

## Tarsal Organ Morphology and the Phylogeny of Goblin Spiders (Araneae, Oonopidae), With Notes on Basal Genera

NORMAN I. PLATNICK,<sup>1</sup> NAIARA ABRAHIM,<sup>2</sup> FERNANDO ÁLVAREZ-PADILLA,<sup>3</sup>  
DANIELA ANDRIAMALALA,<sup>4</sup> BARBARA C. BAEHR,<sup>5</sup> LÉON BAERT,<sup>6</sup> ALEXANDRE  
B. BONALDO,<sup>2</sup> ANTONIO D. BRESOVIT,<sup>7</sup> NATALIA CHOUSOU-POLYDOURI,<sup>8</sup>  
NADINE DUPÉRRÉ,<sup>1</sup> BEATA EICHENBERGER,<sup>9</sup> WOUTER FANNES,<sup>10</sup> EVA  
GAUBLOMME,<sup>6</sup> ROSEMARY G. GILLESPIE,<sup>8</sup> CRISTIAN J. GRISMADO,<sup>11</sup> CHARLES  
E. GRISWOLD,<sup>12</sup> MARK S. HARVEY,<sup>13</sup> ARNAUD HENRARD,<sup>10</sup> GUSTAVO  
HORMIGA,<sup>4</sup> MATÍAS A. IZQUIERDO,<sup>11</sup> RUDY JOCQUÉ,<sup>10</sup> YVONNE KRANZ-  
BALTENSBERGER,<sup>9</sup> CHRISTIAN KROPE,<sup>9</sup> RICARDO OTT,<sup>14</sup> MARTÍN J. RAMÍREZ,<sup>11</sup>  
ROBERT J. RAVEN,<sup>5</sup> CRISTINA A. RHEIMS,<sup>7</sup> GUSTAVO R.S. RUIZ,<sup>15</sup> ADALBERTO J.  
SANTOS,<sup>16</sup> ALMA SAUCEDO,<sup>12</sup> PETRA SIERWALD,<sup>17</sup> TAMÁS SZÜTS,<sup>12</sup> DARRELL  
UBICK,<sup>12</sup> AND XIN-PING WANG<sup>18</sup>

<sup>1</sup>Division of Invertebrate Zoology, American Museum of Natural History; <sup>2</sup>Museu Paraense Emílio Goeldi, Belém, Brazil; <sup>3</sup>Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico; <sup>4</sup>George Washington University, Washington, DC; <sup>5</sup>Queensland Museum, Brisbane, Australia; <sup>6</sup>Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium; <sup>7</sup>Instituto Butantan, São Paulo, Brazil; <sup>8</sup>Essig Museum of Entomology, University of California, Berkeley; <sup>9</sup>Natural History Museum, Bern, Switzerland; <sup>10</sup>Royal Museum for Central Africa, Tervuren, Belgium; <sup>11</sup>Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; <sup>12</sup>California Academy of Sciences, San Francisco, CA; <sup>13</sup>Western Australian Museum, Perth, Australia; <sup>14</sup>Museu de Ciências Naturais, Porto Alegre, Brazil; <sup>15</sup>Universidade Federal do Pará, Belém, Brazil; <sup>16</sup>Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; <sup>17</sup>Field Museum of Natural History, Chicago, IL; <sup>18</sup>Hebei University, Baoding, China.

## ABSTRACT

Based on a survey of a wide variety of oonopid genera and outgroups, we hypothesize new synapomorphies uniting the Oonopidae (minus the South African genus *Calculus* Purcell, which is transferred to the Orsolobidae). The groundplan of the tarsal organ in Oonopidae is hypothesized to be an exposed organ with a distinctive, longitudinal ridge originating from the proximal end of the organ, and a serially dimorphic pattern of 4-4-3-3 raised receptors on legs I–IV, respectively. Such organs typify the diverse, basal, and ancient genus *Orchestina* Simon. Several other genera whose members resemble *Orchestina* in retaining two plesiomorphic features (an H-shaped, transverse eye arrangement and a heavily sclerotized, thick-walled sperm duct within the male palp) are united by having tarsal organs that are partly (in the case of *Cortestina* Knoflach) or fully capsulate (in the case of *Sulsula* Simon, *Xiombarg* Brignoli, and *Unicorn* Platnick and Brescovit). The remaining oonopids are united by the loss of the heavily sclerotized palpal sperm duct, presumably reflecting a significant transformation in palpal mechanics. Within that large assemblage, a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement seem to be retained only in the New Zealand genus *Kapitia* Forster; the remaining genera are apparently united by a reduction in the tarsal organ pattern to 3-3-2-2 raised receptors on legs I–IV and by the acquisition of a clumped eye arrangement. Three subfamilies of oonopids are recognized: Orchestinae Chamberlin and Ivie (containing only *Orchestina*; *Ferchestina* Saaristo and Marusik is placed as a junior synonym of *Orchestina*), Sulsulinae, new subfamily (containing *Sulsula*, *Xiombarg*, *Unicorn*, and *Cortestina*), and Oonopinae Simon (containing all the remaining genera, including those previously placed in the Gamasomorphinae). The type species of *Sulsula* and *Kapitia*, *S. pauper* (O. P.-Cambridge) and *K. obscura* Forster, are redescribed, and the female of *S. pauper* is described for the first time. A new sulsuline genus, *Dalmasula*, is established for *Sulsula parvimana* Simon and four new species from Namibia and South Africa.

## INTRODUCTION

Goblin spiders (the family Oonopidae) have long been among the most poorly known groups of spiders; the bulk of the species and much of the generic-level diversity of the family have remained undescribed, and the phylogenetic relationships of its members have been poorly understood, at all levels. Thanks to a Planetary Biodiversity Inventory (PBI) project, initiated in September 2006 with support from the U.S. National Science Foundation (NSF), knowledge of these animals has expanded rapidly; at present, the PBI project involves over 45 participants in more than a dozen countries, and almost one-third of the total project budget comes from sources other than NSF, in several nations. Through the efforts of these participants, enough information has now accumulated to allow testing some preliminary hypotheses about the higher-level relationships of oonopids. We present here results based on investigations of the tarsal organ morphology of a wide variety of oonopids and their outgroups.

## HISTORICAL BACKGROUND: OUTGROUPS

As treated in the classical literature (e.g., Simon, 1893; Dalmas, 1916; Chickering, 1951; Forster, 1956; Hickman, 1979), oonopids were poorly delimited, and certainly not a monophy-

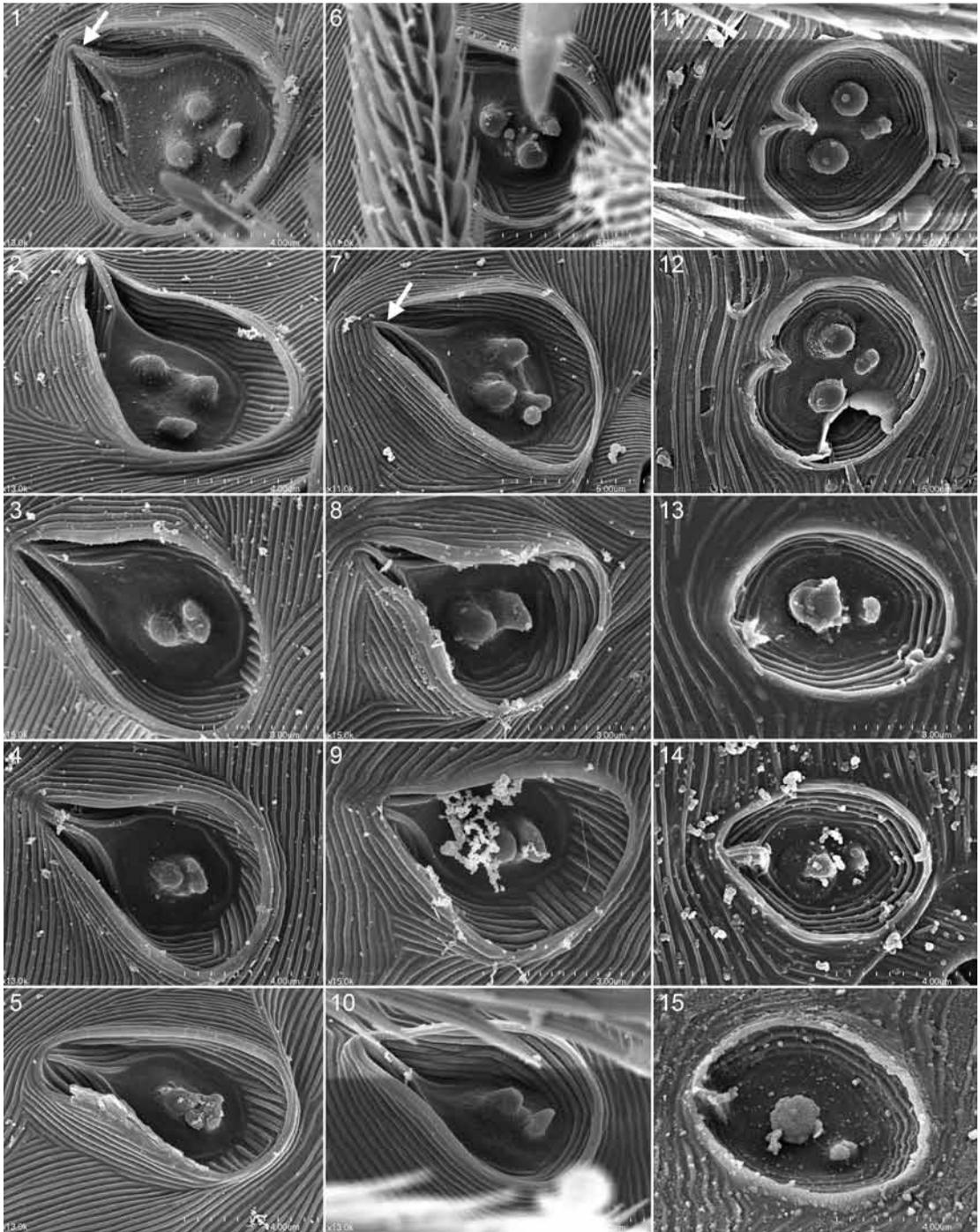
letic group. Some of the major problems were solved by Forster and Platnick (1985), who used scanning electron microscopy of the tarsal organ (a chemosensory structure found near the tips of the legs and palps) to show that many of the austral genera previously assigned to the Oonopidae are actually more closely related to *Orsolobus* Simon (which was then placed in the Dysderidae) than they are to true oonopids. Forster and Platnick suggested that the monophyly of the superfamily Dysderoidea is supported by a peculiar specialization of the internal female genitalia (the development of a receptaculum associated with the posterior wall of the bursal cavity), and argued that four families of dysderoids should be recognized: the Dysderidae (primarily a Mediterranean group, but with one synanthropic, cosmopolitan species), Segestriidae (a worldwide group of three genera), Orsolobidae (a Gondwanan group, found in Australia, New Zealand, and southern South America, and subsequently discovered in southern Africa by Griswold and Platnick, 1987), and the Oonopidae. This grouping of families was also supported in more recent, matrix-based phylogenetic analyses by Platnick et al. (1991), which incorporated new data obtained by scanning electron microscopy of the spinneret spigots, and by Ramírez (2000), which added new data on respiratory system morphology.

The latter study placed the family Caponiidae as the sister group of dysderoids, based on the shared advancement of the posterior spiracles to a position just behind the epigastric furrow. Resolution within the Dysderoidea was not strongly supported in any of these studies; Platnick et al. (1991: 67) concluded that “familial relationships within the Dysderoidea (and the monophyly of the Oonopidae) remain uncertain” but favored a sister-group relationship between oonopids and orsolobids, and that sister-group relationship was also supported in the later analysis by Ramírez (2000).

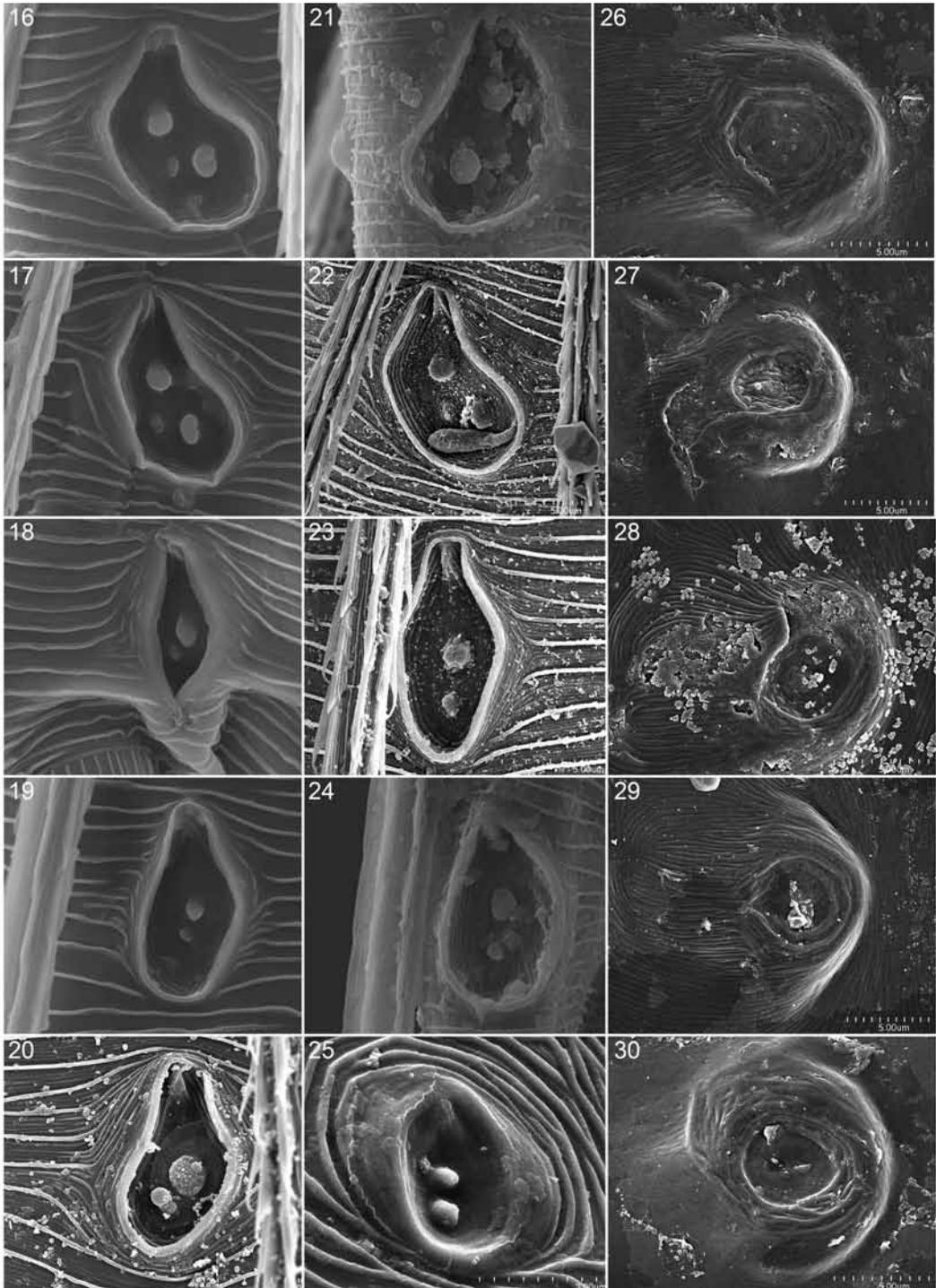
More recently, Burger and Michalik (2010) presented the first evidence in support of oonopid monophyly, showing that (unlike all other spiders previously observed) males of a wide variety of oonopid genera have an unpaired, completely fused testis. The single orsolobid species they examined, in contrast, had the paired, unfused testes typical of most other spiders. Interestingly, some dysderids and segestriids have been reported to have partially fused testes, but similar structures also occur in the more distantly related family Scytodidae (Michalik, 2009).

#### HISTORICAL BACKGROUND: INGROUP

The traditional classification of oonopids stems from the treatment of the family in Simon's (1893) classic volume on the *Histoire naturelle des araignées*, where he recognized two informal groups, the “Oonopidae molles,” containing soft-bodied species in which the abdomen either lacks scuta entirely or has only a weakly sclerotized epigastric scutum, and the “Oonopidae loricatae,” containing hard-bodied species in which the abdomen has additional (and more heavily sclerotized) scuta. Simon intended these groupings only as artificial aids to identification; he explicitly stated (1893: 292) “Pour en faciliter l'étude, je répartis les Oonopides en deux sections, qui ne correspondent cependant pas à des groupes naturels.” Nevertheless, Petrunkevitch (1923) and subsequent workers recognized these groups formally, as the subfamilies Oonopinae and Gamasomorphinae, respectively. Neither Petrunkevitch nor the other workers who have used the names provided any phylogenetic justification for either of those subfamilies.



FIGURES 1–15. Tarsal organ, dorsal view, *Oonops pulcher* Templeton, female (1–5) and male (6–10), *Triaeris stenaspis* Simon, female (11–15). 1, 6, 11. Leg I. 2, 7, 12. Leg II. 3, 8, 13. Leg III. 4, 9, 14. Leg IV. 5, 10, 15. Palp. Arrows point to the proximally situated, longitudinal ridge here considered synapomorphic for the Oonopidae.



FIGURES 16–30. Tarsal organ, dorsal view, *Ischnothyreus peltifer* (Simon), female (16–20) and male (21–25), *Segestria senoculata* (Linnaeus), female (26–30). 16, 21, 26. Leg I. 17, 22, 27. Leg II. 18, 23, 28. Leg III. 19, 24, 29. Leg IV. 20, 25, 30. Palp.

Two later papers also attempted to establish formal, subfamilial groupings. Chamberlin and Ivie (1942: 6) erected a monotypic subfamily, the Orchestininae, but provided no relevant evidence, indicating only that “The genus *Orchestina* is sufficiently distinct from the other genera of the Oonopidae to warrant its separation into a separate subfamily.” Their action seemingly ignored prior work, including that of Simon (1893: 292), who grouped *Orchestina* Simon with *Sulsula* Simon, and Dalmas (1916: 205), who added *Calculus* Purcell to this grouping, commenting that “Les trois genres *Orchestina*, *Calculus* et *Sulsula* sont les seuls de la famille offrant un groupe oculaire complètement transverse.” Much later, Dumitresco and Georgesco (1983: 103, 114) attempted to establish a subfamily containing only the gamasomorphine genera *Tri-aeris* Simon and *Ischnothyreus* Simon, but as they did not designate a type genus for the group, and did not base its name on either of the included genera, their subfamilial name “Pseudogamasomorphinae” is not available.

Given Simon’s intentions, it is hardly surprising that modern workers have found at least the Oonopinae to be paraphyletic. Platnick and Dupérré (2010a) noted that two putatively synapomorphic features, the acquisition of a clumped eye arrangement (rather than a transverse, H-shaped arrangement with a strongly recurved posterior row) and the loss of the heavily sclerotized, thick-walled sperm duct within the male palp, place *Oonops* Templeton as more closely related to the gamasomorphines than to some of the other genera currently placed as oonopines (including *Orchestina* and several other basal groups that retain the plesiomorphic states of these characters). Platnick and Dupérré (2010a: 6) also indicated that the limits of the Gamasomorphinae are unclear, and suggested that “gamasomorphy” be treated “as a syndrome of increasing sclerotization that starts, phylogenetically, with the cephalothorax.” Under that view, several genera placed as “molles” by Simon (1893) may be more closely related to the Gamasomorphinae than to *Oonops*. However, the monophyly of the classical Gamasomorphinae may be supported by at least one synapomorphic character, the presence of a sperm pore on the epigastric scutum of males.

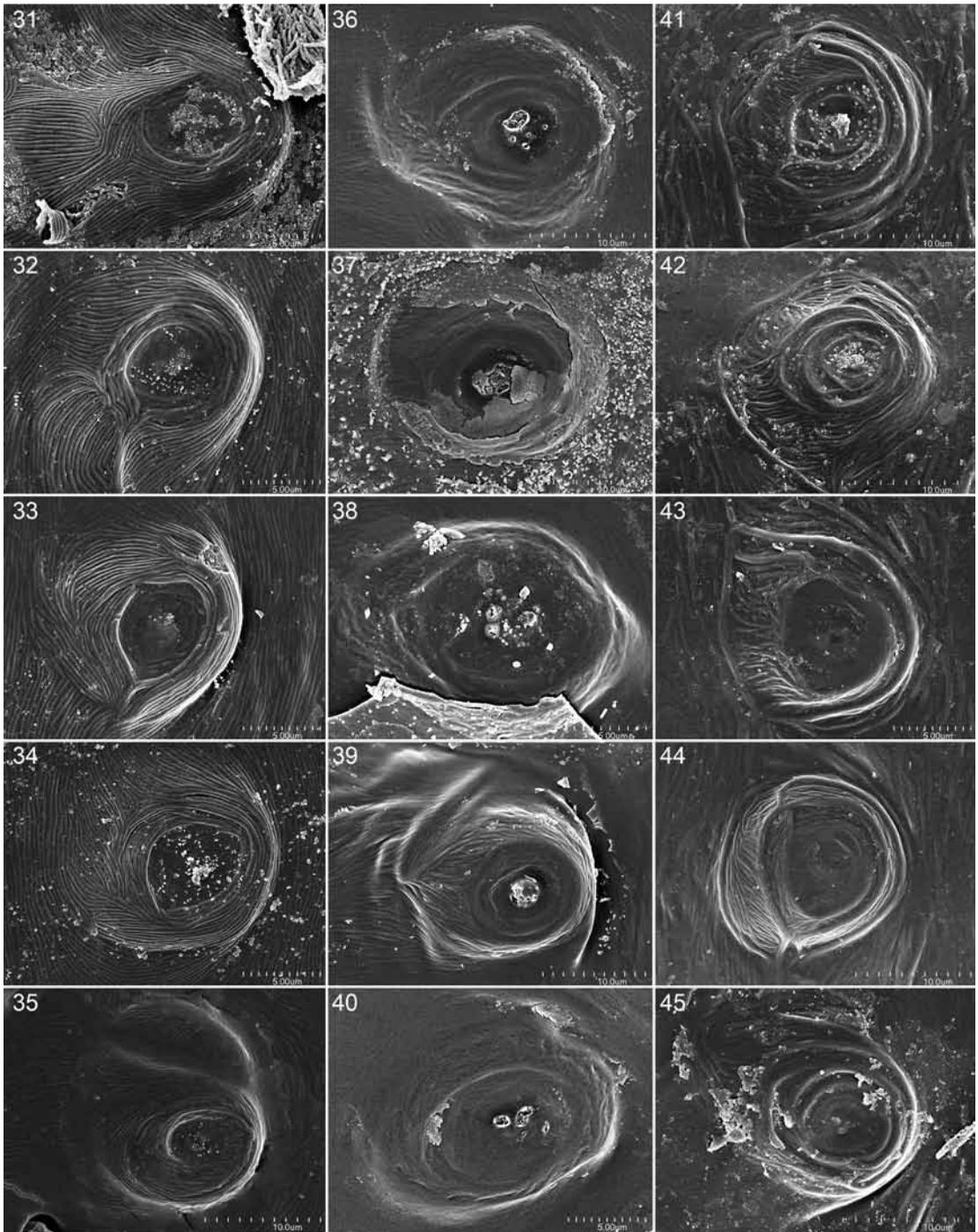
#### TYPICAL OONOPID TARSAL ORGANS

Study of a wide variety of oonopid genera indicates that the tarsal organ morphology most commonly encountered within the family is that shown by its type species, *Oonops pulcher* Templeton. In the first comprehensive study of spider tarsal organs, Blumenthal (1935: 669) indicated that in all cases where he succeeded in locating the tarsal organ, the organ occurred on the tarsus of each leg and on the palpal tarsus, always with the same structure (although not always with the same size). In that regard, as is frequently the case, oonopids simply don’t play by the same rules as other spiders. As shown here for *O. pulcher* (figs. 1–10), both sexes typically show serial dimorphism in their tarsal organ morphology; on the anterior legs, the tarsal organ has three raised receptors (figs. 1, 2, 6, 7), whereas on the posterior legs (and palps) the tarsal organ has only two receptors (figs. 3–5, 8–10). In *O. pulcher* and most other oonopids, the two most proximal receptors on the anterior legs are arranged transversely, whereas the two receptors found on the posterior legs and palps are arranged longitudinally.

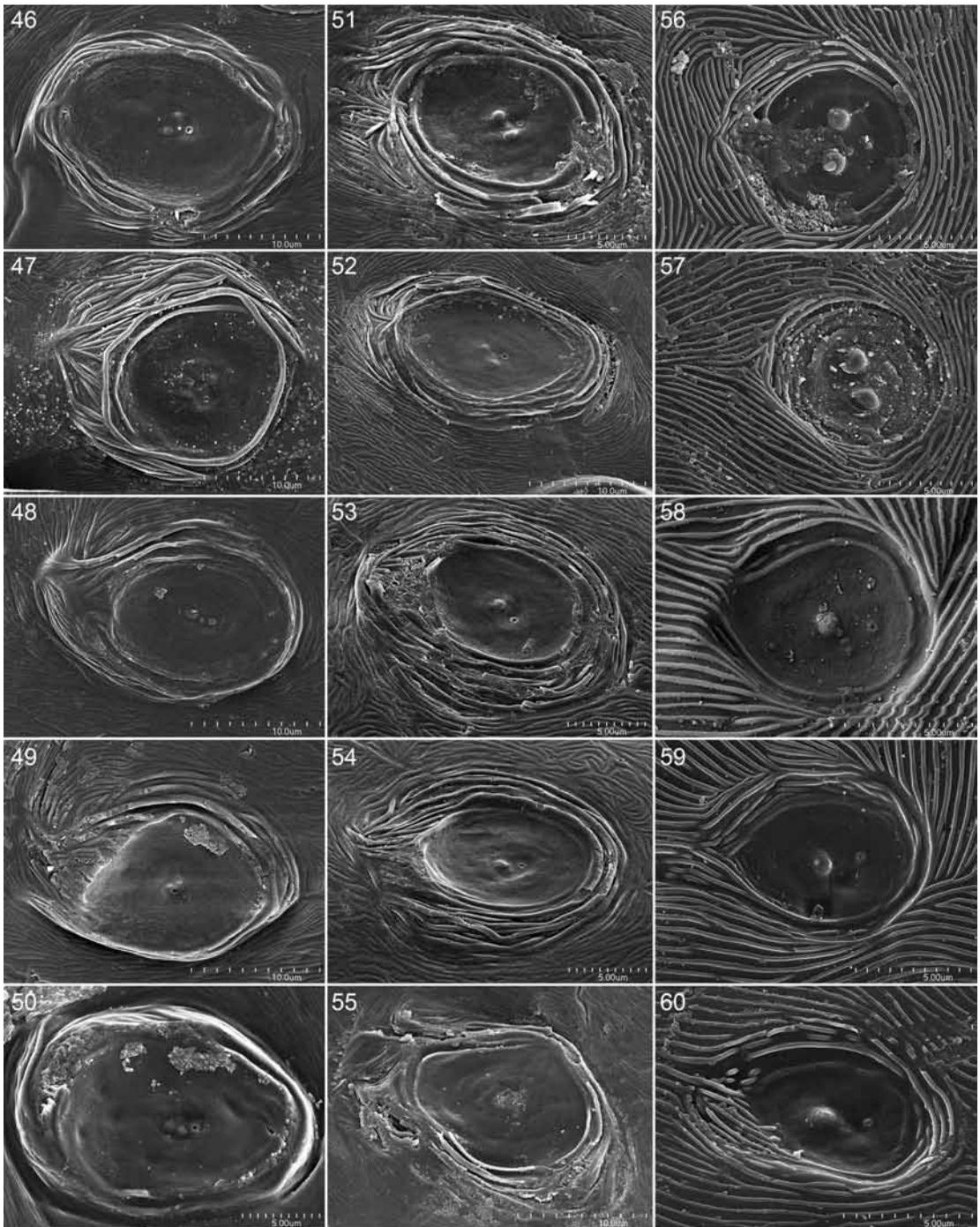
In addition to this unusual anterior/posterior dimorphism, most oonopid tarsal organs have a distinctive longitudinal ridge that originates at the proximal end of the tarsal organ (figs. 1, 7, arrows). Such ridges have not been detected, to date, in the relevant outgroup families (Orsolobidae, Dysderidae, Segestriidae, and Caponiidae). We therefore hypothesize that both the anterior/posterior, serial dimorphism in raised receptor number and orientation, and the presence of the proximal, longitudinal ridge, are synapomorphic for the Oonopidae.

To date, tarsal organs showing this typical morphology have been demonstrated to occur in the following oonopid taxa: *Antoonops corbulo* Fannes and Jocqué (see Fannes and Jocqué, 2008: fig. 47), *Australoonops granulatus* Hewitt (see Platnick and Dupérré, 2010b: figs. 755–759, 782, 796, 797), *Birabenella pizarroi* Grismado (see Grismado, 2010: fig. 14), *Brignolia parumpunctata* (Simon) (see Platnick et al., 2011: figs. 41–44, 49, 66, 77–80), *Camptoscapphiella paquini* Ubick (see Baehr and Ubick, 2010: figs. 91–94, 103–107), *Cavisternum clavatum* Baehr et al. (see Baehr et al., 2010: figs. 67–70), *Costarina plena* (O. P.-Cambridge; see Platnick and Dupérré, 2012: figs. 26–30, 56–60), *Coxapopha yuyapichis* Ott and Brescovit (see Ott and Brescovit, 2004: fig. 21), *Epectris apicalis* Simon (see Platnick and Dupérré, 2009a: figs. 137, 138), *Heteroonops castellus* (Chickering) (see Platnick and Dupérré, 2009c: figs. 287–290, 298), *H. spinimanus* (Simon) (see Platnick and Dupérré, 2009c: figs. 121–125), *Malagiella ranomafana* Ubick and Griswold (see Ubick and Griswold, 2011a: figs. 57–61), *Melchisedec thevenot* Fannes (see Fannes, 2010: fig. 44), *Molotra milloti* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 311–314), *M. molotra* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 123–128), *M. tsingy* Ubick and Griswold (see Ubick and Griswold, 2011b: figs. 266–268), *Niarchos baragani* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 59–63, 95–99), *N. foreroi* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 509–513, 542–546), *N. palenque* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 602–606, 633–637), *N. scutatus* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 250–254, 287–291), *Opopaea deserticola* Simon (see Platnick and Dupérré, 2009a: figs. 51–54), *Paradysderina watrousi* Platnick and Dupérré (see Platnick and Dupérré, 2011d: figs. 14, 25–28, 62, 67–70), *Pescennina arborea* Platnick and Dupérré (see Platnick and Dupérré, 2011b: figs. 119–123, 164–168), *Scaphidysderina palenque* Platnick and Dupérré (see Platnick and Dupérré, 2011a: figs. 149, 160–163, 183, 197–200), *Scaphiella williamsi* Gertsch (see Platnick and Dupérré, 2010a: figs. 510–514, 560–564), *Scaphios yanayacu* Platnick and Dupérré (see Platnick and Dupérré, 2010c: figs. 739–743, 786–790), *Semidysderina lagila* Platnick and Dupérré (see Platnick and Dupérré, 2011d: figs. 755, 766–769, 803, 809–812), *Simonoonops craneae* (Chickering) (see Platnick and Dupérré, 2011c: figs. 19–23, 50–54), *Stenoonops peckorum* Platnick and Dupérré (see Platnick and Dupérré, 2010b: figs. 33, 34, 66–70), and *S. pretiosus* (Bryant) (see Platnick and Dupérré, 2010b: figs. 379–383, 426–430).

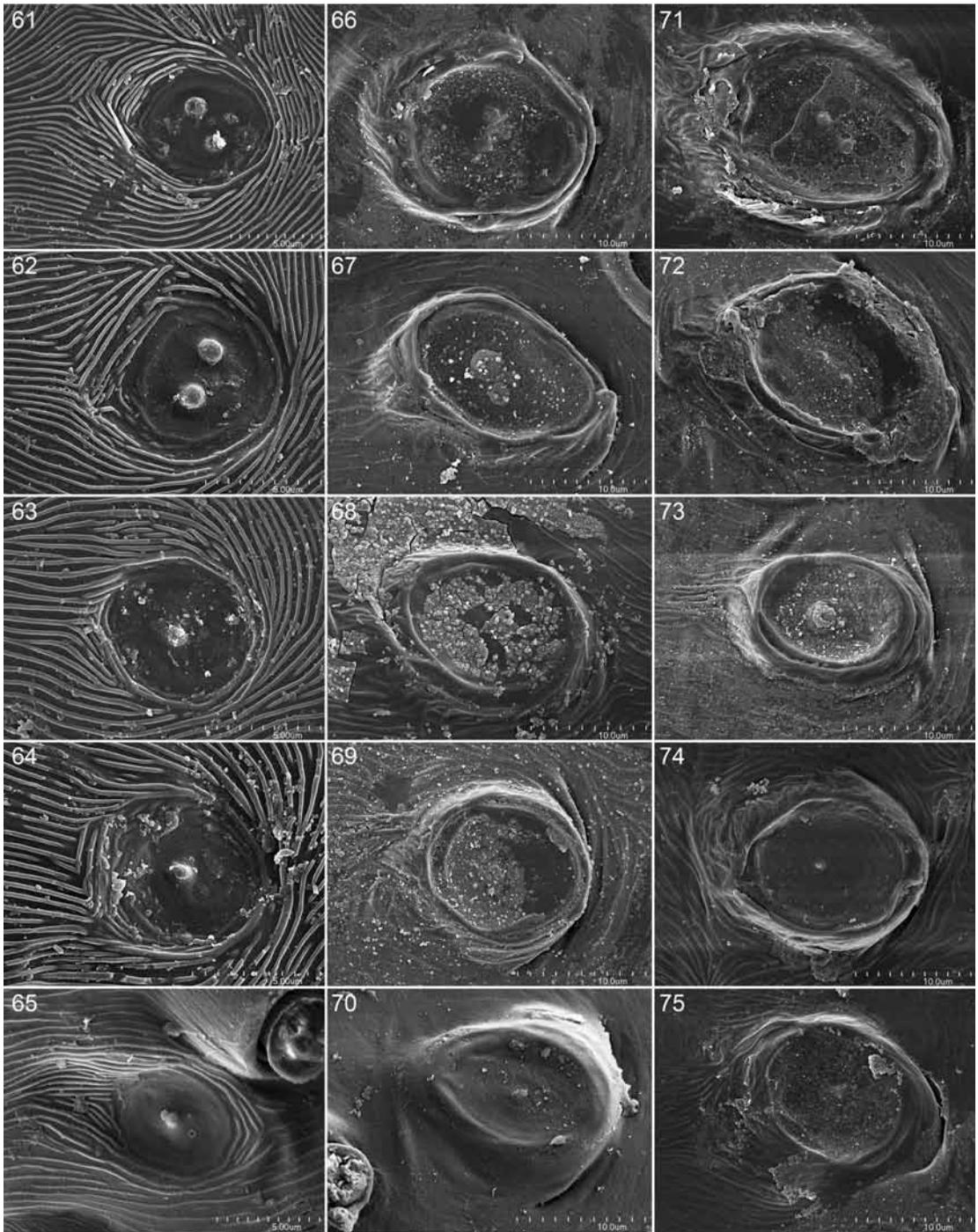
This range of taxa constitutes a reasonable sampling of oonopid diversity, particularly as studies in preparation show that tarsal organs of this type occur also in many taxa that are not yet revised or described, including members of the genera *Gamasomorpha* Karsch (Eichenberger et al., in press), *Neoxyphinus* Birabén (Abraham et al., in press), *Zyngoonops* Benoit (Fannes, in prep.), *Lionneta* Benoit (Andriamalala, in prep.), and *Trilacuna* Tong and Li (Gris-



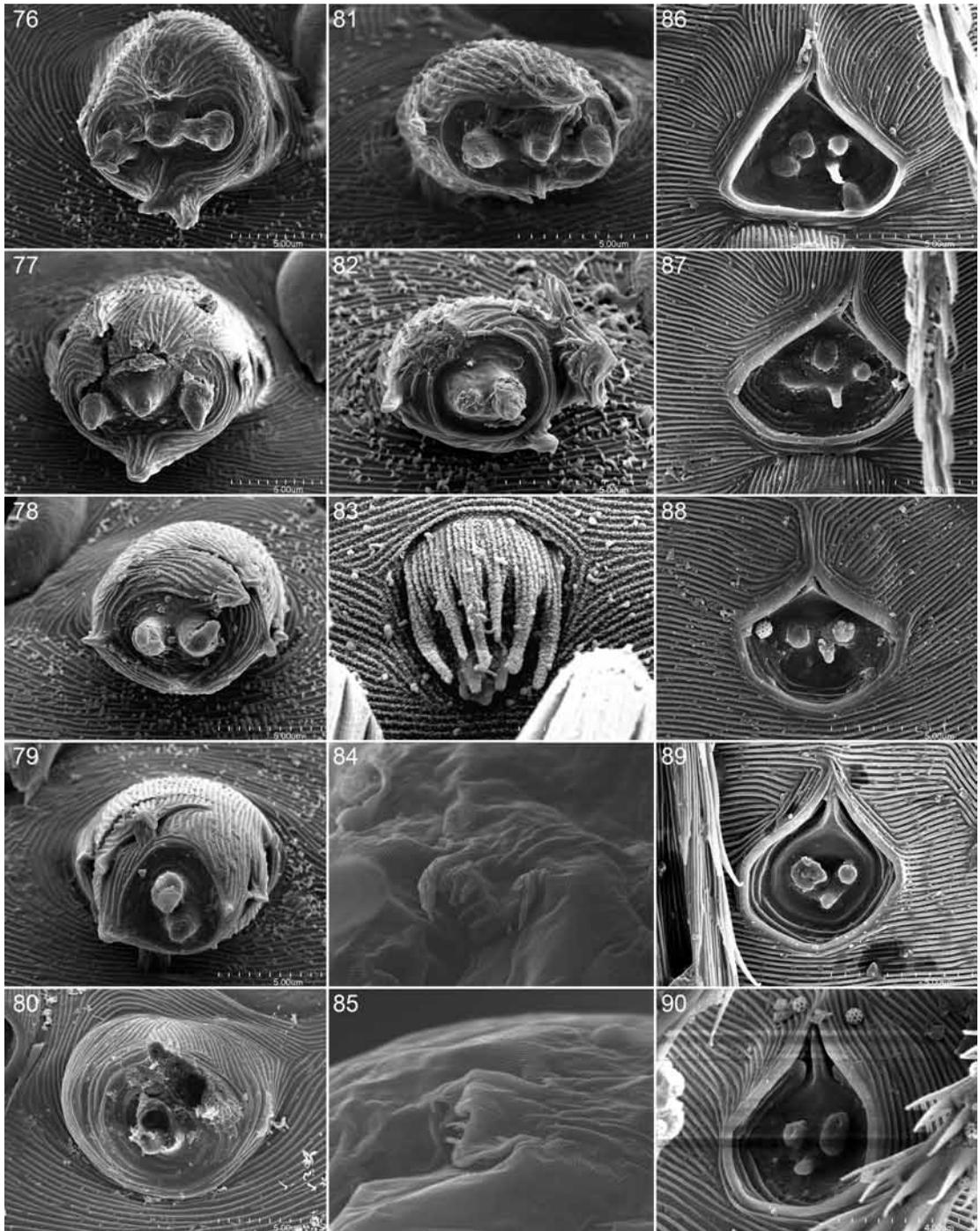
FIGURES 31–45. Tarsal organ, dorsal view, *Segestria senoculata* (Linnaeus), male (31–35), *Ariadna bicolor* (Hentz), female (36–40) and male (41–45). 31, 36, 41. Leg I. 32, 37, 42. Leg II. 33, 38, 43. Leg III. 34, 39, 44. Leg IV. 35, 40, 45. Palp.



FIGURES 46–60. Tarsal organ, dorsal view, *Dysdera crocata* C.L. Koch, female (46–50) and male (51–55), *Harpactea lepida* (C.L. Koch), female (56–60). 46, 51, 56. Leg I. 47, 52, 57. Leg II. 48, 53, 58. Leg III. 49, 54, 59. Leg IV. 50, 55, 60. Palp.



FIGURES 61–75. Tarsal organ, dorsal view, *Harpactea lepida* (C.L. Koch), male (61–65), *Harpactocrates drasoides* (Simon), female (66–70) and male (71–75). 61, 66, 71. Leg I. 62, 67, 72. Leg II. 63, 68, 73. Leg III. 64, 69, 74. Leg IV. 65, 70, 75. Palp.



FIGURES 76–90. Tarsal organ, dorsal view (except 85, lateral view), *Tasmanoonops parvus* Forster and Platnick, female (76–80, proximal end at top of image except 79, proximal end at right of image) and male (81, 82), *Hickmanolobus* sp., female (83), *Calculus bicolor* Purcell (84, 85), *Orchestina* sp. from Africa, female (86–90). 76, 84–86. Leg I. 77, 81, 83, 87. Leg II. 78, 82, 88. Leg III. 79, 89. Leg IV. 80, 90. Palp.

mado and Piacentini, in prep.), as well as in new genera from Brazil (Brescovit et al., in press), southern South America (Grismado and Ramírez, in prep.), Madagascar (Álvarez-Padilla et al., in press), and Australia (Baehr et al., in press).

The largest gap in the sampling that has been done to date concerns the two genera, *Triaeris* and *Ischnothyreus*, that were treated by Dumitresco and Georgesco (1983) as members of their stillborn subfamily “Pseudogamasomorphinae.” We therefore present here scans of the tarsal organs of the type species of those genera, *Triaeris stenaspis* Simon (figs. 11–15) and *Ischnothyreus peltifer* (Simon) (figs. 16–25). Although the late Ray Forster doubted that *Ischnothyreus* is an oonopid, its type species has tarsal organs that are typical for the family. The longitudinal ridge is relatively short, but the same is true for many other typical oonopids (e.g., Platnick and Dupérré, 2011a: figs. 160–163).

#### OUTGROUP TARSAL ORGANS

The tarsal organs of the putative sister group of oonopids, the family Orsolobidae, have been documented in detail (see Forster and Platnick, 1985; Griswold and Platnick, 1987; Brescovit et al., 2004; Lise and Almeida, 2006; Baehr and Smith, 2008) because they constitute the best evidence for the monophyly of that family and provide many characters for grouping subsets of its members. Orsolobids resemble oonopids in many respects, but have distinctively elevated tarsal organs, usually accompanied by several cuticular lobes, that are unlike those of any other spiders studied to date (figs. 76–83). Interesting in that regard is one of the basal oonopid genera associated with *Orchestina* by Dalmás (1916), *Calculus*. The type (and only known) species of that genus, *Calculus bicolor* Purcell, is known only from juveniles from South Africa (Purcell, 1910); although they are poorly preserved, their tarsal organ morphology (figs. 84, 85) shows clearly that these juveniles are orsolobids rather than oonopids. Simon (1893: 294) identified similar juveniles from South Africa as members of *Sulsula pauper* (O. P.-Cambridge), a species otherwise then known only from Egypt. Dalmás (1916: 205) suggested that those South African juveniles actually belong to *C. bicolor* rather than *S. pauper*; we have scanned the tarsal organs of one of those juveniles, and can confirm that it does indeed belong to the Orsolobidae rather than the Oonopidae. On the basis of these results, we here transfer *Calculus* from the Oonopidae to the Orsolobidae.

The tarsal organs of the other dysderoid families, the Segestriidae and Dysderidae, are less well known. Blumenthal (1935) considered that all spider tarsal organs belong either to “der primitive Typus” or “die normale Form.” His studies of the primitive type were based primarily on two species of *Segestria* Latreille, and his distinction was maintained by Forster (1980), who substituted the more descriptive terms “exposed” and “capsulate” for Blumenthal’s primitive and normal types, respectively.

Forster and Platnick (1985: 219, figs. 958–962) provided characterizations of the tarsal organs for each of the dysderoid families, as well as a few scans of oonopid, dysderid, and segestriid tarsal organs. Here we present detailed sets of scans for several representative genera, including *Segestria* (figs. 26–35), *Ariadna* Audouin (figs. 36–45), *Dysdera* Latreille (figs. 46–55),

*Harpactea* Bristowe (figs. 56–65), and *Harpactocrates* Simon (figs. 66–75). The primary relevance of these figures is to show that the typical oonopid tarsal organ morphology detailed above does not occur in those outgroup taxa.

The same is true for the putative sister group of dysderoids, the family Caponiidae. Caponiid tarsal organs have been well documented, for example, in *Cubanops alayoni* Sánchez-Ruiz et al. (see Sánchez-Ruiz et al., 2010: figs. 88–91, 112–115) and *Nopsides ceralbonus* Chamberlin (see Jiménez et al., 2011: figs. 34–37, 64–67). Those taxa show neither the anterior/posterior, serial dimorphism nor the proximally originating, longitudinal ridge characteristic of oonopids.

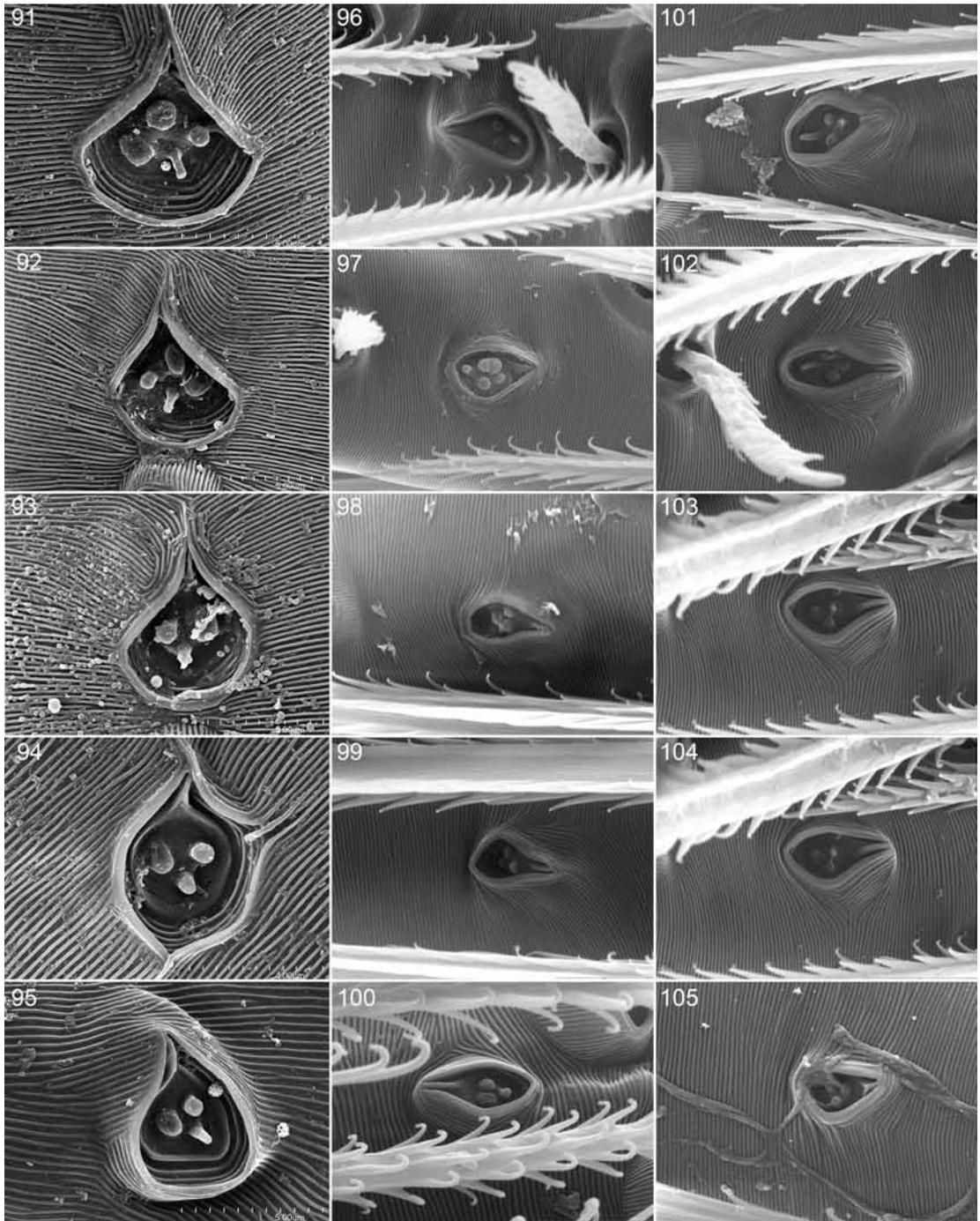
The tarsal organs of the dysderids we have examined offer several features of potential phylogenetic interest. In *Dysdera crocata* C.L. Koch, there is no longitudinal ridge, and there seem to be two different types of receptors. One type resembles the raised receptors of oonopids, except that they each seem to have a tiny pore (figs. 46, 51–54); the second type are just small pores, surrounded by an elevated rim (fig. 52). Because the raised receptors are relatively low and the small pores are easily occluded by dirt and debris, it is difficult to determine how many receptors are present on a given tarsal organ. For example, the tarsal organ of leg I seems to have four receptors in females (fig. 46), two raised and two rimmed, whereas in the male only one rimmed and two raised receptors are clearly visible on leg I (fig. 51). There may be some serial dimorphism as well; females seem to have one, rather than two, rimmed receptors on legs III, IV, and the palps (figs. 48–50).

In *Harpactea lepida* (C.L. Koch), the tarsal organ of leg I seems to have two rimmed and two raised receptors in males (fig. 61), and probably in females as well (fig. 56). Interestingly, in this species both sexes have two raised receptors on legs I and II, but only one on legs III, IV, and the palps (figs. 56–65). It seems likely that this pattern of serial dimorphism is a parallelism with oonopids, but the apparent presence of two rimmed receptors on the female palpal tarsal organ (fig. 60) suggests that it is also possible that one of the raised receptors has been transformed into a rimmed receptor, rather than lost. Our scans of *Harpactocrates drassoides* (Simon) are not clean enough to show the rimmed receptors, but they do indicate that a similar serial dimorphism occurs in that species, with two raised receptors on legs I and II, but only one on legs III, IV, and the palps (figs. 66–75).

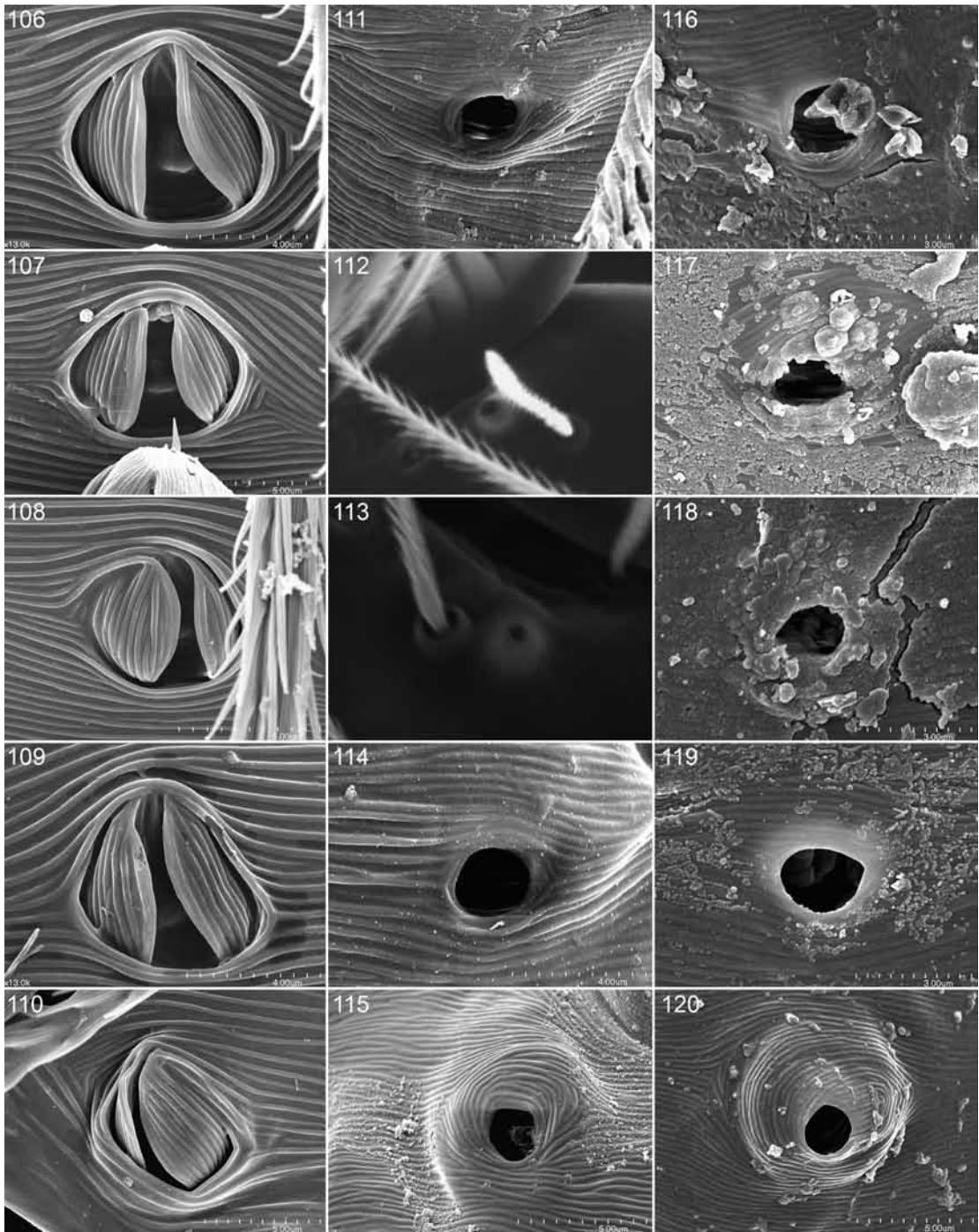
Interestingly, our scans of *Ariadna bicolor* (Hentz) indicate that the rimmed receptor type also occurs in that species (figs. 36, 41), and the same may also be true for *Segestria senoculata* (Linnaeus) (see fig. 31) and *Segestria florentina* (Rossi) (see Giroti and Brescovit, 2011: figs. 11–14). The rimmed receptors may therefore prove to be a synapomorphy uniting Dysderidae plus Segestriidae, although a much broader survey will be required to test that conjecture. Similarly, more thorough sampling of tarsal organ morphology is also likely to prove useful for future work on orsolobids, as our scans suggest that serial dimorphism occurs in both sexes of at least one species (figs. 76–82).

## BASAL OONOPID TARSAL ORGANS

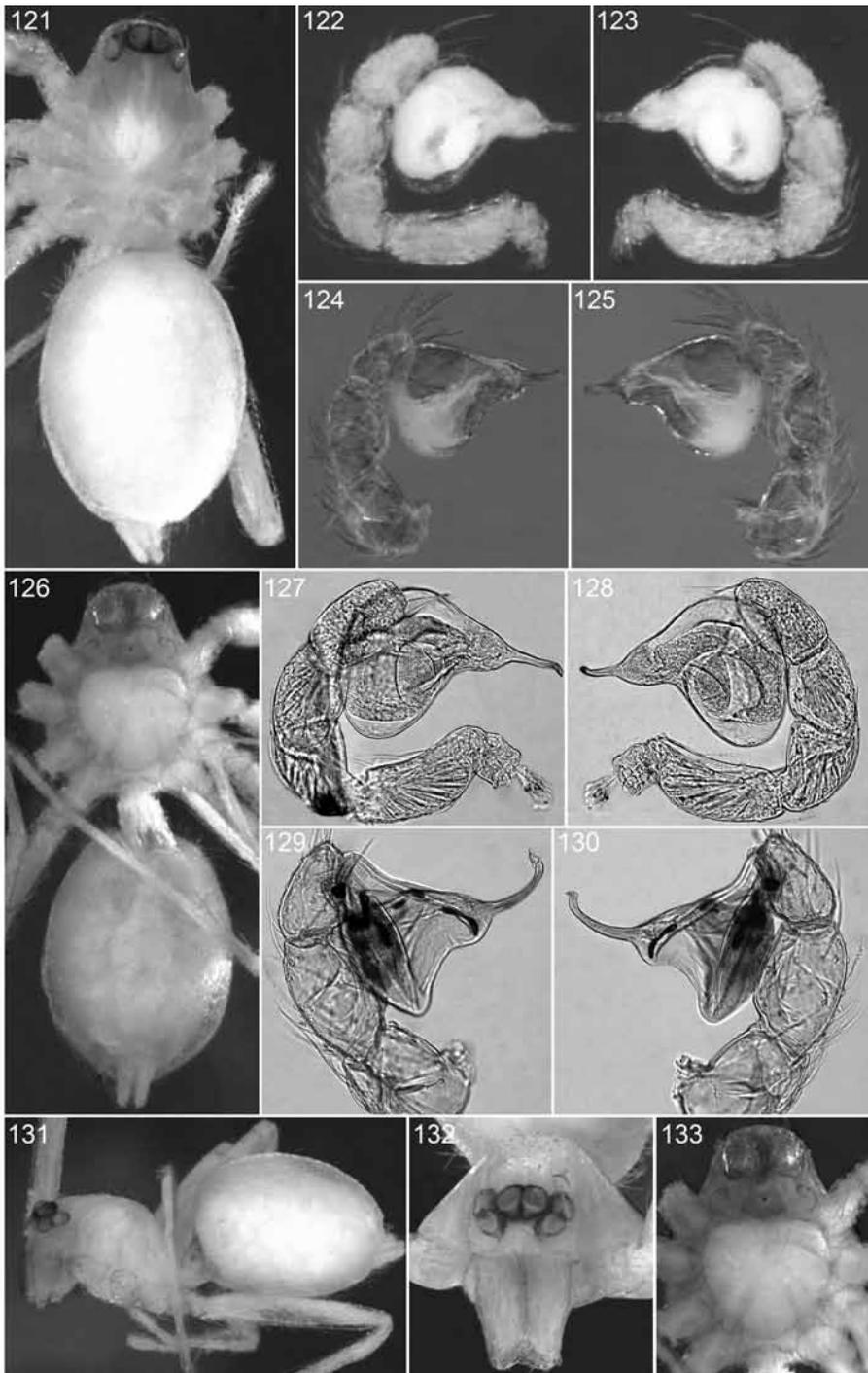
Given that the groundplan for typical oonopids seems well supported by the observations listed above, and clearly different from that of the relevant outgroups, our attention focused on



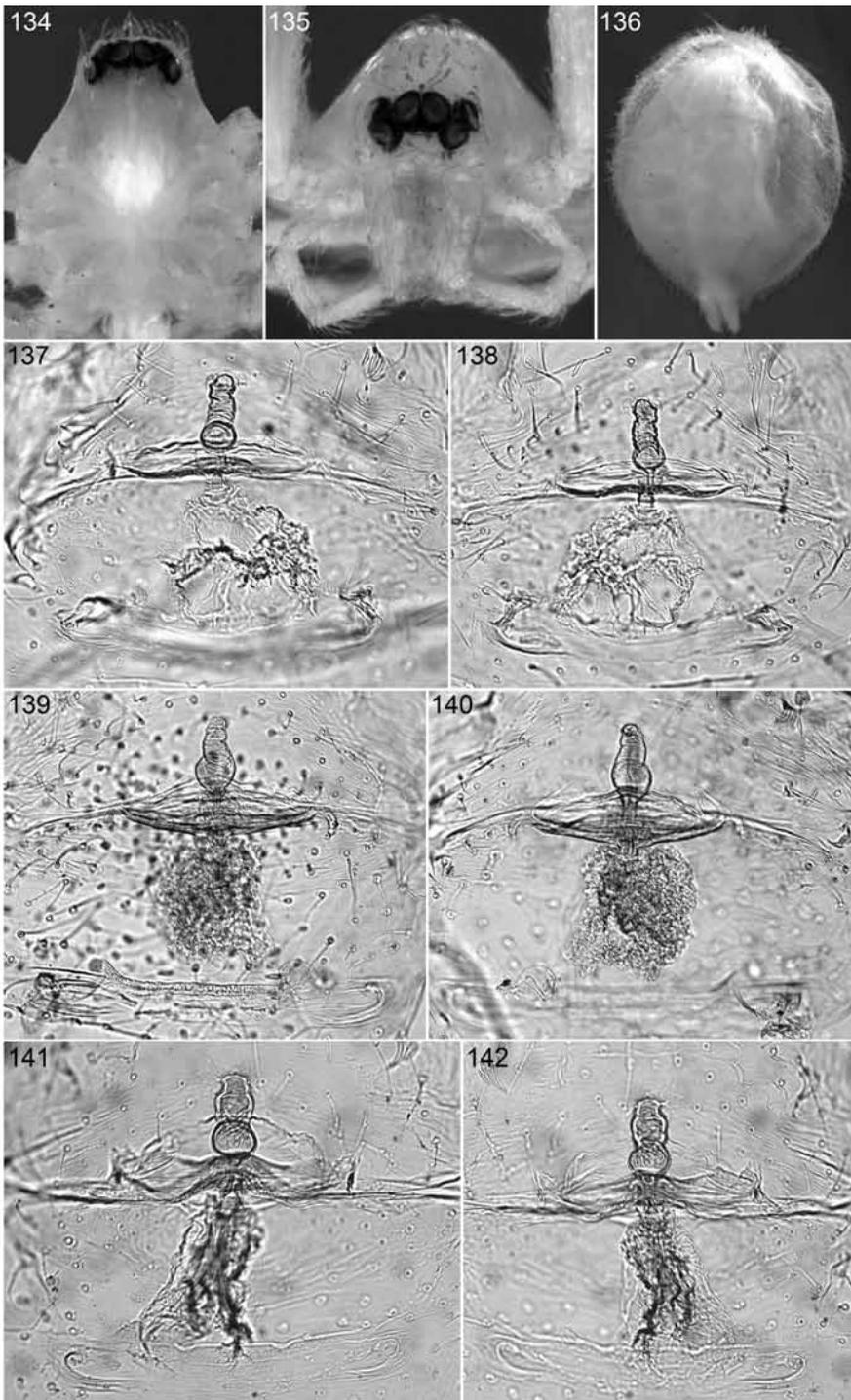
FIGURES 91–105. Tarsal organ, dorsal view, *Orchestina* sp. from Africa, male (91–95), *Orchestina* sp. from South America, female (96–100) and male (101–105). 91, 96, 101. Leg I. 92, 97, 102. Leg II. 93, 98, 103. Leg III. 94, 99, 104. Leg IV. 95, 100, 105. Palp.



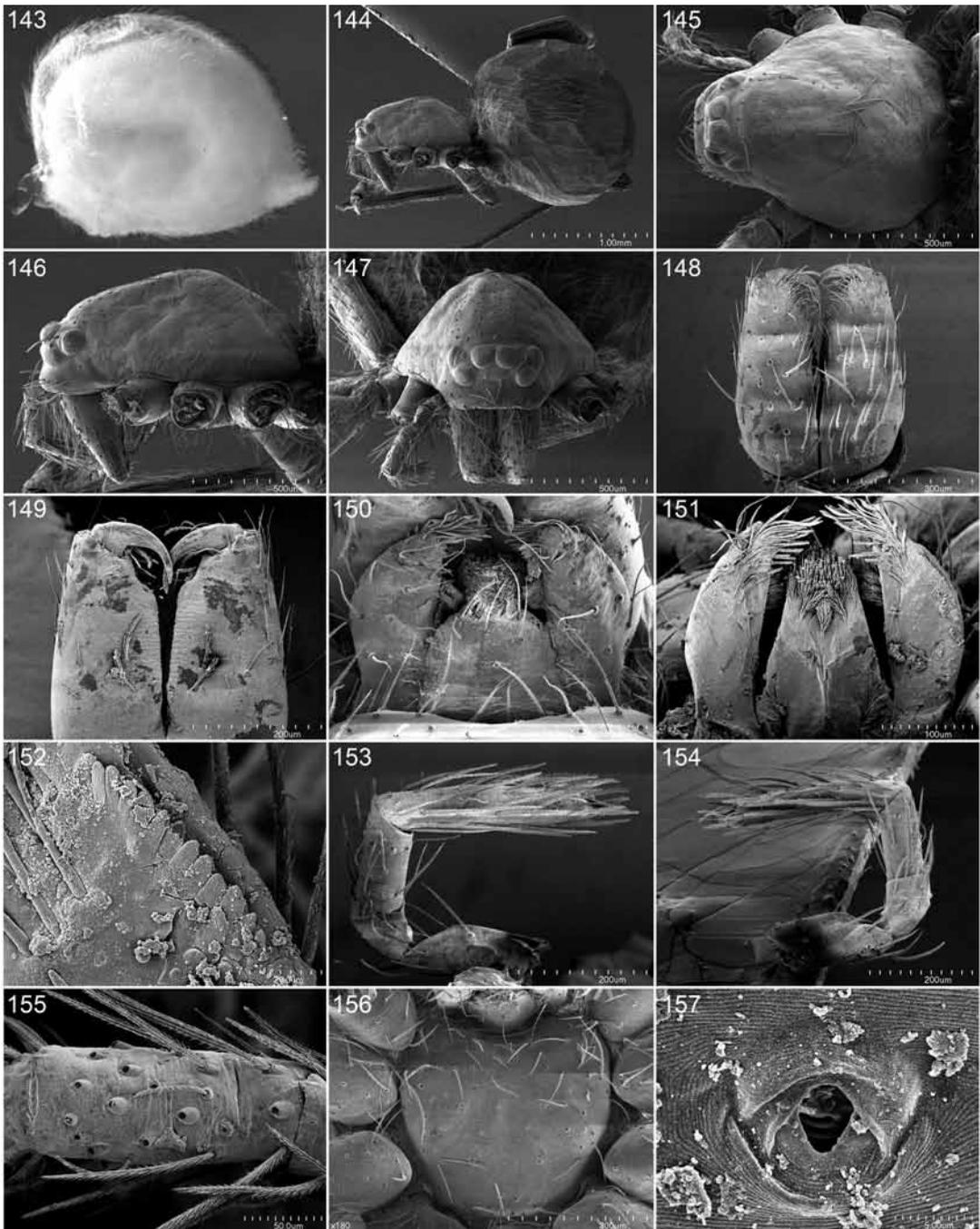
FIGURES 106–120. Tarsal organ, dorsal view, *Cortestina thaleri* Knoflach, male (106–110), *Xiombarg plaumanni* Brignoli, male (111–115), *Unicorn catleyi* Platnick and Brescovit, male (116–120). **106, 111, 116.** Leg I. **107, 112, 117.** Leg II. **108, 113, 118.** Leg III. **109, 114, 119.** Leg IV. **110, 115, 120.** Palp.



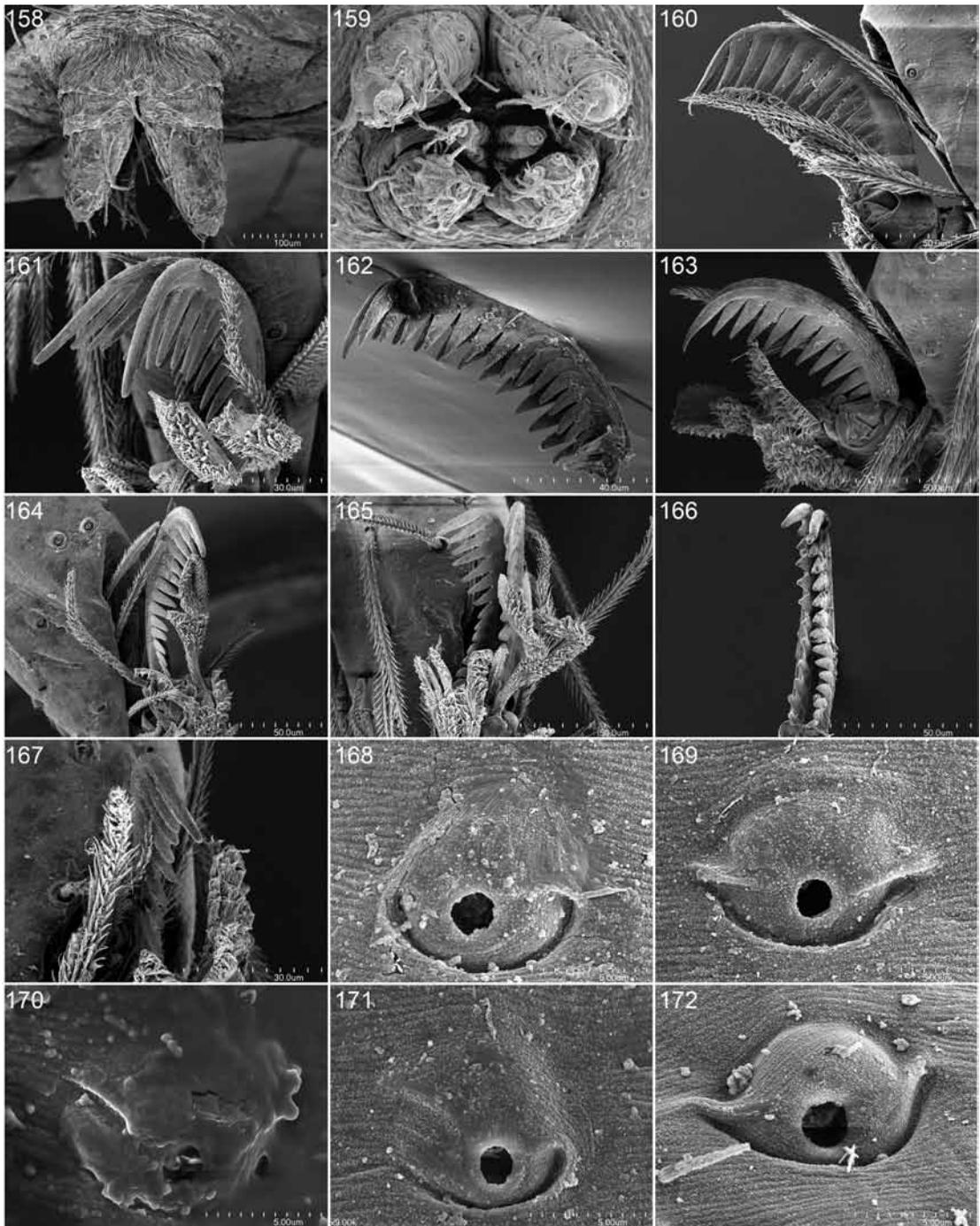
FIGURES 121–133. *Salsula pauper* (O. P.-Cambridge), male. **121.** Habitus, dorsal view. **122, 127.** Left palp, Algeria, pro-lateral view. **123, 128.** Same, retrolateral view. **124, 129.** Left palp, Egypt, pro-lateral view. **125, 130.** Same, retrolateral view. **126.** Habitus, ventral view. **131.** Same, lateral view. **132.** Carapace, anterior view. **133.** Sternum, ventral view.



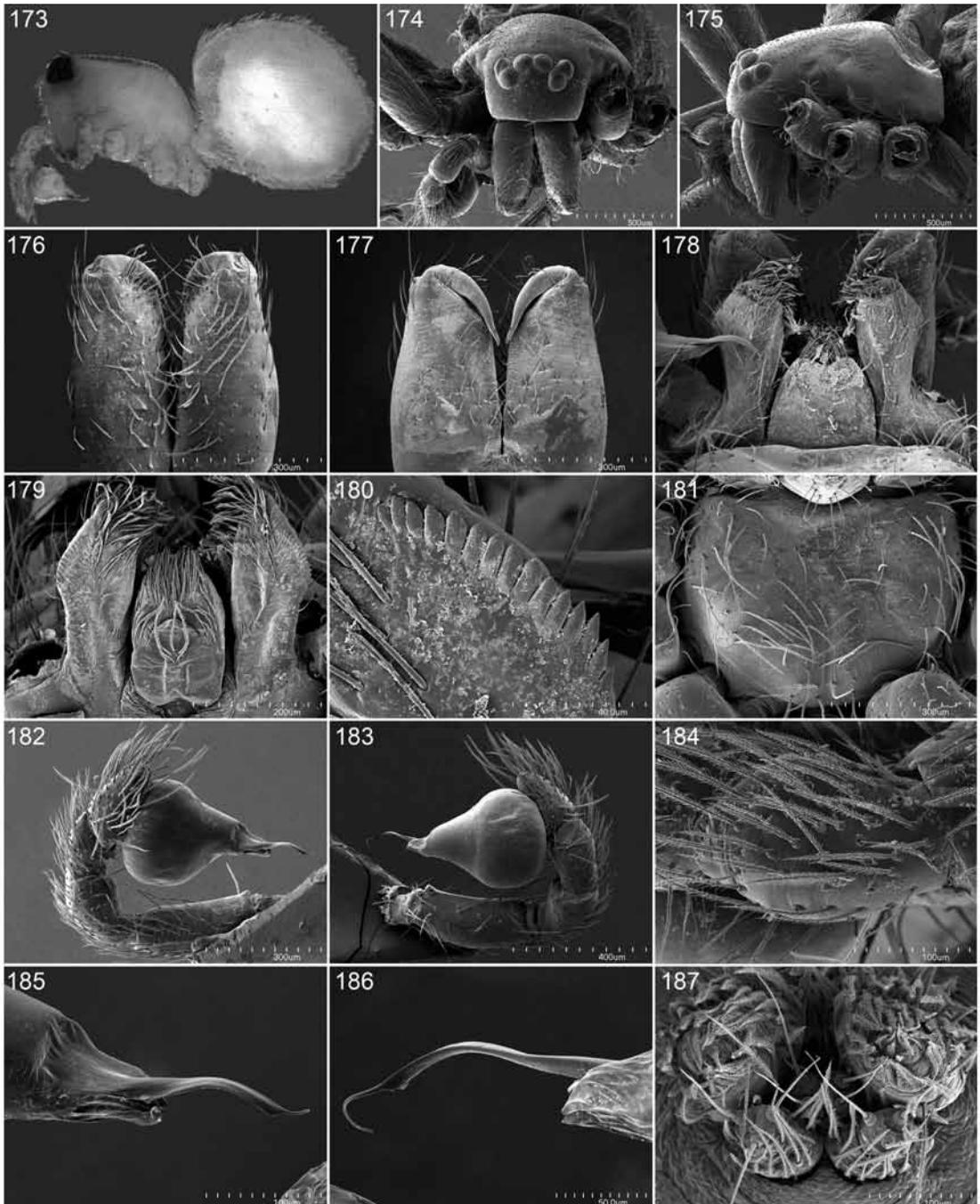
FIGURES 134–142. *Salsula pauper* (O. P.-Cambridge), females from Algeria (134–138), Egypt (139, 140), and Sudan (141, 142). 134. Carapace, dorsal view. 135. Same, anterior view. 136. Abdomen, ventral view. 137, 139, 141. Genitalia, ventral view. 138, 140, 142. Same, dorsal view.



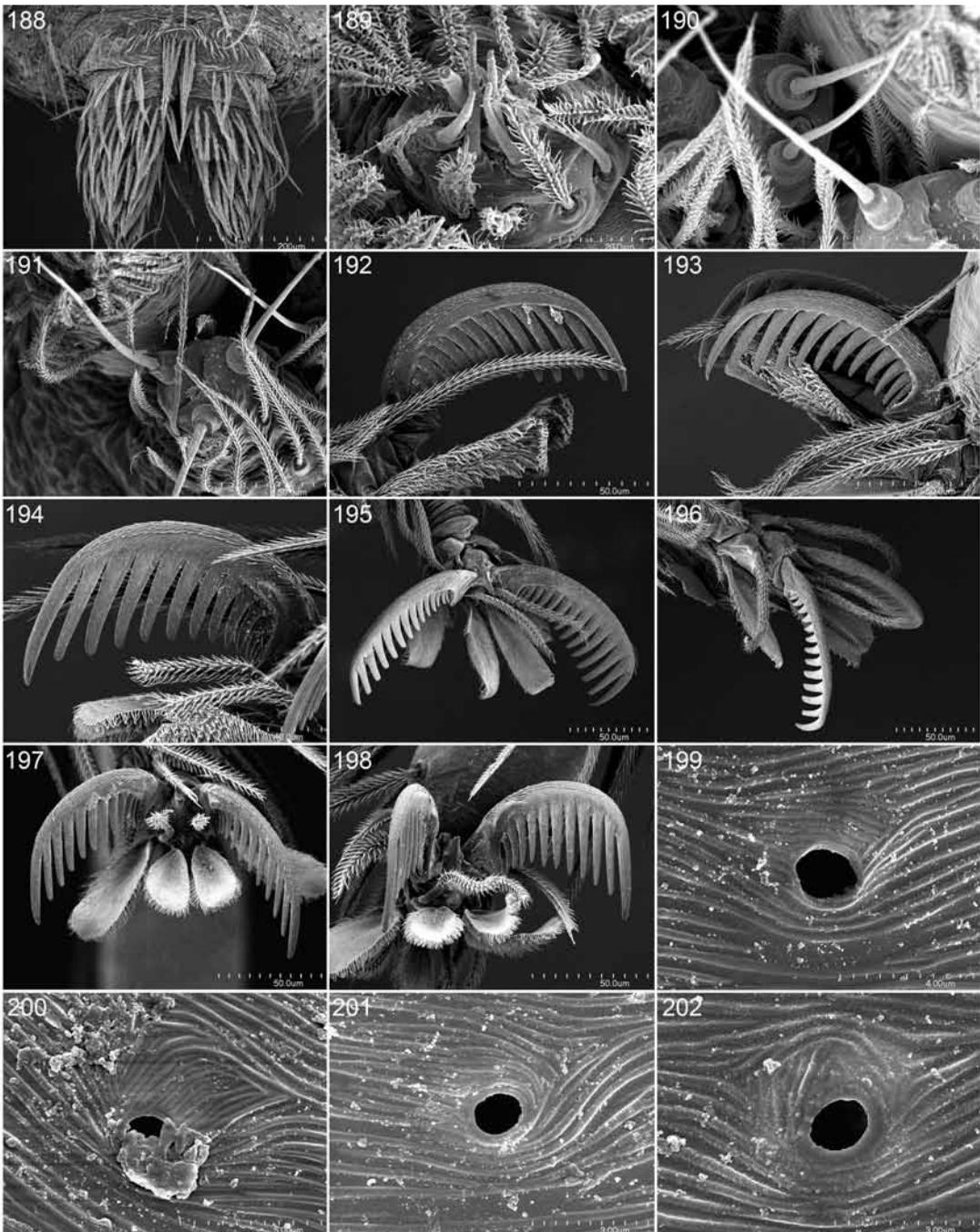
FIGURES 143–157. *Sulsula pauper* (O. P.-Cambridge), female. 143. Abdomen, lateral view. 144. Habitus, lateral view. 145. Carapace, dorsal view. 146. Same, lateral view. 147. Same, anterior view. 148. Chelicerae, anterior view. 149. Same, posterior view. 150. Labium and endites, ventral view. 151. Labrum and endites, dorsal view. 152. Serrula, dorsal view. 153. Palp, prolateral view. 154. Same, retrolateral view. 155. Palpal tibia, dorsal view. 156. Sternum, ventral view. 157. Trichobothrial base from tibia IV, dorsal view.



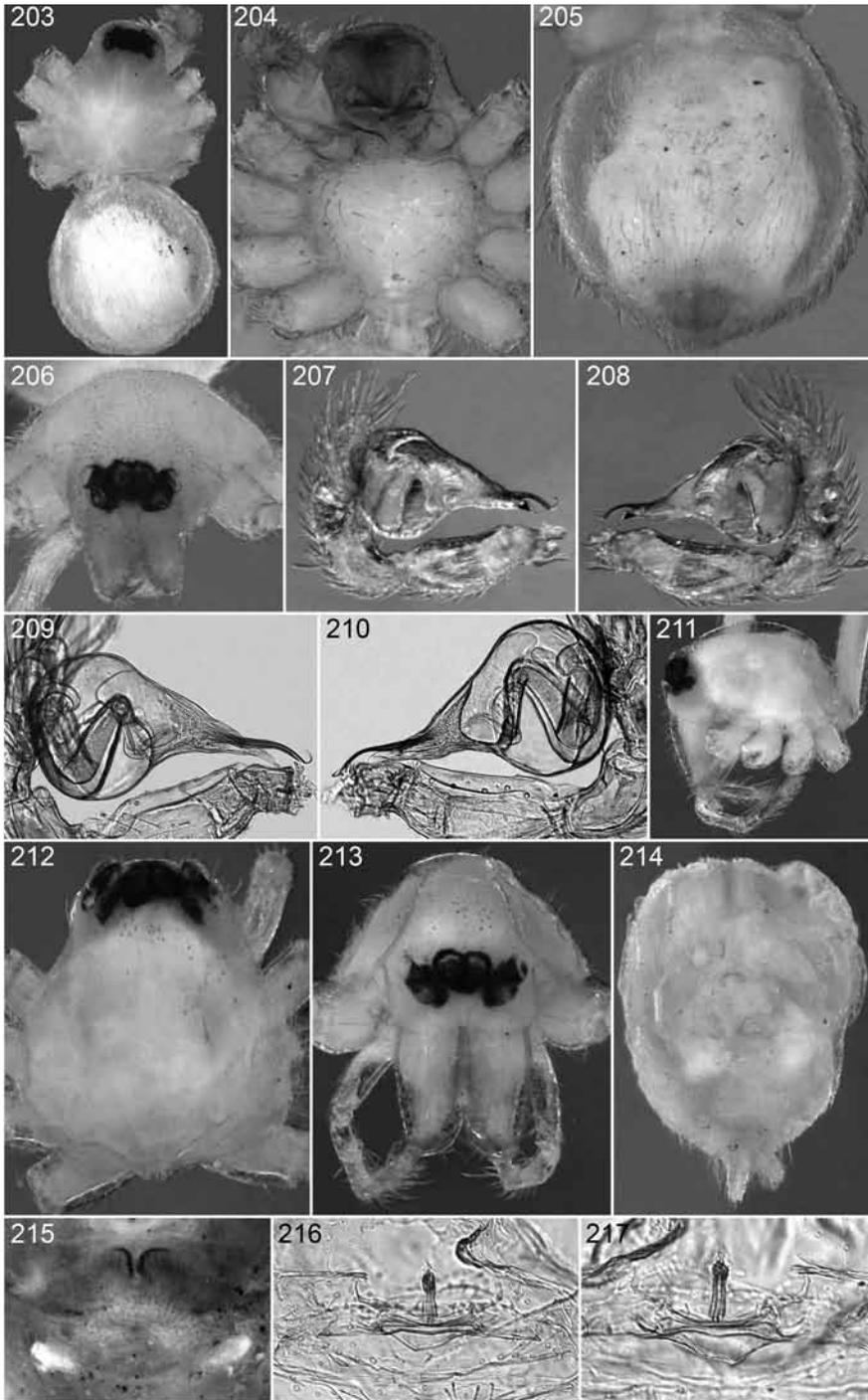
FIGURES 158–172. *Salsula pauper* (O. P.-Cambridge), female. 158. Spinnerets, ventral view. 159. Same, apical view. 160. Claws of leg I, lateral view. 161. Same, leg II. 162. Same, leg III. 163. Same, leg IV. 164. Claws of leg I, apical view. 165. Same, leg II. 166. Same, leg III. 167. Same, leg IV. 168. Tarsal organ from leg I, dorsal view. 169. Same, leg II. 170. Same, leg III. 171. Same, leg IV. 172. Same, palp.



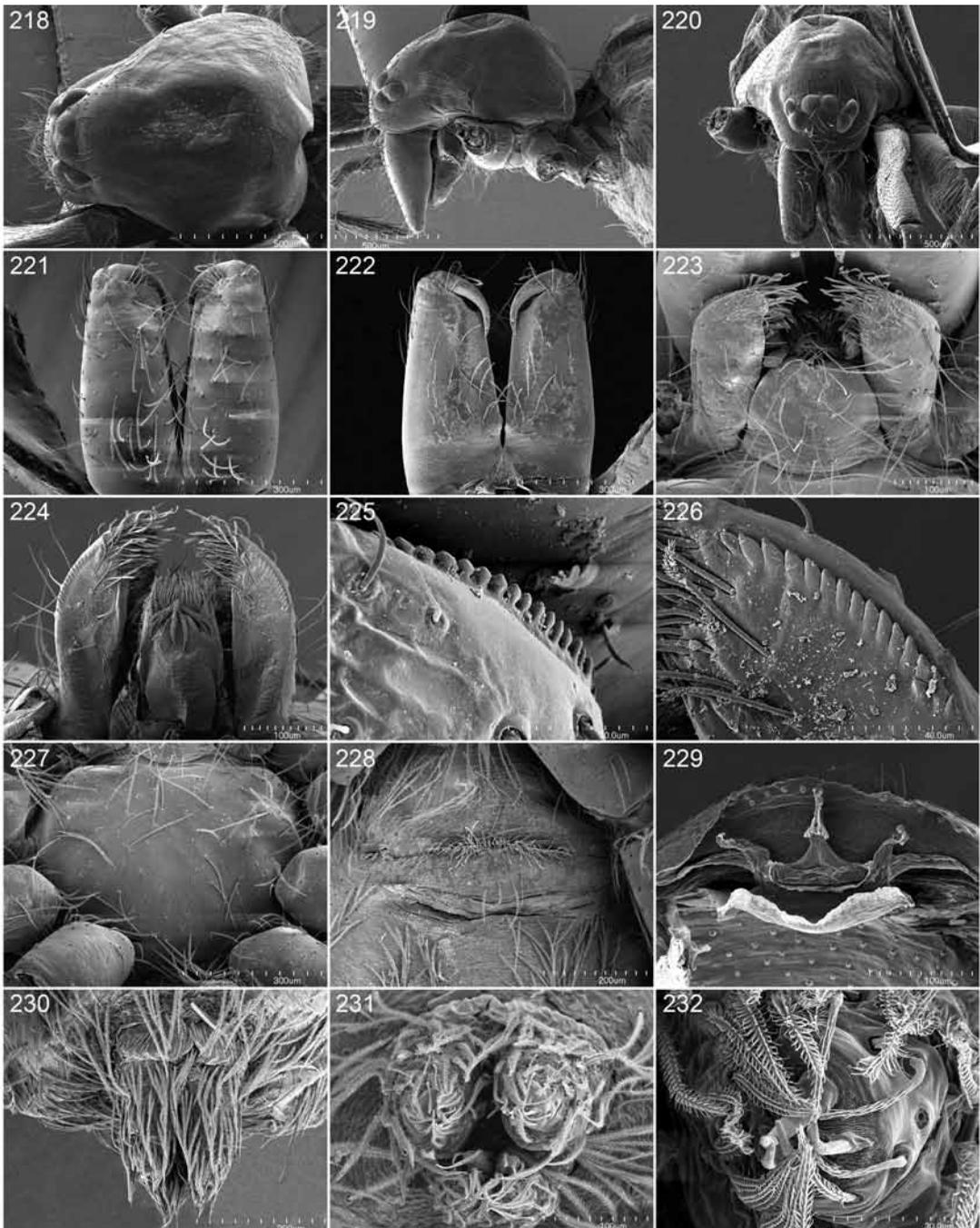
FIGURES 173–187. *Dalmasula lorelei*, new species, male. 173. Habitus, lateral view. 174. Carapace, anterior view. 175. Same, lateral view. 176. Chelicerae, anterior view. 177. Same, posterior view. 178. Labium and endites, ventral view. 179. Labrum and endites, dorsal view. 180. Serrula, dorsal view. 181. Sternum, ventral view. 182. Left palp, prolateral view. 183. Same, retrolateral view. 184. Palpal tibia, dorsal view. 185. Embolus, prolateral view. 186. Same, retrolateral view. 187. Spinnerets, apical view.



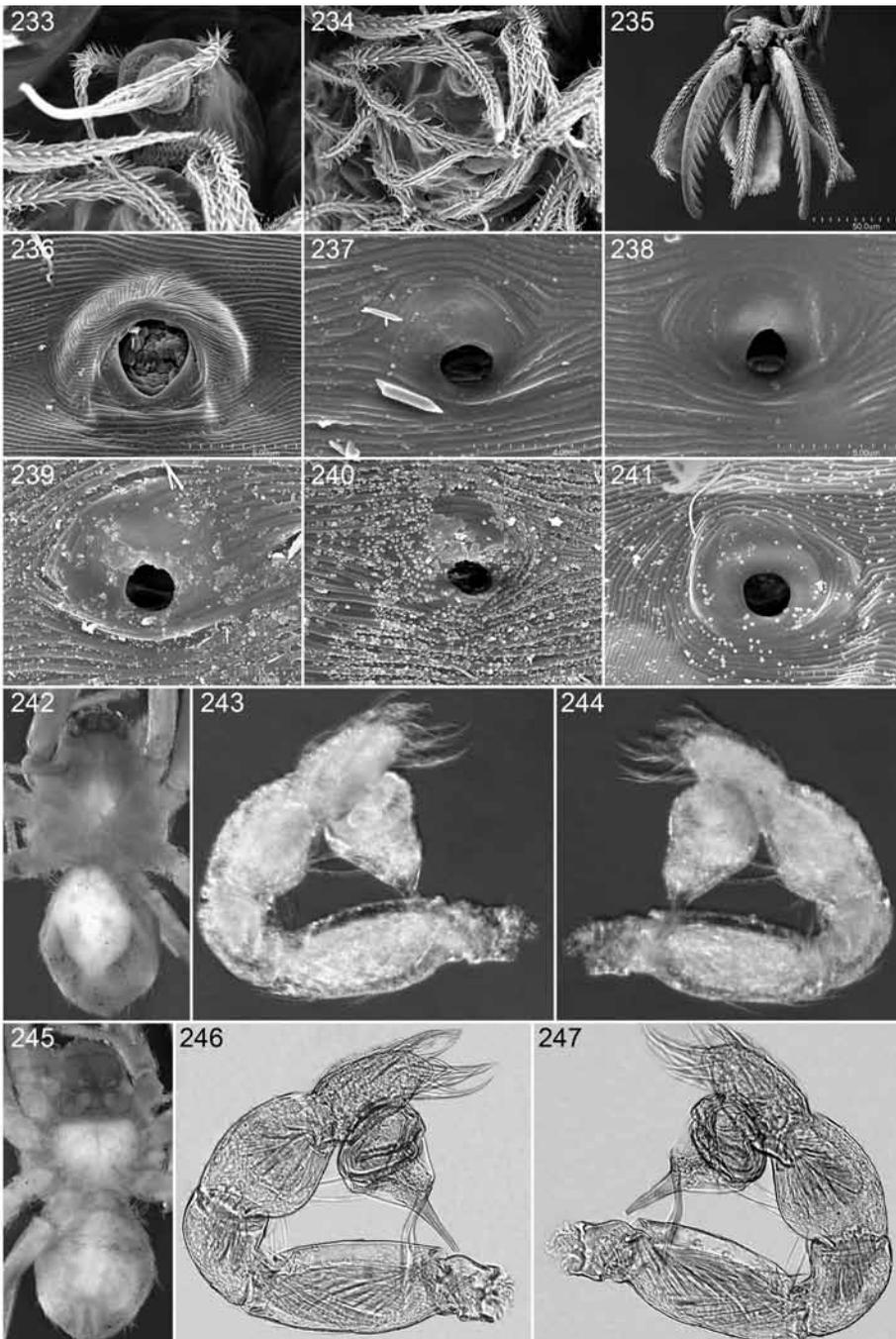
FIGURES 188–202. *Dalmasula lorelei*, new species, male. **188.** Spinnerets, ventral view. **189.** Anterior lateral spinneret, apical view. **190.** Posterior median spinneret, same. **191.** Posterior lateral spinneret, same. **192.** Claws of leg I, lateral view. **193.** Same, leg III. **194.** Same, leg IV. **195.** Claws of leg I, apical view. **196.** Claws of leg II, dorsal view. **197.** Claws of leg III, apical view. **198.** Same, leg IV. **199.** Tarsal organ from leg I, dorsal view. **200.** Same, leg II. **201.** Same, leg III. **202.** Same, leg IV.



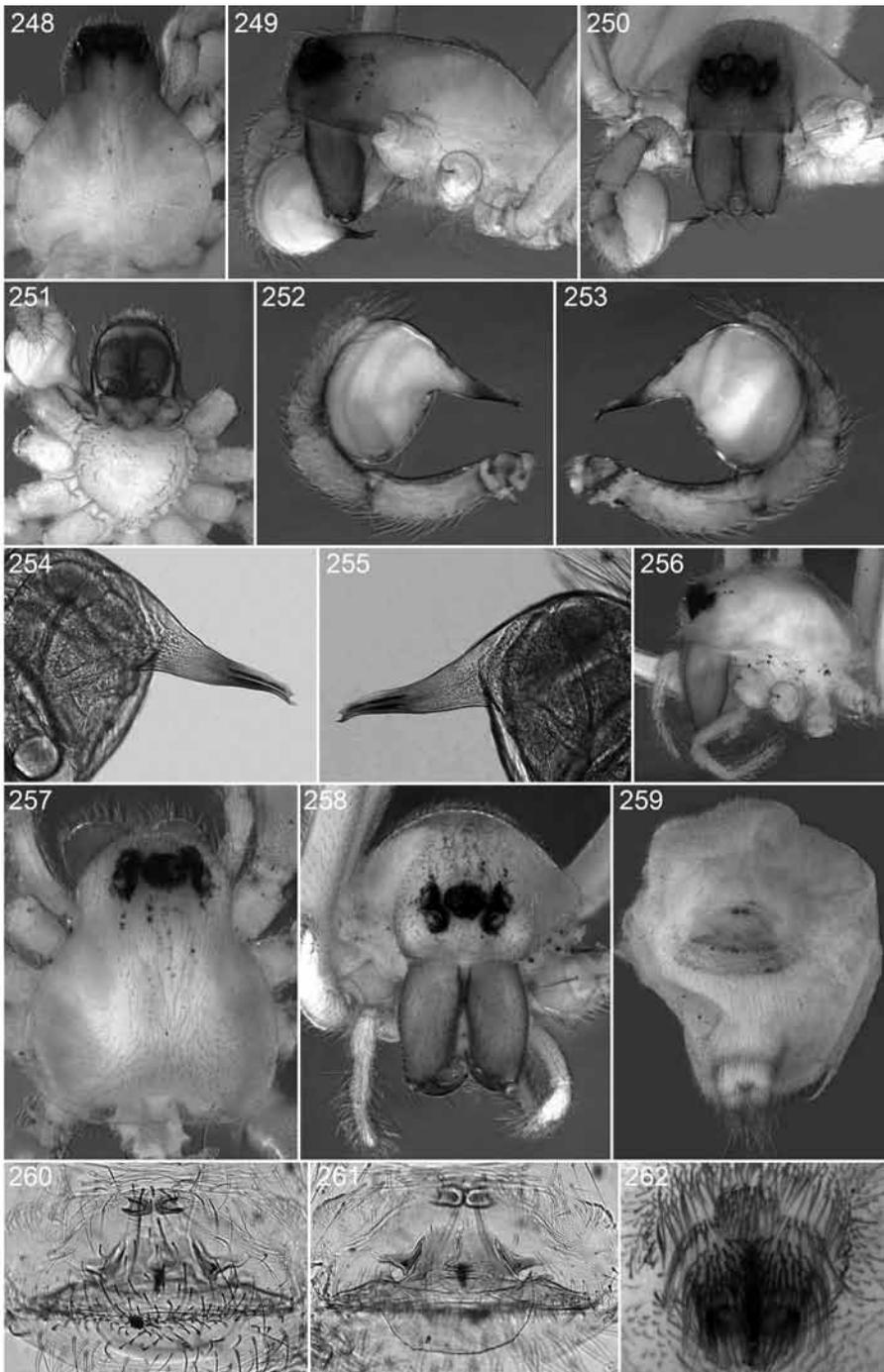
FIGURES 203–217. *Dalmasula lorelei*, new species, male (203–210) and female (211–217). **203.** Habitus, dorsal view. **204.** Sternum, ventral view. **205, 214.** Abdomen, ventral view. **206, 213.** Carapace, anterior view. **207, 209.** Left palp, prolateral view. **208, 210.** Same, retrolateral view. **211.** Carapace, lateral view. **212.** Same, dorsal view. **215, 216.** Genitalia, ventral view. **217.** Same, dorsal view.



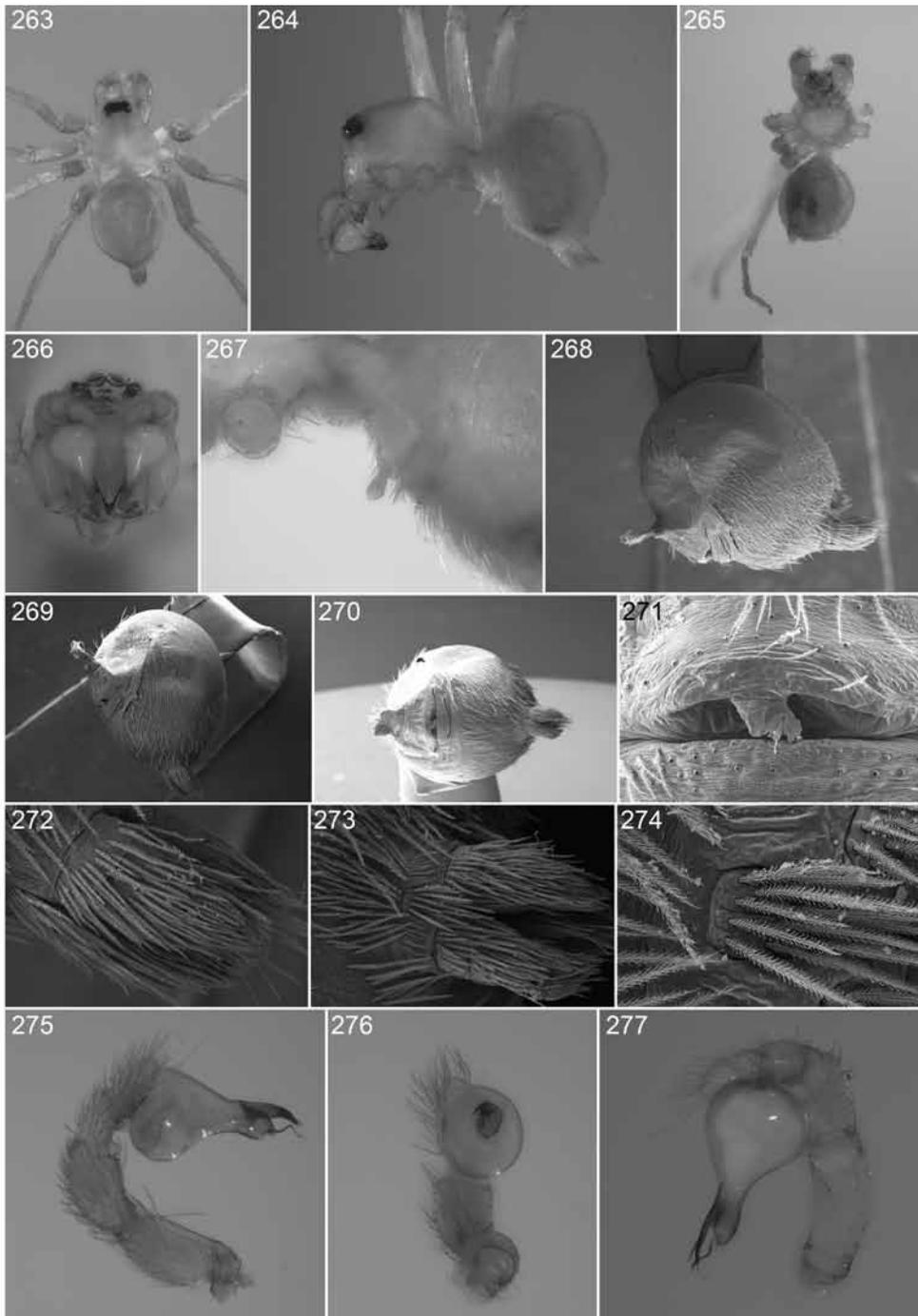
FIGURES 218–232. *Dalmasula lorelei*, new species, female. **218.** Carapace, dorsal view. **219.** Same, lateral view. **220.** Same, anterior view. **221.** Chelicerae, anterior view. **222.** Same, posterior view. **223.** Labium and endites, ventral view. **224.** Labrum and endites, dorsal view. **225.** Serrula, ventral view. **226.** Same, dorsal view. **227.** Sternum, ventral view. **228.** Epigastric region, ventral view. **229.** Genitalia, dorsal view. **230.** Spinnerets, ventral view. **231.** Same, apical view. **232.** Anterior lateral spinneret, apical view.



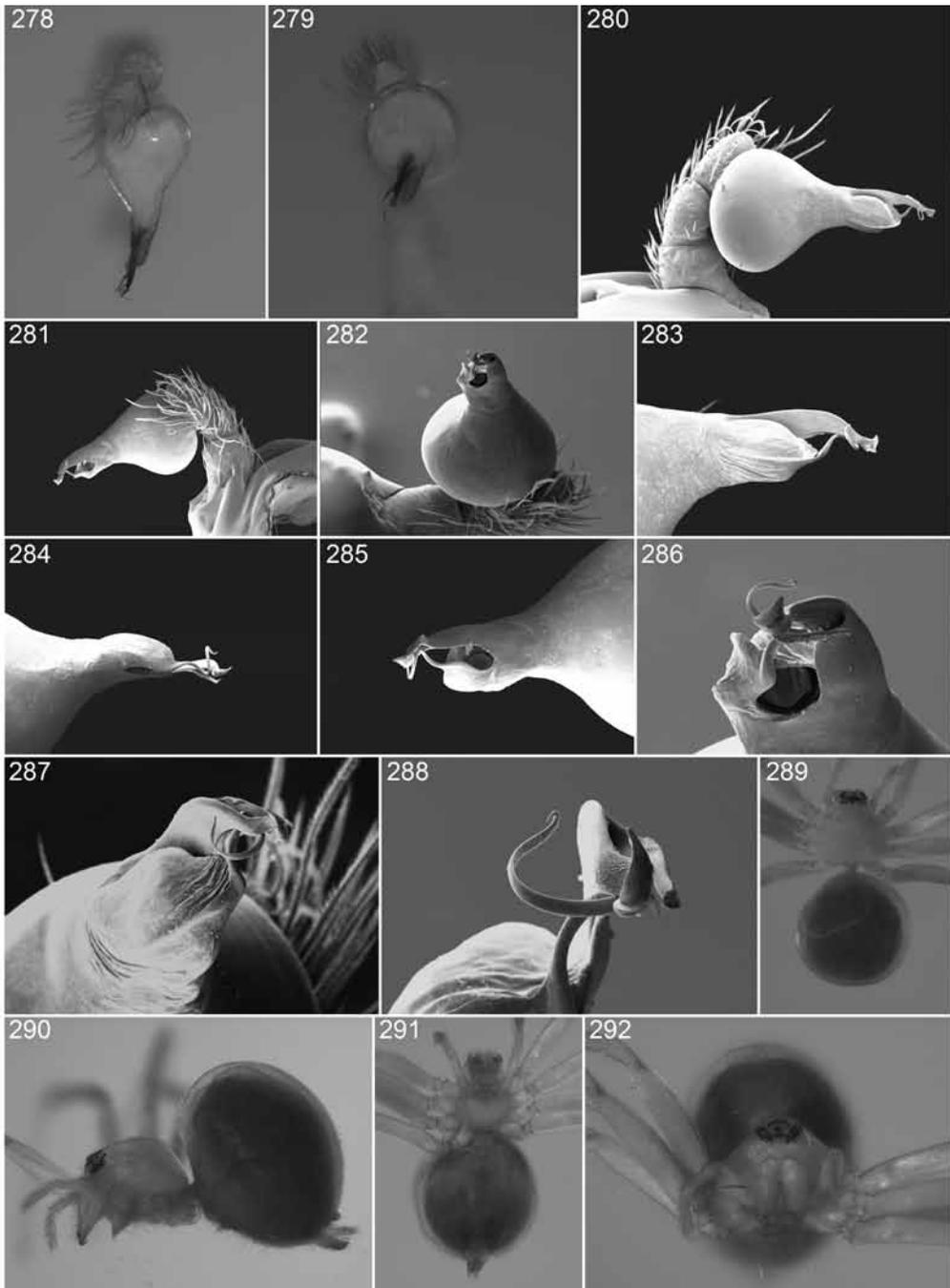
FIGURES 233–247. *Dalmasula lorelei*, new species, female (233–241), *D. parvimana* (Simon), male (242–247). 233. Posterior median spinneret, apical view. 234. Posterior lateral spinneret, apical view. 235. Claws of leg I, anterior view. 236. Trichobothrial base from tibia III, dorsal view. 237. Tarsal organ from leg I, dorsal view. 238. Same, leg II. 239. Same, leg III. 240. Same, leg IV. 241. Same, palp. 242. Habitus, dorsal view. 243, 246. Left palp, prolateral view. 244, 247. Same, retrolateral view. 245. Habitus, ventral view.



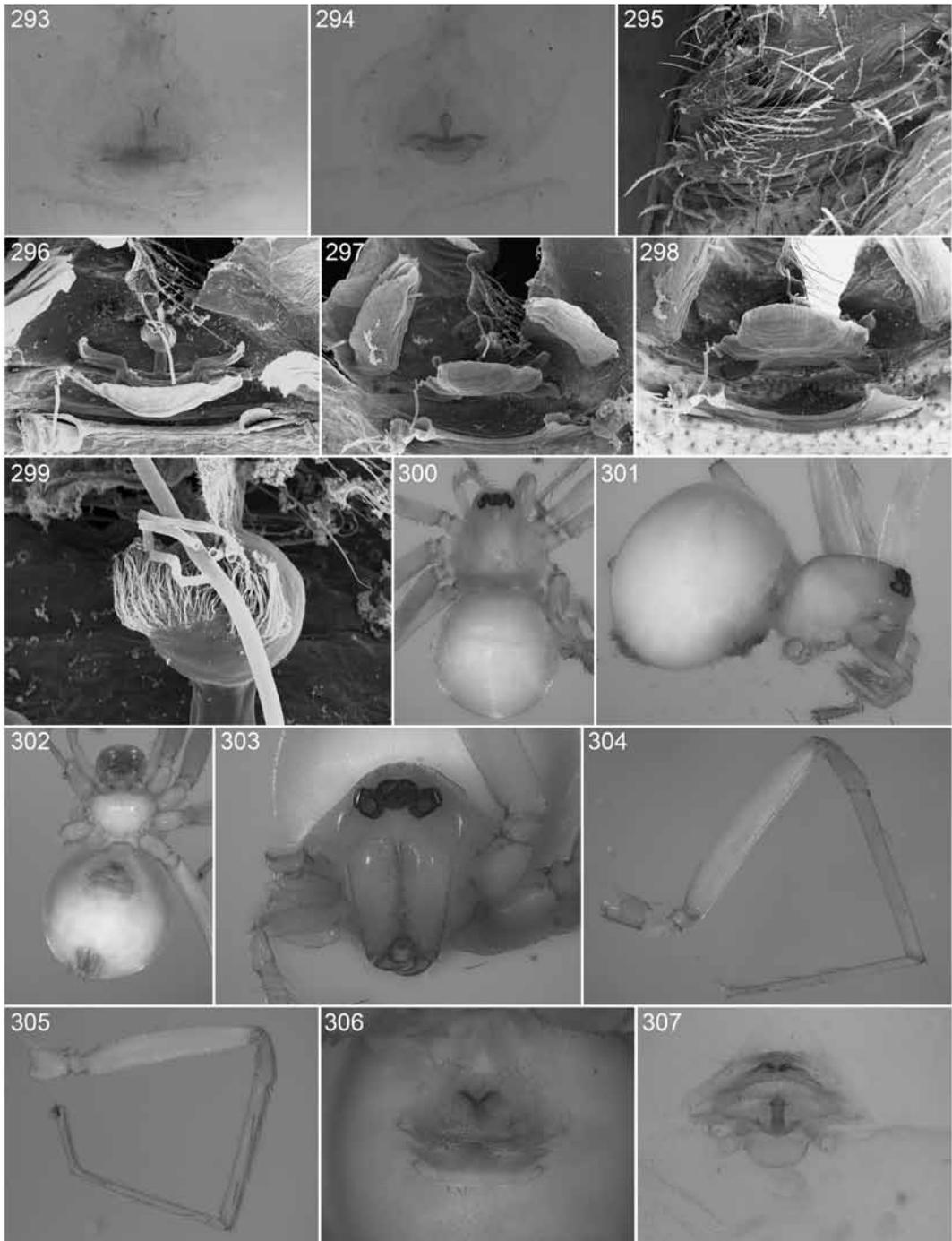
FIGURES 248–262. *Dalmasula tsumkwe*, new species, male (248–255) and female (256–262). **248, 257.** Carapace, dorsal view. **249, 256.** Same, lateral view. **250, 258.** Same, anterior view. **251.** Sternum, ventral view. **252.** Left palp, prolateral view. **253.** Same, retrolateral view. **254.** Embolus, prolateral view. **255.** Same, retrolateral view. **259.** Abdomen, ventral view. **260.** Genitalia, ventral view. **261.** Same, dorsal view. **262.** Spinnerets, ventral view.



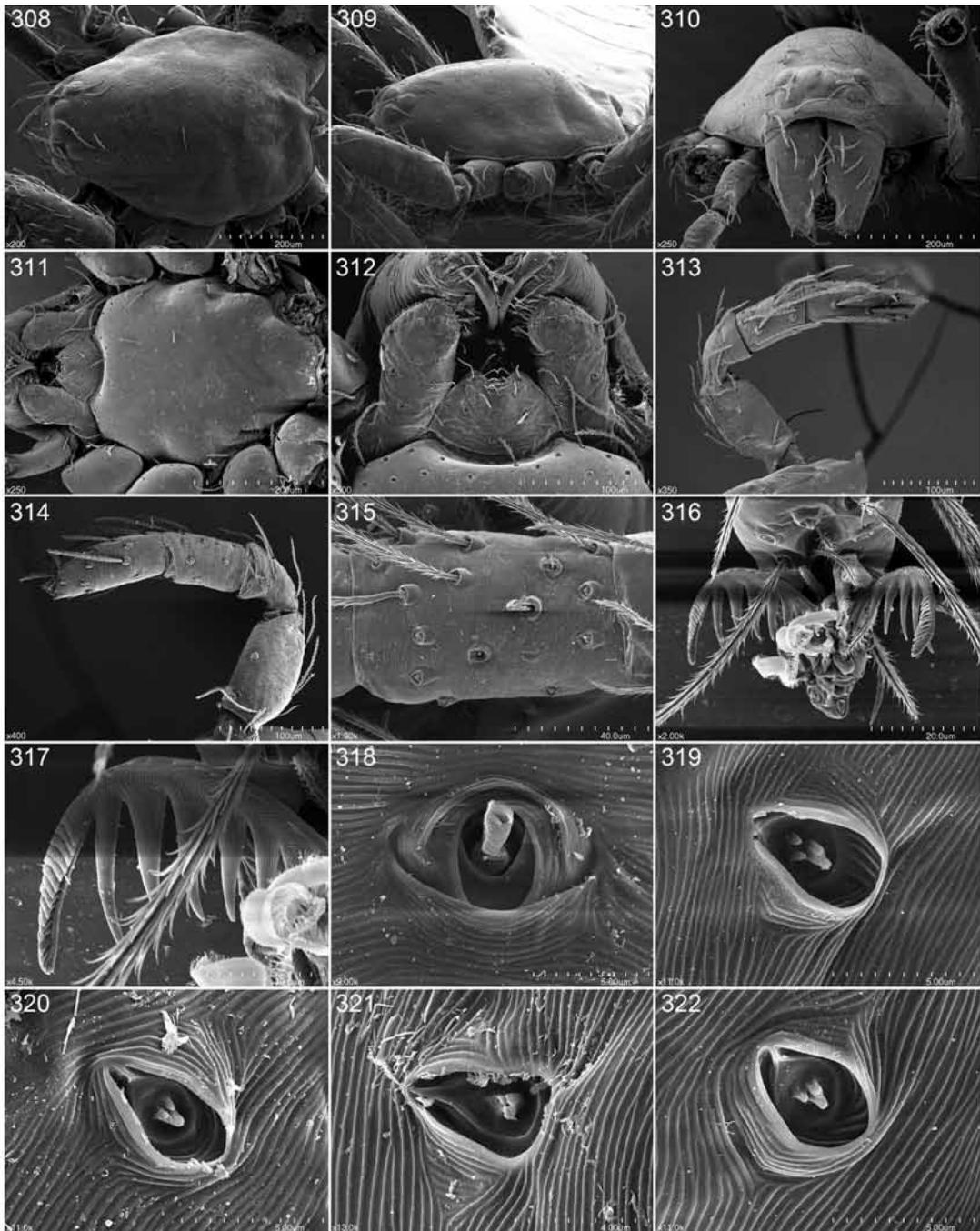
FIGURES 263–277. *Dalmasula griswoldi*, new species, male. **263.** Habitus, dorsal view. **264.** Same, lateral view. **265.** Same, ventral view. **266.** Carapace, anterior view. **267, 268.** Abdomen, lateral view. **269.** Same, oblique lateral view. **270.** Same, ventral view. **271.** Epigastric area, ventral view. **272.** Spinnerets, lateral view. **273.** Same, ventral view. **274.** Colulus, ventral view. **275.** Left palp, prolateral view. **276.** Same, ventral view. **277.** Same, retrolateral view.



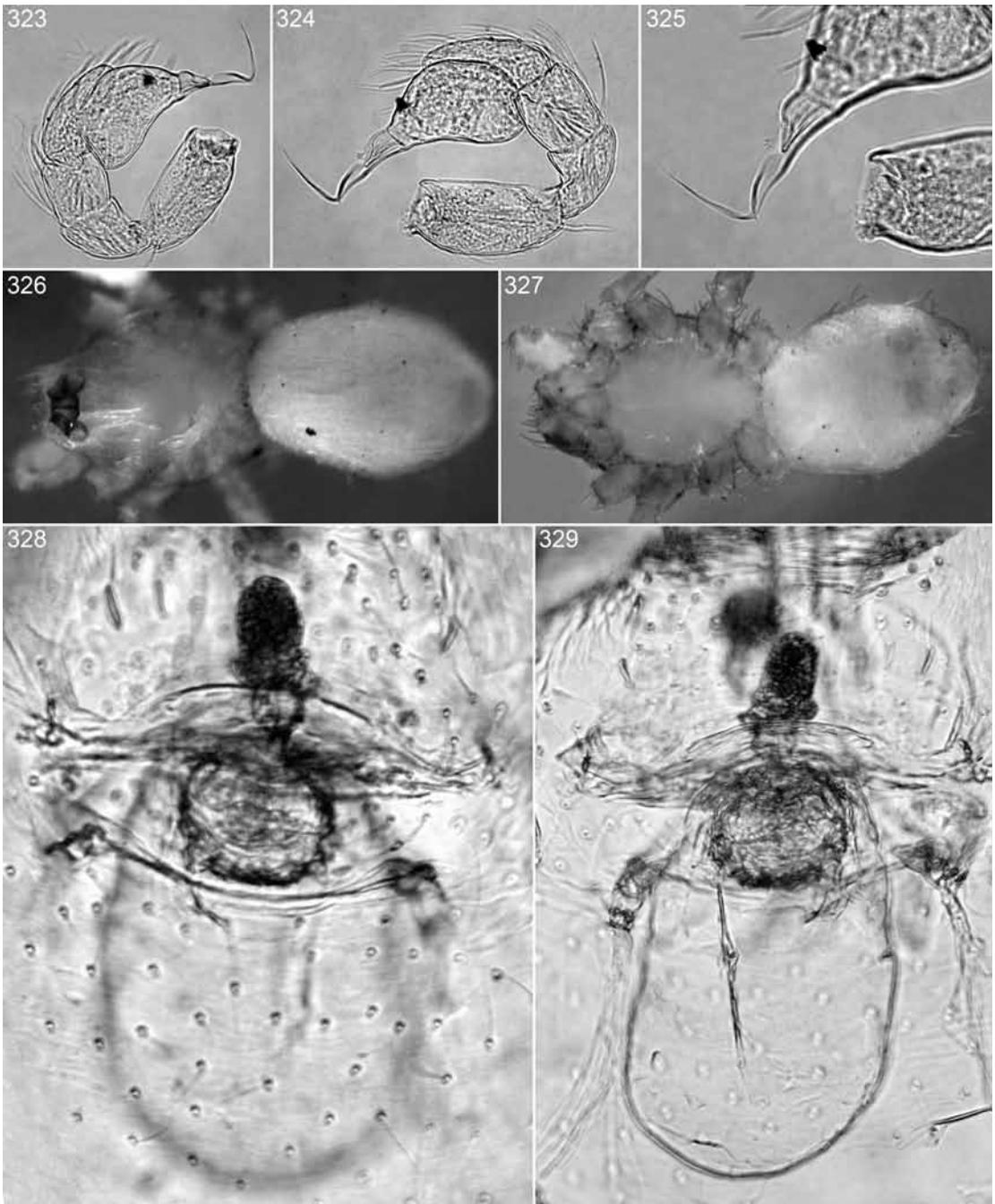
FIGURES 278–292. *Dalmasula griswoldi*, new species, male (278–288) and female (289–292). 278. Left palp, dorsal view. 279. Same, apical view. 280. Left palpal bulb, prolateral view. 281. Same, retrolateral view. 282. Same, apical view. 283. Embolus, prolateral view. 284. Same, ventral view. 285. Same, retrolateral view. 286. Same, apical view. 287. Conductor, ventral view. 288. Same, apical view. 289. Habitus, dorsal view. 290. Same, lateral view. 291. Same, ventral view. 292. Same, anterior view.



FIGURES 293–307. *Dalmasula griswoldi*, new species, female (293–299), *D. dodebai*, new species, female (300–307). 293, 306. Genitalia, ventral view. 294, 296, 299, 307. Same, dorsal view. 295. Epigastric area, ventral view. 297, 298. Genitalia, oblique dorsal view. 300. Habitus, dorsal view. 301. Same, lateral view. 302. Same, ventral view. 303. Same, anterior view. 304. Leg II, prolateral view. 305. Same, lateral view.



FIGURES 308–322. *Kapitia obscura* Forster, female. **308.** Carapace, dorsal view. **309.** Same, lateral view. **310.** Same, anterior view. **311.** Sternum, ventral view. **312.** Labium and endites, ventral view. **313.** Palp, prolateral view. **314.** Same, retrolateral view. **315.** Palpal tibia, dorsal view. **316.** Claws of leg II, anterior view. **317.** Same, lateral view. **318.** Trichobothrial base from metatarsus II, dorsal view. **319.** Tarsal organ from leg II, dorsal view. **320.** Same, leg III. **321.** Same, leg IV. **322.** Same, palp.



FIGURES 323–329. *Kapitia obscura* Forster, male (323–327) and female (328, 329). 323. Left palp, prolateral view. 324. Same, retrolateral view. 325. Embolus, retrolateral view. 326. Habitus, dorsal view. 327. Same, ventral view. 328. Genitalia, ventral view. 329. Same, dorsal view.

the types of tarsal organs found among the more basal oonopid genera (i.e., *Orchestina* and similar taxa). *Orchestina* is a highly diverse, nearly worldwide group of species united by the presence of enlarged femora on leg IV; the enlarged femora enable the animals to jump several times their body length. Its members dominate both the oonopid canopy fauna and the oonopid fossil record (including the oldest known oonopids, from Cretaceous amber, Saupe et al., in press; Marusik and Wunderlich, 2008). The tarsal organs of several undescribed species from South America, Africa, and Madagascar have been examined (see figs. 86–105); they resemble those of typical oonopids in having the longitudinal ridge originating from the proximal edge of the organ, and in showing serial dimorphism between the anterior and posterior legs, but differ in having one additional raised receptor (four on the anterior legs and three on the posterior legs), so that their receptor formula is 4-4-3-3, for legs I–IV, rather than 3-3-2-2 (as in typical oonopids).

Forster (1980), based on an extensive survey including most spider families, identified a general trend in tarsal organ evolution: the transformation from an exposed to a capsulate structure. The basal oonopid genera other than *Orchestina* illustrate this trend well. In the genus *Cortestina* Knoflach, the tarsal organ is partly capsulate (figs. 106–110; Knoflach et al., 2009, figs. 50, 51). The receptor-bearing portion of the organ is sunken well below a pair of elevated lateral folds, but one can still see at least some of the raised receptors as well as the longitudinal ridge.

In the remaining basal genera, the tarsal organ has become fully capsulate; in dorsal view, the aperture of the tarsal organ is a tiny circle, and the receptors are situated too far below the opening to be visible in scanning electron microscopy. These fully capsulate structures occur in the North African genus *Sulsula* Simon (figs. 168–172) and the South American genera *Xiombarg* Brignoli (figs. 111–115) and *Unicorn* Platnick and Brescovit (figs. 116–120; Platnick and Brescovit, 1995: figs. 9, 10; González-Reyes et al., 2010: fig. 1c). They also occur in the new genus described below as *Dalmasula*, from Namibia and South Africa, and in an undescribed genus from Argentina (Izquierdo et al., in prep.).

Forster's (1980) view that the transformation from exposed to capsulate tarsal organs has occurred repeatedly in spider evolution is born out also within the Oonopidae. Among the typical oonopids, the genus *Escaphiella* Platnick and Dupérré is notable for having an almost fully capsulate tarsal organ (see Platnick and Dupérré, 2009b: figs. 50–53, 100). The aperture, however, is quite different from that found in the basal genera, forming a long, narrow slit rather than a circle. The structure in *Escaphiella* is clearly modified from that found in the sister group of that genus, *Scaphiella* Simon, where the exposed tarsal organ has become elongated and narrowed (see Platnick and Dupérré, 2010a: figs. 510–514, 560–564). A similarly narrowed tarsal organ shape is found in another member of the *Scaphiella* complex, *Pescennina* Simon (see Platnick and Dupérré, 2011b: figs. 119–123, 164–168), suggesting that *Pescennina* may be the sister group of *Scaphiella* plus *Escaphiella*. A similarly slit-shaped opening occurs also in the more distantly related *Grymeus robertsi* Harvey (see Harvey, 1987: fig. 8), and the tarsal organs of *Longoonops bicolor* Platnick and Dupérré and *L. padiscus* (Chickering) are notably narrowed (see Platnick and Dupérré, 2010b: figs. 598, 599, 623–625, 670, 671, 692, 693), but all the transformations from exposed to capsulate tarsal organs detected to date within the typical oonopids are morphologically easily distinguishable from the character states found in *Cortestina* and the fully capsulate basal genera.

## PHYLOGENETIC CONCLUSIONS

We hypothesize that the groundplan of oonopids includes an exposed tarsal organ like that of *Orchestina*, having a distinctive longitudinal ridge originating from the proximal end of the organ, and a serially dimorphic 4-4-3-3 pattern of raised receptors on legs I–IV. So far as we can tell, all oonopids retain the longitudinal ridge, but the ridge (like the receptor nodes) is not visible externally in those taxa that have acquired a fully capsulate tarsal organ morphology. The presence or absence of the ridge (and the number of receptors) in such taxa could be confirmed only by histological sectioning. The majority of oonopid species fit the trend identified within the Orsolobidae by Forster and Platnick (1985: 219), where the number of receptors becomes reduced (from five or six in some species of basal genera such as *Tasmanoonops* Hickman to only two or three). In the vast majority of oonopids, the tarsal organ is exposed and the receptor pattern is reduced from 4-4-3-3 to 3-3-2-2 (i.e., one raised receptor is lost on each tarsal organ).

The reduction to a 3-3-2-2 pattern of raised receptors occurs in the same set of taxa that show a clustered eye arrangement and have lost the heavily sclerotized, thick-walled sperm duct within the male palp, with a single known exception. The only described oonopid species from New Zealand, *Kapitia obscura* Forster, appears to retain the plesiomorphic 4-4-3-3 tarsal organ receptor pattern (figs. 319–322) and an H-shaped eye arrangement (figs. 308, 310, 326), even though its male palp clearly lacks a sclerotized sperm duct (compare figs. 323, 324 with 127, 128, 209, 210). These characters suggest that *Kapitia* Forster is the sister group of the many genera with a 3-3-2-2 tarsal organ receptor pattern and a clustered eye arrangement, and all these taxa, including those previously placed in the Gamasomorphinae, are assigned below to the subfamily Oonopinae. A new subfamily is established below for those more basal genera that share a partly or fully capsulate tarsal organ; that subfamily is here named Sulsulinae, as *Sulsula* appears to be the oldest available name for any of its members. We thus recognize three subfamilies: the Orchestininae Chamberlin and Ivie, the Sulsulinae, and the Oonopinae Simon.

Although the Oonopinae are united by the “loss” of the heavily sclerotized, thick-walled sperm duct that is typical of other araneomorphs, the absence presumably reflects a major transformation in how sperm are stored within the palp, and possibly also changes in the physiological mechanisms involved in the induction of sperm into the palp, and the expulsion of sperm into the female genitalia.

The question of whether sulsulines are more closely related to oonopines or to *Orchestina* remains unanswered. Although the tarsal organ receptor patterns of the fully capsulate sulsuline genera are unknown, our scans of *Cortestina* (figs. 106–110) suggest that in that genus the number of receptors is greatly reduced, probably to 2-2-1-1, so we would expect the fully capsulate basal genera to have a similarly reduced receptor pattern. The apparent retention of a 4-4-3-3 pattern in *Kapitia* suggests, however, that the reduction in the number of tarsal organ receptors has followed different pathways within the sulsuline and oonopine lineages. Unfortunately, without studies of their ultrastructure or innervation, it doesn't seem possible to

homologize individual receptors across the three subfamilies. Thus, other characters should be sought to resolve the basal three-taxon statement within the family.

We are far from being able to present a comprehensive, quantitative analysis of oonopid interrelationships. Fully half of the family's generic-level diversity may still be undescribed. Although a few groups of putatively closely related genera have been recognized (e.g., the *Scaphiella*, *Dysderina*, *Gamasomorpha*, *Pelcinus*, and *Stenoconops* groups), we are not yet able to assign many of even the currently described genera to such groups, making the choice of exemplars to be included in any such analysis highly problematic. Although our descriptive database includes a substantial amount of character information on a substantial number of species, those characters were chosen primarily for their efficacy at the species level. Many other characters that are important for higher-level relationships will need to be added before such analyses will become realistic; female genitalic characters, for example, are largely uncoded in the descriptive database. Even though a detailed analysis would therefore be premature at this point, the hypotheses we have presented above can effectively be summarized in the following matrix:

<i>Dysdera</i>	0000000
<i>Orsolobus</i>	0000000
<i>Orchestina</i>	1110000
<i>Cortestina</i>	1101000
<i>Sulsula</i>	1101000
<i>Dalmasula</i>	1101000
<i>Xiombarg</i>	1101000
<i>Unicorn</i>	1101000
<i>Kapitia</i>	1100100
<i>Oonops</i>	1100111
<i>Gamasomorpha</i> , etc.	1100111

where the characters are:

- 1 tarsal organ with proximal longitudinal ridge
- 2 tarsal organ with raised receptors only, in serially dimorphic pattern (either 4-4-3-3 or a modified, reduced form of that pattern, i.e., 3-3-2-2 or 2-2-1-1)
- 3 femur IV enlarged
- 4 tarsal organ at least partly capsulate
- 5 male palp without heavily sclerotized sperm duct
- 6 tarsal organ receptor pattern reduced to 3-3-2-2
- 7 ocular group clumped

Computer analysis is not needed to discern that these seven characters support the following groups, respectively:

- 1 Oonopidae (all taxa except *Dysdera* and *Orsolobus*)
- 2 Oonopidae (all taxa except *Dysdera* and *Orsolobus*)
- 3 Orchestininae (*Orchestina*)

4 Sulsulinae (*Cortestina*, *Sulsula*, *Dalmasula*, *Xiombarg*, *Unicorn*)

5 Oonopinae (*Kapitia*, *Oonops*, *Gamasomorpha*, etc.)

6 higher Oonopinae (*Oonops*, *Gamasomorpha*, etc.)

7 higher Oonopinae (*Oonops*, *Gamasomorpha*, etc.)

Note, however, that (as indicated above) the entries for characters 1 and 2 for the fully capsulate genera (*Sulsula*, *Dalmasula*, *Xiombarg*, *Unicorn*) represent inferences (based on *Cortestina*) rather than direct observations (which would require histological sectioning).

#### COLLECTIONS EXAMINED

AMNH	American Museum of Natural History, New York, NY
CMC	Canterbury Museum, Christchurch, New Zealand
HDO	Hope Department of Entomology, Oxford University, Oxford, England
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MCTP	Museu de Ciências e Tecnologia de Pontifícia Universidade Católica, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NMNW	National Museum of Namibia, Windhoek, Namibia
OMD	Otago Museum, Dunedin, New Zealand
PPRI	Plant Protection Research Institute, Pretoria, South Africa
QMB	Queensland Museum, Brisbane, Australia
SAM	South African Museum, Cape Town, South Africa
ZMB	Museum für Naturkunde, Humboldt Universität, Berlin, Germany

#### VOUCHERS

Figs. 1–10, *Oonops pulcher* Templeton: PBI\_OON 36412, 36413 (see Platnick and Duperré, 2009c: 17).

Figs. 11–15, *Triaeris stenaspis* Simon: Trinidad: Simla, Apr. 1964 (A. Chickering, MCZ 71487, PBI\_OON 26533).

Figs. 16–25, *Ischnothyreus peltifer* (Simon): Trinidad: University Campus, St. Augustine, Apr. 7–9, 1964 (A. Chickering, MCZ 71345, PBI\_OON 27411); Brazil: Amazonas: Base de Operações Geólogo Pedro de Moura, Urucu River, Coari, July 11–20, 2003 (A. Bonaldo, J. Dias, D. Guimarães, MPEG 10214, PBI\_OON 40693); Brazil: Pará: Belém, Oct. 2005 (L. Macambira, MPEG 10709, PBI\_OON 40692).

Figs. 26–35, *Segestria senoculata* (Linnaeus): Switzerland: Basel (AMNH).

Figs. 36–45, *Ariadna bicolor* (Hentz): United States: Colorado: Fremont Co.: 3 mi E Texas Creek, Aug. 29, 1961 (W. Gertsch, W. Ivie, AMNH).

Figs. 46–55, *Dysdera crocata* C.L. Koch: United States: New Mexico: Grant Co.: Silver City, Apr. 12, 1950 (H. Shantz, AMNH); Pennsylvania: Bucks Co.: E Jamison, Apr.–June 1954 (W. Ivie, AMNH).

Figs. 56–65, *Harpactea lepida* (C.L. Koch): Switzerland: Basel (AMNH).

Figs. 66–75, *Harpactocrates drassoides* (Simon): Switzerland: Basel, July–Aug. (AMNH).

Figs. 76–82, *Tasmanoonops parvus* Forster and Platnick: Australia: Queensland: Lamington National Park, Mar. 20, 2007 (D. Putland, K. Staunton, QMB 22286, PBI\_OON 23260).

Fig. 83, *Hickmanolobus* sp.: Australia: Queensland: Lamington National Park, July 27, 2007 (S. Wright, AMNH PBI\_OON 31359).

Figs. 84, 85, *Calculus bicolor* Purcell: South Africa: Western Cape: Cape Flats (SAM PBI\_OON 2190).

Figs. 86–95, *Orchestina* sp.: Democratic Republic of Congo: Luki Forest Reserve, Sept. 22, 2007, canopy fogging (D. De Bakker, J.-P. Michiels, MRAC 228967, PBI\_OON 33693).

Figs. 96–105, *Orchestina* sp.: Argentina: Jujuy: Parque Nacional Calilegua (MACN 17674, 17677, 17678, 18015, 18016, PBI\_OON 14896, 14905, 14922, 14924).

Figs. 106–110, *Cortestina thaleri* Knoflach: Austria: Tirol: Innsbruck, May 2006 (F. Stauder, AMNH PBI\_OON 43544).

Figs. 111–115, *Xiombarg plaumanni* Brignoli: Brazil: Rio Grande do Sul: Parque Estadual de Itapuã (MCTP 17255, 17274, 17293, PBI\_OON 11635, 11636, 43543).

Figs. 116–120, *Unicorn catleyi* Platnick and Brescovit: Chile: Tarapacá: Parinacota, Feb. 3, 1994 (N. Platnick, K. Catley, R. Calderon, R. Allen, AMNH PBI\_OON 43542).

## SYSTEMATICS

Our methods follow those of Platnick and Dupérré (2009a, 2009b); only differences from the males (beyond the obvious lack of male endite modifications) are mentioned in the descriptions of females. Scans were taken from uncoated right male palps, and the images were flipped for consistency. All measurements are in mm. High-resolution versions of the images, the geocoded locality data, and a distribution map for each species will be available on the goblin spider Planetary Biodiversity Inventory (PBI) project's website (<http://research.amnh.org/oonopidae>).

### Oonopidae Simon

Oonopidae Simon, 1890: 80.

**DIAGNOSIS:** Oonopids resemble orsolobids but lack the elevated tarsal organs characteristic of that family (figs. 76–85) and have instead a flat, exposed, or capsulate tarsal organ with a distinctive longitudinal ridge originating at the proximal end of the organ (figs. 1, 7, arrows), raised receptors only, and dimorphism between the anterior and posterior legs, with legs I and II having one more receptor than do legs III, IV, and the palpal tarsi (figs. 1–25). Males of

representative studied species have a single, fused testis (Burger and Michalik, 2010); females lack a claw on the palpal tarsus (the claw is typically retained in orsolobids).

One other character that has traditionally been used to delimit oonopids is the absence of cheliceral teeth (see, for example, Simon, 1893: 287; Kaston, 1948: 60; Platnick and Brescovit, 1995: 5). However, the presence of cheliceral teeth has now been documented in a wide variety of oonopids (see, for example, Bristowe, 1948: 883; Fannes and Jocqué, 2008: fig. 26; Ubick and Griswold, 2011a: figs. 25, 136).

INCLUDED SUBFAMILIES: Orchestinae, Sulsulinae, Oonopinae.

MISPLACED GENERA: *Calculus* Purcell, here transferred to the Orsolobidae.

### Orchestinae Chamberlin and Ivie

Orchestinae Chamberlin and Ivie, 1942: 6.

DIAGNOSIS: Orchestines are easily recognized by their enlarged femora IV. So far as is known, their 4-4-3-3 tarsal organ receptor pattern is shared only with the basal oonopine genus *Kapitia*. In *Orchestina*, however, the tarsal organs are typically narrowed at the proximal end, producing a neck-shaped appearance (figs. 86–105) that does not occur in *Kapitia*. Most species of *Orchestina* have the posterior median eyes advanced to form a straight row with the anterior lateral eyes (much as in *Segestria*), but at least some undescribed African species have the posterior median eyes situated more posteriorly, in the more H-shaped pattern shared by the sulsulines and *Kapitia*.

INCLUDED GENERA: Only *Orchestina* Simon; 51 Recent species have been described to date (Platnick, 2012), but as many additional species have already been identified by Matias Izquierdo, Arnaud Henrard, and Natalia Chousou-Polydouri. Saaristo and Marusik (2004) established a monotypic genus, *Ferchestina*, for a single species from the Russian Far East. Those authors noted (2004: 51) that five of the oonopid genera then recognized are each widely distributed and together constitute more than half of the family's then known species diversity, and somehow concluded from those observations that "it is quite safe to postulate that all these five genera are more or less polyphyletic." The argument is nonsensical, as neither the number of included species, nor how widely they occur, are evidence of monophyly or polyphyly; only synapomorphic characters, and their distribution among taxa, are relevant to that question. Saaristo and Marusik (2004: 51) noted that *Orchestina*, in particular, does have at least one putative synapomorphy: "A single key-character used to separate members of *Orchestina* from other non-scutate oonopids is the markedly swollen tibia [sic, lapsus for femur] IV."

In our view, there are no convincing characters supporting the placement of *Ferchestina storozhenkoi* Saaristo and Marusik in a genus separate from *Orchestina*; that type species clearly shares the primary synapomorphy of *Orchestina*, the enlarged femur IV. Saaristo and Marusik provided no characters suggesting that their species represents the sister group of all other orchestines (i.e., that all the other *Orchestina* species form a monophyletic group that excludes *Ferchestina*). The differences they cited in their generic diagnosis, such as the prominent humps on the male carapace, the projection at the tip of the cheliceral paturon, and the details of the

male and female genitalia, are all presumably just species-level autapomorphies, and are therefore irrelevant to the question of what the closest relative(s) of the species may be. Saaristo and Marusik commented that compared to *Orchestina pavesii* (Simon), the type species, femur IV is “not so thick” but provided no illustration of that supposed difference. The thickness of the fourth femur varies among the many species of *Orchestina*, possibly in allometric correlation with the total size, which also varies significantly (with some species attaining almost twice the total length of others). The diagnostic character is that the fourth femora are much thicker than femora I–III of the same specimen, not that they are of any particular given thickness (indeed, proportionately much less emphatically enlarged femora IV are also found in some soft-bodied, Neotropical oonopine species currently misplaced in *Oonops*). Both the male and female genitalia of *Ferchestina* fit well within the extensive range of variation shown by *Orchestina* species. We conclude that *Ferchestina* represents just a highly autapomorphic species of *Orchestina*, and that its recognition as a separate genus is positively misleading phylogenetically; we therefore place the name as a junior synonym of *Orchestina* (NEW SYNONYMY).

Although our conclusion is that the recognition of *Ferchestina*, as currently constituted, renders *Orchestina* a paraphyletic group and is therefore unacceptable, it is of course possible that future phylogenetic analyses will be able to discern monophyletic subgroups of orchestinines that are each supported by putatively synapomorphic characters. If, at that time, the type species of *Ferchestina* can be shown to belong to a subgroup that does not also include the type species of *Orchestina*, then it may be possible to resurrect *Ferchestina* as a usable name, but it would have to be on the basis of new evidence, not the insufficient data provided by Saaristo and Marusik (2004).

#### Sulsulinae Platnick, new subfamily

TYPE GENUS: *Sulsula* Simon (1882).

DIAGNOSIS: This subfamily includes taxa that resemble *Orchestina* in having a transverse, unclumped eye arrangement and a heavily sclerotized sperm duct within the male palp, but have partly or fully capsulate tarsal organs and a normal, rather than expanded, femur IV.

INCLUDED GENERA: *Sulsula* Simon (1882) from North Africa; *Xiombarg* Brignoli (1979) from Brazil and Argentina; *Unicorn* Platnick and Brescovit (1995) from Chile, Bolivia, and Argentina; *Cortestina* Knoflach (see Knoflach et al., 2009) from Austria and Italy, plus two new genera: *Dalmasula*, described below from Namibia and South Africa, and an undescribed genus from Argentina (Izquierdo et al., in prep.). Based on its partly capsulate tarsal organs, the Laurasian genus *Cortestina* probably represents the sister group of the other, fully capsulate, Gondwanan genera. The monophyly of the fully capsulate genera may also be supported by the presence of a single row of teeth on the tarsal claws; most other oonopids, and orsolobids, have two rows of teeth on each claw. However, there are typical oonopids in which one of the tooth rows has been lost in males (as in *Heteroonops* Dalmas; see Platnick and Dupérré, 2009c) or in both sexes (as in *Birabenella* Grismado; see Grismado, 2010).

#### *Sulsula* Simon

*Sulsula* Simon, 1882: 237 (type species by monotypy *Sulsula longipes* Simon).

*Salsula*: Simon, 1893: 294.

NOTE: Simon (1893) regarded the original spelling of the genus as a printer's error, but the spelling occurs twice in Simon (1882) and his alternate spelling was rejected by Dalmas (1916: 204) and subsequent authors.

DIAGNOSIS: Members of *Sulsula* resemble those of *Dalmasula* in having a globose abdomen (figs. 143, 144), but can be distinguished by the absence of cheliceral teeth, the much smaller colulus (fig. 158; cf. figs. 188, 273, 274), and the uniquely modified tarsal organs, which have a distal, semicircular groove as well as a pair of laterally directed ridges (figs. 168–172). Males have a simple embolus, without a conductor (figs. 127, 128), and the female genital area lacks the anterior sclerotizations found in *Dalmasula* (fig. 136).

*Sulsula pauper* (O. P.-Cambridge)

Figures 121–172

*Oonops pauper* O. P.-Cambridge, 1876: 549 (juvenile holotype from Alexandria, Alexandria, Egypt, in HDO; examined).

*Sulsula longipes* Simon, 1882: 237 (male holotype from Ramleh, Alexandria, Egypt, in MNHN; examined). First synonymized by Simon, 1910: 178.

*Salsula longipes*: Simon, 1893: 294.

*Salsula paupera*: Simon, 1910: 178.

*Salsula pauper*: Simon, 1911: 308.

*Sulsula pauper*: Dalmas, 1916: 205.

NOTE: Simon (1882) mentioned only a single male specimen, but the vial with that specimen includes also a female, which we suspect Simon erroneously considered to be juvenile.

DIAGNOSIS: With the characters of the genus, a male embolus with a relatively short, terminally curved tip (figs. 127–130), and female genitalia with a tubular, sclerotized anterior receptaculum (figs. 137–142) and an oval, unsclerotized posterior receptaculum (collapsed in those figures).

VARIATION: It is possible that more than one species is represented, but the few available specimens do not provide sufficient evidence to substantiate the description of additional species at this time. Females are available from three sites, but the one from Sudan (figs. 141, 142) has genitalia that seem more similar to that of a female from Algeria (figs. 137, 138) than to the geographically much closer one from Egypt (figs. 139, 140). Only two males are available, from Algeria and Egypt. Under a dissecting microscope, the Algerian male appears to have a bulb that extends farther toward the palpal patella (figs. 122–125), but under a compound microscope, that difference is not obvious (figs. 127–130; unfortunately, the bulb of the Egyptian male collapsed in clove oil under the compound microscope). The embolus shows differences under the compound microscope, but at least some of those differences reflect different positioning of the palps and consequent foreshortening in the photographs of the Algerian male.

MALE (PBI\_OON 813, figs. 121–133, images of nonsexual characters based on female): Total length 2.16. **Cephalothorax:** Carapace white, without any pattern, piriform in dorsal view (figs. 134, 145), pars cephalica flat in lateral view (fig. 131), anteriorly narrowed to 0.49 times its maxi-

mm width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent; marginal and nonmarginal pars cephalica and pars thoracica setae dark, needlelike. Clypeus margin unmodified, straight in front view (fig. 147), vertical in lateral view (fig. 146), high, ALE separated from edge of carapace by their radius or more, median projection absent; setae dark, needlelike. Chilum absent. Eyes six, well developed, PME largest, ALE oval, PME squared, PLE oval; posterior eye row recurved from above, straight from front; ALE separated by more than their diameter, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by PME radius to PME diameter (figs. 121, 132, 135, 145). Sternum wider than long (fig. 156), white, uniform in coloration, not fused to carapace, median concavity absent, without radial furrows between coxae I–II, II–III, III–IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles absent, lateral margins unmodified, without posterior hump; setae sparse, dark, needlelike, densest laterally, originating from surface, hair tufts absent (figs. 126, 133). Mouthparts yellow. Chelicerae straight, anterior face unmodified; without teeth on promargin or retromargin (figs. 148, 149); fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae dark, needlelike, evenly scattered; paturon inner margin with scattered setae, distal region unmodified, posterior surface unmodified, promargin unmodified, inner margin unmodified, laminate groove absent. Labium triangular, not fused to sternum, anterior margin not indented at middle, same as sternum in sclerotization; with six or more setae on anterior margin, subdistal portion with unmodified setae (fig. 150). Endites distally not excavated, serrula present in single row (figs. 151, 152), anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen:** White, without scuta or color pattern, globular (figs. 136, 143, 144), without long posterior extension, rounded posteriorly; book lung covers large, ovoid, without setae, anterolateral edge unmodified; posterior spiracles connected by groove; pedicel tube short, unmodified, scutopedicel region unmodified, abdomen extending anteriorly of pedicel, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, and postepigastric setae light, needlelike; dense patch of setae anterior to spinnerets absent. Spinnerets probably with unsclerotized strip crossing base of anterior lateral pair (fig. 158), all spinnerets with few spigots (fig. 159). Colulus small, with two setae. **Legs:** White, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spination (only surfaces bearing spines listed, legs in poor condition, most spines lost, their bases not detectable without scanning): tibia IV r1-0-0. Tarsi without inferior

claw, superior claws with single row of teeth (figs. 160–167). Trichobothrial bases with arched ridge (fig. 157). Tarsal organ capsulate, with distal, semicircular groove and pair of laterally directed ridges (figs. 168–172). **Genitalia:** Epigastric region with sperm pore not visible; furrow without  $\Omega$ -shaped insertions, without setae. Palp of normal size, not strongly sclerotized, proximal segments yellow; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, slightly widened, without prolateral row of ridges, setae unmodified; cymbium yellow, narrow in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, plumose setae, stout setae, distal patch of setae all absent; bulb yellow, more than 2 times as long as cymbium, stout, tapering apically; embolus dark, curved distally, without prolateral excavation; conductor absent (figs. 122–125, 127–130).

**FEMALE** (PBI\_OON 813, figs. 134–172): Total length 3.19. Palpal tarsus without claws (figs. 153, 154); tibia with trichobothria (fig. 155); spines present, tibia p1-0-0; patella without prolateral row of ridges. Leg spination (only surfaces bearing spines listed, all spines longer than segment width): femora: I d0-0-2, p0-1-1; II d0-0-2; III, IV d0-0-1; patellae: III d1-0-0, p1-0-0, r1-0-0; tibiae: I p0-0-1, v0-0-1, r0-0-1; II p0-0-1, v0-0-1; III d1-1-0, p1-1-1, r1-0-1; IV d1-1-0, p1-1-1, v1-0-0, r1-1-1; metatarsi: I p1-1-0, r1-0-0; II p1-0-0, r1-0-0; III r1-0-0; IV d0-1-0, p1-1-0, r1-0-1. Anterior receptaculum sclerotized, short, tubular, narrowed at about one-third its length; posterior receptaculum unsclerotized, oval (figs. 137–142).

**MATERIAL EXAMINED:** **Algeria:** *Biskra:* Biskra (MNHN 12281, PBI\_OON 814), 1 ♂, 2 ♀. **Egypt:** *Alexandria:* Alexandria, Apr. 1864, under stone (O. P.-Cambridge, HDO PBI\_OON 3012), 1 juv. (holotype); Ramleh (M. Letourneux, MNHN 3230, PBI\_OON 813), 1 ♂ (holotype), 1 ♀. **Sudan:** *Red Sea:* Port Sudan, July 1962 (J. Cloudsley-Thompson, MRAC 127163, PBI\_OON 815), 1 ♀.

**DISTRIBUTION:** North Africa (Algeria, Egypt, Sudan).

**SYNONYMY:** It appears that Simon (1910, 1911) was able to borrow the holotype of *Oonops pauper*, compared it directly to his material of *Sulsula longipes*, and concluded that the specimens are conspecific. Although the holotype of *O. pauper* is a juvenile, there is no evidence that disputes Simon's conclusion. The specimens came from the same area (Ramleh is one of the beaches of Alexandria) and are clearly congeneric; it is unlikely that multiple species of *Sulsula* occur within Alexandria.

### *Dalmasula* Platnick, Szüts, and Ubick, new genus

**TYPE SPECIES:** *Dalmasula lorelei*, new species.

**ETYMOLOGY:** The generic name is a contraction of "Dalmas' *Sulsula*" and is feminine in gender. It honors Raymond de Dalmas and his pioneering study of *Orchestina*, in which (after discussing the similarities of *Sulsula* and *Calculus* with that genus) he commented (1916: 205) that: "On peut ajouter que *Sulsula parvimanus* E. Simon (1910: 178), décrit du pays des Namaquas, dans le Sud-Ouest Africain, et dont le *type* unique est en Allemagne, deviendra peut-être le *type* d'un quatrième genre de cette série." The existence of this genus in South Africa was discovered independently by Charles Griswold (in Platnick and Brescovit, 1995: 6).

**DIAGNOSIS:** Members of this genus resemble those of *Sulsula* in having a globose abdomen (fig. 173), but can be distinguished by the presence of a promarginal cheliceral tooth (fig. 176) and a very wide, hirsute colulus (fig. 274), and the absence of a distal, semicircular groove and laterally directed ridges on the tarsal organ (figs. 199–202, 237–241). Males typically have both an embolus and a conductor (figs. 275, 277), although they appear to have fused in *D. tsumkwe*, new species (figs. 254, 255); the female genital area has peculiar, distinctive anterior sclerotizations that probably function as coupling ridges (figs. 215, 259–261, 293, 306). Males also have unusual modifications of the mouthparts; in those of *D. lorelei*, *D. parvimana*, and *D. griswoldi*, the base of the endites bears a triangular projection directed toward the chelicerae (fig. 175). Males of *D. tsumkwe* apparently lack those projections, but have a similar spur situated distally on the cheliceral paturon (figs. 250, 251).

**DESCRIPTION:** Total length of males 1.7–2.8, of females 2.2–3.1. **Cephalothorax:** Carapace yellow or pale orange, without any pattern, ovoid to piriform in dorsal view (fig. 218), pars cephalica usually flat or slightly elevated in lateral view in males (fig. 175), slightly elevated in females (fig. 219), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent; pars cephalica and pars thoracica setae dark, needlelike. Clypeus margin unmodified, curved downwards in front view, vertical in lateral view, high, ALE separated from edge of carapace by their radius or more (figs. 174, 220), median projection absent; setae dark, needlelike. Chilum absent. Eyes six, well developed, PME largest, ALE oval, PME squared, PLE oval; posterior eye row recurved from above, straight or slightly procurved from front; ALE separated by more than their diameter, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separated by PME radius to PME diameter. Sternum yellow, wider than long (figs. 181, 227), uniform, not fused to carapace, median concavity absent, without radial furrows between coxae I-II, II-III, III-IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles present, lateral margins unmodified, without posterior hump; setae sparse, dark, needlelike, densest laterally, originating from surface; hair tufts absent. Mouthparts yellow. Chelicerae straight; promargin with one tooth (figs. 176, 221), retromargin without teeth; fangs without toothlike projections, directed medially, slightly sinuous at tip (figs. 177, 222), without prominent basal process, tip unmodified; setae dark, needlelike, evenly scattered; paturon inner margin with scattered setae, distal region unmodified (except in males of *D. tsumkwe*, figs. 250, 251), posterior surface unmodified, promargin unmodified, inner margin unmodified, laminate groove absent. Labium not fused to sternum, slightly narrowed in front, anterior margin, slightly indented at middle (figs.

178, 223), with six or more setae, same as sternum in sclerotization, subdistal portion with unmodified setae. Endites distally not excavated, serrula present in single row (figs. 179, 180, 224–226), anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization; males (except in *D. tsumkwe*) with triangular process situated at base of dorsal surface, directed toward chelicerae (fig. 175). Female palp without claw, sometimes with spines; patella without prolateral row of ridges; tarsus unmodified. **Abdomen:** White, globular, without long posterior extension, rounded posteriorly, interscutal membrane without rows of small sclerotized platelets; dorsum soft portions without color pattern; book lung covers large, ovoid, without setae, anterolateral edge unmodified; posterior spiracles connected by groove; pedicel tube short, unmodified, scutopedicel region unmodified, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, postepigastric, and spinneret scuta absent; dorsal, epigastric, and postepigastric setae light, needlelike, epigastric setae not basally enlarged; dense patch of setae anterior to spinnerets absent. Spinnerets (scanned only in *D. lorelei*) with conspicuous unsclerotized strip crossing base of anterior lateral pair (figs. 188, 230, 262, 272); anterior laterals large (figs. 187, 231), with one major ampullate gland spigot and five piriform gland spigots in male (fig. 189), three in female (fig. 232); posterior medians with two long spigots in males (fig. 190), one in females (fig. 233); posterior laterals with three long spigots in males (fig. 191) and females (fig. 234). Colulus extremely wide, hirsute (figs. 188, 273, 274). **Legs:** Yellow or pale orange, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spines present, longer than segment width. Tarsal proclaws and retroclaws with inner face striate, with single row of nine or more teeth; inferior claw absent (figs. 192–198, 235). Trichobothria base rounded, aperture internal texture not gratelike, hood covered by numerous low, closely spaced ridges (fig. 236). Tarsal organ capsulate (figs. 199–202, 237–241). **Genitalia:** Male epigastric region with sperm pore not visible; furrow without  $\Omega$ -shaped insertions, without setae. Male palp yellow or pale orange, of normal size, not strongly sclerotized, right and left palps symmetrical; embolus dark, prolateral excavation absent; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia with trichobothria (fig. 184); cymbium not fused with bulb, not extending beyond distal tip of bulb, narrow to ovoid in dorsal view, without plumose setae, stout setae, or distal patch of setae; bulb more than twice as long as cymbium, stout, tapering apically; embolus accompanied by conductor, conductor sometimes partially fused with embolus (figs. 182, 183, 185, 186). Female genitalia with gonopore region swollen (fig. 228), bearing distinctive sclerotizations, probably functioning as coupling ridges, situated anteriorly on epigastric area (figs. 215, 259–261, 293, 306); internal genitalia with long anterior projection (fig. 229).

**DISTRIBUTION:** Known only from Namibia and South Africa.

*Dalmasula lorelei* Platnick and Dupérré, new species

Figures 173–241

**TYPES:** Male holotype and female allotype taken in pitfall traps at a site 10 km east of Lorelei Mine, Lüderitz District, Karas, Namibia (Aug. 9–22, 1990; C. Roberts, E. Marais), deposited in NMNW (ex 41492, PBI\_OON 33774).

**ETYMOLOGY:** The specific name is a noun in apposition taken from the type locality.

**DIAGNOSIS:** Males differ from those of *D. parvimana* in having a longer embolus (figs. 185, 186), from those of *D. tsumkwe* in lacking cheliceral apophyses and having an unsclerotized palpal conductor (figs. 209, 210), and from those of *D. grismoldi* in having a narrow embolus (figs. 185, 186); females have much larger ridges at the anterior end of the genital area (fig. 215) than do those of the other known females.

**MALE** (PBI\_OON 33774, figs. 173–210): Total length 2.13. Posterior eye row straight from front. Chelicerae anterior face unmodified. Epigastric furrow unmodified. Leg spination: tibiae: I d0-1-1, p1-0-1, v0-0-2, r1-0-1; II d0-0-1, p1-0-1, v0-0-2, r1-0-0; III d0-0-1, p0-0-1, v1p-1p-2, r0-0-1; IV d0-0-1, p0-0-1; metatarsi: I p1-0-0, v0-0-1p, r1-0-0; II p0-0-1, v0-0-1p; III v0-1p-1p; IV p0-1-0, v0-1p-1p, r0-1-0. Palp with embolus long, thin, basally sinuous, accompanied by long, thin, parallel, translucent conductor.

**FEMALE** (PBI\_OON 33774, figs. 211–241): Total length 2.24. Palpal spines absent. Leg spination: tibiae: I p1-0-1, v0-0-1r, r1-0-1; II p1-0-1, v0-1p-1r, r1-0-1; III, IV d0-0-1, p1-0-1, v0-1p-1p, r1-0-1; metatarsi: I, II d1-0-0, p1-0-0, r1-0-0; III d1-0-0, v2-0-1p, r1-1-0; IV d1-1-0, p1-1-0, v1p-0-1p, r1-1-0. Epigastric area with pair of elevated, anteriorly and medially sclerotized paramedian ridges, anterior genitalic projection with narrow anterior extension.

**OTHER MATERIAL EXAMINED:** **Namibia:** *Erongo:* Lower Ostrich Gorge, 22°20'S, 14°58'E, Rössing Mine Survey, June 6, 1984, in web at base of tree trunk (E. Griffin, NMNW 38953, PBI\_OON 33761), 1 ♀; 3.5 km N Okondeka, 18°57'S, 15°50'E, May 16–June 15, 1986, pitfall trap (E. Griffin, NMNW 39382, PBI\_OON 33776), 1 ♀. *Karas:* Lüderitz District: 10 km E Lorelei Mine, Aug. 9–22, 1990, pitfalls (C. Roberts, E. Marais, NMNW 41492, PBI\_OON 33774), 7 ♂.

**DISTRIBUTION:** Namibia (Erongo, Karas).

*Dalmasula parvimana* (Simon), new combination

Figures 242–247

*Salsula parvimanus* Simon, 1910: 178 (male holotype from Rooibank, Erongo, Namibia, in ZMB; examined).

*Sulsula parvimana:* Roewer, 1942: 281.

**DIAGNOSIS:** Males resemble those of *D. lorelei* but have a much shorter embolus, which extends only about half as far as the conductor (figs. 246, 247).

**MALE** (PBI\_OON 822, figs. 242–247): Total length 1.77. Posterior eye row straight from front. Chelicerae anterior face unmodified. Epigastric furrow unmodified. Leg spination: tibia

IV p1-0-0, v1p-0-2; metatarsus IV v0-1p-0. Embolus extending only about half as far as divergent, translucent conductor.

FEMALE: Unknown.

MATERIAL EXAMINED: Only the male holotype (ZMB 32720, PBI\_OON 822).

DISTRIBUTION: Namibia (Erongo).

***Dalmasula tsumkwe*** Platnick and Dupérré, new species

Figures 248–262

TYPES: Male holotype, female allotype, and female paratype from the CDM Camp at Tsumkwe, Bushmanland, Otjozondjupa, Namibia (May 1993; S. Green), deposited in NMNW (43119, PBI\_OON 33771).

ETYMOLOGY: The specific name is a noun in apposition taken from the type locality.

DIAGNOSIS: Males can easily be distinguished by the cheliceral apophysis near the fang (figs. 250, 251), females by the very small ridges at the front of the genital area (figs. 260, 261).

MALE (PBI\_OON 33771, figs. 248–255): Total length 2.68. Posterior eye row straight from front. Chelicerae anterior face with conical apophysis. Epigastric furrow unmodified. Leg spination: tibia IV p0-0-1, v0-0-1p, r0-0-1; metatarsi: I, II v0-0-2; III v0-0-2; IV p1-2-1. v1p-2-2. r0-0-1. Embolus only slightly longer than conductor; conductor apparently fused with embolus.

FEMALE (PBI\_OON 33771, figs. 256–262): Total length 3.18. Chelicerae without apophyses. Palpal spination: tibia p0-1-2; tarsus p0-1-2, v0-1-2, r0-2-2. Leg spination: tibiae: III p0-1-1; IV p0-1-1, v0-0-2, r0-0-1; metatarsi: I v0-0-1p; II p0-0-1, v0-0-2; III v0-0-2; IV p0-2-2, v1p-1p-2, r0-1-1. Anterior edge of weak epigastric scutum with pair of paramedian, sharply recurved ridges.

OTHER MATERIAL EXAMINED: None.

DISTRIBUTION: Namibia (Otjozondjupa).

***Dalmasula griswoldi*** Szüts and Ubick, new species

Figures 263–299

TYPES: Male holotype, female allotype, and three male and one female paratypes taken from dunes to the north of Muizenberg, 34°06'S, 18°27'E, Western Cape, South Africa (June 16–30, 1991; R. Legg), deposited in MRAC (173912, PBI\_OON 36053).

ETYMOLOGY: The specific name is a patronym in honor of Charles Griswold, who first discovered the South African members of this genus.

DIAGNOSIS: Males differ from those of the other *Dalmasula* species in having a more complex embolar region with a dorsal lobe terminating in two ribbonlike lamellae and a broad ventral lobe terminating in a slender spiral prong (figs. 275–288); females differ in having an epigynum with the anteromedian coupling ridges C-shaped and widely separated, and an internal median process with a slender stalk and a rounded head (figs. 293–299).

MALE (PBI\_OON 36091, figs. 263–288): Total length 2.33. Posterior eye row procurved from front. Chelicerae anterior face unmodified. Epigastric furrow with anterior margin swollen, glabrous, with median projection (extrusion through torn cuticle?). Leg spination: tibiae:

I, II p1-1-0; III p1-1-0, r1-1-0; IV d1-0-0, v0-0-2, r1-0-1; metatarsi: I, II p1-1-1; IV d1-1-2, p1-1-0, r1-1-1. Embolar opening apparently between bases of dorsal lamellae; distal portion of bulb terminating in two main divisions: dorsal lobe, with two distal lamellae, and ventral lobe, broad basally with distal attenuation, thin, twisted, in contact with dorsal lamellae.

**FEMALE** (PBI\_OON 36091, figs. 289–299): Total length 3.05. Palpal spines absent. Leg spination: tibiae: I p1-1-0, v1-1-2, r1-1-0; II d1-1-1, p1-1-0, v1-1-2, r1-1-0; III d1-1-1, p1-1-1, v1-1-1, r1-1-0; IV d1-1-1, p1-1-0, v1-1-1, r1-1-0; metatarsi: I p1-1-1, v1-1-1, r1-1-1; II d1-1-1, p1-1-1, v1-1-1, r1-1-1; III d1-1-1, v1-1-0, r1-1-1; IV d1-1-1, p1-1-1, v1-1-2, r1-1-1. Gonopore margins swollen, densely setose, anteriorly with pair of median pockets, evenly curved, separated; dorsally, anterior margin with median process, stalked, with round head bearing pores and strands; posterior margin with pair of lateral apodemes and oval posterior receptaculum.

**OTHER MATERIAL EXAMINED: South Africa: Western Cape:** dunes to N of Muizenberg, 34°06'S, 18°27'E, May 19–June 2, 1991 (R. Legg, MRAC 173909, PBI\_OON 36091), 3♂, 4♀.

**DISTRIBUTION:** South Africa (Western Cape).

### *Dalmasula dodebai* Szüts and Ubick, new species

Figures 300–307

**TYPE:** Female holotype taken in pitfall trap at Koiingnaas, 30°21.357'S, 17°19.664'E, Northern Cape, South Africa (July 13, 2007; C. Lyons, J. Mingo), deposited in PPRI (PBI\_OON 36069).

**ETYMOLOGY:** The specific name is a patronym in honor of the Belgian arachnologist Domir De Bakker, in recognition of his assistance at the MRAC throughout the visit there during which Tamás Szüts found the specimen described here, formed by combining the first two letters of each of his names.

**DIAGNOSIS:** Females differ from those of the other *Dalmasula* species in having an epigynum with the anteromedian coupling ridges straight and posteriorly contiguous, and an internal median process with a thick stalk and an angular head (figs. 306, 307).

**MALE:** Unknown.

**FEMALE** (PBI\_OON 36069, figs. 300–307): Total length 2.69. Posterior eye row procurved from front. Palpal spines absent. Leg spination: tibiae: I, II d1-1-0, p1-1-0, v1-1-2, r1-1-0; III, IV d1-1-0, p1-1-0, v1-1-2, r1-1-0; metatarsi: I p1-1-1, v1-1-1, r1-1-1; II d1-1-1, p1-1-1, v1-1-1, r1-1-1; III d1-1-1, v1-1-1, r1-1-1; IV d1-1-0, p1-1-1, v1-1-2, r1-1-1. Gonopore with margins swollen, setose, anteriorly with pair of curved, median, posteriorly contiguous pockets; dorsally with anterior stalked process, shaft thick, as broad as head, posterior part with foliate lateral apodemes and large rounded receptaculum.

**OTHER MATERIAL EXAMINED:** None.

**DISTRIBUTION:** South Africa (Northern Cape).

### Oonopinae Simon

Oonopidae Simon, 1890: 80.

Gamasomorphinae Petrunkevitch, 1923: 172.

“Pseudogamasomorphinae” (nomen nudum): Dumitresco and Georgesco, 1983: 103.

**DIAGNOSIS:** The bulk of the currently recognized oonopid genera (i.e., all those except *Orchestina*, *Sulsula*, *Dalmasula*, *Xiombarg*, *Unicorn*, and *Cortestina*) are here assigned to the Oonopinae, and are characterized by the absence of a heavily sclerotized, thick-walled sperm duct in the male palp. This absence presumably reflects a major transformation in palpal mechanics. With the exception of the New Zealand genus *Kapitia*, all known oonopines have a distinctively clumped eye arrangement and a 3-3-2-2 tarsal organ receptor pattern.

**RELATIONSHIPS:** So far as is known, a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement are retained only in *Kapitia*, suggesting that this enigmatic, seldom collected New Zealand genus is the sister group of all the other oonopines. Aside from the original description by Forster (1956), information on *Kapitia* has been supplied only by Paquin et al. (2010), so we present below a redescription of the species. Of particular interest are the teeth on the tarsal claws (figs. 316, 317); it appears that the inner tooth row has been displaced entirely to the tip of the claw, presumably representing a stage in the loss of that tooth row.

Within the massive assemblage of remaining oonopine species united by the reduction to a 3-3-2-2 tarsal organ receptor pattern and a clustered eye arrangement, we can recognize only a few large groupings at this point. Platnick and Dupérré (2010b) suggested that those genera with a distinctly sclerotized cephalothorax might form a monophyletic group; if so, then several genera that were classically placed in the Oonopinae are actually more closely related to the classical gamasomorphines than to *Oonops* and such similarly soft-bodied taxa as *Heteroonops* and *Oonopoides* Bryant. These anteriorly hard-bodied genera include at least *Stenoonops* Simon, *Australoonops* Hewitt, *Scaphioides* Bryant, *Khamisia* Saaristo and van Harten, and *Longoonops* Platnick and Dupérré. The classical gamasomorphines might also represent a monophyletic subgroup of this enlarged group. It remains to be seen, for example, whether taxa in the *Scaphiella* complex, where males have dorsal abdominal scuta that are lacking in females, or the similarly sexually dimorphic taxa in the *Dysderina* complex, represent independent gains of dorsal scuta in males, or independent losses of dorsal scuta in females. However, even if the presence of a dorsal scutum does not turn out to be a synapomorphy of the classical gamasomorphines, the movement of the male gonopore onto the epigastric scutum may well be synapomorphic for that group. Nevertheless, neither the classical nor the enlarged group could be recognized as a subfamily unless a separate subfamily were to be established for *Kapitia* and the many other genera that (like *Oonops*) have both a soft-bodied cephalothorax and a soft-bodied abdomen can also be shown to constitute a monophyletic group (i.e., a smaller Oonopinae). At present, we know of no potentially synapomorphic characters supporting that smaller group.

#### *Kapitia* Forster

*Kapitia* Forster, 1956: 166 (type species by original designation *Kapitia obscura* Forster).

**DIAGNOSIS:** The lack of a heavily sclerotized sperm duct within the male palp, combined with the presence of a 4-4-3-3 tarsal organ receptor pattern and an H-shaped eye arrangement, is diagnostic for the genus.

*Kapitia obscura* Forster

## Figures 308–329

*Kapitia obscura* Forster, 1956: 166, figs. 140–144 (male holotype and female allotype from Kapiti Island, New Zealand, in CMC; examined). – Paquin et al., 2010: 32, figs. 10.1–10.4.

**DIAGNOSIS:** With the characters of the genus, an abruptly bent embolus (figs. 323–325), and receptacula as in figures 328, 329.

**MALE** (PBI\_OON 26044, figs. 323–327, images of nonsexual characters based on female): Total length 1.26. **Cephalothorax:** Carapace yellow, without any pattern, ovoid in dorsal view, pars cephalica flat in lateral view (fig. 309), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of elevated portion of pars cephalica smooth, sides smooth, pars thoracica without depressions, fovea absent, without radiating rows of pits; lateral margin straight, smooth, without denticles; plumose setae near posterior margin of pars thoracica absent (fig. 308). Clypeus margin unmodified, straight in front view, vertical in lateral view, low, ALE separated from edge of carapace by less than their radius, median projection absent. Eyes six, well developed, all subequal, ALE oval, PME oval, PLE circular; posterior eye row recurved from above; ALE separated by their radius to diameter, ALE-PLE touching, PME touching throughout most of their length, PLE-PME touching (fig. 310). Sternum longer than wide, white, uniform in coloration, not fused to carapace, median concavity absent, without radial furrows between coxae I–II, II–III, III–IV, radial furrow opposite coxae III absent, surface smooth, without pits, microsculpture absent, sickle-shaped structures absent, anterior margin unmodified, posterior margin extending posteriorly beyond anterior edges of coxae IV as single extension, anterior corner unmodified, lateral margin without infracoxal grooves, distance between coxae approximately equal, extensions of precoxal triangles absent, lateral margins unmodified, without posterior hump; setae sparse, light, needlelike, evenly scattered, originating from surface, without hair tufts (fig. 311). Mouthparts white. Chelicerae slightly divergent, without teeth, anterior face unmodified; fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified; setae light, needlelike, evenly scattered. Labium rectangular, not fused to sternum, anterior margin indented at middle, same as sternum in sclerotization; with one or two setae on anterior margin, subdistal portion with unmodified setae (fig. 312). Endites distally not excavated, serrula present as single row of teeth, antero-median tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen:** Ovoid, without long posterior extension, rounded posteriorly, interscutal membrane rows of small sclerotized platelets absent posteriorly; dorsum soft portions yellow, without color pattern; book lung covers small; pedicel tube short, unmodified, scutopedicel region unmodified, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent; dorsal, epigastric, postepigastric and spinneret scuta absent; setae light, needlelike, epigastric area setae not enlarged at base; dense patch of setae anterior to spinnerets absent. Colulus absent. **Legs:** Yellow, without color

pattern; femur IV not thickened, same size as femora I–III, tibia I unmodified, tibia IV specialized hairs on ventral apex absent, tibia IV ventral scopula absent, metatarsi I, II mesoapical comb absent, metatarsi III, IV weak ventral scopula absent. Leg spines absent. Tarsal claws with inner tooth row displaced to tip of claw, inner faces striated, inferior claw absent (figs. 316, 317). Trichobothrial base with arched ridge (fig. 318). Tarsal organs apparently with four receptors on anterior legs, three on posterior legs and palps (figs. 319–322). **Genitalia:** Epigastric region with sperm pore not visible; furrow without  $\Omega$ -shaped insertions, without setae. Palp of normal size, not strongly sclerotized, right and left palps symmetrical, proximal segments white; embolus light, prolateral excavation absent; trochanter of normal size, unmodified; femur of normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia with trichobothria; cymbium white, ovoid in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, without stout setae, without distal patch of setae; bulb white, without sclerotized sperm duct (figs. 323, 324), embolus abruptly bent (fig. 325).

**FEMALE** (PBI\_OON 26045, figs. 308–322, 328, 329): Total length 1.63. Palpal tarsus without claw or spines, unmodified, patella without prolateral row of ridges (figs. 313, 314), tibia with three trichobothria (fig. 315). Anterior receptaculum with ventral expansion at base, tip microphone-shaped, posterior receptaculum long, ovoid (figs. 328, 329).

**MATERIAL EXAMINED:** **New Zealand:** *North Island:* Cook Strait: Kapiti Island, May 1947, leaf litter (R. Forster, CMC 1192, 1193, PBI\_OON 26044, 26045), 1 ♂, 1 ♀ (holotype, allotype); Nigger Head, Apiti-Utawai, Sept. 28, 1972, roadside (C. Wilton, OMD PBI\_OON 26512), 2 ♀; summit, Three Kings, Nov. 28, 1970 (G. Ramsay, OMD PBI\_OON 26508), 1 ♂.

**DISTRIBUTION:** The few available records span the full length of the North Island of New Zealand.

#### ACKNOWLEDGMENTS

This paper, like the PBI project itself, would not have been possible without the support of NSF (through grant DEB-0613754) and agencies in several other countries. We are grateful to all our funders for giving us the chance to demonstrate that an international group of systematists can indeed collaborate to make major advances in the study of a poorly known, megadiverse, microdistributed group of organisms, within a relatively short time frame. As always, we thank the curators who have supplied essential specimens: Tharina Bird (NMNW), Ansie Dippenaar-Schoeman (PPRI), Jason Dunlop (ZMB), Cody Fraser (OMD), Gonzalo Giribet and Laura Leibensperger (MCZ), Dawn Larsen (SAM), Arno Lise (MCTP), Simon Pollard (CMC), Christine Rollard (MNHN), and Zoe Simmons (HDO). We also thank Steve Thurston for composing the plates, and Joel Ledford and Michael Rix for their helpful comments on a draft of the manuscript.

## REFERENCES

- Abraham, N., et al. In press. A revision of the Neotropical goblin spider genus *Neoxyphinus* Birabén, 1953, (Araneae, Oonopidae). American Museum Novitates.
- Álvarez-Padilla, F., D. Ubick, and C.E. Griswold. In press. *Noideattella* and *Tolegnaro*, two new genera of goblin spiders from Madagascar, with comments on the gamasomorphoid and silhouetteloid oonopids (Araneae, Oonopidae). Bulletin of the American Museum of Natural History.
- Baehr, B.C., and H.M. Smith. 2008. Three new species of the Australian orsolobid spider genus *Hickmanolobus* (Araneae: Orsolobidae). Records of the Western Australian Museum 24: 325–336.
- Baehr, B.C., and D. Ubick. 2010. A review of the Asian goblin spider genus *Camptoscaphiella* (Araneae: Oonopidae). American Museum Novitates 3697: 1–65.
- Baehr, B.C., M.S. Harvey, M. Burger, and M. Thoma. In press. The new Australasian goblin spider genus *Prethopalpus* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History.
- Baehr, B.C., M.S. Harvey, and H.M. Smith. 2010. The goblin spiders of the new endemic Australian genus *Cavisternum* (Araneae: Oonopidae). American Museum Novitates 3684: 1–40.
- Blumenthal, H. 1935. Untersuchungen über das “Tarsalorgan” der Spinnen. Zeitschrift für Morphologie und Ökologie der Tiere 29: 667–719.
- Brescovit, A.D., L.A. Bertonecello, R. Ott, and A.A. Lise. 2004. Description and ecology of two new species of the Brazilian spider genus *Losdolobus* Platnick & Brescovit (Araneae, Dysderoidea, Orsolobidae). Revista Ibérica de Arachnología 9: 249–257.
- Brescovit, A.D., C.A. Rheims, A.B. Bonaldo, A.J. Santos, and R. Ott. In press. The Brazilian goblin spiders of the new genus *Predatoroonops* (Araneae: Oonopidae). American Museum Novitates.
- Brignoli, P.M. 1979. Ragni del Brasile V. Due nuovi generi e quattro nuove specie dello stato di Santa Catarina (Araneae). Revue Suisse de Zoologie 86: 913–924.
- Bristowe, W.S. 1948. Notes on the structure and systematic position of oonopid spiders based on an examination of the British species. Proceedings of the Zoological Society of London 118: 878–891.
- Burger, M., and P. Michalik. 2010. The male genital system of goblin spiders: evidence for the monophyly of Oonopidae (Arachnida: Araneae). American Museum Novitates 3675: 1–13.
- Cambridge, O. P.-. 1876. Catalogue of a collection of spiders made in Egypt, with descriptions of new species and characters of a new genus. Proceedings of the Zoological Society of London 1876: 541–630.
- Chamberlin, R.V., and W. Ivie. 1942. A hundred new species of American spiders. Bulletin of the University of Utah 32 (13): 1–117.
- Chickering, A.M. 1951. The Oonopidae of Panama. Bulletin of the Museum of Comparative Zoology 106: 207–245.
- Dalmas, R. de. 1916. Révision du genre *Orchestina* E.S. [Arachn. Oonopidae], suivie de la description de nouvelles espèces du genre *Oonops* et d’une étude sur les Dictynidae du genre *Scotolathys*. Annales de la Société Entomologique de France 85: 203–258.
- Dumitresco, M., and M. Georgesco. 1983. Sur les Oonopidae (Araneae) de Cuba. Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba 4: 65–114.
- Eichenberger, B., et al. In press. Morphology of new Indian/Indonesian *Gamasomorpha* and *Xestaspis* species (Araneae: Oonopidae). Zootaxa.
- Fannes, W. 2010. On *Melchisedec*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). American Museum Novitates 3702: 1–28.

- Fannes, W., and R. Jocqué. 2008. Ultrastructure of *Antoonops*, a new, ant-mimicking genus of Afro-tropical Oonopidae (Araneae) with complex internal genitalia. *American Museum Novitates* 3614: 1–30.
- Forster, R.R. 1956. New Zealand spiders of the family Oonopidae. *Records of the Canterbury Museum* 7: 89–169.
- Forster, R.R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. In J. Gruber (editor), *Verhandlungen 8. Internationaler Arachnologen-Kongress*: 269–284. Vienna: Verlag H. Egermann.
- Forster, R.R., and N.I. Platnick. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. *Bulletin of the American Museum of Natural History* 181 (1): 1–230.
- Giroti, A.M., and A.D. Brescovit. 2011. The spider genus *Segestria* Latreille, 1804 in South America (Araneae: Segestriidae). *Zootaxa* 3046: 59–66.
- González Reyes, A.X., J.A. Corronca, and M.B. Cava. 2010. New species of *Unicorn* Platnick & Brescovit (Araneae, Oonopidae) from north-west Argentina. *Munis Entomology & Zoology* 5: 374–379.
- Grismado, C.J. 2010. Description of *Birabenella*, a new genus of goblin spiders from Argentina and Chile (Araneae: Oonopidae). *American Museum Novitates* 3693: 1–21.
- Griswold, C.E., and N.I. Platnick. 1987. On the first African spiders of the family Orsolobidae (Araneae, Dysderoidea). *American Museum Novitates* 2892: 1–14.
- Harvey, M.S. 1987. *Grymeus*, a new genus of pouched oonopid spider from Australia (Chelicerata: Araneae). *Memoirs of the Museum of Victoria* 48: 123–130.
- Hickman, V.V. 1979. Some Tasmanian spiders of the family Oonopidae, Anapidae and Mysmenidae. *Papers and Proceedings of the Royal Society of Tasmania* 113: 53–79.
- Jiménez, M.L., N.I. Platnick, and N. Dupérré. 2011. The haplogyne spider genus *Nopsides* (Araneae, Caponiidae), with notes on *Amrishoonops*. *American Museum Novitates* 3708: 1–18.
- Kaston, B.J. 1948. Spiders of Connecticut. *Bulletin of the State Geological and Natural History Survey of Connecticut* 70: 1–874.
- Knoflach, B., K. Pfaller, and F. Stauder. 2009. *Cortestina thaleri*—a new dwarf six-eyed spider from Austria and Italy (Araneae: Oonopidae: Oonopinae). *Contributions to Natural History: Scientific Papers from the Natural History Museum Bern* 12: 743–771.
- Lise, A.A., and L. Almeida. 2006. A new species of *Losdolobus* Platnick & Brescovit, 1994 (Araneae: Dysderoidea: Orsolobidae) from southern Brazil. *Zootaxa* 1277: 23–27.
- Marusik, Y.M., and J. Wunderlich. 2008. A survey of fossil Oonopidae (Arachnida: Aranei). *Arthropoda Selecta* 17: 65–79.
- Michalik, P. 2009. The male genital system of spiders (Arachnida: Araneae) with notes on the fine structure of seminal secretions. *Contributions to Natural History: Scientific Papers from the Natural History Museum Bern* 12: 959–972.
- Ott, R., and A.D. Brescovit. 2004. Three new species of the haplogyne spider genus *Coxapopha* Platnick from the Amazon region (Araneae, Oonopidae). *Revista Ibérica de Aracnología* 9: 127–135.
- Paquin, P., C.J. Vink, and N. Dupérré. 2010. Spiders of New Zealand: annotated family key & species list. Lincoln, New Zealand: Manaaki Whenua Press, vii + 118 pp.
- Petrunkovitch, A. 1923. On families of spiders. *Annals of the New York Academy of Sciences* 29: 145–180.
- Platnick, N.I. 2012. The world spider catalog, version 12.5. New York: American Museum of Natural History, Internet resource (<http://research.amnh.org/iz/spiders/catalog>). [doi: 10.5531/db.iz.0001]

- Platnick, N.I., and A.D. Brescovit. 1995. On *Unicorn*, a new genus of the spider family Oonopidae (Araneae, Dysderoidea). *American Museum Novitates* 3152: 1–12.
- Platnick, N.I., and N. Dupérré. 2009a. The goblin spider genera *Opopaea* and *Epectris* (Araneae, Oonopidae) in the New World. *American Museum Novitates* 3649: 1–43.
- Platnick, N.I., and N. Dupérré. 2009b. The American goblin spiders of the new genus *Escaphiella* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 328: 1–151.
- Platnick, N.I., and N. Dupérré. 2009c. The goblin spider genus *Heteroonops* (Araneae, Oonopidae), with notes on *Oonops*. *American Museum Novitates* 3672: 1–72.
- Platnick, N.I., and N. Dupérré. 2010a. The goblin spider genus *Scaphiella* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 332: 1–156.
- Platnick, N.I., and N. Dupérré. 2010b. The goblin spider genera *Stenoonops* and *Australoonops* (Araneae, Oonopidae), with notes on related taxa. *Bulletin of the American Museum of Natural History* 340: 1–111.
- Platnick, N.I., and N. Dupérré. 2010c. The Andean goblin spiders of the new genera *Niarchos* and *Scaphios* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 345: 1–120.
- Platnick, N.I., and N. Dupérré. 2011a. The Andean goblin spiders of the new genus *Scaphidysderina* (Araneae, Oonopidae), with notes on *Dysderina*. *American Museum Novitates* 3712: 1–51.
- Platnick, N.I., and N. Dupérré. 2011b. The goblin spider genus *Pescennina* (Araneae, Oonopidae). *American Museum Novitates* 3716: 1–64.
- Platnick, N.I., and N. Dupérré. 2011c. The goblin spider genus *Simoonops* (Araneae, Oonopidae). *American Museum Novitates* 3724: 1–30.
- Platnick, N.I., and N. Dupérré. 2011d. The Andean goblin spiders of the new genera *Paradysderina* and *Semidysderina* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 364: 1–121.
- Platnick, N.I., and N. Dupérré. 2012. The goblin spider genus *Costarina* (Araneae, Oonopidae), part 1. *American Museum Novitates* 3730: 1–64.
- Platnick, N.I., J.A. Coddington, R.R. Forster, and C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *American Museum Novitates* 3016: 1–73.
- Platnick, N.I., N. Dupérré, R. Ott, and Y. Kranz-Baltensperger. 2011. The goblin spider genus *Brignolia* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 349: 1–131.
- Purcell, W.F. 1910. The phylogeny of the tracheae in Araneae. *Quarterly Journal of Microscopical Science* 54: 519–564.
- Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *Journal of Arachnology* 28: 149–157.
- Roewer, C.F. 1942. *Katalog der Araneae von 1758 bis 1940*. Budy, Bremen, 1: 1–1040.
- Saaristo, M.I., and Y.M. Marusik. 2004. *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei: Oonopidae). *Arthropoda Selecta* 13: 51–54.
- Sánchez-Ruiz, A., N.I. Platnick, and N. Dupérré. 2010. A new genus of the spider family Caponiidae (Araneae, Haplogynae) from the West Indies. *American Museum Novitates* 3705: 1–44.
- Saupe, E.E., et al. In press. New *Orchestina* (Simon, 1882) (Araneae: Oonopidae) from Cretaceous ambers of Spain and France: first spiders described using phase-contrast x-ray synchrotron microtomography. *Palaeontology*.
- Simon, E. 1882. Études arachnologiques. 13<sup>e</sup> Mémoire. XX. Descriptions d'espèces et de genres nouveaux de la famille des Dysderidae. *Annales de la Société Entomologique de France* (ser. 6) 2: 201–240.

- Simon, E. 1890. Études arachnologiques. 22<sup>e</sup> Mémoire (I). XXXIV. Étude sur les arachnids de l'Yemen. *Annales de la Société Entomologique de France* (ser. 6) 10: 77–124.
- Simon, E. 1893. *Histoire naturelle des araignées*: 1: 257–488. Paris: Roret.
- Simon, E. 1910. Arachnoidea. Araneae (ii). *In* L. Schultze, *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika*. *Denkschriften Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 16: 175–218.
- Simon, E. 1911. *Catalogue raisonné des arachnids du nord de l'Afrique* (1<sup>re</sup> partie). *Annales de la Société Entomologique de France* 79: 265–332.
- Ubick, D., and C.E. Griswold. 2011a. The Malagasy goblin spiders of the new genus *Malagiella* (Araneae, Oonopidae). *Bulletin of the American Museum of Natural History* 356: 1–86.
- Ubick, D., and C.E. Griswold. 2011b. The Malagasy goblin spiders of the new genus *Molotra* (Araneae, Oonopidae). *American Museum Novitates* 3729: 1–69.

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from <http://www.amnhshop.com> or via standard mail from:

American Museum of Natural History—Scientific Publications  
Central Park West at 79th Street  
New York, NY 10024

Ⓢ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).