woody vines, but with comparatively little low vegetation, the ground being covered with dead leaves and leaf mold rather than grass or herbs.

Two main types of rain forest exist in the Australian Region: tropical (including subtropical) (Figs. 1, 2) and south temperate (Figs. 3, 4). Tropical rain forest is widely distributed in New Guinea at low and middle altitudes, although in the drier country of southern New Guinea it is replaced by open savannah woodland like that of much of northern Australia. Tropical rain forest occurs also on the eastern edge of Australia in separate tracts spaced irregularly from parts of Cape York south through Queensland and northern New South Wales (map, Fig. 6). The best of this forest in tropical and subtropical Australia as well as in New Guinea is real, Malaysian-type rain forest, although some tracts in Australia are lighter and seasonally drier, and light rain forest sometimes grades into semi-deciduous monsoon forest.

The northernmost rain forest in Australia is the tip-of-peninsular (Lockerbie or Somerset) tract on the tip of Cape York. It is lowland rain forest, but somewhat depauperate (see p. 17).

²This trip was supported in part by a fellowship of the John Simon Guggenheim Memorial Foundation. I am especially indebted to Dr. L. J. Webb, of the Commonwealth Scientific and Industrial Research Organization, for information on the distribution of rain forest in Queensland, to many members of the Queensland Department of Forestry who aided or guided us in the field, and to Mr. P. J. Killoran, of the Queensland Department of Native Affairs, who arranged our visit to Bamaga and the tip of Cape York. I very much regret that I do not have space to acknowledge other assistance in detail here.

EXPLANATION OF PLATE 1

Fig. 1. Tropical rain forest, Lake Barrine, Atherton Tableland, North Queensland (P. J. D. 1932).

Fig. 2. Interior of tip-of-peninsular (tropical) rain forest, from edge of new clearing, Lockerbie, Cape York, Queensland (P. J. D. 1958). This is the habitat of *Mecynognathus*.



1



2



3



4

Next in order southward is a gap more than 100 miles wide of drier, open savannah woodland (Fig. 5) in which may be an isolated piece of rain forest near the head of the Jardine River, unknown biologically (Brass 1953, pp. 154, 161).

Next is the mid-peninsular rain forest system. It extends irregularly and with perhaps slight interruptions from near Iron Range and Mt. Tozer south to the "Rocky Scrub" east of Coen. Altitudinally it extends from near sea level (*e.g.* at Iron Range) to about 2,000 ft. on the higher summits of the McIlwraith Range. It includes fairly heavy rain forest, although its quality varies locally.

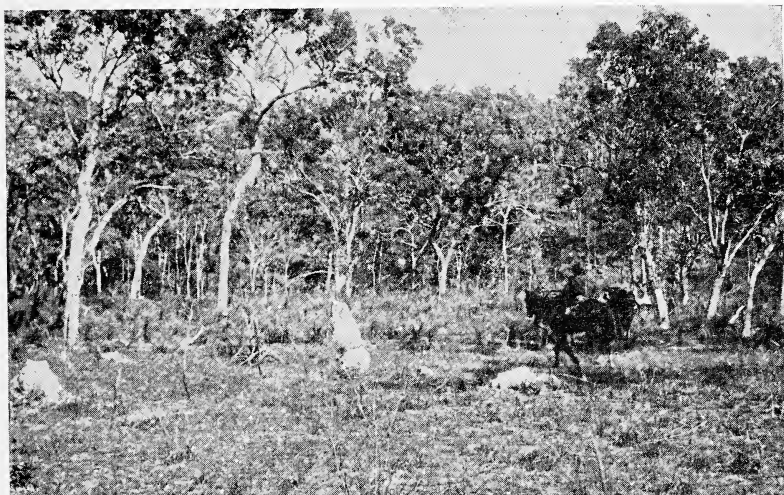


Fig. 5. Rather dry savannah woodland northeast of Coen, Cape York peninsula. (P. J. D. 1932). Such woodland is an effective barrier to rain forest Carabidae in the tropics.

Next, after another gap more than 150 miles wide of drier, open woodland, is the base-of-peninsular or main tropical rain forest system of North Queensland. Outlying pieces of semi-rain forest of this system are within sight of Cooktown, and heavier rain forest begins on the coastal mountains (Mt. Amos, Mt. Finnigan) about 20 miles to

EXPLANATION OF PLATE 2

Fig. 3. South temperate rain forest, Lake St. Clair, Tasmania (P. J. D. 1957). On left is transitional wet forest with overstory of big eucalypts; center, heavy rain forest including *Nothofagus*.

Fig. 4. Interior of old south temperate rain forest, Cradle Valley, northern Tasmania (courtesy Mr. H. J. King, Honorary Photographer, and Mr. Frank Ellis, Director, Queen Victoria Museum, Launceston).

the south. From here an irregular system of good rain forests extends somewhat discontinuously but with no very wide breaks south to and across the Atherton Tableland and farther south along a series of plateaus and ranges to the Mt. Spec plateau (Paluma Range) almost within sight of Townsville. Much of this forest system lies between 1,000 and 5,000 ft. altitude, but areas of good rain forest belonging to it occur (or occurred before being cleared) also on the coastal plain east of the Atherton Tableland and in the Mossman-Daintree region.

From the southern end of the main tropical rain forest system to below Rockhampton is a gap of nearly 500 miles of dry, open woodland broken only (so far as I know) by two noteworthy islands of rain forest. One is at about 3,000-4,000 ft. on the crest of the Elliot Range, within sight of (southeast of) Townsville but separated from the northern rain forests by a low, comparatively dry valley. The other, more important island of rain forest is on the Eungella Range about 40 miles inland from Mackay, at about 2,000-4,000 ft. altitude. Scattered fragments of semi-rain forest, for example near Proserpine (Repulse Bay) and Yepoon (Byfield), are relatively unimportant so far as carabid distribution is concerned.

South of Rockhampton, in the edge of the south temperate zone, begins what I call the subtropical rain forest system. The first piece of (rather poor) rain forest of this system is on Mt. Jacob east of Many Peaks. Other tracts are widely scattered in southeastern Queensland at low altitudes as well as on mountains (Blackall Range, Bunya Mts., Mt. Tamborine, McPherson Range on the New South Wales border, etc.). The different forest tracts vary in quality, but the best of them approximate tropical rain forest. This system of rain forests extends into northeastern New South Wales at rather low altitudes, although much of it has now been cleared. The more important pieces that still remain are listed and briefly described in my published locality list (1961). The most southern *good* tract that seemed to me to be tropical-type rain forest is on "Mt. Dorrigo", on the lower (eastern) edge of the Dorrigo Plateau, at about 30° 20' S., but small pockets of more or less similar forest occur still farther south, even south of Sydney, especially in wet ravines.

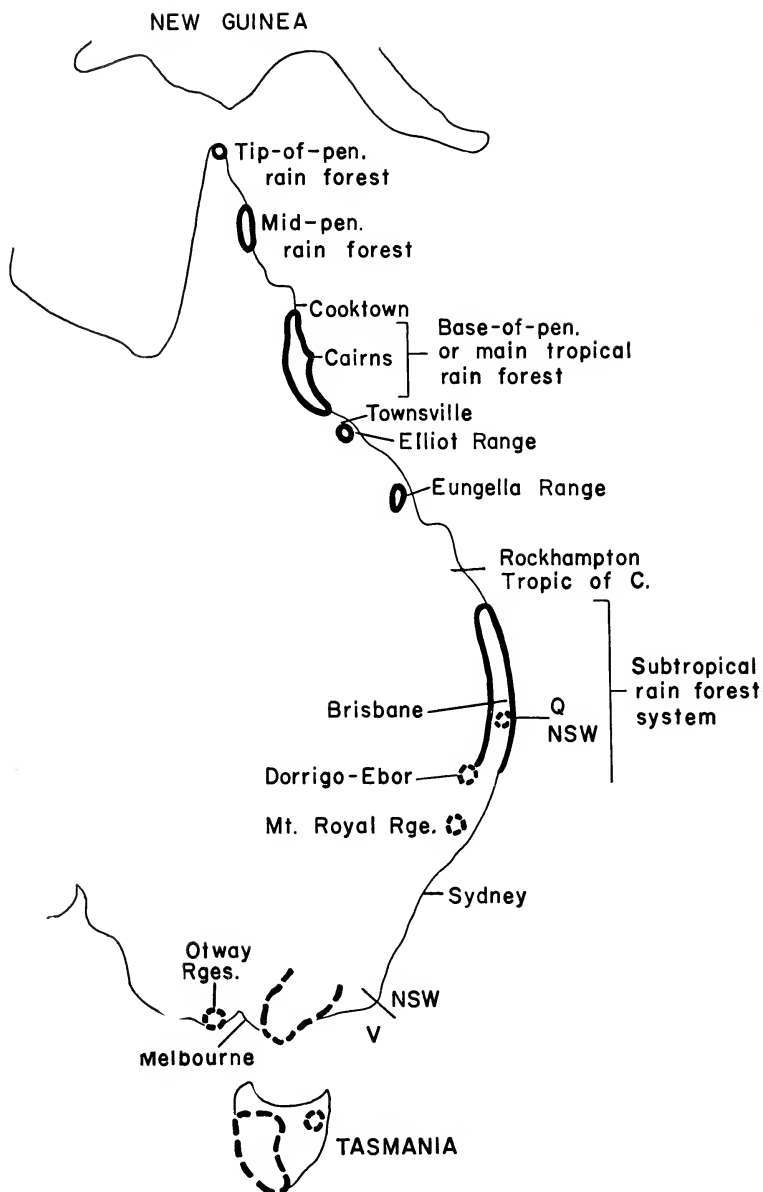
South temperate rain forest (see again Figs. 3, 4) is different in aspect from tropical rain forest (fewer vines, etc.) and different botanically, often dominated by southern beeches (*Nothofagus*). Such forest is widespread in southwestern Tasmania and occurs in isolated tracts elsewhere in Tasmania (see paper referred to above for details). Isolated tracts of similar forest occur on plateaus and mountains in southern Victoria including the Otway Ranges southwest of

Melbourne and some of the southern "Victorian Alps" east of Melbourne. This kind of forest occurs also, at wide intervals, on isolated plateaus in eastern New South Wales, notably on the plateau of the Mt. Royal Range (Barrington Tops and Tomalla Tops) at about $31^{\circ} 50'$ S. and on the higher part of the Dorriggo-Ebor Plateau (especially at Point Lookout in New England National Park) at about 30° S. Both these plateaus reach about 5000 ft. above sea level. The northernmost *Nothofagus* in Australia is still farther north, on the southern border of Queensland, where small tracts of old trees exist on the highest points of the McPherson Range, at about $28^{\circ} 20'$ S. and 4,000 ft. altitude. *Nothofagus* does not occur on the mountains of tropical North Queensland but is dominant in New Guinea in mountain forests between about 6,500 and 10,000 ft. (Womersley and McAdam 1957, p. 25). However, south temperate groups of Carabidae do *not* occur in the New Guinean *Nothofagus* forests.

The distribution of tropical (including subtropical) and south temperate rain forest is shown, rather diagrammatically, on the accompanying map (Fig. 6). The map is based partly on the vegetation map in "The Australian Environment" (CSIRO 1950, pp. 88-89) and on Brass's (1953, p. 152) map of Cape York rain forests, but many details are modified according to my own observations. In most cases rain forest is not continuous within the boundaries shown, but occurs as irregular, sometimes discontinuous tracts and strips interspersed with savannah woodland (in the north) and/or sclerophyll forest (in the south). The two kinds of rain forest overlap widely in New South Wales. Within the area of overlap south temperate rain forest is usually above (at higher altitude than) tropical rain forest, but there is some mixing.

The Carabidae

The wet-forest Carabidae of New Guinea and Australia, including Tasmania, are numerous, diverse, and complex in ecology and distribution. They form three general ecological groups. Those that live on the ground without being specially associated with surface water are mesophiles or *geophiles*. Those that live on the ground beside streams or ponds or in swamps are *hydrophiles*. And those that live on tree trunks or in foliage above the ground are *arboreal*. According to my (1943, p. 41) rough analysis of the Australian carabid fauna, at least half the species are geophiles, not quite a quarter hydrophiles, and not quite a quarter arboreal. The carabid fauna of New Guinea divides in something like the same way, although I cannot yet give exact figures.



State of wings of Carabidae is correlated with ecology and distribution. Most Carabidae in most parts of the world have fully developed inner wings and can fly, but some have lost their wings (except for vestiges) and become flightless. The Australian carabid fauna includes an unusually large proportion of flightless species: according to my rough analysis (*loc. cit.*), nearly 45% of all Australian Carabidae have atrophied wings, and many genera and even some tribes are wholly flightless. Most hydrophiles and arboreal forms have retained their wings and can fly, but about 75% of Australian geophile Carabidae are flightless, and flightless groups are common everywhere in Australia, at low and high altitudes and in wet and dry climates, and some are well represented in the tropical as well as the temperate parts of the continent. In New Guinea flightlessness is rare among lowland Carabidae. This accords with the general rule that most Carabidae in most wholly tropical lowland areas are winged. On mountains in New Guinea, however, as on many tropical mountains elsewhere, flightless geophile Carabidae are numerous.

New Guinea-Tropical Australian Relationships

Probably the first fact that strikes entomologists collecting in the rain forests of tropical Australia is that some of the insects are species that occur in New Guinea. This is expected. The Australian rain forests themselves are predominantly New Guinean (or Malaysian) both in aspect and in botanical relationships (CSIRO 1950, pp. 95-96; Brass 1953, p. 154); many mammals in the North Queensland rain forests belong to New Guinean genera or even species; and so do many birds. Some Carabidae are common to New Guinean and Australian rain forests. For example *Syleter papua* Darl. extends to the tip of Cape York, living on the ground in shaded swamps. *Morion longipenne* Putz. of New Guinea extends to the main North Queensland rain forests, on and in fallen logs. And *Violagonum violaceum* (Chd.) is common in rain forest in New Guinea and eastern Australia south at least to near Rockhampton, in accumulations of dead leaves on the ground and in thick foliage. Besides shared species like these (there are many others among Carabidae) the New Guinean and Australian rain forests share some geographically restricted genera, for example *Platycoelus* (*Chlaenioidius*), *Loxandrus*, and *Stricklandia*,

EXPLANATION OF PLATE 3

Fig. 6. Distribution of rain forests in eastern Australia. Solid lines enclose principal areas of tropical (including subtropical) rain forest; broken lines, of south temperate rain forest. In most cases rain forest is not continuous within the boundaries shown but occurs in discontinuous or scattered tracts. See text for further details.

as well as many more-widely distributed genera. Up to a point, therefore, the Carabidae agree with the forest trees, mammals, and birds in showing a considerable number of species and genera common to the rain forests of New Guinea and tropical Australia.

When I was collecting on the Atherton Tableland in northeastern Australia in 1932, I found not only many Carabidae of obviously New Guinean groups but also, in rain forest, many species of Australian groups not known to occur in New Guinea. Included were striking endemic species of *Notonomus*, *Trichosternus*, *Leiradira*, *Pamborus*, and *Mystropomus*. Knowing, as I did, that the rain forests of Australia and New Guinea had much in common, and knowing that the Carabidae of New Guinea were poorly collected, I imagined in New Guinea a rich fauna of the genera just named, perhaps in rain forest at middle altitudes, but wholly unknown. It was a sort of El Dorado for the future, to a young and enthusiastic carabid student. But now that I have collected in New Guinea and seen thousands of Carabidae collected there by other persons, I know that this El Dorado does not exist, and I know why. All the Carabidae common to the New Guinean and Australian rain forests are winged and probably fly. All the genera mentioned above as represented in rain forest on the Atherton Tableland are wholly flightless, and I know now that there is no direct relationship between any flightless Carabidae of the New Guinean and Australian rain forests.³

The difference between the flightless Carabidae of Australia and New Guinea goes far beyond mere differences of species and genera. The composition and origins of the two faunas are fundamentally different. Flightless Carabidae are numerous everywhere in Australia, even at low altitudes in the tropical part of the continent including Cape York. Many of the species belong to wholly flightless genera or even flightless tribes that have evidently been in Australia a long time. Derivatives of old Australian flightless groups dominate the flightless ground-living carabid fauna of tropical rain forest in Australia. In New Guinea, in contrast, no primarily flightless groups of Carabidae occur at low altitudes. A very few species of the primarily winged

³If tiger beetles are considered Carabidae, *Tricondyla aptera* Ol. is an exception to this rule. The genus *Tricondyla* is primarily Oriental and is wholly flightless. Nevertheless *T. aptera* has reached New Guinea, probably rather recently (it is only slightly differentiated there), and has got beyond New Guinea to the mid-peninsular rain forests of Cape York. (It has reached the Solomon Islands and New Hebrides too.) It is a good sized (nearly an inch long), big-eyed, ant-like, active insect, which lives on tree trunks in rain forest. It has probably dispersed on floating trees, which ground-living Carabidae are not likely to do.

genera *Clivina*, *Tachys*, *Lesticus*, *Platycoelus*, and *Loxandrus* have undergone wing atrophy at low altitudes in New Guinea (Darlington in press), but they have evidently done it recently, *in situ*. Some of the species are still dimorphic, with fully winged individuals occurring with the short winged ones, and all the short winged lowland species are closely related to long winged ones that still exist in New Guinea. It is only above about 5000 ft. in the mountains that flightless Carabidae become numerous in New Guinea, and they too have apparently undergone wing atrophy *in situ*. That is, they have been derived on the mountains of New Guinea from winged ancestors, and do not represent flightless stocks of other regions. This is my conclusion after making formal studies of the New Guinean representatives of the two principal tribes concerned, the Agonini (Darlington 1952, especially table p. 108) and Pterostichini (in press).

Besides the change of specific flightless stocks from New Guinea to Australia there is a change of dominance of tribes. In New Guinea, Agonini are much more numerous than Pterostichini, and most flightless Carabidae of the island are agonines. But in Australia, even in the tropical rain forest, Pterostichini are overwhelmingly dominant and include most of the flightless forms. This striking shift of dominance is further discussed on page 22.

The first important finding of the present study, then, is that, although the rain forests of New Guinea and tropical Australia are similar and share many species of plants, mammals, birds, and winged insects including many winged Carabidae, they have wholly different faunas of flightless Carabidae, which differ not only in taxonomic details but also in general ecology (in relation to altitude), in origin of the flightless stocks, and in relative dominance of tribes.

Transition in Australia: South from the Tropics

Now to be considered is the transition of wet forest carabid faunas within the limits of Australia and Tasmania.

Five important genera of flightless geophile Carabidae are mentioned above as occurring in rain forest on the Atherton Tableland. Of these five genera, *Notonomus* is most dominant. It is a genus of about 100 species, confined to eastern and southeastern Australia and Tasmania except for one species isolated in southwestern Australia. The genus' northern limit is between Daintree and Cooktown. It is represented by several species (some very localized) in the main tropical rain forest system of North Queensland, where it seems to be confined to rain forest. It is well represented in the subtropical rain forests of South Queensland and northern New South Wales and south through

eastern New South Wales and southern Victoria; in these areas some species occur not only in rain forest (including south temperate rain forest) but also in wet sclerophyll forest and good savannah woodland. However only two groups of the genus reach Tasmania and only one group (two related, primarily allopatric species) occurs in rain forest there.

Trichosternus is a genus of 25 or more species confined to eastern Australia, except that one species is isolated in southwestern Australia (Darlington 1953, p. 94). The genus' northern limit is between Daintree and Cooktown. It occurs (several species, some very localized) throughout the main rain forest system of North Queensland, where it is apparently confined to rain forest. It is well represented also in the subtropical rain forest system of South Queensland and northern New South Wales, and in this area some species occur in savannah woodland as well as in tropical-type rain forest, and some have entered south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range. The southern limit of the genus is somewhere in east-central New South Wales, probably not far north of Sydney.

The northern limit of *Leiradira* (or of the group of genera that includes *Leiradira*) is between Daintree and Cooktown. This genus too occurs in much of the main tropical rain forest system of North Queensland, being represented there by several distinct species each more or less localized, but the genus may be absent in the southern extension of the main tropical rain forest system south of the Atherton Tableland. It is represented also by several species in the subtropical rain forests of South Queensland etc. Its southern limit is apparently on the lower, eastern edge of the Dorrigo plateau. It is confined to eastern Australia. It is wholly or chiefly a rain forest genus in all parts of its range.

The three preceding genera are all Pterostichini. All their species are flightless geophiles. Additional flightless geophile pterostichines are localized in all the different rain forest areas of Australia from Cape York to Tasmania. Examples are *Mecynognathus* in the tip-of-peninsular forests; *Paranurus* in the mid-peninsular forests; *Loxogenius* and undescribed genera in the main tropical rain forest system; *Nursus* s. s., *Liopasa*, *Ceratoferonia*, *Zeodera*, and *Notolestes* in the subtropical rain forest system; *Loxodactylus* in the wet forests of southern Victoria; and *Rhabdotus* in those of Tasmania. (It should be added that Australia possesses many winged pterostichines as well as these and other flightless genera.)

Of non-pterostichines, *Pamborus* is noteworthy. It is confined to eastern Australia and is one of the two known genera of the tribe Pamborini. (The other is monotypic *Maoripamborus* in New Zealand — Brookes 1944.) The northern limit of *Pamborus* is probably near Cooktown. Four species of the genus occur in the main tropical rain forest system of North Queensland, chiefly or wholly in rain forest. Six other species occur in South Queensland and New South Wales. Some of them occur mainly in (sub)tropical rain forest, but *viridis* inhabits savannah woodland and some other species occur in open woods as well as rain forest, and some enter south temperate rain forest on the high plateaus of north-central New South Wales. The southern limit of the genus is near the Shoalhaven River about 70 miles south of Sydney. (Old records for Victoria are probably errors.)

The genus *Mystropomus* is the only Australian representative of the pantropical tribe Ozaenini. The genus is confined to eastern Australia. Its northern limit is between Daintree and Cooktown. A single species (two subspecies) occurs throughout the main tropical rain forest system of North Queensland, and is apparently confined to rain forest. Another, variable species (two subspecies) occurs in the subtropical rain forest system, and extends into more open woodland. The southern limit of the genus is apparently near Sydney.

These five genera dominate the flightless geophile carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia. Their distribution is notable in several ways. All five genera reach an approximately common northern limit, north of Daintree and south of or near Cooktown. All five genera are widely distributed both in the main tropical and in the subtropical rain forest systems. These two forest systems are separated by a wide barrier of comparatively dry, open forest in which is one important "island" of rain forest, on the Eungella Range west of Mackay, and all five of the genera in question are represented there.⁴ In the tropics, these genera occur only or chiefly in rain forest,⁵ although most of them enter opener forest too in the south temperate zone.

⁴Of the 5 genera in question on the Eungella Range, the one *Pamborus* has close relatives in both North and South Queensland. The one *Mystropomus* is a South Queensland species. Of 2 *Trichosternus*, one probably belongs to a South Queensland group and the other is doubtful. The one *Notonomus* belongs to a North Queensland group. And the one *Leiradira* belongs to a South Queensland subgenus. These genera in the Eungella rain forest therefore show 2 close ties with North Queensland (in *Pamborus* and *Notonomus*) and 4 with South Queensland.

⁵*Trichosternus cordatus* Chd. occurs outside rain forest in the southern edge of the tropics.

Southward, through New South Wales, rain forest of (sub)tropical type diminishes in area and quality, and the Carabidae associated with it diminish too. Of the five genera just discussed, *Leiradira* may not extend south of the Dorrigo. *Trichosternus*, *Mystropomus*, and *Pamborus* go a little farther south, reaching different limits probably in this order, but do not reach Victoria. And *Notonomus* reaches Victoria (in numbers) and Tasmania (only one stock in rain forest). Toward their southern limits, all these genera, except *Leiradira*, occur not only in tropical-type rain forest but also in opener forest, and all, except again *Leiradira*, have entered or even evolved endemic species in south temperate rain forest on the Dorrigo-Ebor plateau and the Mt. Royal Range.

Transition in Australia: North from Tasmania

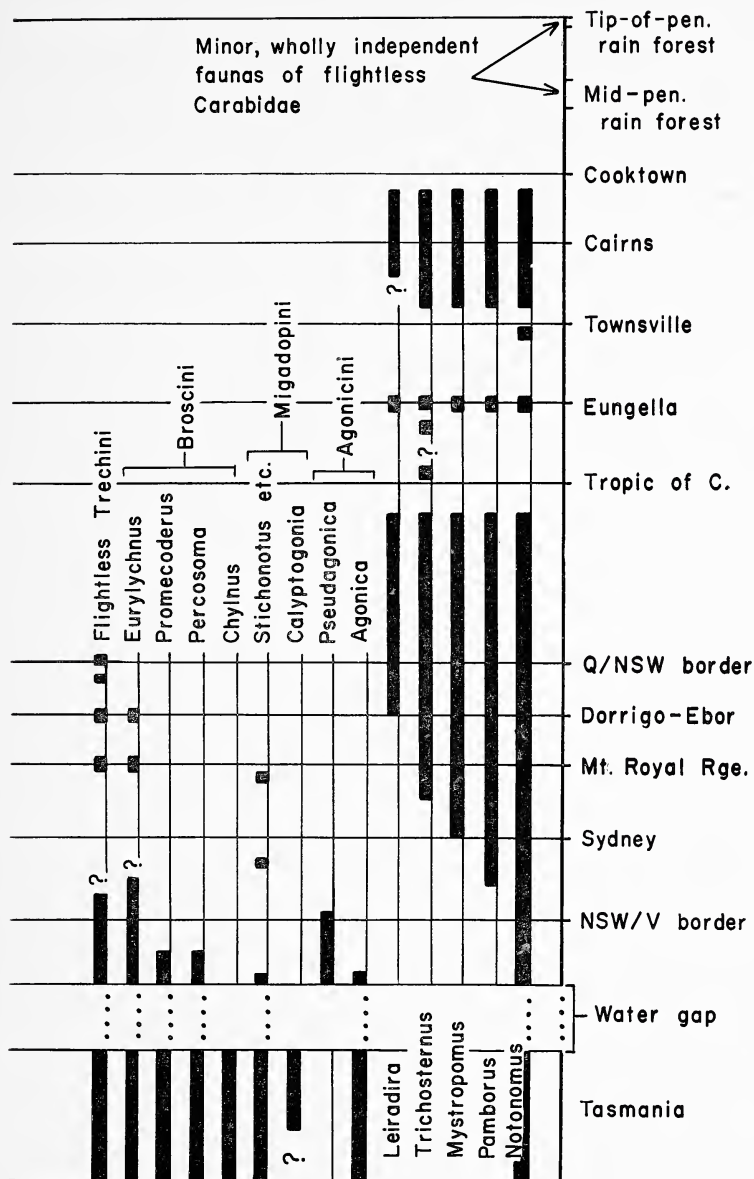
The ground-living Carabidae of the south temperate rain forest of Tasmania are dominated by or include flightless genera of four special tribes in addition to the more widely distributed Pterostichini, Licinini, etc.

The tribe Broscini is well represented in both the north and the south temperate zones of the world (Ball 1956) but is absent in the tropics or nearly so. Some northern broscines have well developed wings, but I think that all those of the southern hemisphere have atrophied wings and are flightless. Four genera occur in Tasmania. *Promecoderus* is represented there by several rain forest species and by other species that live in drier, opener woodland. The genus is widely distributed across southern Australia, but chiefly in dry forest and arid country, although one or two species occur in rain forest in Victoria. Of the other Tasmanian genera, *Chylmus* is confined to Tasmania, in wet forest. *Percosoma* occurs in Tasmania and the mountains of southeastern Victoria, in wet forest. And *Eurylychnus* occurs in Tasmania, southern Victoria etc. including the Otway Ranges, and east and north into southern New South Wales, and two separate stocks of the genus have species isolated (chiefly in south temperate rain forest) on the Mt. Royal Range and the Dorrigo-Ebor plateau. The latter is the northern limit of wet-forest broscines in Australia.

The tribe Trechini (subfamily Trechinae of Jeannel 1926-1928)

EXPLANATION OF PLATE 4

Fig. 7. Diagram of transition of selected flightless geophile Carabidae in rain forests of eastern Australia. The 5 genera at bottom of the diagram are primarily tropical and subtropical; the other genera and tribes, primarily south temperate. See text for further details.



is world-wide in distribution. It includes both flying and flightless genera, but the flying genera usually live beside standing or running water and are not forest-living geophiles. Flightless geophile Trechini are numerous both north and south of the tropics. In Tasmania they are numerous in south temperate rain forest and hardly enter other habitats at low altitudes, although some occur in open country above timber line, on cold mountain tops. Flightless Trechini are less numerous but still widely scattered in wet forests and on mountain tops in southern Victoria, including the Otway Ranges (Moore 1960), east nearly to the New South Wales border and north to Mt. Kosciusko in southern New South Wales, and endemic species perhaps representing one original flightless stock of spotted "*Trechus*" are isolated on the Mount Royal Range, the Dorriggo-Ebor plateau, and the McPherson Range on the Queensland border.⁶

The tribe Migadopini (Jeannel 1938; Darlington 1960, p. 663) is confined to the southern hemisphere, with different genera localized in Tasmania and southeastern Australia, New Zealand, and the southern tip of South America, etc. Two flightless genera of the tribe occur in Tasmanian rain forest: *Calyptogonia* is confined to Tasmania; *Stichonotus* extends to the mainland, but only to the Otway Ranges. A third Australian genus of the tribe is known from a single specimen collected long ago near Kiama south of Sydney, and a fourth genus occurs still farther north, in subtropical forest on the low (c. 2,000 ft.) Comboyne plateau at about 31° 35' S. This last genus, *Decognus*, differs from all other Migadopini in being winged.

Finally, the flightless tribe Agonicini is confined to Tasmania and southeastern Australia (Moore 1960). There are two genera. One is widely distributed in Tasmania and occurs also in the mountains of southern Victoria east of Melbourne (B. P. Moore, in letter). The other is confined to the mainland, including the Otway Ranges and the "Victorian Alps," north to Mt. Kosciusko. Agonicines live on the ground in rain forest, and sometimes in open snow gum woods on mountains.

Although there are other Carabidae in Tasmanian rain forests (especially various Pterostichini and Licinini) the four tribes just discussed make up a large part, and zoogeographically the most important part, of the flightless wet forest Tasmanian carabid fauna. It will be seen from details given above that all four tribes occur both in

⁶A second "*Trechus*", *diemensis* Bates, extends from Tasmania and southeastern Australia north to the McPherson Range, but this species is winged or dimorphic.

Tasmania and on the adjacent mainland of Australia, but that they all diminish rapidly northward.

The transition of selected elements of the flightless geophile carabid faunas of tropical and south temperate rain forests is diagrammed in Fig. 7.

Isolated Australian Faunules

To return to the five carabid genera discussed above as characteristic of the main tropical and subtropical rain forests, these genera have distributions that are alike in many details. Within the main (base-of-peninsular) tropical rain forest system, they all have almost the same northern limits and (excepting perhaps *Leiradira*) the same southern limits. All are represented on the Eungella Range. In South Queensland, all apparently find their northern limit on Mt. Jacob (except that *Trichosternus cordatus* extends farther north in drier woodland), and all extend well into New South Wales, although they reach different limits there. They illustrate a general fact, that the carabid faunas of the main tropical and subtropical rain forest systems of eastern Australia, although separated by several hundred miles of comparatively dry country, are fundamentally similar, dominated by the same tribes, and share many genera some of which coincide remarkably in details of distribution, although some other genera and most species are different. However three isolated pieces of Australian rain forest have carabid faunules that do not fit into this main pattern. They are the tip-of-peninsular and mid-peninsular rain forests of Cape York and the rain forest on the Elliot Range south of Townsville.

The tip-of-peninsular tract is light rain forest and is limited both botanically and zoologically. For example, stinging trees (*Laportea*), which occur in other Australian rain forests and in New Guinea, are apparently absent in the tip-of-peninsular forest, and land leeches and itch mites, which are pests in rain forest elsewhere, are apparently absent in the tip-of-peninsular tract. The winged Carabidae of this tract are not remarkable, except that they include New Guinean species. But the flightless Carabidae form a faunule wholly different from that of any other rain forest, consisting (so far as I could find) of only two flightless species. One is *Mecynognathus dameli* MacL., an enormous carabid, the largest males $2\frac{1}{2}$ inches long with mandibles like stag beetles. The genus occurs nowhere else on earth, although it may be rather closely related to *Paranurus* (see below). The other is a large flightless *Clivina* (probably *kershawi* Sl.), which is fairly common both in the rain forest and in adjacent savannah woodland. The nature of this forest and of its flightless Carabidae suggests that

the tip-of-peninsular tract is not a remnant of a larger, continuous rain forest but has been constituted or reconstituted separately, by gradual accumulation of a limited variety of plants and animals.

The mid-peninsular rain forests of Cape York are heavier and more extensive than the tip-of-peninsular tract, more like the base-of-peninsular forests at least superficially, but their flightless Carabidae form a second independent faunule. None of the flightless genera characteristic of the other rain forests is represented in the mid-peninsular system. In their place is a single large species of *Paranurus*. This is a genus of probably only one, geographically variable species, which occurs from the tip of Cape York (and islands off the tip) south to below Cairns mainly in good savannah woodland. In most parts of its range it apparently does not enter rain forest, but it has done so in the mid-peninsular system, where it is now widely distributed. It seems to have invaded this system recently. An earlier invasion of the tip-of-peninsular rain forest by the ancestral stock of *Paranurus* may have produced *Mecynognathus*. There is also in the mid-peninsular rain forest a flightless *Coptocarpus*, but it is small and rare and I am not sure of its habitat or relationships. And also in this forest is a large form of *Lesticus chloronotus* Chd. It is winged, but its distribution and behavior suggest that it may eventually become flightless, as several stocks of the same genus have done in New Guinea. The Carabidae, then, suggest that the mid-peninsular rain forest has not been connected with the main base-of-peninsular system but, like the tip-of-peninsular tract, has derived or is deriving its flightless Carabidae independently.

The rain forest on the Elliot Range is poorly known. The only insect collecting ever done in it, so far as I know, was done March 2, 1958, when my son and I climbed from Double Creek to near the peak of Sharp Elliot and worked for three or four hours in the forest there. It seemed to be real but rather light rain forest. We found there series of two conspicuous flightless Carabidae: a very big *Nurus* and a *Notonomus*, both endemic. No trace of the four other genera (other than *Notonomus*) discussed above as characteristic of the main tropical and subtropical rain forests of Australia was found. Judging from my experience elsewhere, we would probably have found specimens or fragments of other species if the carabid fauna were diverse. I think, therefore, that the rain forest of the Elliot Range probably has a limited, endemic faunule of flightless Carabidae presumably received across a barrier and not by way of continuous rain forest. The valley that separates the Elliot Range from the main mountain

system of North Queensland is not much more than ten miles wide, but it seems to have been a more effective barrier than the much wider gaps of dry hilly country between the North Queensland, Eungella, and South Queensland rain forest areas.

Summary of Transition from New Guinea to Tasmania

The transition of wet forest carabid faunas from New Guinea to Tasmania involves two main changes. First, between the rain forests of New Guinea and those of tropical Australia is a complete change of flightless stocks of Carabidae and also a change from Agonini to Pterostichini as dominant tribes, although the change is overlain and superficially concealed by many winged species and genera of Carabidae that are common to New Guinea and Australia and that form a broad and complex transition, not fully described here. Between the tropical rain forests of North Queensland and the subtropical ones of South Queensland etc. are very many changes of species and genera but no fundamental change in the nature of faunas or in dominant groups. The second main change is farther south, and is a complex transition from tropical to south temperate groups. The area of transition (of overlapping and mixing of faunal elements) is from the southern edge of Queensland to Tasmania. And the transition involves not only changes of species and genera but a second partial change of dominant tribes, from Pterostichini as principal dominants to (in Tasmania) dominance shared by Broscini and Trechini (and Licinini) as well as some Pterostichini. This change has been described as it occurs among selected flightless geophile Carabidae, but it is reinforced and made more complex by changes of winged Carabidae too.

The whole transition of wet forest carabid faunas from New Guinea to Tasmania might be described as a very irregular stepcline of flightless groups overlain by a more regular transition (or cline of many smaller steps) of winged groups. The flightless Carabidae of the isolated rain forests of Cape York and the Elliot Range are outside the main pattern and complicate it, and of course the situation as a whole is much more complex in detail than I can describe here.

Historical Implications: Two Land Bridges

It is a good working principle of zoogeography that situations should be analyzed first by study of the best known and most significant groups of animals, especially mammals, but that other groups may add important details to what the mammals show. In the present case, two former land bridges are involved: from New Guinea to Australia

and from Australia to Tasmania. Mammals show, by occurrence of many identical or closely related species on opposite sides of the existing water gaps, that both bridges did exist recently and that some forest-living animals crossed both of them. Carabidae show additional, different things about the two bridges. In the case of the Australian-Tasmanian bridge, the Carabidae agree with the mammals. Many wet forest Carabidae including many flightless ones evidently crossed this bridge without meeting important ecological barriers, although cold climate stopped some other animals, especially some reptiles (Darlington 1960, p. 659). In the case of the New Guinea-Australian bridge, however, the flightless rain forest Carabidae show that there was an ecological barrier upon the land, and that the barrier existed for a long time. New Guinea and Australia cannot have been connected by a continuously rain-forested ridge within the time of existing carabid faunas. The recent connection was evidently low and rain forest was probably not continuous across it, although it was nearly enough continuous to allow certain forest trees, mammals, birds, and winged insects to get across. These organisms probably crossed the bridge by way of more or less separate forest "stepping-stones" and strips of gallery forest that did not allow continuous passage of flightless rain forest Carabidae, which do not disperse easily across even narrow gaps of unsuitable land. Rain forest is discontinuous on Cape York now. The Carabidae suggest that it has been so for a long time in the past, and that conditions on Cape York now are like the conditions that existed on the land bridge when New Guinea and Australia were connected.

Historical Implications: Climatic Fluctuations

The present distribution of wet forest Carabidae shows that many of them have been able to move up or down the eastern edge of Australia between North and South Queensland, across what are now wide gaps of comparatively dry country. The degree of relationships of different Carabidae in the tropical and subtropical rain forest systems varies. In some cases (*e. g. Pamborus* of the *tropicus* group) the North and South Queensland representatives of single original stocks are only slightly differentiated, but in other cases (*e. g. Leiradira* and its allies) they have diverged as subgenera or genera. This suggests either several periods of dispersal and isolation, accompanying fluctuations of rainfall and rain forest, or occasional trickling of dominant wet forest Carabidae across the drier gaps of central Queensland. In either case wet forest Carabidae seem to have followed a rather narrow path along the continental divide, and have usually

not been able to reach such slightly isolated places as the rain forest on the Elliot Range. The whole pattern, of occasional or limited exchange between North and South Queensland and of isolation of endemic faunules on the Elliot Range and in the Cape York rain forests, is consistent with climates and forests fluctuating only within moderate limits, not profoundly.

Ecological Correlations

It is a fact not sufficiently understood by some zoogeographers that the climatic zones, the differences between tropical and cool temperate climates, are very important to Carabidae and other insects. In eastern Australia, where climate is the only permanent barrier to dispersal, many old groups of Carabidae are confined to either the tropical (including subtropical) or the cooler south temperate areas. Evidently whole tribes may persist for long periods in small areas protected only by climatic barriers, and even dominant tribes do not always easily cross from one climatic zone to another.

Carabid distribution is correlated with climate and ecology in several more specific ways. For example some rain forest Carabidae, including five genera specially considered above, seem to be more strictly limited to rain forest in the tropics than in the south temperate zone. This suggests that ecological factors are more intense in the tropics, as they may well be if temperature and evaporation rates are involved. That ecological factors are intense in the tropics is suggested also by groups of Carabidae that occur in diverse habitats in the temperate zones but enter or cross the tropics only when associated with surface water, which probably tempers the intensity of tropical climate. I have discussed this elsewhere (1959, especially pp. 332, 342). In Australia, for example, the only Trechini that occur in the tropics are winged hydrophiles: *Perileptus* and *Trechodes* by running water and *Trechobembix* (which extends north to Cairns) in deep swamps. *Mecyclothorax* occurs in many habitats in temperate southern Australia, but I found only one species (apparently *cordicollis* Sl.) in the tropics, in thick vegetation over deep, cool water on the Atherton Tableland. And *Notagonum* ("*Agonum*") *submetallicum* (White), which, though always associated with water, occurs in a variety of waterside habitats in both humid and arid parts of south temperate Australia, I found in the tropics (Atherton Tableland) only in thick vegetation over cool, moving water.

There is also a notable correlation of wings and flight of Carabidae with climate and altitude. Carabidae (mostly geophiles) often become flightless at low altitudes in temperate climates, and on moun-

tains everywhere, but rarely at low altitudes in the tropics. The fewness of flightless Carabidae at low altitudes in New Guinea is an example. I have discussed this subject, with other examples, elsewhere (1943).

Finally there is a partial correlation between size of Carabidae and climate. Very large Carabidae (over 1 to 2½ inches long) are numerous in the forests of warm temperate to tropical eastern Australia but relatively few or absent in both cool temperate Tasmania and wholly tropical New Guinea. If *Catadromus tenebrioides* (ol.) is introduced, as I think it is, the largest carabids in New Guinea are hardly an inch long and few are that large. I suspect that this correlation has a complex ecological basis which may include direct action of physiological factors, correlation of size with state of wings and flight, and competition with other insects. Of insects that might compete with carabids, ants are most obvious. I have suggested (1943, p. 42, Fig. 4) that ants may take the place of most flightless geophile Carabidae especially in the lowland tropics.

Geographical History of Carabidae

Carabidae, like other old, complex groups of animals (mammals etc.), have presumably had complex geographical histories, with successive dominant groups evolving, spreading over the world, and replacing older groups. The present distribution of Carabidae in the Australian Region may reflect this. Some localized tribes that are now confined to the cool south temperate zone may be remnants of an ancient fauna (see Darlington 1960 for further discussion of some of these groups). Pterostichini, now dominant in most of Australia, may be more recent and may be replacing more ancient Carabidae. And Agonini may be still more recent, now dominant in New Guinea (and in the whole tropical Asiatic-Australian area), and spreading to Australia.

Pterostichini and Agonini tend, as dominant tribes, to be complementary over the world as a whole. I have discussed this before (1956, pp. 1-3), but what I said then is worth repeating briefly now, with counts of species brought up to date. Both tribes are cosmopolitan, but unevenly so. In some parts of the world they occur in nearly equal numbers, in others, one tribe or the other is overwhelmingly dominant. The tribes tend to be complementary within the Australian Region, as already indicated. In Australia itself (with Tasmania) Pterostichini are dominant, with more than 350 known species against probably less than 20 species of Agonini, a ratio of nearly 40/1. But

in New Guinea Agonini are dominant, with considerably more than 100 known full species (some discovered since my 1952 paper) against about 40 species of Pterostichini (manuscript in press), a *reversed* ratio of about 3/1.

One reason for the number of Agonini in New Guinea is that species of this tribe have multiplied on the mountains there. In Australia, however, Pterostichini, not Agonini, have multiplied in what seem to be comparable habitats on the mountains. This difference can hardly be accounted for in simple ecological terms but is probably due to a complex combination of ecological, historical, and geographical factors. Over the world as a whole, there is a tendency for Agonini to be better represented in the tropics; Pterostichini, in the temperate zones. Also it is probable that Agonini, which are phylogenetically less diverse, are more recent in origin than Pterostichini and that they have dispersed more recently. It is therefore likely that Pterostichini are dominant in Australia partly because Australia is more temperate than tropical in climate and partly because Pterostichini reached Australia before Agonini did, and it is likely that Agonini are dominant in New Guinea partly because the climate there is fully tropical and partly because the carabid fauna of New Guinea is more recent in its origins than that of Australia, as I think it is. Add to this that the mountain carabid faunas of Australia and New Guinea have been derived independently, each from the lowland fauna adjacent to it, and not by dispersal along a connecting mountain chain, and we have an adequate and probably correct explanation of the great difference in composition of the carabid faunas on the mountains of Australia and New Guinea.

As to direction of recent movements of Carabidae, movements of (winged) species have evidently occurred in both directions between Australia and New Guinea, although I cannot take space to give details now. Movements have apparently occurred also in both directions between the tropical and subtropical forests of Australia. This is indicated by the relationship of the species now on the Eungella Range (p. 13), although I am not ready to give further details now. South of the tropics, patterns of distribution (Fig. 7) suggest withdrawal of cool temperate groups and southward spreading of tropical or subtropical groups. This is probably primarily an adjustment to recent warming of climate rather than an invasion of south temperate habitats by tropical Carabidae, although *Pamborus*, *Trichosternus*, and *Notonomus* have invaded *Nothofagus* forest on high plateaus in New South Wales.

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A RECONSIDERATION OF THE GENUS *EPIPOMPILUS* (HYMENOPTERA: POMPILIDAE)¹

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The genus *Epipompilus* was described by Kohl in 1884, with *maximiliani* Kohl, from Mexico, as type. It was next treated by Ashmead in 1902, who at the same time described a related genus, *Aulocostethus*, with *bifasciatus* Ashmead, from "Peru", as type. Haupt, in 1930, erected the tribe Epipompilini for these two genera and several others; the others were shortly thereafter removed to another tribe. In 1944 Bradley presented a revision of the American species of *Epipompilus* and *Aulocostethus*. Ashmead, Haupt, and Bradley all separated the two genera by whether or not the eyes are hairy. Since Ashmead said that *Epipompilus* has glabrous eyes, it is clear that he was unfamiliar with the genus; and both Haupt and Bradley admit they had never seen the genus. Thus we have the curious phenomenon of a genus being treated by three persons, none of whom had ever seen any specimens belonging to the genus as he conceived it. As a matter of fact the eyes of *maximiliani* are hairy, and *Epipompilus* as conceived by these three workers is a nonexistent genus: in actuality the name *Epipompilus* is a senior synonym of *Aulocostethus*.

This is only one of several sources of confusion in the genus. Ashmead described *Aulocostethus* by merely placing it in a key and listing *bifasciatus* n. sp. as type. His description of *bifasciatus* can be and has been considered valid, but he gives no information other than the generic characters and the type locality ("Peru"), not even as to color pattern, which is of much value in separating species in this genus. Haupt used Ashmead's name for a specimen from Costa Rica, while Bradley, unable to find Ashmead's type, followed Haupt while expressing doubt that he had correctly identified Ashmead's species. However, there is a specimen in the U. S. National Museum labeled as *Aulocostethus bifasciatus* Ashmead in Ashmead's handwriting and marked as type of that species. But to add to the confusion this specimen bears the locality Bahia, Brazil, not "Peru" as it should. Now Costa Rica (Haupt's specimen) is actually closer to Peru than is Bahia, Brazil, but I find it hard to reason away the identification label in Ashmead's handwriting. Specimens of this genus are so rare that one is unlikely to make an error in labeling; in fact I doubt if Ashmead

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ever saw any other specimens of the genus. On the other hand, Ashmead was a sufficiently careless person so that it is quite believable that he may have jotted down "Peru" when he meant "Brazil". At any rate, I accept this as the type of *bifasciatus* and have presented a description of it below, along with a new name for Haupt's specimen from Costa Rica.

Still further problems remain. Was Ashmead correct in placing *maximiliani* in the synonymy of Cresson's *aztecus*, or was Bradley correct in resurrecting it? If *Epipompilus* and *Aulocostethus* are synonyms, what is the status of Banks' *Epicostethus*, said to share some of the characters of both genera? What is the correct generic placement of *Epipompilus insularis* Kohl, from New Zealand? Finally, what is the male sex of *Epipompilus*?

On the following pages I have presented a brief synopsis of *Epipompilus* in which answers to all of these questions are proposed. I do not mean to imply that all problems in the genus are solved: my synopsis is based on a mere 18 specimens of these exceedingly rare insects. There are doubtless undiscovered species, and the males of most of the species have yet to be found. But at least I hope that I have supplied a sounder framework for future studies than has previously been available.

Genus *Epipompilus* Kohl

Epipompilus Kohl, 1884, Verh. K. K. Zool.-Bot. Gesell. Wien, 34: 57. [Type species: *Epipompilus maximiliani* Kohl, 1884 (= *aztecus* Cresson 1869) (designated by Ashmead, 1900)].

Aulocostethus Ashmead, 1902, Canad. Ent., 34: 132. [Type species: *Aulocostethus bifasciatus* Ashmead, 1902 (monobasic and original designation)]. New synonymy.

Epicostethus Banks, 1947, Bull. Mus. Comp. Zool., 99: 445. [Type species: *Epicostethus williamsi* Banks, 1947 (monobasic)]. New synonymy.

Generic characters. — Maxillary palpi unusually elongate, antepenultimate segment the longest and distinctly longer than third antennal segment; labial palpi with the penultimate segment broadly ovate, the ultimate segment attached to one side of it; mandibles stout, rather smooth, with a few setae but without a lamina on the inferior margin which subtends a fimbriate groove, inner margin with a single strong tooth well back from apex; labrum partially exerted, broad and short, apical margin of clypeus broadly truncate or arcuately concave; flagellum with rather coarse, bristling, semi-erect pubescence, particularly on the inner side of the basal segments of the female and on the outer side of the entire flagellum of the male; head broader than high, front with distinct small punctures; eyes densely covered with short hairs (reduced and scarcely noticeable in some females and in

the known males); front rather swollen above, between the antennal bases abruptly declivous to the much lower plane of the area frontalis and clypeus. Pronotum short or fairly long, sides of disc rather prominent, streptaulus absent or ill-defined; mesoscutellum and metanotum prominent medially, latter with distinct lateral foveae; postnotum of variable length, front and hind margins subparallel; propodeum with smooth contours, slope low and even, almost flat behind; front femora of female slightly to quite noticeably incrassate; front tibiae and tarsi without spines, middle and hind tibiae with or without scattered short spines; segments of front tarsus of female unusually short; claws slender, with a strong, subapical tooth which is nearly parallel to the apical tooth; ultimate tarsal segments without spines beneath, pulvillar pads small but giving rise to some strong setulae. Hind wing with anal lobe small, about .3-.5 as long as submedian cell, anal vein extending very slightly or not at all beyond junction of transverse median vein, latter vein leaving it at an angle, oblique, meeting media much before origin of cubitus; fore wing with venation extending relatively close to outer wing margin, marginal cell acute, removed from wing-tip much less than its own length; three submarginal cells present, second and third receiving recurrent veins near middle, third much wider at apex than at base. Abdomen fusiform, in the female somewhat depressed apically, apical sternite rather flat, even obscurely grooved medially; male with or without conspicuous brushes of hair on sternites four and five, subgenital plate of remarkable structure, forming a very slender, hairy process apically, its basal plate (morphological sternite 8) unusually broad; male genitalia with short, simple parameres, volsellae short-setose, not expanded apically, basal hooklets double, aedoeagus small and of simple structure.

Remarks. — *Epipompilus* possesses a remarkable array of unusual structural features; if one follows the practice of Bradley and Arnold of splitting the Pompilinae into numerous tribes, there can be no question that the genus deserves a tribe of its own. Personally, I am much impressed with certain similarities with *Aporus* and related genera: the pronotum is similar, the front legs of the female somewhat incrassate, and the head shape and hairiness of the eyes suggestive of certain Aporini. The male genitalia suggests *Allaporus*, as does the venation of the hind wing. Any division of the Pompilinae into tribes can be no more than tentative until such time as the classification of the family from a world point of view is more satisfactorily worked out. In the meantime, I prefer to place *Epipompilus* in the Aporini.

As here construed, the genus *Epipompilus* is strictly Neotropical

is distribution. However, Kohl included a New Zealand species, *insularis* Kohl, in his conception of the genus, and various workers since have listed *Epipompilus* from the Australian region. I have studied two females determined by Banks as *insularis* and agreeing well with Kohl's description of this species. There can be no question that this species is closely related to the several Neotropical species of *Epipompilus*. Indeed, it agrees well with the above diagnosis except in the following characters (the males are unknown): maxillary palpi not greatly lengthened, about as usual in the family; labial palpi unmodified; eyes with only minute, scarcely noticeable hairs; transverse median vein of hind wing reaching media a short distance before origin of cubitus. The generic name *Epipompiloides* is here proposed for *insularis* Kohl, 1884. I know of no other species assignable to this genus, but the pompilid fauna of the Australian region is, of course, very inadequately known. This genus is related to *Epipompilus* and should be placed in the Aporini next to that genus.

Key to known species of the genus *Epipompilus*

Males

- Antennae moderately long, crenulate in profile; claws of front tarsus nearly alike; thorax in considerable part rufous; parameres of genitalia with extremely long hairs, abdominal venter with hair-tufts 9. *innubus* n. sp.
- Antennae very short, with coarse, dark pubescence but only very weakly crenulate in profile; outer claws of front tarsus much more strongly curved than inner claws; thorax black; parameres and abdominal venter with only short hairs 6. *excelsus* (Bradley)

Females

1. Wings wholly fuliginous; abdomen wholly rufous; pronotum patterned with red and black (Florida and Bahamas) 1. *pulcherrimus* (Evans)
- Wings hyaline, fore wing with two prominent brownish bands; abdomen not wholly rufous, more or less patterned with black, rufous, and/or whitish, pronotum all black or all rufous 2
2. Abdomen black, with a pattern of whitish spots 3
- Abdomen in part rufous, with or without whitish spots 5
3. Body wholly black except for a pair of whitish spots on second abdominal tergite; hind tibiae with a few short spines; pronotum very short, subangulate behind (Ecuador) 2. *williamsi* (Banks)
- Thorax largely rufous; hind tibiae without spines 4

4. Abdomen with whitish markings on tergites 2 and 5, none on sternites; posterior lobes of pronotum rufous (Mexico) 3. *aztecus* (Cresson)
Abdomen with whitish markings on tergites 2, 3, 4, and 5, also on sternites 2 and 3; posterior lobes of pronotum whitish (Brazil) 4. *bifasciatus* (Ashmead)
5. Size larger (8-11 mm.); abdomen with whitish markings on tergite five, this tergite otherwise black (Brazil) 6
Size small (6-7 mm.); abdomen not marked with whitish on tergite five, tergites five and six brownish-ferruginous (Central America) 7
6. Antennae black; propodeum black except for limited yellowish markings; hind tibiae unarmed 5. *haupti* (Arlé)
Antennae rufous except darker apically; propodeum wholly rufo-castaneous; hind tibiae weakly spinose 6. *excelsus* (Bradley)
7. Second abdominal segment with a pair of whitish spots; hind tibiae unarmed (Panama) 7. *delicatus* Turner
Second abdominal tergite without whitish spots; hind tibiae with scattered, short spines (Costa Rica) 8. *insolitus* n. name

1. *Epipompilus pulcherrimus* (Evans) new combination

Aulocostethus pulcherrimus Evans, 1955, Ent. News, 66: 150. [Type: ♀, Everglades Nat. Park, Florida, 30 December 1953 (U. S. Nat. Mus.)].

Remarks.— Since describing this species from the unique type, I have seen one additional specimen, from Mangrove Cay, Andros Island, May-June 1917 (W. M. Mann) [Amer. Mus. Nat. Hist.]. This specimen agrees well with the type except that it is smaller (about 5 mm. long, fore wing 4.3 mm.) and the pronotum has a broad median streak of pale rufous as well as being rufous anteriorly and posteriorly. This species is colored quite differently from any other. The pronotum is much shorter than in *aztecus*, nearly as short as in *williamsi*. The claws are the same as in *aztecus* and other species of the genus, my statement to the contrary in the original description being in error.

2. *Epipompilus williamsi* (Banks) new combination

Epicostethus williamsi Banks, 1947, Bull. Mus. Comp. Zool., 99: 446. [Type: ♀. Baños, Oriente, Ecuador, 6000 feet, 30 Oct. (Mus. Comp. Zool.)].

Remarks.— Bank's description is detailed and there is no reason to repeat it here. The pronotum is short and subangulate behind, the front femora are barely incrassate, and the hind tibiae have several spines. The first two of these characters are shared (more or less)

with *pulcherrimus* and *delicatus*, the third with *insolitus*, *excelsus*, and *innubus*. Thus the species is not as unique as Banks supposed, and his generic name must be added to the synonymy of *Epipompilus*. I have seen no specimens of this species other than Banks' type.

3. *Epipompilus aztecus* (Cresson) new combination

Ferreola azteca Cresson, 1869, Proc. Boston Soc. Nat. Hist., 12: 376 [Type: ♀, Veracruz, Mexico (Acad. Nat. Sci. Phila.)].

Epipompilus maximilian Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146 34: 57 [Type: ♀, Cuernavaca, Mexico, 1871 (Bilimek) (Vienna Mus.)].

(Placed in synonymy with *azteca* by Ashmead, 1902). — Haupt, 1930, Mitt. Zool. Mus., Berlin, 16: 762.

Epipompilus maximilian Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146 (Misspelling of *maximiliani* Kohl).

Aulocostethus aztecus Bradley, 1944, *ibid.*, p. 142.

Remarks. — Bradley has recently provided a detailed description of this species, drawn from Cresson's type of *azteca*. He states that this specimen "does not at all agree with Kohl's description of *maximiliani*". Since I found myself unable to agree with this statement, I asked to borrow the type of *maximiliani* from the Vienna Museum for comparison. At first the type could not be located, but later Dr. R. M. Bohart visited the museum and at my request searched for and found it; Dr. Max Fischer then sent it to me by mail, and I took it to Philadelphia and compared it directly with the type of *azteca*. I am very much indebted to Drs. Bohart and Fischer for their assistance with this problem.

The two type specimens differ considerably in size, that of *aztecus* being much larger, 13.5 mm. long, fore wing 10 mm.; *maximiliani* measures 7.5 mm. long, fore wing 6 mm. The front femora are slightly more incrassate in *aztecus* ($2.6 \times$ as long as maximum width as compared to $2.75 \times$ in *maximiliani*). The whitish maculations are exactly the same in the two specimens, but they type of *aztecus* has the posterior third of the propodeum blackish and the middle and hind legs blackish except for the white spurs and white streaks on the hind tibiae; in the type of *maximiliani* the propodeum is wholly rufous, the middle and hind coxae rufous above, the middle and hind femora rufous, and the tibiae partially suffused with rufous. Besides these two specimens, I have seen one other, a female from Cuernavaca, taken by my wife inside the window of a house on March 24, 1959. This specimen is about the same size as the type of *aztecus*, from Veracruz, and the front femora are incrassate to the same degree. However, the propodeum is wholly rufous (as in the type of *maximiliani*, also from Cuernavaca) and the leg coloration intermediate between that of the two types (middle femora rufous, hind femora

black, middle tibiae slightly suffused with rufous but hind tibiae black and whitish, middle and hind coxae with a small amount of rufous above). There is no question at all in my mind that these three specimens are conspecific.

4. *Epipompilus bifasciatus* (Ashmead) new combination

Aulocostethus bifasciatus Ashmead, 1902, *Canad. Ent.*, 34: 132 [Type: ♀, Bahia, Brazil, 19 March 1883 (but stated by Ashmead to be "Peru") (U. S. Nat. Mus., no. 58858)]. (Not *Aulocostethus bifasciatus* of Haupt, 1930; see no. 8, *insolitus* n. name).

Description of type female. — Length 11 mm., fore wing 8.7 mm. Head black; inner orbits narrowly pale yellow up to emargination of eyes; antennae wholly brownish, darker apically; apical half of clypeus and labrum pale yellowish; mandibles dull rufous; palpi light reddish-brown. Thorax rufo-castaneous, except mesonotum with black streaks over wing bases, and the following pale yellow: posterior lobes of pronotum, extreme lower posterior corner of mesopleurum, posterior rim of propodeum (interrupted medially), and apical posterior parts of middle and hind coxae; legs otherwise reddish like thorax, middle and hind tibiae weakly infuscated, spurs all whitish. Abdomen black, spotted with pale yellow (almost white) as follows: two large lateral spots on tergite two, two much smaller spots on tergite three, two spots on tergite four slightly larger than those on three, two large spots on tergite five broadly connected by a basal band; also sternites two and three with small lateral spots. Wings bifasciate, hyaline with a strong band over the basal and transverse median veins and a broader band filling the marginal cell and extending to the posterior wing margin. Body and legs clothed with short, white hair; eyes short-haired.

Clypeus broadly truncate; labrum small, exserted. First four antennal segments in a ratio of about 13:5:11:12, segment three .55 × upper interocular line. Head 1.2 × as broad as high; middle interocular line .57 × width of head; upper interocular line .8 × lower interocular line. Ocelli in a broad, flat triangle, front angle greater than a right angle; postocellar line much greater than ocello-ocular line. Pronotum of moderate length, posterior margin subangulate. Propodeum with smooth contours except posterior slope finely transversely striolate and with rather long pubescence; median line not impressed. Posterior tibiae without spines. Fore wing with basal and transverse median veins interstitial; radial vein somewhat angulate at junction of second intercubital vein, marginal cell removed from wing-tip by about .7 its own length.

Remarks. — This is a rather typical member of the genus, in fact

rather close to *aztecus*. As mentioned in the introduction, Ashmead provided no real description of the species, and Bradley did not see the type and therefore followed Haupt, who had misidentified the species. Presumably Ashmead was merely in error when he gave "Peru" as the type locality of the species, as the type is labeled in Ashmead's handwriting.

5. *Epipompilus haupti* (Arlé) new combination

Aulocostethus haupti Arlé, 1936, Festschr. für Embrik Strand, 1: 514 [Type: ♀, Serra do Realengo, Rio de Janeiro, Brazil, 7 Oct. 1934].—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 144. —Banks, 1947, Bull. Mus. Comp. Zool., 99: 445.

Remarks.—Bradley has provided a translation of the description of this species. I have studied the specimen mentioned by Banks (Campinas, Brazil). The legs of this specimen are more extensively rufous than described for the type, but there is agreement in most other details; the eyes of this species are more weakly hairy than is usual in the genus.

6. *Epipompilus excelsus* (Bradley) new combination

Figs. 3 and 4

Aulocostethus excelsus Bradley, 1944, Trans. Amer. Ent. Soc., 70: 143 [Type: ♀, Nova Teutonia, Santa Catarina, Brazil, 25 January 1939 (Mus. Comp. Zool.)]. —Wahis, 1957, Bull. Ann. Soc. R. Ent. Belg., 93: 47-49 (Remarks on color variation).

Remarks.—I have seen several additional females of this species from the type locality, as well as a female from Rio de Janeiro, October 1938 (R. C. Shannon) [U. S. Nat. Mus.]. The type, as well as all the other specimens I have seen, has a pair of connected whitish spots on the fifth tergite, Bradley's description being in error on this point. Wahis has discussed this matter and also pointed out that some specimens have whitish markings on the second and sixth tergites.

A male *Epipompilus* in the Canadian National Collections, Ottawa, is almost certainly that of *excelsus*, even though it is colored very differently from the female. Like the type female *excelsus*, it was taken at Nova Teutonia, Brazil, by Fritz Plaumann, in this case on 19 June 1946. The spinose hind tibiae, as well as the locality, suggest that this male belongs here rather than with *haupti* or *bifasciatus*.

Description of male.—Length 5.8 mm., fore wing 4.8 mm. Body wholly shining black, with a weak bluish luster; face with a pair of small whitish spots beside and below the antennal sockets, next to the eyes; apical two thirds of mandibles whitish, the teeth rufous; palpi

light brown; antennae dark brown; tegulae dark brown; front and middle legs with the coxae black, suffused with brown apically, remainder of these legs brown, middle femora with a tinge of rufous, front tibiae yellowish-brown; hind legs wholly black except tibia with a sub-basal whitish spot which nearly encircles them; fore wing weakly tinged with brownish, especially along the basal vein and on the apical third, setulae dark, veins and stigma brown.

Maxillary palpi with segments 3-6 in a ratio of about 15:19:15:13. Mandibles with a single large tooth well back from apex. Clypeus arcuately emarginate apically, exposing the small labrum. Eyes strongly convergent below, lower interocular line about $.75 \times$ upper interocular line; middle interocular line $.59 \times$ width of head; head about $1.15 \times$ as wide as high; ocelli in a broad triangle, postocellar line $1.3 \times$ ocello-ocular line. Front with distinct punctures which are separated by about their own diameters. Eyes with minute hairs except near the tops, where they are somewhat longer. First four antennal segments in a ratio of about 15:5:8:9, segment three about $1.6 \times$ as long as thick; flagellum short, very weakly crenulate in profile, with coarse, dark pubescence which is especially long and suberect on the upper and outer sides of the basal segments.

Pronotum of moderate length, its posterior margin subangulate. Mesonotum wholly and uniformly covered with small punctures. Postnotum nearly as long as metanotum, polished, with a median impression and some weak basal striations. Propodeum with the slope low and even; median line not impressed. Femora slender; middle tibiae with a few spines, hind tibiae with many fairly strong spines above; all tarsi weakly spinose; longer spur of hind tibiae nearly as long as basitarsus. Claws with the inner tooth of all claws strong, sloping so that the claws appear bifid; outer claws of front tarsus much more strongly curved than inner claws. Fore wing with basal vein arising a very short distance beyond transverse median vein, basal part of basal vein distinctly arched; marginal cell large, acute apically, radial vein distinctly angulate at its junction with the second transverse cubital vein.

Abdomen fusiform, covered with short setae but without distinct ventral hair-brushes. Subgenital plate (fig. 3) consisting of a long, hairy apical process arising from a basal section which also bears some long hairs. Genitalia (fig. 4) with the parameres weakly setose; volsellae simple, weakly setose; basal hooklets large, double; parapenial lobes somewhat knobbed apically, very slightly exceeding the volsellae.

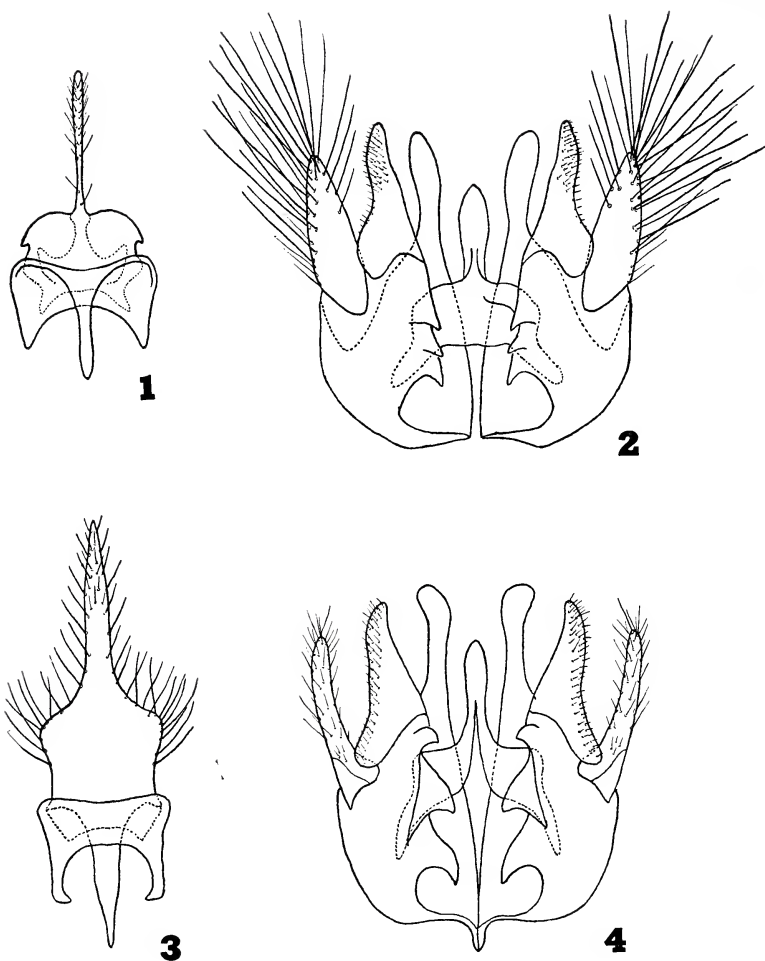


FIG. 1 Subgenital plate of *Epipompilus innubus* new species. FIG. 2 Genitalia of *E. innubus*. FIG. 3 Subgenital plate of *E. excelsus* (Bradley). FIG. 4 Genitalia of *E. excelsus*. All figures show the ventral aspect.

7. *Epipompilus delicatus* Turner

Epipompilus delicatus Turner, 1917. Ann. Mag. Nat. Hist., (8) 20: 359 [Type: ♀, Bugaba, Panama (Champion) (British Mus.)].—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 146.

Remarks.—I have not seen the type of this species, nor had Bradley. It is a small species, comparable in size to *pulcherrimus* and *insolitus*. It is reported to have a short pronotum and unarmed hind tibiae, as well as a color pattern distinct from that of other species.

8. *Epipompilus insolitus* new name

Aulocostethus bifasciatus Haupt, 1930. Mitt. Zool. Mus. Berlin, 16: 763. — Bradley, 1944, Trans. Amer. Ent. Soc., 70: 145 (*Nec* Ashmead, 1902, Canad. Ent., 34: 132; misidentification).

Type.—♀, Turrialba, Costa Rica (Coll. H. Haupt, Halle/Saale, Germany).

Description (from Haupt, 1930).—Length 7 mm. Yellowish-brown, the following black: head, apical half of antennae, tergites 1, 3, and 4, apex of hind femora, and outer base of hind tibia. Fore wing with two dark brown bands. Hind tibiae with a whitish area behind the black base, tips of front and hind coxae also whitish. Whole body with short, thick whitish hair; eyes and wings hairy.

Wings (Haupt's fig. 64) yellowish-hyaline, a brown transverse band before the middle and one before the apex. Fore wing with three cubital cells, the second somewhat pentagonal, the third trapezoidal, the latter removed from tip by its own length. Radial cell longer than second and third cubital cells together, also somewhat higher than these. Pterostigma cell-like, translucent, somewhat attenuate. Lower section of basal vein about twice as long as upper and weakly arched; transverse median vein interstitial. Hind wing with transverse median vein short, oblique, reaching media more than its own length before origin of cubitus.

Head thick, flattened and weakly concave immediately behind the eyes, temples barely developed. Ocelli large, forming a weakly acute angle in front, postocellar and ocello-ocular lines equal. Front strongly swollen, eyes thick, their inner margins subparallel, the eyes together about equal to width of front. Antennae filiform, relatively thick, third segment somewhat shorter than scape. Clypeus short, trapezoidal, its entire anterior margin weakly arcuately concave. Segments of maxillary palpi very long, third segment about ten times as long as thick (Haupt's fig. 65). Pronotum short, hind margin obtusely angled, sides parallel, with distinct longitudinal swellings. Mesoscutum twice as long as pronotum medially; scutellum and metanotum

elevated. Postnotum distinct, half as long as metanotum, lightly impressed medially. Propodeum somewhat longer than broad, narrowed and less steeply sloping behind, without discernible sculpturing except indication of a median groove. Fore tarsi without a comb, second to fourth segments short, the second as long as broad, the following shorter. Hind tibiae with scattered, short spines. Claws slender, with a sharp tooth before the apex, also with a distinct fan of bristles (Haupt's fig. 84J); claw-comb with a very short plate, its barbules sparse, surpassing the pulvillus.

Remarks.—I have not seen this species, but since it has been described and figured by Haupt in considerable detail, it seems desirable to provide a name for it.

9. ***Epipompilus innubus*** new species

Figs. 1 and 2

Type.—♂, Cucharas, 750 m., Valley of Huallaga, Dpt. Huanuco, Peru, June 1954 (F. Woytkowski) [Coll. H. K. Townes].

Description.—Length 6 mm., fore wing 5.7 mm. Head black except as follows: inner orbits pale yellow up to middle of eyes; clypeus, labrum, and mandibles pale yellow, almost white; palpi very light brown; antennal sockets connected by a light yellow band; first five antennal segments yellowish-brown below, dark brown above, rest of antenna nearly black. Thorax rufo-ferruginous except shining blue-black as follows: propleura and extreme anterior parts of pronotum, mesosternum and anterior half of mesopleurum, sides of metanotum, all of postnotum, all of metapleurum except upper anterior margin, all of propodeum except for sides of posterior rim, which are pale yellow. Coxae blackish except middle and hind coxae tipped with white; middle and hind trochanters blackish; front and middle legs otherwise light reddish-brown, hind legs nearly black except tarsi paler and tibiae with a white basal annulus; tibial spurs whitish except middle and hind spurs suffused with black basally. Abdomen shining blue-black except apical tergite ivory-white. Wings hyaline, with dark setulae, veins and stigma brown, fore wing weakly clouded in and about third submarginal cell.

Maxillary palpi very long, segments in a ratio of about 2:4:8:10:8:7. Mandibles rather smooth, with a few setae, inner margin with a strong tooth well back from apex. Labrum broad and short, truncate, exerted well beyond truncate apical margin of clypeus, latter about twice as broad as high. Front prominent above antennal orbits, narrow, middle interocular line .56 times width of head; head nearly 1.2 × as wide as high; ocelli in a broad, flat tri-

angle, postocellar line twice the ocello-ocular line. Front with distinct punctures which are separated by less than their own diameters. Eyes with very short, barely noticeable hairs. First four antennal segments in a ratio of about 15:5:13:12, segment three about twice as long as thick; each flagellar segment, but more particularly the middle ones, with a distinct swelling below and toward the base, giving the antennae a somewhat crenulate profile below.

Pronotum very short, its posterior margin subangulate. Mesonotum with distinct small punctures like the front; postnotum smooth, transversely striate, about half as long as metanotum. Propodeum with even contours, median line weakly impressed, surface of declivity very finely transversely striolate. Femora not notably swollen; middle and hind tibiae with short spines scattered amongst the pubescence; longer spur of hind tibia nearly as long as basitarsus; claws of front and middle legs strongly dentate, those of hind legs obscurely dentate. Fore wing with basal vein arising well beyond junction of transverse median vein, basal part of basal vein strongly arched; marginal cell large, acute, removed from wing-tip by only about half its length; other features of wing about as in other species of the genus.

Abdomen fusiform, covered with short setae; sternites four and five each with a transverse brush of longer setae, longer on the sides than medially, the setae curved at their tips; genitalia also giving rise to some long setae which protrude from sides of subgenital plate. Subgenital plate (fig. 1) of unusual form, consisting of a long, slender, hairy process arising from complex basal plates (the modified ultimate and penultimate sternites). Genitalia (fig. 2) with parameres short, bearing some very strong setae; volsellae weakly setose, narrow in ventral view but mesal surface wide and concave; basal hooklets double, unusually well separated; parapenial lobes slightly shorter than volsellae; aedoeagus very small.

Remarks. — The spinose hind tibiae and short pronotum suggest *williamsi* as the possible female of this species, and the type localities of these two are not too far distant (Ecuador and Central Peru). However, the difference in coloration is great, and it seems to me best to consider the two distinct for the present.

THE REDISCOVERY AND PROBABLE
PHYLOGENETIC POSITION OF
PSILOPSOCUS (PSOCOPTERA)

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The genus *Psilopsocus* has posed a puzzle to students of the Psocoptera since the time of its discovery. The original description by Enderlein (1903:305) was based on a single specimen. Although adequate for identification, this description does not permit the genus to be placed beyond suborder in recent classifications. Enderlein placed *Psilopsocus* in the Mesopsocidae, but gave no reasons for this. Roesler (1944), apparently without re-examining the type, erected a new family for this genus and placed it in the group Epipsocetae on the basis of similarity of the lacinia in the Epipsocidae and Psilopsocidae.

It is the purpose of this paper to describe a new species of *Psilopsocus* from the Philippine Islands, to add to the knowledge of the morphology of the genus, and to re-interpret its phylogenetic position.

Genus *Psilopsocus* Enderlein, 1903.

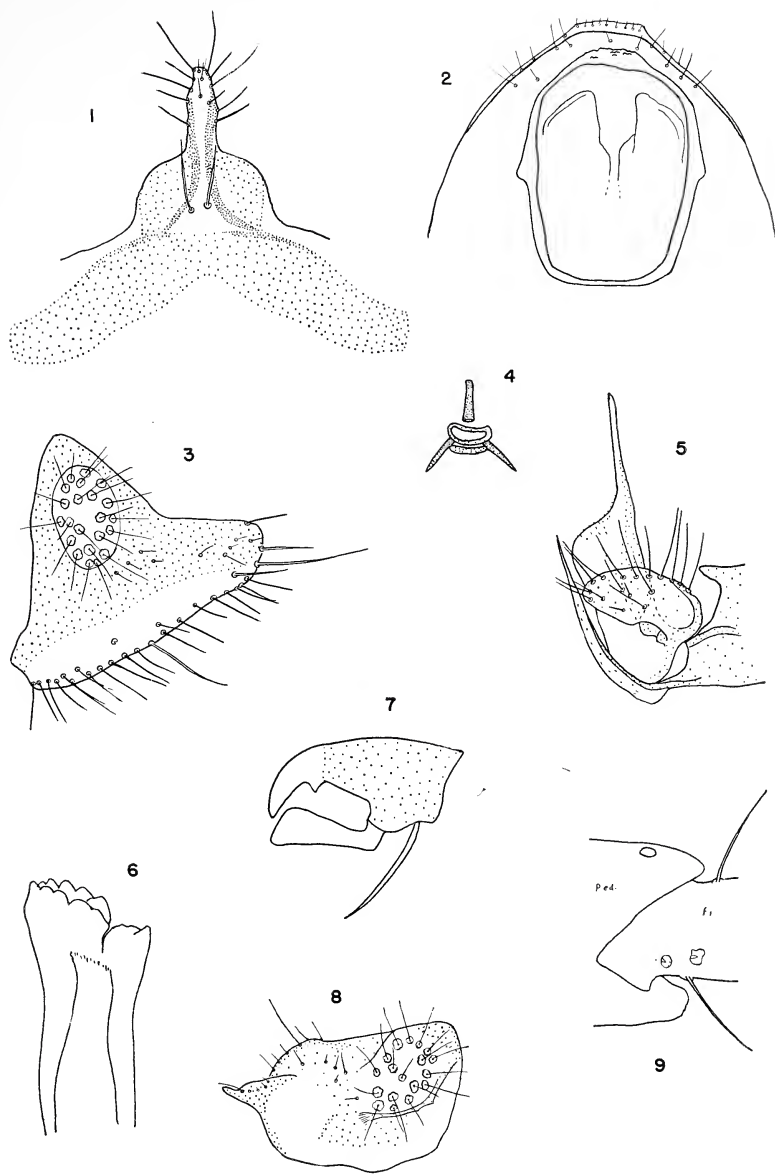
In addition to the characters included by Enderlein in the original description, the following characters are probably important in delimiting this genus:

1. Male phallic sclerotizations in the form of a simple frame with no indication of external parameres (fig. 2.).
2. Ovipositor valvulae complete, i.e. three pairs.
3. Female subgenital plate with a slender central process (fig. 1.).
4. Female paraproct with a decided elongation of the posterior margin (fig. 3.).
5. Male paraproct with a pointed apical process on its posterior margin (fig. 8.).
6. Labrum not of the *Epipsocus* type, lacking a pair of diagonal strap-like sclerites.

The character mentioned by Enderlein of lack of junction of the

EXPLANATION OF PLATE 5

Psilopsocus nebulosus n. sp. Fig. 1, ♀, subgenital plate. Fig. 2, ♂, hypandrium and phallic frame. Fig. 3, ♀, left paraproct. Fig. 4, ♀, sclerites of 9th abdominal sternite (dorsal view). Fig. 5, ♀, ovipositor valvulae. Fig. 6, ♂, lacinial tip. Fig. 7, ♂, tarsal claw. Fig. 8, ♂, right paraproct. Fig. 9, ♂, tip of pedicel (Ped.) and base of first flagellar segment (fl).



MOCKFORD — PSILOPSOCUS

bases of Radius and Media + Cubitus in the hindwing is not found in the species described below, although a fold in the wing membrane running from the Radius just above this junction, to the wing base produces the appearance of two closely parallel veins.

In the species described below, the coxal organ is well developed, with both rasp and tympanum. The rasp is composed of tiny indentations with raised edges.

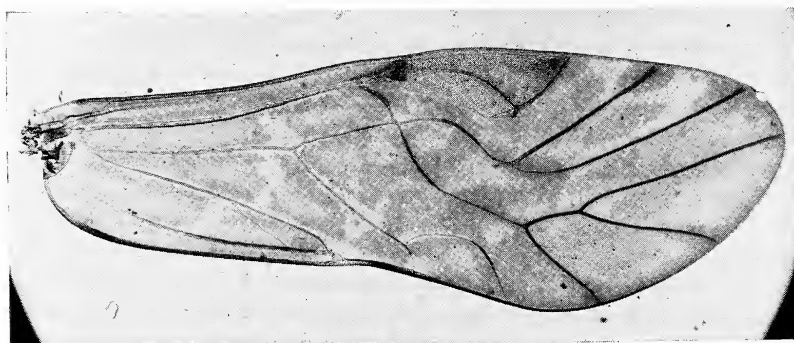
***Psilopsocus nebulosus*, new species**

Plate 5 and Text Fig. 1

Diagnosis: differs from the generotype, *P. nigricornis* End., possibly in number of teeth on lacinial tip (6 indicated for *nigricornis*, 11 in *nebulosus*), number of ctenidia on basal segment of hind tarsus (15 in *nigricornis*, 16 to 19 in *nebulosus*), shape of the pterostigma (less deep in *nebulosus*), and details of the forewing markings (text figure 1), colorless areas being more numerous in *nebulosus*, but there being no colorless areas bordering the wing apex in this species.

Holotype ♂. Measurements (see table I.).

Morphology: IO/D (distance between eyes divided by greatest dorsal diameter of eye, method of Badonnel) = 0.78, PO (lateral diameter of eye from above divided by greatest dorsal diameter of eye) = 0.94. Apex of lacinia (fig. 6.) broad, with a distinct lateral and median cusp, the lateral broadest and bearing 10 denticles. Coeloconic sensilla of first flagellar segment two in number, both situated at the extreme base of the segment (fig. 9.). Distinct tarsal ctenidia present only on posterior tarsi, with a row of 17 on T1 and one each on T2 and T3 (T1 = basal tarsal segment). Hypandrium weakly sclerotized, its margin rounded except slightly flattened at the apex; this flattened apex slightly more heavily sclerotized than



Text figure 1. *Psilopsocus nebulosus* n. sp., ♂, photomicrograph of right forewing.

the rest of the hypandrium and bearing a row of tiny cilia (fig. 2.). Phallic frame (fig. 2.) a simple ring, slightly oblong, rather uniform in width except somewhat thickened apically and for a short distance along each side. Within the frame are a pair of membranous lobes. Paraproct (fig. 8.) with the usual field of trichobothria extending obliquely downward from its antero-dorsal angle. Posterior margin of the paraproct extended as a lobe tipped with a pointed process.

Color (in alcohol): compound eyes black. General body color dull ivory marked with medium to pale brown. Labrum, antennae, ocellar interval, and terminal two segments of maxillary palpi medium brown. Clypeal striations, cloudy spots around compound eyes and antennal bases, and a band bordering epicranial suture pale brown. Thorax irregularly mottled with large pale brown areas including most of the pleura and large areas of the tergal lobes. Brown areas of mesothoracic tergal lobes darkest at their borders, pale in their centers. Legs dull ivory except medium brown on each coxa, distal end of each femur, distal end of each tibia, and all of each tarsus. Forewing hyaline, marked with extensive pale brown cloudy bands and spots as in text figure 1. Abdomen ringed with irregular pale brown cloudy bands. Terminal segments medium brown.

Allotype ♀. Measurements (see table I).

Morphology: IO/D = 1.56, PO = 0.72. Tarsal ctenidia present only on posterior tarsi with a row of 18 on T₁ and one each on T₂ and T₃. Subgenital plate (fig. 1.) with basal pigmented area in the form of two widely diverging arms. Median process of subgenital plate broad basally, abruptly narrowing to a slender tongue about half-way toward its tip; the broad basal portion bearing two large setae and the slender apical portion bearing many setae of various sizes. Sclerites of the 9th abdominal sternite (fig. 4.) in the form

Table I. Length (in mm.) of various characters of
Psilopsocus nebulosus

Character	♂	♂	♂	♂	♀
Entire body	2.87	2.82	2.61	3.03	3.67
Forewing	4.44	4.40	4.44	4.59	4.65
Hind tibia	1.39	1.43	1.43	1.57	1.43
Hind tarsus, T ₁ *	0.465	0.440	0.476	0.476	0.405
Hind tarsus, T ₂	0.071	0.071	0.059	0.071	0.059
Hind tarsus, T ₃	0.119	0.119	0.131	0.131	0.119

* First posterior tarsal segment.

of a transverse ring with three straps radiating from it and a transverse strap basal to it. Ovipositor valvulae (fig. 5.) with first valvula slender; second valvula broad basally, terminating in a long, slender process; third valvula a broad flap bearing many setae. Paraproct (fig. 3.) with field of trichobothria in its antero-dorsal angle. Posterior margin of paraproct markedly protruding; ventral and posterior margins bearing many setae.

Variation: aside from variations noted in the descriptions and measurements (table I), four male paratypes have wing and body markings somewhat paler than the holotype male, but this may be due to tenerality. IO/D ratios for three male paratypes are 0.69, 0.70, and 0.70; PO ratios for these are 0.88, 0.85, and 0.91; numbers of ctenidia on posterior basal tarsal segment are 16, 19, and 18.

Nymph: one nymph taken with adults of *P. nebulosus* is with little doubt this species. The association is made on the basis of similarity in size, color, (except the distal two-thirds of the abdomen is dark brown in the nymph), and general body shape, also on the structure of the lacinia and tarsal claws. The lacinia is broad apically with several indistinct denticles on the outer cusp. The tarsal claw bears a preapical tooth and a pulvillus of medium width bent at a decided angle near its base, as in the adult (fig. 7.).

Type locality: Philippine Islands: Mindanao, east slope of Mt. McKinley, Davao Province, August and September, 1946, in mossy forest, elevation 6400 feet, H. Hoogstraal collector; holotype ♂, allotype ♀, 4 ♂ paratypes and one nymph, all in collection of Chicago Natural History Museum.

Discussion: *Psilopsocus* is apparently very close to the Myopsocidae. The following points of similarity were noted:

1. Tarsal structure
 - a. Number of segments same.
 - b. Distribution of ctenidia same.
 - c. Both with preapical tooth on tarsal claw.
 - d. Pulvillus in both of medium width with a decided bend near its point of attachment.
2. Lacinial structure. The lacinial tip of *Lichenomima sparsa* has a broad lateral cusp bearing 13 stubby denticles, and a short median cusp, hence it shows marked similarity to the lacinial tip of *Psilopsocus*.
3. Male genitalia.
 - a. Hypandrial margin. The rounded hypandrial margin of *Psilopsocus* is similar to that of several species of *Rhaptoneura*, *Phlotodes*, and *Lichenomima*.

b. Phallic frame. The simple, rounded phallic frame of *Psilopsocus* bearing a pair of lateral thickenings and enclosing a pair of membranous lobes is reminiscent of this structure in *Lichenomima pauliani* Bad. (Badonnel, 1955, fig. 529) and *Rhaptoneura eatoni* McL. (Badonnel, 1943, fig. 143). It differs little from this structure in *Lichenomima maxima* Sm. (Smithers, 1957, fig. 6).

c. Paraproct. The paraproct of *Psilopsocus* is similar to those of most Myopsocids in bearing a pointed process on its posterior margin. Although several species of Myopsocids have two such processes, there is only one in *Phlotodes angolensis* Bad. (Badonnel, 1955, fig. 514). The male paraproct of the latter species resembles that of *Psilopsocus* in several other respects, including shape of the field of trichobothria and presence of a roughened area antero-dorsad of this field.

4. Female genitalia.

a. Subgenital plate. The subgenital plate of *Psilopsocus* is similar in structure to that of *Rhaptoneura*. The resemblance is especially marked in the case of *R. africana* Bad. (Badonnel, 1955, fig. 508). In both forms the pigmented basal area consists of a pair of widely diverging arms; the central process is broad basally, narrowing abruptly to a slender tongue which bears setae on or near its apex.

b. Ovipositor valvulae. Both *Psilopsocus* and the Myopsocids have three pairs of ovipositor valvulae. The second valvula terminates as a long, slender process in both groups, although this is generally much longer in the Myopsocidae than in *Psilopsocus*. The third valvula is a simple flap bearing many setae in both groups.

c. Sclerites of the ninth abdominal sternite. These sclerites in several *Lichenomima* species (Badonnel, 1955, figs. 522-525; Smithers, 1957, fig. 11) are composed of three main sclerotized areas, and are thus similar in appearance to the same group of sclerites in *Psilopsocus nebulosus* with their three radiating sclerotized straps.

d. Paraproct. The female paraproct is similar in shape, ciliation, and position of the field of trichobothria in the two groups.

The differences between the Myopsocidae and the Psilopsocidae are not great. The only ones which I have found are (1) presence in Myopsocidae of a connection between areola postica and medial stem in the forewing and absence of this in Psilopsocidae, (2) presence in Psilopsocidae of a spur vein from the pterostigma and its absence in Myopsocidae, and (3) much more complex markings of the forewing in Myopsocidae than in Psilopsocidae, with characteristic alternating dark and light areas on veins in the former group.

Pearman (1936) has designated the families Myopsocidae, Psocidae, and Thyrsophoridae as constituting the group Psocetae. To this group should be added the Psilopsocidae. It appears that this group represents an ancient phylogenetic line within the suborder Psocomorpha, in which the most primitive forms share a broad, multidenticulate lacinial tip with the Group Epipsocetae. It seems likely that this type of lacinial tip, found also in the Amphientomidae (Suborder Troctomorpha) was present in the earliest forms of the Suborder Psocomorpha.

ACKNOWLEDGEMENTS

I wish to thank the officers of the Chicago Natural History Museum, Mr. Henry Dybas in particular, for arranging the loan of material discussed in this paper. The accompanying photomicrograph (text figure 1) was made by Dr. Robert D. Weigel of the Department of Biological Sciences, Illinois State Normal University.

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The illustration on the front cover of this issue of *Psyche* is a drawing of a myrmecophilous weevil, *Liometophilus manni* Fall. The original figure was included in H. C. Fall's article in *Psyche*, Volume 19, 1912, plate 3. The weevil itself was collected by the late W. M. Mann in the Huachuca Mts., Arizona.

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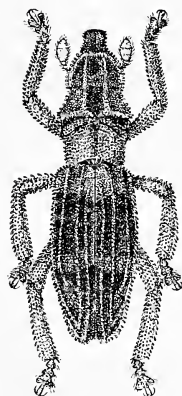
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Nos. 2-3

A NEW EARWIG IN THE GENUS *VOSTOX* (DERMAPTERA: LABIIDAE) FROM THE SOUTHWESTERN UNITED STATES AND MEXICO¹

BY W. L. NUTTING² AND ASHLEY B. GURNEY³

During the summer of 1958 a single male earwig was taken from a light trap in southwestern New Mexico and sent to the U. S. National Museum for identification. Apparently a new species of *Vostox*, it was put aside with the hope that more specimens might be collected. In the fall of 1959, during a study of the Dermaptera in the University of Arizona collection, six adults and three nymphs of this same earwig were discovered among some undetermined specimens. A further search finally resulted in the completion of the series of six males, seven females, and three nymphs upon which the following description is based. This new earwig brings the total number of Dermaptera in the United States, both native and adventive, to 19 species and 1 subspecies.⁴ Probably not more than six or seven of them are representatives of our endemic fauna.

There are about seven previously described species of *Vostox*, of which only *brunneipennis* (Serville) occurs in the United States; the others are all Neotropical. *V. brunneipennis* ranges from Virginia, Indiana, and Illinois south to Florida and westward to eastern Texas, with a few records from Panama and the states of Vera Cruz and Sinaloa in Mexico. So far as the available material demonstrates, the new species ranges from southern New Mexico and Arizona into the Mexican states of Sinaloa and Baja California. Neither of the species

¹Arizona Agricultural Experiment Station Technical Paper No. 642.

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⁴Several changes, which have occurred in the list of United States Dermaptera since the paper by Gurney (1950) appeared, may be noted. *Prolabia* has been found to be a synonym of *Marava*, and *M. wallacei* (Dohrn) a synonym of *M. arachidis* (Yersin), the latter current combination replacing *Prolabia arachidis* (see Hincks, 1954). *Pyragropsis buscki* (Caudell), a recent addition to the list, occurs in Florida (Gurney, 1959). *Prolabia pulchella* (Serville) has been transferred to *Laprobia*, a genus described as new by Hincks (1960).

of *Vostox* found in the United States is apparently very common over most of its range, though fairly numerous specimens of *brunneipennis* have been seen from Florida and other southeastern states, where it occurs beneath loose bark of trees. *Spongovostox apicedentatus* (Caudell) is similar superficially to the new species and is one of the commonest earwigs native to the southwestern United States and northwestern Mexico. The following keys serve to distinguish the latter and the two United States species of *Vostox*, in spite of their general similarity in habitus, size, and coloration.

Keys to Species of *Vostox* and *Spongovostox* Found in
Continental United States
(Males)

1. Forceps armed with a conspicuous subapical tooth *Spongovostox apicedentatus* (Caudell)
Forceps armed with at least one conspicuous tooth at or considerably anterior to middle (if tooth is absent, forceps are definitely concave internally on basal third) 2
2. Forceps sparsely tuberculate beneath, not concave internally, typically bearing a prominent, rounded tooth considerably anterior to middle (if two prominent teeth occur, the smaller, secondary tooth is at the middle); pygidium as in Figs. 10 or 11; parameres with conspicuous preapical curvature, Fig. 9. *Vostox brunneipennis* (Serville)
Forceps smooth beneath, generally conspicuously concave internally on basal third, larger specimens with tooth near middle; pygidium as in Figs. 2, 3 or 7; parameres less conspicuously curved, Fig. 8. *Vostox excavatus*, new species

(Females)

1. Forceps armed with a basal, quadrate tooth, projecting but little beyond dorso-internal margin; abdominal sterna moderately clothed with fine yellow-brown setae and bearing many long, brown setae on posterior margins (males and nymphs as well); suggestions of lateral folds on segments four, five, and sometimes six (sometimes subtle but, when prominent, each fold bearing a long, light brown seta); pygidium much like Fig. 5. *Spongovostox apicedentatus* (Caudell)
Forceps armed with a large, basal, quadrate tooth, projecting well beyond dorso-internal margin (Fig. 1) 2
2. Dorsal surface of anal segment with a scattering of prominent tubercles over posterior third (Fig. 13); ventro-internal margin of forceps prominent and crenulate, dorso-internal margin

broadly rounded and beset with a few widely spaced tubercles, inner face thus scarcely concave for more than half its length; pygidium as in Fig. 12, but scarcely diagnostic.

..... *Vostox brunneipennis* (Serville)
Dorsal surface of anal segment comparatively smooth; dorso- and ventro-internal margins of forceps prominent and closely set with small tubercles (almost crenulate), inner face thus distinctly concave as a longitudinal groove nearly to tip; pygidium as in Fig. 4. *Vostox excavatus*, new species

***Vostox excavatus*, new species**

Figures 1-8

Description. Male (holotype): Size medium, form usual for genus; body depressed with sides of abdomen (except for slightly narrower segments 1 and 10) subparallel and as wide as elytra; abdomen minutely punctulate above and below, less so on segments 1-3, increasingly so posteriorly, body practically smooth elsewhere; fine, short setae rather densely covering labrum, antennae and limbs, but sparse on remainder of body including forceps, elytra and wing scales; a few longer setae on posterior margin of head, anterior margin of pronotum, cephalic faces of femora, near bases of coxae, and on the posterior margins of all abdominal sterna except the last.

Head cordate in dorsal outline, with greatest width through the eyes equal to the median length; occipital margin broadly and obtusely emarginate; caudal angle of genae broadly rounded; eyes not especially prominent, slightly shorter in length than the postocular portions of genae; ecdysial cleavage lines very faintly impressed; antennae broken, one with 11, the other with 12 segments, the first segment equal to the sixth in length, considerably shorter than the fourth and fifth together.

Pronotum subquadrate, with greatest width at caudal third nearly equal to its median length, cephalic margin produced mesad to form a narrow cervical flange, laterocephalic angles obtuse and narrowly rounded, lateral margins straight and diverging slightly to the broadly rounded caudal margin, anterior two-thirds of disc convex with lateral margins flaring upward, thus forming shallow furrows which broaden and become confluent with the flattened posterior third of disc; median longitudinal sulcus moderately impressed on convex portion of disc, but becoming obsolete in posterior third.

Elytra with median length 2.1 times the greatest width of a single elytron; lateral margins nearly straight and subparallel, humeral angles broadly rounded, distal margin subtruncate. Exposed portions

of wings projecting posteriorly almost one-half the median elytral length with external margins converging gradually to the truncated distal extremities.

Abdomen broadened slightly in the middle, with basal segment notably narrower than anal segment; lateral folds moderately prominent on second and third terga; posterior margin of terga four, five, and six bordered with small tubercles, becoming obsolete laterad; anal segment transversely rectangulate with sides subparallel, posterior margin truncated, but with a small lobe laterad above dorso-internal margin of each forceps.

Forceps, as in figure 7, about three-fourths as long as the normally exposed portion of abdomen, relatively smooth, slender, and straight except for gentle incurving of the apical third, a prominent, slightly rounded tooth just anterior to middle on dorso-internal margin; inner faces rather strongly excavate anteriorly, this becoming obsolete proximad from tooth; ventro-internal margin bearing a few irregularly spaced tubercles anterior to tooth; pygidium, as in figure 7, with sides parallel at base, converging acutely to the narrowly rounded apex; subgenital plate slightly less exposed than the last tergum, its lateral margins oblique and broadly rounded into the somewhat concave distal margin; concealed genitalia as in figure 8.

Femora moderately inflated, anterior pair most strongly so, and subequal in length to anterior tibiae; tarsi long, slender, their ventral margins (particularly of metatarsi) bearing numerous, stiff setae; posterior metatarsus subequal to the combined length of the remaining two tarsal segments, the ventral surface with 2 rows of setae along the outer (lateral) margin, inner (mesal) margin with 2 longitudinal rows and numerous shorter marginal setae which are arranged in about 12 to 15 short, oblique, comblike rows to give a "stepped" or "staircase" effect. (The combs are best seen on clean specimens, in a mesal view, with magnification of 50 or more times, in a strong light.)

Coloration: Similar to *brunneipennis*; head, pronotum, median third of wing scales and abdomen dark chestnut brown, paler on antennae, elytra, anal segment and forceps; outer two-thirds of wing scales yellowish-white; limbs honey yellow; eyes black.

Measurements (in millimeters): Body length (exclusive of forceps and pygidium), 9; median length of head, 1.5; length of pronotum, 1.5; median length of elytron, 2.5; internal length of exposed wing scale, 1.1; length of forceps, 4.3.

Female (allotype): General form as in male, but somewhat more robust and differing as follows: head broader and longer; eyes larger

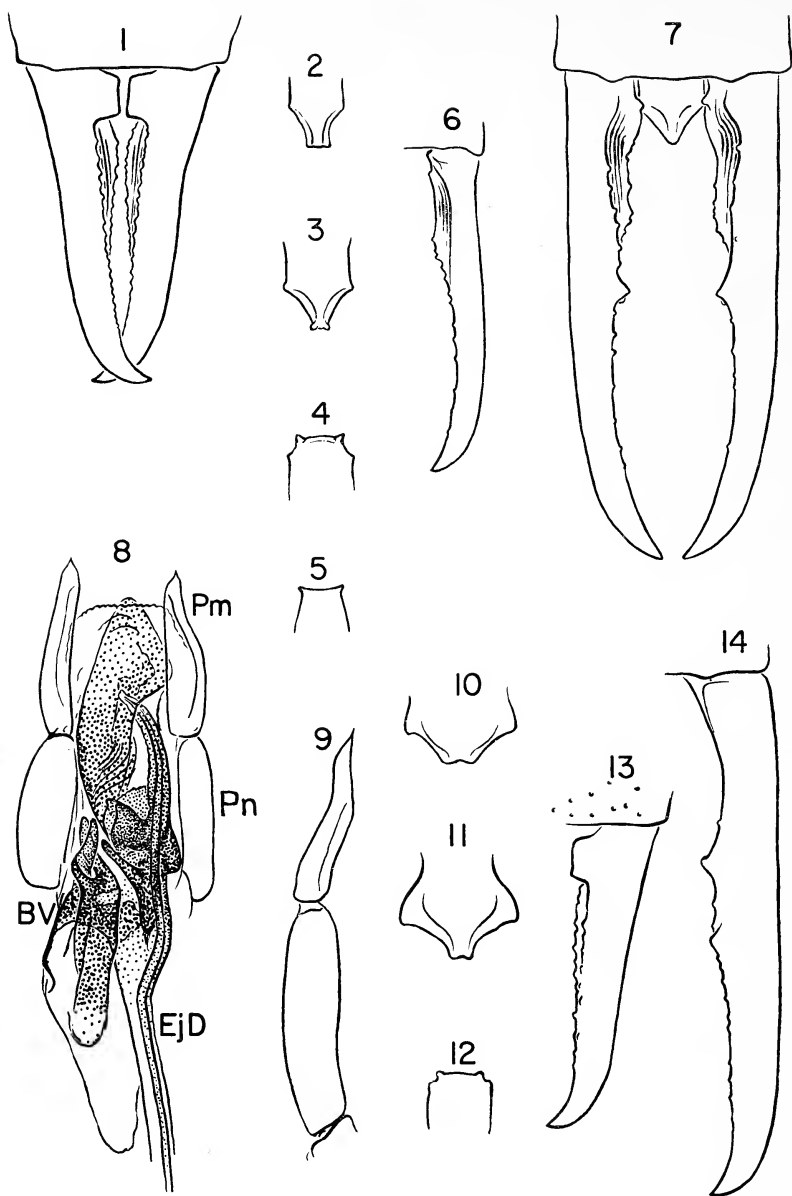
and slightly longer than cheeks; antennae broken, one with 9, the other with 12 segments; abdomen notably wider, but with anal segment considerably narrower than the basal segment; marginal tubercles absent from terga four, five, and six; forceps typically shorter, stouter, and shaped as in figure 1, with a large quadrate tooth on dorso-internal margin at base, both dorso- and ventro-internal margins prominent and irregularly but closely set with small tubercles, inner faces thus distinctly concave nearly to tips; pygidium shaped as in figure 4.

Coloration: Differs from male in no important respect except for being a shade darker over-all, especially on the anal segment and forceps.

Measurements (in millimeters): Body length (exclusive of fore- and pygidium), 9; median length of head, 1.5; length of pronotum, 1.5; median length of elytron, 2.5; internal length of exposed wing scale, 1.1; length of forceps, 4.3.

Variation: There are five male paratypes, three of which do not vary significantly in size from the type; the length (in mm.) of various parts of the smallest specimen (Tucson) follow: body 7.2, head 1.5, pronotum 1.2, elytron 2.1, wing scale 1.1, forceps 2.8. The eyes of all but the smallest agree with the type in being shorter than the genae, whereas in the smallest specimen they are slightly longer. The complete number of antennal segments varies from 12 to 16. The Tucson specimen also lacks the marginal tubercles on terga four, five, and six. Although the forceps of all are distinctively excavated, the large tooth is absent in the two smaller specimens (Fig. 6), and its position marked only by a tubercle in the third. The shape of the pygidium apparently varies considerably as in *brunneipennis*; in two specimens it is unlike the type in that it is truncated at the tip (Figs. 2 and 3). All genitalia are preserved in glycerol and show close agreement with those of the type in the shape of the parameres, details of the sclerotized armature of the basal vesicle, and the bend of the ejaculatory duct.

The six female paratypes show considerably less variation in size and configuration of characters; the lengths (in mm.) of various parts of the smallest specimen ("Venodio") follow: body 8.6, head 1.6, pronotum 1.4, elytron 2.3, wing scale 1.2, forceps 2.2. The length of the eye of two agrees with the allotype in being longer than the cheeks, whereas in three it is shorter, and in the remaining specimen these measurements are equal. The number of antennal segments ranges from 13 to 16. Most of the paratypes vary but little in the shades of brown described above; however, the two females from



Baja California are a dark, smoky brown over-all, nearly black on the head, and diminishing posteriorly to a dark chestnut brown on the forceps. The appendages and outer portions of the wing scales are a lighter smoky brown.

Nymphs: Three nymphs, presumably collected with one of the adult males, are included with the paratypes. These specimens are probably more than half-grown, for they range in length from 6.5 to 7 mm., and each bears moderately developed, fused wing pads. The antennae are 10- to 12-segmented. Each of the first six abdominal sterna bears two long setae, which are conspicuously arranged in contralateral rows, one-third of the width of the abdomen from each margin. (This pattern may exist in the adult stage but is not evident in any of our specimens.) The smooth forceps range from 1.8 to 2.2 mm. in length but show none of the specializations of either sex beyond the minute tubercles along the dorso- and ventro-internal margins. Figure 5 shows the configuration of the pygidium which suggests that all three may be females. Their coloration is similar to the holotype, except that the outer two-thirds of both pairs of wing pads are dark brown and the inner third is a lighter, yellow-brown.

Holotype: U.S.N.M. No. 65696

Type locality: Santa Catalina Mts. (2000-3000 ft.), Pima Co., Ariz.

The holotype male was collected by Andrew A. Nichol on August 15, 1924. In reply to a recent inquiry as to the exact locality, Dr. Nichol has recalled that it was in the lower parts of either Sabino Canyon (south slope of the range) or Cañada del Oro (north and west slopes), probably the former. The allotype (U.S.N.M.) was taken under lights on the bridge over the Salt River (dry), Tempe, Maricopa Co., Ariz., on July 18, 1947, by Floyd G. Werner.

Paratypes: U. S. National Museum (1 ♂, 1 ♀, 2 nymphs); Department of Entomology, College of Agriculture, University of Arizona,

EXPLANATION OF PLATE 6.

Figs. 1-8, *Vostox excavatus*, new species. 1. Forceps of female allotype, dorsal view. 2. Male pygidium (Tucson), dorsal view. 3. Male pygidium (Virden), dorsal view. 4. Pygidium of female allotype, ventral view. 5. Nymphal pygidium, ventral view. 6. Male forceps (Tucson), dorsal view. 7. Forceps and pygidium of male holotype, dorsal view. 8. Concealed genitalia of male holotype: Pm, paramere; Pn, penis; BV, basal vesicle; EjD, ejaculatory duct. Figs. 9-14, *Vostox brunneipennis* (Serv.). 9. Left penis and paramere (Gainesville, Fla.), dorsal view. 10. Male pygidium (Dallas, Tex.), dorsal view. 11. Male pygidium (Gainesville), dorsal view. 12. Female pygidium (Paris, Tex.), ventral view. 13. Female forceps (Mobile, Ala.), dorsal view. 14. Male forceps (Gainesville), dorsal view. Figs. 1-7, 10-14, x15; Figs. 8 and 9, x34. (Drawings by senior author).

Tucson (1 ♂, 2 ♀, 1 nymph); Arizona State University, Tempe (1 ♂); Museum of Comparative Zoology, Cambridge, Mass. (1 ♂, 1 ♀); California Academy of Sciences, San Francisco, Calif. (1 ♂); Academy of Natural Sciences of Philadelphia (1 ♀); British Museum (N. H.), London, England (1 ♀).

The paratypes are from the following localities:

NEW MEXICO: Virden, Hidalgo Co., one male, Aug. 27, 1958. light trap, G. L. Nielsen.

ARIZONA: Tempe, one male, Nov. 22, 1955, Jones; Tucson, Pima Co., one male and three nymphs, Dec. 4, 1924, C. T. Vorhies; one female, Nov. 7, 1939, Wayne Enloe; two females, Dec. 29, 1939, Tom Embleton; Sabino Canyon, Sta. Catalina Mts., Pima Co., one male, July 25, 1955, at light, G. D. Butler and F. G. Werner; 2 mi. sw. Patagonia (4050 ft., Sonoita Creek bottom, willow-cottonwood), Sta. Cruz Co., one male, Aug. 21, 1949, F. H. Parker.

MEXICO: SINALOA, "Venodio", one female, 1918, Kusche; BAJA CALIFORNIA, 25 mi. w. La Paz (ca. 500-foot plateau, relatively rich shrubby vegetation), one female, light trap, Aug. 30, 1959, K. W. Radford and F. G. Werner; 10 mi. sw. San José del Cabo (100 yd. from ocean in sandy wash, sparse shrubs), one female, light trap, Sept. 1, 1959, K. W. Radford and F. G. Werner. Aside from the few notes appended to the above localities, there is no information of any sort available on this apparently rare earwig.

Morgan Hebard (1923, and other papers) described many Orthoptera collected by J. A. Kusche in Sinaloa, at "Venvidio", which probably is our "Venodio." Workers have been unable to locate either locality since, and Irving J. Cantrall, of the University of Michigan, has written us of having prepared a manuscript dealing with the Kusche locality. Thanks to Dr. Cantrall's cooperation, we are able to report that Venadillo apparently is the correct name. This small town is 5 miles northeast of Mazatlán on Mexican Highway 15, which goes to Culiacan.

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SOME COMMENTS ON WALCKENAER'S NAMES OF
AMERICAN SPIDERS,
BASED ON ABBOT'S DRAWINGS¹

BY HERBERT W. LEVI AND LORNA R. LEVI
Museum of Comparative Zoology, Harvard University

In 1887 McCook rediscovered the Abbot drawings, basis of many of Walckenaer's spider descriptions, and initiated a controversy in spider nomenclature by synonymizing spider names then in use. Emerton replied that the drawings represent the spiders in so general and indefinite a way that identification would only increase the uncertainty of nomenclature. Banks' comments about the Walckenaer descriptions were blunt: "They rank with 'hearsay evidence.' I shall not use them nor list them; I shall ignore them." Later Gertsch (1933) expressed the fear that these names would be revived and cause permanent instability: "The problem at hand is not the question of validity, which should be unchallenged, but one of recognition." In 1944 Chamberlin and Ivie made a serious attempt to establish the Walckenaer names *en masse*. Their synonymies were accepted by Archer (1946, 1950), Levi (1954), and Levi and Field (1954), but not by Gertsch (1953). We were at first inclined to follow Chamberlin and Ivie in using the Walckenaer names, but during the course of the theridiid studies, had an opportunity to examine the Abbot drawings. We are convinced that in the Theridiidae at least, Chamberlin and Ivie were ill-advised to attempt the synonymies, and, indeed, that establishment of such synonymies would be a disservice to araneology.

English-born John Abbot immigrated in 1776, as a young man, to Screven County, Georgia, and lived in Georgia for 65 years as a schoolmaster and naturalist. He painted birds, butterflies and other animals, and his drawings were sold by John Francillan, a London silversmith (Dow, 1914). Sixteen volumes of Abbot's drawings are in the British Museum (Natural History) in London; many volumes

¹We wish to thank the following for reading a draft of this manuscript and for making suggestions (without implying that they necessarily agree with the conclusions): Mrs. D. L. Frizzell (Dr. Harriet Exline), Dr. R. Crabill, Dr. C. Dondale, Prof. E. Mayr, and Dr. W. J. Gertsch. Dr. Gertsch kindly sent us a manuscript, prepared ten or twelve years ago but never published, in which he discussed the problem of the Walckenaer names. Although he believed the names were correctly synonymized by Chamberlin and Ivie (1944), he pleaded their rejection in the interests of nomenclatural stability. Dr. Gertsch and Dr. Dondale called our attention to pertinent literature. A National Science Foundation grant made possible our trip to Europe in 1958, at which opportunity we examined the Abbot manuscript drawings.

are in other institutions, several at the Houghton Library of Harvard University. According to Chamberlin and Ivie (1944), Walckenaer purchased drawings from the entomologist Mackay. In the eighteen forties Walckenaer named and described some of the drawings of the 1792 Abbot volume (now in the British Museum), in *Histoire Naturelles des Insectes Aptères*. There is some doubt about the date of publication of Walckenaer's second volume. Our personal volume has two inscriptions, one of Walckenaer, addressed to Mr. Adam White and dated 4 June 1841, and another presumably in White's handwriting: "Adam White Villeneuve, St. Germ. Walckenaer's study June 7, 1841." Thus the publication date is undoubtedly 1841, not 1842 as stated by Chamberlin and Ivie and Bonnet (1945).

Dr. McCook visited the British Museum in 1887 and his attention was called to the Abbot drawings of American spiders. In a report to the Philadelphia Academy of Sciences (1888a), he discussed some of the questions raised by this discovery. McCook was much concerned about the changing of names in use, but he also wanted to credit the earliest author: "the laws of priority must be considered, and honesty and justice can give no room for considerations of convenience and sentiment." Several argiopid names of Hentz were identified with those of Walckenaer.

McCook's paper was reviewed by Emerton (1888). Emerton had looked over the Abbot drawings at the time of his visit to the British Museum in 1875, "and like Mr. McCook made hasty identifications of such few of them as I could. . . . A comparison of the numbers shows that only five of these identifications agree with those of McCook showing the uncertainty of off-hand identifications of these drawings by two persons both familiar with the common spiders of the northern states. The greater number of Abbot's drawings represent the spiders only in the most general and indefinite way and it seems to me improbable that any large number of them can ever be identified."

Included in McCook's self defense (1888b) were excerpts from a congratulatory letter from Thorell. Banks followed: "The descriptions of new species in Walckenaer's *Insectes Aptères* fall into two classes: descriptions based on specimens, and descriptions based on figures. The former class are undoubtedly valid and I intend to accept them wherever I can apply them. Descriptions of figures, however, I hold, have no claim on the naturalist. Not only are they based on figures, but the figures have never been published. Many of the descriptions are sufficient for identification, but most are not.

But no matter how complete, they are not descriptions of spiders; but of figures of spiders. They rank with 'hearsay evidence'. I shall not use them nor list them; I shall ignore them."

Chamberlin and Ivie (1944) undertook "initially to determine, as far as possible from available evidence, the proper application of the names based by Walckenaer upon Abbot's drawings of the spiders of Georgia." Chamberlin made color photographs of Abbot's drawings at the time of a London visit, and Ivie spent a month in April 1943 collecting spiders in Georgia. Some other collections were obtained during brief stops in Georgia in August 1933 and June 1935. Chamberlin and Ivie listed the collections (including many determined juveniles), and synonymized many well established spider names of many families with names of Walckenaer.

However, in our own examination of the Abbot manuscript drawings, we found that the majority do not show diagnostic characters; interpretation must be subjective, and authors may differ. For instance, McCook synonymized the name *Tetragnatha lacerta* Walckenaer with *Tetragnatha caudata* Emerton; Chamberlin and Ivie synonymized the same name with *Rhomphaea fictilium* (Hentz), of a different family. Most of McCook's synonymies concerned argiopid spiders that have a characteristic dorsal abdominal pattern. However a modern author has to consider the possibility of sympatric sibling species.

Further, and to be expected, students working with groups never revised make errors in identification. Thus Chamberlin and Ivie synonymized *Argyroides trigonum* (Hentz) with *Linyphia rufa* Walckenaer. However, the specimens so labelled were not Hentz's species, but were *Argyroides furcatus* (O.P.-Cambridge), a species more common in Georgia. *Tidarren fordum* (Keyserling) was synonymized with *Theridion sisypoides* Walckenaer, but specimens so labelled were not *Tidarren fordum*. Female specimens of *Theridion alabamense* Gertsch and Archer were misidentified as *Theridion americanum* Walckenaer, and the male was described as new. Walckenaer's description of *T. americanum* does not fit *T. alabamense*. Figure 43, Walckenaer's *Theridion ansatum*, was not recognized as the species otherwise called *Tidarren sisypoides* (Walckenaer), easily recognized by the white line on the posterior part of the abdomen. Probably half the examined theridiids of the Chamberlin and Ivie Georgia collection had incorrect identifications, and the same may be true of specimens of other families. While these errors can easily be understood, they invalidate many of the synonymies of Walckenaer's names.

Chamberlin and Ivie apparently were unaware of the earlier exchanges about the synonymies, for they neither referred to them nor listed them in their bibliography. Also they apparently did not consider the possibility of additional plates, letters and notes concerning the Abbot spiders, in other libraries. Such sources of evidence might have relevance in interpreting Abbot's drawings, which must be considered the types for the Walckenaer names.

As recently as twenty years ago, some considered the discovery of an "older name" a matter to be admired, and priority was frequently invoked to rationalize changing a name in widespread use. Today the attitude toward stability of names has changed, partly due to criticism of zoologists in fields other than taxonomy. Perplexed by the constant change of names, these other biologists leveled the charge that some taxonomists were spending more time in historical than in biological research.

Two approaches to stability of names present themselves: Some taxonomists think that through priority, the supply of older names will eventually become exhausted; at the same time, strict priority leads nomenclature back to the oldest and most uncertain names. Other taxonomists favor established usage of the name as the basis of stability, though usage may be hard to define.

The new (1961) Zoological code of Nomenclature combines the criteria of priority and usage through a statute of limitations. Also, and more important, the new code emphasizes in its Preamble the reason for its existence — to keep names stable — a reflection of the present needs of zoologists. The establishment of sweeping synonymies of the Walckenaer names based on Abbot's drawings, so inconsistent with stability, should be questioned.

A more acceptable treatment of the Walckenaer names was demonstrated by Bishop (1924), in his revision of the North American Pisauridae. By restricting himself to one family he was able to treat each nomenclatural problem individually and authoritatively, rather than all in one arbitrary sweep. The largest number of specimens, the greatest grasp of the literature, and the keenest understanding of the particular spider group were brought into each judgement.

Our purpose, then, is to urge that spider students adopt the Walckenaer synonymies proposed by Chamberlin and Ivie only after thorough study of the spider genera in question, including, in addition to a study of the Abbot drawings, investigation of usage of names, species problems, and distributions, giving due consideration to the basic principles of nomenclature: to stability and universality of names.

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THE NEOTROPICAL SPECIES OF THE ANT GENUS
STRUMIGENYS FR. SMITH:
MISCELLANEOUS CONCLUDING STUDIES

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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 in the same journal, in Psyche, and in Studia Entomologica, Petrópolis, Brazil. This section is a final one so far as currently available material in the genus indicates; only one more section, which will be composed chiefly of an illustrated key to the New World members of the genus, is planned at present.

S. micretes and *S. lacacoca*

Following the descriptions of what I called the *emeryi* group (Brown, 1959) the species were discussed as follows:

"The four species *emeryi*, *nevermanni*, *micretes* and *lacacoca* are very close, and seem, from the limited material available, to replace one another in a chain extending from Mexico to Panama, and perhaps beyond. So far as I can see now, the differences are complex enough and strong enough to indicate that each form is a distinct species; perhaps together [they constitute] one superspecies. However, it is not beyond possibility that one or more of these forms intergrades with a neighbor. More material is needed."

Since that writing, material has turned up which, though small in amount, tends to bridge the gap between *S. micretes* Brown and *S. lacacoca* Brown, indicating perhaps that they belong to a single variable species. Nevertheless, the new material poses certain problems itself, and the discussion next offered is intended to give details that should help in eventually straightening this complex out.

A sample consisting of parts of four nest series from Boquete, Chiriqui Province, Panama (F. M. Gaige leg., see below) contains 25 workers with highly variable preapical mandibular dentition, the denticles varying in number from 1 to 4 in the two mandibles taken together, and also varying markedly in size, acuteness and position, so as to bridge virtually completely the chief diagnostic character-gap between *micretes* (each mandible with a small but acute preapical tooth, and a little farther up a minute denticle) and *lacacoca* (man-

dibles completely without teeth or denticles basad of the apical fork in the preapical region). This sample indicates that the preapical dentition, usually so constant in species of *Strumigenys*, may sometimes be unreliable. The Boquete sample would clearly indicate synonymy between *micretes* and *lacacoca* were it not for one disturbing fact: the Boquete sample differs from the available samples of both species in its larger size and in having the promesonotum very distinctly and closely longitudinally striate throughout (arched striate along the anterior pronotal margin). This sculpture is somewhat shining, especially on the sides, where a large section becomes smooth or nearly so. The rest of the sides of the alitrunk are also smooth and shining for the most part. Postpetiole predominantly smooth and shining, crossed by a few longitudinal costulae. Propodeal teeth also longer, more slender and more nearly horizontal than in the *micretes* or *lacacoca* type series. Anterior coxae smooth or nearly so, shining.

Some specimens of *micretes* and *lacacoca* have feebly indicated longitudinal rugulae or costulae on the pronotum (in addition to the median carinula), but in these the predominant sculpture is the usual opaque reticulo-punctulation over at least the discal portion. The size, head width and sculptural traits of the Boquete sample could well be diagnostic of still another species in this close-knit complex, or they could merely mark a local population of a single variable species that would also include the types of *micretes* and *lacacoca*. For the present, it seems wise to avoid introducing new species names for members of this complex and also to hold off from synonymizing *micretes* and *lacacoca* until the distribution and variation of the complex are better known. For the convenience of future workers, I list here the material of the complex that I have studied, with such measurements, proportions and other observations as I have obtained from them (n = number of workers measured for each sample):

Colombiana Farm, Santa Clara, Costa Rica (W. M. Mann leg.), TL 2.9-3.1, ML 0.70-0.74, ML 0.45-0.47, WL 0.72-0.76 mm; CI 71-74, MI 62-65 (n = 12), type series of *S. micretes*. Progreso, Chiriqui Prov., Panama, (F. M. Gaige leg., no. 332), TL 3.1-3.3, HL 0.75-0.76, ML 0.50-0.51 mm; CI "about as in the type series" of *micretes*, MI 66-68 (n = 6), series placed with *micretes* in the original description of that species. Boquete, Chiriqui Prov., Panama (F. M. Gaige leg., nos. 208, 497, 504 and one series with no number) TL 3.7-4.0, HL 0.86-0.90, HW 0.66-0.68, ML 0.58-0.61, WL 0.92-0.99 mm; CI 75-76, MI 67-68 (n = 25), *Strumigenys* near *micretes*, discussed above. Cerro Campana, west of Chorrera, Panama Prov., Panama, at about 950 m altitude in montane rain forest (cloud for-

est), in rotten wood (G. B. Fairchild and W. L. Brown leg., no. B-86), TL 3.3, HL 0.76, HW 0.52, ML 0.53, WL 0.82 mm; CI 68, MI 70 ($n = 1$), specimen here placed as *S. lacacoca*; this worker has a single extremely minute denticle in the preapical concavity of the left mandible, perhaps representing a vestige of a distal preapical tooth. Rio Chinillo, Panama Canal Zone (T. E. Snyder leg.), TL 2.8-3.2, HL 0.70-0.75, ML 0.45-0.48, WL 0.72-0.75 mm; CI 67-71, MI 60-66 ($n = 7$), type series of *S. lacacoca*.

Though the known variation of the *micretes-lacacoca* is considerably expanded by the new material reported above, this variation is mainly away from the direction of *S. nevermanni* Brown, from Costa Rica, a species that is generally smaller, with a relatively shorter head and mandibles and narrow infradental lamellae.

A new species of the *Tococae* group

***Strumigenys fairchildi* new species**

Holotype worker: TL 4.1, HL 0.96, HW 0.72, ML 0.59, WL 1.01, scape L 0.68 mm; CI 75, MI 61.

Aside from its larger size and relatively longer mandibles, this species closely resembles *S. tococae* Wheeler from the Amazon Basin. The upper propodeal teeth are somewhat longer (about as long as the distance between the centers of their bases, and about twice as long as the lower teeth), and the lamella between the upper and lower teeth is lower and more cariniform. The eyes are about the same size (greatest diameter about 0.14 mm), and the petiole and postpetiole are similar, but with slightly less voluminous spongiform appendages. The best distinction lies in the sculpture and pilosity of the nodes and gastric dorsum:

(1) Postpetiolar disc convex, evenly reticulo-punctulate, with only feeble anterior traces of longitudinal costulae. First gastric tergite finely longitudinally striolate, opaque-sericeous throughout (in *S. tococae*, the gaster is costulate at the base, but otherwise smooth and shining).

(2) Ground pilosity strongly reduced, virtually absent on nodes and gastric dorsum (plentiful and conspicuous in *S. tococae*). Fine erect flagelliform hairs of nodes and gaster shorter and apparently fewer than in *S. tococae*.

The color is ferruginous yellow, the gaster somewhat brighter yellow than the rest of the body.

Holotype [MCZ] a unique worker from the wooded ravine next to the inn near the top of Cerro Campana, Panama Prov., Panama, 17 January, 1960, at an altitude of 800 to 850 m (G. B. Fairchild

and W. L. Brown leg.). The worker was found walking on a rotten stick lying on the leaf litter on the shaded slope of the ravine; hasty search of the litter and soil nearby failed to uncover more specimens. Since the very closely related *S. tococae* was found at Belem, Brazil, nesting in foliar sacs of the plant *Tococa*, it is possible that *S. fairchildi* was also nesting in a plant cavity above the ground. Since the relationships of *S. fairchildi* were not recognized until it was critically examined in the laboratory, the possibility of a plant-cavity habitat was not investigated in the field.

Group of *S. lanuginosa* Wheeler

Two species, *S. lanuginosa* Wheeler and *S. hindenburgi* Forel, share a number of traits that apparently indicate a fairly close relationship between them: Mandibles lying close together at full closure, their bases sharply narrowed from the outside; apical fork moderate in length, with a single intercalary tooth; inner (masticatory) margin concave near apex, the concavity with a short but acute preapical tooth (*S. hindenburgi* has an additional minute denticle near the apical third of the margin). Clypeus broadly triangular, with convex anterior margin. Antennal scape slender, tapered toward both ends, very slightly curved at basal third.

Pronotum with humeral angles developed, bluntly tuberculate; anterior margin present (weak in *S. lanuginosa*); alitrunk in side view with convex dorsal profile, broken only at the impressed metanotal groove. Propodeal teeth of modest size, but acute, each subtended by a low, concave infradental lamella ending in a ventral convexity. Petiole distinctly pedunculate and with a short, dorsally rounded node; postpetiolar disc convex; both nodes with complete and well-developed spongiform appendages. Gaster normal in form, with a strong anterodorsal spongiform margin and a thick anteroventral spongiform pad; basigastric costulae well developed.

Head, alitrunk and both nodes densely and finely reticulo-punctulate, opaque; postpetiolar disc usually with weak rugulosity or costulation superimposed. Underside of gaster smooth and shining; mandibles weakly shining in some lights, punctulate; legs and antennae finely and densely punctulate. Sides of pronotum, anterolateral surfaces of anterior coxae, and lower lateral surfaces of infradental lamellae of propodeum with patches of fine reclinate hairs and frequently encrusted with whitish material; apparently these represent secretory areas.

Ground pilosity of head, promesonotum, posterior propodeum; scapes and legs consisting of fine, abundant reclinate and arched-reclin-

ate hairs. Larger specialized hairs all fine, long, flagelliform, more or less erect: a pair on each lateral occipital border (2 pairs in *lanuginosa*), a pair on the middle occiput, a pair on the humeri and another pair on the mesonotum. Both nodes and both upper and lower surfaces of the gaster with a luxuriant growth of abundant, long, fine flagelliform hairs, the longest of which, on the gastric dorsum, are as long as or longer than the petiole. Each inner mandibular border bears a row of fine oblique sensory hairs.

Males of neither species have yet been found. *S. lanuginosa* occurs in Central America and southern Mexico, and has apparently been introduced into the Bahamas, while *S. hindenburgi* is known from southern Brazil and northern Argentina.

Strumigenys lanuginosa Wheeler

Strumigenys lanuginosa Wheeler, 1905, Bull. Amer. Mus. Nat. Hist. 21: 104, fig. M, worker, female. Type loc.: Fort Charlotte, Nassau, Bahama Islands. Syntypes in AMNH, MCZ, several examined.

Worker: TL 2.4-2.7, HL 0.55-0.60, ML 0.35-0.38, WL 0.58-0.64 mm; CI 79-80, MI 63-64. Measurements from 5 workers, including a syntype, Panamanian and Mexican specimens.

Main distinguishing features:

- (1) Small size and slender build.
- (2) Dorsolateral borders of head merely cariniform, not lamellate.
- (3) Mandibles without a trace of a denticle basad of preapical tooth.
- (4) Basal costulae of gaster extended as fine, sericeous striation (striolation) over the basal third or more of the first segment. Gastric pilosity also more abundant and crowded than in *S. hindenburgi*.
- (5) Two pairs of flagellate hairs on the lateral occipital margins.
- (6) Postpetiole usually with traces of fine longitudinal striolation or costulation overlying the punctulation.

Color light ferruginous, gaster often slightly more brownish. Mandibles and appendages lighter, more yellowish.

Female (dealate): TL 2.9-3.0, HL 0.62-0.63, ML 0.36-0.38, WL 0.72-0.73 mm; CI 80-84, MI 57-61 (from 2 syntypes). Males unknown.

Distribution: Southern Mexico, Panama; in Bahamas, where probably introduced historically.

Localities for material examined: Bahama Islands, Nassau (W. M. Wheeler leg.), type locality. Mexico, Veracruz: Cordoba (C. H. Seevers leg.), one worker under stone. Pueblo Nuevo, near Tetzonapa (E. O. Wilson leg.), strays from leaf litter in tropical evergreen for-

est, and foraging on surface of log in degraded rain forest. Panama Canal Zone: Barro Colorado Island (J. Zetek leg.), a single worker. This species is here reported from the American mainland for the first time; apparently it is widespread.

Strumigenys hindenburgi Forel

Strumigenys Hindenburgi Forel, 1915, Bull. Soc. Vaud. Sci. Nat., 50: 357, worker. Type loc.: "Argentine," La Plata from label on syntypes. Syntypes in Coll. Forel, Museum d'Histoire Naturelle, Geneva, and MCZ, several examined.

Strumigenys hindenburgi, Kempf, 1958, Stud. Ent. (n.s.) 1:555, record from 10 km sw of Agudos, S. Paulo State, Brazil, among dry leaves in wooded gully.

Worker: TL 2.8-3.2, HL 0.60-0.69, ML 0.38-0.40, WL 0.63-0.71 mm; CI 83-88, MI 58-64. Measurements from 3 syntypes and 6 additional Argentinian specimens representing 3 nest series.

Within the *lanuginosa* group, this species is distinguished by its large size and relatively broad head, as well as the following characters:

(1) Dorsolateral borders of the head (dorsal scrobe borders) on each side produced as a narrow but distinct lamellar margin that gradually narrows posteriad and ends in a shallow concavity behind the level of the eye.

(2) Mandibles each with an extra minute preapical denticle, best seen in oblique view in dark silhouette against a bright background, near the apical third of the shaft.

(3) Basigastric costulae extending less than half the length of the first segment, the rest of which is smooth and shining.

(4) Lateral occipital margins each with only one flagellate hair, arising from the concavity at the end of the lamellate dorsolateral margin.

(5) Occiput, pronotum and postpetiolar disc with traces of feeble reticulate rugulation superimposed on the basic densely punctulate sculpture.

Color medium ferruginous; legs, mandibles and antennae more yellowish; gaster mostly brown.

Pseudogyne or ergatoid female from Itatiaia: TL 2.7, HL 0.60, HW 0.49, ML 0.34, WL 0.60 mm; CI 82, MI 57. This small individual has the mesonotum developed in the direction of the full female, with raised margins dorsad, and the differentiated scutellum acutely projecting posteriad. The petiolar and postpetiolar nodes are wide, as expected in females of this genus, but the gaster is not unusually bulky for a worker. A tiny apparent remnant of a median ocellus occurs in the central vertex. This specimen appears to me to

be classifiable as a pseudogyne, or pathological worker-female intermediate.

Distribution: Northern Argentina, extending into southeastern Brazil.

Localities for material examined: Argentina: La Plata (C. Bruch leg.), 3 syntypes. Salinas, near Tucumán (Kusnezov and Golbach leg., no. 1677). Parque Avellanida, Tucumán (P. Wygodzinsky leg.), a small series of workers. Brazil: Rio de Janeiro State, Itatiaia, Lago Azul (R. Barth leg.), the single pseudogyne described above.

The Variation and Synonymy of *Strumigenys louisianae*

Strumigenys louisianae Roger

Strumigenys louisianae Roger, 1863, Berlin. ent. Zeitschr. 7: 211, worker. Type loc.: "Louisiana." Type in Zoologisches Museum der Humboldt Universität, Berlin, not examined.

Strumigenys unidentata Mayr, 1887, Verh. zool.-bot. Ges. Wien 37: 575 and in key, p. 570, worker. Type loc.: "St. Catharina." Lectotype, by present designation, in Naturhistorisches Museum, Vienna, examined. NEW SYNONYMY.

Strumigenys fusca Emery, 1894, Bull. Soc. ent. ital. 26: 215, pl. 1, fig. 8, worker. Type loc.: Manicore, Amazonas. Holotype in Museo Civico di Storia Naturale, Genoa, examined. NEW SYNONYMY.

Strumigenys clamospongia Brown, 1953, Psyche 60: 2, worker. Type loc.: Petropolis, Rio de Janeiro State, Brazil. Holotype in Coll. W. W. Kempf (ex Coll. T. Borgmeier), São Paulo, Brazil; paratypes in Coll. Kempf, USNM, MCZ, several reexamined. NEW SYNONYMY.

In my "Revisionary Studies" of 1953, I showed that *S. louisianae* is a very variable species ranging from warm temperate North America south into Bolivia and northern Argentina. However, variation at that time was thought to involve mainly body size and proportions of the head and mandibles. After prolonged study, a number of names (see synoptic synonymy below) was placed in the synonymy of *S. louisianae*; types were compared in most of these cases. The variety *longicornis* was also synonymized on the basis of its original description.

In another paper entitled, "Three new ants related to *Strumigenys louisianae* Roger" (Brown, 1953a), I described *S. clamospongia*, *S. producta* and *S. mixta*, stating that "each of the three forms has been compared with all other neotropical species known to me, both described and undescribed, except *S. fusca* and *S. unidentata*, two species to be placed among the *species inquirendae*." Since that writing, I have been able to study the (previously unavailable) types of *S. fusca*, *S. unidentata* and *S. unispinulosa* var. *longicornis* on deposit in Vienna and Genoa, through the kindness of Dr. Max Beier and Dott. Delfa Guiglia respectively. From the first comparison, it was clear that my

clasmospongia was only a larger, relatively narrow-headed variant of *unidentata*. The unique type of *S. fusca* was more puzzling, being a rather large *louisianae*-like worker with fairly broad head and longish mandibles, but having the posterior half of the first gastric tergite nearly completely smooth and definitely shining. Var. *brevicornis* turned out as expected: a large *louisianae* female fitting fairly well with the largest worker forms from South American samples of the species, so that my earlier synonymy was confirmed.

In addition to these types, I have been able during the last few years to examine an increasing accumulation of *louisianae*-related forms from southeastern Brazil and northern Argentina, and scattered specimens have even come in from central Brazil and Surinam, previously blanks on the map. These samples are due mostly to the kindness of Father Borgmeier and Father Kempf. Study of this new material has completely changed my ideas on relationships of the species within the *louisianae* complex. First, the relatively slender, long-mandibulate forms with shining gastric dorsum were shown to be common in southeastern Brazil; it is these forms to which the names *unidentata* and *clasmospongia* have been applied. Taken in combination, the distinctive "*unidentata* characters" give the impression of a distinct species inhabiting southeastern Brazil, but all attempts to define a species with these characters have failed. The reason for this failure is that the new material clearly shows that each of the characters going to make up the *unidentata* in its "typical" manifestation actually has its own independent pattern of geographical and individual variation within *louisianae*. The long mandibles (MI up to 67) of the southeastern Brazilian samples are approached by samples from Bolivia (MI 60-63), and some series from southeastern Brazil have much shorter mandibles (MI as low as 56, and perhaps even lower in some samples seen but not measured), in this respect being not far from average for the species *louisianae* taken as a whole. The gastric sculpture of the *unidentata* pattern, in which basigastric costulae of moderate length are followed by a smooth or nearly smooth, shining surface (though this surface may be obscured by secretion or other foreign matter), is not confined to southeastern Brazilian specimens with long mandibles; in fact, it is found in series with much shorter mandibles from localities as far away as Tucuman, in northern Argentina; Goias, Amazonas and Surinam in the northwest and north; and even in southern Mexico (Veracruz, Puebla). Furthermore, certain series even in southeastern Brazil contain workers with shorter mandibles, some individuals of which have the reticulate, opaque "*louisianae* sculpture", while others from the same nest sample have

the gaster predominantly smooth and shining. Variation in the queens is poorly known because not many of the "*unidentata*" workers are accompanied by females in the collections I have seen. In general, *louisianae*-complex queens have stronger gastric sculpture than the workers accompanying them.

In view of the discordant nature of the variation in the only good distinctive characters available, I am forced to consider *fusca*, *unidentata*, and *clasmospongia* as synonyms of *louisianae*. It is possible that the variation of this very plastic species is even greater in central and northern South America, from which our samples are so few, and perhaps even the large, very long-mandibulate *producta* is only another extreme variant of *louisianae*. The type of *fusca* does show tendencies in the direction of *producta*, but we shall need more material from Western Brazil and Bolivia before we decide this question. Of course, the possibility must not be overlooked that *louisianae* really is made up of a number of cryptic species, inseparable by conventional morphological study.

A fact of continuing interest is the absence of *S. louisianae* from the forest on Barro Colorado Island in the Panama Canal Zone. Intensive collecting by a number of myrmecologists on the Island was repeated in January 1960 by Dr. E. S. McCluskey and myself, making full use of Berlese funnels and other modern collecting techniques, but no one has yet found *S. louisianae* on the Island or elsewhere in Panama. This is especially strange in view of the fact that the species is common in banana plantations on both the Atlantic and Pacific sides of Costa Rica near the Panama border (El Palmar and Coto in the Golfo Dolce, E. O. Wilson leg.). While we now have very inadequate ecological information, it does seem possible that *S. louisianae* may be a species that has adapted to habitats marginal to the rain forest of the South American continent, and that this has something to do with its present wide distribution — the widest of any New World dacetine. In this sense, *S. louisianae* may fit Wilson's (1959) "Stage-I" category of expanding species. It is also of interest to note that the species is much less variable ("more typical") in the North American extremities of its range than in the presumed evolutionary center in South America. Furthermore, the "typical" characteristics of short mandibles and reticulate gastric sculpture, while discordant one with the other geographically, tend to prevail at the extremities of the range in North America and South America as well, indicating a centrifugal evolution and movement of these characters.

Below I have listed some of the available samples of *S. louisianae* by geographical regions, with special emphasis on some of the more

significant South American samples reviewed since 1953, and giving certain measurements and proportions as known for the combined samples from each region (n = number of workers in each combined sample).

Southeastern United States (8 localities in 5 states): HL 0.52-0.61, ML 0.27-0.23 mm; CI 82-87, MI 52-57 (n = 15). Guatemala and Costa Rica: HL 0.50-0.58, ML 0.27-0.33 mm; CI 83-85 (n = 11). Cuba and Puerto Rico: HL 0.52-0.60, ML 0.26-0.32 mm; CI 83-87, MI 51-56 (n = 11). Colombia (Rio Porce and Medellin, leg. N. A. Weber): HL 0.54-0.61, ML 0.32-0.34 mm; CI 71-84, MI 55-56 (n = 3). Surinam (La Poulle and Dirkshoup, leg. I. van der Drift): HL 0.49-0.53, ML 0.29-0.30 mm; CI 83-86, MI 57-59 (n = 2). Goiás (Anapolis, leg. W. W. Kempf): HL 0.47, ML 0.23 mm; CI 85, MI 49 (n = 1). Southeastern Brazil (States of Rio de Janeiro, São Paulo, Santa Catarina and Rio Grande do Sul): HL 0.46-0.58, ML 0.28-0.37 mm; CI 77-92, MI 56-67 (n = 22). Bolivia (Rosario, leg. W. M. Mann): HL 0.50-0.53, ML 0.31-0.32 mm; CI 81-83, MI 60-63 (n = 6). Holotype female of var. *longicornis* from Coroico, Bolivia: TL 3.0, HL 0.66, ML 0.38, WL 0.77 mm; CI 85, MI 58. Northern Argentina (3 localities): HL 0.49-0.64, ML 0.26-0.35 mm; CI 83-89, MI 52-56 (n = 6).

An additional record of interest is a sample of *S. louisianae* from Yuma, Arizona, "on cotton," "HAGA" leg.

Descriptive Note on the Holotype of *S. fusca*

Holotype worker: TL 3.4, HL 0.67, ML 0.40, WL 0.71 mm; CI 82, MI 59. A large variant of *S. louisianae*; mandibles farther apart and relatively more slender than in North American *louisianae* samples; inner margins not so sharply concave near apex. Apical fork: dorsal tooth about 0.12 mm long, ventral about 0.09 mm; two subequal intercalary denticles. Preapical tooth about 0.05 mm long, and its tip situated about 0.05 mm from dorsal apical tooth; slightly curved toward mandibular apex; larger and farther from apical fork than in most *S. louisianae*. No other teeth or denticles on inner mandibular border. Scape L 0.44, funiculus L 0.58 mm.

Promesonotum high, with convex profile, promesonotal suture (sulcus) visible in some lights. Metanotal groove weak. Propodeal teeth acute, elevated, with narrow infradental lamellae approaching cariniform; teeth about $\frac{4}{5}$ as long as the distance between their basal centers. Petiolar peduncle longer than node; node broader than long. Postpetiole robust, fully punctulate, opaque. Spongiform appendages as usual for *S. louisianae*. Gastric costulae extending about $\frac{1}{2}$ the

length of the basal tergite, interspersed with reticulo-punctulation; remaining half of tergite nearly completely smooth, distinctly shining. Pilosity as usual in *S. louisianae*, but a little coarser than the average. Color dark ferruginous, but not as dark as some specimens of the "*unidentata*" conformation from the wet Serra do Mar, the coastal mountain strip of São Paulo; these latter samples approach black.

The *fusca* type is similar to *producta* as well as to more "typical" *louisianae*, but differs in details of cephalic proportions and in sculptural details. The body of the *fusca* type is more robust, and the hairs of the pilosity are larger throughout. The preapical tooth is larger and is situated a little farther from the apical fork.

Descriptive Note on the Lectotype of *S. unidentata*

Lectotype worker: TL 2.2, HL 0.55, ML 0.36, WL 0.54 mm; CI 79, MI 66. Despite its slightly smaller size and wider head, there is little doubt that this type and the species I described as *clasmospongia* are conspecific. I have partially cleaned and reexamined the postpetiole and gaster in the available types of *unidentata* and *clasmospongia*, and the postpetiole is now seen to vary from weakly to moderately shining discal, while the gastric dorsum now appears as smooth and shining, with reticulation nearly or quite absent, except for the basal costulae. The frequent presence of a refractory hardened secretion (?) on the gastric dorsum is misleading when describing sculpture in a number of dacetine groups. The specimen now in the Naturhistorisches Museum in Vienna has been selected as lectotype, and is so labeled.

Synoptic Synonymy of *Strumigenys louisianae*

In the list below are found the names currently considered to be synonyms of *S. louisianae*. Full page references for each synonym are to be found in Brown, 1935b, p. 28, or, in the case of new synonymy, with the species heading above.

S. louisianae Roger, 1863

- = *unidentata* Mayr, 1887, n. syn.
- = *unispinulosa* Emery, 1890.
- = *unispinulosa* var. *longicornis* Emery, 1894.
- = *fusca* Emery, 1894, n. syn.
- = *louisianae* var. *obscuriventris* Wheeler, 1908.
- = *bruchii* Forel, 1912.
- = *infidelis* Santschi, 1919.
- = *eggersi* var. *cubaensis* Mann, 1920.
- = *louisianae* subsp. *laticephala* M. R. Smith, 1931.
- = *louisianae* subsp. *soledadensis* Weber, 1934.
- = *louisianae* subsp. *guatemalensis* Weber, 1934.
- = *louisianae* subsp. *costaricensis* Weber, 1934.
- = *clasmospongia* Brown, 1953, n. syn.

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A NOTE ON THE ANT *GNAMPTOGENYS HARTMANI* WHEELER.—Workers and winged females of this ant were received recently from Dr. M. R. Smith of the U. S. National Museum and were determined by direct comparison with the type in the Museum of Comparative Zoology. The sample represents a nest taken in the soil of a banana plantation on Zapote Farm, La Lima, Honduras, May 18, 1961 (E. Mólendez leg.). This is the first record of the species to come to light since the original description, published in 1915, based on a single worker specimen from Huntsville, Texas (C. G. Hartman leg.). The type locality in northeastern Texas has always seemed anomalous for a genus otherwise confined to a more strictly tropical climate and not known from any other samples occurring natively within the continental United States, but until the present find, the good possibility remained that *G. hartmani* was an extralimital relict. It now seems more likely that the Texas record represents either a locality error or an adventive specimen taken from bananas. No ecological data accompanied the original find. At least, the occurrence of this (or other) species of *Gnamptogenys* in Texas remains to be convincingly demonstrated.—W. L. BROWN, JR., DEPARTMENT OF ENTOMOLOGY, CORNELL UNIVERSITY.

ANTHICUS TOBIAS MARSEUL,
ANOTHER TRAMP SPECIES
(COLEOPTERA: ANTHICIDAE)

BY F. G. WERNER
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Among the rather numerous collections of Anthicidae examined by the author during the past ten years there have been small numbers of an unidentified species of *Anthicus* from a truly amazing variety of localities. In the United States, which yielded the first examples seen, specimens have turned up from the Atlantic to the Pacific and from New England to Florida, including such places as Catarina, Texas and the Sierra Ancha Mountains of Arizona. The author must admit that he held these specimens to represent an undescribed species and had prepared a description for publication and designated types. Then a specimen was sent from Guam, in the Marianas, others from Oahu identified as *Anthicus mundulus* Sharp, and, most recently, others from Jamaica and Venezuela. By this time it had become apparent that the species must have been introduced into part of the localities. Structurally, it is quite unlike any other species in the New World, especially in the details of the very elaborate structure surrounding the male primary gonopore. So an Old World source was likely.

The true identity of the species was revealed in the British Museum collection, which the author was privileged to study recently. Specimens identified as *Anthicus tobias* Marseul from Aden, India and Java are the same as those previously seen. The type specimen of *tobias* has not been examined but the specimens at hand agree perfectly with the original description. Both *Anthicus mundulus* Sharp and *A. cervinus* LaFerté, under whose names most specimens have been misidentified, are quite different.

In the United States, at least, this is not a very abundant species. In most cases only one or a very few specimens have been seen from any one locality. It may be more abundant on Oahu, if one can judge from the number of specimens that have accumulated in collections. In order to help prevent further misidentification in any new areas where the species may be found, a brief description and figure are given here. The male genitalia are very distinctive. In most cases an examination of the tip of the tegmen will suffice for the identification of the species; none other has been seen with a similar conformation. A quick perusal of the British Museum collection and the Pic collection in Paris failed to disclose any species that might be likely close

relatives, at least on external features. However, the author is not thoroughly familiar with the Old World fauna and may have missed some species.

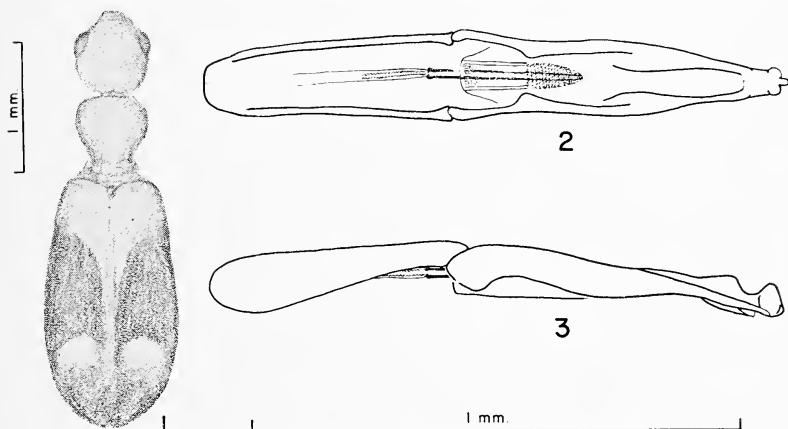
Anthicus tobias Marseul

(Figs. 1-3)

Anthicus Tobias Marseul, 1879, L'Abeille 17: 125. Pic, 1911, Coleop. Cat., pars 36: 77.

Rufous, the antennae, palpi and legs luteous; elytra with a ferruginous to piceous area that extends from the basal $2/5$ to $1/4$ to the apex, with the suture pale anteriorly, and with a very pale spot on each elytron at about $1/5$ from the apex. Prothorax and elytra flattened.

Head subquadrate, but base rounded and slightly notched at the middle. Surface smooth, with dense, rather small punctures throughout, even on the midline. Pubescence moderately dense and short, fine, decumbent. Eyes moderately large, prominent. Antennae slender but slightly thickened apically. Prothorax widest at apical third, flattened, with punctures and pubescence similar to those of head. Elytra subparallel, flattened; omoplates slightly elevated; suture elevated on apical half. Surface smooth, moderately densely punctured, the punctures on the basal portion slightly larger and feebly asperate, those behind fine and small. Pubescence golden in the pale zone, brown over the dark markings, decumbent, fine, directed obliquely laterally in the basal fourth, not conspicuous. Tactile setae very short but erect. Male pygidium flattened, with truncate apex; hypopy-



Figs. 1-3. *Anthicus tobias* Marseul. 1. Habitus sketch, with sculpture and pubescence omitted. 2. Aedeagus, in ventral view as it lies in the abdomen. 3. Aedeagus, in left lateral view.

gium with a shallow, V-shaped notch. Aedeagus with a dorsal ridge and subapical notch on the tegmen; gonopore armature very large and complex, not inverted.

The total length of the specimens examined ranges from 2.6 to 3.1 mm. Both the pale area at the base of the elytra and the subapical spots vary somewhat in size. The most similar-looking species in the North American fauna is *Anthicus cervinus*, which has curved pubescence on the elytra in most parts of its range, elytra that are not flattened, and very different male genitalia.

Range: Except for the localities followed by a bibliographic citation, the author has seen specimens from each of the following localities: *ASIA*: Arabia (Pic, 1911); W. Aden Prot.: Lahej — XI-27-1937 — Scott & Britton; Iraq (Marseul, 1897); Turkestan (Pic, 1911); India (Pic, 1911) and U. P.: Fyzabad — Hingston. *INDIAN OCEAN*: Mauritius (Pic, 1911). *E. INDIES*: Java: Preange-Tijembong — 4-'15 — Corporaal. *PACIFIC OCEAN*: Marianas: Guam: Agana — X-10-1952 — J. W. Beardsley; Hawaiian Islands: Oahu: Ewa — X-1958 — lt. trap; Waipio — I-22-1946 and VIII-1949 — lt. trap — Pemberton; Manoa — IX-10-1949 — at lt. — O. H. Swezey. *NORTH AMERICA*: CANADA: Quebec: Granby — VI-15-1911 — P. E. Mercier. U. S. A.: MASS.: Boston — VIII-13-1911 — found dead on Boston Common — Fall Coll.; Bedford — VII-15-1911 — C. A. Frost; Nahant — VI-3-1935 — P. J. Darlington; Framingham — VIII-12-1944 — C. A. Frost; Dover — VIII-3-1949 — K. Christiansen. CONN.: Hamden — VIII-25-1939 — lt. trap — N. Turner. WIS.: Wood Co.: Nekoosa — VIII-23-1948 — lt. trap — W. W. Barrett. ILL.: Chicago — IX-6-1909 — Fall Coll. and X-24-1921 — A. B. Wolcott; LaSalle Co.: VIII-24-1936 — F. Werner, and Lowell — VIII-24-1948 — lt. trap — F. Werner & W. Nutting. PENN.: Delaware Co. — IX-10-1941 — R. C. Casselberry; Williamsport — VIII-3-1949 — at lt. D. C.: Washington — VIII-15-1911 — at lt. — H. S. Barber. FLA.: Jacksonville — VI-10 — R. L. Blickle; Broward Co.: Pineland — X-1956 — L. N. Bell. ALA.: Mobile — VI-23-1950 — E. O. Wilson. TEX.: Dimmit Co.: Catarina — VII-7-1948 — at lt. — F. Werner & W. Nutting. ARIZ.: Sierra Ancha Mts. — X-1-1925 — D. K. Duncan. ORE.: Jackson Co.: Ashland — Black & Davis. *W. INDIES*: Jamaica: Spanish Town — flying at dusk; Morant Bay; and Gordon Town, all II-1937 — E. A. Chapin and R. E. Blackwelder. *S. AMERICA*: Venezuela: Caracas — V-VI-1957 — M. J. & S. Sargent.

CHEMICAL AND BIOLOGICAL CHARACTERIZATION OF VENOM OF THE ANT *SOLENOPSIS XYLONI* McCOOK

BY MURRAY S. BLUM¹, J. E. ROBERTS, JR.², AND A. F. NOVAK³

The reaction of human beings to the sting of the indigenous southern fire ant (*Solenopsis xyloni* McCook) is in marked contrast to that produced by the sting of the closely related imported fire ant (*Solenopsis saevissima* [Fr. Smith]). Whereas the sting of *S. saevissima* is characterized by a painful edema and marked necrosis (Caro *et al.* [1957]), we have found that the sting of *S. xyloni* seldom results in more than a mild prurience. These facts strongly indicate that the venoms of these two species of *Solenopsis* differ chemically. The purpose of this present paper is to compare the chemical and biological properties of these *Solenopsis* venoms in order to possibly determine what is responsible for their different dermatological effects.

Materials and Methods

Venom was collected from major or media workers employing a previously described method (Blum *et al.* 1958). The chemical and biological properties of *S. xyloni* venom were studied by procedures described elsewhere (Blum *et al.* 1958; Blum and Callahan 1960). A crystalline derivative of the main component in *S. xyloni* venom was prepared from an ether extract of 450 poison glands dissected from major workers. The derivative was isolated by the method of Blum and Callahan (1960).

The dermatological effects of the sting of *S. xyloni* to human beings were studied by observing reactions at sting sites.

Results and Discussion

The chemical properties of the venom of *S. xyloni* parallel those of the venom of *S. saevissima* in nearly all respects. Like the venom of *S. xyloni*, the venomous secretion of *S. saevissima* consists of an alkaline two-phase system in which the suspended droplets represent the minor phase (Blum *et al.* 1958). The main constituent in the venom of *S. xyloni* is an amine which is chemically comparable to the amine isolated from the venom of *S. saevissima* (Adrouny *et al.* 1959; Blum and Callahan 1960). The infrared spectrum of the venom of *S. saevissima* is virtually superimposable on the spectrum of the venom of *S. xyloni* and it is probable that the amine constituents which these

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spectra represent are very similar. On the other hand, whereas the venom of *S. saevissima* contains two rhodamine-complexing minor components, the venom of *S. xyloni* contains only one.

The chemical similarities of the two venoms are paralleled by their biological properties. The venomous principles of *S. xyloni* exhibit the same antimycotic and antibacterial activities as are found in the venom of *S. saevissima* (Blum *et al.* 1958). The pronounced hemolytic effect and insecticidal activity of *S. xyloni* venom compare to these same properties in the venom of *S. saevissima* (Adrouny *et al.* 1959; Blum *et al.* 1958). Thus the venoms of both of these fire ants feature the same broad-spectrum activity against diverse types of cells.

The skin responses of human beings to the stings of these two fire ants are similar only during the first few hours, both being characterized by an immediate flare followed by a wheal. However, whereas the sting of *S. saevissima* is always characterized by an umbilicated pustule at the sting site (Caro *et al.* 1957), we have found that the response to the sting of *S. xyloni* seldom results in more than a mild prurience. In the few cases where minute pustules were observed, they were on individuals who were quite sensitive to the sting of *S. saevissima*. At least three explanations seem possible: (1) minor structural modifications of the necrotoxin in the venom of *S. saevissima* are associated with a large increase in necrotoxicity when compared to its counterpart in the venom of *S. xyloni*, (2) the concentration of the necrotoxin in the venom of *S. saevissima* is greater than its counterpart in the venom of *S. xyloni*, (3) the minor components contribute to the necrotoxic action of the venom. These hypotheses remain to be determined experimentally.

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MASS INSECT CONTROL PROGRAMS: FOUR CASE HISTORIES*

BY WILLIAM L. BROWN, JR.

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PREFACE

Insect control is a vast subject. It encompasses many methods of approach meant to protect a wide diversity of human resources, including the lives and health of humans themselves. Upon the success or failure of insect control programs have rested the fate of armies, of great canals and populous lands. Yet, though man has registered many practical successes against particular insect menaces, we do not yet understand fully the underlying dynamics of insect populations (or for that matter, of other animals, including man himself), and until we do, perfect control will probably continue to elude us in many cases.

However, there exist practical measures that have been used successfully to control or eradicate many kinds of insects, even though

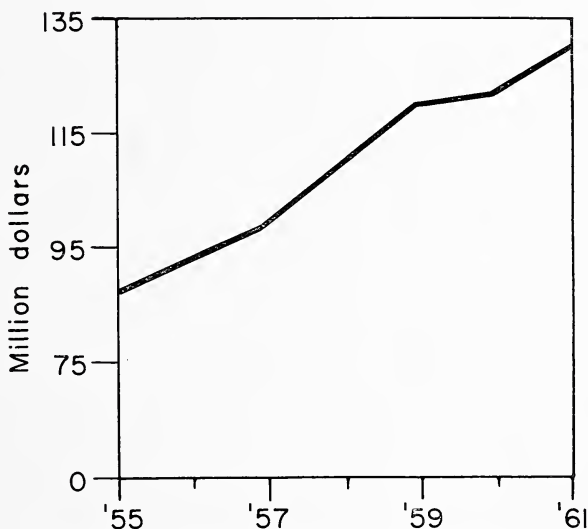


Figure 1. Insecticide sales by U. S. producers in recent years, projected through to the end of 1961. Domestic consumption of insecticides actually declined slightly during 1960 in the U. S., but exports more than made up this dip. From Chemical Week, July 22, 1961, by permission.

*This study and the report were sponsored and supported by the Conservation Foundation, New York.

we may not understand exactly how a particular measure takes its effect. In recent years, developments in practical insect control have come thick and fast, particularly in the field of pesticides. The development since World War II of chlorinated hydrocarbons, carbamate and organic phosphate insecticides, distributed by mass aerial spray techniques, has revolutionized control work and has raised insecticide production and aerial application to the status of big businesses. But, promising as it seemed in the immediate postwar years, simple mass aerial broadcasting of toxic materials has not always led to efficient control of the target pest. Furthermore, the extensive application of this relatively unselective technique inevitably caused damage to incidental targets — plants and animals or property valued by humans — and there even arose a threat to human health itself.^{9, 20} As such damage and threat of damage became more obvious, protest against mass air-spraying increased in volume, and naturally the demand grew for research into alternative means of control.

It is my intention now to attempt to illuminate the current status and outlook of insect control methods in the United States by outlining four case histories of large-scale insect control programs. It is difficult to say how representative these case histories may be, considering the very diverse nature of insects and the damage each kind does. All four of the programs are large and expensive ones as such operations go, all have been considered to be eradication programs at one time or another, and all have been guided or conducted by agencies of the United States Department of Agriculture (hereinafter referred to as USDA).

Since these great programs affect or involve many people and many diverse vested interests, they are all to some extent controversial. Because controversy about them involves many contradictory findings and interpretations, it is often difficult to gain a true and unbiased conception of what is going on in a given instance. For this reason, I have tried to draw my information from as large and varied a group of sources as I could find (see Acknowledgements and References Cited). Let us now see if a resumé of four programs — Gypsy Moth, Fire Ant, Mediterranean Fruit Fly and Screwworm — will help us to appreciate the problems of mass insect control.

THE GYPSY MOTH

Introduction

The Gypsy Moth, *Porthetria dispar* (formerly *Lymantria dispar*), is a variable insect, a native of Eurasia, where it ranges from Portugal and North Africa to Japan. The insect was imported to the Boston

area from France in 1869 by a misguided naturalist who believed that he could cross it with silkworms. Moths escaped from his breeding colony, but it was not until 1889 that the first severe outbreak defoliated fruit and shade trees in many towns of eastern Massachusetts. Control work was started by the state and apparently was successful, for populations were so low by 1899 that control operations were ended. The moth soon again built up extensive populations, and control work was resumed in 1905, but it had spread by this time to western Massachusetts and parts of Maine, New Hampshire and Rhode Island. In 1906, Congress voted aid to the infested states to help prevent the spread of the moth, but despite all efforts it continued to expand its range.

Biology and Nature of the Damage

The gypsy moth has a single generation per year. The winter is passed in the egg stage, and in New England the larvae hatch in mid-spring and feed through May and June, entering the quiescent pupal stage in early July. The larvae feed on a wide variety of broad-leaved trees and shrubs, especially oak, willow, poplar, birch, fruit trees and, in heavy infestations, even hemlock and pine. Dense populations may completely defoliate large areas of forest, weakening many trees and killing others outright.

The heavy-bodied female does not fly, but puts out a powerful scent to which the strong-flying male responds, even to extremely minute amounts carried on the air great distances, by flying upwind until contacting the source individuals and copulating with them.¹⁸ The female deposits her eggs on tree trunks, fences, rocks and other solid objects. The young larvae spin silken threads on which they are easily spread by the wind before they start to feed.

According to Campbell⁴ the strong fluctuations in abundance of the moth are density-reactive, a most critical factor in this reactivity being the larval behavior. At low densities, the caterpillars tend to descend to the leaf litter to rest during the daytime, and feed mainly at night out on the foliage. When density is intermediate, the larvae rest during the day under loose bark on the tree trunks, a habit that has been used to advantage in control work (bands of burlap placed around trunks of infested trees are removed daily and the caterpillars found beneath them are destroyed). At high densities, the larvae remain on the foliage day and night, and are subject to heavy losses due to disease, desiccation and attack by ichneumon-wasp parasites. Population "crashes" are correlated with previous high densities of larvae.

Control Problems

Early control efforts by the State of Massachusetts and the Federal Government included laborious and expensive methods such as hand-creosoting of egg masses, shelter-band and tanglefoot trapping on tree trunks, and various kinds of spray operations from the ground. For many years, control and quarantine programs appear to have confined the infestation to the area east of the "barrier" at the Berkshires and Green Mountains. Occasional extralimital infestations appearing in New Jersey, Ohio, Pennsylvania and Canada, particularly after egg masses were spread widely by the hurricane of 1938, apparently were eradicated before getting out of hand. Extensive introductions of predatory and parasitic insects from Europe and Japan were made beginning in 1905, and about ten such insects have taken hold in North America. Much of the subsequent history of the infestation was summarized in the report of the Gypsy Moth Eradication Meeting¹ held in Ithaca, New York, in September, 1957:

"Following World War II, DDT was found to be a specific insecticide for the gypsy moth. At about the same time application of insecticide by plane became a practical undertaking. It was a new day for gypsy moth control. Heavy infestations within the area of general spread were suppressed or brought under control, and new infestations beyond the barrier were detected and held in check. Pennsylvania eradicated with reasonable effort and expenditure the gypsy moth on an area of 300,000 acres. Unfortunately more than 20 million acres were infested in this country before a practical control was discovered.

For some unexplained reason, the gypsy moth infestations seemed to explode* in 1950 and there was rapid spread beyond the barrier zone. Following the outbreaks in 1953 and 1954, surveys revealed the new areas of infestation west of the barrier zone in New York, New Jersey and Pennsylvania, aggregating nearly 9 million acres. An isolated infestation found in the vicinity of Lansing, Michigan, was immediately scheduled for eradication. The occurrence of these infestations west and south of the barrier posed a serious threat of spread to the hardwood forests throughout the eastern and southern United States. The control and quarantine programs that had successfully held the moth in check for so long were no longer adequate. . . ."

*The explosion might better be said to have fairly begun in 1951 or 1952; see Figure 2. Its inception so soon after mass air spraying of DDT began on an operational basis is a phenomenon which, curiously enough, seems to have attracted little attention. It was first pointed out to me by Prof. F. M. Carpenter of Harvard University. — W. L. B.

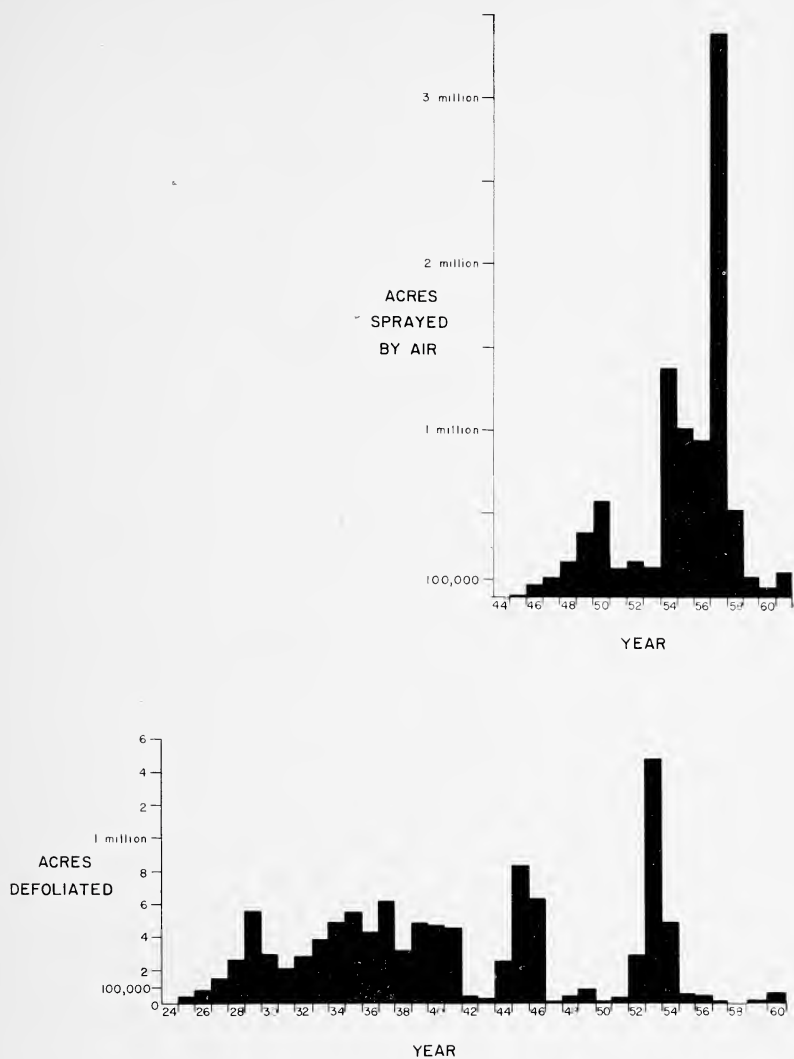


Figure 2. Graphs to show the ups and downs of the struggle against the gypsy moth in the U.S. Acreage showing substantial defoliation by gypsy moth larvae each year (below) is compared with acreage sprayed from the air (above) mostly with DDT at 1 lb per acre. Some suppression treatments used only 1/2 or 3/4 lb. of DDT per acre, and sevin has partly replaced DDT in recent years. For details, see summaries by USDA in Appendix A, upon which these graphs are based.

In spite of the difficulties involved, Federal and some state authorities were still speaking in terms of "eradication" of the gypsy moth in 1956 and 1957, while other state and local people were by this time hesitant about backing an all-out eradication effort.

In 1957, after about three and one-half million acres had been sprayed (two and one-half millions of them in New York State), DDT residues were found on forage crops and in the milk of cows that had grazed on treated areas in New York State, as well as in eggs from poultry farms that had received spray.¹⁶ DDT tolerances for milk are set at zero by the Federal Food and Drug Administration and by health authorities in New York among other states.

When the DDT residues were found persisting on forage crops and in the raw milk for periods up to a year, New York suspended eradication efforts ". . . so that," as the USDA's *Cooperative Plant Pest Control Programs* for 1958 put it, "the 1957 work could be fully evaluated and any required 'mopping up' could be done; however, during the eradication season tests were made of several alternate insecticides more suitable than DDT for use on pasture and forage crops."

Since 1958, New York has been doing a greatly reduced amount of spraying by air, using in part the new insecticide *sevin*, a carbamate having very low toxicity to mammals and birds, and one leaving no residue in the milk. Unfortunately, *sevin* is not as good against the gypsy moth as is DDT, it is highly toxic to honeybees, and it injures plants to some extent.

Aside from the dairy-linked residue problem, DDT has received rather good marks from most biologists checking the general ecological effects of mass spray at one pound to the acre. A few fish are sometimes killed, birds that catch insects on the wing depart, and certain aquatic insects suffer, but the known damage does seem tolerable. Long-term residual effects on soil organisms are, however, not well known.

The chief short-range danger of mass aerial DDT campaigns lies with the loose spray practices or accidents that result in duplication (or worse) of spray strips in a given area. Field insect control men often complain about the quality of pilots available for some spray programs, and numerous incidents have occurred to illustrate the point that some of the pilots are irresponsible or incompetent, or that they are poorly directed. For this and other reasons, it seems certain that operational mass spraying does not always give the same safe results as are found for the neatly-sprayed test strips of some of the studies, and landowners are often justified in complaining of double or triple

doses of spray on their land. In view of these difficulties, DDT must be considered as only a marginally safe compound even at the 1 lb per acre dosage.

The issue of mass spraying has come to one court battle that attracted considerable attention. A group of plaintiffs led by Dr. Robert Cushman Murphy, the well-known ornithologist, sought injunctions against mass spraying of DDT for gypsy moth on or near their land, which was situated near New York City and mostly on Long Island. Most of the plaintiffs were organic gardeners and nature-lovers, and much of their testimony tended to be emotional in tone but rather insubstantial as to verifiable facts. The government defended itself with toxicologists and entomologists who presented a generally factual picture, and the case was decided against the plaintiffs by the Federal judge, although he warned the government to use more care in spray operations. The main effect of the case appears to have been to make the spray agencies hesitant about treating Long Island and many other farm areas. Also, by agreement with New York health authorities, a wide belt is left unsprayed around the large reservoirs of the metropolitan water supply. Such areas can of course provide refuges for the moth from which it is potentially able to recolonize adjacent treated areas.

Thus, for various reasons, the large key "border state" of New York has in fact been forced to abandon the "eradication" campaign, and the Plant Pest Control Division of the USDA now speaks instead of a "containment program" which would include chemical treatments within the infested area and along its periphery to back up the continued quarantines.

Infestations in Pennsylvania and Michigan, thought on several past occasions to have been eradicated or nearly so by DDT spray, still survive. Directly menaced are the hardwood forests of the Atlantic Slope, the Appalachians and the Mississippi Valley.

What Can Be Done About the Gypsy Moth?

I gather from conversations and correspondence with entomologists and foresters responsible for gypsy moth control at the state and local level that they generally share an uneasiness about the use of air-sprayed non-specific poisons such as DDT and sevin on forest and watershed areas. Most of them expressed the hope that some substitute control method eventually would be found. So far as we can see now, potential substitute methods lie in four different areas: predator-parasite manipulation, propagation of bacterial or viral diseases,

baiting with attractants, and genetic disruption. In briefly discussing these topics, we should not overlook the possibility that there may exist entirely different modes of attacking the problem that have not yet occurred to anyone.

Predators and parasites. As already mentioned, a number of predaceous, parasitic and parasitoid insects, mainly beetles, flies and wasplike types, have been successfully colonized in the United States after being brought from Europe and Asia. Different ones attack every stage of the moth, from egg through adult, but few of them are strictly specific to the gypsy moth. The efficacy of the parasites is now open to question, since they have obviously not prevented serious outbreaks in areas where they are known to be established. Nevertheless, some natural enemies are known to be very effective at high densities of the host, and their value in the absence of possibly disturbing chemical control has not been thoroughly checked in recent years. Furthermore, it is likely that the established introductions represent only a fraction of the potentially useful arthropod enemies of the moth existing in Eurasia or elsewhere. In theory at least, there remains the possibility of keeping the moth at a tolerable population level by means of natural enemies, especially if used in conjunction with other biological control methods. Further research on natural enemies of the moth would certainly be desirable.

Disease propagation. The gypsy moth larva is susceptible to certain bacterial and viral diseases, among which *Bacillus thuringiensis* shows enough promise to have stimulated large-scale tests by Federal and state agencies. These tests, only partly completed, employ a "sticker" of tung oil or one of the improved English Lovol products to fasten the bacterial spores to the foliage. The suspension of spores in sticker can be sprayed from the air, and presumably is not harmful to plants or wildlife. So far, results have not been encouraging.

Attractants. The female gypsy moth, as already stated, can flutter along the ground or over low plants, but she cannot truly fly for any distance. The strong-flying males, like those of many moths, are strongly activated, even over long distances, by scent released by the female from the terminal segments or "tip" of her abdomen. Upon sensing even minute amounts of this scent, the male responds by flying upwind, in this way automatically approaching the scent-producing female, and ultimately coming near enough to mate with her. The scent obtained by extracting the female tips in benzol has been used for years as a lure in metal or paper traps to survey suspected areas in order to determine whether males, and therefore a likely infestation, are present. The female tips are obtained by the laborious and extremely expensive rearing of thousands of hand-collected female

pupae, many of them imported from Europe and North Africa. Costs have ranged up to a half dollar per tip in poor collecting years.

In 1960, after producing several moderately effective synthetic lures, M. Jacobson and his co-workers of the Entomology Research Division, Agricultural Research Service, USDA, succeeded in isolating the principal sex attractant from some half a million female gypsy moth tips collected in Connecticut and Spain. The substance was prepared synthetically and found to be an ester alcohol with 16 carbon atoms in its main chain. In the course of preparing the natural lure, a closely related substance (with 18 carbon atoms in its main chain) was also found to act as a strong gypsy moth lure.¹⁷ This preparation, named *gyplure*, has the advantage that it can be synthesized cheaply and in quantity from ricinoleic acid, a common component of castor oil. Tested in field traps, quantities of this substance as small as one microgram proved equal in luring power to traps baited with the natural lure. In 1961, as this is written, field trials are being carried out to test the efficacy of gyplure-toxicant combination baits in reducing moth populations. Included in this program are "confusion" tests with saturated levels of gyplure in granular and spray formulations. Initial technical difficulties have been met, but it is hoped that these can be cleared up during the 1962 season. It will be appreciated that many hopes ride on these crucial trials.

Genetic methods. The success of the screwworm eradication program (see below) has raised the possibility that the release of sterilized males might be used to control or eradicate gypsy moth populations. This possibility remains to be explored by further studies of the moths' mating behavior and physiology and the practicability of rearing, sterilization and release procedures. Sterile male release might be made much more effective after reduction of the population by bait attractants or other means.

Other theoretical possibilities for control rest in the fact, discovered years ago by R. B. Goldschmidt, that certain different native Old World populations of *P. dispar* differ in their sex-determining mechanisms in such a way that crosses made between them produce intersexes. It can be argued that the overall fitness of a population might be cut by introducing north Japanese strains into the American populations, which originated in France. The possibility is worth investigation despite some theoretical difficulties.

THE IMPORTED FIRE ANT

Introduction

The fire ants belong to seven or eight New World species in the *geminata* group of genus *Solenopsis*. The group as a whole has a

tropical warm temperate distribution throughout the Americas, from southeastern and southwestern U. S. to central Argentina and Chile. The species are quite closely related and are similar in their habits. All form populous nests, at maturity containing 25,000 to more than 200,000 active and aggressive adult workers. The workers in a mature nest vary considerably in size from large soldiers down to much more numerous minor workers only 2-3 mm. long, and usually only a single functional queen is present. Nest foundation follows the pattern typical for ants, in which virgin winged females mate with males during a nuptial flight, then quickly shed their wings and, as young queens, burrow into the soil and begin the rearing of the first brood in a small chamber. Later, as the nest grows, it usually comes to be capped by an earthen mound sometimes two feet or more high and often two or three feet in diameter.

Up to the First World War, only three of the fire ant species were known to occur in the U. S., of which two, *Solenopsis xyloni* and *S. geminata* (native fire ant) were found in the southeastern states. It seems possible that the "native" fire ant is itself a post-Columbian introduction, and it has been spread widely over the tropics of both hemispheres by human commerce. In past years, *S. geminata* had gathered to itself much the same reputation as a nuisance now generally assigned to the late-coming imported fire ant (*S. saevissima*) that is the subject of this discussion. The imported fire ant arrived at Mobile, Alabama in produce or ballast at or a few years after the end of the First World War. At first the ant (then represented solely, so it seems, by a blackish phase with a dull orange band at the base of its gaster — the so-called "variety *richteri*," common in Argentina and Uruguay) spread only very slowly in Mobile and its environs. At some time around the beginning of the 1930's, a smaller, light reddish form of *saevissima* appeared in the Mobile area. This phase corresponds to populations of the species common in southern Brazil and Paraguay, and it seems most likely that its appearance marks a second introduction of *saevissima* into the Mobile Bay port area.

Coincident with the advent of the red phase, the entire *saevissima* salient in southern Alabama entered upon a period of rapid expansion that carried the main infestation across state lines by 1940. The expansion apparently has not yet reached its full extent, although infestations are or have been known to occur in ten states ranging from Texas and Arkansas to North Carolina and Florida. Expansion occurs in two main ways — by steady widening of the main infested areas due to short-range aerial spread of winged females, and through

colonization ahead of the main infested area by queens and colony fragments transported by vehicular traffic. Nursery stock used to be a prime source of new infestations, but since nursery treatments and quarantine regulations have come into effect, fertilized females accidentally carried in automobiles are probably responsible for most colonization.

Wherever the red phase has expanded to overcome the dark phase, the two extreme forms have interbred to produce a series of intermediates, and in most cases the red form soon comes to predominate by a process of genetic swamping coupled with its greater success in warfare between nests. In fact, it may not be too extravagant a speculation to conclude that it was the injection of the red-form genes into the existing dark population that sparked the spectacular spread of the species in the last three decades. At present, the North American population consists mainly of light reddish ants, the dark phase surviving mainly in peripheral situations and cool swamplands.

Wherever it spreads, *S. saevissima* tends to replace the populations of *S. xyloni* and *S. geminata* in its path, though this is less true of the dark-colored *geminata* occupying woodlands in Florida and perhaps elsewhere²⁶; *saevissima* in the U.S. generally avoids shaded situations. The imported fire ant is able to build up remarkably dense populations. I have seen pastures in eastern Mississippi in which it was literally possible to walk for a considerable distance by stepping from mound to mound without touching a foot to the ground between. Such situations are exceptional, and usually mark the entry of the species into a new area, or else follow control measures that have knocked out a stable population of old, large nests. When the old nests are eliminated, large numbers (up to 185 per acre) of smaller new ones take their places, but as they grow, nests are gradually eliminated until the density is again relatively low (10-50 nests per acre usually).

Studies made to date have not been critical enough to detect possible widespread population fluctuations in untreated areas, but about a century ago, Bates noted a radical change in a native population of *S. saevissima* in the Amazon Basin.

A small number of parasites of this ant are known in its native habitat, including several known or suspected inquiline species of ants and a phorid fly, but no real study has ever been made of this phase of the ant's biology. These parasites have been lightly dismissed as a control possibility by previous writers, but it seems to me that the whole subject of parasitism should be looked into. Parasites might do

much better in the U. S. than in their native range, and even a minor reduction in fire ant populations might reduce it appreciably as a nuisance in some areas.

Nature and Extent of Damage

The kind and extent of the damage done by fire ants has been the subject of much dispute. Generally, control agencies, and especially the USDA-affiliated ones, have emphasized the deleterious effects produced by the ant, while some zealous anti-insecticide writers have written it off as doing negligible harm. Both groups admit that the ant mounds do interfere with the harvesting of forage crops. Harvesting machinery is often damaged by striking the hard mounds, and field hands are stung by the ants — in some cases so badly that they refuse to work infested fields. Occasionally, land values have fallen somewhat in badly infested areas. The health threat must also be considered in cities and towns, where the ants may infest lawns and gardens and even sometimes enter houses. Small children and unusually sensitive adults have occasionally suffered grave illness, or in two or three cases may even have died as a result of fire ant stings. Numerous stings result in a rash-like group of pustules that can be very annoying for several days or more. Still, the fire ant as a health menace must be ranked far below ordinary bees and wasps, which are responsible for many times the deaths that fire ants cause during a given period of years, in the same states. It is difficult to see how the ant can be classed as a serious public health problem despite scare stories in the press, television and in a USDA-sponsored film. Professor F. S. Arant, head of the entomological contingent at Auburn University, current president of the Entomological Society of America, and a top authority on the fire ant, agreeing with Dr. J. L. George¹⁰ and other state entomologists in the Southeast, calls the fire ant a "major nuisance," but deprecates its role as a crop pest. Studies made at Auburn¹⁴ and elsewhere in the South generally have borne out this evaluation. It is interesting to note that the studies^{6, 27} that have found more or less serious damage done to crop plants were made before 1953. These studies were mainly concentrated in south-central Alabama, near the Mobile Bay center of fire ant spread, and were based on personal investigation as well as uninvestigated farmer reports. That some crop damage was done in this area in the late 'forties and early 'fifties is incontestable, but even then, the damage does not seem to have been insupportable. That more recent studies have failed to find serious crop damage is probably to be laid to a gradual change in the habits of the ants or their population density,

or both. Whatever is the case, it does seem that the damage currently being done by the imported fire ant in the untreated sections infested in this country is less than would seem to justify the massive campaign that has been mounted against it. Agencies in all but two infested states do not even grant the fire ant a place in their lists of the more important plant pests. The USDA cites farmer support for the program, and this support certainly exists at least in some sections. But the enthusiasm of farmers for the spray programs is too often based merely on a vague feeling that insecticides in general are a good thing. When, as in large areas covered by the present program, the farmers individually get the spray free, they tend to overlook possible bad effects it may bring with the benefits. In any case, the satisfaction of farmers is certainly no substitute for a careful and extensive professional check of current fire ant damage. No such check has been made by the USDA, or at least none has been reported upon, since 1952.

Control Operations

Control efforts directed against the imported fire ant were first initiated on a small scale by the State of Mississippi in 1948, without notable success. A survey of the infested area was begun by the USDA in the fall of 1948, and, together with limited investigation of the biology of the ant and control measures against it,⁶ ran until research funds were stopped in 1953. This investigation did not deal with aerial control measures, and little attention was paid to wildlife damage. It is important to note that from 1953 until 1958, after the USDA had started its mass spray program, it spent no money for fire ant research.²² Meanwhile, several independent agencies had done part-time research on various aspects of fire ant biology and control, including medical studies of the effects of the venom on humans at Tulane University, biological and control studies at Auburn and Mississippi State Universities, and behavioral and other investigations by Dr. E. O. Wilson and others (including the present author) at Harvard University and in the field. The Fish and Wildlife Service, although greatly hampered by lack of research funds for this purpose, was giving some attention to the prospect of mass broadcasting of insecticides as it could be expected to affect wildlife.

Against this patchy research background, in March, 1957, the USDA noted that it had requested the approval of Congress for control of the fire ant, and Congress forthwith passed a special "Federal Plant Pest Act," authorizing the USDA to take measures against

the ant. For the 12 months beginning July, 1957, 2.4 million dollars was appropriated, to be matched by funds from state agencies, local sources and/or individual farmers. (In practice, actual matching appears to have been spotty at best, and the government has waived farmer contributions in Georgia and parts of Florida since early in the program.)

On April 18, 1957, after a brief correspondence with officers in the Entomology Research Division of the Agricultural Research Service, USDA, I received a letter from Dr. A. W. Lindquist, head of one of the sections in the Division, which started in part as follows:²²

"The idea of airplane spraying and dusting for control probably stems from the fact that extensive areas are infested. This method of application would of course be fine if it were effective. However, we would want to see considerable research conducted to determine if it would be effective and, if so, to determine what insecticides and special precautions would be necessary for maximum results. As far as we know, no research along these lines has been conducted."

This answer may be compared with that received from Dr. M. R. Clarkson,²³ Acting Administrator of the Agricultural Research Service, dated January 3, 1958, stating in part:

"In planning field operations, all available results of applicable research and practical experience are taken into account. Close liaison has been established with the Fish and Wildlife Service of the Department of the Interior and the states involved. Competent wildlife observers have been assigned to the work and experience to date indicates that a successful program can be carried out without serious consequence to wildlife resources. . . . Both the Agricultural Research Service and State Experiment Stations have *expanded* their research program in a *continuing* effort to improve operational procedures." (Italics mine — W.L.B.)

In May, 1957, as a matter of record, Dr. Ross Leffler of the Department of the Interior had written to Representative H. C. Bonner, Chairman of the House Committee considering the bill, as follows in part:

"Sufficient basic research has not been accomplished to predict losses or to properly advise operating agencies on the means of obtaining effective control and at the same time avoiding unnecessary fish and wildlife mortality."

With astonishing swiftness, and over the mounting protests of conservation and other groups alarmed at the prospect of another airborne "spray" program, the first insecticides were laid down in November, 1957. The rate of application was two pounds of dieldrin or heptach-

lor per acre, the insecticides being incorporated in granules of an inert material to cut down wind drift and lessen loss by foliage interception. It had been established that this formulation would be spread in the upper soil layers when rain dissolved the granules, and that its effect would last at least three years.¹ Dieldrin was used at three pounds per acre wherever another pest, the white fringe beetle, occurred as well as the ant, thus treating for both pests at once. Where the ant occurred alone, heptachlor was usually the choice. Dieldrin and heptachlor are extremely toxic substances — about 4-15 times as toxic to wildlife as is DDT.⁸ Many wildlife experts and conservationists, as well as entomologists both basic and economic, felt a sense of foreboding at the start of a program that would deposit poisons with 8-30 times the killing power of the common forest dosage of DDT (one pound per acre in gypsy moth control).

The spray campaign got off to such a fast start that both state and Federal agencies were caught without being able properly to organize programs that year for assessing the effects of the poisons on wildlife, so that results of such programs were delayed until after large amounts of toxicants had already been laid down.

Now that some of these results are finally available, we can see that they were acutely needed before the program was ever begun. The misgivings of the wildlife people seem to have been justified on the whole, since the kill of wildlife in sample treated areas appears to have been high in most of those that were adequately checked.^{5, 8, 10, 12, 21} The USDA disputes many of the claims of damage, but their own statements often tend to be vague and general. It does seem to be true that quail and perhaps other wildlife species will make a good comeback on treated land after two or three years, *provided that untreated areas are available nearby* to furnish replenishment stocks once the treated land begins to recover. Still, most of the information on wildlife repopulation comes from the accounts of hunters and other sources not subject to proper checking, and we still have little in the way of published studies by competent authorities on ecological recovery of treated lands.

Wash-off into streams and inlets has led to heavy losses among fish, crayfish and aquatic insects. Dieldrin at only one pound per acre sprayed on a salt marsh at Vero Beach, Florida, killed all the fish (including young tarpon) and Crustacea in the marsh and adjacent waters, and the effect lasting for weeks.¹² This particular test, meant to control sandfly populations, applied only half of the dosage of dieldrin originally used for fire ant control, and one-third the dosage actually used on white fringe beetle together with fire ant.

Although the USDA claims that the evidence is inconclusive in some cases, there does exist contrary information^{7, 10} indicating that stock losses from fire ant poisons may sometimes be significant. Various newspaper accounts, while sensational in tone and possibly exaggerated, add further to the impression that damage to cattle, horses, poultry and household pets may on several occasions have been locally serious. Even a few livestock deaths, if added to the time and effort spent by farmers in carrying out awkward measures to protect their animals from spray measures, must more than balance out any cumulative loss that fire ants may have inflicted directly on farm stock since the infestation began.

In 1959, the formulation was changed to a dosage of 1.25 lb of dieldrin or heptachlor per acre, and more recently an alternative dosage of a quarter pound per acre has been most widely used. This latter dosage, used twice at three- to six-month intervals, was developed because of the growing concern about wildlife and the residue problem. At this rate of application, wildlife apparently suffers much less seriously, but the fire ant is also much safer than under the old rate of two pounds per acre, and can probably come back in many places a year or two after the "light treatment" has been applied, according to the data of Blake, Eden and Hays¹ for similar dosages. Wildlife officials claim to have heard from Plant Pest Control officers that there still exist stockpiles of the formulation yielding two pounds of actual heptachlor or dieldrin per acre, and that this product was still being used for treating junkyards as of March, 1961, but Dr. E. D. Burgess of Plant Pest Control denies that this is so.

A serious blow was dealt the program in late 1958, when treatments were only one year old; Senator Sparkman and Congressman Boykin of Alabama asked that the fire ant campaign be suspended until its benefits and dangers could be evaluated properly. Then, in the beginning of 1960, the Food and Drug Administration of the Department of Health, Education and Welfare lowered the tolerance for heptachlor residues on harvested crops to zero, following the discovery that heptachlor was transformed by weathering into a persistent and highly toxic derivative, heptachlor epoxide, residues of which turn up in meat and milk when fed to stock. Some state entomologists now definitely advise farmers against the use of heptachlor on pasture or forage.

At just about the time that the residue question arose, the Alabama State Legislature refused to appropriate state funds for participation in the program after hearing evidence from state entomologists and some farmers that the fire ant is a nuisance rather than a direct source

of serious harm to crops or farm animals. (Alabama voted some participation funds again in 1961.) Alabama was followed out of the program by Florida in the spring of 1960. According to a U. P. release on March 26 of that year, Florida Plant Commissioner W. G. Cowperthwaite announced, "Efforts to stamp out the fire ant permanently in Florida have failed." He said that "the all-out attack on the pest is being abandoned. In its place a control program centered on badly contaminated areas will be set up. We thought at one time we could eradicate the fire ant, but it is impossible."

It seems likely that Mr. Cowperthwaite's words accurately express the situation for the South insofar as the present means of control are employed. The original plan set forth in 1957 called for eradication of the ant on the North American continent, by rolling back the infestation from its borders, applying eradication measures to more central foci in the main infestation, and instituting an effective program of treatment of especially dangerous sources of spread, such as nurseries. Nearly four years and perhaps 15 million dollars after that plan was announced, the fire ant is still turning up in new counties, and is being rediscovered in counties thought to have been freed of the pest in Arkansas, Louisiana, Florida and North Carolina. Undoubtedly, as the task of surveying for an elusive quarry continues, more reinfestations will turn up, and further "spot control" will be needed. Some two and one-half million acres, a little less than one-tenth of the total acreage known to have been infested, have now been treated with one or more of the formulations discussed above (July, 1961).

What Can Be Done About The Fire Ant?

Even before the aerial spray program began, independent research workers had brought to the attention of the USDA authorities the potentialities for fire ant control residing in the use of baits, both poisoned and otherwise. New approaches to the use of baits were being explored at the time at Harvard, and a good start was being made at Auburn University; the two investigations have since brought forth different but very promising results.

Difficulties in using most poison baits against ants include the development of social "bait shyness," a term that describes the fact that ant colonies will often "learn" to avoid baits that have been taken by, and presumably have killed, some of their foraging workers. It is not known how bait shyness arises in the colony. Hays and Arant¹³ have developed a new peanut butter bait in which very low concentrations of a new, extremely slow-acting poison called Kepone® are

mixed and squeezed into short lengths of paper soda straws. These baits have proven to be extremely effective against the fire ant in test plots in Alabama, probably because the Kepone takes five to seven days to kill, and thus puts off bait shyness until the entire colony has fed upon the poison. The USDA has also recently completed some bait tests. The effect of these formulations upon wildlife has not yet been fully tested, and there may be a hitch in this direction.

Perhaps even more promising is work done over the last few years by E. O. Wilson at Harvard²⁵ and M. S. Blum and his associates at Louisiana State University² with the so-called "trail substance" of the fire ant. This material, found in one of the sting glands of the ant, is used by the ants to mark trails leading back to the nest from food sources or other attractive objects. This liquid is released through the sting, which is used like a pen to draw a trail on the ground. The odor of the trail substance induces stereotyped foraging behavior, and also serves as the marker along which the ants run. Apparently, each species of fire ant has its own distinctive trail substance. At the present writing, the chemical composition of the trail substance is not known, but like other natural products, it will eventually be worked out, and synthesis of its components and related compounds should be possible. The trail substance has the advantage that it is a necessary part of the ants' communication system, and it is extremely potent. Presumably, it could be used to lead the ants to poison baits, or, more hypothetically, it might be used as a "confusion lure," broadcast in high concentrations, leading the ants to forage fruitlessly in all directions.

THE MEDITERRANEAN FRUIT FLY

Introduction

The Mediterranean fruit fly (or "medfly," *Ceratitis capitata*) and other fruit flies of greatest importance belong to a family (Trypetidae) of the two-winged or true flies (Diptera). They are not to be confused with the fruit flies of genetics, which are primarily yeast-feeders of the genus *Drosophila*, belonging to another family of the same order.

Biology and Nature of Damage Done

The adult true fruit flies vary from much smaller than a house-fly to somewhat larger, and they usually have their wings "pictured" with dark markings. In the usual case, the fruit fly female, after mating, will puncture unripe fruit and deposit one or more eggs in the incision. The larvae are whitish or yellowish maggots that feed in the fruit on the branch, and then either drop to the ground, or leave the fruit after it drops, and pupate in the soil. Infested fruit is, of

course, rendered unfit for human consumption. Host fruits infested are citrus, peach, mango and about 200 other fruits and vegetables. Although some true fruit fly species are found in temperate regions, most, including the medfly, are at home in tropical or subtropical climates.

In a climate like that of Florida, the medfly can produce about 10-12 generations per year, since the life cycle is completed in slightly under one month in warm weather. The medfly is a native of Africa, but it has spread to most of the world's citrus-producing areas in infested fruits carried by human commerce; the United States is one of the few such countries that have managed to exclude it. Since 1912, U. S. Plant Quarantine has intercepted the medfly over 1600 times at various ports of entry in this country, and it became established here twice, in 1929 and again in 1956, both times in Florida. On both occasions, vigorous efforts by combined Federal and state forces eradicated the fly before it could become established outside of Florida, and at present writing, the pest has no known breeding population in the continental United States.

The 1929 Campaign

On April 6, 1929, larvae were discovered in grapefruit at Orlando, Florida, and by April 10, adult flies had been found and positively identified as Mediterranean fruit fly. The Florida State Plant Board and the USDA sprang into action immediately, shifting inspectors to the area, and by May 1, 1929, a quarantine was invoked in connection with a program aimed at prevention of spread of the pest and its eventual eradication. Quarantine stations were set up on railways, roads and ports on coastal waters and inland waterways. The quarantine of automobiles moving north and south from the infested area proved difficult, but was strictly enforced — when necessary, with the help of the National Guard. Between 410,000 and 625,000 vehicles were examined each month, of which 6,900 to 13,100 were found carrying contraband material, including fruits, vegetables, soil, nursery stock, compost, etc.

Within the affected area, all actual infestations discovered and the area surrounding each one for one mile were designated as "infested zones," while a "protective zone" extended for another nine miles beyond every infested zone. Within the infested zones all known fruits and vegetables were destroyed in order to deprive the flies of breeding opportunities. Removal of host fruit was continued in the infested zones, and no vegetables were planted there. Packing houses were supervised in order to prevent shipping leaks through this channel and to enforce sanitary measures against possibly infested

fruit lying around their premises. In both infested and protective zones, the foliage was sprayed with a bait preparation containing brown sugar and molasses plus a poison — lead arsenate or copper carbonate.

The extent of the effort may be judged from these figures: the treatment extended onto 1,002 properties in 20 counties with about 10,000,000 acres of land (containing nearly three-fourths of all the bearing citrus land in Florida), including 120,000 acres of citrus and 160,000 of non-citrus crops. About 609,000 boxes of fruit were destroyed in this area, and 25,000 outside it. Fifty thousand bushels of host vegetables were destroyed, and about 300,000 pounds of lead arsenate were used in the bait spray. Infested shipments were found in ten localities in seven states outside Florida, owing to the fact that three-fourths of the citrus crop had been marketed by the time the fly was discovered.

It was found that kerosene and certain fermenting materials were attractive to adult male flies, and glass traps containing these were used to check on the presence of the pest.

By July, 1930, the medfly could no longer be trapped in the continental United States. Its elimination took an expenditure of about seven and one-half million dollars and the employment of a peak work force of some 6,000 men. Reimbursement of those who sustained losses through confiscation of fruit or other control measures cost another seven million dollars. The "scorched earth" policy plus effective quarantine and the crude bait spray had paid off; the medfly had been eradicated for the time being on this continent.

The 1956 Campaign

The second medfly infestation began when infested grapefruit was found at Miami Shores in April of 1956. By June of that year, infestations were found in 19 Florida counties. Again, Federal and state forces were marshalled with admirable alacrity, but this time, after a brief initial period of fruit-stripping in some of the southeastern Florida counties, a new strategy was employed. In large part, this plan was devised by L. F. Steiner, USDA fruit fly expert, who had been working out control and detection methods for various pest fly species in Hawaii. Fruit-stripping was abandoned, and quarantine zones of one mile were established around each known infestation. All fruit or produce moving out of these areas had to be fumigated or processed immediately. New improved fumigation methods employing methyl bromide and ethylene dibromide were found quite satisfactory for most fruit, and could be applied at a rate of only five

cents a box. Some loopholes were exposed. For instance, mangoes, which do not stand up well to fumigation, were sent unfumigated to Chicago, but were found to have been transshipped to Louisiana, a state vulnerable to the fly because of its mild winters.

Although over four and one-half million automobiles were examined at roadblocks, the spread of the fly mainly followed the highways, indicating that contraband fruit or adult female flies were moving by car. Other minor routes of dispersal occurred through Indian reservations, where mangoes were peddled after being transported by canoe and otherwise away from the roads, and through the traffic of guava pickers, who are independent and have their own pickup stations.

Direct control methods employed a spray containing a bait of protein hydrolysate ("sauce base" of the food industry) plus a poison component, the organic phosphorus compound, wettable malathion, mixed in just enough water to make up a spray that could be applied by air. This bait attracted flies from distances of over 200 yards away, instead of the few inches or feet over which the 1929 sweetened bait had proved effective. The new bait lured and killed almost all flies within 100 feet a few hours after their emergence, so that swaths missed by the planes did not matter so long as they were not excessively wide. By proper timing of sprays at seven to ten days apart, the flies were prevented from ripening to sexual maturity after eclosing from the pupal stage. Since the maggots were able to survive (in grapefruit and oranges left on the tree) for up to 20 days after reaching the final larval stage, the spray was continued for one full generation (50-90 days) after the last fly find.

Detection methods depended primarily upon substances that would lure male flies. Angelica seed oil in plastic traps with poison proved to be a highly effective attractant for males, but the different lots of the oil that were tried were found to be very uneven in their effectiveness. Furthermore, this commodity was rare and expensive — \$100 or more per pound. By early 1957, some 800 pounds of the oil (the entire world production of ten years) had been used for fly baiting, virtually exhausting the world supply. The last angelica seed oil was offered on the world market at \$500 a pound. Fortunately, at just about this time the chemists came through with an effective and relatively inexpensive substitute that they called siglure, containing certain simple esters of cyclohexane carboxylic acid. It was learned that the fruit flies tend to disperse from areas after fruit production has ceased, and this was a good reason for leaving fruit on the trees in infested areas. Fallen fruit was destroyed wherever possible.

An auxiliary control used in heavily infested zones was the application of a formulation at the rate of five pounds of dieldrin per acre to the soil under infested trees. This was aimed at pupating larvae and adults leaving the pupal stage.

The program progressed steadily. Infestations were found in a total of 28 counties, most of them south of the 1929 zone. While the 1929 infestation had affected mainly the major commercial citrus groves of central Florida, the 1956 invasion was centered more in the ornamental and dooryard plantings of residential areas in the southern part of the state. This required the use of more of the safer twin- and four-engined planes in the low altitude bait-application flights.

One year after the first discovery of 1956, nine-tenths of the total acreage had been treated, and only about 12,000 acres of new infestations remained to be discovered. One by one, during late 1956 and early 1957, counties were released from the aerial spraying routine after no more flies could be found in them, and in November, 1957, the last known infestation was eliminated from an island off the coast in Manatee County. The cost of the eradication program, paid jointly by the state and Federal governments, was about \$11 million, but only small quantities of fruit had had to be stripped from the trees and destroyed.

Eight hundred thousand acres were sprayed one or more times — some of them up to a dozen times — for a total of six and one-half million spray-acres. Twelve million pounds of malathion and a million gallons of sauce base went into the bait spray, and 1,667,217 pounds of dieldrin were used in the bait treatment. A maximum of 800 personnel was involved in the 1956 struggle, as compared to the 6,000 of the 1929 campaign — labor costs of course having risen steeply since the earlier campaign. At the peak of the campaign, some 54,000 detection traps were in use all over Florida, and additional trapping was done in other southern states and Cuba in areas where preferred host fruits grow. About 12,000 fly specimens were caught, and none of these came from states outside Florida. The Florida Legislature has voted funds for continued lure trapping, using combined lures for several fruit fly species in addition to the medfly. In June, 1958, 32,000 traps were still in use throughout Florida.

Harmful Effects of the Campaign

It seems reasonably clear that the two medfly campaigns were completed with little serious loss of wildlife or damage to non-infested crops, domestic animals and human property. The 1956 program

received good publicity in the press and on television and radio, and most tropical fish producers were able to cover their ponds, while paint and plastic testing laboratories could spread plastic sheeting over their test plates. Housewives were advised to withhold wash from clotheslines, and automobile owners to cover or be prepared to wash their cars. Some damage was noted on cars with lacquer finishes, but not on those with enamel, and the spotting proved to have been caused by malathion. Some loss of tropical fish was also reported, but not in ponds with deep enough water. Reported losses of birds, mammals and beneficial insects were not confirmed upon investigation. One C-84 twin-engine aircraft crashed at Boca Raton while ferrying materials, killing a crew of five men.

Side benefits from the spray included control or depression of insect pests such as houseflies, mosquitoes and the papaya fruit fly during the period of application.

THE SCREWORM

Introduction

The screwworm is the maggot (larva) of a large fly (*Callitroga hominivorax*, plus at least one other species occurring outside the area concerned). The maggot lives in the flesh of warm-blooded animals and gets its name from its fancied resemblance to a wood screw. All sorts of mammals are attacked, but from the human standpoint in this country, the damage it inflicts on cattle has been most important. The screwworm has a year-round range in the American tropics and sub-tropics, from Texas and other border states south to Argentina. Each summer, screwworm flies migrate northward to spread the infestation into the midwestern states, and infestations are known to have been introduced into Illinois, Iowa, New Jersey, South Dakota and other northern states in livestock shipments carrying the pest. Each year up to 1933, winter cold killed the infestation back to the southern parts of the border states and to Mexico, where the winter weather is mild enough to permit permanence of the fly population.

In the summer of 1933, screwworms appeared for the first time in the southeastern United States, probably shipped in infested southwestern livestock, and before they could be controlled they had spread into peninsular Florida. Here they found the climate mild enough to support a year-round population, and thus a permanent infestation became established in the Southeast. Each summer this infestation spread outward from Florida into additional southeastern states, and each winter it died back to Florida and the warmer parts of Georgia and Alabama. During 1935-1937, the affected states in cooperation

with the USDA applied the best known animal husbandry practices and tried larvicides and repellents to treat and protect livestock wounds directly. While these expensive measures did help to cut livestock losses, enough larvae survived in neglected livestock and wild animals to keep the infestation alive and dangerous. By 1957, the State of Florida and the Federal Government were ready to support the then new technique of eradication based on male sterilization, and funds were appropriated to begin the campaign against the screw-worm.

Biology and Nature of Damage

The screwworm is an obligatory feeder in the flesh of living mammals. Each female fly lays her eggs in a mass of about 200 on scratches or near exposed wounds on the animals, and the eggs take 12-24 hours to hatch. The larvae then enter the wound and feed extensively on the muscle tissue. As tissue decomposition advances, more and more female flies are attracted to infested wound areas, and the maggot populations at such sites increase correspondingly. The larvae burrow in the tissues for five to seven days, after which they leave the wound and drop to the ground, where they burrow into the soil to pupate. The pupal stage lasts a week or more, depending upon the temperature. The pupa is vulnerable to low temperatures, and freezing soil or prolonged cold kills it. After eclosing from the puparium, the adult flies disperse and seek food. Flies have been found to disperse to distances as great as 35 miles in one week. In the summer, mating begins two days after eclosion, and four to six days later the females have been mated and have laid fertile eggs. The sexes reach adulthood in about equal numbers, and the females mate only a single time, although the males normally mate several times. (Some attention has been given to breeding males that will mate a greater number of times.) Females segregated from males in the laboratory to prevent fecundation oviposit as readily as do mated females. In summer conditions, females live two to four weeks as adults, and may deposit three, four or more egg masses during this span.

Because oviposition is triggered only by the presence of a wound on a suitable host animal, and because of predation of mature larvae by insects, especially by ants, the number of adults produced is rarely high. Uvalde County, Texas, has had the heaviest infestations in the United States, with 100-500 flies produced per square mile per week, but infestations south of the border may be even heavier.

Massive infestations of screwworm can quickly weaken and kill even full-grown cattle, and very small animals often succumb before

the flies can complete their larval growth. The pest has caused livestock losses of 20-40 millions of dollars annually, about half of this figure in the Southeast.

Eradication Operations

The story of screwworm eradication in the Southeast begins in 1936 with the work of Melvin and Bushland,³ who learned how to culture the insect in the laboratory *en masse* on ground meat, blood and water containing a small amount of formaldehyde to retard spoilage. Dr E. F. Knipling, now heading entomological research in the USDA, speculated in conversation in 1938 that the known habits of the females suggested that they might mate only once, which if true meant that laboratory-reared sterile males might be used to control isolated populations such as the one in Florida. The idea was not followed up until after the war, when Knipling directed that the mating habits and physiology of screwworm flies be studied in detail, and that attempts be made to find chemicals capable of rendering the males sterile. In 1950, a general paper was published by H. J. Muller, in which this famed geneticist pointed out that *Drosophila* fruit flies in the laboratory were sterilized by irradiation. A colleague, A. W. Lindquist, passed this paper on to Knipling, who then contacted Muller about the possibility of employing radiation sterilization on screwworms. The reply encouraged Knipling to initiate experiments, and Bushland and Hopkins eventually established that screwworms were readily sterilized by irradiating pupae that had been held at 80° F. for five days. A dose of 2,500 r sterilized males, and 7,500 r prevented egg production altogether. Adult males emerging from irradiated pupae proved able to mate normally with untreated females, but the egg masses resulting were of course infertile. Determination of critical doses proved to be laborious and time-consuming, but cooperation with cytogeneticists soon gave rise to important short-cuts in the process, because damage could be assessed by cytological examination instead of waiting for the full life cycle to carry through in order to get results.

Field tests run on Sanibel Island, two miles off the Florida coast, proved that its screwworm population could be reduced by the release of 100 sterilized males per square mile per week, a figure that surpassed the number of native males. But Sanibel is so close to the mainland that it was easily reinfested, so eradication could not be attempted there.

The conclusive eradication test was finally performed on the Dutch island of Curaçao in the south Caribbean Sea. Screwworms were

reared at Orlando, Florida, and irradiated in a cobalt-60 source built at Oak Ridge. At first, flies were released by air at a rate of 100 males per square mile per week, but this proved only fractionally effective because the swarming, unattended goats and sheep of Curaçao harbored a much larger screwworm population than had been encountered in Florida. The release rate was accordingly increased from 100-400 males per square mile per week, and the first saturation of the island with sterilized flies caused substantially more than half of the egg masses laid on test animals to be sterile. After a month of continued releases, when another generation of adults emerged, the native flies were so reduced in numbers that the percentage of sterile matings increased greatly. The emergence of the second generation of wild flies saw the proportions so altered that practically all matings were sterile ones. By generation III, only two egg masses were found in goat pens on the island, and both of these were sterile. No more screwworm eggs were found during the additional two months that flies were released on Curaçao, and release was terminated in January, 1955, less than six months after the first flies were let go.

The Curaçao experiment, heartening as it was, also showed the need for improved procedures for mass production of sterilized males. At a rate of 400 males per square mile, the 50,000 square miles of the overwintering area in Florida was estimated to require 20 million males weekly. The females produced equal the males in numbers and are not easily separated from them in practice, so these doubled the necessary weekly rate of release to 40 million flies. An additional ten million flies had to be reared to make up for mortality of pupae and to provide for breeding stocks. This came to a weekly grand total of 50 million flies, in contrast to the 170,000 larvae raised each week for the Curaçao test.

To meet this demand, experts on insect rearing, irradiation methods and mass production engineering cooperated to transform a large airplane hangar near Sebring, Florida, into a wonderfully efficient plant capable of producing more than the needed number of sterile screwworm flies each week. This plant employed fully modern production line techniques, with the larvae being carried through their feeding life and thence to the pupal stage and the irradiation chamber on a continually moving line of stacked trays suspended from a monorail. Full safeguards were provided against possible escape of unsterilized flies, and elaborate precautions set up to protect the employees from radiation and from the odor of the meat-blood larval food.

Designed, built and equipped on a "crash" basis in just nine months, and at a cost of under a million dollars, the plant moved into full-

scale production in July, 1958. By early spring of 1959, it was producing for release at the phenomenal rate of 50-60 million flies per week. The flies were placed in special cardboard cartons that could be opened as dropped from the plane. About 20 light planes were used at the peak of operations, each flying five to six hours a day over prearranged flight patterns based on a few strategic release centers spaced over Florida. Three long trap lines covering the state from north to south provided information on the effectiveness of the operation, and a field force of about 50 livestock inspectors worked on quarantine patrol duty. Stringent quarantine regulations were set up to prevent infested livestock from entering the Southeast from across the Mississippi.

The program had a swift and dramatic effect on the Florida screwworm population. By the middle of March, 1959, all attempts to find egg masses or active screwworm infestations in Florida proved negative. On June 13 of that year the USDA and the Florida Livestock Board could announce, "Southeast free of screwworms for 16th consecutive week." This record was marred in the following week by the discovery of a single case of screwworm infestation in Highlands County, Florida. The releases continued at a rate of about 42 million flies a week, blanketing the area from southern Alabama and Georgia south to Key West. After some weeks during which no signs of a wild fly population were found, the rate of releases was dropped to 30 million flies per week and lower, and finally, on November 14, 1959, fly releases were terminated. The total eradication of the southeastern screwworm population had been achieved.

In the months since the release ended, an infested dog has been found in Florida — evidently brought in from the outside — and during the spring and summer of 1961, infestations have appeared at points along the Gulf Coast from the west, apparently originating from infested livestock shipped from the Southwest. It seems that these new threats to the Southeast can be handled with the available weapons, and the long-range problem now is centered on rolling the screwworm menace back across a defensible line in southern Mexico or Central America, and holding it there by quarantine and possibly by a constantly maintained belt of sterile flies.

COMPARISONS OF THE FOUR PROGRAMS

In comparing operations against the four pests we have just considered, it is well to recall once again that each insect is a separate and distinct problem in control. Some insects have characteristics

that lend themselves to simple control methods, while others are just naturally tougher, faster-spreading or faster-breeding, and defy all control methods that have been tried. However, it is also evident that the four programs do differ considerably among themselves in basic ways, especially in the resourcefulness and insight of their planning and operating personnel, in the kind and amount of information upon which control operations are based, and in the adaptability of the operating plans to conditions as they are met while the campaign proceeds. The first factor — personnel — is of course very difficult for one outside of the agencies involved to evaluate, and in any case, judgements are bound to be influenced by hindsight according to the success of the particular program concerned.

The second factor for analysis is the nature and quantity of the information on which each program proceeded. Ideally, of course, a control campaign is based on a full knowledge of the target pest, its life history, ecology, physiology and behavior; on a basic understanding of the efficacy of various methods that might be used against the target; and on a reasonable assurance that these methods do not have seriously harmful effects on valuable plants, animals, microorganisms, inanimate human property, or on man himself. Such knowledge, of which we can never get enough, is provided by previous investigations, by pilot trials, and by continuing evaluation of operational results. These activities, collectively known as research, are the counterparts of intelligence-gathering in a military campaign. The public as well as the technicians involved have come to take research for granted in insect control programs, just as they confidently assume that the proper tests of safety have been applied when a new antibiotic or vaccine is issued by medical authorities.

If we look at the details of the four projects as they have been dealt with in recent years, the differences among them in research effort are very striking. The research behind the screwworm program has been extensive, imaginative and persistent, and obviously it has paid off handsomely. The second medfly campaign, unlike the desperate, scorched-earth first one, was carried out with an efficiency grounded on solid long-term research into the bionomics of fruit flies in general, particularly that conducted by L. F. Steiner and his colleagues in their Hawaiian installation. Here again, it is clear that previous research was crucial in a successful eradication campaign.

The gypsy moth campaign has the longest history, and also the oldest research program, of any of the four efforts considered here. In the years before mass air-spraying, many kinds of measures were tried against the moth, including the introduction of natural enemies

already mentioned, as well as cultural methods (such as tree banding and egg mass destruction) and poisons sprayed from the ground. Also built up during the years was a store of knowledge concerning the life history, foodplants, enemies and distribution of the moth, and particularly a fund of information on the effect of the female attractant on males. All this has proven very useful in developing control methods. Nevertheless, the recent work of Campbell (some results of which are outlined above) indicates that there was and is much more of importance to be learned about the behavior of gypsy moth populations than has been generally appreciated. The preparation of gyplure and other attractants in the last few years had doubtless been made easier by technical developments in natural-product chemistry, but perhaps even without these developments more could have been done in the past with attractant research had more time and money been spent on it. To sum up gypsy moth research, one might say that it began rather well and then tended to get into a rut, from which it has been pulled only during the last few years. The present research program is expanding and striking out in new directions, and the outlook now seems rather good for the eventual control of the moth.

As we have already seen, the fire-ant mass spraying program began full blast in the fall of 1957. Considering the very high potency of the poisons used and the great areas over which they were to be sprayed, the research background of the fire-ant program was so sketchy as to be virtually non-existent. USDA investigations ran from 1948 to 1953, and consisted mainly of survey scouting for new infestations plus routine life history, ecological and insecticide-testing work. As already emphasized,²² no research was done by the USDA from 1953 until *after* the mass spraying had gotten well under way. The Gulfport Methods Improvement Laboratory was not opened until 1958. Nevertheless, in their letters and releases,²³ USDA officials spoke of "expanding" the "continuing research effort," thus giving the impression that an unbroken chain of research studies stretched back from the start of the spray program. The USDA releases emphasize the liaison with the U. S. Fish and Wildlife Service "from the outset," and even seem to imply concurrence of the Service in the mass spray program.²⁴ As we have already seen from Dr. Leffler's letter,¹⁹ this concurrence could not possibly have been granted at that time. The first meeting of USDA and Fish and Wildlife officers on the fire-ant program took place, according to the USDA, in Washington on December 12, 1957, about a month after the spraying had started. The delay is important in view of the time needed by wildlife researchers to set up and carry out a

complicated wildlife survey in an area about to be treated. In fact, the Fish and Wildlife Service seems to have been presented with a *fait accompli* upon which to make its studies.

What about outside research? In the years between 1948 and 1957, Dr. E. O. Wilson at Harvard had continued his work on fire-ant variation, distribution and social behavior, and had discovered the existence of a trail-forming chemical laid down by foraging worker ants. Research on this substance was continued by M. S. Blum and co-workers at Louisiana State University, and is still going on. The active group at Auburn in Alabama studied fire-ant crop damage (which had unaccountably dwindled practically to nothing by 1957) and worked on promising bait formulations. The findings of these groups swerved the spray program not at all. The Gulfport Laboratory is now working on baits and other angles of attack, but insofar as their results have affected the operations to date, emphasis still seems to fall on mass spray methods. No recent specific, detailed study of the damage caused by the ant seems to have been reported, despite the claims of competent state entomologists that crop damage is now negligible. We are left, then, with no concrete information to counter the claims of wildlife experts and state entomologists that the ant is not a major pest deserving of the effort and funds expended upon it. For research effort, the fire-ant program must take low marks.

The last factor to be compared among the programs is their adaptability to conditions met as operations proceed. This is so closely related to the research facet of the respective program that we are not surprised to find the flexibility of operations more or less closely paralleling the quality and amount of research. The screwworm and medfly programs made major adjustments smoothly and without delay as the information available indicated they should.

The gypsy moth campaign has varied; sometimes the operational response to changing conditions was rapid and efficient, while at other times it lagged. Curiosity about the obviously great fluctuations in abundance of the moth, and especially about the great peak following the first extensive air spraying, are not reflected in the impassively literal Annual Reports on gypsy moth control work. Even the overstepping of the Berkshire-Green Mountain barrier seems never to have raised much doubt on the part of the government control officials that the mass spray program in progress would eventually bring about the eradication of the insect in North America, at least to judge from the reports. But events have caught up with the program. The milk residue problem in New York State first halted the program in much of this key "frontier area," and later forced a switch to the less effec-

tive sevin for most districts. Finally, a new Methods Improvement Laboratory is opening this year at Otis Air Force Base in Massachusetts, and one way or another we may hope to see some more sophisticated control measures tried against the gypsy moth.

After five stormy years of air spraying, the fire-ant control program goes on pretty much as before, but with greatly reduced dosage in many areas. The reduction seems to have been forced in part by serious wildlife kills and perhaps some destruction of livestock and poultry, as well as by the threat of residues. Where the new double quarter-pound treatment is being applied, damage to warm-blooded animals is apparently not serious. It is, of course, effective against the ants for a much shorter time, and it is doubtful whether its residual effect is up to the task of preventing reinfestation of treated areas. Recently, "mopping-up" activities have been required after treatment in a number of places.

There is a question, already decided in the negative by some of the infested states, whether the eradication campaign should continue in its present form. Not without some logic, wildlife experts have called the fire-ant program, "scalping to cure dandruff." But this campaign has so much momentum, fueled annually with 2.4 million dollars in Federal appropriations, that even the defection of such key participant states as Alabama and Florida has failed to halt it. As the possibility of eradicating the fire ant by the present mass spray techniques recedes into future decades, it will be interesting to see how many more years Congress will vote to keep the present control machinery rolling.

CONCLUSIONS AND RECOMMENDATIONS

The case histories we have reviewed illustrate, I think, the point that mass air spraying of non-selective insecticides can be disappointing as control agents and are in some cases dangerous to the living human environment as well, perhaps, as to man himself. These dangers are usually discussed as "side effects," a term which in itself reflects the special viewpoint of many of the control men on the job. These are "practical" people, absorbed in managing large teams with complex apparatus, and often caught up in the direct urgency of "crash programs." Their efforts are directed at a clear and simple goal — the eradication or control of a particular insect. In the heat of such campaigns, complaints arising from damage to humanly-valued resources are likely to appear as mere incidental annoyances to the control men, and the damage itself is minimized and shrugged off. But the side effects of the control men may in reality amount to catastrophes from other viewpoints, as in the case of the fire-ant

campaign. When the cost of a campaign in dollars plus the losses in wildlife, stock or other resources destroyed begins to balance or exceed the benefits to be gained by eradication of the pest, then it is time to give thought to cutting off or drastically modifying the program. In such a case, side effects become main effects, and we should never forget it. The dangers involved in the mass use of pesticides has recently been dramatically recognized in Great Britain,¹⁵ where a Parliamentary Investigation Committee of 43 Members has accused the Ministry of Agriculture of negligence in insecticide research and has recommended that pesticide use be intensively investigated and rigidly controlled, and has called for the "immediate prohibition" of heptachlor, dieldrin and aldrin.

Our case histories illustrate another point: alternative control measures are increasingly available, and we should expect their development to be accelerated. The medfly and screwworm campaigns are shining examples of the results of real thinking and hard work, but most of all they point up the value of new approaches and a sound knowledge of the pest to be dealt with — in other words, they bear the stamp of thorough research.

The issue is clearcut: in the face of a new and spreading insect menace, do we rush out the planes and the poison, or do we first find out what we ought to do and how it should be done, on the basis of adequate information?

The problem of urgency is sure to be raised in answering this question; otherwise, there could be only one answer. In the light of past insect invasions, however, urgency has rarely been so great as to preclude some kind of research assessment of the problem before mass control could begin. Furthermore, research can be called upon to provide a sound body of general background information and principles before the emergency occurs. Our insect control programs often lack this kind of a background, as the makeshift fire-ant campaign illustrates, but when they do have it, as in the case of the medfly, the success of control efforts may be rapid and brilliant.

But in the USDA, entomological research is often hampered at the basic level. Even in such fundamental fields as insect taxonomy and morphology, USDA specialists are for the most part overworked and overcrowded. Daily the cartons of insects submitted for identification pile up on each man's desk, and most of these highly qualified researchers must work on their own time to get any basic investigations completed. The same is often true of extension entomologists at the state level. Permanent workers in the new and vital disciplines of population dynamics and insect behavior have scarcely begun to be

hired by the Federal Government or the states for work in their own fields; yet, as our case histories demonstrate, these fields will surely be pivotal in future control developments. Bright spots in the entomological research picture are the grants from other governmental agencies for the support of basic research, mostly in the universities. But such grants are no substitute for an adequate research establishment within the USDA itself.

From all of these considerations, I think the recommendations must be clear. They are as follows:

1. Every mass control campaign should have an adequate research program functioning as far ahead as possible before control operations get under way. The control work should be guided by the research findings, and not the reverse, and every campaign should be reevaluated frequently to see if a need for it continues.

2. The USDA quickly should be granted funds to expand all permanent research facilities related to pest control. Special attention needs to be given to basic fields such as systematics, physiology, behavior, ecology and genetics. The study of the natural-product chemistry of insects should be stepped up.

3. Mass broadcasting of non-selective poisons, especially spraying and dusting from the air, should be deemphasized and the development of other measures, especially selective lures and sterilization techniques, correspondingly augmented. Over lands other than intensively cultivated agricultural blocks, mass insecticides should be used with the greatest caution and only in real emergencies after other measures have failed. Non-selective insecticides in general should be considered only as stopgap remedies, pending the development of better means of control for all types of land.

4. There should be established a strong permanent inter-agency office to coordinate policies and activities related to pesticidal operations as they affect the biotic environment and human health. This office should have ample funds to allot to the proper agencies for research on specific problems. It would be made up of representatives from the USDA Agricultural Research Service, the Fish and Wildlife Service of the Department of the Interior, and the Food and Drug Administration of the Department of Health, Education and Welfare.

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I am grateful to the many individuals and organizations who made this essay possible, although I cannot mention them all by name here. Particularly helpful were the information and criticisms offered by

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Appendix A

[Data furnished by Plant Pest Control Division, Agricultural Research Service, August 25, 1961.]

SUMMARY OF ACREAGE SPRAYED FOR GYPSY MOTH CONTROL, SUPPRESSION AND ERADICATION

(All DDT Except As Noted)

	Application By Aircraft (Acres)	Application By Ground Equipment (Acres)	Totals (Acres)
1945	5,103	1,092	6,195
1946	62,201	19,427	81,628
1947	106,677	56,932	163,609
1948	212,260	53,650	265,910
1949	390,576	34,239	424,815
1950	582,895	17,205	600,100
1951	177,713	2,499	180,212
1952	202,109	15,032	217,141
1953	179,451	6,970	186,421
1954	1,371,199	29,817	1,401,016
1955	1,083,169	25,129	1,108,298
1956	926,073	15,391	941,464
1957	3,395,248	27,695	3,422,943
1958	516,150	18,426	534,576
1959	115,078 ¹	35,343	150,421
1960	65,538 ²	33,369	98,907
1961	141,270 ³	19,583 ⁴	160,853
Totals	9,532,710	411,799	9,944,509

	<i>By Aircraft</i>		<i>By Ground Equipment</i>	
1959 ¹	DDT	29,518 acres	All DDT	
	Sevin	85,560 "		
		115,078 acres		
1960 ²	DDT	54,103 acres	All DDT	
	Sevin	11,435 "		
		65,538 acres		
1961 ³	DDT	104,770 acres	⁴ DDT	19,342 acres
	Sevin	30,000 "	Sevin	241 "
	Methoxychlor	6,500 "		19,583 acres
		141,270 acres		

SUMMARY OF GYPSY MOTH DEFOLIATION

Calendar Years 1924 to 1960

<i>Year</i>	<i>Acres</i>	<i>Year</i>	<i>Acres</i>
1924	825	1943	34,845
1925	48,560	1944	250,148
1926	80,822	1945	821,487
1927	140,920	1946	622,919
1928	262,514	1947	7,422
1929	551,133	1948	32,467
1930	288,226	1949	78,673
1931	204,721	1950	5,368
1932	286,395	1951	21,314
1933	397,730	1952	293,052
1934	492,361	1953	1,487,077
1935	540,769	1954	491,448
1936	428,622	1955	52,061
1937	608,760	1956	43,158
1938	313,954	1957	6,458
1939	492,640	1958	125
1940	485,636	1959	14,467
1941	468,021	1960	48,722
1942	44,577	1961	data incomplete

Moorestown, N. J.

August 16, 1961

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The illustration on the front cover of this issue of *Psyche* is a drawing of a myrmecophilous weevil, *Liometophilus manni* Fall. The original figure was included in H. C. Fall's article in *Psyche*, Volume 19, 1912, plate 3. The weevil itself was collected by the late W. M. Mann in the Huachuca Mts., Arizona.

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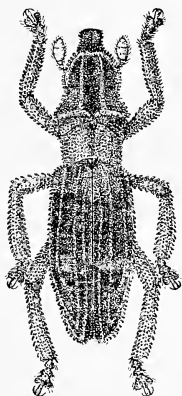
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DECEMBER, 1961

No. 4



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PSYCHE

Vol. 68

December, 1961

No. 4

AUSTRALIAN CARABID BEETLES VII. *TRICHOSTERNUS*, ESPECIALLY THE TROPICAL SPECIES

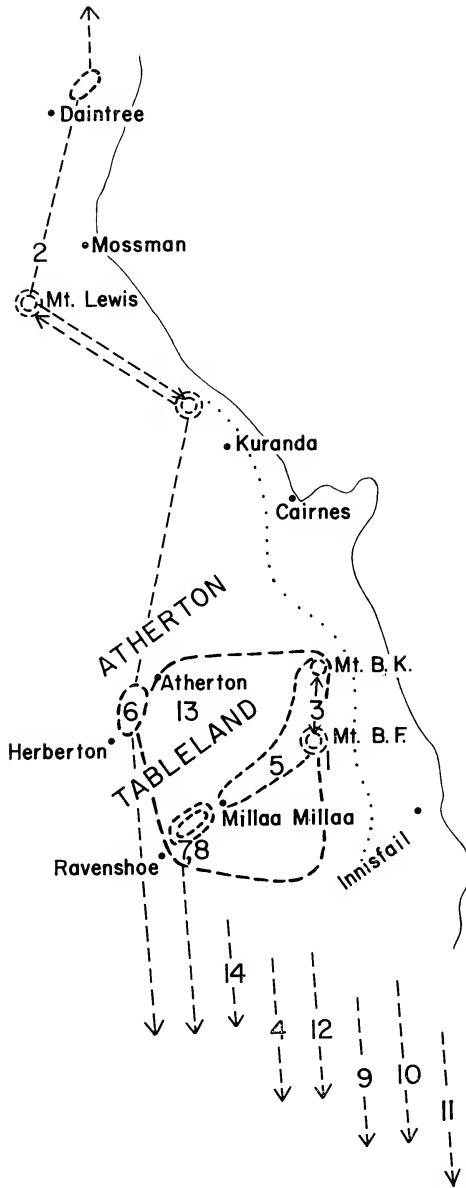
BY P. J. DARLINGTON, JR.

Museum of Comparative Zoology, Cambridge, Mass.

This is one of a series of papers describing new Carabidae of zoogeographic importance referred to in my account (1961b) of transition of Australian wet forest carabid faunas. Some other papers of the series, including a list of my localities, are referred to below (p. 130). The present paper is concerned with *Trichosternus*, especially with the comparatively little known tropical species. Types of new species are placed, at least for the time being, in the Museum of Comparative Zoology; paratypes, with C. S. I. R. O. at Canberra and usually in the Queensland Museum. Proportions given in the descriptions are calculated from actual measurements.

Items of geographic or evolutionary interest derived from *Trichosternus* are its total distribution; the occurrence of two very distinct (relict or primitive?) species, *fax* and *montorum*, high on Mt. Bartle Frere (one reaching Mt. Bellenden Ker too); the distribution of *T. frater* and its apparent allies (*subvirens* and *simplicipes* of South Queensland and *nudipes* to *fisheri* in the tropics), which form a group of mostly allopatric forms in which the male front tarsi have apparently been simplified in two different stocks and in which double invasion or hybridization may have occurred in a very limited area on part of the Atherton Tableland (pp. 122-125). Another case of hybridization (of *eungella* and *mixtus*) may have occurred on the Eungella Range (p. 127). See map for distribution of species on and north of the Atherton Tableland.

I cannot give an exclusive definition of *Trichosternus*. Characters used by Sloane (1894 etc.) and Tschitschérine (1902) fail among recently discovered species. Compared with *Nurus*, *Trichosternus* is usually smaller, more lightly built, with ♂ front tarsi usually dilated and with 3 segments squamulose below, while in *Nurus* the ♂ front tarsi are usually simple, rarely (*e.g.* in *N. atlas* Cast.) slightly dilated and with 2 segments squamulose. However, exceptional *Trichosternus*



DARLINGTON — TRICHOSTERNUS

resemble *Nurus* in having ♂ tarsi simple (*T. subvirens* Chd., *simplificipes* Sl., *nudipes* Darl., *soror* Darl.) or with only 2 segments squamulose (*setosiceps* Sl.). Compared with *Notonomus*, *Trichosternus* is usually larger, often with prosternal process setose (rarely in *Notonomus*), often with alternate intervals of elytra raised, and often without distinct 10th intervals at outer edges of elytra, but all these characters fail in some species. A generic revision of the larger Australian pterostichines is much needed. The Australian genera should be compared with the New Zealand ones (Britton 1940) and phylogenies should be worked out if possible, and the old types, many of them in Europe, should be re-examined. However, I cannot undertake all this now.

The known range of *Trichosternus* is the eastern edge of Australia from the base of the Cape York peninsula (south of Cooktown) to central New South Wales (perhaps a little north of Sydney), with one species isolated in southwestern Australia (Darlington 1953) and another on New Caledonia. All the *tropical* Australian species (except *cordatus*) live in rain forest, but some more-southern species occur in savannah woodland, and some enter or are confined to south temperate rain forest on the Dorriggo-Ebor and Mt. Royal plateaus.

Before considering the tropical *Trichosternus*, I give the following tentative key to species south of the tropics, as a basis for comparison (cf. Sloane's key, 1899, pp. 567-569, and Tschitschérine's, 1902, pp.

EXPLANATION OF PLATE 7

Known distribution of *Trichosternus* in tropical Queensland. The finely dotted line is the approximate eastern edge of high land (Atherton Tableland etc.). Arrows indicate occurrence southward, at increasing distances beyond the limits of the map, of the species indicated. The species are numbered in the order in which they are treated in the text. No. 1, on Mt. B(artle) F(rere), is *Trichosternus fax*; 2, *obscuripennis*, which extends north beyond the limits of the map nearly to Cooktown; 3, *montorum*; 4, *nudipes*, on the Mt. Spec plateau; 5, *soror*; 6, *frater*, which occurs north to Mt. Lewis and south beyond the limits of the map on the Kirrama Range; 7, *mutatus*; 8, *fisheri*; 9, *eungella*, and 10, *mixtus*, both on the Eungella Range; 11, *cordatus*, at the southern edge of the tropics; 12, *spec*, on the Mt. Spec plateau; 13, *setosiceps*, which is widely distributed on the south-central Atherton Tableland and occurs also south of the limits of the map on the Kirrama Range; and 14, *kirrama*, on the Kirrama Range. Nos. 1, 2, 3, 13, 14 are very distinct, phylogenetically isolated species. Nos. 4, 5, 6, 7, 8 are apparently interrelated, chiefly allopatric members of the *frater* group (see text). Nos. 9, 10, both on the Eungella Range, though structurally distinct, may be related to each other and may hybridize (see text). No. 11 represents a primarily south temperate rather than tropical stock. No. 12, on the Mt. Spec plateau north of Townsville, is apparently related to another south temperate (New South Wales) species.

523-530). I have specimens of all the 16 full species named in this key except *cyaneotinctus*.

*Tentative key to Trichosternus of eastern
Australia south of tropics*

1. Elytral intervals 3, 5, 7 with seta-bearing punctures (Mt. Royal Range and highest part of Dorrigo-Ebor plateau; 2 species?) *australicus* Sl.
 - Only 3rd interval (if any) with seta-bearing punctures on elytral disc 2
2. Mesosternum setose anteriorly 3
 - Mesosternum not setose anteriorly 7
3. Male front tarsi not dilated, not squamulose 4
 - Male front tarsi dilated, 3 segments squamulose below 5
4. Alternate discal elytral intervals scarcely differentiated; greenish (extreme SE. Q. & adjacent N. S. W. border) *subvirens* Chd.
 - Alternate discal intervals slightly elevated; black or nearly so, with cupreous or greenish margins (Bunya Mts., S. Q.) *simplicipes* Sl.
5. Seventh elytral intervals sharply carinate at base; prothorax relatively broad at base; length *c.* 22 mm. (extreme NE. N. S. W. and adjacent Q. border) *angulosus* Chd.
 - Seventh intervals roundly costate at base 6
6. Very large, *c.* 33-40 mm. (SE. Q. to Blackall and Bunya Mts. etc.) *renardi* Chd.
 - Not so large, *c.* 25-32 mm. (N. S. W. S. to Dorrigo, Williams River, Booral, etc., and N. to Stanthorpe-Dalveen area, S.Q.) *vigorsi* Gory
7. Three supra-ocular setae each side 8
 - Two supra-ocular setae each side 9
8. Purplish (savannah woodlands of N. N. S. W. chiefly west of the rain forest zone) *superbus* Cast.
 - Greenish (unknown to me; may be another savannah woodland species) *cyaneotinctus* Boisd. incl. *atroviridis* Sl.
9. Additional lateral prothoracic setae present (savannah woodland and drier rain forest of S.Q., N. into edge of tropics; probably includes *hecate* Tsch.) *cordatus* Chd.
 - Only usual 2 pairs lateral prothoracic setae present 10
10. Very large, 34 mm. or more 11
 - Smaller, 34 mm. (maximum size of *cyaneus* only) or less 12
11. Prosternal process setose; black; length 37-42 mm. (extreme NE. N. S. W. and adjacent Q. border) *perator* Sl.

- Prosternal process not setose; purplish; length 34-39 mm. (Blackall Range, SE. Q.) *porphyriacus* Sl.
- 12. Posterior-lateral prothoracic setae near base at least 3 species:
 wilsoni Cast., *nitidicollis* Cast., and *speciosus* Sl.
- Posterior-lateral prothoracic setae about $\frac{1}{8}$ of prothoracic length before base 13
- 13. Smaller, length *c.* 21-27 mm.; black sometimes slightly bluish or purplish (widely distributed in NE. N. S. W. and S. Q., from Dorrig to Blackall Range *marginiferus* Chd.
- Larger, length *c.* 28-34 mm.; wholly purple or blue (Mt. Royal Range, Dorrig, etc.; possibly 2 species) *cyaneus* Cast.

The following key to tropical Australian *Trichosternus* differs from the preceding key in form (ranges and authorities omitted) because the tropical species are discussed individually. All the species have rather long, strong, curved mandibles; rather short, irregular, subparallel frontal foveae; well developed, emarginate mentum tooth; palpi not strikingly modified; elytra margined at base; 8th (submarginal) stria lined with very small ocellate punctures; lower surface impunctate or nearly so except for usual "fixed" punctures; and (so far as my observations go) other usual characters of the genus, except as otherwise stated.

Key to Species of Trichosternus of

Tropical Australia

- 1. Mesosternum setose anteriorly; dorsal elytral intervals equal or nearly so (except in *montorum*) 2
- Mesosternum not setose anteriorly; alternate elytral intervals elevated (except scarcely so in *kirrama*) 9
- 2. Seventh intervals of elytra not sharply carinate at base (at most somewhat swollen); elytra without dorsal punctures 3
- Seventh intervals sharply carinate at base; elytra with (small) dorsal punctures 4
- 3. Subparallel, prothorax quadrate; humeri subdentate; color blue-purple *fax*
- Elytra oval, prothorax subcordate; humeri not dentate; black, elytra dull *obscuripennis*
- 4. Elytra with alternate intervals moderately raised; (form depressed; color greenish or bluish) *montorum*
- Elytra with discal intervals equal or nearly so, except at extreme base (*frater* group) 5
- 5. Male front tarsi not dilated, without squamules 6
- Male front tarsi more or less dilated, always with some squa-

- mules below 7
6. Broader; greenish *nudipes*
 - Narrower; bluish or purplish *soror*
7. Greenish *frater*
 - Black or purplish 8
8. Black or faintly purple; smaller (18-20 mm.) *mutatus*
 - Purple; larger (23-25 mm.) *fisheri*
9. Only 2 pairs supra-ocular *and* 2 pairs lateral prothoracic setae (but extra apical ventral setae) present *eungella*
 - Extra supra-ocular *and/or* lateral prothoracic setae present 10
10. Prosternal process setose; if prosternal setae broken or not visible, note 3 supra-ocular and 4 or more median-lateral prothoracic setae each side, and odd elytral intervals costate *mixtus*
 - Prosternal process not setose 11
11. Only 2 pairs supra-ocular setae present, *and* odd elytral intervals raised 12
 - Extra supra-ocular setae present, *or* odd elytral intervals (except 7th) scarcely raised and humeri scarcely dentate 13
12. Black *cordatus*
 - Purple *spec*
13. Only 1 pair median-lateral prothoracic setae present; odd elytral intervals costate *setosiceps*
 - Extra lateral prothoracic setae present; odd elytral intervals (except 7th) not costate *kirrama*

Trichosternus fax new species

Form as figured (Fig. 1), subparallel, not strongly convex; black, head slightly metallic, pronotum with green or bluish marginal channels and copper-purple on disc brightest in baso-lateral areas, elytra with marginal channels blue or greenish blue; pronotum shining, head and elytra slightly duller. *Head* *c.* 3/4 or slightly more width prothorax; eyes moderate, genae *c.* wide as eyes, rounded and somewhat narrowed to neck; antennae rather short (in genus), passing base of prothorax by 1 or 2 segments; 2 supra-ocular setae each side. *Prothorax* subquadrate, *c.* 1/3 wider than long at middle, not much narrowed behind; base *c.* 1/10 or more wider than apex (variable); apex broadly emarginate but angles not otherwise advanced, not margined; base subtruncate, slightly emarginate at middle, strongly margined at sides; sides weakly arcuate for much of length, broadly, slightly sinuate before *c.* right, well defined posterior angles; lateral margins narrow, slightly wider posteriorly, each with a seta about 1/3 from apex and on margin at basal angle; disc rather flat, middle

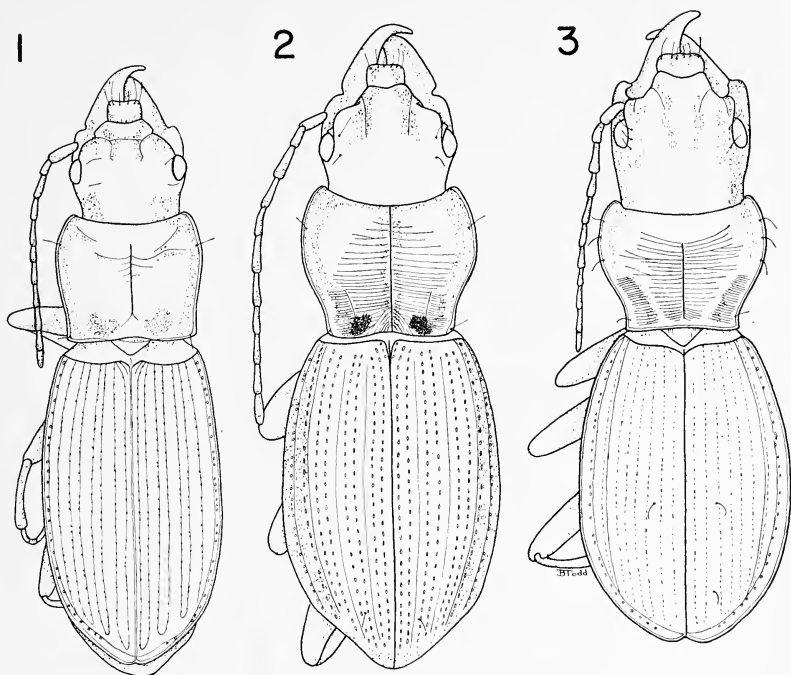


Fig. 1. *Trichosternus fax* n. sp. Fig. 2. *T. montorum* n. sp. Fig. 3. *T. kirrama* n. sp.

line deep, transverse impressions almost obsolete except for subbasal foveae each side midway between middle and sides, separated from margins by strong convexities; disc and foveae not punctate. *Elytra* c. $1/5$ wider than prothorax, usually slightly narrowed anteriorly; margin rectangular or almost acute at subdentate humeri; elytra with striae well impressed and punctate; intervals slightly convex but not costate, 3, 5, and 7 slightly wider than others but not more elevated, except 7th slightly elevated at base; narrow 10th interval indicated posteriorly; dorsal punctures lacking. Mesosternum anteriorly and prosternal process setose. Male front tarsi slightly dilated, 3 segments squamulose; ♂ with 1, ♀ 2 setae each side last ventral segment. Length 20-23; width 6.5-7.7 mm.

Holotype ♂ (M. C. Z. Type No. 30,355) and 15 paratypes all from Mt. Bartle Frere, North Queensland, west slope 3000-5000 ft. (not found lower), Dec. 1957, collected by my wife, my son, and myself, in mountain rain forest.

This new species is sufficiently distinguished from others in the preceding key. It is not closely related to any other known species. It may prove to be generically distinct from *Trichosternus*, or it may be a relict of the ancestral stock of the genus.

Trichosternus obscuripennis (Macl.)

This is the northernmost *Trichosternus*, and it descends to relatively low altitudes. Macleay (1887, p. 220) described it from the Mossman River. Sloane had it from Helenvale south of Cooktown. I have it from Mt. Finnigan south of Cooktown, Thornton Peak near Daintree, Mt. Lewis near Mossman, and Black Mt. about 20 miles north of Kuranda. Although most of my specimens were taken at 2000 or 3000 ft. altitude, several were found at or below 1000 ft. in strips of rain forest along the trail between Thornton Peak and the Daintree River.

T. obscuripennis is a very distinct species but hardly a separate subgenus. Its lack of humeral teeth is approached in *T. kirrama*, and lack of dorsal elytral punctures is matched by *fax*, although neither of these species is close to *obscuripennis* in other ways.

***Trichosternus montorum* new species**

Form as figured (Fig. 2), rather broad, depressed; black with bluish, purplish, or sometimes greenish reflections, head and pronotal disc moderately shining, elytra a little duller. *Head* about $4/5$ width prothorax; eyes rather small, genae as wide or wider than eyes, irregularly arcuate and somewhat narrowed to neck; antennae rather long (in genus); 2 supra-ocular setae each side. *Prothorax* cordate; $1/3$ (\pm) wider than long at middle; base slightly ($\pm 1/10$) narrower than apex; sides rounded for about $3/4$ of length, then rather strongly sinuate before *c.* right, scarcely blunted posterior angles; side margins moderate, not much wider basally, each with a seta about $1/3$ from apex and on margin at basal angle; apex not margined, broadly emarginate but angles not otherwise advanced; base broadly emarginate at middle, slightly rounded toward sides, vaguely margined at sides but not at middle; disc depressed, middle line deep, transverse impressions weak; baso-lateral foveae elongate but not strictly linear, slightly nearer margins than middle, not quite reaching middle of length, densely transversely rugulose, the rugulose areas meeting at middle posteriorly, with middle of base longitudinally rugulose; disc otherwise impunctate. *Elytra* oval, usually slightly narrowed anteriorly; margin somewhat obtusely angulate and finely toothed at humeri; elytra with finely punctate discal striae; intervals more or less convex, 3, 5, 7 increasingly elevated, 7th being sharply carinate for

most of length (most strongly so near base); 10th interval indicated but not well developed; each 3rd interval with 0, 1, or 2 dorsal punctures behind middle (often asymmetrical in number and position). Mesosternum anteriorly and prosternal process setose. Male front tarsi slightly dilated, 3 segments squamulose below; ♂ with 1, ♀ 2 setae each side last ventral segment. Length 23.5-27; width 7.9-9.1 mm.

Holotype ♂ (M. C. Z. Type No. 30,356) and 39 paratypes all from west slope Mt. Bartle Frere, North Queensland, 3000-5000 ft. (none lower), Dec. 1957, collected by the Darlingtones, in mountain rain forest. Also 6, not types, from east side Mt. Bellenden Ker, 3000-4500 ft., Dec. 1957, taken by myself, in mountain rain forest.

This seems to be a typical, rather generalized (primitive?) *Trichosternus*, without known close relatives. It is of course distinguished from other species in the preceding key.

***Trichosternus nudipes* new species**

Form about average; greenish black, the green most distinct at sides and baso-lateral areas of pronotum and marginal channels of elytra; head and pronotum shining, elytra duller. *Head* $c. 3/4$ (by measurement) width prothorax; eyes small but abrupt, genae $c.$ wide as eyes, convex, somewhat narrowed to neck; antennae of moderate length; 2 supra-ocular setae each side. *Prothorax* subcordate, moderately narrowed at base, $c. 1/3$ (\pm) wider than long at middle; base slightly (less than $1/10$) wider than apex; apex broadly emarginate with angles (lateral channels) slightly advanced, not margined; base broadly emarginate at middle, slightly rounded laterally, margined laterally; sides broadly rounded for much of length, moderately sinuate near $c.$ right or slightly obtuse, scarcely blunted basal angles; lateral margins narrow, not wider basally, each with 1 or sometimes 2 setae each side $1/3$ or less from apex and 1 seta on margin at basal angle; disc not very convex, middle line fine, transverse impressions weak; baso-lateral impressions deep, $c. 1/3$ length prothorax, separated from lateral margins by convexities but extending inward somewhat vaguely nearly to middle; disc of pronotum impunctate except base irregularly rugulose. *Elytra* $1/3$ or less wider than prothorax, sub-oval, slightly narrowed anteriorly; margins forming $c.$ right or slightly obtuse, finely raised-dentate angles at humeri; dorsal striae very fine, finely punctate; each elytron with 7 (including suture) rather weak but almost entire costae, 7th carinate basally; 10th interval indicated toward apex; 3rd interval usually 2-punctate, the punctures at or before apical $1/3$ and near apex, but individual punctures some-

times absent or obscured. Mesosternum anteriorly and prosternal process (sometimes slightly) setose. Male front tarsi narrow, without squamules; ♂ with 1, ♀ 2 setae each side last ventral segment. Length 22.5-26; width 7.9-9.5 mm.

Holotype ♂ (M. C. Z. Type No. 30,357) and 87 paratypes all from Mt. Spec plateau (Paluma Range), c. 40 miles north of Townsville, North Queensland, 2000-3000 ft., Dec. 1957 and Feb. 1958, taken by the Darlingtons, in rain forest; and 1, same locality, June 7-10, 1955, E. O. Wilson.

This is similar to and perhaps related to *T. subvirens* Chd. of South Queensland, but *subvirens* has an entire mentum tooth (emarginate in *nudipes*), posterior lateral pronotal setae just inside (not on) the margin, and lacks or nearly lacks rugulose sculpture on the base of the pronotum.

Trichosternus soror Darl.

I described this species (1953) from 3 specimens from Millaa Millaa, on the Atherton Tableland. I did not find it at this locality during my last trip, but found it on both the lower and upper western slopes of Mt. Bartle Frere, at 2000-3500 and 3000-5000 ft., and on the east side of Mt. Bellenden Ker, at 3000-4500 ft.

Although this small, bluish species has simplified male tarsi, like the preceding species, it may not be directly related to it but may be independently derived from a common ancestor perhaps resembling *frater* (below).

***Trichosternus frater* new species**

Slightly more slender than average of genus, rather convex; greenish or bluish black, head and pronotum moderately shining, elytra somewhat duller. *Head* 4/5 or more width prothorax; eyes small, genae about wide as eyes, rounded and somewhat narrowed to neck; 2 supra-ocular setae each side; antennae of moderate length. *Prothorax* subcordate, c. 1/4 wider than long at middle; base slightly narrower than apex; apex broadly emarginate but angles otherwise scarcely advanced, apex not margined; base emarginate at middle, rounded toward sides, margined at sides; sides broadly arcuate through much of length, moderately sinuate toward base; basal angles c. right or slightly obtuse, scarcely blunted; side margins rather narrow; not much wider posteriorly, each with 1 seta near or before anterior 1/3 and 1 on margin at basal angle; disc with distinct middle line, less distinct transverse impressions, and moderate baso-lateral foveae which reach posterior margin but are separated from lateral margins by convexities; surface of disc nearly smooth except with some (variable)

transverse strigulation in baso-lateral impressions. *Elytra* slightly more than $1/4$ wider than prothorax, subparallel, slightly narrowed anteriorly; margin forming obtuse (nearly right), slightly dentate angles at humeri; dorsal striae formed by fine vaguely punctulate impressed lines in low spaces between intervals; latter subequal on disc, slightly raised but not costate, except 7th strongly raised and costate basally, 10th interval indicated posteriorly; each 3rd interval 1- or 2-punctate posteriorly, position of punctures variable. Mesosternum anteriorly and prosternal process (sometimes inconspicuously) setose. Male front tarsi moderately dilated, 3 segments squamulose below; ♂ with 1, ♀ 2 setae each side apex last ventral segment. Length 20-23; width 6.5-8.0 mm.

Holotype ♂ (M. C. Z. Type No. 30,358) and 73 paratypes all from Kirrama Range, inland from Cardwell, North Queensland, 2000-3000 ft. altitude, Dec. 1957 and Feb. 1958, collected by the Darlingtons, in rain forest. Also the following specimens, not types: 12, mountains above (SW of) Atherton, Atherton Tableland, 3000-4000 ft., Dec. 1957 and Feb. 1958; 1, near Black Mt., c. 20 miles north of Kuranda, probably near 2000 ft. altitude, May 1958; and 3, Mt. Lewis, near Mossman, probably near 3000 ft., Dec. 1957; all collected by the Darlingtons, in rain forest. These localities are all on the Dividing Range system, which has probably been the principal path of north-south dispersal of wet forest Carabidae in North Queensland.

T. frater may represent the ancestral stock, with dilated, squamulose male tarsi, from which *nudipes* of the Mt. Spec plateau, *subvirens* and *simplicipes* of South Queensland, and also (independently) *soror* of the Atherton Tableland etc. have been derived. These 5 species (including *frater* itself) are all allopatric and are generally similar in form and technical characters except for the differences in the ♂ tarsi. The two following new species may be local derivatives of the same stock with ♂ tarsi still dilated and squamulose. See map for distribution of tropical species of the *frater* group.

Trichosternus mutatus new species

Small; form about average for genus but rather convex; black, sometimes with faint purplish reflections; moderately shining, elytra slightly duller. Head $3/4$ to $4/5$ width prothorax; antennae rather short, scarcely extending beyond base of prothorax; eyes moderate, genae c. wide as eyes, rounded and narrowed to neck; 2 supra-ocular setae each side. Prothorax subcordate, $1/4$ (\pm) wider than long at middle; base equal to or slightly narrower than apex; sides broadly

but not strongly rounded in much of length, weakly sinuate before base; basal angles *c.* right or slightly obtuse, scarcely blunted; apex subtruncate or very broadly emarginate with angles scarcely advanced, apex not margined; base subtruncate or slightly emarginate at middle, slightly rounded-oblique toward sides, weakly margined only toward angles; lateral margins narrow, scarcely wider basally, each with 1 seta about $1/4$ from apex and 1 on margin at basal angle; disc convex, middle line well impressed, transverse impressions rather weak; baso-lateral foveae rather weak and irregular, reaching posterior margin but separated from side margins by convex areas, not punctate and not much more rugulose than disc. *Elytra* slightly more than $1/4$ wider than prothorax, rather short, slightly narrowed anteriorly; humeral angles nearly right, slightly toothed; striae represented by depressed spaces between intervals; latter subequal on disc, convex but not much elevated except 7th elevated and costate basally; 10th interval indicated posteriorly; each 3rd interval with 2 or 3 dorsal punctures posteriorly. Mesosternum anteriorly and prosternal process (sometimes inconspicuously) setose. Male front tarsi moderately dilated, 3 segments squamulose; ♂ with 1, ♀ 2 setae each side apex last ventral segment. Length 18-20; width 6.5-7.0 mm.

Holotype ♂ (M. C. Z. Type No. 30,359) and 4 paratypes from Mt. Fisher (see below), *c.* 4000 ft., Feb. 1958; and 5 additional paratypes from mountains above (SW of) Millaa Millaa, *c.* 3500 ft., Dec. 1957; all specimens taken by the Darlingsons, in rain forest. The two localities are close together in the mountain mass between Raven-shoe and Millaa Millaa on the Atherton Tableland, North Queensland.

This species differs from the preceding one (*frater*) in smaller size, color, smoother basal pronotal foveae, and other details. It differs from *soror* in form of ♂ tarsi, in being a little broader, different in color, and in other details. For further comments, see under following species.

Trichosternus fisheri new species

Larger than preceding; black with strong purplish reflections, moderately shining except elytra slightly duller. *Head* slightly more than $4/5$ width prothorax; eyes moderate, genae *c.* wide as eyes, rounded and narrowed to neck; antennae rather long (in genus), passing base of prothorax by 2 or 3 segments; 2 supra-ocular setae each side. *Prothorax* subcordate, *c.* $1/4$ or less wider than long at middle; base *c.* $1/10$ narrower than apex; apex subtruncate or very broadly emarginate, with angles scarcely advanced; apex not distinctly margined; base

slightly emarginate at middle, faintly rounded toward sides, rather vaguely margined at sides; sides rather weakly rounded for much of length; moderately sinuate posteriorly before *c.* right, scarcely blunted basal angles; margins rather narrow, not much wider posteriorly; each with a seta about $1/3$ from apex and on margin at basal angle; disc convex, with fine middle line and weak transverse impressions; basolateral foveae deep but irregular, more or less transversely striolate; surface of disc otherwise nearly smooth, except some striae radiating from a point near base. *Elytra* nearly $2/5$ wider than prothorax, slightly narrowed anteriorly; margin forming strong but slightly obtuse, slightly toothed angles at humeri; striae vaguely punctate in clean specimens; intervals slightly raised but not strongly costate on disc, subequal except 3rd and 5th slightly more prominent at base and 7th carinate especially basally; 10th interval scarcely indicated; 3rd interval with usually 4 to 6 punctures, irregularly spaced. Mesosternum anteriorly and prosternal process (sometimes inconspicuously) setose. Male front tarsi only slightly dilated but usually with some squamae on 1st three segments (sometimes visible only on first segment — it is not clear whether they are worn off or originally missing on other segments in this case); ♂ with 1, ♀ 2 setae each side apex last ventral segment. Length 23-25; width 8.1-8.9 mm.

Holotype ♂ (M. C. Z. Type No. 30,360) and 3 paratypes from Mt. Fisher (see below), *c.* 4000 ft., Feb. 1958; and 2 paratypes from mountains above (SW of) Millaa Millaa, *c.* 3500 ft., Dec. 1957; all specimens taken by the Darlingtons, in rain forest. Both these localities are in the mountain system between Ravenshoe and Millaa Millaa, on the Atherton Tableland, North Queensland.

This species differs from the 2 preceding ones (in different ways) in details of form and color and size, in having ♂ tarsi less dilated, and in having more punctures on 3rd elytral intervals. It and *mutatus* appear to be confined to the same local mountain mass. Their occurrence together, localized between the ranges of *frater* on one side and *soror* on the other (see map), suggests some sort of double invasion or hybridization, although all the species in question now seem fully distinct.

***Trichosternus eungella* new species**

Rather small, broad, depressed; black, virtually without metallic reflections, moderately shining, elytra (except marginal intervals and tops of costae) dull. Head $3/4$ (\pm) width prothorax; eyes moderate, genae wide as or slightly wider than eyes, rounded and narrowed to neck; antennae rather long (in genus), passing base of prothorax by

about 2 segments; 2 supra-ocular setae each side. *Prothorax* subcordate, *c.* $2/5$ or slightly more wider than long at middle; base slightly narrower than apex; apex broadly emarginate with angles slightly advanced, not margined; base broadly emarginate at middle subtruncate at sides; sides broadly rounded through much of length, rather strongly sinuate basally; posterior angles right or slightly acute, scarcely blunted; side margins moderate, not much broader basally, each with a seta about $1/3$ from apex and on margin at or very near basal angle (additional setae rarely present anteriorly); disc with well impressed middle line and anterior transverse impression, weak posterior transverse impression but large irregular baso-lateral impressions; latter strongly transversely strigulose. *Elytra* $1/5$ (\pm) wider than prothorax, slightly narrowed anteriorly; margin forming *c.* right (slightly obtuse) dentate angles at humeri; discal striae in clean specimens indicated by rows of rather vague punctures; even discal intervals scarcely convex, odd intervals costate; no distinct 10th interval; each 3rd interval usually 2-punctate, behind middle and on declivity. Mesosternum and prosternal process not setose. Male with front tarsi slightly dilated, 3 segments squamulose; ♂ with 2 or 3, ♀ with 3 or 4 (often asymmetrical) setae each side last ventral segment. Length 20-25; width 7.8-8.3 mm.

Holotype ♂ (M. C. Z. Type No. 30,361) and 53 paratypes all from the Eungella Range, west of Mackay, Queensland, 2000-3000 ft. altitude, Nov. 1957, taken by the Darlingtons, in rain forest.

This is apparently related to *T. wilsoni* Cast. of South Queensland etc., but *eungella* is slightly broader and more depressed, with stronger elytral costae. For possible hybrids of this and following species, see under latter.

***Trichosternus mixtus* new species**

Form about average for genus, but prothorax strongly cordate and elytra oval; black without metallic color, head and pronotum moderately shining, elytra duller. *Head* large, $4/5$ width prothorax; eyes moderate, genae *c.* wide as eyes, rounded and somewhat narrowed to neck; antennae rather long, passing base of prothorax by about 2 or more segments; usually 3 supra-ocular setae each side (only 2 on right side in one specimen, 4 on both sides in another). *Prothorax* *c.* $2/5$ (\pm) wider than long at middle; base *c.* $4/5$ or slightly more width apex; apex strongly emarginate, angles (marginal channels) advanced in arc of emargination; apex not margined; base slightly emarginate, finely margined; sides rounded for much of length, strongly sinuate about $1/6$ of length before base, then subparallel to base;

posterior angles right or slightly acute, scarcely blunted; side margins moderate anteriorly, slightly wider posteriorly, each with 4 to 9 setae near and before middle (at least 4 on each side in all specimens) and 1 seta posteriorly well before angle; disc with usual middle line, weak transverse impressions, and rather weak baso-lateral foveae separated from base by transverse elevation; foveae strongly transversely strigulose, and base longitudinally strigulose. *Elytra* *c.* $1/4$ wider than prothorax; margin forming *c.* right or slightly obtuse, dentate angles at humeri; striae in form of lines of small punctures (often obscured); even intervals scarcely elevated but intervals 3, 5, and 7 carinate, carinae of 3 and 5 not reaching base but 7th very strongly carinate basally; no 10th interval; each 3rd interval 2-punctate posteriorly. Mesosternum without but prosternal process with setae (all specimens — most setae broken off in 2 specimens but vestiges visible). Male front tarsi moderately dilated, 3 segments squamulose; ♂ with usually 2 or 3, sometimes 4 (often asymmetrical), ♀ with usually 4, sometimes 5 setae each side last ventral segment. Length 24-29; width 8.4-9.5 mm.

Holotype ♂ (M. C. Z. Type No. 30,362) and 23 paratypes all from Eungella Range, west of Mackay, Queensland, 2000-3000 ft., Nov. 1957, taken by the Darlingtons, in rain forest.

Superficially, *mixtus* is almost a miniature of *cordatus* but has extra supra-ocular setae, posterior pronotal setae farther from base, and a setose prosternal process. From *eungella*, with which it occurs, *mixtus* differs in form, extra supra-ocular and lateral prothoracic setae, position of posterior pronotal setae, and setose prosternal process. Most individuals of both species are unquestionably distinct. However, I have 5 specimens from the Eungella Range that have intermediate characters and that may be hybrids. They are intermediate in form; like *eungella* in having only 2 pairs of supra-ocular setae; intermediate in lateral pronotal setae (2 or 3 each side at and before middle, but with posterior setae near base); and like *eungella* in having prosternal process not setose. Only field study can determine the real status of these specimens.

Trichosternus cordatus Chd.

Although *cordatus* is primarily a South Queensland species, it extends into the tropics. It lives in drier woodland than most other members of the genus except *superbus* Cast. I found it at Beechmont (Queensland-New South Wales border); Benarkin; Yarraman; Biggenden (SW of); near Monto (in dry scrubby woods with *Pamborus*

viridis); and, in the tropics, at Byfield (N. of Yepoon) in semi-rain forest, and c. 40 miles S. of Mackay in good savannah woodland.

Trichosternus spec new species

Form nearly of *T. superbus*, with strongly cordate prothorax and oval elytra narrowed anteriorly; purple or purplish, not strongly shining, elytra slightly duller. *Head* large, slightly more than $4/5$ width prothorax; eyes small, genae slightly wider than eyes, subparallel anteriorly, rounded and slightly narrowed to neck; antennae rather long, passing base of prothorax by about 2 segments; 2 supra-ocular setae each side (all specimens). *Prothorax* c. $2/5$ or less wider than long at middle; base slightly more than $3/4$ width apex; apex broadly emarginate except rounded toward sides, with angles (marginal gutters) slightly advanced; apex not margined; base broadly emarginate except oblique near angles, rather vaguely margined; sides rounded through much of length, strongly sinuate before basal angles; latter right or slightly obtuse, not much blunted; lateral margins rather narrow anteriorly, broader posteriorly, each with several (usually 4 or 5) setae at and before middle and 1 before basal angle; disc with middle line distinct, transverse impressions weak; baso-lateral foveae rather deep but vaguely limited, with weak convexities toward lateral margins, and closely transversely strigulose, the strigulations extending onto disc across base. *Elytra* c. $1/4$ wider than prothorax, widest behind middle; forming c. right (slightly obtuse), slightly dentate angles at humeri; striae indicated by weakly punctate impressions; even intervals slightly convex, odd ones 3, 5, and 7 subcostate to costate on disc, 7th strongest and sharply carinate anteriorly; no 10th interval; each 3rd interval usually 2-punctate, with punctures behind middle and on declivity. Mesosternum and prosternal process not setose. Male front tarsi slightly dilated, 3 segments squamulose. Length 24-30; width 8.5-10.3 mm.

Holotype ♂ (M. C. Z. Type No. 30,363) and 33 paratypes all from the Mt. Spec plateau (Paluma Range), c. 40 miles north of Townsville, North Queensland, 2000-3000 ft., Nov. 1957 and Feb. 1958, taken by the Darlingsons in or on the edges of rain forest.

In spite of their wide geographical separation, this species and *superbus* Cast. (of New South Wales) may represent one original stock. The new species resembles *superbus* in form, color, and many details, but differs from it in having only 2 (instead of 3) supra-ocular setae on each side and in having better defined posterior prothoracic angles.

Trichosternus setosiceps Sl.

Sloane (1923, p. 23) described *setosiceps* from the South Johnstone River and Malanda, which are on or near the Atherton Tableland. The species is widely distributed on the Tableland, except apparently the northern part, and reaches the lower slopes of Mt. Bellenden Ker and extends south to the Kirrama Range.

This species differs from all other *Trichosternus* in having 2 segments of each male front tarsus squamulose.

***Trichosternus kirrama* new species**

Form as figured (Fig. 3), large, with strongly cordate prothorax and oval elytra; black, head and prothorax moderately shining, elytra dull. *Head* large, $4/5$ or slightly more width prothorax; eyes small, genae slightly wider than eyes, broadly rounded and narrowed posteriorly to neck; antennae rather long, passing base of prothorax by *c.* 2 segments; 2 or 3 supra-ocular setae each side (often asymmetrical); frontal foveae as usual except area between them slightly depressed and/or with longitudinal prominences outside them. *Prothorax* strongly cordate, nearly $1/2$ wider than long at middle; base *c.* $4/5$ (\pm) width of apex; apex emarginate at middle, rounded toward sides, with angles (lateral channels) advanced; apex not margined; base broadly emarginate except subtruncate near angles, rather irregular, vaguely margined; sides rounded through much of length, strongly sinuate about $1/6$ before base, thence subparallel to *c.* right, well defined posterior angles; lateral margins moderate anteriorly, slightly wider posteriorly, each 2 to 4 (rarely 5) setae at and before middle and one a little before base; disc with usual middle line, transverse impressions weak; baso-lateral impressions irregular, transversely strigulose, the strigulose area extending forward at sides and across base; extreme basal strigae longitudinal. *Elytra* $1/5$ or slightly more wider than prothorax; margin somewhat obtusely angulate but only vaguely toothed at humeri; striae formed by lines of small punctures; even intervals slightly convex, odd intervals 3 and 5 slightly more raised but not costate, interval 7 strongly raised, costate at base; no 10th interval; each 3rd interval 2-punctate, behind middle and on declivity. Mesosternum and prosternal process not setose. Male front tarsi moderately dilated, 3 segments squamulose; 2 or 3 (often asymmetrical) setae each side last ventral segment in both sexes. Length 30-33; width 9.9-10.6 mm.

Holotype ♂ (M. C. Z. Type No. 30,364) and 11 paratypes all from Kirrama Range, near Cardwell, North Queensland, 2000-3000 ft., Dec. 1957 and Feb. 1958, taken by the Darlingtons, in rain forest.

In form, appearance, and some characters (near obliteration of

humeral teeth, lowness of elytral intervals) this species approaches *obscuripennis*, but the arrangement of setae is very different. I do not know the real relationships of either species.

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ADRITYLA, A NEW MILLIPED GENUS (CHORDEUMIDEA: CONOTYLIDAE)

BY NELL B. CAUSEY¹

Introduction

This is the second of a series of papers on the widely dissimilar North American species formerly assigned to the genus *Conotyla*. In the first (Causey, 1961), the genus *Austrotyla* was proposed for *coloradensis*, *humerosa*, *montivaga*, and *specus*. The remaining species will be reviewed and the basal region of the gonopods described in subsequent papers.

A grant from the National Science Foundation (G-14486) made the completion of this paper possible.

I am grateful to Dr. Herbert W. Levi for the loan of the specimens of *Conotyla deseretae* in the Museum of Comparative Zoology.

Genus *Adrityla*, new

Type species. *Conotyla deseretae* Chamberlin, 1910, by monotypy.

Diagnosis. Large bodied (length to 24 mm.), pigmented conotylids of 30 body segments, distinguished especially by the modification of legpair 10 (8¹), of which the coxa is greatly enlarged and lobate and the telepodite is reduced to 2 or 3 minute segments. The sternum of the anterior gonopods is divided, and the small sternites are fused to the base of the gonopods. The latter are unsegmented and larger than the coxites of the posterior gonopods.

Relationships. The inclusion of this genus in the subfamily Conotylinae is justified by the following sexual characters of the male: the unsegmented anterior gonopods, the retention of a division between the coxal and prefemoral segments of the posterior gonopods, and the absence of coxal glands on legpair 11 (8²). The divided sternum of the anterior gonopods suggests a close relationship with the *Austrotyla-Taiyutyla* line rather than with *Conotyla*, which has this sternum undivided. The remarkable modification of legpair 10 surely occurred independently in *Adrityla*, as it has in other widely separated chordeumids.

Distribution. Utah.

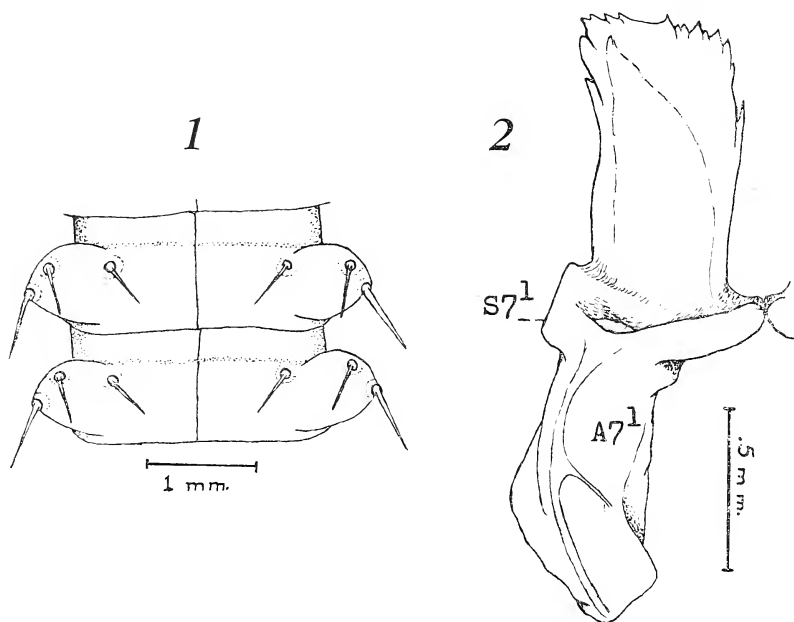
Adrityla deseretae (Chamberlin), new combination

Figures 1-4

Conotyla deseretae Chamberlin, 1910, Ann. Ent. Soc. Amer. 3(4): 235-236, pl. 31, figs. 3-8; pl. 32, figs. 1-7. Loomis, 1943, Bull. Mus. Comp. Zool. Harvard 92(7): 381. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212: 98.

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Types. Present location of male holotype unknown. Two larvae, undoubtedly metatypes, from Mill Creek Canyon, Salt Lake Co., Utah, and my plesiotypes (σ , φ) from South Willow Canyon, Tooele Co., Utah, are in the Museum of Comparative Zoology.



Figures 1, 2. *Adrityla deseretae* (Chamberlin). 1. Segments 10 and 11, dorsal view. 2. Left anterior gonopod, anterior view.

Type locality. The Wasatch Mountains, Salt Lake Co. and Utah Co., Utah.

Range. The Wasatch Mountains in central and northern Utah (Chamberlin and Hoffman, 1958).

Description. Length 22 to 24 mm., width 2.6 to 3 mm., the σ larger than the φ . Body reaches its greatest width at segment 8 or 9. Dorsum with a dark brown medial longitudinal band; pleura with a brown longitudinal band along the lower surface of the paranota; venter, legs, and remainder of dorsum light brown to yellowish; antennae dark brown. Ratio of length and width of collum approximately $\frac{1}{2}$. Paranota with the typical conotylinid shape and position are on segments 2 through 25 (Fig. 1). Segmental setae acute; on typical segments the external setae are markedly longest, about 0.5 mm., and the medial and internal (nearest the dorsomedial furrow)

setae are about 0.35 mm.; the relative distances between them are as follow:

$$\frac{\text{med. seta} - \text{ext. seta}}{\text{med. seta} - \text{int. seta}} = \frac{1}{3} \qquad \frac{\text{dorsal furrow} - \text{int. seta}}{\text{int. seta} - \text{med. seta}} = \frac{1}{3/4}$$

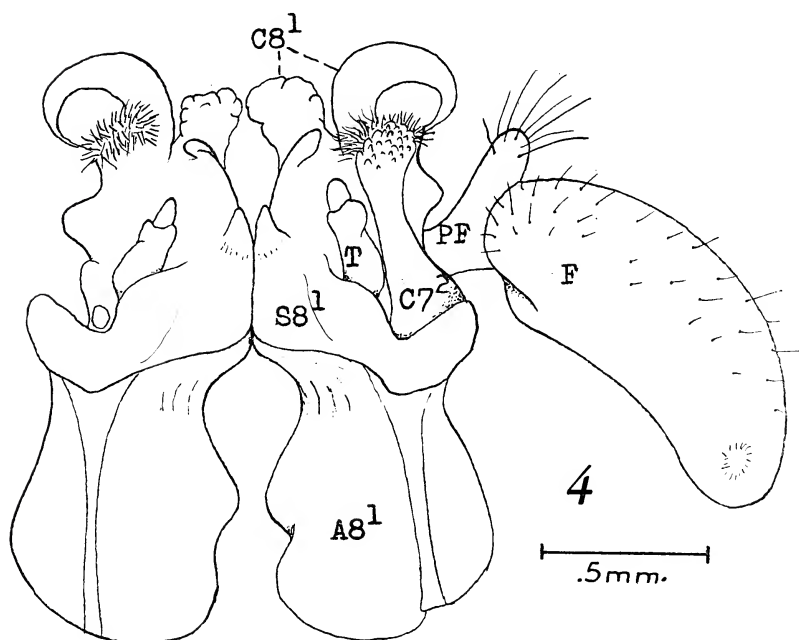
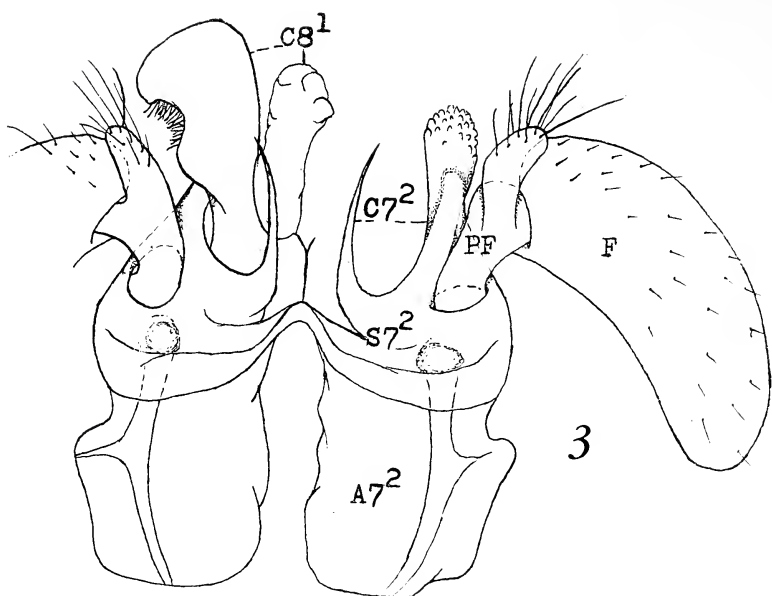
Mentum undivided. Clypeus, frons, and vertex with the usual short, unequal setae. Eyes triangular, from 23 to 25 black ocelli arranged compactly, but not touching, in rows of 1, 7, 6, 5, 4 (3), 2 (1), Antennae slender, the length approximately 4.3 mm. in the ♂ and 3.3 in the ♀.

In the male, legpairs 1 and 2 are about two-thirds the length and thickness of the following legs; legpairs 3 through 7 are shorter and thicker than the postgonopodal legs and segment 4 bears an inconspicuous rounded protuberance on the mesioproximal surface; the ventral surface of the coxa of legpair 7 is conspicuously swollen; the ventral surface of the tarsus of all legs from the third to about the middle of the body is pulvillar; legpair 10 (8¹) is highly modified by the enlargement of the coxa and the coxal sac and by the reduction of the telopodite; and legpair 11 (8²) has the coxa slightly swollen but lacks a coxal sac or coxal perforation; the ectoventral surface of segment 2 of legpair 11 bears a small, rounded, caudally directed lobe.

The anterior gonopod (Fig. 2) is an unsegmented, rectangular piece irregularly serrated on the ventral margin and directed down and slightly forward. In the coxosternal region it is contiguous with its homologue along a movable suture. The spiracle opens into a large depression near the anterior margin of the coxosternum.

The posterior gonopod (Figs. 3 and 4) consists of the usual three segments: 1) a coxa with two elongated coxites, the mesial one inconspicuous and narrowly attenuated, and the more lateral one longer, stouter, clavate, warty on the apical surface, and covered distad by the larger coxite of legpair 10; 2) a slender prefemur (one-third the length of the femur) with a setose lobe on the mesiodistal surface; and 3) a large oval femur (the ratio of the length to the thickness is 1/3) with an irregular pigmented pit on the caudal surface near the apex. The sternum is thin in the midline and bent sharply ventrad; laterad it is fused with the coxae and thickened; the spiracles open from large pigmented pits near the ectocephalic angles.

Leg 10 consists of two regions: 1) an enlarged coxosternum with one massive coxite that curves back over leg 11 and covers the apical region of the larger of the two coxites of the posterior gonopod, and 2) a minute telopodite of 2 or 3 unequal segments that cannot be



seen unless leg 11 is removed. The coxite is elongated, broadened and rounded distad, smooth on the anterior surface, and thickly setose over part of the more complex posterior surface; a subapical flange is on the ectal surface, and near the base of the mesial surface is a large perforation through which the enlarged, soft coxal sac projects. The coxal sac is contiguous with its homologue in the midline. The sternum is divided and coalesced with the coxa, forming a thick, short coxosternum which is contiguous with its homologue along a movable suture; the inconspicuous spiracles open on the ectal surface of the coxosternum.

Appendages 7² and 8¹ (the posterior gonopods and legpair 10, respectively) fit close together, but there is no fusion, and with careful dissection they can be completely separated.

In the female, the setae on the vulvae are unusually long. The legs are typical of the family.

Emendations. In the original description, Chamberlin (1910, p. 236) incorrectly interpreted the coxites of legpair 10 (8¹) as part of the anterior (7¹) and posterior (7²) gonopods. The correct legends of plate 31, figures 4-7 are: figure 4, legpair 10, caudal aspect; figure 5, anterior gonopods and parts of posterior gonopods and legpair 10, cephalic aspect; figure 6, left gonopods and tenth leg, lateral aspect; posterior gonopods, cephalic aspects. Only legpairs 4 and 5 were represented (Pl. 32, Figs. 2-6) as having a small lobe on the mesioproximal surface of segment 4. I have found that legpairs 3 through 7 have segment 4 similarly modified; possibly there is some variation of this character. A large promentum was indicated in plate 32, figure 7. There is no promentum; the small triangular space anterior to the mentum is covered only by a membrane.

Variations. The ventral margin of the anterior gonopods is irregularly serrated in each of the 4 male specimens that I have examined. The serrations vary between 3 and 14 or 15. A possible variation in the lobation of the pregonopodal legs was mentioned in the preceding paragraph.

Material Examined. UTAH: Mill Creek Canyon, Salt Lake Co., larvae (MCZ) [? metatypes]; South Willow Canyon, Tooele Co.,

Figures 3, 4. *Adrityla deseretae* (Chamberlin). 3. Posterior gonopods and left tenth leg, anterior view. 4. Left posterior gonopod and legpair 10, posterior view. (Abbreviations: A7¹, A7², A8¹, sternal apodemes of anterior gonopod, posterior gonopod, and leg 10, respectively; C7², C8¹, coxites of posterior gonopod and leg 10, respectively; F, PF, femur and prefemur of posterior gonopod, respectively; S7¹, S7², S8¹, coxosternites of anterior gonopod, posterior gonopod, and leg 10, respectively; T, telopodite of leg 10.)

July 5, 1953, 1 ♂, 1 ♀, W. D. Hester (MCZ); American Fork Canyon, Timpanogos Park, Utah Co., June 14, 1952, W. D. Hester, 3 ♂, 8 ♀, larvae (NBC).

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ANTS FROM THREE REMOTE OCEANIC ISLANDS

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The three islands (Raoul, Clipperton, St. Helena) whose ant faunas are described below have in common only extreme geographic isolation. That ants occur on them at all confirms the idea that these insects, with man's help, have now populated every part of the earth capable of supporting them. These and other remote oceanic islands will undoubtedly attract more of the ecologist's attention in the future, since many animal taxa inhabiting them, including most or all of the ant species, have only arrived within historical times and present simple case histories of faunas in the first stages of local adaptation.

We are grateful to Dr. J. S. Edwards, Dr. C. F. Harbinson, Mr. Arthur Loveridge and Dr. B. A. Holloway of the Dominion Museum, Wellington, New Zealand, for making these unusual collections available. The study has been supported in part by a research grant from the National Science Foundation.

RAOUL ISLAND, KERMADEC ISLANDS

The Kermadecs are a group of forest-clad volcanic islands lying in the South Pacific between S. lat., 29.10 and 31.30; and W. long., 177.45 and 179.00. The nearest sizable land mass is the North Island of New Zealand, about 650 miles to the southwest, and the nearest major Polynesian island is Tongatabu of the Tongan group, about 700 miles to the north. Australia lies about 1,700 miles to the west.

The ants listed below were taken on Raoul or Sunday Island, the largest of the group (11.25 sq. miles), or on its tiny outlier, Meyer Island. Most of the material was collected during June 1956 for the University of Auckland, New Zealand, by Dr. J. S. Edwards of Cambridge University. A few records are from the collections of the Museum of Comparative Zoology, Harvard University, or from the Dominion Museum, Wellington, New Zealand. Unless otherwise noted all collections were made by Dr. Edwards.

The collection includes a number of Berlese funnel samples as well as hand-collected specimens, and although only three species are listed, it is thought that they represent most, if not all, those present on Raoul in 1956.

Ponera gleadowi Forel

The systematics and distribution of this ant have been discussed by Wilson (1958). *P. gleadowi* is a widespread species, originally

described from India, and found throughout South East Asia, Melanesia and Polynesia. It is apparently native throughout most of its range, but may have been distributed in part by man (i.e., it is a member of "Class II" discussed below).

Material examined: RAOUL ISLAND: June 5, 1956; under rock, watercourse, June 8, 1956 (nest with ergatomorphic male pupae); ex Pohutakawa logs (*Metrosideros* sp.), June 3, 1956. Crater: June 4, 1956; ex moss caps on pumice boulders, June 4, 1956; ex Pohutukawa log, June 4, 1956 (nest with alate queens). Denham Bay: ex *Narcissus* litter Berlese funnel sample, June 7, 1956. Denham Bay swamp: ex Pohutakawa litter Berlese funnel sample, June 2, 1956. Hostel Bay: Berlese funnel sample, June 7, 1956; *Coxnocarpus* litter Berlese funnel sample, June 8, 1956. Oneraki Beach: beneath cow dung under trees, June 9, 1956 (J. S. Soeberg). MEYER ISLAND: Berlese funnel samples, June 7, 1956; June 16, 1956.

Ponera gleadowi is apparently the most abundant ant on Raoul and was "commonly found (by Dr. Edwards) under stones or in decaying logs or branches, frequently associated with termites." Moreover it was present in about half of the Berlese funnel samples processed by Dr. Edwards. As indicated, winged queens are present in the nests during June. No adult males were located, but several pupae from the nest collected on June 8, 1956, were found to contain almost fully developed ergatomorphic males. Except for genital differences these are similar to the workers, and like them have twelve-segmented antennae.

Tetramorium guineense (Fabricius)

This is one of the most common pantropical formicid tramp species. It evidently originated in Africa and ranges widely throughout the Old and New World tropics, and Northern Australia. It is widespread in Polynesia (Wheeler, 1935) and has recently been found established near Auckland, New Zealand. Dispersal by man has clearly been of primary importance in the distribution of this species.

Material examined: RAOUL ISLAND: June 4, 1956; quarry, under rock, June 5, 1956, (nest with alate females). MEYER ISLAND: Berlese funnel sample, June 7, 1956.

Monomorium antarcticum (White)

At present the name *M. antarcticum* is applied to what is almost certainly a complex of species found in New Zealand and its outlying islands, including the Chatham group, some 470 miles to the east

of South Island. It has undoubtedly been carried to the Chatham Islands by man (Brown, 1958). (It is further likely that *Monomorium rapaëense* Wheeler (1936) of Rapa Island in the Austral group, is conspecific with some New Zealand form belonging to the present *M. antarcticum* complex. If this should be so the fact that New Zealand and Rapa were both important whaling ports in the nineteenth century may be significant with regard to the dispersal of this form.)

Material examined: **RAOUL ISLAND:** Crater: nest in warm soil beside fumarole, June 3, 1956. Four workers without further data from the M. C. Z. collection.

The M. C. Z. specimens were studied by Wheeler in preparing his 1935 paper and were probably collected by the W. R. B. Oliver expedition to Raoul Island during 1907-08. Wheeler apparently intended using these specimens as the types of a new species, to be described in a later paper which, however, was never published due to his death. It seems unlikely that they are specifically separate from some North Island samples of the *antarcticum* complex, and they have almost certainly been introduced to Raoul from New Zealand.

The Kermadec ant fauna is thus characterized by a lack of endemic or native species and includes forms derived either from tropical Polynesia, or the nearest large land area, and known to have capacities for passive dispersal by man. The faunal tally of only three species is probably well below the possible maximum carrying capacity of the island (see Wilson, 1961). Although the present human settlement on Raoul consists only of the staff of a weather station, there have been several attempts to colonize it in the past. The parties concerned are known to have travelled from Fiji and New Zealand, and to have carried much produce as well as plants and seeds, thus providing adequate passage for ants. In its relationships and depauperate nature the ant fauna resembles those of other insect groups which have been studied (see Miller, 1956 p. 420 for references).

Some interesting comparisons can be made with the faunas of Lord Howe and Norfolk Islands, which are about the same size as Raoul, and lie at approximately the same latitude, but much closer to Australia.

The ants of these three islands may be grouped for analysis into three classes.

Class I. Species which are probably native to the island concerned. This category includes forms found also in Australia, and endemic species (all of which are clearly derived from Australian stock).

Class II. Species native to, and sometimes widespread in the Indo-Australian region which appear to have been distributed in part by man.

As the islands under discussion are rather peripheral to the main part of the Indo-Australian area it is difficult to estimate whether "Class II" species listed from them are truly native, or whether they have originated from propagules carried by man. This difficulty is especially evident with respect to the Lord Howe and Norfolk Island forms, but in our opinion, it is highly probable that the "Class II" Kermadec species (*Ponera gleadowi* and *Monomorium antarcticum*) were carried to Raoul by man.

Class III. Widespread pantropical or cosmopolitan forms well known as "tramp species" and distributed largely by man.

The numbers of species referable to each of these classes on the islands concerned are shown in Table I.

	Lord Howe Island	Norfolk Island	Raoul Island
South latitude	30° 30'	29° 48'	29° 10'
Size (mi ²)	5	13	11.25
Distance from Australia (mi)	400	900	1700
No. ants Class I (endemics bracketed)	10(5)	8(1)	—
No. ants Class II	3	1	2
No. ants Class III	1	3	1
Total number of ants	14	12	3

Table I. Certain geographical features of Lord Howe Island, Norfolk Island, and Raoul Island; with details of the class composition of their ant faunas. Further explanation in text [data based in part on Wheeler (1927), modified by recent revisionary studies].

Although native ants are apparently absent from Raoul they are present on both Lord Howe and Norfolk Islands. The species concerned are all of Australian origin, and more of them are present on Lord Howe than on Norfolk, in spite of the considerably larger size of the latter. Faunal size on these islands is thus negatively correlated with their areas, a reverse situation from that observed by Wilson (1961) in various Moluccan and Melanesian Islands. Judging from the Melanesian faunal curves published by Wilson, we believe that Lord Howe Island probably supports a saturated ant fauna. Norfolk Island, however, would be expected to carry more

species than it does — and considerably more than Lord Howe. The reason for the apparently sub-normal size of the Norfolk Island fauna may be sought in the correlation between faunal size on the two islands and the following two factors:

1. Ecological Diversity: The published reports of the terrain and the state of the vegetation on these islands suggest that Lord Howe is ecologically much more diverse than is Norfolk Island. In spite of its much smaller size it may, therefore, be capable of supporting a larger and more varied ant fauna. Conversely, Norfolk Island may have a lower carrying capacity due to its lower ecological diversity, so that its fauna, although proportionately smaller than that of Lord Howe, is nevertheless saturated.

2. Distance from Australia: The apparent correlation between faunal sizes on these islands and their distances from Australia contrasts with Wilson's (1961) finding in Melanesia, where such correlation is lacking. This situation may be due to the absence of intermediate islands between those under discussion and Australia — islands which might provide assistance as "stepping stones" to colonists. According to this hypothesis the small size of the Norfolk ant fauna is due to the fact that too few species have reached the Island to saturate its carrying capacity.

If mere distance from Australia does have the filtering effect envisaged it may be assumed that there is a maximum range of natural overseas dispersal of the Australian fauna. As far as the ants are concerned, Raoul, in lacking indigenous Australian elements, may be considered to be outside this range.

It is not possible, at present, to evaluate the relative importance of these two factors in determining the size of the Norfolk Island ant fauna, but the problem would certainly be worthy of attention by future field workers in these areas.

Lord Howe Island also has significantly more endemic ant species than has Norfolk; each of these represents a stock which has diverged from its Australian progenitor and in no case has splitting or radiation taken place *in situ* on the island. The ecological diversity of the island, coupled with the competitive pressures which must arise in such a dense fauna, has probably caused this specialization of stocks, with consequent phyletic change to the point of formation of an endemic species in some lineages.

CLIPPERTON ISLAND

Clipperton Island is a lonely coral atoll about four miles in diameter, lying at N. lat., 10.18 and W. long., 109.15. It is 1,800

miles due west of the Panama Canal, and about 670 miles southwest of the nearest part of the Mexican coast. Most of the island is barely 10 feet high, but it rises to about 70 feet at one point. The vegetation consists of grasses, shrubs, and wild tobacco and there are several coconut groves.

The island is now uninhabited but it was occupied by a Mexican garrison from 1879-1917, and by about 100 phosphate miners from 1906-1917. Both of these groups received regular supplies from Mexico. Clipperton was occupied by the United States Navy during the Second World War.

The ants listed below were collected for the Museum of Comparative Zoology by A. M. Peterson and C. F. Harbinson during August 1958; the collection is almost certainly fully representative.

Odontomachus insularis (Guérin)

This species is widespread in Central America and the West Indies, and ranges north to Florida and Georgia. It also occurs on Cocos Island and the Tres Marias Islands in the Eastern Pacific. It is noteworthy that the Island of Clarion in the Revillagigedo group is occupied by a second species, *O. clara* Roger (= *haematoda clarionensis* Wheeler), which is widespread in Mexico and the West Indies. A third far ranging species, *O. bauri* Emery (= *haematoda div. auct.; nec haematoda* L.), occurs on the Galapagos. All of these exclusively New World species are to be distinguished from the closely similar Indo-Australian *O. simillimus* Fr. Smith, (= *haematoda div. auct.; nec haematoda* L.), which ranges eastwards only to Tahiti. Three series collected.

Tetramorium simillimum (Fr. Smith)

Like *T. guineense* this is a pantropical tramp species of African origin, widespread both in Central America and Polynesia. Its total range closely approximates that of *guineense*. Ten series collected.

Triglyphothrix striatidens (Emery).

A species of tropical Oriental origin, spread by commerce throughout the Pacific, and established in North Africa and Queensland, Australia. Seven series collected.

Like Raoul, Clipperton has a depauperate ant fauna, consisting entirely of species which have probably been introduced by man.

SAINT HELENA ISLAND

Saint Helena (S. lat., 15.57, W. long., 5.42) is a small volcanic island 47 sq. miles in area, lying in the south Atlantic about 1,800

miles from South America, and 1,200 miles from Africa. The Island differs in several respects from those discussed above, in that it is well populated and is visited more regularly by shipping. Indeed, it has at times been a major port-of-call for trade between Europe, and South Africa and India. The ants listed below have probably all been introduced to the island by man. They were collected for the Museum of Comparative Zoology between 1958 and 1960 by Mr. Arthur Loveridge. The collection is probably less representative than those already discussed, so that no faunal analysis can be attempted at present.

Tetramorium simillimum (Fr. Smith)

The distribution of this species has been discussed above. One series collected at Varneys.

Pheidole megacephala (Fabricius)

This is one of the most widespread and notorious of the commercial tramp ant species, it is now virtually cosmopolitan in warm humid areas. Sandy Bay: under rocks. Prosperous Bay: nest with alates, under rocks, February 24, 1958. Varneys: alate males from a storeroom cabinet, February 19, 1960.

Solenopsis (Diplorhoptrum) sp.

The subgenus *Diplorhoptrum* includes a number of taxonomically confused, and in some cases widespread, cryptobiotic species, several of which appear to be commercial tramps. A single series labeled Varneys, 1000 feet.

Plagiolepis alluaudi Forel

This species, probably of East African origin, is a widespread pantropical tramp species. A single series from Varneys.

Paratrechina bourbonica Forel

A widespread pantropical tramp species, apparently of African origin. A single series from Varneys.

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STUDIES ON CARBONIFEROUS INSECTS OF
COMMENTRY, FRANCE: PART III.
THE CALONEURODEA

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Introduction

This is the third in a series of papers redescribing certain of the Carboniferous insects of the Commentry Basin, France.¹ It treats those Commentry species which now appear to belong to the order Caloneurodea. This extinct order was erected by Martynov in 1938 for the Carboniferous family Caloneuridae and for related families represented in Permian deposits of the USSR. It now includes additional families established by Carpenter (1943) for Permian species from Kansas. At the present time seven families are known in the order and of these only one, the Caloneuridae, is of Carboniferous age. The Commentry specimens are by far the most important of the Caloneuridae but Handlirsch's and Meunier's publications have given us a superficial and confused knowledge of these fossils. The present paper, which is based upon direct study of all the known Commentry material, consists of redescriptions of the fossils and a revision of their taxonomic assignments.

Survey of Commentry Species

A historical account of the Commentry collections and of the general literature on the insects was included in the first part of this series of papers (Carpenter, 1943). Among the species first described by Brongniart (1885) from the Commentry shales was a single specimen, designated *Caloneura dawsoni*, and assigned to the family Palaeacridiidea of the order Orthoptera. In his later monograph of the Commentry insects (1894) Brongniart included drawings of five additional specimens of *dawsoni* and gave a more extensive account of the genus, which he placed in the same family, designated at that time as Palaeacrididae. Handlirsch, in his 1906 treatise, established the family Caloneuridae for the genus, assigning it to the extinct order Protorthoptera.

¹This research has been aided by a grant (NSF-G14099) from the National Science Foundation and by a previous grant (1938) from the Penrose Fund of the American Philosophical Society. I am indebted to the authorities of the Laboratoire de Paleontologie of the Muséum National d'Histoire Naturelle in Paris for placing at my disposal the unique collections of Commentry insects in the Muséum, both in 1938 and in 1961; and to the authorities of the British Museum (Natural History) for allowing me to examine the Commentry fossils in that institution.

In 1917 Lameere, following an examination of the Commentry fossils in the Muséum in Paris, placed in the Caloneuridae two species (*similis* and *royeri*) which Meunier had originally described (1911) in the order Paleodictyoptera. At about the same time (1919) Handlirsch described four more species of *Caloneura*, all based on the Commentry specimens illustrated in Brongniart's monograph (1894). Finally in 1925 Bolton described an additional species (*subtilis*) from Commentry in the British Museum (Natural History) and also figured a specimen of *dawsoni* included in the same collection.

As a result of my examination of all of these fossils and of additional specimens in the Muséum in Paris, not previously published upon, I propose the following classification of the Commentry Caloneuroidea:

Family Caloneuridae Brongniart

Genus *Caloneura* Brongniart (synonym: *Confusio* Handlirsch)
dawsoni Brongniart (synonyms: *picta* Handlirsch, *major* Handlirsch, *longicornis* Handlirsch, *robusta* Handlirsch, *royeri* Meunier).

Family Apsidoneuridae, new (type species, *Apsidoneura flexa* Carp., Permian Kansas)

Genus *Homaloptila* Handlirsch
similis Meunier

The Commentry species which Bolton (1925) described as *Caloneura subtilis* (British Museum [Natural History], type 17280) is not, in my opinion, a caloneurid or even a member of the order Caloneuroidea. However, since the poor preservation of the specimen prevents satisfactory determination even to order, I refer this species to Insecta Incertae Sedis.

Family Caloneuridae Handlirsch

Fore and hind wings similar. Sc terminating well before the wing apex; CuA and CuP very close together and nearly parallel; MP forked nearly dichotomously; 4 anal veins; cross veins numerous. Body and legs slender.

This family is known only by the genus *Caloneura*. The Carboniferous genera *Caloneurella* Carp. (Pennsylvania) and *Pruvostiella* Handl. (Nord, France), both of which have previously been placed here, should probably be included under Caloneuroidea Incertae Sedis.

Genus *Caloneura* Brongniart

Caloneura Brongniart, 1885, soc. Amis Sci. Nat. Rouen., 21:59; 1894, Recherches Hist. Ins. Foss.: 562. Handlirsch, 1906, Foss. Ins.: 141. Carpenter, 1943, Proc. Amer. Acad. Arts Sci., 75:69.

Confusio Handlirsch, 1919, Denkschr. Acad. Wiss. Wien, 96:37 (New synonymy).

Fore wing with a somewhat broader costal space than the hind wing

and with the costal space abruptly narrowed basally; hind wing narrower at base than the fore wing and with the costal margin nearly straight basally. Rs with five or six main branches, one of these usually having a short distal branch. MP usually forked, CuA and CuP unbranched.

Type species: *Caloneura dawsoni* Brongniart.

Confusio was based upon *royeri*, which Meunier described in the palaeodictyopterous genus *Homaloneura*, and which I consider a synonym of *dawsoni*.

Caloneura dawsoni Brongn.

Figure 1

Caloneura dawsoni Brongniart, 1885, Soc. Amis Sci. Rouen, Bull., 21:59, pl. [4], fig. 2; 1894, Recherches Hist. Ins. Foss., 562, pl. 36, fig. 5-11. Lameere, 1917, Mus. Nat. Hist. Natur. Bull., 23:181. Handlirsch, 1919, Denkschr Akad Wiss., 96:35, fig. 36. Bolton, 1925, Brit. Mus. Fossil Insects, 2:15, fig. 5.

Caloneura picta Handlirsch, 1919, *ibid.*, p. 35, fig. 37.

Caloneura major Handlirsch, 1919, *ibid.*, p. 35, figs. 38, 39.

Caloneura longicornis Handlirsch, 1919, *ibid.*, p. 35, fig. 40.

Caloneura robusta Handlirsch, *ibid.*, p. 36, fig. 41.

Homaloneura royeri Meunier, 1911, Bull. Mus. Nat. Hist. Natur., 17:119, fig. 2; 1912, Ann. Paleont., 7:9, pl. 7, fig. 2; Lameere, 1917, Mus. Nat. Hist. Natur., Bull., 23:181.

Confusio royeri Handlirsch, 1919, Denschr. Acad. Wiss., 96:37, fig. 44.

This species was originally based on the single specimen figured in Brongniart's 1885 paper but was later known to Brongniart by five additional fossils, all illustrated in his *Recherches* (1894). Five other specimens (here designated as C1-C5), which have not previously been mentioned in the literature, are contained in the Muséum National d'Histoire Naturelle in Paris. To these may be added the specimen of *dawsoni* described by Bolton (1925), and the type of *royeri* Meunier. Since I am convinced for reasons given below that these thirteen specimens, all of which I have been able to examine, are one species (*dawsoni*), I have used them as a basis of the following account of this insect.

Wings (Figure 1): The fore wing, which is completely preserved in several specimens, is from 45-48 mm in length, and from 10-12 mm in width. The type specimen has a fore wing length of 45 mm and a width of 10 mm. The hind wings of the several specimens are about the same dimensions as the fore wings but are somewhat narrowed basally. The costal area of the fore wing narrows abruptly just at the level of the separation of CuP and 1A. In the hind wing the costal space is not narrowed at this point, continuing its full width as far as it is preserved in all specimens.

The general venational pattern is shown in figure 1, but this is subject to much individual variation. The subcosta terminates on the costal margin well before the end of R1; it does not extend to the apex of the wing as shown by Bolton in his drawing of a specimen in the British Museum. The number of main branches of Rs varies from 5 to 6 in the several specimens showing those veins, but usually one of these branches has a short fork, which occurs most often on R2 or R3. The branching varies in the fore and hind wings (and presumably in the right and left wings) of individual insects. In the holotype specimen (36.5)², for example, this fork occurs on R3 in the fore wing but on R2 in the hind wing. MP is less variable; it forks broadly at about mid-wing. In only one specimen (C4) does either branch of MP clearly fork again (see figure 1), but in several one or both branches

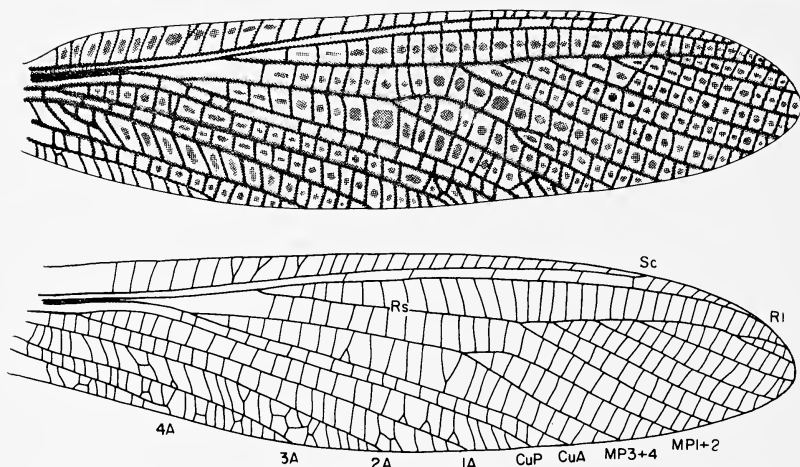


Figure 1. *Caloneura dawsoni* Brongn. Fore and hind wings based on the holotype and other specimens in the Muséum National, Paris. Sc, subcosta (—); R1, radius (+); Rs, radial sector (—); MP1 + 2 and MP3 + 4, branches of posterior media (—); 1A, 2A, 3A, 4A, anal veins.

appear to have a small, terminal fork. CuA and CuP are consistently unbranched; the divergence of CuP and 1A, near the base of the wing, is either shallow or somewhat broader. The four anal veins are consistently present.

The most striking characteristics of the wings of *dawsoni* are the

²Since the Commeny insects in the Muséum National are not numbered, I am using here the figure number on Brongniart's plates for the number of the specimen. Hence, specimen 36.5 is the fossil illustrated on Brongniart's plate 36, figure 5.

markings, as mentioned by Brongniart in his original description. The main veins and most of the cross-veins are margined with dark pigment; the veins appear to be very thick but careful examination of the wing shows that the actual veins are only of usual thickness. In addition, nearly all cells of the fore wing contain a dark, irregular pigment spot. The size of the spots varies in different wings but the pattern formed in the wing as a whole is fairly constant. The hind wings appear to be without both types of these markings; at any rate, no specimens that can clearly be recognized as hind wings show them. In a few fossils some of the wings appeared blotched (as in the holotype, 36-5), but the extreme irregularity of this and its absence in other hind wings strongly indicates that it is the result of preservation.

Body structure: Very little is known of the body structure of *dawsoni*. Several specimens show fragments and portions of the thorax and four specimens (36-8, 36-9, 36-10, 36-11) include parts of the legs and antennae but the abdomen is entirely unknown. The legs are slender, nearly homonomous and apparently cursorial. The fore and middle legs are about 34 mm long and the hind legs, 45 mm long. The dimensions of the leg segments are given in Table 1. The tarsi of all three pairs of legs are about the same length.

	<i>Femur</i>	<i>Tibia</i>	<i>Tarsus</i>
Fore leg	12 mm	10 mm	12 mm
Middle leg	12 mm	10 mm	12 mm
Hind leg	18 mm	15 mm	12 mm

Table 1. Dimensions of leg segments in *Caloneura dawsoni* Brongn.

The femora and tibiae of the fore and middle legs are about the same length, but the hind femur and tibia are slightly longer than those of the other pairs. The antennae are obviously long and slender, though they are not completely preserved in any fossil. In specimen 36-10 one antenna is preserved to the edge of the rock containing the specimen; the preserved part is 55 mm long, which is considerably in excess of the wing length.

So far as known, therefore, the body structure of *dawsoni* is similar to that of the best-known Permian species, *Paleothygramma tenuicornis* Mart. (see Martynov, 1938b, p. 126).

Synonymy: As mentioned above, Brongniart figured in his *Recherches* (1894) five specimens of *dawsoni* which were not known to him when he described the species in 1885. In 1919 Handlirsch, basing his conclusion on Brongniart's illustrations, established four

additional species for these fossils: *picta*, *major*, *longicornis*, and *robusta*. No specific characteristics were even mentioned for *robusta* and those used for the others involved the nature of the branching of Rs. Having examined all these specimens, I cannot accept any of Handlirsch's species as valid.

Meunier's *royeri*, originally placed in the paleodictyopterous genus *Homaloneura*, was transferred to the Caloneuridae by both Lameere (1917) and Handlirsch (1919), the latter making the new genus, *Confusio*, for it. Meunier's drawing of the fossil (1911, p. 119, fig. 2), although incorrect in many details, was more accurate than Handlirsch's (1919, p. 37, fig. 44), which was based solely on the small photograph contained in Meunier's later account (1912). The wing, which I have examined at the Paris Muséum, is characteristic of *dawsoni*: Rs has six branches and MP is forked as usual in the species, — not narrowly branched as in Meunier's figure or unbranched as in Handlirsch's. CuP and 1A are close together, as usual, not widely separated as represented by Meunier. This specimen is clearly *dawsoni* and since the costal margin is straight (not curved as in Meunier's figure), it is almost certainly a hind wing.

Specimens studied: The following is a list of the specimens of *dawsoni* which are now known and which I have been able to examine. In the Muséum National, Paris; (1), no. 36-5, the holotype of *dawsoni*, consisting of a nearly complete fore wing and two overlapped hind wings. (2), no. 36-7 (type of *picta* Handl.), distal two-thirds of a hind wing. (3), no. 36-8 (syntype of *major* Handl.), a nearly complete insect, with the fore wings overlapped and the hind wings also overlapped; some parts of thorax and legs. (4), no. 36-9 (type of *longicornis* Handl.), a wing base, parts of thorax, legs and antennae. (5), no. 36-10 (type of *robusta* Handl.), wing bases, portions of thorax, legs, antennae. (6), no. 36-11 (syntype of *major* Handl.), nearly complete fore wing, basal third of hind wing, parts of thorax and legs. (7), no. C1, two overlapped wings, probably hind, bases absent. (8), no C2, a well preserved fore wing, showing details of fore wing and posterior margin, parts of thorax and legs. (9), no. C3, distal third of a wing, probably hind. (10), no. C4, a very clear fore wing, and basal parts of a hind, parts of thorax and legs. (11), no. C5, basal half of a hind wing, posterior margin very clear. (12), the type of *royeri* Meunier, a nearly complete hind wing, lacking only the very base. In the British Museum (Natural History), London: (13), no. I7292, consisting of at least three (probably four) overlapped wings; also parts of thorax and legs, poorly preserved. Bolton

(1925) was in error in describing a large precostal area in this fossil; he apparently did not realize that more than two wings were overlapped, resulting in a confused jumble of veins.

Apsidoneuridae, new family

Fore and hind wings similar. Sc extending to about the apex of the wing; CuA and CuP very close together and nearly parallel; MP forked broadly and unevenly, the anterior branch (MP 1 + 2) arching strongly away from MP 3 + 4; 3 anal veins; cross-veins numerous. Body unknown.

This family is related to the Caloneuridae but differs in the length of Sc, the number of anal veins and the nature of the fork on MP. It is based on the type-genus *Apsidoneura* Carpenter (Permian, Kansas), which was originally placed in the Permian family Paleuthygrammatidae. Study of additional specimens of Caloneurodea from Permian strata of Oklahoma and of the type of *similis* from Commen-try has led me to conclude that *Apsidoneura* and *Homaloptila* represent a distinct family.

Genus *Homaloptila* Handlirsch

Homaloptila Handlirsch, 1919, Denkschr. Acad. Wiss., 96:36.

Rs with four main branches, one of these usually having a terminal fork; MP 3 + 4 continuing in a nearly straight line the stem MP, which arises from CuA at a considerable distance from the separation of CuA from R. In *Apsidoneura*, MP arises from R or the junction of R and CuA.

Type-species: *Homaloneura similis* Meunier. This is the only species known in the genus.

Homaloptila similis (Handlirsch)

Figure 2

Homaloneura similis Meunier, 1911, Bull. Mus. Nat. Hist. Natur., 17:118, fig. 1. 1912, Annal. Paleont., 7:8; fig. 6; pl 6, fig. 5.

Homaloptila similis Handlirsch, 1919, Denkschr. Akad. Wiss. 96:36, fig. 42, 43.

Fore wing: length, 30 mm., maximum width, 7 mm. Rs with four main branches, at least two of which are forked distally. MP 1 + 2 arched away from MP 3 + 4 as characteristic of the family, but curved strongly towards MP 3 + 4 distally. There is a tendency for the formation of an irregular network of cells in the distal parts of Rs and MP. Base of wing slender but not as slender as in *Apsidoneura flexa*. Hind wing: similar to the fore wing in size and venation but having a straight costal margin towards the base. The venational pattern is shown in figure 2.

Holotype: Muséum National, Paris. This is a well preserved specimen showing a fore wing and hind wing, their bases overlapped but otherwise independent. The veins are distinct and can be clearly seen under good illumination.

Meunier's drawing of this specimen is incorrect and misleading; he completely overlooked in both wings the fork on MP and the proximity of CuA and CuP. Handlirsch's drawing, based on Meunier's

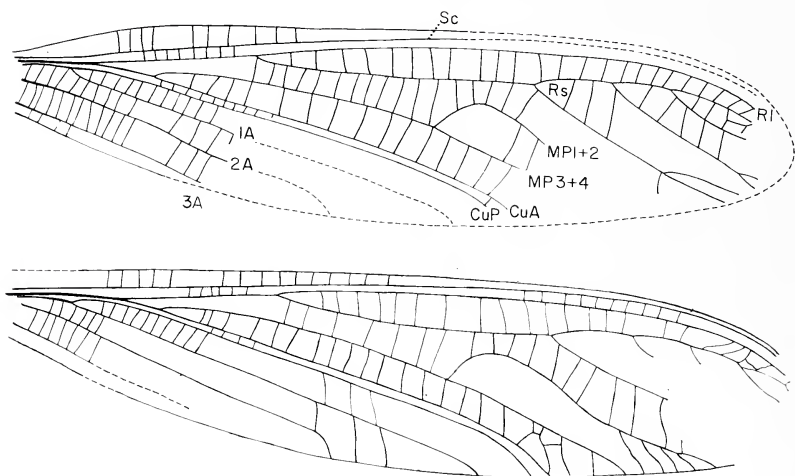


Figure 2. *Homaloptila similis* (Meunier). Fore and hind wing, based on holotype in Muséum National, Paris. Lettering as in figure 1.

published photograph, was equally inaccurate, showing the hind wing with a broad anal area. However, even though the wings are slightly overlapped basally, the margins of the wings are distinct.

The presence in the Commeny shales of this genus, allied to *Apsidoneura*, is an interesting example of a Permian element in the Commeny fauna. A similar occurrence was noted (Carpenter, 1943) in the Order Protodonata, the genus *Meganeurula* of Commeny being virtually indistinguishable from the Permian genus *Typus*.

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A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:00 p.m. in Room B-455, Biological Laboratories, Divinity Ave., Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

The illustration on the front cover of this issue of *Psyche* is a drawing of a myrmecophilous weevil, *Liometophilus manni* Fall. The original figure was included in H. C. Fall's article in *Psyche*, Volume 19, 1912, plate 3. The weevil itself was collected by the late W. M. Mann in the Huachuca Mts., Arizona.

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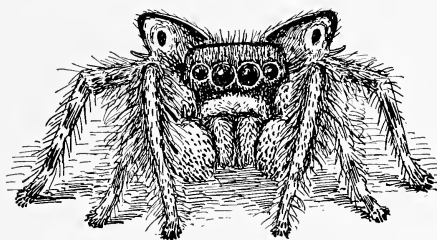
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PSYCHE

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March, 1962

No. 1

A CHEMICAL ALARM RELEASER IN HONEY BEE STINGS (*APIS MELLIFERA* L.)¹

BY RALPH L. GHENT AND NORMAN E. GARY
Department of Entomology
Cornell University

Chemicals that function to communicate alarm among the members of hymenopteran colonies have been discovered in recent years by several investigators. These chemicals, released by disturbed insects and detected in the gaseous state by other members of the colony, have been shown to elicit various forms of alarm behavior, differing according to species, but always related to the defense of the colony. Certain species of ants in particular have been shown to employ such "alarm releasers" (Wilson, 1958; Butenandt and Lindauer, 1959; Brown, 1960; Ghent, 1961). Preliminary evidence presented by Huber (1814) suggests that the honey bee (*Apis mellifera*) also possesses such a mechanism.

It is a common observation among beekeepers that the probability of being stung increases after the first sting. The frequency of stinging often appears to rise exponentially: for example, a beekeeper working with colony after colony becomes increasingly liable to be stung. This phenomenon suggests that bees possess some means of labelling an intruder, presumably by applying an alarm releaser to the victim during the act of stinging.

A characteristic, pleasantly sweet scent is noticeable at the site of stinging. This scent, although not detectable from undisturbed bees, becomes quite concentrated in a closed container of agitated bees and is most perceptible from newly-inserted stings. One exception is that the stings of recently emerged bees bear no such scent. When the bee stings, the barbed sting and its basal motor apparatus are torn from the departing worker and remain imbedded in the skin. The fragrant

¹This investigation was supported by a research grant (MY 3368) from the Mental Health Division, U. S. Public Health Service.

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substance associated with the sting would, therefore, seem to be an efficient tagging mechanism. Subsequent stings would then replenish and augment this chemical label.

An examination of the sting apparatus to determine the source of this scent revealed several facts. The contents of neither the large poison reservoir nor the so-called "alkaline" accessory gland have any detectable odor. A minute amount of fluid, immiscible with water, is held between the bulbous base of the sting shaft and the setose lobe of membrane which folds over it. The sting odor is particularly associated with this membrane, although it is sometimes detectable on other basal structures as well.

No glandular tissue was found to be immediately associated with the setose lobe covering the bulb of the sting shaft. There are, however, two masses of glandular cells, lying against the inner surface of the quadrate plates, which secrete by individual ducts onto the outer surface of these plates (Snodgrass, 1956). There is a continuous space surrounding the sting base through which this secretion can flow, eventually to collect beneath the setose lobe.

It may be significant that under natural circumstances the under surface of this lobe is exposed only when the sting is partially extruded, or during the act of stinging. The sting is frequently extruded by alarm bees, particularly when bees in the winter cluster are disturbed.

Exposure of honey bees to stings pulled from freshly-frozen workers results in a marked change in behavior. Pieces of filter paper, bearing one or more stings, were introduced into an observation hive containing a normal colony, and the subsequent behavior observed. A sudden agitation was first observed in the vicinity of the introduced stings, spreading quickly outward to a radius of about 15-20 cm. After the first sharp wave of agitation, during which most of the bees in the area buzzed momentarily, a general orientation to the stings occurred, with many bees converging on the paper. Individual bees standing near or over the introduced stings assumed an abnormally high stance, with the antennae constantly waving, and the wings partially extended, in marked contrast to the normal posture of resting bees. These individuals successively accosted approaching workers, turning from side to side and sometimes making short flights to do so. Apparently identical behavior may be observed in guard bees at the entrance of a hive. Control pieces of filter paper, introduced into other parts of the hive, or alternately with those bearing stings, elicited no such behavior if the introduction was made carefully without mechanical disturbance.

An experiment was conducted to determine whether the presence

of a fresh sting on an introduced object increases the probability of its being stung. Captured workers were first induced to sting a disk of suede leather 1.5 cm. in diameter. This was lowered on a wire into

TABLE 1. Response to suede leather disk bearing three fresh stings compared to response to an untreated control disk.

	(a) <i>Disk Bearing Stings</i>		(b) <i>Control Disk</i>	
	No. of bees clustered on disk	No. of additional stings	No. of bees clustered on disk	No. of additional stings
Test #1	50	4	0	0
#2	12	3	0	0
#3	10	0	1	0
#4	5	1	0	0
#5	100	3	0	0
#6	30	1	0	0

Test of significance for difference in number of additional stings:

$$\chi^2 = 12 \text{ with 1 degree of freedom}$$

$$P < .001$$

an observation hive and held about 5 cm. above the comb for one minute, then carefully removed. Allowing 30 seconds between introductions, this disk and other control disks bearing no stings were alternately introduced in the same manner. The number of bees which congregated on the disks during each test was estimated and the newly deposited stings were counted after each removal. The data in table (1) clearly exhibit greater attractiveness of the leather disk bearing stings, as well as a significantly ($P < .001$) greater number of stings retained in it.

These results seemed to indicate that the presence of a fresh sting alone is sufficient to provoke stinging attacks. In subsequent observations, however, it was demonstrated that one or more secondary stimuli are usually necessary to elicit stinging. Although stings invariably attract bees, we observed very few cases of stinging unless the test object was moved or jarred. Indeed, bees that congregated about an introduced sting tended to fly at any moving object in the vicinity. Since the loss of the sting is often fatal to the worker, there is an obvious selective pressure against the stinging of immobile objects, even though coated with an alarm releaser.

In subsequent experiments, it was found that extracts of stings attracted worker bees, and induced a pattern of behavior which was apparently identical to that of workers exposed to fresh stings.

The alarm reaction was further characterized in an experiment relating the quantity of extract to the number of bees attracted to it. Three hundred whole uncrushed stings, pulled from freshly-frozen workers, were extracted in 1 ml. of methylene chloride. Measured

quantities were pipetted into vials (4.5 cm. long by 1.3 cm. in diameter) with an inner lining of filter paper. Each vial was placed in a cylindrical screen cage 10 cm. long by 3 cm. in diameter, which was

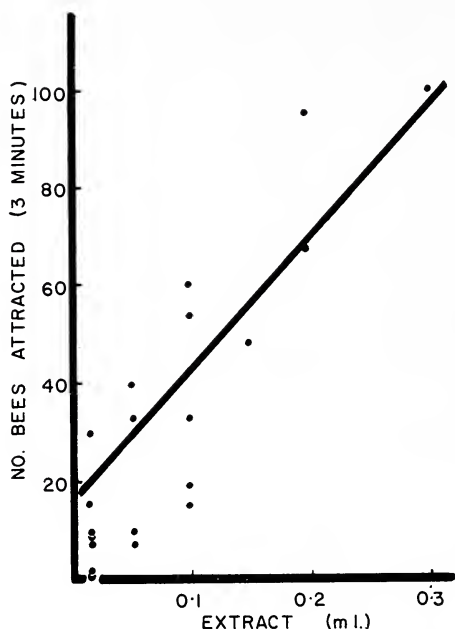


Figure 1. Attraction of worker bees to an extract of bee stings in methylene chloride. The extract was pipetted onto filter paper and introduced in screen cages laid over the combs of a colony. Bees attracted to each cage were collected and counted.

open at one end. The cages were laid in groups of four across the top bars of an open colony, immediately enclosed by an empty hive body and cover, and left in this dark chamber for 3 minutes. Each was then carefully transferred with the adhering bees into a closed container. The bees thus collected were anesthetized and counted (Fig. 1). Although the data show considerable variation, there was a positive correlation between the quantity of extract per vial and the number of bees attracted.

An extract containing about 5,000 stings in 10 ml. of methylene chloride was distilled, beginning at 35° C. and slowly rising to 90° C. The colorless distillate was collected in three approximately equal fractions. The last two fractions, distilled at temperatures over

60° C., had the characteristic bee sting scent. Some of this scent was retained by the yellow residue.

Vapor phase chromatograms of the first fraction showed evidence of only the solvent, methylene chloride. In both of the last two fractions only two components in addition to the solvent were detected: water and the scented substance presumed to be the alarm releaser. Attempts to concentrate the odoriferous component by evaporation of the methylene chloride were only partially successful. Vapor phase chromatograms indicated that, although it was slightly concentrated during evaporation, the greater part was lost.

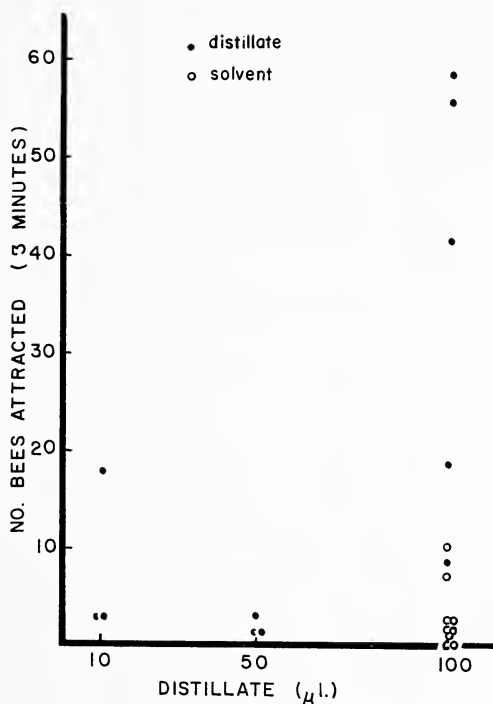


Figure 2. Attraction of worker bees to distilled extract of bee stings. The distillate was pipetted onto filter paper and introduced in screen cages laid over the combs of the colony. Bees attracted to each cage were collected and counted.

The effect of the whole distillate on bee behavior was tested by the same method as that used for the crude extract. Data on attraction

confirmed the presence of the alarm releaser in the distillate (Fig. 2). The behavior of bees exposed to the distillate was indistinguishable from that observed in the presence of fresh bee stings. Moreover, it was evident that bees attracted to filter papers bearing the distillate demonstrated an extraordinary tendency to sting upon the slightest provocation.

We have not yet succeeded in concentrating sufficient quantities of the alarm releaser to permit chemical characterization. Our observations indicate that extremely small traces of the scented substance of bee stings are detectable both by humans and by honey bee workers, and that the amount borne by single stings is in fact minute.

Alarm behavior in honey bees is governed by many factors, and the presence of the alarm releaser is not essential to stinging. Bees often attack moving objects or animals in the vicinity of the hive where no alarm releaser could possibly have been applied previously. Movement, odor, and texture probably all determine to some degree whether the response is aggressive. Unless accompanied by a supplementary stimulus, for example movement, the odor of the alarm releaser rarely precipitates stinging. The function of the alarm releaser, besides serving as an efficient recruiting mechanism, must be considered as an intensifier of the normal defensive responses of the colony.

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THE MALE OF *PLATYPATROBUS LACUSTRIS*
DARLINGTON (COLEOPTERA: CARABIDAE)*

BY CARL H. LINDROTH
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The discovery of a new genus among the Patrobini from Lake Superior (Darlington, 1938) was most unexpected. It was founded on a single female from Batchawaung Bay, Ontario, in the Leconte collection in the Museum of Comparative Zoology at Harvard, and, in the absence of a male, the author hesitated to state the true relationship of the new genus. This female is the only specimen of the genus *Platypatrobus* (species, *lacustris* Darl.) heretofore known.

Quite recently, in September, 1961, Dr. Darlington and I visited the well-known coleopterist, Mr. C. A. Frost, Framingham, Mass., and, looking through his large collection, made the exciting discovery of a male of *Platypatrobus lacustris*, received by him from Dr. A. E. Brower. According to the label, the beetle had been taken at "black light," July 30th, a few years ago (exact year not stated) at Sinclair in northernmost Maine. Its capture in a light trap and its well developed hind-wings indicate that it is able to fly.

The new male, except for the two dilated basal segments of the pro-tarsi, matches the type completely. The extra setae on prothorax and elytra are considerably irregular in number and position: laterally on the prothorax are 3 (left) and 4 (right) (in the type 4 + 3) setae; on the elytra, 1st interval, 2 + 2 (type 1 + 2), 3rd interval, 12 + approximately 9 (type 11 + 12), 5th interval, 10 + 8 (type 5 + 6).

I was allowed to borrow the specimen and have dissected the genitalia (fig. 1). The *parameres* are of the normal Patrobine type, almost identical with those of the two related genera, *Patrobus* and *Diplous* (*Platidius*), that is, approximately symmetric with long, narrow apical prolongations bearing 4 setae at tip. The accessory sub-apical setae are inconspicuous, only 2 in number, and there is no suggestion of the hairy membrane externally that is characteristic of the *septentrionis* group of *Patrobus*.

The *penis* (median lobe) is non-sclerotized dorsally, as in *Patrobus* and *Diplous*, but not entirely open, as in *Deltomerus*, *Platidiolus* (*Patroboidea*), and related genera. The hook-shaped basal part is a common feature of all Patrobini. The apex is long and slender as

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in *Patrobus longicornis* and *foveocollis*, but without the subapical left side tooth of *longicornis* and, compared with *foveocollis*, symmetric. The shape of the apex, however, generally has little generic value in carabid beetles.

The *internal sac* of the penis is less complicated than in most *Patrobus*. The "apical plate" (Darlington; "Manschette", Kühnelt, 1941), forming the bottom (anterior part) of the eversible sac when in repose, is slightly spiral, but not at all to the extent of the *sibiricus* group of *Diplous* (Kühnelt). It is not prolonged into a spine, as in the North American *Diplous* (contrasted with the Siberian repre-

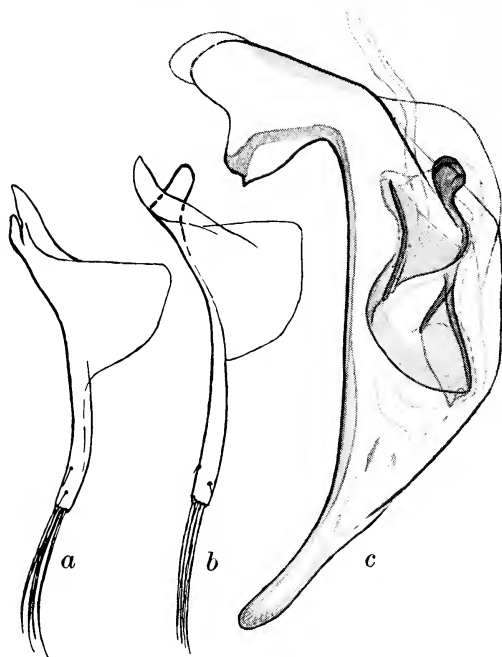


Fig. 1. *Platypatrobis lacustris* Darl. Penis (c) and parameres (a, right; b, left). The dark parts of the internal sac are not isolated sclerites but thickened margins of lamellae.

sentatives of the genus). It lacks accessory spine(s), in contrast to *Patrobus*. Presence of spines was used as a generic character of *Patrobis* by Darlington, but there is no spine in the Palaearctic *P. assimilis* Chd.

The most characteristic feature in the internal sac of *Platypatrobis* is the dorso-basal part of the "apical plate", which protrudes into

the softwalled section of the dorsum. In side view it resembles a stalked button, but in dorsal view it is revealed as the side-face of a horizontal though somewhat elevated and irregular lamella with thickened margin. It seems to have no direct counterpart in any species of *Patrobus* or *Diplous*.

In summary, the male genitalia of *Platypatrobus* provide no clue to its taxonomic relationship with its two closest relatives, *Patrobus* and *Diplous*. The intrageneric variation of the internal sac is so great in both genera that no single consistently separating detail could be discovered. And the male genitalia of *Platypatrobus* itself show little peculiarity. Possibly, the general simplicity of the internal sac, with complete lack of spine-like sclerites, could be regarded as a sign of primitive organization. But it should be remembered that the same applies to the *depressus* group of *Diplous* (Kühnelt, 1941) as well as to *Patrobus assimilis*.

The taxonomic position of genus *Platypatrobus*, therefore, has still to be judged on external characters. In these, the genus is clearly closer to *Patrobus* than to *Diplous*. This is shown by the protruding eyes and the strongly constricted neck, as well as by several structural details of the prothorax: the central furrow is deepened at base; the basal foveae are deep and well defined; the front margin is strongly elevated (almost as in *P. longicornis*), delimited basad by a deep transverse impression which is coarsely punctured (as in *P. septentrionis*) and prolonged laterally to front-angles as an engraved line (as in *P. longicornis*, *septentrionis*, and *foveocollis*). However, as in *Diplous*, there is no defined latero-basal carinula inside the hind angles.

There are also good characters separating *Patrobus* and *Diplous* in the marginal region of the elytra¹, not observed by earlier students (Darlington, 1938; Kühnelt, 1941; Lindroth, 1961): (1) the raised lateral bead is complete to apex in *Patrobus*, rather suddenly disappearing well before apex in *Diplous*²; (2) the 9th stria is better developed in *Diplous*, still evident at the level of the meso-coxae, whereas in *Patrobus* it disappears anteriorly well behind this point; (3) the marginal row of setiferous punctures (on 9th interval) is almost continuous in *Diplous*, consisting of about 20 (19-24) punctures, whereas in *Patrobus* it is \pm interrupted at middle and the number of punctures is reduced (8-14). Jeannel (1941, p. 565ff)

¹Studied in the North American and (*Patrobus*) Scandinavian representatives of the two genera.

²This, however, is not quite constant in *Diplous*. An apparently undescribed species from the Kolyma River district, E. Siberia (V. N. Kurnakov). has the elytra margined to apex.

has used the last character as the main distinction between the "sub-families" *Deltomeritae* (represented in North America by genus *Platidiolus*, syn. *Patroboidea*) and *Patrobitae*, in spite of the fact that *Diplous* is referred to the latter group which he defines as having constantly 8 setiferous punctures! In the three points mentioned above (1-3), *Platypatrobis* agrees with *Patrobis* in points 1 and 2 but is intermediate in point 3, the marginal row consisting of 16 punctures on each side in the male investigated and being less interrupted at middle than in *Patrobis*.

Platypatrobis, though generically distinct, is closely allied to *Patrobis* and no "missing link" to *Diplous*. Its extreme rarity and restricted distribution undoubtedly give the impression of a relict, on the verge of extinction. On the other hand, it does not seem possible to tell whether *Platypatrobis* is the phylogenetically older genus. It should perhaps be regarded as "more simple" in general construction (lack of prothorax carinula, nearly continuous marginal row of setiferous punctures of elytra, simple internal sac of penis), but evolution sometimes goes toward simplification. How often is it actually defensible to state, without fossil evidence, what is "primitive" and what "derivative"?

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THE SPIDER GENERA *STEATODA* AND
ENOPLOGNATHA IN AMERICA*
(ARANEAE, THERIDIIDAE)

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The previous revisions (Levi, 1957a, 1957b) of the two genera *Enoplognatha* and *Steatoda* considered only the North American species. Since the revisions were published, large South American collections have become available and the types of South American species could be consulted.

The majority of species of both genera are found in the north temperate zone and are fairly well known. The additional species described here from the neotropical area are sometimes intermediate between the two genera. *Enoplognatha peruviana* may lack the tooth on the posterior margin of the chelicerae as in *Steatoda* species. The males of several *Steatoda* (e.g. *S. andina*) have the chelicerae enlarged as is characteristic of *Enoplognatha*. South American *Enoplognatha* species are found only in southern Peru and northern Chile (Map 1). The genus has no representatives in Central America or the West Indies. *Steatoda* species are found in all parts of South America, with several endemic species and several that are widespread (*S. ancorata*, *S. grossa*, *S. moesta*). Unlike *Anelosimus* species (Levi, in press) *Steatoda* species cross the desert or mountain barrier into Chile (Map 2).

The types of species could be examined through the hospitality and cooperation of Dr. G. Owen Evans and Mr. D. Clark of the British Museum (Natural History); Prof. G. C. Varley of the Hope Department of Entomology, Oxford; Dr. L. Brundin of the Natural History Museum, Stockholm; Prof. M. Birabén of the Museo de la Plata; Prof. M. Vachon of the Muséum National d'Histoire Naturelle, Paris; Mr. J. Prószyński of the Polish Academy of Sciences, Warsaw; Dr. L. Forcart of the Naturhistorisches Museum, Basel and Dr. M. Beier of the Naturhistorisches Museum, Vienna. I would like to thank the following for the loan of specimens for study: Prof. M. Vachon, Muséum National d'Histoire Naturelle (MNHN); Mr. J. Kekenbosch of the Institut Royal des Sciences Naturelles, Brussels (ISNB); Dr. W. J. Gertsch of the American Museum of Natural History (AMNH); Dr. O. Kraus of the Senckenberg Museum,

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Frankfurt (SMF); Dr. E. S. Ross of the California Academy of Sciences (CAS); Dr. H. Exline (Mrs. D. Frizzell) for specimens from northern Peru and Ecuador collected by herself and others; Dr. R. X. Schick of California; Miss H. Zapfe (Mrs. G. Mann) of Santiago de Chile; Dr. J. Abalos of Santiago del Estero and Prof. H. Stahnke of Arizona. A trip to European museums to examine types was made possible by a National Science Foundation Grant (G-4317) and the research was supported by a grant from the National Institutes of Health (E-1944).

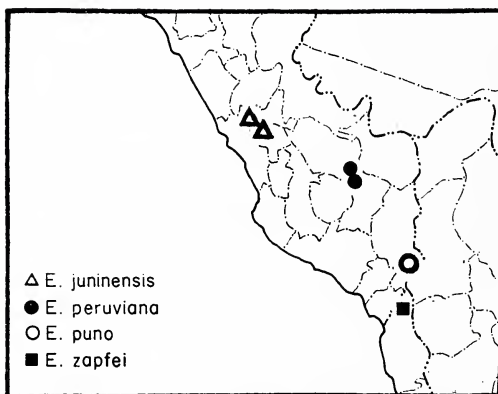
Enoplognatha Pavesi

Enoplognatha Pavesi, 1880, Ann. Mus. Civ. Stor. Nat. Genova, vol. 15, p. 325.

Type species by original designation and monotypy *Theridion mandibulare* Lucas.

Diagnosis. Medium sized to large theridiid spiders. *Enoplognatha*, like *Steatoda*, has a large colulus and a subspherical abdomen. Females have a tooth on the posterior margin of the chelicerae. Males usually have enlarged chelicerae, with enlarged teeth and have the paracymbium on the margin of the cymbium (Levi and Levi, 1962).

Species misplaced. *Enoplognatha dubia* Chamberlin, 1916 = *Anelosimus studiosus* (Hentz, 1850). *Enoplognatha triangulifera* Simon, 1902 = *Anelosimus recurvatus* (Tullgren, 1901).



Map 1. Distribution of South American *Enoplognatha* species.

Key to American Species of *Enoplognatha*

- | | |
|--|---|
| 1a. Species found in South America | 2 |
| 1b. Species found in north of Mexico | 5 |

- 2a. Epigynum with a large central depression (Figs. 12, 13, 15) 3
- 2b. Epigynum otherwise 4
- 3a. Epigynum with central depression surrounded by a lip (Figs. 12, 13); ducts coiled (Fig. 11); Peru *E. juninensis* (Keyserling)
- 3b. Epigynum with central depression lacking a lip posterior (Fig. 15); ducts with a sclerotized loop (Fig. 14); Chile *E. zapfei* n. sp.
- 4a. Fused ducts extending anterior and surrounding seminal receptacles (Fig. 9) *E. puno* n. sp.
- 4b. Fused ducts not extending anterior of seminal receptacles (Fig. 7) *E. peruviana* Chamberlin
- 5a. Yellow-white coloration with black or red lines on carapace and abdomen (1957a, fig. 4); introduced in northeastern and Pacific coast states *E. ovata* (Clerck)
- 5b. Gray, brown or black coloration 6
- 6a. Males 7
- 6b. Females 14
- 7a. Lacking paracymbium on cymbial margin (Fig. 4); Arizona, southeastern California *E. maricopa* n. sp.
- 7b. With paracymbium on cymbial margin 8
- 8a. Conductor with a stalked distal apophysis (1957a, fig. 13-16) 9
- 8b. Conductor otherwise 10
- 9a. Conductor apophysis widened distally and truncate (1957a, figs. 15, 16); California *E. selma* Chamberlin and Ivie
- 9b. Conductor apophysis pointed distally (1957a, figs. 13, 14); introduced in Oregon *E. thoracica* (Hahn)
- 10a. Chelicerae with two subequal teeth on posterior margin (1957a, figs. 24, 25) 11
- 10b. Chelicerae with one large mesal tooth (1957a, figs. 46-48) 12
- 11a. Abdomen with a spotted dorsal pattern (1957a, fig. 33); median apophysis in ventral view only in distal half of alveolus (1957a, fig. 26); widespread throughout United States and southern Canada, Mexico *E. marmorata* (Hentz)
- 11b. Abdomen with a foliate dorsal pattern (1957a, fig. 37); median apophysis in ventral view extending into proximal half of alveolus (1957a, fig. 28); east of Rocky Mountains to Newfoundland *E. tecta* (Keyserling)
- 12a. Ectal portion of conductor with long axis almost parallel to axis of cymbium (1957a, figs. 42-45); western states, rare in east *E. joshua* Chamberlin and Ivie

- 12b. Long axis of ectal portion of conductor at almost right angles to axis of cymbium (1957a, figs. 38, 40) 13
- 13a. Embolus more proximal, conductor with a longer ectal portion (figs. 38, 39); South Dakota to Utah at lower elevations *E. wyuta* Chamberlin and Ivie
- 13b. Embolus more distal, conductor with a shorter ectal portion (1957a, figs. 40, 41); Alaska to Greenland, in Rocky Mountains above timberline and in spruce-fir forest, Minnesota, Pennsylvania, New England *E. intrepida* (Sørensen)
- 14a. Epigynum with a light posterior transverse bridge (1957a, fig. 55); western states, rare in east .. *E. joshua* Chamberlin and Ivie
- 14b. Epigynum otherwise 15
- 15a. Epigynum with an oval depression having dark marks of openings on the anterior of the depression (1957a, fig. 20); California *E. selma* Chamberlin and Ivie
- 15b. Epigynum otherwise 16
- 16a. Epigynum with a transverse swelling, with a seam on the anterior and openings on each end of seam (1957a, fig. 18); introduced in Oregon *E. thoracica* (Hahn)
- 16b. Epigynum otherwise 17
- 17a. Epigynum with distinct dark marks indicating openings 19
- 17b. Epigynum with diffuse dark marks 18
- 18a. Swelling of epigynum divided by a transverse groove (1957a, figs. 31, 32), spotted dorsal abdominal pattern (1957a, fig. 33); widespread throughout United States and southern Canada, Mexico *E. marmorata* (Hentz)
- 18b. Epigynum swelling undivided with only a slight depression posterior (1957a, figs. 35, 36), foliate dorsal pattern of abdomen (1957a, fig. 37); east of Rocky Mountains to Newfoundland *E. tecta* (Keyserling)
- 19a. Dark mark of epigynum anterior to a light swelling (Fig. 2); Arizona, southeastern California *E. maricopa* n. sp.
- 19b. Dark mark anterior to a transverse ridge 20
- 20a. Posterior edge of dark mark of epigynum straight (1957a, fig. 50); South Dakota to Utah at lower elevations *E. wyuta* Chamberlin and Ivie
- 20b. Dark mark dumb-bell shaped (1957a, fig. 52); Alaska to Greenland, in Rocky Mountains above timberline and in spruce-fir forest, Minnesota, Pennsylvania, New England *E. intrepida* (Sørensen)

Enoplognatha selma Chamberlin and Ivie

Additional record. California. Los Angeles Co.: Big Tujunga Canyon, San Gabriel Mts., 3 June 1955 (R. X. Schick).

Enoplognatha marmorata (Hentz) and
Enoplognatha tecta (Keyserling)

Although these are common species in the eastern United States, we still have few observations on their habits. Mature *E. tecta* have been collected on a garage door in Cambridge, Massachusetts and numerous specimens were collected rolled up in leaves in herbaceous vegetation along forest edge about 40 cm above ground in southern Minnesota, in an area where *E. marmorata* was collected under boards in gardens.

Additional records of E. marmorata. Canada. British Columbia: Muskeg near Little Prairie (D. Rounds). Mexico. Hidalgo: Guerrero Mill (W. M. Mann).

***Enoplognatha maricopa* new species**

Figures 1-5

Type. Male from Phoenix, Maricopa County, Arizona, 11 March 1960 (H. L. Stahnke) in the Museum of Comparative Zoology.

Description. Male carapace, sternum, legs red-brown. Abdomen mottled purplish. Sclerotized portion of epigastric area and plate above pedicel on abdomen red-brown. Carapace with a circular thoracic depression. Anterior median eyes smallest, anterior laterals largest. Anterior median eyes a little less than a diameter apart, their radius from laterals. Posterior median eyes a little less than a diameter apart, one diameter from laterals. Chelicerae heavy but not elongated, with one large anterior tooth (Fig. 5). Total length 3.4 mm. Carapace 1.8 mm long, 1.3 mm wide. First patella and tibia 1.4 mm; second 1.3 mm; third 1.0 mm. Fourth femur 1.3 mm; patella and tibia 1.6 mm; metatarsus 1.2 mm; tarsus 0.5 mm.

Female carapace, sternum and legs mottled brown or yellowish. Abdomen with a black pattern on dorsum as in *Enoplognatha wyuta* Chamberlin and Ivie (1957a, fig. 53). Anterior median eyes smaller than others. Anterior medians one and one-half diameters apart, one diameter from laterals. Posterior median eyes one diameter apart, a little more than one diameter from laterals. Chelicera with one anterior tooth and three denticles between tooth and base of fang.

Posterior margin of chelicera with one small tooth (missing on one side of one specimen). Total length one female 2.9 mm, another 3.8 mm. Carapace of the latter 1.5 mm long, 1.2 mm wide. First femur 1.6 mm; patella and tibia 1.8 mm; metatarsus 1.0 mm; tarsus 0.8 mm. Second patella and tibia 1.5 mm; third 1.1 mm; fourth 1.8 mm.

Comments. It is not certain that the male and female described here belong together. However, since large collections of spiders are available from southern and southeastern Arizona and no specimens of *Enoplognatha* have been found, I assume that the distribution of *Enoplognatha maricopa* is north from the type locality, where the females were found, a poorly collected area.

Diagnosis. The palpus differs from other North American species in that there is no paracymbium on the margin of the cymbium (Fig. 4). However, the transparent edge of the cymbium is difficult to see. On the mesal side of the bulb is a sclerite, probably part of the conductor, which has two projections, one toward the venter and one toward the distal end of the palpus (Fig. 3). The female differs from *Enoplognatha intrepida* (Sørensen) in that it has two dark openings connected by a black groove; posterior to the groove is a swelling having a lighter center (Fig. 2).

Records. California. Placer Co., near Emigrant Gap, 8 July 1956, 2 ♀ (V. Roth, W. J. Gertsch, AMNH); Tahoe City, 8 July 1956, ♀ (W. J. Gertsch, V. Roth, AMNH).

Enoplognatha peruviana Chamberlin

Figures 6-8

Enoplognatha peruviana Chamberlin, 1916, Bull. Mus. Comp. Zool., 60: 232, pl. 16, figs. 8-11, ♀. Female type from Urubamba, 3100 m alt., [Cuzco], Peru, in the Museum of Comparative Zoology, examined.

Description. Carapace, sternum, legs red-brown. Abdomen black with a dorsal pattern as in *Enoplognatha tecta* (Keyserling), (1957a, fig. 37). Anterior median eyes two-thirds diameter apart, one diameter from laterals. Posterior median eyes two-thirds diameter apart, one and one-half diameters from laterals. Anterior median eyes slightly smaller than others. Chelicera with three large teeth on anterior margin, the first and third larger than the middle one; none on posterior margin of the type. However, another specimen seems to have the posterior tooth. Colulus relatively small with two setae. Total length of female type 6.5 mm. Carapace 3.6 mm long, 2.4 mm wide. First femur, 2.7 mm; patella and tibia, 3.4 mm;

metatarsus, 2.0 mm; tarsus, 1.1 mm. Second patella and tibia, 3.0 mm; third, 2.3 mm; fourth, 3.2 mm.

The male illustrated (Fig. 6) may belong to this species; this is uncertain, as is the locality where it has been found.

Records. *Peru.* "Pampa Machei, 4400 m," Feb. 1947, ♂ (Brecht, AMNH). *Cuzco:* Cuzco, 3500 m, July 1947, ♀ (W. Weyrauch, AMNH).

***Enoplognatha puno* new species**

Figures 9, 10

Type. Female from 32 km north of Desaguadero, Puno, Peru, 27 Feb. 1951 (E. I. Schlinger, E. S. Ross), in the California Academy of Sciences. The specific name is a noun in apposition, after the type locality.

Description. Carapace, sternum, legs dark brown. Abdomen brownish black with an indistinct dorsal pattern as in *E. peruviana*. Venter with some white pigment on each side. Anterior median eyes much smaller (two-thirds their diameter) than oval posterior eyes. Anterior median eyes two-thirds diameter apart, more than their diameter from laterals. Posterior median eyes less than their shorter diameter apart, two and one-half times their shorter diameter from laterals. Chelicerae with three large anterior teeth and a minute denticle on posterior margin. Total length 6.1 mm. Carapace 2.6 mm long, 2.0 mm wide. First femur 2.3 mm; patella and tibia 2.9 mm; metatarsus 1.7 mm; tarsus 1.0 mm. Second patella and tibia 2.5 mm; third 2.1 mm; fourth 3.0 mm.

Diagnosis. Only the epigynum (Fig. 10) and ducts of the internal genitalia (Fig. 9) separate this species from *E. peruviana*; the pattern and the structure are very similar. It is possible that this species belongs to a geographical race of *E. peruviana*.

***Enoplognatha juninensis* (Keyserling)**

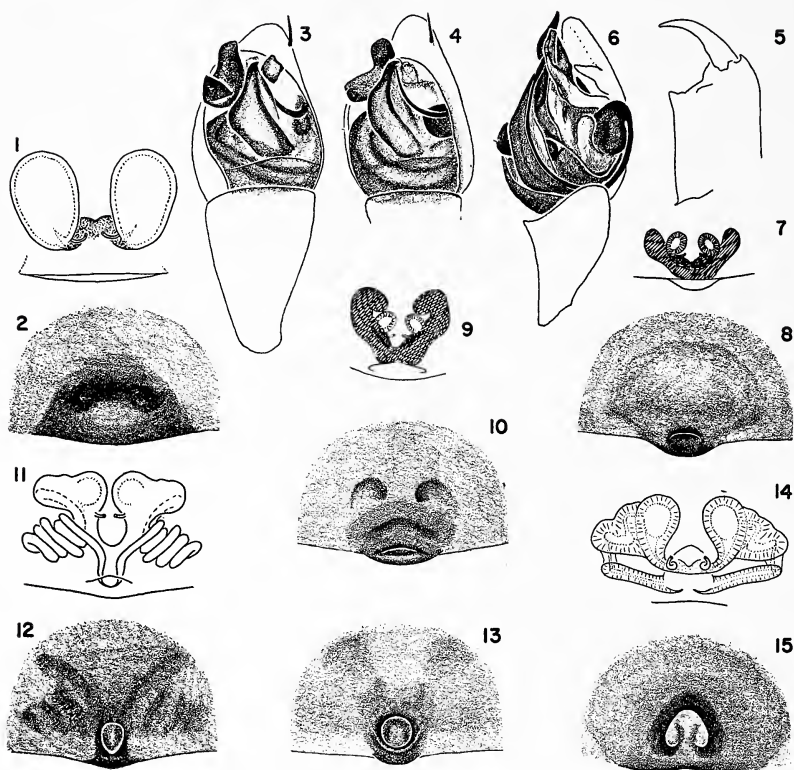
Figures 11-13

Lithyphantes juninensis Keyserling, 1884, Die Spinnen Amerikas, Theridiidae 2(1):143, pl. 6, fig. 90, ♀. Female lectotype here designated from Maraynioc, Junín, Peru in the Polish Academy of Sciences, Warsaw, examined.

Enoplognatha juninensis, Simon, 1894, Histoire Naturelle des Araignées, 1: 578.

The specimen examined from Pasco, Peru has the abdomen dark gray with a light area on each side on dorsum; the venter is also dark

gray with a light area on each side between epigynum and spinnerets. The chelicerae have three large teeth on the promargin, a minute



Figs. 1-5. *Enoplognatha maricopa* new species. 1. Female genitalia, dorsal view. 2. Epigynum. 3, 4. Left palus. 3. Ventral view. 4. Ectal view. 5. Left male chelicera, posterior view.

Figs. 6-8. *E. peruviana* Chamberlin. 6. Palpus (doubtful determination). 7. Female genitalia, dorsal view. 8. Epigynum.

Figs. 9-10. *E. puno* new species. 9. Female genitalia, dorsal view. 10. Epigynum.

Figs. 11-13. *E. juninensis* (Keyserling). 11. Female genitalia, dorsal view. 12, 13. Epigynum.

Figs. 14-15. *E. zapfei* new species. 14. Female genitalia, dorsal view. 15. Epigynum.

tooth on the posterior margin. The colulus is large, almost transparent white, with two setae from the base.

Records. Peru. Pasco: near Huayllay, 4400 m, 10 Aug. 1953,

♀ (H. W. Koepcke, SMF). *Junín*. Maraynioc, ♀ paratype with ♀ paratype (BMNH).

***Enoplognatha zapfei* new species**

Figures 14, 15

Type. Female from Putre, Province Tarapacá, Chile, Feb. 1948 (Avilés), in the Museum of Comparative Zoology. The species is named after Miss H. Zapfe of Santiago de Chile.

Description. Carapace dark yellow, darker around anterior median eyes. Chelicerae red-brown. Sternum, legs dark yellow. Abdomen gray with darker gray mottled pattern on dorsum and a pair of longitudinal lighter bands between genitalic area and spinnerets. Anterior median eyes slightly smaller than others. Anterior lateral eyes on slight tubercles. Anterior median eyes slightly less than one diameter apart, a little more than one diameter from laterals. Posterior median eyes three-quarters diameter apart, two diameters from laterals. Chelicerae with three teeth on anterior margin, a blunt indistinct tooth posterior. Total length 9.2 mm. Carapace 4.5 mm long, 3.4 mm wide. First femur, 4.1 mm; patella and tibia, 5.0 mm; metatarsus, 3.4 mm; tarsus, 1.6 mm. Second patella and tibia, 4.3 mm; third, 3.7 mm; fourth, 5.1 mm.

Diagnosis. This large species of *Enoplognatha* can be separated from *E. juninensis* by the lack of posterior lip in the opening of the depression of the epigynum (Fig. 15) and by lack of the internal coiled duct. The ducts of *E. zapfei* are heavily sclerotized adjacent to the seminal receptacles (Fig. 14).

Steatoda Sundevall

Steatoda Sundevall, 1833, *Conspectus Arachnidum*, p. 16. Type species designated by Thorell, 1869, *On European Spiders*, p. 93. *S. castanea* (Clerck, 1757).

Diagnosis. Medium-sized to large theridiid spiders, usually dark in coloration. Colulus very large. Chelicerae armed with a tooth or several teeth on anterior margin. But unlike *Enoplognatha*, it has no teeth on the posterior margin of female chelicerae. Abdomen subspherical. Males often with enlarged chelicerae and a sclerotized ring around pedicel on anterior end of abdomen. The abdomen of most species has a white line around anterior of dorsum, in addition to other lines or spots (Levi and Levi, 1962).

Note. The common species of North America were described in

a previous paper (Levi 1957b). In this paper the ventral view of the genitalia (cleared epigynum) was illustrated, not the dorsal as in most of my papers on theridiid spiders. Gertsch (1960) has taken issue with my treatment of species of the "fulva" group in the previous paper and has named several new species. However, insufficient ecological and life history data are available for the possible species involved to permit making a final decision now (Levi, 1960). Thus the only species recognized are those of my previous revision.

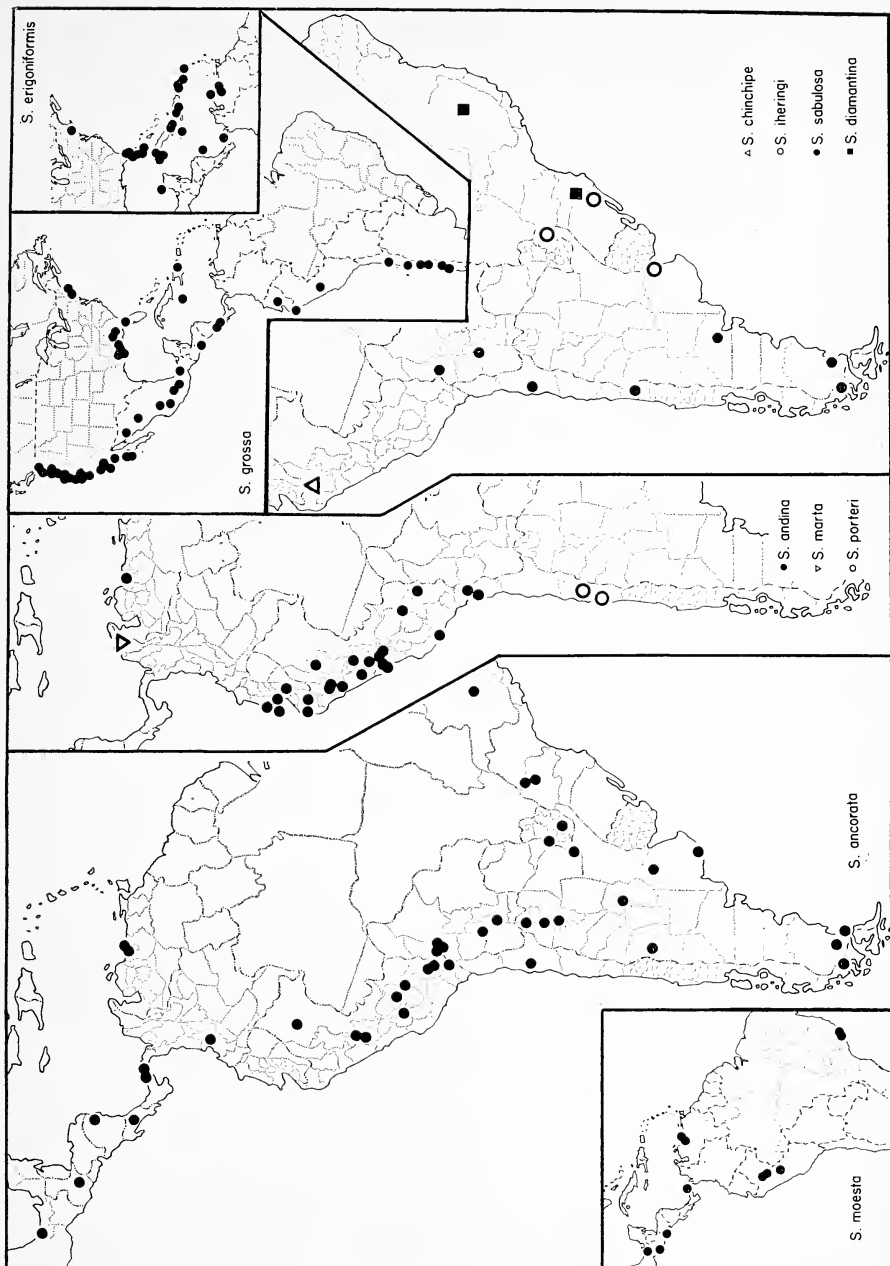
Steatoda brasiliana Keyserling, 1884, Die Spinnen Amerikas Theridiidae, 2(1): 115, pl. 5, fig. 75, ♂. Male type from Rio de Janeiro, Brazil in the Naturhistorisches Museum, Vienna, examined is a male *Steatoda bipunctata* (Linn.) from Europe (NEW SYNONYMY). The female described by Keyserling in 1886 as *S. brasiliana* is probably a specimen of *S. moesta* (Keyserling).

Species misplaced: *Lithyphantes juninensis* Keyserling = *Enoplognatha juninensis* (Keyserling).

Steatoda rubra Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2): 239, pl. 20, fig. 294, ♀. Female type from Blumenau, Brazil = *Theridion rubra* (Keyserling).

Key to American Species of *Steatoda*

- 1a. Epigynum with a prominent, wide, transverse bridge; areas anterior and posterior to bridge shallow depressions (1957b, figs. 43, 44, 46, 47, 49, 50); palpus with thread-like embolus on venter, evenly curved, with a membrane inside embolus loop from base supporting a portion of embolus (1957b, figs. 32-41); North America *S. fulva* group
- 1b. Epigynum without transverse bridge or if with bridge, then areas anterior and posterior to it not depressed; embolus otherwise or if similar South American 2
- 2a. Seminal receptacles thickened, sclerotized, coiled ends of ducts (1957b, figs. 88, 92, 98, 116); epigynum having a U-shaped depression (1957b, figs. 105, 107-109) or a shallow circular depression containing anterior a deeper depression on each side of a septum (rarely absent) (1957b, figs. 93, 97, 99-103) or epigynum as in 1957b, fig. 89; palpus with a prominent U-shaped radix on mesal side (1957b, figs. 119, 124, 129, 134, 145, 155); North America *S. bipunctata* group



- 2b. Seminal receptacles oval or spherical; epigynum and palpus otherwise or if similar, not North American 3
- 3a. Males 4
- 3b. Females 17
- 4a. Palpus with a large mesal projecting radix (1957b, figs. 59, 68) 5
- 4b. Palpus otherwise 6
- 5a. Embolus short, radix longer than half length of bulb (1957b, fig. 59); southern Canada to central Mexico
..... *S. albomaculata* (DeGeer)
- 5b. Embolus long, radix less than half length of bulb (1957b, fig. 68); southern Canada to central Mexico, common in north-eastern states *S. americana* (Emerton)
- 6a. Palpal tibia one and one-half times length of cymbium (1957b, fig. 76); probably introduced and widespread in United States, rare in South America *S. triangulosa* (Walckenaer)
- 6b. Palpal tibia as long as or shorter than cymbium 7
- 7a. Palpal embolus visible as a prominent loop supported by conductor (1957b, fig. 73); probably cosmopolitan, Florida, Caribbean *S. erigoniformis* (O. P.-Cambridge)
- 7b. Palpus otherwise 8
- 8a. Palpus with a transverse, ventral embolus base and a prominent short thread-shaped embolus portion (1957b, fig. 74); cosmopolitan; coast states, wide-spread in Mexico and South America
..... *S. grossa* (C. L. Koch)
- 8b. Palpus otherwise 9
- 9a. Palpal embolus ventral, with a short distal hook as in 1957b, fig. 18; southern Mexico to southern Brazil
..... *S. moesta* (O. P.-Cambridge)
- 9b. Palpus otherwise 10
- 10a. Palpus with biforked embolus (Fig. 22); northern Colombia
..... *S. marta* n. sp.
- 10b. Palpus otherwise 11
- 11a. Palpus with spine on base of embolus and complex U-shaped radix (1957b, fig. 11; Figs. 44-48); southern Mexico to southern Patagonia *S. ancorata* (Holmberg)
- 11b. Palpus otherwise 12
- 12a. Palpus with prominent ventral embolus (Fig. 18); chelicerae tuberculate (Fig. 19); Venezuela, Ecuador, Peru to Chile
..... *S. andina* (Keyserling)
- 12b. Palpus and chelicerae otherwise 13

- 13a. Palpal embolus appearing as a tightly coiled structure supported by the conductor (Fig. 30). Minas Gerais, Brazil *S. diamantina* n. sp.
- 13b. Palpus otherwise 14
- 14a. Palpus with a long narrow radix (in ventral view) whose axis is parallel to that of the cymbium (Fig. 27); Bolivia, Chile, Argentina *S. sabulosa* (Tullgren)
- 14b. Palpus otherwise 15
- 15a. Palpal embolus small, on distal, ventral side of bulb (1957b, fig. 14); Mexico *S. quaesita* (O. P.-Cambridge)
- 15b. Palpus with embolus on ectal side or hidden in ventral view.. 16
- 16a. Palpus with prominent ventral radix (1957b, fig. 27); southern California, Texas, Mexico *S. transversa* (Banks)
- 16b. Palpus otherwise (1957b, fig. 30); Georgia, Gulf states, West Indies, Mexico to Venezuela *S. quadrimaculata* (O. P.-Cambridge)
- 17a. Epigynum with a wrinkled area (Figs. 39, 43) 18
- 17b. Epigynum with all parts smooth 20
- 18a. Epigynum with a shield having its anterior margin lobed (1957b, fig. 67); ducts coiled (1957b, fig. 66); southern Canada to central Mexico; common in northeastern states *S. americana* (Emerton)
- 18b. Epigynum without lobed anterior margin; ducts not coiled .. 19
- 19a. Epigynum as in Figure 39; Chile *S. porteri* (Simon)
- 19b. Epigynum as in Figure 43; southern Mexico to southern Patagonia *S. ancorata* (Holmberg)
- 20a. Epigynum with a light, transverse, oval, surrounded on sides and behind by a raised area (Fig. 26); Bolivia, Chile, Argentina *S. sabulosa* (Tullgren)
- 20b. Epigynum otherwise 21
- 21a. Epigynum with a median lobe extending from anterior (Figs. 17, 21) 22
- 21b. Epigynum without anterior lobe 27
- 22a. Posterior margin of epigynum heavily sclerotized and projecting in middle (Fig. 21), northern Colombia *S. marta* n. sp.
- 22b. Epigynum otherwise 23
- 23a. Epigynum with a depression along posterior margin (1957b, figs. 58, 72) 24
- 23b. Epigynum otherwise 25
- 24a. Posterior median depression bordered on each side by a thorn

- (1957b, fig. 58); southern Canada to central Mexico
S. albomaculata (De Geer)
- 24b. Posterior depression not bordered on sides (1957b, fig. 72);
 cosmopolitan; Florida, Caribbean
S. erigoniformis (O. P.-Cambridge)
- 25a. Epigynum with two widely separated depressions (Figs. 34,
 35); southern Brazil, Paraguay, Argentina
S. iheringi (Keyserling)
- 25b. Epigynum otherwise 26
- 26a. Depression of epigynum bordered all around (Fig. 17); Vene-
 zuela, Ecuador, Peru to Chile *S. andina* (Keyserling)
- 26b. Depression on each side of lobe not bordered behind (1957b,
 figs. 84, 85); cosmopolitan, coast states, widespread in Mexico
 and South America *S. grossa* (C. L. Koch)
- 27a. Epigynum with a narrow, transverse bridge (1957b, fig. 81);
 probably introduced and widespread in United States and South
 America *S. triangulosa* (Walckenaer)
- 27b. Epigynum otherwise 28
- 28a. Epigynum with a median dark spot (1957b, fig. 17); southern
 Mexico to southern Brazil *S. moesta* (O. P.-Cambridge)
- 28b. Epigynum otherwise 29
- 29a. Epigynum with a posterior directed lobe, posterior to the opening
 (Fig. 32); Peru *S. chinchi* n. sp.
- 29b. Epigynum otherwise 30
- 30a. Epigynum with a slit-like opening on each side (1957b, fig. 20);
 Mexico *S. saltensis* Levi
- 30b. Epigynum otherwise 31
- 31a. Epigynum with shallow longitudinal oval depression (Fig. 29);
 Minas Gerais, Brazil *S. diamantina* n. sp.
- 31b. Epigynum otherwise 32
- 32a. Epigynum with a deep transverse depression (Fig. 24); Peru
 *S. variipes* (Keyserling)
- 32b. Epigynum otherwise 33
- 33a. Epigynum with two black spots on posterior margin (1957b,
 fig. 24); southern California, Texas, Mexico
S. transversa (Banks)
- 33b. Epigynum otherwise 34
- 34a. Epigynum with a pair of shallow depressions each with a black
 spot (1957b, fig. 29); Georgia, Gulf States, West Indies,
 Mexico to Venezuela *S. quadrimaculata* (O. P.-Cambridge)
- 34b. Epigynum as in 1957b, fig. 22; Mexico .. *S. autumnalis* (Banks)

Steatoda moesta (O. P.-Cambridge)

Asagena moesta O. P.-Cambridge, 1896, *Biologia Centrali-Americana*, Araneidea, 1:209, pl. 25, fig. 4, ♀. Female type from Guatemala in the British Museum, Natural History.

Steatoda moesta, Levi, 1957, *Bull. Mus. Comp. Zool.*, 117: 3, p. 379, figs. 15-18, ♀, ♂.

Distribution. Southern Mexico to southern Brazil.

Additional Records. *Venezuela*: "Caracas, Tovar," 1888 (E. Simon, MNHN). *Peru. Huánuco*: 27 km N of Huánuco, Dec. 1954 (E. I. Schlinger, E. S. Ross, CAS). *San Martín*: Tarapoto (MNHN); Moyobamba (MNHN). *Brazil. Rio de Janeiro*: Mendes (Eidmann, SMF); Teresópolis (MNHN).

Steatoda erigoniformis (O. P.-Cambridge), new combination

Theridion erigoniforme O. P. - Cambridge, 1872, *Proc. Zool. Soc. London*, p. 284. Female, male syntypes from Jordan in the Hope Department of Entomology, Oxford, examined.

Asaganella erigoniformis, Schenkel, 1937, *Festschrift E. Strand*, 3: 381, fig. 3, ♂.

Lithyphantes septemmaculatus Keyserling, 1884, *Die Spinnen Amerikas*, 2(1): 141, pl. 6, fig. 88, ♀. Female syntypes from "Denver in Columbia" collected by Marx. (Marx's labels are often wrong and the Denver type locality is undoubtedly an error). NEW SYNONYMY.

Distribution. Cosmopolitan. Florida, Caribbean, Panama, Venezuela in America. Kaston (1948, *Bull. Connecticut Geol. Nat. Hist. Surv.* no. 70: 79) reports a specimen from Connecticut. O. Kraus (in a letter) tells of a specimen from Japan in the Senckenberg Museum. It also has been found in the Near East.

Additional Records. *Panama Canal Zone*: Gamboa, 7 Jan. 1958, ♂ (A. M. Chickering). *British West Indies*: Antigua: St. John, 1955 (A. M. Nadler, AMNH). *Venezuela. Aragua*: Tovar, 1888, ♀ (E. Simon, MNHN). *Carabobo*: San Estebán, 1888, ♀ ♂ (E. Simon, MNHN).

Steatoda triangulosa (Walckenaer)

Aranea triangulosa Walckenaer, 1802, *Faune Parisienne*, 2: 207. Type from Paris, France, lost.

Steatoda triangulosa, Levi, 1957, *Bull. Mus. Comp. Zool.* 117(3): 407, figs. 75, 76, 80-82, ♀ ♂.

Distribution. Central and southern Europe, southern Russia, Mediterranean, United States from Massachusetts to Oregon, south to southern Texas. The city-dwelling habit suggests that it has been

introduced in America. It has previously been reported from South America, but only one specimen was seen.

Additional Records. Argentina. Santiago del Estero: Santiago del Estero, 12 June 1961, ♀ (J. Abalos).

Steatoda grossa (C. L. Koch)

Theridion grossum C. L. Koch, 1938, Die Arachniden, 4:112, fig. 321, ♀. Female types from Greece.

Steatoda punctilineata Mello-Leitão 1939, Rev. Suisse de Zool., 46:61, figs. 30, 31, ♀. Two female syntypes from Leones, Argentina, in the Naturhistorisches Museum, Basel, examined. NEW SYNONYMY.

Steatoda grossa, Levi, 1957, Bull. Mus. Comp. Zool., 117(3):404, figs. 74, 83-85, ♀ ♂.

Note. Mello-Leitão (1939) figure 31 is printed upside down; if it had been turned around the synonymy with the common *S. grossa* would have been recognized earlier. *Steatoda grossa* females can be confused with females of *S. andina*. Only details of the posterior rim of the epigynum seem to separate females of the two species. The male palpi, however, are very different.

Natural History. The species has been collected in subtropical rain forests in Oxapampa, and under stones on guano islands.

Distribution. Cosmopolitan; along coast of United States, Mexico, South America.

Additional records. Ecuador. Tungurahua: Ambato, June 1943 (H. E., D. L. Frizzell). *Peru.* Isl. Don Martín (Guano Isl.) (L. Peña, SMF); *Piura:* Negritos (H. E., D. L. Frizzell). ? *Ancash:* Chimbote, Feb. 1953 (W. Weyrauch). *Pasco:* Oxapampa, 1600 m, E of Oroga (W. Weyrauch). *Chile. Antofagasta:* Taltal (H. Zapfe). *Coquimbo:* La Serena (H. Zapfe); Los Vilos (H. Zapfe). *Aconcagua:* San Felipe (L. Peña, ISNB). *Santiago:* Santiago (H. Zapfe). *Linares:* Linares (L. Peña, ISNB). *Malleco:* Angol, 1950 (D. S. Bullock). *Osorno:* Osorno (L. Peña, ISNB).

Steatoda andina (Keyserling), new combination

Figures 16-19

Lithyphantes andinus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1):132, pl. 6, fig. 82, ♀ ♂. Male and female syntypes from Junín, Amable Maria, Lima and San Mateo, Peru in the Polish Academy Sciences, Warsaw. A female specimen determined by Keyserling, in the British Museum, Natural History, examined.

Description. Carapace, sternum reddish brown, legs lighter. Abdomen purplish black with a narrow white line around sides, crossed

in front by a median narrow white line. Very variable, sometimes with a longitudinal white line or almost black. Venter with a lighter W-shaped mark and lighter spots on sides. Eyes subequal in size, anterior median eyes one diameter apart, one and one-half diameters from laterals. Posterior median eyes about one diameter apart, two diameters from laterals. Chelicera of female with a blunt, fleshy tooth on anterior margin, that of male enlarged as in the genus *Enoplognatha*, with a large tooth on anterior margin (Fig. 19); there is no tooth, however, on posterior margin. Measurements of specimens from Lima, Peru. Total length of female 8.3 mm. Carapace, 3.7 mm long, 2.9 mm wide. First femur, 4.3 mm; patella and tibia, 5.1 mm; metatarsus, 3.7 mm; tarsus, 1.6 mm. Second patella and tibia, 4.1 mm; third, 3.3 mm; fourth, 5.0 mm. Total length of male, 8.6 mm. Carapace, 4.2 mm long, 2.7 mm wide. First femur, 4.7 mm; patella and tibia, 5.5 mm; metatarsus, 4.3 mm; tarsus, 1.9 mm. Second patella and tibia, 4.3 mm; third, 3.6 mm; fourth, 5.0 mm.

Variation. The epigynum (fig. 17) is variable in proportion. A male from Chile has a shorter embolus than males examined from central Peru.

Diagnosis. The more discrete posterior rim of the depression of the epigynum (Fig. 17) separates this species from *S. grossa* (1957b, figs. 84, 85) with which it may be confused. The palpus (Fig. 18) is very different from that of *S. grossa*.

Natural History. Collected in stony grassland near Lake Junín, shrubs in dry valley in Cajamarca and in Eucalyptus forest in Ancash.

Records. *Venezuela.* *Aragua:* Maracay (SMF). *Ecuador.* *Manabí:* Manta (D. L. Frizzell). *Guayas:* Baños de San Vicente, Santa Elena Peninsula (R. W. Landes); W of Guayaquil (R. W. Landes); Colonche (R. W. Landes). *Azuay:* 22 km E of Cuenca (E. I. Schlinger, E. S. Ross). *Peru.* *Piura:* El Alto (R. Wells); Río Quíroz (H. E., D. L. Frizzell); Negritos (H. S. M.); Pariñas Valley (H. E., D. L. Frizzell); Quebrada Mogollon (H. E., D. L. Frizzell); Máncora (H. E., D. L. Frizzell). *Cajamarca:* Cajamarca, 2700 m (W. Weyrauch) between Lives and Mirador, near San Miguel de Pallaques, 1050 m (H. W. Koepcke, SMF). *Libertad:* Otusco (E. I. Schlinger, E. S. Ross, AMNH). *San Martín:* Hara, 32 km SE of Moyobamba (F. Woytkowski, AMNH). *Ancash:* Puna near Huarás, 4300 m (W. Weyrauch, AMNH); Huarás (H. W. Koepcke, SMF). *Huánuco:* 27 km S of San Rafael (E. I. Schlinger, E. S. Ross); Tingo María, 670 m (W. Weyrauch, AMNH). *Lima:* 3 km E of San Mateo (E. I.

Schlenger, E. S. Ross). San Mateo, 3000 m (W. Weyrauch, AMNH). Lima (H. E., D. L. Frizzell); Canta, 2800 m (W. Weyrauch); Matucana, 2300-2500 m (H. W. Koepcke, SMF); Atocongo Lomas, rocky hills (H. W. Koepcke, SMF). *Junín*: Tarma, 3100 m (W. Weyrauch, AMNH). Laguna Algacocha, near Laguna Junín, 4300 m (H. W. Koepcke, SMF). Laguna Junín, 4140 m (H. W. Koepcke, SMF). *Cuzco*: Cuzco, 4000 m (J. C. Pallister, AMNH). *Arequipa*: Atiquipa, Chala, 200 m (W. Weyrauch). *Puno*: 10 km S of Oroya (E. S. Ross, E. M. Michelbacher, CAS). *Chile*. *Tarapacá*: Putre, (Aivilés); Oasis de Miñimiñe, (Aivilés).

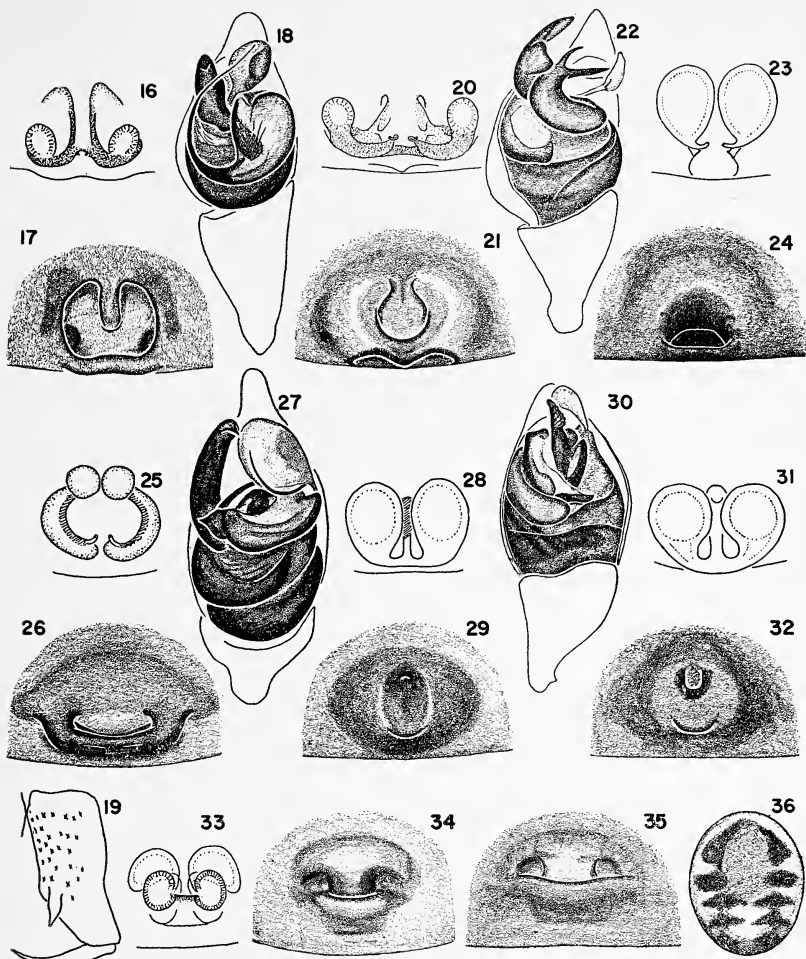
***Steatoda marta* new species**

Figures 20-22

Type. Male from Sierra Nevada de Santa Marta, Magdalena, Colombia (Dulm), in the Muséum National d'Histoire Naturelle, Paris (no. 18389). The specific name is a noun in apposition, after the type locality.

Description. Carapace, sternum, legs rich dark red-brown. Abdomen purplish black with a median dorsal longitudinal white line and a white line around the anterior edge of the abdomen. Anterior median eyes slightly smaller than others, their diameter apart, one and one-half to two diameters from laterals. Posterior median eyes one and one-quarter diameters apart, two diameters from laterals. Laterals separated by about their radius. Chelicerae of male corniculate, with a blunt tooth. Female chelicerae smooth with a short tooth on anterior margin. First and fourth legs subequal in length. Abdomen of male with four sclerotized round spots on dorsum. Total length of male 7.2 mm. Carapace 3.0 mm long, 2.3 mm wide. First patella and tibia, 3.5 mm; second, 2.9 mm; third, 2.5 mm. Fourth femur, 3.0 mm; patella and tibia, 3.7 mm; metatarsus, 2.5 mm; tarsus, 1.2 mm. Total length of female 8.0 mm. Carapace 3.2 mm long, 2.5 mm wide. First patella and tibia, 3.5 mm; second, 2.9 mm; third, 2.6 mm. Fourth femur, 3.3 mm; patella and tibia, 4.0 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm.

Diagnosis. This species is very close to *Steatoda andina* (Keyserling) but differs in having the embolus shorter with a spur, in having a smaller conductor, and having a median apophysis of different shape (Fig. 22). The female epigynum differs in having a scape in a shallow depression. The depression is not bordered. The posterior edge of the



Figs. 16-19. *Steatoda andina* (Keyserling). 16. Female genitalia, dorsal view. 17. Epigynum. 18. Left palpus. 19. Left male chelicera, anterior view.

Figs. 20-22. *S. marta* new species. 20. Female genitalia, dorsal view. 21. Epigynum. 22. Palpus.

Figs. 23-24. *S. variipes* (Keyserling). 23. Female genitalia, dorsal view. 24. Epigynum.

Figs. 25-27. *S. sabulosa* (Tullgren). 25. Female genitalia, dorsal view. 26. Epigynum. 27. Palpus.

Figs. 28-30. *S. diamantina* new species. 28. Female genitalia, dorsal view. 29. Epigynum. 30. Palpus.

Figs. 31-32. *S. chinchipe* new species. 31. Female genitalia, dorsal view. 32. Epigynum.

Figs. 33-36. *S. iheringi* (Keyserling). 33. Female genitalia, dorsal view. 34, 35. Epigynum. 34. Type. 35. (Paraguay). 36. Female abdomen, dorsal view (Paraguay).

epigynum is heavily sclerotized (Fig. 21). The scape is sometimes subcircular, sometimes not constricted anteriorly (its sides being nearly parallel), and is sometimes constricted at its posterior point and widens again; its shape seems to be variable in different specimens collected together.

Records. Several ♀ paratypes from type collection.

Steatoda sabulosa (Tullgren), new combination

Figures 25-27

Lithyphantes sabulosus Tullgren, 1901, Svenska Exped. Magellansländern 2(10):193, pl. 1, fig. 3, ♂. Male type from Santa Cruz, in South Argentina, in the Naturhistoriska Riksmuseum, Stockholm, examined.

Steatoda albiornata Mello-Leitão, 1940, Rev. Mus. La Plata, n.s., 2:36, fig. 34, ♀. Female type from Valcheta, Río Negro, Argentina in the Museo de la Plata, examined. NEW SYNONYMY.

Description. (Specimens from Magellanes, Chile). Carapace, sternum, legs yellow-brown to reddish brown. Abdomen purplish black; dorsum of female abdomen with pigment missing in some areas; white line around anterior of abdomen on dorsum and median, dorsal, longitudinal white line which may be broken. Anterior median eyes slightly smaller than others, two-thirds diameter apart, two-thirds diameter from laterals. Posterior median eyes a little less than a diameter apart, one diameter from laterals. The posterior median eyes of the male are slightly farther from laterals. Male chelicerae not large, with one large tooth, fang widened and short. Total length of female 10.5 mm. Carapace 3.2 mm long, 2.9 mm wide. First patella and tibia 4.0 mm; second 2.9 mm; third 2.7 mm. Fourth femur 3.5 mm; patella and tibia 4.2 mm; metatarsus 3.6 mm; tarsus 2.3 mm. Total length of male 8.0 mm. Carapace 3.3 mm long, 2.5 mm wide. First patella and tibia 4.0 mm; second 3.6 mm; third 2.9 mm. Fourth femur 3.5 mm; patella and tibia 4.2 mm; metatarsus 3.1 mm; tarsus 1.4 mm.

The internal female genitalia (Fig. 25) are heavily sclerotized. A female from northern Chile has the seminal receptacles slightly wider apart and the ducts forming a V rather than a circle.

Record. Bolivia. La Paz: La Paz, (MNHN); 48 km N of Potosí, 22 Feb. 1951 (E. S. Ross, A. E. Michelbacher, CAS). *Chile.* Antofagasta: Tumbre, 3600 m, Cord. Antofagasta, Dec. 1955 (L. Peña, ISNB). *Santiago:* Santiago (SMF); Los Valdes, 2000 m, Cordilleras near Santiago (G. Mann, AMNH). *Magallanes:* Laguna Amarga, Natales, Dec. 1960, ♀ ♂ (L. Peña).

Steatoda iheringi (Keyserling), new combination
Figures 33-36

Lithyphantes iheringi Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):240, pl. 20, fig. 295, ♀. Female type from Rio Grande do Sul, Brazil, in the British Museum, Natural History, examined.

Lithyphantes cancellatus Mello-Leitão, 1944, Rev. Mus. La Plata, n.s., 3:325, fig. 8, ♀. Female type from José C. Paz, Provincia de Buenos Aires, Argentina in the Museo de la Plata, examined. NEW SYNONYMY.

Description. Specimen from Paraguay. Carapace yellow-brown, cephalic area brown, sternum red-brown, legs yellow, ends of tibiae darker. Abdomen with two series of dark spots on dorsum; sides and area between posterior spots with some white pigment. Venter darker with a small white mark just posterior to the epigynum. Anterior median eyes slightly smaller than others, one diameter apart, one diameter from laterals. Posterior median eyes three-quarters diameters apart, one and one-half diameters from laterals. Chelicerae with one tooth on the anterior margin. Legs quite thick, first equal in length to fourth. Epigynum (Figs. 34, 35) with a transverse fold. Internal genitalia difficult to study; the anterior ducts are very transparent and in the single specimen available, could not be seen completely. Total length of female type 2.9 mm. Carapace 1.30 mm long, 1.08 mm wide. First femur, 1.04 mm; patella and tibia, 1.43 mm; metatarsus, 0.84 mm; tarsus, 0.52 mm. Second patella and tibia, 1.10 mm; third, 0.95 mm; fourth, 1.50 mm.

The palpus illustrated by Figure 48 may belong to the male of this species. It was collected with females of *S. ancorata* in Rio Grande do Sul and belongs to the Keyserling collection in the British Museum.

Records. *Paraguay:* Taquararapa, Alto Parana, 1908, ♀ (AMNH). *Argentina.* Buenos Aires, ♀ (Latarte, MNHN).

Steatoda diamantina new species
Figures 28-30

Type. Female from Mina Serinha, Diamantina, Minas Gerais, Brazil, December 1944 (Mrs. E. Cohn), in the American Museum of Natural History. The specific name is a noun in apposition, named after the type locality.

Description. Carapace, sternum, legs red-brown. Abdomen black except for one or two thin jagged white lines around sides and anterior. A median, longitudinal, dorsal white line varies in thickness and has several short pairs of lateral branches. Eyes subequal in size, in female. Anterior median eyes two-thirds diameter apart.

Posterior median eyes their radius apart and one diameter from laterals. Anterior median eyes of male slightly larger than others, one-third diameter apart, one-quarter diameter from laterals. Posterior median eyes one-third diameter apart, one diameter from laterals. Chelicerae of male with one tooth on anterior margin. First femora of male swollen and corniculate on venter. Total length of male 6.6 mm. Carapace 3.3 mm long, 2.4 mm wide. First femur 4.3 mm; patella and tibia 3.9 mm; metatarsus 2.9 mm; tarsus 1.5 mm. Second patella and tibia 3.2 mm; third 2.7 mm; fourth 3.9 mm. Total length of female 6.1 mm. Carapace 2.9 mm long, 2.1 mm wide. First femur 3.5 mm; patella and tibia 3.9 mm; metatarsus 3.0 mm; tarsus 1.4 mm. Second patella and tibia 2.9 mm; third 2.3 mm; fourth 3.5 mm.

Diagnosis. This species is separated from other *Steatoda* by the epigynum (Fig. 29), which has a shallow, oval to round depression, the anterior end of which is dark and contains the opening. The male can be separated by the structure of the palpus (Fig. 30).

Records. *Brazil. Santa Catarina:* Nova Teutonia, lat 27° 11' S, long 52° 23' W, ♀, ♂ (F. Plaumann, SMF).

***Steatoda chinchipe* new species**

Figures 31, 32

Type. Female from Río Chinchipe, San Ignacio, 800 m elev., Cajamarca, Peru, July 1948 (W. Weyrauch) in the Museum of Comparative Zoology. The specific name is a noun in apposition, after the type locality.

Description. Carapace, sternum, legs brown. Abdomen evenly purplish black with a wavy line around sides and anterior on dorsum; center of dorsum with a fine longitudinal white line having two crosslines. Anterior median eyes smaller than other eyes. Anterior median eyes three-quarters their diameter apart, one diameter from laterals. Posterior median eyes their radius apart, slightly more than one diameter from laterals. Lateral eyes slightly separated. Total length 7.5 mm. Carapace 3.2 mm long, 2.5 mm wide. First femur 3.5 mm; patella and tibia 4.2 mm; metatarsus 2.7 mm; tarsus 1.3 mm. Second patella and tibia 2.9 mm; third 2.2 mm; fourth 3.7 mm.

Diagnosis. The epigynum differs from that of other *Steatoda*. It has a raised circular area containing an anterior opening with a lip on three sides (Fig. 32). The internal genitalia (Fig. 31) are heavily sclerotized.

Records. *Ecuador. Tungurahua:* Baños, 7 May 1942 (H. E.

Frizzell); 32 km SE of Ambato, 8 Feb. 1955 (E. I. Schlinger and E. S. Ross, CAS); Río Pastaza between Baños and Mapoto, Aug. 1938 (W. C. Macintyre).

Steatoda variipes (Keyserling), new combination

Figures 23, 24

Theridium variipes Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1):93, pl. 4, fig. 61, ♀. Female lectotypes here designated from Amable María [Junín], Peru in the Polish Academy of Science, Warsaw, examined.

Description. Carapace rich brown, sternum yellow-brown with darker margin and darker spot in middle. Legs yellow-brown with darker bands as wide as lighter arcs. Abdomen probably mottled black. Eyes about subequal in size, anterior median eyes one diameter apart, one-quarter diameter from laterals; posterior median eyes one diameter apart, one-third diameter from laterals. Muscle impressions on abdomen and bases of setae slightly sclerotized. Colulus relatively small with two setae. Total length of female lectotype 5.0 mm; carapace 1.0 mm long, 1.9 mm wide. First femur 2.7 mm; patella and tibia 2.9 mm; metatarsus 1.6 mm; tarsus 0.9 mm. Second patella and tibia 2.3 mm; third 1.6 mm; fourth 2.4 mm.

Record: One ♀ paratype with type.

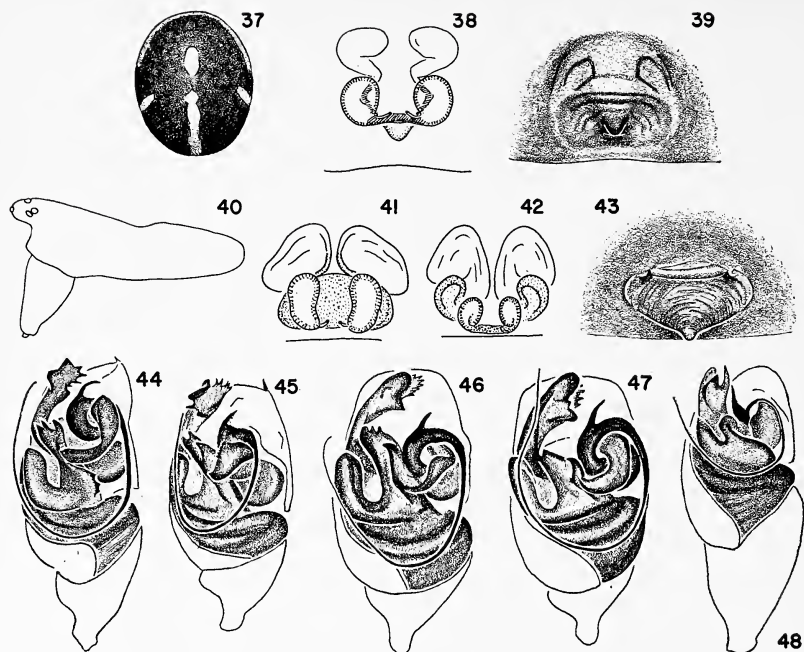
Steatoda porteri (Simon), new combination

Figures 37-39

Lithyphantes porteri Simon, 1900, Rev. Chileana, 4:50. Female type from Chañarcillo, [Prov. Atacama], Chile, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace, sternum, legs yellow-brown; fourth leg darker than others. Abdomen purplish black with dorsal white marks (Fig. 37) and a small white spot posterior to genital groove on venter. Anterior median eyes slightly smaller than others, one and one-half diameters apart, one diameter from laterals. Posterior median eyes one diameter apart, slightly more than one diameter from laterals. One broad tooth on anterior margin of chelicerae. Fourth leg slightly longer than first. Epigynum (Fig. 39) with a wrinkled knob pointing posterior. Total length 4.7 mm. Carapace, 1.8 mm long, 1.4 mm wide. First patella and tibia, 2.1 mm; second, 1.7 mm; third, 1.4 mm. Fourth femur 2.0 mm; patella and tibia, 2.4 mm; metatarsus, 1.6 mm; tarsus, 0.9 mm.

Record. Chile. Coquimbo: El Tofo, Sept. 1957 (H. Zapfe).



Figs. 37-39. *Steatoda porteri* (Simon). 37. Female abdomen, dorsal view. 38. Female genitalia, dorsal view. 39. Epigynum.

Figs. 40-47. *S. ancorata* (Holmberg). Fig. 40. Male carapace and chelicerae. Figs. 41, 42. Female genitalia, dorsal view. 43. Epigynum. 44-47. Palpus. 44. (northern part of range). 45. (southern Peru). 46. (Bolivia). 47. (southern Chile).

Fig. 48. *S. ? iheringi* (Keyserling), palpus.

Steatoda ancorata (Holmberg), new combination

Figures 40-47

Theridium ancoratum Holmberg, 1876, An. Agr. Rep. Argentina, 4:72, fig. 16.

Type from Argentina, lost.

?*Lithyphantes vittatus* Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1):134, pl. 6, fig. 83. Juv. type from Minas Gerais, Brazil, in the Hope Department of Entomology, Oxford, examined. NEW SYNONYMY.

Lithyphantes nigrofemoratus Keyserling, 1884, *op. cit.* 2(1):139, pl. 6, fig. 87, ♀. Female type from Monte Rico, [Ayacucho], Peru, in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY.

Asagena alticeps Keyserling, 1886, *op. cit.* 2(2):4, fig. 136, ♂. Male type from N. Granada [Panama, Colombia, Venezuela] in the British Museum, Natural History. NEW SYNONYMY.

Lithyphantes lactus O. P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, 1:181, pl. 22, fig. 12, ♂. Male type from Costa Rica, in the British Museum, Natural History. NEW SYNONYMY.

Asagena patagonica Tullgren, 1901, Svenska Exped. Magellanslåndern 2: 194, pl. 15, fig. 4, ♀. Female type from Ultima Esperanza and Puerto Gallegus, Patagonia [? Magellanes, Chile] in the Naturhistoriska Riksmuseum, Stockholm, examined. NEW SYNONYMY.

Asagena melanomela Mello-Leitão, 1944, Rev. Mus. La Plata, n.s., 3:325, fig. 5, ♂. Male type from Pergamino, [Buenos Aires], Argentina in the Museo de la Plata, examined. NEW SYNONYMY.

Steatoda nigrofemorata, Levi, 1957, Bull. Mus. Comp. Zool., 117(3):377, figs. 11-13, ♀ ♂.

Note. This species is the most common *Steatoda* in Argentina, the type locality of *T. ancoratum*. Specimens of this species from Argentina determined by Mello-Leitão and by Birabén were named *Lithyphantes ancoratum*. The synonymy of *L. vittatus* Keyserling remains uncertain, however, as the type is a juvenile and no specimens of *S. ancorata* have been examined from Minas Gerais, the type locality.

The palpi are variable in structure, (Figs. 44-47). Since the palpal sclerites are unusually complex, any slight change in position changes the appearance of the palpus.

Natural History. Specimens have been found "near rockpile in weathered shale" and "under flat rock" in Bolivia. In Mendoza, Argentina it has been found in chaparral area.

Distribution. Southern Mexico to southern Patagonia.

Additional records: *Venezuela.* *Dist Federal:* Caracas (E. Simon, MNHN). *Aragua:* Tovar (E. Simon, MNHN). *Colombia.* *Valle:* 10 km W of Cali (E. I. Schlinger, E. S. Ross, CAS). *Peru.* *Huánuco:* Monzón Valley, Tingo María (E. I. Schlinger, E. S. Ross, CAS); Huánuco (E. I. Schlinger, E. S. Ross, CAS). *Ayacucho:* Ayacucho (W. Weyrauch). *Cuzco:* Cuzco, 3800 m (W. Weyrauch); Huadquiña, 1600 m (W. Weyrauch). *Puno:* 95 km N of Puno (E. S. Ross, A. E. Michelbacher, CAS); Puno (W. Weyrauch); near Juliaca, 3900 m (H. W. Koepcke, SMF); Mazo Cruz, 3800 m (L. Peña, ISNB); Camacani (L. Peña, ISNB). *Bolivia.* Chaco (MNHN). *La Paz:* Timari, Nevada de Chicani (MNHN); La Paz 4400 m (R. Walsh, MNHN); 65 km NE of La Paz (R. Walsh); Altiplano near Huayna Potosí Mtn., 5100 m (R. Walsh). *Chiquisaca:* 26 km N of Camargo (E. S. Ross, A. E. Michelbacher, CAS). *Potosí:* 45 km N of Potosí, 4300 m (E. S. Ross, A. E. Michelbacher, CAS). *Brazil.* *Paraná:* Bela Vista (MNHN). *Rio Grande do Sul.* (BMNH). *Paraguay.* Asunción (MNHN). *Caazapá:* Pastoreo (D. Wees). *Argentina.* *Jujuy:* 8 km N of Humacuaca, 2900 m (E. S. Ross, A. E. Michelbacher, CAS). *Salta:* Salta (Reimoser); Cafayate (M. Birabén). *Chaco:* Resistencia

(MNHN). *Córdoba*: Alta Gracia (Bruch). *Mendoza*: 8 km SSW Estación Cachenta, Dept. Luján, 1500 m (B. Patterson). *Buenos Aires*: Necochea (M. Birabén); "Bahia" (MNHN). *Chile. Antofagasta*: Tumbre, 3600-3700 m, Cord. Antofagasta (L. Peña, ISNB). *Magallanes*: Cerro Castillo, Natales (L. Peña).

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A PERMIAN MEGASECOPTERON FROM TEXAS¹

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A collection of six Permian insects recently received from Dr. Sergius H. Mamay, of the U. S. Geological Survey, includes an unusually interesting species belonging to the extinct order Megasecoptera. The other specimens are fragments of cockroach wings, which, in the light of our present knowledge, cannot be satisfactorily placed in families and do not warrant description. The megasecopter, however, is sufficiently well preserved to enable family and generic diagnoses. It clearly belongs to the family Bardohymenidae, of the suborder Eumegasecoptera.

Family Bardohymenidae

This family was based on *Bardohymen magnipennifer* Zal., from a Permian outcrop along the Barda River, near Perm, Russia (Zalessky, 1937). Two other genera, *Sylvohymen* Martynov (Permian of Oklahoma and of Chekarda, Russia) and *Calohymen* (Permian of Oklahoma) have also been placed here (Carpenter, 1947). The family includes species which are related to Protohymenidae but which differ in lacking the coalescences of Rs and MA, and of MP and CuA.

Actinohymen, new genus

Related to Bardohymen, but having the cross-vein between R₁ and R₂ very strong, thickened at the costal end, and situated well basad of the apex of the wing. Pterostigmal area thickened; Rs with three main branches.

Type-species: *Actinohymen russelli*, n. sp.

Actinohymen russelli, new species

Text-figures 1 and 2; plate 1.

Length of wing, as preserved, 28 mm; width, 8.5 mm; estimated complete wing length, 50 mm. Wing markings: pterostigmal and

¹This research has been aided by a grant from the National Science Foundation.

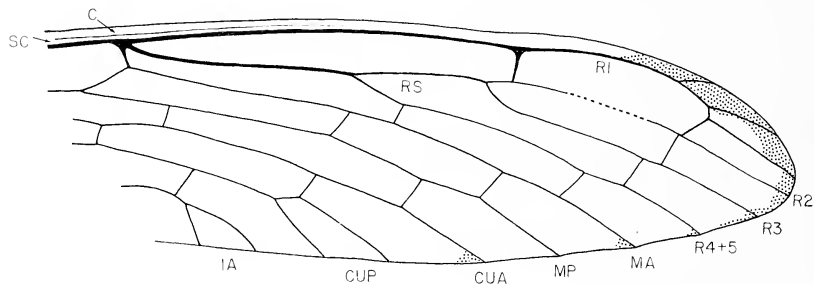
Manuscript received by the editor January 4, 1962.

apical region margined with dark pigment; isolated triangular spots at end of $R_4 + 5$, MA, and CuA. Eight outer cross-veins, forming a distinct row; CuP and 1A forked distally. Other details of venation are shown in text-figure 1.

Holotype: No. 140898, Paleozoic Catalogue #29, U. S. National Museum, Washington; collected by Dr. S. H. Mamay, in an outcrop on the Emily Irish land grant, about 18 miles south-southeast of Seymour, Baylor County, Texas. The fossil is very clearly preserved and consists of about the distal half of a wing; the proximal half was apparently broken away in the counterpart, which is missing. Slight distortion of the anterior margin, just basal of the pterostigma, results from a pronounced depression in the rock. Although incomplete, this is the best-preserved specimen of a bardohymenid which has yet been found.

Geological age: Lower Permian; Belle Plains Formation (Wichita Group); this may be approximately correlated with the lower part of the Wellington Formation of Oklahoma and Kansas. (See Dunkle and Mamay, 1956; and Dunbar, *et. al.*, 1960).

The species is named for Mr. Mart Russell, of Seymour, Texas, in recognition of the cooperation, hospitality and interest shown to Dr.



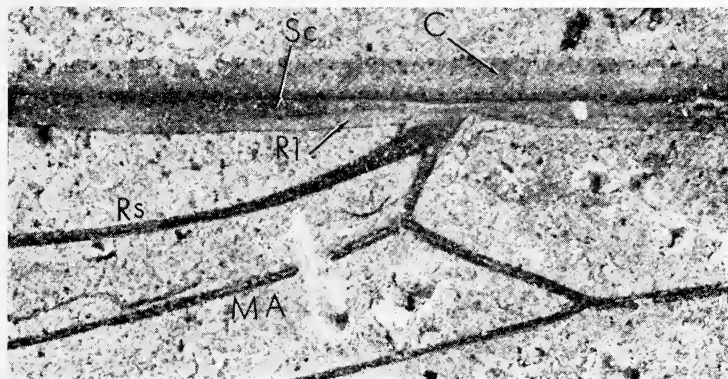
Text-figure 1. Drawing of *Actinohymen russelli*, n. sp., based on holotype. C, costa (+); Sc, subcosta (—); R1, radius (+); Rs, radial sector (—); R2, R3, R4+5, branches of radial sector (—); MA, anterior media (+); MP, posterior media (—); CuA, anterior cubitus (+); CuP, posterior cubitus (—); 1A, first anal vein. The irregularities in the costal margin have been restored.

Mamay and his associates during their collecting trips at the Emily Irish deposit.

This remarkable fossil shows a number of interesting features, mostly specializations of the anterior marginal area of the wing. As in many Eumegasecoptera, such as Prothymenidae and Bardohy-

menidae, the subcosta and radius (R₁) are very close together and also to the anterior wing margin (text-figure 2). The costa is flattened and wide for its entire length. In the region of the pterostigma the costa widens even more and is somewhat thickened, but at the distal end of the pterostigma it disappears. The subcosta appears to be flattened and to be contiguous with the costa and is not readily distinguished from the latter. The radius (R₁) is contiguous with the subcosta (in the preserved part of the fossil) or with the costa beyond the end of the subcosta, except in the very distal part of the wing. Beyond the short but distinct pterostigmal veinlet the radius seems to fork, the more distal branch leading to the very apex of the wing. The cross-vein at the basal part of the pterostigma forms a heavy bar, which is especially thick at its costal end.

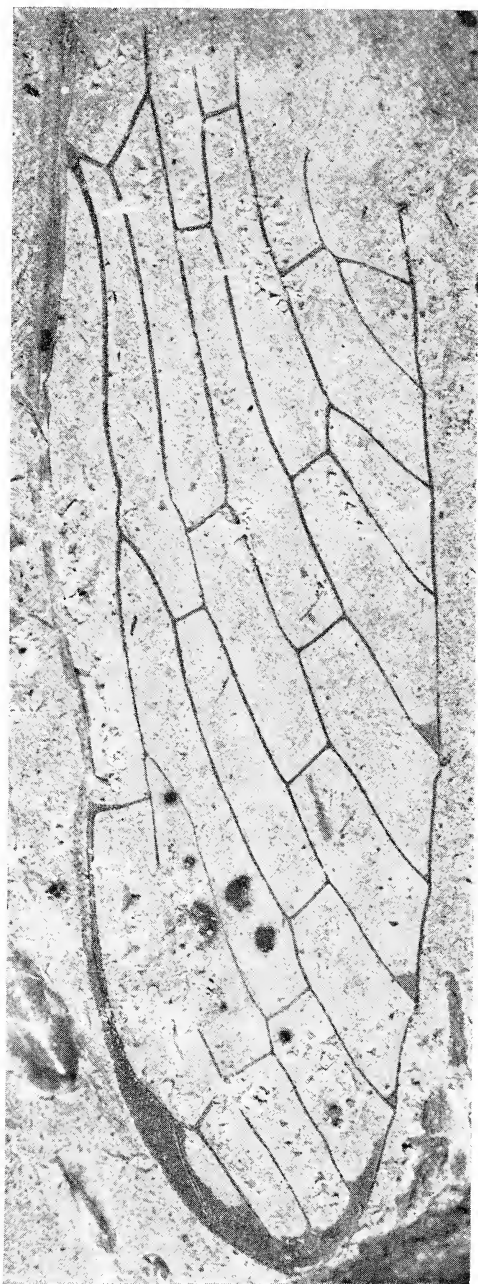
The flattened costa, subcosta and even parts of R₁ bear several irregular rows of setal bases or sockets (text-figure 2), as in some



Text-figure 2. Photograph of part of wing of *Actinohymen russelli*, n. sp. (holotype), showing proximity of C, Sc and R₁, and the origins of Rs and MA. Setal bases can be seen along the costa.

Palaeodictyoptera, *e. g.* *Dunbaria*. It is curious that no setae are preserved, especially since they are often visible on the wings of *Dunbaria*.

The wing markings are not unlike those of other species of Megasecoptera, especially the Carboniferous *Aspidothorax triangularis* Brongn. (Commentry, France). *Eumartynovia raaschi* Carp. (Permian, Oklahoma), though not at all closely related (*i. e.*, belonging to the Paramegasecoptera), has almost identical markings.



Photograph of holotype of *Actinohymen russellii*, n. sp., $\times 6$.

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A REMARKABLE NEW GENUS OF LYGAEIDAE
FROM SUMATRA (HEMIPTERA: HETEROPTERA)*

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Many species of Lygaeidae possess fore femora that are strongly incrassate and armed on the ventral surface with sharp spines. Many workers have assumed that these powerful legs were associated with predatory habits and indeed as recently as 1956 Miller illustrated species of Blissinae (*Spalacocoris* and *Chelochirus*) as examples of legs modified for raptorial purposes. However, it has been evident for a long time that this was at best an oversimplification and that very strongly incrassate and heavily spinous legs were known in such subfamilies as the Pachygronthinae and Oxycareninae whose members so far studied are entirely phytophagous, whereas in the predaceous Geocorinae the fore femora are slender and not at all adapted for seizing prey. The enlarged leg is best expressed in the great subfamily Rhyparochrominae where nearly all of the many hundreds of species possess enlarged and ventrally spined fore femora. Putshkov (1956) and Sweet (1960) have shown that most, if not all, of the rhyparochromines are seed feeders. Thus the function of these legs remains unknown. They do not appear to be used in mating behavior or in antennal cleaning, nor to any appreciable extent in carrying food etc. Yet it seems unlikely that legs of this type would persist throughout hundreds of species in many different genera distributed in several different subfamilies and in all of the major zoogeographic regions without having an important function. Solution of this problem should be a matter of considerable interest to those concerned with the question of correlation of form and function from inferred evidence. Recently Sweet (*in litt.*) has noticed some remarkable threatening behavior, displayed intraspecifically by several species of rhyparochromines in defense of food, that involves the use of the fore femora. This may offer a clue to an understanding of this interesting biological problem.

Despite our lack of knowledge of the function of these fore legs we do know enough of their occurrence in the family Lygaeidae to conclude that they are not of random distribution. The presence of incrassate fore femora is the predominant condition in the Rhyparochrominae, Pachygronthinae and Oxycareninae whereas they are

*Manuscript received by the editor December 20, 1961.

absent or infrequently developed in the Lygaeinae, Orsillinae, Ischnorhynchinae and Geocorinae. Thus it can be seen that the presence of incrassate fore femora is at least roughly correlated with ventrally located spiracles. The latter is the less specialized condition. The correlation may well be more than coincidental and at least give some indication that an enlarged femur represents the generalized condition within the family.

It is thus most interesting to encounter a member of the Ischnorhynchinae with forelegs as strongly developed as in any of the subfamilies whose members are usually provided with incrassate fore femora. Except for the remarkable front legs this insect appears to be a conventional ischnorhynchine. It possesses dorsally located spiracles, a large claval commissure, a punctate clavus, hyaline membrane of the fore wing, hind wing with hamus and intervannals present, a "pruinose" body bloom, and a non-depressed posterior pronotal margin.

Macellocoris new genus

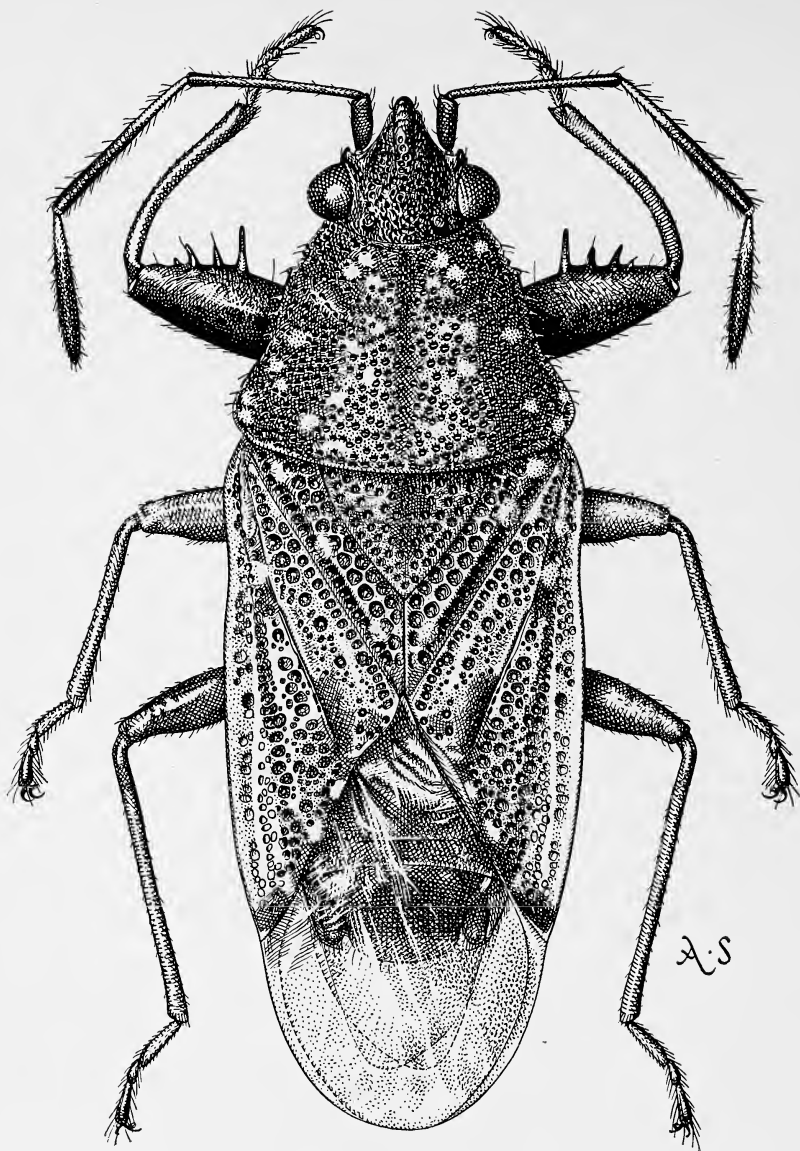
Fore femora strongly incrassate, armed below with four sharp, prominent, elongate spines; lateral margins of pronotum non-explanate but sinuate, bearing a series of prominent setigerous tubercles; clavus with a closely set row of punctures adjacent to claval suture and two inner rows of very large coarse punctures; membrane transparent, hyaline, exceeding apex of abdomen; eyes prominent, in contact with antero-lateral pronotal angles; apex of head attaining but not exceeding first antennal segment; preocular distance greater than eye length; lateral margin of corium explanate.

Type species: *Macellocoris incrassatus* new species.

Macellocoris incrassatus new species

Plate 2

General coloration reddish-brown, pronotum lighter on either side of midline posterior to calli and near anterior margin; hemelytra opaque whitish, the irregular punctures brown; legs yellow with anterior femora bright tan; antennae with segment one, two except extreme apex, basal one-half of three and basal one-fourth of four yellowish with remaining antennal areas fuscous; venter reddish brown; mesal area of sternum black; head with large, coarse, contiguous placed punctures that give a rugose appearance; pronotum and scutellum with rather small, deep evenly spaced punctures; claval punctures very large and deep, those on corium irregular in size and



SLATER — MACELLORIS

position with a definite row adjacent to the claval suture; surface nearly glabrous, head, pronotum and scutellum with short semi-decumbent setae in the punctures; appendages sparsely but definitely pubescent.

Head non-declivent, moderately acuminate, tylus projecting well beyond the juga; first antennal segment about attaining apex of tylus; eyes large not produced, strongly in contact with anterolateral pronotal angles; length head .70 mm.; width across eyes .85 mm., interocular space .48 mm.; pronotum evenly narrowing anteriorly, lateral margins slightly sinuate, narrowly carinate, bearing 6-7 setose tubercles, transverse impression absent mesally but faintly indicated by depressed area near lateral margin, dorsal surface slightly convex becoming less so in area of calli and anteriorly, length pronotum 1.05 mm., width pronotum 1.55 mm.; scutellum evenly tumid with depressed base, no median carina, length .60 mm.; corium with broad slightly upturned explanate margin, this laterally rounded becoming sinuate adjacent to apex of scutellum; apical corial margin sinuate, concave along basal one-third; distance apex clavus to apex corium 1.10 mm., distance apex corium to apex membrane .90 mm.; membrane greatly exceeding apex of abdomen; distance apex abdomen to apex membrane .75 mm.; middle and hind femora slightly enlarged, with basal one-fourth slender, giving a clavate appearance; labium elongate, attaining posterior margin of first abdominal sternite, first segment exceeding base of head, second segment extending onto anterior portion of mesosternum; length labial segments I .65 mm., II .62 mm., III .60 mm., IV .35 mm.; antennae slender, segments two and three terete, fourth segment narrowly fusiform; length antennal segments I .25 mm., II .75 mm., III .82 mm., IV .70 mm. Total length 4.65 mm.

Holotype: Male. SUMATRA: Pematang Siantar, June 1937. (CT & BB Brues). In Museum of Comparative Zoology (Harvard).

Acknowledgements

I should like to extend my appreciation to Drs. P. J. Darlington and W. L. Brown (now at Cornell University), of the Museum of Comparative Zoology, for the opportunity to study this interesting

EXPLANATION OF PLATE 2

Macellocoris incrassatus new species. Drawing by Arthur Smith, British Museum (Natural History).

insect. Appreciation is also extended to the University of Connecticut Research Foundation for providing funds for the execution of the plate by the distinguished Arthur Smith of the British Museum (Natural History).

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NOTES ON FOSSIL CLEONINAE (COLEOPTERA: CURCULIONIDAE)¹

BY JOHN M. KINGSOLVER
Illinois Natural History Survey

Dr. Samuel H. Scudder probably described more species of North American fossil Rhynchophora than any other worker, yet he was not a specialist in the weevils. His monograph of the fossil Rhynchophora found in the middle Oligocene beds of Florissant, Colorado, however, is one of the most extensive treatments of any group from that site.² Whereas most fossil beetle species have been described on the basis of elytra, a high percentage of the Florissant weevils are preserved so that the dorsal or the lateral aspect of the whole specimen is visible. In most examples from this site, according to the illustrations, the rostrum is well preserved, and even antennal and tarsal segments are intact but the body is usually compressed and distorted and parts are often disarranged. Details of the mouthparts are obliterated and the ventral surface of the body is seldom visible. In these latter two areas lie some of the critical characters needed for subfamilial and tribal differentiation in existing keys to extant forms of the Rhynchophora.

There is a basis for comparison of the fossils with extant forms where the modern classifications of groups are based on the characters that happen to be well preserved in the fossil specimen. Fossil beetles, however, are seldom preserved in enough detail to be of much value at the specific level and in many cases at the generic level, except in amber. Unless some diagnostic structure is particularly well preserved in a specimen, most fossil beetles have not been of much value in taxonomic studies.

Workers in the Rhynchophora should use caution in interpreting Scudder's illustrations. If reference to any of his fossil species is contemplated, the type specimen or specimens should be checked, and decisions should be based upon this examination instead of upon the original description and illustration.

Through the kindness of Dr. F. M. Carpenter, I was recently privileged to examine the type specimens of fossil species of Cleoninae

¹This study was made possible by a travel grant from the Society of Sigma Xi.

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²Tertiary Rhynchophorus Coleoptera of the United States. U. S. Geological Survey Monographs, Vol. 21, 206 pp., 12 pls., Washington, 1893.

which had been described by Scudder in 1893. The types are part of the collection at the Museum of Comparative Zoology, Harvard University, and were all collected at Florissant. This type study was in conjunction with a survey being made to circumscribe the weevil subfamily Cleoninae and to revise the included genus *Lixus*.

The characters which separate the Cleoninae from other subfamilies of the Curculionidae are: (1) antennal scrobes originating on the sides of the beak and curving abruptly downward to terminate beneath the base of the beak, (2) tarsal claws connate at the base, (3) labial palpi short and positioned on the ventral face of the labium at either end of the ligular suture, (4) ligula attached to the terminal margin of the prementum, (5) tegmen of the male lacking posterior dorsal lobes, (6) anal veins 2dA₂ and 2dA₃ usually entire in the hind wings, (7) eyes either vertically elongated, ovate or reniform. Obviously, dissection of a specimen would be required to examine the genitalia and the wings. The other five characters in order to be visible would require a precise orientation of the beak and tarsal claws, yet the combination of all these characters is necessary for inclusion of a weevil in the Cleoninae.

In none of the six cotype specimens of *Cleonus exterraneus* Scudder, the two of *Cleonus degeneratus* Scudder, or in the genotype of *Eocleonus subjectus* Scudder are the labium or the tarsal claws visible. Neither are the eyes nor the antennal scrobes sufficiently well preserved or correctly positioned to permit accurate determination except in the genotype specimen of *Eocleonus subjectus*. Two characters in this latter specimen rule out the probability of its inclusion in the Cleoninae. First, the visible eye is elongated horizontally instead of dorso-ventrally as is the case in every modern, narrow-eyed Cleonine weevil I have seen. Second, the antennal scrobe is directed toward the eye as in some of the broad-nosed weevils. Not only are the characters that are preserved in all of the examined specimens insufficient to permit the species to be placed in the Cleoninae, but they are also too vague to allow accurate placement in any other subfamily. There is simply not enough detail preserved to give any substantial clues to the correct taxonomic status of the specimens.

In his 1893 report, Scudder also described *Cleonus foersteri* and *Cleonus primoris*, each based on a single specimen. The illustration of *foersteri* indicates that this species most nearly approaches a true *Cleonus* in the shape of the beak and eye, but other Cleonine characters are not apparent. The location of the type specimen is not known.

The illustration of *Cleonus primoris* indicates that the specimen is badly distorted and that it probably will yield few clues to its correct placement in the Curculionidae. The type was stated by Scudder to be in the Princeton University collections, but Dr. A. G. Fischer assures me that the type is not presently in that collection and that its whereabouts is unknown.

On the basis of my examination of the types, I suggest that the three fossil species, *Cleonus exterraneus*, *Cleonus degeneratus* and *Eocleonus subjectus* be relegated to *incertae sedis* status in the Curculionidae until such time as their true position can be determined, if that is possible. Likewise, *Cleonus foersteri* and *Cleonus primoris* should be placed in *incertae sedis* in the Curculionidae until the types can be located and examined.

PSEUDOSCYMNUS, A NEW GENUS OF ASIATIC SCYMNINI (COLEOPTERA: COCCINELLIDAE)*

BY EDWARD A. CHAPIN
Museum of Comparative Zoology

In the course of work on a report on the Coccinellidae of Micronesia, my attention was attracted by the figure of the antenna of *Scymnus kurohime* Miyatake and the figures of receptacula of unusual form of several species, mostly from Japan. Paratypes of *S. kurohime* were generously presented to me by Mr. M. Miyatake and a series of this species was found in a collection from Naha, Okinawa, made by Mr. N. L. H. Krauss. Mr. Miyatake also supplied, at my request, a series of *S. hareja* Ws. An analysis of the characters of these species shows that they form a group which is intermediate between *Scymnus* proper and *Cryptogonus*. It should be noted here that the eyes of *Cryptogonus* and its close relatives are sparsely set with fine erect setae, a character which has long been recognized as definitive of the Scymnini.

When compared with *Scymnus nigrinus* Kugel. and *Cryptogonus orbiculus* (Gyll.), the respective type-species, one finds the characters of *S. hareja* and *S. kurohime* to be closer to *Cryptogonus* than to *Scymnus*. In *Scymnus* the antenna is of the usual coccinelline form and consists of eleven segments. The tarsus is also similar to the large majority of coccinellids in being composed of four segments. In *Cryptogonus* and *Pseudoscymnus* the antenna is very short and consists of nine segments and is of an unusual form for the family. The tarsus is truly three segmented, differing from those of most coccinellids.

Genus **Pseudoscymnus** new genus

Body form and size of *Scymnus* Kugelann, upper surface set with fine, short pubescence. Antenna nine-segmented; basal segment stout, almost as wide at its widest part as long; second segment stout barrel-shaped, nearly equilateral, clearly separated from the basal; third through ninth segments forming a fusiform club, the third longer than wide, fourth through seventh wider than long, each wider than the preceding, eighth segment usually shorter than wide and slightly narrower than seventh, ninth segment a little more than half as

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wide as eighth, subconical. The ninth segment bears at its apex several long setae. Maxillary palp with the three segments nearly equal in width, the terminal segment parallel-sided with apex sharply oblique. Terminal segment of labial palp stout barrel-shaped with truncate apex. Mandible with subapical tooth. Prosternum not produced anteriorly to cover mouthparts, prosternal lobe rather narrow, carinate. Abdomen with six visible sternites. Coxal arc incomplete, much as in *Nephus* Mulsant. Tibiae simple, rather slender. Tibial spurs absent. Tarsus three segmented. Claw with subquadrate basal tooth. Elytral epipleura nearly flat and horizontal, not distinctly foveolate.

Male — aedeagus symmetrical.

Female — receptaculum seminis with ramus short and stout, nodulus long, drawn out in a slender, curved tube, or short and stout, cornu curved, sausage-shaped. Sperm duct very short if nodulus is elongate tubular, otherwise moderately long. Infundibulum absent. Hemisternites intermediate between the "blade and handle" type of the majority of the Coccinellidae and the "ovipositor" type of most of the Scymnini.

Type-species — *Scymnus hareja* Weise.

I am including the following species in *Pseudoscymnus* —

Pseudoscymnus hareja (Ws.) 1879, Deutsch. ent. Zeit., 23: 150;

Miyatake, 1958, Japanese Journ. Appl. Ent. Zool., 2: 251-256, figs. 1 A-D, 3 A-B, 4 E-H, 5 A-C.

Pseudoscymnus kurohime (Miyatake) 1959, Mem. Ehime Univ., (6) 4: 136-138, figs. 50-61.

It is probable that the following four species also should be referred to *Pseudoscymnus* —

Scymnus seboshii Ohta 1929, Ins. Matsumurana, 4: 11; Miyatake, 1958, Japanese Journ. Appl. Ent. Zool., 2: 251-256, figs. 2 A-C, 3 C-D, 4 A-D, 5 D-F.

Scymnus sylvaticus Lewis 1896, Ann. Mag. Nat. Hist., (6) 17: 36; Bielawski 1957, Trans. Shikoku Ent. Soc., 5: 71, figs. 5-11.

Scymnus pilicrepus Lewis 1896, op. cit., p. 36; Bielawski, 1957, op. cit., p. 72-73, figs. 12-15.

Scymnus quinquepunctatus Weise, 1923, Arch. Naturg., 89. A. 2: 188; Miyatake 1959, Mem. Ehime Univ., (6) 4: 138, figs. 62-64.

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The illustration of a spider on the front cover of this issue of *Psyche* was reproduced from an original drawing made by J. H. Emerton and contained in the Museum of Comparative Zoology. First published in the Transactions of the Connecticut Academy of Arts and Sciences (1909, vol. 14, plate 7, fig. 5), it shows the displaying posture of the male of *Habronattus viridipes* (Hentz).

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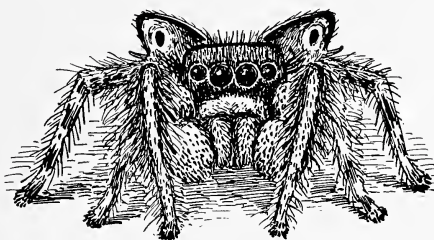
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No. 2

DEFENSE MECHANISMS OF ARTHROPODS. X. A PHEROMONE PROMOTING AGGREGATION IN AN APOSEMATIC DISTASTEFUL INSECT.¹

By T. EISNER AND F. C. KAFATOS²

Department of Entomology, Cornell University, Ithaca, N. Y.

A striking feature of many aposematic insects is their habit of maintaining dense and often conspicuous aggregations (Cott, 1957). Rather than spacing themselves more or less evenly throughout what is seemingly a uniformly favorable habitat, they occur in distinct, sporadically distributed clusters. Many meloid and coccinellid beetles, as well as a variety of pentatomid, coreid, and lygaeid Hemiptera, among others, are well known for this habit. These insects possess chemical defense mechanisms that protect them against predators, and their tendency to advertise themselves to visually oriented predators such as birds by pooling their aposematic resources in a collective display, appears to have obvious adaptive value. Moreover, by restricting themselves to a few relatively widely-spaced sites, the insects are exposed to but a fraction of the total number of predators in the area. This is likely to be of particular importance with respect to predators such as birds, which are known in many cases to have well-delimited foraging territories, and each of which may be expected to inflict a toll upon the insect population during the training period when the bird is learning to discriminate against the insect. Clearly, the fewer the foraging territories occupied, the greater will be the number of insects spared.

Hitherto no studies have been made on the mechanism by which such aggregations are established and maintained. The purpose of

¹This study was supported by Grant E-2908 of the U. S. Public Health Service. The work was done at the Southwestern Research Station of the American Museum of Natural History, Portal, Arizona. We are indebted to the director of the Station, Dr. Mont A. Cazier, for his generosity with equipment and facilities, and to Miss Abby Rockefeller, who assisted ably in this and related studies.

²New address: Biological Laboratories, Harvard University, Cambridge, Mass.

Manuscript received by the editor January 9, 1962.

this note is to present evidence indicating that in at least one case, a gregarious beetle of the family Lycidae, the clustering behavior of both sexes seems to be mediated by a volatile attractant produced by the males alone.

Lycids are widely distributed through the tropics and subtropics, commonly are aposematic, are known to be distasteful to many vertebrate and invertebrate predators, and frequently figure as dominant Müllerian elements in mimetic associations. They form dense aggregations, sometimes being found by thousands, closely spaced on the exposed inflorescences of the host plants on which they feed and mate.

The particular species on which we worked, *Lycus loripes* (Chevrolat), is abundant on the grounds of the Southwestern Research Station of the American Museum of Natural History, Portal, Arizona, where this study was made. The locality has been described in some detail elsewhere (Linsley et al., 1961), and it will suffice here to mention that, at the time of the experiments (July 15-25, 1961), the lycids were found almost exclusively on a patch (ca. 80 x 160 ft.) of sweet white clover (*Melilotus alba*) directly facing the principal laboratory building of the Station (Plate 3, fig. 1). Over 3000 *L. loripes* inhabited the patch at the time, distributed more or less irregularly in dense clusters. These lycids are uniformly yellow-orange in color (except for some black on the appendages), and are conspicuous on the white flowers of the clover, particularly on those branches where they are densely aggregated (Plate 3, fig. 2). They are sluggish and do not take readily to flight when disturbed. They fly relatively little even on their own initiative, and when they do, it is usually during the noon hours.

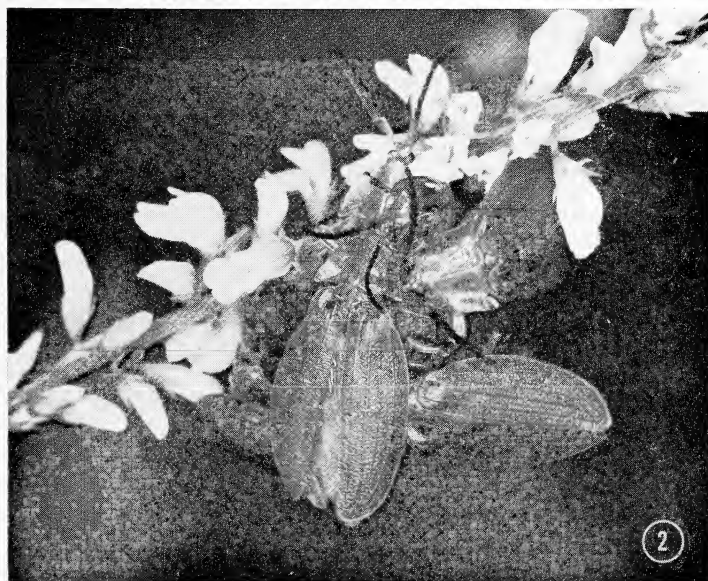
Behind the laboratory building there was a second stand of *Melilotus*, roughly equal in area to the front patch, but almost entirely devoid of lycids. This uninhabited patch became the test arena in which formation and growth of aggregations was experimentally induced.

Initial tests, designed to see whether one could induce lycids to aggregate after distributing them singly throughout the test area were bound to failure, since these lycids, rather than being attracted to one

EXPLANATION OF PLATE 3

Figure 1. The open field, densely overgrown with *Melilotus alba*, directly in front of the main laboratory building of the Southwestern Research Station, Portal, Arizona. On this field was found the main standing aggregation of *Lycus loripes*.

Figure 2. A cluster of *Lycus loripes* on an inflorescence-bearing branch of *Melilotus alba*. Within the main lycid aggregation, dozens of branches bore one or more such clusters, as well as isolated individuals and mating pairs.



EISNER AND KAFATOS — DEFENSE MECHANISMS

another, were lured back to the main standing aggregate in the front of the building. Instead of being scattered individually, the lycids were then put out in a number of isolated incipient aggregations to see whether these would tend to consolidate and attract newcomers. This they were found to do. Five groups of *L. loripes*, each comprising 75 individuals of both sexes, were placed on single *Melilotus* plants (or on compact clusters of branches) in such a way that three of the groups were closely spaced and roughly equidistant (5-6 m.), whereas the other two were spaced about 25 m. from each other and from the center of the triangle formed by the other three. Within five days (see Table I) the three closely spaced aggregations became consolidated around one of the loci, which now numbered 390 individuals. The two neighboring clusters had dwindled to 27 and 1 respectively. Recruitment had taken place also from the two outlying clusters, one of which had disappeared altogether, while the other now had only 15 lycids. Although the individuals of each lot had originally

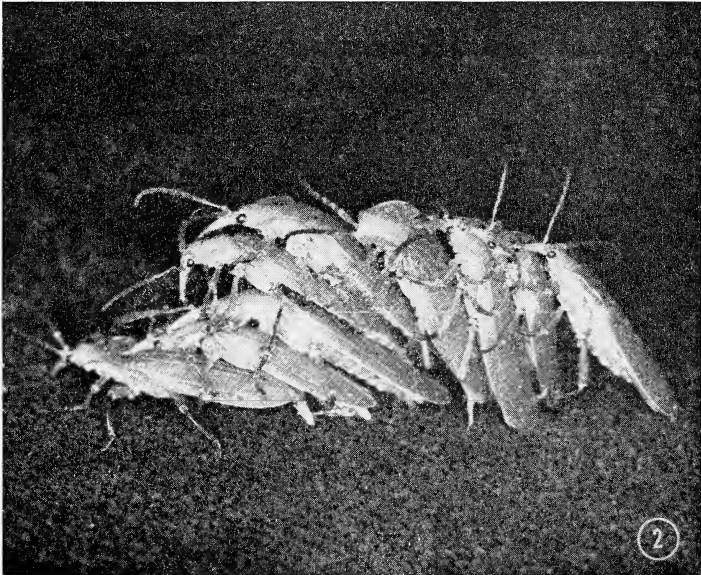
AGGREGATION						
	I	II	III	IV	V	
TIME (hrs.)	LYCID COUNT PER AGGREGATION					LYCIDS ELSEWHERE
0	75	75	75	75	75	5
4	22	23	35	35	82	5
30	2	21	30	9	178	30
56	2	21	26	3	309	24
119	0	15	27	1	390	30

Table I. Fate of five artificially-established incipient aggregations (each consisting of 75 lycids of both sexes) observed over a period of five days. Aggregations III, IV, and V were 5-6 m. from one another. Aggregations I and II were 25 m. from each other and from the center of the triangle formed by the other three. The times given for the various counts are measured from when the aggregations were first put in the field. The column on right gives the lycid count for the entire remainder of the *Melilotus* test patch behind the laboratory building.

EXPLANATION OF PLATE 4

Figure 1. One of the nets (enclosing *Melilotus* with lycids) used as a lure. This particular net, which held males alone, was one that successfully attracted other lycids (a few of the newcomers are seen on the net itself).

Figure 2. Group of male lycids, in the typical sequential arrangement they often assume when confined by themselves.



EISNER AND KAFATOS — DEFENSE MECHANISMS

been labelled with a distinct color marking, these tended to flake off after some days, and the exact course of the migration patterns could therefore not be followed. However, judging from the number of unmarked specimens present, which outnumbered by far the calculated maximum that could have lost its markings, it was clear that a substantial number of lycids were new arrivals in the test area, probably stemming from the principal aggregation at the opposite side of the laboratory building. Conversely, as expected, some marked individuals had been lured back to the front field.

It remained to be determined what particular attracting stimulus is responsible for luring the lycids. Visual cues were eliminated by

DECOY GROUP

A	B	C	D
150 ♂♂	150 ♂♂	150 ♀♀	150 ♀♀

TIME(hrs.) NEWCOMER COUNT PER DECOY GROUP

	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
20	39	7	65	13	4	2	4	3
45	41	16	25	8	0	1	0	0
72	29	17	19	5	0	1	0	0

	A	
	150 ♀♀	
	♂♂	♀♀
96	5	2
119	0	0
145	0	0

	D	
	150 ♂♂	
	♂♂	♀♀
	23	12
	31	7
	26	13

Table II. Attraction of lycids to male and female decoy aggregates placed in nets. The four decoy groups (A-D) were placed at the corners of a square, roughly 25 m. to the side. The times given for the various newcomer counts are measured from when the decoy groups were first staked out. At 72 hours, the females from group D were exchanged with the males from A.

using porous nets of white cloth to enclose the groups of lycids, distributed as before on close clusters of *Melilotus* branches (Plate 4, fig. 1). The technique had the added advantage of preventing dispersal of the decoy group, while at the same time facilitating the count of newcomers assembled around the nets. Four nets were staked out with 150 lycids each, two of them containing only males, the other two only females. Spacing was maximized within the area available, each net being about 25 m. from its neighbors. The loci selected were known to have supported no previous aggregations. Table II summarizes the results. Only those lycids were counted as newcomers which were either directly upon the nets, or on *Melilotus* branches within a few feet around them. It is clear that the males, but not the females, exerted immediate and persistent attraction for lycids of both sexes. The fact that the newcomers included a preponderance of males should not be taken to reflect a greater susceptibility of this sex to the attracting stimulus, since the males were actually the more numerous in the population at the time (actual counts made, based on samplings from the main population site, showed the ratio to vary between 3:1 and 6:1).

The possibility was ruled out that ecological factors, rather than the males themselves, were the source of attraction. After the third day, the males from *net A* were exchanged with the females from *net D*. The other two nets were dismantled, and the lycids within them, plus the assemblages that had accumulated around both original male sites, were scattered at 1 m. intervals throughout the test area. Over the next three days only one assemblage built up, this time around the new male site (Table II). Clearly, the attracting stimulus is emitted by the males, and it is most likely a diffusible chemical factor.

An additional observation is worth mentioning. On two separate occasions, when artificially induced aggregations were allowed to persist over a period of several days, and were subsequently removed, the *Melilotus* branches that had harbored the beetles were found to retain the potential to lure lycids, presumably as a result of residual attractant with which the plants had been labelled. When the lycids that would subsequently accumulate on these branches were systematically removed once a day, and redispersed, the attractiveness of the plants dwindled to extinction within a few days.

The attraction of lycids to each other in the presence of males was also demonstrated in captive specimens. Mixed lots of males and females confined in glass-topped observation enclosures would soon distribute themselves into individual mating pairs or small clusters of

pairs. Females alone remained distributed singly and showed no attraction for each other. Males, by contrast, clustered closely, usually one on top of the other in overlapping sequence, as shown in Plate 4, fig. 2.

A chemical attractant of the type involved here may appropriately be called a pheromone. Pheromones, by definition (Karlson and Butenandt, 1959), are substances secreted by one individual to the outside, capable of eliciting specific behavioral or developmental responses in another individual of the same species. Among insects, these social chemical messengers include the sex attractants, the queen substance of honeybees, the trail substances of ants and termites, the releasers of alarm behavior in ants, etc. It is clear that the lycid attractant, aside from its obvious function in maintaining the aposematic population densely congregated, also serves appropriately in bringing together the sexes preparatory to mating. But since it lures both males and females with apparently equal effectiveness, there must be additional short-range stimuli operating within the aggregation to insure that males and females will ultimately be properly paired. One wonders what evolutionary justification accounts for the production of attractant by the males alone, rather than by the females, or by both sexes. Not enough is known about the life cycle of lycids, but the possibility that the males are the first to emerge in the season and hence are the ones that carry the aggregations through their incipency, is worth considering.

It is hoped, now that the groundwork of this problem has been laid, that additional more precise experimentation on this unusual type of attractant will be pursued. With *L. loripes* there are some especially intriguing aspects to the problem. This lycid is the dominant Müllerian element of an elaborate mimetic complex (Linsley et al., 1961) that includes among others, a congeneric sibling species of lycid [*Lycus simulans* (Schaeffer)], a cerambycid beetle (*Elytroleptus ignitus* LeConte), and a geometrid moth [*Eubaphe unicolor* (Robinson)]. Whether the attractant produced by *L. loripes*, which far outnumbers the others, exerts its action also on all or some of the mimetic associates, thus insuring that these are lured to "safety" within the aggregations of the dominant model element, remains unknown. Unfortunately all of these mimetic forms were extremely scarce at the time of our experiments, and could not be included for study.

Future work should concentrate also on some of the many other gregarious aposematic insects known, in which similar attractant mechanisms, or perhaps interesting alternatives, are likely to be at play.

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THE TRINIDAD CAVE ANT *EREBOMYRMA*
(= *SPELAEOMYRMEX*) *URICHI* (WHEELER), WITH
A COMMENT ON CAVERNICOLOUS ANTS
IN GENERAL*

By EDWARD O. WILSON

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In 1922 W. M. Wheeler described a new pheidologetonine ant, *Spelaeomyrmex urichi*, which he regarded as allied to *Erebomyrma* but sufficiently removed to justify the erection of a separate genus. The eleven syntypes, all minor workers, were collected in "Guacharo Cave," Trinidad, occupied by the oil-bird or "guacharo" (*Steatornis caripensis* Humboldt). Their pale color, minute eyes, and long bristly pilosity suggested to Wheeler that they represent a truly cavernicolous, i.e. troglobitic, species. In addition, Wheeler speculated that "the Texan *E. longi* Wheeler, which is certainly subterranean and has been taken only once (during a nuptial flight), is really a cavernicolous ant." In 1938, however, Wheeler reported the collection of workers of *Spelaeomyrmex urichi* by P. J. Darlington from leafmold in Cuba, thereby casting doubt on the status of the species as a troglobite.

Certainly no more likely troglobite than *S. urichi* has been found among the ants. Further information on its biology has promised to be of exceptional interest. In the course of field work in Trinidad in 1961, the present author undertook to rediscover the species. The first problem was to find the type locality. No fewer than six caves in various parts of the island harbor the guacharo and could correctly be called "Guacharo Cave." The itinerary of the collector, the late Prof. F. M. Urich, was not known. After the author had visited one cave, on the Spring Hill Estate, without success, Dr. David Snow, who was conducting an ecological study of the guacharos, suggested the Oropouche Cave, near Cumaca, as the most likely locality. A single visit to this cave, on April 18, resulted in the immediate finding of two colonies of *Spelaeomyrmex*. Later, a surprising discovery was made: a colony collected from savanna forest at Bernhardsdorp, Surinam, in March 1961 and first identified as *Erebomyrma*, was on second examination determined to be conspecific with *Spelaeomyrmex urichi*. These findings have shed new light on the generic distinctness of

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Spelaeomyrmex, on its status as a troglobite, and on the ecological singularity of cave ants in general.

TAXONOMY

Erebomyrma Wheeler

Erebomyrma Wheeler, 1903, Biol. Bull., 4:137-148, minor worker, queen, male. Type species (monobasic): *Erebomyrma longi* Wheeler.

Spelaeomyrmex Wheeler, 1922, Amer. Mus. Novitates, 45:9, minor workers. Type species (monobasic): *Spelaeomyrmex urichi* Wheeler. NEW SYNONYMY.

Following is a list of the known species of *Erebomyrma*, with attendant bibliography:

eidmanni Menozzi, in H. Eidmann, 1936, Arb. phys. Angew. ent. Berlin-Dahlem, 3:47-48, fig. V (1-4), worker, soldier, queen. Type locality: Mendes, Rio de Janeiro, Brazil.

longi Wheeler, 1903, Biol. Bull., 4:137-148, figs. 1-5, minor worker, queen, male. Type locality: Denton, Texas.

morai Menozzi, 1931, Bull. Lab. Zool. Gen. Agr., Portici, 25:271-272, fig. 7, worker. Original localities: Apaican, Vulcano; and San José (Costa Rica). Borgmeier, 1949, Rev. Brasil. Biol., 9:207-208, figs. 8-9, "ergatogyne" (= soldier), second record from San José, Costa Rica.

nevermanni Mann, 1926, Psyche, 33:103-104, worker. Type locality: Hamburg Farm, Reventazon, Santa Clara, Costa Rica.

peruviana Emery, 1905, Bull. Soc. Ent. Ital., 37:139, nota, queen. Type locality: Marcapata, Peru.

urichi (Wheeler), 1922, Amer. Mus. Novitates, 45:9-11, fig. 1A-B, minor worker. Type locality: "Guacharo Cave," Trinidad. (*Spelaeomyrmex urichi*). Other records: Cuba, Yucatan, Surinam.

The minor-worker characters cited by Wheeler as most strongly separating *urichi* from *longi*, and hence *Spelaeomyrmex* from *Erebomyrma*, are: larger head size; angulate (vs. round) humeri; proportionately larger first gastric segment; and minor features in the shape of the petiole, postpetiole, and legs. These differences probably signify a specific distinction between *urichi* and *longi*, but they are not great enough to justify a generic break, even by liberal standards. The synonymy is supported by the fact that the newly-discovered queen and male of *urichi* are closely similar to these castes in *longi*. One possible difference of generic magnitude, unknown to Wheeler, still remains: *eidmanni*, *morai*, *nevermanni*, and *urichi* are now known to

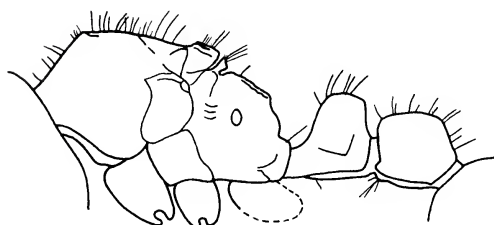
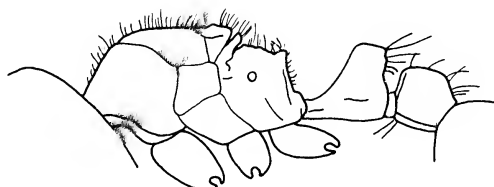
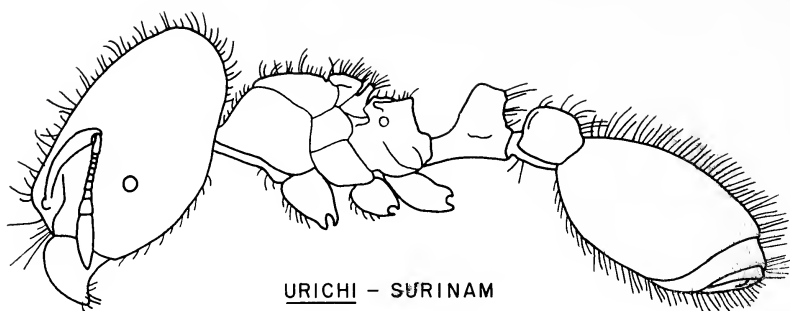


Figure 1. Soldiers of *Erebomyrma urichi* from Bernhardsdorp, Surinam, and Oropouche Cave, Trinidad, and *E. ?nevermanni* from Barro Colorado, Panama, showing variation in thoracic and pedicellar structure in this little known caste.

have a soldier caste, while none has been discovered in *longi*. However, *longi* is known from but a single collection, made under circumstances in which the scarce soldier caste could easily have been overlooked. It

seems a fairly safe conjecture that *longi* soldiers will be discovered when whole colonies of that species are collected.

As just noted, the Oropouche *urichi* and a colony taken at Bernhardsdorp, Surinam, are considered conspecific. The minor workers of the two colonies are virtually identical. In the Oropouche soldier the anterior face of the petiolar node is slightly more inclined posteriorly (thus forming a greater angle with its anterior peduncle), the anterodorsal nodal angle somewhat more rounded, the propodeal angles are more pronounced and acute, and there are some differences in thoracic form and sculpturing (see text-figure). The Oropouche queens have slightly more developed propodeal spines and larger ocelli. In other respects the soldiers and queens appear identical between the two colonies.

Together, the Trinidad and Surinam *urichi* differ markedly from those in a series of *Erebomyrma* collected recently at Barro Colorado (W. L. Brown and E. S. McCluskey *leg.*) and tentatively determined as *nevermanni* Mann. The *urichi* minor worker has distinctly narrower, more erect propodeal spines; while the *urichi* soldier is much smaller and with more pronounced propodeal spines (text-figure).

ECOLOGY

Trinidad. The Oropouche Cave is the source of the Oropouche River, which extends back into the cave as a clear stream several meters in width. A colony of *Erebomyrma urichi* was found approximately 30 meters inside the cave on the bank of the stream, in very feeble light coming from the plainly visible cave mouth. Much of the ground was covered by guano dropped from the large numbers of guacharos nesting overhead. The arthropod fauna at this point was rich and diverse, consisting of ants [*Mesoponera constricta* Mayr, *Odontomachus haematodus* (Linné), and *Solenopsis (Diplorhoptrum) tenuis* Mayr], as well as the *Erebomyrma*, entomobryid collembolans, cave crickets, dermapterans, small flies, and mites. The ant species, other than *Erebomyrma*, have been collected outside caves in Trinidad. *Mesoponera constricta*, which was the most common forager in the vicinity of the *Erebomyrma* nest, was also a dominant ant along the trails through cacao plantations in the Cumaca area. Most of the other insects appeared to be troglaphiles. Fifteen meters farther in, and in almost total darkness, a large *Bufo marinus* was found. In short, at the site of the first *Erebomyrma* nest, troglaphilic (facultatively cavernicolous) animals predominated.

A second group of foraging *Erebomyrma* workers, almost certainly

representing another colony, was encountered between 200 and 300 meters from the cave entrance. This spot was reached only after passing five major twists in the cave and was in apparently total darkness. It was the final outpost of the guacharo nests. Here there were no other ant species; in fact, none of the other three found at the first site ventured beyond the lighted portion of the cave. The arthropod fauna was sparse in species and biomass and consisted wholly of blind, white entomobryids, campodeids, isopods, and snails.

Just past the second site the cave ceiling dipped to within less than a meter of the stream surface, and the passage continued tortuously for another twenty meters or so. Beyond, the cave opened into a final oblong chamber before dipping beneath the stream surface. In this terminal room there were no guacharos; only bats had left a sprinkling of guano on the floor. A careful search revealed no *Erebomyrma* workers in the terminal chamber.

The nest at the first site, near the cave entrance, was located and excavated. It was enclosed entirely within a large, smooth shale slab partly buried in the cave soil and covered with a thin layer of dense clay. The rock was soft, naturally fractured, and could easily be broken apart with a steel trowel. Columns of workers were observed traveling from the guano piles to two entrance holes twelve centimeters apart on the upper edge of the rock. The holes were each about two millimeters in diameter, and each was surrounded by low, inconspicuous piles of excavated clay. The nest, located only a few centimeters below the surface, consisted of several flat, irregular cavities between five and ten centimeters wide and several millimeters in height. Probably the great majority of workers and all of the other adult castes were collected, both alive and preserved in alcohol. The sample, censused the following day, had the following composition: 547 minor workers, 1 soldier, 10 dealate queens, 10 males. Also present was a large quantity of brood, in all stages of development, including one male pupa. It was estimated that the entire worker population, including that part left foraging or missed in the nest, was not less than 600 and not greater than 1000.

Previous to the excavation, the foraging workers were observed briefly. Workers were found up to $1\frac{1}{2}$ meters from the nest entrances, but the great majority was within a meter's radius. Most were hunting singly or moving in loose files through guacharo guano, just as Urich had found them forty years earlier. Workers returning to the nest converged in two separate files, which, judging from the precision

with which they repeated each twist and turn, must have been following odor trails. Several were carrying objects: a mite, an entomobryid collembolan, and two unidentified arthropod eggs. The mite and entomobryid were freshly killed and had evidently been captured as prey. This conjecture is supported by the fact that *Erebomyrma* workers were most densely concentrated at points where large numbers of entomobryids occurred. Later, in captivity, workers fed readily on a wide variety of larger moths and flies presented to them, but only after these had been killed and cut open. In the original nest over a hundred unidentified globular objects resembling arthropod eggs were found piled with the brood. These were cared for by the captive colony in the artificial nest and may have been used sporadically for food, although direct feeding was not observed. Similar structures were found by Eidmann (1936) in the nests of *Erebomyrma eidmanni*.

Surinam. On March 14 a *urichi* colony was found in open, dry, second growth forest at Bernhardsdorp, near Lelydorp. It was nesting in a small rotting log partly buried in moist leaf litter in a well-shaded part of the forest. The population consisted of a single dealate queen, four soldiers, an estimated 500-1000 minor workers, and a large quantity of brood in every stage of development. Adjacent to the *Erebomyrma* colony was a large colony of the termite *Armitermes minutus* Emerson (det. A. E. Emerson). The *Erebomyrma* colony and a fraction of the *Armitermes* colony were placed alive in separate but interconnected artificial nests. Within a few hours after establishment *Erebomyrma* workers entered the still chaotic termite chamber and began carrying off eggs. They were unopposed by the much larger *Armitermes* adults, and in turn did not molest the *Armitermes* adults or nymphs. While the response of the *Erebomyrma* workers was clear-cut in this instance, it does not necessarily mean that the species is termitolestic on undisturbed *Armitermes* colonies in nature. The colony was kept alive for only a few days and there was no opportunity to extend the experiment. In this connection it is worth noting that Emerson (in Wheeler, 1936) found evidence that *Solenopsis (Diplorhoptrum) laeviceps* Mayr collects and stores eggs of *Nasutitermes cavifrons* (Holmgren) and *N. costalis* Holmgren in British Guiana.

BEHAVIOR

The Trinidad colony was kept under observation in an artificial nest for two months and notes taken on selected aspects of behavior. The ethology of this species is of considerable interest because nothing

has been recorded hitherto on *Erebomyrma*, and, in fact, very little information is available on the entire tribe Pheidologetonini.

The self-grooming movements of the minor worker are given as follows, according to the classification proposed recently for ants as a whole (Wilson, 1962): (1) oral leg cleaning, (2) antenna wiping, (3) four-leg wiping, (4) three-leg wiping, (5) two-front-leg wiping, (7) head wiping (8) abdomen wiping (front legs). The queen repeated all of these movements and in addition (10) metapleuron wiping, conspicuously missing in the worker. Other-grooming was as frequent as in most other myrmicines. The workers were especially attentive to the large queens, and a populous retinue followed each as it moved about. As many as six were seen riding on one queen's body at the same time.

Worker-to-worker regurgitation was frequent. The queens apparently were fed exclusively by worker regurgitation, and they never approached the prey. In several emigrations studied, adult transport was never observed. In one exceptional instance a worker carried a newly eclosed worker by its left middle and fore legs clumsily and a short distance over the brood pile, as though it were a piece of brood.

DISCUSSION: THE ECOLOGY OF CAVERNICOLOUS ANT SPECIES

Penetration of caves by ants occurs chiefly in the tropics and is limited mostly to the dimly lighted (twilight) zone near entrances. The great majority of records belong to species that are obviously either trogloxenic (penetrating as foragers from nests outside) or troglophilic (facultatively cave-nesting). Further, these species are typically those that are among the most abundant, widespread, and adaptable members of the ant fauna in habitats outside the caves. For instance, a collection of ants made in 1959 in the Batu Caves, Malaya, by Mr. H. E. McClure and studied by the author, consisted primarily of three identifiable species [*Bothroponera tridentata* (Fr. Smith), *Leptogenys diminuta* (Fr. Smith), *Pheidole javana* Mayr] that are among the most widespread and common members of their genera in the Oriental Region. Wheeler (1924) records *Triglyphothrix striatidens* Emery from 400 feet inside the entrance of Siju Cave, Garo Hills, Assam; this ant is a notably adaptable pantropical "tramp" and by far the most widely distributed *Triglyphothrix*. Of 16 species recorded from Yucatan caves by Wheeler (1938), 15 are identifiable, and of these 13 have very extensive ranges in the New World tropics; most are known further to be abundant in various habitats. The remaining two species [*Brachymyrmex cavernicolus* Wheeler, *Paratrechina* (*Nylanderia*) *pearsei* Wheeler] belong to genera whose

taxonomy and ecology are too poorly known to allow further generalization. Kempf (1961) records *Labidus coecus* (Latreille) from "guacharo" caves in northern Peru and Venezuela. Both collections were made in zones of total darkness, at 90 m. and 800 m. respectively from the cave mouths. As Kempf points out, *L. coecus* is one of the commonest and most adaptable army ant species and ranges, at widely varying elevations, from the southern United States to northern Argentina. Santschi (1914) records eight species collected by Ch. Alluaud and R. Jeannel from caves at Tanga and Shimoni, Tanganyika. These can be roughly characterized as follows: *Ponera dulcis* Ford, widespread but known from only a few records; *Leptogenys jeanneli* Santschi, known only from the type collection but an unexceptional member of the epigeic *falcigera* group; *Odontomachus haematoda* L. var. *troglydites* Santschi, probably the same as the very widespread, abundant African "*haematoda*" or "*haematoda stanleyi*" (? *nec haematoda* L. of the New World); *Dorylus fimbriatus* (Shuckard), very widespread and abundant; *Monomorium rhopalocentrum* Emery subsp. *speluncarum* Santschi, probably equals *rhopalocentrum*, a widespread and apparently relatively common species, collected at Shimoni only at a cave entrance; *Strumigenys stygia* Santschi, known only from the type collection but otherwise a morphologically unexceptional species of the *rogeri* group (see Brown, 1954); *Miccostruma marginata* (Santschi), known only from the type collection taken at cave entrance and not morphologically peculiar; *Paratrechina (Nylanderia) jaegerskioldi* (Mayr), very widespread and abundant. Thus this African cave fauna is made up of five more or less common widely distributed species together with three species still known only from the type caves. The latter exceptional group, however, belong to genera (*Leptogenys*, *Strumigenys*, *Miccostruma*) in which rare, local species are usual, so that no particular ecological significance can be attached to the fact that their known range is at present so limited.

Cave ants do not as a group possess the usual morphological modifications found in extreme cave dwellers. For the most part, they show no exceptional pigment or eye reduction when compared with their congeneric relatives, and, in the cases where their habits are known, they are no less epigeic in their foraging behavior. Conversely, the majority of the most highly modified hypogeic and subterranean tropical ant taxa are unknown from caves, e.g., extreme species of *Amblyopone*, *Centromyrmex*, *Solenopsis (Diplorhoptrum)*, *Tranopelta*, *Acropyga*. We may conclude that the troglloxenes and trogllophiles are characteristically generally adaptable rather than pre-

adapted for cave life. Ants are not exceptional in this regard. Other adventitiously cavernicolous animal taxa are often very varied in their ecology; some other arthropod groups, such as the European copepods, resemble the ants in that the cave species are typically widely distributed on the outside (Hesse, Allee, and Schmidt, 1951).

The question can now be raised, whether there are any ant species that are troglotic, i.e. limited to caves. *Erebomyrma urichi* is clearly excluded on the basis of information just given, and the accumulated evidence makes it improbable that any other member of the genus is troglotic. *Paratrechina* (*Nylanderia*) *troglydites* Weber of Cuba, originally recorded from a shallow cave, has been shown to be a junior synonym of *P. (N.) myops* (Mann), which has been found in soil away from caves in two montane localities in Cuba (Brown, 1955). A related species, *microps* M. R. Smith, occurs in places remote from caves on Puerto Rico. *Proceratium cavernicola* (Borgmeier), described from a queen found in the Chilibrillo Caves of Panama, has been recognized as a synonym of *P. micrommatum* (Roger), known from several non-cavernicolous series collected in Central America and Cuba (Borgmeier, 1957; Brown, 1958).

There remain at least four ant species known only from single collections made in caves. *Brachymyrmex cavernicolus* Wheeler (1938) was found beneath a stone near the mouth of Balaam Canche Cave, Chichén Itzá, Yucatan. It is pale yellow in color and has small eyes, which perhaps suggest a normally cavernicolous habit. But it belongs to a genus the taxonomy of which is in outstandingly poor condition, so that the possibility exists that non-cavernicolous series have been recorded in the literature under other names, as in the cases of the *Paratrechina* and *Proceratium* species just mentioned. The African cavernicoles *Leptogenys jeanneli*, *Strumigenys stygia*, and *Smithistruma marginata* have already been discussed. They belong to otherwise non-cavernicolous groups and show no apparent morphological adaptation to cave life themselves. Clearly, until stronger evidence is produced, the existence of troglotic cave ant species must be considered in great doubt.

Enlarging on this point, let us ask why there are so few (if any) troglotic ants or, for that matter, troglotic social insects of any sort. The following hypothesis is proposed. The reproductive unit in social insects is the colony, and it follows that natural selection operates on the colony as a unit. Further, the singly prefertilized mother queen of a monogynous colony ordinarily contains the whole of the transferable genetic material, and, since she stores the sperm of

her mate (or mates), is genetically the equivalent of two or several individuals, the female and sexual consorts in a normal population of non-social animals. Hence, what may be referred to as the "equivalent size" of the reproductive population, N_d , in an idealized deme of social insects outside the nuptial season can be estimated as

$$N_d = \frac{N_t}{N_c} (Q + mQ)$$

where N_t is the total adult population of the deme, including workers, m is the average number of males that fecundated the queens assuming approximately equal sperm contributions, Q is the average number of mother queens assuming approximately equal egg contributions, and N_c is the average mature colony size. Thus in a cave deme containing 10,000 adult individuals with an average mature colony size of 1000 and single fertilizations of single queens, the reproductive population size equivalent would be only 20. We may note that a deme of 10,000 adults, the non-social condition, would perhaps be large enough and contain enough genetic variability to be stable and self-maintaining. Demes of this size are quite common in nature. But a deme-equivalent of 20 adults, the social condition, must be below the critical threshold or dangerously close.

In short, if species of social insects never become truly troglobitic it may be simply because they are unable to maintain sufficiently large cave demes. Due to limited habitable space, the Oropouche Cave could not have contained more than 20 colonies of *Erebomyrma urichi* and probably held considerably fewer. *Erebomyrma* colonies are sometimes polygynous, as we know from the single Oropouche example. If ten queens per colony is accepted as the upper limit, and each were assumed to be singly fertilized, the reproductive-population equivalent of the Oropouche *Erebomyrma* is calculated not to exceed 400. Since the excavated colony was the only obviously populous colony found, the actual equivalent was probably far less.

But let us suppose that social insects do occasionally become troglobitic; what characteristics might they be expected to have? In addition to the well-known morphological changes common to most troglophilic animals, there are several features of social structure that might be affected. There would likely be one or more of three devices to increase N_d ; namely, (1) decreased colony size, (2) increased polygyny, and (3) increase in m (polygamy). The Oropouche colony of *Erebomyrma urichi* was markedly polygynous, with the added result that the estimated N_d of the colony was large (20). In fact, *urichi*, although not a troglobite, may be pre-adapted for marginal cave exis-

tence. Finally, it is interesting to note that the predicted social modifications are just as likely to be developed in any ant species sufficiently ecologically restricted to be partitioned into very small demes.

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A NEW ANT OF THE GENUS *AMBLYOPONE* FROM PANAMA¹

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As known before 1960, the genus *Amblyopone* in the New World was restricted to temperate North America and the southern half of South America. In my 1960 review of the Amblyoponini (Bull. Mus. Comp. Zool., 122: 143-230) I described as new *A. orizabana* from Mt. Orizaba in southern Mexico, and the aberrant *A. mystriops* from Guatemala. In a very recent paper, Kempf [1961, Studia Ent., Petropolis, Brazil (n. s.) 4: 489] has recorded *A. degenerata* Borgmeier — previously known only from southern Brazil — as being collected in Surinam. Now, a new species, to be described below, has been found in lowland forest on the Isthmus of Panama, closing the last significant gap in the distribution of *Amblyopone* in this hemisphere. The genus is now seen to range from British Columbia and the St. Lawrence Valley south into southern Chile, and it seems likely that it reaches Tierra del Fuego, even though no specimens have yet come in from that far south. As it stands, *Amblyopone* is the most widely distributed New World ant genus. While it is clear that the genus is very sparsely distributed in the tropics, and that it reaches its best development in cool temperate regions to the north and south, it does seem likely that further collecting will show it to have a continuous or near-continuous range in all but the driest and coldest parts of the Americas.

Amblyopone tropicalis sp. nov.

Holotype worker: TL 3.0, HL (including clypeal teeth) 0.60, HW 0.52 (CI 87), WL 0.74, petiolar node L 0.26, W 0.35, post-petiole W 0.38, scape L 0.34, outside straightline length of mandible 0.46 mm.; measurements as in my 1960 review.

Habitus that of the smaller "*Fulakora*" group of *Amblyopone*, especially *A. orizabana* Brown and *A. chilensis* Mayr. Head with nearly straight (feebly sinuate) occipital border, sides feebly convex, diverging anteriorly, widest across anterior corners, which are furnished

¹The work in Panama was supported by a Small Grant from the Milton Fund of Harvard University.

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with small but acute genal teeth. Frontal lobes approximate, separated only by a narrow linear groove. Anterior clypeal apron gently convex in outline, with 5 large truncate teeth, of which the middle tooth is much the largest, being composed of two median teeth completely fused to about their apices, and projecting nearly twice as far as the smaller teeth close on each side of them; corner (lateral clypeal) teeth still shorter, each composed of a mesal and a smaller lateral element which are fused at the base. Mandibles rather slender, their external margins feebly convex (almost straight along basal $2/3$), inner margins convex except for apical quarter, each bearing 7 teeth: a triangular basal tooth, followed by a spaced series of 5 acute, slightly recurved teeth, of which each of the distal 3 or 4 has a shorter dorsal spur (difficult to see in normal full-face view) representing the vestigial twin of a pair common in species of this group; an indistinct reclinate tooth lies near the narrow mandibular apex. The mandibles when closed cross each other, but leave a fairly large triangular space between themselves and the clypeal margin. Antennal scapes short and rather broad (thinnest near their midlength), feebly sigmoidal, reaching back to about the posterior fifth of the head length. Funiculus 11-segmented, conspicuously enlarged apicad, but gradually so, without a definite number of segments in the club; all segments except first and apical broader than long. No eyes detected.

Alitrunk feebly convex in profile; as seen from above, broadest across the middle pronotum; promesonotal suture apparently flexible and accompanied by a strong groove along the anterior mesonotal border, at alitruncal midlength. Mesonotum transverse, forming narrowest point of alitrunk; metanotal groove distinct but shallow; propodeal dorsum broader than long, its sides diverging posteriad; declivity plane, rounding into dorsum, much broader than high. Inferior borders of pronotum broadly rounded.

Petiole sessile, with vertical anterior and horizontal dorsal faces both convex, the dorsal face broader than long as seen from above. Ventral process of petiole a rounded, forward-thrust lobe with a conspicuous oval thinned area or fenestra. Postpetiole broader than petiole, but shorter, and also shorter than the succeeding segment, which is the widest. Gastric apex not laterally compressed; sting stout. Legs robust; femora flattened and incrassate; tibial spur vestigial on middle legs, but on each hind tibia there is a short but very thick, curved, pectinate tibial spur and an adjacent, much smaller, straight, slender spur.

Head densely reticulate-punctulate and opaque. Antennal scapes,

mandibles and clypeus obscurely longitudinally striate-punctate, opaque to subopaque. Lower sides of propodeum with the usual faint longitudinal striae. Remainder of body smooth or nearly smooth and shining, with fine spaced punctures, these most dense on petiolar dorsum and on two succeeding segments, where integument almost appears loosely coriaceous in some lights, but is still definitely shining.

Pubescence appressed and subappressed, moderately dense, generally distributed over body and appendages (not on sides of alitrunk); erect pilosity short, mostly oblique, moderately abundant, becoming longer on gastric apex, antennal apices and mandibles; very sparse on legs. Color ferruginous yellow, the head capsule very slightly darker, appendages somewhat lighter.

Paratype female (dealate): TL 3.1, HL 0.65, HW 0.57 (CI 88), WL 0.91, petiolar node L 0.26, W 0.38, scape L 0.37, greatest diameter of compound eye 0.11 mm.

Similar to the holotype worker, but with the usual differences of caste: fairly large compound eyes (no eyes could be detected in the worker), ocelli developed and with blackened calli, wing stumps present and blackened; meso- and metathoracic flight sclerites well developed, but rather flat, continuing the weakly convex surface of the alitrunk without major interruption. As usual for females of this genus, the petiole and gaster are relatively a little wider than in the worker, and the head, while still light ferruginous, is a trifle darker than in the worker. Alitrunk also rather coarsely and closely punctate above, but still distinctly shining.

The holotype worker and female paratype, the only adults taken, were found on Barro Colorado Island, Panama Canal Zone, on January 6, 1960 [W. L. Brown, Jr., leg.], and deposited in the Museum of Comparative Zoology. The specimens were found together with a few larvae and pupae in a cavity in the underside of a small rotten branch lying in moist leaf litter on the forest floor, in what is variously described as rain forest or monsoon forest, close to Snyder-Molino Trail and less than 100 meters from the Laboratory Clearing of the Smithsonian Institution's Canal Zone Biological Area. These specimens were the very first ants I collected during a three-week stay on the island. When first collected, they were mistaken for *Prionopelta*, a related genus found very rarely on the island, but common elsewhere in Central and South America. After closer examination revealed their true identity, I searched energetically for the species in likely habitats for the remainder of my stay, as did my companion, Dr. E. S. McCluskey, but we never found it again. This is only one

of many ant species that have been collected on Barro Colorado a single time, despite the very intensive collecting of its whole area by several ant specialists, as well as the long-time Resident Naturalist, James Zetek. It has been said that Barro Colorado is so well collected for ants that scarcely anything in the way of new species can be collected there. That McCluskey and I, engaged in what was primarily an ecological survey not particularly directed toward the finding of novelties, were able to find this *Amblyopone* and at least two other undescribed ant species in the square mile centered on the Laboratory Clearing, speaks for the virtual inexhaustability of the island's ant fauna and for the richness of tropical forest faunas in general.

In the key to the New World *Amblyopone* in my 1960 review (p. 191 to 192), *A. tropicalis* runs to couplet 8, where its intermediate size makes it fall ambiguously into either 8 or 9. Of the three species in these two couplets [*orizabana* Brown, *bierigi* (Santschi), *chilensis* Mayr], *A. tropicalis* is closest to *orizabana* in structure and to *chilensis* in size, but differs from these in the reduced number of teeth in the clypeal armament, in the strongly projecting, large median fusion tooth, and in the nearly obsolete dorsal members of the mandibular double teeth, rendering the tooth row apparently single as seen from dorsal view. *A. tropicalis* is larger than *orizabana*, has relatively longer and more slender mandibles and a broader head.

A NEW ANT OF THE GENUS *EPITRITUS* FROM SOUTH OF THE SAHARA*

BY WILLIAM L. BROWN, JR.

Department of Entomology, Cornell University

Recently Mr. G. E. J. Nixon, of the Commonwealth Institute of Entomology in London, sent me a small series of a curious ant that he had recognized as an aberrant and possibly undescribed species of tribe Dacetini. Upon receiving the specimens, I found that the sample represented a new *Epitritus*, the first member of the genus from Ethiopian Africa, and the first to be found in the tropics. I am grateful to Mr. Nixon for making available this most interesting new species.

***Epitritus laticeps* sp. nov.**

Figures 1-4

Holotype worker: TL 2.2, HL 0.47, HW 0.58 (CI 123), ML 0.22 (MI 47), WL 0.49, scape L 0.29, funiculus L 0.43 mm, of which about half is taken up by the apical segment. Measurements and proportions are those standard in my other dacetine studies (see Brown, 1953, Amer. Midl. Nat. 50: cf. pp. 7-15).

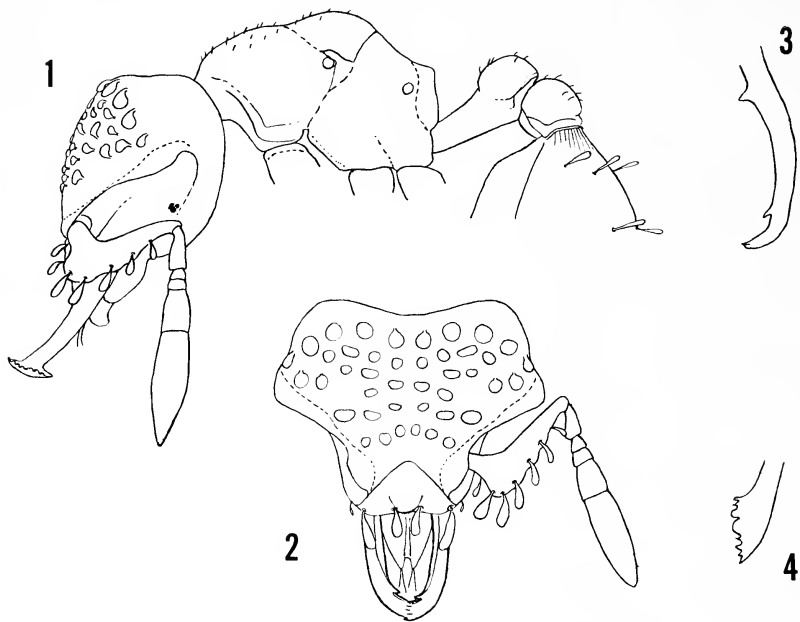
Shape of head, body and mandibles as shown in Figs. 1-4. Especially characteristic of the known species of *Epitritus* and (judging from two occipital lobes (which make the head distinctly broader than long); the wide, basally lobiform antennal scapes; the large, conical labral lobes; the 4 long straplike clypeal hairs and the peculiar mandibles, lacking a long, spiniform dorsal "apical" tooth and with only a single preapical tooth. The apex of the mandible is of the "inverted" type characteristic of the known species of *Epitritus* and (judging from two paratype workers of which the mandibles were opened) has 7 or 8 denticles, of which one or two in the middle are round-edged, and the rest are acute. The basal lamella is small, with acutely rounded apex (Fig. 3), and the ventro-medial margin below it is obtusely denticulate or angulate (not shown in figures). Eyes minute, with only 4-6 facets. Antennal funiculus clearly 5-segmented.

Promesonotum seen from above broadly oval, almost circular, narrowest behind, where it is terminated by the fine but distinct metanotal groove, which crosses just behind the highest point of the swollen mesonotum. Propodeum much narrower than pronotum, with high,

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angular lamellae guarding the concave declivity, the declivity reaching far up towards the metanotal groove.

Petiolar node distinct from its anterior peduncle, as seen from above transverse, subrectangular, about twice as broad as long. Postpetiole



Figures 1-4. *Epitritus laticeps* sp. nov., paratype worker. Fig. 1, side view of head and body. Fig. 2, dorsal full-face view of head and mandibles. Fig. 3, oblique dorsal view of opened left mandible. Fig. 4, ventral inside oblique view of apical group of teeth or denticles. Drawn by F. A. McKittrick.

much broader than petiole and more than twice as broad as long, convex above with a shallow median impression, articulated to the entire width of the anterior gastric margin. Spongiform appendages limited to narrow posterodorsal lamelliform collars on both nodes, and absent from anteroventral face of gaster. Gaster laterally submarginate at the extreme base; short, coarse costulae fade caudad into superficial, indistinct reticulation reaching nearly to the midlength of the basal segment; gaster otherwise shining and smooth.

Body reticulate-punctulate, opaque, except for the gaster, the inner mandibular surfaces and the labral lobes, which are smooth and shining. Specialized pilosity, especially the large orbicular, cochlear hairs

of the head, and the spatulate ones of the scapes and clypeus, as shown in the figures. Slender, erect spatulate-to-clavate hairs in rows of 4 or 6 on gastric dorsum, totalling about 32. Ground pilosity reduced to minute stubby hairs, chiefly on promesonotum and nodes, and sparse, short reclinate hairs on gastric dorsum and legs. Tibiae and tarsi with longer reclinate hairs, some of them spatulate. Gula with fine reclinate hairs. Color medium ferruginous; head feebly infuscated dorsally; appendages more yellowish.

Holotype [British Museum (Natural History)] and six paratype workers [deposited with holotype and in Museum of Comparative Zoology at Harvard College] taken in northern Nigeria near Zungeru on the Kaduna Road, 19 December, 1956, from "base of dead tree" by W. A. Sands of the Termite Research Unit (Collection No. S 780). The paratypes are quite similar to the holotype, and range from the same size down to the smallest specimen: TL 2.0, HL 0.46, HW 0.55 (CI 120), ML 0.22 (MI 48), WL 0.49 mm. Cephalic index range for the entire type series is 119-125. There is slight variation in the size and shape of the small teeth or denticles in the apical complex. Female and male unknown.

E. laticeps can be separated from its two congeners by means of the following key:

1. Tooth at apparent (dorsal) apex of mandible small, about equal to or slightly longer than the other largest teeth of the apical group; promesonotum without conspicuous hairs of any kind (Nigeria) *laticeps* Brown
Tooth at apparent (dorsal) apex of mandible long, straight and spiniform, about 2 or 3 or more times as long as the largest of the other teeth in the apical group; promesonotum with numerous large orbicular scale-like hairs like those of the dorsum of the head 2.
2. Funiculus with 5 separate segments; mandible with two pre-apical teeth (Japan: Kyushu, Honshu) *hexamerus* Brown
Funiculus with only 3 separate segments; mandible with 4 pre-apical teeth (Mediterranean lands n. to Hungary) *argiolus* Emery

The finding of a species of *Epitritus* south of the Sahara marks the genus as a zoogeographical curiosity of more than usual interest. Of the two previously known species, *E. argiolus* is widespread in southern Europe and North Africa, while *E. hexamerus* has been taken twice in Japan. Evidently, *Epitritus* is a relict-distributed group that was once more widely distributed in the tropical and warm temperate

parts of the Old World. The insects are cryptobiotic in habits, and are small and inconspicuous, so we may look forward to the discovery of species elsewhere in the Old World.

Another interesting thing about the new species is its close convergence in many morphological details to *Talaridris mandibularis* Weber (tribe Basicerotini) of Trinidad and British Guiana (see Brown and Kempf, 1960, Stud. Ent., Petropolis, (n.s.) 3: 233, 241-242).

A NEW *DAMOTHUS*
AND A KEY TO THE NORTH AMERICAN
DIGNATHODONTID GENERA
(CHILOPODA : GEOPHILOMORPHA :
DIGNATHODONTIDAE)¹

By R. E. CRABILL, JR.
U. S. National Museum, Washington, D. C.

The genus *Damothus* was proposed by R. V. Chamberlin in 1960 (p. 239) for the reception of a single species, *montis*, which had been collected in the Wasatch Mountains of Utah. While collecting arachnids and myriapods at Ophir in the Oquirrh Mountains of that State, Dr. H. W. Levi unwittingly uncovered the second-known specimen of the genus, which I judge to represent a new species, *alastus*, here described. I wish to express my thanks to Dr. Levi for his kindness in placing this and much other valuable material in my hands for study.

On the basis of all available information, the two most distinctive features of the genus are the massively crassate and essentially tubular ultimate legs of the male, and the presence of two basal denticles on the prehensorial tarsungula. Indeed, the latter character alone will distinguish *Damothus* from all other known chilopod genera of whatever order. After more is known about *Damothus*, it may well be seen that two other features have significance diagnostically: the peculiar shape of the 1st maxillary medial lobes; the relatively strongly-developed labral sidepieces.

Comparing the Harvard specimen with Dr. Chamberlin's original description of *montis*, I find the following to be significant distinguishing features. *D. montis*: (1) The first maxillae are without lappets. (2) The coxopleural pores are concentrated along and mostly concealed beneath the margins of the ultimate pedal sternite. (3) Ventral pore-fields are absent. *D. alastus*, n. sp.: (1) The first maxillary coxosternum bears a pair of conspicuous and relatively long lappets. (2) The coxopleural pores are all exposed and are not concentrated along and beneath the ultimate pedal sternite. (3) Small but conspicuous pore-fields are present on all pedal sternites except the last.

¹This study was undertaken with the assistance of a grant from the National Science Foundation.

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Damothus alastus new species

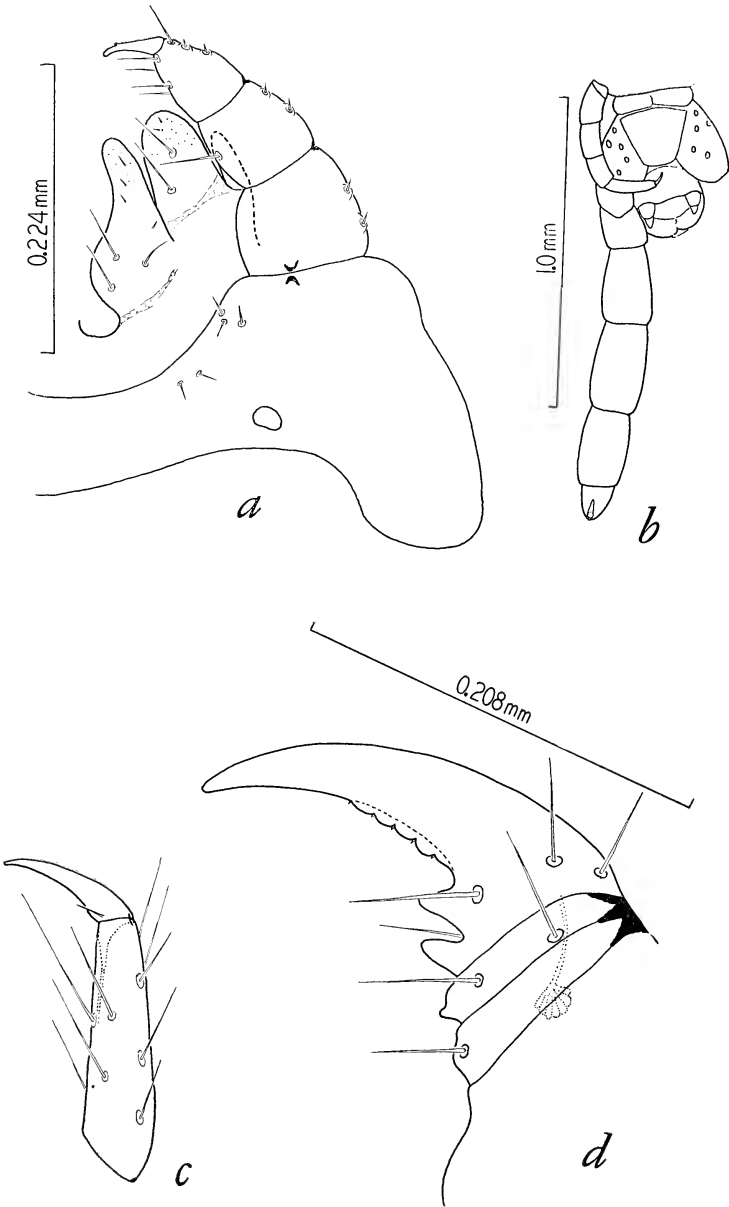
Plate 5

Holotype, male. Utah: Tooele County, Ophir, Oquirrh Mountains, 2000 m. 25 April 1961. Herbert W. Levi, leg., in cottonwood, sage. Specimen preserved in the Myriapod Collection of the Museum of Comparative Zoology, Harvard University.

GENERAL. Length: 11.5 mm. Pedal segments: 37. Body widest over posterior third, anterior to which it is gradually acuminate. Color: generally pale yellow; the head and prehensors yellowish-orange. **ANTENNAE.** Length: (expanded in Hoyer's) 1.65 mm. Shape: strictly filiform, neither attenuate nor clavate. Setae gradually increasing in number and decreasing in length on articles 1-14. Ultimate article twice as long as penult; its upper third with short, flat, special sensory setae on outside and inside surfaces. **CEPHALIC PLATE.** Length: 0.416 mm. Greatest width: 0.406 mm. Shape: sides evenly excurved; rear margin perfectly straight. Clothed with straight, relatively short, stiff setae. Frontal suture absent. Prebasal plate completely concealed. **CLYPEUS.** Paraclypeal sutures broadly membranous, complete. Transbuccal sutures vague, passing only half-way to lateral margin. With a pair of small and extremely weakly consolidated areas (plagulae) on extreme posterior margin. Setae: postantennals, 1 + 1, very long; midclypeals, 2 + 2, the inner pair much longer than the outer pair; prelabrals absent. **LABRUM.** Midpiece very wide, armed over entire width with long, hyaline, thin serratures. Sidepieces: strongly-developed, well-sclerotized; each with a few delicate, hyaline serratures; widely separated centrally; separated from clypeus by wide membranous strip. **FIRST MAXILLAE.** Coxosternum: without setae; medially undivided; very vaguely separated from medial lobes and telopodites; with a pair of concealed, relatively long lappets. **SECOND MAXILLAE.** Isthmus very wide from side to side but narrow antero-posteriorly. Each coxosternite very weakly sclerotized, with few setae; without special thickenings or similar appurtenances. Telopodite: with strongly-developed dorsal and ventral basal condyles; the articles separated by distinct sutures; outer marginal setae extremely short and robust; inner marginal setae much longer; apical claw long and thin,

EXPLANATION OF PLATE 5

Damothus alastus sp.n. a. First and Second Maxillae. Left halves, all setae shown. b. Ultimate Pedal and Postpedal Segments. Ventral aspect, setae deleted. c. Left Sixth Leg, Tarsus and Pretarsus. Anterior surface, all setae shown. d. Tarsungula and Intercalary Articles of Left Prehensor. Ventral aspect, principal setae shown.



CRABILL — DAMOTHUS

smooth except for minute protuberance as shown in figure. PROSTER-
NUM. Without subcondylic sclerotic lines. Pleuroprosternal sutures
arching obliquely laterally, complete anteriorly. Anterior margin
without diastema or denticle. PREHENSORS. When closed, not sur-
passing anterior head margin. Trochanteroprefemur: basally bulging
on inner side; without a denticle; outside length, 0.198 mm; inside
length, 0.094 mm; basal width, 0.146 mm. Femoroid without den-
ticle. Tibioid with a distinct but small denticle. Tarsungula: rela-
tively short and robust; basally with two large denticles; dorsal edge
smooth; ventral edge over proximal half dissected into about 4 coarse
and rounded serrations; length, 0.208 mm. Poison calyx: of the simple
type, consisting of bunched digitiform appendices; situated in femoroid.
Poison gland situated entirely in the trochanteroprefemur. TERGITES.
Without evident paramedian grooves. Tergites and intertergites
clothed with long, stiff, robust setae. STERNITES. On the anterior
third of body each with a midlongitudinal, shallow depression. Pore-
fields: anterolaterals absent; each sternite from the first through the
penult with two small, subcircular fields on extreme posterior margin.
Pro- and metacoxal porefields present on the first through the penult
pedal segments. Setae; few in number; arranged in regular horizontal
rows. LEGS. Clothed with stiff, long, robust setae. Pretarsi: very
long and thin, curved; parungues acicular, short, approximately equal
in length. ULTIMATE PEDAL SEGMENT. Pretergite fused with its
pleurites, i.e. without sutures or divisions bilaterally. Tergite: greatest
width to length, 35 : 28; anterior corners rounded; sides straight and
posteriorly convergent; rear margin broadly rounded. Presternite
with a vague midlongitudinal suture. Sternite with sides essentially
straight and convergent, its rear margin weakly rounded. Coxopleuron:
barely inflated; ventrally with small, freely-opening, deeply-pigmented
pores; 5 on each coxopleuron. Ultimate leg: greatly swollen, essential-
ly tubular, notably much longer and more massive than the penults;
tarsus consisting of two articles, the second about half as long as the
first and conical in shape; pretarsus is a robust, dark claw; the whole
leg clothed with robust, stiff setae; ventral and inner surfaces of all
articles including and distal to the femur pierced by relatively large
glandular pores. POSTPEDAL SEGMENTS. Gonopod distinctly bipartite,
conical. Anal pores present and not concealed.

To assist in locating *Damothus* within the growing complex of
North American dignathodontid genera, I have presented a generic
key here: it is the first to be published since that of Attems of 1947,
p. 129. To some extent it had to be based upon information only

available from the literature. Included are all of the genera now known from North America including Mexico.

Excluded are three genera which had been previously reported from the area under discussion: *Leptodampius* Chamberlin, 1938, p. 255; *Diplochora* Attems, 1903, p. 281; *Paraplanes* Verhoeff, 1933, p. 22. The original description of *Leptodampius* is not sufficiently full and detailed to permit its confident placement within my key. The recent examination of the holotype of *fusata* Attems, the type species of *Diplochora*, shows it to be referable to *Tomotaenia* Cook (new synonymy), and to the subgenus *Korynia* Chamberlin. Verhoeff's Californian *Paraplanes californicus*, whose types I have studied at Munich, all are referable to *Tomotaenia fusata* (Attems) (new synonymy). The details of these cases will be discussed in a separate paper soon to be issued.

- 1a. Each coxopleuron with two subsurface gland-pits, but without freely-opening and exposed pores. (Mexico)
..... *Pagotaenia* Chamberlin
- 1b. Each coxopleuron with freely-opening pores most or all of which are exposed. Subsurface gland-pits absent. 2
- 2a. Prehensorial tarsungula with 1 or 2 prominent basal denticles
..... 4
- 2b. Prehensorial tarsungula without a basal denticle 3
- 3a. Coxopleural pores numerous, opening over most or all of coxopleural surface. Ultimate pedal sternite narrow and elongate. (Idaho). *Zantotaenia* Chamberlin.
- 3b. Coxopleural pores few in number and opening only along and under the margins of the ultimate pedal sternite which is wider than long. (southeastern United States). *Agathothus* Bollman
- 4a. Tarsungula with 2 prominent basal denticles. (Utah)
..... *Damothus* Chamberlin
- 4b. Tarsungula with 1 prominent basal denticle 5
- 5a. Ventral pore-fields absent. (California)
..... *Malochora* Chamberlin
- 5b. Ventral pore-fields present. 6
- 6a. Coxopleural pores concentrated along and beneath margins of ultimate pedal sternite; this sternite always wider than long. (United States, Missouri westward to the Pacific Coast; eastern Asia) *Tomotaenia* Cook (*sensu lato*²)

²If *Tomotaenia* is divided into subgenera on the basis of the presence or absence of sutures on the ultimate pedal pretergite, then the oldest available

- 6b. Coxopleural pores freely dispersed *at least* over ventral surface of coxopleuron; not restrictively concentrated along and beneath ultimate sternite margins; this sternite usually longer than wide or at most as wide as long. (Holarctic Region) .. *Strigamia* Gray 7
- 7a. Ultimate pedal pretergite fused with its pleurites, i.e. not bilaterally impressed with sutures. *S. (Linotaenia)* C. L. Koch
- 7b. Ultimate pedal pretergite not fused with its pleurites, i.e. set off from them by prominent sutures or fissures. *S. (Strigamia)* Gray³

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name for the bisuturate specimens would have to be *Diplochora* Attems, 1903. The non-suturate specimens would take the nominate generic name. The explanation for this is complicated and beyond the scope of this paper; however, it is fully treated in another paper being published in *Entomological News*.

³Historically three contending generic names have been applied to this zoological entity. Some workers continue to apply the wrong generic name. The only correct generic name is *Strigamia*; it is neither *Scolioplanes* nor *Linotaenia*. The whole matter was thoroughly discussed and clarified by me in a 1953 publication: see *Entomological News*, 64(7), pp. 169-172.

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The illustration of a spider on the front cover of this issue of *Psyche* was reproduced from an original drawing made by J. H. Emerton and contained in the Museum of Comparative Zoology. First published in the Transactions of the Connecticut Academy of Arts and Sciences (1909, vol. 14, plate 7, fig. 5), it shows the displaying posture of the male of *Habronattus viridipes* (Hentz).

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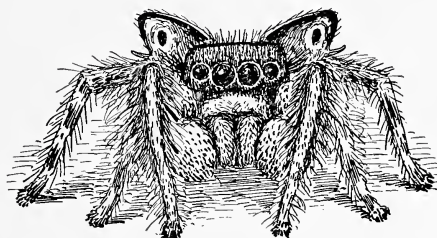
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THE CYTOTAXONOMY OF THE LARVAE OF SOME MEXICAN FRUIT FLIES IN THE GENUS *ANASTREPHA* (TEPHRITIDAE, DIPTERA)¹

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INTRODUCTION

During a study of host relations of the Mexican fruit fly, *Anastrepha ludens* (Loew), difficulty was encountered in obtaining positive identification of tephritid larvae recovered from field infested fruit. Existing larval keys based on morphological characters (e.g. Phillips, 1946) were not adequate for differentiating between some closely related Mexican representatives of the family. Accurate identifications could only be obtained by rearing larvae to the adult stage. This proved time consuming and increased the chance of losing valuable host records when larvae failed to mature. For this reason, a preliminary cytotaxonomic study was made on some of the more common fruit infesting *Anastrepha* found in Mexico to see if chromosome morphology would be of any use in identifying larvae.

This method of species differentiation is not new. It has been used for many years by plant taxonomists to establish a more natural classification within certain groups of plants (Darlington, 1956). Its application to animal taxonomy has been somewhat restricted owing, in part, to the difficulties of handling some animal material. Many of these difficulties have now been eliminated through the use of new and improved techniques. A great deal is now known about the cytogenetics of animals and particularly of the insects. White (1954) has presented an excellent summary of our present knowledge of comparative cytology and its application to the study of animal evolution and taxonomy, while Patterson and Stone (1952) have

¹This study was conducted under the auspices of the United States Department of Agriculture while the author was employed by that organization in Mexico, D.F., Mexico, from 1955 to 1957.

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discussed chromosome evolution in the genus *Drosophila* in detail.

Several investigations have been made concerning the cytology of the Tephritidae. Metz (1916), after investigating the chromosomes of *Euresta melanogaster* Loew [probably *Dyseuaresta mexicana* (Wied.)], concluded that flies of the family Tephritidae were not suitable for detailed chromosome studies. He did state, however, that this species appeared to have a haploid number of six, though he presented no figures. Keuneke (1924), on the other hand, obtained clear metaphase complements from *Tephritis arnicæ* L., which had an interesting XO instead of the normal XY sex determining mechanism found in most Diptera. This configuration resulted in a diploid number of 11 in the male and 12 in the female. A reduced number of chromosomes has also been reported for *A. ludens* by Emmart (1935). A haploid number of 5 was found in spermatogenesis, though the findings of the present study do not support these observations for this species.

In more recent studies, Frizzi and Springhetti (1953) described the karyotype of the olive fruit fly, *Dacus oleae* Gmel., as having a haploid number of 6. This same modal number of 6, which seems to be common in most higher Diptera (White, 1954), has also been reported for six out of seven species of Queensland Dacinae by Davis (1955). One species had a haploid number of 7. Davis apparently encountered some technical difficulty, as he was unable to observe any details in the morphology of the chromosomes. Mendes (1958), however, was able to find distinct morphological differences in the chromosomes of two species of Brazilian tephritids, *Anastrepha fraterculus* (Wied.) and *Ceratitis capitata* (Wied.), both of which had the characteristic haploid number of 6. His description of the karyotype of *A. fraterculus* is of particular interest in that he found morphologically differentiated sex chromosomes. These distinguishable heterochromosomes were not found in the Mexican population of this species by the author. The importance of these differences will be discussed later.

METHODS

The chromosomes of the following nine species of tephritids were analyzed during the course of this investigation: *Anastrepha ludens* (Loew); *A. zuelaniae* Stone; *A. fraterculus* (Wied.); *A. mombin-praeoptans* Seín; *A. distincta* Greene; *A. spatulata* Stone; *A. striata* Schiner; *A. serpentina* (Wied.); and *A. aphelocentema* Stone.

Larvae were reared from field collected fruit which was held in

racks over moist sand in well ventilated wooden boxes. A sample of each collection was reared to the adult stage to confirm preliminary identification. Some species, such as *A. ludens*, *A. mombinpraeoptans*, *A. fraterculus*, and *A. serpentina*, were also reared on a laboratory diet of ground carrots and yeast (Finney, 1956). Eggs of these species were collected from females which were induced to oviposit in wax impregnated cheese cloth shells, formed and pigmented to represent fruit (McPhail and Guiza, 1956). For most cytological investigations only larvae in the prepupal stage were used. Other larval stages had suitable but fewer metaphase plates.

The supraoesophageal and suboesophageal ganglion were used for the evaluation of all karyotypes with the exception of those of *A. spatulata* whose host and larva are not known, though the adult is collected in large numbers at certain times of the year. Adult spermatogonial metaphase plates were therefore used to establish the karyotype of this species. Attempts were made to obtain suitable oögonial metaphase plates, but these were unsuccessful. Larval and adult tissues were dissected out in normal saline (0.75 NaCl) and transferred immediately to a saturated solution of coumarin in distilled water for six to ten minutes following the technique of Sharma and Bal (1953) and Manna (1956). The majority of the species, including those treated statistically, were pretreated in coumarin for seven minutes. Care had to be taken not to exceed ten minutes as chromosomes tended to become condensed and unsuitable for study (Fig. 8). However, the shortening effect of coumarin, if used judiciously, makes it possible to obtain well flattened metaphase plates that show the structural features of the chromosomes distinctly. Without the use of coumarin, chromosomes remained bunched and no structural detail could be observed.

Tissue that had been pretreated in coumarin was then transferred either directly into aceto-orcein (2% orcein in 45% glacial acetic acid) for 30 minutes to one hour, or hydrolyzed in 1N HCl for 30 seconds to one minute at room temperature prior to staining. Hydrolysis improved the over-all qualities of the preparations. Squashes were then made in a drop of aceto-orcein on albuminized slides using coverslips treated with a silicon anti-wetting agent, such as Desicote³, and made permanent following the simple and rapid quick-freeze method of Schultz *et al.* (1949), as modified by Conger and Fairchild (1953).

³Beckman Desicote 18772, Beckman Scientific Instruments Division, Fullerton, California.

Photomicrographs were taken on 35 mm. Adox KB-14 film with the aid of a Micro Ibsa attachment using a Zeiss 90x apochromatic oil immersion objective of NA 1.3 and a Leitz 10x ocular. All films were developed with Neofin blau.⁴ Prints were made on No. 5 Kodabromide paper. Final magnification of all prints used in statistical analysis was 3750x.

Measurements of chromosome lengths were made from photomicrographs after the method of Boyes and Wilkes (1953), as modified by Robertson (1957), on *A. fraterculus*, *A. mombinpraeoptans*, and *A. distincta* whose karyotypes could not be distinguished by visual inspection. All measurements were carried out to the nearest 0.5 mm. and the percent of the total complement length of each chromosome pair calculated. A sine transformation was then made on the resulting percentages to reduce any correlation between the means and their corresponding variances (Snedecor, 1956). An analysis of variance was made on both the longest and the shortest chromosome pairs which were the only chromosomes that could be consistently identified with certainty. There was not sufficient evidence to reject the null hypotheses that in these three species the mean lengths of the long chromosomes are the same or that the mean lengths of the short chromosomes are the same. (Short chromosome: $F=2.28 < F_{.05(2, 69)}=3.13$. Long chromosome: $F=2.51 < F_{.05(2, 69)}=3.13$.) The karyotypes of *A. fraterculus*, *A. mombinpraeoptans*, and *A. distincta* therefore could not be distinguished from one another on the basis of mensural observations.

DESCRIPTION OF KARYOTYPES

The terminology used throughout the following descriptions and discussion of metaphase chromosomes is the same as that outlined by White (1957) except for the terms used to designate the position of the kinetochore or centromere. Major chromosome arms (MCA) were considered only when they were clearly visible in the metaphase plate as a point of flexion or bend in the chromosome. This does not rule out the possibility of missing a short arm that would be visible only in anaphase configuration. Such chromosomes would be considered acrokinetic. A metakinetic chromosome has two major arms with the kinetochore located near the center. Acrokinetic chromosomes have the kinetochore located near the end of the chromosome giving the appearance at metaphase of being one-armed. Dot chromosomes are treated as though acrokinetic, although in future investigations

⁴Neofin blau, Tetenal-Photowerk, Hamburg, Germany.

these may prove to be metakinetically as has been shown in the IV chromosomes of *Drosophila melanogaster* Meigen (Kaufmann, 1934).

The locality and the host fruit from which the karyotype was described is also included in anticipation that future studies may uncover chromosomal polymorphism or sibling species within this genus. Whenever observable sex chromosomes were present, the heterogametic sex was always the male, as is normal for Diptera. This characteristic was checked by studying spermatogonial metaphase plates of adult males.

Anastrepha ludens (Loew)

Figure 1

The diploid number is 12. The MCA number is also 12 in both sexes as all chromosomes are acrokinetic. No secondary constrictions were noted. The male has a small dot Y chromosome about $1/4$ to $1/3$ the length of the rod-shaped X chromosome. Forty-seven metaphase plates were photographed from 16 larvae. A total of over 300 larval brain squashes from various localities were studied but not photographed.

Source of cytological material. Cuernavaca, Morelos, Mexico.

Host plant. Mango (*Mangifera indica* L.).

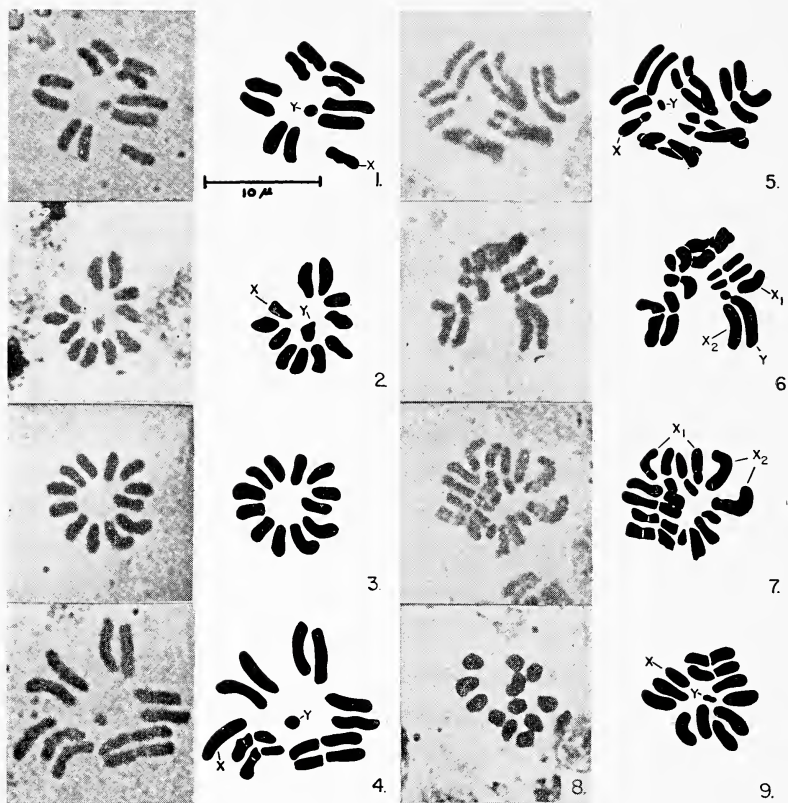
Collections of this species were made throughout the year from many host plants other than mango. These included sapote dominguito (*Mammea americana* L.); avocado (*Persea americana* Mill.); yellow chapote (*Sargentia greggii* S. Wats.); white sapote (*Casimiroa edulis* Llave and Lex.); sweet orange (*Citrus sinensis* (L.) Osbeck); sour orange (*Citrus aurantium* L.); and grapefruit (*Citrus grandis* (L.) Osbeck).

Collections were also made in the states of Colima, Veracruz, Chiapas, Tamaulipas, Jalisco, Mexico, and Michoacan. No variation in the karyotype from these localities was noted.

Anastrepha zuelaniae Stone

Figure 2

The diploid number is 12 in both sexes. The MCA number is 12 with all chromosomes acrokinetic. No secondary constrictions were noted. The male has a rod-shaped Y chromosome about $2/3$ the length of the X chromosome. Thirty-nine metaphase plates were photographed from nine larvae. Sixty-three larval brain squashes were studied but not photographed.



Figs. 1-9. Metaphase plates from the brain of: (1) *Anastrepha ludens*; (2) *A. zuelaniae*; (3) *A. fraterculus* (*A. mombinpraeoptans* and *A. distincta* are closely similar); (4) *A. striata*; (5) *A. aphelocentema*; (6) *A. serpentina* ♂ showing X_1X_2Y sex chromosomes; (7) *A. serpentina* ♀ showing $X_1X_1X_2X_2$ sex chromosomes. (8) Extreme contraction of chromosomes of *A. ludens* resulting from extended pre-treatment in coumarin. (9) Spermatogonial metaphase plate from testes of adult *A. spatulata*. (Magnification of all plates 1500X)

Source of cytological material. Tamazunchale, San Luis Potosi, Mexico.

Host plant. Volador (*Zuelania guidonia* Britt. and Millsp.).

Collections were made from late May to early July 1957. The larvae were found only in the fruit of the above host plant.

Anastrepha fraterculus (Wiedemann)

Figure 3

The karyotype of this species cannot be distinguished from those of *A. mombinpraeoptans* and *A. distincta* at metaphase. The diploid number in both sexes is 12. The MCA number is also 12, with all chromosomes acrokinetic. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed. One hundred twenty-eight metaphase plates were photographed from 32 larvae. Over 250 larval brain squashes were studied but not photographed.

Source of cytological material. Monte Blanco, Veracruz, Mexico.

Host plant. Rose apple (*Eugenia jambos* L.).

Collections were made from early July to late August, 1957.

Anastrepha mombinpraeoptans Seín

cf. Figure 3 (*A. fraterculus*)

The karyotype of this species cannot be distinguished from those of *A. fraterculus* and *A. distincta*. The MCA number in both sexes is 12. No morphologically differentiated heterochromosomes (XY) or secondary constrictions were observed. Forty-six metaphase plates were photographed from 14 larvae. More than 150 larval brain squashes were studied but not photographed.

Source of cytological material. Cocoyoc, Morelos, Mexico.

Host plant. Hog plum (*Spondias mombin* L.).

Collections were made from September through October, 1957. Larvae which were reared from mangoes (*M. indica*) collected from Veracruz from June through July, 1957 were also studied.

Anastrepha distincta Greene

cf. Figure 3 (*A. fraterculus*)

This species cannot be distinguished from either *A. mombinpraeoptans* or *A. fraterculus*. It has an MCA number of 12 in both sexes. No morphologically differentiated heterochromosomes (XY) or sec-

ondary constrictions were observed. Forty metaphase plates were photographed from seven larvae. Over 80 larval brain squashes were studied but not photographed.

Source of cytological material. Cocoyoc, Morelos, Mexico.

Host plant. *Inga inicuil* Cham. & Schlecht.

Collections were made from August through October, 1957.

Anastrepha spatulata Stone

Figure 9

The diploid number is 12 in the male. The MCA number is 14, as one pair of chromosomes is metakinetically. The male has a small rod-shaped Y chromosome about $1/4-1/3$ the length of the X chromosome. Only eight adult males were available for study; three of these gave suitable preparations for analysis. From these, four spermatogonial metaphase plates were obtained. Several photographs were taken of one particularly good metaphase plate that regrettably did not lie in one plane. A drawing made from a composite photograph is therefore presented in Figure 9.

Source of cytological material. Canyon de Lobos, Morelos, Mexico.

Host plant. Unknown.

Adults were collected from January to March 1957 in glass traps, using fermenting brown sugar as a lure (Baker *et al.*, 1944). Each adult was maintained for two weeks in the laboratory on a standard laboratory diet (Rhode, 1957) prior to examination.

Anastrepha striata Schiner

Figure 4

The diploid number is 12 in both sexes. The MCA number is 16. Two pairs of chromosomes are metakinetically. The shorter metakinetically chromosomes have secondary constrictions on their longest arms. The dot Y chromosome is present in the male and is about $1/4$ to $1/3$ the length of the X chromosome. Seventy-one plates were photographed from 20 larvae. Approximately 175 larval brain squashes were studied but not photographed.

Source of cytological material. Tequila, Jalisco, Mexico.

Host plant. Guava (*Psodium guajava* L.).

Collections were made from Tequila during the month of August 1957. Other collections were made from guava in the states of Veracruz, Chiapas, Morelos, and Michoacan in 1956 and 1957 with no variation in chromosome morphology noted.

Anastrepha aphelocentema Stone

Figure 5

The diploid number in both sexes is 12. The MCA number is 22 as there are five pairs of metakinetic autosomes. The dot Y chromosome is about $1/4$ the length of the rod-shaped X chromosome which has a proximal secondary constriction. Twenty-five metaphase plates were photographed from five larvae. Approximately 35 larval brain squashes were studied but not photographed.

Source of cytological material. Tamazunchale, San Luis Potosi, Mexico.

Host plant. Socavite (*Lucuma standleyana* Pittier).

This species was studied only from the area surrounding Tamazunchale during the months May through July, 1957.

Anastrepha serpentina (Wiedemann)

Figures 6 and 7

The diploid number in the male is 11 and in the female 12. The male (Fig. 6) has an MCA number of 20 as there are four metakinetic pairs of autosomes, one of which in some metaphase complements has a secondary constriction on its longest arm (not visible in photomicrograph of the male metaphase plate). There are also three heteromorphic acrokinetic sex chromosomes designated X_1X_2Y . Both the X_1 , which is the shortest, and the X_2 have small proximal secondary constrictions which are not always visible. The long Y chromosome is easily distinguished as it has a short arm separated from the rest of the chromosome by what has been interpreted as the kinetochore, though future studies may show this to be a secondary constriction. The female karyotype (Fig. 7) has an MCA number of 20 with four pairs of metakinetic autosomes and two acrokinetic pairs of sex chromosomes. Since the X_1 is much shorter than the X_2 (X_1 ca. $2/3$ X_2), these two chromosomes are easily differentiated. Thirty-nine metaphase plates were photographed from 13 larvae. Approximately 75 larval brain squashes were studied but not photographed.

Source of cytological material. Monte Blanco, Veracruz, Mexico.

Host plant. Mamey (*Calocarpum mammosum* (L.) Pierre).

Collections were also made from the states of San Luis Potosi and Morelos in 1957. It should be noted here that one collection of this species was made from Tapachula, Chiapas in 1956 from mamey. Samples taken from this population did not demonstrate the com-

pound⁵ sex determining mechanism. The diploid number was 12 and the MCA number was 24. No heteromorphic chromosomes were present. However, the collection was made at the beginning of the study when methods were not yet perfected for making temporary squashes permanent, and before photographic equipment was available. For this reason, only a few drawings were made. This difference in karyotype morphology may have resulted from inadequate technique, but more likely it represents a different species.

DISCUSSION

To date at least 19 species representing 10 genera in the family Tephritidae have been investigated cytologically by several authors. It is apparent even from the few species thus far studied that a great deal of chromosomal variation exists within the family. Such variation not only includes characteristic positions of the kinetochore, secondary constrictions, and chromosome length, but also involves differences in chromosome number and sex determining mechanisms as well. These differences can be put to good use in the identification of immature forms and may possibly aid in establishing phylogenetic relationships. It must be stressed that cytotaxonomy is seldom if ever a "solve all" method of identification, and it is not surprising that three species of *Anastrepha* show no distinct chromosome differences. It is probable that as more species in this genus are investigated chromosome patterns will be found similar to the ones reported here as morphologically distinct. A combination of several criteria, including chromosomal variations, gross morphology of the larvae, and various ecological aspects of the species in question, may therefore be necessary before accurate identification can be made.

With such limitations in mind, the following key is presented as a tentative means of separating the larvae of six of the nine Mexican Tephritidae investigated cytologically so far. Due to the similarities of some female karyotypes, the key is based on the chromosome morphology of the male karyotype whenever it is known. This makes it advisable to study at least eight larvae (assuming a 1:1 sex ratio) in a given collection to be fairly certain that all are not of the same sex. No suitable means has yet been found to determine the sex of immature forms in this family without resorting to karyotype analysis.

⁵Schrader's (1928) terminology is followed here. A compound sex determining mechanism is one in which the X or the Y is represented by more than one element in contrast to a multiple sex determining mechanism in which there is an adherence of chromosomes belonging to different pairs.

*Cytotaxonomic Key to the Metaphase Plates of the Common
Species of Mexican Anastrepha (males only)*

1. All chromosomes evidently acrokinetic (MCA=12) 2
- All chromosomes not all acrokinetic (MCA=13 or more) 4
2. No heteromorphic chromosome pairs present at metaphase
A. mombinpraeoptans, *A. fraterculus*, *A. distincta*
- Heteromorphic chromosome pair present 3
3. Small dot Y chromosome present ($Y < 0.5 X$) *A. ludens*
- Rod-shaped Y chromosome present but shorter than
X chromosome ($Y > 0.5 X$) *A. zuelaniae*
4. MCA=14 to 16 5
- MCA=17 to 22 6
5. MCA=14 *A. spatulata*
- MCA=16 *A. striata*
6. MCA=20, X_1X_2Y sex mechanism present ($2n=11$)
A. serpentina
- MCA=22, secondary constriction on X chromosome
A. aphelocentema

Though cytological evidence *per se* is not always suitable for distinguishing some species of Tephritidae, it can support and elucidate certain phylogenetic relationships within the group. The cytogenetics of certain Diptera has been extensively studied in the past three or four decades so that many of the mechanisms of chromosome evolution in this group are now fairly well understood (Patterson and Stone, 1952; White, 1954; da Cunha, 1960). Since the number of species of Tephritidae so far investigated is extremely limited, it is as yet impossible to determine any conclusive generic or interspecific relationships, though some interesting possibilities do appear, particularly at the interspecific level in the genus *Anastrepha*.

It is possible that *A. mombinpraeoptans*, *A. distincta*, *A. ludens*, *A. zuelaniae*, and the Mexican and Brazilian forms of *A. fraterculus* may form part of a chromosome complex representing a subgenus or species group within the genus *Anastrepha*. This is supported by the similarity in the morphology of the adults of these species. The difference in karyotypes between the Mexican form of *A. fraterculus* reported here and the Brazilian population described by Mendes is interesting since this difference may represent a case of chromosomal polymorphism or, more likely, sibling species. Biological data support the latter (A. C. Baker *et al.*, 1944; E. W. Baker, 1945) in that slight but consistent morphological differences exist in the adults

from these widely separated areas. Such differences could be attributed to geographical variation; however, they also have distinctly different host preferences. The Brazilian population has a wide host range and is a destructive pest of citrus, while the Mexican population is of no economic importance, infesting the rose apple and only occasionally the guava.

The case of the compound sex determining mechanism encountered in *A. serpentina* is also interesting as this type of system appears to be rare in Diptera. Dobzhansky (1935) reported X_1X_2Y system in *Drosophila miranda* Dobzh. believing it to be an example of determinate disjunction. Cooper (1946), however, clearly showed that a X_1YX_2 trivalent was actually formed during meiosis. Boyes (1952) found the same type of trivalent formed in *Hylemya fugax* (Meig.). It is possible that *A. serpentina* may also produce a trivalent, but the preparations of gonadal tissue using the squash technique were not suitable for establishing the interaction of the three sex chromosomes.

The different chromosome number of $2n=10$ reported by Emmart (1935) for *A. ludens* probably resulted from an incorrect interpretation of chromosome morphology in her study of meiosis in pupal and adult testes. In the present study, larvae as well as adults were studied from Cuernavaca, Morelos, the same locality from which Emmart collected most of her material. A diploid number of 12 was always recorded. Meiotic figures in the testes without exception had a characteristic haploid number of 6.

Little can be said about the other *Anastrepha* species at this time. It is likely that a more thorough investigation of the karyotypes within this genus will uncover many interesting phylogenetic relationships which can now only be hinted at on the basis of the present study.

Spermatogonial metaphase plates can be put to good use in evaluating the chromosome morphology of those species of tephritids whose larvae are unknown, as in the case of *A. spatulata*, or whose larvae cannot be readily maintained in the laboratory. Such determinations can also be used to obtain tentative identification of larvae collected for the first time, and whose chromosome morphology is known only from previously captured adults.

From the cytological data thus far accumulated for the family Tephritidae, it appears that the variation between karyotypes is sufficient to warrant more attention from the taxonomists of this group. New methods of handling animal chromosomes, such as the many pre-treatments now available, followed by simplified squash tech-

niques, have eliminated many arguments against inclusion of cytological data in taxonomic studies. Cytological information in many cases offers the taxonomist who is interested in establishing better phylogenetic relationships a tool which can often supplement and strengthen his conclusions based on morphological data, as well as provide information not available by any other means. In the family Tephritidae this seems particularly true.

SUMMARY

The karyotypes of nine species of *Anastrepha* (Tephritidae, Diptera) are described on the basis of mitotic metaphase morphology. The species include *A. ludens*, *A. fraterculus*, *A. distincta*, *A. mombinpraeoptans*, *A. zuelaniae*, *A. spatulata*, *A. striata*, *A. serpentina*, and *A. aphelocentema*. All species have a diploid number of 12, with the exception of the males of *A. serpentina* where an X_1X_2Y sex determining mechanism resulted in a diploid number of 11. Only six of the nine species investigated could be identified on the basis of chromosome morphology. It is suggested that *A. distincta*, *A. mombinpraeoptans*, and Mexican *A. fraterculus*, which have cytologically indistinguishable karyotypes, as well as *A. ludens*, *A. zuelaniae*, and the Brazilian form of *A. fraterculus* may represent part of a chromosome complex within the genus *Anastrepha*. The differences between the karyotypes of the Brazilian and Mexican populations of *A. fraterculus*, along with differences in external morphology and biology, suggest that these two forms may represent sibling species. In general, it is concluded that the metaphase chromosomes of the family Tephritidae can be used for critical cytotoxic and phylogenetic studies.

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REDESCRIPTION OF *LITHOPHOTINA FLOCCOSA* COCK. (MANTEODEA) WITH SOME NOTES ON THE MANTEOD WING VENATION

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Dr. G. M. Byers recently sent to me for study the wing of an insect from the Miocene deposits of Colorado. I determined this wing to be the hind wing of a manteod, close to *Lithophotina floccosa* Cock., which Cockerell described in 1908 from the same deposits. At my request and with the approval of Dr. Hugo Rodeck (University of Colorado Museum) Professor F. M. Carpenter brought the holotype of *L. floccosa* to Moscow with him at the time of his visit to the Paleontological Institute. A study of the holotype led me to the conclusion that the hind wing which Dr. G. M. Byers sent most probably belongs to the same species, i.e. *L. floccosa*. A comparison with the venation of the fore and hind wings of the living manteod *Chaeteesa filata* Burm., which belongs to the primitive relict family Chaeteesidae, confirms this. *L. floccosa* also ought to be referred to this family. Since the description of *L. floccosa* given by Cockerell is very short, and since drawings are lacking and the photograph in the article is poorly reproduced, a redescription of *L. floccosa*, with a description of the hind wing of this species, is given below.

FAMILY CHAETESIDAE

Lithophotina floccosa Cock.

Figure 1

Lithophotina floccosa Cock., 1908, Canad. Ent., 40: 343-344.

The fore wing of this species (Figure 1A) was found in the Miocene deposits of Colorado (Florissant) at Station No. 14. The length of the wing is 21.5 mm, the width 7 mm. The wing is narrowed at the base. Sc is long, taking up more than two-thirds the length of the wing, ending at its widest portion. The branches of Sc close to the base of the wing have the character of cross-veins; in the center, together with the cross-veins which join them, they form a double row of cells; and close to the apex they take on the character of gently curving branches. At the apical portion of the

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wing, R has 4-5 branches in pectinated form, which are directed toward the fore margin. MA at the center of the wing length forms two branches, of which the fore branch divides again close to the apex, and the hind one forms two short branches at the very apex. The vein MP is merged with CuA and its base apparently forms one of the cross-veins. MP + CuA dichotomizes and forms seven branches.

Between R, M and their branches there is a double row of cells. The anal portion in the holotype is missing; evidently it was torn off while the wing was being carried by currents of water before it was buried. The longitudinal and cross-veins are colored with brown pigment.

The hind wing (Figure 1B) was found by G. M. Byers in July of 1953 in the same deposits at the Park County station. The length of the hind wing is 18 mm. The different character of the venation of the fore and hind wings, and also the ratio of the length of the fore wing to the length of the hind wing of *L. floccosa*, is very close to that of *Chaeteessa filata* Burm. (Figure 2), which is the reason for placing the specimen of the hind wing found by G. M. Byers in the same species, i.e. *L. floccosa*.

Sc ends at a distance less than two-thirds of the length of the wing from the base. R has three oblique branches. Rs is simple and does not branch. M is joined with R only at the base of the wing, proximal to the beginning of MP. MA forms three branches in the same sequence as in the fore wing. MP has the character of a cross-vein but is stronger in comparison with the other cross-veins. MP + CuA forms three branches. In the distal portion of the wing between the longitudinal veins there is a double row of cells. Both the longitudinal and the cross-veins are colored with brown pigment.

Although there is no doubt about the closeness of the Manteodea to the Blattodea, the interpretation of the venation of the former, particularly with respect to the hind wing, remains questionable (see Smart, 1956, p. 550). In such cases the study of fossil material is extremely desirable, and the fossil representative of the Manteodea examined here actually permits a simple solution of some debatable questions on the venation of these insects. (See figure 2).

Chopard (1949) and Ragge (1955) find an independent RS in the fore wing of some Manteodea, the nature of which becomes clear upon examination of the fore wing of *Lithophotina*, where R has the same type of pectinated branching as in most Blattodea. In *Chaeteessa*, as Smart (1956) has correctly noted, the remains of these

branches are short oblique veinlets on the end of R. In *Mantis*, *Ameles* and several other Manteodea only two of these branches are preserved, the hind one usually being mistaken for Rs.

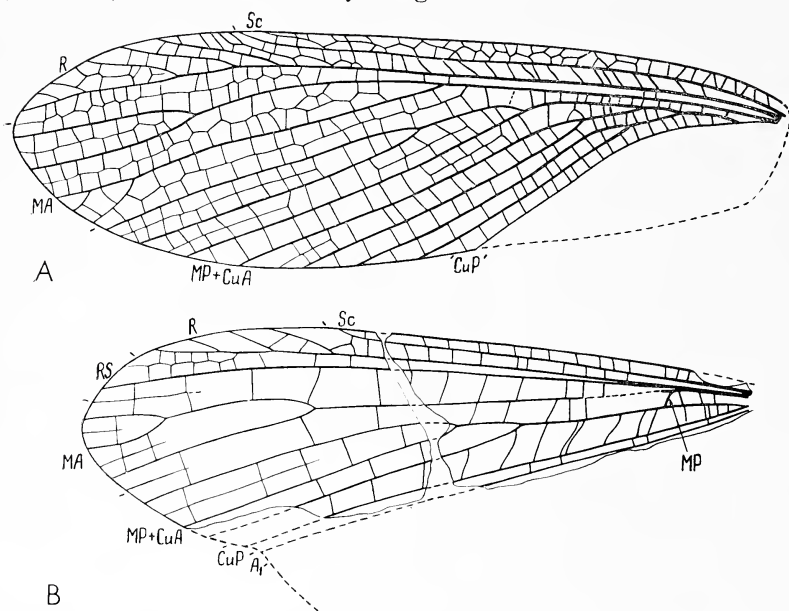


Fig. 1. Drawing of *Lithophotina floccosa* Cock.; A. Holotype (fore wing); B. Homeotype (hind wing).

The stem following R which is mistakenly identified in Blattodea and Manteodea as M, in the opinion of the author, is this only in the proximal portion. Its distal portion together with the branches is really the fore branch of M, i.e. MA, whereas the hind branch, MP, is merged with CuA. Only in some Paleozoic Blattodea (*Archimylacris pruvosti* Laur., *Aphtoroblattina shottoni* Laur.) is the base of MP in the fore wings represented as an oblique vein, which in the rest of the Blattodea and in all known Manteodea is missing or has the character of a cross-vein, just as has occurred in the evolution of the Plecoptera (Sharov, 1960).

The peculiarities of the venation of the hind wing of *L. floccosa* confirm the correctness of the interpretation of R and Rs in the hind wings of the Manteodea proposed by Ragge (1955) on the basis of the study of the tracheation and accepted later by Smart (1956), although with some reservations (p. 550). In *L. floccosa* Rs is separated from M and cannot be considered as the fore branch of M.

Thus, there cannot be any doubt about the fact that, in the hind wings of the Manteodea, the vein which is situated behind R is Rs, which is characteristic also for the hind wings of the Paleozoic and Mesozoic Blattodea.

In the hind wings of the Manteodea a free base of MP, which Smart (1956) designates as the "oblique cross-vein", is preserved. Among the Polyneoptera a similar vein is preserved in the hind wings

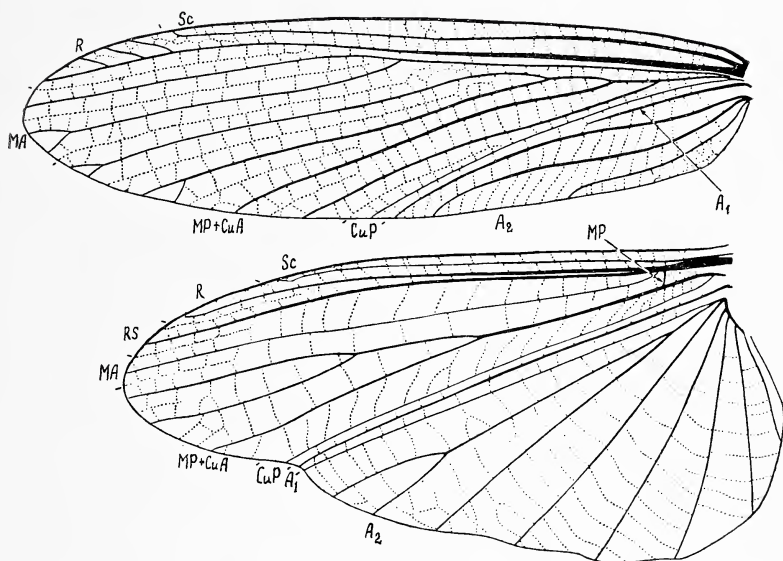


Fig. 2. Drawing of the fore and hind wings of *Chactes filata* Burm. (After Smart, 1956, with changed designations of the veins.)

of Plecoptera and Orthoptera. Its homology with the same vein in the fore wings, in the cases where it is preserved, seems obvious.

ACKNOWLEDGEMENTS

I wish to thank Professor F. M. Carpenter and Dr. Hugo Rodeck (University of Colorado) for giving me the opportunity to study the holotype of *L. floccosa* and for the photographs of this fossil insect, which were used for the preparation of the drawings. I am very grateful also to Dr. G. M. Byers for sending the specimen of the hind wing of this insect.

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THE INFRABUCCAL POCKET OF A FORMICINE ANT: A SOCIAL FILTRATION DEVICE¹

BY T. EISNER AND G. M. HAPP

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The importance of regurgitative feeding as a means for distributing liquid nutrient among workers, and from workers to larvae and queen, has long been recognized, and it is now generally agreed that this process is a most fundamental bond in the social life of many ants (Le Masne, 1953; Wallis, 1961; Wheeler, 1923; Wilson and Eisner, 1957). Unlike honeybees, which also feed one another by regurgitation, but which have their principal food reservoir outside their own bodies in the honeycomb, ants store liquids exclusively within the crops of the individual living workers. Crop storage and regurgitative feeding are probably most highly developed in the specialized and successful subfamilies Formicinae and Dolichoderinae. It is in these ants that the crop is most capacious (witness the fact that ants with "replete" castes are restricted to these subfamilies), and it is these that have a special device, in the form of an elaborately refined proventriculus, adapted to dam the posterior outlet of the distended crop (Eisner, 1957; Eisner and Brown, 1958).

In its basic features, the proventriculus of Dolichoderinae and Formicinae is really no different from that of other ants and of Hymenoptera in general. It is a mechanical pump, consisting of a strongly muscled bulb, with an anterior intake valve communicating with the crop, and a posterior outlet valve leading to the midgut. When nutrient is to be passed from foregut to midgut, the bulb is put into operation, and through a series of rhythmic compressions and decompressions, liquid is effectively pumped along. Whereas in most Hymenoptera the intake valve of the proventriculus is a more or less mobile portal, incapable of effective prolonged closure, and hence ill-adapted to withstand for protracted periods the liquid pressure from a filled crop, in formicine and most dolichoderine ants the portal valve is permanently restricted to a narrow cruciform cleft through which leakage of crop contents is virtually impossible. It is only during proventricular pumping that liquid is passed through the clefts under

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suction pressure from the activated bulb (Eisner, 1957; Eisner and Brown, 1958).

Aside from its obvious advantage in making prolonged crop storage possible, the permanent restriction of the proventricular portal poses a problem. Solid particles passed into the crop have no place to go, since they obviously cannot be pumped through the proventriculus. What, then, happens to indigestible solids that are swallowed? Or are they perhaps not swallowed at all? Ants, as well as many other Hymenoptera, have a so-called infrabuccal chamber, a ventral infolding of the hypopharyngeal surface, that could conceivably act as an effective solid-withholding device, guarding the opening to the crop. Janet (1895a, 1895b, 1905) has described the anatomy of this structure, and has shown that in both ants and wasps, debris gathered while cleaning themselves or their nestmates, as well as solid residue from food ingested, often collects in this pocket and is ejected intermittently as small discrete pellets. His observations were excellent, but left some basic questions unanswered. The present study deals with an experimental evaluation of the function of the infrabuccal pocket of a formicine ant, *Camponotus pennsylvanicus* (DeGeer), in which crop storage and regurgitative food transmission are known to be well-developed social attributes (Plate 6).

Several laboratory-maintained colonies of *Camponotus* were available, but only nestmates, rather than internidally mixed lots, were used for any one series of tests. For experimental purposes they were fed honey mixed with various samples of corundum powder ranging in particle diameter from 10μ to 300μ .

EXPERIMENTS WITH INDIVIDUAL ANTS

An initial series of tests was designed to determine just how effective a filtering device the infrabuccal pocket really is. Individual ants, including only medium-sized workers, were confined in Petri dishes in which they had access to single drops of honey-corundum mixture. Eight corundum samples were tested (10, 20, 30, 80, 100, 150, 200, and 300μ), each on 10-15 ants. The ants were starved for one or more days before the tests, and, when introduced into the dishes, each would promptly commence feeding and remain at the food source uninterrupted for up to several minutes. Only in a few exceptional cases would an ant pause briefly partway through the meal and, after backing away slightly and spreading its mandibles, would regurgitate a small, typically kidney-shaped infrabuccal pellet, consisting of a densely clumped packet of corundum plus small pieces of wood and other

residual matter that the infrabuccal pocket must have contained before the meal. As soon as the ants had gorged themselves and ceased feeding they were drowned and their crops and infrabuccal chambers examined under a microscope for corundum content. The crops were dissected out and mounted intact in clearing medium, while the infrabuccal pockets were induced to discharge their contents simply by pressing the sides of the heads, causing the pockets to be everted. An alternative technique was to examine crops and infrabuccal chambers in intact corpses, after rendering their body cuticle transparent by prolonged immersion in 10% aqueous KOH. The results were clear-cut. Ants fed on the 200 μ and 300 μ samples had no corundum particles in their infrabuccal pockets and none in their crops: particles of such caliber are evidently excluded altogether by the mouthparts themselves, and they never even reach the infrabuccal chamber. Particles of the next smaller size tested (150 μ) did get taken in, but only as far as the infrabuccal pocket, which was invariably packed tightly with them; the crops were always clear. With the remaining samples (10-100 μ) the infrabuccal chambers were also replete with corundum, but a substantial amount of particles had also been swallowed into the crop (Plate 7). Evidently the narrow transverse slit by which food gains entrance to the pharynx just above the infrabuccal chamber is of such aperture as to bar particles larger than 150 μ but not those of 100 μ or less.

An additional experiment supported these findings. A group of ten ants were fed individually on a honey sample as before, but this time the mixture had particles of three sizes (10, 100, and 300 μ). As expected, the crops contained primarily 10 μ -particles, the infrabuccal chambers mainly 100 μ -particles, and the 300 μ -particles were not recovered at all.

It is clear from the preceding that the filtering action of the infrabuccal chamber is far from perfect, at least for particles smaller than 150 μ . Since the capacity of the chamber is limited, and since the individual ant as a rule does not pause to rid itself of an infrabuccal pellet every time the chamber is filled, but continues feeding even after the chamber is full and no longer operative, one is led to believe that in the normal course of food gathering a considerable amount of particulate matter is likely to find its way into the crop of the individual foraging ant. The experiments described next below were designed to establish the fate of such particles, which must obviously be voided in some fashion, or the crop would become solid-bound and the proventriculus obstructed.



EISNER AND HAPP — INFRABUCCAL POCKET

EXPERIMENTS WITH GROUPS OF ANTS

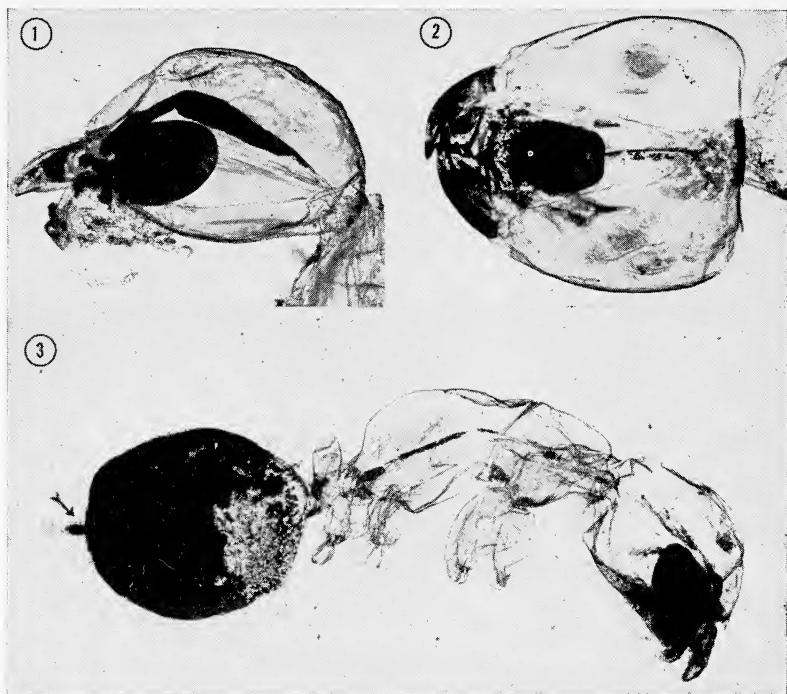
Within the formicine ant society, such evidence as we have suggests that regurgitative food transmission proceeds more or less continually — at least during that part of the year when the colony is active. Judging from the increased number of individual regurgitative exchanges that can be witnessed in laboratory colonies that are given renewed access to food following a period of deprivation, it is clear that the arrival of returning foragers with new crop-loads greatly stimulates the overall rate of intranidal exchange. Actual measurements made with species of *Formica*, fed on food labelled with radioactive tracer, have shown that the crop contents from single foragers may become shared by an entire colony in a matter of hours (Wilson and Eisner, 1957). Although no measurements have been made with *Camponotus*, it is unlikely that the results with this close relative of *Formica* would be much different. Evidently, an incoming crop-load, in the course of being passed from ant to ant, and channelled, as it were, through one infrabuccal chamber after another, could be expected to undergo progressive filtration and ultimately be completely cleared of all debris. The following experiments proved that regurgitative feeding does in fact provide a means by which the communal crop supply is filtered and cleared.

Seven ants, fed to repletion on a honey-10 μ corundum mixture, were each placed in a Petri dish with five unfed nestmates. A color marking differentiated the laden ant from the others. Regurgitative donations took place immediately, at the end of each of which the recipient (previously unfed) worker was removed and killed before it in turn had a chance to donate to others. Dissection of 25 recipients taken in this fashion showed 22 of them to have corundum in their infrabuccal pockets. Thirteen of these had their infrabuccal pockets packed full, and some particles had already passed into their crops.

EXPLANATION OF PLATE 6

Fig. 1. Intact worker of *Camponotus americanus* Mayr, shown next to two individuals whose appendages have been clipped, and whose gasters have been dissected away to expose the digestive tract. Only crop (A), proventriculus (B), and midgut (C) are shown; the entire hindgut has been removed. Notice the enormously distended crop in the freshly-fed forager (center), contrasted with the crop of a starved individual (right). In *Camponotus*, as in many other ants, the crop acts as a social stomach, capable of storing amounts of nutrient far in excess of the demands of the individual forager.

Fig. 2. Regurgitative food exchange between two workers of *Camponotus pennsylvanicus* (DeGeer). This is the process by which the liquid food supply in the crops of incoming foragers is shared with the remainder of the society.



EISNER AND HAPP — INFRABUCCAL POCKET

Fig. 1. Profile view of head of worker of *Camponotus pennsylvanicus* (DeGeer), killed shortly after feeding and cleared in KOH, showing infrabuccal chamber, plus pharynx and portion of oesophagus, densely packed with corundum particles.

Fig. 2. Same as preceding, but of another individual, in dorsal view. The infrabuccal chamber is full, but only few particles are seen in the oesophagus.

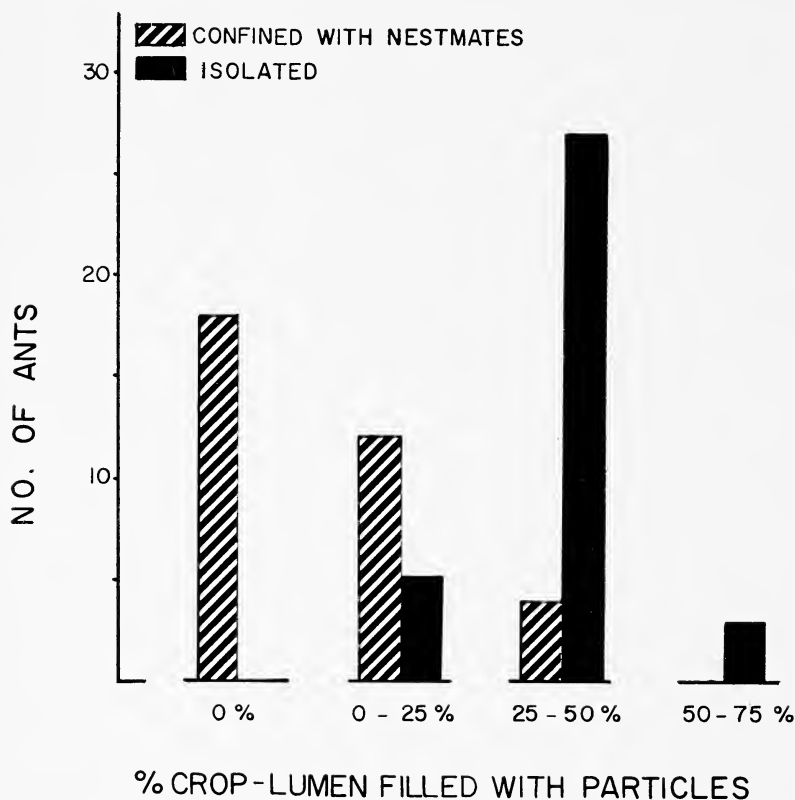
Fig. 3. Worker of *Camponotus pennsylvanicus* (DeGeer), killed shortly after a meal and cleared in KOH, with cuticular shell of gaster dissected away to expose the crop and proventriculus. Notice corundum particles in the infrabuccal chamber, oesophagus, crop, and in the "calyx" (arrow) of the proventriculus.

Another experiment was designed to replicate more closely the crowded conditions prevailing in actual nests. A total of 35 ants, fed on honey-10 μ corundum and provided with color markings, were divided into seven groups of five each, and each group was introduced into an observation arena containing 50-75 unfed nestmates. Another 35 ants, similarly fed, served as controls, and were confined each ant by itself. At the end of twelve hours both lots were killed, and a visual estimate made of the corundum contents of their individual crops (one ant of the first lot escaped). The results (text fig. 1) were strikingly different in the two batches. Of the isolated ants, nearly every one had the crop filled with corundum to one quarter or more of its capacity. Of those that had been confined socially, about half had completely clear crops, and in most of the remainder the crops were less than one-quarter full with particles. Evidently, in the context of the society, debris is rapidly filtered from the communal crop supply. One might add that, whereas in each of the arenas containing the ants in groups there were found at the end of the 12-hour period a dozen or more infrabuccal pellets of corundum, the ants confined singly produced only an occasional single pellet. The pellets recovered in the group-tests stemmed not only from the five introduced food donors, but were actually seen in some cases to have been ejected by residents that had received food by regurgitation. (Ants confined singly over a period of several days sometimes produced more than one pellet. Since during this period they often regurgitated their particle-laden crop contents onto the walls of their glass enclosures, the production of more than one pellet may signify that their crop loads had undergone a series of filtrations as a result of reingestion of the regurgitate. These observations may be of no more than incidental interest, since prolonged lone confinement is obviously not the rule in nature.)

DISCUSSION

The above experiments show the infrabuccal chamber of *Camponotus* to be an organ of considerable social importance, in that it serves to maintain the liquid communal crop supply particle-free. It would be interesting to know whether the chamber is a similarly effective filtering apparatus in other ants. In formicines, and in the more advanced dolichoderines, the proventriculi of which are so constructed as to preclude passage of solids, one would certainly expect this to be so. Since the midgut of these ants is never likely to be exposed to the abrasive action of particulate matter, it is noteworthy that a peritrophic

membrane has been found lacking in those species (including a *Camponotus*) of these two subfamilies that have been examined. The primitive Myrmeciinae, the proventriculi of which have gaping portals through which small particles could presumably pass, do have a membrane (Waterhouse, 1953).



Text fig. 1. Frequency distribution of ants classified according to corundum content of their crops. The ants were fed 12 hours earlier on honey laden with 10μ -corundum powder, and were confined immediately after the meal either in isolation (black bars), or together with groups of unfed nestmates (striped bars). See text for details.

One wonders whether, despite the effectiveness of infrabuccal filtration, enough detritus sometimes remains in the crop to interfere — perhaps only temporarily — with the normal operation of the proventriculus: particles accumulated over the portal clefts might effectively

block the passage of fluid during proventricular pumping. In this connection it is of interest that some formicine proventriculi have a special device that apparently serves to wipe the clefts of obstructing solids (Eisner, 1957). In *Camponotus*, as well as in other formicines with so-called "sepalous" proventriculi, such a device is missing, but since the "calyx" of the proventriculus presumably undergoes rhythmic constriction and dilation during the pumping cycle (the calyx is enveloped by circular muscles), the space within it is likely to be stirred sufficiently to prevent particles from accumulating over the portal clefts on the sepals (Eisner, 1957).

In ants of some of the other subfamilies, the infrabuccal chamber has been shown to serve special functions. Thus, in *Atta* and certain other fungus growers (subfamily Myrmicinae), the chamber provides the receptacle in which a supply of fungal spores is carried from the parent colony by the departing nest-founding female that must ultimately start a new fungus garden of her own (von Ihering, 1898; Huber, 1905). In yet another subfamily, the Pseudomyrmecinae, the larvae are fed with food pellets compacted in the infrabuccal pockets of the workers, which deposit the pellets in a special postoral receptacle (trophothylax) of the larva (Wheeler and Bailey, 1920).

In honeybees, the infrabuccal chamber is apparently inoperative as a filter (Snodgrass, 1956). These insects rely on the intake and digestion of pollen as a protein source for the subsequent manufacture of brood food, and this special requirement can obviously be met only in the absence of thorough preoral filtration. Interestingly, the proventriculus of honeybees is especially adapted to transmit dense pollen suspensions to the midgut without becoming choked (Bailey, 1952).

A representative comparative study of the infrabuccal chamber of Hymenoptera has never been made. In the absence of such a study, it is difficult to speculate on the evolutionary justification for the chamber as it first arose within the order. But since adult Hymenoptera are predominantly fluid feeders, one may reasonably presume that the chamber functioned as a filter from the very outset [its filtering action in at least some wasps has been demonstrated by Duncan (1939) and Janet (1895b)]. To ants like *Camponotus*, as well as to all other formicines and dolichoderines with an intranidal organization heavily dependent on crop storage and regurgitative food transmission, the infrabuccal filter is thus seen to represent an evolutionary preadaptation of considerable importance. In the absence of an adequate preoral filtration mechanism by which the communal crop supply is maintained particle-free, the proventriculus could not have evolved toward pro-

gressive restriction of its aperture, and the crop might never have achieved the extremes of storage capacity that it has in formicines and dolichoderines.

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AUSTRALIAN CARABID BEETLES XI. SOME *TACHYS*¹

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The preceding part of this series (Darlington 1962) dealt with the Australian species of *Bembidion*. The present part deals with some smaller Bembidiini of the genus *Tachys*. Australian *Tachys* have been treated twice by Sloane (1896; 1921), whose papers should be consulted for references and synonymy. I shall now consider only selected groups of the genus about which I have something new to say.

Australian species of *Tachys* are much more numerous and less well known than those of *Bembidion*. They are phylogenetically diverse as well as numerous and include several peculiar groups which may be relict, or specialized. For example *Tachys amplipennis* Macleay has the elytron fully striate with grooved striae and seems to lack the apical stria that characterizes most *Tachys*. However the apex of the 7th stria is deeply impressed, with a puncture beside it on the inner side, and this part of the 7th stria is almost separated from the main part of the stria in some individuals. This condition may be primitive and may show how the apical stria originated. However, some other *Tachys* have the apical stria attached to the 3rd stria (see *Tachys ectromioides* group in the following pages, and also *Tachys yarrens* Blackburn, which will be treated in the next paper of this series).

Species of *Tachys* are numerous, diverse, and frequently collected almost everywhere on the continent of Australia, including Victoria, but are comparatively few in Tasmania. Sloane (1920, 151) records only four, well known Australian species from the island. In four months' collecting on Tasmania I encountered *Tachys* on only three occasions: once in stone and gravel banks and bars of the King River at the crossing of the Queenstown road, where I found *T.* ("*Bembidion*") *hobarti* Blackburn and a related new species; once on the bank of the Mersey River, where I took one *hobarti* by washing gravel; and once beside the Arve River in southern Tasmania, where I found one specimen of *T. australis* Schaum under a stone.

The distribution of *Tachys* in Tasmania and southern Australia

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is complementary to that of the Trechini. The latter are numerous in Tasmania and decrease rapidly northward on the mainland, where *Tachys* increases in numbers. The two groups tend to be complementary ecologically too. Most *Tachys* live beside standing or running water or in swamps, often in open as well as forested country. Most Australian (including Tasmanian) Trechini live on the ground in wet forest but not beside open water. [What I have just said about complementarity of *Tachys* and Trechini is true and important, but an oversimplification. The two groups overlap both geographically and ecologically in ways that are too complex to describe here.]

Tachys hobarti group

In 1921 (p. 193) Sloane mentioned as unknown to him two supposed *Bembidion* described by Blackburn: *hobarti* of Tasmania and *wattsense* of Victoria. I can now say that *hobarti* is a *Tachys*, not a *Bembidion*. The oblique truncation of the outer angle of the anterior tibia is (as Blackburn said) less marked in *hobarti* than usual in *Tachys*, but absence of a scutellar stria and presence of a (modified) apical striae mark the species as *Tachys*. I think that the Victorian *wattsense* may be a synonym of *hobarti*. The former is described as having 5 and the latter 6 dorsal striae on each elytron, but both conditions occur in my series of *hobarti* from the King River. Sloane's *leai* may be the same thing, although I do not want to declare the synonymy without comparing specimens. Sloane's *murrumbidgeensis* is a related species. And 3 additional species that seem to be new, one of them remarkable for reduction of elytral striation, are described below. All these species, and perhaps additional ones still to be discovered, form what may be called the *hobarti* group of *Tachys*. Although they are certainly *Tachys* rather than *Bembidion* by current classification, the species of this group are anomalous (primitive ?) in some ways and should be specially considered by students of bembidiine phylogeny.

Characteristics of the *hobarti* group are: form subparallel (but elytra considerably wider than prothorax), moderately convex; upper surface usually punctulate (scarcely so in *lutus*). Head large (short but wide, with neck very wide and not impressed); eyes of moderate size but rather prominent; antennae rather short, with median segments $2\times$ or less long as wide, and segment 3 usually slightly longer than 2; clypeus truncate or broadly emarginate, impressed at middle anteriorly in some species; mentum not perforated at base, with a simple tooth at middle. Prothorax subcordate, more or less lobed across base,

so that posterior angles are sometimes not quite basal (but I have measured width of base of prothorax across the prominent sub-basal angles); apex subtruncate; lateral margins narrow, each with usual 2 setae; disc with anterior transverse impression obsolete, middle line moderately or lightly impressed but extending posteriorly behind transverse sulcus, and latter variably impressed, sometimes interrupted at middle. *Elytra* with rather prominent but more or less rounded humeri; margins not serrate or faintly so; sutural stria entire and deeply impressed; 5th stria deeply impressed at base (except in *lutus*); 8th stria absent excepting an apparent remnant deeply impressed near apex and including 2 strong punctures; apical striole ending anteriorly in or (usually) reduced to a conspicuous elongate puncture; 3rd interval or stria 3-punctate. Inner wings fully developed. Abdomen sparsely, inconspicuously pubescent; front tibia with outer apical angle less strongly oblique than usual in *Tachys*; posterior tarsi rather short; males with 2 segments each front tarsus widely dilated, and males with 1, females 2 setae each side apex last ventral segment.

The known range of the *hobarti* group is Tasmania and temperate southeastern Australia north to Rockhampton. All the species occur in sand or gravel or under stones by rivers or brooks. Some of the species superficially resemble *Perileptus*, with which they sometimes occur.

Key to species of *Tachys* of *hobarti* group

1. Dorsal striae (except sutural) obliterated *lutus*
 - Stria 5 and usually some other dorsal striae distinct at least in part 2
2. Striae 1 and 5 well impressed but 2-4 light, irregular, sometimes hardly traceable; clypeus not impressed anteriorly; rather shining; size small (length c. 1.8 mm.) *kingi*
 - Striae 2-4 distinct and individually traceable at least behind anterior dorsal puncture, although less impressed than 1 and 5; other characters variable, but none of the following species has all the characters given above for *kingi* 3
3. Black; more shining, with microsculpture less distinct; clypeus not distinctly impressed; length 2.3-2.7 mm. (may include *wattsense* Blackburn and *leai* Sloane) *hobarti*
 - Reddish; less shining, with microsculpture (microreticulation and punctulation) more distinct; clypeus impressed at middle anteriorly 4.

4. Length *c.* 1.75-2.4 mm. *murrumbidgensis*
 - Length *c.* 2.5-2.8 mm. *fitzroyi*

***Tachys lutus* n. sp.**

Figure 1

With characters of *hobarti* group as given above, but dorsal striae (except sutural) obliterated; form (Fig. 1) rather slender but convex; dark reddish piceous, appendages reddish testaceous; shining, virtually without dorsal microsculpture or punctulation. *Head* .89 width pro-

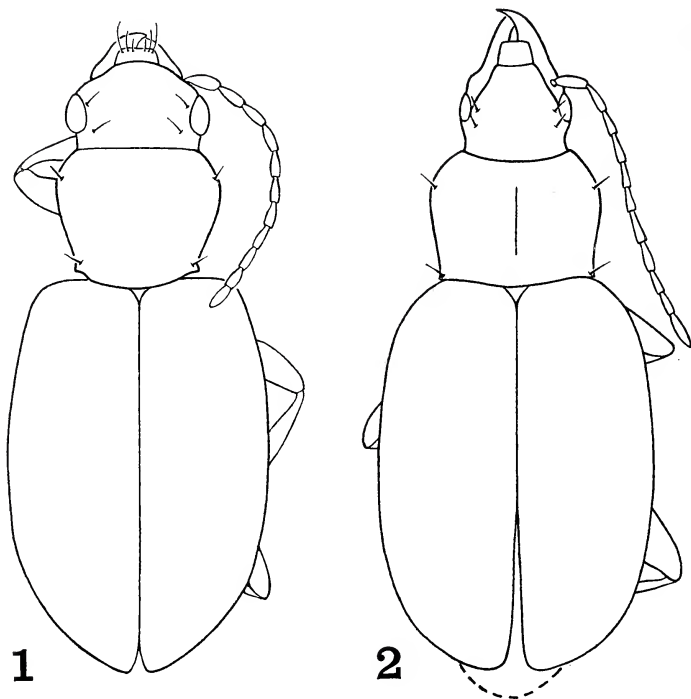


Fig. 1. *Tachys lutus* new species. Fig. 2. *Tachys bolus* new species.

thorax; eyes moderate in size and prominence; antennae with median segments (not counting pubescence) hardly $2\times$ long as wide; clypeus subtruncate (slightly emarginate), not impressed anteriorly; frontal sulci irregularly subparallel, extending onto clypeus; front slightly convex, impunctate except faintly punctulate at $54\times$ in good light; mentum with an entire tooth. *Prothorax* subcordate; width/length 1.21; base/apex *c.* 1.04; base/head .85; sides arcuate anteriorly,

oblique and strongly converging posteriorly, strongly but briefly sinuate before posterior angles; latter forming small, sub-basal, rectangular projections; apex truncate; base subtruncate; disc with anterior transverse impression and middle line almost obsolete but latter coarse basally; sulcus coarsely foveate. *Elytra* more than $\frac{1}{2}$ wider than prothorax (E/P 1.57), probably widest about middle (slightly spread), not margined basally (margin ending a little inside humeri); margins not visibly serrate or setulose (at $54\times$); sutural stria entire, punctate anteriorly, groove-like posteriorly; other dorsal striae obliterated, including 5th, which is at most faintly indicated toward base; apical striole reduced to a coarse slightly elongate puncture on declivity, nearer margin than suture; 3 dorsal punctures on each elytron before anterior $\frac{1}{4}$, near middle, and behind $\frac{3}{4}$. Length c. 2.5; width c. .95 mm.

Holotype (M. C. Z. Type No. 30327) ♀ from Termeil (north of Bateman's Bay and east of the upper Clyde River), southern New South Wales, October 1957, taken by myself. It was actually found northwest of Termeil, well up in the hills, where I followed a system of wood roads nearly to (south of) a conspicuous summit called the Pigeon House. Here, in a small valley of eucalyptus woods, was a small brook, nearly dry but with water still in the pools, which were margined by sand bars. The single specimen of the present species was taken by washing sand at the water's edge.

The obliteration of the elytral striae (except the sutural) makes this a distinct and easily recognizable species.

***Tachys kingi* n. sp.**

With characters of *hobarti* group as described above. Small, moderately elongate, moderately convex; dark rufous, head slightly darker, appendages not much paler; shining, reticulate microsculpture faint above but head and pronotum distinctly, sparsely punctulate. *Head* .86 & .87 width prothorax (in ♂♀ measured); antennae with middle segments not quite $2\times$ long as wide; clypeus truncate, not impressed anteriorly (checked in all specimens); frontal sulci irregularly sub-parallel, reaching and diverging on clypeus. *Prothorax* subcordate, width/length 1.30 & 1.28; base/apex .89 & .93; base/head .81 & .79; sides rounded anteriorly, oblique and strongly converging posteriorly, rather strongly sinuate before angles; latter sub-basal, forming nearly rectangular projections; disc with anterior impression obsolete, middle line lightly impressed, basal sulcus moderate, faintly punctulate, not

foveate unless at intersection of middle line. *Elytra* $1/3$ or more wider than prothorax (E/P 1.34 & 1.44); margins behind humeri faintly subserrate and setulose; sutural striae entire, stria 5 well impressed in about basal half and reaching humerus, stria 2 less impressed, and striae 3 and 4 irregularly and usually rather faintly indicated; apical stria reduced to a conspicuous elongate puncture. Length *c.* 1.8; width *c.* 0.7 mm.

Holotype ♂ (M. C. Z. Type No. 30328) and 10 paratypes all from the King River just below the crossing of the road from Lake St. Clair to Queenstown. The specimens were taken with *hobarti*, under stones, on stone-and-gravel bars.

This species is about the size of typical *T. murrumbidgensis*. I do not have specimens of the latter, but *kingi* evidently differs in having elytral striae 2-4 less distinct, clypeus not impressed, and upper surface more shining.

Tachys hobarti (Blackburn)

Bembidium hobarti Blackburn 1901, 123.

?*Bembidium wattsensae* Blackburn 1901, 123.

?*Tachys leai* Sloane 1896, 358, 370.

A rather elongate, black or blackish species, with characters of *hobarti* group. *Head* .87 & .88 width prothorax; clypeus not or not distinctly impressed anteriorly (checked in all specimens). *Prothorax* subcordate; width/length 1.31 & 1.34, base/apex .93 & .91; base/head .82 & .81; posterior angles right-acute, nearer base than in preceding species but separated from basal lobe by brief, strong sinuations. *Elytra* much wider than prothorax (E/P 1.47 & 1.46); each with 5 or 6 discal striae (stria 6 variable). Length 2.3-2.7; width 0.8-1.0 mm.

This species was described from near Hobart, Tasmania. I rediscovered it at the King River and later found a specimen by the Mersey River, Tasmania, as noted in the preceding general discussion of *Tachys*. If the synonymy suggested above is correct, this species has been found on the mainland of Australia on the bank of the Watts River, a tributary of the Yarra, east of Melbourne, Victoria (*wattsense*), and at Tamworth, New South Wales (*leai*).

Tachys murrumbidgensis Sloane

Sloane 1895, 407.

A small, piceous species, with clypeus impressed anteriorly (noted by

Sloane). Measurements (of types, *t.* Sloane): length 1.75; width 0.75 mm.

Described from 2 specimens from Narrandera, New South Wales, and later (1921, 203) recorded by Sloane from "sand banks and pebble beds" by the margins of the following rivers, all in New South Wales: Murray (at Mulwala), Murrumbidgee (at Narrandera), Cudgegong (at Mudgee), and Macquarie (at Narromine).

Tachys fitzroyi n. sp.

With characters of *hobarti* group as described above. Larger and slightly broader than most species of group; dark rufous, appendages not much paler; not very shining, reticulate microsculpture distinct above but not deeply impressed, and whole upper surface sparsely punctulate. *Head* .91 & .90 width prothorax; clypeus subtruncate or slightly emarginate, impressed at middle anteriorly so that it is sub-tuberculate each side at apex (in all specimens); frontal sulci sub-parallel, diverging posteriorly, extending across clypeus as sharply defined parallel grooves. *Prothorax* broadly subcordate; width/length 1.33 & 1.37, base/apex .85 & .85, base/head .75 & .78; sides rather broadly rounded for much of length, strongly converging posteriorly, abruptly sinuate before posterior angles; latter sub-basal, forming rather small *c.* rectangular prominences; disc with middle line distinct, basal sulcus moderate, not foveate but vaguely punctulate. *Elytra* about 3/10 wider than prothorax (E/P 1.32 & 1.29); margin behind humeri finely scalloped and setulose; sutural striae entire, stria 2 nearly entire but less impressed, stria 5 strongly impressed basally to humerus, striae 3-4 light and slightly irregular but plainly traceable except less distinct at extreme base, striae 6-7 at most faintly indicated; apparent apical striole present but irregularly impressed, ending anteriorly in a coarse impression; 3rd stria 3-punctate, anterior puncture before $\frac{1}{4}$ of elytral length and almost joining 3rd to 4th stria, other punctures near middle and behind $\frac{3}{4}$ of elytral length. Length 2.5-2.8; width *c.* 0.9-1.1 mm.

Holotype ♂ (M. C. Z. Type No. 30329) and 22 paratypes all from the Fitzroy River a few miles north of Rockhampton, Queensland, November 1957, taken by myself. They were in gravel and cobble stone river bars and occurred with *Perileptus*, which they resembled superficially.

This is probably the supposed large form of *Tachys murrumbidgeis* referred to by Sloane (1921, 203) as occurring with the smaller

typical form at Narromine. I have two reasons for considering it a distinct species. First, the size range given by Sloane (*loc. cit.*) for *murrumbidgeensis* (1.75-2.75 mm.) is greater than expected in a population of one species. And second, my series from the Fitzroy River includes only the large form, which apparently therefore exists separately.

Tachys ectromioides group

Tachys ectromioides Sloane is a very distinct, large, rare species. The reason for its rarity is probably its habitat. It, like the related species described below, probably lives in debris, loose soil, or rotten wood on the ground in heavy, damp woods, not associated with surface water. This is a habitat where (in southern Australia) one expects to find "*Trechus*" rather than *Tachys*, and in fact I mistook *Tachys bolus* for a trechine when I collected it. Small Carabidae in this habitat are rarely found by ordinary collecting methods. They can be taken by sifting, but this is laborious and must be done persistently in just the right place in order to get specimens. They can be taken more easily and in greater numbers by shoveling debris and loose soil into quiet water and catching the insects as they come to the surface. I have not found *T. ectromioides* itself, but I have collected series of 2 new related species by this method. The 3 species concerned may be considered to form the *Tachys ectromioides* group.

Important characters of the *Tachys ectromioides* group are: form broad with base of prothorax broad; color variable; upper surface not punctulate (but with reticulate microsculpture). *Head* rather long; frontal sulci not extending onto clypeus but produced posteriorly and vaguely joining depressed areas behind eyes, so latter on poorly defined ocular hemispheres; antennae varying in length, segment 3 not or slightly longer than 2; mentum with 2 deep impressions at base (but not perforated) and with entire median tooth. *Prothorax* with posterior angles costate. *Elytra* with humeri broadly rounded; margins ending inwardly about opposite ends 6th striae, not serrate or setulose; striation entire or nearly so but lightly impressed laterally and apically; 8th stria parallel to margin, deep posteriorly, lighter or irregular anteriorly; apical striole well impressed, long, approaching or joining end of 3rd stria anteriorly, with a fixed puncture on inner side well back; dorsal punctures present or absent, if present, 2 on each 3rd interval. Inner wings long and folded, probably fit for flight in *bolus*, perhaps not in *bolellus*. Lower surface almost impunctate, not (or at

most very inconspicuously) pubescent. Male with 2 segments each front tarsus slightly dilated, inconspicuously squamulose; ♂ with 1, ♀ 2 setae each side last ventral segment.

Key to species of *Tachys ectromioides* group

1. Elytra fasciate, brown on testaceous; dorsal elytral punctures present, though small; length *c.* 3 mm. *ectromioides*
- Elytra unicolorous; dorsal elytral punctures absent 2
2. Bicolored, head and prothorax rufous, elytra castaneous; length 3.2-3.6 mm. *bolus*
- Color wholly castaneous; length 2.6-2.8 mm. *bolellus*

Tachys ectromioides Sloane

Sloane 1896, 356, 359; 1898, 477; 1921, 195 (prothorax), 198, 204.

Sloane described this species as with "... elytra testaceous, a very wide dark piceous fascia across disc considerably behind base, apex widely piceous ..." and "... third elytral interval with two small setigerous punctures — the anterior just before, the posterior just behind discoidal piceous fascia ..." The type of the species (now in the Macleay Museum at Sydney) was said to be from Donnybrook, Western Australia, but Sloane later (1898) suggested that this was probably an error. The species has been found at the Richmond River, northern New South Wales (Sloane 1898); on the Blue Mts., New South Wales; and near Melbourne, Victoria (Sloane 1921, 204). I have not collected it but have briefly examined a specimen at the British Museum, unfortunately without looking for the dorsal elytral punctures. The possible habitat of the species is suggested in discussion of the group.

***Tachys bolus* n. sp.**

Figure 2

With characters of *Tachys ectromioides* group as here defined; form as figured (Fig. 2). Head and prothorax rufous, former darker posteriorly and at sides, elytra dark reddish castaneous, appendages rufous; moderately shining but with distinct microsculpture isodiametric on front, isodiametric or slightly transverse on pronotum, present as very fine transverse lines on elytra, which are vaguely iridescent. Head .66 & .65 width prothorax; antennae rather long, middle seg-

ments *c.* $3 \times$ long as wide; palpi slender, last segments rather long (in genus) but slender, subulate. *Prothorax* strongly narrowed anteriorly, slightly so posteriorly; width/length 1.32 & 1.33; base/apex *c.* 1.58 & 1.47; base/head 1.38 & 1.37; apex subtruncate, slightly lobed at middle; base subtruncate, broadly and slightly lobed at middle; sides broadly arcuate through much of length, broadly but rather slightly sinuate posteriorly; posterior angles *c.* right, well defined, costate; lateral margins moderate anteriorly, slightly broader posteriorly, each with usual 2 setae about $2/5$ from apex and near basal angle; anterior transverse impression of disc broad, not sharply defined; middle line rather coarse and well impressed, coarser basally and reaching base; basal sulcus distinct but not foveate, interrupted at middle by longitudinal impression; baso/lateral areas broadly depressed. *Elytra* broad (E/P 1.59 & 1.61), somewhat rounded at sides, widest about middle; striae moderately impressed, slightly, irregularly punctulate; dorsal punctures lacking. Length 3.2-3.6; width 1.3-1.6 mm.

Holotype ♂ (M. C. Z. Type No. 30332) and 19 paratypes all from Bellangry Forest, northwest of Wauchope, New South Wales, about 3000 ft. altitude, April 1958, taken by myself. Also one specimen, not a type, from Barrington Tops, Mount Royal Range, about 4000 ft., October 1957, also taken by myself. All specimens were taken among lumps of dirt and in loose soil in damp situations. The first one at Bellangry Forest was washed from dirt and leaf litter from the ground in wet forest. After finding it, I searched for additional specimens without success until I started kicking the actual broken earth bank of a small brook into the water. Then the series here recorded was collected without much trouble. The Barrington Tops individual was taken among lumps of earth beside a seepage near the top of the road that led up from the Allyn River toward (but at that time not quite to) the plateau.

This species was very *Trechus*-like in life. It is somewhat *Trechus*-like even under the microscope, although its technical characters (subulate palpi, elytral striation, etc.) leave no doubt that it is a *Tachys*. It is evidently related to *ectromioides*, but differs as indicated in the key. The absence of dorsal elytral punctures in this and the following species is unexpected, but I have examined all specimens of both the present and following species at about $100\times$ under fluorescent illumination, which reduces surface reflection and makes minute details clear, and have not found any trace of dorsal punctures in any specimen.

***Tachys bolellus* n. sp.**

With characters of *ectromioides* group as here defined. Color dark reddish castaneous, appendages rufous; rather shining, reticulate microsculpture of upper surface isodiametric on front, finer and strongly transverse on disc of pronotum but isodiametric and in part actually longitudinal in anterior-median area of pronotum, scarcely resolved on elytra but probably present as very fine transverse lines, for elytra slightly iridescent. *Head* .68 & .64 width prothorax; antennae relatively short, middle segments *c.* $1\frac{1}{2}\times$ or slightly more long as wide. *Prothorax* strongly narrowed anteriorly, much less so posteriorly; width/length 1.29 & 1.39; base/apex 1.46 & 1.43; base/head 1.27 & 1.34; apex subtruncate or very broadly emarginate; base subtruncate, very slightly lobed at middle; sides rather broadly arcuate anteriorly, nearly straight and moderately converging posteriorly, slightly or scarcely sinuate before base; lateral margins moderate anteriorly, slightly broader posteriorly, each with usual 2 setae at apical $2/5$ and basal angle; basal angles slightly obtuse (nearly right), sharply defined, costate; disc with rather vague anterior transverse impression, strongly impressed middle line, broader basally, and reaching base; basal sulcus well impressed, interrupted at middle; baso-lateral impressions rather large, deep, margined posteriorly, and margined exteriorly by strong costae. *Elytra* broad (E/P 1.49 & 1.48), oval, widest near or slightly behind middle; all striae indicated, but outer ones faint or almost obsolete; dorsal punctures lacking. Length 2.6-2.8; width 1.1-1.2 mm.

Holotype ♂ (M. C. Z. Type No. 30333) and 8 paratypes all from the Williams River Valley a little above Barrington House, at the foot of the Mount Royal Range, New South Wales, October 1957, taken by myself. All the specimens were taken by washing wood-debris from a rotten log lying on the ground in heavy gallery forest near the river.

The present new species is sufficiently distinguished from *bolus* and *ectromioides* in the preceding key.

(Some additional *Tachys* will be treated in the next number of this series.)

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THE SPIDER GENUS *SOSIPPUS* IN NORTH AMERICA,
MEXICO, AND CENTRAL AMERICA
(ARANEAE, LYCOSIDAE)¹

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Introduction. The genus *Sosippus* contains the only spiders in the Nearctic Region of the subfamily Hippasinae, members of which are unique among the Lycosidae in producing a large funnel-web resembling that of the Agelenidae. The posterior spinnerets are more elongate than in other Lycosidae, concomitant with their web building habits. Although similar to the Agelenidae in these respects, they represent typical Lycosidae in other characters. In *Sosippus* the eyes are arranged in three rows: four small eyes on a vertical front form the anterior row; two large posterior median eyes form the second row, and two somewhat smaller posterior lateral eyes form a third row. The trochanters are notched and the egg case is carried attached to the spinnerets. These features are characteristic of all Lycosidae, but are not found in the Agelenidae. The tarsi and metatarsi of leg I and leg II are more densely scopulate in *Sosippus* than in most other lycosids. *Sosippus* is found in tropical and subtropical America from Costa Rica to the southern United States.

Porrina, found in South America, appears to be the closest relative of *Sosippus*. Females of *P. diversa* (O. P.-Cambridge) and the male holotype of *P. harknessi* Chamberlin resemble *Sosippus* in coloration and especially in external genitalia (Figs. 12, 33), but are readily separated by differences in the eye arrangement (Fig. 11). The Hippasinae of the Neotropical Region, in addition to eight described species of *Porrina*, are represented by two species of *Birabenia* and the monotypic genus *Hippasella*. C. F. Roewer (1959) splits *Porrina* into three genera on the basis of the number of posterior cheliceral teeth and slight differences in the eye arrangement. On the basis of great variation of these characters in *Sosippus*, it seems best to maintain the eight species in question in the single genus *Porrina* until further study.

In the Ethiopian, Oriental, and Australian Regions the Hippasinae are represented by 12 genera containing numerous species according to C. F. Roewer (1959). These Lycosidae have in common one feature

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that separates them from other lycosids, namely, the greater length of the posterior pair of spinnerets. If the greater length of the spinnerets is concomitant with web-spinning habits, then it would seem that this assemblage might constitute a natural group deserving subfamilial rank. If, however, the length of the spinnerets does not indicate a web-spinning function, but is simply a structural convergence found in otherwise diverse groups, it should not be used as a criterion to establish a subfamily. It may be that some species of *Euprosthenoops* placed in the Pisauridae also belong to this group since the genitalia are similar to those of Lycosidae and the eye arrangement resembles that of *Porrina*.

Acknowledgements. This investigation was carried out as a graduate research program under the direction of Dr. H. W. Levi of the Museum of Comparative Zoology to whom I am especially indebted for encouragement, helpful advice, and constructive criticism. I thank sincerely Dr. W. J. Gertsch of the American Museum of Natural History, who placed the collections of his institution at my disposal. I thank also Dr. H. K. Wallace of the University of Florida for making large collections from Florida available for study. Measurement of Wallace's specimens was not undertaken because the paper was near completion at the time of their arrival. Study of these specimens elucidates certain facts that I will stress, and supports the conclusions already reached before their arrival. Locality data was utilized and certain structural features were checked. Mr. J. A. Beatty provided a number of specimens from Arizona and Sonora and supplied ecological data for *S. californicus*. I am grateful to Dr. G. Owen Evans and to Mr. D. Clark of the British Museum, Natural History, for loan of the male of *S. mexicanus*. Collections in the field during the summer of 1961 were made possible by a grant from the Sigma Xi-RESA Research Fund. A National Institutes of Health Grant (E-1944) helped defray some of the expenses.

Sosippus Simon

Sosippus Simon, 1888, Ann. Soc. Ent. France, 8(6): 206.

Types species: The problem of the type species has been discussed by Bonnet (1958). I follow him for the sake of nomenclatural stability. Simon (1888) established the genus *Sosippus* and designated *Dolomedes oblongus* C. L. Koch as the type. At the same time he described *Sosippus mexicanus* as a new species. In 1898 Simon transferred *D. oblongus* to the genus *Lycosa* (*Diapontia*) and established

S. mexicanus as the type species. *Sosippus mexicanus* has been assumed to be the type for the last 64 years.

Characteristics. Anterior eye row, as seen from in front, procurved. Lateral eyes subequal to the median eyes and mounted on distinct tubercles. Anterior eye row wider than the middle row; the posterior row wider than the anterior row (Fig. 10). Chelicerae robust, with prominent bosses. Anterior cheliceral margin with three teeth on each side. Posterior cheliceral margin with three or four cheliceral teeth on each side, rarely five. Usually constant within a species, but sometimes variable, e. g. *S. mimus*. Labium longer than wide, as long as wide, or slightly wider than long. Endites, heavily scopulate, slightly converging in front of labium, less heavily scopulate. Carapace with conspicuous longitudinal thoracic groove. Carapace of females highest in the cephalic region, of males usually highest in the thoracic region. Sternum always longer than wide. Fourth leg longest. Patella-tibia IV longer than metatarsus (except in males of *S. californicus*, which have the metatarsus longer). Order of length of patellae and tibiae: IV, I, II, III. Tarsi and metatarsi of legs I and II heavily scopulate. Tibia I and II usually scopulate at distal ends. Males with legs longer than those of females and more heavily scopulate.

Female epigynum characterized by a relatively narrow anterior median septum connected to an expansive posterior blade (Fig. 19). Male palpi with numerous sclerites (Fig. 36).

The variable nature of certain morphological characters is emphasized because some earlier authors considered such characters to be diagnostic for the genus. Some are diagnostic at the species level.

Discussion. Spiders of the genus *Sosippus* represent a closely related group of species as evidenced by their structural similarity and web-spinning habits. It is probable that the group has diverged relatively recently in geologic time. Two species groups might be established on the basis of structural similarities and distribution. One group contains *S. floridanus*, *S. mimus*, and *S. texanus*. The other group includes *S. californicus*, *S. mexicanus*, *S. agalenoides*, *S. michoacanus* and *S. plutonus*. The illustrations of the color patterns and the drawings of the genitalia indicate the affinities within these two species groups.

C. F. Roewer, first in the Katalog der Araneae (1954) without giving reasons, and then in 1959 attempted to separate *Sosippus* into two groups, giving each generic rank. This division is based entirely upon the number of teeth on the posterior cheliceral margin. Species with four cheliceral teeth on each side were left in *Sosippus* and those with three on each side were placed in the newly erected genus *Sosip-*

pinus. The division of the genus on this basis alone becomes untenable since the number of teeth on the posterior cheliceral margin is extremely variable within certain species (*S. mimus*). Similarities in color pattern, eye arrangement, spination, relative length of leg segments, and especially the genitalic characteristics indicate that the eight species considered in this paper should be maintained in a single genus.

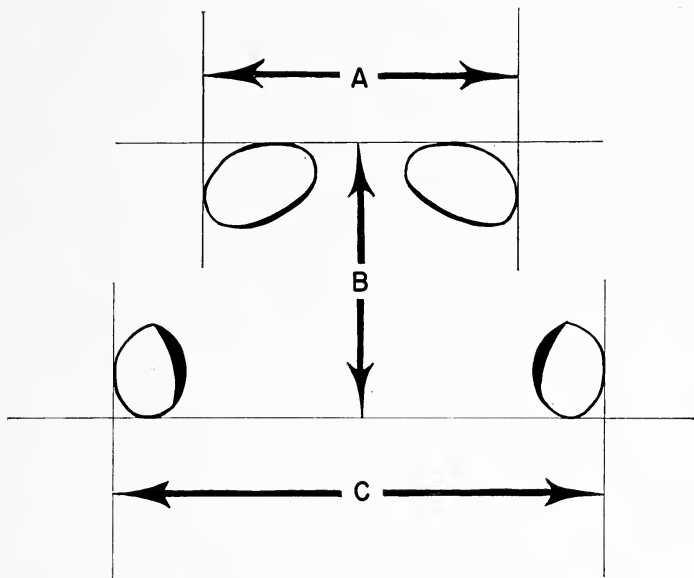
Simon described *S. mexicanus* (type of the genus) as having four posterior cheliceral teeth on each side. F. Pickard-Cambridge (1902) reported that the most abundant species of *Sosippus* in Mexico, which he felt surely was the one described by Simon, had only three cheliceral teeth on each side. Of the two females of *S. mexicanus* examined, one has 4-3 posterior cheliceral teeth. It is very possible that the specimens of *S. mexicanus* that Simon had before him actually had four posterior cheliceral teeth on each side, which, in the case of *mexicanus*, turns out to be the exception rather than the rule. It is also very probable that F. Pickard-Cambridge was describing the same species. Roewer's criterion of the number of posterior teeth of the chelicerae for defining genera is completely artificial in the case of *Sosippus* and probably other lycosid genera as well. J. Buchar (1959) has recently found that the lycosid genus *Trochosa* in Central Europe shows considerable variation within the same species in the number of posterior cheliceral teeth. The similarities among the eight species of *Sosippus* far outweigh any differences that might be used to separate them into two or more genera.

Incorrect Placement. *Sosippus insulanus* Bryant (1923), described from Barbados, is an immature lycosid, evidently at the penultimate stage of development. The coloration, scopulae of the tarsi and metatarsi, and spinnerets are not like those found in *Sosippus*. Although the true identity of this specimen can be ascertained only after association with adult individuals from the same locality, it is best referred to the genus *Lycosa* at the present time.

Measurements. Two sets of oculars with accompanying grids were used in combination with low and high power objectives for making measurements. From measuring a selected set of specimens several times, it was determined that the higher power combination was accurate to 0.02 mm and the lower power combination was accurate to 0.1 mm. In all cases the greatest dimension of the structure was measured, e.g. patella-tibia length was measured as the greatest distance between a line tangent to the most proximal part of the patella to a line tangent to the most distal part of the tibia. Measurements were made under conditions as uniform as possible. Conditions for the most important

measurements are specified below. A series of 20 measurements involving various components of the spider were made for each specimen. The most diagnostic of these measurements are recorded for comparison in Table 1.

The posterior median eyes (PME) and the posterior lateral eyes (PLE), which form two rows in the Lycosidae, are referred to in this



Text Fig. 1. Measurement of the Posterior Ocular Quadrangle.

paper as the *posterior ocular quadrangle* (POQ). The measurement of the POQ is illustrated in Text Figure 1.

The distance A is the width of the anterior row of the POQ, the distance B is the length of the POQ, and the distance C is the width of the posterior row of the POQ. The length of the carapace was measured as the distance from the line tangent to the posterior-most part of the carapace to the line tangent to the anterior-most part of the AME. Total length was measured from the most anterior part of the AME to the tip of the anal tubercle, when this structure was visible, or to the posterior tip of the abdomen. When the specimen was stretched so that the lorum of the pedicle was visible (an abnormal attitude in the living spider), the abdomen was measured and the length of the carapace was added as the distance from the anterior

TABLE 1

MALES:

Species	N	Anterior Eye Row	POSTERIOR OCULAR QUADRANGLE		
			Anterior Row	Posterior Row	Length
<i>S. californicus</i>	22	1.397 ± 0.075	1.190 ± 0.051	1.717 ± 0.069	1.031 ± 0.049
<i>S. mexicanus</i>	1	1.44	1.17	1.80	1.10
<i>S. floridanus</i>	3	1.29	1.12	1.62	1.04
		1.17	1.05	1.52	0.99
		1.24	1.10	1.57	1.04
		1.47	1.22	1.79	1.00
<i>S. mimus</i>	4	1.50	1.25	1.84	1.17
		1.49	1.22	1.84	1.05
		1.50	1.27	1.89	1.14
		1.75	1.45	2.17	1.25
<i>S. texanus</i>	2	1.79	1.42	2.17	1.25

FEMALES:

<i>S. californicus</i>	38	1.615 ± 0.563	1.311 ± 0.129	1.949 ± 0.199	1.171 ± 0.121
<i>S. mexicanus</i>	2	1.35	1.15	1.74	1.05
		1.15	0.99	1.34	0.92
<i>S. agalenooides</i>	4	2.10	1.67	2.59	1.45
		2.00	1.57	2.40	1.42
		2.12	1.65	2.40	1.50
		2.10	1.62	2.45	1.39
<i>S. michoacanus</i>	5	1.64	1.45	2.12	1.25
		1.59	1.39	2.02	1.19
		1.57	1.34	2.00	1.17
		1.54	1.34	1.95	1.19
		1.39	1.24	1.79	1.09
<i>S. plutonus</i>	1	1.34	1.19	1.70	1.07
<i>S. floridanus</i>	16	1.434 ± 0.113	1.238 ± 0.090	1.803 ± 0.146	1.144 ± 0.080
<i>S. mimus</i>	4	1.59	1.30	2.12	1.20
		1.54	1.32	2.00	1.22
		1.37	1.17	1.72	1.04
		1.97	1.49	2.29	1.39
<i>S. texanus</i>	10	1.794 ± 0.313	1.459 ± 0.240	2.218 ± 0.381	1.308 ± 0.185

All measurements are in mm with the mean and standard deviation calculated where 10 or more specimens were available.

TABLE 1 (Continued)

MALES:

Species	CARAPACE		LABIUM		Total Body Length
	Length	Width	Length	Width	
<i>californicus</i>	6.90 ± 0.50	5.01 ± 0.14	1.037 ± 0.065	1.021 ± 0.067	13.92 ± 1.09
<i>mexicanus</i>	6.4	4.6	0.99	0.94	12.0
<i>floridanus</i>	6.3	4.5	0.89	0.84	11.9
	6.0	4.3	0.84	0.75	11.2
	5.8	4.5	0.84	0.78	—
<i>mimus</i>	7.2	5.4	1.07	0.97	13.3
	7.3	4.7	1.12	1.04	13.1
	7.2	5.4	1.15	1.04	14.2
	7.6	5.4	1.14	1.00	14.2
<i>texanus</i>	9.4	6.9	1.40	1.25	20.1
	9.5	7.1	1.40	1.29	18.0

FEMALES:

<i>californicus</i>	7.34 ± 1.01	5.32 ± 0.74	1.165 ± 0.154	1.20 ± 0.157	16.16 ± 2.46
<i>mexicanus</i>	5.7	4.4	0.99	0.94	13.4
	4.7	3.7	0.78	0.78	12.6
<i>agalenoides</i>	9.8	7.4	1.62	1.39	20.1
	9.7	7.4	1.57	1.50	22.9
	10.6	7.9	1.77	1.62	25.0
	10.0	7.2	1.65	1.50	22.2
<i>michoacanus</i>	7.5	5.4	1.29	1.17	15.1
	6.7	5.0	1.14	1.07	13.5
	6.7	4.8	1.15	1.05	13.2
	6.5	4.7	1.10	1.04	14.3
	5.7	4.1	0.99	0.95	11.4
<i>plutonius</i>	6.1	4.3	0.94	0.95	11.8
<i>floridanus</i>	6.44 ± 0.65	4.59 ± 0.51	1.029 ± 0.124	0.988 ± 0.099	13.25 ± 1.63
<i>mimus</i>	7.5	5.5	1.20	1.12	14.6
	7.3	5.2	1.22	1.14	16.1
	5.7	4.3	0.95	0.97	12.9
	8.8	6.2	1.45	1.35	18.2
<i>texanus</i>	8.61 ± 1.84	6.25 ± 1.33	1.434 ± 0.305	1.327 ± 0.232	17.88 ± 3.25

TABLE 1 (Continued)

MALES:

SEGMENTS OF LEG IV

Species	Femur	Patella- Tibia	Metatarsus	Tarsus	Total
<i>S. californicus</i>	8.02 ± 1.96	9.43 ± 2.31	9.95 ± 2.36	3.76 ± 0.79	31.16 ± 2.28
<i>S. mexicanus</i>	7.6	8.8	8.6	3.7	28.7
<i>S. floridanus</i>	6.4	7.4	6.7	3.3	23.8
	6.1	7.1	6.7	3.0	22.9
	6.2	7.5	7.0	3.2	23.9
<i>S. mimus</i>	7.3	8.4	8.0	3.7	27.4
	7.5	9.0	8.5	4.1	29.1
	7.9	9.4	9.2	4.2	30.7
	7.5	9.2	8.7	4.2	28.6
<i>S. texanus</i>	9.5	11.6	11.0	5.7	37.8
	9.6	11.8	11.0	5.5	37.9

FEMALES:

<i>S. californicus</i>	7.65 ± 1.06	8.86 ± 1.16	8.26 ± 1.06	3.31 ± 0.37	28.11 ± 3.55
<i>S. mexicanus</i>	6.0	7.0	6.5	2.6	22.1
	5.5	6.3	5.9	2.3	20.0
<i>S. agalenoidea</i>	9.8	11.2	9.6	2.7	33.3
	9.7	10.9	9.4	—	—
	10.1	11.5	9.7	—	—
	9.6	10.8	9.4	—	—
<i>S. michoacanus</i>	7.0	8.1	7.5	2.9	25.5
	6.5	7.6	6.9	2.8	23.8
	6.5	7.7	7.0	2.9	24.1
	6.3	7.5	6.9	2.9	23.6
	—	—	—	—	—
<i>S. plutonus</i>	5.7	6.7	5.8	2.7	20.9
<i>S. floridanus</i>	5.72 ± 0.63	6.63 ± 0.69	5.83 ± 0.59	2.84 ± 0.96	21.08 ± 2.12
<i>S. mimus</i>	7.0	7.6	6.9	2.9	25.4
	7.0	7.6	6.9	2.9	24.4
	6.0	7.3	6.2	2.8	22.3
	7.4	8.3	7.0	3.6	26.3
<i>S. texanus</i>	7.43 ± 1.62	8.86 ± 1.79	7.30 ± 1.24	3.74 ± 0.75	27.33 ± 5.38

All measurements are in mm with the mean and standard deviation calculated where 10 or more specimens were available.

part of the indentation in the posterior edge to the tangent of the AME, thus allowing for the abdomen over-hanging the carapace. For measurements of the POQ the specimen was placed in a horizontal attitude such that a definite space was visible between the PME and the AME when viewed from above (as in Fig. 3 and not as in Fig. 4). This gives the greatest length to the POQ. The anterior eye row was measured by placing the specimen vertically in such a position that a face view was obtained. The measurement of the AME was again checked in this position. The measurement of leg segments was taken from the prolateral aspect of the anterior pairs of legs and the retrolateral aspect of the posterior pairs of legs for all segments except the femora. The femora of the anterior pairs of legs were measured from the retrolateral aspect and those of the posterior pairs of legs from the prolateral aspect to avoid breaking legs from specimens.

EXPLANATION OF FIGURES

The color descriptions and illustrations of *S. texanus*, *S. floridanus*, and *S. californicus* were based on fresh specimens and represent these species much as they appear in life. The color description and illustration of *S. mimus* (Fig. 3) is based on the holotype, which is in very good condition. *Sosippus michoacanus*, *S. agalenooides*, *S. mexicanus*, *S. mimus* (Fig. 2), and *S. plutonus* were drawn from specimens that have been in alcohol for some time, but have remained in a good state of preservation. The relative condition of these specimens is indicated by the order in which they are listed above. The description and illustration of the type of *S. plutonus* probably deviates more from that of the living spider than any of the rest since hair appears to have been rubbed from the carapace and the abdomen is shrivelled.

Two drawings of the female genitalia were made for each species: a ventral external view of the epigynum after all the hair had been removed (thus revealing some internal structure through the integument), and a dorsal internal view with the genitalia removed and submerged in clove oil for clearing.

Two views of the male palpi were drawn for each species: a ventral view and a retrolateral view. The left palpi of the males were used after gently scraping them free of hair (quite abundant in the living spider) and spines (one or more at the ventral apex and several along the retrolateral edge of the cymbium). These hairs and spines obstruct the palpal sclerites and since the sclerites of the palpi are of much greater diagnostic value, no attempt was made to indicate hirsuteness or spination in the drawings of the male palpi.

SPECIES DESCRIPTIONS

Before analyzing the individual species a few comments should be made concerning the treatment of certain sections.

Structure. Under this heading follows a description of structural features not covered in the table of measurements and not defined specifically under generic characters. Tibial spination is relatively constant for each sex within a given species and there is a basic pattern throughout the genus. Therefore, two tables are constructed showing the typical patterns of tibial spination in *S. californicus* and subsequent species are compared to these.

When the difference between two dimensions is less than 0.05 mm these dimensions are considered *subequal*.

Color. Color descriptions are based on specimens submerged in alcohol and viewed at low power ($10\times$) under a dissecting scope with illumination from a microscope lamp. In fresh alcoholic specimens the color is much the same as in the living spiders. The contrasting light and dark markings, particularly on the carapace and dorsum of the abdomen, are created by light and dark hairs. When these hairs become rubbed off, the underlying color of the integument no longer provides such marked contrast. All of the figures and descriptions are based on specimens with the hairs present. In some cases, of course, this is very difficult because of damage to the specimen.

Records. Locality records for states are listed geographically, counties alphabetically under states, cities and towns alphabetically under counties. The records are for specimens examined except where noted. The lower case "o" is used to indicate a juvenile specimen in the same manner that the normal ♂ and ♀ signs represent a mature specimen. The oo, ♂♂ and ♀♀ signs indicate more than one specimen collected at a single locality.

KEY TO SPECIES

- 1a. Four posterior cheliceral teeth 2
- 1b. Three posterior cheliceral teeth 3
- 2a. Carapace with a distinct white median stripe beginning at second eye row and continuing to posterior edge; and with two broad white submarginal stripes as in Figure 1. Epigynum as in Figures 18-20. Palp as in Figures 40-43. Found in Florida only. *S. floridanus*
- 2b. Carapace without a distinct median white stripe running length of carapace, and without distinct white submarginal stripes. Three yellowish white stripes converging behind second eye row and spreading posteriorly, but continuing for only a short distance, as

- in Figures 2, 3. Epigynum as in Figures 13-17. Palp as in Figures 34, 35. *S. minimus*
- 3a. Without a conspicuous white median stripe running length of carapace and without distinct submarginal white stripes. Pattern as in Figures 2, 3, 4 or 5. 4
- 3b. With a definite median white stripe beginning behind second eye row and continuing to posterior edge of carapace, and with distinct broad white marginal or submarginal stripes. Pattern as in Figures 6, 7, 8, or 9. 6
- 4a. Black in color without distinct lighter markings as in Figure 5. Epigynum as in Figures 25, 26. Found at high elevations in Mexico. *S. plutonus*
- 4b. Dark brown or gray with distinct white markings on carapace and dorsum of abdomen as in Figures 2-4. 5
- 5a. Epigynum as in Figures 21, 22. Palp as in Figures 37-39. Found in southern Texas. *S. texanus*
- 5b. Epigynum as in Figures 13-17. Palp as in Figures 34, 35. Found from eastern Louisiana to southern Florida. *S. minimus*
- 6a. Abdomen with wide median brown stripe bordered by white lines at the anterior end, these lines broken posteriorly as a series of white dashes. No white chevrons crossing the median brown stripe, as in Figure 6. Epigynum as in Figures 23, 24. Palp as in Figures 46, 47. *S. mexicanus*
- 6b. Abdomen with wide median brown stripe with indentations accented by white spots anteriorly and with a series of white chevrons crossing the median stripe posteriorly. 7
- 7a. Epigynum with broad median septum and greatly expanded blade as in Figures 31, 32. *S. michoacanus*
- 7b. Epigynum with relatively narrow median septum and rounded blade as in Figures 27-30. 8
- 8a. Epigynum as in Figures 27, 28. Palp as in Figures 44, 45. *S. californicus*
- 8b. Epigynum as in Figures 29, 30. *S. agalenooides*

Sosippus californicus Simon

Figures 8, 27, 28, 43, 44. Map 1.

Sosippus californicus Simon, 1898, Ann. Soc. Ent. Belgique, 42:25. Female holotype from Lower California in the Paris Museum. Simon, 1898, Histoire naturelle des Araignées, 2(2):323-325, fig. 331 ♀. Banks, 1913, Proc. Acad. Nat. Sci. Philadelphia, 65:182, pl. 9, fig. 13 ♀. Comstock, 1913, The Spider Book, p. 622; 1940, op. cit., rev. ed., p. 639. Bonnet, 1958, Bibliographia Araneorum, 2(4): 4093.

Sosippus pragmaticus Chamberlin, 1924, Proc. Calif. Acad. Sci., 12:674, fig. 117. Female holotype from San Carlos Bay, 8 Jul. 1921 (J. C. Chamberlin) in Museum of California Academy of Sciences. NEW SYNONYMY. *Sosippinus californicus*: Roewer, 1954, Katalog der Araneae, 2:313; 1959, Exploration du Parc National de l'Upemba, Araneae Lycosaeformia II (Lycosidae), p. 1002.

Structure. For comparison of certain diagnostic measurements of *S. californicus* to other species see Table 1.

Posterior cheliceral margin with three teeth on each side. Of 39 females examined, 36 had 3-3 posterior cheliceral teeth, two 3-4; of 23 males, 22 had 3-3 posterior cheliceral teeth. A female and male from Mecatan, Nayarit had 4-4 teeth on the posterior margin of the chelicerae and two immature specimens from Acaponet, Nayarit have the same number.

In the following table the denotation of tibial spines is from proximal to distal end, e.g. 1-2-2 indicates that there is one proximal spine, one pair midway of the tibia, and one distal pair; 1-1 indicates one spine one-third the length of the leg segment from the proximal end and another the same distance from the distal end. Of the 39 female specimens examined 18 had the following tibial spination:

Tibial Spination	Dorsal	Ventral	Prolateral	Retrolateral
Leg I	0	2-2-2	1-1	0
Leg II	0	2-2-2	1-1	0
Leg III	0	2-2-2	1-1	1-1
Leg IV	0	2-2-2	1-1	1-1

Sixteen females differed from the above only in the ventral spination of leg II which was 1-2-2. The five remaining specimens varied in different respects.

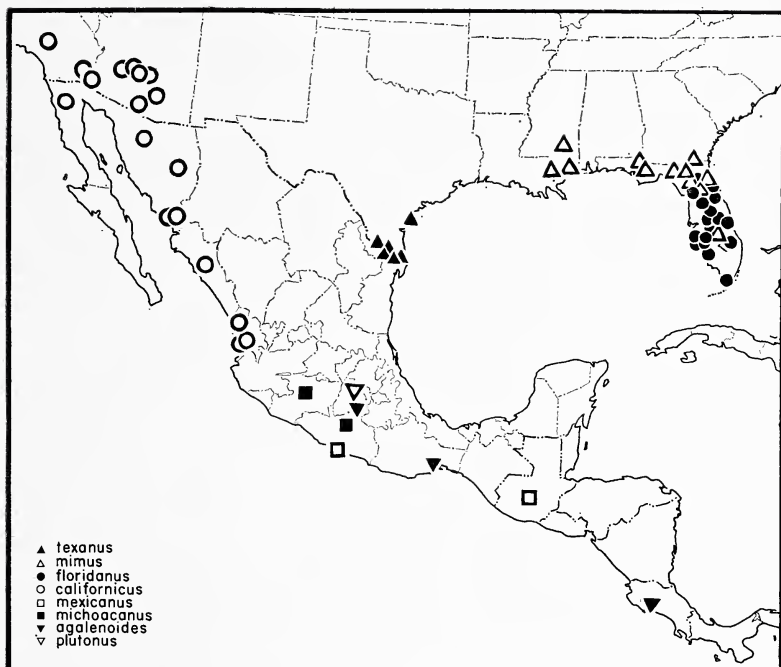
Sixteen of the 23 males examined showed the following arrangement of tibial spines:

Tibial Spination	Dorsal	Ventral	Prolateral	Retrolateral
Leg I	0	2-2-2	1-1	1-1
Leg II	0	2-2-2	1-1	1-1
Leg III	0-1-0	2-2-2	1-1	1-1
Leg IV	0	2-2-2	1-1	1-1

The seven remaining specimens showed variable dorsal spination on leg III and the ventral spination of leg II was 1-2-2 in three specimens, otherwise the spination was constant except for malformities, e. g. regeneration.

On all legs there appear on the dorsal surface of the tibiae, as well

as the metatarsi, and tarsi a series of trichobothria. These are extremely variable on all leg segments. The usual pattern is one or two large proximal trichobothria and then a series of smaller ones decreasing in size distally, although there may be one or two large trichobothria at the distal end of the tibiae. Occasionally the basal trichobothria are spine-like particularly on the tibia of leg III. A spine is distinguished from a trichobothrium by its greater thickness at the base and the



Map. 1. Distribution of *Sosippus* species.

socket within which it articulates. This basal socket leaves a scar whenever the spine is broken off, whereas it is difficult to distinguish an empty socket where a trichobothrium has been broken off.

Of 37 females measured the clypeus height was subequal to the diameter of the AME in 32, in three clypeus height was less than the diameter of the AME, and in two clypeus height was greater than the diameter of the AME. Of 23 males examined the clypeus height

was subequal to the diameter of the AME in 13, and less than the diameter of the AME in ten.

Labium. Of 39 females measured: 26 have length subequal to width, 11 wider than long, and two longer than wide. Of 23 males measured: 19 have length subequal to width, two longer than wide, and two wider than long.

Color. Female. Pattern illustrated in Figure 8. Carapace dark brown with the eye region darkest. Eyes outlined with black. A narrow pale brownish yellow median stripe beginning just behind the second eye row and running the length of the carapace. Broad marginal stripes of the same color. Both the marginal stripes and the median one densely clothed with white hair. Marginal stripes broadening anteriorly and extending to edge of clypeus. Chelicerae dark reddish brown, almost black.

Sternum brownish yellow. Endites darker reddish brown with distal ends brownish yellow. Proximal segments of legs brownish yellow without distinct contrasting markings, metatarsi and tarsi darker brown.

Dorsum of abdomen with a broad dark brown median stripe from base to tip, with two pairs of white spots at lateral indentations of stripe anteriorly, and transverse chevrons clothed with white hair posteriorly. Brownish yellow area adjacent to brown median stripe on each side, thickly clothed with white hair; lateral edges of dorsum darker brown, mottled with tufts of white hair. Venter brownish yellow.

Male. Very similar to the female in coloration.

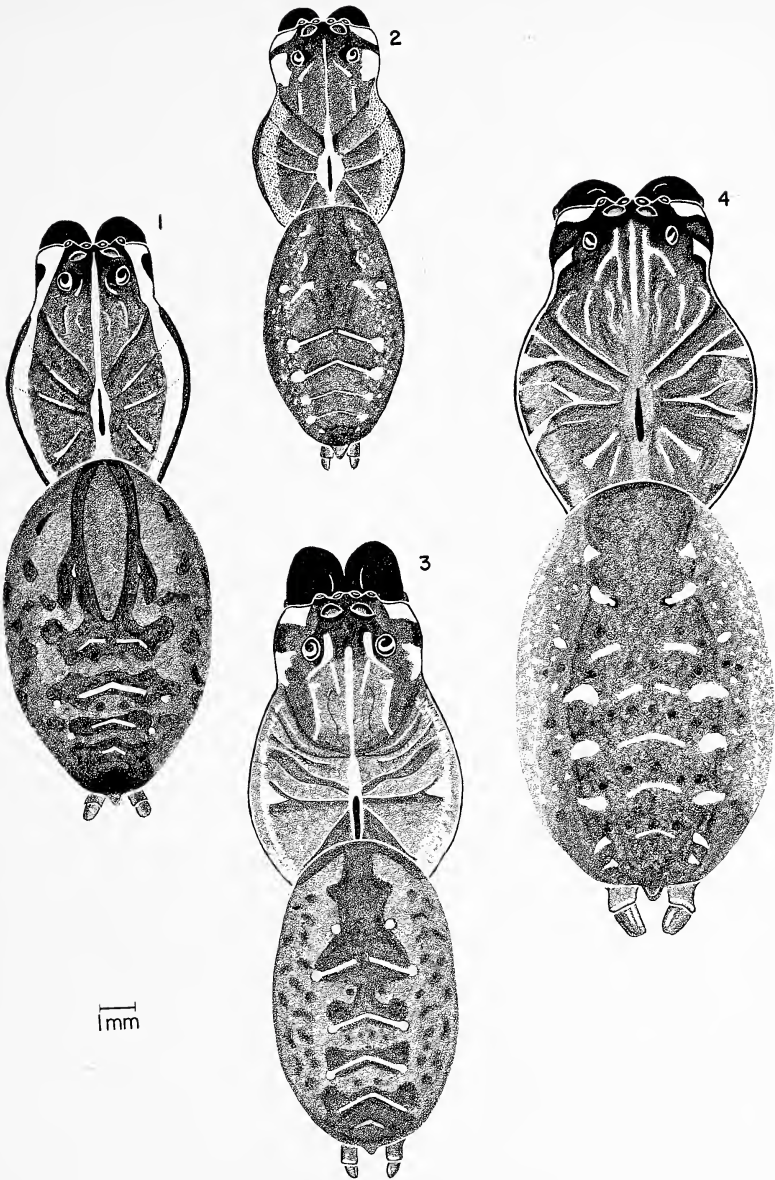
Diagnosis. *Sosippus californicus* resembles *S. agalenoides* and *S. michoacanus* in color pattern. *S. michoacanus* is darker in color, however, and both it and *S. agalenoides* can be separated from *S. californicus* by the form of the epigynum. (compare Figs. 27, 28 with Figs. 29, 30 or 31, 32.) *Sosippus plutonus* is closest to *S. californicus* in the form of the epigynum, but is a very dark, almost black species and smaller than *S. californicus* (compare Fig. 8 with Fig. 5). *Sosippus*

EXPLANATION OF PLATE 8

Fig. 1. *Sosippus floridanus* Simon, ♀ from Highlands Hammock State Park, Highlands Co., Florida, 9 Jun. 1961.

Figs. 2-3. *S. mimus* Chamberlin. 2. Female from Archibold Biological Station, Lake Placid, Highlands Co., Florida, 24 Jan. 1943. 3. Female holotype from Mandeville, Saint Tammany Par., Louisiana, 1 May 1921. Note size of abdomen, due to having recently constructed an egg case.

Fig. 4. *S. texanus* sp. n., ♀ paratype from Goose Island State Park, Aransas Co., Texas, 15 Jun. 1961.



BRADY — GENUS SOSIPPUS

mexicanus is separated from *S. californicus* by the form of the epigynum and by the dorsal color pattern of the abdomen (compare Fig. 8 with Fig. 6).

Natural History. In southern Arizona, according to J. A. Beatty (unpublished, 1961), *S. californicus* is found primarily in riparian woodland formations. These associations occur in or adjacent to drainageways and their floodplains and are characterized by different vegetation than that of the surrounding non-riparian community. This spider occurs at varying elevations depending upon the amount of vegetation and moisture available. In the Santa Catalina Mountains it was collected at about 850 m.

Sosippus californicus constructs expansive webs with a central funnel-shaped retreat leading to the base of vegetation, into crevices, or under rocks. In El Coyote, Sonora it was collected from webs leading under rocks in a dry stream bed at about 1000 m. A female with egg case was collected from beneath a rock in a canyon filled with Palm trees, 26 km east of Magdalena, about 1300 m elevation.

Distribution. Baja California, southern California, Arizona, south to Nayarit (Map 1).

Records. *Baja California.* ♀ holotype. *California.* Imperial Co.: NE corner ♀ (J. Anderson). Los Angeles Co.: Claremont (Baker). *Arizona.* Maricopa Co.: Buckeye, 19 Feb. 1956 o (T. Barry); Mesa, 21 Mar.-23 May oo, 16 Jul.-11 Nov. ♂ ♂ ♀♀ (sev. coll.); Phoenix, 12-23 Feb. 1956 oo (sev. coll.); Santa Cruz River Valley, 9 May 1940 o (R. H. Crandall); Tempe, 14 Feb.-27 Mar., 20 Nov. 1960 oo (sev. coll.). Pima Co.: Baboquivari Mountains, Brown's Canyon, 22 Apr. 1961 oo (J. A. Beatty), 9 Jun. 1952 ♂ ♂ ♀♀ with egg cases (M. Cazier, W. J. Gertsch, R. Schrammel), 4 Sep. 1951 ♀♀ (W. S. Creighton), Rancho El Mirador, 4 Sep. 1950 ♀ (W. J. Gertsch); Santa Catalina Mountains, Sabino Canyon, 10 Apr. 1959, 26 Sep. 1959, 20 Nov. 1960 oo, 26 Jun.-21 Aug. 1960 ♂ ♂ ♀♀ (J. A. Beatty), 6 Jun. 1952 ♂ ♂ (M. Cazier, W. J. Gertsch, R. Schrammel). Yuma Co.: Yuma, 12 Feb. 1961 o (J. A. Beatty). *Sonora.* El Coyote, 28 km E of Rio Bavisbee, 1000 m, 19-24 Jul. 1960 ♀♀ with egg case, 26 km E of Magdalena, 1300 m, 16 Jul. 1960 ♀ (J. A. Beatty); Minas Nuevas, 8 Aug. 1952 ♀ (P., C. Vaurie); Navajoa, 6 Aug. 1956 ♀ (V. Roth & W. J. Gertsch). *Sinaloa.* Culiacán, 19 Jun. 1939 ♂ (A. M., L. I. Davis). *Nayarit.* Acaponeta, 20 Nov. 1939 oo (C. M. Bogert, H. E. Vokes); Mecatan, 23 May 1949 ♂ (G. M. Bradt); San Blas, 6 Aug. 1947 ♀ (C., M. Goodnight, B. Malkin).

Sosippus mexicanus Simon

Figures 6, 23, 24, 46, 47. Map 1.

Sosippus mexicanus Simon, 1888, Ann. Soc. Ent. France, 8(6):206. Female holotype from Mexico in the Paris Museum. Simon, 1898, Histoire naturelle des Araignées, 2(2):325, 327. F. P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, 2:332, p. 31, figs. 30, 31a-c. Banks, 1909, Proc. Acad. Nat. Sci. Philadelphia, 61:217. Bryant, 1948, Psyche, 55(2):55. Roewer, 1954, Katalog der Araneae 2:314. Bonnet, 1958, Bibliographia Araneorum, 2(4):4093. Roewer, 1959, Exploration du Parc National de l'Upemba, Araneae Lycosaeformia II (Lycosidae), p. 1004.

Structure. For comparison of certain diagnostic measurements of *S. mexicanus* to other species see Table 1.

Posterior cheliceral margin with three teeth on each side. Of two females examined one had 3-3 posterior cheliceral teeth, the other 4-3. The male specimen, described by F. Pickard-Cambridge (1902), has 3-3 posterior cheliceral teeth. According to F. P.-Cambridge all the specimens that he examined had 3-3 posterior cheliceral teeth.

Tibial spination in the two females examined was the same as in *S. californicus* with the following exceptions: ventral spines on leg II 1-2-2, dorsal spines on tibia III and IV 1-1. These spines slightly smaller than the lateral spines.

Clypeus height of one female subequal to the diameter of the AME, in the other greater than the diameter of the AME. Clypeus height of the male subequal to the diameter of the AME.

Labium. Length subequal to width in the male and two females.

Color. Female. Pattern illustrated in Figure 6. Carapace brown, darker in the eye region with the eyes circled in black. A thin pale brownish yellow median stripe beginning immediately behind the second eye row and continuing to the posterior edge of the carapace. Broad marginal stripes of the same color starting at the edge of the clypeus and extending the length of the carapace. The marginal stripes, as well as the median stripe, clothed with short white hair. Darker brown lines radiating from the thoracic groove. Chelicerae dark reddish brown.

Sternum brownish yellow. Labium and endites darker reddish brown. Legs brownish yellow without distinct darker markings.

Dorsum of the abdomen with a wide brown median stripe, enclosed by two very light broken lines in the anterior region. Posteriorly the lines are broken-up into a series of dots, the broken lines and dots accented with white hair. Lateral to the light lines and dots the dorsum is brownish yellow mottled with brown. Venter of the abdo-

men with a concentration of white pigment under the integument, overlaid with yellow, producing a cream color.

Male. Median longitudinal stripe of carapace not as distinct as in the female. Dorsum of abdomen with a series of paired white spots outlining wide brown median stripe, otherwise similar to female in coloration.

Diagnosis. This species is similar to *S. agalenoides* in the form of the epigynum. It is separated from *S. agalenoides* most easily on the basis of size in the limited number of specimens examined. *Sosippus mexicanus* does not exceed 15 mm in total body length and *S. agalenoides* is not less than 20 mm. *Sosippus mexicanus* also differs from *S. agalenoides* in the dorsal pattern of the abdomen (compare Fig. 6 to Fig. 9) and tibial spination. *Sosippus agalenoides* is more hairy than *S. mexicanus*, especially on the dorsum of the abdomen. The venter of the abdomen in *S. mexicanus* is characterized by white pigment underlying the integument, which is not found in *S. agalenoides*. If the differences in tibial spination remain consistent upon examination of a larger series of specimens, this will provide an easy method of separation.

Natural History. According to F. Pickard-Cambridge (1902), "The spiders of this genus are very much like *Agelenae*, not only in the shape of their body and the appearance of their legs, but to some extent their markings. Still more do they resemble them in habits, for the web consists of a very large sheet of fine silk spun over the bushes, with a tube-like tunnel running down into some place of safety. Their movements are exceedingly rapid, and one cannot at first sight believe they are not true *Agelenae*."

Distribution. Guerrero to Guatamala.

Records. Guerrero. Acapulco de Juárez, 1 Sep. 1940 ♀♀ (H. E. Frizzell). Guatamala. ♂ (Sarg). N. Banks (1909) reported this species from Costa Rica, but the specimens in question are immature and appear to be *S. agalenoides*, which Banks described from Costa Rica.

Sosippus agalenoides Banks

Figures 9, 29, 30. Map 1.

Sosippus agalenoides Banks, 1909, Acad. Nat. Sci. Philadelphia, 61:217, pl. 6, fig. 33. Three female syntypes and one juvenile from Puntarenas, Costa Rica, in the Museum of Comparative Zoology, examined. Roewer, 1954, Katalog der Araneae, 2:313. Bonnet, 1958, Bibliographia Araneorum, 2(4):4093. Roewer, 1959, Exploration du Parc National de l'Upemba, Araneae Lycosaeformia II (Lycosidae), p. 1004.

Structure. For comparison of certain diagnostic measurements of *S. agalenoides* to other species see Table 1.

Posterior cheliceral margin with three teeth on each side. Of four female and one juvenile specimens examined all have 3-3 posterior cheliceral teeth.

Tibial spination in each of the four females is exactly the same as that shown in the table for *S. californicus*.

Clypeus height is greater than the diameter of the AME in three specimens, in one specimen it is subequal to the diameter of the AME.

Labium longer than wide.

Color. Pattern illustrated in Figure 9. Carapace light orange-brown, darkest in the eye region. A thin median stripe, clothed with white hair, begins slightly in front of the third eye row and continues to the thoracic groove. Broad marginal longitudinal stripes, not as distinct as in *S. californicus*; white hairs along these stripes heaviest laterally just behind the clypeus, more diffuse posterior to this region. The lateral edges of the carapace clothed with fine white hair. Chelicerae dark reddish brown, almost black; boss on each side prominent, with dense white hair surrounding it except at the point of articulation.

Sternum light brownish yellow. Endites and labium darker reddish brown, yellowish at distal ends. Legs light brownish, yellow with metatarsi and trasi darker reddish brown.

Dorsum of the abdomen with a wide brown median stripe beginning at the base and continuing to the spinneretes. The anterior end of this stripe bordered by three white dashlines on each side, and interrupted posteriorly by a series of white chevron markings. These markings clothed with white pubescence. A series of dark brown dots alternate crossing the dorsum with the white chevrons and continue laterally for some distance. Lateral area of abdomen light brownish yellow, venter lighter, almost cream colored.

Diagnosis. *Sosippus agalenoides* is most similar to *S. californicus* in coloration. It is separated from this species by the shape of the epigynum (compare Figs. 29, 30 to Figs. 27, 28). *Sosippus agalenoides* is similar to *S. mexicanus* in the form of the epigynum. It differs from *S. mexicanus* in size and other characters discussed under that species.

Natural History. Banks (1909) does not supply any information concerning the natural history of this species. Presumably it builds the same type of sheet web and tubular retreat as found in *S. californicus*.

Distribution. Morelos, Oaxaca, Costa Rica.

Records. Morelos. Miacatlán, 4 Oct. 1942 o (C. Bolivar).
Oaxaca. Tehauantepec, 15 Dec. 1947 o, 6-10 Feb. 1948 o (T. MacDougall); Cerro del Armadillo, 7 Jan. 1948 ♀ (T. MacDougall).
Costa Rica. Puntarenas, 1909 ♀♀ (P. Biolley).

***Sosippus michoacanus* sp. n.**

Figures 7, 31, 32. Map 1.

Type. Female holotype from Tzararacua Falls, 11 km from Uruapan, Michoacan, Mexico, 14 Jun. 1948 (A. M., L. I. Davis) in the American Museum of Natural History. The species named after the type locality.

Structure. For comparison of certain diagnostic measurements of *S. michoacanus* to other species see Table 1.

Posterior cheliceral margin with three teeth on each side. Of five females examined, all had this arrangement.

Tibial spination was the same as in *S. californicus* with the exception that four specimens had 1-2-2 ventral spines on tibia II.

Clypeus height subequal to the diameter of the AME. Labium longer than wide.

Color. Pattern illustrated in Figure 7. Carapace reddish brown, overlaid with black pubescence giving it a darker appearance. Eye region dark brown, almost black, with eyes encircled with black. Thin median stripe beginning some distance behind the third eye row, continuing to posterior edge of carapace. This stripe not conspicuous, with white hairs sparsely covering it, densest along the thoracic groove. Broad submarginal stripes extending from clypeus to posterior edge of carapace, clothed with white pubescence. Chelicerae very dark reddish brown, almost black, with intermitent, long black hairs. Conspicuous boss on each side, light brown.

Sternum light brown with gray overtones. Endites and labium reddish brown, yellowish at distal ends. Femora brown with dusky

EXPLANATION OF PLATE 9

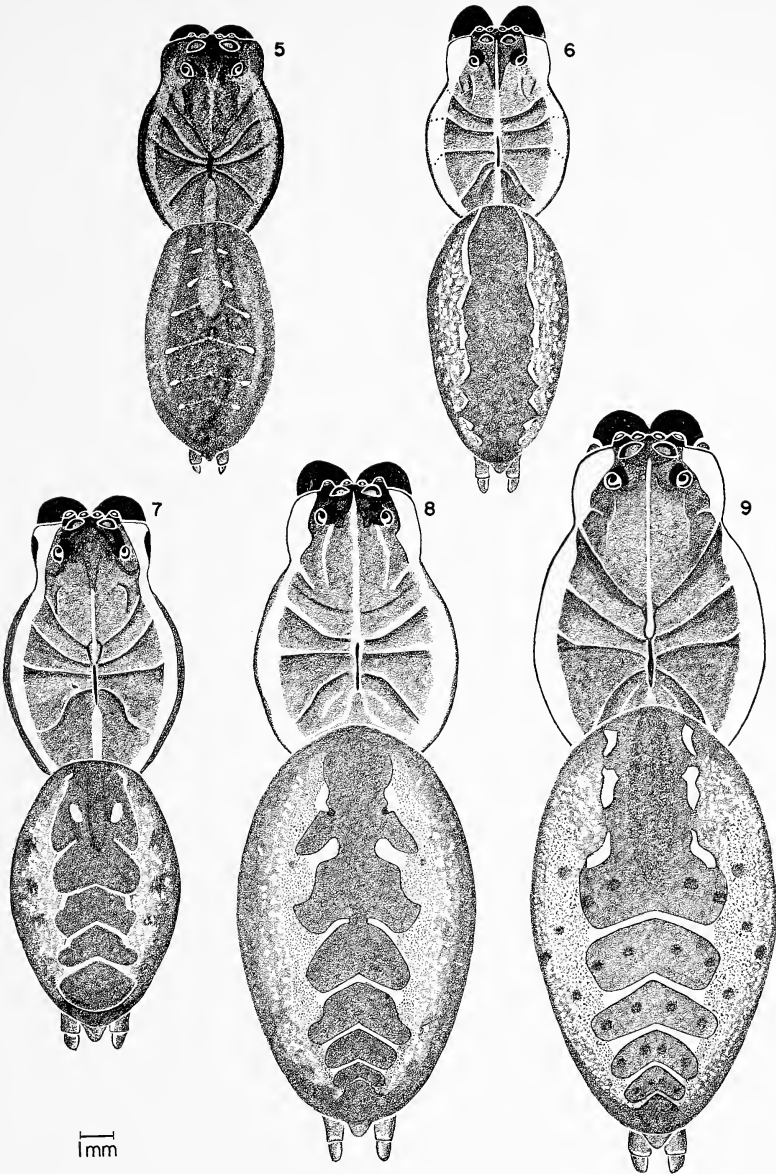
Fig. 5. *Sosippus plutonus* sp. n., ♀ holotype from Tenango del Valle, Mexico, Mexico, 25-26 Aug. 1946.

Fig. 6. *S. mexicanus* Simon, ♀ from Acapulco de Juárez, Guerrero, Mexico, 1 Sep. 1940.

Fig. 7. *S. michoacanus* sp. n., ♀ holotype from Tzararacua Falls, 11 km from Uruapan, Michoacan, Mexico, 14 Jun. 1948.

Fig. 8. *S. californicus* Simon, ♀ from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 Jun. 1952 (pattern and color same as specimens from Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, 26 Jun. 1960).

Fig. 9. *S. agalenooides* Banks, ♀ syntype from Puntarenas, Costa Rica, 1909.



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markings, uniformly gray on ventral surface, but forming bands on the lateral and dorsal surfaces. Patellae and tibiae of same color, but darker markings form more indefinite pattern. Metatarsi and tarsi yellowish brown, without dusky markings.

Dorsum of abdomen with basal lanceolate reddish brown mark, enclosed by typical wide dark brown stripe heavily pigmented with black. Dark brown median stripe bordered by lighter brown area, with lateral regions again becoming dark brown. Venter light yellowish brown.

Diagnosis. *Sosippus michoacanus* has an abdominal pattern similar to *S. californicus*. It is much darker in color than *S. californicus* and is readily recognized by the female epigynum, which has a wide median septum and greatly expanded blade (Fig. 32).

Natural History. No information concerning the habits is available. It presumably constructs a funnel-web like that of *S. californicus*.

Distribution. Michoacan and Guerrero.

Records. *Michoacan.* Tzararacua Falls, 11 km from Uruapan, 14 Jun. 1948 ♀♀ (A. M., L. I. Davis). *Guerrero.* Mexcala, 2 Jul. 1941 ♀ (L. I. Davis).

***Sosippus plutonus* sp. n.**

Figures 5, 25, 26. Map 1.

Type. Female holotype from Tenango del Valle (Tenango de Arista), 2400 m elev., Mexico, Mexico, 25-26 Aug. 1946 (H. Wagner) in the American Museum of Natural History.

Structure. For comparison of certain diagnostic measurements of *S. plutonus* to other species see Table 1.

Female holotype with 3-3 posterior cheliceral teeth. Of seven immature specimens examined, six had 3-3 posterior cheliceral teeth, one 3-4.

Tibial spination was the same as in *S. californicus* with the following exceptions: ventral spination of leg II 1-2-2, dorsal spination of leg III 0-1-0.

Clypeus height equal to the diameter of the AME. Labium slightly wider than long.

Color. Pattern illustrated in Figure 5. Carapace very dark reddish brown with the eye region black. A few white hairs along the mid-line might be indicative of a thin median white line once present. Broad submarginal stripes, brownish yellow and covered with white pubescence, beginning about the third eye row and continuing to the

posterior edge of the carapace. Chelicerae black with lighter colored boss on each side.

Sternum brown. Endites and labium dark brown, lighter at distal ends. Coxae dark gray-brown on ventral surface with lighter amber color at basal regions. Other leg segments gray-brown with lighter amber colored stripes as follows: dorsal paired stripes at proximal and distal ends of femora, stripe covering almost entire dorsal surface of patellae, paired stripes at distal end of tibiae.

Abdomen (considerably shrivelled) dark brown, almost black, with a series of paired lighter spots formed from tufts of white hair. Venter brown.

Diagnosis. *Sosippus plutonus* is most similar to *S. californicus* in the shape of the epigynum. The median septum in *S. plutonus* (Fig. 26) is shorter than in *S. californicus* (Fig. 28). *Sosippus plutonus* is much darker than *S. californicus*, being almost black, hence the specific name.

Natural History. *Sosippus plutonus* presumably constructs a funnel web similar to that of *S. californicus*. *Sosippus plutonus* is probably a montane species being found at extremely high altitudes in Mexico.

Distribution. Mexico, Mexico.

Records. *Mexico.* Tenango del Valle (Tenango de Arista), 2400 m elev., 25-26 Aug. 1946 oo ♀ (H. Wagner); Tenancingo, 2050 m elev., 27 Sep.-7 Oct. 1946 oo (H. Wagner).

Sosippus floridanus Simon

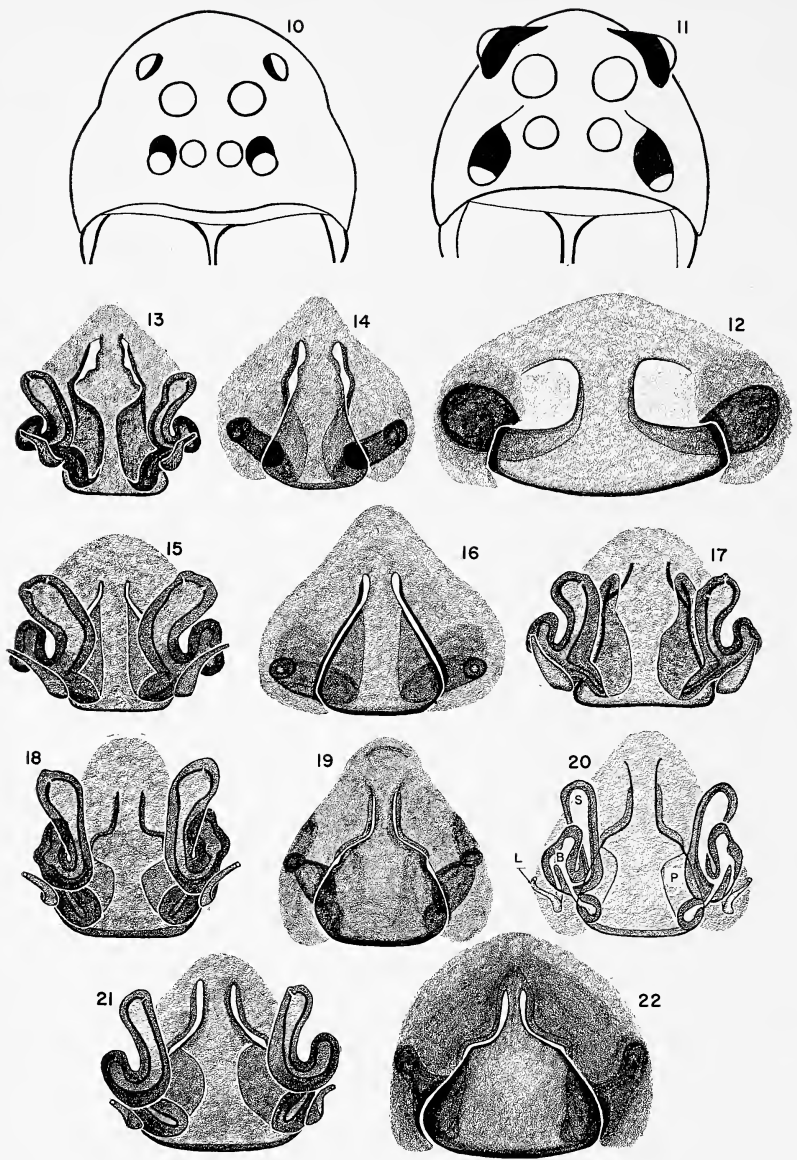
Figures 1, 19, 20, 40-43. Map 1.

Sosippus floridanus Simon, 1898, Ann. Soc. Ent. Belgique, 42:25. Female holotype from Florida in the Paris Museum. Simon, 1898, Histoire naturelle des Araignées, 2(2):323, 325. Comstock, 1913, The Spider Book, p. 622, op. cit. rev. ed., p. 639. Banks, 1904, Proc. Acad. Nat. Sci. Philadelphia, 56:121, 135. Chamberlin, 1908, Proc. Acad. Nat. Sci. Philadelphia, 60:293, pl. 23, fig. 2, pl. 11, figs. 1 ♂, 4 ♀. Wallace, 1950, Florida Ent., 33:76. Roewer, 1954, Katalog der Araneae, 2:314. Bonnet, 1958, Bibliographia Araneorum, 2(4):4093. Roewer, 1959, Exploration du Parc National de l'Upemba, Araneae Lycosaeformia II (Lycosidae), p. 1004.

Structure. For comparison of certain diagnostic measurements of *S. floridanus* to other species see Table 1.

Posterior cheliceral margin with four teeth on each side. Of 37 females examined, 35 had 4-4 posterior cheliceral teeth; two had 4-5 posterior cheliceral teeth. Of 11 males examined 10 had 4-4 posterior cheliceral teeth, one had 4-5 posterior cheliceral teeth.

Tibial spination in 16 females was the same as in *S. californicus* with the exception of ventral spination on leg II. In this position nine



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females had 1-2-2 spines, five had 1-1-2, and two females had 1-2-2 on one leg and 1-1-2 on the other leg. Tibial spination in three males was the same as in *S. californicus* except for 1-1 dorsal spines on leg III and IV in *S. floridanus*.

Clypeus height in nine females is greater than the diameter of the AME, in seven females clypeus height is subequal to the diameter of the AME. In the three males examined clypeus height is subequal to the diameter of the AME.

Labium longer than wide in 14 females, length equal to width in two females. In the three males the labium is longer than wide.

Color. Female. Pattern illustrated in Figure 1. Carapace dark brown, overlaid with black pubescence, black in eye region. Narrow median longitudinal white stripe beginning at second eye row and continuing to the posterior edge of carapace. Broad submarginal white stripes originating at edge of clypeus and running to the posterior edge of carapace. The white color of these stripes is due to presence of short appressed white hairs. The fine white hairs and the black pubescence provide contrasting pattern illustrated. If these hairs become rubbed off the underlying integument is almost unicolorous, the regions of the white stripes may remain somewhat lighter, however.

Chelicerae black with stout black hairs, lighter orange brown boss on each side. Sternum brownish yellow. Endites and labium reddish brown, lighter at distal ends. Coxae light brownish yellow on ventral

EXPLANATION OF PLATE 10

Fig. 10. Frontal view, showing eye arrangement of *Sosippus texanus*, sp. n., ♀ from Goose Island State Park, Aransas Co., Texas, 15 Jun. 1961.

Fig. 11. Frontal view, showing eye arrangement of *Porrina diversa* (O. P.-Cambridge) from Rockstone, British Guiana, 1 July (determined by W. J. Gertsch).

Figs. 13-17. *S. mimus* Chamberlin. 13-14. Female with 3-3 posterior cheliceral teeth from Archibold Biological Station, Lake Placid, Highlands Co., Florida, 24 Jan. 1943. 13. Genitalia, dorsal view. 14. Epigynum. 15-16. Female holotype with 3-3 posterior cheliceral teeth from Mandeville, Saint Tammany Par., Louisiana, 1 May 1921. 15. Genitalia, dorsal view. 16. Epigynum. 17. Genitalia, dorsal view of specimen with 4-4 posterior cheliceral teeth from Alachua Co., Florida, 18 Apr. 1935.

Figs. 18-20. *S. floridanus* Simon, ♀ from Highlands Hammock State Park, Highlands Co., Florida, 9 Jun. 1961. 18. Genitalia, dorsal view. 19. Epigynum. 20. Diagrammatic ventral view showing route of various ducts.

Abbreviations: S, seminal receptacle; B, copulatory bursa; P, copulatory pouch (usually not heavily sclerotized); L, dorsal bursal ligament (difficult to see unless the epigynum is tipped on edge). The route of this ligament is difficult to trace, due to its transparency, and inaccuracy in its placement in the drawings might occur, since it can hardly be seen from a dorsal view.

Figs. 21-22. *S. texanus* sp. n., ♀ paratype from Goose Island State Park, Aransas Co., Texas, 16 Jun. 1961. 21. Genitalia, dorsal view. 22. Epigynum.

surface. Femora gray on ventral surface, gray color continuing around leg segment at proximal and distal ends and toward the center as a pair of wide bands against a brownish yellow background clothed with white pubescence. Remaining leg segments brownish yellow, thickly clothed with black hair.

Dorsum of abdomen with a reddish brown lanceolate mark at the base, enclosed by a wide black median stripe. This broad stripe with tufts of white hair forming two pairs of spots at indentations in the anterior end and with chevrons clothed with white hair crossing it at the posterior end. Lateral to dark median stripe are areas of brown with scattered black spots. Venter of abdomen grayish brown, produced by black hair overlying brownish yellow integument.

Male. The white spots and chevrons on the dorsum of the abdomen are not as conspicuous as in the female, otherwise the coloration and markings are much the same.

Diagnosis. *Sosippus floridanus* is most similar to *S. mimus*. The form of the epigynum in these two species is similar but consistently different (compare Figs. 18, 19 to Figs. 13-17). The male palpi are much alike, but in *S. floridanus* the tarsal segment is usually only twice as long as wide, while in *S. mimus* the tarsal segment is usually more than twice as long as wide (compare Figs. 40-43 to Figs. 34, 35). The most clear-cut difference between these two species is in the color patterns (compare Fig. 1 to Figs 2, 3).

Natural History. *Sosippus floridanus* was collected from tubular webs leading under the trunks of Palmetto bushes and into the bases of tufts of high grass in areas of white, sandy soil. The webs were not extensively developed, the tubular portion usually being hidden and the sheet portion of the web consisting of radiating lines of silk forming a very loose meshwork. Additional specimens were collected from holes and ruts along a path of white sand that had once been cleared

EXPLANATION OF PLATE 11

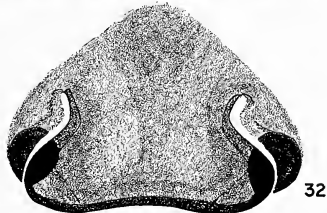
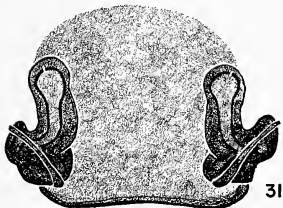
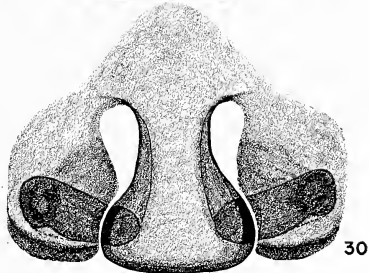
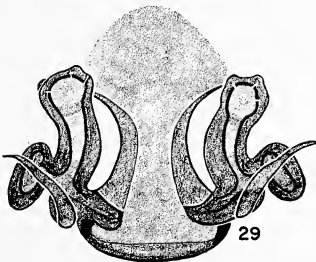
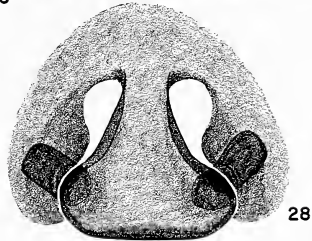
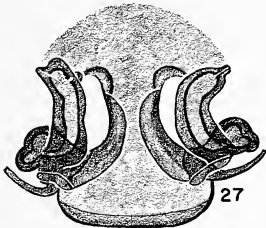
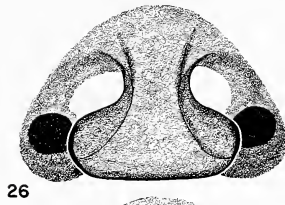
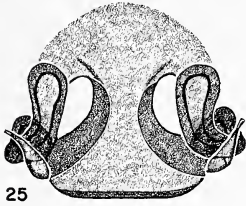
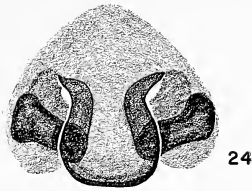
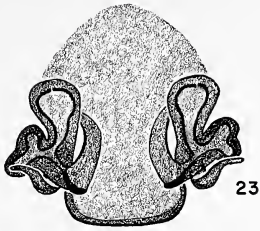
Figs. 23-24. *Sosippus mexicanus* Simon, ♀ from Acapulco de Juarez, Guerrero, Mexico, 1 Sep. 1940. 23. Genitalia, dorsal view. 24. Epigynum.

Figs. 25-26. *S. plutonus* sp. n., ♀ holotype from Tenango del Valle, Mexico, Mexico, 25-26 Aug. 1946. 25. Genitalia, dorsal view. 26. Epigynum.

Figs. 27-28. *S. californicus* Simon, ♀ from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 Jun. 1952. 27. Genitalia, dorsal view. 28. Epigynum.

Figs. 29-30. *S. agalenooides* Banks, ♀ syntype from Puntarenas, Costa Rica, 1909. 29. Genitalia, dorsal view. 30. Epigynum.

Figs. 31-32. *S. michoacanus* sp. n., ♀ paratype from Tzararacua 11 km from Uruapan, Michoacan, Mexico, 14 Jun. 1948. 31. Genitalia, dorsal view. 32. Epigynum.



for vehicles. In these situations the webs were not typical funnel webs at all. However, most of these specimens were immature and this may account for their under-developed webs.

Distribution. Florida.

Records. Florida. Alachua Co.: 1-10 May 1934-37 ♂ ♂ ♀ (H. K. Wallace, A. F. Carr); Gainesville, 12 Jun. 1935 ♀ (W. J. Gertsch). Desoto Co.: 29 Jun. 1935 ♂ ♀♀ (H. K. Wallace); 8 mi. W. of Arcadia, 21 Mar. 1938 ♀ (W. J. Gertsch). Flagler Co.: 2 Sep. 1958 (H. K. Wallace). Highlands Co.: 1 Jun. 1958 ♀ (N. Causey); 29 Jun. 1935 ♀ (H. K. Wallace); Highlands Hammock State Park near Sebring, 24 Mar. 1938 ♀ (W. J. Gertsch), 9 Jun. 1961 ♂ ♀♀ (A. R. Brady); Lake Placid, Archibold Biological Station, 25 Jun.-4 Feb. 1943 oo (M. Cazier). Indian River Co.: 17 Mar. 1936, ♂ (H. T. Townsend). Lake Co.: 21 Apr. 1933 ♂ (H. K. Wallace); Emerald Canal, 6 Mar. 1936 ♀ (Bishop coll.); Umatilla, Jul. 1934 ♀ (M. Broyles). Martin Co.: Port Mayaca on Lake Okeechobee, 29 Mar. 1938 ♂ ♀♀ (W. J. Gertsch). Monroe Co.: Flamingo, 13 Mar. 1920 ♀ (W. S. Brooks). Lee Co.: 14 Apr. 1949 o ♀♀ (H. K. Wallace). Levy Co.: 9 Apr. 1937 oo ♀ (H. K. Wallace). Orange Co.: 7 mi. E of Apopka, 29 Aug. 1944 ♀ (M. Nirenberg); Dec. 1934 ♂ (K. Boyer). Osceola Co.: Runnymede ♀ (N. Banks). Polk Co.: Hobbs, 5.6 mi. W of Lake Wales, 13 Mar. 1937 oo ♀; 27 Jun. 1935 ♀♀ (H. K. Wallace). Sarasota Co.: 19 Jul. 1937 ♀ (M., A. Carr); Englewood, 1-5 Apr. 1938 ♀ (W. J. Gertsch). Volusia Co.: Enterprise, 7 Jun. 1946 ♂ ♀ (F. N. Young).

Sosippus mimus Chamberlin

Figures 2, 3, 13-17, 34, 35. Map 1.

Sosippus mimus Chamberlin, 1924, Proc. U. S. Nat. Mus. 63:27, pl. 6, fig. 43. Female holotype from Mandeville, Louisiana, 1 May 1921 (H. E. Hubert) in Museum of Comparative Zoology, examined. Comstock, 1940, The Spider Book, p. 639. Bonnet, 1958, Bibliographia Araneorum, 2(4):4093.

Sosippinus mimus: Roewer, 1954, Katalog der Araneae 2:313; 1959, Exploration du Parc National de l'Upemba, Araneae Lycosaeformia II (Lycosidae), p. 1002.

Structure. For comparison of certain diagnostic measurements of *S. mimus* to other species see Table 1.

Number of cheliceral teeth on posterior margin extremely variable. Of 12 females examined, nine had 4-4 posterior cheliceral teeth, two had 3-3 posterior cheliceral teeth, and one had 3-4 posterior cheliceral teeth. Of nine males examined, two had 3-3 posterior cheliceral teeth,

two had 3-4 teeth, three had 4-4 teeth, one had 3-5 teeth, and one had 4-5 teeth.

Tibial spination in four females examined was the same as in *S. californicus* with the following exceptions: ventral spination of leg II 1-2-2. Tibial spination in four males was the same as in *S. californicus* with the following exceptions: dorsal spination of legs III and IV 1-1, one male lacked the dorsal spines on leg IV.

Clypeus height in three females greater than the diameter of the AME, in one female clypeus height subequal to the diameter of the AME. Clypeus height in two males greater than the diameter of the AME, clypeus height in one male subequal to the diameter of the AME, diameter of the AME greater than the clypeus height in one male.

Labium longer than wide except that in one female it is slightly wider than long.

Color. Female. Pattern illustrated in Figures 2, 3. Carapace dark reddish brown (mahogany), darkest in eye region, with eyes circled in black. Three longitudinal stripes beginning just in front of third eye row and consisting of: one median stripe continuing to thoracic groove, two lateral stripes passing inside of eyes of third row and ending in the cephalic region. These three stripes yellowish white in color. Lateral bands of the same color at anterior edge of carapace and another pair of yellowish white bands below eyes of third row running downward and diagonally backwards. No distinct stripe along margins of carapace, diffuse yellowish white hairs instead. Black lines radiating from thoracic groove, accented by yellowish white pubescence.

Chelicerae black, clothed with large black hairs, with orange brown boss on each side. Sternum yellowish brown. Labium and endites orange-brown, lighter at distal ends. Leg segments yellowish brown without distinct banding. Ventral surface of femora sometimes having a gray appearance due to heavy clothing of black hairs. Dorsal surface of femora clothed with short white hair.

Dorsum of abdomen with a wide brown median stripe from the base of the abdomen to the posterior end, interrupted at intervals. A pair of whitish spots at lateral edges of median stripe anteriorly, followed by a series of five white chevrons crossing the median stripe; the ends of the chevrons merging with white spots at the lateral edges. Bands of brown dots alternately crossing the median stripe with the chevrons. Lateral areas of dorsum yellowish brown mottled with darker brown. Venter of abdomen brownish yellow.

Male. The pattern in the male is very similar to that of the female.

Diagnosis. *Sosippus mimus* resembles *S. floridanus* in male and female genitalia and is much like *S. texanus* in color pattern. *Sosippus mimus* is separated from the former by characters discussed under that species. *Sosippus mimus* is smaller than *S. texanus* (see Table 1). Although the males are difficult to separate by differences in the palpi, the females are easily separated by differences in the epigyna (compare Figs. 13-17 to Figs. 21, 22). It is possible that the specimens considered in this paper under *S. mimus* constitute more than one species. There is considerable variability of certain characters in this species, but these characters do not show geographic variation that would permit separation, e. g. the holotype from Mandeville, Louisiana and specimens from Lake Placid, Florida have 3-3 posterior cheliceral teeth, while some specimens between these two localities have 4-4 posterior cheliceral teeth. The specimens considered under *S. mimus* all agree in color pattern and genitalia. Additional collections and field studies will provide a more definite answer.

Natural History. *Sosippus mimus*, according to R. V. Chamberlin (1924), was collected from a funnel web much like that of other species in the genus.

Distribution. Georgia, south into Florida and along the Gulf Coast to eastern Louisiana.

Records. Georgia. Charlton Co.: Chesses Island, Pinebarrex, 15 Jun. 1922 ♀ (Wright). Florida. Alachua Co.: 13 Apr.-18 May 1935-50 ♂ ♀♀ (H. K. Wallace). Columbia Co.: 27 Apr. 1935 ♂ ♀ (H. K. Wallace). Highlands Co.: Lake Placid, Archibold Biological Station, 24 Jan.-4 Feb. 1943 oo ♀ (M. Cazier). Jackson Co.: 3 Apr. 1953 ♂ (H. K. Wallace). Levy Co.: 20 Apr. 1935 ♂ ♀♀ (H. K. Wallace). Liberty Co.: Blountstown, 17 Apr. 1938 ♀ (W. J.

EXPLANATION OF PLATE 12

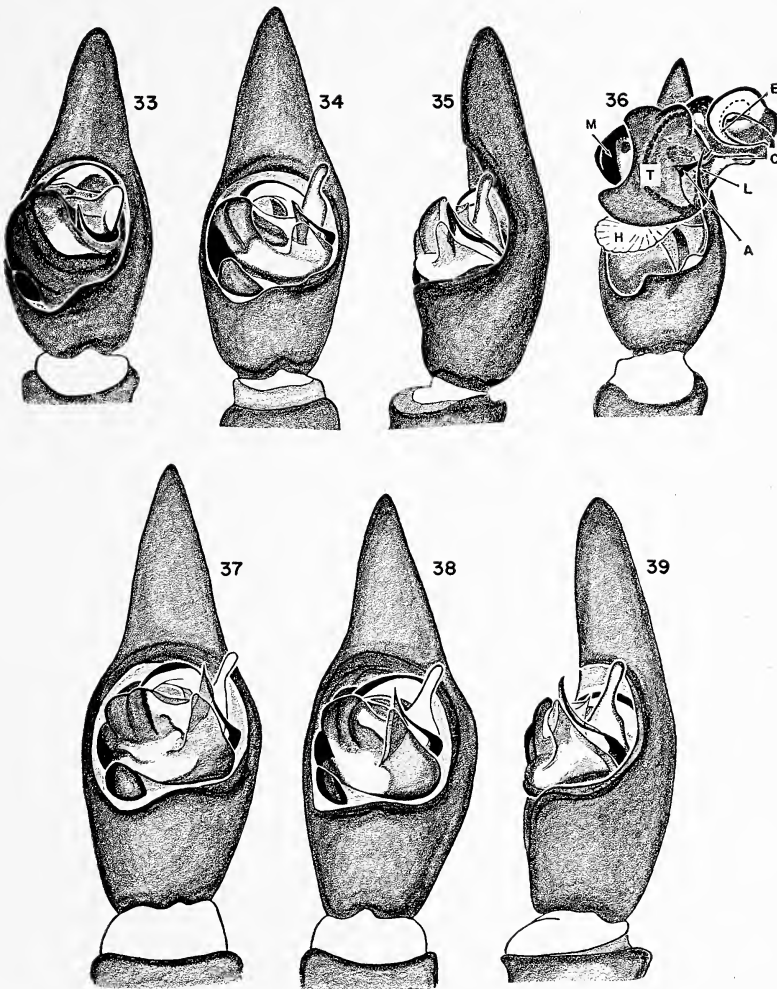
Fig. 33. Left palpus, ventral view of *Porrima harknessi* Chamberlin, ♂ holotype from Huadquina, Peru, July, 1911.

Figs. 34-35. *Sosippus mimus* Chamberlin, ♂ from Blountstown, Liberty Co., Florida, 17 Apr. 1938. 34. Left palpus, ventral view. 35. Left palpus, retrolateral view.

Fig. 36. *S. californicus* Simon, ♂ from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 Jun. 1952. Expanded left palpus.

Figs. 37-39. *S. texanus* sp. n., ♂ from Goose Island State Park, Aransas Co., Texas. 37. Palpus, ventral view. 38. Palpus, ventral view (more retrolateral than 37). 39. Palpus, retrolateral view.

Abbreviations: C, conductor; E, embolus; H, basal haematodocha; L, lateral apophysis of conductor; M, median apophysis; A, mesal apophysis of tegulum; T, tegulum.



BRADY — GENUS SOSIPPUS

Gertsch). Marion Co.: Kerr Park near Lake Kerr, Oct. 1956 ♀ with egg case (H. K. Wallace). Saint Johns Co.: Hastings, Jul. 1927 ♂ (J. L. Scribner). Suwanee Co.: 25 Mar. 1933 ♂ (H. K. Wallace). *Mississippi*. Forrest Co.: Hattiesburg, 2-6 Jan. 1942 oo (E. L. Bell). Jackson Co.: Ocean Springs, 10 May 1931 ♂ (Dietrich). *Louisiana*. Saint Tammany Par.: Mandeville, 1 May 1921 ♀ with egg case (H. E. Hubert).

***Sosippus texanus* sp. n.**

Figures 4, 21, 22, 37-39. Map 1.

Type. Female holotype from Goose Island State Park, Aransas Co., Texas, 15 Jun. 1961 (A. R. Brady) in the Museum of Comparative Zoology.

Structure. For comparison of certain diagnostic measurements of *S. texanus* to other species see Table 1.

Posterior cheliceral margin with three teeth on each side. Of 11 females examined all have 3-3 posterior cheliceral teeth. Two males also have 3-3 posterior cheliceral teeth.

Tibial spination in 10 females is the same as *S. californicus* with the following exceptions in the case of ventral spines on leg II: six females with 1-2-2 spines, three females with 1-2-2 spines on one leg and 1-1-2 spines on the other leg, and one female with 1-1-2 spines. Two males have the same tibial spination as *S. californicus* with the exception of the dorsal spination of legs III and IV which is 1-1 on each leg.

Clypeus height in seven females is greater than the diameter of the AME, in three females the clypeus height is subequal to the diameter of the AME. In the two males clypeus height is subequal to the diameter of the AME.

Labium longer than wide in eight females and length subequal to width in two females. Labium longer than wide in the two males.

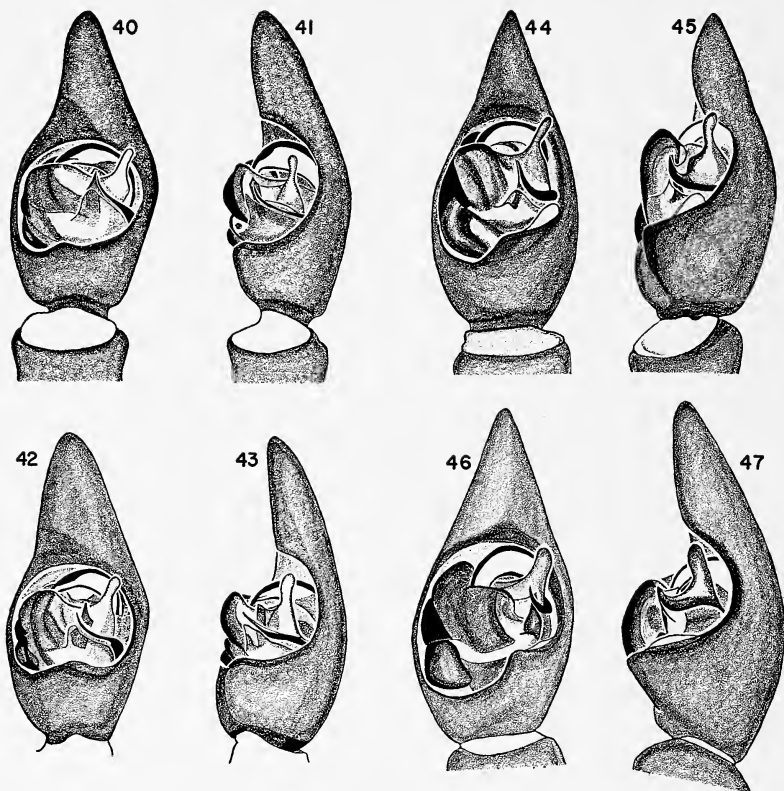
Color. Female. Pattern illustrated in Figure 4. Carapace dark brown, covered with black pubescence, black in eye region. Three longitudinal white stripes beginning behind the second eye row where they are convergent, consisting of one median stripe and two lateral stripes passing on the inside of the eyes of the third row, ending at edge of cephalic region. Marginal areas of carapace lighter, but no definite stripe present. Sides of cephalic region with a white band behind the clypeus, followed by a black band, then another white band below eyes of third row running diagonally backward and downward. Black lines, accented with white hair, radiating from the thoracic groove.

Chelicerae black, clothed with long black hairs, conspicuous orange-brown boss on each side. Sternum yellowish brown. Endites and labium dark reddish brown, brownish yellow at distal ends. Ventral surface of coxae yellowish brown. Femora gray-brown on ventral surface. White hairs on dorsal surface of femora forming alternating bands, consisting of: proximal gray-brown, white, gray-brown, white, and distal gray-brown. Remaining leg segments dark brown with tarsi and metatarsi darker. Heavy scopulae on tarsus and metatarsi of legs I and II dark gray in color.



Text Fig. 2. Funnel web of *S. texanus* constructed in corner of cardboard box with retreat behind large stick.

Dorsum of abdomen with a wide brown median stripe running the length of the abdomen, with diffuse black hairs covering it. Two pairs of white dots at the lateral edges of the stripe anteriorly, posterior to these a series of six paired white spots connected by white chevrons crossing the brown stripe. Usually the first chevron is represented by two dashes and the arms of the second chevron do not quite join at the midline. Alternating with the white chevrons are bands of darker brown dots. The areas on each side of the median stripe are speckled



BRADY — GENUS *SOSIPPUS*

Figs. 40-43. *Sosippus floridanus* Simon. 40-41. Male from Alachua Co., Florida, 8 May 1934. 40. Left palpus, ventral view, showing lateral apophysis of conductor resting normally against mesal apophysis of tegulum. 41. Left palpus, retrolateral view. 42-43. Male from Port Mayaca, Lake Okeechobee, Martin Co., Florida, 29 Mar. 1938. 42. Palpus, ventral view showing lateral apophysis of conductor lying below median apophysis of tegulum. 43. Palpus, retrolateral view.

Figs. 44-45. *S. californicus* Simon, ♂ from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 Jun. 1952. 44. Palpus, ventral view. 45. Palpus, retrolateral view.

Figs. 46-47. *S. mexicanus* Simon, ♂ from Guatamala. 46. Palpus, ventral view. 47. Palpus, retrolateral view.

with tufts of white hair intermixed with dark brown dots on a lighter brown background. Venter light brown.

Male. The pattern in the male is very similar to that of the female. There are fewer black hairs over the body and in over-all appearance the male is more brown than the female, which appears dark gray or even black.

Diagnosis. *Sosippus texanus* is most similar to *S. mimus* in coloration. The white spots and chevrons on the abdomen of *S. texanus* are usually more distinct. *Sosippus texanus* is also larger (see Table 1) and slightly darker than *S. mimus*. The male palpal organs are very similar, but the females are readily separated by differences in the epigyna (compare Figs. 21, 22 to Figs. 14-17).

Natural History. Specimens of *S. texanus* were collected and observed in the field at Goose Island State Park. This is a peninsular area of dry sandy soil, characterized by dense stands of Live Oak (*Quercus virginiana*). *Sosippus texanus* was collected in an area at the edge of a clearing from conspicuous funnel webs with tubular retreats running under logs and holes in the ground. The sheets of these funnel webs were not as extensive as those observed in *Agelenopsis*. *Sosippus texanus* was also collected from funnel webs at the base of the trunks of these trees. Again the sheet portion of the webs was not highly developed. The emphasis upon the tubular portion of the webs may have been due to their situation, especially those webs at the base of trees.

The spider rests at the mouth of the funnel and rushes forth with great speed to grab insects that have touched the sheet portion of the web. The prey consists chiefly of grasshoppers and ground beetles that have fallen upon or run across the lines of radiating silk forming the sheet. Upon grabbing the insect the spider retreats rapidly into the tubular portion of the funnel so that the struggles of the victim are impeded.

Spiders whose retreats dead-end into a hole or crevice construct a second short tube that they utilized for an escape exit. Most spiders seemed to have escape exists running off at angles from the main tube rather than having an exit directly to the rear.

Several spiders from this locality were reared to maturity and were observed for several months. One spider kept in a cardboard box, provided with sand and sticks for a retreat, constructed a funnel web like that found in the field at the base of Live Oak trees. This web is shown in the accompanying photograph (Text Fig. 2).

Distribution. Southern Texas.

Records. Texas. Aransas Co.: Goose Island State Park, 7 Mar. 1959 oo, 15 Jun. 1961 ♂♂ ♀♀ paratypes (A. R. Brady). Cameron Co.: Brownsville, 30 Nov. 1934 ♀ (S. Mulaik). Hidalgo Co.: Resaca, 5 mi. SE of Brownsville, 26 Sep. 1937 ♀ (L. I. Davis, M. Fones), Edinburgh, Sep.-Dec. 1933 ♀ (S. Mulaik), La Joya, 30 Oct. 1938 ♀♀ (L. I. Davis). Zapata Co.: Lopeno, 15 Apr. 1952 ♀ with egg case (Willie).

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The illustration of a spider on the front cover of this issue of *Psyche* was reproduced from an original drawing made by J. H. Emerton and contained in the Museum of Comparative Zoology. First published in the Transactions of the Connecticut Academy of Arts and Sciences (1909, vol. 14, plate 7, fig. 5), it shows the displaying posture of the male of *Habronattus viridipes* (Hentz).

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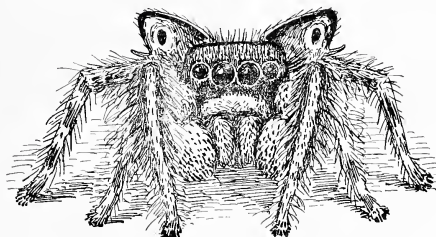
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DECEMBER, 1962

No. 4

A COMPARATIVE STUDY OF OÖCYTE DEVELOPMENT IN FALSE OVOVIVIPAROUS COCKROACHES*

BY LOUIS M. ROTH AND BARBARA STAY¹

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Recently Engelmann (1960) compared various internal and external factors which affect the activity of the corpora allata in *Leucophaea maderae* (Fabricius) and *Diploptera punctata* (Eschscholtz). In these two species the stimuli resulting from mating, food intake, gestation, and parturition differed in the degree to which they influenced production of gonadotropic hormone.

In this paper we report our experiments on control of oöcyte development in several species of cockroaches that incubate their eggs internally in a brood sac or uterus. We classify these species as false ovoviviparous forms because the uterine eggs increase in water content only (Roth and Willis, 1955) as opposed to false viviparous species, like *Diploptera*, in which the embryos take up both water and solids from the mother (Roth and Willis, 1955a). In both groups the oviposition behavior is similar. The eggs do not pass directly from the ovaries into the uterus but are first extruded to the outside of the body and then retracted into the brood sac (Roth and Willis, 1954, 1958).

Cockroaches that incubate their eggs internally have two birth products, the egg and nymph (Roth and Willis, 1958). Ovulation and oviposition refer to the eggs being released from the ovaries, oriented by the ovipositor, and covered by the oötheca. After the eggs are in the uterus the females are pregnant (gestation) for a certain period of time and give birth (parturition) to nymphs.

MATERIALS AND METHODS

Except for one series of experiments on *Nauphoeta* (see page 174), all insects were reared on dog chow checkers and maintained at 24°

*Manuscript received by the editor August 1, 1962.

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to 25° C. and 50 to 70% relative humidity. Engelmann (1957, 1959) showed that yolk deposition and growth of the oöcytes are correlated with and dependent upon activity of the corpora allata in *Leucophaea* and *Diploptera* and we have used oöcyte development as an indicator of endocrine activity. Measurements were made, with an ocular micrometer, of oöcytes that were dissected from ovaries in Ringer's solution. Our measurements of the oöcytes of *Leucophaea* are larger than those reported by Engelmann (1960). This discrepancy is probably due to the fact that he measured the oöcytes after fixation (Engelmann, 1957). We measured one large oöcyte per female; in establishing the normal ovarian cycle or the sizes of the oöcytes at a specific period a number of females were usually dissected to give some indication of the extent of variation. Various operations (allatectomy, nerve cord severance, etc.) were performed on insects kept under carbon dioxide anesthesia.

The species reported on in this paper are *Pycnoscelus surinamensis* (Linnaeus), *Byrsotria fumigata* (Guérin), *Blaberus craniifer* Burmeister, *Blaberus giganteus* (Linnaeus), *Nauphoeta cinerea* (Olivier), and *Leucophaea maderae*. There are two strains of *Pycnoscelus surinamensis* which differ physiologically. The bisexual strain cannot reproduce parthenogenetically and the parthenogenetic strain females when mated to males of the bisexual form show a reduction in fertility and the resulting offspring are all females which reproduce parthenogenetically (Roth and Willis, 1961). Practically all of the experiments on *Pycnoscelus* were done on the parthenogenetic strain but a few were performed on the bisexual form. A similar study on control of oöcyte development in *Diploptera* and two species of *Blattella* has been reported elsewhere (Roth and Stay, 1961, 1962).

RESULTS AND DISCUSSION

Oöcyte development in virgin and mated females

Pycnoscelus surinamensis: Biological data for the two strains are given in table 1. The basal oöcytes of the ovarioles of females less than a day old are large and may already contain yolk. In fact yolk may be present in the oöcytes of some newly-emerged adults indicating that perhaps gonadotropic hormone had already been released in the nymphal stage. The ovarian cycle from emergence to the formation of the second oötheca in the parthenogenetic strain is shown in figure 1. During gestation the oöcytes remain small and increase only slightly in length during the development of the eggs in the uterus. Yolk deposition occurs after parturition and the oöcytes increase rapidly in size.

Table 1 — Biological Data For Two Strains of *Pycnoscelus surinamensis*

BIOLOGICAL OBSERVATION	PARTHENOGENETIC STRAIN				BISEXUAL STRAIN			
	Min.	Max.	Mean \pm S.E. ¹	N ²	Min.	Max.	Mean \pm S.E.	N
Length (mm.) of oöcytes less than 1 day after emergence of adult	0.86	0.99	0.91 \pm 0.03	5	0.73	0.94	0.85 \pm 0.02	10
Length (mm.) of mature oöcytes at oviposition ³	2.97	3.36	3.21 \pm 0.04	10	2.69	3.36	2.99 \pm 0.04	15
Length (mm.) of new basal oöcyte at time of oviposition	0.50	0.57	0.53 \pm 0.01	6	0.50	0.74	0.60 \pm 0.02	16
Length (mm.) of basal oöcytes less than 1 day after parturition	0.67	0.79	0.74 \pm 0.01	10	0.69	0.79	0.74 \pm 0.01	5
Age (days) at first ovulation								
Virgins	10	20	12.8 \pm 0.1	244	8	25	13.6 \pm 0.2	138
Mated	—	—	—	—	9	22	11.9 \pm 0.1	59
Gestation (days) ³								
Virgins	53	58	55.4 \pm 0.3	20	—	—	—	—
Mated	—	—	—	—	50	56	52.8 \pm 0.2	37
Number days to ovulation following parturition ³	14	17	15.5 \pm 0.3	11	10	16	14.2 \pm 0.7	8

¹S.E. = standard error, here and in all following tables.²N = number of insects, here and in all following tables.³Data from Roth and Willis (1961).

In the parthenogenetic strain the first ovulation occurs when the female is about 13 days old whereas the second ovulation takes place about 16 days after birth of young. This 3 day difference is explained by the difference in size of the oöcytes in the newly-emerged female and in the female at parturition; the oöcytes are smaller after the female gives birth and it takes about 3 days to attain the same degree of development as they are at adult emergence. In *Diploptera* the reverse is true and the second preovulation period is 3 days shorter than the first although, as in *Pycnoscelus* the growth rate of the oöcytes is about the same during the first and second preovulation periods. In *Diploptera* the oöcytes at parturition are about the size of those of a 3-day-old mated female which explains the shorter period required for ovulation after parturition (Engelmann, 1959).

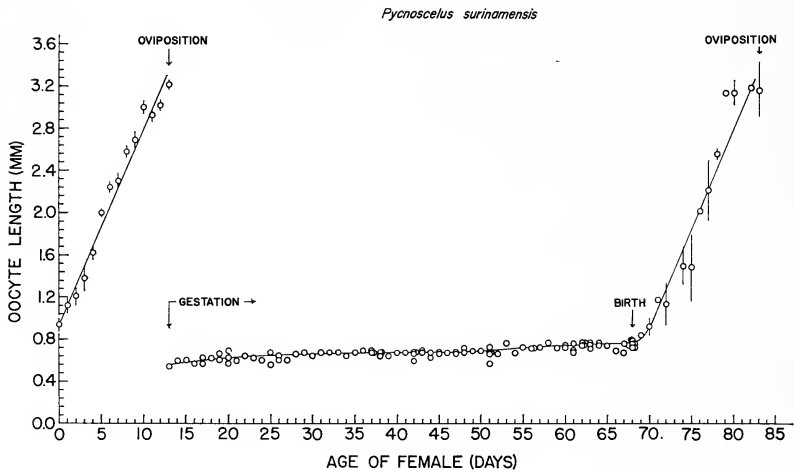


Fig. 1. Ovarian cycle of *Pycnoscelus surinamensis* (parthenogenetic strain). Each point on the curve for oöcyte development from 0 to 13 days is the mean of 6 to 13 measurements ($N=134$). Each point for the gestation period from 13 to 68 days represents individual measurements ($N=99$; when 2 or more points were similar for a particular age only one is indicated). The part of the curve representing the growth of the oöcytes after parturition (birth) is based on 1 to 3 individuals ($N=24$) for each point. Vertical bars = standard errors of mean values.

In the parthenogenetic strain of *Pycnoscelus* it is obvious that mating is unnecessary for development of the oöcytes. The initial development of the oöcytes in the bisexual strain is similar to that found in the parthenogenetic form but differs in that mating slightly stimulates the growth rate and also is necessary for normal retraction of the oötheca into the uterus. Mating a parthenogenetic strain female with a male

of the bisexual strain has no stimulating effect on growth of the oöcytes as indicated by age of the female at ovulation (Roth and Willis, 1961).

Six parthenogenetic strain females, allatectomized when 1-2 days old, did not oviposit within a month after the operations. Five of these females had 2 pairs of corpora allata implanted at 29 to 30 days after allatectomy. Four produced oöthecae in less than 35 days and one died after 44 days. At 111 days after allatectomy one female that still had not ovulated received corpora allata implants and oviposited in less than 21 days. This strain normally oviposits about 13 days after emergence (table 1). The delay in oviposition after implanting corpora allata may have been due to the presence of degenerating oöcytes in the ovaries since the oöcytes already have yolk one to two days after emergence (the age at which allatectomy was performed). In *Leucophaea*, oöcytes in resorption inhibit the corpora allata (Engelmann, 1957).

Table 2 — Effect of mating on oöcyte development and oviposition in *Byrsotria fumigata*

OBSERVATION	MATED	VIRGIN
Total number observed	63	213
Number oviposited	53 (84%)	102 (48%)
Oötheca retracted normally	46	92
Oötheca incompletely retracted	7	5
Oötheca dropped	0	5
Number failed to oviposit	10 (16%)	111 (52%)
Oöcytes large, well developed or matured but degenerating and being resorbed	4 ¹	68 ²
Oöcytes small, abnormal in shape, being resorbed	6 ³	35 ⁴
Oöcytes small, normal in appearance but only slightly or not at all developed	0	8

¹Three of the 4 females had sperm in their spermathecae; one lacked sperm.

²These females were 35 to 60 days old when dissected.

³All had sperm in their spermathecae.

⁴Twenty-one of these females were 32 to 60 days old. The other 14 were 11 to 24 days of age but since their oöcytes were small and abnormal they would not have oviposited.

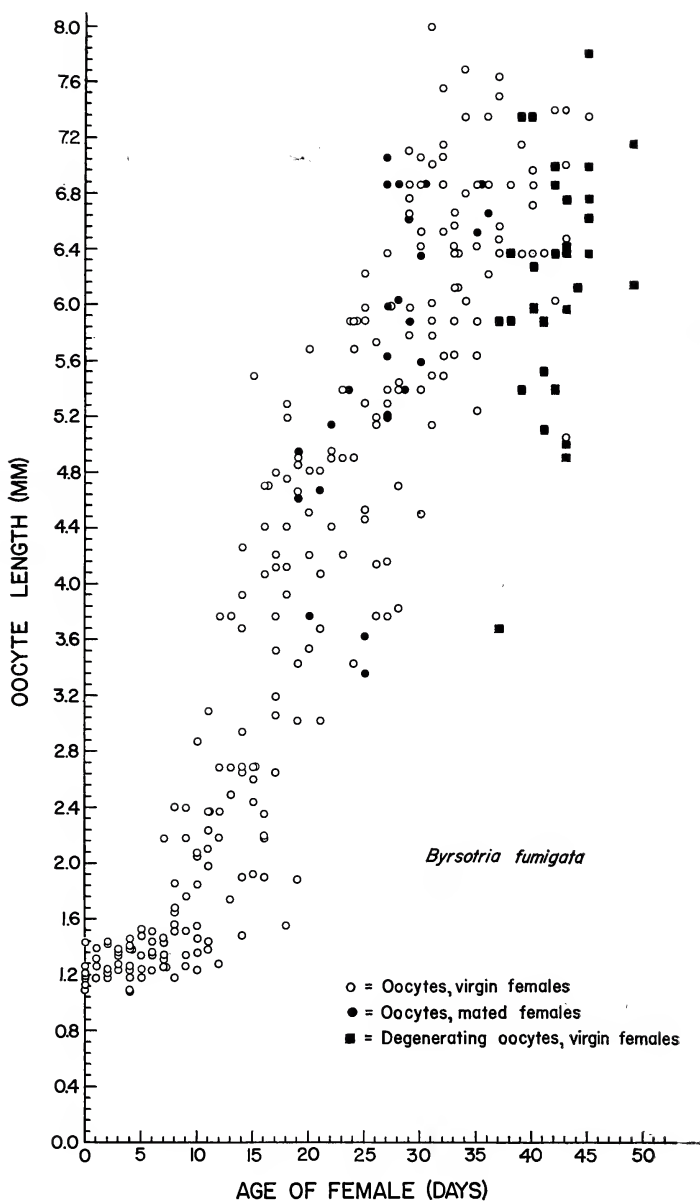


Fig. 2. Growth of oöcytes in virgin and mated females of *Byrsotria fumigata*. Each point represents one female. Females were mated when 1 to 17 days old.

Byrsotria fumigata: The effects of mating on oöcyte development and oviposition in *Byrsotria* are shown in table 2 and figure 2. About 50 percent of the virgin females failed to oviposit but of these 111 females 61% had large well-developed oöcytes that were degenerating or were being resorbed (fig. 14E). It is evident from figure 2 that after the thirty-fifth day of age the oöcytes of many virgins degenerate although most of them may reach a length of 5 mm. or more. About 16% of the virgins and about 10% of the mated females had small abnormally-shaped oöcytes that were being resorbed. It is unlikely that lack of hormone is responsible for this type of abnormality since Barth (personal communication) has dissected pheromone-producing *Byrsotria* females which had small degenerating oöcytes but accessory glands filled with secretion.

In those females that mate, copulation has little, if any, effect on the growth rate of the oöcytes (fig. 2). Mated females oviposited at 26 to 41 days of age ($\bar{x}=32.4\pm0.4$ days; $N=53$); virgin females oviposited 26 to 44 days after emergence ($\bar{x}=34.3\pm0.4$ days; $N=121$). That there is little effect on the rate of growth resulting from mating is further borne out by the fact that the females oviposit at about the same age regardless of their age when mated. In our series the females were with males continuously until they mated; copulation occurred from 4 to 25 days after female emergence. The oöcytes may vary considerably in size in females between these age limits (fig. 2). A female with large oöcytes mated when 25 days old may ovulate 10 days later whereas one with small oöcytes mated at 4 days of age may take 30 days to ovulate (fig. 3). This is quite different from the effect of mating in *Leucophaea* (Engelmann, 1960) where the average interval between mating and oviposition is about the same regardless of the age of the female when mated (fig. 3) because the females tend to mate more readily when their oöcytes reach a certain size (see below). Barth (1961) found that *Byrsotria* females begin to produce sex pheromone 10 to 30 days after the imaginal molt; however, recently (1962) he has found that some females may mate as early as 4 days after adult emergence.

It seems that in *Byrsotria* mating (perhaps the presence of sperm in the spermathecae) serves as a stimulus to oviposition. This is indicated by the fact that the oöcytes in many virgin females apparently mature yet ovulation does not occur. The oöcytes in virgin females at ovulation vary in length from 5.90 to 7.60 mm. ($\bar{x}=6.79\pm0.06$; $N=7$). Although the mean ages at ovulation of mated and virgin females are very similar a breakdown of the data (fig. 4) shows that

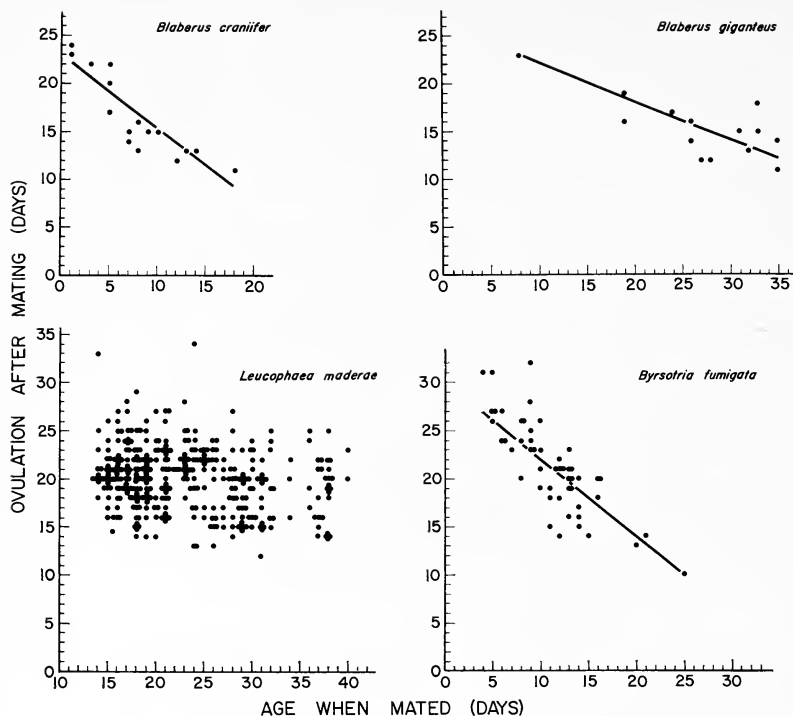


Fig. 3. Relationship between age at mating and ovulation (as indicated by oviposition) in 4 species of cockroaches. Each point represents one female. (N=356 for *Leucophaea*).

38% of the virgins oviposited after the thirty-fifth day as compared to 13% of mated females.

Fifteen virgin females allatectomized when 1 to 2 days old did not produce oöthecae within more than 50 days. At 52 to 210 days after allatectomy, corpora allata were implanted; 9 females ovulated in less than 82 days and one oviposited in 128 days; 3 died without ovipositing and two dissected after 150 days had small undeveloped oöcytes. One allatectomized female that oviposited after receiving corpora allata implants had well developed oöcytes although the oötheca was in the uterus (fig. 14D). Of 25 sham operated females 16 oviposited in less than 56 days. We don't know how to account for the delay in ovulation after implantation of corpora allata into allatectomized females. Four pregnant females (i.e. with an oötheca in the brood sac) had corpora allata implanted and were dissected at 35 to 41 days of pregnancy. Their oöcytes measured 4.90 to 6.81 mm. in length

indicating renewed growth of the ovarian eggs as a result of the implants.

Nauphoeta cinerea: The oöcytes of virgins develop but unless mating occurs the oöcytes in many females may degenerate before they reach ovulation size (fig. 5). Virgin females that ovulate do so in 31 to 47 days ($\bar{x}=35.8\pm1.2$ days; $N=17$). Mating results in stimu-

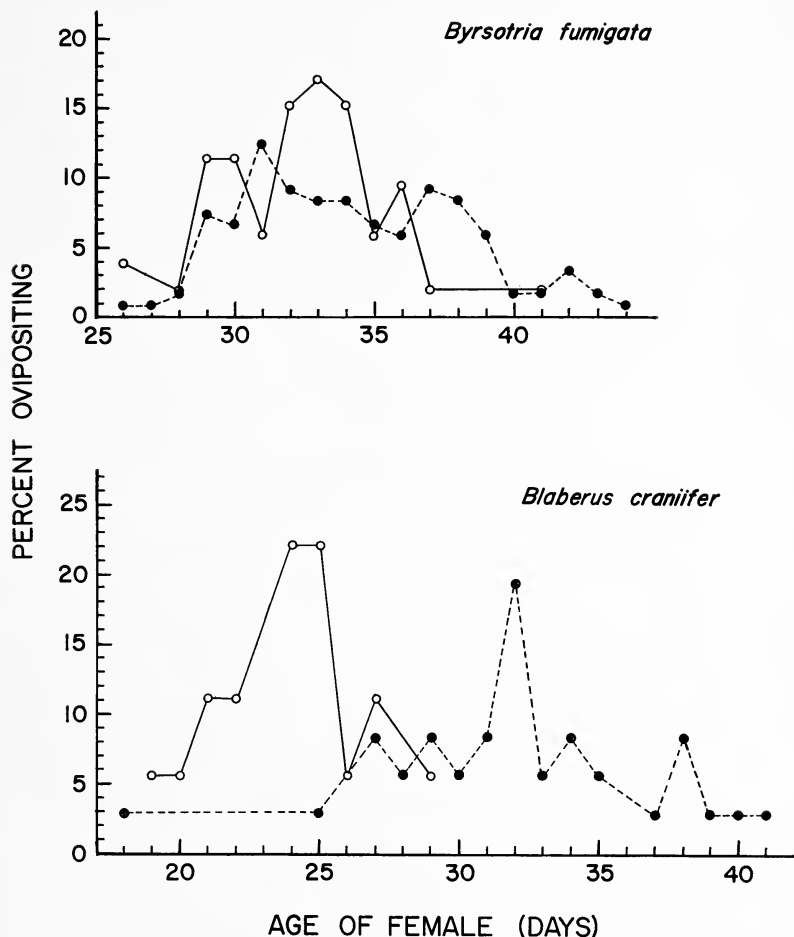


Fig. 4. Effect of mating on oviposition. Solid circles=virgin females. Open circles=mated females. The curves for *Byrsotria* are based on 53 mated and 121 virgin females. The curves for *Blaberus* are based on 18 mated and 36 virgin females.

lation of the corpora allata so that the oöcytes develop rapidly (fig. 5) and oviposition occurs in 18 to 21 days ($\bar{x}=18.9\pm0.40$; $N=8$). Copulation is completed in 17 to 30 minutes ($\bar{x}=20.4\pm0.81$ min.; $N=17$). Of 22 females kept with males continuously, 19 mated 5 days after emergence; the other 3 mated after 6, 8, and 10 days respectively.

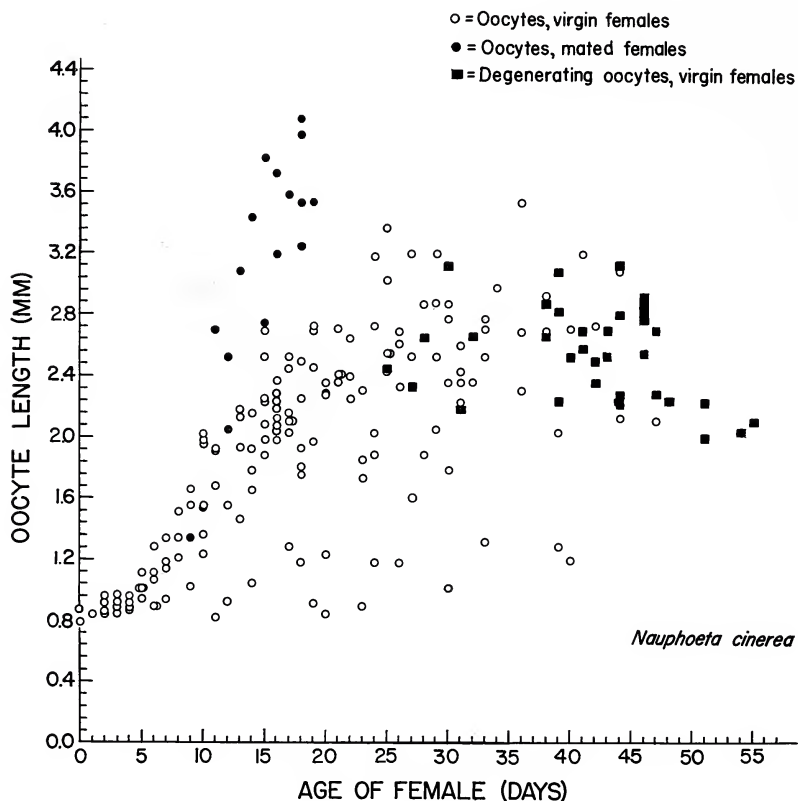


Fig. 5. Growth of oöcytes in mated and virgin females of *Nauphoeta cinerea*. Each point represents one female. Except for 2 individuals mated at 8 and 10 days of age, all others were mated when 5 days old.

In a series of experiments performed at Harvard University, temperature was uncontrolled but usually higher than 24° to 25° C.; the insects were maintained on Purina Laboratory Chow. Both virgin and mated females oviposited earlier than in the above experiment but virgin females still oviposited later (24 to 35 days) than mated indi-

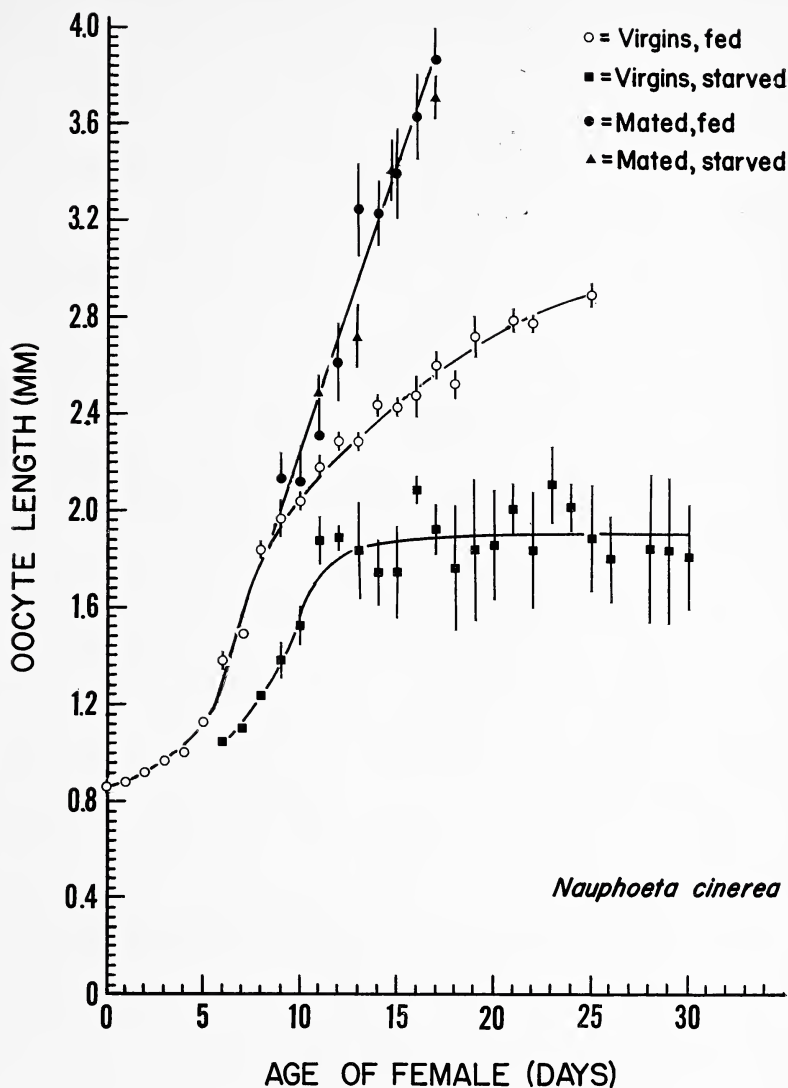


Fig. 6. Effect of mating, starvation, and combined starvation and mating on oöcyte development in *Nauphoeta cinerea*. The points are mean values; fed virgins, N=707; starved virgins, N=133; fed mated, N=58; starved mated, N=21. Females were mated when 4 to 6 days old. Vertical bars are one standard error (only positive halves of standard errors are indicated wherever errors overlapped); no vertical bars indicate standard errors of ± 0.02 mm. or less.

viduals (15 to 18 days). The difference in rate of oöcyte development in virgin and mated females is shown in figure 6. The oöcytes of starved females that have mated develop at the same rate as fed mated females (fig. 6).

Of 17 virgin females that oviposited, 10 retracted the oötheca completely into the uterus; several of these females aborted the egg cases several days after oviposition. Four females partly retracted the egg cases so that some of the eggs remained protruding from the abdomen; three dropped the egg cases while or after they were formed without retracting them. In most virgin females (including those that retract the oötheca normally) some mature oöcytes remain in the ovaries.

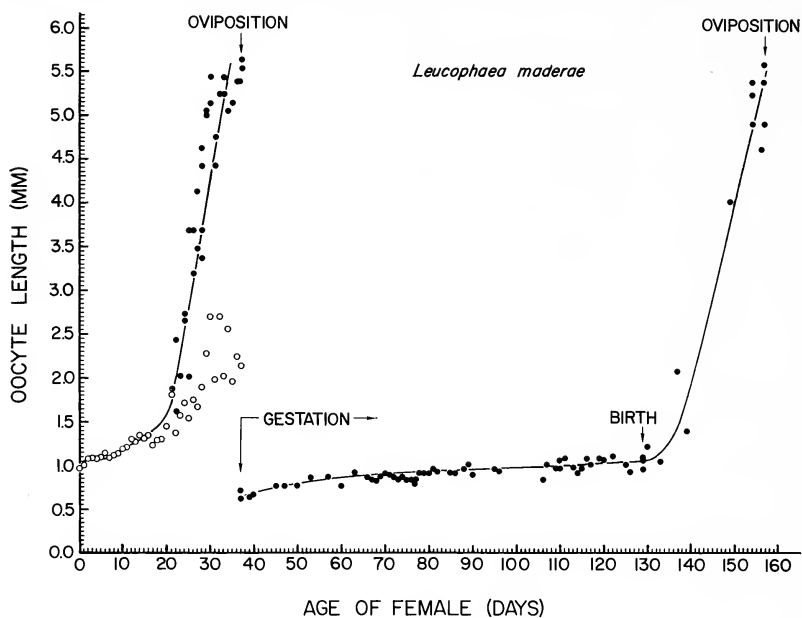


Fig. 7. Ovarian cycle (first and second ovipositions) in *Leucophaea maderae*. The points for the oöcytes of unmated females (open circles) are means of 5 to 21 individuals ($N=349$). For the first preoviposition period, females were mated (solid circles) when 16 days old and each point represents 1 individual. Each point for the gestation and post parturition periods represents one individual.

Leucophaea maderae: At emergence the oöcytes of *Leucophaea* are 0.97 ± 0.01 mm. ($N=10$). Mature oöcytes at ovulation are 5.56 ± 0.12 mm. ($N=20$: 10 mated and 10 virgin females). The new basal oöcyte at oviposition is 0.66 ± 0.01 mm. ($N=11$) and at parturition 1.05 ± 0.01 mm. ($N=4$). Under our conditions gestation lasted 91.8

± 0.7 days ($N=35$) and the second oviposition occurred 27.8 ± 0.3 days ($N=10$) after parturition.

The ovarian cycle in this species is shown in figure 7. Mating shortens the egg maturation period so that the female ovulates at a more or less definite time (fig. 3) after copulation (Engelmann, 1960). It is almost impossible to predict what the extent of oöcyte development would be in virgins of known age (fig. 8). Only 25 of 381 mated females failed to oviposit. These were 16 to 40 days old when mated and were dissected 30 to 62 days later. Eighteen had large degenerating oöcytes; 5 had small (1.01 to 1.73 mm.) and 2 had large but normal appearing oöcytes. As Engelmann found mating results in the rapid growth of the oöcytes (fig. 7). Of the large number of virgin females dissected (fig. 8) only 2 had oöcytes that were degenerating.

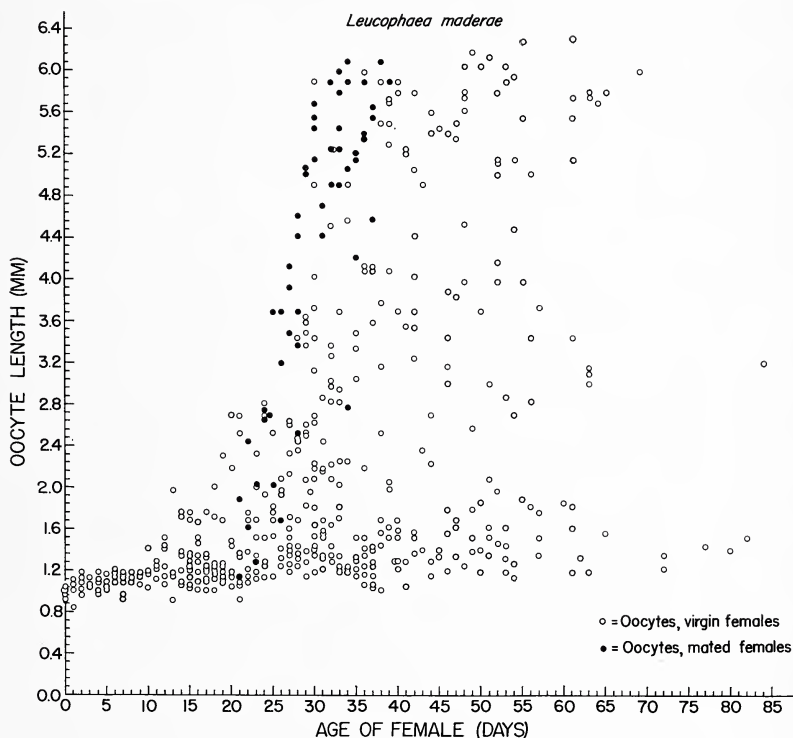


Fig. 8. Growth of oöcytes in mated and virgin females of *Leucophaea maderae*. Each point represents one female. Females were mated when 17 to 23 days old.

Of 47 virgin females that oviposited, only 11 retracted the oötheca into the uterus; the others dropped the egg cases while they were being formed. Virgin females frequently retain mature oöcytes in their ovaries and the egg cases are incomplete (Engelmann, 1957a).

Engelmann (1960) found that when females of *Leucophaea* had constant access to males, mating occurred when their oöcytes averaged 1.08 ± 0.01 mm. and none mated that had oöcytes exceeding a size of 1.46 mm. He concluded (1960, 1960a) that the corpus allatum hormone must be present in low titer for mating to occur, and as soon as a certain titer is surpassed, the females did not mate even with ready access to males. We exposed females of various ages to males for relatively brief periods (the longest time females were with males was 2 days), and measured the oöcytes of those that did and did not mate. One hundred and fifteen females between 14 and 52 days of age were mated and their oöcytes varied in size as follows:

1.08 mm. to 1.95 mm. ($\bar{x} = 1.43 \pm 0.02$, $N = 83$)

2.00 mm. to 2.97 mm. ($\bar{x} = 2.34 \pm 0.06$, $N = 21$)

3.11 mm. to 3.72 mm. ($\bar{x} = 3.30 \pm 0.08$, $N = 9$)

4.90 mm. to 5.88 mm. ($\bar{x} = 5.39 \pm 0.49$, $N = 2$)

A breakdown of the data into two age groups when mated was as follows:

Size of oöcytes (mm.) when mated	Age (days) when mated and number mated	
	14-25	26-52
1.08 - 1.95	50	33
2.00 - 2.97	8	13
3.11 - 3.72	0	9
4.90 - 5.88	0	2

As pointed out earlier our measurements are larger than Engelmann's because in our experiments the oöcytes were dissected and measured in Ringer's solution whereas he measured fixed oöcytes. The majority of the females mated when their oöcytes averaged 1.43 ± 0.02 mm. This value probably corresponds to Engelmann's mean of 1.08 ± 0.01 mm. However, 28% of the females mated when their oöcytes were more developed. Thirty-six females that failed to mate when exposed to males along with the above females that copulated had oöcytes that ranged from 1.01 to 1.68 mm. ($\bar{x} = 1.19 \pm 0.02$ mm.; $N = 25$) and 2.05 to 5.88 mm. ($\bar{x} = 4.54 \pm 0.38$ mm.; $N = 11$).

There was a slight but not very significant shortening of the inter-

val between age at mating and age at ovulation when older females mated (Engelmann, 1960). Engelmann suggested that this shortening of the period needed for egg maturation could be explained by the presence of larger amounts of reserve substances that would allow for more rapid growth of the eggs and might not be due to the presence of larger oöcytes at the later mating. Our findings confirm Engelmann's in that *Leucophaea* tend to mate more readily when their oöcytes reach a certain size. However, some females mate even though their oöcytes have grown beyond this critical size and the shortening of the period between mating and ovulation is undoubtedly due to the presence of large oöcytes in these older females; some females mate even when there is a high titer of corpus allatum hormone (as indicated by large oöcytes).

Engelmann (1960) found that when the nerve cord of *Leucophaea* was severed 0 to 2 days after mating, oöcyte maturation occurred about a week later than normal mated females. When the cord was severed 3 to 19 days after mating, the females oviposited at the same age as normal mated females indicating that an intact nerve cord is necessary for at least 2 days after mating for the mating stimulus to be effective. When the nerve cords of virgin females were severed and they were not mated, ovulation occurred at the same time as females that had their nerve cords severed 0 to 2 days after mating. Engelmann concluded that severance of the ventral nerve cord in virgins either stimulates the corpora allata or cuts off an inhibitory center for the corpora allata but he favored the latter hypothesis.

We severed the nerve cords of females *prior* to mating them and found that in most cases the spermatophore was not inserted properly. Of 27 females that mated after their nerve cords were severed, only 8 had spermatophores that were apparently transferred by the male normally. Four females had spermatophores that were visible in the genital region but they had not been inserted properly in the bursa. In one mating the spermatophore was dropped by the male without being transferred to the female. Fourteen females had no spermatophores after mating and originally it was believed that none had been transferred by the male. However, it was discovered that in some females the male pierced the wall of the uterus and inserted the spermatophore in the body cavity near the right ovary (fig. 13C). This was found in 7 females but may have occurred in 6 others that apparently had no spermatophore inserted but were not dissected because we did not realize that the spermatophore could be inserted into the body cavity. One female had no spermatophore after mating, based on dissection. It seems that the female takes an active role in the

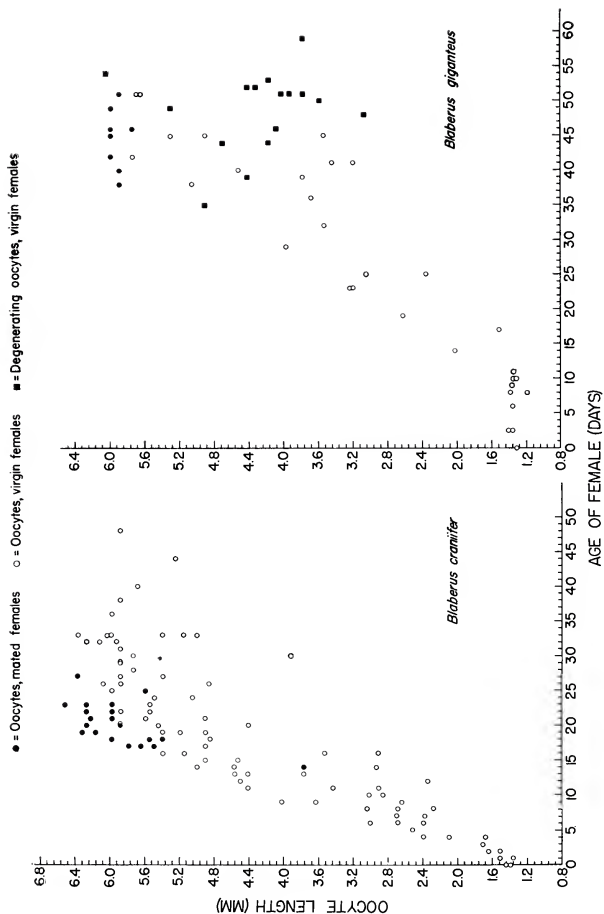


Fig. 9. Oocyte development in mated and virgin females of *Blaberus*. Each point represents one individual. Females of *B. craniifer* were mated when 1 to 16 days old. Females of *B. giganteus* were mated at 19 to 35 days of age and all were ovipositing when their oocytes were measured.

proper positioning of the spermatophore in the bursa copulatrix, and an intact nerve cord is needed for proper muscular movements of the female genitalia. Of 11 nerve-cord-severed virgin females that oviposited 7 dropped their egg cases when they were formed and 4 retracted the oötheca into the uterus but aborted some time later.

Blaberus craniifer: The growth of the oöcytes of virgins is rapid but mating affords sufficient additional stimulation (fig. 9) so that ovulation occurs about a week earlier than in unmated individuals (fig. 4). Eighteen mated females oviposited in 19 to 29 days ($\bar{x}=23.9\pm0.6$ days); sixteen oviposited normally, 1 dropped its oötheca and 1 failed to retract the egg case completely. Virgin females oviposited in 18 to 41 days ($\bar{x}=32.0\pm0.8$; $N=36$). Stimulation from mating results in either an additional production of gonadotropic hormone or it may possibly serve as an oviposition stimulus. The relationship of age at mating and age at oviposition of the female is similar to that found in *Byrsotria* (fig. 3). The older the female when mated the shorter the interval to ovulation indicating that the oöcytes of these older females are large when mating occurs.

Of 40 virgin females that oviposited 23 (58%) failed to retract the egg case completely and some of the eggs protruded beyond the abdomen. This may be due to the fact that in some females the eggs are not aligned properly in the oötheca and may even be arranged in 3 rows (rather than 2) which may make it difficult to retract the egg case completely into the uterus. Generally, in most virgin females that ovulate, the proper amount of colleterial gland secretion does not flow out over the eggs since the accessory glands are usually quite full even after the egg case is formed. Sometimes not all of the eggs are laid and mature oöcytes remain in the ovaries and are eventually resorbed. Thirteen females retracted the oötheca normally into the uterus. Four females dropped the oötheca although some eggs remained in the uterus. Perhaps this is related to the lack of proper amount of colleterial gland secretion being poured out around the eggs; the result may be the formation of a weak oötheca which cannot support the weight of the eggs as they are extruded some distance beyond the end of the abdomen prior to their being retracted. In addition to the above 40 females, 5 unmated females that did not oviposit in 46 to 51 days had oöcytes that had obviously matured (based on size) but were degenerating.

Six allatectomized virgin females that had not ovulated had corpora allata implanted at 62 to 82 days of age; all 6 oviposited within 31 days after implantation. Nine allatectomized virgin females kept for 66 to 238 days failed to ovulate.

All the nerves to the corpora allata were severed in 11 virgin females and the glands were left in the animals; ten oviposited in 21.8 ± 0.49 days which is similar to ovulation in mated females. This would indicate that the brain tends to inhibit the corpora allata in virgin *B. craniifer* and mating overcomes this inhibition.

Blaberus giganteus: The oöcytes of virgins grow and yolk is deposited but after about a month they may degenerate unless mating occurs (fig. 9). In general mating appears to be necessary for completion of oöcyte development, at least more so than in *B. craniifer*. Fourteen females kept with males until mating occurred, mated at 8 to 35 days of age and oviposited when 35 to 51 days old ($\bar{x} = 42.6 \pm 1.3$ days). Of 8 virgin females, not shown in figure 8, kept for 51 to 68 days, only 2 oviposited when 51 days old, and in both individuals the oöthecae were dropped and not retracted; the 6 females that did not oviposit had small abnormally shaped oöcytes that failed to develop.

The relationship between age when mated and age at ovulation (fig. 3) appears to be similar to *Byrsotria* and *B. craniifer* rather than *Leucophaea*. The females of *B. giganteus* which have continuous access to males, mate over a rather wide age range, and their oöcytes may vary considerably in size at the time of mating.

Thirteen of 14 virgin females that had all the nerves to the corpora allata severed at 0 to 19 days of age ovulated in 35.1 ± 1.2 days after the operations; one oviposited 153 days after the operation at 163 days of age. Severing the connectives to the corpora allata apparently removed the inhibition from the brain.

The effects of mating vary in degree among the species of cockroaches that incubate their eggs internally or carry them externally during the incubation period. In the summary given below, data from Engelmann, (1957, 1959, 1960), Roth and Willis (1961) Roth and Stay (1961, 1962), and the present study have been used.

I. Effect of mating on oöcyte development.

1. Oöcytes of virgins may degenerate:

- a. before reaching ovulation size (*Nauphoeta cinerea* and *Blaberus giganteus*)
- b. before or after reaching ovulation size (*Byrsotria fumigata*)

Mating prevents degeneration of the oöcytes in the above 3 species. The oöcytes of virgins generally do not degenerate in *Blaberus craniifer* (rarely), *Diploptera punctata*, *Leucophaea maderae*, *Pycnoscelus surinamensis* (parthenogenetic and bisexual strains), *Blattella germanica*, and *Blattella vaga*.

2. Mating increases rate of oöcyte development so that the first preoviposition period is less than in virgin females. Preoviposition period shortened on an average of about:
 - a. 1 day (*Pycnoscelus surinamensis*, bisexual strain; *Blattella*).
 - b. 9 or more days (*Blaberus craniifer*, *Blaberus giganteus*).
 - c. 17 days (*Nauphoeta cinerea*).
 - d. 30 or more days (*Leucophaea maderae*).
 - e. Majority of virgins do not oviposit for months or not at all. Oviposition occurs about 10 days after mating (*Diploptera punctata*).
3. Mating apparently has little effect on the rate of oöcyte development but may stimulate oviposition (*Byrsotria fumigata*).
4. Mating has no effect on rate of oöcyte development or on the length of the preoviposition period (*Pycnoscelus surinamensis* — parthenogenetic strain mated to males of the bisexual form).

II. Effect of mating on ovulation and oviposition.

1. Ovulating virgins frequently retain mature oöcytes in some part of the reproductive tract so that not all of the eggs are laid (*Blaberus craniifer*, *Blattella vaga*, *Byrsotria fumigata*, *Leucophaea maderae*, *Nauphoeta cinerea*, *Pycnoscelus surinamensis* bisexual strain).

Mated females usually oviposit all of the mature oöcytes.

2. Oötheca is incompletely formed and oviposition is abnormal in a large percentage of virgins.
 - a. Oötheca usually dropped when formed (*Leucophaea maderae*, *Pycnoscelus surinamensis* [bisexual strain], *Blattella vaga*).
 - b. Oötheca dropped or partly retracted into the uterus (*Nauphoeta cinerea*).
 - c. Oötheca usually only partly retracted into the uterus so that some of the eggs protrude from the end of the abdomen (*Blaberus craniifer*).

Mating in a large percentage of females results in normal formation of the oötheca and complete retraction of the egg case into the uterus in the above species.

3. Oötheca may be retracted normally into the uterus in a high percentage of virgins (*Byrsotria fumigata*, *Diploptera punctata*, and *Nauphoeta cinerea*).
4. Mating has no effect on normal oviposition (*Pycnoscelus*

surinamensis — parthenogenetic strain mated to males of the bisexual form).

From the preceding summary one finds two extremes of dependence upon mating for stimulation of the corpora allata. In *Diploptera*, the majority of females require mating for maturation of the oöcytes and its effect is the most striking since ovulation occurs about 10 days after mating, whereas virgin females may go for months without ovipositing or they may never do so (Engelmann, 1959, 1960; Roth and Stay, 1961). At the other extreme is the parthenogenetic strain of *Pycnoscelus surinamensis* where mating is unnecessary and the oöcytes mature in virgins about 13 days after emergence. In this species some newly-emerged females already may have yolk in their oöcytes. Between these two extremes are species which show varying degrees of dependence on external mating stimuli for overcoming inhibition of the corpora allata. The oöcytes in virgins grow but unless mating occurs the ovarian eggs do not mature and may degenerate before reaching ovulation size. This is particularly true in *Nauphoeta*, *Byrsotria*, and *Blaberus giganteus* and apparently in these species the corpora allata in many virgin females secrete an insufficient amount of hormone for the oöcytes to mature; and in many of these females the partly developed oöcytes are not maintained but degenerate unless the corpora allata are stimulated by mating.

Various species show different degrees of dependence on mating for normal formation and retraction of the oötheca into the uterus. This is of particular interest, for the ability of virgin females to place the oötheca in the brood sac is a prerequisite to the evolution of parthenogenesis in false ovoviviparous cockroaches (Roth and Willis, 1961). Not all females of a species behave similarly which explains why some forms are included in more than one category in the above summary. It is this variation in behavior which may make possible the evolution of parthenogenesis in bisexual species of cockroaches. From the few species studied one can arrange the forms in a series to show the gradual evolution of retraction of the oötheca into the uterus in virgin females, although we do not imply that one gave rise to the other. Almost invariably in the bisexual strain of *Pycnoscelus surinamensis* the oötheca is dropped at formation in virgins. In *Nauphoeta* the oötheca is dropped at formation, partly retracted, or completely retracted. In *Blaberus craniifer* the oötheca is usually only partly retracted into the uterus. In *Byrsotria* the oötheca of virgins that ovulate is usually normally retracted into the brood sac. Although parthenogenesis is uncommon in false ovoviviparous cockroaches (other than the parthenogenetic strain of *Pycnoscelus*) it does occur

rarely. Nine females of *Nauphoeta cinerea* had eggs that developed parthenogenetically and in 8 individuals the eggs hatched; two unmated females that developed from unfertilized eggs gave birth to 3 nymphs (Roth and Willis, 1956). We have encountered only one case of parthenogenesis in *Leucophaea* (20 undeveloped eggs and 5 well developed embryos with pigmented eyes in an oötheca 89 days after ovulation) and one in *Byrsotria* (2 well developed embryos, 55 days after oviposition); Barth (personal communication) has reared a single adult female of *Byrsotria* that was produced parthenogenetically. Only one unmated female of the bisexual strain of *Pycnoscelus* was found that had a developed embryo in one of the eggs of the oötheca (Roth and Willis, 1961). Parthenogenesis in false ovoviviparous cockroaches depends upon (1) the ability of virgin females to mature their oöcytes, ovulate, and form and retract the oötheca into the uterus, and (2) the capacity for unfertilized eggs to develop. Although parthenogenesis cannot occur unless the above requirements are met, the insects must first be capable of retracting the oötheca into the uterus for unless this occurs the eggs desiccate since the oötheca does not prevent water loss in cockroaches that incubate their eggs internally (Roth and Willis, 1955).

No experiments were performed on the species, in this study, to determine the mechanism of stimulation during mating. However, in *Leucophaea* (Engelmann, 1960) and *Diploptera* (Engelmann, 1959, 1960; Roth and Stay, 1961) it is a mechanical stimulus that activates the corpora allata and it is probably similar in *Pycnoscelus* (bisexual strain), *Nauphoeta*, and *Blaberus*.

Food intake and maturation of the oöcytes

Food intake stimulates maturation of the oöcytes in *Leucophaea* (Scharrer, 1946; Johansson, 1955; Engelmann, 1960) and *Blattella germanica* and *B. vaga* (Roth and Stay, 1962) but is unnecessary for oöcyte development in *Diploptera* (Engelmann, 1960; Roth and Stay, 1961). The effect of starvation on oöcyte development in several species used in this study was determined; all females were isolated from food at emergence.

Pycnoscelus surinamensis: Fifteen females of the parthenogenetic strain were starved without water. All oviposited in 14.1 ± 0.4 days, which was about 1 day more than in unstarved females (table 1). Nine virgin females of the bisexual strain starved without water oviposited in 14.3 ± 0.5 days, which was similar to unstarved individuals (cf. table 1). Food is unnecessary in both strains to activate the corpora allata or for maturation of the eggs for the first ovulation.

Nauphoeta cinerea: The effect of starvation on oöcyte development in *Nauphoeta* is shown in figure 6. The oöcytes of starved virgin females develop more slowly and to a lesser degree than those of fed virgin females. When starved females were mated the oöcytes matured in the same period as fed mated females. In *Leucophaea*, females that were starved but mated failed to deposit yolk in the oöcytes and Engelmann (1960) concluded that the brain properly integrated the different afferent stimuli (inhibitory during starvation and activating from mating) into messages to the corpora allata and the endocrines were not activated. *Nauphoeta* differs from *Leucophaea* in that the oöcytes of starved females become well developed and mating adds sufficient stimulation to the corpora allata for the oöcytes to mature normally in spite of the absence of food.

Blaberus craniifer: Seven virgin females of *Blaberus craniifer* were starved (with water) for 22 to 39 days. In 6 females the oöcytes measured 4.82 ± 0.19 mm.; one female had oöcytes that did not develop (1.38 mm.). The oöcytes of fed females 22-38 days of age were 5.61 ± 0.11 . Although there may be a slightly slower rate of growth of the oöcytes in starved females, food is unnecessary for initiating activity of the corpora allata.

Byrsotria fumigata: Twenty-four virgin *Byrsotria* were starved (with water) for 20 to 45 days. Six females starved 20 to 24 days had oöcytes 4.22 ± 0.35 mm. long. Eight starved 29 to 40 days had oöcytes 4.86 ± 0.36 mm. in length (several had oöcytes that had begun to degenerate). Two females had small undeveloped oöcytes (0.88 ± 0.01 mm.) and 8 had small, round, abnormally shaped oöcytes. Thirty-three virgin females were starved without water for 26 to 50 days. Nine (starved 26 to 43 days) had oöcytes 5.01 ± 0.30 mm. long. Twelve had large oöcytes that were degenerating. Five females oviposited in 34 to 38 days; four had undeveloped oöcytes (1.14 ± 0.08 mm.) and 3 had small abnormally shaped oöcytes. The oöcytes of virgin females fed for 20 to 24 days were 4.85 ± 0.32 ($N=17$) and for 29 to 40 days, 6.36 ± 0.22 ($N=39$). Although the oöcytes of starved females may not grow quite as rapidly as unstarved individuals, neither food nor water are necessary for growth of the oöcytes in *Byrsotria*.

The degree to which cockroaches depend upon food intake for stimulation of the corpora allata varies among the species. The forms may be arranged in a series showing complete dependence to complete independence upon food for oöcyte development. The effects of starvation may be summarized as follows:

1. Oöcytes do not develop (*Leucophaea*, *Blattella germanica*, and *Blattella vaga*).

2. Oöcytes develop but at a slower rate and to a lesser degree than in fed females (*Nauphoeta*).
3. Oöcytes develop at a normal or slightly slower rate than fed females (*Blaberus craniifer*, *Byrsotria*).
4. Oöcytes mature about as rapidly as fed females (*Diploptera*, *Pycnoscelus surinamensis* — bisexual and parthenogenetic strains).

Inhibition of the corpora allata during pregnancy

During the first gestation the basal oöcytes, in all of the species investigated in this study, usually remain undeveloped except for a small increase in length; some *Nauphoeta* females may have oöcytes containing yolk at parturition. Yolk deposition occurs in these basal oöcytes only after parturition (except in *Diploptera* and some *Nauphoeta*). This has already been pointed out in *Pycnoscelus* (fig. 1). Very similar cycles occur in *Blattella* (Roth and Stay, 1962), *Leucophaea* (Engelmann, 1957) and *Diploptera* (Engelmann, 1959; Roth and Stay, 1961). However in *Diploptera* the oöcytes begin to show deposition of yolk about 3 days before parturition (Engelmann, 1959; Roth and Stay, 1961). Although complete ovulation cycles are not given for *Blaberus*, *Byrsotria*, and *Nauphoeta*, measurements of the new oöcytes at ovulation, and at parturition show that inhibition of the corpora allata during gestation also occurs in these forms. In *Leucophaea* (Engelmann, 1957, 1960), *Diploptera* (Engelmann, 1959; Roth and Stay, 1961), and *Pycnoscelus* (Roth and Stay, 1959) removal of the oötheca results in resumption of growth of the oöcytes prematurely, indicating that the oötheca in the uterus, in some manner, inhibits the activity of the corpora allata. The following experiments were performed to investigate the nature of inhibition of the corpora allata during gestation.

Pycnoscelus surinamensis: The oöthecae were removed from 84 females of the parthenogenetic strain, 62 (74%) of which subsequently ovulated. Of the 22 females that failed to oviposit 25 to 37 days after the operation, 15 had oöcytes that showed essentially no development (0.64 to 0.79 mm.) and 7 had oöcytes with definite yolk deposits (0.84 to 2.39 mm.); one female had oöcytes that had apparently matured but had not been laid and were being resorbed. There is an inverse relationship between the age of the oötheca at the time it is removed from the uterus and the time required to ovulate again. Less time is required to ovulate again, the older the uterine eggs are when removed (fig. 10). This relationship also has been found in *Blattella* and *Diploptera* (Roth and Stay, 1961, 1962). One

of the factors which might account for this may be that the oöcytes increase in size during gestation so that at the time an older oötheca is removed the oöcytes are larger when again subjected to gonadotropic hormone. The larger oöcytes may contain greater amounts of reserve substances allowing for a more rapid maturation of the eggs.

Since the period between the first and second ovulations is about 70 days (table 1) it is evident from figure 10, showing the relatively

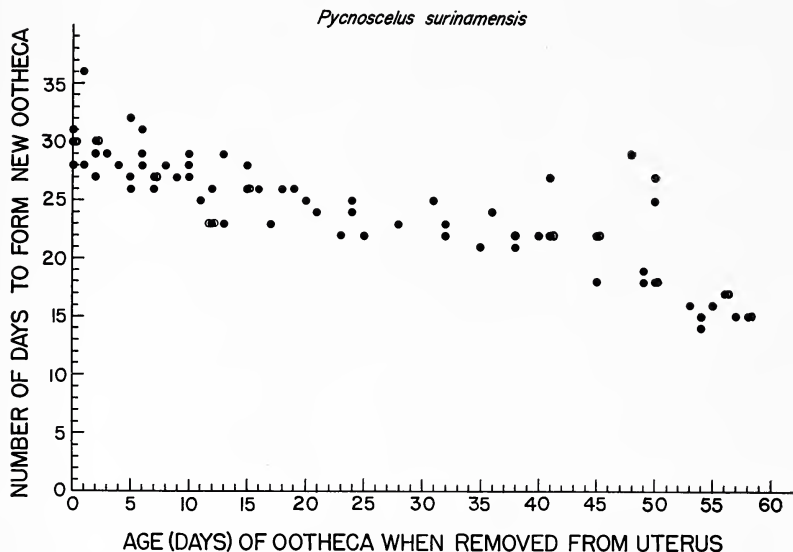


Fig. 10. Relationship between the age of the oötheca at the time it was removed from the uterus of *Pycnoscelus surinamensis* (parthenogenetic strain) and the time required to form a new oötheca. Each point represents one individual. The points at 53 to 58 days on the x axis, are for females that gave birth normally; all of the other points are based on females that had their oöthecae removed manually.

rapid development of the oöcytes (as indicated by oviposition) after removal of the oötheca, that the oöcytes are inhibited by the presence of the eggs in the uterus.

Virgin females of the bisexual strain of *Pycnoscelus* almost invariably fail to retract their oöthecae into the uterus (Roth and Willis, 1961). Fourteen virgin females that had dropped their oöthecae when they were formed, oviposited again in 28 to 39 days ($\bar{x}=32.9\pm 1.1$ days). The normal interval between the first and second ovulations in this strain is about 67 days (53 days of gestation plus 14 days postparturition, table 1) and the absence of uterine eggs in the brood sac resulting from aberrant oviposition hastened the development of

the oöcytes. Three mated bisexual form females that failed to retract their oöthecae also formed the second egg case in 30.3 ± 2.7 days. Three mated females that had their oöthecae removed 2, 5, and 7 days after oviposition ovulated again in 32 to 33 days. Both strains of *Pycnoscelus* are similar in that the presence of an oötheca in the uterus inhibits the development of the oöcytes.

Leucophaea maderae: The oöthecae were removed from 102 pregnant females at different stages in pregnancy to determine the time required for the next ovulation. Forty-three females oviposited during the period of the experiment and these results are plotted in figure 11. As in *Pycnoscelus* the time required to ovulate after removal of the oötheca varied with the age of the oötheca when it was removed; the younger the oötheca the longer it took to mature the oöcytes. Of the remaining females, 45 showed little or no growth of the oöcytes; those whose oöthecae were removed 0 to 18 days after ovulation had oöcytes 1.06 ± 0.03 mm. ($N=22$), 62 to 82 days later and 23 females whose

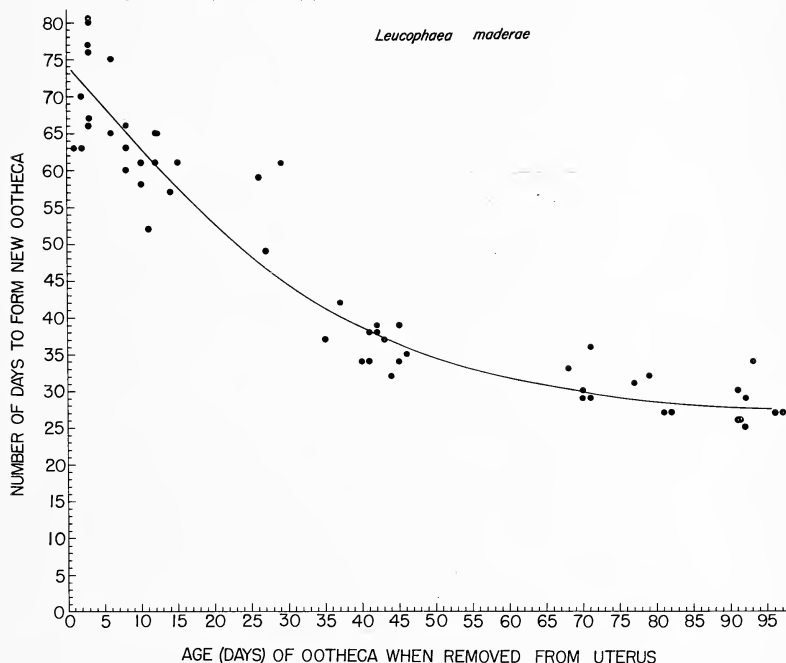


Fig. 11. Relationship between the age of the oötheca at the time it was removed from the uterus of *Leucophaea maderae* and the time required to form a new egg case. The points plotted at 82 to 97 days on the x axis are for females that gave birth normally; all of the other females had their oöthecae removed manually. Each point represents one female.

oöthecae were removed 23 to 76 days after oviposition had oöcytes 1.19 ± 0.04 mm., 34 to 63 days later. Fourteen females that had their oöthecae removed 0 to 77 days after ovulation had developed oöcytes 3.72 ± 0.30 mm. long, 34 to 71 days later. It is unknown why about 45% of the females failed to show oöcyte development after removal of the oötheca; the presence of degenerating oöcytes that were not laid in the first ovulation may account for some of these cases.

Byrsotria fumigata: In *Byrsotria* gestation lasts from 71 to 82 days ($\bar{x}=76.2 \pm 1.4$; $N=6$). The basal oöcytes at parturition vary in length from 1.43 mm. to 1.71 mm. ($\bar{x}=1.53 \pm 0.04$ mm.; $N=10$). The second ovulation occurs 21 to 30 days ($\bar{x}=24.8 \pm 1.6$; $N=5$) after parturition. Oöcyte development during pregnancy in mated females is inhibited and no yolk is deposited until after the young are born.

Five mated females had their oöthecae removed at various periods during pregnancy. One whose oötheca was removed 27 days after ovulation oviposited 45 days later. Two females whose oöthecae were removed 28 and 40 days after oviposition had practically mature oöcytes, 5.98 mm. and 6.22 mm. (fig. 14B) respectively, 32 days later. The oöcytes (1.23 and 1.29 mm. long) of two females whose oöthecae were removed on the first and thirty-first day of pregnancy failed to develop when examined after 75 and 32 days. The oöthecae of 10 virgin females were also removed with the following results. Three females whose oöthecae were removed 29 to 34 days after ovulation had mature oöcytes that were being resorbed 53 days later. One female whose oötheca was removed 38 days after oviposition ovulated again 39 days later. Six females whose oöthecae were removed from 1 to 24 days after oviposition failed to develop their oöcytes ($\bar{x}=1.53 \pm 0.05$ mm.) when examined 35 to 59 days after the operations. In the mated and virgin females that failed to develop oöcytes after removal of the oöthecae, several unlaid degenerating oöcytes were present from the previous ovulation which may account for the results.

Virgin females of *Byrsotria* that deposit their unfertilized eggs normally in the brood sac frequently carry these oöthecae for a longer period of time than mated females. When the undeveloped eggs are finally extruded the ovarian oöcytes may be large and contain considerable yolk in spite of the fact that an oötheca was present in the uterus during the entire "pregnancy" period. Thirteen females that carried their unfertilized eggs for 71 to 90 days had oöcytes 1.51 ± 0.04 mm. which is normal for the size of the oöcytes at parturition of mated females. However, the oöcytes of 14 virgins that had carried their oöthecae for 87 to 97 days had oöcytes that varied in length from

2.86 to 6.12 mm. ($\bar{x}=4.60\pm0.23$ mm.). One mated female that aborted an oötheca with undeveloped eggs after carrying for 79 days had oöcytes 3.72 mm. long. It is apparent that toward the end of the "gestation" period in virgin females or once the time at which parturition should normally take place is passed, the inhibition of the corpora allata (due to the presence of the oötheca in the uterus) breaks down and these endocrines again secrete the gonadotropic hormone. Eleven virgin females that aborted their oöthecae 91 to 104 days after ovipositing, were kept until they ovulated a second time. Five of the females oviposited in 21 to 30 days ($\bar{x}=25.6\pm1.6$) which is the same as mated females indicating that their oöcytes at the time of aborting were relatively undeveloped. The other 6 virgin females ovulated in 11 to 18 days ($\bar{x}=14.8\pm1.4$) undoubtedly because their oöcytes were already well developed when the egg cases containing undeveloped eggs were extruded from the uterus.

Blaberus craniifer: The oöcytes of this species at emergence are about 1.39 to 1.44 mm. ($N=2$) in length. The mature oöcytes are about 6.12 to 6.37 mm. ($N=3$) and at oviposition the new basal oöcytes vary from 1.02 to 1.16 mm. ($\bar{x}=1.09\pm0.03$; $N=7$). At parturition the oöcytes are 1.34 to 1.85 mm. ($\bar{x}=1.56\pm0.07$; $N=6$). Gestation lasts 73 to 87 days ($\bar{x}=79.2\pm2.4$; $N=5$). After birth, a second ovulation occurs in 16 to 27 days ($\bar{x}=22.0\pm1.9$; $N=5$).

Six virgin females had their oöthecae removed on the day of oviposition. One oviposited again 47 days later. The others were dissected 44 to 60 days later and all had well-developed oöcytes (3.96 ± 0.43 mm.). One female whose oötheca was removed 8 days after ovulation had oöcytes 5.88 mm. long, 54 days later. Two females whose oöthecae were removed 73 days after oviposition (i.e. close to parturition in mated females) had oöcytes 3.23 mm. and 3.82 mm. long, only 10 days later. Removal of the oötheca in *B. craniifer* results in renewed development of the oöcytes.

The principal evidence for Engelmann's (1957) hypothesis that a hormonal factor from uterine eggs inhibits the corpora allata via the brain was his claim that implantation of uterine eggs into the abdomen of females of *Leucophaea* inhibited oöcyte development, and nerve cord severance of pregnant females only had a slight but temporary effect on growth of the oöcytes. However, more recently, Engelmann (1960) found that severance of the nerve cord in pregnant females results in growth of the oöcytes indicating that nervous stimuli may also be responsible for inhibition of the corpora allata during pregnancy.

We have repeated these and performed additional experiments on the following species of cockroaches:

Pycnoscelus surinamensis (parthenogenetic strain): Some of the experiments on this species were briefly described elsewhere (Roth and Stay, 1959). The oötheca was removed from the uterus of each of 10 females 1 to 16 days after oviposition and one-half of each oötheca was implanted into the body cavity of the donor female. Twenty-three days after the operation the oöcytes ranged in length from 2.12 mm. to 3.19 mm. ($\bar{x}=2.70\pm0.10$ mm.) clearly larger than the oöcytes of females that have been pregnant for 24 to 39 days which vary from 0.59 to 0.66 mm. Implantation of uterine eggs into the abdomens of females that had their oöthecae removed did not prevent subsequent growth of the oöcytes. Two of the 10 females had oöcytes that had practically matured and the oöcytes of the remaining 8 females were approaching maturity (2.97 to 3.36 mm., cf. table 1) and undoubtedly would have matured in about the time one would expect ovulation following removal of the oötheca (cf. fig. 10). One-half of young oöthecae were implanted into the body cavities of 6 females one day old or less; after 11 days the oöcytes were 2.65 to 3.14 mm. ($\bar{x}=2.91\pm0.10$) in length. The oöcytes of untreated 11-day old females averaged 2.93 ± 0.06 mm. ($N=10$). These results show that uterine eggs when implanted into the abdomen of a recently emerged female have no effect on the initial development of the oöcytes. Nor does implantation of uterine eggs into the abdomen of a female that had her oötheca removed inhibit subsequent development of the oöcytes.

The oöthecae of 20 pregnant females were removed 13 to 25 days after ovulation and a wax "oötheca" about the size and shape of a normal oötheca was inserted into the uterus. Examined 20 to 37 days later all had small oöcytes (fig. 13A) similar in size to those found in females that were pregnant for 36 to 52 days (table 3). However

EXPLANATION OF FIGURE 12

Fig. 12A. *Pycnoscelus surinamensis* (parthenogenetic strain). Oötheca (upper) and ovaries (lower) of a female that had been pregnant 60 days and whose nerve cord was severed on the thirty-second day of pregnancy. When dissected 28 days after the operation, the embryos in the oötheca began to hatch. The oöcytes in the ovary had matured but were being resorbed. (Note the abundant colleterial gland secretion [arrow]). Vertical line=3 mm.

Fig. 12B, 12C. *Blaberus craniifer*. B. Mated female whose nerve cord was severed 26 days after oviposition. The oötheca (0) containing well developed embryos (note pigmented eyes) was being aborted 34 days after the operation. The oöcytes (arrow) were 5.88 mm. long. C. Virgin female that had carried an oötheca with undeveloped eggs for 93 days (well beyond the normal gestation period). The oöcytes were 3.92 mm long. Vertical line=5 mm.

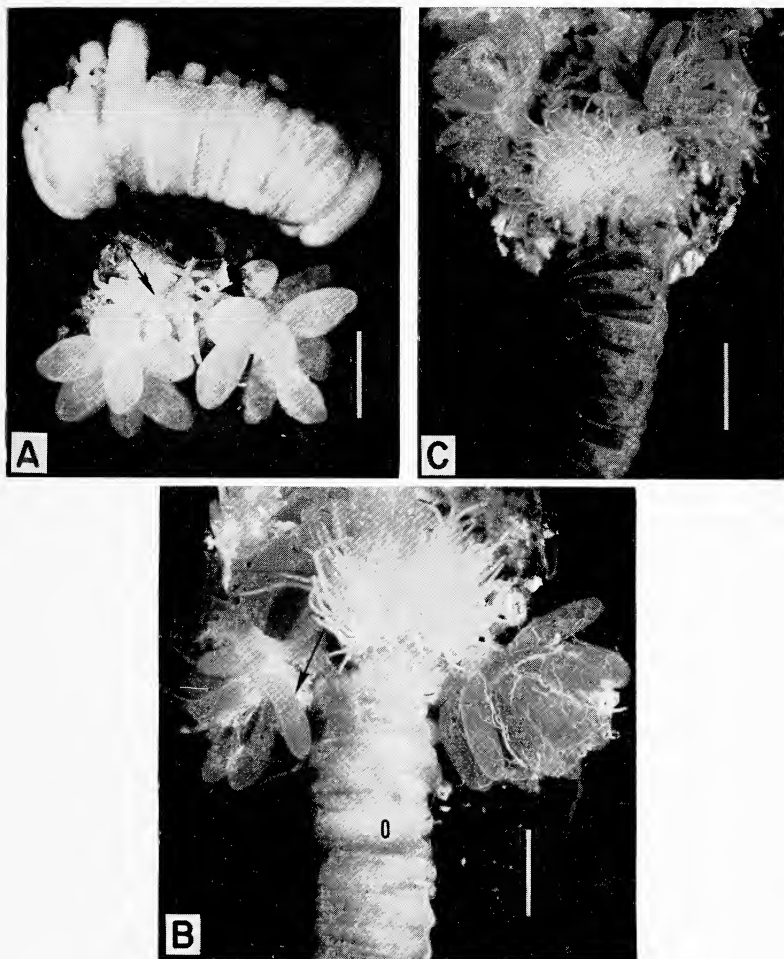


Table 3 — Effect of inserting a wax "oötheca" into the uterus and subsequent nerve cord severance on oöcyte development in the parthenogenetic strain of *Pycnoscelus surinamensis*

AGE (DAYS) OF OÖTHECA WHEN REMOVED AND WAX WAS INSERTED INTO UTERUS	DAYS AFTER INSERTION OF WAX, OÖCYTES WERE MEASURED	DAYS ♀ HAD OÖTHECA OR OÖTHECA THEN WAX IN UTERUS	OÖCYTES (MM.) MEAN \pm S.E.	N
13-25	20-37	36-52	0.70 ± 0.01	20
Control (oötheca in uterus)	—	36-52	0.71 ± 0.01	17
Nerve cord severed after insertion of wax				
15	32 (8) ¹	47	1.09	1
15	33 (9)	48	1.18	1
13	37 (13)	50	2.40 ± 0.03	3
Control (oötheca in uterus; nerve cord intact)	—	47-50	0.72 ± 0.01	8

¹Numeral in () = number of days, prior to measuring oöcytes, nerve cord was severed.

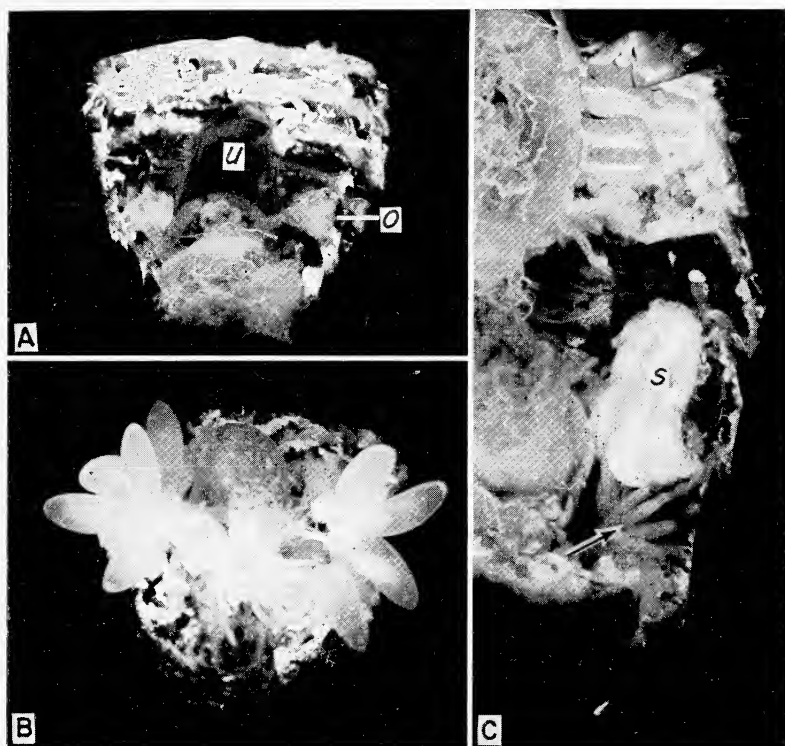


Fig. 13A-B. *Pycnoscelus surinamensis* (parthenogenetic strain). A. Ovaries (O) undeveloped as the result of the presence of a wax "oötheca" in the uterus (U). The oötheca was removed on the thirteenth day of pregnancy, and replaced with wax. The female was dissected 37 days later. B. Oöcytes which developed in a female that had a wax "oötheca" in its uterus for 37 days. The oötheca was removed 13 days after ovulation and replaced by wax. Twenty-four days later the nerve cord was severed and the female was dissected 13 days later.

Fig. 13C. *Leucophaea maderae*. Dissection of a female that mated after her nerve cord had been transected. The spermatophore (S) was inserted by the male into the body cavity near the right ovary (arrow).

Table 4 — Effect of nerve cord severance on oöcyte development in the parthenogenetic strain of *Pycnoscelus surinamensis*

DAYS AFTER OVIPOSITION NERVE CORD WAS SEVERED	DAYS AFTER OPERATION OÖCYTES WERE MEASURED	OÖCYTES (MM.) MEAN \pm S.E.	N
< 1	24	2.08 \pm 0.07	3
4	25	2.94	1
< 1	26	2.57 \pm 0.30	2
0 ¹	29	3.06 ²	1
< 1	31	3.52 \pm 0.16 ²	2
< 1	32	2.94	1
27-32	23-33	Oöcytes matured and degenerating ³	5
Controls (sham operated)			
1-4	25	0.67 \pm 0.01	4
< 1	29	0.65 \pm 0.02	4
1	38	0.66 \pm 0.02	5

¹Operated on just after the female retracted the oötheca.

²Oöcytes matured.

³The uterine eggs of these females were completely developed and parturition was imminent. The eggs began to hatch (fig. 12A) from 3 of the 5 females after their oöthecae were removed from the uterus.

when the nerve cords were severed in five females that had been carrying a wax "oötheca" in the uterus for 24 days, the oöcytes were well developed (fig. 13B) 8 to 13 days later (table 3).

The effect of nerve cord severance in pregnant females on development of the oöcytes is shown in table 4. The oöcytes could mature (2.97 to 3.36 mm., table 1), in females carrying oöthecae once the nerve cord was severed. The time required for the oöcytes to mature in pregnant nerve-cord-severed females was essentially the same as that taken by females after their oöthecae were manually removed. When removed at 0 days a new oötheca was formed in about 28 to 31 days. When removed after 27 to 32 days of pregnancy ovulation occurred about 22 to 25 days later (fig. 10). The five females that had their nerve cords severed 27 to 32 days after oviposition all had mature oöcytes that were degenerating or being resorbed 23 to 33 days later at the time the uterine eggs were ready to hatch (fig. 12A). Apparently oviposition could or did not occur while an oötheca was

in the brood sac, and the mature oöcytes degenerated. In addition to the fifteen females shown in table 4, two females had their nerve cords severed prior to ovulation and oviposited normally; 24 and 25 days later their oöcytes had grown considerably and were 2.18 mm. and 2.72 mm. respectively. The nerve cord may be severed at any site between the second and sixth segments to eliminate the inhibition of the corpora allata during pregnancy. Two females had their nerve cords severed between the second and third abdominal segments 4 days after oviposition; 29 days later their oöcytes were 2.75 ± 0.01 mm. Six females had their cords severed between the third and fourth, fourth and fifth or fifth and sixth abdominal segments, 4 days after oviposition; 22 days later their oöcytes were 1.89 ± 0.24 mm. long. Six pregnant females taken from cultures (histories unknown) had their nerve cords severed between the fourth and fifth, or fifth and sixth segments; 20 days later their oöcytes measured 2.28 ± 0.33 mm.

Unmated females of the parthenogenetic strain oviposited normally in 98 percent of 248 individuals examined (Roth and Willis, 1961). Twenty-two females had their nerve cords severed prior to oviposition. Of these, 15 (68%) ovulated in the normal period of time and deposited eggs in the uterus; 8 oviposited all their eggs and had normal oöthecae but the other 7 had small abnormally shaped oöthecae and from 1 to 12 mature oöcytes remained in their ovaries. The remaining 7 of the 22 females operated upon failed to retract the oötheca into the brood sac; in 4 of these one or more mature oöcytes remained in the ovaries but in the others all the eggs were laid. Of 9 females that were sham-operated when 1 to 4 days old, all oviposited normally and no mature oöcytes remained in their ovaries. Apparently an intact nerve cord is necessary for normal deposition of mature oöcytes and for normal formation and retraction of the egg case in some females of *P. surinamensis* (parthenogenetic strain). Some center, possibly in the brain, may be involved in this behavior.

Virgin females of the bisexual strain almost invariably fail to retract their oöthecae into the uterus (99% of 138 females, Roth and Willis, 1961) and drop the incompletely formed oötheca. Thirteen virgin females had their nerve cords severed when 1 to 9 days old. All oviposited abnormally, which is the typical behavior of virgins of the bisexual strain; 10 dropped their oöthecae and all had mature oöcytes left in their ovaries. The other 3 carried their oöthecae extruding from the abdomen but failed to retract them; 2 had some mature oöcytes left in the ovaries but the third had none. Virgin females of the bisexual strain with severed nerve cords behaved like unoperated virgin females in oviposition and deposition of mature oöcytes.

In *Blattella* pressure on the oöthecal chamber by the oötheca appears to be responsible for the inhibition of the oöcytes, the stimulus being transmitted via the nerve cord (Roth and Stay, 1959, 1962). When the oötheca is in the uterus of *Pycnoscelus* the ovipositor is bent forward and is held in that position by the egg case. This suggested the possibility that the gonapophyses might be involved in transmitting nervous stimuli to the brain which then inhibits the corpora allata. Two experiments on *Pycnoscelus* were performed to test this hypothesis. Glass beads (3-3.5 mm. in diameter) were inserted into the vestibule of 7 females 1 to 2 days of age. A small drop of ferrule cement on the anal segments prevented the beads from being extruded; the beads exerted pressure on the ovipositor. The oöcytes were measured at 3 different periods. At 5 days of age they were 1.77 ± 0.13 mm. ($N=4$), at 7 days, 2.20 mm. ($N=1$), and at 13 days, 2.85 ± 0.01 mm. ($N=2$). Normal females at 5, 7, and 13 days of age had oöcytes 2.03 ± 0.08 mm. ($N=9$), 2.28 ± 0.08 mm. ($N=15$), and 2.94 ± 0.04 mm. ($N=6$) respectively. The presence of a bead and the resulting pressure on the ovipositor of recently-emerged females had essentially no effect on the development of the oöcytes.

To determine if release of pressure by the oötheca on the ovipositor during gestation would result in resumption of oöcyte development, the oöthecae of pregnant females were partly extruded, a portion of the egg case was cut off and the remainder was pushed back into the uterus. This was done to 8 females 11 to 12 days after oviposition and their oöcytes were measured on the fifty-fourth to fifty-sixth days of pregnancy when the females gave birth or parturition was imminent. Five operations were successful in that the ovipositors were

EXPLANATION OF FIGURE 14

Fig. 14. Reproductive organs of *Byrsotria fumigata*.

A. Normal mated female sham operated (nerve cord) when pregnant 38 days and dissected after 70 days of pregnancy. The eggs (arrows) in the ovaries are undeveloped; U=uterus containing oötheca.

B. Mated female whose oötheca was removed 40 days after oviposition and dissected 32 days later. The eggs in the ovaries have almost matured (6.22 mm. long).

C. Mated female whose nerve cord was severed at 39 days of pregnancy and dissected 32 days after the operation (71 days pregnant). The eggs (arrows) in the ovaries have nearly matured (5.88 mm. long); U=uterus containing oötheca.

D. Virgin female allatectomized at one day of age. After 52 days, corpora allata from two females 9 to 10 days of age were implanted. Oviposition occurred 28 to 35 days after implantation of corpora allata. The eggs (arrows) in the ovary are almost full grown (5.88 mm.) although an oötheca remains in the uterus (U).

E. Ovary of a virgin female 43 days old. The oöcytes are large and degenerating (A-D= $\times 2$; E= $\times 4$).

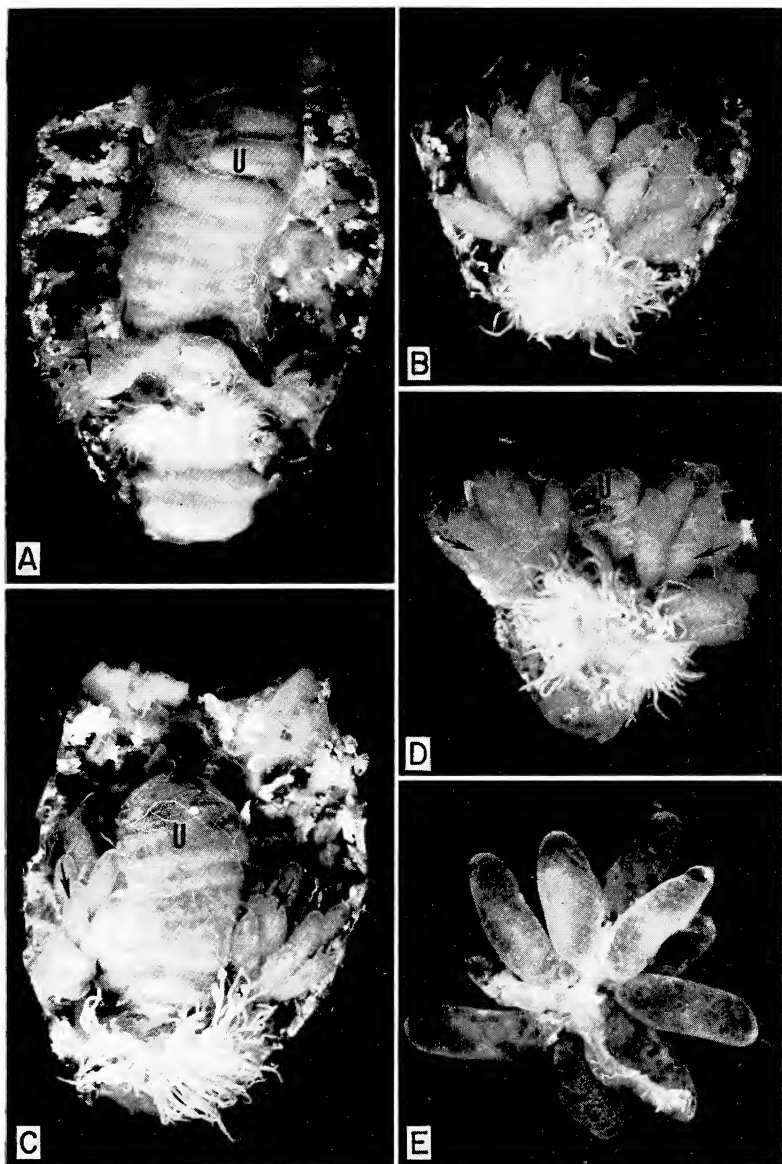


Table 5 — Effect on oöcyte development of various implants into the abdomens of virgins of *Byrsotria fumigata*

TYPE OF IMPLANT INSERTED INTO ABDOMEN	AGE (DAYS) OF FEMALE AT OPERATION	AGE (DAYS) WHEN OÖCYTES WERE MEASURED	OÖCYTES (MM.) MEAN \pm S.E.	N
Portion of an oötheca of <i>Byrsotria</i>	< 1	17	3.21 \pm 0.28	5 ¹
	1	19	3.77	1
	< 1-1	20	4.38 \pm 0.17	4 ¹
	1	23	4.53 \pm 0.12	2
	< 1	17	3.56 \pm 0.02	2
Entire oötheca of <i>Pycnoscelus</i>	2	20	4.50 \pm 0.20	4
Portion of an oötheca of <i>Leucophaea</i>	< 1,2	17	3.56 \pm 0.02	2
Controls				
Wax "oötheca"	1	17	3.69 \pm 0.14	3 ¹
	1	20	4.70 \pm 0.29	4
	-	17	3.81 \pm 0.23	7
Untreated	-	19	3.79 \pm 0.50	6
	-	20	4.55 \pm 0.35	5
	-	23	4.83 \pm 0.34	3

¹One female had oöcytes that were abnormally shaped and was not included in the measurements.

Table 6 — Effect of severing the nerve cord on development of the oöcytes, in *Byrsotria* females that were carrying oöthecae

DAYS AFTER OVULATION NERVE CORD WAS SEVERED	DAYS AFTER OPERATION OÖCYTES WERE MEASURED	OÖCYTES (MM.) MEAN \pm S.E.	N
<i>Virgin Females</i>			
O ¹	56-59	3.69 \pm 0.39	4
18	27, 33	4.03 \pm 1.11	2
28	33	5.39	1
O ¹	43-62	1.34 \pm 0.01	13
21-27	33	1.39 \pm 0.07	4
<i>Controls (sham operated)</i>			
O ¹	43-57	1.37 \pm 0.02	7
<i>Mated Females</i>			
12, 19	41, 43	6.01 \pm 0.02	2
27-28	29-32	3.68 \pm 0.48	4
30-36	31-32	5.02 \pm 0.40	6
42-44	32	5.50 \pm 0.71	3
21-39	30-37	1.39 \pm 0.02	5
<i>Controls (sham operated)</i>			
12, 30, 38	32, 43	1.43 \pm 0.02	4

¹The nerve cords of these females were severed prior to oviposition and therefore they may be considered to have had the cords cut when the female was ovipositing.

freed for the period of the experiment. The oöcytes of these females measured 0.78 ± 0.01 mm. In 3 females the remaining portion of the oötheca in the uterus continued to apply pressure on the ovipositor and their oöcytes measured 0.77 ± 0.05 mm. As controls 6 females were sham operated, i.e. their oöthecae were partly extruded and pushed back, without being cut off, into the uterus 11 to 13 days after ovulation. They all gave birth at 54 to 56 days of age and their oöcytes measured 0.74 ± 0.01 mm. These experiments indicate that relieving the pressure of the oötheca on the gonapophyses during pregnancy had no effect on oöcyte development.

One mated female of the bisexual strain that had oviposited normally failed to give birth in the usual period of time (53 days). It was

dissected after 62 days of pregnancy and the oöcytes were 1.56 mm. long and contained yolk. The uterine eggs were degenerating and were undeveloped but the oöcytes had developed although the egg case had been in the uterus. This failure of endocrine inhibition during "pregnancy" was also found in *Blaberus* and *Byrsotria* (see below).

Byrsotria fumigata: The effect of various implants into the abdominal cavities of virgins is shown in table 5. Portions of egg cases of *Byrsotria* and *Leucophaea* and entire oöthecae of *Pycnoscelus* failed to inhibit the development of the oöcytes in *Byrsotria*.

Severance of the nerve cord in pregnant virgin and mated females resulted in resumption of oöcyte development in some females (cf. figs. 14A and C) although an oötheca was in the uterus (table 6). However, the oöcytes developed only in 7 of 24 virgins as compared to 15 of 20 mated individuals. All of the virgins that failed to develop oöcytes had many degenerating oöcytes that had not been laid during the initial ovulation which may account for the negative results in many of these females. Of the 7 virgin females that developed their oöcytes after nerve cord severance, 5 had no old degenerating oöcytes, one had one old oöcyte and the last had several oöcytes that had remained from the previous oviposition. In addition to the 24 virgin females that had been operated upon after ovulating (table 6), 11 females had their nerve cords severed 7 to 24 days after emergence and 8 others were sham operated when 5 to 20 days old. These females failed to oviposit and were dissected 31 to 38 days after the operations. Of the nerve-cord-severed females 7 had matured degenerating oöcytes and 4 had small oöcytes with some yolk but these had degenerated. Of the sham operated females 5 had mature degenerated oöcytes, 2 had small degenerated oöcytes and 1 had oöcytes that failed to develop. The oöcytes in females that had been operated on prior to oviposition were essentially similar to those found in unoperated virgin females.

Experiments were performed on several females to determine the effect of removing the ovipositors or relieving the pressure of the oötheca on the gonapophyses. The ovipositors were cut off of 9 virgin females 6 to 26 days after oviposition. The oöcytes were measured after the females had carried their oöthecae for 75 to 84 days. In 8 females the oöcytes measured 1.62 ± 0.06 mm. indicating no growth other than might be expected in unoperated females (1.53 ± 0.04 mm. at parturition). One female whose ovipositor was cut off 13 days after ovulation had oöcytes 6.37 mm. after 82 days of pregnancy. The oöthecae of 13 virgin females were partly extruded

manually, part of the egg cases were cut off and the remainder pushed back into the uterus in an attempt to free the pressure normally exerted on the ovipositor. In 6 successful operations the ovipositors were freed 9 to 12 days after ovulation, and at 73 to 75 days of "pregnancy" their oöcytes were 1.47 ± 0.03 mm. Seven females in which the operations (7 to 18 days after ovulation) did not free the ovipositors, had oöcytes 1.49 ± 0.05 mm. after carrying their oöthecae for 71 to 76 days; one female that was unsuccessfully operated upon 8 days after ovulation had oöcytes 3.77 mm. 64 days later. These experiments indicate that removing the ovipositor or releasing the pressure of the oötheca on the ovipositor during the gestation period does not influence the development of the oöcytes. The two individuals in which the oöcytes grew may be explained by the fact that inhibition of the corpora allata in some virgins of *Byrsotria* may break down during gestation.

Blaberus craniifer: Parts of oöthecae (about 5 mm. x 10 mm.) of *B. craniifer* were implanted into the abdomens of 9 virgin females less than 1 to 3 days old (one female had an entire oötheca implanted). Eight females dissected 15 to 30 days later had well developed oöcytes 4.84 ± 0.28 mm.; one female dissected 28 days after the implant showed no growth of oöcytes (1.48 mm. long). The oöcytes of unoperated virgins 15 to 30 days old were 5.10 ± 0.05 mm. The length of mature oöcytes are about 6.25 ± 0.07 mm. ($N=3$); the new basal oöcyte at ovulation is 1.10 ± 0.03 mm. ($N=5$). Uterine eggs implanted into the abdomens of virgin females did not inhibit oöcyte development in *B. craniifer*.

Six mated females had their nerve cords severed on the twenty-second to twenty-sixth days of pregnancy and were dissected 34 to 39 days later. Four of these females (operated on the twenty-fifth to twenty-sixth day of pregnancy) had oöcytes 4.09 ± 0.84 mm., 34 to 38 days later (fig. 12 B); two females operated on the twenty-second and twenty-third days of pregnancy showed very little oöcyte development (1.74 ± 0.12 mm.), 34 and 39 days later (the oöcytes at parturition are 1.56 ± 0.07 mm. long; $N=6$).

Two virgin females of *B. craniifer* carried their oöthecae for 93 and 107 days, which is longer than the normal gestation period (about 79 days) of mated females. When the undeveloped uterine eggs were extruded the oöcytes measured 3.92 mm. and 3.68 mm. respectively (fig. 12C). Inhibition of the corpora allata in *B. craniifer* apparently can break down in the late stage of "pregnancy" in virgin females, as it does in *Byrsotria* and in *Pycnoscelus*.

Blaberus giganteus: Eight pregnant females were taken from cul-

tures (histories unknown), their nerve cords were severed and their oöcytes were measured on the day they gave birth or aborted their oöthecae. Five females gave birth and 3 extruded oöthecae containing well developed embryos in 19 to 33 days after the operations. In every female the oöcytes grew, as a result of nerve severance, and measured 4.24 ± 0.33 mm. At ovulation the mature oöcyte is 5.86 ± 0.04 mm. ($N=11$) and the new basal oöcyte is 0.97 ± 0.01 mm. ($N=6$). Normally at parturition the oöcytes are 1.67 ± 0.03 mm. long ($N=10$). Gestation in this species lasts about 95 to 103 days. Nerve cord severance at least 33 days before parturition eliminated the inhibition of the corpora allata resulting from the presence of the egg case in the uterus.

Leucophaea maderae: The oöthecae of 7 females were removed and part of the egg cases were implanted into the abdomens of the female donors. Five females which had their egg cases removed and implanted 10 to 15 days after oviposition, ovulated 61 to 65 days later. This is about the time one would expect ovulation after removal of the oötheca (fig. 11). One female had oöcytes 2.18 mm. long 65 days after an implant (made 10 days after ovulation). One female whose oötheca was removed and implanted 22 days after ovulation had oöcytes 5.14 mm. long 41 days later. Four females whose oöthecae were removed 14 to 40 days after ovulation and had a wax "oötheca" inserted into the uterus showed no yolk deposition in the oöcytes (1.05 ± 0.05 mm.) 58 to 65 days later.

The implantation of uterine eggs into the abdomens of females did not prevent the oöcytes from maturing. The results with wax "oöthecae" insertions indicate that the corpora allata may be inhibited by pressure of the oötheca in the uterus.

To determine whether there was a hormonal influence on oöcyte development in *Leucophaea*, Engelmann (1957) removed the eggs from the uterus and implanted about one half of the oötheca into the abdominal cavity. He found that the eggs (in the oötheca) still affected the corpora allata when they were implanted into the abdomen (as they did when in the uterus). To rule out any possible effect of a mechanical pressure on the abdomen, or the effect of other substances resulting from decay of tissues (i.e. decaying implanted uterine eggs) he implanted paraffin blocks, muscle tissue, or agar blocks of about the size of half an oötheca after removal of the egg case. These implants did not inhibit the corpora allata and Engelmann concluded that the arrest of the corpora allata was not caused by mechanical pressure. However, it should be pointed out that pressure exerted by an implant in the abdominal cavity may be quite different from pres-

sure exerted in the uterus by the growing eggs (or by an implant into the uterus). In his more recent work (1960) Engelmann found that nerve cord severance did in fact result in renewed growth of the oöcytes in pregnant females and that nervous stimuli are primarily responsible for inhibition of the corpora allata during pregnancy. However, he found a statistically significant delay of egg maturation after severance of the nerve cord, compared with animals from which egg cases were removed (35.2 ± 0.7 versus 39.1 ± 1.4 days in animals operated on 29 to 37 days after ovulation; 64.7 ± 1.9 vs. 73.4 ± 1.5 days in animals operated on 0 to 1 day after ovulation). He concluded that other factors play an important role in inhibiting the corpora allata during pregnancy. By injecting 0.1 ml. of clear supernatant fluid from homogenized uterine eggs every fifth day for 30 days, he inhibited the corpora allata of *Leucophaea*. However, the injection of muscle homogenate resulted in a similar inhibition and Engelmann suggested that a non-specific substance inhibited the corpora allata during pregnancy.

Although Engelmann has shown a delay in ovulation in females that had nerve cords cut compared to females from which oöthecae were removed and has demonstrated that extracts of uterine eggs and muscle tissue have an inhibitory effect on the corpora allata, he has not demonstrated that there is a substance normally produced by the uterine eggs which acts to inhibit the corpora allata. Our experiments do not corroborate Engelmann's finding that a substance from uterine eggs inhibits the corpora allata. We find that removing eggs from the uterus and implanting them into the abdomen (in *Pycnoscelus*, *Byrsotria*, *Blaberus craniifer* and *Leucophaea*) removed inhibition of oöcyte development, i.e. oöcytes developed in the ovaries. We also find that cutting the nerve cord of pregnant females allows the oöcytes to develop in the ovaries of *Pycnoscelus*, *Byrsotria*, *Blaberus craniifer*, and *B. giganteus*; we therefore conclude that the inhibition of the corpora allata during gestation, in these species at least, is dependent upon nervous stimuli resulting from the presence of the egg case in the uterus.

Engelmann (1960) concluded that in *Leucophaea* the inhibitory influence of the oötheca may act on the last abdominal ganglion either by nervous or chemical factors and that there was "no reason to believe that the presence of an egg case in the brood sac is mechanically recorded in the brain (Roth and Stay, 1959). The question is still undecided." Our conclusions in the 1959 paper were based on studies of *Pycnoscelus surinamensis* and *Blattella germanica*. In the parthenogenetic strain of *Pycnoscelus* there is no inhibition of corpora allata

in virgin females prior to the first pregnancy, and severance of the nerve cord may affect the ability of the female to oviposit but has no influence on the rate of maturation of the oöcytes. There is no inhibitory center in the last abdominal ganglion in this species before the first oviposition. The insertion of wax into the uterus, after removal of the oötheca, results in inhibition of the corpora allata, and indicates that a chemical substance from uterine eggs is not necessary for inhibition of corpora allata in *Pycnoscelus*. We interpret these results to mean that pressure from the stretched uterus regulates the secretion of the corpora allata. As suggested by Engelmann (1962) the inhibitory center may be caudal to the site of the operation and "the brain may act only as a way station for the transmission of nervous impulses."

In *Rhodnius prolixus* the release of brain hormone was triggered by the distension of the insect's abdomen following a blood meal. Since cutting the nerve cord eliminated this effect, Wigglesworth (1934) inferred that the neurosecretory cells were influenced by nerve impulses arising in abdominal proprioceptors. The two stretch receptors found in each abdominal segment of *Rhodnius* adapt scarcely at all and will continue to discharge as long as the abdomen is stretched (Van der Kloot, 1961). In all of the false ovoviviparous cockroaches the uterus becomes greatly distended as the eggs increase in size as a result of water uptake and growth (Roth and Willis, 1955). It is possible that inhibition of the oöcytes during pregnancy may be due to pressure on abdominal stretch receptors as in *Rhodnius*. However, it is also conceivable that there are mechanoreceptors in the uterus itself. The present evidence indicates that the ovipositor is not involved in transmitting the pressure stimulus from the oötheca in the uterus or genital chamber of *Pycnoscelus* and *Byrsotria*; similarly, the ovipositor in *Blattella germanica* is not involved in corpora allata inhibition while the female carries its egg case (Roth and Stay, 1962).

In *Blattella*, which carries its oötheca externally, and in all cockroaches that incubate their eggs internally, the oötheca swells during embryogenesis, particularly in the latter species (Roth and Willis, 1955, 1955a, 1958). We (Roth and Stay, 1959, 1961, 1962) have suggested that during pregnancy inhibition of the corpora allata is due to nervous stimuli resulting from pressure of the oötheca. The changing pressure stimulus resulting from the increase in size of the oötheca would tend to prevent or retard adaptation of the receptors involved so that the corpora allata are inhibited during the entire (except in *Diploptera* and some *Nauphoeta*) gestation period. However, in virgins of *Blattella germanica* (Roth and Stay, 1962) *Blaberus craniifer*, *Byrsotria fumigata*, and *Pycnoscelus surinamensis*

(mated bisexual strain females whose uterine eggs do not develop) where the oötheca does not increase markedly in size because the eggs remain undeveloped, inhibition of the corpora allata, resulting from the presence of the oötheca, ceases, and consequently the oöcytes develop in spite of the presence of the egg case; it seems that because of the constant, more or less unchanging pressure stimulus resulting from an oötheca that is not increasing in size, pressure receptors (or the central nervous system) become adapted and nervous inhibition of the corpora allata ceases.

ABSTRACT

The effect of mating on oöcyte development and oviposition in *Pycnoscelus surinamensis*, *Byrsotria fumigata*, *Blaberus craniifer*, *Blaberus giganteus*, *Nauphoeta cinerea*, and *Leucophaea maderae*, all cockroaches that incubate their eggs internally, was investigated. In *Diploptera punctata*, the majority of females require mating for maturation of the oöcytes. In *Pycnoscelus* mating is unnecessary for egg maturation. Between these two extremes are species which show varying degrees of dependence on external mating stimuli for overcoming inhibition or for stimulating corpora allata. Various species also show different degrees of dependence on mating for normal formation and retraction of the oötheca into the uterus.

The extent to which cockroaches depend upon food intake for stimulation of the corpora allata also varies. The species may be arranged in a series showing complete dependence to complete independence upon food for oöcyte development.

Experiments to determine the nature of inhibition of the corpora allata during pregnancy indicate that inhibition is due to nervous stimuli resulting from pressure of the growing eggs in the uterus.

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MORE AMERICAN SPIDERS OF THE GENUS *CHRYSSO* (ARANEAE, THERIDIIDAE)*

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In a previous paper (Levi, 1955) I revised the genus *Chrysso*, which I thought at the time to be a compact group of closely related species quite distinct from *Theridion*, and all coming from America. However, soon after publishing a description of the genus *Arctachaea* for only two species (Levi, 1957), I discovered species intermediate between the new genus and *Chrysso*.

Though species bridging genera have been found in various groups of theridiids, it was a surprise to see the description of *Argyria venusta* Yaginuma, 1957 (Figs. 3-5) from Japan, a species close to *Chrysso* and having similar habits, but less specialized in genitalic structure. Soon several other species were examined that are best placed in *Chrysso* unless we want numerous monotypic genera. One of these species is *Argyrodes nigra* O. P.-Cambridge (Figs. 1, 2) from Ceylon (with genitalia superficially resembling those of *Theridion punctosparsum* Emerton) though it has the palpus still less specialized than does *Chrysso venusta* (Yaginuma). Allied to *Chrysso nigra* (O. P.-Cambridge) is the American *Chrysso nigrosternum* Keyserling (Fig. 13). Several of the species now placed in *Chrysso* have the cymbium modified [e.g. *Chrysso perplexa* (Keyserling), Fig. 18], and bridge the gap to the two species previously placed in *Arctachaea*. Further, a male of *Chrysso cambridgei* (Petrunkevitch) (Figs. 43-47) bridges the gap between the latter groups and the species tentatively placed in *Meotipa*. *Meotipa* is a genus of doubtful validity; the male of the type species remains unknown. The three species placed in *Meotipa* differed from *Chrysso* mainly by their longer legs and by a somewhat different shape of abdomen.

There is still some doubt that the groups considered in this paper are monophyletic. Certainly all are related to *Theridion*, from which they can be separated by the modified shape of the abdomen and by the more specialized palpus. The specialization of the palpus, however, may go in different directions. Most species resemble the *T. frondeum* group. A distally truncate cymbium, otherwise rare in theridiids, is common in *Chrysso* and probably indicates relationship. Another unusual character, grooves on the sides of the abdomen, is found in some of the species here considered to belong to *Chrysso* and

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may be further evidence of common origin. In addition, several species have teeth on the posterior margin of the chelicerae.

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Chrysso O. P.-Cambridge

- Chrysso* O. P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 429. Type species by original designation *Chrysso albomaculata* O. P.-Cambridge.
Meotipa Simon, 1892, Histoire Naturelles des Araignées, 1: 519. Type species by original designation *Meotipa picturata* Simon.
Physcoa Thorell, 1895, Descriptive Catalog of the Spiders of Burma, p. 83. Type species by original designation *Physcoa scintillans* Thorell.
Argyria Yaginuma, 1957, Acta Arachnologica, 15: 11. Type species by original designation *Argyria venusta* Yaginuma. Homonym of *Argyra* Huebner, 1818, and *Argyria* Robineau-Desvoidy, 1863.
Argyroaster Yaginuma, 1958, Acta Arachnologica, 15: 37. New name for *Argyria* Yaginuma preoccupied.
Arctachaea Levi, 1958, Psyche, 64: 102. Type species by original designation *Arctachaea pelyx* Levi.

Diagnosis. *Chrysso* differs from *Theridion* by a hump or posterior dorsal extension of the abdomen; from *Achaearanea* by having a much more complicated palpus containing a radix; from *Argyrodes* and *Spintharus* by lacking a colulus (Levi and Levi, 1962).

Comments. The types of *Chrysso nigriceps* Keyserling and *Helvibis sulcata* Keyserling have been examined since publishing my paper in

1957. The specimens given those names were correctly identified.

The following species have recently been misplaced in *Chryso*: *Chryso maronica* Caporiacco, 1954 (Comm. Pontificia Acad. Sci. 16: 74) is *Achaearanea hirta* (Taczanowski). NEW SYNONYMY. *C. pentagona* Caporiacco, 1954, ibid., 16: 75 belongs to *Achaearanea*.

While many species of *Chryso* are strikingly colored, the coloration usually cannot be used for determination or as a key character. As in most theridiids, it is variable, e.g. *Chryso compressa* (Keyserling) has a striking black sternum and abdomen with a black venter in Brazil, but the venter is yellow in Peruvian specimens. Uyemura (1957) has observed rapid color change in *Chryso venusta* (Yaginuma) when disturbed. Probably other species of *Chryso* can also change color.

Species of *Chryso* are absent from the United States and Canada except *C. albomaculata* and *C. clementinae* (Map) found in the southeastern states and the two species previously placed in *Arctachaea* found from Wyoming to Alaska. None are known from Chile or southern Argentina. Most species are found in the hotter parts of America, where the spider fauna is least known, and our knowledge of the species and their distribution is fragmentary.

Key to the American species of *Chryso*

- 1a. Mesal tip of male cymbium with teeth (1957, figs. 11-13), female chelicerae toothless; Wyoming to Alaska 2
- 1b. Cymbium without teeth; female chelicerae usually with teeth; southeastern United States to South America 3
- 2a. Mesal corner of cymbium projecting (1957, figs. 12, 13); female abdomen higher than long *C. pelyx* (Levi)
- 2b. Mesal corner of cymbium rounded (1957, fig. 11); female abdomen longer than high *C. nordica* (Chamberlin and Ivie)
- 3a. Males 4
- 3b. Females 25
- 4a. Thread-shaped portion of embolus originating in center of bulb, looping towards outside and base before continuing straight towards distal end (1955, figs. 1-5) 5
- 4b. Embolus otherwise 11
- 5a. Width of area enclosed by embolus loop almost equals width of basal portion of embolus (1955, fig. 15); Huánuco, Peru *C. mariae* Levi
- 5b. Width of area enclosed by embolus loop at least twice width of basal portion of embolus thread (1955, figs. 7, 9, 13) 6
- 6a. Median apophysis with a large thorn (1955, fig. 13); Amazon, Peru *C. sulcata* (Keyserling)

- 6b. Median apophysis without thorn 7
- 7a. A thorn on ectal side of palpal bulb (1955, figs. 7, 9) 8
- 7b. No thorn on ectal side of bulb 9
- 8a. Radix with evenly rounded swelling; ectal thorn large (1955, fig. 7); Panama *C. vallensis* Levi
- 8b. Radix with round boss; ectal thorn small (1955, fig. 9); Panama, Peru *C. diplosticha* Chamberlin and Ivie
- 9a. Radix with a swelling; conductor almost lanceolate in ventral view (1955, fig. 11); coloration as in 1955 fig. 12; Panama *C. indicifer* Chamberlin and Ivie
- 9b. Radix without swelling; conductor hook-shaped (1955, fig. 1-6); coloration otherwise 10
- 10a. Radix with a mesal fold, (1955, figs. 1-4); abdomen usually with spots; North Carolina to Brazil *C. albomaculata* O. P.-Cambridge
- 10b. Radix without fold (1955, figs. 5, 6); abdomen without discrete spots; Panama to Argentina *C. vexabilis* Keyserling
- 11a. Prominent ventral embolus biforked (Figs. 8, 13) 12
- 11b. Embolus otherwise 13
- 12a. Embolus long, reaching base of bulb (Fig. 13); southern Brazil *C. nigrosternum* Keyserling
- 12b. Embolus short, covering distal two-thirds of bulb (Fig. 8); Minas Gerais *C. gounellèi* sp. n.
- 13a. Distal end of cymbium truncate 14
- 13b. Distal end of cymbium rounded 15
- 14a. Ventral view as in Fig. 18; southern Barzil *C. perplexa* Keyserling
- 14b. Ventral view as in Fig. 28; Venezuela *C. simoni* sp. n.
- 15a. With long thread-shaped embolus of even diameter (Fig. 23); Costa Rica to Trinidad *C. questona* sp. n.
- 15b. Embolus otherwise 16
- 16a. Embolus corkscrew-shaped, on distal end of bulb (Figs. 89, 94) 17
- 16b. Embolus otherwise 18
- 17a. Embolus larger than remaining portion of bulb (Fig. 89); abdomen higher than long; Panama to Ecuador *C. silva* sp. n.
- 17b. Embolus one-third length of remaining portion of bulb (Fig. 95); abdomen longer than high; Costa Rica, Panama *C. volcanensis* sp. n.
- 18a. Embolus with distal portion hook-shaped (Fig. 47); Mexico to Venezuela *C. cambridgei* (Petrunkovitch)
- 18b. Embolus otherwise 19

- 19a. Two transparent sickle-shaped structures on venter of bulb (Fig. 42); Colombia to Bolivia *C. vittatula* (Roewer)
- 19b. Palpal bulb without sickle-shaped structures 20
- 20a. Conductor prominent and with distal hook (Fig. 74); cosmopolitan *C. clementinae* (Petrunkevitch)
- 20b. Conductor otherwise 21
- 21a. Embolus a ventral bottle-shaped structure (Fig. 69); Peru to Brazil *C. compressa* (Keyserling)
- 21b. Embolus otherwise 22
- 22a. Median apophysis not apparent in ventral view (Fig. 30); southern Brazil *C. arops* sp. n.
- 22b. Median apophysis visible in ventral view 23
- 23a. Median apophysis in distal half of bulb, palpus lightly sclerotized (Fig. 79); Panama *C. melba* sp. n.
- 23b. Median apophysis mostly on proximal half of bulb; palpus heavily sclerotized 24
- 24a. Palpus as in Figure 36, 37; Colombia to Bolivia
..... *C. ecuadorensis* Levi
- 24b. Palpus as in Figure 51; Venezuela
..... *C. barromachadoi* Caporiacco
- 25a. Epigynum with openings in coiled borders of fossa (Fig. 78); Costa Rica to Trinidad *C. questona* sp. n.
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- 26a. Ducts showing through epigynal wall long and coiled, openings indistinct (Figs. 82, 84) 27
- 26b. Epigynum otherwise 28
- 27a. Ducts loosely coiled in large loops (Fig. 83); Panama
..... *C. alecula* sp. n.
- 27b. Ducts tightly coiled (Fig. 85); Trinidad *C. arima* sp. n.
- 28a. Epigynum with a central black mark (Fig. 45); sternum, venter black; Mexico to Venezuela *C. cambridgei* (Petrunkevitch)
- 28b. Epigynum otherwise; sternum and venter usually not black (except *C. compressa*, *C. nigrosternum*) 29
- 29a. Openings of epigynum widely separated (Fig. 88); Panama to Ecuador *C. silva* sp. n.
- 29b. Epigynum otherwise 30
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- 30b. Epigynum otherwise 32
- 31a. A dark mark anterior to swelling (Figs. 34, 35)
..... *C. ecuadorensis* Levi
- 31b. A dark mark posterior to swelling (Fig. 40)
..... *C. vittatula* (Roewer)

- 32a. Epigynum with a light swelling bordered anterior and sides (Fig. 50); Venezuela *C. barromachadoi* Caporiacco
- 32b. Epigynum otherwise 33
- 33a. Epigynum with openings near posterior margin in a depression, ducts loop anterior (Fig. 54); southern Brazil *C. ribeirao* sp. n.
- 33b. Epigynum otherwise 34
- 34a. Epigynum with a central fossa 35
- 34b. Epigynum without fossa 41
- 35a. Two openings in center of fossa (Fig. 93); Costa Rica, Panama *C. volcanensis* sp. n.
- 35b. Epigynum otherwise 36
- 36a. A black circular mark on each lateral end of fossa (Fig. 73); cosmopolitan *C. clementinae* (Petrunkévitch)
- 36b. Epigynum otherwise 37
- 37a. Fossa far anterior, usually bordered on sides only (Fig. 27); Venezuela *C. simoni* sp. n.
- 37b. Fossa in center or posterior, bordered anterior or posterior as well as sides 38
- 38a. Fossa in a dark spot; ducts visible posterior to fossa (Figs. 16, 17); Brazil, Argentina *C. rubrovittata* (Keyserling)
- 38b. Epigynum otherwise 39
- 39a. Narrow ducts leading from sides into fossa (Figs. 57, 62) 40
- 39b. Ducts wider and leading from anterior into fossa (Figs. 64, 66, 67), Peru to Brazil *C. compressa* (Keyserling)
- 40a. Fossa bordered on sides and posterior (Fig. 57); southern Brazil *C. pulchra* (Keyserling)
- 40b. Fossa bordered on sides and anterior (Fig. 62); Minas Gerais .. *C. caraca* sp. n.
- 41a. Epigynal openings in a slit anterior to a dark area (Fig. 60); ducts simple (Fig. 59); San Fernandez Isl. *C. backstromi* (Berland)
- 41b. Epigynal openings otherwise; usually with internal sacs 42
- 42a. Epigynum a central transverse connected dark mark as in Figure 21; Brazil *C. antonio* sp. n.
- 42b. Epigynum otherwise 43
- 43a. Epigynum with two central dark curved marks (Figs. 10, 12); southern Brazil *C. nigrosternum* (Keyserling)
- 43b. Epigynum otherwise 44
- 44a. Epigynum with an anterior dark mark and light posterior as in 1955, fig. 33; head region blackened; Colombia, Ecuador *C. nigriceps* Keyserling
- 44b. Epigynum otherwise, coloration usually otherwise 45

- 45a. Epigynum with two lines, diverging posterior (1955, fig. 31); Panama to Peru *C. diplosticha* Chamberlin and Ivie
 45b. Epigynum otherwise 46
 46a. Epigynum with a transverse dark mark posterior to two spots (1955, fig. 29); Panama *C. vallensis* Levi
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 47a. Epigynum with a transverse line anterior to two spots (1955, fig. 37); southern Brazil *C. sicki* Levi
 47b. Epigynum otherwise 48
 48a. Epigynum with a pair of longitudinal lines in light area posterior to transverse dark mark (1955, fig. 35); dorsum of abdomen with two black long lines which fuse at posterior end; Panama *C. indicifer* Chamberlin and Ivie
 48b. Epigynum otherwise 49
 49a. Carapace dark brown; abdomen with a longitudinal dark band (1955, fig. 20); Peru *C. huanuco* Levi
 49b. Coloration otherwise 50
 50a. Abdomen without discrete white spots; Panama to Argentina *C. vexabilis* Keyserling
 50b. Abdomen usually with white spots; North Carolina to Brazil *C. albomaculata* O. P.-Cambridge

Chrysso albomaculata O. P.-Cambridge

Argyrodes elegans Taczanowski, 1872, Horae Soc. Ent. Rossicae, 9: 118, pl. 5, fig. 11, ♀. Female syntypes from Uassa, French Guiana [now Rio Uaçá, Amapa, Brazil] in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY. Not *Theridion elegans* Blackwall, 1862.

Chrysso albomaculata O. P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 429, fig. 6, ♀, ♂. Male, female syntypes from the Amazon in the Hope Department of Entomology, Oxford, examined.—Levi, 1955, Jour. New York Ent. Soc., 68: 61, figs. 1-4, 18-19, 25-27, ♀, ♂.

Chrysso elegans, — Keyserling, 1884, Die Spinnen Amerikas, Theridiidae 2 (1): 151.

Theridion elegans, — Simon, 1903, Histoire Naturelle des Araignées, 2: 990. *Theridion emendatum* Roewer, 1942, Katalog der Araneae 1: 429. New name for *Argyrodes elegans* Taczanowski. NEW SYNONYMY.

Distribution. Southeastern United States, Mexico, West Indies, northeastern South America to Bahia, Brazil.

Additional records. *Lesser Antilles. Grenada:* St. George's (N. L. H. Krauss, AMNH). *Trinidad:* Mt. St. Benedict (J. G. Myers). *Venezuela. Carabobo:* San Esteban, 1888 (E. Simon, MNHN). *Grand Elang. Dist. Fed.:* hacienda Corosal, N of Mt. Silla, 1888 (E. Simon, MNHN). *British Guiana.* Georgetown (A. M. Nadler, AMNH). *Surinam.* Paramaribo. *Brazil. Ceara:* Sierra Com-

munaty (E. Gounelle, MNHN). *Pernambuco*: Recife (SMF; A. M. Nadler, AMNH). *Bahia*: Salvador (A. M. Nadler, AMNH); Terra Nova (MNHN).

Chrysso vexabilis Keyserling

Chrysso vexabilis Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 155, pl. 7, fig. 96, ♀, ♂. Syntypes from N. Granada [now Ecuador, Colombia, Panama, Venezuela] in the British Museum, Natural History, examined. — Levi, 1955, Jour. New York Ent. Soc., 63: 63, figs. 5, 6, 23, 24, ♀, ♂.

Steatoda rubicunda F. P.-Cambridge, 1902, Biologia Centrali-Americana, Araneidea, 2: 386, pl. 36, fig. 21, ♂. Male type from Bugaba, Panama in the British Museum, Natural History, examined. (Not *Theridion rubicunda* Nicolet, 1849.) NEW SYNONYMY.

Theridion rubicundulum Roewer, 1942, Katalog der Araneae, 1: 498. New name for *Theridion rubicunda* (F. P.-Cambridge). NEW SYNONYMY.

Examination of Keyserling's type indicated that this species had been correctly determined. The internal female genitalia of Argentine specimens like the ones from Panama, have the posterior portion of the sacs of the internal genitalia ending in narrow extensions (Levi, 1955, fig. 23) quite different from the broadly rounded sacs of *C. albomaculata*. Unlike *C. albomaculata* it has no white spots on abdomen.

Distribution. Panama to Argentina.

Additional records. *Venezuela*. *Dist. Fed.*: hacienda Corosal, ♀, ♂ (E. Simon, MNHN). *Ecuador*. *Guayas*: Milagro, ♀, ♂ (H. E., D. L. Frizzell); Río Chimbo, ♂ (Edwards, MNHN). *El Oro*: Arenillas (E. L. Moore). *Brazil*. *Bahia*: Salvador, ♀, (E. Göldi, MNHN); Rio Salobro, ♀ (E. Gounelle, MNHN, doubtful det.). *Argentina*. *Córdoba*: Cosquín, ♀.

Chrysso diplosticha Chamberlin and Ivie

Chrysso diplosticha Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., 3(5): 36, fig. 83, ♀. Female type from Barro Colorado Island, Panama Canal Zone in the University of Utah Collection. — Levi, 1955, Jour. New York Ent. Soc., 63: 65, figs. 9, 30, 31, ♀, ♂.

Distribution. Nicaragua, Panama, Trinidad and Dept. Huánuco, Peru.

Additional records. *Nicaragua*: Musawas, Waspuc River, ♂ (B. Malkin, AMNH). *Lesser Antilles*. *Trinidad*: Simla near Arima, ♂ (A. M. Nadler, AMNH).

Chrysso indicifer Chamberlin and Ivie

Chrysso indicifer Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., 3(5): 36, figs. 82, 96, ♀. Female type from Barro Colorado Island in the

University of Utah collection. — Levi, 1955, Jour. New York Ent. Soc., 63: 66, figs. 11, 12, 17, 34, 35, ♀, ♂.

Distribution. Panama to Peru.

Additional records. *Venezuela.* *Dist. Fed.* Caracas, (E. Simon, MNHN). *Carabobo:* La Cumbre, S. of San Esteban, (E. Simon, MNHN). *Ecuador.* *Guayas:* Milagro, (H. E., D. L. Frizzell); Río Chimbo, (MNHN). *El Oro:* Arenillas, (E. L. Moore); Pasaje, (R. Walls). *Peru.* *Huánuco:* Monzón Valley, Tingo María, ♀, ♂ (E. I. Schlinger, E. S. Ross, CAS).

Chrysso gounellei sp. n.

Figures 6-8

Type. Male from Caracá, Minas Gerais, Brazil (E. Gounelle), in the Muséum National d'Histoire Naturelle, Paris (no. 9487). The species is named after E. Gounelle who collected for E. Simon.

Description. Carapace orange, eye region black. Sternum black. Legs yellowish to gray. Abdomen white with two black spots above spinnerets (Fig. 7), sometimes also with a pair of anterior spots. Carapace low and flat. Anterior median eyes larger than others, one and one-third their diameter apart, three-quarters from laterals. Posterior median eyes one and one-quarter their diameter apart, one and one-half from laterals. Chelicerae with three teeth on anterior margin, the middle one smallest, five sharp teeth posterior (Fig. 6). Abdomen longer than wide with indistinct grooves on sides (Fig. 7). Total length 1.9 mm. Carapace 1.0 mm long, 0.8 mm wide. First femur, 1.1 mm; patella and tibia, 1.1 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 0.9 mm; third, 0.6 mm; fourth, 0.9 mm.

Diagnosis. The two prongs of the embolus (Fig. 8) of *C. gounellei* are shorter than those of the related *C. nigrosternum* (Keyserling).

Record. 6 paratypes collected with holotype.

Chrysso nigrosternum Keyserling

Figures 9-13

Theridium rotundum Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, 3: 191, pl. 6, fig. 137, ♀. Female type from N. Freiburg [Nova Friburgo, Est. Guanabara], Brazil in the British Museum, Natural History, examined. NEW SYNONYMY.

Chrysso nigrosternum Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, 3: 206, pl. 7, figs. 148, ♀, ♂. Female, male syntypes from Taquara do Mundo Novo, [Rio Grande do Sul], Brazil in the British Museum, Natural History, examined. The female syntype is in poor condition.

Note. The similarity of my illustrations of the female types of the two names was not noted until some time after the examination. Keyserling's descriptions, except for the color of the abdomen, are also similar. Although *rotundum* has page priority, the name *Chrysso nigrosternum* Keyserling is used here, because the male palpus is very distinct while the epigyna are not. Figures 11, 12 were made from the type of *T. rotundum*, Figures 9, 10, 13 from those of *C. nigrosternum*.

Chrysso rubrovittata (Keyserling), new combination
Figures 14-17

Faiditus rubrovittatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 159, pl. 7, fig. 98, ♀. Female type without locality in the Hope Department of Entomology at Oxford University, examined. It probably came from South America.

Faiditus lacteovittatus Mello-Leitão, 1945, Rev. Museo La Plata, nueva serie, sec. Zool., 4: 233, fig. 7. Female type from Puerto Victoria, Misiones, Argentina in the La Plata Museum, examined. NEW SYNONYMY.

Description. Female from Pernambuco. Carapace, sternum, legs yellow. Abdomen grayish white with a dorsal, longitudinal white band and some white pigment spots (Fig. 14). Eyes subequal in size. Anterior median eyes one and one-half diameters apart, their radius from laterals. Posterior median eyes one and one-half diameters apart, their radius from laterals. Chelicerae with two teeth on anterior margin. Abdomen without lateral grooves (Fig. 14). Epigynum with central, sclerotized opening having a posterior lip (Figs. 16, 17). Total length 3.9 mm. Carapace 1.11 mm long, 1.02 mm wide. First femur 2.10 mm; patella and tibia 1.95 mm; metatarsus 1.62 mm; tarsus 0.78 mm. Second patella and tibia 1.17 mm; third 0.75 mm; fourth 1.30 mm.

EXPLANATION OF PLATE 14

Figs. 1, 2. *Chrysso nigra* (O. P.-Cambridge) (Ceylon). 1. Left palpus. 2. Epigynum cleared.

Figs. 3-5. *C. venusta* (Yaginuma) (Japan). 3. Female genitalia, dorsal view. 4. Epigynum. 5. Palpus.

Figs. 6-8. *C. gounellei* sp. n. 6. Male left chelicera, posterior view. 7. Abdomen, dorsal view. 8. Palpus.

Figs. 9-13. *C. nigrosternum* Keyserling. 9, 11. Female genitalia, dorsal view. 10, 12. Epigynum. 13. Palpus.

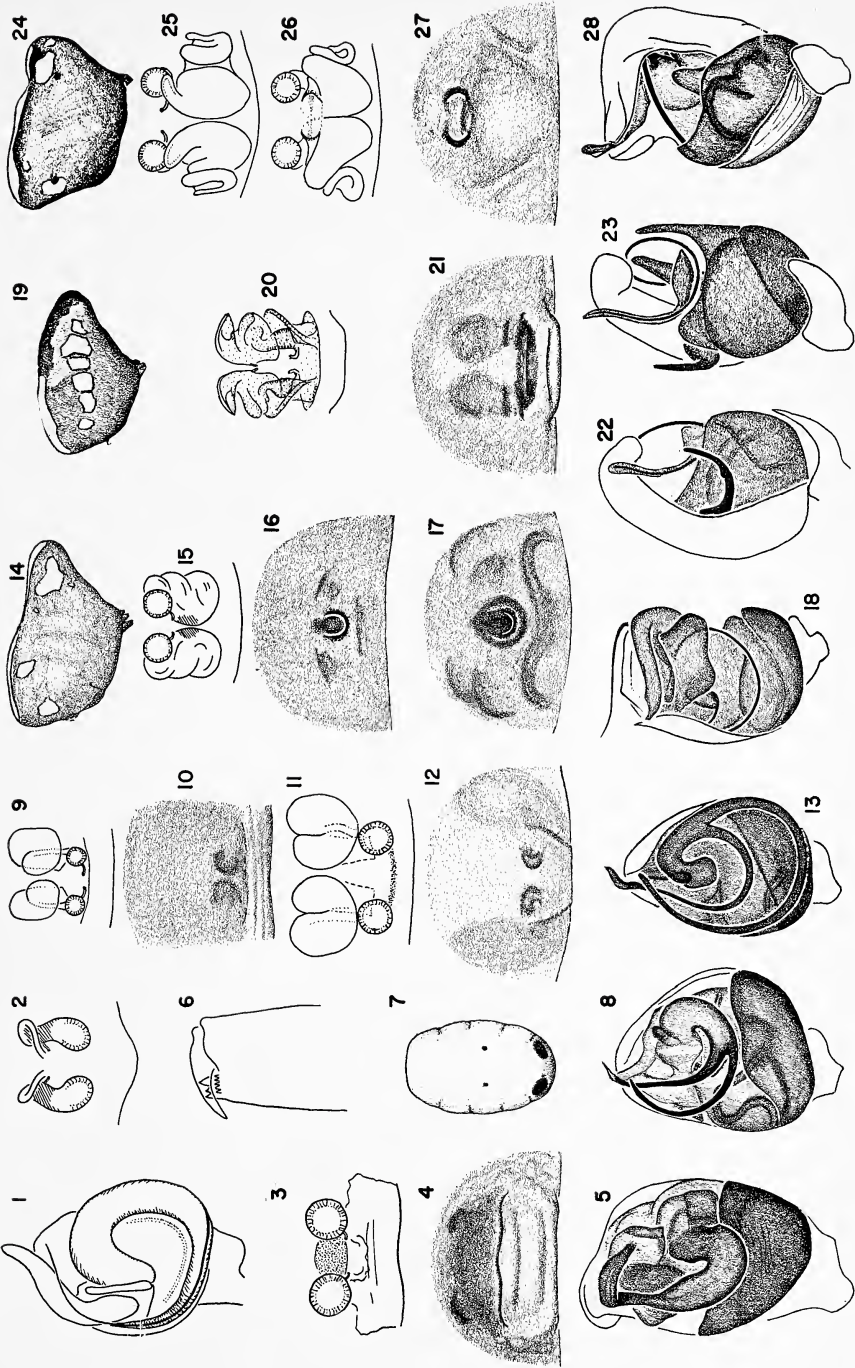
Figs. 14-17. *C. rubrovittata* (Keyserling). 14. Female abdomen, lateral view. 15. Female genitalia, dorsal view. 16, 17. Epigynum.

Fig. 18. *C. perplexa* Keyserling. Palpus.

Figs. 19-21. *C. antonio* sp. n. 19. Female abdomen, lateral view. 20. Female genitalia, dorsal view. 21. Epigynum.

Figs. 22, 23. *C. questona* sp. n. palpus. 22. Mesal view. 23. Ventral view.

Figs. 24-28. *C. simoni* sp. n. 24. Female abdomen, lateral view. 25. Female genitalia, dorsal view. 26. Epigynum cleared. 27. Epigynum. 28. Palpus.



Figures 15, 16 were made from the type of *Faiditus rubrovittatus*.
Distribution. Brazil, Argentina.

Record. Brazil. *Pernambuco*: Recife, ♀ (SMF); *Minas Gerais*: Caraça, ♀ (E. Gounelle, MNHN).

Chrysso perplexa Keyserling
 Figure 18

Chrysso perplexa Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2): 242, pl. 20, fig. 296, ♂. Male type from Blumenau, [Santa Catarina], Brazil in the British Museum, Natural History, examined. Figure 18 was prepared from the type.

Record. Brazil. *Santa Catarina*: Nova Teutonia, lat 27° 11' S, long 52° 23' W, ♂ (F. Plaumann, SMF).

Chrysso antonio sp. n
 Figures 19-21

Type. Female from São Antonio de Barro [Condeúba, Bahia], Brazil (E. Gounelle), in the Muséum National d'Histoire Naturelle, Paris (no. 11518). The specific name is a noun in apposition after the type locality.

Description. Carapace dark brown, dusky on sides. Chelicerae, sternum black. Legs yellowish. Abdomen with dorsal white patch and five white spots on sides on gray background a darker, indistinct gray band behind dorsal white spot continuing to a black posterior tip (Fig. 19). Eyes subequal in size. Anterior median eyes one diameter apart, their radius from laterals. Posterior eyes their diameter apart. Chelicerae with two long teeth on anterior margin. Abdomen without grooves (Fig. 19). Total length 2.5 mm. Carapace 0.85 mm long, 0.65 mm wide. First femur, 1.20 mm; patella and tibia, 0.98

EXPLANATION OF PLATE 15

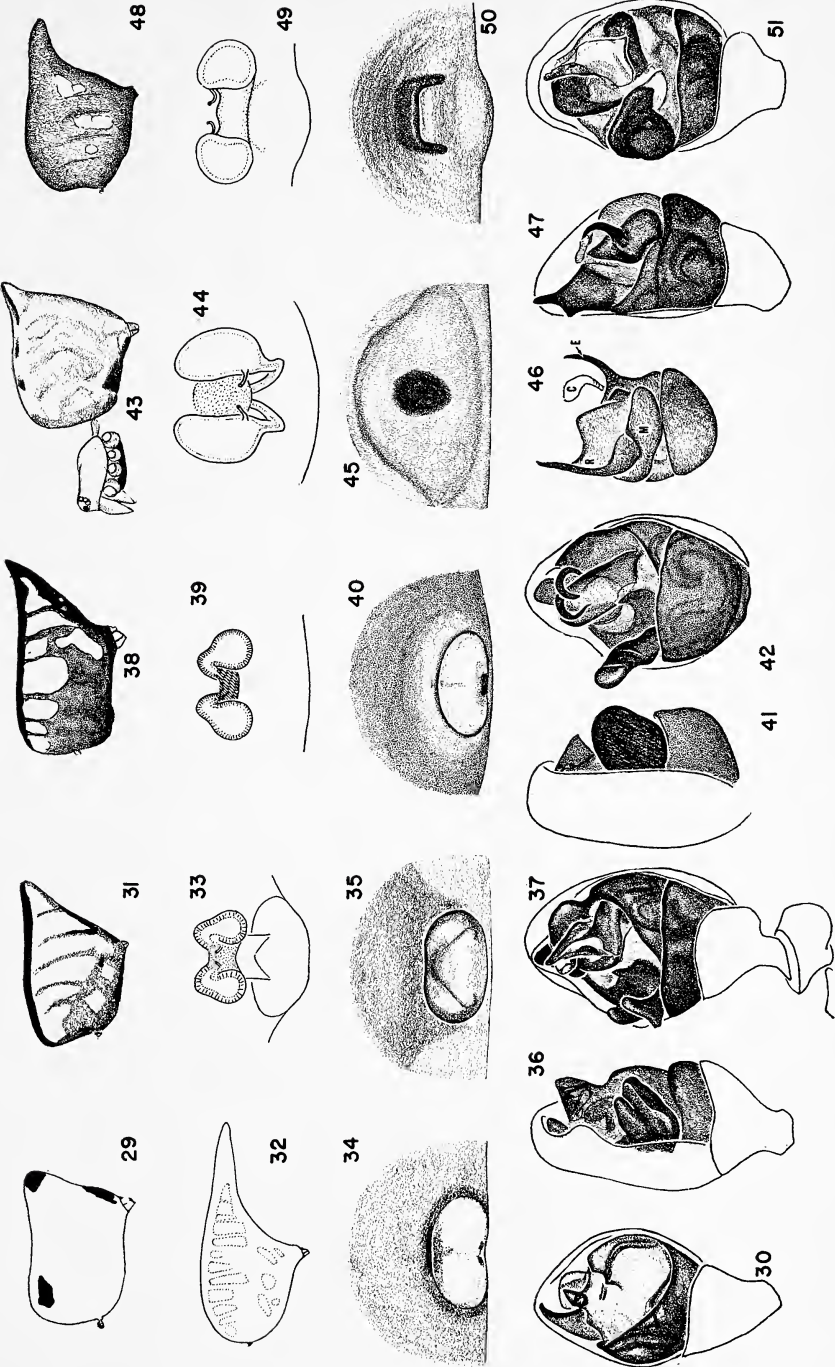
Figs. 29-30. *Chrysso arops* sp. n. 29. Male abdomen, lateral view. 30. Left palpus.

Figs. 31-37. *C. ecuadorensis* Levi. 31, 32. Female abdomen, lateral view. 33. Female genitalia, dorsal view. 34, 35. Epigynum. 36, 37. Palpus. 36. Mesal view. 37. Ventral view.

Figs. 38-42. *C. vittatula* (Roewer). 38. Female abdomen, lateral view. 39. Female genitalia, dorsal view. 40. Epigynum. 41, 42. Palpus. 41. Mesal view. 42. Ventral view.

Figs. 43-47. *C. cambridgei* (Petrunkevitch). 43. Female, lateral view. 44. Female genitalia, dorsal view. 45. Epigynum. 46. Palpus expanded, mesal view (cymbium removed; C, conductor; E, embolus; M, median apophysis; R, radix). 47. Palpus.

Figs. 48-51. *C. barromachadoi* Caporiacco. 48. Abdomen of juvenile, lateral view. 49. Female genitalia, dorsal view. 50. Epigynum. 51. Palpus.



mm; metatarsus, 0.78 mm; tarsus, 0.50 mm. Second patella and tibia, 0.71 mm; third, 0.52 mm; fourth, 0.91 mm.

Diagnosis. The epigynum, which has a dark patch in a light transversely folded area (Fig. 21), separates this species from *C. albomaculata*. The sacs of the internal genitalia (Fig. 20) are more complex in shape than in related species.

***Chrysso questona* sp. n.**

Figures 22, 23, 76-78

Type. Female from El Valle, Panama, July 1936 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs whitish. Legs with black rings on middle and distal ends of segments. Abdomen whitish with some black patches (Fig. 76). Chelicerae with two anterior teeth. Anterior median eyes one and one-fourth diameters apart, three-fourths from laterals. Posterior median eyes slightly more than a diameter apart, one diameter from laterals. Eyes of male smaller and slightly farther apart. Legs very long. Total length of female 4.5 mm. Carapace 1.3 mm long, 1.0 mm wide. First femur, 4.9 mm; patella and tibia, 4.5 mm; metatarsus, 4.9 mm; tarsus 1.4 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 2.0 mm. Total length of male 3.0 mm. Carapace, 1.6 mm long. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.3 mm.

Diagnosis. The coiled rim of the epigynum (Fig. 78), the coiled ducts (Fig. 77) and the long embolus and narrow cymbium (Figs. 22, 23) distinguish this species from *C. volcanensis*.

Records. *Costa Rica.* San Isidro del General, 600-1200 m, ♀ (D. Rounds). *Panama:* Chiriquí Prov., 1938, ♂ (UU). *Trinidad:* Simla, 29, 30 Dec. 1954, ♀; 26 Feb. 1954, ♀ (A. M. Nadler, AMNH).

***Chrysso simoni* sp. n.**

Figures 24-28

Type. Male from Caracas, Venezuela, December 1887 to February 1888 (E. Simon), in the Muséum National d'Histoire Naturelle, Paris (no. 16392). The species is named after the great araneologist E. Simon.

Description. Carapace yellow-brown, slightly darker in cephalic region. Sternum, legs yellow-brown. Abdomen gray with variable white, darker gray or black patches. Some specimens have a median

dorsal white longitudinal band, in others the band is almost black (Fig. 24). Eyes subequal in size. Anterior median eyes about one and two-thirds diameter apart, three-quarters from laterals. Posterior median eyes less than two diameters apart, one from laterals. Anterior median eyes of male slightly farther apart than in female. Chelicerae with two teeth on anterior margin, none on posterior. Abdomen longer than wide or high, with posterior tip of female overhanging (Fig. 24) but posterior tip of male more blunt. Total length of female 3.1 mm. Carapace 1.1 mm long, 1.0 mm wide. First femur, 2.2 mm; patella and tibia, 2.0 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm. Second patella and tibia 1.3 mm; third 0.9 mm; fourth 1.4 mm. Total length of male 2.5 mm. Carapace 1.1 mm long, 0.9 mm wide. First femur, 2.2 mm; patella and tibia, 2.0 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm. Second patella and tibia, 1.3 mm; third, 0.8 mm; fourth, 1.3 mm.

Diagnosis. The palpus of the male (Fig. 28) is quite similar to that of *C. perplexa* Keyserling but can be separated from the latter by the shape and length of the embolus, the base of which lies against the alveolus of the cymbium. The internal female genitalia have a lateral duct loop (Figs. 25, 26) unlike that of the related *C. rubrovittata* (Keyserling). The internal genitalia are asymmetrical in the specimens examined.

Records. 3 ♂ and 3 ♀ paratypes from type collection.

Chrysso barromachadoi Caporiacco

Figures 48-51

Chrysso barromachadoi Caporiacco, 1955, Acta Zool. Venezuelica, 1: 337.

Juvenile type from Rancho Grande, Aragua, Venezuela, in the Museum at Caracas, examined.

Description. Carapace, sternum dark brown. Legs yellow. Abdomen gray to black with white patches on sides of female (Fig. 48) but lacking in male. Anterior median eyes slightly smaller than others, one and one-half diameters apart, two from laterals. Posterior median eyes one diameter apart one and one-half from laterals. Anterior eyes are slightly closer in male. Abdomen with lateral grooves; female abdomen extension, two-thirds length of abdomen between spinnerets and pedicel. Male abdomen blunt and short. This species can be diagnosed by the genitalia (Figs. 49-51).

Figure 48 was made from the juvenile type specimen.

Records. *Venezuela. Aragua:* Rancho Grande, March 1945; 20 Dec. 1954 (A. M. Nadler, AMNH); Choróni, 9 March 1959, (A.

M. Nadler, AMNH); *Carabobo*: Le Cumbre, S of San Esteban, 1888 (E. Simon, MNHN).

Chrysso cambridgei (Petrunkevitch), new combination

Figures 43-47

Achaea vittata O. P.-Cambridge, 1894, *Biologia Centrali-Americana*, Araneidea, 1: 130, pl. 17, fig. 11, ♀. Female type from Teapa, [Tabasco, Mexico] in the British Museum, Natural History, examined. Not *Argyrodes vittata* Keyserling, *Theridion vittatum* Nicolet.

Thwaitesia vittata, — O. P.-Cambridge, 1896, *op. cit.*, p. 197.

Thwaitesia lepida O. P.-Cambridge, 1896, *op. cit.*, p. 197, pl. 25, fig. 5, ♀. Female type from Teapa, [Tabasco, Mexico] in the British Museum, Natural History, examined.

Chrysso splendida Banks, — 1898, *Proc. California Acad. Sci.*, (3)1: 237, pl. 14, fig. 13, ♀. Female syntype from Tepic, Nayarit, Mexico in the Museum of Comparative Zoology, examined.

Theridion vittatum, — F. P.-Cambridge, 1902, *Biologia Centrali-Americana*, Araneidea, 2: 391, pl. 37, figs. 6, 7, ♀, ♂.

Theridion splendidum, — F. P.-Cambridge, 1902, *op. cit.*, p. 391.

Theridion cambridgei Petrunkevitch, 1911, *Bull. Amer. Mus. Nat. Hist.*, 29: 192. New name for *Achaea vittata* thought preoccupied by *Theridion vittatum* Nicolet and for *Thwaitesia lepida* thought preoccupied by *Theridion lepidum* Walckenaer. Reimoser, 1939, *Ann. Naturhist. Museum Wien*, 50: 346. Roewer, 1943, *Katalog der Araneae*, 1: 490. Kraus, 1955, *Abhandl. Senckenbergischen Naturf. Gesell.* 493: 17.

Theridion splendens Roewer, 1942, *op. cit.* p. 498. New name for *Chrysso splendida* thought preoccupied by *Theridion splendidum* Taczanowski.

Conopistha acuminata Schenkel, 1953, *Verh. Naturf. Gesell. Basel*, 64: 12, fig. 12, ♀. Two female syntypes from El Pozon, Venezuela in the Naturhistorisches Museum, Basel, examined. NEW SYNONYMY.

Comments. F. P.-Cambridge first suspected that Bank's *splendida* is a synonym of *vittata*. The epigynum, a shallow black depression (Fig. 45) sometimes has an anterior lip. The only male examined was caught in December at Barro Colorado Island by Dr. A. M. Chickering.

Distribution. Mexico to Venezuela.

Records. Mexico. *Veracruz*: 16 km S of San José del Carmen (L. I. Davis, AMNH). *Tabasco*: 3 km NE of Comalcalco (G. Ekholm). *Guatemala*: Variedades, 300 m (C., P. Vaurie, AMNH). *El Salvador*. (Kraus, 1955). *Costa Rica*. (Reimoser, 1938). *Panama*: El Valle. *Panama Canal Zone*: Barro Colorado Island (sev. collections).

Chrysso vittatula (Roewer), new combination

Figures 38-42

Argyrodes vittatus Keyserling, 1884, *Die Spinnen Amerikas*, Theridiidae, 2(1): 191, pl. 9, fig. 114, ♀. Female syntypes from St. Fe de Bogota [Bogotá, Colombia] and female, male syntypes from Pumamarca,

[Junín], Peru in the British Museum, Natural History, examined. Homonym of *A. vittatus* Bradley, 1877.

Argyroides vittatula Roewer, 1942, Katalog der Araneae, 1: 439. New name for *A. vittatus* Keyserling.

Description. Carapace, sternum dark brown, legs yellow. Abdomen with a longitudinal dorsal black band, series of white patches on sides and venter partly black. Eyes subequal in size. Anterior median eyes one and one-half diameters apart, almost two from laterals. Posterior median eyes one diameter apart, one and one-half from laterals. Chelicerae with two teeth on anterior margin. Total length of female 6.7 mm. Carapace 1.6 mm long, 1.2 mm wide. First femur 3.5 mm long; patella and tibia 3.4 mm long; metatarsus 3.0 mm long; tarsus 1.1 mm. Second patella and tibia 1.8 mm; third 1.2 mm; fourth 2.3 mm.

It is uncertain if females have been correctly separated from *C. ecuadorensis*. Females of *C. vittatula* have a dark spot posterior in the light area of the epigynum (Fig. 40). No other differences were noted. The male palpi, however, are very distinct (Figs. 41, 42). Only the availability of larger collections will permit finding characters separating the females. Illustrations were made from the syntypes.

Distribution. Colombia to Bolivia.

Records. Peru. Junín: Pumamarca, ♀, ♂ (PAS). Cuzco: San Miguel, ♀ (H. W. Foote). Bolivia: Tunari-Massiv, 4000 m, 1948, ♀ (Zischka, AMNH).

Chryso ecuadorensis Levi

Figures 31-37

Chryso ecuadorensis Levi, "1955" (1957) Jour. New York Ent. Soc. 63: 66, figs. 16, 38, 39, ♀. Female type from Runtun Trail, Baños, [Tungurahua], Ecuador in the American Museum of Natural History.

Description. Carapace, sternum red-brown. Legs yellow with ends of first tibiae and all tarsi darker to brown. Abdomen with white patches on sides and above spinnerets and with some black pigment in a median dorsal longitudinal line and above spinnerets (Figs. 31, 32). Posterior median eyes slightly larger than other eyes. Anterior median eyes one and one-half diameters apart, two from laterals in female, slightly more than two in male. Posterior median eyes one diameter apart, one and three-quarters from laterals in female; in male one and one-quarter diameters apart, two and one-half from laterals. Chelicerae with two teeth on anterior margin, apparently none posterior. Total length of female from Bolivia 5.5 mm. Carapace 1.7 mm long, 1.3 mm wide. First femur, 3.9 mm; patella and tibia, 3.6 mm; metatarsus, 3.6 mm; tarsus, 1.2 mm. Second patella and tibia, 1.9 mm; third, 1.3 mm; fourth, 2.5 mm. Total length of male from

Bolivia 4.0 mm. Carapace 1.7 mm long, 1.4 mm wide. First femur, 3.7 mm; patella and tibia, 3.5 mm; metatarsus, 4.2 mm; tarsus, 1.2 mm. Second patella and tibia, 2.1 mm; third, 1.4 mm; fourth, 2.3 mm.

Diagnosis. It is not certain whether females have been correctly separated from *C. vittatula* Roewer. The light area of the epigynum has a dark spot anterior (Figs. 34, 35). Only large collections of accompanied females will make the separation of the species possible.

Distribution. Colombia to Bolivia.

Records. *Colombia.* Cauca: 43 km S Popayán, March 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Ecuador.* Los Rios: Macuchi, copper mining camp inland from Río Palenque, March, 1943 ♀ (H. E. Frizzell). Tungurahua: Mt. Tungurahua, 1900-2000 m, Apr. 1939, ♀ (W. C. Macintyre); Baños, 1850-2000 m, Apr. 1939, ♀ (W. C. Macintyre, AMNH). *Bolivia.* Chaco, 2000 m, ♀, ♂ (MNHN).

Chrysso compressa (Keyserling), new combination

Figures 63-70

Achaea compressa Keyserling, 1882, Die Spinnen Amerikas. Theridiidae, 2(1): 107, pl. 5, fig. 69, ♀. Female type from Amable María, [Junin], Peru in the Polish Academy of Sciences, Warsaw.

Theridion conspersa, — Simon, 1894, Histoire Naturelle des Araignées, 1: 535 (misspelling).

Theridion compressum, — Roewer, 1942, Katalog der Araneae, 1: 491.

Comments. A specimen, presumably collected with the type, in the British Museum, Natural History, was examined. The abdomen resembles *C. cambridgei*, it has slight grooves on sides; a black band covers dorsum.

Description. Carapace yellow-white, yellowish in head region. Sternum yellow in Peruvian specimens, black in Brazilian. Legs yellow-white, distal ends of most leg segments darker yellow with denser, darker hairs. Abdomen with median dorsal colorless area and with white pigment on each side. Brazilian specimens have genital area

EXPLANATION OF PLATE 16

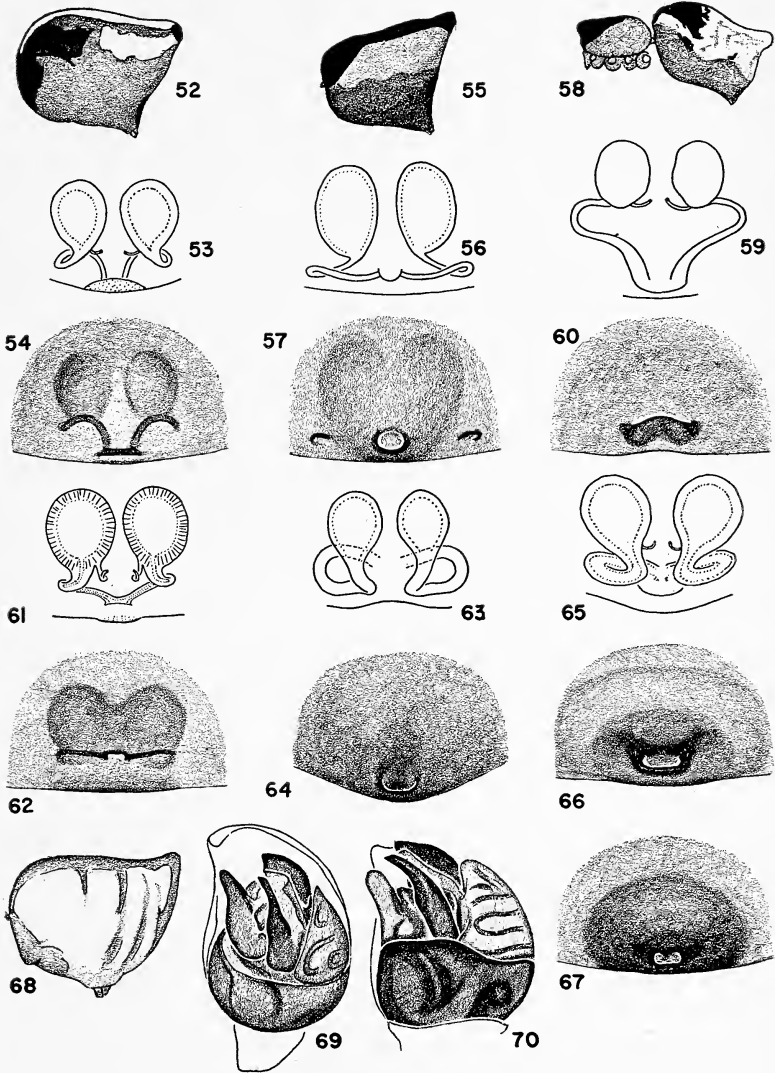
Figs. 52-54. *Chrysso ribeirao* sp. n. 52. Female abdomen, lateral view. 53. Female genitalia, dorsal view. 54. Epigynum.

Figs. 55-57. *C. pulchra* (Keyserling). 55. Female abdomen, lateral view. 56. Female genitalia, dorsal view. 57. Epigynum.

Figs. 58-60. *C. backstromi* (Berland). 58. Female. 59. Female genitalia, dorsal view. 60. Epigynum.

Figs. 61, 62. *C. caraca* sp. n. 61. Female genitalia, dorsal view. 62. Epigynum.

Figs. 63-70. *C. compressa* (Keyserling). 63, 65. Female genitalia, dorsal view. 64, 66, 67. Epigynum. 68. Female abdomen, lateral view. 69, 70. Left palpus.



black and a black spot anterior to spinnerets. Anterior median eyes slightly larger than others or subequal, their diameters apart, and one-third from laterals. Posterior median eyes slightly oval, their shorter diameter apart, and one and one-half from laterals. Chelicerae with two teeth on anterior margin. Abdomen usually without grooves. Total length of female from Peru 6.1 mm. Carapace 1.8 mm long, 1.4 mm wide. First femur 5.4 mm; patella and tibia 5.4 mm; metatarsus 5.5; tarsus 1.8 mm. Second patella and tibia 3.0 mm; third 1.8 mm; fourth 3.2 mm. Total length of male from Brazil 4.1 mm. Carapace 1.7 mm long. First femur 6.1 mm; patella and tibia 6.1 mm; metatarsus 3.6 mm; tarsus 1.8 mm. Second patella and tibia 3.3 mm; third 1.8 mm; fourth 3.3 mm.

The shape of the epigynum fossa is variable (Figs. 64, 66, 67). Figures 63, 64 were prepared from the types.

Distribution. Peru to southeastern Brazil.

Records. Peru. *San Martín:* Mishqui-yacu, 1600 m, 20 km NE of Moyobamba, Aug. 1947, ♀ (F. Woytkowski, AMNH). *Huánuco:* Monzón Valley, Tingo María, Oct. 19, 1954, ♀, ♂ (E. I. Schlinger, E. S. Ross, CAS). Brazil. *Minas Gerais:* Matosinhos, ♀ (MNHN). *Guanabara:* Teresópolis, 900-1000 m, March, 1946, ♀ (H. Sick, AMNH). *São Paulo:* São Paulo, Jan. 1960, ♂ (A. M. Nadler, AMNH); Jabaquara, Cidade São Paulo, 700-800 m, Dec. 1945, ♀, ♂ (H. Sick, AMNH). *Santa Catarina:* Nueva Teutonia, lat 27° 11' S, long 52° 23' W, ♀, ♂ (F. Plaumann, SMF).

***Chrysso arops* sp. n.**

Figures 29, 30

Type. Male from Teresópolis, 900-1000 m alt., Est. Guanabara, Brazil (H. Sick), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace with clypeus, labium, maxillae orange. Sternum black, except anterior portion. Legs orange to gray. Abdomen orange-white with several black spots (Fig. 29). Eyes subequal in size. Anterior median eyes one diameter apart, their radius from laterals. Posterior median eyes one and one-fourth diameters apart, one and one-half from laterals. Chelicerae with one tooth on the anterior margin. Abdomen as illustrated with a hump above spinnerets but without grooves (Fig. 29). Total length 2.4 mm. Carapace 0.98 mm long, 0.93 mm wide. First femur 2.58 mm; patella and tibia 2.50 mm; metatarsus 2.34 mm. Fourth patella and tibia 1.28 mm.

Diagnosis. This species probably belongs to *Chrysso*, it is not cer-

tain whether the palpus (Fig. 30) has a radix. The palpal structure separates *C. arops* from other *Chryssso*.

***Chryssso ribeirao* sp. n.**

Figures 52-54

Type. Female from Ribeirão Pires, 700-800 m alt., Est. São Paulo, Brazil, Dec. 1945 (H. Sick), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace yellow-white with some gray around posterior margin. Sternum all black in most specimens, in some only partially. Legs yellow-white with a black band on distal end of first femora and first tibiae. Abdomen with black and white areas and a median dorsal white band (Fig. 52). Eyes subequal in size. Anterior median eyes their diameter apart, almost touching laterals. Posterior median eyes their diameter apart, two-thirds from laterals. Abdomen without grooves (Fig. 52). Total length 2.7 mm. Carapace 0.89 mm long, 0.77 mm wide. First patella and tibia 1.8 mm; second 1.04 mm; third 0.74 mm. fourth 1.22 mm.

Diagnosis. The curved connecting ducts opening near the posterior rim (Figs. 53, 54) separates this species from others. The distance between the opening and the rim is variable.

Records. *Brazil.* *Guanabara:* Teresópolis, March 1946, 3 ♀ paratypes (H. Sick, AMNH).

Chryssso pulchra (Keyserling), new combination

Figures 55-57

Achaea signata Keyserling, 1891, *Die Spinnen Amerikas*, Brasilianische Spinnen, 3: 199, pl. 7, fig. 143, ♀. Female type from Alto da Serra do Novo Friburgo [Nova Friburgo, Est. Guanabara], Brazil in the British Museum, Natural History, examined. NEW SYNONYMY.

Achaea pulchra Keyserling, 1891, *op. cit.*, p. 200, pl. 7, fig. 144, ♀. Female type from Alto da Serra do Novo Friburgo [Nova Friburgo, Est. Guanabara], Brazil in the British Museum, Natural History, examined.

Theridion pulchrum, — Roewer, 1942, *Katalog der Araneae*, 1: 497.

Theridion signatellum Roewer, 1942, *op. cit.*, p. 498. New name for *signata*, thought to be preoccupied by *Theridion signata* Walckenaer, 1805. NEW SYNONYMY.

Comments. Although *signata* has page priority, it will help nomenclatural stability to use the name *pulchra*, since *Theridion signata* is preoccupied and some authors might consider *Chryssso* and *Theridion* synonymous. The types of *signata* and *pulchra* differ only in the coloration of the abdomen, a variable character. *Chryssso pulchra* has the

dorsum of the abdomen black, the sides white, and the venter yellowish without pigment (Fig. 55). The carapace and palpi of this species are black. The illustrations were prepared from the types of *Achaea pulchra*.

***Chrysso caraca* sp. n.**

Figures 61, 62

Type. Female from Caraca, Minas Gerais, Brazil (E. Gounelle), in the Muséum National d'Histoire Naturelle, Paris (no. 8881). The specific name is a noun in apposition after the type locality.

Description. Carapace yellow. Sternum yellow, gray or black. Legs yellow, sometimes with irregular black marks. Abdomen with a median longitudinal dorsal white band and white patches on sides; a black spot on each side of posterior tip and sometimes a black patch on each side. Carapace fairly high. Anterior median eyes slightly smaller than others, their diameter apart, one-quarter from laterals. Posterior median eyes one diameter apart, their radius from laterals. Chelicerae with two teeth on anterior margin, probably none posterior. Abdomen barely longer than high. Total length 2.9 mm. Carapace 0.98 mm long, 0.79 mm wide. First femur, 1.71 mm; patella and tibia, 1.69 mm; metatarsus, 1.43 mm; tarsus, 0.62 mm. Second patella and tibia, 1.00 mm; third, 0.59 mm; fourth, 1.12 mm.

Diagnosis. The opening of the epigynum is bordered by an anterior lip (Fig. 62) unlike *C. pulchra*; the shorter, straighter ducts (Fig. 61) separate this species from *C. ribeirao*.

Records. 3 paratypes collected with type.

Chrysso backstromi (Berland), new combination

Figures 58-60

Theridion backströmi Berland, 1924, The Natural History of Juan Fernandez and Easter Island, 3: 426, figs. 4-6, ♀. Female type from Juan Fernandez Island, [Chile] in the Naturhistoriska Riksmuseum, Stockholm, examined.

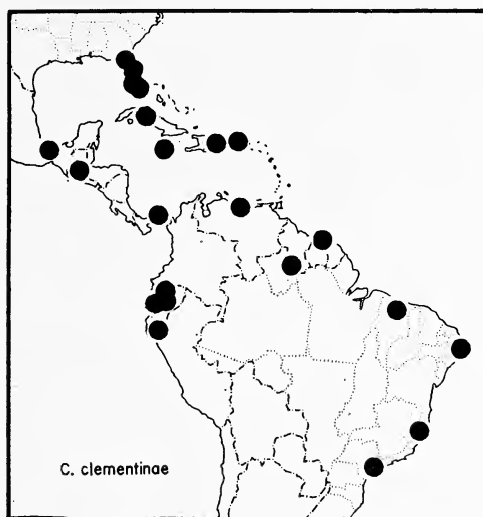
Description. Yellow-white with white and black markings (Fig. 58). Legs yellow-white with black rings on ends of femora and tibiae of fourth leg. Anterior median eyes smaller than others, a little more than one diameter apart, their radius from laterals. Posterior eyes two-thirds their diameter apart. Eyes appearing white and relatively large. Chelicerae without teeth. Abdomen with a hump (Fig. 58). Total length 2.5 mm. Carapace, 1.1 mm long, 1.0 mm wide. First femur, 2.2 mm; patella and tibia, 2.2 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 1.3 mm; third, 0.9 mm; fourth 1.5 mm.

Chryso clementinae (Petrunkévitch), new combination

Figures 71-75; Map 1

Meotipa clementinae Petrunkévitch, 1930, Trans. Connecticut Acad. Sci., 30: 212, fig. 61, ♀. Female type from Bayamón, Puerto Rico, in Petrunkévitch personal collection. Schmidt, 1956, Zool. Anz., 15: 240. [Not Bryant, 1940, Bull. Mus. Comp. Zool., 86: 314, figs. 79, 80, ♂].

Description. Color white, with narrow reddish line in thoracic region, some scattered black spots on venter of legs and white pigment spots and some scattered small spots on dorsum of abdomen. Eyes subequal in size. Anterior median eyes a little more than one diameter



Map. 1. Distribution of *Chryso clementinae* (Petrunkévitch).

apart, almost touching laterals. Posterior eyes separated by about one diameter. Abdomen often with several strong feather shaped (? movable) spines near tip (Fig. 71). Epigynum with two dark spots in a lightly sclerotized area (Fig. 73). Male palpus with a short embolus and large conductor (Figs. 74, 75). Total length of a female from Puerto Rico 2.3 mm. Carapace 0.85 mm long, 0.78 mm wide. First femur, 2.45 mm; patella and tibia, 2.31 mm; metatarsus, 1.51 mm; tarsus, 0.61 mm. Second patella and tibia, 1.30 mm; third, 0.81 mm; fourth, 1.55 mm. Total length of a male from Venezuela 2.0 mm. Carapace 1.00 mm long, 0.78 mm wide. First femur 3.60 mm; patella and tibia, 3.35 mm; metatarsus, 3.45 mm; tarsus, 0.91 mm. Second patella and tibia, 2.05 mm; third, 1.13 mm; fourth, 1.96 mm.

Natural History. This species is found on the underside of leaves of shrubs and small trees. Schmidt (1956) reports that it is commonly brought with bananas to Europe.

Distribution. Probably cosmopolitan; the absence of closely related species in America might suggest that it has been introduced. (Schmidt, 1956, records having obtained specimens with fruit from Guatemala, Colombia, French West Africa and Belgian Congo).

Records. Florida. Alachua Co.: Gainesville (H. K. Wallace, Hubbell, AMNH). Dade Co.: Kendall (A. M. Nadler, AMNH). Highlands Co.; 3 mi. S of Lk. Istokpoga (A. M. Nadler, AMNH). Seminole Co.: near Geneva (W. J. Gertsch, AMNH). *Mexico. Veracruz.* 30 km S of Jesús Carranza; Lake Catemaco, 300 m (C. P. Vaurie, AMNH). *Panama Canal Zone.* Pedro Miguel; Corozal; Barro Colorado Island; Summit; France Field (all A. M. Chickering). *Cuba.* Vega Alta, Santa Clara (P. Bermudez); Soledad, Las Villas (P. J. Darlington). *Jamaica.* Mona, St. Andrew Par.; Gas-tonbury, Trelawny Par.; Rio Cobre Gorge, St. Catherine Par.; Ewarton, St. Catherine Par. (all A. M. Chickering); Kinloss (A. M. Nadler, AMNH). *Dominican Republic.* near Ciudad Trujillo (A. M. Nadler, AMNH); Boca Chica (A. M. Nadler, AMNH). *Puerto Rico.* Rio Piedras (A. M. Nadler, AMNH). *Venezuela. Aragua:* Maracay; Rancho Grande (A. M. Nadler, AMNH). *Dto. Federal:* Caracas (A. M. Nadler, AMNH). *British Guiana.* Sauri-Wau River near Rio Tacutae (W. G. Hassler, AMNH). *Surinam:* Paramaribo (A. M. Nadler, AMNH). *French Guiana.* Cayenne (A. M. Nadler, AMNH). *Ecuador. Pichincha:* 35 km NW of Santo Domingo de los Colorados (A. M. Nadler, AMNH). *Tun-*

EXPLANATION OF PLATE 17

Figs. 71-75. *Chrysso clementinae* (Petrunkévitch). 71. Female, lateral view. 72. Female genitalia, dorsal view. 73. Epigynum. 74. Left palpus. 75. Palpus expanded, submesal view.

Figs. 76-78. *C. questona* sp. n. 76. Female abdomen, lateral view. 77. Female genitalia, dorsal view. 78. Epigynum.

Fig. 79. *C. melba* sp. n., palpus.

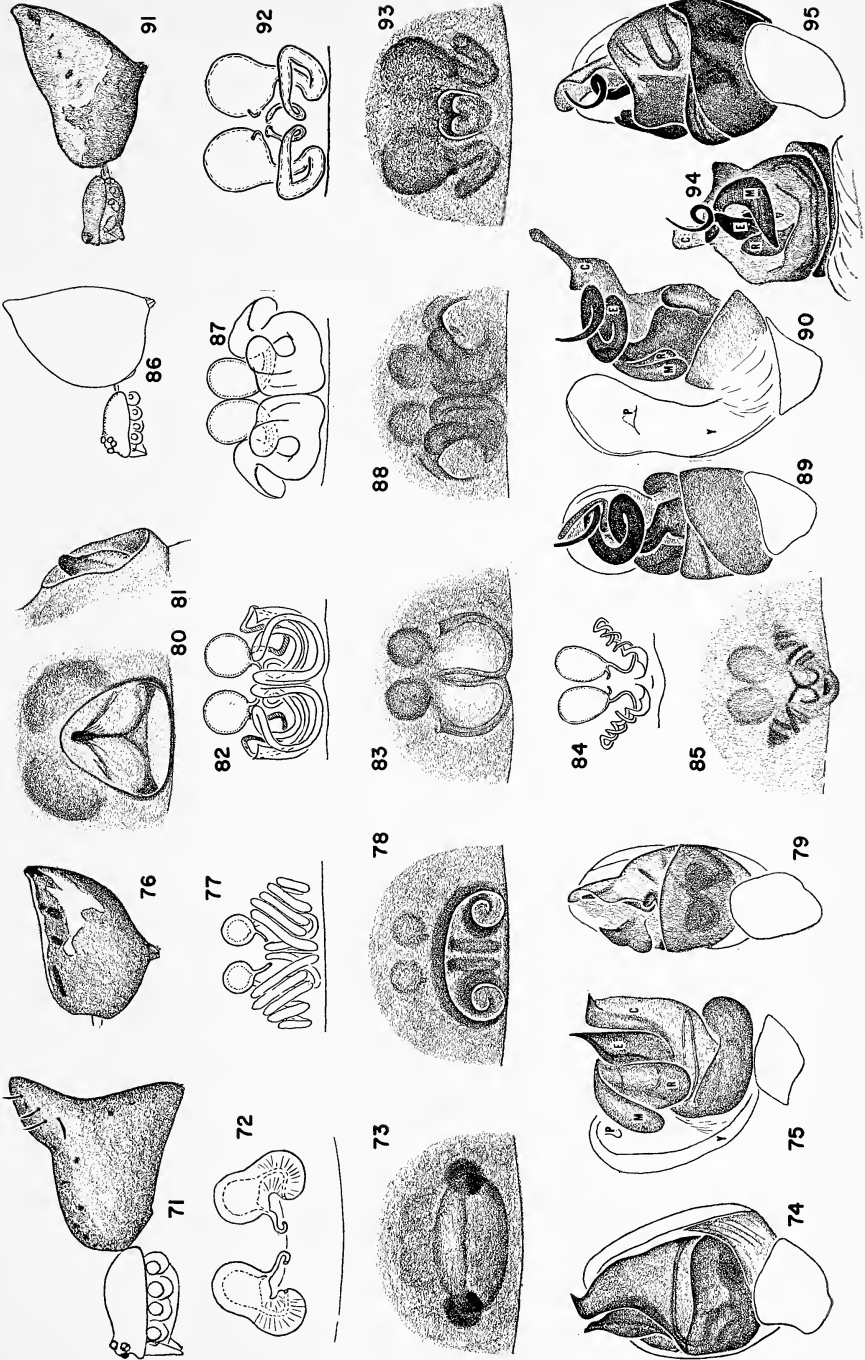
Figs. 80, 81. *C. vesiculosa* (Simon) (Philippines), Epigynum.

Figs. 82, 83. *C. alecula* sp. n. 82. Female genitalia, dorsal view. 83. Epigynum.

Figs. 84, 85. *C. arima* sp. n. 84. Female genitalia, dorsal view. 85. Epigynum.

Figs. 86-90. *C. silva* sp. n. 86. Female. 87. Female genitalia, dorsal view. 88. Epigynum. 89. Palpus. 90. Palpus expanded, subventral view.

Figs. 91-95. *C. volcanensis* sp. n. 91. Female. 92. Female genitalia, dorsal view. 93. Epigynum. 94. Palpus expanded, cymbium removed, dorsal view. 95. Palpus. (C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; Y, cymbium).



gurahua: Baños (H. E. Frizzell); Puñapi (H. E., D. L. Frizzell). *Guayas*: Milagro (H. E., D. L. Frizzell). *Peru*. "San Martin" (J. C. Pallister). *Piura*: Bellavista, Prov. Jean, (D. L. Frizzell). *Brazil*. *Maranhão*: São Luís (A. M. Nadler, AMNH). *Pernambuco*: Recife (A. M. Nadler, AMNH). *Espírito Santo*: Santa Teresa (A. M. Nadler, AMNH). *São Paulo*: São Paulo (A. M. Nadler, AMNH). *Paraguay*. San Luis [?].

***Chrysso melba* sp. n.**

Figure 79

Type. Male from Summit, Panama Canal Zone, July 21-29, 1950 (A. M. Chickering) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Yellow-white with a dusky median band on carapace, ends of femora, on patella, and distal ends of tibiae and metatarsi. Dorsum of abdomen with two rows of about ten dusky bars. Eyes subequal in size; anterior median eyes, one and one-third diameters apart, their radius from laterals. Posterior median eyes one and one-half diameters apart, a little more than one from laterals. Chelicerae with two teeth on anterior margin. Abdomen longer than wide or high; highest above spinnerets. Total length 2.2 mm. Carapace 1.0 mm long, 0.9 mm wide. First femur, 3.5 mm; patella and tibia, 3.5 mm; metatarsus, 3.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.0 mm; third 0.9 mm; fourth, 1.7 mm.

Diagnosis. The palpal structure (Fig. 79) separates this species from *C. clementinae*.

***Chrysso alecula* sp. n.**

Figures 82, 83

Type. Female from El Valle, Panama, July 1936 (A. M. Chickering) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Yellow-white with a dusky median band on carapace, small dark spots on venter of legs and white pigment spots and some dusky marks on dorsum of abdomen. Eyes subequal in size. Anterior median eyes their diameter apart, one-fourth from laterals. Posterior median eyes one-half diameter apart, one-fourth from laterals. Shape of abdomen like that of *C. silva* (Fig. 86). Total length of female, 1.6 mm. Carapace, 0.68 mm long 0.65 mm wide. First femur, 1.71 mm; patella and tibia, 1.61 mm; metatarsus, 1.43 mm; tarsus, 0.50

mm. Second patella and tibia, 1.06 mm; third, 0.71 mm; fourth, 1.17 mm.

Diagnosis. The long loosely coiled ducts of the genitalia (Figs. 82, 83) separate this species from *C. arima*.

Records. *Panama*: El Valle, July 1936, ♀ paratypes (A. M. Chickering).

***Chrysso arima* sp. n.**

Figures 84, 85

Type. Female from Simla, near Arima, Trinidad, 28 Dec. 1954 (A. M. Nadler) in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Yellow-white with white pigment spots on dorsum of abdomen. Eyes subequal in size. Anterior median eyes separated by one diameter, one-fourth from laterals. Posterior eyes separated by one diameter. Total length of female 1.6 mm. Carapace, 0.63 mm long, 0.52 mm wide. First femur, 1.42 mm; patella and tibia, 1.28 mm; metatarsus, 0.98 mm; tarsus, 0.50 mm. Second patella and tibia, 0.80 mm; third, 0.53 mm; fourth, 0.98 mm.

Diagnosis. The narrow, tightly coiled ducts of the genitalia and the median opening (Figs. 84, 85) separate this species from *C. alecula*.

Record. *Trinidad.* Simla near Arima, ♀ paratype (A. M. Nadler).

***Chrysso silva* sp. n.**

Figures 86-90

Type. Male from Forest Reserve, Panama Canal Zone, 25-28 July 1954 (A. M. Chickering) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Yellow-white with a median longitudinal dusky band on carapace; abdomen with white pigment patches on dorsum, dusky on sides. Anterior median eyes subequal or slightly larger than others, three-quarters diameter apart, almost touching laterals. Posterior eyes separated by one-third their diameter. Abdomen much higher than long in female (Fig. 86). Total length of a female, 1.6 mm. Carapace 0.65 mm long, 0.59 mm wide. First femur, 1.56 mm; patella and tibia, 1.43 mm; metatarsus, 1.30 mm; tarsus, 0.45 mm. Second patella and tibia, 0.88 mm; fourth, 0.97 mm. Total length of male 1.4 mm. Carapace, 0.66 mm long, 0.66 mm wide. First femur, 1.70 mm; patella and tibia, 1.75 mm; metatarsus, 1.53 mm; tarsus, 0.52 mm. Second patella and tibia, 1.09 mm; third, 0.63 mm; fourth, 0.98 mm.

Diagnosis. The larger diameter and shortness of the female ducts (Figs. 87, 88) separate this species from *C. alecula* and *C. arima*. The large coiled embolus of the palpus (Fig. 89) is distinctive.

Natural History. This species is found by beating vegetation.

Records. *Panama.* Porto Bello, ♀ (A. M. Chickering). *Panama Canal Zone.* Forest Reserve, ♂ paratype (A. M. Chickering); Summit, ♀ paratype (A. M. Chickering, A. M. Nadler, AMNH); Barro Colorado Island, ♀, ♂ paratypes (A. M. Chickering, A. M. Nadler, AMNH); Madden Dam (A. M. Chickering); Ft. Randolph (A. M. Chickering). *Ecuador.* *El Oro:* Río Jubanes, Pasaje, Oct. 23, 1942, ♂ (R. Walls).

***Chrysso volcanensis* sp. n.**

Figures 91-95

Thwaitesia vittata, — Banks, 1929, Bull. Mus. Comp. Zool., 69: 86. Not *C. vittata* O. P.-Cambridge.

Type. Male from El Voicán, Panama, Aug. 9-14, 1950 (A. M. Chickering) in the Museum of Comparative Zoology. The species is named after the type locality.

Description. Carapace, sternum, legs yellow-white. Legs with dark bands on middle and ends of segments. Abdomen yellow-white with white pigment areas on dorsum, sometimes with small black spots (Fig. 91). Anterior median eyes one and one-half diameters apart, their radius from laterals in female; one diameter apart, one-third diameter from laterals in male. Posterior median eyes a little more than one diameter apart, one from laterals. Total length of females 3.5-4.5 mm. One female measured 3.7 mm total length. Carapace, 1.2 mm long, 0.8 mm wide. First femur, 5.0 mm; patella and tibia, 5.0 mm; metatarsus, 5.4 mm; tarsus, 1.4 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.6 mm. Total length of a male 2.5 mm. Carapace 1.2 mm long, 1.0 mm wide. First femur, 5.9 mm; patella and tibia, 6.0 mm; metatarsus, 7.5 mm; tarsus, 1.7 mm. Second patella and tibia, 3.6 mm; third, 1.4 mm; fourth, 2.6 mm.

Diagnosis. The shorter ducts and embolus (Figs. 92-95) distinguish this species from *C. questona*. The epigynum (Fig. 93) has an indistinct shallow depression of variable shape. The small palpal embolus (Figs. 94, 95) separate the species from *C. silva*.

Records. *Costa Rica:* Santa María Dota (Tristan). *Panama.* El Volcán, ♀, ♂ paratypes (A. M. Chickering).

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THE NEOTROPICAL SPECIES OF THE ANT GENUS *STRUMIGENYS* FR. SMITH: SYNOPSIS AND KEYS TO THE SPECIES¹

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Introduction

The New World *Strumigenys* have been revised through a series of twelve papers bearing the general foretitle, "The Neotropical species of the ant genus *Strumigenys* Fr. Smith," plus several articles by Dr. W. W. Kempf and by myself, beginning with my "Preliminary generic revision of the higher Dacetini" (Brown, 1948). It now seems appropriate to offer a unifying synopsis of the New World species of the genus, along with keys for identification and some general remarks.

Species Synopsis of New World *Strumigenys*

The synopsis below includes the names, each with author and date of publication, plus citation of the principal references in the Brown or Kempf papers already mentioned, which are listed in the section of "References" at the end of this article. These papers contain references to original descriptive and distributional material for each species, but I have included in the synopsis new or supplementary information wherever it seemed useful to do so. The species are listed by groups in order of apparent relationship, as closely as it is possible to place them in a purely linear order. The probable relationships within the genus in the New World are discussed at the end of the synopsis. It will be noticed that the group placement of some species differs from that of the previous parts published. The present grouping represents a reconsideration of all of the New World species taken together.

Group of *mandibularis*

1. *Strumigenys mandibularis* Fr. Smith, 1860
Brown, 1953b: 53-55, worker, synonymy.

Frederick Smith confused two species under this name; one of these was later described as *S. prospiciens* by Emery. In order to fix these names unambiguously according to present usage, I hereby designate as lectotype of *S. mandibularis* the worker in the British Museum (Natural History), which was called "holotype" in my 1953 paper.

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Manuscript received by the editor January 25, 1962.

Although this specimen is labeled as "type," Smith never designated a type in print, and at least some of his original specimens exist elsewhere (e.g., in the Munich Museum).

Distribution: Amazon Basin; known only from the type series.

Synonym: *S. batesi* Forel.

2. *Strumigenys godmani* Forel, 1899

Brown, 1953b: 55-56, worker, female, variation.

Biology: Lives in wet forest. The nest I found in Panama was in a small rotten log in cloud forest.

New records: Panama: Progreso, Chiriqui Prov. (F. M. Gaige leg.); Cerro Campana, about 950 m altitude, Panamá Prov. (W. L. Brown, Jr. leg.).

Distribution: Costa Rica, Panama, British Guiana.

Synonym: *S. ferox* Weber.

3. *Strumigenys planeti* Brown, 1953

Brown, 1953b: 57-59, worker, female, variation, distribution.

Biology: Apparently a rain forest species. Weber (1952) reports a nest taken in a wet mossy log in a cacao plantation on Trinidad.

New record: Peru: Monson Valley, Tingo Maria, winged female (E. I. Schlinger and E. S. Ross leg.).

Distribution: Trinidad, Amazon Basin to Bolivia and Peru.

4. *Strumigenys smithii* Forel, 1886

Brown, 1953c: 104-107, worker, variation, distribution, biology.

Biology: Nests in rotten logs, rotten twigs or, on St. Vincent, rarely in sod. Primarily a forest species.

New records: Colombia: Loma Larga, Sierra Santa Marta (F. M. Gaige leg.). Panama: Cerro Campana, 800 m, Province of Panamá (G. B. Fairchild and W. L. Brown, Jr. leg.).

Distribution: Costa Rica south to Santa Catarina, Brazil, and Amazonian Bolivia; St. Vincent, B. W. I.

Synonym: *S. smithi* var. *inaequalis* Emery.

5. *Strumigenys hemidisca* Brown, 1953 (Fig. 22)

Brown, 1953c: 107-108, worker.

Biology: The type series came from orchid plants intercepted in U. S. plant quarantine, and so were probably nesting amid the epiphytes in trees.

Distribution: Venezuela; known only from the type series.

6. *Strumigenys prospiciens* Emery, 1906

Brown, 1953c: 108-110, worker, female, distribution.

Distribution: Amazon Basin south to Bolivia and to northern Argentina: Misiones.

7. *Strumigenys biolleyi* Forel, 1908 (Fig. 28)

Brown, 1953c: 101-104, worker female, variation, distribution.

Biology: A forest species, nesting mainly in rotten logs.

New records: Ecuador: 10 miles north of Manglar Alto, Guaymas (E. I. Schlinger and E. S. Ross leg.). Panama: Cerro Campana, Panamá Prov., 800 m altitude (W. L. Brown, Jr. leg.).

Distribution: Southern Mexico (Chiapas) south through Central America to Ecuador.

Synonyms: *S. tridens* Weber, *S. luctuosa* Menozzi.

8. *Strumigenys saliens* Mayr, 1887

Brown, 1954b: 55-57, worker, female, distribution, biology.

Biology: Nests in rotten logs and branches lying on the floor of forest.

Distribution: Southeastern Brazil and northeastern Argentina: Misiones.

Synonyms: *S. saliens* var. *procera* Emery and var. *angusticeps* Forel.

9. *Strumigenys borgmeieri* Brown, 1954

Brown, 1954b: 57-59, worker.

Distribution: Brazil: Pernambuco; known only from the holotype.

10. *Strumigenys trinidadensis* Wheeler, 1922 (Figs. 14, 23)

Brown, 1954b: 59-62, worker, male, distribution.

New record: Esmeralda, Ecuador (J. Foerster leg.).

Distribution: Trinidad, northeastern Brazil, Ecuador, Amazonian Bolivia; probably widespread in the interior of South America.

11. *Strumigenys sanctipauli* Kempf, 1958 (Fig. 24)

Kempf, 1958b: 556-559, figs. 1-4, worker.

Distribution: Brazil: Serra do Mar, São Paulo State; known only from the holotype.

12. *Strumigenys sublonga* Brown, 1958

Brown, 1958a: 221-222, fig. 1C, D, worker, female.

Distribution: Bolivia: Lower Rio Madidi; known only from type series.

13. *Strumigenys rehi* Forel, 1907

Brown, 1958a: 222-223, worker.

Biology: This species was taken from orchid plants arriving at Hamburg, Germany, a circumstance agreeing with the large eyes of the worker to indicate an arboreal habitat.

Distribution: Amazon Basin; exact type locality unknown.

14. *Strumigenys cordovens* Mayr, 1887 (Figs. 25, 26, 27)

Brown, 1958a: 218-220, fig. 1B, E, F, G, worker, variation, distribution.

Distribution: Southern Mexico to Trinidad and the Guianas.

15. *Strumigenys mokensis* Forel, 1905

Brown, 1958a: 221, raised from variety to provisional species rank.

This is a very doubtful form, most likely a synonym of *cordovens*. The whereabouts of the type is unknown. The species is not included in the key.

Distribution: La Moka, Venezuela, type locality.

16. *Strumigenys dolichognatha* Weber, 1934

Brown, 1958a: 223-224, fig. 1A, worker.

Distribution: British Guiana: Kartabo; known only from the type series.

Group of *cultriger*

17. *Strumigenys cultriger* Mayr, 1887 (Fig. 9)

Brown, 1957: 97-99, worker.

New record: Xaxim, Santa Catarina (F. Plaumann leg.).

Distribution: Southeastern Brazil.

18. *Strumigenys deltisquama* Brown, 1957

Brown, 1957: 99-101, fig. 1a, b, worker.

Distribution: Panama Canal Zone: Barro Colorado Island; known from types only.

Group of *tococae*

19. *Strumigenys tococae* Wheeler, 1929

Brown, 1957: 101-102, fig. 1c, worker.

Biology: The types were taken from an abundant population inhabiting the foliar sacs of *Tococa formicaria*, a tall myrmecophytic shrub, in the outskirts of Belém. From this circumstance and the large size of the eyes, *S. tococae* is judged to be an arboreal or subarboreal specialist.

Distribution: Belém, Brazil, at the mouth of the Amazon; known only from the type series.

20. *Strumigenys fairchildi* Brown, 1961

Brown, 1961: 60-61, worker.

This species, described from a single worker, is very close to *S. tococae*, but differs markedly in gastric sculpture and pilosity. It is

not known whether *S. fairchildi* lives in plant cavities, but it does seem likely that it is a subarboreal forager.

Distribution: Panama: Cerro Campana, Panamá Province ca. 800 m altitude; known only from the holotype.

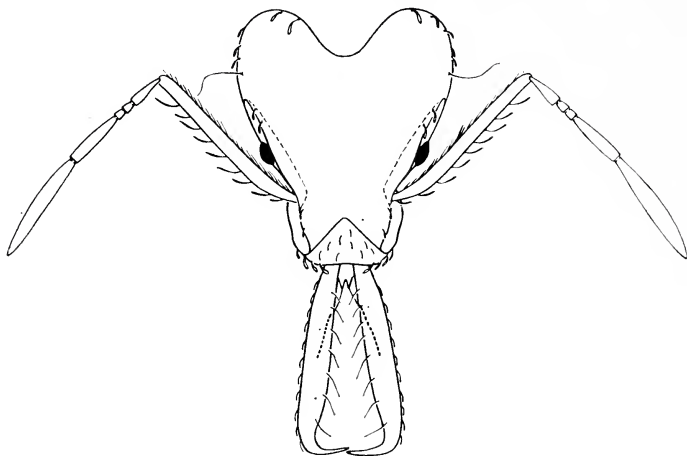


Figure 1. *Strumigenys ludia*, worker from Veracruz, dorsal full-face view of head showing fringing pilosity only.

Group of *ludia*

21. *Strumigenys longispinosa* Brown, 1958

Brown, 1958b: 123-126, figs. 1, 2, worker.

Biology: Nests in the soil of tropical forest.

Distribution: Panama.

22. *Strumigenys marginiventris* Santschi, 1931

Brown, 1958b: 126-128, fig. 3, worker, female.

Biology: Nests in the soil, often in paths or other other openings, in rain forest or plantations, and the workers forage over the open ground among leaves or herbs by day as well as night. Common on Barro Colorado Island.

New records: Palmar, Puntarenas Dept., Costa Rica, in soil of banana plantation, several collections (E. O. Wilson leg.).

Distribution: Golfo Dolce region of Costa Rica to northern Colombia.

23. *Strumigenys ludia* Mann, 1922 (Figs. 1, 5)

Brown, 1954a: 194-196, worker, female.

Biology: *S. ludia* has been investigated at length in the field by

Wilson and in the artificial nest by Wilson and Brown, and the details will be published elsewhere. *S. ludia* is a forest species and usually nests in rotten branches or twigs lying on the forest floor. The food is chiefly entomobryoid Collembola caught alive in the manner usual for the genus.

New records: Mexico: Ridge between Antiguo Morelos and Nuevo Morelos (E. S. Ross leg.). Pueblo Nuevo, near Tetzonapa, Veracruz (E. O. Wilson leg.). Costa Rica: Abaca Plantation, Bataan (C. H. Batchelder).

Distribution: Southern Mexico to Costa Rica.

Synonym: *S. ludia* subsp. *tenuis* Weber.

Group of *hindenburgi*

24. *Strumigenys hindenburgi* Forel, 1915 (Fig. 8)

Brown, 1961: 61-64, worker, pseudogyne, distribution.

Distribution: Northern Argentina extending into southeastern Brazil.

25. *Strumigenys lanuginosa* Wheeler, 1905 (Fig. 4)

Brown, 1961: 61-63, worker, female, distribution.

Distribution: Southern Mexico, Panama; Bahamas, where probably introduced.

26. *Strumigenys ogloblini* Santschi, 1936

Brown, 1958c: 136-137, fig. 1b, worker, female.

Distribution: Northern Argentina, probably also in southern Brazil.

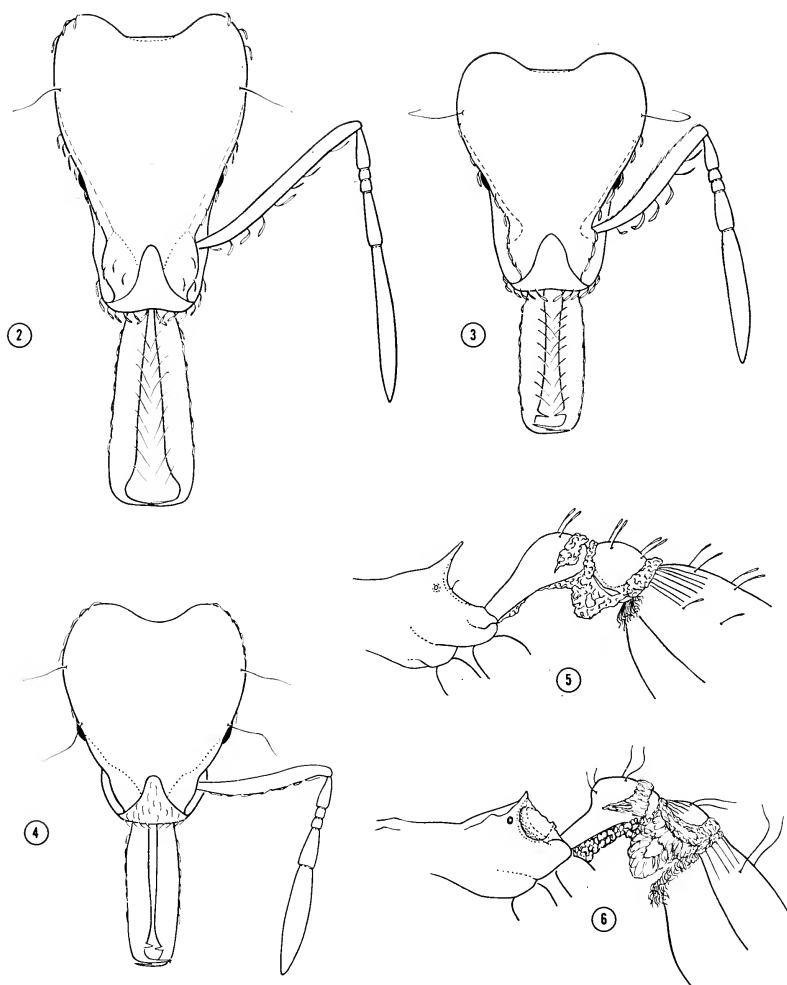
Group of *elongata*

27. *Strumigenys precava* Brown, 1954 (Fig. 7)

Brown, 1954a: 196-200, worker, female.

Biology: I found this species rather common on Barro Colorado Island in the Panama Canal Zone, nesting in red- or chocolate-rotten logs. One nest found was very large, containing several hundred — perhaps a thousand or more — workers. Workers were seen carrying a mycetophilid larva and a termite nymph into this nest as it was being opened, and a captive colony fed on a wide variety of small arthropods, including entomobryoid collembolans.

New record: Panama: Cerro Campana, Panamá Province, about 800 m altitude, in a small rotten log in a cloud forest ravine, with winged females, Jan. 16, 1960 (G. B. Fairchild and W. L. Brown, Jr. leg.).



Figures 2-6. *Strumigenys* spp., workers. Figure 2, *S. lacacoca*, paratype, dorsal full-face view of head, showing fringing pilosity only. Figure 3, *S. nevermanni*, same. Figure 4, *S. lanuginosa*, same. Figure 5, *S. ludia*, Veracruz, side view of posterior alitrunk, nodes and anterior part of gaster. Figure 6, *S. lacacoca*, paratype, same. Roughly to same scale.

Distribution: Panama, British Guiana, Amazonian Bolivia; probably widespread in hylaeon South America.

28. *Strumigenys elongata* Roger, 1863

Brown, 1954a: 189-192, worker, female, male, variation, synonymy, distribution, biology.

Biology: This species is definitely a collembolan feeder, common in the leaf litter of tropical forest. It seems to tolerate drier as well as wet forest types.

New records: Mexico: Pueblo Nuevo and El Palmar, near Tetzonapa, Veracruz (E. O. Wilson leg.). Ocosingo Valley, Chiapas (C. and M. Goodnight and L. Stannard leg.).

Distribution: Southern Mexico to Bolivia and southeastern Brazil.

Synonyms: *S. imitator* Mayr, *S. elongata* subsp. *nicaraguensis* Weber.

29. *Strumigenys consanii* Brown, 1954

Brown, 1954a: 192-194, worker.

A larger, more robust relative of *elongata* with smooth and shining postpetiolar disc.

Distribution: Costa Rica: La Palma, near San José, 1500 m altitude; known only from the type series.

Group of *emeryi*

30. *Strumigenys emeryi* Mann, 1922

Brown, 1959a: 97-99, worker, variation, distribution.

Distribution: Honduras, southern Mexico.

31. *Strumigenys boneti* Brown, 1959 (Fig. 12)

Brown, 1959a: 103-104, worker.

Distribution: Southern Mexico.

32. *Strumigenys nevermanni* Brown, 1959 (Fig. 3)

Brown, 1959a: 99-100, worker, female.

Distribution: Costa Rica: Hondura, 1050 m altitude; known only from types.

33. *Strumigenys micretes* Brown, 1959 (Figs. 13, 19)

Brown, 1959a: 100-101, worker. Brown, 196: 58-60, variation, distribution.

As mentioned in the note in couplet 21 of the key (below), this species and *S. lacacoca* may actually represent different populations of the same species.

Biology: A species of rain forest and cloud forest.

34. *Strumigenys lacacoca* Brown, 1959 (Figs. 2, 6)

Brown, 1959a: 101-102, worker. Brown, 196: 58-60, worker variation, distribution.

Distribution: Central Panama.

Group of *silvestrii*

35. *Strumigenys silvestrii* Emery, 1905 (Fig. 18)

Brown, 1959c: 25-28, fig. 1, worker, female, synonymy, variation, distribution.

Distribution: Northern Argentina, southern Brazil; also in Cuba and Louisiana, U. S. A., where probably introduced by commerce.

Synonym: *S. caribbea* Weber.

36. *Strumigenys carinithorax* Borgmeier, 1934

Brown, 1959c: 29-30, worker, female, male.

Distribution: Dutch Guiana: vicinity of Paramaribo.

37. *Strumigenys schmalzi* Emery, 1905

Brown, 1959c: 28-29, worker.

Distribution: Southeastern Brazil.

38. *Strumigenys perparva* Brown, 1958

Brown, 1958c: 133-135, fig. 1a, worker, female.

Distribution: Trinidad and the Guianas to São Paulo; probably interior Brazil.

Group of *louisianae*

39. *Strumigenys mixta* Brown, 1953 (Figs. 15, 21)

Brown, 1953a: 4-5, worker.

Biology: One of the two original series was taken in orchid plants at quarantine, so the species may be arboreal or subarboreal.

Distribution: Guatemala; known only from the types (two localities).

40. *Strumigenys louisianae* Roger, 1863

Brown, 1953a: 2-3, description of synonymous *S. clasmosporgia*, worker.

Brown, 1953d: 28-31, figs. 1, 3, worker, variation, synonymy, distribution.

Brown, 1961: 64-68, geographical variation, synonymy.

Biology: The feeding habits of this species have been studied in some detail by Wilson (1950, 1954) and by myself. The food consists of a variety of small arthropods found in and on the soil cover and caught by the workers with their trap-like jaws. The preferred prey are entomobryoid and symphypleonan Collembola; poduroid collembolans are not taken.

Distribution: Widespread in the Americas from Virginia and Tennessee south at least to the Tucumán area of Argentina; north-

ward in Mexico to sheltered canyons and cultivated areas of southern Arizona; greater Antilles (except Jamaica). Unaccountably absent from certain well-collected areas within this range, such as parts of the Canal Zone, Trinidad and British Guiana, although plentiful in Costa Rica and at least some localities in Colombia. This species tolerates much drier conditions and will live in plantations and other cultivated situations, so perhaps it is found mostly in habitats outside the primary forest in the central parts of its range. Its range and ecological amplitude are greater than those of any other New World *Strumigenys*.

Synonyms: *S. unidentata* Mayr, *S. unispinulosa* Emery, *S. unispinulosa* var. *longicornis* Emery, *S. fusca* Emery, *S. louisianae* var. *obscuriventris* Wheeler, *S. bruchi* Forel, *S. infidelis* Santschi, *S. eggersi* var. *cubaensis* Mann, *S. louisianae* subsp. *laticephala* M. R. Smith, *soledadensis* Weber, *guatemalensis* Weber, and *costaricensis* Weber, *S. clamospongia* Brown. The long list of synonyms reflects in part the rather extreme variation shown by this species on the South American continent. More peripheral populations (North and Central America, West Indies, Argentina) tend to be more uniform both within and among themselves.

41. *Strumigenys producta* Brown, 1953

Brown, 1953a: 3-4, worker.

This species is a larger, long-mandibulate version of *S. louisianae*. In view of the extensive variation now known for the latter species in South America, it would not be surprising to find that *S. producta* is just an extreme local variant of *S. louisianae*.

Distribution: Basin of the Rio Beni, Bolivia; known only from the types.

Group of *connectens*

42. *Strumigenys connectens* Kempf, 1958 (Fig. 11)

Kempf, 1958a: 59-64, figs. 1-3, worker, variation.

Biology: The paratype series was taken in orchid plants in U. S. quarantine, so the species is presumably arboreal.

Distribution: The species is known from two localities, both in Colombia.

43. *Strumigenys laevipleura* Kempf, 1958

Kempf, 1958a: 64-65, figs. 5-7, worker.

Biology: Like *S. connectens*, this species was also taken from an orchid shipment, and it may therefore be arboreal in habits.

Distribution: Known only from the type series from Colombia, apparently from the vicinity of Medellin.

44. *Strumigenys xenognatha* Kempf, 1958

Kempf, 1958a: 65-66, fig. 4, female.

Biology: The holotype female, a unique, was taken from orchid plants and bears the same data as the *S. laevipleura* types, from which it differs too widely to be their queen. Perhaps it is a social parasite of *S. laevipleura*.

Distribution: Colombia.

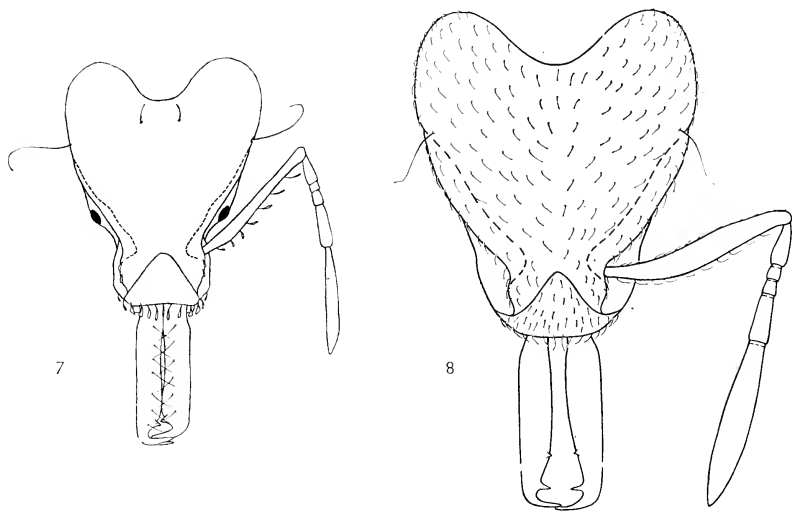
Group of *gundlachi*45. *Strumigenys subedentata* Mayr, 1887

Brown, 1960: 48-50, figs. 7, 9, worker, female, male, variation, distribution, biology.

Biology: This species nests in small colonies in the soil or soil cover in mesic tropical forest and feeds chiefly on entomobryoid Collembola.

Distribution: Southern Mexico south to southeastern Brazil; Trinidad; probably widespread in interior South America.

Synonyms: *S. tristani* Menozzi, *S. clavata* Weber.



Figures 7-8. *Strumigenys* spp., workers, dorsal full-face view of head. Figure 7, *S. precava* from Panama Canal Zone, showing fringing pilosity only. Figure 8, *S. hindenburgi* from Tucumán, Argentina. Not to same scale.

46. *Strumigenys trieces* Brown, 1960

Brown, 1960: 50-51, fig. 8, worker.

Distribution: Costa Rica; known only from the holotype.

47. *Strumigenys denticulata* Mayr, 1887

Brown, 1960: 47-48, fig. 3, worker, female.

Biology: Occurs in both primary and second-growth forest, in leaf litter; epiphytes and in termite nests.

Distribution: Trinidad and the Guianas south to southeastern Brazil; probably occurs widely in interior South America as well.

48. *Strumigenys jamaicensis* Brown, 1959

Brown, 1959b: 6, worker. Brown, 1960: 45-46, fig. 4, worker.

Distribution: Mountains of Jamaica.

49. *Strumigenys gundlachi* (Roger, 1862)

Brown, 1960: 40-45, figs. 1, 5, worker, female, synonymy, distribution, biology.

In addition to the characters cited in the key, it may be mentioned that fully-colored *S. gundlachi* workers and females are usually darker in color (brownish-red to dark brown) than are those of *S. eggersi* (ferruginous yellow).

Biology: *S. gundlachi* feeds chiefly if not entirely on entomobryoid and sminthuroid Collembola, which it catches by employing a relatively inactive "ambush" type of hunting, but if the prey struggles after being struck, it may be lifted off the ground and stung in the manner of other *Strumigenys*. In many parts of the Caribbean countries, this is a very abundant ant in the leaf litter of tropical forest, thickets and plantations, and it tolerates a wide variety of ecological conditions.

Distribution: Central America and southern Mexico, southern Florida, West Indies to Trinidad.

Synonyms: *S. eggersi* varieties *vincentensis* Forel, *banillensis* Santschi, *isthmica* Santschi and *berlesei* Weber; *S. eggersi* subsp. *infuscata* Weber, and *S. bierigi* Santschi.

50. *Strumigenys eggersi* Emery, 1890 (Figs. 10, 20)

Brown, 1960: 46-47, figs. 2, 6, worker, female, variation, distribution, biology.

Biology: Found in forests, thickets, gardens, etc. Almost certainly a collembolan feeder.

Distribution: Trinidad and the Guianas to southeastern Brazil and Amazonian Bolivia. Widespread (possibly by recent introduction) in the West Indies; southern Florida; southern Mexico.

Group of *rogeri*51. *Strumigenys rogeri* Emery, 1890 (Figs. 16, 17, 29)

Brown, 1954, Bull. Mus. Comp. Zool., 112: 20-23, worker, female, feeding habits.

Although *S. rogeri* was first described from West Indian material, I

showed in 1954 that it is a tramp belonging to a characteristically African species-group, and itself probably West African in origin.

Distribution: Widespread in the West Indies, from Cuba to Trinidad; British Guiana; West Africa; Hawaii, Tahiti, Fiji, Micronesia; greenhouses in England and Scotland; apparently spreading rapidly through commerce.

Synonyms: *S. incisa* Godfrey, *S. sulfurea* Santschi.

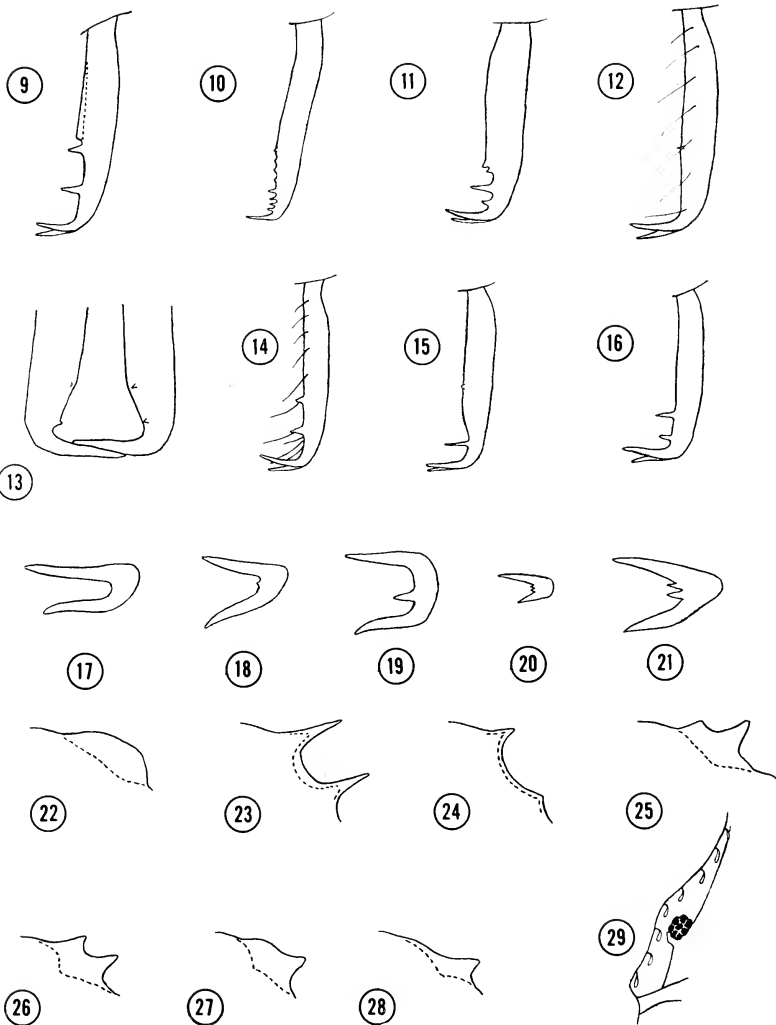
Phylogeny of the New World *Strumigenys*

I belong to the school that believes that since Darwin phylogenetic reasoning is inseparably a part of the taxonomic ordering of any group. The work of the more outspoken "aphyletic taxonomists" shows that they have not escaped the influence of evolutionary thinking, either, when it comes to revising a species-group or genus or family. Phylogenetic thinking is usually more or less implicit in the grouping of species, as I have grouped the New World species (above). In Figure 30 I have shown my best guess as to how the species groups are related one to the others. This diagram should not be taken too seriously, because *Strumigenys* species are very likely to be convergent from different groups, and the convergence may be very close and may involve several to many characters.

The most serious problem in *Strumigenys* is the question of *direction* of evolution; in other words, which species or groups are primitive, and which derived? One can look to the other two faunas of the genus (Ethiopian-Malagasy and Indo-Australian), but these give little help at present. I used to think, for no very good reason, I suppose, that certain species with large, ruggedly modelled heads and heavy, more or less closely approximate mandibles [*chyzeri* group of Melanesia,

EXPLANATION OF PLATE 18

Figures 9-29. *Strumigenys* spp., workers. Figures 9-12 and 14-16 show left mandibles in dorsal view; Figure 13 is a dorsal enlarged view of the apices of both mandibles. Figure 9, *S. cultriger*. Figure 10, *S. eggersi*. Figure 11, *S. connectens*, paratype. Figure 12, *S. boneti*, paratype. Figure 13, *S. sp.* near *micretes* from Boquete, Panama — one of several variants from this locality. Figure 14, *S. trinidadensis*. Figure 15, *S. mixta*, paratype. Figure 16, *S. rogeri*. Figures 17-21 are end-on views of the apical fork of the mandibles, much enlarged. Figure 17, *S. rogeri*. Figure 18, *S. silvestrii*. Figure 19, *S. micretes*, paratype. Figure 20, *S. eggersi*. Figure 21, *S. mixta*, paratype. Figures 22-28, lateral view of propodeal lamella. Figure 22, *S. hemidisca*, holotype. Figure 23, *S. trinidadensis*, paratype. Figure 24, *S. sanctipauli*, holotype after Kempf. Figure 25, *S. cordovensis*. Figures 26, 27, same, showing extremes of variation in different individuals; the pattern of Figure 27 is common in southern Mexico. Figure 28, *S. biolleyi*. Figure 29, *S. rogeri*, left side of head near eye as seen from dorsal full-face view, to show "detached" eye.



BROWN — STRUMIGENYS

grandidieri Forel of Madagascar, *precava* of the present study (Fig. 7)], were primitive types within the genus, but now it seems to me that the opposite is true. *S. loriae* Emery (of the *chyzeri* group) and *S. precava* are viewed as derivative species with secondarily broadened prey specificity, and it is predicted that *S. grandidieri* will also eventually be found to feed on a wide range of small arthropods instead of the usual *Strumigenys* diet consisting mainly of collembolans. The powerful head and mandibles of these species are probably an adaptation to prey less fragile than *Collembola*.

Mandibular armament is probably the best character to use for determining direction of descent within *Strumigenys*. More primitive dacetine genera (*Acanthognathus*, *Orectognathus*, *Microdacton*) have strumigenite mandibles with three long teeth in the apical fork; often the most dorsal of the three is also displaced slightly basad. In cases where such displacement has taken place, we have what in the genus *Strumigenys* would be called an apical fork (with two teeth) plus a preapical tooth. This is the condition found, with greater or lesser modification, in most Indo-Australian members of the genus as well as several New World species. In the African group, the species judged to be the more primitive ones have two preapical teeth, and derivative species mostly are smaller in size and tend to lose one or both *distal* preapical teeth. Quite a few of the New World forms, most notably those of the *mandibularis* group, have two well-developed preapical teeth on each mandible. In other New World forms, chiefly among smaller species, one or both of these teeth are present in greatly reduced form — in fact, in form so greatly reduced as to suggest that they serve no present function in holding struggling prey. It seems more likely to me that such feeble denticles represent vestiges of larger, functional teeth rather than the reverse, especially since so many of the species, and particularly the smaller species, have them. From this hint (which is no more than that), I take it that in the New World fauna of *Strumigenys* the *mandibularis* groups two large preapical teeth represent the primitive condition. The extensive radiation of undoubted *mandibularis* group species also speaks for a relatively long-term existence of this armament pattern. I have accordingly placed the *mandibularis* group at the base of my phyletic scheme (Fig. 30), despite the very good possibility that the earliest *Strumigenys* on a *world* basis may have had but a single preapical tooth.

The *mandibularis* group shows what appears to be a clear double morphocline. Beginning with a more “normal” or “average” species such as *S. smithii*, a string of species of increasing size and development (width) of occipital lobes, concurrent with a shortening and

thickening of the mandibles, leads through *S. planeti* and *S. godmani* to *S. mandibularis*. In the other direction, we find a trend toward lengthening of the mandibles through the series *S. biolleyi*, *S. saliens*, *S. sanctipauli* and so on to the species near *S. cordovens*, climaxed by the remarkable *S. dolichognatha*, the mandibles of which are relatively longer than in any other ant known to me. Side offshoots of the *mandibularis* group are species such as *S. borgmeieri* and *S. trinidadensis*; the greatly weakened proximal preapical tooth of the last species shows the first stages of a trend that apparently led to groups such as the *hindenburgi* and *emeryi* assemblages, and beyond these to the *elongata* and *silvestrii* groups respectively. Species such as *S. perparva* and *S. ogloblini*, both of which have a single preapical tooth on each mandible, were previously grouped together, but now I think it more likely that their similarities are due to convergence. Such highly reduced species are doubtfully placed at best.

The *emeryi* group, especially *S. emeryi* itself, is linked to the *louisianae* group by the virtually perfect intermediate *S. mixta*. The *louisianae* group leads to the *connectens* group and through this to the *gundlachi* group. These last three groups all have two (or rarely more) intercalary denticles between the main teeth of the apical fork. The genus *Neostruma* represents a further development of the *louisianae* group → *connectens* group → *gundlachi* group trend or morphocline.

The three remaining species groups, all small, appear to be derivable directly from the *mandibularis* group: the *tococae* group by addition of a second intercalary denticle in the apical fork, the *cultriger* group by development of a mandibular lamella, and the *ludia* group by the serial loss of mandibular teeth.

Identification of Species

This section is intended to provide materials with which any competent entomologist can hope to identify quickly and surely the *Strumigenys* species at present known from the New World. Of course, there are certainly species remaining to be discovered in this hemisphere, but I believe that we now know all or nearly all of the species that are both widespread and reasonably common, and many of the rare or local species as well.

Before discussing the species, though, it is necessary that we characterize the genus *Strumigenys* well enough to recognize it in this hemisphere. It will be enough to say that any New World ant with the following combination of characters is a *Strumigenys*: Worker and

female — Exactly 6 antennal segments, of which the third and fourth are very short and the first (scape) and sixth (apical) are very long (Figs. 1-4); mandibles long and linear, straight or bowed, more than $1/3$ as long as the head proper, with an apical fork of two prominent teeth, other teeth absent to few, usually separated (Figs. 1-4, 7-16); occiput with a deep median posterior excision between two broad, rounded lobes, head in front distinctly narrowed (Figs. 1-4); spongi-form appendages, or at least their vestiges, present on petiole and postpetiole (Figs. 5, 6); head and often most of alitrunk reticulate-punctulate and opaque, rarely with superimposed rugulation. Males are not dealt with here, since few of them are known, and they cannot be separated as a group from a number of other dacetine genera.

Measurements, and the proportions derived from them, are very important in dacetine taxonomy, so it is necessary to measure with a high degree of accuracy. Measurements should be made to the nearest hundredth of a millimeter at least. A stereomicroscope magnifying at least $90\times$ is required, plus a carefully calibrated reticule of the ocular squared disc type having finer subdivisions in one or more of the squares. The art of measuring dacetines is discussed at length elsewhere (Brown, 1953d: 7-15), so I shall repeat here just the essentials for use with this paper.

Head length (HL), maximum measureable length of head proper as seen from dorsal full-face view, including all of clypeus and occipital lobes.

Head width (HW) is the maximum width of the cranium measured in the same view as for HL.

Mandible length (ML), exposed length of mandibles, including apical teeth, measured in same view from which HL is obtained.

Weber's length (WL), oblique length of alitrunk from side view, measuring from base of anterior pronotal declivity to metasternal extremity.

Total length (TL) of the body is the summed lengths of ML, HL, WL plus the axial lengths of petiole, postpetiole and gaster measured separately.

Cephalic index (CI), head width expressed as a percentage of head length, or $HW/HL \times 100$.

Mandibulo-cephalic index (MI), $ML/HL \times 100$.

In addition to the dichotomous key to the species, I have constructed a table giving known ranges of values for the seven quantitative characters most used in species-level taxonomy of the genus. This table may be used either as a primary key or as a check on the determinations made with the dichotomous key. Number of individuals

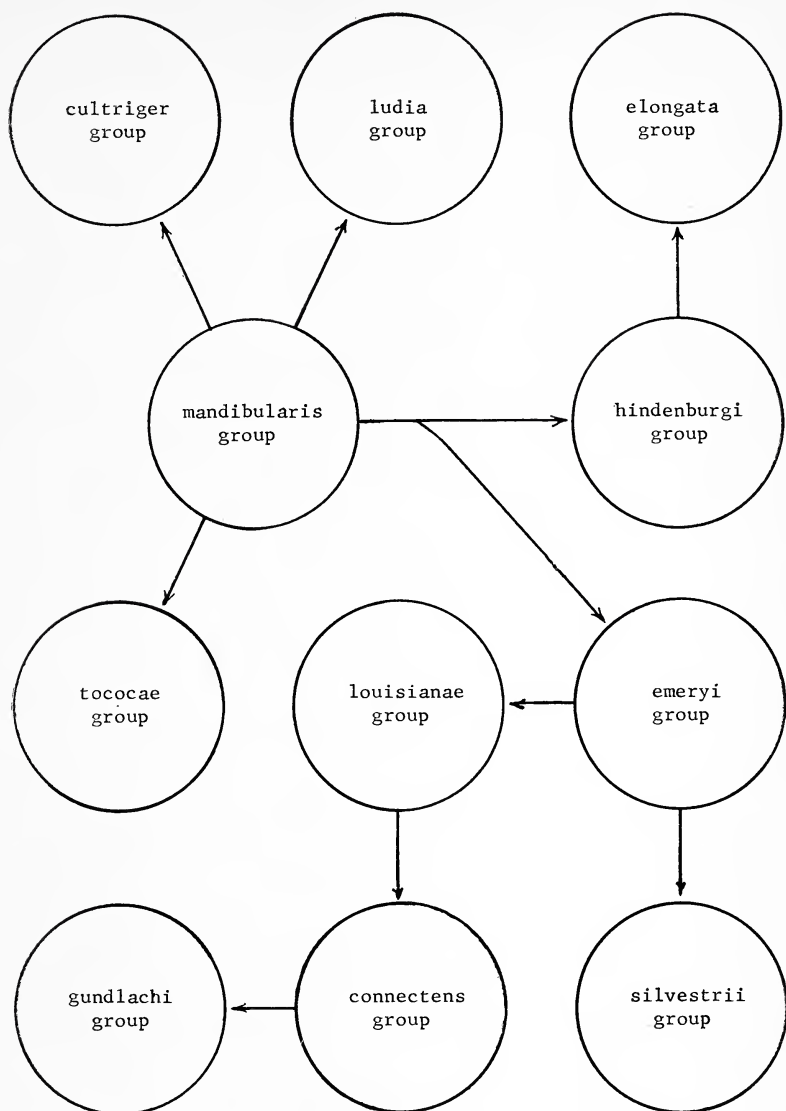


Figure 30. Diagram to illustrate the possible phyletic relationships among the species-groups of New World *Strumigenys*, based upon the hypothesis that the group of *S. mandibularis* represents the primitive stock in this hemisphere. *S. rogeri*, being African in origin, does not figure in this scheme.

and localities on which the measurements were based are given under "Sample" so that the user can judge crudely how nearly the natural variance may be represented by the range of values given.

Following the dichotomous key is a glossary of the most important morphological terms used in species identification.

Table of the most valuable quantitative characters of the
Strumigenys species of the New World

The table is arranged in order of size as based chiefly on head length. The measurements (in hundredths of millimeters) HL (head length), ML (mandibular length) and WL (Weber's diagonal length of alitrunk), as well as the proportions CI (cephalic index) and MI (mandibulo-cephalic index), are explained in the preceding section. ID indicates the number of small teeth or denticles lying between the two main teeth of the apical fork of the mandible, and PT is the number of teeth along the inner margin of the mandible proximad of the dorsal apical tooth (not counting the basal lamella, which is usually hidden beneath the clypeal margin); these preapical teeth may be large and spiniform or may be reduced to exceedingly minute denticles. The sample indicates the number of specimens measured and, following a dash, the number of separate localities represented by the specimens.

Species	HL	CI	ML	MI	WL	ID	PT	Sample
<i>mandibularis</i>	131	~102	~51	~38	—	1	2	1
<i>godmani</i>	106-120	87-93	51-55	46-48	109-122	1	2	8-2
<i>sanctipauli</i>	98	76	96	98	103	1	2	1
<i>fairchildi</i>	96	75	59	61	101	2	2	1
<i>precava</i>	87-101	71-79	50-56	54-61	81-97	1	1	92-7
sp. nr. <i>micretes</i>	86-90	75-76	58-61	67-68	92-99	1	0-2	25-1
<i>saliens</i>	81-95	69-77	50-60	60-65	82-97	1	1	38-9
<i>dolichognatha</i>	84-90	75-77	104-108	119-124	—	1	2	6-1
<i>cultriger</i>	85	77	51	60	90	1	2	1
<i>planeti</i>	80-89	80-86	45-50	52-57	80-90	1	2	39-5
<i>tococae</i>	80-85	75	44-47	55	80-87	2	2	8-1
<i>trinidadensis</i>	78-83	78-82	52-56	66-69	80-88	1	2	12-6
<i>longispinosa</i>	78-80	72-74	71-72	90-91	80-81	0	1	2-1
<i>cordovens</i>	73-82	76-80	83-92	109-123	—	1	2	40-8
<i>prospiciens</i>	74-80	79-83	41-46	56-60	75-82	1	2	8-3
<i>sublonga</i>	74-79	76-80	72-75	96-98	73-79	1	2	7-1
<i>rehi</i>	76	76	76	100	80	1	2	1
<i>borgmeieri</i>	74	65	52	67	77	1	2	1
<i>lacacoca</i>	70-76	67-71	45-53	60-70	72-82	1	0-1	8-2

<i>micretes</i>	70-76	71-74	45-51	62-68	72-	1	2	18-2
<i>smithii</i>	67-76	80-87	36-42	52-61	70-78	1	2	26-6
<i>biolleyi</i>	60-81	78-85	35-51	58-66	-86	1	2	51-11
<i>ludia</i>	67-74	81-84	49-56	73-76	62-73	1	0	9-6
<i>marginiventris</i>	68-73	78-82	51-57	75-79	68-72	0	1	11-3
<i>producta</i>	65-70	78-82	45-48	69-70	69-74	2	1	15-1
<i>consanii</i>	64-66	78-80	41-42	63-64	76-80	0	0	5-1
<i>hindenburgi</i>	60-69	83-88	38-40	58-64	63-71	1	2	9-3
<i>deltisquama</i>	62-67	95-97	34	51-55	60-63	1	2	12-1
<i>xenognatha</i> ♀	65	79	41	63	84	2	2	1
<i>connectens</i>	60-65	81-86	33-37	53-56	64-73	2	3-4	7-2
<i>nevermanni</i>	61-63	77-80	36-38	58-60	67-	1	1	8-1
<i>emeryi</i>	59-64	80-82	38-40	61-64	65-69	1	2	10-4
<i>laevipleura</i>	58-62	79-82	33-35	56-57	65-66	2	3	3-1
<i>hemidisca</i>	60	82	39	65	64	1	2	3-1
<i>rogeri</i>	57-62	70-74	30-34	53-55	—	0	2	11-9
<i>trieces</i>	58	78	28	48	62	2+	3	1
<i>elongata</i>	50-63	72-79	28-41	56-67	47-62	0	0	161-25
<i>ogloblini</i>	55-56	80-81	28-29	51-52	~55	1	1	2-1
<i>louisianae</i>	46-64	77-92	23-37	49-67	—	2	1	130-71
<i>mixta</i>	51-59	80-84	28-32	54-60	51-60	2	2	20-2
<i>jamaicensis</i>	52-56	81-82	40-42	75-77	55-57	2	6-8	12-2
<i>boneti</i>	50-56	80-82	28-30	50-60	50-57	1	1	4-3
<i>subedentata</i>	48-56	82-86	26-30	53-54	47-60	2	4-6	36-15
<i>denticulata</i>	42-48	77-80	31-39	74-83	42-49	2	5-9	11-6
<i>gundlachi</i>	40-49	79-86	24-32	59-66	40-50	2	4-9	36-20
<i>silvestrii</i>	42-47	77-81	24-26	55-60	41-50	1	2	11-4
<i>eggersi</i>	39-47	83-88	22-27	56-64	39-46	2	4-8	32-22
<i>schmalzi</i>	42	79	27	64	44	0	2	1
<i>perparva</i>	40	81	20	50	40	0	1	2-1
<i>carinithorax</i>	36	81-83	21-22	59-61	41	0	2	3-1

Dichotomous key to the known species of *Strumigenys* occurring in the New World, based chiefly on the worker caste, but applying to the females of most species as well

1. Apical fork of mandible without distinct intercalary teeth or denticles (Fig. 17) 2.
- Apical fork of mandible with a single intercalary tooth or denticle, either separate or occurring as a spur on the inner side of the ventral tooth (Figs. 18, 19) 9.
- Apical fork of mandible with 2 (rarely 3-4) intercalary denticles (Figs. 20, 21) 38.
2. Mandible without preapical teeth or denticles (Fig. 1) 3.
- Mandible with 1 or 2 preapical teeth and/or denticles (Fig. 16) 4.

3. Postpetiole large and convex, its dorsum smooth and shining; larger, more robust species (Costa Rica) *consanii* Brown
Postpetiole small, its dorsum densely punctulate and opaque; smaller, more slender species (s. Mexico to se. Brazil and Bolivia) *elongata* Roger
4. First segment of gaster margined for its full length on each side by a strong, raised dorsolateral carina (Costa Rica to Colombia) *marginiventris* Santschi
First gastric segment smoothly rounded dorsolaterally, without raised margins apart from the basal costulae 5.
5. Larger species with very long mandibles; combined length of head + mandibles > 1.10 mm (Panama) *longispinosa* Brown
Smaller species with mandibles not so long; combined length of head + mandibles < 1.10 mm 6.
6. Compound eye anteriorly detached, i.e., bounded in front by a narrow cleft or notch in the ventrolateral margin of the head (Fig. 29); combined length of head + mandibles > 0.80 mm; 2 preapical teeth on each mandible, the distal being smallest (Figs. 16, 17) (West Indies, Trinidad, British Guiana, introduced from Africa) *rogeri* Emery
No preocular notch in ventrolateral border of head; combined length of head + mandibles < 0.80 mm 7.
7. Each mandible with a single preapical tooth; no minute denticle near mandibular midlength (Trinidad to se. Brazil) *perparva* Brown
In addition to the preapical tooth, each mandible bears a minute denticle somewhere near the midlength of its inner margin 8.
8. Mandibles (MI 54-61), scape (L 0.23 mm) and apical funicular segment (L ca. 0.22 mm) shorter; promesonotum with a distinct median longitudinal carina (Dutch Guiana) *carinithorax* Borgmeier
Mandibles (MI > 61), scape (L > 0.27 mm) and apical funicular segment (L > 0.25 mm) longer; no distinct carina in the middle of the promesonotum (se. Brazil) *schmalzi* Emery
9. Mandible with no preapical teeth, or with a single preapical tooth or denticle, or with a preapical tooth or denticle plus another minute denticle proximal to it (Figs. 1-4, 7, 8, 12, 13) 10.
Mandible with 2 well-developed preapical teeth (Figs. 9, 14) 22.
10. Mandible without preapical teeth or denticles (Fig. 2) 11.
Mandible with a preapical tooth or denticle, or both (Figs. 3, 4, 7, 8, 12, 13, 15) 12.
11. Petiole claviform, the node only feebly differentiated from its

- anterior peduncle; gastric hairs mostly stiff, remiform (i.e., with broadened apices) (Fig. 5); head broader ($CI > 79$; Fig. 1) (Nicaragua to s. Mexico) *ludia* Mann
- Petiolear node with a steep anterior face, set off from its anterior peduncle; gastric hairs long, finely flagelliform (Fig. 6); head narrower ($CI < 78$; Fig. 2) *lacacoca*; go to 21
12. Large hairs of gastric dorsum remiform (i.e., oar- or paddle-shaped at apex); smaller species 13.
- Large hairs of gastric dorsum fine, long, flagelliform 15.
13. First gastirc tergite reticulate-punctulate and opaque; preapical armament of mandible reduced to a single minute denticle situated somewhat distal to the midlength of the inner border, but remote from the apex (Fig. 12) (s. Mexico) *boneti* Brown
- First gastric tergite smooth and shining beyond the basal belt of longitudinal costulae; preapical armament of mandible consisting of a distinct tooth, with or without an additional minute denticle near mandibular midlength 14.
14. Dorsal borders of antennal scrobes broad, lamellose; preapical armament of mandible consisting of a single strong tooth (n. Argentina) *ogloblini* Santschi
- Dorsal scrobe borders merely narrowly cariniform; preapical mandibular armament consisting of a tooth near the apex plus an additional minute denticle near the midlength (n. Argentina to s. Brazil; also Cuba and Louisiana, where probably introduced) *silvestrii* Emery
15. Ventral ends of propodeal lamellae at most rounded or bluntly angulate, not dentiform 16.
- Propodeal teeth large and acute, matched on each side below by a (metasternal) tooth of nearly the same size and shape arising from the ventral end of the infradental lamella (Fig. 23) *trinidadensis*; go to 26.
16. Long fine flagelliform hairs on nodes of petiole and postpetiole and on gastric dorsum very numerous, too many to count, and evidently always $> 16 + 20 + 50$, or > 86 total (partially denuded specimens or those with hairs plastered down can of course be deceptive) 17.
- Long flagelliform hairs of nodes and gastric dorsum much fewer, at most about $8 + 10 + 34$, or about 52 hairs total 18.
17. Dorsal scrobe border on each side produced as a narrow but distinctly lamellar margin; inner mandibular border with a minute denticle near the apical third, in addition to the preapical tooth; basal gastric costulae short, coarse, remainder of first

- tergite smooth and shining (Fig. 8; Argentina, se. Brazil)
 *hindenburgi* Forel
 Dorsal scrobe borders merely narrowly cariniform, not lamellate;
 mandibles without preapical denticle proximad of preapical tooth;
 basal costulae of gastric dorsum extended over basal third or
 more of first tergite as fine, sericeous-opaque striolation (Fig. 4;
 C. America to s. Mexico; Bahamas) *lanuginosa* Wheeler
18. Head with a strong concavity anterior to each eye, and thus
 appearing constricted in full-face view (Fig. 7); humeral tuber-
 cles large and produced (mandibles broad, contiguous or nearly
 so when closed, each with a single short, broad preapical tooth;
 Fig. 7) (Panama; hylaeon S. America to Bolivia)
 *precava* Brown
 Head parallel-sided or gently tapered in front of eyes, without
 marked preocular concavities; humeral tubercles or angles small,
 not produced (mandibles slender, not contiguous at full closure,
 preapical dentition diverse, but not as above) 19.
19. Smaller species, with mandibles < 0.42 mm long; head broader
 (CI > 75) 20.
 Larger species, with longer mandibles (ML > 0.42 mm); head
 narrow (CI 75 or less) 21.
20. Inner mandibular margin with a minute denticle near the apical
 third in addition to the preapical tooth; head distinctly longitudi-
 nally rugulose (s. Mexico, Honduras) *emeryi* Mann
 Mandible with a single preapical tooth and no additional denticles
 proximad of this (Fig. 3); head at most weakly and indistinctly
 rugulose above (Costa Rica) *nevermanni* Brown
21. Mandible with a small preapical tooth or denticle and, near it
 proximally, an additional minute denticle (Fig. 13; Costa Rica,
 Panama) *micretes* Brown
 Mandible with no teeth or denticles, or with a single minute
 preapical denticle (Fig. 2; Panama) *lacacoca* Brown
 (A population from Boquete, Chiriqui Prov., Panama, has 1 or
 2 preapical denticles on the inner mandibular border, and is thus
 intermediate between *micretes* and *lacacoca*, but this population
 is also distinctive in having the promesonotum coarsely longitudi-
 nally striate. The specimens are also larger. Possibly *micretes*,
lacacoca and the Boquete sample are simply local variants of a
 single unusually variable species, or perhaps three distinct species
 are represented here.)
22. Inner mandibular border extended as a straight-edged lamella
 that terminates abruptly and subangularly at its distal end near

- the proximal preapical tooth (Fig. 9) 23.
 Inner mandibular border without a lamellar extension, or, if a lamella of sorts is present, its form is not as above (Fig. 14) .. 24.
23. Lamelliform margin of inner mandibular border ending near mid-length of mandible (Fig. 9) ; propodeal teeth very small; gastric dorsum predominantly smooth and shining, with vestiture of abundant fine, short reclinate hairs (se. Brazil) .. *cultriger* Mayr
 Lamelliform margin of inner mandibular border ending near apical quarter of mandible; propodeal teeth large; first gastric tergite predominantly reticulate-striate, opaque, with about 20 apically-broadened, short erect hairs (Panama)
 *deltisquama* Brown
24. Large forms (head width > 0.85 mm) with massive head and short, heavy mandibles (MI 50 or less) 25.
 Smaller forms with narrower heads (head width under 0.85 mm) and longer, more slender mandibles (MI > 50) 26.
25. First gastric tergite finely longitudinally striolate for most or all of its length; head about as broad as, or broader than, long (Amazon Basin) *mandibularis* Fr. Smith
 Gastric dorsum smooth and shining, with only a narrow basal band of reduced costulae; head slightly longer than broad (Guiana to Costa Rica) *godmani* Forel
26. Gastric dorsum predominantly finely longitudinally striolate, sericeous-opaque, with very abundant, fine, erect flagelliform pilosity; proximal preapical mandibular tooth small (only about half the length of the distal preapical) and situated toward the mandibular midlength (Fig. 14; Trinidad to Bolivia and Ecuador) *trinidadensis* Wheeler
 Gastric dorsum with either sculpture or pilosity or both different from the above; proximal preapical tooth of mandible more than half as long as distal preapical tooth and situated well beyond the mandibular midlength 27.
27. Mandibles very nearly as long as, to distinctly longer than, the head proper (MI > 90) 28.
 Mandibles relatively shorter (MI < 75) 32.
28. Mandibles slightly > 1.00 mm long; distal preapical tooth closer to proximal than to apical fork (British Guiana)
 *dolichognatha* Weber
 Mandibles < 1.00 mm long; distal preapical tooth closer to apical fork than to proximal preapical tooth 29.
29. Mandibles > 0.80 mm long; longitudinal costulation of post-petiolar disc absent or incomplete 30.

- Mandibles < 0.80 mm long; longitudinal costulation on post-petiolar disc complete from anterior to posterior border 31.
30. Size larger (HL 0.98 mm in holotype worker); infradental lamella of propodeum low and cariniform, terminating below in a small, obtuse ventral angle that is much smaller than the dorsal tooth (Fig. 24); antennal scape straight to its base (se. Brazil) *sanctipauli* Kempf
 Size smaller (HL < 0.85 mm); infradental lamella high, terminating below in a prominent tooth or angle which is subequal to, or often larger than, the dorsal propodeal tooth (Figs. 25-27); antennal scapes gently but distinctly curved in basal half (s. Mexico to Trinidad and the Guianas) *cordovens* Mayr
31. Pilosity of head, alitrunk and nodes rather abundant and conspicuous, narrow-spatulate; eyes 0.09 mm in greatest diameter; MI $100 \pm$ (Amazon Basin) *rehi* Forel
 Pilosity less abundant and conspicuous, that of nodes and first gastric segment sparse, fine and filiform; eyes 0.07 - 0.08 mm in greatest diameter; MI 94 - 99 (Amazon Basin) .. *sublonga* Brown
32. Propodeal lamellae evenly rounded, without dorsal or ventral angles or teeth (Fig. 22; Colombia) *hemidisca* Brown
 Propodeal lamellae angulate or toothed above and/or below, more or less as in Figs. 23, 24 or 28 33.
33. Propodeal lamellae without dorsal teeth or angles; ventral angle present and prominent (Fig. 28; C. America s. to Ecuador) *biolleyi* Forel
 Propodeal lamellae angulate or toothed both above and below (more or less as in Figs. 23-26) 34.
34. Mandibles longer and more slender (MI > 63); head narrower (CI < 80) 35.
 Mandibles shorter and more robust (MI < 63); head broader (CI 80 or more) 36.
35. Smaller (HL < 0.80 mm), more slender (CI < 68); preapical teeth small and crowded toward apical fork, occupying little or no more than the apical $1/5$ of the mandibular length (Brazil: Pernambuco) *borgmeieri* Brown
 Larger (HL 0.80 mm or more), not so slender (CI > 68); preapical teeth more widely spaced, occupying the apical $2/5$, more or less, of the mandibular length (se. Brazil, n. Argentina) *saliens* Mayr
36. Larger (HL 0.80 mm or more), with heavy, distinctly arcuate mandibles *planeti* Brown

- Smaller (HL < 0.80 mm); mandibles narrower, not or only indistinctly arcuate 37.
37. Basigastric costulae absent or extremely reduced, never much longer than the space separating one from the next; anterodorsal face of petiolar node convex in both directions (Amazon Basin to Bolivia) *prospiciens* Emery
Basigastric costulae fine but numerous, extending at least 1/8 the length of gastric tergite I; anterodorsal face of petiolar node obliquely depressed, nearly or quite plane (tropical S. and C. America, St. Vincent I.) *smithii* Forel
38. Mandible with a single small preapical tooth; no additional preapical teeth or denticles on inner border 39.
Mandible with 2 or more preapical teeth and/or denticles 40.
39. Larger form with long mandibles (ML > 0.42 mm; MI 68 or more; see discussion, p. 247) (Bolivia) *producta* Brown
Smaller form with shorter mandibles (ML < 0.42 mm; MI < 68) (Tennessee and Arizona to n. Argentina and Bolivia, W. Indies) *louisianae* Roger
40. Mandible with at most 2 preapical teeth and/or denticles (Fig. 15) 41.
Mandible with 3 or more preapical teeth and/or denticles (Figs. 10, 11) 44.
41. Mandible with 1 preapical tooth and a single additional minute denticle near the apical third of the mandibular length (Fig. 15); gastric dorsum predominantly reticulate-striate, opaque, with stiff remiform erect hairs (Guatemala) *mixta* Brown
Mandible with two well-developed preapical teeth 42.
42. Smaller species, HL < 0.75 mm; erect hairs of gaster stiff, slightly clavate or remiform (known from female only; possibly an inquiline in nest of *S. laevipleura*; Colombia)
..... *xenognatha* Kempf
Larger forms, HL > 0.75 mm; erect hairs of gaster few, straggling flagelliform 43.
43. Dorsum of basal gastric segment with longitudinal costulae only at base, otherwise smooth and shining; short, thickened reclinate ground hairs of gastric dorsum abundant and conspicuous (Amazon Basin) *tococae* Wheeler
Dorsum of basal gastric segment longitudinally striolate for its full length; reclinate ground hairs of gastric dorsum obsolete or apparently so (Panama) *fairchildi* Brown
44. Postpetiolar node smooth and shining when clean; mandible with 2 preapical teeth and a denticle (Colombia) *laevipleura* Kempf

- Postpetiolar node densely reticulate-punctulate, opaque 45.
45. Preapical armament of mandible consists of 2 close-set preapical teeth, of which the second is much the longer, followed closely basad by 1 or 2 denticles (Fig. 11) (Colombia) *connectens* Kempf
Preapical armament otherwise; consisting either of three small subequal teeth, or of 4-9 minute teeth and/or denticles (Fig. 10) 46.
46. Antennal scape 0.33 mm or more long; larger, dark-colored species (Jamaica) *jamaicensis* Brown
Antennal scape < 0.33 mm long 47.
47. Mandibles short and thick (MI < 56); robust species, worker HL mostly > 0.48 mm 48.
Mandibles longer and slender (MI 56 or more); smaller species, worker HL mostly 0.48 or less (Fig. 10) 49.
48. Mandible short (MI 48 in unique holotype), with exactly 3 small preapical teeth; ground pilosity of head nearly or quite obsolete; pronotum markedly flattened (Costa Rica) *trieces* Brown
Mandible relatively longer (MI ca. 53-54), with > 3 preapical teeth and/or denticles; ground pilosity abundant and conspicuous on head; promesonotum strongly rounded, not depressed (Mexico to s. Brazil) *subedentata* Mayr
49. Mandibles very long and slender (MI > 70), bowed outward (Trinidad to n. Argentina) *denticulata* Mayr
Mandibles not so long (MI < 70), their shafts approximately straight (Fig. 10) 50.
50. Ventral spongiform appendages of postpetiole small but distinctly developed (side view); gastric dorsum of worker predominantly smooth and shining (when clean!), at most with a few basal longitudinal costulae, but female gaster commonly shagreened above (Caribbean countries) *gundlachi* (Roger)
Ventral spongiform appendages of postpetiole obsolete; gastric dorsum of both worker and female with fine, mostly opaque reticulation (Brazil, Bolivia, Caribbean countries) *eggersi* Emery

Glossary

Alitrunk: The second tagma of the body in Hymenoptera, incorporating the thorax and the closely fused propodeum (first true abdominal segment).

Antennal scrobes: Broad longitudinal excavations or grooves, one on each side of the head above the eye, for the reception of the folded antennae.

Apical fork: The two large teeth at the extreme apex of the mandible, converging to form a U or V; between them may occur one or more intercalary denticles (Figs. 9-21).

Basal costulae (basigastric costulae): Numerous raised longitudinal lines of the integumental sculpture originating from the base of the first gastric segment (tergite) and extending caudad for distances varying with the species (Figs. 5, 6).

Basal tooth (or lamella): A process, usually digitiform or dentiform, arising from the inner mandibular border at its base, and usually covered by the clypeus when the mandibles are closed; not to be confused with the preapical teeth.

Flagelliform hairs: Very long, slender, tapered setae, often wavy, looped or otherwise contorted, i.e., whip-like (Figs. 4, 6).

Intercalary tooth (or denticle): Abbreviated "ID," a tooth (or denticle) occurring between the main teeth of the apical fork of the mandible, or as a spur on the inner side of one of the main teeth (Figs. 18-21).

Preapical tooth (or denticle): Abbreviated "PT," a tooth (or denticle), one or more of which occur along the inner mandibular border proximal to the apical fork, but not at or beneath the clypeal margin; not to be confused with the basal tooth, q. v. (Figs. 3, 4, 7-16).

Propodeal lamella: One of a pair of raised lobes or flanges guarding the sides of the propodeal declivity, sometimes incorporating the (dorsal) propodeal tooth and/or a ventral (metasternal or metapleural) tooth or angle (Figs. 5, 6, 22-28).

Remiform hairs: Setae with a more or less oar-like form (Fig. 5).

Spongiform appendages: Lobes, flaps and collar-like strips of light-colored spongy integumental material situated in definite, symmetrical positions on the petiole, postpetiole and anteroventral face of the gaster (Figs. 5, 6), and sometimes even on the alitrunk, in the higher dacetines and a few other ants. Their function is unknown.

INDEX TO NAMES OF STRUMIGENYS SPECIES OF THE NEW WORLD AND THEIR SYNONYMS

(Names in *italics* are synonyms; page references are to the accompanying article)

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THE EGG-SAC IN THE IDENTIFICATION OF SPECIES OF *LATRODECTUS* (BLACK-WIDOW SPIDERS)¹

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Santiago del Estero, Argentina

The genus *Latrodectus* comprises a few species very hard to classify. The geographical distribution of some spreads across several continents, making the problem even more complex and, at the same time, the synonymy richer. The difficulty lies in the lack of taxonomic characters which allow true differentiation among the species. Levi (1959)² used for species identification, among other devices, the male genitalia as well as the female; thanks to this the problem of systematics of so ill-treated a group begins to be clearer.

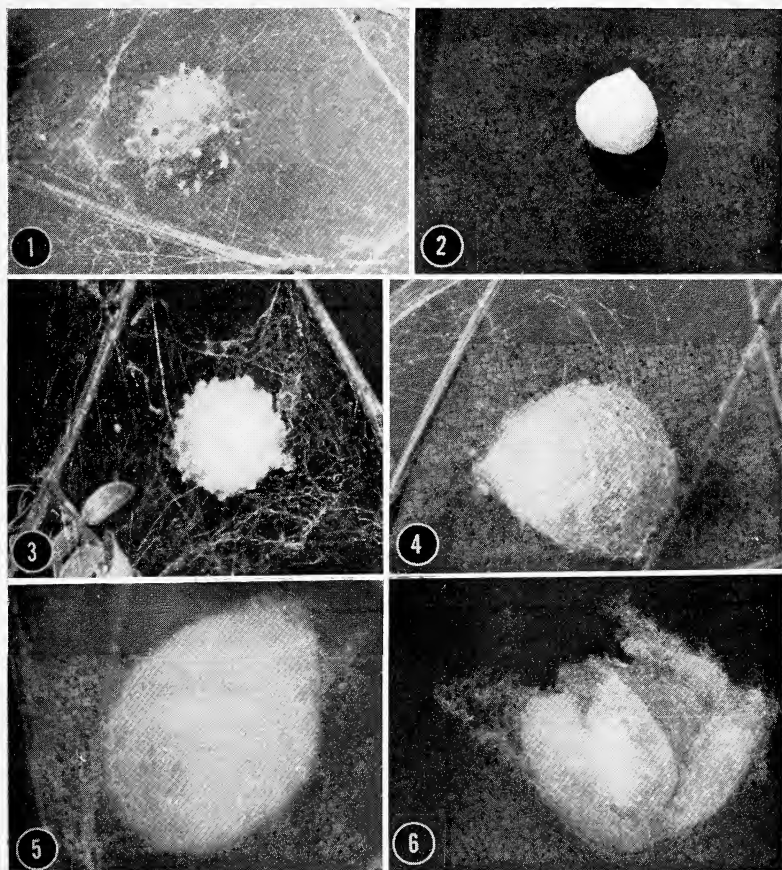
In the course of the research we are carrying out on *Latrodectus* in Santiago del Estero (north-central region of Argentina) we have recognized the presence of five different species living in the same area. We were able to separate two of them according to their morphological characters; *L. geometricus* C. L. Koch, a domestic species we identified by its well-defined color and genitalic characters, among them the coils of the embolus of the male palpus, coils corresponding to those in the connecting ducts of the female. The other species, temporarily named *Latrodectus* No. 1 in order not to add further confusion of names, resembles *L. curacaviensis* (Müller) in the genitalic characters pointed out by Levi: the embolus of the male palpus and the connecting ducts of the female with two coils. The three remaining species correspond to what we call "*L. mactans* complex" with their three coiled embolus and female ducts. The morphological characters are not enough to separate these species. The width of the red spots on the abdomen guides the identification but is not reliable. The three of them live in the same area and ecologic environment. The only elements that allow us at present to separate these species in an accurate way are the size, shape and texture of the egg-sacs. We have temporarily called these species: *Latrodectus* No. 2, *Latrodectus* No. 3, and *Latrodectus* No. 4. However, many names are available for the species.

Latrodectus No. 2: The egg-sac is white when just formed, but usually turns yellowish in the course of days; it is spheroidal, slightly

¹Research under the sponsorship of Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina.

²Levi, H. W. 1959. The spider genus *Latrodectus* (Araneae, Theridiidae) Trans. Amer. Micros. Soc., 78 (1):7-43.

Manuscript received by the editor October 31, 1962.



ABALOS — LATRODECTUS

Figs. 1-6. Egg-sacs of *Latrodectus*. Fig. 1. *Latrodectus geometricus* C. L. Koch. Fig. 2. *Latrodectus* No. 1. Fig. 3. *Latrodectus* No. 2. Fig. 4. *Latrodectus* No. 3. Figs. 5-6. *Latrodectus* No. 4.

pyriform and its most frequent size is about 10 mm. The sac is formed by threads 8 microns in diameter. They form a tissue, not very dense, but tight, that constitutes a thin cover, soft to pressure of the fingers. On the surface of the egg-sac we can observe numerous little web pompons that give a characteristic granulous aspect (Fig. 3). These little pompons are made by the spider with the hind legs; they are not firmly joined to the surface of the egg-sac and they usually fall off with handling.

Latrodectus No. 3: The egg-sac of this spider generally has the same shape as the one mentioned above, even though it sometimes changes, up to the point of presenting the aspect of an elongated pear; its size varies, but it is always bigger than the former species, reaching 21 mm in its biggest diameter. The sac wall is thicker and is formed by threads of a diameter of about 16 microns. These threads form a tight tissue, with a parchment texture that makes the egg-sac resistant to pressure. The egg-sac completely lacks pompons or any other ornament on its surface (Fig. 4).

Latrodectus No. 4: The egg-sac is white, pyriform, and its common size is about 10 mm. The sac-wall is thin, with threads of about 8 microns in diameter forming a less compact tissue. On this cover the spider weaves a coat about 3 mm thick, of loose tissue, that gives the egg-sac the appearance of a spherical woolen tuft (Figs. 5, 6).

We can also observe that *Latrodectus* No. 1 differs from the other species in its egg-sac. Its size is always smaller than in any of the former species, about 7 mm, although it sometimes reaches 10 mm; its shape is spherical pyriform. Its color is white, often turning greyish in the course of days. The cover is thin with threads of about 8 microns in diameter, forming a very tight tissue of smooth surface, with a paper texture, and completely lacking exterior ornaments (Fig. 2). The egg-sac is fairly resistant to finger pressure.

The egg-sac of *L. geometricus*, many times figured, is very characteristic: its color is whitish when just formed; turning yellowish in the course of days. It is spherical; its size about 10 mm in diameter; it is covered with conic protuberances that give it the curious aspect of a war-mace (Fig. 1).

We are thankful to Dr. Herbert W. Levi, for his generosity and advice on the publication of this note and to Emilio Clementi for taking the photographs.

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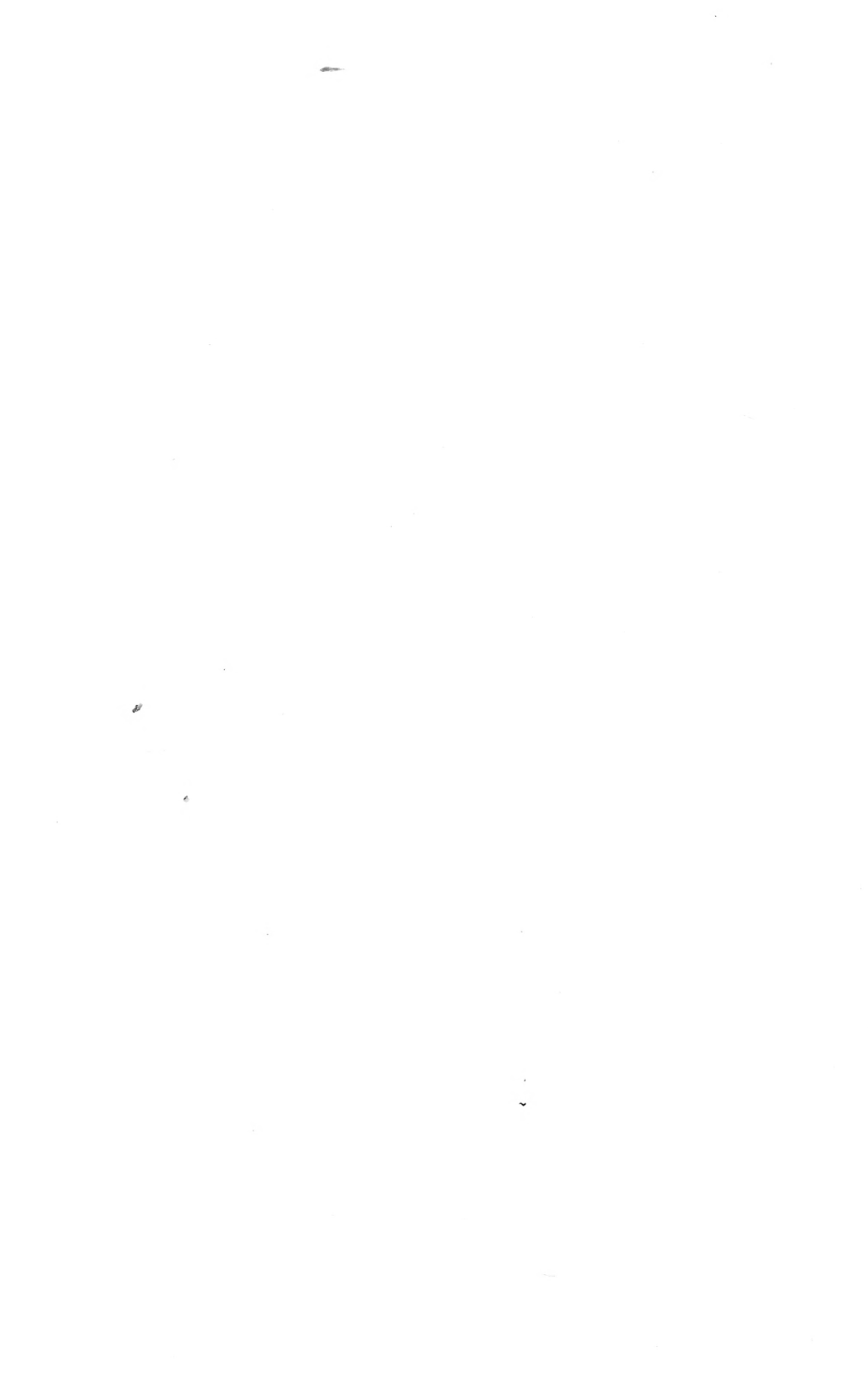
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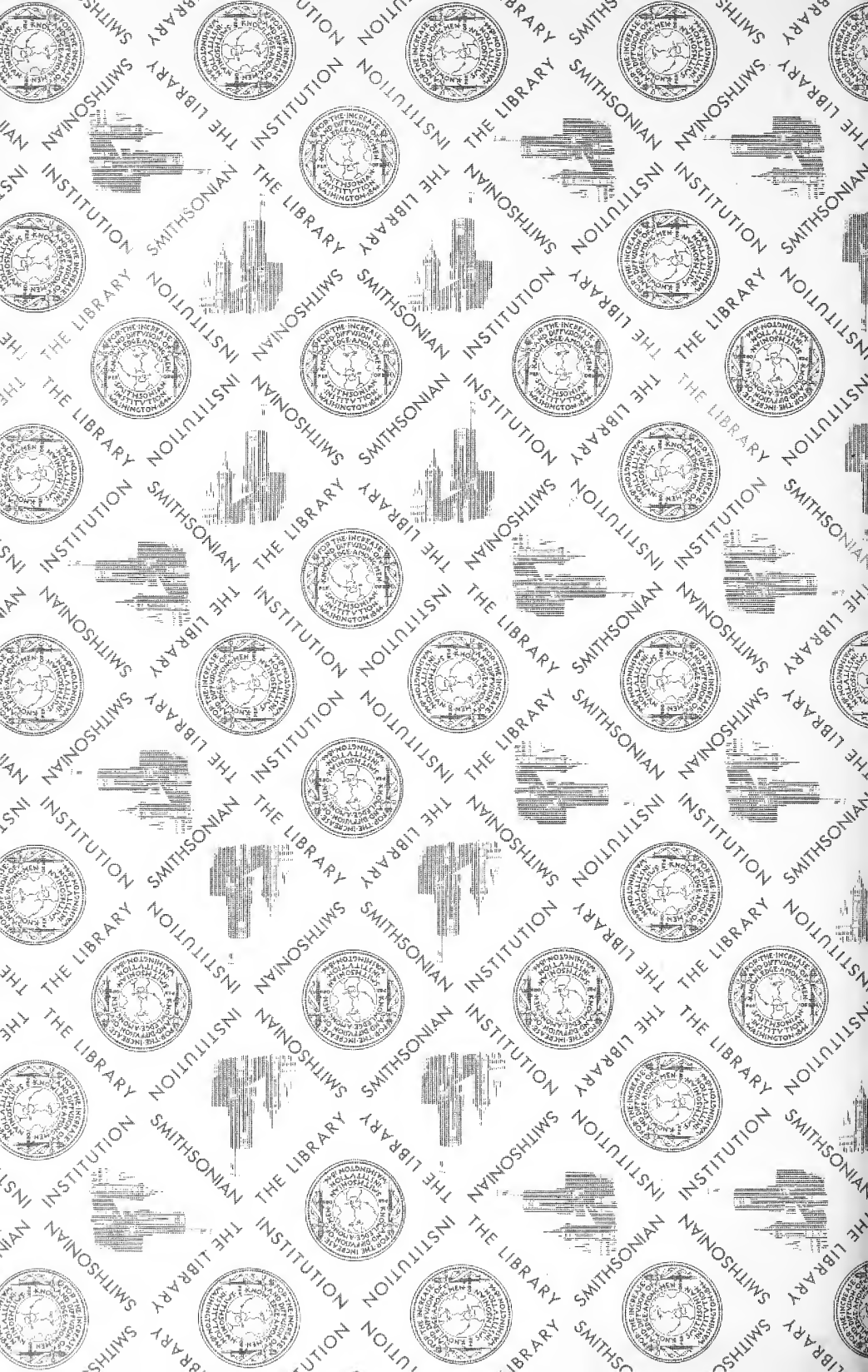
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