The Genera of the Spider Family Theridiosomatidae

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ABSTRACT

Coddington, Jonathan A. The Genera of the Spider Family Theridiosomatidae. *Smithsonian Contributions to Zoology,* number 422, 96 pages, 220 figures, 8 maps, 1 table, 1986.—The cosmotropical spider family Theridiosomatidae is revised at the generic level to contain 9 genera: *Theridiosoma* O. Pickard-Cambridge, 1879, *Ogulnius* O. Pickard-Cambridge, 1882, *Wendilgarda* Keyserling, 1886, *Epeirotypus* O. Pickard-Cambridge, 1894, *Baalzebub,* new genus (type-species *B. baubo,* new species), *Epilineutes,* new genus (type-species *Theridiosoma globosum* O. Pickard-Cambridge), *Plato,* new genus (type-species *P. troglodita,* new species), *Naatlo,* new genus (type-species *N. sutila,* new species), and *Chthonos,* new name. Of the 22 genera historically associated with the family, 17 have been rejected, transferred, or synonymized. *Theridilella* Chamberlin and Ivie, 1936 (damaged specimen), and *Allototua* Bryant, 1945 (unique specimen lost), are considered unrecognizable nomina dubia; *Haliger* Mello-Leitão lacks the defining features of theridiosomatids and is considered incertae sedis. *Diotherisoma* di Caporiacco, 1947, is transferred to the Araneidae and *Totua* Keyserling, 1891, to the Linyphiidae. The previous transfers of *Colphepeira* Archer, 1941, to the Araneidae, *Billima* Simon, 1908, *Helvidia* Thorell, 1890, and *Spheropistha* Yaginuma, 1957, to the Theridiidae, *Cyatholipulus* Petrunkevitch, 1930, to the Symphytognathidae, *Cyatholipus* Simon, 1894, and *Tekella* Urquhart, 1894, to the Cyatholipinae (Tetragnathidae), and *Parogulnius* Archer, 1953, and *Phricotelus* Simon, 1895, to the Mysmenidae are not contested. The genus *Andasta* Simon, 1895, is synonymized with *Theridiosoma,* and *Enthorodera* Simon, 1907, and *Cyathidea* Simon, 1907, with *Wendilgarda. Theridiosoma argentatum* Keyserling, 1886, and *T. radiosum* (McCook, 1881) are synonymized with *T. gemmosum* (L. Koch, 1878), and *Wendilgarda panamica* Archer, 1953, *W. hassleri* Archer, 1953, and *W. theridionina* Simon, 1895, with *W. clara* Keyserling, 1886. *Tecmessa tetrabuna* Archer, 1958, and *Epeirotypus gloriae* Petrunkevitch, 1930, are transferred to *Ogulnius. Maymena bruneti* Gertsch, 1960, and *Wendilgarda guacharo* Brignoli, 1972, *W. miranda* Brignoli, 1972, and *W. bicolor* Keyserling, 1886, are transferred to *Plato. Theridiosoma fauna* Simon, 1897, *T. splendidum* (Taczanowski, 1873), and *T. sylvicola* Hingston, 1932, are transferred to *Naatlo. Theridiosoma albinotatum* Petrunkevitch, 1930, and *T. brauni* Wunderlich, 1976, are transferred to *Baalzebub. Theridiosoma nigrum* (Keyserling, 1886) is returned to *Wendilgarda.* The genus *Tecmessa* O. Pickard-Cambridge, 1882, is valid but the name is preoccupied (*Tecmessa* Burmeister, 1878: Lepidoptera); the new name *Chthonos* replaces it. The new genera *Baalzebub, Epilineutes, Naatlo,* and *Plato,* and the new species *Baalzebub baubo, Plato troglodita, Naatlo sutila,* and *Epeirotypus chavarria* are described. The sister taxon of the Theridiosomatidae is the Mysmenidae-Symphytognathidae-Anapidae clade. A cladogram for theridiosomatid genera is presented.

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The Genera of the Spider Family Theridiosomatidae

Jonathan A. Coddington

Introduction

The spider family Theridiosomatidae exemplifies a common taxonomic problem: a vaguely defined, little-known, poorly understood, supposedly small, and yet exotic cosmotropical group of animals. The exasperatingly small size of the spiders (often less than 2 mm total length) invited superficial descriptive work by taxonomists and ensured neglect of their natural history. However, the recent series of papers by Forster and Platnick (1977), Platnick and Shadab (1978a,b, 1979), Eberhard (1981, 1982), and Coddington (in press) on related araneoid spiders demonstrates that knowledge of these small groups will probably be critical for our understanding of the superfamily Araneoidea.

Study of theridiosomatids is important for a number of reasons. Refutation of their traditional placement within or near Araneidae (sensu lato) makes the latter group more homogeneous, thus facilitating the eventual recognition of monophyletic groups within that ill-defined assemblage. The behavior and morphology of theridiosomatids will also help to advance our understanding of the superfamily Araneoidea. Understanding of that superfamily has always been based primarily on character polarities inferred from a few very large taxa (Araneidae, Linyphiidae, Theridiidae). As groups of tropical araneoids become better known, they become reliable outgroups for the remaining Araneoidea. Delimitation of these taxa thus can only improve our understanding of character transformations in the superfamily as a whole.

Theridiosomatidae promises to be a much larger family than catalogs suggest (e.g., Roewer, 1942; Bonnet, 1955–1959; Brignoli, 1983). At present roughly 120 species, described and undescribed, are known world-wide, and certainly that is only the beginning. Probably rather few of the 60-odd available species names will turn out to be synonyms. Most species are known only from the type series.

This revision was originally envisaged as a treatment of the neotropical theridiosomatid species. Tropical Africa, Australia, Malaysia, and New Guinea, however, are rich in theridiosomatid species. As it turned out, putative synapomorphies inferred for the neotropical groups were contradicted by those in the Old World Tropics; distribution patterns of characters in some cases are neither simple nor obvious. Therefore, it was clearly unwise to diagnose any genus in the Neotropics without simultaneous treatment of the family on a world-wide basis. This result expanded the work to its present scope and rendered the idea of an exhaustive revision of theridiosomatids at the species level impractical. The results published herein are a compromise: the family is revised on a generic

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basis, interfamilial and intergeneric relationships are reviewed, a key to genera is provided, but treatment of each genus is synoptic rather than complete. For each genus I have described or redescribed one, two, or three species to illustrate diversity, including the type-species, and have discussed the placement of all species in the genus. By no means were all species redescribed, however. That task will be taken up in a series of generic revisions.

Even so, several more new genera could have been described. In this initial work, however, a rather conservative approach has been taken toward the description of new genera. For example, ***Theridiosoma gemmosum*** forms a monophyletic group with *T. epeiroides,* and possibly also with *T. goodnightorum* and its relatives. Taken together this group may be the sister taxon of another species group including at least *T. savannum, T. nechodomae, T. davisi,* and *T. benoiti,* but more research is necessary to confirm that conclusion. The two groups together are monophyletic, and the name *Theridiosoma* is applied to that more inclusive taxon. A similar situation occurs in *Ogulnius,* which ranks with *Theridiosoma* as one of the largest genera in the family (20 to 30 species each).

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Specimens or locality data used during this study were made available by the following people and institutions (abbreviations in parentheses): G. Arbocco and L. Capocaccia, Museo Civico di Storia Naturale (MCSN), Genoa; N.P. Ashmole (specimens collected by the joint Ecuadorean-British Los Tayos Expedition, deposited in the Museum of Comparative Zoology, Harvard University (MCZ), Cambridge); D. Azuma, Academy of Natural Sciences of Philadelphia (ANSP); C.L. Craig; C.D. Dondale, Canadian National Collection (CNC), Ottawa; W.G. Eberhard; W.J. Gertsch (deposited in the American Museum of Natural History (AMNH), New York); J. Gruber, Naturhistorisches Museum (NMW), Vienna; P.D. Hillyard, British Museum (Natural History) (BMNH), London; J. Heiss; H. Homann; M. Hubert, Muséum National d'Histoire Naturelle (MNHN), Paris; J.A. Kochalka (JAK); T. Kronestedt, Naturhistoriska Riksmuseet (NRS), Stockholm; A. La Touche; H.W. Levi, (MCZ); G.H. Locket; Y. Lubin; N.I. Platnick, (AMNH); S.E. Riechert; C.L. Remington and D. Furth, Peabody Museum of Natural History (PMNH), New Haven; M.J. Scoble and I. Lansbury, Hope Department of Entomology (HDEO), Oxford; W.C. Sedgwick; W. Starega, Polska Akademia Nauk Instytut Zoologiezny (PANIZ), Warsaw; M.K. Stowe; University of Vermont Collection

(UVM), Burlington; C.E. Valerio, Universidad de Costa Rica (UCR), San Jose; J. Wunderlich.

METHODS

This revision is based primarily on the large theridiosomatid collections of the AMNH and the MCZ. I made no thorough attempt to borrow non-type material from other institutions, partly because the goal was treatment at the generic level, and partly because most theridiosomatid material is not sorted as such, but usually is mixed in with theridiids, araneids, or other small araneoid groups.

Specimens examined with the AMR 1000 scanning electron microscope (SEM) were first cleaned by hand agitation or ultrasonics, dehydrated in acetone, and critical point dried in carbon dioxide. Specimens were sputter-coated with carbon and gold palladium prior to observation. Micrographs of right-hand structures were flipped during printing to make the structure appear left-handed in order to ease comparison between species.

Most drawings of genitalia were prepared with an Olympus drawing tube mounted on a Leitz Smith Interference Contrast compound microscope. Specimens on the stage were manipulated and oriented as described in Coddington (1983).

Male palpi were expanded by quick (2–5 min) immersion in concentrated KOH (0.2–1.0 g/ml H_2O), followed by several rinses with, and then prolonged soaking in, distilled water. Full expansion in many cases was only obtained after several KOH-H_2O cycles. Also, in the case of genera with extensive conductors covering the embolic division (*Ogulnius, Theridiosoma, Baalzebub, Epilineutes, Wendilgarda*) the embolic division had to be levered out from under the conductor with a fine needle, an operation that often damaged the conductor. Full expansion can be ascertained by examination with interference microscopy; in an incompletely expanded palp, the hematodochal folds are still visible inside the bulb. The complex routing of the reservoir was duplicated in a wire model, then checked against the specimen in several orientations.

Female genitalia of non-type material were dissected out from the abdomen, macerated in a warm trypsin solution for 1 to 5 hours to remove all proteinaceous tissue, and then mounted for observation with compound microscopy as in Coddington (1983). In the case of holotypes, the entire spider was cleared in clove oil, mounted as above, and examined with incident and transmitted light by compound microscopy.

Features consistent for the family or for genera are described in the family description or in the general generic description and not repeated under each species description. Measurements of somatic morphology were taken with a grid reticle in a dissecting microscope. In the case of leg article lengths, the legs were separated from the specimen and mounted on a glass slide under a cover slip (accuracy usually ±0.02–0.03 mm). Eye diameters are difficult to measure accurately on such small spiders, and, in any case, the eyes are rarely round. For the eyes themselves, the dimensions given are of the span of the lens, not including any raised tubercle or pigment. Measurements are of the maximum span with the eye feature in question oriented perpendicular to the optical axis, insofar as that is possible. Similarly, accurate measurements of carapace or abdomen dimensions are difficult to obtain. Cephalothorax height measurements were made in lateral view, from the surface of the sternum to the top of the carapace (or posterior median eyes, if higher). Carapace lengths were measured in side view from the rearmost extension of the cephalothorax to the clypeal rim (or anterior median eyes, if longer). Carapace width was measured in dorsal view. I have not routinely reported data on cheliceral teeth, because the great variation in tooth size and placement defies simple description (e.g., Figure 2). Length and height of the abdomen were measured in side view, the former parallel, and the latter perpendicular to the sagittal plane of the cephalothorax, not including any extension of the spinnerets below the ventral surface of the abdomen. Total length ranges reported in the taxonomic descriptions are for at least 10 specimens, or of all specimens available, if less than 10.

I give detailed locality information only for species known from few specimens, otherwise to the level of county (USA) or elsewhere to the level of state or similar political unit (e.g., Comisaría, Departamento, Estado, Intendencia, Provincia, etc.). In the taxonomic treatments and figure legends, these units are set in small capital letters.

As a rule, most old theridiosomatid "type" material is a syntype series. Some authors favor routine lectotype designation in such cases, but I feel that for species in which the syntype series is wholly of that taxon, such designation circumscribes the action of future taxonomists, and ought to be avoided. Also, in some cases (e.g., *Epeirotypus brevipes* O. Pickard-Cambridge, 1894, or *Theridiosoma radiosum* (McCook, 1881) (= *T. gemmosum* (L. Koch, 1878)), the only specimens located thus far are probably not of the type series. Neotypes might be designated, but again as long as the available specimens fit the original description and no confusion over the name exists, I have avoided such action.

For phylogenetic analysis I initially used the Wagner tree algorithm written by Joe Felsenstein (PHYLIP). Those results were corroborated with the PHYSYS package written by J.S. Farris and M.F. Mickevich and maintained at the University of Maryland by the Maryland Center for Systematic Entomology. Characters were coded as presence-absence states, with additive binary coding employed where necessary to represent complex characters.

Abbreviations Used in the Figures and Text.

AC's	aciniform spigots
AG's	aggregate gland spigots
ALE	anterior lateral eyes
ALS	anterior lateral spinneret
AM	ampullate spigot
AME	anterior median eyes
C	conductor
CL	cymbial lamella
CY (CY's)	cylindrical gland spigot(s)
E	embolus
EA	embolic apophysis
ED	embolic division
FL	flagelliform gland spigot
MA	median apophysis
O	opening of ejaculatory duct
P	paracymbium
PI's	piriform gland spigots
PLE	posterior lateral eyes
PLS	posterior lateral spinneret
PME	posterior median eyes
PMS	posterior median spinneret
ST	subtegulum
T	tegulum

TAXONOMIC HISTORY

Neither the family Theridiosomatidae nor any of the genera properly included in it have ever been revised. Archer (1953) reviewed the family, but his work was not in any sense revisionary. He accepted all the genera then placed in the family (e.g., Roewer, 1942) and described a new genus (*Parogulnius*) and several new species. He also transferred *Chthonos* (= *Tecmessa*) to the theridiids. Unfortunately he did not borrow any type specimens and therefore based his nomenclatural and taxonomic conclusions on published descriptions and figures. The opinions of earlier authors are often accurate, but usually are so poorly documented that no sound inferences can be drawn from their illustrations.

The literature on the family is meager (less than 100 papers, including original descriptions of species), and rather few papers discuss the status of the group as a whole (cf. Archer, 1953; Brignoli, 1979; Wunderlich, 1980). Theridiosomatid taxonomy has been chaotic, mainly due to the lack of a clear, objective diagnosis of the family. For example, all the genera originally described in Theridiosomatidae (except, obviously, the type genus *Theridiosoma*) seem to belong elsewhere (or are synonyms), and no genus accepted herein as a valid theridiosomatid taxon was ever originally described as belonging to the family. More or less complete turnover in group membership at the generic level has occurred (Table 1). Of the 21 genera historically associated with the family, 17 clearly belong in

TABLE 1.—Allocation of genera historically associated with Theridiosomatidae (* indicates monotypy; citations in parentheses indicate authority for previous generic transfers).

Genus	Family	Comments
* *Allototua* Bryant, 1945	?	nomen dubium, type lost
Andasta Simon, 1893	Theridiosomatidae	= *Theridiosoma*, new synonymy
* *Billima* Simon, 1908	Theridiidae (Levi, 1968)	
* *Colphepeira* Archer, 1941	Araneidae (Levi, 1978)	
* *Cyathidea* Simon, 1907	Theridiosomatidae	= *Wendilgarda*, new synonymy
* *Cyatholipulus* Petrunkevitch, 1930	Symphytognathidae (Wunderlich, 1978)	
Cyatholipus Simon, 1894	Tetragnathidae	Cyatholipinae (Wunderlich, 1978)
* *Diotherisoma* di Caporiacco, 1947	Araneidae	
* *Enthorodera* Simon, 1907	Theridiosomatidae	= *Wendilgarda*, new synonymy
Epeirotypus Cambridge, 1894	Theridiosomatidae	
* *Haliger* Mello-Leitão	?	incertae sedis
* *Helvidia* Thorell, 1890	Theridiidae (Levi, 1972)	
Ogulnius Cambridge, 1882	Theridiosomatidae	
* *Parogulnius* Archer, 1953	?	incertae sedis
* *Phricotelus* Simon, 1895	?Mysmenidae (Brignoli, 1982)	
* *Spheropistha* Yaginuma, 1957	Theridiidae (Brignoli, 1982)	
Tecmessa O. Pickard-Cambridge, 1882	Theridiosomatidae	= *Chthonos*, new name
* *Tekella* Urquhart, 1894	Tetragnathidae	Cyatholopinae (Wunderlich, 1978)
* *Theridilella* Chamberlin and Ivie, 1936	?	nomen dubium
Theridiosoma Cambridge, 1879 (in part)	Theridiosomatidae	
Theridiosoma Cambridge, 1879 (in part)	Theridiosomatidae	= *Epilineutes*, new genus
Theridiosoma Cambridge, 1879 (in part)	Theridiosomatidae	= *Baalzebub*, new genus
Theridiosoma Cambridge, 1879 (in part)	Theridiosomatidae	= *Naatlo*, new genus
* *Totua* Keyserling	Linyphiidae	
Wendilgarda Keyserling, 1886 (in part)	Theridiosomatidae	
Wendilgarda Keyserling, 1886 (in part)	Theridiosomatidae	= *Plato*, new genus (Platoninae, new subfamily)

other families, are synonyms, or are nomina dubia. Most of the genera whose placement has been unstable are monotypic.

Taczanowski described the first theridiosomatid as *Theridium splendidum* in 1873, based on material from Brazil; however, the affinities of that species were not recognized until later (Keyserling, 1884). The type genus of the family is instead *Theridiosoma* O. Pickard-Cambridge, with *T. gemmosum* (L. Koch), one of the few temperate taxa, as type-species. Koch described it in 1878 from Germany as *Theridium gemmosum*, Pickard-Cambridge in 1879 from Britain as *Theridiosoma argenteolum*, and McCook in 1881 from North America as *Epeira radiosa*.

Keyserling, O. Pickard-Cambridge, and Simon further established the character of Theridiosomatidae by describing or transferring *Andasta*, *Epeirotypus*, *Ogulnius*, *Wendilgarda*, and *Phricotelus* to the group. Petrunkevitch (1923:178, 1928:144) broadened the definition by including *Cyatholipus*, *Cyathidea*, *Helvidia*, and *Totua*. Petrunkevitch also described *Cyatholipulus luteus* in 1930, Mello-Leitão *Haliger corniferus* in 1943, Bryant *Allototua guttata* in 1945(a), L. di Capriacco *Diotherisoma strandi* in 1947, and Archer *Parogulnius hypsigaster* in 1953. Archer (1953) also included *Colphepeira catawba* in the theridiosomatids, and Roewer (1942) transferred *Billima* and synonymized *Cyatholipulus* with *Cyatholipus*. Levi and Levi (1962) transferred *Enthorodera, Spheropistha, Theridilella,* and *Tekella*. In this, its most engorged state, the family contained 21 genera.

Since that time the group has shrunk. Levi (1968b, 1972, 1978) transferred *Helvidia* and *Billima* to the theridiids and *Colphepeira* to the araneids. Gertsch (1960) synonymized *Parogulnius* with *Trogloneta* (Mysmenidae). Wunderlich (1978) provisionally placed *Cyatholipus* and *Tekella* with the tetragnathids, and Brignoli (1981) returned *Spheropistha* to theridiids and provisionally placed *Phricotelus* in the Mysmenidae.

To what extent these transfers are valid remains to be seen. For example, Brignoli (1981) gave no diagnosis of Mysmenidae that supported the transfer of *Phricotelus*. If the relimitation of Mysmenidae by Platnick and Shadab (1978a) is accepted, neither *Phricotelus* nor *Parogulnius* shares the synapomorphies those authors listed for Mysmenidae. *Parogulnius* has a structure reminiscent of a parmula in its epigynum—perhaps it is a linyphiid. Wunderlich (1978) based the monophyly of cyatholipines (*Teemenaarus, Tekella, Tekellatus,* and *Cyatholipus*) on a wide, posterior tracheal spiracle situated far in advance of the spinnerets, a character otherwise known in diverse taxa (not necessarily araneoids) whose affinities are not well established (Forster, 1959). The alliance of those genera with tetragnathids (Wunderlich, 1978) because of a low clypeus and the absence of a cheliceral condyle is certainly grouping on the basis of symplesiomorphies, as outgroup comparison with Dinopidae or Uloboridae demonstrates (see Coddington (in press) for justification of Dinopoidea as the sister taxon to Araneoidea). *Cyatholipulus, Cyatholipus, Haliger, Parogulnius, Phricotelus, Spheropistha, Tekella, Tekellatus,* and *Teemenaarus* should probably be incertae sedis until a convincing argument based on synapomorphies allies them with some other taxon. By incertae sedis I mean "of uncertain affinities"; if the genera can't be placed with assurance in any well-defined araneoid family, it can only compound systematic and nomenclatural confusion to shuffle them between poorly defined groups. On the other hand, no positive evidence is available that these transfers are incorrect, so they may as well stand. Certainly the above taxa exhibit no known characters that justify their retention in Theridiosomatidae. *Diotherisoma* di Caporiacco, 1947, is a synonym of *Bertrana* (Levi, pers. comm.), and *Totua* Keyserling, 1891, and *Parogulnius* Archer, 1953, have epigyna very like linyphiids. At any rate, all of the genera excluded from Theridiosomatidae in Table 1 lack the defining synapomorphies of the family (see below).

Two names in Table 1 are nomina dubia. The monotypic *Theridilella* Chamberlin and Ivie, 1936 (type-species *T. zygops*, in AMNH, examined), is a theridiosomatid. Levi and Levi (1962) state that the specimen was immature; in any case the genitalic region has been dissected out and lost. Without the genitalia nothing definite can be said, but somatically the animal does resemble *Theridiosoma goodnightorum* Archer, 1953. The specimen is undoubtedly a *Theridiosoma* and, in any case, is undiagnosable, hence the name is a nomen dubium. By the published figures, the monotypic *Allototua* Bryant, 1945 (type-species *A. guttata*, lost), may be a synonym of *Ogulnius;* on the other hand, it may not be a theridiosomatid at all. Bryant (1945a) described the genus from a single adult female, but at present it cannot be found. She mentioned that the labium was fused to the sternum; in all theridiosomatids, however, the labial suture is distinct. Also, she gives the order of leg lengths as 1-2-4-3, whereas in Ogulnius the order is 4-1-2-3. Eye proportions and sternum shape are similar to *Ogulnius*. Without any extant specimens, *Allototua* is also a nomen dubium.

Since the inception of the family, theridiosomatids have been heterogeneous and difficult to place. Their superficial appearance obviously suggested Theridiidae to many authors (*Chthonos* (= *Tecmessa*), *Epeirotypus, Enthorodera* (= *Wendilgarda*), *Ogulnius, Theridiosoma,* and *Wendilgarda* were originally described as theridiids). Web architecture, however, linked theridiosomatids with the araneoid orb weavers (McCook, 1881, 1889a). In synonymizing *Theridium gemmosum* and *Theridiosoma argenteolum,* Simon (1881) mentioned that a closely related species occurred in North America, but presumably he was unaware or skeptical of its status as an orb weaver, because he placed the monotypic genus in its own section in the "Theridionidae" (= Theridiidae). He cited L. Koch in stating that its web is "formée de quelques fils irréguliers" (Simon, 1881:27); thus he was unaware that the species spun an orb web. Theridiosomatids were also placed as theridiids by Keyserling (1884, 1886). McCook (1889a) reiterated his evidence that *Theridiosoma* was an araneoid orb weaver (his European colleagues apparently thought it might be a cribellate orb weaver), and Simon (1895) soon concurred by making the group a subfamily of his Argiopidae. Simon's concept of Argiopidae was so broad, however, that by modern standards that placement is equivalent to giving it family status.

Most subsequent authors have treated theridiosomatids as a subfamily of Araneidae (= Argiopidae), e.g., Comstock (1912), Simon (1926), Petrunkevitch (1928), Wiehle (1931), Gerhardt and Kaestner (1938), and L. di Caporiacco (1938). Berland (1932:95) apparently still considered them theridiids, but in view of his training under Simon it is difficult to believe that the assignment was not a mistake. Apparently, Vellard (1924) was the first author to propose full family status for the taxon, but the suggestion was ignored by his colleagues. Kaston (1948) again assigned the group family status, but Archer (1953) argued against family rank. Opinion since then has continued to be divided. Some authors maintained it as a subfamily of araneids (Locket and Millidge, 1953; Lehtinen, 1967), although others give it family status (Kaestner, Levi, and Levi, 1980; Yaginuma, 1968; Wunderlich, 1976, 1980; Brignoli, 1983).

The controversy over theridiosomatids as a subfamily or family is not a puerile argument about taxonomic rank; valid issues involving sister group relations are involved. Subfamilial status in Araneidae implies that theridiosomatids are more closely related to araneids than to any other araneoid higher taxon. Inclusion of the group in Araneidae has been due primarily to the occurrence of orb webs in both groups. Indeed, the operational definition of Araneidae, for the most part, has been "a generalized araneoid spider producing an orb web," as demonstrated by the steady transfer of "theridiid" species into Theridiosomatidae upon discovery of their orb webs. For example, O. Pickard-Cambridge (1894:135) described his new genus *Epeirotypus* as a theridiid, saying:

> This spider, which is allied to both *Theridiosoma,* Cambr., and *Ogulnius,* Cambr., is even nearer to the true epeirids [= araneid orb weavers] than the former of these two; it also comes near the genus *Mesopneustes,* Cambr. [= *Theridula,* Theridiidae] . . . .

Two years later O. Pickard-Cambridge (1896:161) transferred *Epeirotypus* to the araneids when he learned that it spun an orb web.

> Mr. Smith has the following note on them [that the spider made an orb web], which is of great interest as showing that the spider belongs to the Epeiridae rather than the Theridiidae, in which family I had first placed it before the facts related by Mr. Smith were known to me . . . .

However, current evidence shows that the orb web, per se, is plesiomorphic for araneoid spiders, and thus cannot be used as evidence of close relationship within the superfamily or even in araneoid family diagnoses (Coddington, in press; Levi and Coddington, 1983).

Although theridiid-nesticids have not been considered closely related to theridiosomatids for over a century, that lineage may well be the sister group of the Theridiosomatidae and symphytognathoids together (see below). By "symphytognathoids" I mean the Mysmenidae, Anapidae, and Symphytognathidae; I do not mean to imply superfamily status for the group. Many of the component groups of Araneoidea still lack explicit, objective diagnoses (for example, the monophyly of araneids, tetragnathids, metids, and linyphiids is tenuous). At present it seems best to split off monophyletic groups from these larger "taxa" and to give them family rank, thus emphasizing both the objectivity of specific groups and also our ignorance of their interrelationships.

Morphology and Phylogeny

MONOPHYLY OF THERIDIOSOMATIDAE

Throughout the taxonomic history of Theridiosomatidae, various characters have been used to define or to identify the group. Here these characters are considered as potentially diagnostic and will be discussed and evaluated in turn.

STERNUM BROADLY TRUNCATE BEHIND.—(Simon, 1895, 1926; Wiehle, 1931; Kaston, 1948; Levi, 1982). The character is often used in keys and does, in general, separate *T. gemmosum* (the best known north temperate theridiosomatid species) from other north temperate araneoids, but the feature is not at all consistent within theridiosomatids (e.g., Figures 76, 85). In addition various other small-sized taxa also have truncate sterna (Platnick and Shadab, 1978a,b; Forster and Platnick, 1984). Finally, how truncate does the sternum have to be before it is "broadly truncate"? Sternum shape is probably influenced by overall body proportions, and certainly by the observer's angle of view, so while the feature might be informative in the context of a more circumscribed phylogenetic analysis, it is too poorly defined and too widespread to use in a family diagnosis.

HIGH CLYPEUS HEIGHT.—(Levi, 1982; Kaston, 1948). Many theridiids, anapids, mysmenids, linyphiids, and even some araneids have a clypeus more than 2 or 3 times the height of an anterior median eye. Also, in some theridiosomatids (*Naatlo, Baalzebub*, Figures 49, 87, 182) the clypeus is relatively low.

LARGE MALE SEXUAL ORGANS.—(Simon, 1895; Archer, 1953). Some male theridiids (*Tidarren*) have palpi that are similarly huge, but the coincidence is surely homoplasy; however, *Chthonos* species uniformly have small palpi, as does *Wendilgarda mexicana*.

LEGS WITHOUT SPINES.—(Simon, 1895, Wiehle, 1931; Kaston, 1948). At present, a "spine" is considered to be a simple extension of the cuticle—solid and immovable with respect to the exoskeleton. In the past authors have not recognized this difference between spines and hairs, setae, macrosetae, or bristles, or more technical differences such as ennervation, so it is difficult to know what "lack of spines" specifically means. At any rate, spiders in general lack spines in this strict sense, whereas theridiosomatids do have robust setae on their legs. The character is bound to cause confusion and does not diagnose theridiosomatids from other araneoids in either its narrow or broad meaning.

FEMALE PALP WITHOUT A CLAW.—(Simon, 1895, 1926; Wiehle, 1931; Kaston, 1948; Levi, 1982). Other minute araneoid female spiders that are probably closely related to theridiosomatids lack palpal claws (Forster, 1959).

RUDIMENTARY PARACYMBIUM.—(Simon, 1926; Archer, 1953; Levi, 1982). The theridiosomatid paracymbium (e.g., Figures 12, 72, 153) is no more rudimentary than that in most araneids—a simple hook on the basal lateral margin of the cymbium. Presence of a paracymbium appears to be plesiomorphic for Araneoidea, and, in any case, the various kinds of araneoid paracymbia (nesticid, araneid, metid, tetragnathid, theridiid, cyatholipid, linyphiid, etc.) have not been analyzed in enough detail to argue that the particular form or placement of the theridiosomatid paracymbium is unique.

HETEROGENEOUS EYES.—(Wiehle, 1931; Kaston, 1948). Homann (1971) showed that canoe tapeta are plesiomorphic features of secondary eyes for a very large group of spiders, as is the absence of tapeta in the "main," or anterior median eyes. The tapeta of the posterior median eyes and sometimes the posterior lateral eyes have been lost in numerous araneoid genera (Levi and Coddington, 1983). Although that loss may be synapomorphic, presence, and therefore the character "heterogeneous eyes," is certainly symplesiomorphic in theridiosomatids.

MEDIAN CLAW ELONGATE.—(Simon, 1895, 1926; Wiehle, 1931; Kaston, 1948). This character (Figure 3) may define a monophyletic group of spiders including theridiosomatids (see below), but it does not define that family alone. It also occurs in mysmenids (Brignoli, 1974; pers. obs.) and nesticids (Wiehle, 1963; pers. obs.).

CHELICERAE WITHOUT A PROXIMAL BOSS.—(Wiehle, 1931; Kaston, 1948; Levi, 1982). The cheliceral boss that appears in some araneoids is absent in many others (linyphiids, theridiids, etc.). Its absence in theridiosomatids is not a useful character.

MEDIAN APOPHYSIS BROAD-BASED OR PRONE AND PROJECTING.—(Archer, 1953). The median apophysis of many araneoids is broad based, or prone and projecting, e.g., *Araniella* (Araneidae: Araneinae). The shape and insertion of the theridiosomatid median apophysis varies from a thin lamina (*Theridiosoma*, Figure 134) to a sclerotized curved spur (*Plato*, Figure 10), to a wide plate (*Ogulnius*, Figure 99). It is difficult to infer what the primitive condition may have been, and hence whether it could be synapomorphic for the family.

LARGE TEGULUM.—(Archer, 1953). Mysmenids (Gertsch, 1960; Platnick and Shadab, 1978a) also have relatively large tegula.

None of the characters traditionally used, therefore, accurately diagnose the family Theridiosomatidae. Undoubtedly this ambiguity has encouraged the use of the taxon as a repository for genera vaguely like *Theridiosoma* but sharing no clear-cut derived features. Wunderlich (1980) made a very valuable contribution to the diagnosis of theridiosomatids when he pointed out that the sternal pit organs, mentioned by Simon (1907) and Archer (1953), were unique to theridiosomatid genera and thus were a convincing synapomorphy of the family. In the course of this revision, other synapomorphies of Theridiosomatidae have been discovered, and so the monophyly of the group can hardly be doubted. These synapomorphies are as follows.

STERNAL PIT ORGANS.—(Wunderlich, 1980). These structures are located on the promargin of the sternum, adjacent to the labium. In museum material they appear as deep pits (Figures 76, 85, 140), but in cleared preparations they are revealed as glandular structures, with sac-like invaginations (Wunderlich, 1980, figs. 3, 4). Their purpose is unknown. Sternal pits are present in all genera of theridiosomatids except *Chthonos*. The presence of several synapomorphies linking that genus with *Plato*, which has pits, implies that pits are secondarily lost in *Chthonos*.

PALP CONFORMATION.—The juxtaposition of sclerites in the unexpanded palp and their orientation to each other is unique to the family (Figures 30, 42, 70, 130, 161, 188, 196; see below for further explanation).

RESERVOIR.—In all theridiosomatid genera, the route of the reservoir of the sperm duct in the male palpus is consistent and similar (Figures 27, 28, 40, 63, 98, 119, 146, 147, 176). Specifically, the ejaculatory duct is limited to the body of the embolus proper. The reservoir (cf. Comstock, 1910, 1912; Opell, 1979, for the definitions of the regions of the sperm duct accepted here) begins at the point where the embolic division inserts on the tegulum, loops retrolaterally to the rear of the tegulum where it makes a sharp U-turn around the base of the conductor (Figure 176), and then circles forward and mesally beneath the median apophysis (Figure 118). It then bends sharply into the center of the tegulum and out again to the lateral surface, where it executes one or more sharp loops (Figures 62, 176). It again curves retrolaterally to the rear of the tegulum, again around the base of the conductor, and mesally forward beneath the median apophysis, thus paralleling the first loop described above (Figure 176). It continues to the ventral wall of the tegulum, and bends sharply into the subtegulum, where it opens into the large, thin-walled fundus (Figures 28, 41, 118). Many features of the course of the reservoir are consistent among all theridiosomatid genera and thus serve as synapomorphies for the family. Outgroup comparison to other orb-weaving groups such as uloborids (Opell, 1979), araneids (Levi, 1971), or theridiids (Levi, 1961; Levi and Levi, 1962) indicates that the primitive course of the reservoir in the bulb is a simple spiral starting at the insertion of the embolus, continuing around the margin of the tegulum for one or more turns, passing into the subtegulum, and ending in the fundus. In a sense theridiosomatid reservoirs do the same, with two significant elaborations. At the outset the reservoir executes a sharp turn around the conductor, thus reversing from a right-handed to left-handed spiral in apical view (Figure 119), and second, in the vicinity of the completion of the first spiral turn (Figures 146, 147, 186), the reservoir executes a number of sharp switchbacks. Of course some theridiids, metids, nephilids, and tetragnathids also have "complex" reservoir trajectories, but no convincing similarity beyond "complexity" itself has been found between the trajectory in these taxa and that in theridiosomatids. (See below for comments on symphytognathoids.)

LONG TIBIAL TRICHOBOTHRIA.—Theridiosomatids have on all tibiae, but especially on their third and fourth, numerous dorsal trichobothria whose length is often 2–4 times the diameter of the tibia (Figures 48, 171, 181). The distal trichobothrium of the fourth tibia is exceptionally long. Tibial trichobothria on the dorsum of the fourth tibia of araneids, anapids, mysmenids, symphytognathids, metids, theridiids, nesticids, and linyphiids are relatively much shorter.

Based on the above suite of characters, the spider family Theridiosomatidae is defined to include *Baalzebub, Chthonos, Epeirotypus, Epilineutes, Naatlo, Ogulnius, Plato, Theridiosoma,* and *Wendilgarda.*

COMPARATIVE MORPHOLOGY OF THERIDIOSOMATID GENITALIA

Theridiosomatid genitalia have not been described or illustrated in detail. In view of the importance of genitalic morphology to phylogenetic studies, it is desirable to explain clearly and to homologize their morphology with that of other monophyletic araneoid groups, where possible.

Terms used to describe the parts of the palp follow Comstock (1910), Merrett (1963), Millidge (1977, 1980), Levi (1971, 1978), and Opell (1979) (see these authors for the basic morphology of the palp of other orb-weaving spider groups). Orienting terms (mesal, lateral, distal, proximal, etc.) in the following description follow the usual morphological conventions. In general the left palp is figured. Terms such as clockwise or counterclockwise are used from an observer's point of view, looking at a left palp in ventral or apical view. Because the sclerites change their orientations to each other and to the cymbium when the palp expands, strictly accurate description would require different orienting terms for both states. The change would be very confusing. In the following description, unless otherwise noted, terms refer to the cymbium, bulb, and sclerites as they appear in the unexpanded bulb.

BASAL PALPAL ARTICLES.—The palpal endites, femur, patella, and tibia are essentially unmodified, lacking the stridulatory structures, tubercles, thorns, or apophyses that sporadically appear on other orb weavers (e.g., uloborids, araneids, anapids, etc).

CYMBIUM.—The cymbium is a broad, cup-shaped segment with the usual basal alveolus on the ventral surface. The mesal basal margin of the cymbium bears a paracymbium (Figures 12, 32, 50, 72, 102, 153, 164, 191, 216), always a more or less simple hook. A spine may (Figure 102) or may not (Figure 216) occur on the distal end of the paracymbium. The cymbium of *Baalzebub* (Figure 164), *Epilineutes* (Figure 191), *Ogulnius* (Figure 102), *Plato* (not figured), and *Wendilgarda* (Figure 216) has an additional lamella situated just distally to the paracymbium on the margin of the cymbium (lacking in *Chthonos, Epeirotypus,* and *Naatlo*). The tip of the cymbium and the distal margin of the alveolus is distinctly pointed in most species of *Plato* and

Chthonos, blunt in the remaining genera. The mesal margin of the cymbium in most species of *Plato* has several notches (Figure 10).

PALPAL BULB.—The theridiosomatid palpal bulb is tripartite, consisting of the subtegulum, tegulum, and embolic division. The bulb is attached to the cymbium by a basal hematodocha. The basal hematodocha attaches proximally to the alveolus of the cymbium, and its distal end inserts on the cylindrical basal margin of the subtegulum. The petiole is apparently absent, but I am not certain of this fact. During expansion, the basal hematodocha inflates considerably and may rotate the bulb through as much as 200 degrees with respect to the cymbium. The bulb always rotates counterclockwise with respect to the cymbium in the left palpus and so the originally mesal median apophysis (e.g., Figure 10, palp unexpanded) approaches the paracymbium on the lateral cymbial margin (Figure 28, palp expanded). In my preparations the median apophysis did not, however, touch or engage the paracymbium as Heimer (1982) would predict. In an unexpanded bulb, therefore, a diagram shows the mesal aspect of cymbium and bulb, but in an expanded bulb it will show, for example, the mesal aspect of the cymbium and the lateral aspect of the bulb or visa versa.

The subtegulum (ST, Figures 11, 30, 42, 70, 135) is a cup-shaped or cylindrical sclerite, slightly longer or deeper on the ventral side than the dorsal (in an unexpanded palp). The distal ventral margin appears to be weakly fused to the tegulum. The point of fusion provides a fulcrum about which the tegulum and embolic division pivot slightly during expansion (Figures 62, 63). Movement of the distal portions is accomplished by expansion of the median hematodocha, by far the largest hematodocha of the palpus. The subtegulum also contains most of the fundus of the sperm duct, a large, thin-walled sac near the ventral wall of the subtegulum, where the reservoir of the sperm duct inserts. In many palps the form of the fundus is difficult to decipher, and so the appearance of the structure in the illustrations is only diagrammatic.

The tegulum is a ring-shaped sclerite whose lateral aspect is hugely expanded. The lateral surface usually has a dark stripe (Figure 27). It is deeply split on its mesal, dorsal side, and the conductor sits inside the cleft (Figure 21). The median apophysis sits at the end of the mesal arm of the split, and the embolic division originates on the lateral margin of the split. The tegulum also contains the reservoir of the sperm duct, whose trajectory, as described above, is extremely complex. Even though the tegulum is much modified, it can be recognized as such because the course of the reservoir is entirely contained within it, and it bears the median apophysis and conductor, as is the case in nearly all spiders. The median apophysis (Figures 10, 29, 42, 70, 99, 133, 163, 188, 196) is an articulated sclerite arising from the mesal arm of the split tegulum. The median apophysis is variously shaped and can have different lobes or apophyses, but in mesal view it is always in the same place, at the distal end of mesal arm of the tegulum. The reservoir of the sperm duct never passes through the median apophysis itself.

The conductor lies within the split of the tegulum. It is a large, over-arching structure that to a greater (*Baalzebub, Epilineutes, Ogulnius, Theridiosoma, Wendilgarda*) or lesser extent (*Chthonos, Epeirotypus, Naatlo, Plato*) covers the embolus when the palp is contracted. The conductor may have various lobes (Figures 11, 30, 133, 137, 189). The more distal apophyses are often pointed, and during expansion the point rocks forward and rubs against the surface of the tegulum (*Epeirotypus, Theridiosoma*). The conductor also seems to have a hematodocha between it and the lateral portion of the tegulum. When expanded, this hematodocha to some extent pushes the embolus away and out from underneath the conductor.

The embolic division of the palp arises from the tegulum near the connection with the conductor. It curls in a counterclockwise fashion (left palp, ventral view). The embolus is a simple strong sclerite (*Chthonos, Plato, Epeirotypus, Naatlo*) or it has a mesal apophysis emerging at the base, here termed the "embolic apophysis" (*Baalzebub, Epilineutes, Ogulnius, Theridiosoma, Wendilgarda*). No hematodocha occurs between the embolic apophysis and the embolus, and none between the embolic division and the tegulum. The embolic apophysis may either be a bifurcate bristle (*Ogulnius,* Figure 101), fragmented (*Theridiosoma,* Figures 131, 133, 136), or tripartite (*Baalzebub, Epilineutes, Wendilgarda,* Figures 162, 190, 198). The embolic apophysis is apparently an autapomorphy of these genera, because the immediate outgroups of theridiosomatids lack any embolic apophyses at all, and furthermore the apophysis of theridiosomatids differs considerably from the "terminal apophysis" of other araneoid taxa such as linyphiids or araneids. *Plato* species may also exhibit mesal embolic apophyses (Figures 10, 22), but the homology of these more distal structures with those discussed above is not certain.

The male palp therefore offers many taxonomically useful characters. No doubt the female genitalia are similarly useful, but because the structures are soft, less sclerotized, and involve dissecting the animal, I have studied them more superficially. Of course, male and female genitalia complement each other. One expects the oversized male genitalia to be equalled by the capacious copulatory bursae of the female. Likewise the simplest routing of the copulatory ducts is matched by those males having simple embolic divisions. Functionally related parts are not, after all, homologues, and thus can be considered independently derived apomorphic features.

The theridiosomatid epigynum is always a continuous, usually simple, plate covering the opening of the copulatory bursae (Figures 25, 37, 112, 151, 206). Similar plates occur in symphytognathoids, but the feature seems too nondescript to use in phylogenetic studies. The posterior rim may (*Chthonos, Epeirotypus, Naatlo, Ogulnius, Plato*) or may not (*Baalzebub, Epilineutes, Theridiosoma, Wendilgarda*) have a transverse groove, sometimes interrupted medially by a slight longitudinal ridge. Most genera also have a knob, pit, or cuticular thickening in the central region of the epigynal plate (Figures 18, 50, 173, 183, 219). The function of this structure is unknown, but in *Epeirotypus* a well-developed muscle extends from it towards the pedicel, probably enabling the female to reflect the epigynal rim while mating (Figure 5). Thus it may be an apodeme.

The copulatory pores are large and widely spaced, often merging into a common atrium. The copulatory bursae, by which I mean the outer ends of the copulatory ducts and their common atrium, are also capacious. It is sometimes difficult to tell from published illustrations, but apparently such capacious bursae are rare in Araneoidea (cf. Theridiidae, Levi and Levi, 1962; Araneidae, Levi, 1968b; metids, tetragnathids, Levi, 1980b; Symphytognathidae, Forster and Platnick, 1977; Anapidae, Mysmenidae, Platnick and Shadab, 1978a,b). In *Baalzebub, Epilineutes,* and *Wendilgarda* the bursae have lateral wings or pockets (Figures 174, 184, 215).

In many cases, the juncture between copulatory bursae and ducts is indistinct. In some preparations the bursae seem to extend as blind pockets beyond the beginning of the narrow spermathecal ducts (Figures 26, 60, 174); in the majority the two seem continuous, the bursae simply narrowing to form the copulatory ducts. Sectioned, stained preparations might settle the question.

The course of the bursae or ducts varies from a simple hairpin turn (*Epeirotypus, Naatlo,* Figures 60, 95) to more convoluted arrangements (e.g., *Ogulnius,* Figure 113; *Wendilgarda,* Figure 215). Duct routings tend to be diagnostic for genera, but no feature beyond their relatively large size seems to be synapomorphic for the family.

On the other hand, the fused condition of theridiosomatid spermathecae (Figures 26, 195, 220) is probably synapomorphic for the family (compare references cited above for other araneoid taxa). The spermathecae share their median wall, although in some derived groups they are connate only at their distal tips (e.g., *Baalzebub, Epilineutes,* Figures 174, 184).

The copulatory ducts usually insert on the lateral sides of the spermathecae, no doubt because the medial sides are fused. However, the ducts of derived genera nevertheless pass over the dorsal surface of the spermathecae towards the posterior and enter the spermathecae more or less on their mesal surfaces (*Baalzebub, Epilineutes, Theridiosoma, Wendilgarda,* Figures 145, 174, 184, 207).

The fertilization ducts are simple, short spurs that pass from the spermathecae to the vagina, and I made no attempt to use them in the analysis. Implications of these characters and others for the phylogeny of the family and its relationship to other araneoid families are evaluated in the following section.

INTERFAMILIAL RELATIONSHIPS

Our understanding of the phylogeny of the Araneoidea is so chaotic that it is impossible to discuss succinctly the placement of Theridiosomatidae in the superfamily. Some attention has to be paid to the phylogeny of the superfamily as a whole, if only to evaluate the data for any particular placement of Theridiosomatidae.

At present, Araneoidea is the largest spider superfamily, containing about 12,000 described species (estimated from Levi, 1982), or about a third of all described spider species. Araneoid spiders have an easily recognized gestalt, and the superfamily is doubtless monophyletic (see Coddington (in press) for a review of the evidence). The only controversy about the composition of Araneoidea concerns the archaeid, micropholcommatid, textricellid, and mimetid lineages. On the basis of two synapomorphies (peg-shaped cheliceral teeth, distinctive cheliceral gland mound), Forster and Platnick (1984) remove these families from the araneoids and place them with the huttoniids, stenochilids, and palpimanids, in the superfamily Palpimanoidea. It may be simpler (in the sense of competing phylogenetic hypotheses) instead to transfer those families into Araneoidea because of the contingent necessity of supposing the similarities between the former taxa and araneoids to be convergent. For example, a paracymbium-like structure occurs in Palpimanoidea, some have serrate hairs, and some also have labia wider than long, all features otherwise typical of Araneoidea. However, the homology of those rather vaguely defined characters in Araneoidea and Palpimanoidea is only speculative, and, in any case, their absence in other spider taxa that might serve as outgroups to either superfamily has not been documented. On the other hand, the removal of archaeids and mimetids conveniently makes Araneoidea a compact group of web-spinning spiders capable of producing sticky silk (as far as is known the Palpimanoidea sensu Forster and Platnick (1984) lack aggregate silk glands and consequently the ability to produce sticky silk). The problem is a difficult one requiring further research on palp, spinneret, and silk gland morphology, at least.

The controversy affects the placement of Theridiosomatidae within the Araneoidea only because Archaeidae and Mimetidae need no longer be considered as potential sister groups of theridiosomatids if their removal to the Palpimanoidea is correct. In any case, I know of no convincing features that would ally theridiosomatids with any of these taxa, so the question then becomes, which araneoid group (theridiid-nesticid, symphytognathoid, linyphiid-araneid, metid-tetragnathid) is the sister group of theridiosomatids? For justification of the monophyly of theridiids-nesticids and symphytognathoids, see Coddington (in press). The monophyly of araneids and linyphiids is simply a working hypothesis, based on the admittedly slim but apparently synapomorphic evidence of a radix in the embolic division of the male palp. On the other hand, the group "metid-tetragnathid" is almost certainly para- or polyphyletic. I link metids and tetragnathids here only to simplify the following arguments. As is argued below, the monophyly of metid-tetragnathids is in any case irrelevant to the question of the placement of theridiosomatids.

The traditional placement of theridiosomatids has been next to the "araneids"—itself apparently not a monophyletic group if broadly defined to include nephilids, metids, and tetragnathids. As mentioned above, theridiosomatid genera were typically first described as theridiids and then, as their orb webs were discovered, transferred to the araneids. Earlier authors tended to include all orb-weaving araneoid spiders in a single taxon—Araneidae or Argiopidae, defined by the orb web. However, all current evidence suggests that the orb web of uloborids and dinopids is homologous to that of the araneoid orb weavers (Coddington, in press). Given that Araneoidea is itself monophyletic, as is Dinopoidea, the orb web is therefore a synapomorphy for the two superfamilies and, therefore, by outgroup comparison also primitive for Araneoidea. Consequently the occurrence of an orb web, per se, is no justification for uniting any orb weavers within the Araneoidea, specifically Araneidae and Theridiosomatidae.

Even though one classic group (Araneidae, sensu lato) based on symplesiomorphic behavioral characters turns out to be paraphyletic, behavioral features still seem to be the most useful character system for placing theridiosomatids with their closest araneoid relatives. These characters are discussed briefly here and at more length in Coddington (in press).

INNER SS LOOP LOCALIZATION.—Orb-weaving spiders have basically two ways that they contact the innermost sticky silk (SS) loop during the construction of the sticky spiral (Eberhard, 1982; Coddington, in press). Uloborids, dinopids, and araneids (Araneinae, Gasteracanthinae, at least) use a lateral tap of the outside first leg to touch the outermost SS loop prior to connecting the SS segment they are currently spinning. Because the Dinopoidea (Uloboridae and Dinopidae) are the sister taxon of the Araneoidea (Coddington, in press), that method would seem to be plesiomorphic for Araneoidea. Metids, tetragnathids, theridiosomatids, symphytognathids, anapids, and mysmenids use a different method, a forward tap of the inside first leg (see Eberhard, 1982, for figures). Eberhard (1982) found surprisingly little homoplasy in this character, and once seen, the difference is very striking and consistent. Hence the feature seems to define a subsidiary monophyletic group of araneoid spiders containing the taxa listed above.

Two problems must be mentioned at this point. First, "metid-tetragnathids" are almost certainly a paraphyletic group (Coddington, in press). Palp structure supports the monophyly of tetragnathids (*Tetragnatha, Mimognatha, Pachygnatha, Glenognatha, Azilia,* at least), but the characters mentioned by Levi and Coddington (1983) (elongate chelicerae, "modified paracymbium") are poorly defined and weak synapomorphies, at best, for a group including *Meta* and tetragnathids. Almost no published information is available on "metids," so the problem can only be acknowledged until more research is completed. An inside first leg forward tap is one of the very few characters systematically investigated across all araneoid lineages and it does support the monophyletic group defined above.

Second, tetragnathids are haplogyne spiders, whereas all the other Araneoidea are entelegyne. Haplogyny and entelegyny are supposed to be fundamentally different conditions, and the former primitive with respect to the latter based on outgroup comparison to Mesothelae and the hypochiloid taxa (Brignoli, 1975; Platnick, 1975; Opell, 1979). Haplogyny in tetragnathids thus implies that they are the sister group of all other araneoids, not part of the subsidiary araneoid group defined above. The behavioral and morphological data conflict. However, as Opell (1979) suggested for Uloboridae, entelegyny can be independently derived within monophyletic lineages. Forster and Platnick (1984) reached the same conclusion for Palpimanoidea. The conflict could be resolved by a detailed study of the entelegyne condition in araneoid lineages. The behavioral evidence suggests that it has arisen twice, and thus one might expect to find two kinds of entelegyny in Araneoidea. Another possibility is that tetragnathids are secondarily haplogyne.

No detailed accounts of theridiid, linyphiid, or nesticid web building have been published. Some theridiids, certainly, sequentially connect sticky silk lines to non-sticky lines, and thus might be scored for the manner in which they "measure" the spacing of the sticky silk line. At any rate, the condition for this character in any of the above three lineages is unknown.

At least three characters, however, link linyphiids with Araneidae (sensu stricto), and so linyphiids may also be discounted as a potential sister group of theridiosomatids. For example, only linyphiids and araneids possess gnathocoxal sexual glands (Lopez, 1977). Likewise, only linyphiids and araneids possess a radix in the male palp. By radix I mean a sclerite articulated to the tegulum and bearing the embolus and a "terminal apophysis." (The "radices" of theridiids (e.g., Levi, 1961) or uloborids (Opell, 1979) do not fulfill this classical definition and thus are probably autapomorphies of each of those taxa, respectively.) The "terminal apophysis" of linyphiids and araneids is also synapomorphic for the two taxa. By terminal apophysis I mean a sclerite of the embolic division (thus not inserting on the tegulum) that inserts on the radix. Alternatively, the composite character "complex embolic division" could be considered a single, complex synapomorphy for linyphiids and araneids. Moreover, no convincing characters linking theridiosomatids to linyphiids have been discovered, and so linyphiids can be dropped from further consideration.

Two morphological characters do link the theridiid-nesticid lineage with Theridiosomatidae and symphytognathoids (i.e., Anapidae, Mysmenidae, and Symphytognathidae). These characters are cheliceral denticles (Figure 2) and elongate median claws (Figure 3). The former character, however, occurs in at least *Hyptiotes* (Peters, 1982) and *Nephila clavipes* (R.R. Forster, pers. comm.; pers. obs.) and thus cannot be a synapomorphy for theridiosomatids, symphytognathoids, and theridiid-nesticids.

An elongate median claw is ubiquitous in nesticids but unknown in theridiids. Nesticidae may be a paraphyletic assemblage of primitive theridiid genera or, at best, the sister group of theridiids (Coddington, in press). If the former case, elongate median claws could indicate the monophyly of theridiid-nesticids, theridiosomatids, and symphytognathoids.

Symphytognathoids themselves are monophyletic by one very consistent behavioral feature and, possibly, two additional morphological features. After the completion of the sticky spiral, the spider adds numerous "accessory" radii, which extend from the hub to the frame lines (described in Eberhard, 1981; photographs in Coddington, in press). Among the web-spinning mysmenids, the genus *Mysmena* is autapomorphic and has lost the behaviors concerned with accessory radii (Coddington, in press). These accessory radii cross the sticky spiral but are not cemented to it, whereas the sticky spiral is cemented to each structural radii it crosses. (By structural radii I mean the radii constructed during the discrete behavioral sequences defined as frame and radius construction in Coddington (in press), not that structural radii necessarily contribute more to the strength of the web.) Eberhard (1981) felt that the silk composing the accessory radii was finer than that of the structural radii, hence perhaps from a different gland altogether.

All symphytognathoids lack paracymbia. If the sister group relationship between Theridiosomatidae and symphytognathoids is accepted, this particular lack of a paracymbium is unique and unreversed in these taxa (see remarks about palpimanoids above). Nearly all other araneoids have some sort of paracymbium (Heimer, 1982). Second, the male palpi of symphytognathoids have, at most, one tegular apophysis, whereas other araneoids usually have two, the median apophysis and the conductor. Whether the remaining apophysis on the symphytognathoid palp is a conductor or a median apophysis is moot. Theridiosomatids have two tegular apophyses. By the same logic applied to the evidence of the paracymbium, the single tegular apophysis of symphytognathoids may be an additional synapomorphy for the group.

The sister taxon of Theridiosomatidae appears to be the symphytognathoid taxa (Mysmenidae, Anapidae, Symphytognathidae) as a whole. Five characters support this relationship—two strong behavioral synapomorphies, one which is debatable, and two morphological features that require more research before their significance can be fully substantiated.

HUB LOOP CONSTRUCTION AFTER SS CONSTRUCTION.—Most araneoids (Coddington, in press) either do not modify the hub region at all after completing the sticky spiral, or they bite out the hub center and either leave it as a hole or fill it in with irregular lines around or across the hole. Theridiosomatids, anapids, mysmenids, and symphytognathids always not only bite out the hub but add a regular outward spiral of loops to the hub region, usually completely replacing the hub (Eberhard, 1981). The behaviors involved (Coddington, in press) closely resemble the same behaviors used to construct the nonsticky spiral that all orb weavers construct prior to beginning the sticky spiral itself. Their appearance in theridiosomatids, anapids, mysmenids, and symphytognathids in a completely different and later part of the overall web-building sequence is a uniquely derived character uniting these families.

EGGSAC DOUBLY ATTACHED.—As far as I know, most symphytognathoids (*Symphytognatha globosa* is an exception; Hickman, 1931) retain the eggsac near the hub of the web, and it is attached to the web by two lines, hence "doubly attached" (photographs in Coddington, in press). The more primitive theridiosomatid genera do the same. Double attachment in *Epeirotypus* (Figure 44) and *Ogulnius* (Figure 104) arises because the spider begins eggsac construction on a transverse silk line, rather than from the bottom of a single pendant line (pers. obs.). Often the eggsac becomes elongate along the axis of the silk line as well. Even if the spider later cuts one of the attachment lines to the eggsac so that it is secondarily pendant (e.g., *Plato*, Figure 13, some *Ogulnius*, Figure 106, some *Epeirotypus*, Figure 68) the slight remnant of the second attachment line visibly persists on the lower apex of the eggsac.

Placement and attachment of eggsacs in metids, tetragnathids, nesticids, and theridiids is diverse within and between taxa. In any case, none of those lineages behave in a manner consistently similar to that uniting theridiosomatids and symphytognathoids.

RADII LENGTHENED.—The third behavioral similarity is ambiguous. Theridiosomatids (except *Ogulnius, Epeirotypus,* and probably *Naatlo*), anapids, mysmenids, and symphytognathids cut and lengthen all structural radii built during frame and radius construction. They do so after adding the secondary hub loops described above. Theridiosomatids also join the lengthened structural radii, thus "anastomosing" them (Figures 157, 159, 192, 194). Symphytognathoids cut and join their accessory radii to the radii built during frame and radius construction, but the latter radii are not joined to each other.

For several reasons the two kinds of radial anastomoses, one joining structural radii together, the other joining accessory to structural radii, seem too dissimilar to infer homology at this point. First, however similar the two kinds of radius-joining behaviors may be, they act on non-homologous substrates, i.e., accessory versus structural radii, and in slightly different ways. The inference of homology in a process such as behavior is more convincing if the substrate on which the behavior acts is also homologous, and in this case it is not. Second, symphytognathoids do have structural radii, and don't anastomose them, although no obvious engineering or functional reason prevents it. On the other hand, theridiosomatids lack accessory radii entirely, so it is unknown whether, if they had the opportunity, they would anastomose those accessory radii. Third, among theridiosomatids, *Epeirotypus* and very probably *Naatlo* do not cut, lengthen, or anastomose structural radii. If, as seems likely, these genera compose the sister taxon to the rest of the theridiosomatids, "radial anastomosis" may have been derived independently in the remaining theridiosomatids and in the symphytognathids. Otherwise, one could presume secondary loss of radial anastomosis in Epeirotypinae, and, consequently, that the anastomosis of radii, whether structural or accessory, is also synapomorphic for theridiosomatids and symphytognathids.

FEMALE PALPAL CLAW ABSENT.—As far as I know, only the females of theridiosomatids, mysmenids, anapids, and symphytognathids among araneoids consistently lack claws on their palpi. Of course, the palp of female anapids is usually somewhat reduced in size, and that of symphytognathids is reduced to a single segment or complete absence, but, nevertheless, the palp lacks a claw. Mysmenidae appears to be the sister group to anapids and symphytognathids, and the clawless palps of mysmenid females are quite comparable in size and development to those of theridiosomatids.

RESERVOIR SWITCHBACK IN MALE PALP.—As mentioned above, the primitive course of the reservoir in araneoids is one or two unreversed spirals. In Theridiosomatidae (see above, and Figure 176) and at least Anapidae and Mysmenidae of the symphytognathoids, the reservoir starts a spiral in one direction but loops back on itself almost immediately and thereafter follows a reasonably consistent spiral course in the other direction. I have not studied the routing of the reservoir in symphytognathids, but in view of the other characters linking the group with Theridiosomatidae, the similarity is suggestive—possibly an additional synapomorphy.

One reason telling against this feature as a synapomorphy for theridiosomatids and symphytognathids is the complexity of the reservoir routing in nephilids, metids, and tetragnathids (Levi, 1980b, 1981). Although no convincing detailed similarities in reservoir routing between the former and the latter taxa have emerged, all these routings are complex and will certainly yield useful phylogenetic information if further studied. One feature does speak against the homology of the reservoir route complexity in the above taxa. In metids, tetragnathids, and nephilids, the complexity occurs immediately proximal to the insertion of the embolus on the tegulum, whereas in theridiosomatids the reservoir completes the first switchback and circuit of the tegulum before becoming markedly complex (Figures 147, 176). Thus the "complexity" arises in somewhat different regions of the reservoir.

In summary, the tetragnathids, metids, theridiosomatids, and symphytognathoids, and possibly also theridiid-nesticids, form a natural group within the Araneoidea (Coddington, in press). With respect to the first four lineages, one component unites theridiosomatids and symphytognathoids, and another unites tetragnathids-metids to that pair of taxa. The placement of Theridiidae-Nesticidae, however, is uncertain; the lineage may eventually be placed at any of the five possible positions within the following three taxon statement (metid-tetragnathids, (theridiosomatids (symphytognathoids))).

INTERGENERIC RELATIONSHIPS

A cladistic analysis of the family indicates four subfamilies, Platoninae, Epeirotypinae, Ogulniinae, and Theridiosomatinae (Figure 1). Characters used in the cladogram draw on a larger matrix of about 150 characters routinely scored for theridiosomatid taxa during the course of this revision. The majority have been omitted from Figure 1 because they are (1) synapomorphies at subgeneric levels; (2) autapomorphic for genera; (3) characters initially thought to be informative but later found to be too vaguely defined to be usable; (4) known only for a small subset of the studied taxa; or (5) important behavioral features. Behavioral features are of course mentioned throughout, but insofar as a major goal of this revision has been to analyze theridiosomatid morphology in preparation for a test of behavioral phylogenetic hypotheses, one cannot first include the behavior to construct a tree, and then use the tree to analyze the behavior. Even if behavioral features are added to the data set presented in Figure 1, no clear resolution of the basal trichotomy results.

The cladogram of Figure 1 is the shortest possible tree by the following argument. No characters substantially refute the monophyly of Platoninae, Epeirotypinae, or the sister group relation between Ogulniinae and Theridiosomatinae. Thus the cladistic issue at the subfamily level is a three-taxon problem. I used the PHYLIP and PHYSYS Wagner algorithms to ascer-

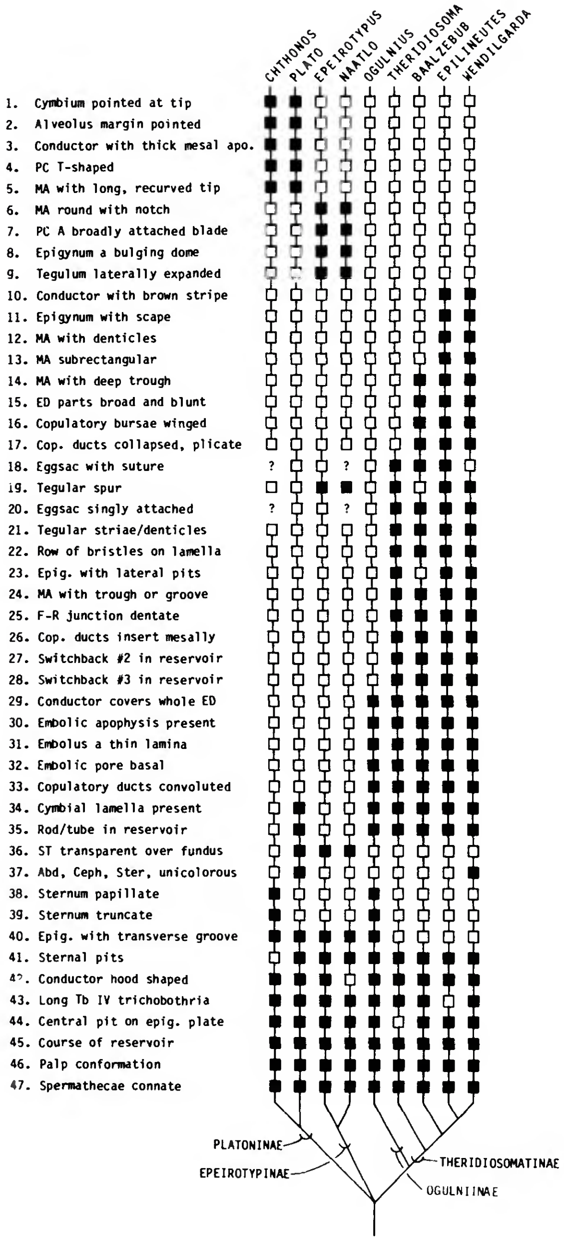


FIGURE 1.—Cladogram of theridiosomatid genera. Consistency index 0.82; autapomorphies of genera omitted; characters discussed in text. (Open squares = primitive states, closed = derived.)

tain that the lengths of each possible solution were equal, thus proving that a basal trichotomy is the appropriate representation of the data. In a like manner, I specified all 105 possible rooted trees for the five-taxon statement (*Ogulnius, Theridiosoma, Baalzebub, Epilineutes, Wendilgarda*), with the root always basal to *Ogulnius*. Figure 1 is the shortest tree, with a consistency index of 0.76. The three implied trees do differ in F ratio. Of these, a sister group relationship between Platoninae and Ogulniinae-Theridiosomatinae affords the least variance between tree and distance matrix (F = 9.4 vs. F = 10.1 and 10.3 for the other two trees). In practice and theory, however, F statistics offer scant reason to prefer one tree to another.

Observation of theridiosomatid web construction shows that the more bizarre webs, for example those of *Ogulnius* (Figures 103, 105) and *Wendilgarda* (Figure 202), employ only a subset of behaviors that by outgroup comparison are primitively part of the orb-web construction algorithm. *Ogulnius* and *Wendilgarda*, for example, lack non-sticky spiral construction, radius construction, frame construction, and hub modification (see Coddington (in press) for brief descriptions). Computer algorithms obviously don't distinguish between secondary loss and primitive absence. If these and other behavioral characters are added to the data set, the consistency index drops considerably, but the form of the tree does not change, because of the massive evidence for the monophyly of Theridiosomatinae.

PLATONINAE.—Platoninae includes the genera *Plato* and *Chthonos*. Five derived characters support the monophyly of the subfamily, all features of the male palpus. First, the cymbium of all *Chthonos* and all except one *Plato* (the exception is undescribed) are distinctly pointed; second, the distal margin of the alveolus is also pointed (Figures 10, 29). Corresponding features in other theridiosomatid genera and family outgroups are rounded. Third, the conductor has a thick, recurved, ventral apophysis, very similar in both taxa (Figures 10, 29). Outgroups to the family lack the particular form of the theridiosomatid conductor in general, and the conductor apophysis in particular. *Theridiosoma* species may have apophyses on the conductor (Figures 133, 156), but they originate from different points on the conductor and are neither so recurved nor so robust. Fourth, the paracymbium of both *Chthonos* and *Plato* is somewhat T-shaped (Figures 12, 32). It hooks toward the tip of the cymbium, as do the paracymbia of other theridiosomatid genera, but also has a backwardly directed lobe that gives it the form of a T. Fifth, the distal tip of the median apophysis is long, recurved, robust, and quite sclerotized (Figures 10, 29). The median apophysis of *Theridiosoma* may be attenuate and recurved, but it is a weakly sclerotized structure with a dorsal groove and pointed tip. That of *Ogulnius* is a much broader lamellar plate with differently shaped apophyses.

Observations of webs of *Plato bruneti,* new combination, in Trinidad and *P. guacharo,* new combination, and *P. miranda,* new combination, in Venezuela confirm that the genus does anastomose radii in the same manner as *Theridiosoma* and *Epilineutes* (e.g., Figures 159, 192). On the other hand, *Plato* species do not isolate a primary radius for use as a tension line as do *Epeirotypus, Naatlo,* and *Theridiosoma* (Figures 45, 69, 157). In that respect, *Plato* is more similar to *Epilineutes* (Figure 192). Moreover, *Epilineutes* and *Plato* often sit at the periphery of their webs exerting noticeable tension on a radial line. *Plato* is more similar to *Epeirotypus* in that they construct numerous closely spaced non-sticky spiral loops during frame and radius construction, whereas in *Theridiosoma* and *Epilineutes* the ratio of frames and/or radii constructed during non-sticky spiral construction is much higher (see Coddington (in press) for definitions and descriptions of these behaviors). Outgroup comparison to very primitive orb weavers (Dinopidae, Uloboridae) indicates that a low ratio is primitive, but more closely related taxa (Anapidae, Mysmenidae) have as high a ratio as theridiosomatines.

The taxonomic affinity of *Chthonos,* of course, has always been controversial, but *Chthonos* is without doubt a theridiosomatid by palp and epigynal characters. *Chthonos* are specialized spiders that do not spin webs, and their body form (Figures 33, 34) certainly differs from that of *Plato* (Figures 14, 23). Female genitalia of both genera are very similar, but the similarities are all primitive features of the family in general.

EPEIROTYPINAE.—This subfamily includes *Epeirotypus* and *Naatlo.* Four derived features define the group. First, the median apophysis is a round, notched disk in both genera, unique among theridiosomatids (Figures 42, 70). Symphytognathoids lack median apophyses altogether. Second, the paracymbium of both genera is a flat, blade-like apophysis, broadly attached to the cymbium (Figures 53, 72). Other theridiosomatid paracymbia are T-shaped (see above) or else rounded hooks. Third, the epigynum in both genera is a convex bulging dome, whose posterior margin is closely appressed to the abdominal ventral wall (Figures 50, 58, 85). The epigyna of other theridiosomatids and symphytognathoids are usually flat plates (or occasionally concave in lateral view), rather different from *Epeirotypus* and *Naatlo.* Fourth, the tegula are much expanded on their lateral faces (Figures 54, 65, 83).

The female genitalia also provide synapomorphic features, probably related functionally to the proportions of the palpi in the males. The route of the copulatory ducts is short, and they make a simple acute turn. The distinction between copulatory bursae and ducts is not marked. Details of surface structure and pigmentation, difficult to illustrate, are also very similar in the two genera.

Behavioral features also support the monophyly of Epeirotypinae. The webs of *Epeirotypus* and *Naatlo* are qualitatively indistinguishable, having many radii, no radial anastomosis, and hubs with two or more persistent hub loops (Figures 67, 69). I have not seen *Naatlo* species build, but in *Epeirotypus* these loops are always added after sticky spiral construction. Finally, members of both genera have tension lines that they use to distort their webs into cones (Figures 66, 69). The large number of radii must increase the force required to distort the web; *Naatlo* and

Epeirotypus species have short, thick legs and "shoulders" on the carapace (Figures 46, 48, 77, 86), presumably because of the increased mechanical advantage provided and because of the muscle mass required to reel in the tension lines. The latter two features also occur in those *Theridiosoma* species that distort their webs excessively. A large number of radii is of course characteristic of symphytognathoids.

OGULNIINAE.—The subfamily includes the single genus *Ogulnius*. It is placed in its own subfamily because they are peculiar spiders quite different from other theridiosomatids in body form and web architecture. *Ogulnius* might have been included in Theridiosomatinae, but placing it in its own subfamily makes each subfamily biologically and morphologically more homogeneous; a single subfamily, although monophyletic, would be heterogeneous and would complicate discussions of theridiosomatid biology. *Ogulnius* is also a large and diverse genus; placing it in its own subfamily anticipates the advisability of splitting the genus into more manageable units at some time in the future. Synapomorphies defining the genus are listed in the systematic section.

No known species of *Ogulnius* spin complete orbs, merely rudimentary networks of non-sticky silk with often very short lengths of sticky silk haphazardly draped across them (Figures 103, 105). Outgroup comparison with all other theridiosomatid genera suggests that the absence of a complete orb is due to secondary loss, and that implication is confirmed by behavioral studies (Coddington, unpubl. data).

THERIDIOSOMATINAE.—This subfamily, including *Baalzebub, Epilineutes, Theridiosoma,* and *Wendilgarda,* is monophyletic by numerous characters. First, the palp has rows or groups of denticles on the tegular surface beneath the conductor (Figures 130, 197), which are absent in other theridiosomatid genera. Second, a row of short, regular bristles occurs on the cymbium at its junction with the cymbial lamella (Figures 153, 186, 211), also absent in other theridiosomatids. Third, the female epigyna are provided with a pair of pits on the lateral parts of the epigynal plate (Figures 151, 173, 213, but absent in *Baalzebub*). These pits are difficult to see except via compound microscopy of mounted epigyna.

Fourth, the median apophysis in all cases is somewhat elongate and has a trough or groove along its upper surface (Figures 134, 163, 189, 196). In *Baalzebub, Epilineutes,* and *Wendilgarda* the groove is deeper, whereas in *Theridiosoma* the groove is shallow and the median apophysis itself less rectangular and more attenuate. Fifth, the junction of the reservoir and the fundus is rugose or perhaps dentate. This feature of course can only be seen on cleared material with compound microscopy, but thus far it is believed to be unique to these three genera. Sixth, the copulatory ducts insert on the spermathecae mesally (Figures 145, 174, 215), not laterally or ventrally as in other theridiosomatid genera. Seventh and eighth, the course of the reservoir in the tegulum has two additional complexities, termed "switchback 2" and "switchback 3" in Figure 1, which are unique to these genera. Last, the eggsacs are singly, not doubly attached, and close examination of the distal tip of eggsacs indicates that these sacs are not doubly attached when they are constructed, because they lack any trace of the second attachment line (see above for more explanation). These inferences have been confirmed by observation of eggsac construction in *Epilineutes globous, Theridiosoma gemmosum,* and several other undescribed *Epilineutes* and *Theridiosoma* species.

Ogulniinae and Theridiosomatinae are sister taxa. They share an embolic apophysis mesal to the embolus proper (Figures 101, 117, 162, 190, 198), a basal, not distal, opening of the ejaculatory duct (Figure 100), and the embolus itself is short and tubular ending in a spatulate lamina, not a long, heavily sclerotized blade as in Platoninae and Epeirotypinae. In addition the copulatory ducts in the females are more convoluted than the simple turns in the latter two subfamilies.

Four characters support the monophyly of

Baalzebub, Epilineutes, and *Wendilgarda.* They all have wrinkled, plicate copulatory bursae (Figure 174, not detailed in Figures 184, 215) with lateral wings (Figures 174, 184, 215). The embolic division is divided into short, blunt elements (Figures 162, 190, 198). The median apophysis has a broad, deep trough (Figures 163, 189, 196).

Wendilgarda and *Epilineutes* are sister taxa by the epigynal scape (Figures 173, 213), the subrectangular form of the median apophysis (Figures 189, 196), the denticles on its distal surface (barely visible in Figure 197), and a distal brown stripe on the conductor, apparently the result of sclerotized thickening of that region. *Baalzebub* lacks the derived features uniting *Wendilgarda* and *Epilineutes* and thus is the sister group to that pair of taxa.

Wendilgarda make derived webs no longer resembling orbs (Figure 202, Coddington and Valerio, 1980), but those of *Epilineutes* (Figure 194) and all *Theridiosoma* species (Figures 157, 159) are rather conventional, with few radii, a widely spaced sticky spiral, and radial anastomosis. The building behavior of *Epilineutes* resembles that of *Theridiosoma* species. Like *Epeirotypus* the latter taxa also construct hub loops after sticky spiral construction, but the ensuing process of radial anastomosis usually destroys all traces of the added hub loops. *Baalzebub* webs have a single persistent hub loop in the web (Figures 165, 167, 168), and radial anastomosis is absent, but that absence is probably due to secondary loss.

Despite the relatively straightforward cladistic structure explained above, the data do not resolve the inter-relationships of Platoninae, Epeirotypinae, and Ogulniinae-Theridiosomatinae, although possible solutions are restricted to three, rather than 15 possibilities, because of the monophyly of Ogulniinae and Theridiosomatinae.

With respect to that unresolved three-taxon problem, the evidence of individual characters is often straightforward—for example, *Plato* and all ogulniine-theridiosomatines have a cymbial lamella adjacent to the paracymbium, as well as a very small rod or tube in the wall of the reservoir, but, discordantly, the subtegulum in *Plato* and epeirotypines is transparent over the region of the subtegulum. This character may also occur in other genera, but its appearance seems to depend on how long the specimen has been preserved. If further study invalidates the transparent subtegulum as a reliable character, the trichotomy could well resolve in favor of (Epeirotypinae (Platoninae (Ogulniinae, Theridiosomatinae))), a solution supported by the presence of radial anastomosis in *Plato* and Theridiosomatinae. On the other hand, the form of the cymbial lamella in *Plato* (a vestige of it may exist in *Chthonos,* although the character is not coded as present in Figure 1) does differ from that in Ogulniinae-Theridiosomatinae. To repudiate the possibility of homology between the structures would nevertheless be disingenuous.

The few characters linking *Chthonos* and *Ogulnius* are convergences, for example, the papillate and truncate sternum. Spiders of these genera are some of the smallest and most heavily sclerotized theridiosomatids. Neither sternum character is reinforced by evidence from any other independent character system. Likewise the presence of a uniform pigment layer (i.e., no abdominal or cephalothoracic "pattern") in *Plato* and *Wendilgarda* is also probably convergent. Species of other genera are often brightly and characteristically marked. *Plato* species usually live in caves, and the lack of abdominal pattern may reflect their troglophilic habit, but that explanation does not explain the lack of pattern in the strictly epigean *Wendilgarda.*

The epigyna of Platoninae, Epeirotypinae, and Ogulniinae have a distinct transverse groove (Figures 25, 37, 50, 78, 124). Probably the male median apophysis engages this groove during mating, although that might be the role of the paracymbium instead. If the former possibility, the presence of a scape and the absence of such a groove in most theridiosomatines becomes intelligible, because the female epigynal scape (functionally defined) in spiders usually engages the male median apophysis. That explanation does not account for the absence of either scape or groove in *Theridiosoma,* however. Symphytognathoids lack scapes (except, perhaps, *Mysmena*), grooves, and median apophyses. Either the epigynal groove is a primitive feature of theridiosomatids lost in the more derived genera (gained once, lost once), or it is convergent in *Ogulnius* and the Platoninae-Epeirotypinae (gained twice). Enough variability in the form and extent of the epigynal groove exists to preclude confidence in either of these resolutions. The epigynal groove character is the major evidence supporting a sister group relationship between Platoninae and Epeirotypinae, one possible resolution of the trichotomy in Figure 1.

Finally, both Epeirotypinae and Theridiosomatinae have the tip of the mesal arm of the tegulum produced into a spur (Figures 43, 70, 133, 187, 197). *Ogulnius* lacks such a lobe or spur altogether, but, as pointed out above, *Ogulnius* is substantially autapomorphic. This tegular spur is the major evidence speaking against a sister group relationship between Platoninae and Ogulniinae-Theridiosomatinae.

In summary, the phylogenetic analysis of the family has identified seven components defining monophyletic groups, each supported by the evidence of several characters, but it fails to resolve a single, and crucial, three-taxon problem—the relationships of Platoninae, Epeirotypinae, and Ogulniinae-Theridiosomatinae. On the whole the behavioral data are as equivocal as the morphological data. Certainly the two classic features of theridiosomatid webs, radial anastomosis and the use of a tension line, do not unambiguously define subsidiary monophyletic groups within the family. Given this discordance in both behavior and morphology, it seems wiser to represent the cladistic relationships among the various lineages of the family as unresolved. Perhaps closer study of each genus in turn will reveal the solution. I identified this recalcitrant cladistic problem early in the study of the family and repeatedly tried to solve it by restudying discordant characters and gathering more information. In the former case, I either confirmed the initial coding of characters or, as in the case of the homology of the cymbial lamellae of Platoninae and Ogulniinae-Theridiosomatinae, I could reach no confident resolution of the conflict. Additional samples of information, surprisingly, yielded further sets of discordant characters in about equal numbers, thus implying that the trichotomy is, in some sense, a "parametric" representation of relationship. Should the trichotomy persist, reconstructions of character evolution in the family will have to be considered from the point of view of each of three possible trees.

THERIDIOSOMATIDAE Simon

THERIDIOSOMATINI Simon, 1881:24 [type genus by monotypy *Theridiosoma* O. Pickard-Cambridge, 1879].

ACTINAE McCook, 1889a:180; 1889b:195 [type genus *Actis* McCook, 1889a:180; genus name proposed and synonymized with *Theridiosoma* in same publication].

THERIDIOSOMATEAE.—Simon, 1895:913.

THERIDIOSOMATINAE.—F.O. Pickard-Cambridge, 1902: 412.—Roewer, 1942:967.—Bonnet, 1959:4435.

THERIDIOSOMATIDAE.—Vellard, 1924:132.

NOTE.—The genus name *Actis,* and the family group name Actinae based on it, are not listed in Bonnet (1959), Roewer (1942), or Brignoli (1983). McCook (1889a) is a record of the proceedings of a meeting of the Philadelphia Academy of Natural Sciences at which McCook spoke and proposed the names (with McCook listed as author of the publication). It seems that McCook (1889a) does fulfill the criteria for valid publication and availablity (ICZN, articles 8, 11, 12, 16), and thus ought to be listed in the above synonymy. McCook (1889a) did state that *Actis* was a synonym of *Theridiosoma,* but he continued to use the family group name Actinae; e.g., in McCook (1889b), a usage conflicting with the requirement that any family group name, when first proposed, must be based on a valid genus group name. As far as I know, however, neither name was ever used subsequently by another author writing about spiders.

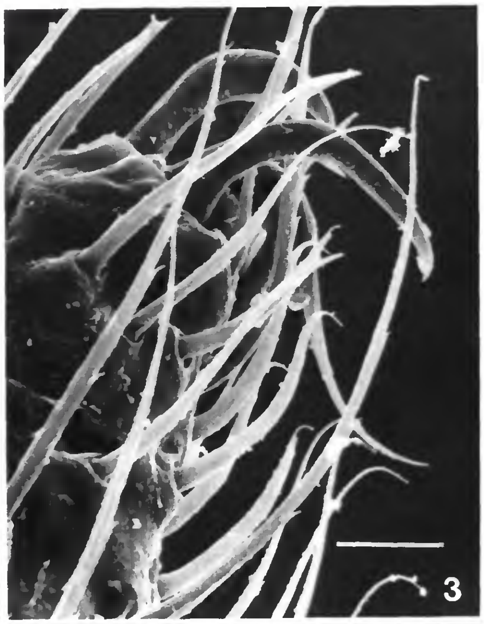
DIAGNOSIS.—Theridiosomatids can be distinguished from all other spiders by the presence of pits on the prolateral margins of the sternum in both sexes (Figure 140, but absent in *Chthonos,* see below), the conformation of the bulb and route of the reservoir of the male palp (e.g., Figures 30, 115, 148, and see above discussion), and the connate spermathecae (e.g., Figure 113). The 4th tibial dorsal trichobothria (Figure 141), which are usually 2 to 4 times longer than the tibial diameter, also diagnose the family but are comparatively short in *Wendilgarda.*

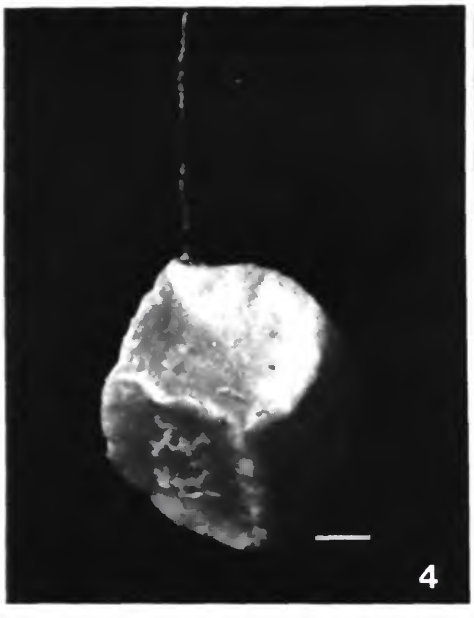
DESCRIPTION.—Small ecribellate, colulate, entelegyne spiders of superfamily Araneoidea. Total length 0.5 to 3.0 mm (usually less than 2.5 mm). Eight subequal eyes in two rows, laterals juxtaposed, AME separation ½ to 1 diameter, PME separation up to twice their diameter or juxtaposed (Figures 111 vs. 172). Laterals separated from medians by about their diameters. Secondary eyes with full canoe tapeta. Seen from above, posterior row straight or procurved (Figure 142), anterior row recurved. AME and sometimes ALE, PLE on slight tubercles in adult males. Clypeus height variable, usually more than 3⁄2 AME diameter. Carapace glabrous (or with few scattered bristles), pear-shaped, length and width subequal, cephalic region frequently elevated (Figure 175). Chelicerae robust, no known stridulatory surfaces; wide range in tooth size in individual animals, from tiny denticles in fang furrow (Figure 2) to larger, often bicuspid teeth irregularly distributed—not usually two simple rows. Endites wider distally, inclined over labium. Labium indistinctly rebordered, wider than long, sternal suture usually distinct. Sternum about as long as wide, smooth or papillate, sparsely bristled; margin smooth or slightly incised, occasionally sharply truncate or even indented behind.

Legs in order of length 1-2-4-3 (4-1-2-3 in *Ogulnius*), of variable proportions, short and thick in *Epeirotypus, Naatlo,* and *Ogulnius* (Figures 48, 77, 109), longer and more slender in *Plato, Epilineutes,* and *Wendilgarda* (Figures 16, 171, 205), intermediate in *Theridiosoma* and *Baalzebub* (Figures 141, 181). Femur diameter ⅓ carapace width in some genera (*Epeirotypus, Naatlo*). Legs of adult males proportionately longer and more slender than in conspecific females. Macrosetae slender, serrate. Irregular group of serrate setae on ventral tarsi, especially fourth, variably developed. Trichobothria grouped on tibiae and single on proximal surface of metatarsi (none on metatarsus IV or femora). Third and fourth tibiae with trichobothria in 3 or 4 rows, much longer than tibial diameter (Figures 77, 141, 181). Lateral claws with 0–3 slight teeth basally, median claw prolonged beyond lateral claw tips, attenuate, and recurved at tip (Figure 3). Female palp without claw.

Abdomen smoothly ovoid (e.g., Figure 169) or with variously placed tubercles (Figures 34, 47, 121) sparsely bristled, usually soft (leathery in *Chthonos*), without scuta, usually higher than long or wide (distance from pedicel to spinnerets very short), attached near its middle to cephalothorax, and to a greater or lesser extent overhanging cephalothorax. Color uniform or with transverse silvery or white bands, or mottled blotches sometimes merging to chevrons posteriorly. Respiratory system diversity largely unknown (see Lamy (1902) for *Theridiosoma gemmosum*), but booklung covers and single median spiracle just anterior to colulus always present. Colulus relatively large, fleshy, bristled. Spinnerets with 16 large spigots and numerous smaller spigots as in most araneoids (Mikulska, 1966; Wasowska, 1966, 1970; Kovoor, 1972). Anterior spinneret in adult females (at least in *Theridiosoma gemmosum*) with single major ampullate and numerous piriform gland spigots (Figure 7); median with minor ampullate, one cylindrical, and several aciniform spigots (Figure 8), posterior with two aggregate, one flagelliform, two cylindrical, and several aciniform gland spigots (Figure 9). (The assignment of gland types to the external morphology illustrated in Figures 6–9 is based on literature descriptions and has not been verified histologically.)

Epigynum usually a flat or domed, sclerotized plate, plate often with central pit (Figure 37) rarely with scape protruding from beneath posterior margin (Figures 173, 206). Copulatory



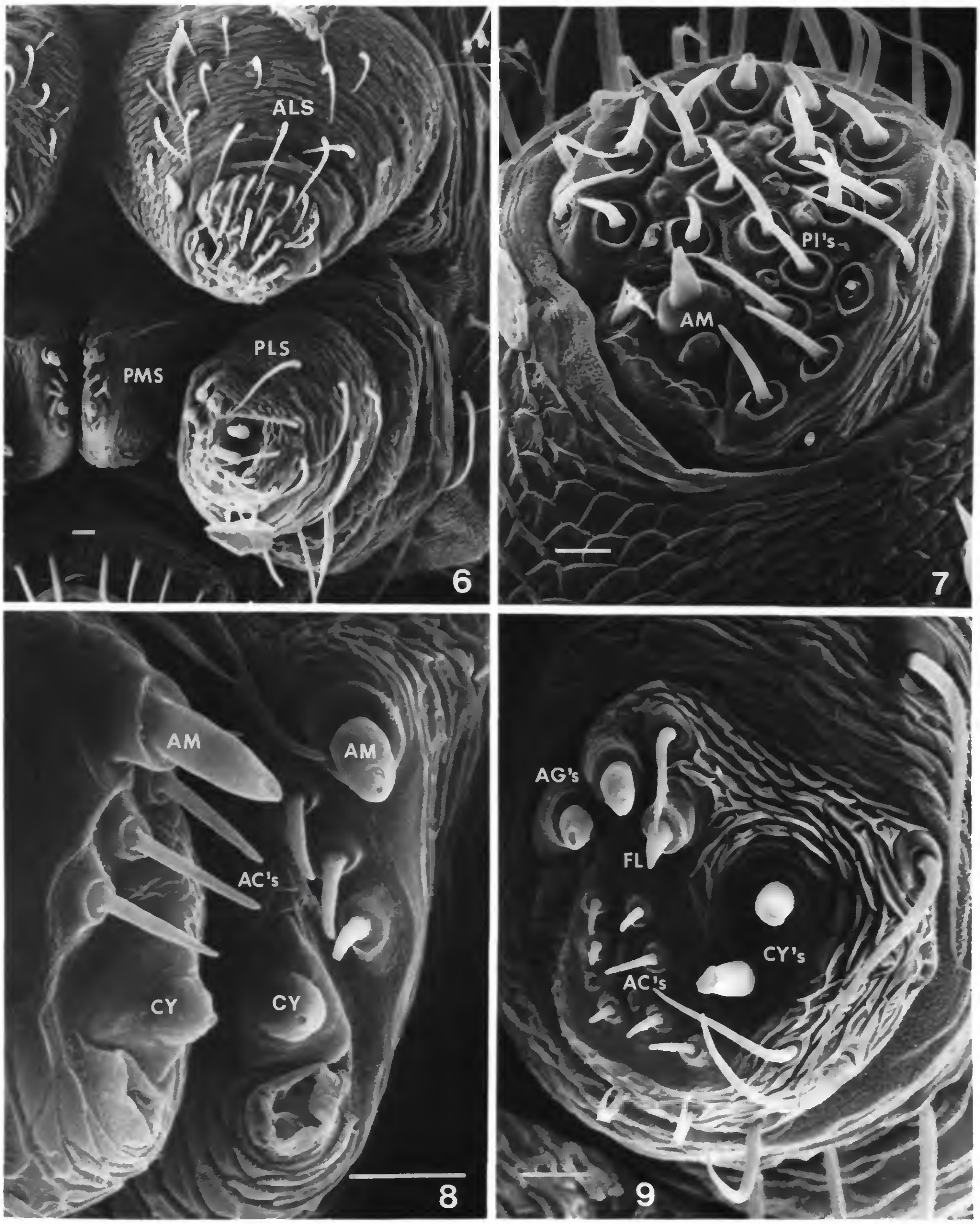


FIGURES 2, 3.—*Ogulnius gloriae* from Puerto Rico: 2, cheliceral denticles on left chelicera, retrolateral; 3, elongate median claw.

FIGURE 4.—Cubical eggsac from Guatemala, IZABAL (not associated with any specimen, possibly made by *Chthonos*). Note opening on lower left facet.

FIGURE 5.—Mating in *Wendilgarda clara* from Puerto Rico; note reflected epigynal plate of female.

Scale lines: 2, 3, 10 μm; 4, 1 mm; 5, 0.5 mm.



FIGURES 6–9.—*Theridiosoma gemmosum* (L. Koch) from Alabama, spinnerets: 6, left spinning field; 7, left anterior lateral spinneret; 8, left posterior median spinnerets; 9, left posterior lateral spinneret.
Scale lines: 10 μm.

bursae well developed (Figure 207); ducts initially capacious, lightly sclerotized, abruptly narrowing just before junction with spermathecae (Figure 26). Coiling of ducts simple (Figure 26) or convoluted (Figure 215). One pair of spermathecae, always juxtaposed, connate (thus sharing median wall, e.g., Figure 20), short fertilization ducts exit from spermathecae laterally (Figure 95). Wall of copulatory ducts adjacent to spermathecae often heavily sclerotized in narrow band (Figure 20).

Male palp with T- or hook-shaped paracymbium (Figures 32, 164), sometimes with additional cymbial lamella (Figure 211), and with basal hematodocha, subtegulum (containing fundus), median hematodocha, and tegulum bearing median apophysis, conductor, and embolus, always in consistent configuration or conformation with respect to one another (e.g., Figure 10). Conductor usually thin, translucent plate more or less covering embolic division. Conductor with small hematodocha on lateral side. Embolus a single, long, robust sclerite (Figure 43) or short tube with variously modified mesal apophysis, herein termed "embolic apophysis" (Figures 100, 131).

NATURAL HISTORY.—Theridiosomatids live almost exclusively in wet or humid, shaded forest habitats. *Plato* is troglophilic, and *Theridiosoma* also is common around cave entrances. All species seem to prefer dark situations.

Web form is diverse, ranging from complete orbs (*Epeirotypus, Naatlo, Baalzebub,* Figures 67, 69, 165), through forms with anastomosed radii (*Plato, Theridiosoma, Epilineutes,* Figures 159, 194), to sparse networks (*Ogulnius, Wendilgarda,* Figures 105, 202), or none (*Chthonos*). The spacing of the sticky spiral is nearly always greater than the body length of the spider (e.g., Figures 105, 192), thus contrasting with that of most other orb-weaving spiders. The web commonly has a line more or less at right angles to the plane of the web, herein termed the "tension line," which the spider reels in to distort the web into a conical form (Figures 45, 66, 157). The occurrence of tension lines throughout the family is sporadic (e.g., present in some *Epilineutes,* all *Theridiosoma, Naatlo,* and *Epeirotypus;* absent in *Baalzebub, Ogulnius, Wendilgarda,* and, reportedly, in *Plato*). Species that distort their webs via tension lines do so by gripping the hub region of the web with their hind four legs and reeling in the tension line with their first four legs. Theridiosomatids consequently have robust anterior legs. The slack of the tension line is either held beneath the spider by the pedipalps or, rarely, piled on top of the eye group. If the plane of the web is perpendicular to the ground, the spider usually tenses the web parallel to the ground (thus normal to the web plane), and in most cases sits dorsal side up at the hub when the web is tensed. The distorted position of the web represents a "prey-ready" posture for the spider. Individuals maintain the posture for hours at a time, and most impacts of prey on the web surface occur with the web in a tensed position. Casual observations of *Epeirotypus chavarria* suggest that this species, at least, responds less rapidly to prey vibrations if the impact occurs on a planar as opposed to a distorted web. Also, the actual force in the tension line appears to vary from 50 to 300 dynes (roughly equivalent to masses of 50 to 300 mg). Theridiosomatids weigh no more than 3 mg, so they are exerting considerable force to tense their webs. The tension is all the more surprising because no morphological structure that could ease the energetic cost of this activity has been found (for example, a cuticular catch mechanism at the femoral-trochanteral joint). Webs typically occur near ground in low vegetation or leaf litter.

Eggsacs are diverse (Figures 4?, 68, 104, 106, 193, 200, 201): usually characteristic of genera, either papery or covered with flocculent silk; often retained near the web hub; cubical, spheroidal, pear-shaped, or fluted; with or without caps or sutures at the proximal tip; and suspended from substrate by a long thread. No deliberate investigation of eggsac contents was undertaken, but Wiehle (1931) examined 15 sacs that each contained 20–35 eggs. Some small *Ogulnius* lay as few as 4 eggs per sac.

Prey, as far as known, is primarily nematocerous Diptera or other similarly weak-flying insects. The family may specialize on this prey type.

Males do not spin webs equipped with sticky silk (*Wendilgarda clara* is an exception, pers. obs.), but frequently they do spin the non-sticky scaffolding of the web, complete with frames, radii, hub loops, and, if characteristic of the species, tension lines. Males are also found "attending" females, i.e., on sparse silk networks juxtaposed and often attached to the web of the female. The nearly ubiquitous presence of "plugs" in the copulatory bursae of females indicates that they mate almost immediately after the final molt.

Mating has been described only for *Theridiosoma gemmosum* (Gerhardt, 1933). Other genera (*Epeirotypus, Wendilgarda,* pers. obs.) seem to follow the same general pattern and sequence of behaviors. In at least the genus *Epeirotypus,* a muscle extends from the epigynal plate to the region of the pedicel, presumably enabling the female to reflect the posterior margin of the epigynal vault during mating (see Figure 5). Interestingly, no muscle that would serve as an adductor to clamp or close the epigynal opening seems to be present.

SPECIES.—Number of species in the family is largely unknown. *Chthonos* and *Plato* are least collected, the former because it is nocturnal and does not spin a web, the latter because it seems to live only in caves or cave-like situations. Probably many more neotropical species of both genera await discovery. *Ogulnius* and *Theridiosoma* are the largest genera, both in terms of described and undescribed species.

Wendilgarda assamensis Fage, 1924, is incertae sedis. It is a theridiosomatid, but, as Brignoli (1981) pointed out, it has little to do with *Wendilgarda*. It does not even share the synapomorphies of Theridiosomatinae, but rather resembles some *Plato* species. *Wendilgarda assamensis* does not fit any of the generic diagnoses and, cladistically, would be placed at the bottom node of the cladogram in Figure 1. Rather than erect a new genus, it seems sensible to let the problem lie until more material is in hand.

RANGE.—Chiefly cosmotropical. At present *Chthonos, Epilineutes,* and *Plato* are restricted to the Neotropics, the other genera occurring in both the Old and New World Tropics. Few species reach the cold temperate regions (*T. gemmosum* in Europe and North America, *T. epeiroides* in Korea and/or Japan). Theridiosomatids are apparently absent from western North America.

Key to the Genera of Theridiosomatidae

1. First and second tibiae, metatarsi, and tarsi with prolateral row of evenly spaced, long, strong macrosetae [Figure 33] .... ***Chthonos***
   First and second legs without prolateral row of macrosetae 2
2. Fourth legs longer than first or, in males, subequal ....***Ogulnius***
   First legs longer than fourth 3
3. Legs relatively short and thick [Figures 48, 77] 4
   Legs long and slender [Figures 16, 141, 171, 181, 205] 5
4. Epigynum with closely fitting, anteriorly hinged flap covering copulatory bursae [Figures 78, 88, 93]; male with striated embolus; tip of embolus blunt, rounded, sawtoothed [Figures 70, 71, 73, 97] .... ***Naatlo***
   Epigynum a domed vault, hind rim appressed to venter [Figures 50, 58]; embolus smooth, tip acute [Figures 42, 43] .... ***Epeirotypus***
5. PME separation 1 diameter or more [Figures 17, 208] 6
   PME separation ½ diameter or less [Figures 142, 172, 182] 7
6. Scape protruding from beneath entire (not notched) posterior epigynal

margin [Figures 206, 213, 219]; palp embolic division with mesal bristle protruding from beneath conductor [Figures 198, 217] (short in *mexicana* only) .... ***Wendilgarda***

Epigynum without scape, usually a blunt knob on a plate with a transverse groove [Figures 18, 23]; conductor with ventral apophysis [Figures 11, 22] .... ***Plato***

7. Posterior epigynal rim blunt, not pointed [Figures 143, 151], not a protruding scape; embolic division fragmented into bristle-like parts, not blunt lobes; median apophysis attenuate, slightly grooved [Figures 132, 134] .... ***Theridiosoma***

Epigynum either triangular [Figures 183] or flat, medially indented plate with short scape protruding [Figure 173]; median apophysis small [Figure 163] or subrectangular in outline [Figure 188], grooved in either case 8

8. Epigynal plate triangular [Figure 183]; median apophysis small but deeply cleft [Figure 163] .... ***Baalzebub***

Epigynum a medially indented plate with apiculate or blunt scape protruding [Figure 173]; median apophysis with dorsal spur [Figure 189] .... ***Epilineutes***

PLATONINAE, new subfamily

DIAGNOSIS.—The subfamily contains the genera *Plato* and *Chthonos*. The following derived features define it: paracymbium a T-shaped lobe (Figures 12, 32), cymbium and distal alveolus margin pointed or bifid median; apophysis with a long, recurved tip; conductor with a thick ventral apophysis (Figures 10, 29).

Platoninae may be distinguished from Epeirotypinae by having slender, proportionately longer legs (Figures 16, 33, vs. 48, 77), less-compact body form, and proportionately smaller male palpi. The subfamily is distinguished from Ogulniinae by the absence of an embolic apophysis encircling the male palpal bulb, and larger body size, and from Theridiosomatinae by the simple embolic division and grooved posterior epigynal margin.

Plato, new genus

TYPE-SPECIES.—*Plato troglodita*, new species (see below).

ETYMOLOGY.—The genus name is masculine and honors the Greek philosopher in referring to the strikingly cubical egg sacs that characterize the genus, as well as their partiality for caves.

DIAGNOSIS.—Members of the genus *Plato* are distinguished from other theridiosomatids by the following combination of characters: fleshy spurs extending from the lateral margins of the epigynal opening toward the midline (Figures 19, 26), notches on the distal, mesal margin of the cymbium (Figure 10), cubical eggsacs suspended by a long thread from one vertex (Figure 13, but see Figure 4 and remarks under *Chthonos*), and a strongly curved ventral apophysis on the conductor (Figure 11). The genus *Chthonos* has a ventral apophysis, but it is shorter and blunt. *Plato* lacks the strong spines on legs I and II that characterize *Chthonos*. In addition, the embolus tip in *Plato* has a thin, spine-like projection on the side nearest the conductor (Figures 10, 27).

DESCRIPTION.—Carapace rather low for a theridiosomatid (Figures 14, 24), pale tan head region not especially elevated. Clypeus 3 times AME diameter. Eyes subequal or laterals very slightly smaller, AME separated by ½ their diameter, PME separation at least their diameter. Sternum tan or slightly darker, as wide as long, convex, rounded behind. Legs long and slender, tarsi-metatarsi shorter than tibiae-patellae, pale tan, no annulations. Abdomen ovoid, higher than long or wide, sparsely setose, of uniform color, whitish gray or tan. Abdominal muscle apodemes not visible.

Conductor of male palp less extensive than in more derived genera, barely covering embolus in contracted palp (Figure 11). Median apophysis variable, basically a lobe tapering distally, frequently bifid, with recurved tip (Figure 10). Embolus single strong sclerite, duct opening distal.

NATURAL HISTORY.—Very little is known. All species known to date live in caves or other dark places but do not seem to have marked troglobitic modifications. The webs of *P. bruneti, P. guacharo, P. miranda* (pers. obs.), and an undescribed species from Colombia (W.G. Eberhard, pers. comm.) are loose orbs with anastomosed radii and no tension line, rather like those of *Epilineutes* (Figures 192, 194).

SPECIES.—As Brignoli (1974) noticed, the species he described (1972a) in the genus *Wendilgarda* (*miranda* and *guacharo*) are closely related to *Maymena bruneti* Gertsch, 1960; all three species are here transferred to *Plato* (*Plato bruneti*, new combination, *Plato miranda*, new combination, *Plato guacharo*, new combination). In addition, *Wendilgarda bicolor* Keyserling has the fleshy lateral spurs on the posterior lip of the epigynal rim and therefore is also transferred to *Plato* (*Plato bicolor*, new combination). Other, as yet undescribed, species occur in the Neotropics.

RANGE.—At present the genus is exclusively neotropical; known from Trinidad, Venezuela, Colombia, Ecuador, and Brazil. (But see previous remarks about *W. assamensis*.)

Plato troglodita, new species

FIGURES 10–12, 23–28; MAP 1

TYPE.—♂ holotype from Ecuador, Morona-Santiago Province, Los Tayos (78°12′W, 3°06′S) in MCZ. Label states "24 July 1976, 78°12′W, 3°06′S, Los Tayos, #783. Clefts by dry stream bed by main cave entrance. 20.00." Collected by joint Ecuadorean-British Los Tayos Expedition.

ETYMOLOGY.—The specific name is a feminine noun in apposition and means "cave-dweller" in Spanish.

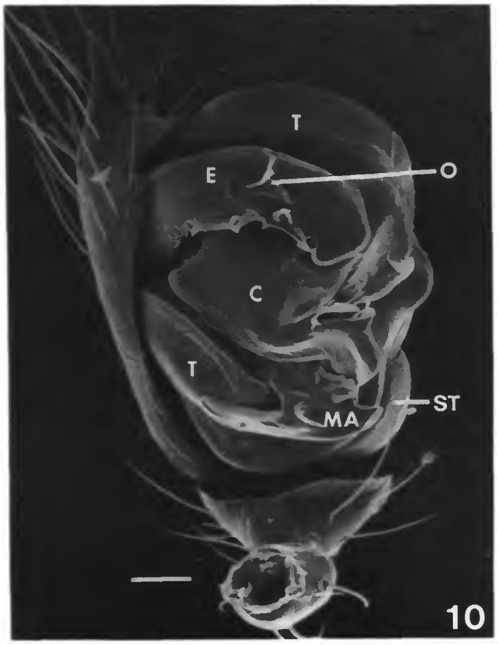
DIAGNOSIS.—*Plato troglodita* is distinguished from other *Plato* species in the female by the thick rounded epigynal rim with a deep central pit in the midline and the denticulate process just anterior to it (Figure 25), and in the male by the form of the median apophysis (Figure 11) and the tip of the embolus (Figure 10).

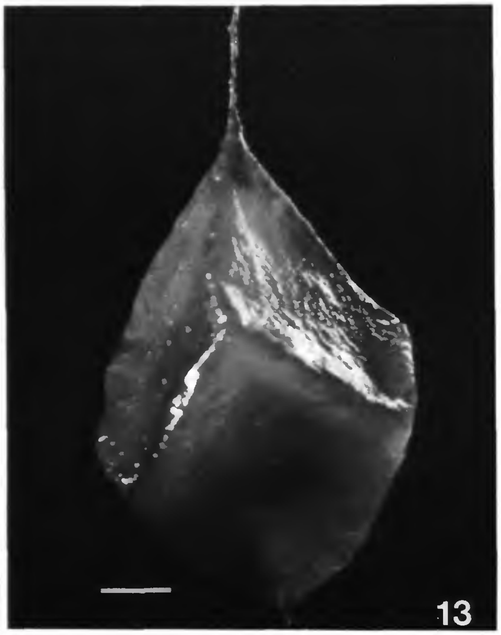
DESCRIPTION.—*Female:* Paratype collected with male holotype. Overall appearance as in *P. bruneti* (cf. Figures 14, 15). Total length 2.4 mm. Cephalothorax 1.03 mm long, 1.26 mm wide, 0.89 mm high. Sternum 0.65 mm long, 0.64 mm wide. Carapace, sternum uniform yellow tan. Abdomen 1.3 mm long, 1.3 mm wide, 1.7 mm high; whitish tan, smoothly ovoid, sparsely setose. AME slightly smaller than PME, AME separation ¾ their diameter, PME separation 1 diameter. ALE, PLE subequal, separated from AME, PME by ~1 diameter. Clypeus 3.3 times AME diameter. Legs yellow tan, more reddish distally. Epigynum a smooth plate with thick posterior rim, rim with deep fossa or pit in midline and denticulate ridge just anterior to it (Figure 25). Dorsal cleared view as in Figure 26.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	1.46	1.24	0.88	1.12
Patella	0.52	0.46	0.40	0.40
Tibia	1.14	0.93	0.65	0.77
Metatarsus	0.81	0.69	0.52	0.60
Tarsus	0.69	0.65	0.48	0.46
Total	4.62	3.97	2.93	3.35

Male: Paratype, specimen #582, from same locality as holotype. Similar in overall appearance to female, slightly smaller (Figures 23, 24). Total length 2.2 mm. Cephalothorax 0.95 mm wide, 1.00 mm long, 0.83 mm high. Sternum 0.52 mm wide, 0.53 mm long. Abdomen 1.3 mm wide, 1.2 mm long, 1.4 mm high. Clypeus 3.6 times AME diameter. Eye proportions and spacing as





FIGURES 10–12.—*Plato troglodita,* new species, from Ecuador, left male palp: 10, mesal, embolic division exposed; 11, ventral, embolic division enclosed; 12, lateral.
FIGURE 13.—*Plato bruneti* (Gertsch) from Trinidad, eggsac.
Scale lines: 100 μm, except 13, 1 mm.

in female, but AME projecting on a slight tubercle (Figure 24). Leg lengths proportionately longer than in female. Color of legs, carapace, sternum, and abdomen as in female. Palp as in Figures 10–12, 27, 28.

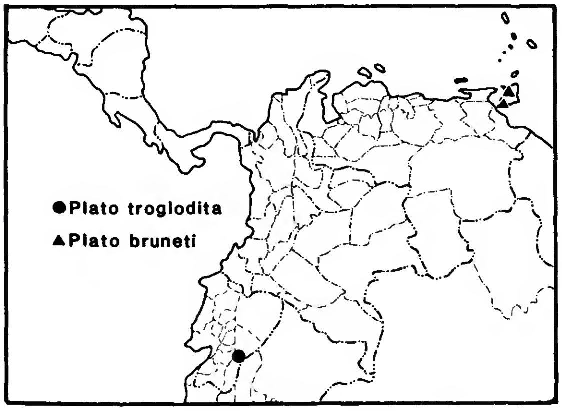
Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	1.34	1.17	0.86	0.98
Patella	0.45	0.43	0.34	0.34
Tibia	1.15	0.98	0.84	0.76
Metatarsus	0.83	0.69	0.52	0.52
Tarsus	0.62	0.57	0.46	0.45
Total	4.39	3.84	3.02	3.05

Variation.—Females (12 specimens) range in length from 2.2 mm to 3.1 mm, males (4 specimens) from 2.1 to 2.2 mm.

Natural History.—Mostly unknown. Label data indicate that the species occurs deep inside caves (e.g., 88 m from entrance in one instance or "bottom of main shaft" in another), as well as around the cave entrance. One label specified "in orb web with eggsacs." Eight cubical eggsacs were present in the type series, all with a fine point on the vertex opposite the suspension line indicating that during construction, at least, the sac is suspended at both ends.

Range.—Known only from the type-locality (Map 1). Los Tayos is the name of the cave system. It does not appear on any map of Ecuador available to me. The species occurs in at least 2 caves.



Map 1.—Distributions of *Plato troglodita*, new species, and *P. bruneti* (Gertsch).

Records.—ECUADOR. MORONA-SANTIAGO: Los Tayos caves, 7 vials from "main cave" at 78°12'W, 3°06'S, and 2 vials from "commando cave" at 78°12'W, 3°10'S; all vials with collection numbers, collected by joint Ecuadorean-British Los Tayos Expedition, deposited in MCZ.

***Plato bruneti* (Gertsch), new combination**

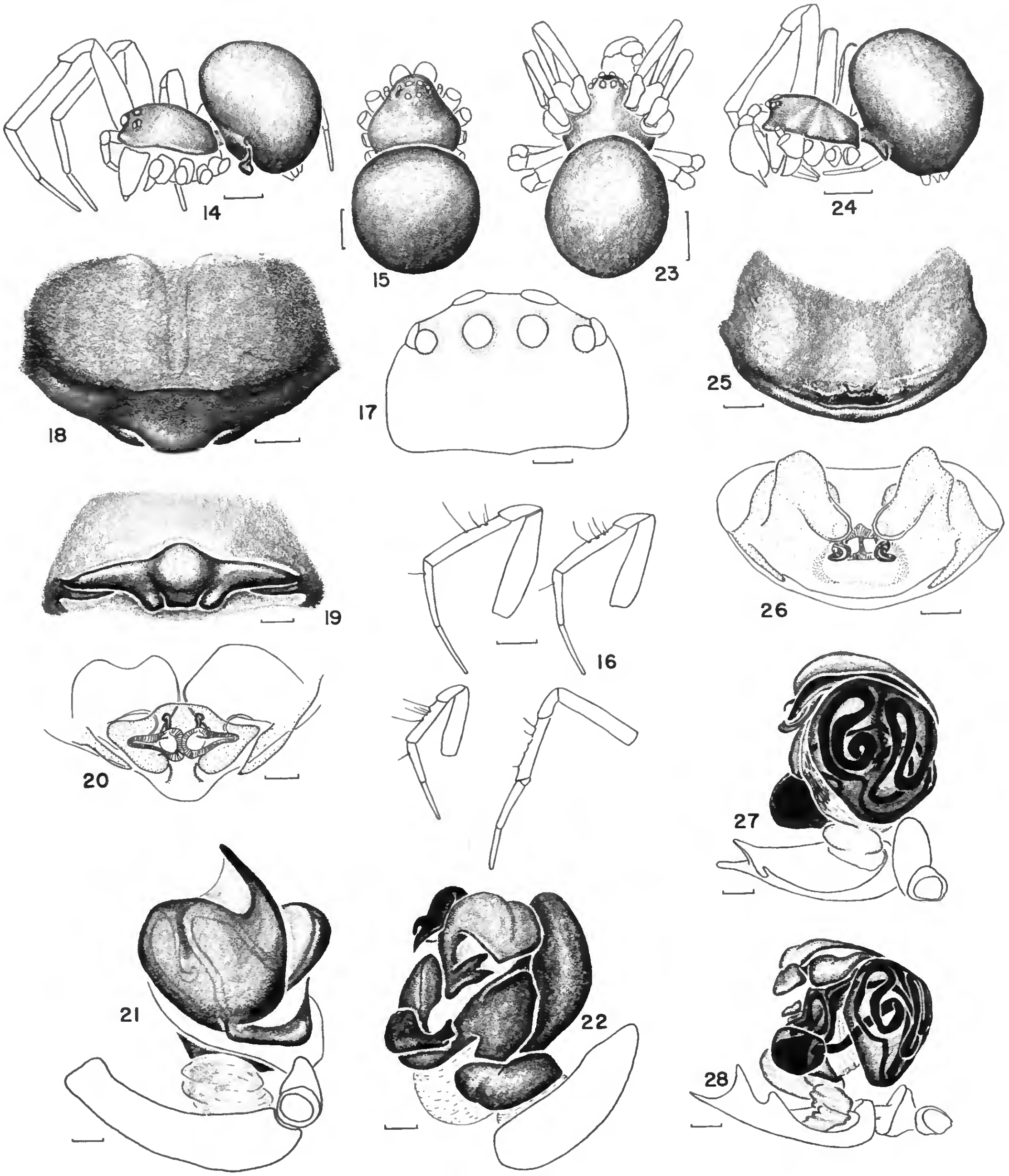
Figures 13–22; Map 1

Maymena bruneti Gertsch, 1960:37, figs. 65–67 [♀].—Brignoli, 1974:226; 1983:377 [♀ holotype from Trinidad, in AMNH, examined].

Note.—For evidence justifying the removal of *bruneti* from *Maymena* and its transfer to *Plato,* see above.

Diagnosis.—*P. bruneti* is distinguished from other *Plato* species by the distinctive epigynum, which presents a rounded tubercle on a transverse ridge in the female (Figure 18), and by the form of the median apophysis and the ventral conductor apophysis in the male (Figure 22).

Description.—*Female:* From Trinidad, ST. GEORGE, Simla. Total length 2.6 mm. Cephalothorax 1.17 mm long, 1.10 mm wide, 0.98 mm high. Sternum 0.65 mm long, 0.64 mm wide. Carapace, sternum, legs uniform tan. Abdomen 1.5 mm long, 1.5 mm wide, 1.8 mm high; grayish white, smoothly ovoid, dorsum covered with strong bristles. AME slightly larger than PME, AME separation ½ their diameter, PME separation 1 diameter (Figure 17). ALE, PLE subequal, separated from AME, PME by 1 diameter. Clypeus height 3 times AME diameter. Epigynum a smooth plate anteriorly, produced posteriorly into transverse ridge with protuberant rounded tubercle medially. In posterior view, dorsal margin of epigynal plate incised laterally, defining a medial lobe (Figure 19).



Figures 14–22.—*Plato bruneti* (Gertsch) from Trinidad. Female: 14, 15, habitus; 16, left legs; 17, eye group, frontal view; 18, epigynum, ventral; 19, same, posterior; 20, same, dorsal, cleared. Left male palp, expanded: 21, lateral; 22, mesal.

Figures 23–28.—*Plato troglodita,* new species, from Ecuador. Male: 23, 24, habitus; 25, epigynum, ventral; 26, same, dorsal, cleared. Left male palp, expanded: 27, lateral; 28, mesal.

Scale lines: 0.1 mm, except 14–16, 23–24, 0.5 mm.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	1.43	1.22	0.71	1.08
Patella	0.50	0.45	0.40	0.40
Tibia	1.17	0.98	0.69	0.86
Metatarsus	0.83	0.72	0.52	0.60
Tarsus	0.65	0.62	0.50	0.48
Total	4.58	3.99	2.82	3.42

Male: From Trinidad: ST. GEORGE, Arima Valley, Simla. Similar in overall appearance to female, slightly smaller. Total length wide, 1.08 mm long, 0.96 mm high. Sternum 0.55 mm wide, 0.57 mm long. Abdomen 1.3 mm wide, 1.5 mm long, 1.6 mm high. Clypeus 3.3 times AME diameter. Eye proportions and spacing as in female, but AME carried on an indistinct tubercle projecting slightly beyond clypeus. Leg lengths proportionately longer than in female. Color pattern of legs, carapace, sternum, and abdomen as in female. Palp as in Figures 21, 22.

Leg lengths of male described above (±0.03 mm).

	I	II	III	IV
Femur	1.38	1.32	0.86	0.98
Patella	0.45	0.43	0.34	0.31
Tibia	1.12	1.00	0.64	0.79
Metatarsus	0.89	0.86	0.69	0.58
Tarsus	0.55	0.53	0.31	0.45
Total	4.39	4.14	2.84	3.11

VARIATION.—At present only 7 females and 1 male are known. Females range in length from 2.6 to 2.7 mm.

NATURAL HISTORY.—Like other *Plato* species, *bruneti* is apparently a troglophile. All collections to date are from caves. The the eggsac has the characteristic cubical form of the genus (Figure 13). A small point on the opposite vertex from the suspension line of the eggsac indicates that during construction this end of the sac is also attached to supporting silk lines, as in *Ogulnius* and *Epeirotypus,* but later the lower attachment is cut.

RANGE.—Apparently endemic to Trinidad (Map 1).

RECORDS.—TRINIDAD. ST. GEORGE, Lopinot (East) Cave, 220445B, P.C.J. Brunet, no date (♀ type and paratypes, AMNH); Mt. El Cerro del Aripo, Cave #1 (670 m), P.C.J. Brunet, no date (♀, AMNH); Arima, cave nr jct. Simla Rd. and Blanchisseuse Rd., L.N. Sorkin, 23.vii.1979 (♀, AMNH); Arima Valley, Simla, J.G. and B.L. Rozen, 7.iii.1968 (♂, ♀, AMNH); Arima Valley, Simla, J. Rozen, 8.ii.1965 (eggsacs). ST. PATRICK, 2 mi south of Fullerton, U.S. Navy base (♀, AMNH).

Plato miranda (Brignoli), new combination

Wendilgarda miranda Brignoli, 1972a:375.

Plato guacharo (Brignoli), new combination

Wendilgarda guacharo Brignoli, 1972a:372.

Plato bicolor (Keyserling), new combination

Wendilgarda bicolor Keyserling, 1886:131.

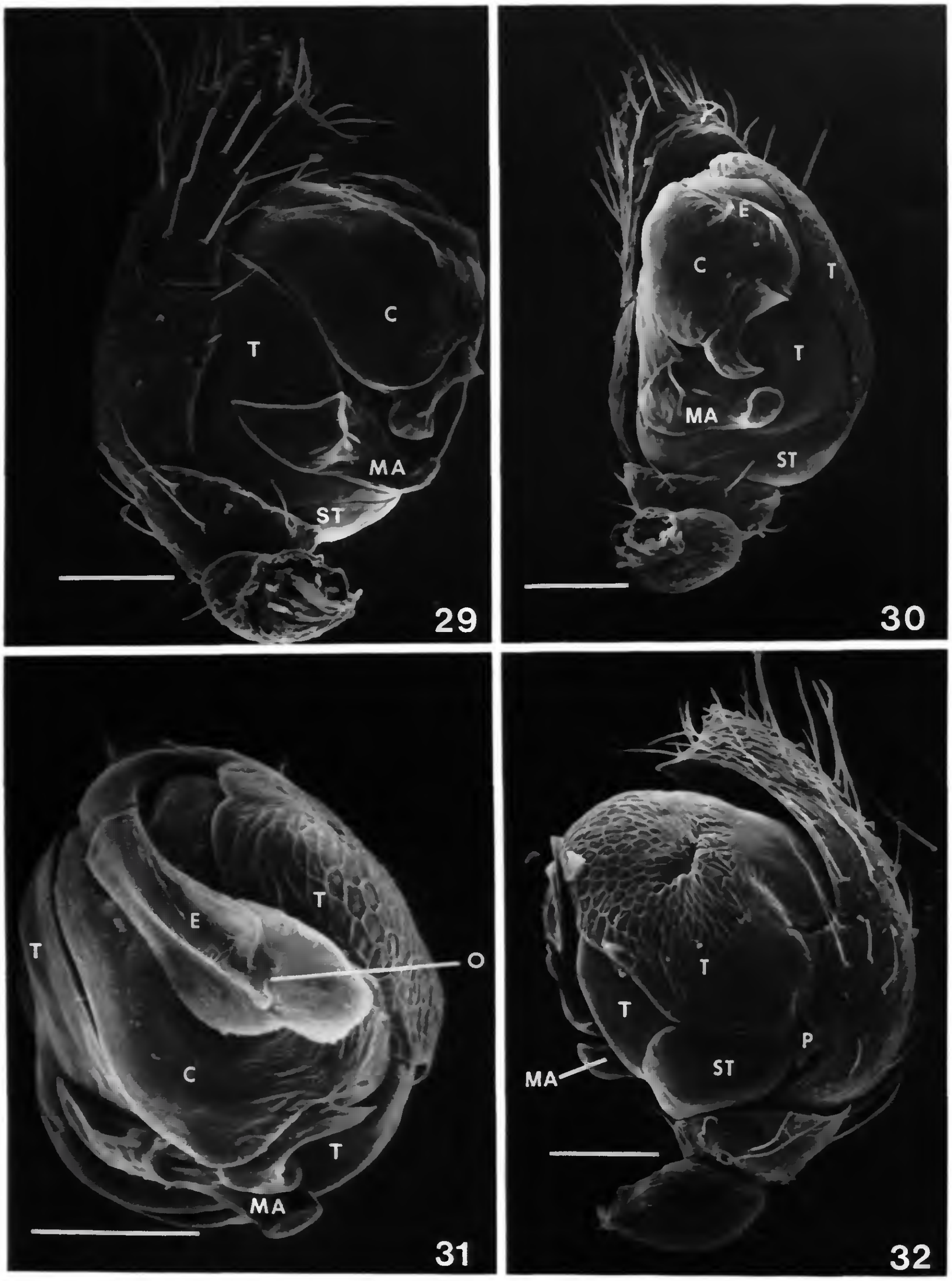
Chthonos, new name

Tecmessa O. Pickard-Cambridge, 1882:433.—Bonnet, 1959:4264.—Roewer, 1942:951.—Archer, 1953:6.—Brignoli, 1983:249. [Type-species by monotypy *T. pectorosa* O. Pickard-Cambridge, 1882:434, pl. 31: fig. 10a–d (♀).]

NOTE.—The name *Tecmessa* O. Pickard-Cambridge, 1882, is preoccupied by *Tecmessa* Burmeister, 1878 (Lepidoptera); the new name *Chthonos* is chosen to replace it.

ETYMOLOGY.—*Chthonos* is feminine and means "of the earth," referring to the habits and habitat of this genus.

DIAGNOSIS.—*Chthonos* is distinguished from other theridiosomatid genera by the lateral rows of strong macrosetae on the first and second tibiae, metatarsi, and tarsi; the sinuate curve of the first and second legs; the protuberant sternum; the well-developed transverse ridges on the epigynum; and the form of the palp (Figures 29, 32, 33, 37, 39).



FIGURES 29–32.—*Chthonos* sp. from Mexico, VERACRUZ, left male palp: 29, mesal, embolic division exposed; 30, ventral, embolic divison enclosed; 31, apical, embolic division exposed; 32, lateral.

Scale lines: 100 μm.

DESCRIPTION.—Carapace tan or reddish brown, cephalic region not higher than thoracic region, clypeus 1 to 2 times AME diameter (Figure 33). Sternum reddish brown, papillate, convex, truncate and indented posteriorly; lateral margins deeply incised, projecting ventrally below level of coxae (Figure 33). AME and PME diameter subequal or AME somewhat larger; AME, PME separation ½ their diameter. Abdomen color overall light yellow to reddish brown, uniform or with whitish guanine blotches; with sparse larger dark sclerotized flecks symmetrically arranged as well as numerous smaller punctate sclerotized flecks; wider above than long or high, tapering below to conical spinneret mound; dorsum with lateral and/or median tubercles, posterior creased; surface leathery (Figures 34–36). Spinnerets on sclerotized ring. Legs uniform brown or light tan; patellae and tibiae sinuate; tibiae, metatarsi, and tarsi of legs I and II with distinctive lateral single rows of long, strong spines (Figure 33). Epigynum a flat, transversely ridged plate with deeper transverse groove just anterior to posterior rim, also a dark spot or pit centrally; transverse ridge toothed in region of spot or pit (Figure 37). Palp with distally pointed cymbium, T-shaped paracymbium; tegulum of only moderate size; conductor covering embolus; embolus as one entire, strong sclerite; duct opening distal; median apophysis a flat plate with backwardly directed prong (Figures 29–32). Sexual dimorphism slight.

NATURAL HISTORY.—Poorly known. Collectors have found the animals walking in leaf litter or on single dry threads between foliage (the animal may have spun the thread, or it may have used the drag line of another spider). Apparently *Chthonos* are wandering predators that do not spin prey-catching webs. The form of the eggsac is also unknown, but both W.G. Eberhard (pers. comm.) and I have seen pink cubical eggsacs (Figure 4) much smaller than those of *Plato* (Figure 13), unassociated with residence webs of any spider, in habitats where *Chthonos* is known to occur. In view of the other characters supporting a sister group relationship between *Chthonos* and *Plato* (see "Intergeneric Relationships") and the cubical eggsac characteristic of *Plato*, these smaller cubical sacs may well be constructed by *Chthonos* species. The leg macrosetae of *Chthonos* may be analogous to those of mimetids. I collected one *Chthonos* individual adjacent to the web of another spider; perhaps like mimetids, *Chthonos* also eats other spiders. No direct evidence, however, supports either of these speculations.

SPECIES.—*Chthonos* at present is an exclusively neotropical genus, but has been very poorly collected. Unsorted material from the AMNH and MCZ collections show fairly uniform genitalia under light microscopy but diverse combinations of tubercles on the abdomen. The latter feature may be a good indicator of species limits (and is taken to be so here), or may simply be intraspecific variation. Available series of specimens are too small to settle the question. Five *Tecmessa* species have been described, four properly placed in *Chthonos: pectorosa* Pickard-Cambridge, 1882, *peruana* Keyserling, 1886 (= *T. peruviana* of Bonnet, 1959:4264; unjustified emendation), *tuberosa* Keyserling, 1886, and *quinquemucronata* Simon, 1893a. The fifth, *tetrabuna* Archer, 1958, belongs in *Ogulnius* (hence *O. tetrabuna* (Archer), new combination).

RANGE.—AMNH and MCZ collections include *Chthonos* individuals from the Antilles, Mexico, Guatemala, Costa Rica, Panama, Venezuela, and Brazil. In addition, *C. peruana* Keyserling, 1886, is from Peru.

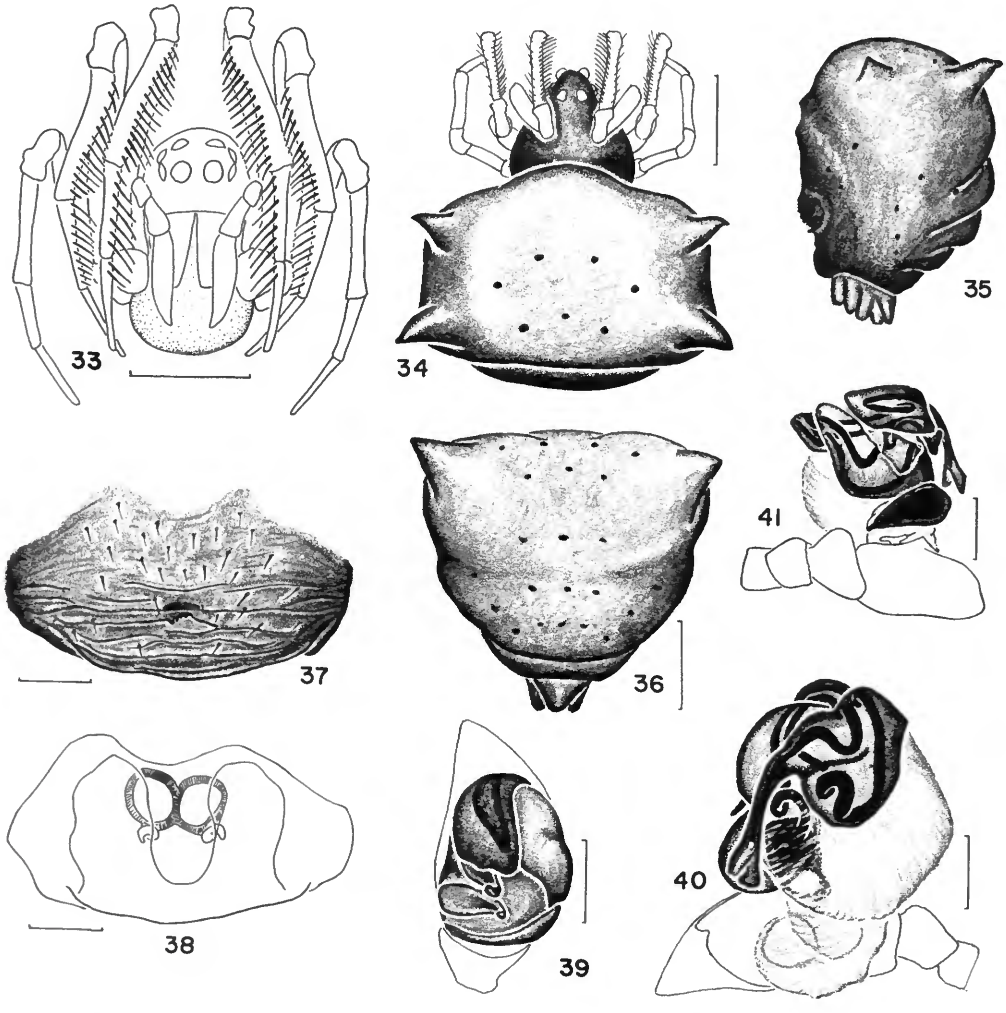
Chthonos pectorosa (O. Pickard-Cambridge), new combination

FIGURES 33–38

Tecmessa pectorosa O. Pickard-Cambridge, 1882:434, pl. 31: fig. 10a–d [♀].—Bonnet, 1959:4264.—Roewer, 1942:951. [Holotype (?) ♀ from "Mr. Traill's Amazon collection," in HDEO, examined. No locality information in vial.]

DIAGNOSIS.—*Chthonos pectorosa* is distinguished from other *Chthonos* species by the two pairs of lateral tubercles on the dorsum of the abdomen (Figure 34). Judging from the figures accompanying the original species descriptions, it appears that *peruana* Keyserling (1886, pl. 11: figs. 144, 144a–c, ♀) has only one pair of lateral tubercles, whereas *tuberosa* Keyserling (1886, pl. 20: figs. 303, 303a, ♀) and *quinquemucronata* Simon (1893a, figs. 1001–1003, ♀) have anterior and posterior median tubercles in addition to lateral tubercles. *Chthonos pectorosa* lacks median tubercles.

DESCRIPTION.—*Female:* Holotype. Abdomen and cephalothorax separated. Total length 1.9 mm (estimated). Cephalothorax 0.74 mm long, 0.69 mm wide, 0.81 mm high. Sternum reddish brown, papillate, 0.46 mm long, 0.48 mm wide, margins deeply incised, projecting be-



FIGURES 33–38.—*Chthonos pectorosa* (O. Pickard-Cambridge), type female: 33, frontal; 34, dorsal; 35, abdomen, lateral; 36, same, posterior; 37, epigynum, ventral; 38, same, ventral, cleared.

FIGURES 39–41.—*Chthonos* sp. from Puerto Rico, left male palp: 39, ventral; 40, expanded, lateral; 41, expanded, mesal.

Scale lines: 0.1 mm, except 33–36, 0.5 mm.

low level of coxae in lateral view. AME and PME diameter subequal, AME, PME separation ½ their diameter. Clypeus height 1.5 AME diameter. Abdomen 1.27 mm long, 1.82 mm wide, 0.81 mm high. Overall color light yellow (probably bleached) with sparse dark flecks symmetrically arranged (Figures 34–36), and four lateral pointed tubercles (Figure 34). Epigynum a flat, transversely ridged plate with deeper transverse groove just anterior to posterior rim; also a dark spot or pit centrally, with its transverse ridge toothed in region of spot or pit. Legs light tan, tarsi longer than metatarsi.

Leg lengths of holotype (±0.03 mm).

	I	II	III	IV
Femur	0.91	0.72	0.46	0.69
Patella	0.26	0.26	0.19	0.19
Tibia	0.74	0.60	0.40	0.41
Metatarsus	0.40	0.34	0.22	0.29
Tarsus	0.48	0.46	0.31	0.26
Total	2.79	2.38	1.58	1.84

Male: Unknown.

VARIATION.—Unknown.

NATURAL HISTORY.—Unknown.

RANGE.—Unknown. In his description, Pickard-Cambridge cites "Amazon" as type-locality.

Chthonos peruana (Keyserling), new combination

Tecmessa peruana Keyserling, 1886:20.

Chthonos tuberosa (Keyserling), new combination

Tecmessa tuberosa Keyserling, 1886:252.

Chthonos quinquemucronata (Simon), new combination

Tecmessa quinquemucronata Simon, 1893a:324.

EPEIROTYPINAE Archer

NOTE.—Archer (1953:5) included *Phricotelus, Colphepeira,* and *Epeirotypus,* with the last named as type genus. The former two genera are not theridiosomatids (see above, under "Taxonomic History"). The subfamily is here relimited to include *Epeirotypus* and *Naatlo,* new genus.

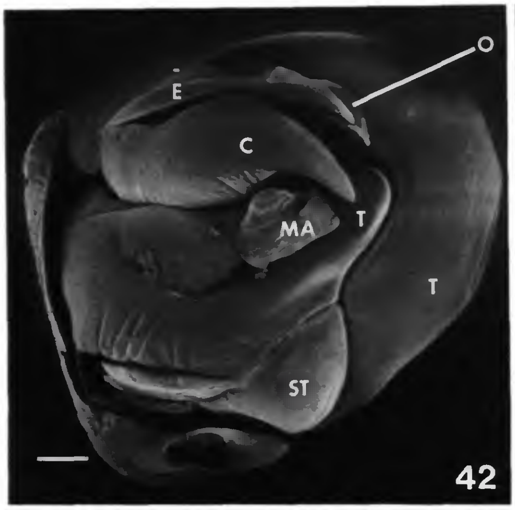
DIAGNOSIS.—The subfamily is defined by the following derived features: the median apophysis is round with a dorsal notch (Figures 42, 55, 64, 70, 82), not elongate, subrectangular, or a thin plate; the epigynum is a bulging dome (Figures 50, 58, 78, 85) with a groove on the posterior rim; the paracymbium is a broadly attached blade; the tegulum is expanded laterally (Figures 53, 72).

Epeirotypines may be recognized more easily by the following combination of characters: larger, strongly built theridiosomatid spiders; PME separated by at least a diameter (some *Naatlo* species have PME separated by ½ diameter); short, stout legs (Figures 48, 77); humps or shoulders lateral to the fovea on the carapace; epigyna either with a closely fitting flap (Figure 78) or with the posterior rim of the bulging dome closely appressed to the abdominal wall; large palpi (Figures 52, 61, 81) with the tegulum expanded laterally (Figure 54), and the emboli as single, robust sclerites (Figures 43, 71). The webs have at least 2 hub circles, often 3 or 4, usually more than 12 radii, tension lines, no radial anastomosis, and in *Epeirotypus* the eggsacs are attached to lines in the web. During the day, the spiders usually maintain their webs in the tensed position.

Epeirotypus O. Pickard-Cambridge

Epeirotypus O. Pickard-Cambridge, 1894:134.—Bonnet, 1956:1706.—Roewer, 1942:968.—Archer, 1953:5.—Brignoli, 1983:239. [Type-species by monotypy *E. brevipes* O. Pickard-Cambridge, 1894:134, pl. 18: figs. 11, 11a–d (♀); 1896:161, pl. 19: figs. 14, 14a–e (♂). The name is masculine.]

DIAGNOSIS.—*Epeirotypus* males are distinguished from all other theridiosomatids by the palp morphology: a very large tegulum, a simple reduced conductor that only partially covers the tip of the embolus, and a long smooth stout embolus with a simple acute tip (Figures 42, 43). *Chthonos* and *Plato* have long stout emboli and



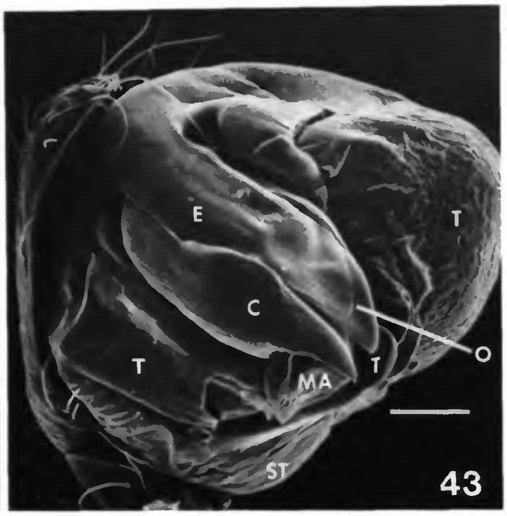


FIGURE 42.—*Epeirotypus* sp. from Costa Rica, PUNTARENAS, left male palp, embolic division exposed, mesal.

FIGURE 43.—*Epeirotypus brevipes* O. Pickard-Cambridge, from Guatemala, IZABAL, left male palp, embolic division enclosed, submesal view.

FIGURES 44, 45.—*Epeirotypus chavarria*, new species, from Costa Rica, HEREDIA: 44, incomplete web showing outer sticky spiral, non-sticky "spiral" as two peripheral circles; note eggsacs doubly attached to web lines; 45, lateral view of web, showing tension line, spider ready posture, and web distortion.

Scale lines: 42, 43, 100 μm; 44, 45, 10 mm.

conductors that only partially cover the embolus, but their median apophyses differ, and they do not have such short stout legs. *Naatlo* is very similar to *Epeirotypus* in overall appearance, but the embolus tip of the former genus is complex and truncate (Figure 73), not simple and pointed. Some *Ogulnius* species superficially resemble *Epeirotypus,* but *Ogulnius* are much smaller and their genitalia are very different.

The epigyna of female *Epeirotypus* are also diagnostic: a strongly sclerotized vault with a transverse groove along the posterior rim, the vault closely appressed to the abdominal venter (Figures 50, 58). The ventral surface of the copulatory bursae is also strongly ridged in all species examined thus far (Figure 59). *Naatlo* epigyna are similar, but they possess a closely fitting flap.

DESCRIPTION.—Total length 1 to 3 mm. Carapace light yellow to almost black, head region not elevated, lateral regions of carapace posterior to head region strongly developed as "shoulders." Eyes subequal, AME separation ~½ their diameter; PME separation usually 1 diameter, occasionally almost juxtaposed. Sternum smooth, convex, margins slightly incised around coxae, bluntly rounded behind. Legs short and stout (Figure 48), light tan or dark and annulate, femora often ⅓–½ carapace width (Figure 57). Tarsi with irregular group of ventral serrated hairs. Fourth tibial trichobothria 2 times tibial diameter. Abdomen ovoid, with (Figure 47), or without posterior lateral tubercles (Figure 56), pointed anteriorly or rounded, usually with some dorsal color pattern, often species specific. Epigynum a broad vault, almost planar in front and gently rounded behind, closely appressed to ventral abdominal wall; posterior margin with distinct, transverse groove (Figure 50). Copulatory ducts with single bend (Figure 60) like *Naatlo.* Male palp large; paracymbium a broadly attached lamella (Figure 53); median apophysis, embolus, and conformation as in Figures 54, 55, 64, 65.

NATURAL HISTORY.—Habitats preferred by *Epeirotypus* species are shrubs or, more commonly, tree trunks or buttresses in shaded, lowland to montane wet forest. *Epeirotypus brevipes* has been taken in limestone karst hollows in Guatemala that become quite xeric by the end of the dry season. All known *Epeirotypus* webs are alike and similar to *Naatlo* webs, with a tension line, profuse (15–25) radii, fairly closely spaced SS loops, and all radii inserting on the hub (lacking radial anastomosis). The hub region has 2–5 hub loops, which in *E. brevipes* and *E. chavarria* are constructed after the completion of the SS spiral (compare Figures 44, 67). The non-sticky "spiral" has two peripheral circles in all species examined thus far (Figure 44). Judging from measurements made on *brevipes, chavarria,* and an undescribed species from Costa Rica and Mexico, it appears that the adult females exert a force about 100 to 200 times their body weight to tense the web into a cone. Eggsacs are kept near the hub, attached to or pendant from the tension line. The sacs are covered with sparse or dense flocculent silk (Figure 68), and lack any suture such as occurs in *Theridiosoma.*

SPECIES.—Bonnet (1956) and Roewer (1942) list only two *Epeirotypus,* the type-species *E. brevipes* and *E. gloriae* Petrunkevitch (1930). *Epeirotypus gloriae* belongs in *Ogulnius* (see below). However, at least 5 other species are known from Latin America, and possibly Malaysia, all undescribed.

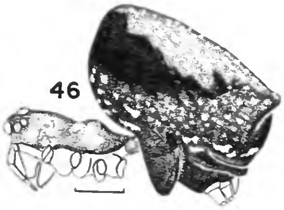
RANGE.—Antilles, Central and South America, possibly Malaysia.

Epeirotypus brevipes O. Pickard-Cambridge

FIGURES 43, 46–55, 68; MAP 2

Epeirotypus brevipes O. Pickard-Cambridge, 1894:134, pl. 18: figs. 11, 11a–d [♀]; 1896:161, pl. 19: figs. 14a–e [♂].—Bonnet, 1956:1706.—Roewer, 1942:968. [Type specimens (BMNH) lost.]

NOTE.—The original description cites specimens from Senahú, ALTA VERAPAZ, Guatemala, but none of the specimens in the BMNH are from that locality. Pickard-Cambridge's second listing of the species (1896:161) cites specimens from Teapa, TABASCO, Mexico, and some of the BMNH vials do include a Teapa label. It seems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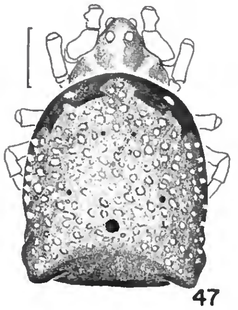
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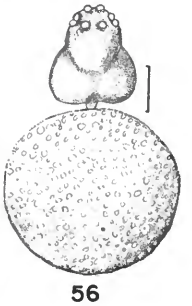
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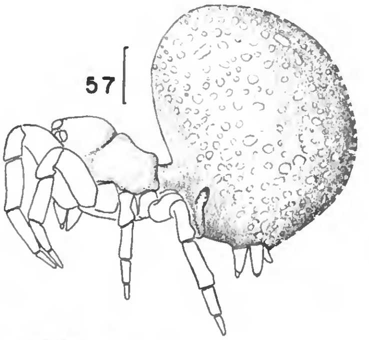
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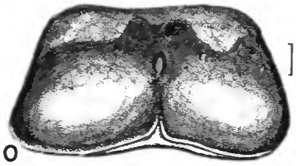
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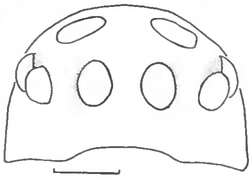
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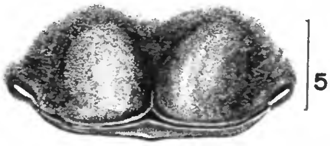
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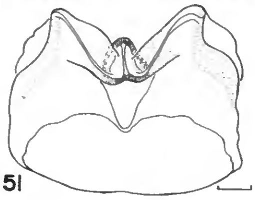
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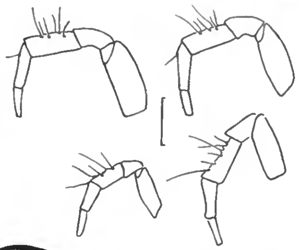
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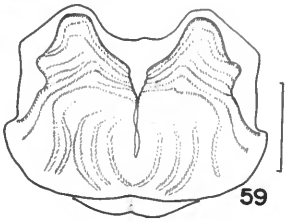
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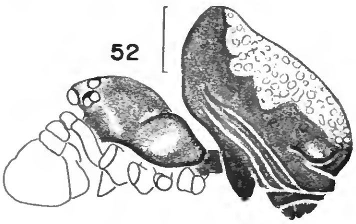
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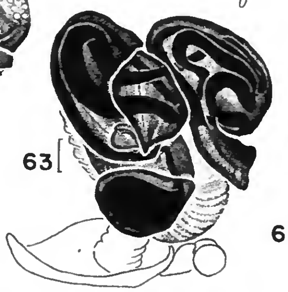
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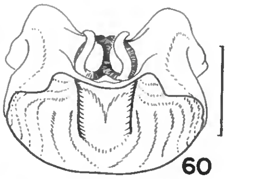
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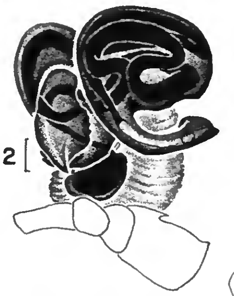
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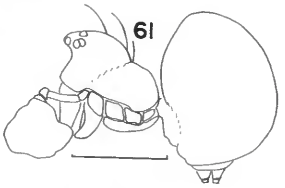
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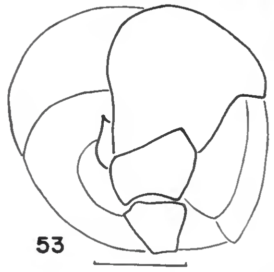
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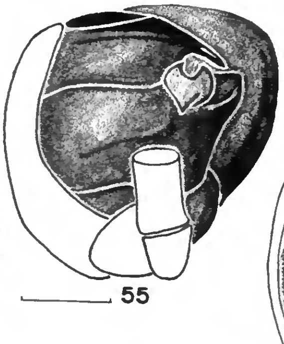
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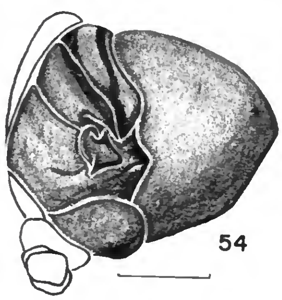
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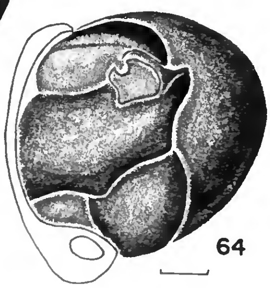
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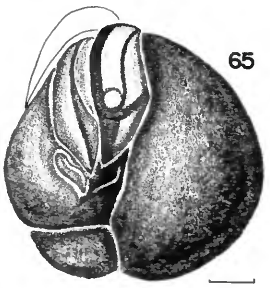
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that the original type series is missing, but the available specimens were indeed identified by Cambridge. *Epeirotypus brevipes* is a well-marked species, easily identified by the abdominal color pattern, and thus there is no doubt about the taxon to which the name refers. Consequently no neotype is designated.

DIAGNOSIS.—Males and females of *brevipes* may be distinguished from all other species of *Epeirotypus* by the white dorsum of the abdomen with a black dot in the middle (Figure 47). The genitalia of both sexes (Figures 50, 51, 54, 55), however, are similar to those of other species in the genus.

DESCRIPTION.—*Female:* From Guatemala, IZABAL. Total length 2.8 mm. Cephalothorax 1.26 mm long, 1.03 mm wide, 0.88 mm high; dark overall, with parallel light streaks on either side of midline (Figure 47). Sternum dusky brown, 0.58 mm long, 0.55 mm wide. Abdomen 1.7 mm long, 1.7 mm wide, 1.9 mm high. Abdominal dorsum white with numerous white small guanine dots and central black patch, dorsum bordered by black; sides black, interrupted by light dots ventrally; venter dark (Figures 46, 47). Abdomen flat above, with posterior lateral tubercles; anterior margin bluntly pointed (Figure 47). PME 5/4 times AME diameter, separated by slightly less than their diameter. AME separated by 3/4 their diameter. ALE, PLE subequal to AME, separated from AME, PME by 2/3 diameter. Clypeus slightly more than AME diameter. Posterior margin of epigynum with transverse groove, rim closely appressed to the surface of abdomen (Figure 50).

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.86	0.73	0.68	0.45
Patella	0.38	0.46	0.41	0.32
Tibia	0.56	0.54	0.54	0.28
Metatarsus	0.50	0.47	0.43	0.34
Tarsus	0.31	0.30	0.25	0.27
Total	2.61	2.50	2.31	1.66

Male: From Guatemala, IZABAL. Total length 2.2 mm. Cephalothorax 1.24 mm long, 0.95 mm wide, 0.74 mm high. Sternum 0.53 mm long, 0.47 mm wide. Abdomen 1.6 mm long, 1.4 mm wide, 1.3 mm high. PME 3/4 AME diameter, separated by slightly more than their diameter; AME separated by 1/2 their diameter, projecting beyond clypeus on slight tubercle (Figure 52). ALE, PLE subequal to PME, separated from AME, PME by 1/2 diameter. Clypeus height 2 times AME diameter. Color pattern of legs, carapace, sternum, and abdomen as in female. Legs proportionately longer, thinner than in female. Palp as in Figures 54, 55. In ventral view palp diameter almost equal to carapace diameter.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.90	0.71	0.48	0.50
Patella	0.40	0.35	0.27	0.37
Tibia	0.61	0.59	0.30	0.47
Metatarsus	0.59	0.55	0.37	0.43
Tarsus	0.39	0.32	0.26	0.27
Total	2.89	2.52	1.68	2.04

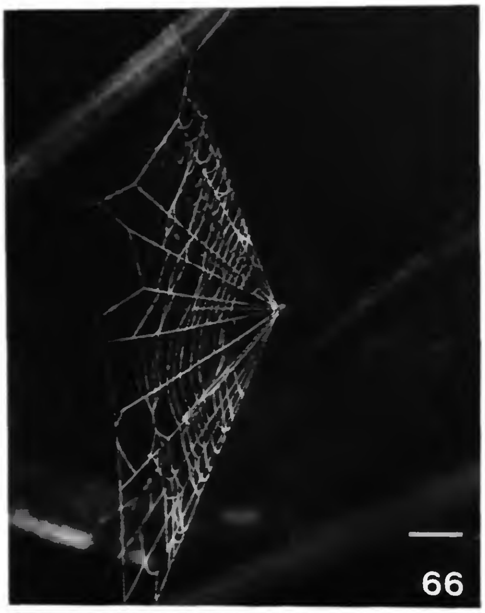
VARIATION.—Females range in length from 2.6 to 3.1 mm, males from 1.9 to 2.4 mm. Intensity of pigmentation varies from very light to almost black.

NATURAL HISTORY.—The web resembles that shown in Figures 66, 67. Females hang eggsacs from the tension line by a single thread. When the eggsacs are made, however, they are doubly attached as in *E. chavarria,* but in the course of web replacement and repair, *brevipes* females sever one of the connecting lines so that the

FIGURES 46–55.—*Epeirotypus brevipes* O. Pickard-Cambridge, from Guatemala, IZABAL. Female: 46, 47, habitus; 48, left legs; 49, eye group, frontal view; 50, epigynum, ventral; 51, same, dorsal, cleared. Male: 52, habitus; 53, left male palp, dorsal; 54, same, ventral; 55, mesal.

FIGURES 56–65.—*Epeirotypus chavarria,* new species, from Costa Rica, HEREDIA. Female: 56, 57, habitus; 58, epigynum, ventral; 59, same, ventral, partially cleared; 60, same dorsal, cleared. Male: 61, habitus; 62, left male palp, expanded, sublateral; 63, same, ventral; 64, left male palp, mesal; 65, same, ventral.

Scale lines: 0.1 mm, except 46–48, 52, 56, 57, 61, 0.5 mm.



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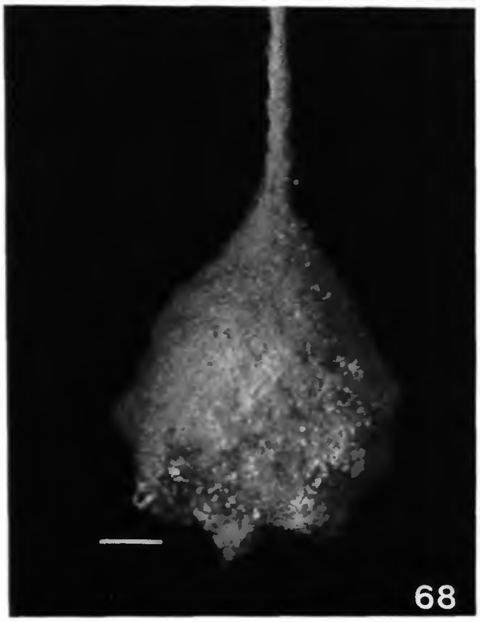

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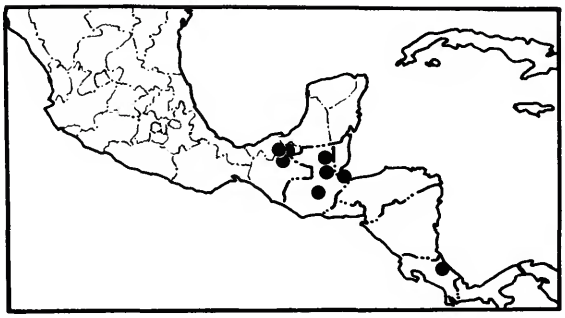
FIGURES 66, 67.—Web of *Epeirotypus* sp. from Guatemala, IZABAL: 66, lateral; 67, frontal, showing persistent hub loops.

FIGURE 68.—Eggsac of *Epeirotypus brevipes* O. Pickard-Cambridge, from Guatemala, IZABAL.

FIGURE 69.—Web of *Naatlo fauna* (Simon) from Panama, PANAMÁ, frontal view; note tension line, hub loops.

Scale lines: 10 mm, except 68, 1 mm.



MAP 2.—Distribution of *Epeirotypus brevipes* O. Pickard-Cambridge.

eggsacs are pendant (Figure 68). The species seems to prefer tree buttresses or rock crevices as web sites, with the tension line facing inward. Males are found at the periphery of the female web.

RANGE.—The species is recorded from Mexico, Guatemala, Honduras, and Costa Rica, but probably occurs throughout Central America (Map 2).

RECORDS.—MEXICO. CHIAPAS: Palenque, Mayan ruins (♂, ♀♀, MCZ). TABASCO: Grutas de Aguas Blanca, 7 km S of Río Tulija, 17°39′N, 92°26′W (♀♀, MCZ); Teapa (♀♀, ♂, BMNH). GUATEMALA. PETEN: Tikal, forest around Mayan ruins (♀, MCZ). ALTA VERAPAZ: Purulhá (♀♀, MCZ). IZABAL: Santo Tomás (♂♂, ♀♀, MCZ). HONDURAS. ATLANTIDA: 6 km S of Tela, Lancetilla, along base of mts. (♀, MCZ). COSTA RICA. HEREDIA: Puerto Viejo, Organization for Tropical Studies field station Finca La Selva (♂♂, ♀♀, MCZ).

Epeirotypus chavarria, new species

FIGURES 44, 45, 56–65

TYPE.—♀ holotype and one ♂, three ♀ paratypes from Costa Rica, Heredia Province, near Puerto Viejo, Organization for Tropical Studies Finca La Selva, 50 m, J. Coddington, coll., 25.iii.1979, in MCZ.

ETYMOLOGY.—The name is a noun in apposition, honoring Sr. Rafael Chavarría, the late administrator of Finca La Selva, of Puerto Viejo de Sarapiqui. The ending of "*chavarria*" conflicts with Recommendation 31a of the ICZN, but in this case an exception seems warranted to ease pronunciation of the name.

DIAGNOSIS.—Males and females of *chavarria* may be distinguished from all other species of *Epeirotypus* by the color pattern: an off-white abdomen with numerous very white guanine speckles. The genitalia are very similar to those of other *Epeirotypus* species.

DESCRIPTION.—*Female:* Paratype. Total length 2.4 mm. Carapace whitish yellow, cephalothorax 0.98 mm long, 0.83 mm wide, 0.86 mm high; white, head region slightly elevated, lateral portions strongly developed into "shoulders" (Figure 57). Sternum 0.52 mm long, 0.45 mm wide, whitish yellow. Abdomen 1.3 mm long, 1.4 mm wide, 1.7 mm high; smoothly ovoid, uniformly white with numerous white small guanine dots on dorsum and sides, absent on venter (Figures 56, 57). AME slightly smaller than PME, separated by ½ their diameter. PME separated by slightly less than their diameter. ALE, PLE subequal to AME, separated from AME, PME by ½ their diameter. Clypeus ⅓ AME diameter. Epigynum with central pit; posterior margin with transverse groove, groove bisected medially by ridge; posterior rim closely appressed to surface of abdomen (Figures 58, 59). Copulatory ducts ridged, simple (Figures 59, 60).

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.67	0.67	0.50	0.63
Patella	0.32	0.31	0.31	0.35
Tibia	0.46	0.41	0.32	0.44
Metatarsus	0.38	0.37	0.27	0.33
Tarsus	0.32	0.30	0.20	0.19
Total	2.15	2.06	1.60	1.94

Male: From type-locality. Total length 1.9 mm. Cephalothorax 0.86 mm long, 0.76 mm wide, 0.83 mm high; head region elevated, lateral portions strongly developed into "shoulders" (Figure 61). Sternum 0.47 mm long, 0.41 mm wide. Abdomen 1.1 mm long, 1.1 mm wide, 1.3

mm high. AME slightly larger than PME, separated by ½ their diameter. PME separated by ⅘ their diameter. ALE, PLE subequal, slightly smaller than AME, separated from AME, PME by ½ their diameter. Clypeus 3 times AME diameter. Color of carapace, sternum, legs, and abdomen as in female. Palp as in Figures 62–65.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.68	0.62	0.35	0.50
Patella	0.33	0.32	0.24	0.24
Tibia	0.60	0.44	0.25	0.46
Metatarsus	0.47	0.43	0.28	0.32
Tarsus	0.32	0.30	0.24	0.22
Total	2.40	2.11	1.36	1.74

VARIATION.—Females range in length from 2.0 to 2.8 mm, males from 1.4 to 2.0 mm. Coloration may be slightly yellowish in life, but never very dark.

NATURAL HISTORY.—The species occurs only in primary, wet lowland rain forest, making its webs within 2 m of the ground, on shrubs or other woody substrates. The web is shown in Figures 44, 45. Females suspend eggsacs between the tension line and other silk lines or the substrate. One female observed for about 2 months constructed a total of 6 eggsacs. Eggsacs in collections contain from 6 to 12 eggs. The species seems to prefer tree buttresses, palm roots, and wind falls as web sites, with the tension line facing inward towards the substrate. Males are found at the periphery of the female web.

RANGE.—Thus far, the species is known only from the type-locality.

RECORDS.—COSTA RICA. HEREDIA: nr Puerto Viejo de Sarapiqui, OTS Finca La Selva (♂♂, ♀♀, numerous records, MCZ). The locality is the same as the southernmost dot on Map 2, *E. brevipes*.

Naatlo, new genus

TYPE-SPECIES.—*Naatlo sutila*, new species.

ETYMOLOGY.—Na'atlo is the name given by Navaho Indians to "cat's cradle" string figures, an art taught to them by a deity known as Spiderwoman. The name is taken to be feminine.

DIAGNOSIS.—*Naatlo* is diagnosed by the presence of the epigynal flap hinged anteriorly and covering the copulatory bursa in the females (Figures 78, 88, 93) and the reduced conductor and the more complex embolic tip in the males (Figures 71, 73, 83, 97). Somatic morphology most resembles that of *Epeirotypus*, but *Naatlo* is readily distinguished by these diagnostic features.

DESCRIPTION.—Total lengths 1.7 to 3.0 mm. Cephalothorax glabrous, light tan, sternum slightly darker. Head region (narrower and less distinct in males) only somewhat higher than thoracic region and set off by deep depression or groove (Figure 74). Lateral region of carapace opposite fovea high, forming "shoulders" (Figure 86). AME ⅔ PME diameter, separation ¾ their diameter and similarly from ALE. PME ovoid, separation ½ their diameter and similarly from PLE. ALE, PLE juxtaposed, subequal to PME. Male eye group more compact, AME projecting slightly beyond clypeus (Figure 81). Chelicerae robust, 2 to 3 prolateral and retrolateral, discrete teeth. Sternum longer than wide, rounded behind. Legs light tan proximally, darker reddish tan distally. Legs I, II much more robust than III, IV; female femur I width about ⅓ carapace diameter. Tarsi with numerous serrated bristles ventrally. Male legs I, II less robust, proportionately longer and thinner than in female. Abdomen ovoid, without prominent humps. Species distinguishable by abdominal shape and color patterns or, in doubtful specimens, by genitalic details.

NATURAL HISTORY.—Preferred habitat is typical of the family, wet or humid shaded forest, from near sea level to montane forest (e.g., 2300 m in Colombia). The webs are similar to those of *Epeirotypus*, with 14–20 radii and a similar number of SS loops. All radii reach the hub (Figure 69). At least two hub loops and a tension line are present. Judging from the robust first and second legs, these spiders also exert considerable force to tense their webs into a cone (cf. remarks under

Epeirotypus). Eggsac form apparently is diverse. One eggsac accompanying a specimen of *splendida* from Colombia was a ball of fluffy silk attached directly to a leaf. An undescribed species from Queensland, Australia, however, had a papery sack suspended from two points (cf. remarks under *Ogulnius*, *Epeirotypus*).

SPECIES.—*Theridiosoma fauna* Simon, 1897b, *T. sylvicola* Hingston, 1932, and *T. splendidum* (Taczanowski, 1873) are here transferred to *Naatlo*. The identity of *sylvicola* is somewhat uncertain, because no Hingston specimens are extant. He did provide a detailed description, in particular mentioning a "subtriangular" epigynum (1932:376). Specimens from Guyana in the MCZ and AMNH agree with Hingston's description, and thus may be referred to *sylvicola*. Archer (1953:12, fig. 25) also provided a brief description and figure of the epigynum, as well as identifying several specimens as *T. sylvicola* (currently in the AMNH). Both authors overlooked that the subtriangular structure on the epigynum is merely the ridge on the epigynal flap, not the epigynum itself. A neotype for *sylvicola* should be designated when *Naatlo* is revised. Undescribed species are known from South America, Australia, and New Guinea.

RANGE.—The genus occurs at least in Central and South America, Australia, and New Guinea.

Naatlo sutila, new species

FIGURES 70–72, 74–83; MAP 3

TYPE.—♀ holotype and ♂ paratype from Colombia, Valle Province, near Saladito (1700 m). III.1976 (W.G. Eberhard, #1064); in MCZ.

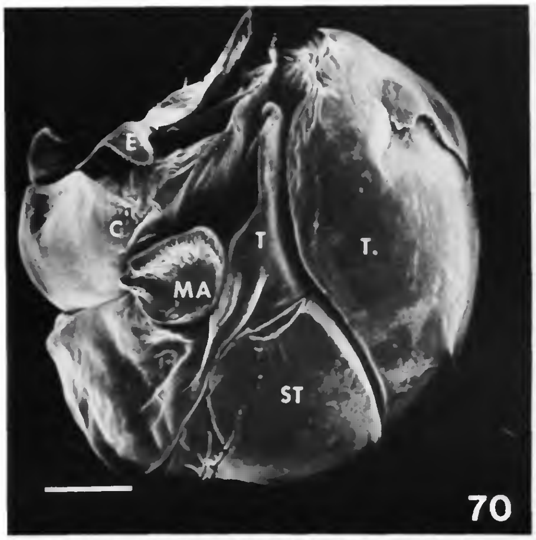
ETYMOLOGY.—The name is a Spanish adjective meaning "refined" or "delicate," and refers to the overall morphology of the species in comparison to other members of the genus.

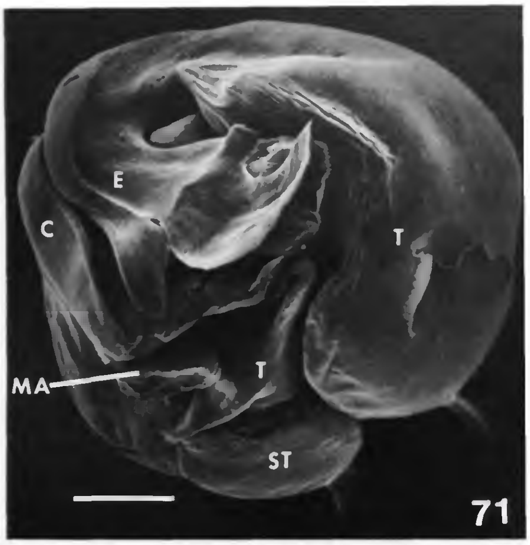
DIAGNOSIS.—Males and females of *sutila* may be distinguished from other *Naatlo* species by the abdomen, which is higher than long, the equatorial, unsilvered, light band on the sides and anterior of the abdomen (incomplete behind), and the dorsal abdominal color pattern (Figures 74, 75). *Naatlo splendida* has a lateral silver stripe on the abdomen, and *Naatlo fauna* has a different dorsal abdominal color pattern. In addition, the width of the epigynal flap in *sutila* is 0.8 or less the width of the sternum (Figure 76), the epigynal flap is less sclerotized than in *splendida* and *fauna*, and the copulatory bursae are more pointed than in *splendida* and *fauna* (Figure 80). The copulatory bursa seen when the epigynal flap is reflected (Figure 79) lacks the prominent lateral lobes characteristic of *splendida* and *fauna*. Thus far the palpal bulbs of the three species appear indistinguishable; abdominal color pattern generally will separate males.

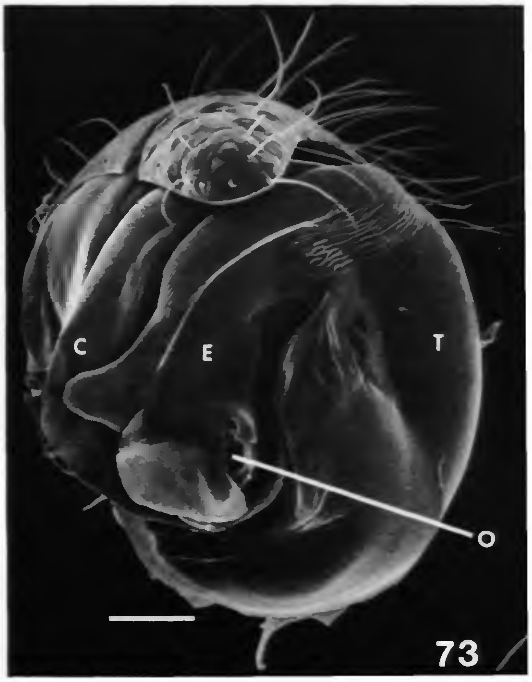
DESCRIPTION.—*Female:* From Colombia, VALLE. Total length 2.0 mm. Carapace yellow tan, dusky around eyes and on carapace midline; cephalothorax 0.91 mm long, 0.69 mm wide, 0.62 mm high. Sternum brownish yellow; 0.43 mm long, 0.38 mm wide, acutely rounded behind (Figure 76). AME ¾ PME diameter, separation slightly less than their diameter, PME separation about ½ their diameter. Clypeus height subequal to AME diameter. Abdomen 1.2 mm long, 1.1 mm wide, 1.3 mm high. Dorsum of abdomen dark with indistinct bilateral pattern of oblique lighter marks (Figure 75); sides and anterior with wide, unpigmented, equatorial band speckled with sparse white dots, band incomplete behind (Figure 74); venter dark laterally, with dark patch between spinnerets and epigynum (Figure 76). Abdomen flattened above, higher than long. Legs light tan, darkening to a reddish brown distally. Epigynal flap with posterior, marginal, transverse groove (Figure 78), flap 2.1 times wider than long, flap width 0.6 the sternum width. In dorsal view, copulatory bursae pointed and spermathecae four-chambered (Figure 80).

Leg lengths of a female described above (± 0.02 mm).

	I	II	III	IV
Femur	0.71	0.57	0.38	0.50
Patella	0.31	0.31	0.20	0.31
Tibia	0.47	0.41	0.25	0.35
Metatarsus	0.47	0.44	0.30	0.36
Tarsus	0.30	0.27	0.22	0.28
Total	2.26	2.00	1.35	1.80







FIGURES 70–72.—*Naatlo sutila,* new species, from Colombia, VALLE, left male palp: 70, submesal, embolic division exposed; 71, subapical, embolic division exposed; 72, cymbium and paracymbium.

FIGURE 73.—*Naatlo splendida* (Taczanowski), from Colombia, META, left male palp, apical. Scale lines: 100 μm.

Male: From Colombia, VALLE. Total length 1.7 mm. Cephalothorax 0.79 mm long, 0.64 mm wide, 0.64 mm high. Sternum 0.34 mm long, 0.34 mm wide. PME ¾ AME diameter, separation ¾ their diameter, AME separation ¾ their diameter. Clypeus height 1.8 AME diameter. Abdomen 1.0 mm long, 0.9 mm wide, 1.0 mm high. Color pattern of carapace, sternum, legs, and abdomen as in female. Palp with large tegulum (Figure 83), embolic blade striated (Figure 71), distal margin saw-toothed (Figure 83).

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.67	0.53	0.32	0.32
Patella	0.27	0.27	0.21	0.22
Tibia	0.59	0.44	0.22	0.35
Metatarsus	0.55	0.50	0.27	0.35
Tarsus	0.32	0.25	0.22	0.22
Total	2.40	1.99	1.24	1.46

VARIATION.—Females range in length from 1.6 to 2.4 mm, males (3 specimens) from 1.2 to 2.0 mm. In gravid females the abdomen is occasionally longer than high, but the abdomen usually does not project as far behind the spinnerets in lateral view as in *splendida* and *fauna*. The color pattern varies in intensity of pigmentation, lighter specimens as in Figure 75, darker ones with the light marks merging to form chevrons posteriorly.

NATURAL HISTORY.—Nothing known, but collecting records indicate the preferred habitat is montane wet forest.

RANGE.—Panama, Colombia, and Surinam (Map 3).

RECORDS.—PANAMA. Illegible label, not mapped (♀♀, MCZ). COLOMBIA. VALLE: nr Saladito, 1700–1800 m (♀♀, ♂, MCZ); Central Hidalgo Anchicayá, 400 m (♂, MCZ). HUILA: 18 km E Santa Leticia, 2300 m (♀♀, MCZ). SURINAM. SARAMACCA: Voltzberg Raleigh Nature Preserve (♀, MCZ).

***Naatlo splendida* (Taczanowski), new combination**

FIGURES 73, 84–90; MAP 3

Theridium (Phrurolithrum) splendidum Taczanowski, 1873:5 [♀ holotype from "Uassa" (probably Brazil, Estado Amapá, Rio Uaçá), in PAN, not examined].

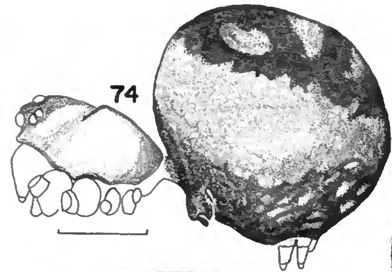
Theridiosoma splendida.—Keyserling 1884:221, pl. 10: figs. 134, 134a–c [♀].

Theridiosoma splendidum.—Bonnet 1959:4435.—Roewer 1942:970.

NOTE.—Although it has been impossible to borrow the holotype from the Polish Academy, Taczanowski described the abdominal proportions for *Naatlo* and the lateral longitudinal silvery stripe diagnostic for *splendida*. In addition, Keyserling (1884) figured specimens from Warsaw, presumably part of the type series.

DIAGNOSIS.—Males and females of *splendida* may be distinguished from other *Naatlo* species by the longitudinal silvery stripes on the abdomen (Figures 84–86). *Naatlo sutila* has a similar lateral stripe, but it lacks the silver pigment, the abdomen is usually higher than long, and the epigynal flap is narrower than the sternum width. *Naatlo fauna* also lacks the silver band and has a dorsal abdominal color pattern, whereas the dorsum in *splendida* is usually uniformly dark (Figure 84). The lateral lobes inside the copulatory bursa in *splendida* are blunt (Figure 89), not pointed, and the bursae are indented in their median sides in dorsal, cleared view (Figure 90).

DESCRIPTION.—*Female:* From Colombia, META. Total length 2.4 mm. Cephalothorax 0.98 mm long, 0.72 mm wide, 0.69 mm high. Sternum 0.46 mm long, 0.43 mm wide. Abdomen 1.51 mm long, 1.08 mm wide, 1.17 mm high. AME slightly smaller than PME, separated by ¾ their diameter. PME separation ½ their diameter. ALE, PLE subequal to PME, separation from AME, PME ⅓ their diameter. Clypeus height 3/2 AME diameter. Dorsum of abdomen uniformly dark, sides with prominent thin longitudinal silvery stripe on dark background (Figure 86). Venter light with dark patches laterally and between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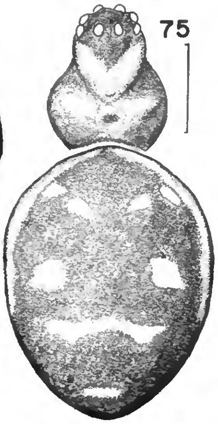
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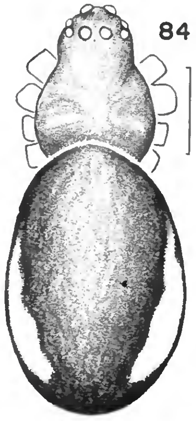
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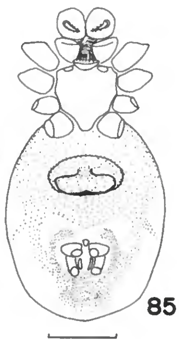
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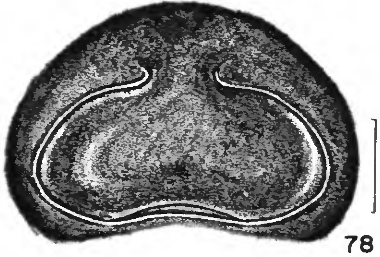
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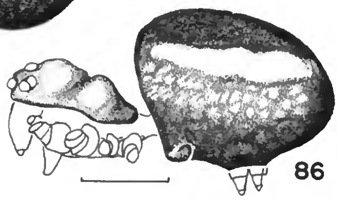
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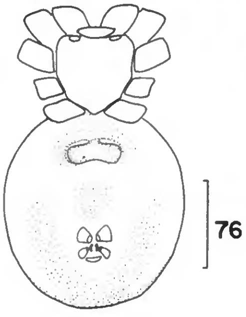
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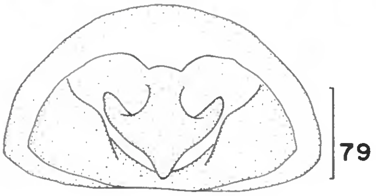
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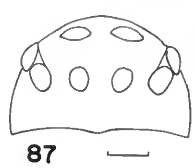
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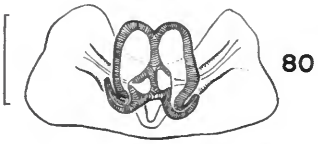
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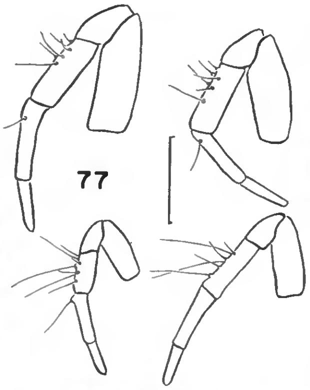
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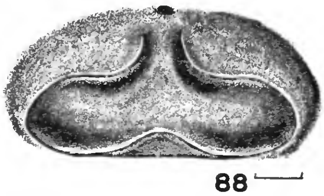
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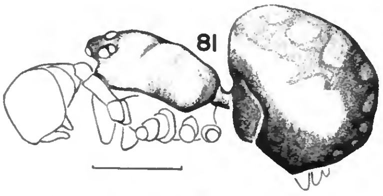
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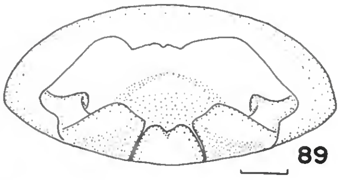
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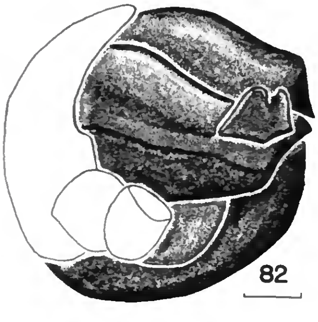
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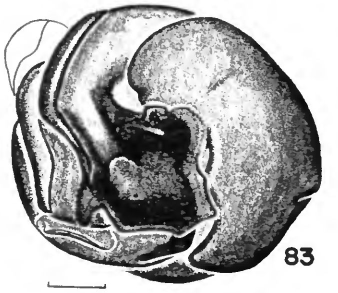
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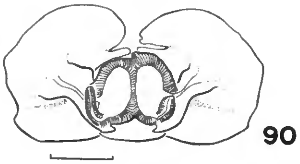
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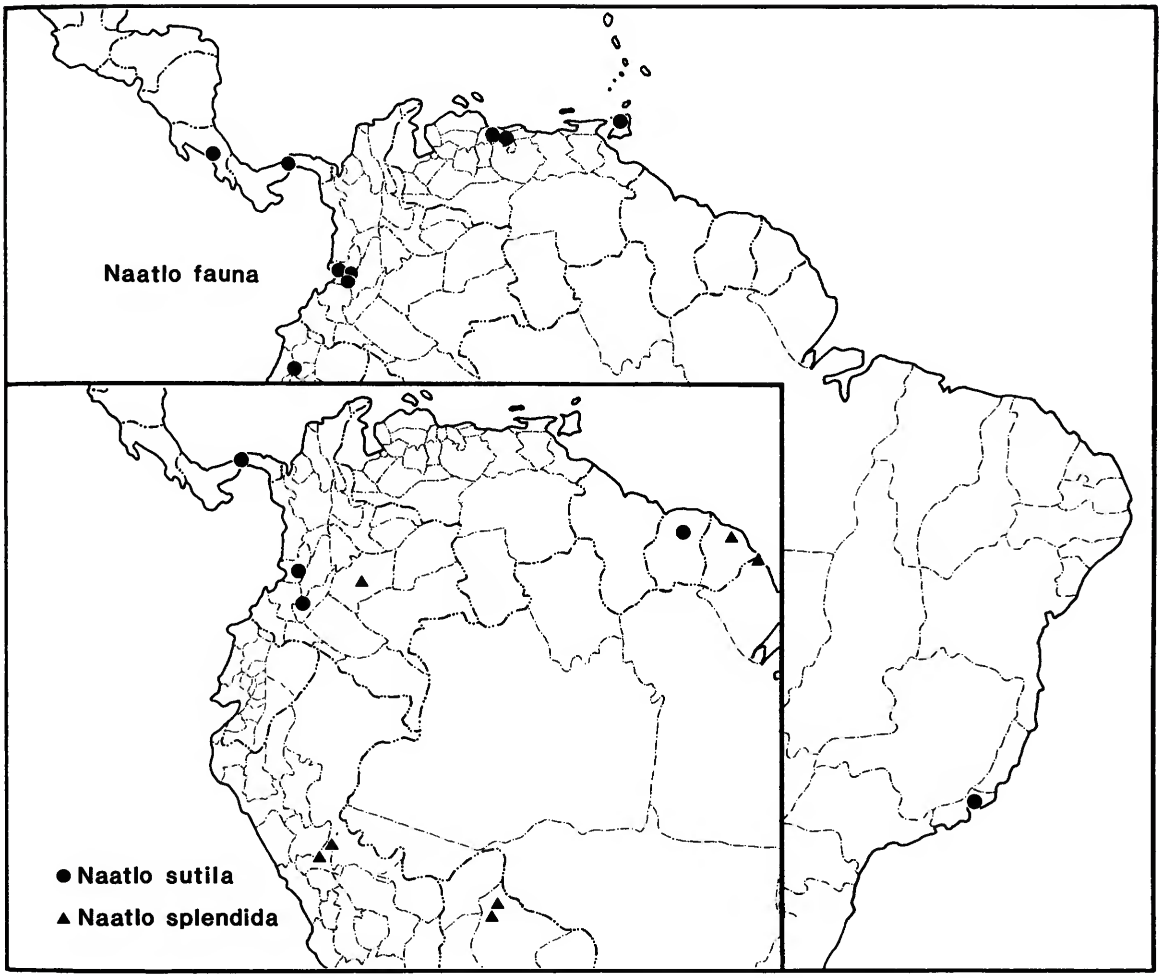


MAP 3.—Distributions of *Naatlo sutila*, new species, *N. splendida* (Taczanowski), and *N. fauna* (Simon).

spinnerets and epigynum (Figure 85). Abdomen rounded above, longer than high. Posterior margin of epigynal flap with groove laterally, medially with triangular mound or ridge (Figure 88); flap 2.8 wider than long, subequal to sternal width.

FIGURES 74–83.—*Naatlo sutila*, new species, from Colombia, VALLE. Female: 74–76, habitus; 77, left legs; 78, epigynum, ventral; 79, same, posterior, flap removed; 80, same, dorsal, cleared. Male: 81, habitus; 82, left male palp, mesal; 83, same apical.

FIGURES 84–90.—*Naatlo splendida* (Taczanowski), from Colombia, META, female: 84–86, habitus; 87, eye group, frontal; 88, epigynum, ventral; 89, same posterior, flap removed; 90, same, dorsal, cleared.

Scale lines: 0.1 mm, except 74–76, 84–86, 0.5 mm.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.74	0.63	0.34	0.50
Patella	0.34	0.31	0.21	0.30
Tibia	0.54	0.53	0.31	0.45
Metatarsus	0.49	0.44	0.32	0.37
Tarsus	0.31	0.30	0.24	0.27
Total	2.42	2.21	1.42	1.89

Male: From Colombia, META. Total length 2.1 mm. Cephalothorax 1.07 mm long, 0.74 mm wide, 0.65 mm high. Sternum 0.41 mm long, 0.40 mm wide. Abdomen 1.1 mm long, 0.9 mm wide, 1.1 mm high. Eye group and color pattern of carapace, sternum, abdomen, and legs as in female. Abdomen more ovoid than in female. Palp morphology (Figure 73) essentially the same as in *fauna* and *sutila*.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.74	0.61	0.34	0.44
Patella	0.31	0.27	0.22	0.27
Tibia	0.58	0.53	0.27	0.38
Metatarsus	0.65	0.53	0.33	0.42
Tarsus	0.38	0.34	0.27	0.27
Total	2.66	2.28	1.43	1.78

VARIATION.—Females range in length from 2.0 to 2.7 mm, males from 1.6 to 2.1 mm. Intensity of pigmentation varies but specimens of *splendida* are usually darker than those of either *sutila* or *fauna*. The ratio of the width of the epigynal flap to the width of the sternum also varies, and overlaps completely that in *fauna*, but it is never so small as that in *sutila*.

NATURAL HISTORY.—This species apparently occurs in lowland as well as cloud forest. One web (photograph supplied by W.G. Eberhard) had 2 hub loops, 19 radii, no radial anastomosis, and a tension line at an angle to the plane of the web. One eggsac was made of fluffy silk and was attached to a leaf, rather than to the tension line or suspended by a silk line. That form of eggsac would be unique among theridiosomatids and, indeed, among symphytognathoids; perhaps the attribution of the eggsac to *splendida* was a mistake.

RANGE.—Colombia, French Guiana, Peru, Bolivia, and Brazil (Map 3).

RECORDS.—COLOMBIA. META: 15 km SW Puerto Lopez, Hacienda Mozambique 200–500 m (♀♀, ♂♂, numerous records, MCZ). FRENCH GUIANA. GUYANA: Cayenne (♀, AMNH). PERU. UCAYALI: Huánuco, Divisoria (probably on Ucayali border between Tingo María and Pucallpa) (♀♀, AMNH). HUÁNUCO: Tingo María (♀♀, AMNH). BOLIVIA. BENI: Río Benicito (♀♀, AMNH); Río Benicito, Chacobo Indian village (♀, AMNH). BRAZIL. AMAPÁ: Río Uaçá (♀, PAN?).

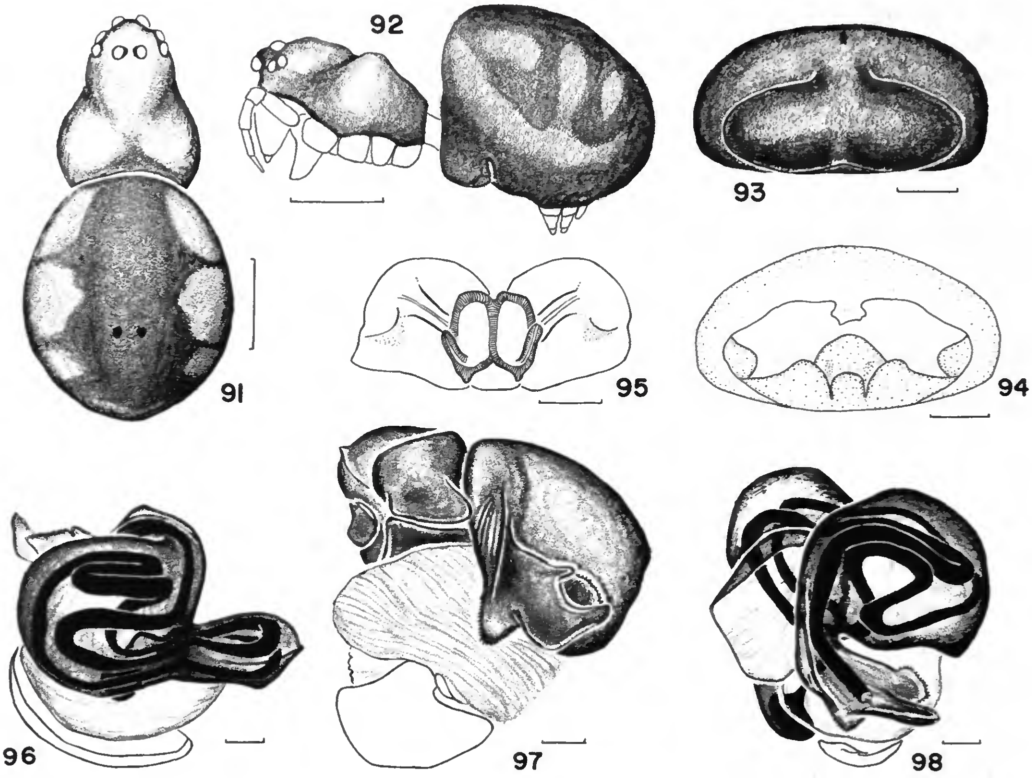
Naatlo fauna (Simon), new combination

FIGURES 69, 91–98; MAP 3

Theridiosoma fauna Simon, 1897a:483, figs. 1, 2, 7, 8 [webs and eggsacs].—Bonnet, 1959:4433.—Roewer, 1942:970. [A syntype series of 1 male and 19 females from San Esteban, CARABOBO, Venezuela, in MNHN, Paris, examined. Female lectotype here designated.]

DIAGNOSIS.—Males and females of *fauna* may be distinguished from other *Naatlo* species by the abdominal color pattern (Figures 91, 92). *Naatlo splendida* has a lateral silver stripe on the abdomen, and no paired spots on the dorsum. The epigynal flap of *sutila* is narrower than the sternum, whereas in *fauna* it is subequal or wider. The lateral lobes in the copulatory bursa are pointed, not blunt (Figure 94).

DESCRIPTION.—*Female:* From Colombia, VALLE. Total length 2.2 mm. Cephalothorax 0.89 mm long, 0.77 mm wide, 0.77 mm high, head region not markedly elevated, carapace opposite fovea higher, forming "shoulders" (Figure 92). Sternum 0.50 mm long, 0.45 mm wide. AME slightly less than PME diameter, separated by ⅔ their diameter. PME separation ⅓ their diameter. ALE, PLE slightly larger than AME, separated from AME, PME by ½ their diameter. Clypeus height 2 times AME diameter. Abdomen 1.3 mm long, 1.2 mm wide, 1.1 mm high. Dorsum of abdomen dusky with distinct large marginal light blotches, blotches paired or forming transverse bands posteriorly (Figure 91); sides dark, venter dark laterally, dark patch between spinnerets and epigynum. Abdomen rounded above, longer than high, extending posteriorly far beyond spinnerets (Figure 92). Epigynal flap with posterior transverse groove (Figure 93), flap 2.6 times wider than long, subequal to sternal width. Bursae rounded (Figure 95).



FIGURES 91–98.—*Naatlo fauna* (Simon), from Colombia, VALLE. Female: 91, 92, habitus; 93, epigynum, ventral; 94, same, posterior, flap removed; 95, same, dorsal, cleared. Left male palp, expanded: 96, lateral; 97, ventral; 98, apical, showing reservoir route. Scale lines: 0.1 mm, except 91, 92, 0.5 mm.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.83	0.70	0.38	0.83
Patella	0.35	0.31	0.20	0.28
Tibia	0.61	0.54	0.27	0.45
Metatarsus	0.56	0.49	0.30	0.41
Tarsus	0.36	0.36	0.24	0.24
Total	2.71	2.40	1.39	2.21

Male: From Colombia, VALLE. Total length 2.2 mm. Cephalothorax 0.91 mm long, 0.72 mm wide, 0.74 mm high, head region not markedly elevated, carapace lateral to fovea higher, forming "shoulders." Sternum 0.44 mm long, 0.41 mm wide. Eye group as in female, clypeus height 5/3 AME diameter. Abdomen 1.3 mm long, 1.1 mm wide, 1.2 mm high. Color of carapace, sternum, abdomen and legs as in female. Abdomen more ovoid in lateral view than in female. Unexpanded palp as in other members of the genus, expanded as in Figures 96–98.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.90	0.75	0.40	0.55
Patella	0.33	0.28	0.21	0.26
Tibia	0.67	0.57	0.27	0.44
Metatarsus	0.72	0.59	0.34	0.43
Tarsus	0.38	0.33	0.27	0.28
Total	3.00	2.52	1.49	1.96

VARIATION.—Females range in length from 2.3 to 2.9 mm, males from 1.7 to 2.2 mm. The color pattern varies in intensity of pigmentation, and in lighter specimens the diagnostic light blotches may be open laterally. Females from Panama are very light, and the abdomen dorsum is almost a uniform dusky color. *Naatlo splendida* and *N. fauna* overlap in many characters, but *splendida* always has silvery stripes on the sides of the abdomen.

NATURAL HISTORY.—The species occurs over a wide altitudinal range (50–1800 m), apparently in wet forest or cloud forest. Web (Figure 69) with numerous radii, hub loops, no radial anastomosis, and a tension line.

RANGE.—Costa Rica, Panama, Colombia, Venezuela, Trinidad, Ecuador, and Brazil (Map 3).

RECORDS.—COSTA RICA. SAN JOSÉ: Quizarrá, 9 km SW San Isidro del General, 2500 m (♀, MCZ). PANAMA. PANAMÁ: Lake Gatún, Barro Colorado Island (♀♀, MCZ). COLOMBIA. VALLE: 28 km E of Buenaventura, nr Saladito, 1800 m (♀♀, ♂♂, numerous records, MCZ); Río San Juan, tributary of Río Dagua nr Queremal, 1300 m (♀, MCZ); above Atuncela, 1800 m (♀♀, MCZ); Central Hidalgo Anchicayá, 400 m (♀, MCZ). VENEZUELA. ARAGUA: Choroní (♀, AMNH). CARABOBO: San Esteban (♀♀, ♂, MNHN). TRINIDAD. ST. GEORGE: Arima Rd., gap to Blanchisseuse (♀, AMNH). ECUADOR. PICHINCHA: Río Palenque, 47 km SW Santo Domingo, on road to Queredo (♀♀, MCZ). BRAZIL. RIO DE JANEIRO: Teresópolis, (♂, MCZ).

Naatlo sylvicola (Hingston), new combination

Theridiosoma sylvicola Hingston, 1932:376.

OGULNIINAE, new subfamily

DIAGNOSIS.—Ogulniinae contains only the genus *Ogulnius* and is diagnosed by the same characters diagnosing *Ogulnius* (see below).

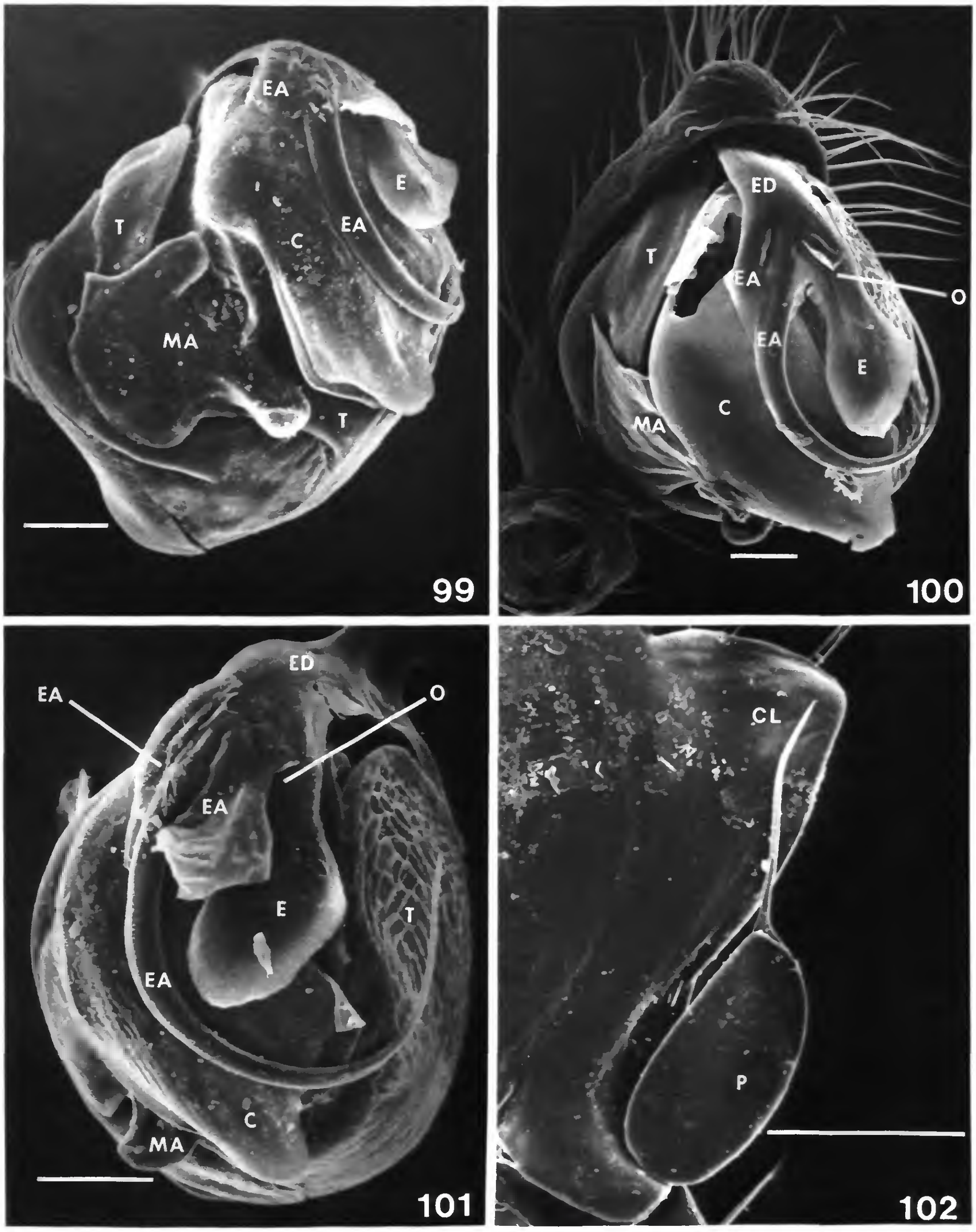
Ogulnius O. Pickard-Cambridge

Ogulnius O. Pickard-Cambridge, 1882:432.—Bonnet, 1958:3157.—Roewer, 1942:968.—Archer, 1953:7.—Brignoli, 1983:239. [Type-species by monotypy *O. obtectus* O. Pickard-Cambridge, 1882:433, fig. 9a–d [♀]. The name is masculine.]

DIAGNOSIS.—*Ogulnius* can generally be recognized by body proportions: the fourth legs are longer than the first (Figures 109, 122 in females; some males with LI, LIV subequal); their small size; the abdomen greatly overbalancing cephalothorax and even obscuring the eye group in dorsal view (Figures 107, 120). The sternum is markedly truncate behind, often incised. In the embolic division of the male palp the mesal apophysis is forked, and its lateral arm is prolonged into a long tapering bristle that encircles the palp (Figure 101). The epigynum resembles *Epeirotypus, Plato,* or *Chthonos* in having a transverse groove sometimes interrupted by a longitudinal median ridge on the posterior margin (Figures 112, 124), but the vault is low and flat, not domed as in *Epeirotypus.*

DESCRIPTION.—Total length 0.5 to 2 mm (rarely to 2.4 mm). Carapace longer than wide, cephalic area much elevated; dark brown to light yellow-tan, or with light central area and periphery marked by characteristic dark figure (Figure 110). AME smaller than or subequal to PME, separated by ½ their diameter, PME separated by at least ¾ diameter, never juxtaposed (Figures 111, 123). Clypeus usually 2 times AME diameter. Sternum smooth or papillate, tan to dark reddish brown, sparsely bristled, always truncate behind, often incised. Legs yellow-tan or annulate dark and light, short and stout. Fourth legs longest, relatively slender, tibial trichobothria quite long. First femur diameter ½ sternum width. Abdomen smoothly ovoid or with anterior and/or posterior tubercles, higher than long or wide, often wider than long, always overhanging carapace; light yellow to dark reddish brown.

Epigynum a flat vault with posterior marginal groove. No scape, lateral spurs, or lateral pits. Interior ducts convoluted (Figure 113). Palp as



FIGURES 99–102.—*Ogulnius gloriae* (Petrunkevitch), from Puerto Rico, left male palp, embolic division exposed: 99, mesal; 100, apical; 101, sublateral; 102, cymbial lamella and paracymbium.
Scale lines: 100 μm.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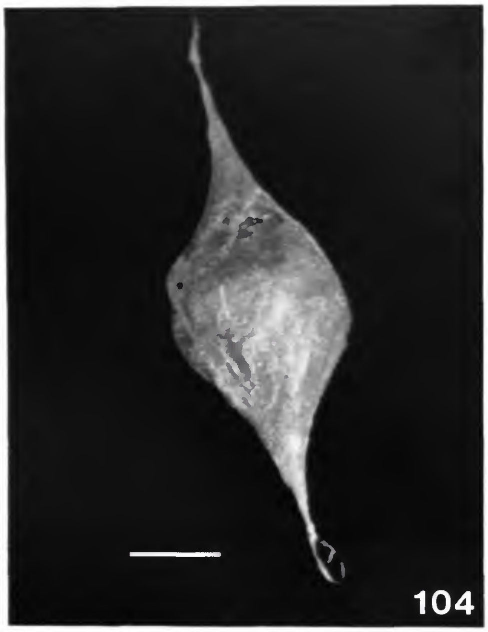
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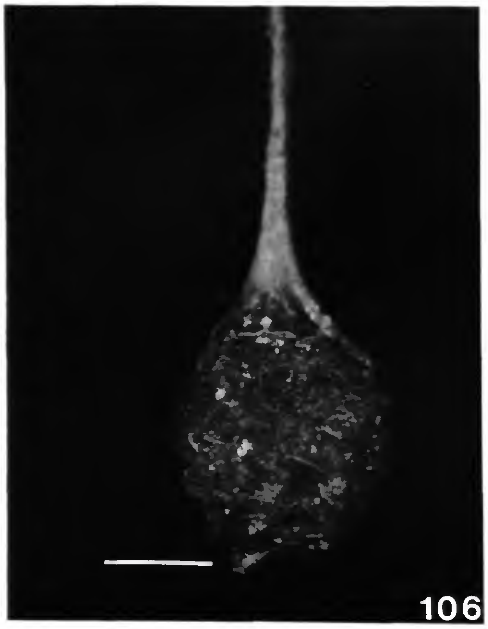
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FIGURES 103, 104.—*Ogulnius* sp. from Guatemala, ALTA VERAPAZ: 103, web; note three dimensional trajectories of radii, sticky spiral; 104, eggsac.

FIGURES 105, 106.—*Ogulnius gloriae* (Petrunkevitch), from Puerto Rico: 105, web; note two-dimensional trajectories of radii, sticky spiral; spider at upper center; 106, eggsac.

Scale lines: 103, 105, 10 mm; 104, 106, 1 mm.

in Figures 99–102, median apophysis a relatively extensive thin plate, often elongate, with one or two apophyses. Routing of reservoir simpler than in other genera (Figures 118, 119).

NATURAL HISTORY.—*Ogulnius* prefer very wet habitats; they usually require a water-saturated humid environment. Usually found within 0.2 m of ground, often in leaf litter, web attachment sites tend to be stationary and inflexible, such as stones, thick branches, or plant stem forks. All species observed construct simple, sparse, non-sticky silk networks on which the SS spiral winds in an irregular trajectory (Figures 103, 105), only vaguely resembling orbs. Frame lines absent, radii always attached directly to substrate, joining each other toward hub in an irregular series of trivalent nodes. Overall shape of web may be planar (Figure 105) or three dimensional (Figure 103). Dimensionality of non-sticky scaffolding strongly influences regularity of SS spiral. Spiders sit at the center of the web or at the end of a radius, face away from hub, and usually tense that radius slightly.

Eggsacs various, either double pointed pentagons or hexagons (Figure 104) or pendant teardrop-shaped leathery sacs (Figure 106). If the former, usually attached to web at both ends of sac, if the latter, suspended from a single silk line. Pendant eggsacs have a minute point opposite the suspension line, indicating that even pendant eggsacs are doubly attached when constructed (Figure 106).

Prey, as far as known, are nematocerous flies or other weak flying ectomorphic insects, often much larger than the spider (e.g., tipulids). General behavior of spider unusually sluggish and slow, never exhibiting the rapid attack behavior characteristic of other genera. Probably rely on extremely viscid, slack silk lines to catch long-legged, relatively weak prey that cannot escape once trapped. As in other genera, males often remain adjacent to female webs in their own small, non-sticky tangles.

SPECIES.—*Ogulnius* is at present second to *Theridiosoma* in numbers of species. It also is circumtropical, diverse, and undercollected. About 10–15 species, described and undescribed, are known from the Neotropics, some apparently endemic to various Antillean islands. The Old World fauna is also diverse. Species are difficult to distinguish because of small size and individual variation (Figures 99–100). *Epeirotypus gloriae* Petrunkevitch (1930) (see below) and *Tecmessa tetrabuna* Archer (1958) belong in *Ogulnius*. The following *Ogulnius* species also seem properly placed in the genus: *agnoscus* Strand, 1918, *pullus* Bösenberg and Strand, 1906, *clarus* Keyserling, 1886 (type examined), *cubanus* Archer, 1958 (type examined), *infumatus* Simon, 1897 (type examined), *obscurus* Keyserling, 1886 (type examined), *pallisteri* Archer, 1953 (type examined), *gertschi* Archer, 1953 (type examined), *fulvus* Bryant, 1945a (type examined), *latus* Bryant, 1948 (type examined), and *yaginumai* Brignoli, 1981. Some of the taxa may, however, be synonyms of each other; the matter needs further research.

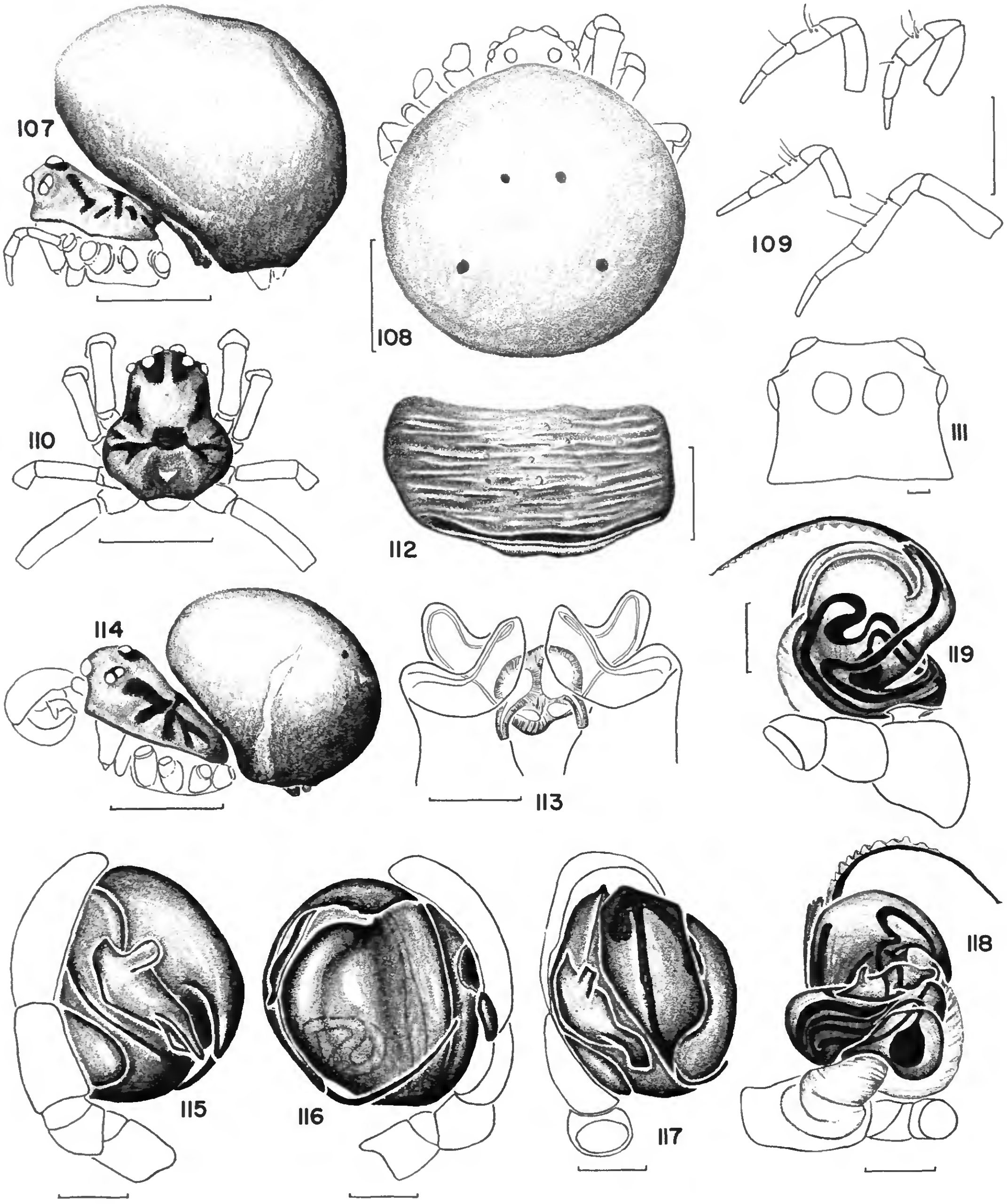
RANGE.—Circumtropical. *Ogulnius pullus* apparently extends its range into north temperate Asia.

Ogulnius obtectus O. Pickard-Cambridge

FIGURES 107–119; MAP 4

Ogulnius obtectus O. Pickard-Cambridge, 1882:433, figs. 9, 9a–d [♀].—Bonnet, 1956:1706.—Roewer, 1942:968.—Brignoli, 1981:12–13, figs. 1–2 [lectotype ♀]. [Lectotype ♀ and paralectotype ♀ designated by Brignoli (1981) from Brazil, "Amazon," in HDEO, examined.]

DIAGNOSIS.—*Ogulnius obtectus* may be recognized by the combination of lateral dark marks on the margin of the carapace (Figures 107, 110), the PME separated by twice their diameter (Figure 111), and the absence of posterior lateral tubercles on the abdomen. *Ogulnius tetrabuna* has the lateral dark marks, but the PME are closer together and the abdomen has posterior lateral tubercles. *Ogulnius gloriae* may have a mottled carapace, but the pattern is indistinct, and the background color of the carapace is much darker. In addition, *gloriae* also has posterior lateral tubercles, but *obtectus* does not.



FIGURES 107–119.—*Ogulnius obtectus* O. Pickard-Cambridge. Female: 107, 108, habitus; 109, left legs; 110, carapace; 111, eye group, frontal view; 112, epigynum, ventral; 113, same, dorsal, cleared. Male: 114, habitus; 115, left palp, mesal; 116, same, lateral; 117, same, ventral; 118, same expanded, mesal; 119, same, lateral.
Scale lines: 0.1 mm, except 107–110, 0.5 mm.

Description.—*Female:* From Colombia. Total length 1.5 mm. Cephalothorax 0.71 mm long, 0.87 mm wide, 0.55 mm high; light yellow, mottled around periphery (Figures 107, 110). PME $\frac{3}{4}$ AME diameter, PME separation twice their diameter, AME separation $\frac{1}{3}$ their diameter. ALE, PLE $\frac{2}{3}$ PME diameter, separated by their diameter from AME, PME. Clypeus height 1.2 AME diameter. Sternum 0.32 mm long, 0.37 mm wide, reddish brown, smooth, evenly truncate behind. Abdomen large for cephalothorax size, 1.2 mm long, 1.3 mm wide, 1.3 mm high; greatly overhanging carapace, almost obscuring eyes (Figure 107). Abdominal dorsum evenly reddish brown. Legs short, thick, yellowish brown, tibia 1 with retrolateral distal light patch, 4th leg longer than 1st.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.36	0.35	0.30	0.49
Patella	0.17	0.18	0.16	0.21
Tibia	0.19	0.20	0.18	0.26
Metatarsus	0.20	0.17	0.20	0.27
Tarsus	0.17	0.18	0.16	0.22
Total	1.09	1.08	1.00	1.45

Male: From Peru, Ucayali. Total length 1.2 mm. Cephalothorax 0.64 mm long, 0.59 mm wide, 0.60 mm high. Eye proportions as in female. Clypeus height 1.7 AME diameter. Sternum 0.38 mm long, 0.35 mm wide. Abdomen 1.0 mm long, 1.0 mm wide, 0.9 mm high. Abdominal shape as in female, with prolateral light streak (Figure 114). Color pattern of carapace, sternum, and legs as in female. Legs 1, IV subequal in length. Palp as in Figures 115–119.

Leg lengths of male described above (±0.03 mm).

	I	II	III	IV
Femur	0.39	0.37	0.25	0.40
Patella	0.16	0.16	0.13	0.16
Tibia	0.26	0.22	0.17	0.25
Metatarsus	0.25	0.25	0.20	0.24
Tarsus	0.20	0.21	0.19	0.21
Total	1.26	1.21	0.94	1.26

Variation.—Females range in lengths from 1.3 to 1.6 mm, males from 0.9 to 1.2 mm (two specimens). Abdominal coloration varies from a uniform reddish brown to forms with bilateral light patches defining a central dark line on the abdomen. All specimens have the characteristic pattern on the carapace. Archer (1953:19) stated that *obtectus* "has a series of pits on either side of the carapace." Neither the type series nor any other specimens referable to *obtectus* have pits on the carapace; presumably Archer mistook pigment for pits.

Natural History.—Nothing known. Collecting labels said "beaten from vegetation."

Range.—Colombia, Peru, and Brazil (Map 4).

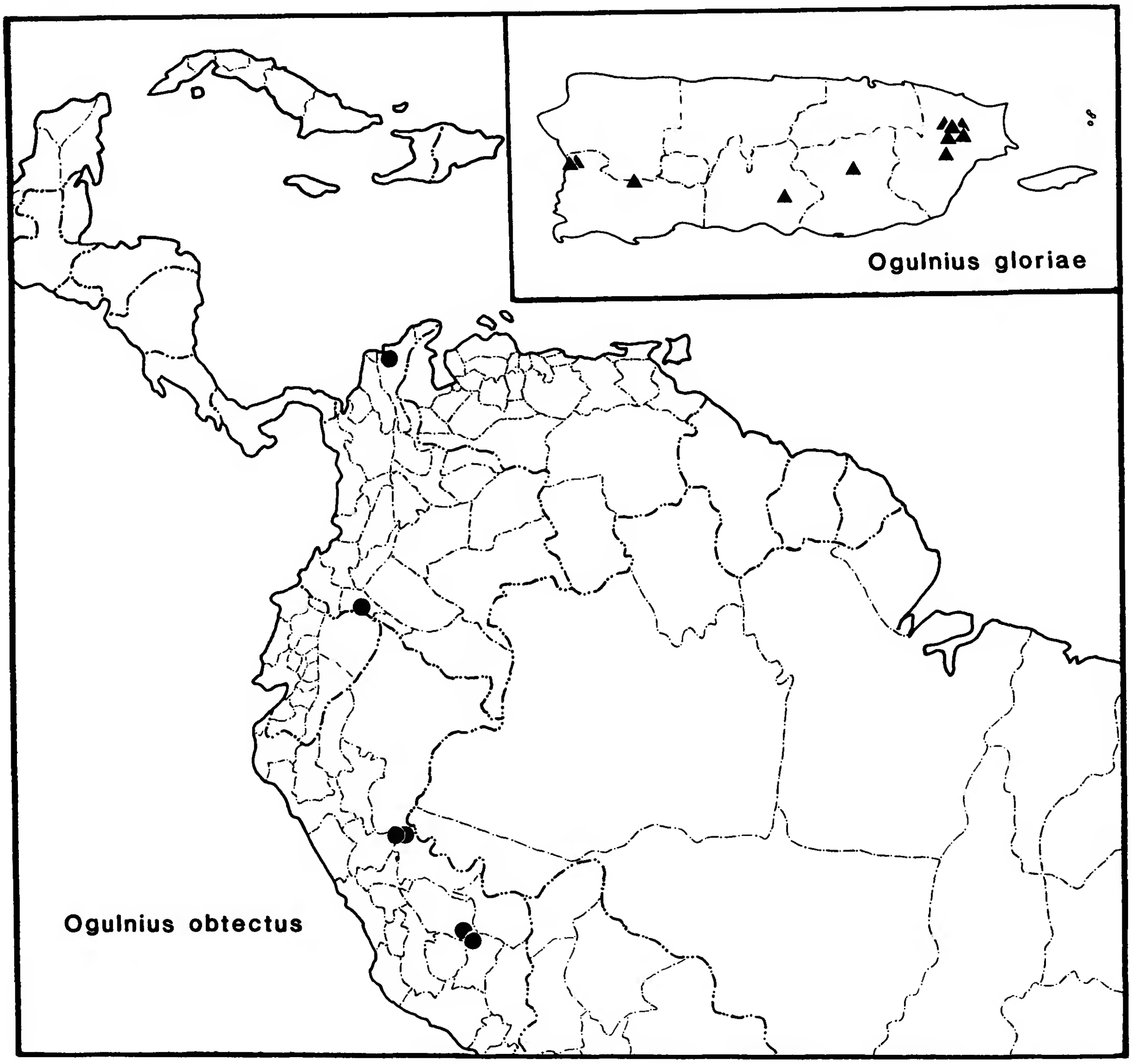
Records.—COLOMBIA. magdalena: Sierra Nevada de Santa Marta, San Pedro–San Javier, 1500 m (JAK). putumayo: Río Putumayo, nr Puerto Asís (probably 00°30′S, 76°31′W) (♀, MCZ). PERU. ucayali: "Colonia Callería, Río Callería," 15 km from Ucayali (♀, AMNH) (probably Callaría at 8°08′S, 74°35′W); Huánuco, Divisoria (probably on ucayali border between Tingo María and Pucallpa 9°05′S, 75°46′W) (♀, AMNH). cuzco: Machu Picchu above ruins, 2060 m (♀♀, ♂, AMNH); Torentoy Canyon, base of Machu Picchu 2000–2200 m (probably Torentoy, 15°10′S, 72°30′W) (♀, AMNH). BRAZIL. amazonas: exact locality unknown, not mapped.

Note.—The type series is from Brazil, but the locality is inexact ("Amazon"). Occurrence of other individuals in southeastern Colombia and northeastern Peru suggests that Mr. Traill collected the animal at the headwaters of the Amazon rather than farther downstream. The species covers a wide altitudinal range (150–2600 m), and abdominal color pattern varies considerably, but throughout this diversity the female genitalia and carapace color pattern remain constant.

Ogulnius gloriae (Petrunkevitch), new combination

Figures 99–102, 105, 106, 120–129; Map 4

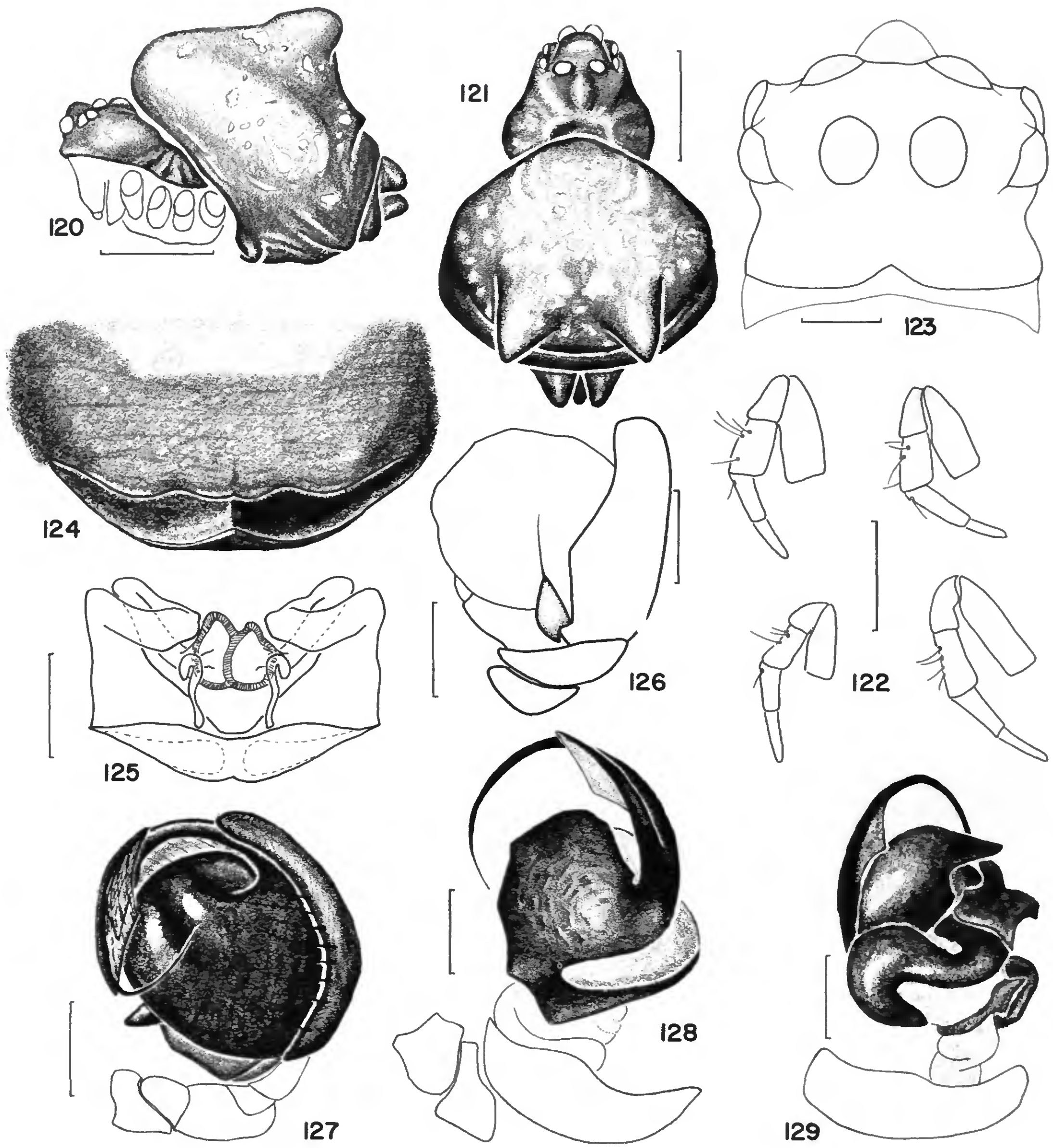
Epeirotypus gloriae Petrunkevitch, 1930:307, figs. 180–183 [♀], fig. 184 [web].—Bonnet, 1956:1706.—Roewer, 1942:968. [Holotype ♀ from Ponce, Coamo Springs (nr Coamo), Puerto Rico, in PMNH, examined.]



Map 4.—Distributions of *Ogulnius gloriae* (Petrunkevitch) and *O. obtectus* O. Pickard-Cambridge.

Diagnosis.—*Ogulnius gloriae* uniquely possesses three closely grouped tubercles (two above, one below) on the posterior of the abdomen (Figures 120, 121).

Description.—*Female:* From Puerto Rico, HUMACAO. Total length 1.9 mm. Cephalothorax 0.89 mm long, 0.65 mm wide, 0.69 mm high; chestnut brown, mottled around periphery, elongate ridge between PME (Figures 120, 121, 123). PME slightly smaller than AME, PME separation slightly more than their diameter, AME separation ⅓ their diameter. ALE, PLE ⅔ PME diameter, separated by ½ their diameter from AME, PME. Clypeus height 1.5 AME diameter. Ster-



Figures 120–129.—*Ogulnius gloriae* (Petrunkevitch), from Puerto Rico. Female: 120, 121, habitus; 122, left legs; 123, eye group, frontal view; 124, epigynum, ventral; 125, same, dorsal, cleared. Left male palp: 126, sublateral; 127, lateral; 128, expanded, lateral; 129, expanded, submesal.

Scale lines: 0.1 mm, except 120–122, 0.5 mm.

num 0.38 mm long, 0.38 mm wide, reddish brown, papillate, sharply truncate and notched behind. Abdomen very large for cephalothorax size, 1.7 mm long, 1.2 mm wide, 1.6 mm high; greatly overhanging carapace, almost obscuring eyes (Figure 120). Abdominal dorsum mottled, light flecks on dark brown background; two large anterior lateral tubercles, two indistinct posterior lateral tubercles, and three grouped small tubercles on posterior midline (Figures 120, 121). Legs short, thick (1st femur diameter ~½ sternum width), annulate with dark and light bands, 4th leg longer than 1st (Figure 122).

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.49	0.40	0.34	0.56
Patella	0.27	0.27	0.21	0.26
Tibia	0.27	0.25	0.22	0.32
Metatarsus	0.21	0.30	0.25	0.28
Tarsus	0.21	0.21	0.19	0.21
Total	1.45	1.43	1.21	1.63

Male: From Puerto Rico, HUMACAO. Total length 1.2 mm. Cephalothorax 0.64 mm long, 0.55 mm wide, 0.55 mm high; cephalic ridge as in female. PME ¾ AME diameter, separation 1 diameter, AME separation ⅓ their diameter. ALE, PLE ⅔ PME diameter, separated by ½ their diameter from AME, PME. Clypeus height 1.5 AME diameter. Sternum 0.34 mm long, 0.34 mm wide. Abdomen 0.7 mm long, 0.8 mm wide, 1.0 mm high. Color of carapace, sternum, abdomen and legs as in female. Leg lengths 1-2-4-3, proportionately longer and more slender than in female. Palp as in Figures 127–129.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.41	0.37	0.27	0.38
Patella	0.21	0.20	0.16	0.18
Tibia	0.28	0.27	0.21	0.24
Metatarsus	0.22	0.21	0.15	0.18
Tarsus	0.19	0.19	0.17	0.13
Total	1.31	1.24	0.96	1.11

Variation.—Females range in length from 1.6 to 2.4 mm, males from 0.9 to 1.2 mm. Color tan to almost black. Posterior lateral abdominal tubercles indistinct in some specimens.

Natural History.—The species occurs in humid shaded forest habitats or similar microclimates (for example, between shaded window bars or under roadside ferns). It seems less restricted to deep primary forest habitats than is typical of theridiosomatids. The web (Figure 105) lacks a hub, the number of radii rarely exceeds 10, and the sticky spiral spacing much exceeds the body length of the spider. The web is roughly planar and oriented vertically. Although the radii appear "anastomosed" as in those of *Theridiosoma* or *Epilineutes*, the anastomosis arises because the animals never make a well-formed hub during the construction of the non-sticky scaffolding. Thus not only does "radial anastomosis" in *Ogulnius* occur before, rather than after sticky spiral construction (in contrast to *Theridiosoma* and *Epilineutes*), but the anastomosis also occurs in a very different way. The two aspects of web architecture are only superficially similar in the final product, not homologous. The spider usually sits at the periphery of one of the upper radii, faces away from the web center, and slightly tenses that radius.

The eggsac is hard, leathery, pear-shaped, and suspended from nearby vegetation by a long silk line whose end nearer the sac is thickened. Spiderlings apparently escape through a hole they make on the side of the sac. A slight point opposite the suspension line (Figure 106) indicates that during construction eggsacs are doubly attached, and the lower end later cut free.

Prey items collected from webs in a window frame comprised mostly tipulids whose body length and certainly leg span much exceeded that of the spiders or the sticky spiral spacing of their webs. Forest spiders caught mainly midges and mosquitos.

Range.—Apparently endemic to Puerto Rico (Map 4), although similar, undescribed species occur on Cuba, Hispaniola, and Jamaica.

Records.—PUERTO RICO. GUAYAMA: Cidra (immature, AMNH). HUMACAO: La Gloria, Luquillo Range (♀ paratype, YALE); El Yunque

(♀♀, ♂, MCZ, AMNH); Río Piedras (♀, AMNH); Luquillo Forest, aviary (♀♀, ♂♂, MCZ); trail to summit of El Toro (♀♀, ♂, MCZ); Rt. 191, roadside (♀♀, MCZ). MAYAGÜEZ: Bosque Estado de Maricao, 2400′ (♂♂, AMNH); Mayagüez (♂, AMNH); Mayagüez, University campus. PONCE: Coamo Springs Hotel, on plants near spring (♀, holotype, PMNH).

Ogulnius tetrabuna (Archer), new combination

Tecmessa tetrabuna Archer, 1965:130.

THERIDIOSOMATINAE Simon

DIAGNOSIS.—Theridiosomatinae includes *Baalzebub, Epilineutes, Theridiosoma,* and *Wendilgarda,* and is diagnosed by the following derived characters: embolic division divided into bristle-like parts or broad, blunt apophyses (Figures 131, 136, 162, 190, 198); median apophysis with dorsal groove or trough (Figures 135, 163, 189, 196); denticles on tegular margin beneath distal lip of conductor (Figures 130, 135, 197); row of short, uniform bristles on cymbial margin opposite cymbial lamella (Figures 147, 153, 186, 211); epigynum with lateral pits (Figures 151, 173, 213, but absent in *Baalzebub*); routing of reservoir inside tegulum more complex than that of other genera (Figures 146, 147); junction of reservoir and fundus dentate.

Theridiosoma O. Pickard-Cambridge

Theridiosoma O. Pickard-Cambridge, 1879:193.—Bonnet, 1959:4432.—Roewer, 1942:969.—Archer, 1953:6.—Brignoli, 1983:240. [Type-species by monotypy *T. argenteolum* O. Pickard-Cambridge, 1879:194, pl. 12: fig. 8a–g (♀) (=*T. gemmosum* (L. Koch)). Female from Bloxworth, Dorset, England, in BMNH, apparently lost. The name is neuter.]

Microepeira Emerton, 1884:320, pl. 34: fig. 7 [♀], pl. 38: figs. 1 [♂], 2–4 [♀] [type-species by monotypy *Epeira radiosa* McCook, 1881; objective synonym of *Theridisoma radiosum* (McCook) (= *T. gemmosum* (L. Koch))].

Actis McCook, 1889a:180 [type-species by monotypy *Epeira radiosa* McCook, 1881 (see above); objective synonym of *Theridiosoma radiosa* (McCook) (= *T. gemmosum* (L. Koch))].

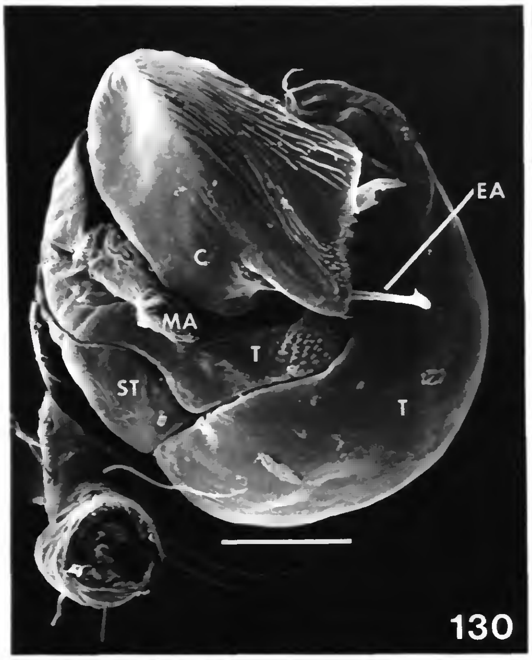
Andasta Simon, 1895:918 [type-species by monotypy *A. semiargentea* Simon; female from Ceylon, in MHNH, Paris, examined]. [New synonymy.]

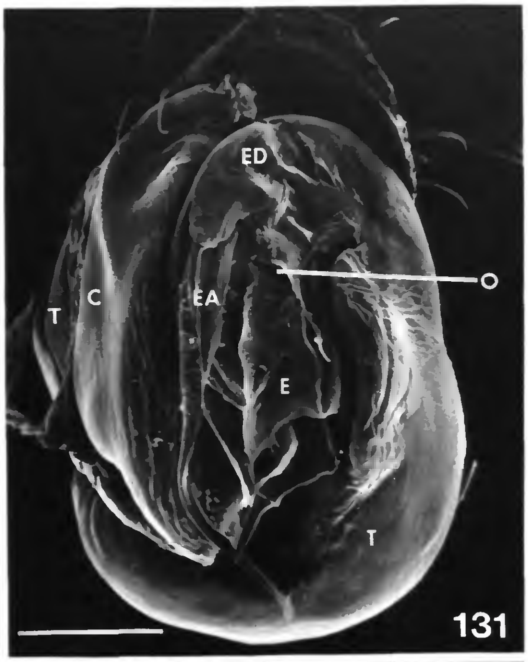
NOTE.—*Andasta semiargentea* does not differ substantially from the generic diagnosis given below, hence the generic name is considered a junior synonym of *Theridiosoma.* Without doubt some species groups of *Theridiosoma* will merit generic status, but much more research is required to assure the monophyly of those groups. Until the cladistic relationships within the genus are better understood, it seems best to adopt a broad definition.

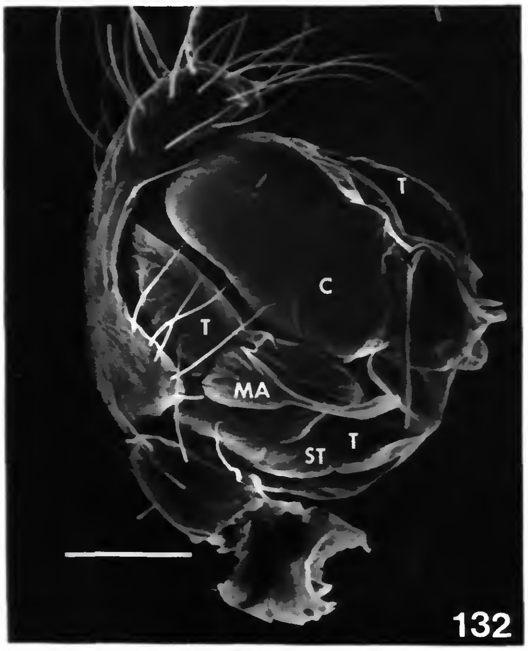
DIAGNOSIS.—*Theridiosoma* differs from all other theridiosomatids by the form of the embolic division—a short, tubular embolus with the embolic apophysis fragmented into several long bristle-like parts (Figures 131, 133, 137). The embolus of *Plato, Chthonos, Epeirotypus,* and *Naatlo* are strongly sclerotized tubes longer than those of *Theridiosoma,* and they have no embolic apophyses. The embolic division of *Ogulnius* is more similar to that of *Theridiosoma* in having an embolic apophysis, but it is at most bifid, not fragmented, and much longer.

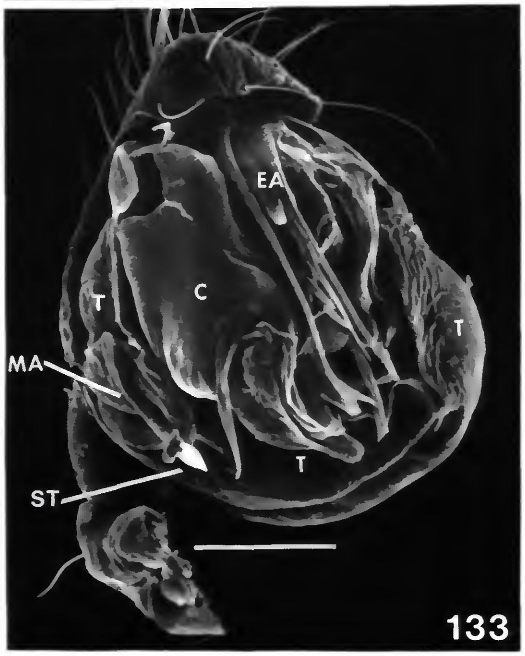
The embolic divisions of *Baalzebub, Epilineutes,* and *Wendilgarda* also have a short tubular embolus and embolic apophyses divided distally, but the apophyses are broad and blunt, three-parted, and not fragmented into many bristle-like parts. The embolic division is normally hidden beneath the conductor, but its form—whether broad and blunt or fragmented and bristle-like—can be discerned without dissection because the conductor is usually translucent (cf. Figures 149, 155, 178, 187).

In addition, the median apophysis of *Theridiosoma* is consistently a curved lobe attenuate distally with a slight groove along its upper long axis (Figures 130, 132, 135). The median apophyses of *Baalzebub, Epilineutes,* and *Wendilgarda* also are grooved along their upper surfaces, but the groove is deeper. The median apophyses of *Epilineutes* and *Wendilgarda* are square or sub-









FIGURES 130, 131.—*Theridiosoma goodnightorum* Archer, from Costa Rica, HEREDIA, left palp: 130, ventral, embolic division enclosed; 131, apical, embolic division exposed.

FIGURES 132, 133.—*Theridiosoma* sp. from Costa Rica, LIMON, left palp: 132, mesal, embolic division enclosed; 133, ventral, embolic division exposed.

Scale lines: 100 μm.

rectangular and they do not taper to a fine point as does that of *Theridiosoma*. The median apophysis of *Baalzebub* somewhat resembles that of *Theridiosoma*, but it is more heavily sclerotized, deeply cleft, and not so attenuate.

Female *Theridiosoma* have relatively firm, robust copulatory ducts leading from the bursa to the spermathecae (Figures 145, 152). Ducts of *Baalzebub, Epilineutes*, and *Wendilgarda* are delicate, plicate, and usually collapsed, and so the lumen of the duct is difficult to discern. The latter genera also have some sort of functional scape—either a spiniform or blunt projection of the ventral epigynal wall, or the entire wall is prolonged posteriorly into a triangle.

The posterior median eyes of *Theridiosoma* species are juxtaposed, nearly or in fact touching. The PME of *Baalzebub* and *Epilineutes* are also juxtaposed, and the genera cannot be separated by this character. Some *Naatlo* and *Epeirotypus* species have PME separated by as little as ⅓ diameter, but these species have "shoulders" lateral to the fovea, and their legs are shorter and thicker.

DESCRIPTION.—Total length 0.5 to 2.5 mm. Carapace dark brown to very light tan, occasionally with distinctive marks around eye region or fovea. Eyes nearly subequal, AME separated by about ½ a diameter, PME separated by at most ½ diameter (Figure 142). Chelicerae typical of family. Sternum smooth, sparsely bristled, usually with a dusky margin (Figure 140). Legs short or long, metatarsi usually shorter than tibiae (except leg III), uniform tan or segments annulate distally. Trichobothria as in family description, 4th trichobothria often 3–4 times tibial diameter.

Abdomen ovoid, higher than long or broad, dorsum very often with transverse thin light band and or symmetric light spots. Sides light grading to dark ventrally, venter dark.

Epigyna often with lateral sclerotized spurs projecting toward the median (*T. savannum, T. nechodomae, T. davisi, T. argenteolunulatum,* not illustrated), or a simple, flat or domed vault (Figures 143, 151). No scape or transverse groove on posterior epigynal lip. At least some species with lateral pits or depressions (Figure 151) in the epigynal plate. Copulatory duct routing moderately complex (Figures 145, 152).

Sexual dimorphism slight, males usually similar to female in color pattern, slightly smaller in stature, legs proportionately longer. The portion of the tegulum beneath the distal point of the conductor usually is a denticulate, smoothly curved surface (Figures 130, 133, 135).

NATURAL HISTORY.—Habitats preferred by *Theridiosoma* species are typical for the family, i.e., wet, shaded forest understory. All species known to date construct simple orbs with the radii joined together, or anastomosed, before they reach the hub. The 4–5 radial lines that do reach the hub are referred to as "hub radii." The spider anastomoses radial lines and constructs the hub radii after completion of the sticky spiral. The web usually has a tension line approximately normal to the plane of the orb, and by reeling it in the spider distorts the web into a cone (Figure 157). In a typical prey-ready posture the spider faces away from the hub, dorsal side up, the back four legs holding onto groups of radii or hub loops, the front four to the tension line, and the slack of the tension line piled on the eye group or held by the palpi. In at least some webs no hub loops exist, so it is only the grip of the spider's back legs on the hub radii that holds the hub together. If disturbed, spiders may "drop" one or more hub radii, and the hub portion then has to be rebuilt before the web can be tensed again. Consequently, many figures of *Theridiosoma* webs (McCook, 1889a,b; Wiehle, 1931) are of webs with rebuilt or repaired hub regions.

The eggsacs of all known species are papery or leathery in texture, pear-shaped, and suspended from twigs, leaves, or stones by a long silk line. Frequently the junction of the sac and line is marked by a distinct suture or cap—the sac dehisces at this point (Figure 158).

SPECIES.—*Theridiosoma* is the largest, most widespread genus in the family, mainly circumtropical, but ranging into north temperate regions in Europe, North America (*gemmosum*), and

Korea (*epeiroides*), and into south temperate regions in Australia and New Zealand (species undescribed). Approximately 20 species, described and undescribed, are known from tropical America, perhaps half that from the rest of the Tropics. Species can be distinguished by genitalic and color differences, but some are very similar (e.g., the *davisi* group).

Past workers tended to place new theridiosomatid species in *Theridiosoma:* hence many described species belong elsewhere. *Theridiosoma fauna* Simon, 1897, *splendidum* (Taczanowski, 1873), and *sylvicola* Hingston (1932) belong in the genus *Naatlo; globosum* (O. Pickard-Cambridge, 1896) in *Epilineutes; albinotatum* Petrunkevitch, 1930, and *brauni* Wunderlich, 1976, in *Baalzebub,* and *nigrum* (Keyserling, 1886) in *Wendilgarda* (where it was originally described). *Andasta semiargentea* Simon, 1901, and *A. genevensium* Brignoli, 1972, belong in *Theridiosoma* as here defined, but *Andasta cyclosina* Simon, 1907, is probably a theridiid.

The following species appear to be properly placed in *Theridiosoma: argenteolunulatum* Simon, 1897 (type examined), *benoiti* Roberts, 1978, *circuloargentum* Wunderlich, 1976, *davisi* Archer, 1953 (type examined), *epeiroides* Bösenberg and Strand, 1906 (figured by Brignoli, 1981), *fasciatum* Workman, 1896 (type examined), *goodnightorum* Archer, 1953, (type examined), *kikuyu* Brignoli, 1979, *lopdelli* Marples, 1955, *lucidum* Simon, 1897 (type examined), *nechodomae* Petrunkevitch, 1930 (type examined), *picteti* Simon, 1893 (figured by Brignoli, 1972b), and *savannum* Chamberlin and Ivie, 1944 (type examined). *Theridiosoma nelsoni* Bryant, 1945 (type examined), as Archer (1953) indicated, is a synonym of *savannum.*

The following species were not examined, and their placement in *Theridiosoma* cannot be confirmed by the existing descriptions: *blaisei* Simon, 1903b, *concolor* Keyserling, 1884, *latebricola* Locket, 1968, *nebulosum* Simon, 1901, and *obscurum* Keyserling, 1886. The holotype and only specimen of *concolor* is apparently lost. Simon (1903b:720) remarked that *blaisei* resembled *Ogulnius* in body form. The reported small size of the type (1.5 mm) lends credence to his comment; perhaps *blaisei* belongs in *Ogulnius.*

RANGE.—Mainly circumtropical, occasional extensions into temperate regions.

Theridiosoma gemmosum (L. Koch)

FIGURES 6–9, 134–137, 138–149, 157–160; MAP 5

Theridium gemmosum L. Koch, 1878:181, figs. 2 [eggsac], 6–8 [♀, ♂] [type series from Nuremberg, West Germany; possible syntypes exist at Vienna (NMW) and Oxford (HDEO)].

Theridiosoma argenteolum O. Pickard-Cambridge, 1879:194, fig. 8a–g [♀] [type ♀ from Bloxworth, Dorset, England, apparently lost (BMNH?, HDEO?)].

Theridiosoma gemmosum.—Simon, 1881:26.—Wiehle, 1931:130–135, figs. 210–213 [♀], 214, 215 [♂], 216, 217 [web, eggsac].—Wiehle, 1967:195, fig. 54 [♀].—Roewer, 1942:971.—Bonnet, 1959:4817.—Archer, 1953:16–17, figs. 29, 30.

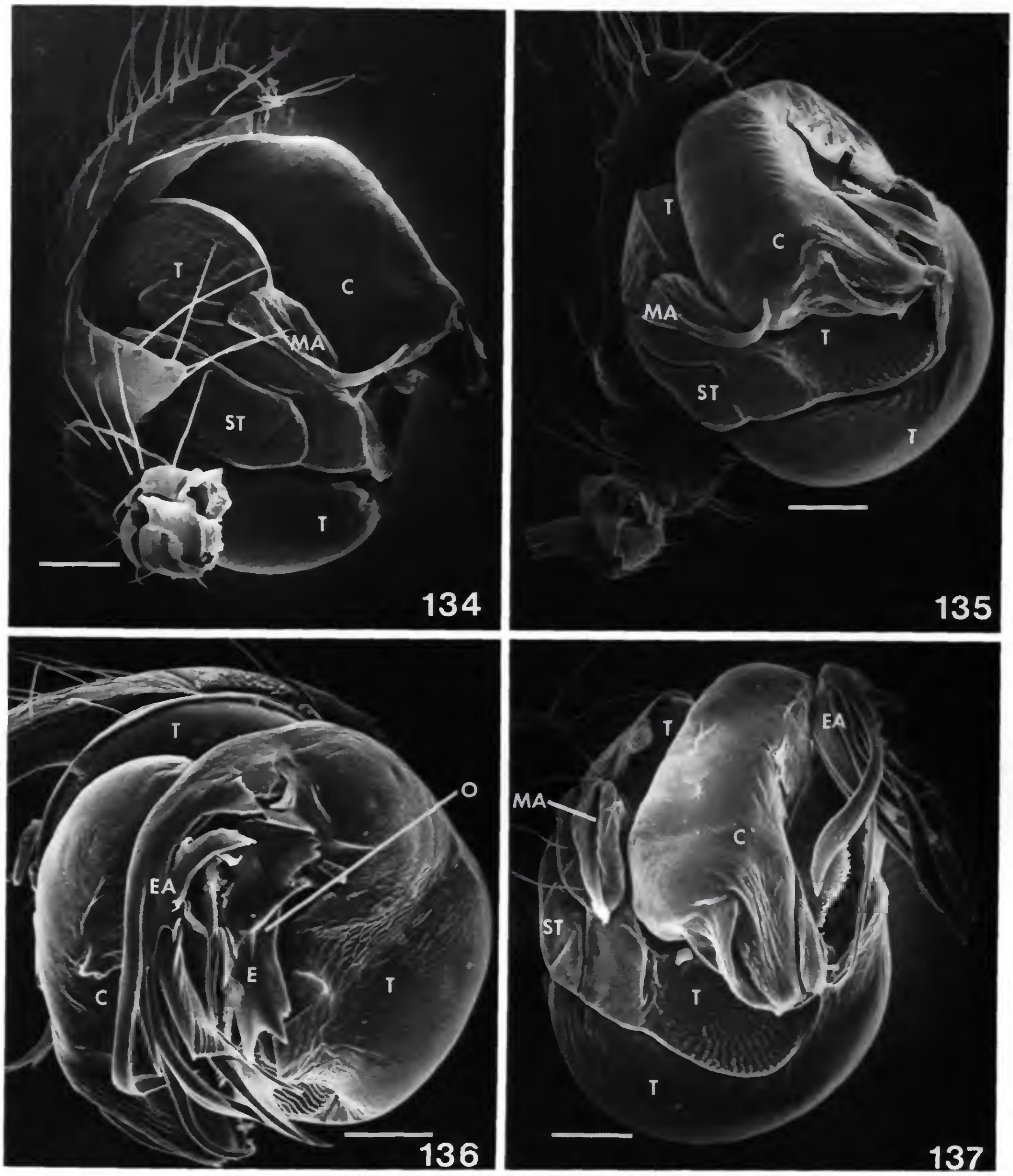
Epeira radiosa McCook, 1881:163, figs. 1–12 [all of webs].—Emerton, 1884:320, pl. 34: fig. 7 [♀], pl. 38: figs. 1 [♂], 2–4 [♀]. [Type probably lost, but specimens from McCook's collection at ANSP examined.]

Theridiosoma radiosum.—McCook, 1889b:195.

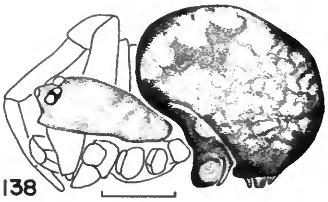
Theridiosoma argentatum Keyserling, 1886:218, fig. 132 [immature male holotype from Georgia, apparently lost (MNHN)]. [New synonymy.]

NOTE.—In his description, Koch based the name "*gemmosum*" on a pair of specimens, male and female. Koch's collection is now much dispersed. The BMNH has most of it, but no specimens that can be confirmed as types of *gemmosum.* Oxford has a series of *gemmosum* specimens, with correspondence documenting that Koch did send specimens of his new species to Pickard-Cambridge soon after he described it. These seem to qualify as syntypes and have been so labeled. Likewise, Vienna, which also has part of the Koch collection, has a male and female with catalog records indicating that they were collected in Nuremberg. These may also be syntypes, and have been so labeled. Because all available type specimens are *gemmosum,* no lectotype is here designated.

No museum seems to have specimens that can qualify as the types of *argenteolum.* Perhaps Pick-



FIGURES 134–137.—*Theridiosoma gemmosum* (L. Koch), left palp: 134, mesal, embolic division enclosed; 135, ventral, embolic division enclosed; 136, apical (damaged), embolic division exposed; 137, subventral, embolic division exposed.
Scale lines: 100 μm.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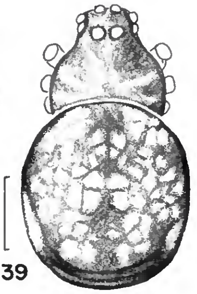
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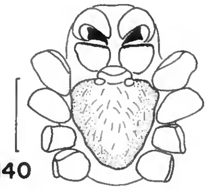
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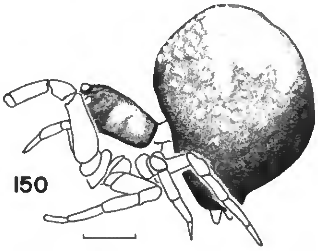
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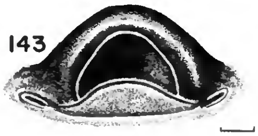
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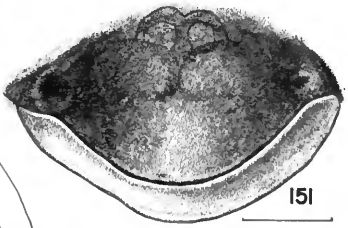
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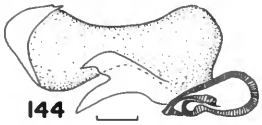
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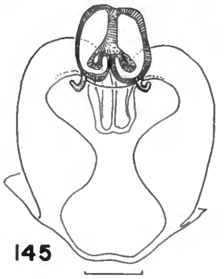
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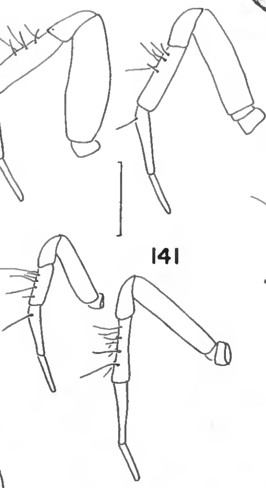
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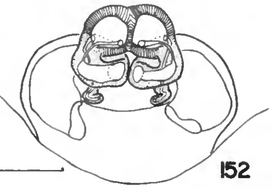
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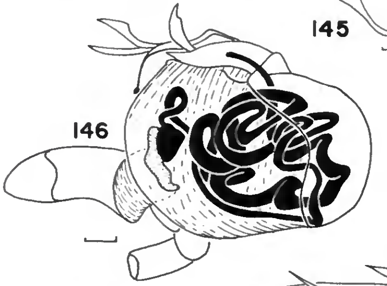
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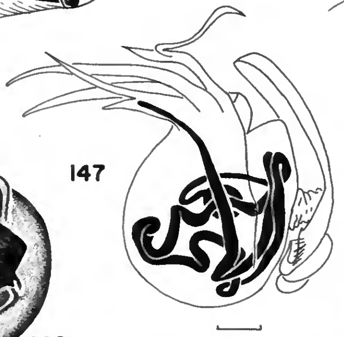
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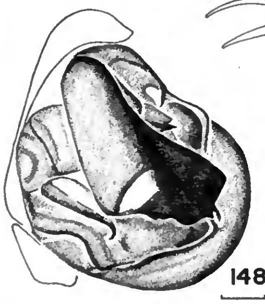
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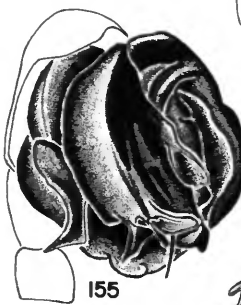
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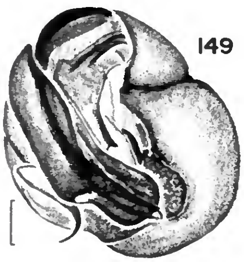
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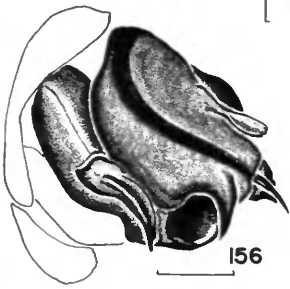
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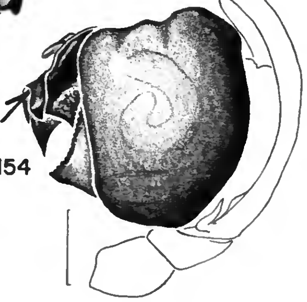
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ard-Cambridge, on receiving Koch's specimens, realized that his were the same and re-labeled them. On the other hand, no specimens located to date bear a Bloxworth label.

McCook did not usually designate holotypes or syntype series when he described species. Only one vial labeled *Theridiosoma radiosum* (lacking any data on locality or date) was found in his collection at the Academy of Natural Sciences in Philadelphia; it contains 12 *gemmosum* females in poor condition. No evidence suggests that these specimens are the ones McCook described in 1881. In fact McCook (1881) mentions having found the species at four localities in two states as well as numerous others not specifically named, and so it is very unlikely that the available specimens are part of the type series. McCook (1881) gave the first locality as "in the vicinity of Philadelphia, June 14, 1881," and other specimens from that region in the MCZ and AMNH are *gemmosum*. Archer collected specimens he labeled as topotypes; these are also *gemmosum*.

The synonymy of *radiosum* with *gemmosum* has, however, been disputed. McCook (1889a:180; 1889b:195) thought they were the same, and Roewer (1942) and Bonnet (1959) synonymized them, as did Kaston (1948), but the most recent author (Archer, 1953) maintained the taxa. Archer (1953:7) stated: "Indeed, there is no justification for uniting the European species with *T. radiosum* (McCook) or any North American species [i.e., *argentatum* or *savannum*]. The genitalia are readily distinguished in both sexes." After a careful study of series of North American material identified by Archer as either *radiosum* or *argentatum* and of several European *gemmosum* kindly provided by Alex La Touche, G.H. Locket, and J. Wunderlich, I find no consistent differences to support a differential diagnosis.

The type of *argentatum* has also apparently been lost. Only two theridiosomatid species occur in the southeastern USA, namely *gemmosum* and *savannum*. The color pattern of *savannum* is striking and distinctive, and Keyserling's verbal description fits *gemmosum;* hence argentatum is a synonym of *gemmosum*.

FIGURES 138–149.—*Theridiosoma gemmosum* (L. Koch). Female: 138, 139, habitus; 140, sternum; 141, left legs; 142, eye group, dorsal view; 143, epigynum, posterior; 144, same lateral; 145, same, dorsal, cleared. Left male palp: 146, expanded, subapical; 147, lateral; 148, ventral (drawing by H.W. Levi); 149, subapical (drawing by H.W. Levi).

FIGURES 150–156.—*Theridiosoma semiargentum* (Simon). Type female: 150, habitus; 151, epigynum, ventral; 152, same dorsal, cleared. Paratype male, left palp: 153, dorsal; 154, lateral; 155, apical; 156, submesal.

Scale lines: 0.1 mm, except 138–141, 150, 0.5 mm.

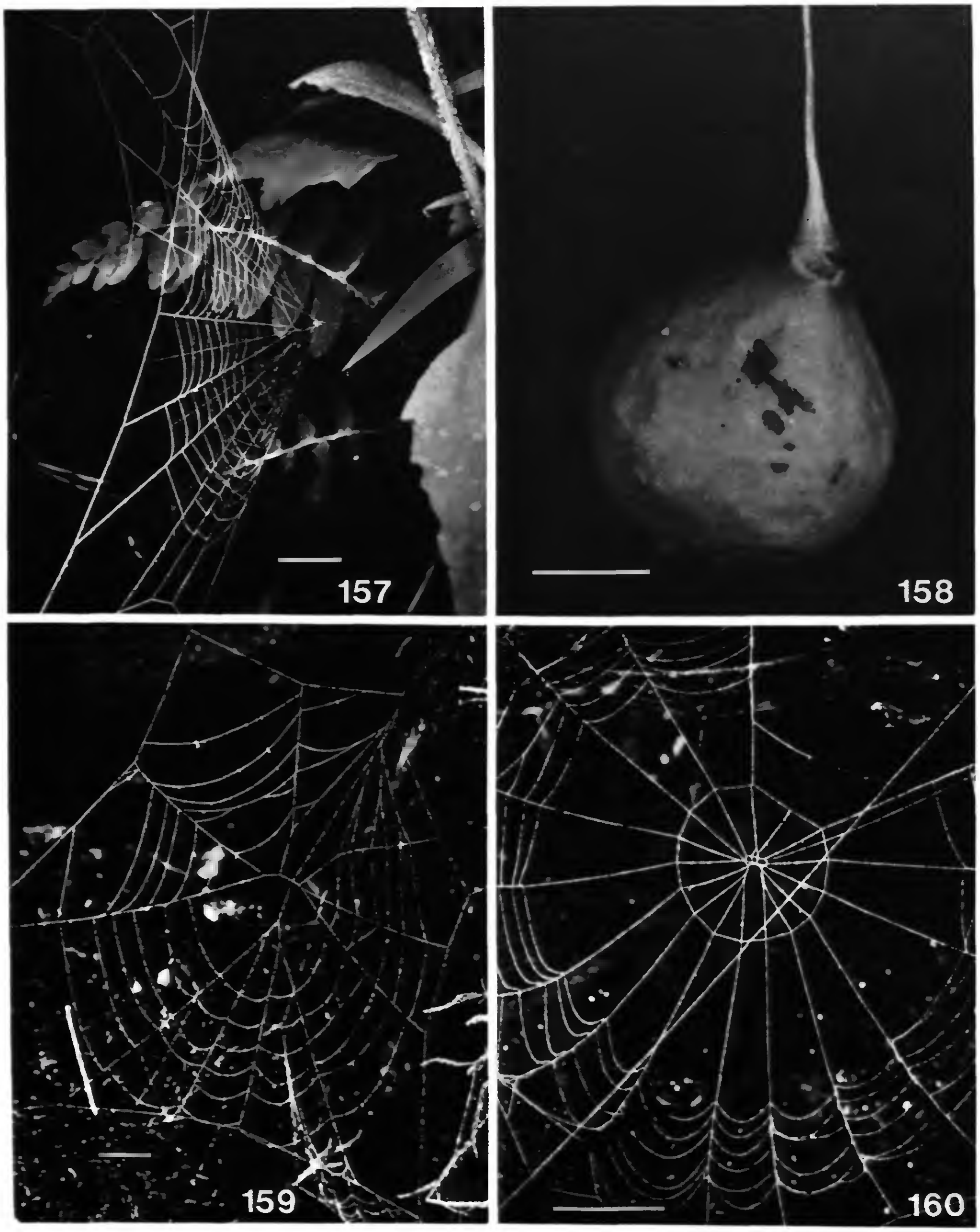
DIAGNOSIS.—*Theridiosoma gemmosum* is distinguished from all other *Theridiosoma* by the strongly sclerotized, protuberant, hood-shaped epigynum in the female (Figures 143–145), and the form of the conductor in the male (Figures 137, 148), which lacks the distal apophyses characteristic of *savannum* or *goodnightorum*.

DESCRIPTION.—*Female:* From USA, GEORGIA. Total length 1.9 mm. Cephalothorax 0.99 mm long, 0.86 mm wide, 0.84 mm high. Sternum 0.51 mm long, 0.49 mm wide. Cephalothorax olive tan with few radiating dark streaks; legs tan, segments darker distally. AME ¾ PME diameter, AME separation ½ their diameter, PME separation slightly less than ½ their diameter. ALE, PLE subequal to PME, separated from AME, PME by ½ their diameter. Clypeus height slightly more than ³⁄₂ AME diameter. Abdomen 1.29 mm long, 1.26 mm wide, 1.22 mm high; smoothly ovoid, overhanging carapace, dorsum (Figure 139) with central dark blotches interrupted by white guanine dots, sides (Figure 138) peppered with white dots, venter dark with fewer dots. Epigynum a smooth domed hood (Figure 143), protuberant in lateral view (Figure 138).

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.94	0.81	0.51	0.77
Patella	0.34	0.35	0.24	0.27
Tibia	0.67	0.57	0.32	0.41
Metatarsus	0.58	0.53	0.38	0.46
Tarsus	0.35	0.33	0.26	0.28
Total	2.88	2.59	1.71	2.19

Male: From USA, NORTH CAROLINA. Total



Figures 157–160.—*Theridiosoma gemmosum* (L. Koch): 157, web, lateral view; note tension line; 158, opened eggsac; 159, web, frontal view; note radial anastomosis and lack of tension line; 160, web showing incomplete sticky spiral and non-sticky "spiral" as a few central loops and one peripheral circle.
Scale lines: 10 mm, except 158, 1 mm.

length 1.9 mm. Cephalothorax 0.86 mm long, 0.83 mm wide, 0.84 mm high. Sternum 0.48 mm long, 0.45 mm wide. Eye group as in female, but AME on slight tubercle; clypeus height $\frac{5}{2}$ AME diameter. Abdomen 1.26 mm long, 1.24 mm wide, 1.29 mm high. Color of carapace, sternum, abdomen, and legs as in female. Palp with conductor produced into strong point (Figures 135, 148, 149) from which bristles of embolic apophysis barely protrude in resting state.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	1.09	0.91	0.56	0.76
Patella	0.38	0.34	0.27	0.30
Tibia	0.90	0.65	0.30	0.38
Metatarsus	0.74	0.62	0.44	0.51
Tarsus	0.35	0.32	0.27	0.27
Total	3.46	2.84	1.84	2.22

VARIATION.—Females range in length from 1.9 to 2.4 mm, males from 1.3 to 1.9 mm. In very light specimens the abdominal color pattern is often only white guanine dots on a light background; in dark specimens almost black. At least some males have paracymbia ending in sharp spines.

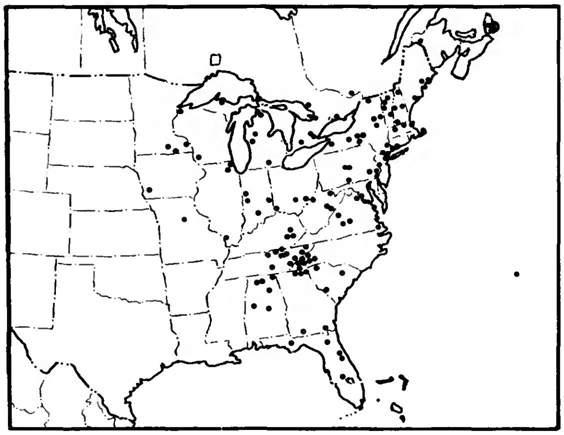
NATURAL HISTORY.—*Theridiosoma gemmosum* is common and widespread in eastern North America (Map 5). The species requires a damp habitat such as ravines, swamps, stream banks, wet cliff faces, or lush undergrowth. It is most typical of old-growth forest, but I have taken it occasionally in second-growth habitat. Only rarely is it found far from running water. Individual animals prefer web sites in dark, shaded situations. Females move away from the wet places they choose as web sites toward drier sites to construct eggsacs. Hence, as Kaston (1948:262) observed, the eggsacs often seem more common than the spiders. The eggsac (Figure 158) is pear-shaped, invariably suspended on a strong silk line at least 3–4 times the length of the eggsac itself. Frequently the suspension line forks before it reaches the substrate. The sac opens at a specific spot at its upper end, the spot marked in the intact sac by a suture.

In colder latitudes animals overwinter as subadults, and so in New England adults can be found as early as March. The adult population reaches a low in June and July in that region, and rises again in August and September. Hatchlings take about 5 weeks to mature. Farther south (e.g., Georgia, Alabama) reproduction is probably not seasonal.

Mating has been described by Gerhardt (1933). In New England males guard females (often even immatures) and will defend against other males. I have observed adult males in webs containing sticky silk—apparently they "rob" functional webs from females, as Eberhard et al. (1978) also observed in *Metazygia*. Males are frequently found on webs with guy lines, frames, and radii, but no sticky spirals, placed adjacent to those of females.

Theridiosoma gemmosum is usually considered a native European species (Locket and Millidge, 1953; Wiehle, 1931). In view of the apparent synonymy of *radiosum* and *gemmosum*, that inference should be questioned. In North America *gemmosum* has a large range, and it is both ubiquitous and common throughout. In Europe and the British Isles its occurrence is reportedly sporadic, despite the presence of suitable habitat. The sister taxa of the species will probably be found either in tropical America or eastern Asia (*epeiroides* is a very close relative). Although such questions cannot be conclusively settled, the evidence suggests that the species may be native to North America, and introduced to Europe. The species in North America often occurs in damp rock heaps or other such places, and might easily be transported with ship's ballast.

Web construction has been described by Wiehle (1931). The web (Figure 159) sometimes resembles that of *Epilineutes globosus*. The nonsticky spiral (Figure 160) has the form of two concentric circles. Most individuals spin webs with tension lines, but some construct completely planar webs. Some populations in the Appalachian Mountains appear to be monomorphic for either state. Individuals that spin tension lines at dawn will often remove them by mid-morning.



MAP 5.—Distribution of *Theridiosoma gemmosum* (L. Koch) in the Western Hemisphere.

Rough measurements indicate that adult females impose a force on the tension line of about 50 times their body weight when in a prey-ready posture.

RANGE.—Eastern North America (Map 5) and, from Wiehle (1931) and Bonnet (1959), England, Ireland, France, Germany, Hungary, Poland, "Balkans," Greece, and Corfu. Saito (1932, 1933, 1935) listed *gemmosum* from the northern Kurile Islands (off Korea) but did not figure the specimens; probably they are the very similar species *epeiroides*, which is native to that region.

RECORDS.—These records primarily include specimens from the MCZ and AMNH collections, and data are given only to county level.

USA. ALABAMA: BALDWIN (♀, AMNH); COOSA (♀♀, ♂♂, AMNH); CONECUH (♀, MCZ); JACKSON (♀, AMNH); TUSCALOOSA (♀♀, ♂♂, MCZ). CONNECTICUT: FAIRFIELD (♀♀, ♂♂, AMNH; see also Kaston, 1948:263). DISTRICT OF COLOMBIA (♀♀, AMNH). FLORIDA: ALACHUA (♀, WJG); CALHOUN (♀♀, ♂, MCZ); HIGHLANDS (♀, MCZ); ORANGE (♀, MCZ); SEMINOLE (♀, AMNH). GEORGIA: CHARLTON (♀♀, MCZ); RABUN (♀, MCZ); THOMAS (♀♀, ♂♂, MCZ); UNION (♀, MCZ). ILLINOIS: JACKSON (♀, AMNH); KANE (♀, AMNH); LAKE (♀, AMNH). INDIANA: LAWRENCE (♀♀, ♂♂, AMNH); MONTGOMERY (♀♀, ♂♂, AMNH); PARKE (♀♀, ♂, AMNH). IOWA: MONTGOMERY (♀, AMNH). KENTUCKY: BREATHITT (♀♀, ♂♂, AMNH); PERRY (?) (♀♂, AMNH); WOLFF (♂, MCZ). MAINE: HANCOCK (♂♂, MCZ, ♀♂, AMNH); LINCOLN (♀, MCZ). MASSACHUSETTS: BARNSTABLE (♀, AMNH); ESSEX (♀♀, ♂♂, MCZ); FRANKLIN (♂, MCZ); MIDDLESEX (♀, MCZ). MICHIGAN: CHEBOYGAN (♀♀, ♂, MCZ, AMNH); EMMET (♀♀, MCZ); HILLSDALE (♀♀, MCZ); MARQUETTE (♀♀, ♂, MCZ, AMNH); NEWAYGO (♀, MCZ); OSCEOLA (♂, MCZ). MINNESOTA: BLUE EARTH (♀, MCZ); FREEBORN (♀, MCZ); WINONA (♀♀, MCZ). MISSOURI: BOONE (♀, AMNH). NEW HAMPSHIRE: CARROLL (♀♀, ♂♂, MCZ); CHESHIRE (♀, MCZ); COOS (♀♀, ♂♂, MCZ); GRAFTON (♀♀, ♂♂, MCZ). NEW JERSEY: BERGEN (♀♀, ♂♂, AMNH); HUNTERDON (♀♀, ♂♂, AMNH).

NEW YORK: CORTLAND (♀, AMNH); DUTCHESS (♀♀, ♂♂, MCZ); ERIE (?) (♀, AMNH); FRANKLIN (♀, AMNH); FULTON (♀♀, ♂♂, MCZ, AMNH); HAMILTON (♂, MCZ); NASSAU (♀♀, ♂♂, MCZ); ROCKLAND (eggsacs, AMNH); SUFFOLK (♀♀, ♂♂, MCZ, AMNH); TOMPKINS (♀♀, ♂♂, MCZ, AMNH); WARREN (♂, AMNH); YATES (♀♀, ♂♂, AMNH). NORTH CAROLINA: BUNCOMBE (♀♀, ♂♂, MCZ, AMNH); HAYWOOD (♀, MCZ); JACKSON (♀♀, ♂♂, MCZ, AMNH); MACON (♀♀, ♂♂, AMNH); MCDOWELL (♀♀, ♂♂, MCZ, AMNH); NANTAHALA (♀♀, ♂♂, UVM); SWAIN (♀♀, ♂♂, MCZ); YANCEY (♀♀, ♂♂, MCZ). OHIO: HAMILTON (♀♀, AMNH); HOCKING (♀♀, ♂♂, AMNH); MEIGS (♀♂, AMNH). PENNSYLVANIA: BERKS (immature, AMNH); BUCKS (♀♀, ♂♂, AMNH); CENTER (♀♀, MCZ); FRANKLIN (♀♀, ♂♂, MCZ); PHILADELPHIA (♀, AMNH). SOUTH CAROLINA: AIKEN (♂, AMNH); OCONEE (♀, WJG); SPARTANBURG (♀, AMNH); SUMTER (♀, MCZ). TENNESSEE: ANDERSON (♀, MCZ); BLOUNT (♀, ♂, MCZ); GRUNDY (♀, AMNH); MACON (♀, WJG); MORGAN (♀, MCZ); OVERTON (♀, MCZ); SEVIER (♀♀, ♂♂, MCZ, AMNH); SULLIVAN (♀, MCZ); UNICO (♀, AMNH). VERMONT: ADDISON (♂, MCZ); CHITTENDEN (♀♀, ♂♂, MCZ); LAMOILLE (♀♀, ♂♂, MCZ); WINDSOR (♂, MCZ). VIRGINIA: AMHERST (♀♀, MCZ); AUGUSTA (♀♀, MCZ); FAIRFAX (♀, MCZ); NANSEMOND (♀, MCZ); PRINCE EDWARD (♀♀, MCZ). WEST VIRGINIA: PLEASANT (♀♀, MCZ); POCAHONTAS (♀♀, MCZ, AMNH); PRESTON (♀♀, MCZ); RANDOLPH (♀, AMNH). WISCONSIN: DOUGLAS (♀♂, MCZ); GRANT (♀♂, MCZ).

CANADA. NEW BRUNSWICK: EDMUNDSTON (CNC). NOVA SCOTIA: VICTORIA (CNC). ONTARIO: ALGOMA (♀♀, AMNH); HALTON (CNC); HASTINGS (CNC); MIDDLESEX (CNC); MUSKOKA (♀, MCZ); NIPISSING (♀♀, AMNH); PETERBOROUGH (CNC); WENTWORTH (♀♀, AMNH). QUEBEC: PERKINS (CNC).

Theridiosoma semiargenteum (Simon), new combination

FIGURES 150–156

Andasta semiargentea Simon, 1895:918.—Roewer, 1942:968.—Bonnet, 1955:320.—Archer, 1953:5.—Brignoli, 1972b:913–915, figs. 13–16 [♀,♂]. [Lectotype female (designation by Brignoli, 1972b) and paralectotype male from Kandy, Sri Lanka, in MNHN, Paris, examined.]

DIAGNOSIS.—*Theridiosoma semiargenteum* is distinguished from other *Theridiosoma* species by the simple epigynal vault (Figure 151), differently shaped from *gemmosum,* and in the palp by the shape of the spur on the conductor (Figure 156).

DESCRIPTION.—*Female:* Lectotype. Total length 2.3 mm (estimated, abdomen and cephalothorax separated). Cephalothorax 0.74 mm long, 0.52 mm wide. Sternum 0.34 mm long, 0.31 mm wide. Cephalothorax olive-brown, light patch around thoracic depression, legs yellow-tan, faint distal annulations. Abdomen 1.47 mm long, 1.70 mm wide, 1.78 mm high; olive brown, transverse light stripe of faint white dots (Figure 150). AME 3/4 PME diameter, separation 1/2 their diameter, PME juxtaposed. ALE, PLE subequal to AME, separated from AME by 1/2 AME diameter. Clypeus height 3/2 AME diameter. Epigynum a smoothly curved plate, with lateral pits barely visible under high magnification (Figure 151). Copulatory ducts as in Figure 152.

Leg lengths of female described above (±0.03 mm).

	I	II	III	IV
Femur	0.57	0.50	0.40	0.46
Patella	0.21	0.21	0.14	0.16
Tibia	0.37	0.34	0.18	0.28
Metatarsus	0.34	0.33	0.22	–
Tarsus	0.24	0.24	0.21	–
Total	1.73	1.62	1.15	?

Male: Not measured. Similar in overall appearance to the female, slightly smaller (total length 1.2 mm), legs proportionately longer, coloration similar. Palp as in Figures 154, 156.

VARIATION.—Only the type series is known.

NATURAL HISTORY.—Nothing known.

RANGE.—Kandy, Sri Lanka. In his original description, Simon also listed the species from the island of Taprobane, just north of Sri Lanka.

Theridiosoma genevensium (Brignoli, 1972), new combination

Andasta genevensium Brignoli, 1972b:911.

Baalzebub, new genus

TYPE-SPECIES.—*Baalzebub baubo,* new species (see below).

ETYMOLOGY.—*Baalzebub* is here taken to be a masculine noun and commemorates the early semitic deity. The Hebrew means literally "Lord of Flies."

DIAGNOSIS.—*Baalzebub* males have elongate tegula (Figure 186), small, pointed median apophyses with a trough so deep that the sclerite appears two-pointed (Figures 163, 187). *Baalzebub* females have epigynal plates shaped like backward-pointed triangles (Figure 183; Petrunkevitch, 1930, fig. 179; Wunderlich, 1976, fig. 18) with a central sclerotized pit.

Epilineutes have a median apophysis with a strong dorsal spine projecting from it, and the median apophysis is much larger and subrectangular. *Wendilgarda* also has a larger, subrectangular median apophysis. The trough of the median apophysis in these genera is only moderately deep compared to that in *Baalzebub.* The embolic division of *Baalzebub* (Figure 162) resembles that of *Epilineutes* in having four blunt, spatulate processes without the prolonged mesal bristle that characterizes *Wendilgarda.* The tegulum of *Baalzebub* is more elongate than in *Epilineutes* or *Wendilgarda* (Figure 186; Wunderlich, 1976, fig. 18); the mesal arm of the tegulum (bearing the median apophysis) angles upward towards the conductor in mesal view (Figures 163, 187), whereas in *Epilineutes* and *Wendilgarda* the tegulum arm dips down or is more or less horizontal.

Baalzebub females lack the lateral pits on the epigynal plate common to *Epilineutes* and *Wendilgarda*. As far as is known, *Baalzebub* spermathecae are fused only at the tip (e.g., Figure 184; Wunderlich, 1976, fig. 24), and, like *Epilineutes*, the course of the ducts as they approach the spermathecae (Figure 184) is less complex than in *Wendilgarda*. *Baalzebub* have juxtaposed PME; in *Wendilgarda* the PME are separated by at least their diameter.

DESCRIPTION.—Total length 1 to 3 mm. Carapace low in eye region (Figure 169), dark olive, dusky or tan, if light usually with dusky region around eye group. Eyes subequal, AME and PME juxtaposed or separated by at most ½ diameter (Figure 182). Sternum smooth, very convex, sparsely bristled, usually with dusky margin. Legs only moderately long and somewhat stout. Fourth tibial trichobothria often 3–4 times tibial diameter.

Abdomen ovoid, higher than long or broad, dorsum dark with symmetric light blotches (Figure 179); sides dark with lighter marks (Figure 182). Epigynum a backward-pointed triangle (Figure 183; Wunderlich, 1976, fig. 22). Spermathecae connate at tips, bursae thin-walled, wrinkled, with lateral wings or pockets (Figure 184). Central but no lateral pits on epigynal plate, and no transverse groove on posterior epigynal lip. Copulatory duct routing simple (Figure 184; Wunderlich, 1976, fig. 24).

Sexual dimorphism slight, male similar to female in color pattern, often subequal in stature, legs longer, clypeus slightly higher (Figure 185). Palp shape and median apophysis distinctive (Figures 161, 163, 187), and elements of embolic division quite short (Figures 162, 163). Conductor lacks apophyses, not geniculate, and bluntly pointed.

NATURAL HISTORY.—*Baalzebub* prefer darker sites than *Epilineutes*. For example, *B. baubo* and related (but undescribed) neotropical species occur in the interior of hollow logs, or under the lee of large fallen trees in Costa Rica and Guatemala. *Baalzebub baubo* has been collected in caves in Panama. *Baalzebub albinotatus*, however, does occur in somewhat sunnier habitats in Puerto Rico. *Baalzebub* don't build as close to water as do *Epilineutes* or *Wendilgarda*. Their webs are distinctive: complete orbs with a single hub circle, and no radial anastomosis (Figures 165, 167, 168). The single hub loop of *baubo* and *albinotatus* is constructed after the completion of the sticky spiral, as in *Epilineutes*, but the latter always removes the hub loop during the process of radial anastomosis. Tension lines are completely absent in *baubo* and *albinotatus*. Spiders do pull slightly on the radii when at the hub.

The eggsac of *baubo* is unknown, but that of *albinotatus* and an undescribed species from Guatemala (Figure 166) resemble those of *Epilineutes*—papery, pear-shaped, and suspended from twigs, leaves or stones by a long silk line. The junction of the sac and line is also marked by a distinct suture, but not a cap.

SPECIES.—*Theridiosoma albinotatum* Petrunkevitch, 1930, and *T. brauni* Wunderlich, 1976, belong in *Baalzebub*, hence *Baalzebub albinotatus*, new combination, and *Baalzebub brauni*, new combination. Perhaps 10–20 species, all undescribed, have been collected.

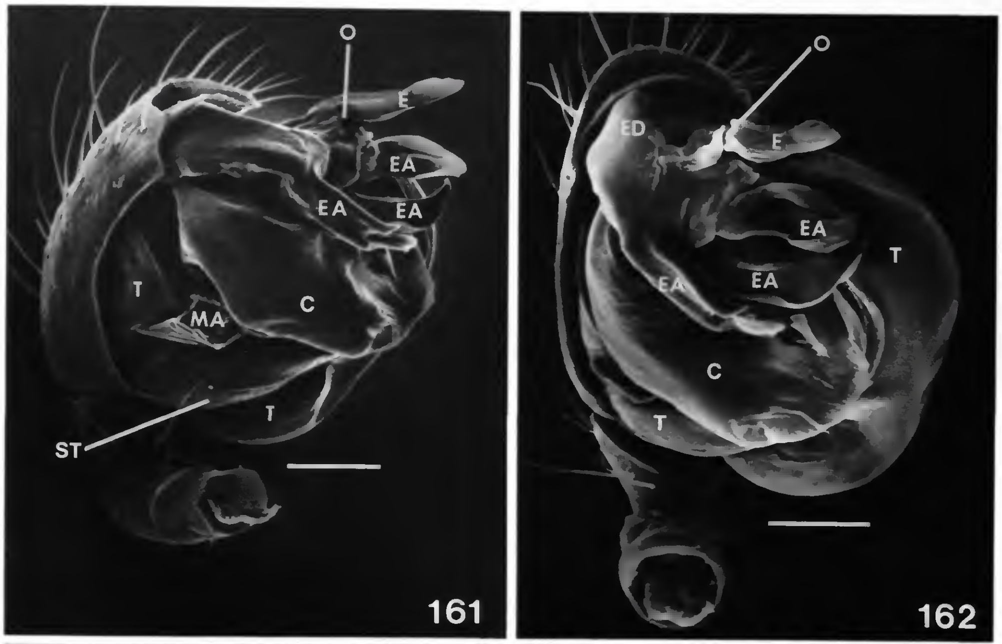
RANGE.—*Baalzebub* is widespread, circumtropical, but ranging into warm temperate regions in Australasia (*brauni*, and undescribed species). Thus far the genus is known from Mexico, Guatemala, Costa Rica, Panama, Colombia, Brazil, South Africa, Malaysia, New Guinea, Australia, and New Zealand.

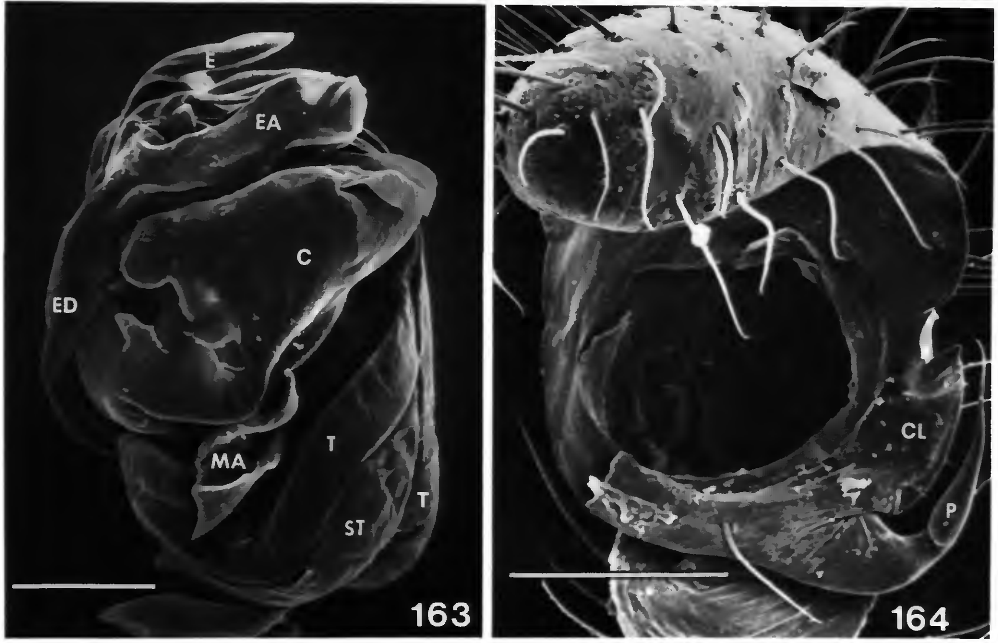
Baalzebub baubo, new species

FIGURES 161, 162, 179–187; MAP 6

TYPE.—♂ holotype from Costa Rica, Heredia Prov. nr Puerto Viejo, Organization of Tropical Studies Field Station Finca La Selva, ~50 m, J. Coddington, 28.ii. 1982: 1, in MCZ. Two paratype ♀♀ from same locality, J. Coddington, 15.xii. 1981: 1, in MCZ.

DIAGNOSIS.—*Baalzebub baubo* can be distin-





FIGURES 161, 162.—*Baalzebub baubo,* new species, left male palp, embolic division exposed: 161, mesal; 162, ventral.

FIGURES 163, 164.—*Baalzebub albinotatus* (Petrunkevitch), left male palp: 163, mesal, embolic division exposed; 164, paracymbium and cymbial lamella.

Scale lines: 100 μm.

guished by the shorter squatter palp proportions from *brauni* and *albinotatus* (Figure 162). *Baalzebub albinotatus* also has a median dorsal white stripe on the abdomen and is restricted to Puerto Rico (Petrunkevitch, 1930, figs. 177, 178). Other, undescribed species of *Baalzebub* occur in at least Guatemala and Colombia in the Neotropics, but their epigynal scapes are either more apiculate or blunter than that of *baubo*.

DESCRIPTION.—*Female:* From Costa Rica, HEREDIA. Total length 1.6 mm. Cephalothorax 0.69 mm long, 0.66 mm wide, 0.60 mm high. Sternum 0.41 mm long, 0.37 mm wide. Carapace olive with dusky blotches, sternum dark yellow, dusky margin, legs yellow with faint annulations. Eye diameters subequal, AME, PME separation ½, ⅓ their diameter. ALE separation from AME ½ diameter, PLE from PME by diameter. Clypeus height AME diameter. Abdomen 0.98 mm long, 0.86 mm wide, 0.98 mm high; smoothly ovoid, dorsum with symmetric light blotches on dark background (Figure 179), sides and venter also blotched. Epigynum as in Figures 183, 184.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.68	0.57	0.38	0.56
Patella	0.30	0.27	0.21	0.24
Tibia	0.38	0.35	0.22	0.34
Metatarsus	0.40	0.37	0.27	0.30
Tarsus	0.30	0.27	0.24	0.24
Total	2.06	1.83	1.32	1.68

Male: From Costa Rica, HEREDIA. Total length 1.5 mm. Cephalothorax 0.77 mm long, 0.65 mm wide, 0.69 mm high. Eye group as in female, cephalic region slightly higher (Figure 185). Clypeus height 2 times AME diameter. Sternum 0.38 mm long, 0.37 mm wide. Abdomen 0.96 mm long, 0.86 mm wide, 1.00 mm high. Color of carapace, sternum, abdomen, and legs as in female. Palp with elongate tegulum (Figure 186) and upturned mesal arm of tegulum (Figure 187). Median apophysis deeply cleft, denticulate on distal surface.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	0.86	0.77	0.48	0.60
Patella	0.31	0.29	0.22	0.22
Tibia	0.69	0.55	0.29	0.40
Metatarsus	0.48	0.43	0.31	0.33
Tarsus	0.29	0.29	0.22	0.24
Total	2.63	2.33	1.52	1.79

VARIATION.—Females range in lengths from 1.5 to 2.0 mm, males from 1.2 to 1.5 mm (3 specimens). Overall coloration usually very dark, posterior abdominal light blotches merge to form chevrons. Males may be much lighter in color. Animals from Panama are larger and lighter.

NATURAL HISTORY.—*Baalzebub baubo* are secretive, somewhat rare animals that live in dark places like hollow logs or under fallen limbs. The web is shown in Figure 168. Animals are usually at the hub at all times, occasionally at the periphery of one of the upper radii. The eggsac is unknown.

RANGE.—Costa Rica and Panama (Map 6).

RECORDS.—COSTA RICA. HEREDIA: nr Puerto Viejo, Organization for Tropical Studies Field Station La Selva (♀♀, ♂♂, MCZ). PANAMA. PANAMÁ: Lake Gatún, Barro Colorado Island (♀♀, ♂, MCZ); Chilibrillo Caves.

Baalzebub albinotatus (Petrunkevitch), new combination

Theridiosoma albinotatum Petrunkevitch, 1930:305.

Baalzebub brauni (Wunderlich), new combination

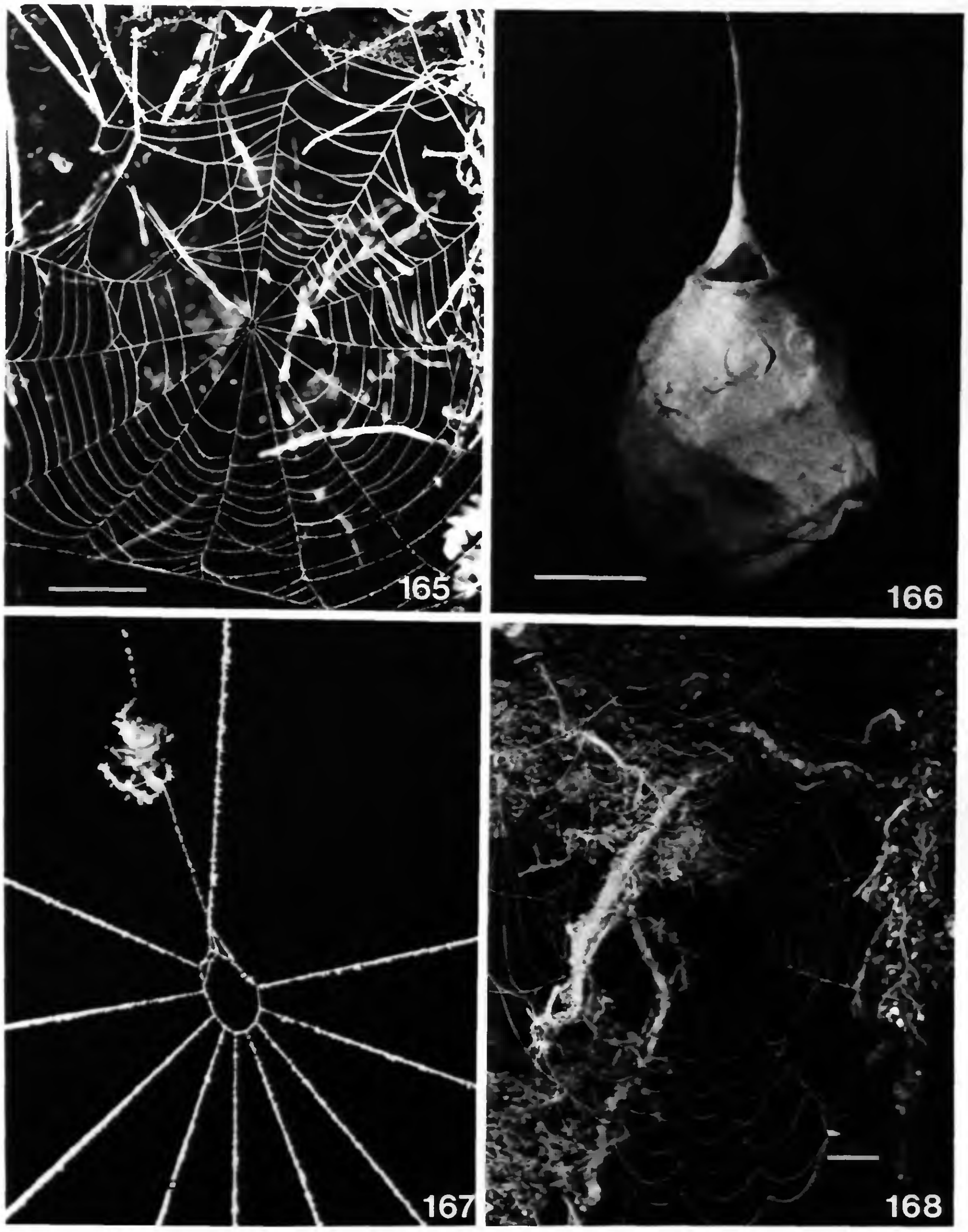
Theridiosoma brauni Wunderlich, 1976:117.

Epilineutes, new genus

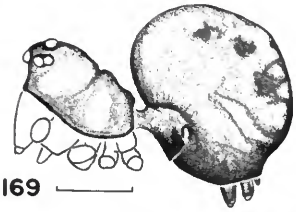
TYPE-SPECIES.—*Andrasta* [sic] *globosa* O. Pickard-Cambridge, 1896:192, pl. 24: figs. 5, 5a–f (♂), figs. 6, 6a–b (♀), see below.

ETYMOLOGY.—*Epilineutes* is a masculine Greek noun meaning "one who catches with a net."

DIAGNOSIS.—Male *Epilineutes* have a median



Figures 165, 166.—*Baalzebub* sp. from Guatemala, ALTA VERAPAZ: 165, web, frontal view; note single hub loop and lack of radial anastomosis; 166, opened eggsac.
Figure 167.—*Baalzebub albinotatus* (Petrunkevitch), from Puerto Rico, close-up of hub.
Figure 168.—*Baalzebub baubo*, new species, from Costa Rica, HEREDIA, web, frontal view; note lack of tension line.
Scale lines: 10 mm, except 166, 1 mm.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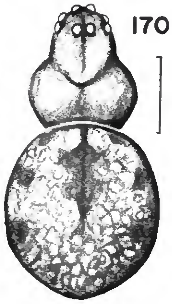
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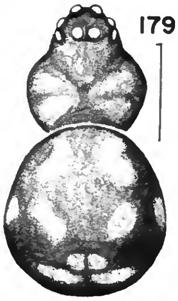
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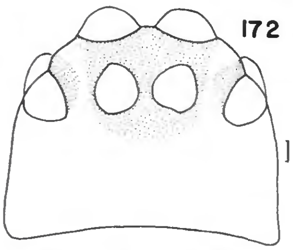
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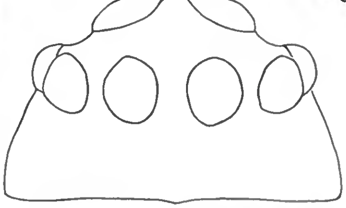
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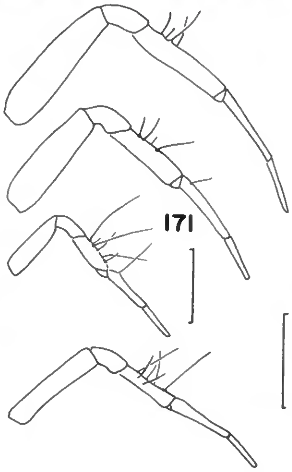
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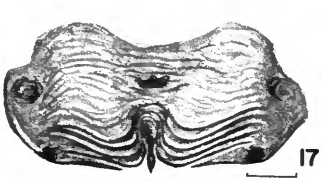
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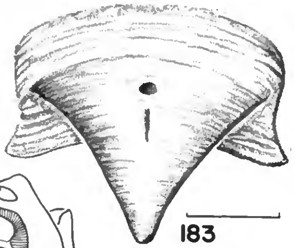
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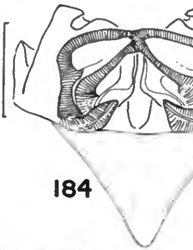
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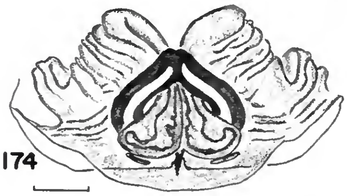
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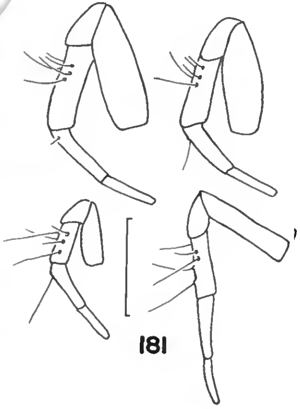
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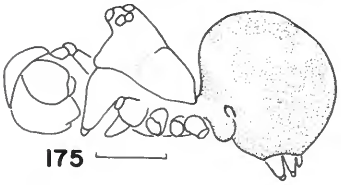
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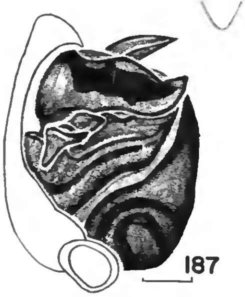
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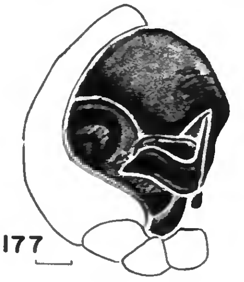
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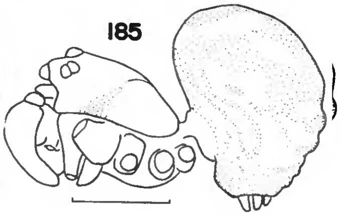
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apophysis with a strong dorsal spine projecting from it (Figure 189), a complex embolic apophysis with the median element prolonged (often greatly so, Figure 190), and a geniculate conductor (Figures 188, 190). Female *Epilineutes* have the posterior epigynal rim notched and a short, blunt or apiculate scape (Figure 174).

The median apophysis is squarish and has a moderately deep trough as in *Wendilgarda*. The embolic division (Figure 190) resembles that of *Wendilgarda*, in having four blunt, spatulate processes, the lateral one containing the distal tip of the embolic duct, the more mesal three composing the embolic apophysis. The embolic apophysis of *Epilineutes*, however, lacks the mesal, attenuate bristle characterizing *Wendilgarda*, and the processes of the embolic apophysis are broader and more blunt than in *Wendilgarda*. Female *Epilineutes* have a scape (Figure 173) reminiscent of that in *Wendilgarda*, but shorter and more pointed. *Epilineutes* spermathecae are connate at the tip, and the course of the ducts as they approach the spermathecae (Figure 174) is less complex than in *Wendilgarda*. Both sexes of *Epilineutes* have juxtaposed PME; in *Wendilgarda* the PME are separated by at least their diameter.

The embolic division of *Epilineutes* resembles that of *Baalzebub*, but usually the embolic apophysis elements are longer and more developed. In addition the embolus of *Epilineutes* does not protrude laterally from beneath the conductor. The median apophysis of *Epilineutes* is larger, squarish, and provided with a dorsal spine, rather than small and pointed as in *Baalzebub*. *Epilineutes* females all have a transverse, notched rim, not a posteriorly pointed, triangular epigynal plate as in *Baalzebub*.

DESCRIPTION.—Total length 0.5 to 2.5 mm. Carapace high in eye region (Figure 169), higher in male (Figure 175), light tan, usually dusky around eye group. Eyes subequal, AME, PME juxtaposed or separated by at most ¼ diameter (Figure 172). Sternum smooth, convex, sparsely bristled, usually with dusky margin. Legs long and slender, metatarsi subequal or longer than tibiae (except leg III); femora distinctively long, robust proximally, slender distally (Figure 171); uniform tan. Trichobothria as in family description, 4th trichobothria often 4–5 times tibial diameter (Figure 171).

Abdomen ovoid, higher than long or broad; coloration various, dorsum with light guanine speckles (Figure 173), dusky, or with broken transverse light bands and symmetric light blotches. Sides light, grading to dark ventrally (Figure 168), venter usually dark.

Epigynum often ridged, with blunt, notched rim, and short, pointed median scape (Figure 173). Spermathecae connate at tips, copulatory bursae thin-walled, wrinkled, with lateral wings or pockets. Epigynal plate with lateral and central pits (Figures 173, 174). No transverse groove on posterior epigynal lip. Copulatory duct routing simple (Figure 174).

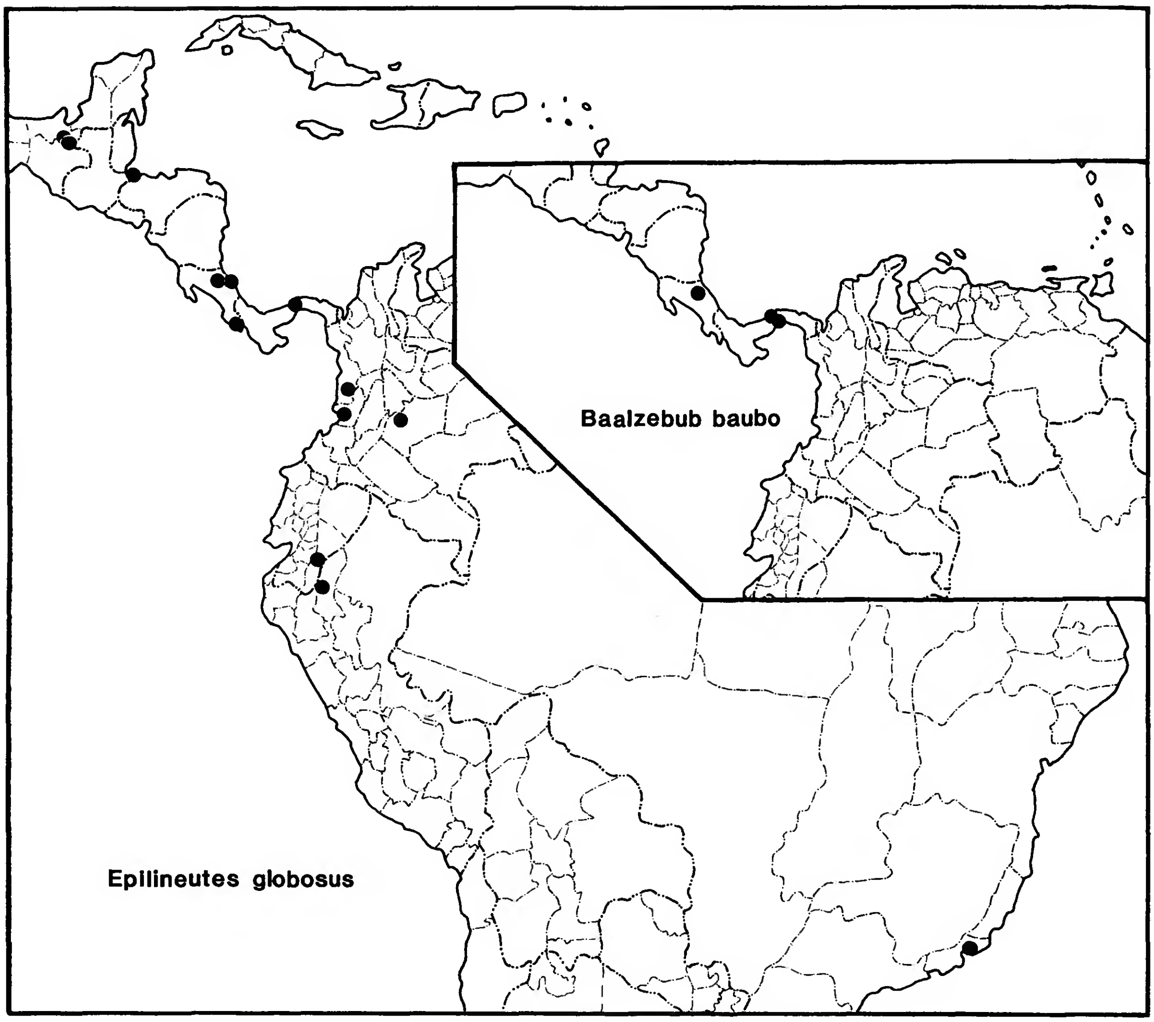
Sexual dimorphism slight, male color pattern usually similar to female, stature slightly smaller, legs proportionately longer, eye group proportionately much higher (Figure 175). Palpi with distinctive median apophysis (Figure 177), and divided embolic division (Figure 190, usually visible through translucent conductor, Figure 178). Conductor without apophyses, somewhat geniculate, prolonged towards tegulum (Figures 178, 188).

NATURAL HISTORY.—*Epilineutes* often build close to or over water in the same habitat as *Wendilgarda*, but they construct complete orbs (Figure 194). The central radii of the web are anastomosed, usually with 4–5 radii reaching the hub (Figure 192). The spider anastomoses radial

FIGURES 169–178.—*Epilineutes globosus* (O. Pickard-Cambridge). Female: 169, 170, habitus; 171, left legs; 172, eye group, frontal view; 173, epigynum, ventral; 174, same, dorsal, cleared. Male: 175, habitus; 176, left male palp, expanded, sublateral; 177, left male palp, mesal; 178, same ventral.

FIGURES 179–187.—*Baalzebub baubo*, new species. Female: 179, 180, habitus; 181, left legs; 182, eye group, frontal view; 183, epigynum, ventral; 184, same, dorsal, cleared. Male: 185, habitus; 186, left palp, lateral; 187, same, submesal.

Scale lines: 0.1 mm, except 169–171, 179–181, 0.5 mm.



MAP 6.—Distributions of *Baalzebub baubo*, new species, and *Epilineutes globosus* (O. Pickard-Cambridge).

lines and constructs the hub radii after completion of the sticky spiral. Tension lines are rare, but do occur occasionally, especially among juveniles or in the first web of the day spun by adults. In webs without tension lines, the spiders often "pull up" on one of the hub radii, although the web is never distorted as much as in *Theridiosoma*, where the tension line is routinely normal to the web surface. In at least some webs of *E. globosus* no hub loops exist, and the spider holds the hub together with its legs, as in many *Theridiosoma*. Also like *Theridiosoma*, the non-sticky spiral is in the form of one peripheral circle (Figure 195).

The eggsacs of all known species are papery, pear-shaped, and suspended from twigs, leaves or stones by a single, long silk line. The junction of the sac and line is marked by a distinct suture, but not a cap (Figure 193). The sac does open at this point.

SPECIES.—*Epilineutes* is thus far believed to be neotropical. Perhaps 5 or 10 undescribed species in this genus occur in the American tropics.

Epilineutes globosus (O. Pickard-Cambridge), new combination

FIGURES 169–178, 188–195; MAP 6

Andrasta [sic] *globosa* O. Pickard-Cambridge, 1896:192, pl. 24: figs. 5, 5a–f [♂], figs. 6, 6a–b [♀].—Bonnet, 1955:321.—Roewer, 1942:970. [A series of 3♂, 5♀ syntypes from Teapa, Tabasco, Mexico in BMNH, examined. *Andrasta* is a lapsus calami for *Andasta* Simon, 1895.]

Theridiosoma globosum.—F.O. Pickard-Cambridge, 1902: 414. Simon, 1903a:1007.—Bonnet, 1959: 4434.—Roewer, 1942:970.—Archer, 1953:11, fig. 16 [♀].

NOTE.—Both F.O. Pickard-Cambridge (1902) and Simon (1903a) questioned whether *globosus* was a synonym of *Theridiosoma argentatum* (= *T. gemmosum*). The ranges of the two species are completely disjunct, and their morphology very different.

DIAGNOSIS.—*Epilineutes globosus* can be distinguished by the large, ridged, protruding epigynal plate with a dark, pointed, short scape and the lateral dark spots on the epigynal plate in the female (Figure 173), and the very large palpal bulb with the embolic apophysis and median apophysis as in Figures 175–178 in the male. In particular the middle division of the embolic apophysis frequently protrudes from beneath the conductor (Figure 190), and shows as a dark stripe under the translucent conductor (Figure 178). Other *Epilineutes* species have scapes but they are more blunt or the epigynal plate is smaller in proportion and not as ridged.

DESCRIPTION.—*Female:* From Costa Rica, HEREDIA. Total length 1.9 mm. Cephalothorax 0.83 mm long, 0.71 mm wide, 0.55 mm high. Sternum 0.42 mm long, 0.40 mm wide. Carapace light yellow, dusky around eyes; sternum darker yellow, dusky margin; legs yellow with faint annulations. AME ⅔ PME diameter, AME, PME separation ¼ their diameter. ALE, PLE subequal to PME, separated from AME, PME by their diameter. Clypeus height 2 times AME diameter. Abdomen 1.29 mm long, 1.08 mm wide, 1.32 mm high; smoothly ovoid, dorsum with guanine speckles on light background (Figure 170), sides and venter also light. Epigynum as in Figures 173, 174.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	0.90	0.78	0.47	0.69
Patella	0.34	0.31	0.21	0.25
Tibia	0.63	0.51	0.27	0.38
Metatarsus	0.54	0.47	0.32	0.39
Tarsus	0.33	0.28	0.24	0.24
Total	2.74	2.35	1.51	1.95

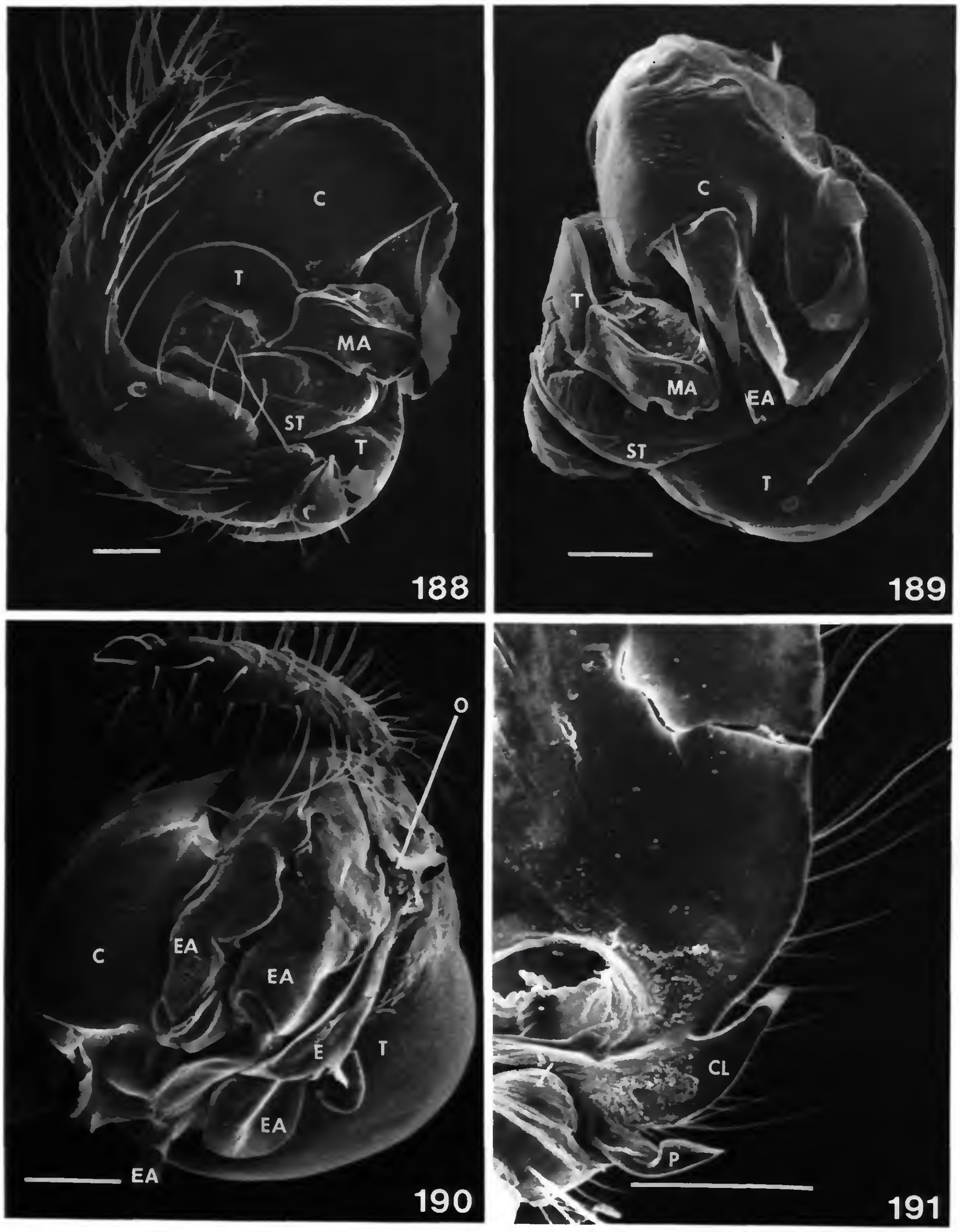
Male: From Costa Rica, HEREDIA. Total length 1.8 mm. Cephalothorax 0.74 mm long, 0.72 mm wide, 0.98 mm high. Eye group more compact than in female, cephalic region very high (Figure 175). Clypeus height 4 times AME diameter. Sternum 0.41 mm long, 0.43 mm wide. Abdomen 1.08 mm long, 1.03 mm wide, 1.20 mm high. Color of carapace, sternum, abdomen, and legs as in female. Palp large, conductor extended, almost touching tegular margin (Figure 178). Dorsal bristle on median apophysis prominent.

Leg lengths of male described above (±0.02 mm).

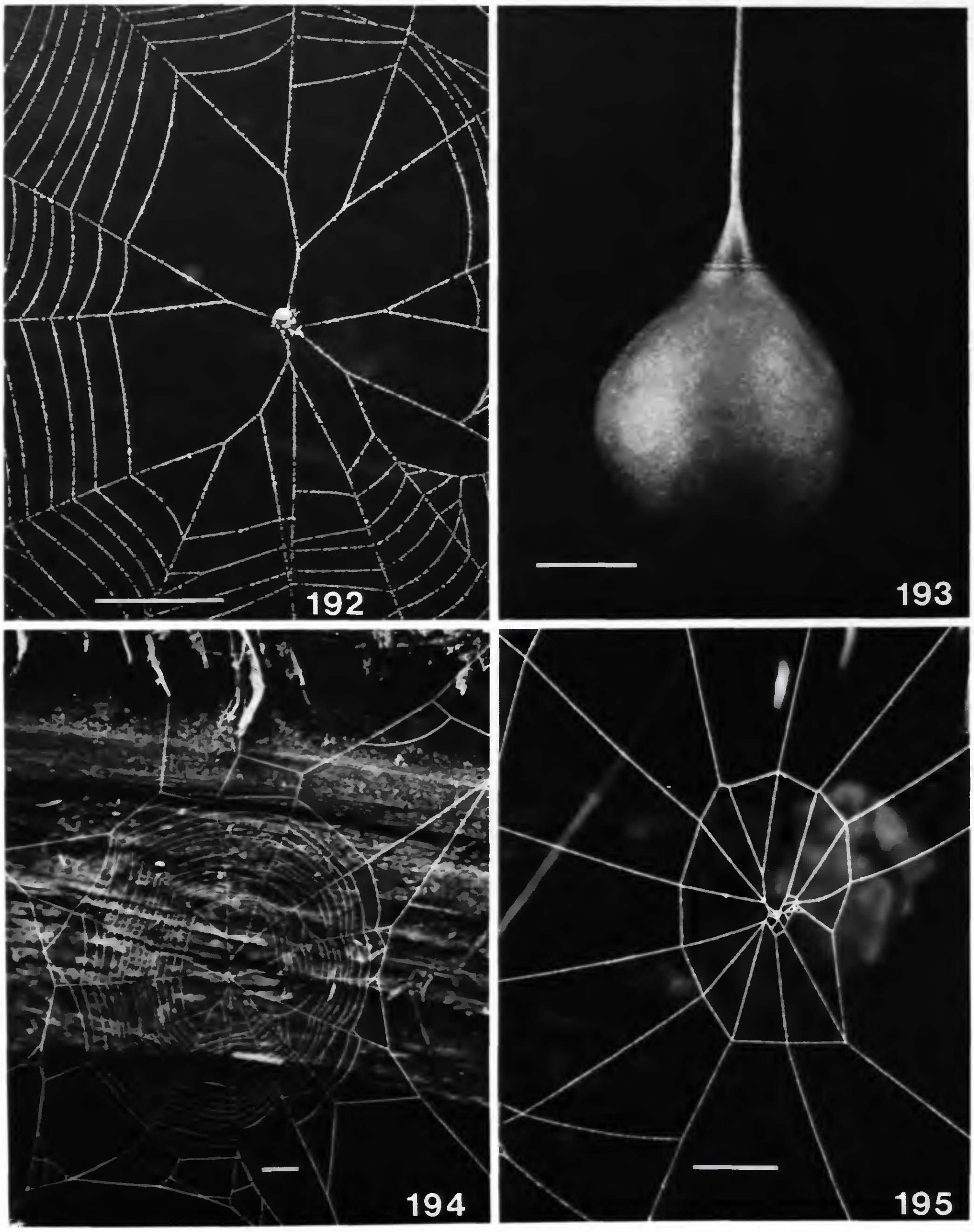
	I	II	III	IV
Femur	1.07	0.89	0.48	0.69
Patella	0.31	0.31	0.22	0.24
Tibia	0.74	0.64	0.29	0.40
Metatarsus	0.69	0.60	0.38	0.46
Tarsus	0.38	0.36	0.26	0.24
Total	3.19	2.80	1.63	2.03

VARIATION.—Females range in length from 1.7 to 2.6 mm, males from 1.5 to 1.9 mm. In very light specimens the abdominal color pattern is often only white guanine dots on a light background; darker specimens have a dark background with a pattern of light blotches. Animals from Mexico, including the type series, are smaller in stature than more southern populations.

NATURAL HISTORY.—*Epilineutes globosus* is a predictable part of the streamside fauna through-



FIGURES 188–191.—*Epilineutes globosus* (O. Pickard-Cambridge), from Panama, PANAMÁ, left male palp: 188, mesal, embolic division enclosed; 189, ventral, embolic division enclosed; 190, subapical, embolic division exposed; 191, paracymbium and cymbial lamella.
Scale lines: 100 μm.



FIGURES 192–195.—*Epilineutes globosus* (O. Pickard-Cambridge): 192, hub region of web; 193, unhatched eggsac; 194, web, frontal view; 195, incomplete web, showing non-sticky "spiral" as a few central loops and one peripheral circle.
Scale lines: 10 mm, except 193, 1 mm.

out the lowland tropics of Central America. Adults prefer the dark, moist hollows created by streamside cave-ins, or similar situations. Juveniles make webs in more open sites, often on snags in the middle of the stream. The web (Figures 192, 194, 195) resembles that of *Theridiosoma gemmosum*. The eggsac is a pear-shaped papery sac with a faint annulation at the junction of the single suspension line and the sac itself, and is laid some distance from the female's web (Figure 193). The males are commonly found on lines at the side of the female web.

RANGE.—Mexico, Guatemala, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, and Brazil (Map 6).

RECORDS.—MEXICO. TABASCO: Teapa (♀♀, ♂♂, BMNH). CHIAPAS: Palenque, Palenque ruins (♀♀, ♂♂, MCZ). GUATEMALA. IZABAL: Santo Tomás; Livingston (♀♀ ,♂♂, MCZ). COSTA RICA. HEREDIA: nr Puerto Viejo, Organization for Tropical Studies field station Finca La Selva (♀♀,♂♂, MCZ). LIMON: Cahuita (♀♀, ♂, MCZ). PUNTARENAS: San Vito, Organization for Tropical Studies field station Las Cruces (♀♀, ♂♂, MCZ). PANAMA. PANAMÁ:, Lake Gatún, Barro Colorado Island (♀♀, ♂♂, MCZ, AMNH); Gamboa (♀, MCZ); El Valle (♀♀, ♂♂, MCZ). COLOMBIA. META: ~15 km SW Puerto Lopez, Hacienda Mozambique, 200 m (♀♀, MCZ). CHOCO: between Cucurripi and Nanama, Quebrada Docordo, Río San Juan (♂, AMNH). VALLE: Central Hidalgo Anchicayá (♀♀, ♂, MCZ); Bajo Colima (on Colima River), nr Puerto Patião (♂, MCZ); Río Querada, Descansion (not located, not mapped, ♀, AMNH). ECUADOR. MORONA-SANTIAGO: Los Tayos Caves (♀♀, MCZ). PERU. AMAZONAS: Montenegro, 350 m (♂, AMNH). BRAZIL. RIO DE JANEIRO: Teresópolis (♀♀, MCZ, AMNH).

Wendilgarda Keyserling, 1886

Wendilgarda Keyserling, 1886:129.—Bonnet, 1959: 4816.—Roewer, 1942:971.—Archer, 1953:14. [Type-species by original designation *Wendilgarda mexicana* Keyserling, 1886:130, pl. 15: fig. 208a–c (♀). The name is feminine.]

Enthorodera Simon, 1907:264 [type-species by monotypy *E. atricolor* Simon, 1907:265]. [New synonymy.]

Cyathidea Simon, 1907:265 [type-species by monotypy *C. merula* Simon, 1907:26]. [New synonymy.]

NOTE.—The holotype females of *E. atricolor* and *C. merula* have blunt scapes as in *W. mexicana*, one central pit and a pair of lateral pits on the epigynal plates, and eye group proportions, leg proportions, and coloration as in *Wendilgarda*. Consequently the genera are judged synonymous with *Wendilgarda*, even though web architecture and eggsac form are unknown.

DIAGNOSIS.—*Wendilgarda* is recognized by the orange-yellow of the cephalothorax combined with uniform abdomen color, the mesal bristle of the embolic apophysis protruding from beneath the conductor and lying along the mesal side of the conductor itself (Figure 198), the complex looping of the copulatory ducts at the junction with the spermathecae (Figure 215), the fluted, double-pointed form of the eggsac (Figures 200, 201), and the web architecture (Figure 202).

Wendilgarda has posterior median eyes separated by at least their diameter, whereas the PME of both *Epilineutes* and *Baalzebub* are juxtaposed. *Epilineutes* has a squarish median apophysis like *Wendilgarda*, but the median apophysis has a strong dorsal spine. The median apophysis of *Baalzebub* is much smaller, and more pointed, and the tegulum in lateral view is elongate. The scapes of female *Wendilgarda* are longer and larger than those of *Epilineutes*, and the spermathecae are connate throughout, not just at their tips. In *Baalzebub* the epigynal plate is triangular.

Two behavioral characters also diagnose *Wendilgarda:* web architecture (Figure 202) and eggsacs fluted in cross-section that taper to fine points along the longitudinal axis (Figures 200, 201). The web architecture is unique, but at least one undescribed species of *Ogulnius* makes a double-pointed, fluted eggsac. It, however, is both much smaller than those of *Wendilgarda* and also is attached at both ends, whereas the eggsacs of *Wendilgarda* are pendant from a single line.

DESCRIPTION.—Total length 1 to 3 mm. Carapace uniform yellow-orange, as long as broad. Cephalic region high in lateral view, clypeus 3 times the diameter of an AME (Figure 208). Sternum reddish brown to yellow, often with dusky margins, as broad as long, slightly convex, sparsely bristled. Posterior margin prolonged between fourth coxae. Legs yellow-tan, slightly darker distally, metatarsi often longer than tibiae and abruptly tapered proximally. Tibial trichobothria long, in two or three irregular rows. Eye diameters subequal or AME largest. PME separated by at least a diameter, never juxtaposed. Abdomen uniform gray to black (sometimes bleached in preserved material) with no pigment pattern; smooth, abdominal muscle apodeme marks prominent. Abdomen wider than long, overhanging carapace, sometimes dorso-ventrally flattened. Venter often with two indentations just forward and lateral to spinnerets. Epigynum with scape (Figures 206, 213, 219), male palp with complex embolic division; embolic apophysis composed of broad, spatulate lobes.

NATURAL HISTORY.—*Wendilgarda* are often common along the margins of slow-moving, lowland tropical streams. They do not seem to occur above an elevation of 500 m, in fast rapids, or along stream courses that become dry for an extended period. Individuals are active at all times of day, except for an apparent siesta in midday during the dry season. Web construction is most frequent at dawn and dusk, although individuals often re-spin their webs once or twice an hour. In appropriate habitats population densities may reach 3–4 individuals/m of stream margin. During heavy rains spiders remain over the stream and simply rise with the flood waters. Their webs are attached to overhanging branches or snags in the stream itself. The web of *Wendilgarda clara* was first described by Simon (1895), and has been redescribed by Coddington and Valerio (1980) (both under the name *W. theridionina*). W.G. Eberhard (pers. comm.) found that at least some individuals of *W. galapagensis* do not attach their webs to water, unlike the other members of the group whose web is known. Prey records from *clara, mustelina,* and *mexicana* include mainly immature Gerridae and nematocerous flies. The web seems to function in two distinct ways, by trapping insects actually on the surface of the water, and by trapping low-flying insects aerially. Because most prey collected from webs were at the junction of the sticky silk vertical line and the water, rather than midway up the line, it seems that the former mode of capture is more frequent. Eggsacs are 2–3 mm in diameter, 4–7 mm long, contain up to 15 eggs, and are suspended on single, reinforced lines about 10 mm long. Unlike *Theridiosoma* eggsacs, there is no distinct cap or operculum. In the appropriate habitat, eggsacs can be common along streams in the upper portions of overhanging vegetation. The eggsacs are laid some distance from the water, the most distant I have seen being almost 4 meters.

SPECIES.—*Wendilgarda assamensis* Fage, 1924, is incertae sedis (see above under family description. *Wendilgarda bicolor* Keyserling, 1886, *W. guacharo* Brignoli, 1972a, and *W. miranda* Brignoli, 1972a, belong in *Plato*. Keyserling (1886) originally described *nigra* in *Wendilgarda,* but Simon (1895) transferred the species to *Theridiosoma*. Examination of the type as well as other material (NRS) confirms Keyserling's original opinion and the species is here returned to *Wendilgarda. Wendilgarda clara* Keyserling, 1886, *mustelina* Simon, 1897, and *galapagensis* Archer, 1953, are also properly placed in *Wendilgarda.* About 10 new species have been collected from the Neotropics.

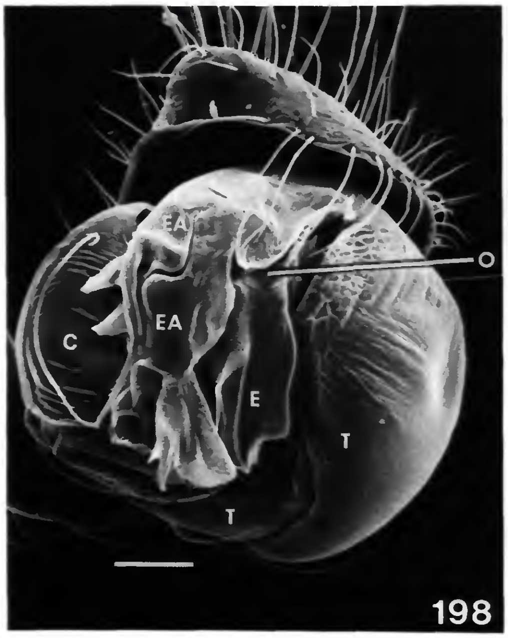
RANGE.—*Wendilgarda* is predominantly neotropical; *W. atricolor* is African.

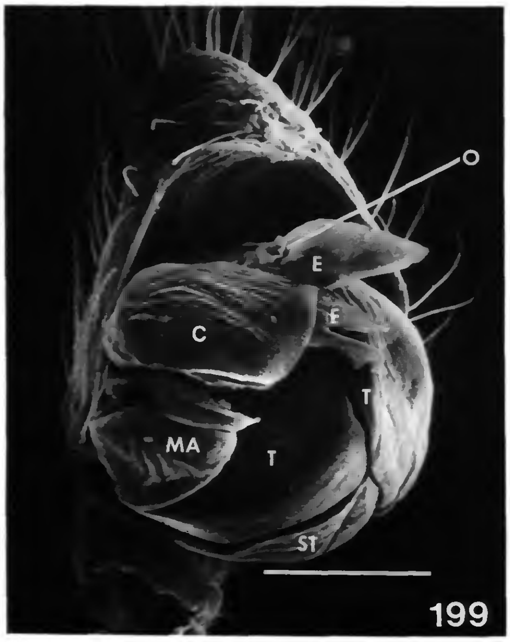
Wendilgarda mexicana Keyserling

FIGURES 199, 200, 203–211; MAP 7

Wendilgarda mexicana Keyserling, 1886:130, pl. 15: fig. 208a–c [♀] [a series of 9 syntype females from Mexico in BMNH, examined].—Roewer, 1942:971.—Bonnet, 1959:4817.—Archer, 1953:14–15.

DIAGNOSIS.—Female *W. mexicana* may be distinguished from other *Wendilgarda* species by the short blunt scape of the epigynum, the differently arranged internal ducts, and the sclerotized transverse bar bridging the spermathecae (Figures 206, 207). Males are distinguished by the

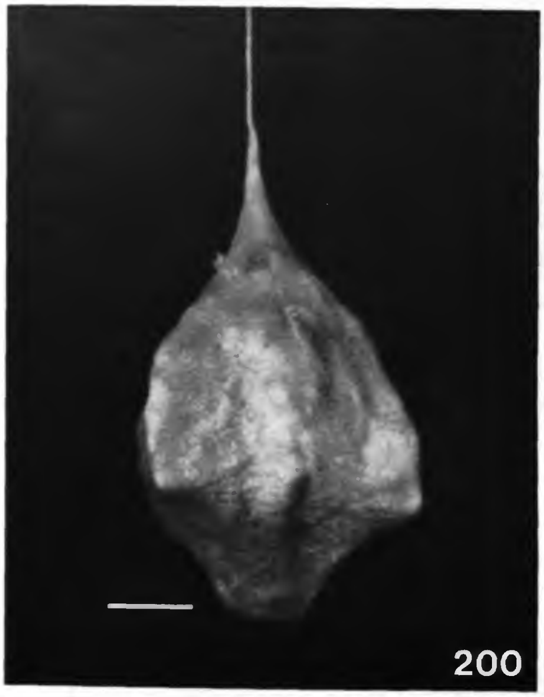




FIGURES 196–198.—*Wendilgarda clara* Keyserling, left male palp: 196, mesal, embolic division exposed; 197, ventral, embolic division enclosed; 198, ventral, embolic division exposed.

FIGURE 199.—*Wendilgarda mexicana* Keyserling, from Mexico, YUCATAN, left palp, ventral.

Scale lines: 100 μm.



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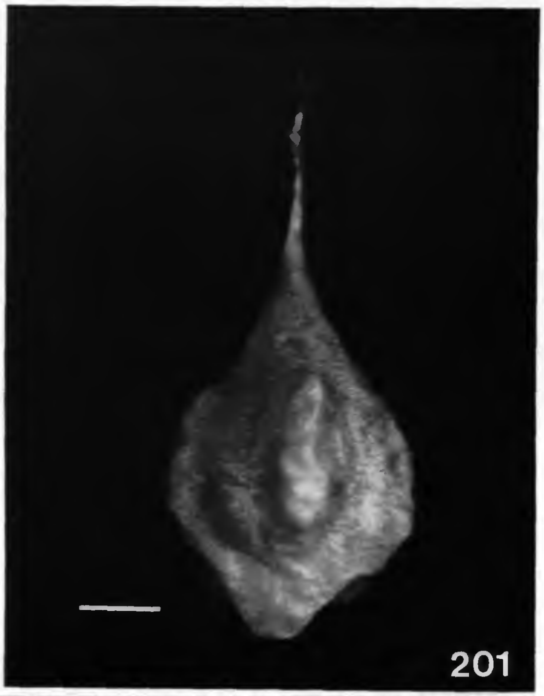

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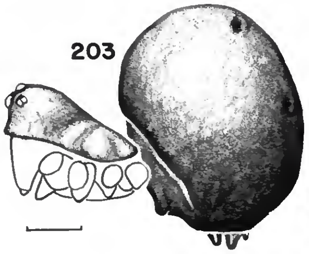
FIGURE 200.—*Wendilgarda mexicana* Keyserling, from Mexico, YUCATAN, eggsac.

FIGURES 201, 202.—*Wendilgarda clara* Keyserling: 201, eggsac; 202, web attached to stream surface (note reflections).

Scale lines: 1 mm, except 202, 10 mm.

relatively small size of the bulb (Figure 210) and the relatively simple embolic division (Figure 199). The conductor also lacks the transverse dark stripe that characterizes the other *Wendilgarda* species. *Wendilgarda mexicana* tends to be larger, more reddish, and the abdomen more flattened than other *Wendilgarda* species, and with smaller PME.

DESCRIPTION.—*Female:* From Mexico, YUCATAN. Total length 2.6 mm. Cephalothorax 1.12 mm long, 1.08 mm wide, 1.01 mm high. Sternum 0.69 mm long, 0.65 mm wide. Carapace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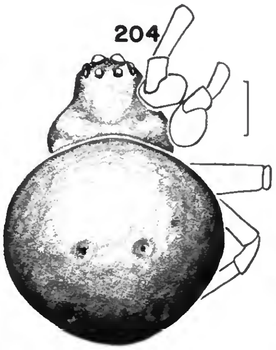
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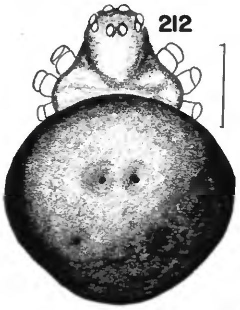
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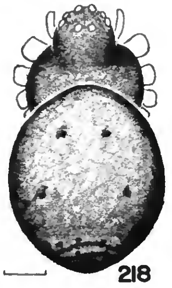
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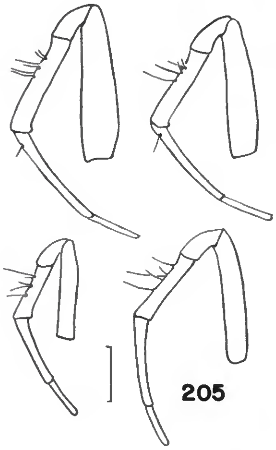
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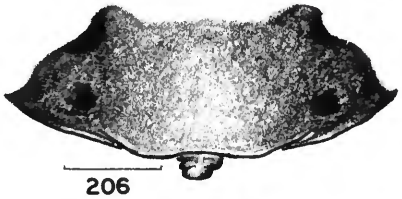
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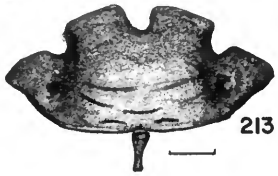
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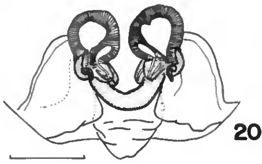
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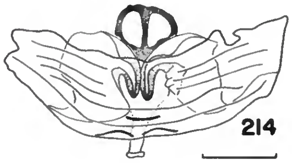
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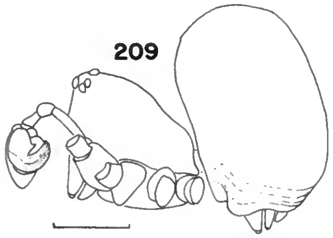
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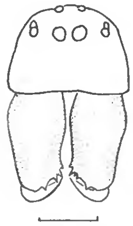
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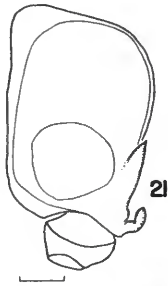
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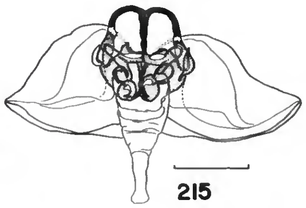
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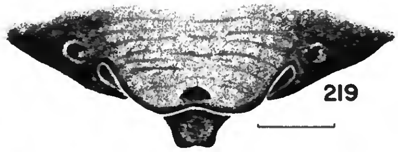
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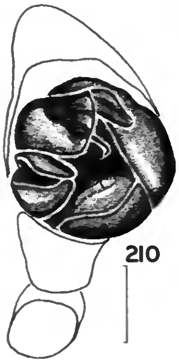
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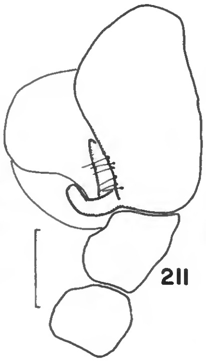
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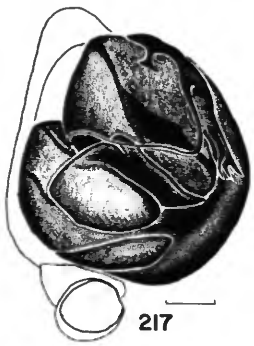
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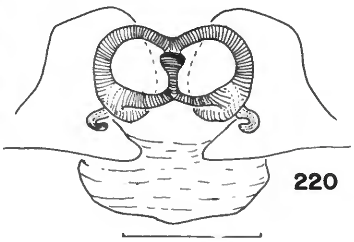

220

uniform orange-yellow, legs proximally same color, darker distally. Abdomen 1.72 mm long, 1.93 mm wide, 2.06 mm high; uniform reddish gray, smoothly ovoid, dorso-ventrally flattened, dorsal muscle scars as four distinct pits. AME 4/3 the PME diameter, AME separation 1/2 their diameter, PME separation 1 diameter. ALE, PLE subequal, separated from AME, PME by their diameter. Clypeus 3 times AME diameter. Epigynum a smooth plate, blunt scape barely visible (Figure 206), dorsal view as in Figure 207.

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	1.43	1.29	0.95	1.17
Patella	0.48	0.43	0.36	0.41
Tibia	0.89	0.77	0.53	0.69
Metatarsus	1.07	0.95	0.72	0.84
Tarsus	0.52	0.48	0.34	0.38
Total	4.39	3.92	2.90	3.49

Male: From Cuba, VILLAS. Total length 2.0 mm. Cephalothorax 0.89 mm long, 0.98 mm wide, 0.95 mm high. Sternum 0.60 mm long, 0.53 mm wide. Abdomen 1.15 mm long, 1.15 mm wide, 1.41 mm high, smaller, more ovoid than female. AME 4/3 PME diameter, AME separation 1/4 their diameter, PME separation slightly more than 1 diameter, ALE slightly larger than PLE, separated from AME, PME by their diameters. Clypeus 3 times AME diameter. Color of carapace, sternum, legs and abdomen as in female. Palp as in Figures 210, 211, relatively small, ratio of palp width in ventral view to sternum width 0.6–0.7; embolic division simple (Figure 199).

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	1.38	1.17	0.83	0.98
Patella	0.40	0.38	0.31	0.36
Tibia	0.91	0.76	0.46	0.57
Metatarsus	1.00	0.86	0.52	0.72
Tarsus	0.45	0.43	0.34	0.29
Total	4.14	3.60	2.46	2.92

VARIATION.—Females range in length from 2.1 to 3.2 mm, males from 1.6 to 2.0 mm. In many cases the epigynal plate of the female is fused to the scape and thus incomplete medially. Populations on Cuba apparently are substantially larger than on the mainland.

NATURAL HISTORY.—The web is qualitatively indistinguishable from that of *clara,* and the eggsac (Figure 200) is typical of the genus. Like other *Wendilgarda* species, *mexicana* is always found over water. Two prey items taken with specimens in Mexico were both immature Gerridae. One eggsac contained 10 eggs.

RANGE.—Mexico, Guatemala, Honduras, and Cuba (Map 7).

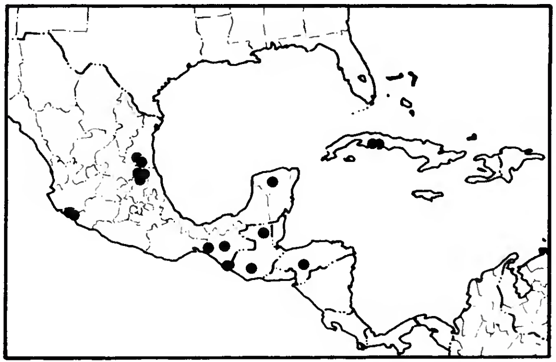
RECORDS.—MEXICO. CHIAPAS: Triunfo (♀, AMNH); 20 km N Huixtla (♀♀, AMNH); San Cristobal de Las Casas (♀, AMNH). COLIMA: Tecoman, Orilla, Rio Ameria (♀♀, AMNH); Boca de Pasquales (♀♀, ♂♂, AMNH). TAMAULIPAS: 1 mi

FIGURES 203–211.—*Wendilgarda mexicana* Keyserling. Female: 203, 204, habitus; 205, left legs; 206, epigynum, ventral; 207, same, dorsal, cleared; 208, eye group, frontal view. Male: 209, habitus; 210, left palp, ventral; 211, same, lateral.

FIGURES 212–217.—*Wendilgarda clara* Keyserling. Female: 212, habitus, dorsal view; 213, epigynum, ventral; 214, same, ventral, cleared; 215, same, dorsal, cleared. Left male palp: 216, cymbium, ventral view; 217, bulb, ventral.

FIGURES 218–220.—*Wendilgarda atricolor* (Simon), holotype female: 218, dorsal view; 219, epigynum, ventral; 220, same, dorsal, cleared.

Scale lines: 0.1 mm, except 203–205, 209, 212, 218, 0.5 mm.



MAP 7.—Distribution of *Wendilgarda mexicana* Keyserling.

SE Villa Juárez (immatures, AMNH); 3 mi SE Ciudad del Mais (♀♀, AMNH). SAN LUIS POTOSI: Pujal (immature, ♀, AMNH); 13 km NE Xilitla (♀♀, ♂♂, AMNH); 10 km W San Joaquin (♀, AMNH). YUCATAN: Chichen-Itza, Cenote Stoloc (♀♀, ♂♂, MCZ, AMNH); "Mexico," more exact locality unknown, not mapped (♀♀, BMNH). GUATEMALA. ESCUINTLA: Tiquisate, 60 m (♀, AMNH). PETEN E end Lago Itza, Tikal (♂, AMNH). HONDURAS. TEGUCIGALPA: Nuevo Rosaria, San Juancita (♀♀, UCR). CUBA. VILLAS: Soledad (nr Cienfuegos) (♀♀, ♂♂, AMNH, MCZ); Mina Carlota, Trinidad Mts (♀♀, MCZ).

Wendilgarda clara Keyserling

FIGURES 196–199, 201, 202, 212–217; MAP 8

Wendilgarda clara Keyserling, 1886:132, pl. 15: figs. 210, 210a–d [♀] [female holotype from Amazonas Prov., Brazil (HDEO), examined].

Wendilgarda theridionina Simon, 1895:919, fig. 986 [♂] [a series of 21 syntype males and 18 females from San Esteban, Carabobo Prov., Venezuela (MHNH), examined].—Simon, 1897a:484, pl. 13: figs. 4–6 [eggsac].—Roewer, 1942:971.—Bonnet, 1959:4817.—Archer, 1953:16–17, figs. 29, 30. [Lectotype female here designated.] [New synonymy.]

Wendilgarda panamica Archer, 1953:15, fig. 23 [female holotype from Barro Colorado Island, Lake Gatún, Panamá, Panama, in AMNH, examined]. [New synonymy.]

Wendilgarda hassleri Archer, 1953:16, figs. 24, 28 [male holotype from upper Shudikar River, Guyana, in AMNH, examined]. [New synonymy.]

NOTE.—Keyserling (1886:133) said the single female specimen of *clara* was in the O. Pickard-Cambridge collection. HDEO has a single female labeled *Bellinda clara*. The genus *Bellinda* is a synonym of *Argyrodes* (Theridiidae), but the name *Bellinda clara* is not listed in Bonnet (1955), Roewer (1942), or Brignoli (1983), and hence was apparently never published. Probably this specimen was the one before Keyserling, and his vial label simply disagrees with his published placement of the species. The *Bellinda clara* specimen agrees in most details with Keyserling's description and figures. It seems simplest to assume that this specimen is the type of *clara* and, consequently, is the oldest available name for the species, even though *theridionina* has been more commonly used.

The type series of *theridionina* contained two theridiid species, *Achaearanea nigrovittata* (Keyserling) and *Dipoena alta* (Simon) (det. H.W. Levi), and one other theridiosomatid, *Epilineutes globosus* (O. Pickard-Cambridge) as well as *theridionina*, which composed the bulk of the series; a lectotype female has been designated to ensure stability. The other specimens have been designated as paralectotypes of *theridionina*.

No features were found that distinguished either *hassleri* or *panamica* from *clara*. Archer was the only person to identify specimens besides the types as *hassleri* or *panamica*, and some of his paratype material is *Epilineutes globosus*. The ranges of *hassleri* and *panamica* are also entirely contained by that of *clara*. Because Archer offered no differential diagnosis of *hassleri* and said only that *panamica* was smaller in stature than *clara*, the three taxa are synonymized.

DIAGNOSIS.—*Wendilgarda clara* is distinguished from *mexicana* and *mustelina* by the short, pointed scape in the female (Figure 213), and by the shape of the median apophysis, the tegular spur, and relative size of the palp in the male (Figure 217). The species is distinguished from *galapagensis* by the lighter color of the abdomen (the abdomen of *galapagensis* is dark brown or black).

DESCRIPTION.—*Female:* From Puerto Rico, HUMACAO. Total length 2.1 mm. Cephalothorax 0.98 mm long, 0.91 mm wide, 0.86 mm high. Sternum 0.52 mm long, 0.52 mm wide. Carapace pale yellow, legs proximally yellow, more orange distally. Abdomen 1.31 mm long, 1.43 mm wide, 1.55 mm high; uniform pale grayish tan, smoothly ovoid, dorsal muscle scars as four distinct pits (Figure 212). Eye diameters subequal, AME, PME separation ½ diameter. ALE, PLE separated from AME, PME by slightly less than their diameter. Clypeus 3 times AME diameter. Epigynum a smooth plate, incised medially, with dark sclerotized spot on center, two lateral pits, and short, tapering scape truncate distally (Figures 213, 214).

Leg lengths of female described above (±0.02 mm).

	I	II	III	IV
Femur	1.20	1.08	0.65	0.91
Patella	0.41	0.40	0.29	0.33
Tibia	0.83	0.65	0.40	0.56
Metatarsus	0.83	0.97	0.50	0.69
Tarsus	0.40	0.34	0.28	0.34
Total	3.67	3.44	2.12	2.83

Male: From Puerto Rico, HUMACAO. Total length 1.8 mm. Cephalothorax 0.95 mm long, 0.89 mm wide, 0.83 high. Sternum 0.52 mm long, 0.48 mm wide. Abdomen 1.20 mm long, 1.20 mm wide, 1.26 mm high. Eye group as in female. Clypeus 2 times AME diameter. Color of carapace, sternum, legs, and abdomen as in female. Ratio of palp width to sternum width 0.9–1.0. Palp as in Figures 196–198, 216, 217.

Leg lengths of male described above (±0.02 mm).

	I	II	III	IV
Femur	1.26	1.17	0.71	0.86
Patella	0.41	0.40	0.26	0.31
Tibia	0.98	0.72	0.43	0.52
Metatarsus	0.86	0.81	0.52	0.64
Tarsus	0.46	0.41	0.31	0.29
Total	3.97	3.51	2.23	2.62

VARIATION.—Females range in length from 1.7 to 2.5 mm, males from 1.5 to 1.9 mm. In fresh specimens the abdomen is sometimes gray rather than tan, but never black. Very large specimens superficially resemble *W. mexicana,* but can be distinguished by the genitalia. *Wendilgarda clara* seems to be the most widespread of all *Wendilgarda,* occurring as least as far south as Ecuador and as far north as Puerto Rico.

NATURAL HISTORY.—The web (Figure 202) is peculiar, consisting of a horizontal non-sticky line from which vertical sticky lines adhere with considerable tenacity to the surface film of flowing tropical streams (Coddington and Valerio, 1980). *Wendilgarda clara* is always found over water. The eggsac (Figure 201) is similar to that of *W. mexicana.* Live animals usually appear distinctly orange.

RANGE.—Antilles, Guatemala south to Colombia, Venezuela, Guyana, and Brazil (Map 8).

RECORDS.—PUERTO RICO. AGUADILLA: Maraicao, El Vivero (♀, MCZ). GUAYAMA: Cidra, Treasure Island (♀, ♂, AMNH). HUMACAO: Caribbean National Forest, Luquillo Division (numerous records, ♀♀, ♂♂, AMNH, MCZ). MAYAGÜEZ (numerous records, ♀♀, ♂♂, AMNH, MCZ). PONCE: Castañer (♀♀, AMNH). SAN JUAN: San Juan (♀, AMNH). DOMINICAN REPUBLIC. EL SEIBO: forest between Hato Mayor and Sabana de La Mar (♀♀, ♂, AMNH). LA VEGA: Constanza (♀, MCZ). PUERTO PLATA: Puerto Plata (♂, MCZ). HAITI. Nr Aux Cayes (♀, AMNH). GUATEMALA. IZABAL: Santo Tomás (♀♀, ♂♂, MCZ, numerous records). COSTA RICA. HEREDIA: nr Puerto Viejo, Organization for Tropical Studies field station Finca La Selva (♀♀, ♂♂, MCZ, numerous records). PUNTARENAS: Corcovado National Park (♀♀, ♂♂, MCZ, numerous records). PANAMA. COLON: Portobelo (♂♂, MCZ); Panamá, Lake Gatún, Barro Colorado Island (♀♀, ♂♂, MCZ, AMNH, numerous records). COLOMBIA. VALLE: Central Hidalgo Anchicayá (♀, ♂♂, MCZ). VENEZUELA. AMAZONAS: upper Río Paciba (♀, AMNH). GUYANA. ESSEQUIBO: Rupunni River between Isherton and Dadawana (♀, ♂, AMNH). ECUADOR. LOS RIOS: Juan Montalvo (♂, AMNH). PICHINCHA: 4.7 km SW of Santo Domingo de los Colorados, Río Palenque (♀, ♂, MCZ). BRAZIL. AMAZONAS? (more exact locality unknown, not mapped).

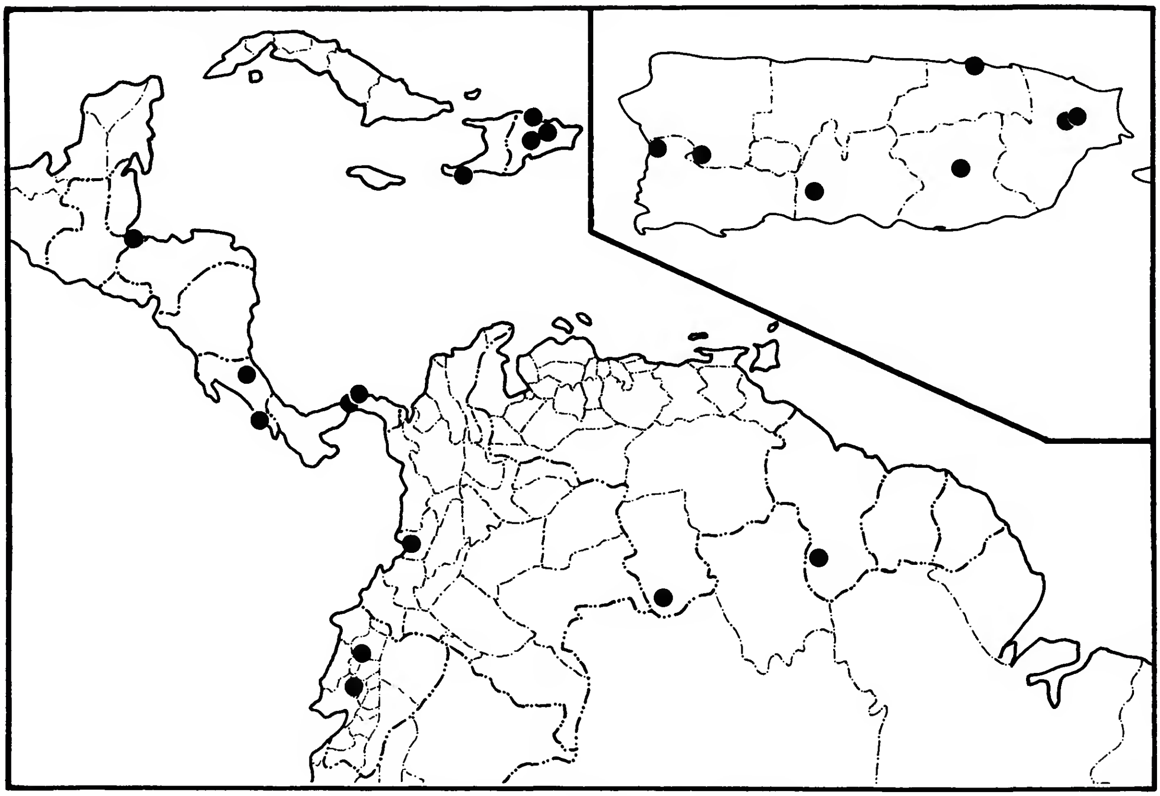
***Wendilgarda atricolor* (Simon), new combination**

FIGURES 218–220

Enthorodera atricolor Simon, 1907:265, no figs. [female holotype from "Roça, inf. d'Henrique," Principe (Republic of Saô Tomé and Principe), in MCSN, Genoa, examined]

Cyathidea merula Simon, 1907:266, no figs. [female holotype from "Agua Izè, Ribeira Palma, Saô Tomé (Republic of Saô Tomé and Principe), in MNHN, Paris, examined]. [New synonymy.]

NOTE.—See remarks under the genus *Wendilgarda* for justification of synonymy of *Enthorodera* and *Cyathidea.* The synonymy of *atricolor* and *merula* is less certain, because only the holotype



MAP 8.—Distribution of *Wendilgarda clara* Keyserling.

females are known. The scape of *atricolor* is definitely slightly bifid, whereas that of *merula* is more rounded, but on the whole the difference between the two specimens is very slight. Somatic morphology seems indistinguishable. Should larger series of males and females refute the synonymy, *merula* would still be the sister taxon to *atricolor* by the posterior ventral pits on the abdomen. The abdomen of the *atricolor* type female is badly damaged and separated from the cephalothorax, and so Figure 218 is a reconstruction. *Wendilgarda atricolor* is taken as the appropriate name for the taxon because Simon used it first in his publication.

DIAGNOSIS.—*Wendilgarda atricolor* most resembles *W. mexicana* in its size, blunt scape, and eye proportions. It can be distinguished by the copulatory pores, which are visible in ventral view, and the shape of the scape (Figure 219).

DESCRIPTION.—*Female:* Holotype. Total length 2.6 mm (estimate). Carapace 1.15 mm long, 0.98 mm wide, 0.77 mm high. Sternum 0.58 mm long, 0.58 mm wide. Cephalothorax light red-tan, legs similar. Abdomen 1.45 mm long, 1.55 mm wide, 1.89 mm high; uniform dull brown, smoothly ovoid, dorsal muscle scars as four distinct pits. AME ¾ PME diameter, separation ½ their diameter. PME separation 0.4 their diameter. ALE, PLE subequal, slightly larger than AME, separated from AME, PME by ¾ their diameter. Clypeus height slightly more than 2 times AME diameter. Epigynum a smooth plate with lateral pits, central transverse pit, posterior rim incised laterally revealing copulatory pores, also medially; short, broad scape notched distally (Figure 219). Dorsal view, Figure 220.

Leg lengths of holotype female (±0.03 mm).

	I	II	III	IV
Femur	1.29	1.24	0.86	1.07
Patella	0.46	0.43	0.36	0.38
Tibia	0.84	0.77	0.53	0.65
Metatarsus	0.81	0.83	0.62	0.71
Tarsus	0.46	0.48	0.41	0.40
Total	3.86	3.75	2.78	3.21

Male: Unknown.

VARIATION.—Unknown.

NATURAL HISTORY.—Unknown.

RANGE.—Islands of Principe and Saô Tomé, off African coast.

References

Archer, A.F.

1941. Supplement to the Argiopidae of Alabama. *Geological Survey of Alabama, Museum Paper,* 18:1–47.

1953. Studies in the Orbweaving Spiders (Argiopidae), 3. *American Museum Novitates,* 1622:1–27.

1958. Studies in the Orbweaving Spiders (Argiopidae), 4. *American Museum Novitates,* 1922:1–21.

1965. Nuevos argiopidos de las Antilles. *Caribbean Journal of Science,* 5:129–133.

Berland, L.

1932. Les Arachnides. *Encyclopédie Entomologique.* Volume 16, pages 79–404. Paris.

Bonnet, P.

1955–1959. *Bibliographia Araneorum.* Volume 2. [1955:1–918 (part 1, A–B); 1956:919–1926 (part 2, C–M); 1958:3027–4230 (part 4, N–S); 1959:4231–5058 (part 5, T–Z).] Tolouse: Les Frères Douladoure.

Bösenberg, W., and E. Strand

1906. Japanische Spinnen. *Abhandlungen von der Senckenbergischen Naturforschenden Gesellschaft,* 30:93–422.

Brignoli, P.M.

1972a. Sur quelques araignées cavernicoles d'Argentine, Uruguay, Brésil et Venezuela récoltées par le Dr. Strinati (Arachnida, Araneae). *Revue Suisse de Zoologie,* 79:361–385.

1972b. Ragni di Ceylon, 1: Misione biospelogica Aellen-Strinati (1970) (Arachnida: Araneae). *Revue Suisse de Zoologie,* 79:907–929.

1974. Notes on Spiders, Mainly Cave-dwelling, of Southern Mexico and Guatemala (Araneae). *In* Subterranean Fauna of Mexico, part II. *Quaderno Accademia Nazionale dei Lincei,* 171:195–238.

1975. Über die Gruppe der Haplogynae. *Proceedings of the 6th International Arachnological Congress, 1974,* pages 33–38.

1979. Un nuovo *Theridiosoma* del Kenya. *Revue Suisse de Zoologie,* 86:485–489.

1981. Spiders from the Phillipines, IV: A New *Ogulnius* and Notes on Some Other Oriental and Japanese Theridiosomatidae (Araneae). *Acta Arachnologica,* 30:9–20.

1983. *A Catalogue of the Araneae Described between 1940 and 1981.* Manchester University Press.

Bryant, E.B.

1945a. The Argiopidae of Hispaniola. *Bulletin of the Museum of Comparative Zoology,* 140:359–418.

1945b. Some New or Little Known Southern Spiders. *Psyche,* 52:178–192.

1948. The Spiders of Hispaniola. *Bulletin of the Museum of Comparative Zoology,* 100:331–447.

Caporiacco, L. di

1938. Il sistema degli Araneidi. *Archivos Zoologico Italiano,* 25:35–155.

1947. Diagnosi preliminari di specie nuove di arachnidi della Guiana Britannica. *Monitore Zoologico Italiano,* 56:20–34.

1948. Arachnida of British Guiana. *Proceedings of the Zoological Society of London,* 118:607–647.

Chamberlin, R.V., and W. Ivie

1936. New Spiders from Mexico and Panama. *Bulletin of the University of Utah, Biological Series,* 27:1–103.

1944. Spiders of the Georgia Region of North America. *Bulletin of the University of Utah, Biological Series,* 35:1–215.

Coddington, J.A.

1983. A Temporary Slide Mount Allowing Precise Manipulation of Small Structures. *In* O. Kraus, editor, Taxonomy, Biology, and Ecology of Araneae and Myriapoda. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg,* new series, 26:291–292.

In press. The Monophyletic Origin of the Orb Web. *In* W.A. Shear, editor, *Spider Webs, Behavior, and Evolution.* Stanford University Press.

Coddington, J.A., and C.E. Valerio

1980. Observations on the Web and Behavior of *Wendilgarda* Spiders (Araneae: Theridiosomatidae). *Psyche,* 87:93–105.

Comstock, J.H.

1910. The Palpi of Male Spiders. *Annals of the Entomological Society of America,* 3:161–185.

1912. *The Spider Book.* New York: Doubleday, Page and Co.

Eberhard, W.G.

1981. Construction Behavior and the Distributions of Tensions in Orb Webs. *Bulletin of the British Arachnological Society,* 5:189–204.

1982. Behavioral Characters for the Higher Classification of Orb-weaving Spiders. *Evolution,* 36:1067–1095.

Eberhard, W.G., M. Barreto, and W. Pfizenmaier

1978. Web Robbery by Mature Male Orb-weaving Spiders. *Bulletin of the British Arachnological Society,* 4:228-230.

Emerton, J.H.

1884. New England Spiders of the Family Epeiridae. *Transactions of the Connecticut Academy of Arts and Sciences,* 6:295–342.

Fage, L.

1924. Araneids from the Siju Cave, Garo Hills, Assam. *Record of the Indian Museum,* 26:63–67.

Forster, R.R.

1959. The Spiders of the Family Symphytognathidae. *Transactions of the Royal Academy, New Zealand,* 86:269–329.

1970. The Spiders of New Zealand, III. *Otago Museum Bulletin,* 3:1–184.

Forster, R.R., and N.I. Platnick

1977. A Review of the Spider Family Symphytognathidae (Arachnida, Araneae). *American Museum Novitates,* 2619:1–29.

1984. A Review of the Archaeid Spiders and Their Relatives, with Notes on the Limits of the Superfamily Palpimanoidea. *Bulletin of the American Museum of Natural History,* 178(1):1–106.

Gerhardt, U.

1933. Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere an Arten der Mittelmeerländer und der Tropen. *Zeitschrift für Morphologie und Ökologie der Tiere,* 27:1–75.

Gerhardt, U., and A. Kaestner

1938. Araneae. *In* Kukenthal, editor, *Handbuch der Zoologie, Berlin,* 3:497–656.

Gertsch, W.J.

1960. Descriptions of American Spiders of the Family Symphytognathidae. *American Museum Novitates,* 1981:1–40.

Heimer, S.

1982. Interne Arretierungsmechanismen an den Kopulationsorganen männlichen Spinnen (Arachnida: Araneae): Ein Beitrag zur Phylogenie der Araneoidea. *Entomologische Abhandlungen der Staatlisches Museum für Tierkunde in Dresden,* 45:35–64.

Heimer, S., and W. Nentwig

1982. Thoughts on the Phylogeny of the Araneoidea Latreille, 1806 (Arachnida: Araneae). *Zeitschrift für Zoologischen Systematik und Evolutionforschung,* 20:284–295.

Hickman, V.V.

1931. A New Family of Spiders. *Proceedings of the Zoological Society of London,* 1931(2):1321–1328.

Hingston, R.W.G.

1932. *A Naturalist in the Guiana Forest.* 384 pages, 150 figures, 16 plates, 1 map. London.

Homann, H.

1971. Die Augen der Araneae. *Zeitschrift für Morphologie der Tiere,* 69:201–272.

Kaestner, A., H.W. Levi, and L.R. Levi

1980. *Invertebrate Zoology.* Volume 2. New York: Robert E. Krieger Publ. Co.

Kaston, B.J.

1948. Spiders of Connecticut. *Bulletin of the Connecticut Geological and Natural History Survey,* 70:1–874.

1972. *How to Know the Spiders.* 3rd edition. Dubuque, Iowa: Wm. C. Brown Co.

Keyserling, E.

1882. Neue Spinnen aus Amerika, III. *Verhandlungen der Zoologische-Botantisch en Gesellschaft in Wien,* 3.

1884. *Die Spinnen Amerikas, Theridiidae.* Volume 2, part 1, 222 pages, 10 plates. Nürnberg.

1886. *Die Spinnen Amerikas, Theridiidae.* Volume 2, part 2, 295 pages, 21 plates. Nürnberg.

1891. *Die Spinnen Amerikas: Brasilianische Spinnen.* Volume 3, 278 pages. Nürnberg.

Koch, L.

1878. Verzeichniss der bei Nürnberg bis jetzt beobachteten Arachniden (mit Ausschluss der Ixoden und Acariden) und Beschreibungen von neuen, hier vorkommenden Arten. *Abhandlungen der Naturhistorischen Gesellschaft zu Nürnberg,* 6: 86 pages, 1 plate.

Kovoor, J.

1972. Étude histochimique et cytologique des glandes séricigènes de quelques Argiopidae. *Annales des Sciences Naturelles, Zoologie* (Paris), 14:1–40.

1977. La soie et les glandes séricigènes des Arachnides. *Annales de Biologie,* 16:97–141.

Lamy, E.

1902. Recherches anatomiques sur les trachées des Araignées. *Annales des Sciences Naturelles, Zoologie,* 8:194–280.

Lehtinen, P.T.

1967. Classification of the Cribellate Spiders and Some Allied Families, with Notes on the Evolution of the Suborder Araneomorpha. *Annales Zoologici Fennici,* 4:199–468.

1975. Notes on the Phylogenetic Classification of Araneae. *Proceedings of the 6th International Arachnological Congress, 1974,* pages 26–29.

1978. Definition and Limitations of Supraspecific Taxa in Spiders. *Symposium of the Zoological Society of London,* 42:255–272.

1980. Trichobothrial Patterns in High Level Taxonomy of Spiders. *Proceedings of the 8th International Congress of Arachnology, Vienna,* 1980:493–498.

Lehtinen, P.T., and M.I. Saaristo

1980. Spiders of the Oriental-Australian Regions, II: Nesticidae. *Annales Zoologici Fennici,* 17:47–66.

Levi, H.W.

1961. Evolutionary Trends in the Development of Palpal Sclerites in the Spider Family Theridiidae. *Journal of Morphology,* 108:1–9.

1968a. The Spider Genera *Gea* and *Argiope* in America (Araneae: Araneidae). *Bulletin of the Museum of*

Comparative Zoology, 136:319–352.

1968b. The Spider Genus *Billima* Simon. *Psyche,* 74:340–341.

1971. The *diadematus* Group of the Orb Weaver Genus *Araneus* North of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology,* 141:131–179.

1972. Taxonomic-Nomenclatural Notes on Misplaced Theridiid Spiders (Araneae: Theridiidae), with Observations on *Anelosimus. Transactions of the American Microscopical Society,* 91:533–538.

1978. The American Orb Weaver Genera *Colphepeira, Micrathena,* and *Gasteracantha* North of Mexico. *Bulletin of the Museum of Comparative Zoology,* 148:417–442.

1980a. Orb-Webs—Primitive or Specialized. *Proceedings of the 8th International Congress of Arachnology, Vienna,* 1980:367–370.

1980b. The Orb Weaver Genus *Mecynogea,* the Subfamily Metinae and the Genera *Pachygnatha, Glenognatha,* and *Azilia* of the Subfamily Tetragnathinae North of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology,* 149:1–74.

1981. The American Orb-weaver Genera *Dolichognatha* and *Tetragnatha* North of Mexico (Araneae: Araneidae: Tetragnathinae). *Bulletin of the Museum of Comparative Zoology,* 149:271–318.

1982. Araneae. *In* S.B. Parker, editor, *Synopsis and Classification of Living Organisms,* 2:77–95. New York: McGraw Hill.

1983. The Orb-weaver Genera *Argiope, Gea,* and *Neogea* from the Western Pacific Region (Araneae: Araneidae, Argiopinae). *Bulletin of the Museum of Comparative Zoology,* 150(5):247–338.

Levi, H.W., and J.A. Coddington

1983. Progress Report on the Orb Weaving Family Araneidae and the Superfamily Araneoidea. *In* O. Kraus, editor, Taxonomy, Biology, and Ecology of Araneae and Myriapoda. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg,* new series, 26:291–292.

Levi, H.W., and L.R. Levi

1962. The Genera of the Spider Family Theridiidae. *Bulletin of the Museum of Comparative Zoology,* 127:1–71.

Locket, G.H.

1968. *Spiders of the Family Linyphiidae from Angola.* 144 pages. Lisbon: Museo do Dundo.

Locket, G.H., and A.F. Millidge

1953. *British Spiders.* Volume 2. London: Ray Society.

Lopez, A.

1977. Contribution à l'étude des caractères sexuels somatiques chez les mâles des Araneides. *Université de Montpellier, Traveaux de Laboratoire de Zoologie,* 2:1–116, 13 plates.

Marples, B.J.

1955. Spiders from Western Samoa. *Journal of the Linnaean Society,* 42:453–504.

McCook, H.C.

1881. The Snare of the Ray Spider (*Epeira radiosa*) A New Form of Orb Web. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 1881:163–175.

1889a. Note on the True Systematic Position of the Ray Spider. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 1889:180–183.

1889b. *American Spiders and Their Spinningwork.* Volume 1. [Published by the author.]

Mello-Leitão, C. de

1943. Catalogo das aranha do Rio Grande do Sul. *Archivos do Museu Nacional, Rio de Janeiro,* 37:147–245.

Merrett, P.

1963. The Palpus of Male Spiders of the Family Linyphiidae. *Proceedings of the Zoological Society of London,* 140:347–367.

Mikulska, I.

1966. The Spinning Structures on the Spinnerets (Thelae) of *Nephila clavipes* (L.). *Zoologica Polonia,* 16:209–222.

Millidge, A.F.

1977. The Conformation of the Male Palpal Organs of Linyphiid Spiders. *Bulletin of the British Arachnological Society,* 4:1–60.

1980. The Erigonine Spiders of North America, Part 1: Introduction and Taxonomic Background (Araneae: Linyphiidae). *Journal of Arachnology,* 8:97–107.

Opell, B.D.

1979. Revision of the Genera and Tropical American Species of the Spider Family Uloboridae. *Bulletin of the Museum of Comparative Zoology,* 148:445–549.

Peters, H.

1982. Wie Spinnen der Familie Uloboridae ihre Beute einspinnen und verzehren. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg,* new series, 25:147–167.

Petrunkevitch, A.

1923. On Families of Spiders. *Annals of the New York Academy of Sciences,* 29:145–180.

1928. Systema Aranearum. *Transactions of the Connecticut Academy of Arts and Sciences,* 29:1–270.

1930. The Spiders of Puerto Rico, II. *Transactions of the Connecticut Academy of Arts and Sciences,* 30:159–355.

1933. An Inquiry into the Natural Classification of Spiders. *Transactions of the Connecticut Academy of Arts and Sciences,* 31:303–389.

Pickard-Cambridge, F.O.

1902. Arachnida: Araneida. *Biologica Centrali-Ameri-*

cana, 2:313–424.

Pickard-Cambridge, O.

1879. On Some New and Rare British Spiders, with Characters of a New Genus. *Annals and Magazine of Natural History,* 24:190–215, plate 12.

1882. On New Genera and Species of Araneida. *Proceedings of the Zoological Society of London,* 1882:423–442.

1886. On Some New and Rare British Spiders. *Proceedings of the Dorset Natural History and Antiquarian Field Club,* 7:70–78.

1894. Arachnida. Araneida. *Biologica Centrali-Americana,* 1:121–144.

1896. Arachnida. Araneida. *Biologica Centrali-Americana,* 1:161–224.

Platnick, N.I.

1975. On the Validity of Haplogynae as a Taxonomic Grouping in Spiders. *Proceedings of the 6th International Congress of Arachnology, 1974,* pages 30–32.

Platnick, N.I., and M.U. Shadab

1978a. A Review of the Spider Genus *Mysmenopsis* (Araneae, Mysmenidae). *American Museum Novitates,* 2661:1–22.

1978b. A Review of the Spider Genus *Anapis* (Araneae, Anapidae) with a Dual Cladistic Analysis. *American Museum Novitates,* 2663:1–23.

1979. A Review of the Spider Genera *Anapisona* and *Pseudanapis* (Araneae, Anapidae). *American Museum Novitates,* 2672:1–20.

Roberts, M.

1978. Contributions à l'étude des la faune terrestre des îles granitiques de l'archipel des Séchelles: Theridiidae, Mysmenidae, and gen. *Theridiosoma* (Araneidae). *Revue Zoologique Africaine,* 92:902–939.

Roewer, C.F.

1942. *Katalog der Araneae.* Volume 1, pages 966–971. Bremen.

Saito, S.

1932. Descriptions of Two New Species of Araneida from the Northern Kurile Islands. *Transactions of the Sapporo Natural History Society,* 12(2):100–104.

1933. Araneida from the Northern Kurile Islands, with Descriptions of Two New Species. *Proceedings of the Imperial Academy of Japan,* 4(2):122–131.

1935. Spiders from the Northern Kurile Islands, II. *Transactions of the Sapporo Natural History Society,* 14:55–56.

Simon, E.

1881. *Les Arachnides de France.* Volume 5, part 1. Paris.

1892. *Histoire naturelle des Araignées.* Volume 1, part 1, pages 1–256. Paris.

1893a. *Histoire naturelle des Araignées.* Volume 1, part 2, pages 257–488. Paris.

1893b. Arachnides de l'archipel malais. *Revue Suisse de Zoologie,* 1893:319–328.

1894. *Histoire naturelle des Araignées.* Volume 1, part 3, pages 489–760. Paris.

1895. *Histoire naturelle des Araignées.* Volume 1, part 4, pages 761–1084. Paris.

1897a. Descriptions d'espèces nouvelles de l'ordre des Araneae. *Annales de la Société Entomologique de France,* 65:466–510, 2 plates.

1897b. On the Spiders of the Island of St. Vincent, III. *Proceedings of the Zoological Society of London,* 1897:860–890.

1897c. *Histoire naturelle des Araignées.* Volume 2, part 1, pages 1–192. Paris.

1898. *Histoire naturelle des Araignées.* Volume 2, part 2, pages 193–380. Paris.

1901a. On the Arachnida Collected during the "Skeet Expedition" to the Malay Peninsula, 1891–1910. *Proceedings of the Zoological Society of London,* 1901:45–84.

1901b. *Histoire naturelle des Araignées.* Volume 2, part 3, pages 381–668. Paris.

1903a. *Histoire naturelle des Araignées.* Volume 2, part 4, pages 669–1080. Paris.

1903b. Études arachnologiques, 35e Mémoire, LII: Étude sur les Arachnides recueillis par M. le lieutenant de vaisseau Blaise dans l'estuaire du Gabon, pendant qu'il commandait la canonnière "La Cigogne" au Congo français (1894–1896). *Annales de la Société Entomologique de France,* 71:719–725.

1907. Arachnides recueillis par L. Fea sur la côte occidentale d'Afrique, Part 1. *Annali del Museo Civico di Storia Naturale di Genova,* 43:218–323.

1908. Araneae, Part 1. *Die Fauna Südwest-Australiens,* 1:359–446. Jena.

1926. *Arachnides de France.* Volume 6, part 2. Paris.

Strand, E.

1918. Zur Kenntnis japanischer Spinnen, I. und II. *Archiv Naturgeschichte,* 82A(11):162–171.

Taczanowski, L.

1873. Les Aranéides de la Guyane française. *Horae Societas Entomologicae Rossicae,* 10:56–115 [and separate pages 1–60].

Thorell, T.

1890. Studi sui Ragni Malesi e Papuani, Part IV. *Annali del Museo Civico di Storia Naturale di Genova,* 30:5–106.

Urquhart, A.T.

1894. Description of New Species of Araneae. *Transactions of the New Zealand Institute,* 26:204–218.

Vellard, J.

1924. Études de Zoologie. *Archivos do Instituto Vital Brazil,* 2:121–170.

Wasowska, S.

1966. Comparative Morphology of the Spinning Fields in Females of Some Spider Species. *Zoologica Po-*

lonia, 16:9–30.

1970. Structures fileuses extérieures sue les filières (thelae) de l'araignée *Argiope bruennichi. Zoologica Polonia,* 20:257–268.

Wiehle, H.

1931. Araneidae. *Tierwelt Deutschlands,* 23:1–136.

1963. über *Nesticus borutzski* Reimoser (Arachnida: Araneae). *Senckenbergiana Biologica,* 44:431–435.

1967. *Meta,* eine semientelegyne Gattung der Araneae (Arachnida). *Senckenbergiana Biologica,* 48:183–196.

Workman, T.

1896. *Mayalasian Spiders.* Parts 4–10, pages 25–80. Belfast. [Published by the author.]

Wunderlich, J.

1976. Spinnen aus Australien, 1: Uloboridae, Theridiosomatidae, und Symphytognathidae (Arachnida: Araneida). *Senckenbergiana Biologica,* 57:113–124.

1978. Zur Kenntnis der Cyatholipinae Simon 1894 (Arachnida: Araneida: ?Tetragnathidae). *Zoologische Beiträge,* 24:33–42.

1980. Sternal-organe der Theridiosomatidae—eine bisher übersehene Autapomorphie (Arachnida: Araneae). *Verhandlungen Naturwissenschaftlichen Vereins, Hamburg,* 23:255–257.

Yaginuma, T.

1957. Two New Conopisthine Spiders from Japan. *Acta Arachnologica,* 15:11–16.

1968. *Spiders of Japan in Color.* Osaka: Hoikusha Publ. Co.

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