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ELONGATED PEDICILLATE SETAE: A PUTATIVE SENSORY SYSTEM AND SYNAPOMORPHY OF SPIDERS

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ABSTRACT. We survey spiders from 43 families, 62 genera, and three arachnid outgroups for the presence and diversity of elongated pedicillate setae (EPS)—a complex system of probably sensory setae hitherto undocumented outside Theridiidae. Although not present in all spiders, these setae are sufficiently widespread to suggest they are primitively present in the order. Because they are absent in related arachnids, they appear to be a synapomorphy of spiders. Based on the morphology and orientation of these setae, it has been suggested that they supplement abdominal slit sensilla in proprioception, documenting the position and movement of the abdomen relative to the cephalothorax. Although still poorly known, the presence and distribution of these setae are informative at lower and higher phylogenetic levels.

Keywords: Araneae, phylogeny, proprioreception

Spiders are typically setose and many of the setae, especially on the appendages, are sensory (Seyfarth 1985; Barth 2001). However, the distribution and function of the many different kinds of setae on spider bodies are poorly known. Morphological, behavioral, histological, and neurobiological research are all necessary to understand setal distribution, function, and to establish interspecific homologies. Morphology can document apparently different types of setae and their distribution on individuals as well as across species. It can also infer function from their detailed structure, distribution, and orientation. Agnarsson (2004) documented the distribution of distinct elongated setae around the pedicel on abdomens of theridiid spiders. The distribution of these setae was phylogenetically informative. They surround the pedicel and are juxtaposed to the cephalothorax so that abdominal movement is likely to cause flexion, which may, in turn, signal the relative positions of the abdomen and cephalothorax. He proposed the name "suprapedicillate proprioceptive setae:" proprioception (or proprioreception) is the perception of the body's position and movement including physical displacement and any changes in tension, or force within the body (e.g., Seyfarth & Pflügler 1984; Seyfarth 1985; Seyfarth et al. 1985).

The proprioceptive hypothesis was based on the morphological, not behavioral, histological, and neurobiological evidence. Here we use a more neutral term, elongated pedicillate setae (EPS) although we hope that the hypothesis of proprioceptive function will be tested in future studies.

Agnarsson's (2004) survey was limited to theridiids and a few outgroups and his discussion focused mainly on their phylogenetic utility within theridiids. Here we document the distribution of EPS and their potential as characters for higher level phylogenetic studies from a broader survey of spider families.

METHODS

Sixty-nine taxa were selected to span the order Araneae and closely related outgroups (many additional species, especially theridiids, were surveyed by Agnarsson 2004). Taxon representation was biased, however, towards Orbiculariae, and Theridiidae by the authors' specialties. Given sufficient specimens, the abdomens were critical point dried, glued to a rivet, and sputter coated with Au/Pd.

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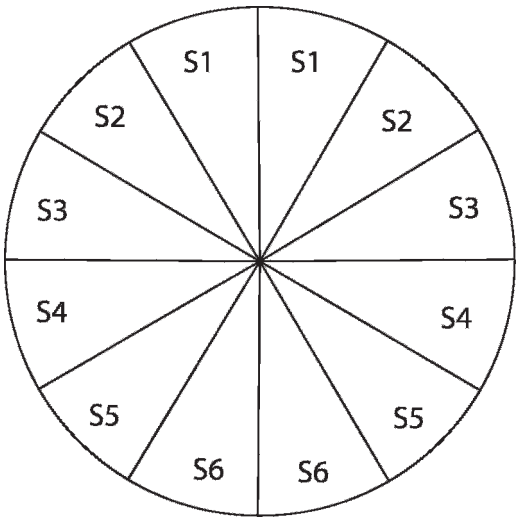


Figure 1.—The six symmetric sectors around the pedicel in which the distribution of EPS were scored.

Scanning electron micrographs were taken of the area around the pedicel from a standard view (normal to the pedicel axis) and other angles when deemed useful. At this rudimentary stage of knowledge, homology of individual setae or setal groups remains ambiguous, so we simply divided the pedicel area into six (paired) sectors, and tabulated the presence and number of EPS in each (Fig. 1). Two people independently scored presence/absence of EPS in each SEM photograph; if any disagreement occurred between the two the taxon in question was scored as "uncertain."

Among Araneae outgroups where EPS seem to be completely absent, presence or absence was verified under a dissecting microscope. For rare taxa (e.g., *Liphistius*) we did not score their distribution because standard view photographs were not available.

RESULTS

The phylogenetic distribution of EPS is given in Table 1 and Figure 2. Three arachnid orders, Amblypygi, Uropygi, and Palpigradi share a narrow pedicel with Araneae, but the pro/opisthosoma connection in spiders is especially flexible, probably to promote mobility of the spinnerets. Amblypygids, uropygids, and schizomids apparently lack EPS. EPS appear to be present in all major spider lineages (Mesothelae, Mygalomorphae, and Araneomorphae). Many of the examined taxa had at least one pair of proprioceptive setae (Figs. 2–36, Table 1).

The distinctiveness of EPS varies widely across spiders. In some taxa, including nearly all examined orbicularians, EPS are easily distinguished from other abdominal setae by the morphology of the robust socket (Fig. 8) and shaft, which is unusually long, slender, and smooth (Figs. 3–36). Their number and position are therefore fairly easy to score (Figs. 3–5). In *Deinopis* and some non-orbicularians the EPS can be distinguished because they are mostly smooth, in contrast to the otherwise serrate or plumose (feathery) abdominal setae (Fig. 30–36). In many other cases, however, the distinction between proprioceptive and other abdominal setae was not clear, and the two scorers often disagreed, usually on their position or number rather than presence or absence. Taxa in which even the existence of EPS was unclear are labeled with parentheses as "uncertain" in Table 1. Given these doubts, for consistency Table 1 indicates only the presence and relative abundance, rather than counts, of EPS in each sector.

Dividing the pedicel region into six radial sectors is purely heuristic. To reify these "sectors" by treating them as biologically meaningful would be a mistake. With that in mind, one can nevertheless use the sector notation simply as a vocabulary to speculate about patterns. Whether uncertainties are counted as presences or absences, the same ten patterns occur: 1-2, 1-2-3, 1-3, 2-3, 2, 3, 3-4, 2-3-4, 1-2-3-4, and 1-2-3-4-5. This is nearly half of the 26 ways 5 digits may be combined. More fundamentally, the two evident axes of variation are extension (some taxa have a more extensive ring of EPS than others), and position (relatively dorsal or ventral). No strongly disjunct groups of setae were observed, e.g. 1-4, 1-5, 2-6, etc. Given the sparse sample, such diversity is not encouraging, but within families the variation may be more regular and informative, as was the case with Theridiidae (Agnarsson 2004, 2006).

DISCUSSION

At this point it seems that EPS is a synapomorphy of spiders and evolved in their common ancestor co-extensively with the increased flexibility of the prosoma-opisthosomal articulation. This supports Agnarsson's (2004) hy-

Table 1.—The distribution of EPS in various arachnid taxa by abdominal "sector" (see Fig. 1). "x" indicates one to few setae, "xx" indicates few to many setae, and parentheses indicate uncertainty. Detail of locality information represents information on collection label. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC. *In *Pardosa* sp. and *Gnaphosa parvula* proprioceptive setae were scored absent by both examiners, however, as discussed in text it is difficult to rule out EPS in these species as they may be hidden by a brush of other seta (see Figs. 41–44).

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
AMBLYPYGI	AMBLYPYGI	*Phrynus longipes* (Pocock, 1894)	Absent	n/a					Puerto Rico, 22.xii.1989
SCHIZOMIDA	SCHIZOMIDA	indet.	Absent	n/a					Marshall Island, 1.i.1977, D.A. Anderson
UROPYGI	UROPYGI	Thelyphonidae indet.	Absent	n/a					USA, Florida, 14.ii.1997.
Liphistiidae	Mesothelae	*Liphistius malayanus* Abraham, 1923	Present	n/a					Malaysia, Pahang, Cameron Highlands, 3–4.vi.1981, W. Sedgwick.
Antrodiaetidae	Mygalomorphae	*Antrodiaetus robustus* (Simon, 1891)	Present	n/a					USA, Preston Co., WV, 26.vi-3.vii.1989, D.T. Jennings
Atypidae	Mygalomorphae	*Atypus muralis* Bertkau, 1890	Uncertain	n/a					Russia, Samara Area Zhiguli Reservation, viii.1981, V.I. Ovtsharenko
Dipluridae	Mygalomorphae	*Ischnothele digitata* (O. P.-Cambridge, 1892)	Present	n/a					Mexico, Los Cocos, Vera Cruz, viii.1908, A. petrunkevitch
Hypochilidae	Hypochilidae	*Hypochilus pococki* Platnick, 1987	Present	(x)	x	-	-	-	USA, Macon Co., NC, 5.ix.1990, J. Coddington
Austrochilidae	Austrochilidae	*Thaida peculiaris* Karsch, 1880	Present	x	x	-	-	-	Chile, Llanquihue Prov., P.N. Vincent P. Rosales, 24–26.xii.2000, J. Miller et al.
Filistatidae	Haplogynae	*Kukulcania hibernalis* (Hentz, 1842)	Present	(x)	x	x	x	-	USA, St. Lucie Co., Florida, 25.ii.1986, P.M. Mikkelsen.
Dysderidae	Haplogynae	*Dysdera crocata* C.L. Koch, 1838	Uncertain	(x)	-	-	-	-	USA, Maryland, Baltimore Co., 17.i.1987, W.E. Steiner et al.
Oonopidae	Haplogynae	sp. "ONO01"	Uncertain	(x)	-	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Scytodidae	Haplogynae	*Scytodes thoracica* (Latreille, 1802)	Present	x	xx	x	-	-	USA, New Britain, 13.vi.1961, B.J. Kaston.
Pholcidae	Haplogynae	*Mesabolivar aurantiacus* (Mello-Leitão, 1930)	Absent	-	-	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Sicaridae	Haplogynae	*Loxosceles deserta* Gertsch, 1973	Present	xx	xx	-	-	-	USA, Utah, Washington Co., 25.viii–9.ix.1991, W.E. Steiner
Eresidae	Eresoidea	*Stegodyphus* sp.	Absent	-	-	-	-	-	Myanmar, Chattin Wildlife Sanctuary, Sagaing Div., 7–12.x.1998, Coddington & Babtista.
Oecobidae	Eresoidea	*Oecobius navus Blackwall, 1859*	Uncertain	-	(x)	-	-	-	no data
Palpimanidae	Palpimanoidea	*sp.* (palpinanid sp 1)	Absent	-	-	-	-	-	Tanzania, Iringa Distr., Uzungwa Scarp Forest, 17–27.v.1997
Malkaridae	Palpimanoidea	*Chilenodes australis* Platnick and Forster, 1987	Absent	-	-	-	-	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Archaeidae	Palpimanoidea	*Eriauchenius vadoni* (Millot, 1948)	Absent	-	-	-	-	-	Madagascar, Steiner
Titanoecidae	Entelegynae	*Titanoeca brunnea* Emerton, 1888	Present	-	-	x	-	-	USA, Sleepy Creek Hunt & Fish Area, Berkeley Co., 16–23.v.1986, P.J. Martinat.
Agelenidae	Entelegynae	*Agelenopsis pennsylvanica* (C.L. Koch, 1843)	Present	xx	xx	xx	-	-	USA, Washington DC, 1.x.1985, K. Smith.
Amaurobidae	Entelegynae	*Amaurobius sp.*	Uncertain	-	-	(x)	-	-	USA, Piscataquie County, Maine, 1.vi.1978. D.T. Jennings & M.WL Houseweart.
Dictynidae	Entelegynae	*Dictyna major* Menge, 1869	Absent	-	-	-	-	-	Russia, Siberia
Oxyopidae	Entelegynae	*Oxyopes salticus* Hentz, 1845	Present	x	x	x	-	-	USA, Massachusetts, Barnstable Co., 2.vi.1989. R.L. Edwards

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Lycosidae	Entelegynae	*Pardosa* sp.	Absent*	-	-	-	-	-	USA, Louisiana
Anyphaenidae	Entelegynae	*Anyphaena* sp.	Present	(x)	-	(x)	-	-	USA, Rock Creek Park, Washington DC, 3.vii.1985, J. Coddington.
Thomisidae	Entelegynae	*Tmarus* sp.	Present	x	x	x	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Clubionidae	Entelegynae	*Clubiona obesa* Hentz, 1847	Uncertain	(x)	(x)	-	-	-	USA, Ellicott Rock Wilderness Area, Rabun Co., Georgia, 20.v.1993, Bond et al.
Gnaphosidae	Entelegynae	*Gnaphosa parvula* Banks, 1896	Absent*	-	-	-	-	-	USA, Maine
Salticidae	Entelegynae	*Lyssomanes taczanowski* Galiano, 1980	Present	x	x	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Deinopidae	Orbiculariae	*Deinopsis* sp.	Present	-	xx	xx	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson and M. Kunter
Uloboridae	Orbiculariae	*Uloborus trilineatus* Keyserling, 1883	Uncertain	-	(x)	-	-	-	Peru, Madre de Dios, Tambopata. 9.vi.1988. J. Coddington (NMNH)
Uloboridae	Orbiculariae	*Philioponella* sp. ("sp. 6")	Present	-	x	x	-	-	Costa Rica, Heredia Prov., Puerto Viejo, La Selva Biological station, 3–5.iv.1989, J. Coddington.
Araneidae	Orbiculariae	*Araneus alboventris* (Emerton, 1884)	Present	-	x	x	-	-	USA, Rock Creek Park, Washington DC, 7.vii.1985, J Coddington
Araneidae	Orbiculariae	*Argiope argentata* (Fabricius, 1775)	Present	-	x	x	-	-	Peru, Madre de Dios, Silva and Coddington
Araneidae	Orbiculariae	*Eustala* sp.	Present	-	x	x	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson
Araneidae	Orbiculariae	*Pronous tuberculifer* (Keyserling, 1881)	Present	-	x	x	-	-	Guyana, Bartika, 20.vii.1999, I. Agnarsson and M. Kunter

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Nephilidae	Orbiculariae	*Nephila* inaurata (Walckenaer, 1842)	Present	-	x	xx	-	-	Madagascar, Ranamofana National Park, iv. 2001, I. Agnarsson and M. Kunter
Tetragnathidae	Orbiculariae	*Leucauge venusta* (Walckenaer, 1842)	Present	(x)	x	x	-	-	USA, Rock Creek Park, Washington DC, 16.vii.1985, J. Coddington
Tetragnathidae	Orbiculariae	*Meta segmentata* (Clerck, 1757)	Present	-	-	xx	-	-	Denmark, Hestehaven, 30.viii.1994, Coddington et al.
Cyatholypidae	Orbiculariae	*Isicabu henriki* Griswold, 2001	Present	-	-	x	x	-	Tanzania, Iringa Distr. Uzungwa Scarp Forest Reserve, 17–27.v.1997. Coddington et al.
Synotaxidae	Orbiculariae	*Synotaxus waiwai* Agnarsson, 2003	Present	x	x	x	x	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Synotaxidae	Orbiculariae	*Physoglenes puyehue* Platnick, 1990	Absent	-	-	-	-	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Synotaxidae	Orbiculariae	*Chileotaxus sans* Platnick, 1990	Present	x	x	x	x	-	Chile, Puyhue National Park, vii. 2000, I. Agnarsson and J. Miller
Mimetidae	Orbiculariae	*Mimetus interfector* Hentz, 1850	Present	-	x	x	-	-	USA, Florida, J. Coddington
Nesticidae	Orbiculariae	*Eidmanella pallida* (Emerton, 1875)	Present	-	x	x	x	-	Trinidad, 1988, Coddington
Theridiidae	Orbiculariae	*Latrodectus geometricus* C.L. Koch, 1841	Present	x	x	x	x	x	Madagascar: Berenty reserve, 2.v.2001, Agnarsson & Kuntner
Theridiidae	Orbiculariae	*Anelosimus vittatus* (C.L. Koch, 1836)	Present	x	x	x	xx	-	Slovenia, Sembpas, 1998, Kuntner et al.
Theridiidae	Orbiculariae	*Anelosimus biglebowski* Agnarsson, 2006	Present	x	x	x	x	-	Tanzania, Iringa District, Uzungwa Scarp forest, 17–27.v.1997, Scharff et al.
Theridiidae	Orbiculariae	*Ariamnes attenuatus* O. P.-Cambridge, 1881	Present	x	xx	x	-	-	Peru, Madre de Dios, Pakitza, 2.x.1987, Silva & Coddington

Table 1.—Continued.

Family (ORDER)	Major clade	Species	EPS	Sector 1	2	3	4	5	Locality
Theridiidae	Orbiculariae	*Dipoena nr. hortoni*	Present	-	x	x	x	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Theridiidae	Orbiculariae	*Episinus maculipes* Cavanna, 1876	Present	(x)	x	x	x	-	Slovenia, Sembpas, 1998, Kuntner et al.
Theridiidae	Orbiculariae	*Faiditus cf. caudatus*	Present	x	-	x	-	-	Colombia, Iguaque, 2850–3000 m, 5.ii.1998, Hormiga et al.
Theridiidae	Orbiculariae	*Kochiura rosea* (Nicolet, 1849)	Present	x	x	x	x	-	Chile, Juan Fernandez Islands, Mas Afuera, Quebrada Vaca, 22.iii.1962, Malkin
Theridiidae	Orbiculariae	*Rhomphaea metaltissima* Soares & Camargo, 1948	Present	x	x	-	-	-	Guyana, Upper Essequibo Reg; 4.42 km S of Gunn's Strip, 7–15 vii. 1999, J. Coddington et al.
Theridiidae	Orbiculariae	*Spintharus flavidus* Hentz, 1850	Present	x	x	x	x	-	Costa Rica, Cartago, RF de Rio Macho, 22–26.iii.1999, Miller.
Theridiidae	Orbiculariae	*Ameridion nr. petrum*	Present	x	x	x	x	-	Costa Rica, Cartago, Reserva forestal de Rio Macho, 2850 m. 22–26.iii.1999, Zujko-Miller
Theridiidae	Orbiculariae	*Theridion varians* Hahn, 1833	Present	x	x	x	x	-	Slovenia, 23.vii.1999,
Theridiidae	Orbiculariae	*Theridion frondeum* Hentz, 1850	Present	x	x	x	x	-	USA, Montgomery Co., MD, 30.v.1985, Smith.
Pimoidae	Orbiculariae	*Pimoa breviata* Chamberlin and Ivie, 1943	Present	-	x	x	xx	-	USA, California
Linyphiidae	Orbiculariae	*Linyphia triangularis* (Clerck, 1757)	Present	-	x	xx	x	-	Denmark, Hestehaven, 30. viii. 1994, Coddington et al.
Linyphiidae	Orbiculariae	*Frontinella communis* (Hentz, 1850)	Present	x	x	x	x	-	USA, Rock Creek Park, Washington DC, J. Coddington

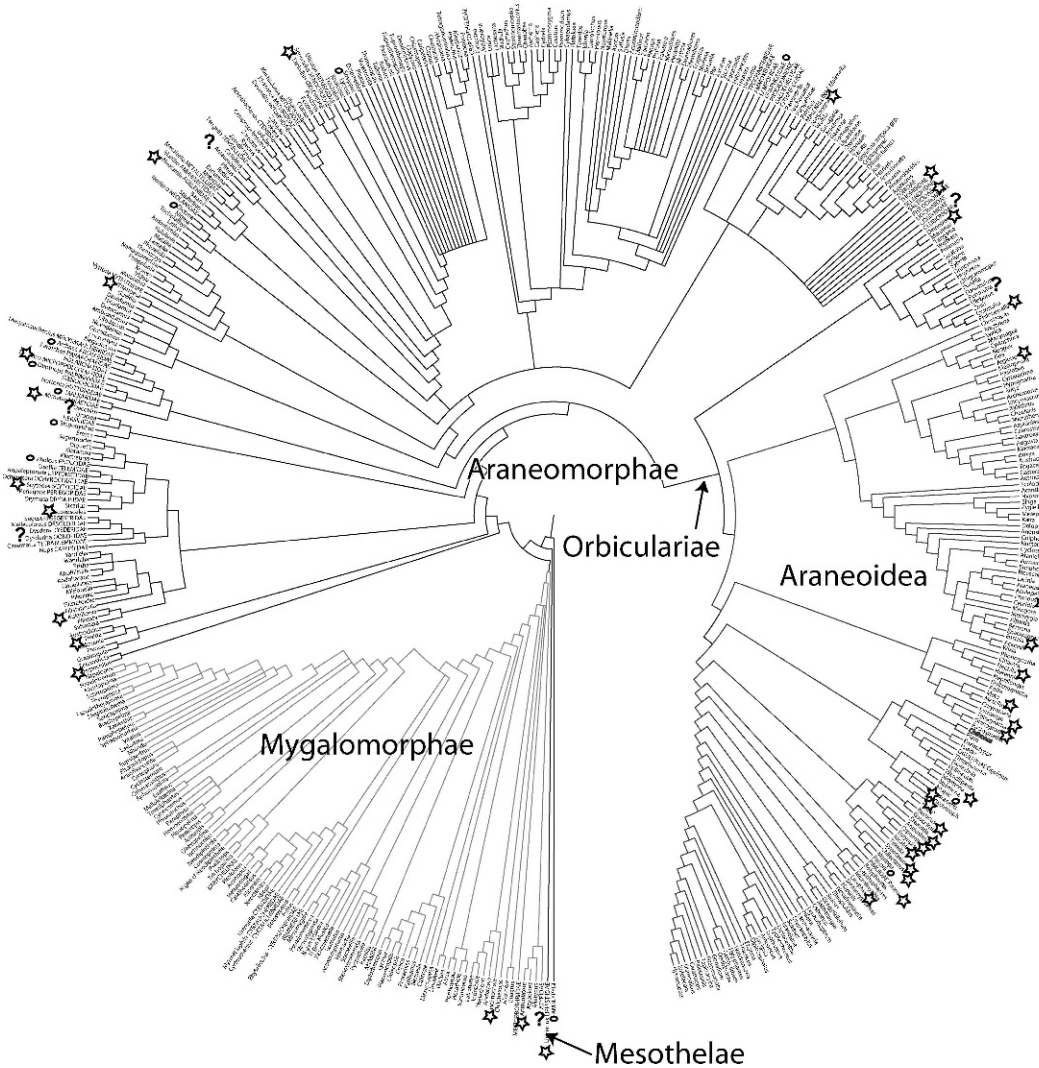
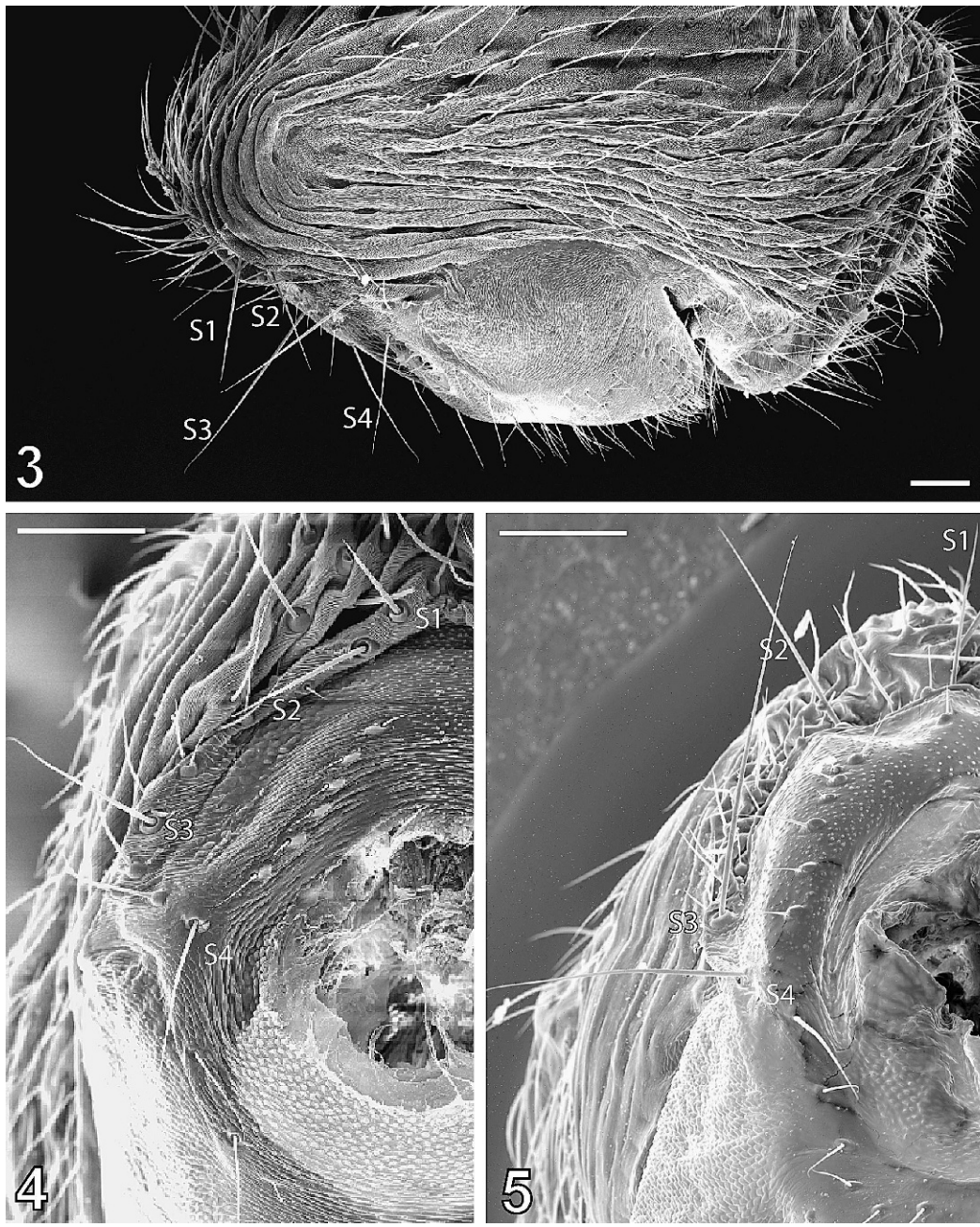


Figure 2.—Known EPS distribution plotted on a qualitative cladogram of spiders, used here to emphasize the overall distribution and scarcity of knowledge of EPS. Stars indicate presence, circles absence, question marks uncertainty.

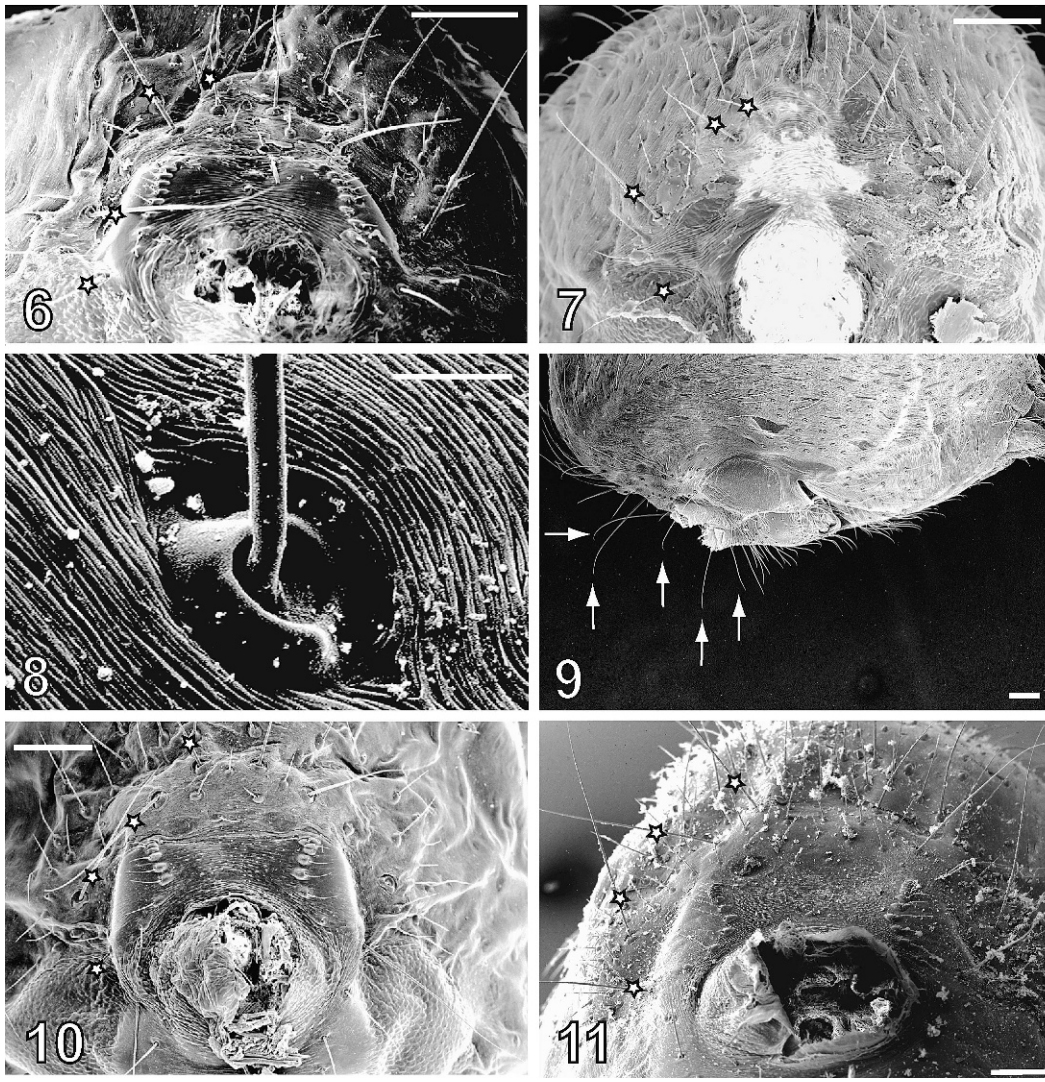
pothesis that EPS supplement the slit sensilla that also detect the relative position of the abdomen (Juberthie & Lopez 1994; Foelix 1996). Similarly, sensory setae at leg joints detect flexion when the setae press against adjacent body parts or the substrate and signal the movement and relative position of segments (Seyfarth 1985; Barth 2001), however, sensory setae on the abdomen are much less well known. Foelix (1979) may have been the first to speculate that particular abdominal setae were proprioceptive in spiders, but he did so only in a brief figure legend illustrating stridulation in *Argyrodes* (fig. 193, p. 270), and without further discussion. Juberthie & Lopez (1994) also described stridulation in male *Argyrodes* (also present in other male theridiids) in which modified and distinctly raised setal bases on the abdomen rub against grooves on the cephalothorax. They suggested that the setae that arise from these bases were proprioceptive. This remains to be confirmed, but it seems unlikely that setal proprioception, unlike stridulation, would be sexually dimor-



Figures 3–5.—Theridiidae males. 3–4. *Kochiura rosea* (Nicolet 1849) male. 3. Abdomen ectal view, ventral side down. 4. Pedicel area. 5. *Chrysso* nr. *albomaculata*. S-numbers indicate allocation of setae to sectors (see Methods). Scale bars = 100 μm.

phic. Regardless, evidence beyond morphology is needed to test the hypothesis of proprioceptive function.

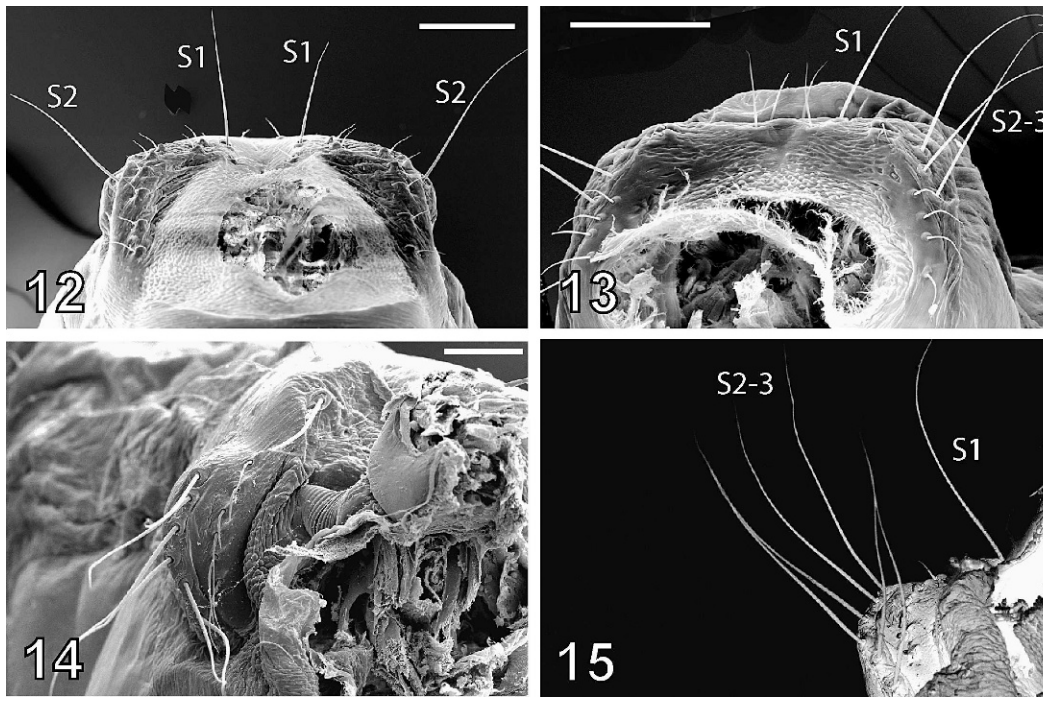
Given the phylogeny of Figure 2, basal araneomorphs (*Hypochilus* and *Austrochilus*) both have EPS in the relatively dorsal sectors 1 and 2. If present in haplogynes, they also tend to occupy sector 1, sometimes 2, and in *Scytodes* also 3. True palpimanoids, thus far, lack EPS. Non-orbicularian Entelegynae fre-



Figures 6–11.—*Anelosimus* (Theridiidae), stars and arrows indicate EPS. 6. *A. biglebowski* male. 7. *A. rupununi* Levi, 1956 female. 8. *A. biglebowski* male, detail of base of EPS setae. 9. *A. analyticus* male ectal view of abdomen with venter facing down. 10, 11. *A. studiosus* (Hentz 1850) males from Florida and Costa Rica, respectively. Scale bars: 6, 7, 9, 10 = 100 μm; 8 = 10 μm.

quently lack EPS and such presumably secondary losses may be informative. The 1-2-3 pattern is most frequent. Among orbicularians (treating *Mimetus* and *Textricella* as such), relatively basal orbicularians (deinopoids, araneids, nephilids, tetragnathids, symphytognathoids) tend to be 2-3 (also *Mimetus*), which may simply be the plesiomorphic 1-2 pattern displaced ventrally. Sheet-web weavers (Linyphiidae, Pimoidae, Synotaxidae, Cyatholipidae, Nesticidae, and Theridiidae) tend to have relatively more, and more ventral, EPS, e.g., 1-2-3-4 or 2-3-4.

None of these patterns may hold up. Observer error, especially in non-orbicularians, is probable. To confirm (or reject) the patterns reported here, verifying the presence of EPS in *Liphistius* and Mygalomorphae, and their absence in non-spider arachnids is a priority. However, proprioception at the pro/opisthosomal connection is *a priori* likely (see Lopez & Juberthie 1996), and certainly its mechanism



Figures 12–15.—Argyrodinae (Theridiidae) males, S-numbers indicate allocation of EPS to sectors (see Methods). 12. *Argyrodes argyrodes* (Walckenaer 1842). 13. *Rhomphaea metaltissima*. 14, 15. *Ariamnes attenuata*. Scale bars = 100 μm.

(EPS, slit sensilla, joint receptors) should be mapped and understood neurobiologically.

Several spider taxa seem to lack EPS (Fig. 37–44), although perhaps they are simply indistinguishable from normal abdominal setae, or greatly modified. In *Pardosa* sp. and *Gnaphosa parvula* Banks 1896 a brush of strong setae is located in sectors 1–2. These differ from typical proprioceptive setae in being stout and serrate, but they may be proprioceptive. Taxa without EPS probably indicate independent secondary losses of this sensory system rather than independent origins. Although patterns related to lifestyle in Table 1 appear weak, spiders do vary in the flexibility of their abdomens (aerial web spiders probably flex their abdomens more, and more precisely), and the patterns discussed above may reflect such differences.

In Theridiidae, EPS distribution defined generic and suprageneric taxa (Agnarsson 2004). Although the taxon sample here is quite sparse, intraspecific (Figs. 10, 11) and intrageneric variation seem low (Figs. 6–11) (see also Agnarsson 2004, characters 163–164; Agnarsson 2006, character 110). Related genera differ in the position and number of EPS. *Argyrodes* has one pair of EPS in sectors 1 and 2 (or 3), *Rhomphaea* has one pair in sector 1 and three pairs in sectors 2–3, and *Ariamnes* has one pair in sector 1 and at least six in sectors 2–3 (Figs. 12–15; generic patterns confirmed in an additional species of each genus, pers. obs.).

In summary, this is the first survey of a poorly known but complex, probably sensory system in spiders—elongated pedicillate setae—that appears to be a spider synapomorphy and useful for generic diagnoses and suprageneric phylogenetic reconstruction. The function of these setae should be investigated neurologically and behaviorally, and their patterns investigated among spiders and their relatives.

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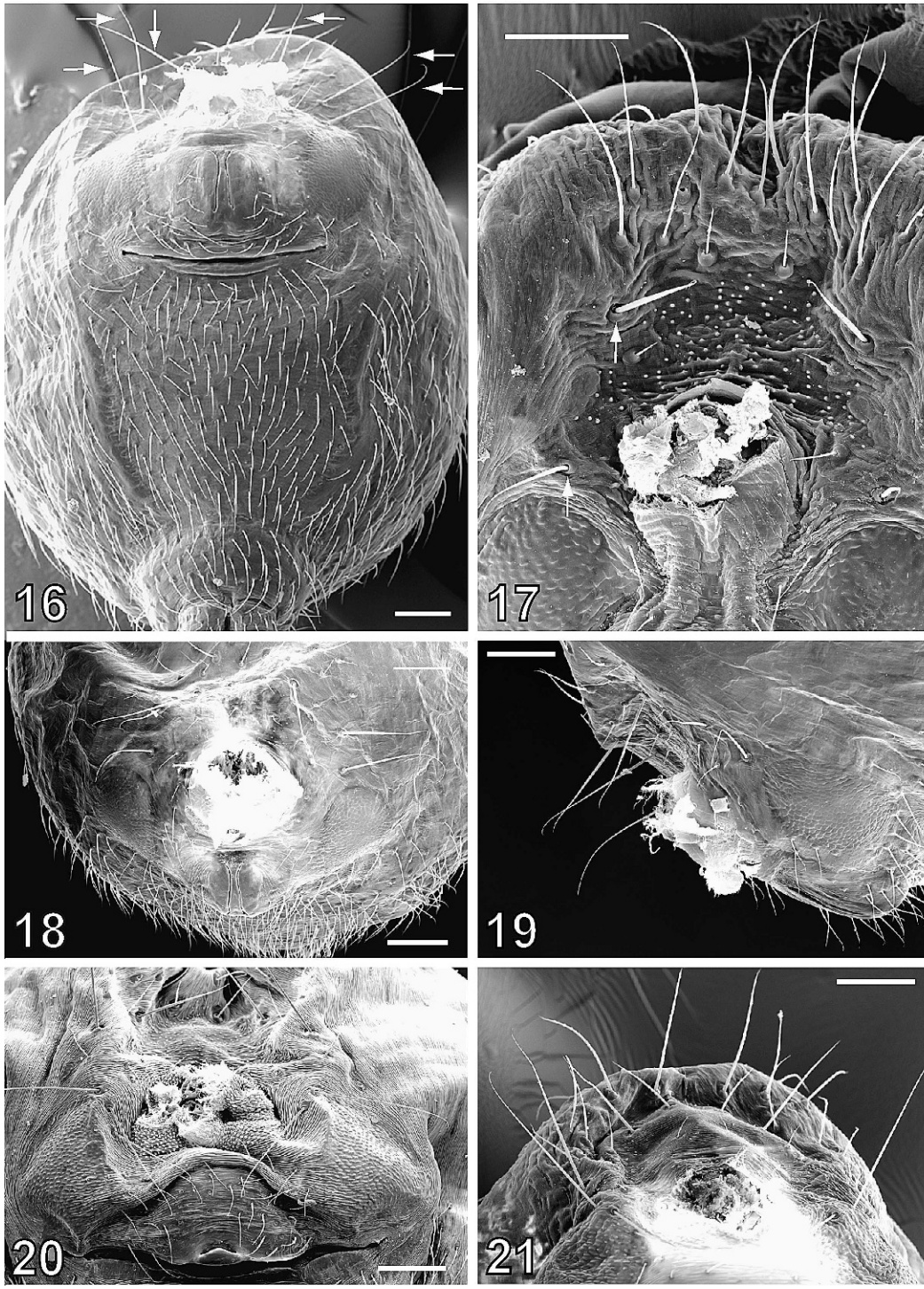
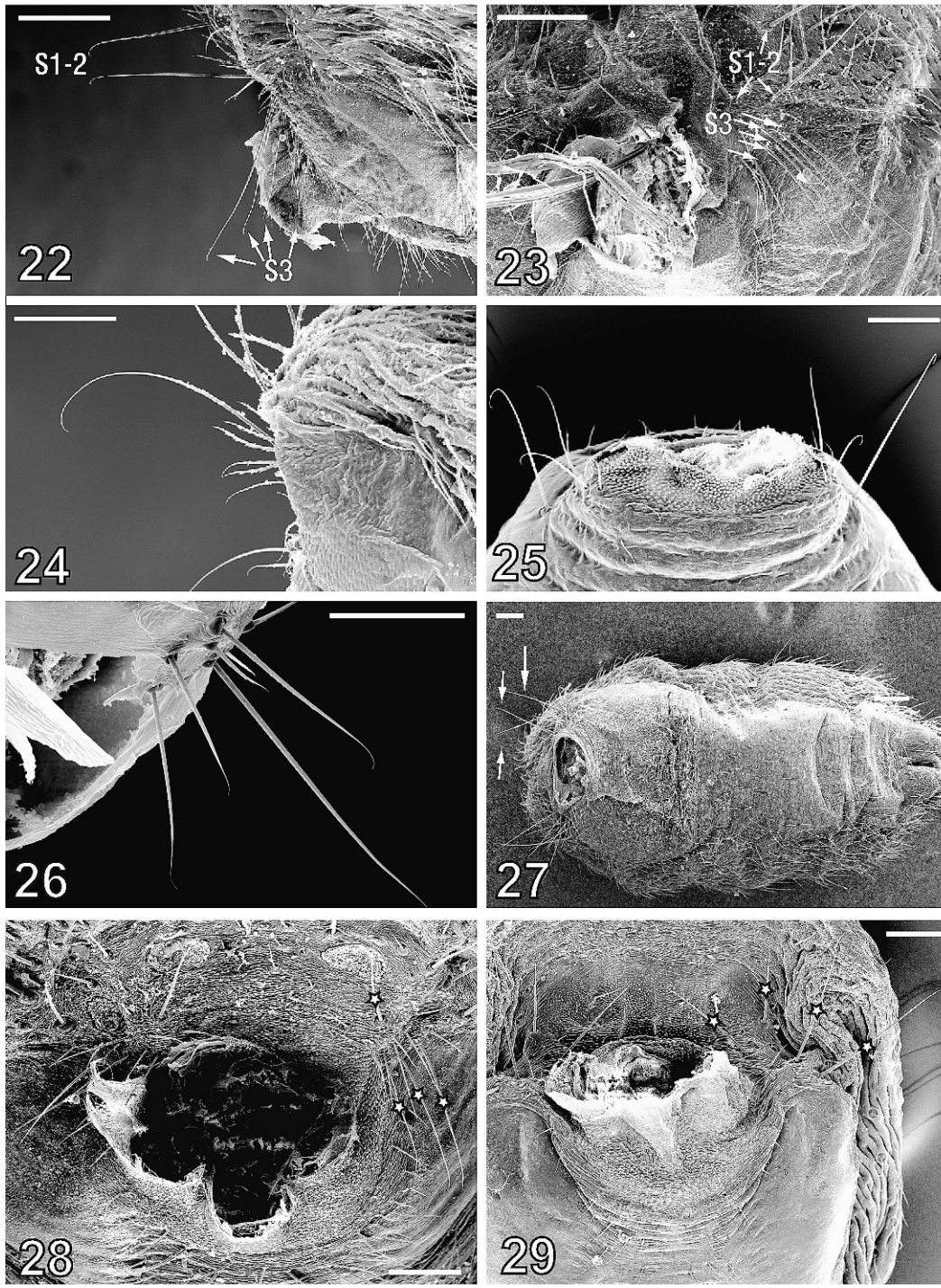
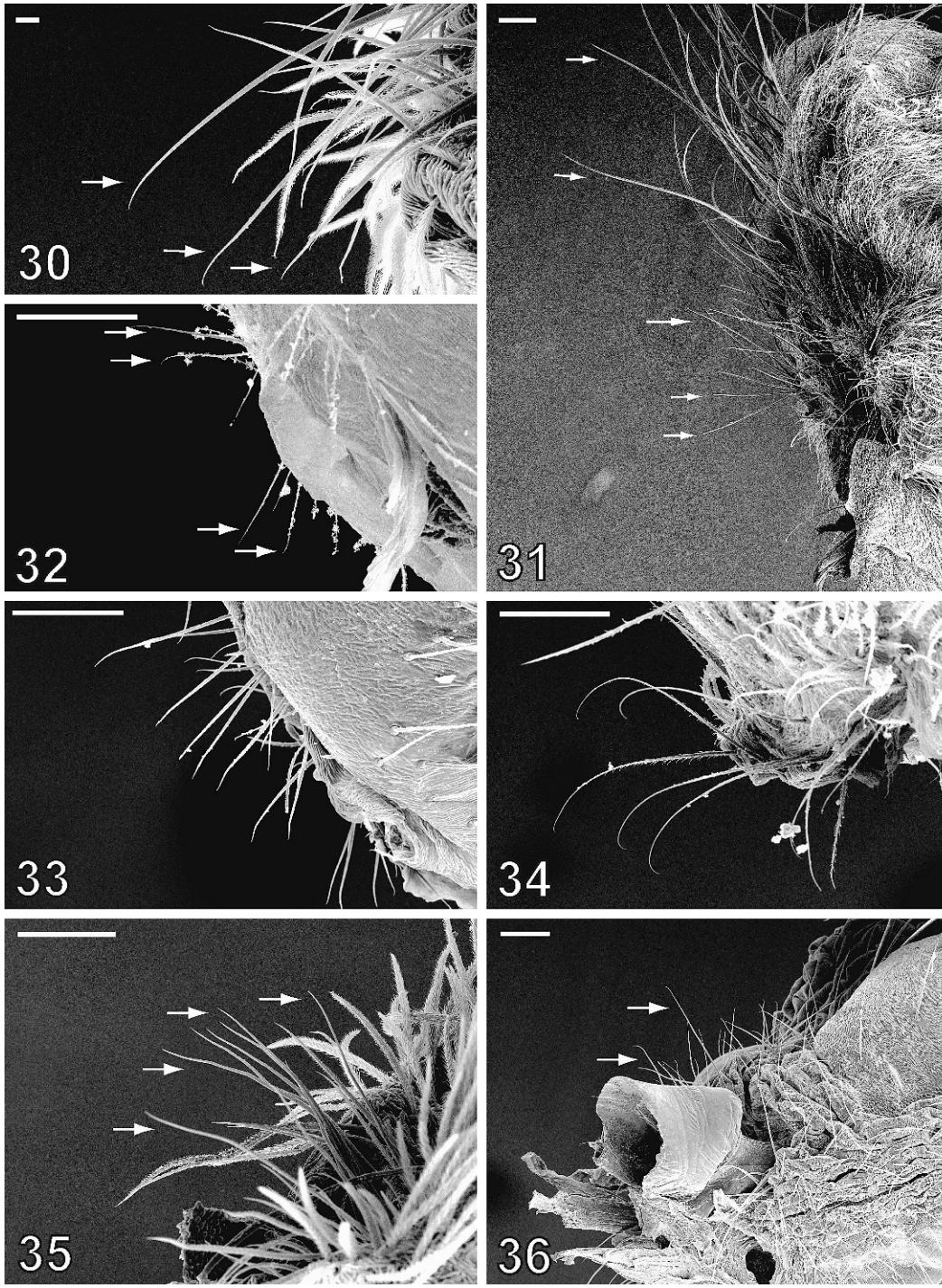


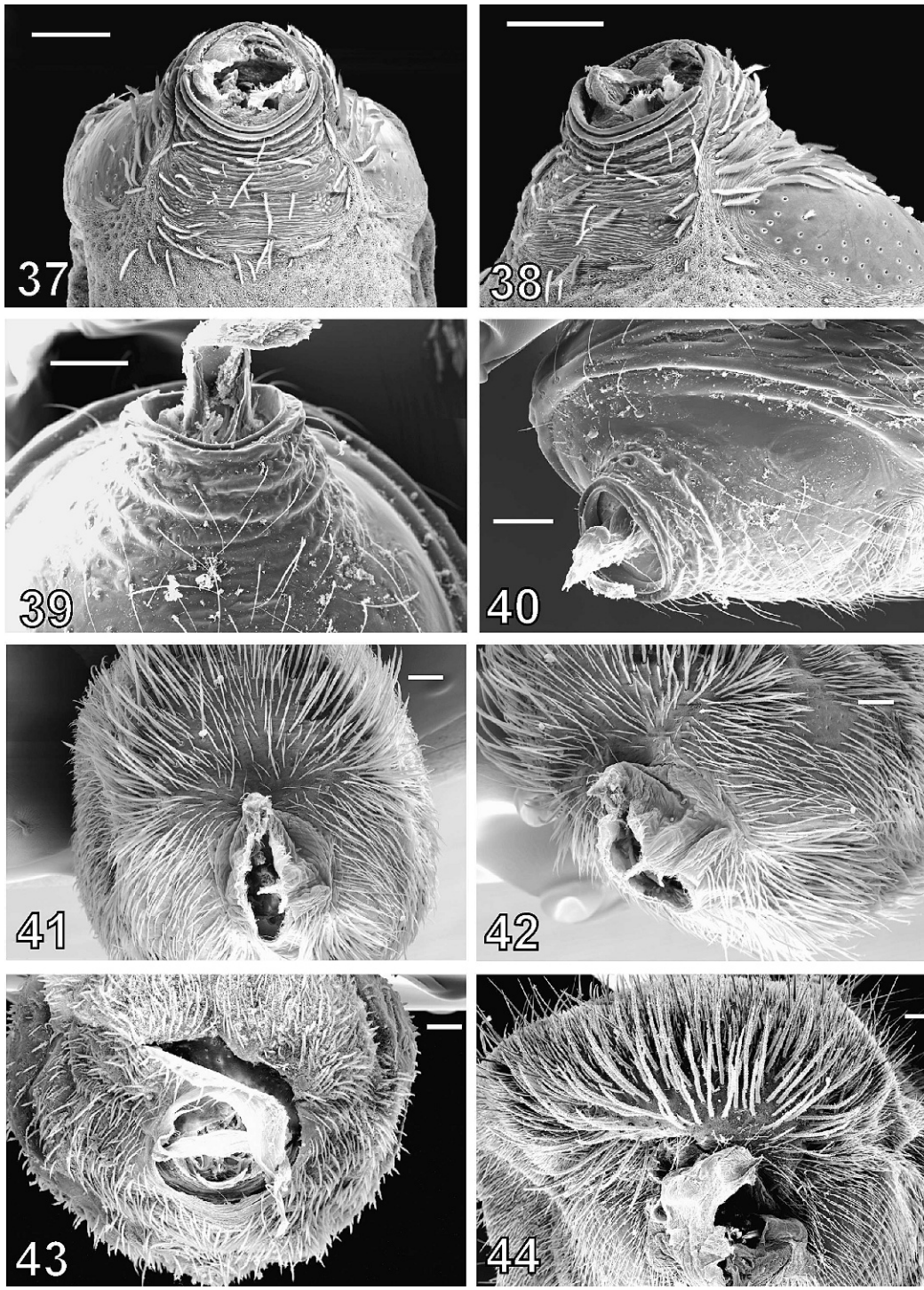
Figures 16–21.—Theridiidae females. 16, 18, 19, *Stemmops bicolor* O. Pickard-Cambridge 1894. 16. Abdomen ventral, arrows indicate EPS. 18. Area around pedicel, ventral view. 19. Area around pedicel, ectal view. 17. *Styposis selis*. Area around pedicel, ventral view. 20. *Selkirkiella magallanes* (Levi 1963). Area around pedicel and epigynum, ventral view. 21. *Selkirkiella* sp. Area around pedicel, ventral view. Scale bars = 100 μm.



Figures 22–29.—Orbiculariae males, stars and arrows indicate EPS and S-numbers their allocation to sectors (see Methods). 22, 23. *Pimoa breviata* (Pimoidae) male. 22. Ventral view. 23. Ectal view. 24. *Eidmanella pallida* (Nesticidae) male. Ectal view. 25. *Isicabu henriki* (Cyatholipidae). Ventral view. 26. *Mimetus interfector* (Mimetidae) male. Mesal view. 27. *Leucauge venusta* (Tetragnathidae) male abdomen. Ventral view. 28. *Nephila inaurata* (Nephilidae) male. 29. *Pronous tuberculifer* (Araneidae) male. Scale bars = 100 μm.



Figures 30–36.—Cribellate orbicularians and non-orbicularians, arrows indicate EPS. 30. *Deinopis* sp. (Deinopidae) male. 31. *Agelenopsis pennsylvanica* (Agelenidae) male. 32. *Oxyopes salticus* (Oxyopidae) male. 33. *Scytodes thoracica* (Scytodidae) male, with multiple EPS. 34. *Loxosceles deserta* (Sicariidae), male with a brush of bent-tipped EPS around the pedicel. 35. *Kukulcania hibernalis* (Filistatidae) male. Note that non-EPS abdominal setae are serrate or plumose (feathery). 36. *Hypochilus pococki* (Hypochilidae) male. Scale bars = 100 μm.



Figures 37–44.—Taxa where the EPS are clearly (37–40) or ambiguously absent (41–44). 37, 38. *Eriauchenius vadoni* (Archaeidae) male. 37. Ventral view. 38. Ectal view. 39, 40. *Chilenodes australis* (Malkaridae) male. 39. Ventral view. 40. Ectal view. Note that both *Archaea* and *Chilenodes* have modified (elongated) pedicels. 41, 42. *Pardosa* sp. (Lycosidae) male. 41. Ventral view. 42. Subectal view. 43. *Dictyna major* (Dictynidae) male. Ventral view. 44. *Gnaphosa parvula* (Gnaphosidae) male. Ventral view. Scale bars = 100 μm.

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