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Spinneret Morphology and the Phylogeny of Ground Spiders (Araneae, Gnaphosoidea)

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ABSTRACT

Scanning electron microscopy is used to survey the spinneret morphology of representatives of 50 genera of gnaphosoid spiders. Adult female gnaphosoids typically have five distinct spigot types. Two types, restricted to the anterior lateral spinnerets, presumably serve the piriform and major ampullate glands. Three other types, restricted to the posterior median and posterior lateral spinnerets, presumably serve the cylindrical, aciniform, and minor ampullate glands, although minor ampullate glands have not been reported to open on the posterior lateral spinnerets of other spiders. The family Gnaphosidae is redefined to include just those gnaphosoids in which the anterior lateral spinnerets bear greatly enlarged and widened piriform gland spigots. The family Prodidomidae is revalidated and expanded to include the former gnaphosid subfamilies Molycriinae and Anagraphidinae as well as the prodidomines and zimirines; as delimited, the prodidomids are united by piriform gland spigots with greatly elongated

bases accompanied by highly plumose setae. Gnaphosoids with piriform gland spigots lacking either type of modification are allocated to the Cithaeronidae, Gallieniellidae, Trochanteriidae, Ammoxenidae (which appear to have lost the piriform gland spigots), and Lamponidae, new rank (removed from the Gnaphosidae and elevated to familial status). The genera of the classical family Platoridae are transferred to either the Gnaphosidae (*Vectius* from South America) or Trochanteriidae (*Plator* from southern Asia and *Doliomalus* from Chile), and Platoridae is considered a junior synonym of Trochanteriidae. The Australasian genus *Rebilus* is transferred from the Hemicleinae (Gnaphosidae) to the Trochanteriidae. The South African genus *Drassodella* is transferred from the Gnaphosidae to the Gallieniellidae. The Iranian genus *Bobineus* is transferred from the Cithaeronidae to the Gnaphosidae and placed as a junior synonym of *Pterotricha*.

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INTRODUCTION

Spiders of the family Gnaphosidae have generally been recognized primarily by spinneret modifications; the anterior lateral spinnerets are enlarged, cylindrical (rather than conical) in shape, widely separated, and heavily sclerotized. Despite the importance of spinneret characters in defining the group, relatively little attention has been paid to the details of spinneret or silk gland morphology in the Gnaphosidae or any of the related families currently assigned to the superfamily Gnaphosoidea. In a recent summary, by family, of the literature on spider silk glands and spinnerets, Kooor (1977: Table 4) noted no studies of gnaphosoids. Aside from Dalmás' (1921: 241, figs. 6–14) analysis of spinneret characters in some gnaphosine genera, there seems to have been little, if any, significant material published since the classic, century-old study of Apstein (1889), who included just two species of gnaphosids in his broad survey of spider silk glands.

A recent paper by Coddington (1989), however, has shown that much systematic information can be obtained from external spinneret morphology, even in the absence of histological and histochemical characterizations of the silk glands themselves, and that (with careful selection and preparation) normal museum specimens can be used for scanning electron microscopic surveys of spinneret morphology. Specimens collected in pitfall traps are often ideal for this purpose, as their spinnerets and spigots are usually fully extended. In this paper, the spinnerets of a wide variety of gnaphosoid genera are surveyed. Except where noted, the micrographs presented were taken from adult females, because they have the fullest complement of spigot types. Entire abdomens (or just the posterior portions in larger species) were ultrasonicated and critical point dried before being coated for SEM observation. The micrographs have the spinnerets positioned with their anterior edge at the top of the image; because they have been reduced about 25 percent for publication, the magnification figures supplied in the legends provide only relative scale information.

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seum of Natural History helped immensely with specimen selection, preparation, and illustration. Peter Croeser (Natal Museum, Pietermaritzburg), Eryn Griffin (State Museum, Windhoek, Namibia), Rudy Jocqué (Musée Royal de l'Afrique Centrale, Tervuren), John Murphy (Hampton, England), Rowley Snazell (Institute of Terrestrial Ecology, Wareham, England), and Song Daxiang (Institute of Zoology, Academia Sinica, Beijing) kindly supplied specimens of rare taxa for SEM examination. Mark Harvey (Western Australian Museum, Perth) generously examined numerous specimens of Australian Hemicloecinae to test the accuracy of the revised classification suggested below. Helpful comments on a draft of the manuscript were received from Jonathan Coddington and Charles Griswold (National Museum of Natural History, Smithsonian Institution), Valerie Davies and Robert Raven (Queensland Museum), Eryn Griffin, Mark Harvey, Rudy Jocqué, Jacqueline Kooor (Muséum National d'Histoire Naturelle, Paris), John Murphy, and Darrell Ubick (California Academy of Sciences).

GNAPHOSID SPINNERET
MORPHOLOGY

Before discussing the differences detected among gnaphosoids and their relatives, and their systematic implications, it seems best to describe the spinneret morphology of a typical gnaphosid. These spiders have only three pairs of spinnerets; the anterior median spinnerets are represented, at most, by a patch of relatively densely clustered setae that are presumably remnants of the colulus. The anterior lateral spinnerets (ALS) and the posterior median spinnerets (PMS) are unisegmented; although sclerotized remnants of a plesiomorphic, separate distal segment still survive on the ALS of some gnaphosoid families, the cuticle of the ALS tip is entirely unsclerotized in true gnaphosids. The posterior lateral spinnerets (PLS) generally have a sclerotized tip representing the distal segment; that tip is usually very short, and seems never to be longer than one-fourth of the proximal segment length.

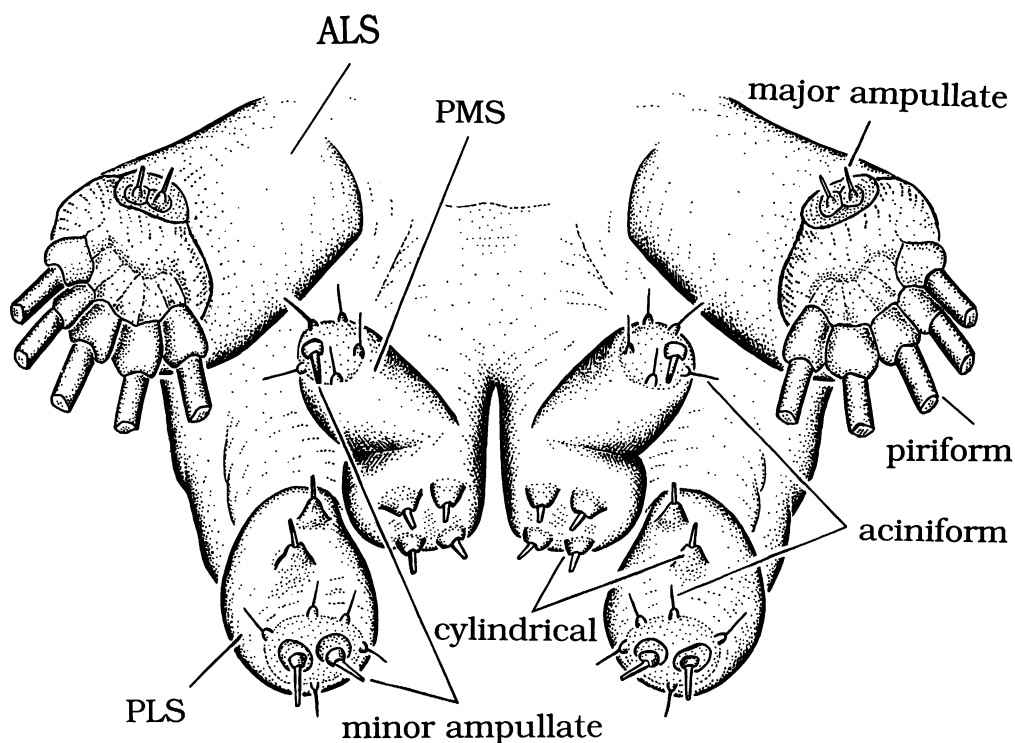


Fig. 1. Spinnerets and spigots of a generalized adult female gnaphosid, showing position of the anterior lateral (ALS), posterior median (PMS), and posterior lateral (PLS) spinneret pairs, along with the distributions of spigots presumed to serve the major ampullate, piriform, cylindrical, aciniform, and minor ampullate glands.

Five types of spigots can be discerned in a typical adult female gnaphosid (fig. 1). The classical names of silk gland types will be used here to refer to these spigot types, but the reader is cautioned that until much more histological work is done on gnaphosoids, predictions about gland characteristics drawn from spigot morphology may prove quite misleading. Running this risk, however, seems preferable to inventing an entirely new series of descriptors referring only to spigots.

The ALS bear two types of spigots. Proximally, a small anteromedian plate near the distal rim of the sclerotized spinneret tube bears two small, short spigots that correspond in their position and morphology with spigots serving the major ampullate glands in other spiders (Coddington, 1989). The spinneret tip itself is encircled by a fringe of enormously enlarged spigots of a characteristic shape, with a widened base, flattened and longitudinally ridged shaft, and large, slitlike opening. Ap-

stein (1889) identified these spigots as serving the tubuliform (= cylindrical) glands, but admitted that his preparations were defective, and that these spigots differ significantly in morphology from those on the PMS and PLS that he also identified as serving the "tubuliform" glands. Apstein's conclusion seems highly unlikely; these spigots are present in both sexes (see figs. 50, 53), whereas in other spiders cylindrical glands are used in egg case construction, occur only in adult females, and open on the PMS and PLS only (Kovoor, 1977, 1987; Coddington, 1989). The highly modified gnaphosid spigots probably serve the piriform glands instead, as in other spiders the numerous piriform gland spigots are in this position on the ALS, and Kovoor (1987: 180) reported that the piriform glands of gnaphosids "are less numerous, but much larger than usual," as is also true of these spigots.

The relatively unsclerotized cuticle of the

TABLE 1
Taxa Figured

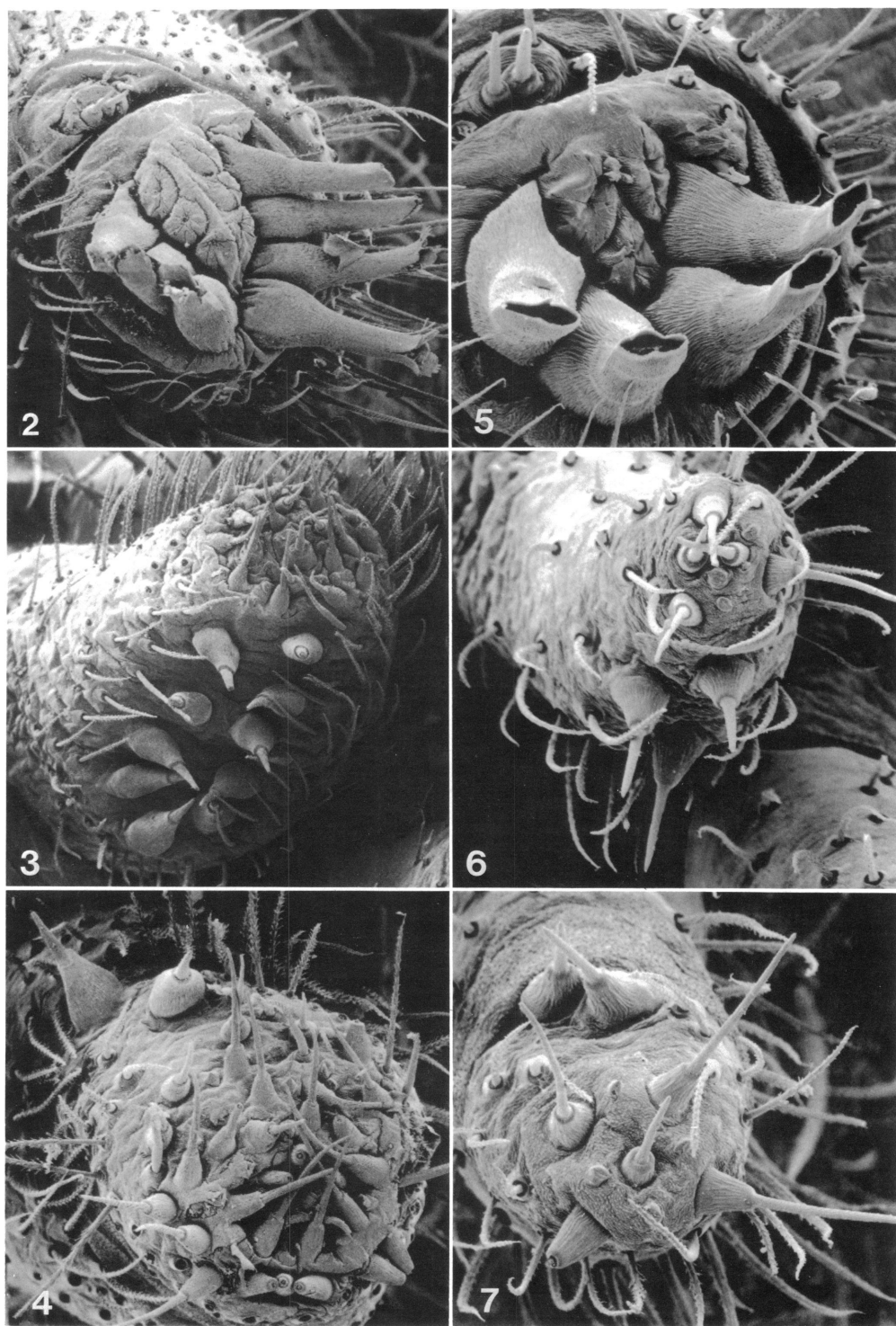
Taxa examined, their previous familial or subfamilial position, and the figure numbers of their spinneret micrographs. No generally accepted subfamilial classification exists for the Gnaphosidae, and the groupings used are a combination of traditional and more recent concepts. The subfamily Drassodinae is used merely as a "wastebasket" group (i.e., for those gnaphosids that do not obviously belong to other subfamilies).

Cithaeronidae	
<i>Cithaeron delimbatus</i> Strand	170-172
Gallieniellidae	
<i>Gallieniella mygaloides</i> Millot	158-160
<i>Legendrena angavokely</i> Platnick	161-163
Undescribed Australian genus	167-169
Ammoxenidae	
<i>Ammoxenus psammodromus</i> Simon	149-152
Undescribed African genus	153-157
Trochanteriidae	
<i>Platyoides walteri</i> (Karsch)	134-136
Platoridae	
<i>Doliomalus cimicoides</i> (Nicolet)	137-139
<i>Plator</i> sp.	140-142
<i>Vectius niger</i> (Simon)	89-91
Gnaphosidae: Hemicloinae	
<i>Hemicloea</i> sp.	147
<i>Rebilus</i> sp.	143-146
Gnaphosidae: Lamponinae	
<i>Lampona</i> sp.	173-175
Gnaphosidae: Prodidominae	
<i>Neozimiris pubescens</i> (Banks)	122-127
<i>Prodidomus dalmasi</i> Berland	128-133
<i>Zimirina</i> sp.	118-121
Gnaphosidae: Anagraphidinae	
<i>Lygromma dybasi</i> Platnick and Shadab	98-102
<i>Theuma</i> sp.	103-107
<i>Tivodrassus farias</i> Platnick and Shadab	92-94
<i>Tricongius amazonicus</i> Platnick and Höfer	95-97
Gnaphosidae: Molycriinae	
<i>Molycria mammosa</i> O.P.-Cambridge	108-112
<i>Myandra</i> sp.	113-117
Gnaphosidae: Micariinae	
<i>Micaria aenea</i> Thorell	86, 88
<i>Micaria pulicaria</i> (Sundevall)	87

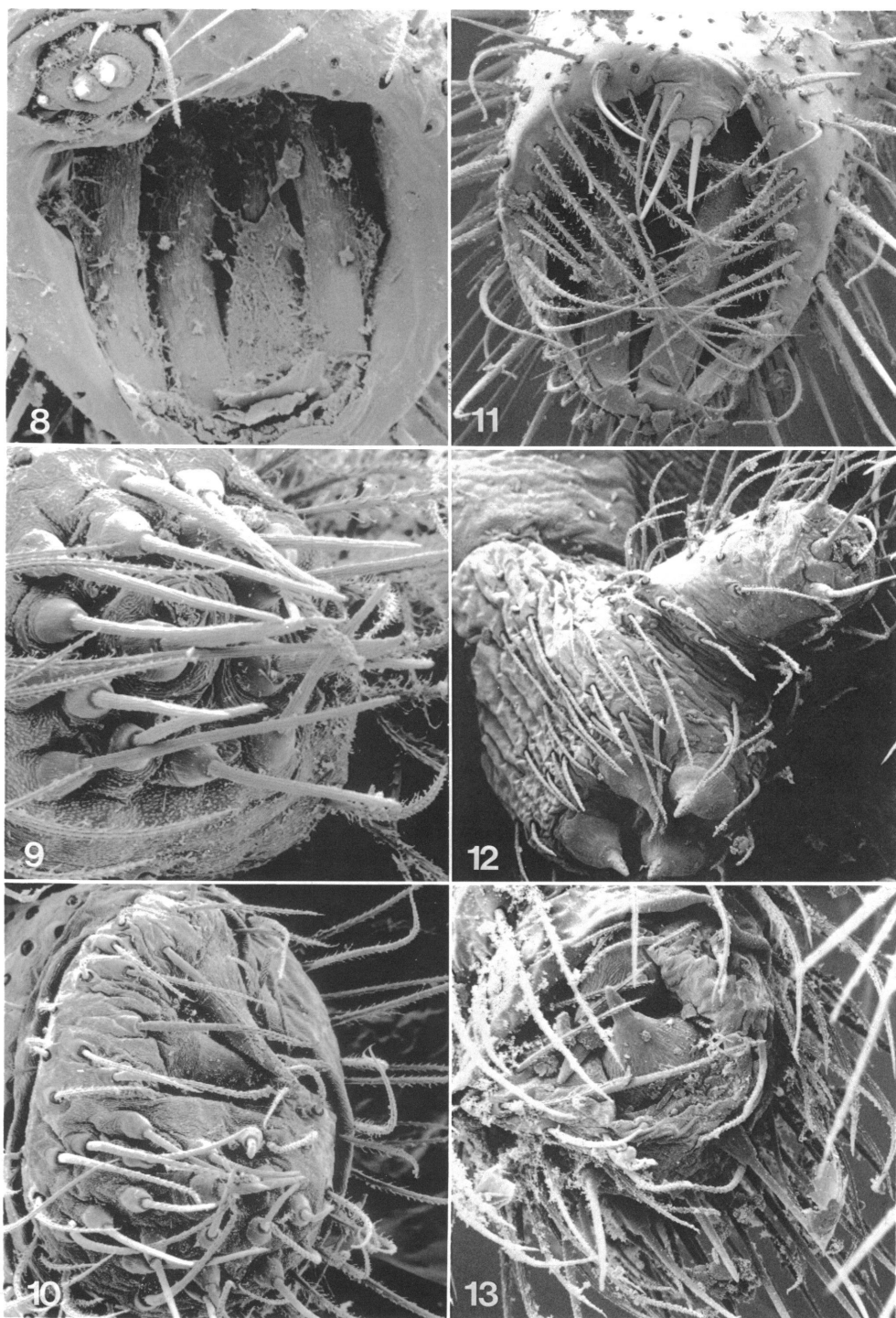
TABLE 1—(Continued)

Gnaphosidae: Drassodinae	
<i>Apodrassodes araucanius</i> (Chamberlin)	62-64
<i>Apopyllus silvestrii</i> (Simon)	65-67
<i>Drassodella septemmaculata</i> (Strand)	164-166
<i>Drassodes saccatus</i> (Emerton)	68-70
<i>Haplodrassus signifer</i> (C. L. Koch)	71-73
<i>Hypodrassodes</i> sp.	74-76, 148
<i>Orodassus coloradensis</i> (Emerton)	77-79
<i>Rachodrassus exlineae</i> Platnick and Shadab	80-82
<i>Synaphosus syntheticus</i> (Chamberlin)	83-85
Gnaphosidae: Herpyllinae	
<i>Cesonia bilineata</i> (Hentz)	50-55
<i>Herpyllus ecclesiasticus</i> Hentz	47-49
<i>Nodocion floridanus</i> (Banks)	56-58
<i>Sergiolus minutus</i> (Banks)	59-61
Gnaphosidae: Zelotinae	
<i>Camillina elegans</i> (Bryant)	35-37
<i>Drassyllus depressus</i> (Emerton)	38-40
<i>Urozelotes rusticus</i> (L. Koch)	41-43
<i>Zelotes fratris</i> Chamberlin	44-46
Gnaphosidae: Echeminae	
<i>Echemoides tofo</i> Platnick and Shadab	26-28
<i>Scopoides naturalisticum</i> (Chamberlin)	29-31
<i>Zimiromus muchmorei</i> Platnick and Shadab	32-34
Gnaphosidae: Laroniinae	
<i>Callilepis imbecilla</i> (Keyserling)	20-22
<i>Eilica bicolor</i> Banks	23-25
Gnaphosidae: Gnaphosinae	
<i>Asemesthes</i> sp.	14-16
<i>Gnaphosa parvula</i> Banks	2-4
<i>Gnaphosa sericata</i> (L. Koch)	5-7
<i>Nomisia exornata</i> (C. L. Koch)	8-10
<i>Pterotricha</i> sp.	11-13
<i>Upognampa</i> sp.	17-19

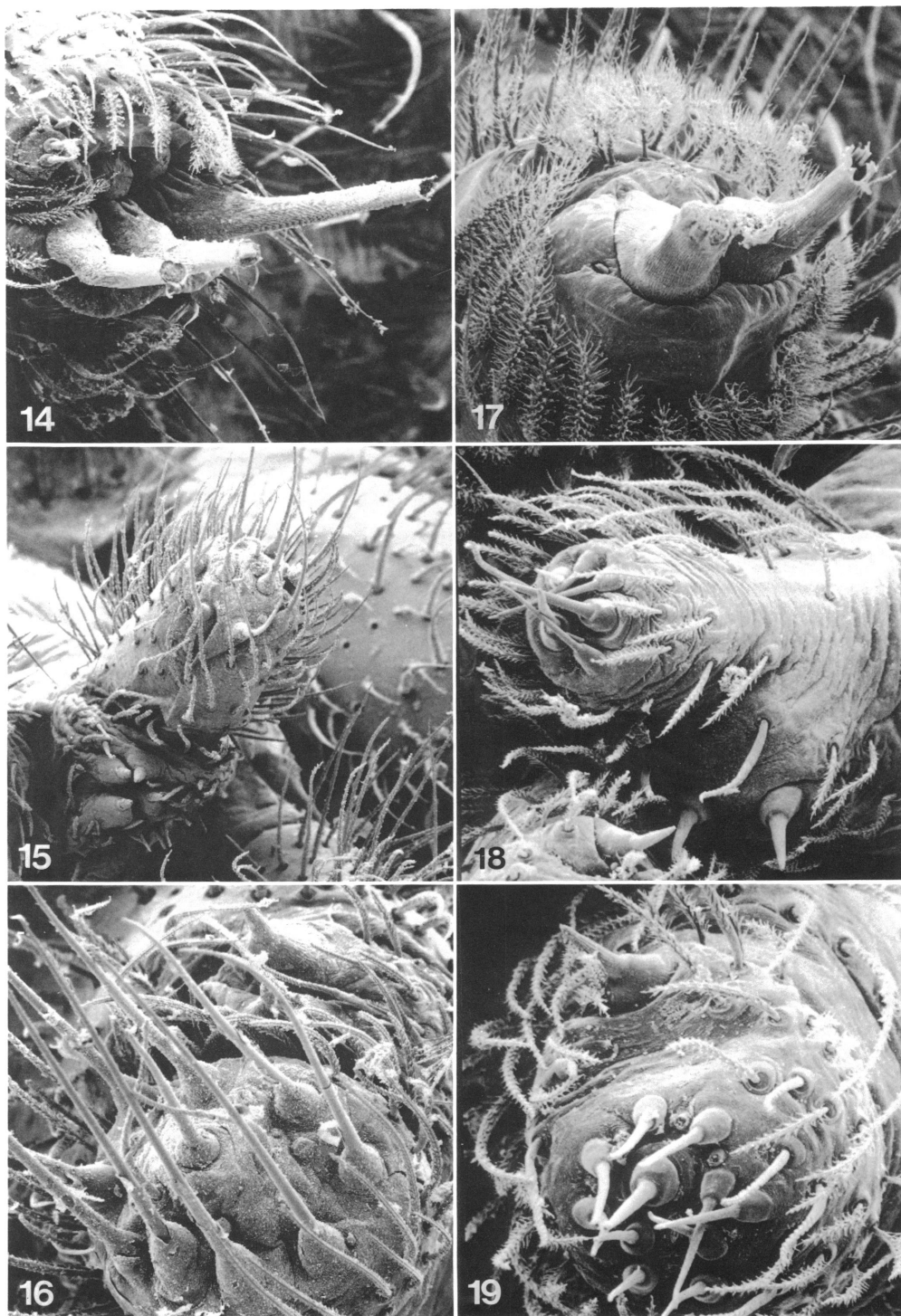
ALS tip is usually divided into large, discrete areas with a crevice at their center (as in figs. 44, 71); these seem to be the "tartipores" of Shear et al. (1989), representing the positions of the piriform gland spigots during the previous instar. Because the number of tartipores is typically one less than the number of adult piriform gland spigots, it is possible



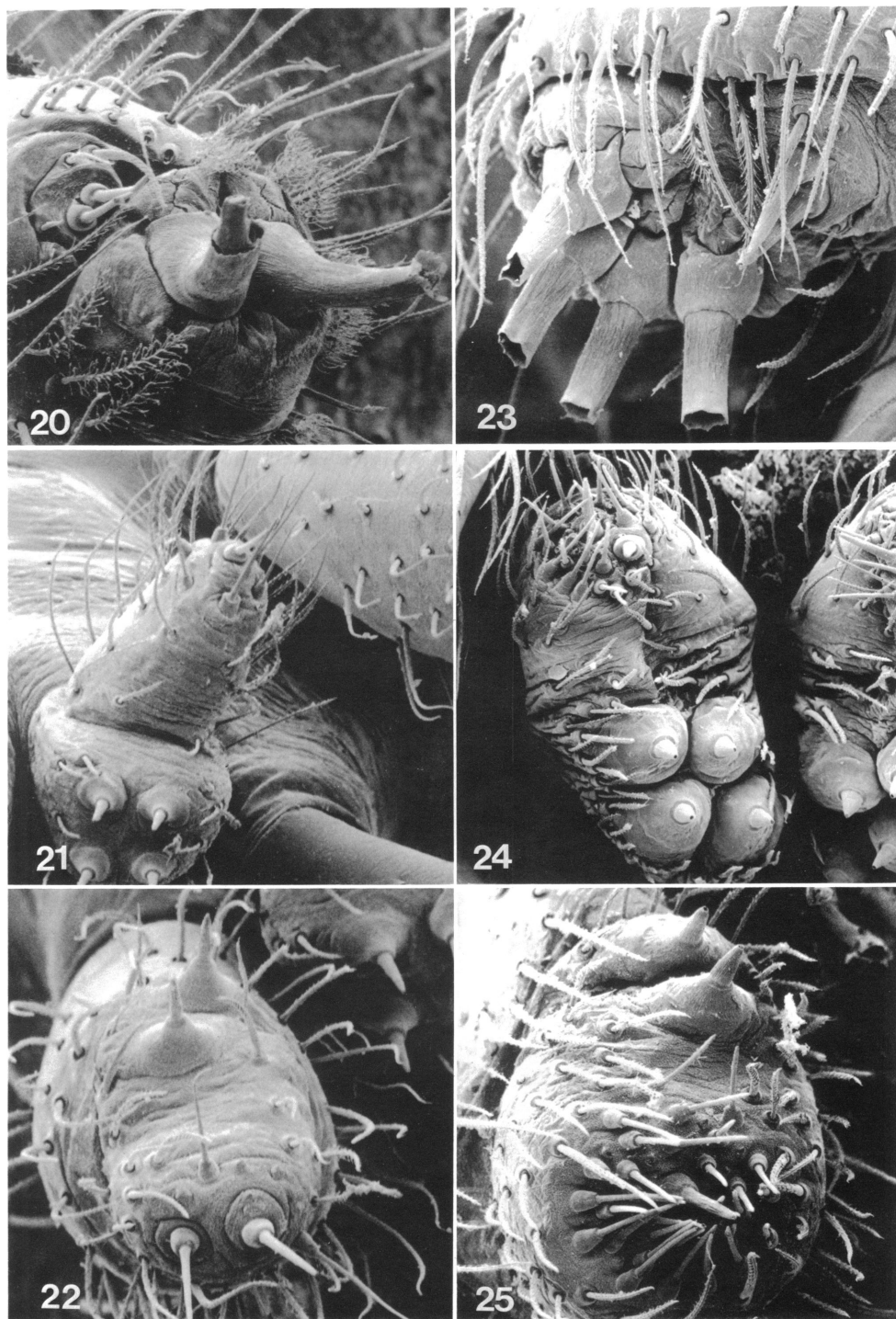
Figs. 2-7. Spinnerets of Gnaphosinae (Gnaphosidae). 2-4. *Gnaphosa parvula* Banks. 5-7. *G. sericata* (L. Koch). 2, 5. ALS, 298 \times , 778 \times . 3, 6. PMS, 328 \times , 680 \times . 4, 7. PLS, 452 \times , 784 \times .



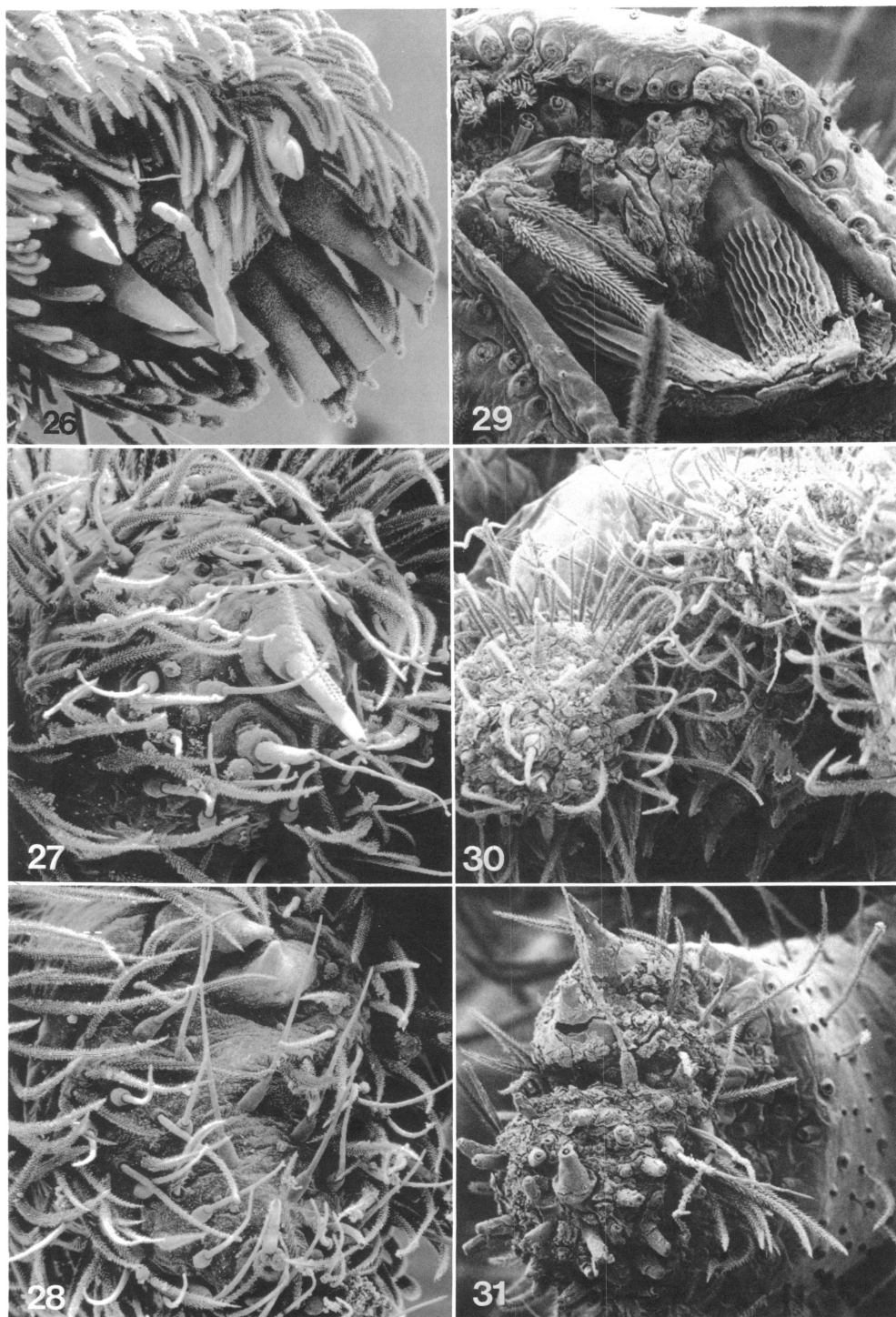
Figs. 8–13. Spinnerets of Gnaphosinae (Gnaphosidae). 8–10. *Nomisia exornata* (C. L. Koch). 11–13. *Pterotricha* sp. 8, 11. ALS, 587 \times , 253 \times . 9, 12. PMS (distal spigots only in fig. 9), 1044 \times , 300 \times . 10, 13. PLS, 554 \times , 426 \times .



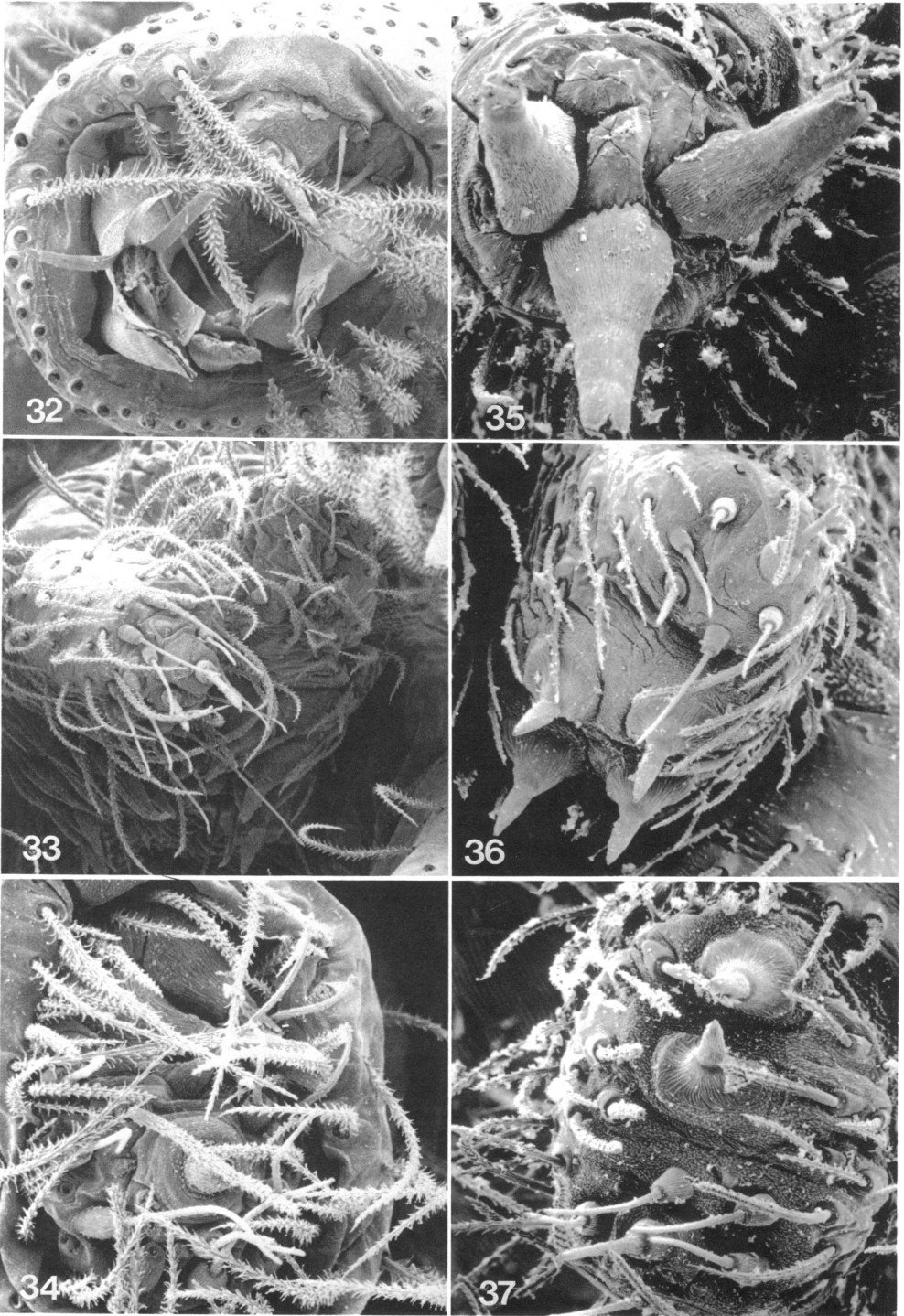
Figs. 14–19. Spinnerets of Gnaphosinae (Gnaphosidae). 14–16. *Asemesthes* sp. 17–19. *Upognampa* sp. 14, 17. ALS, 253 \times , 641 \times . 15, 18. PMS, 245 \times , 662 \times . 16, 19. PLS, 500 \times , 896 \times .



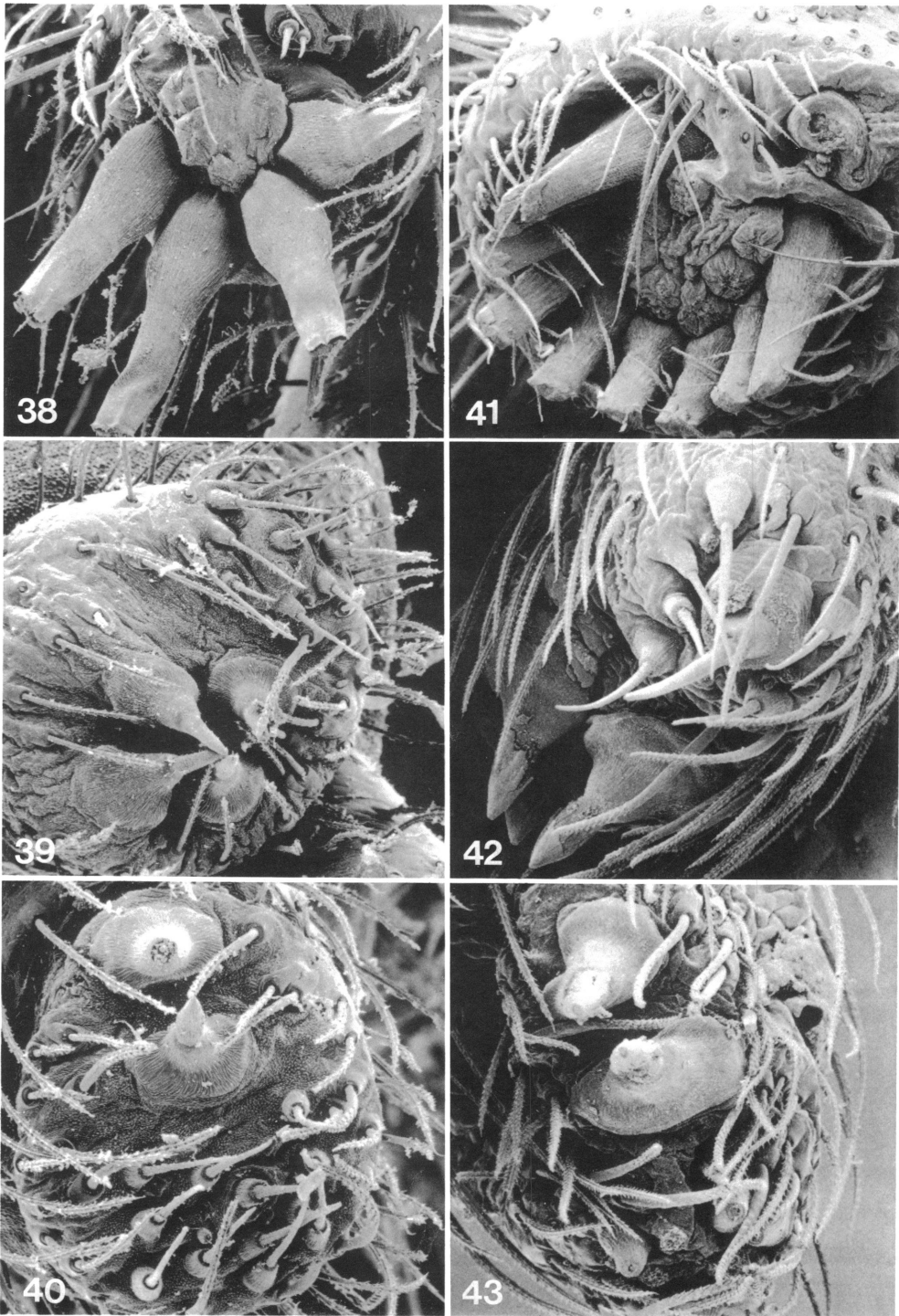
Figs. 20–25. Spinnerets of Laroniinae (Gnaphosidae). 20–22. *Callilepis imbecilla* (Keyserling). 23–25. *Eilica bicolor* Banks. 20, 23. ALS, 617 \times , 545 \times . 21, 24. PMS, 408 \times , 332 \times . 22, 25. PLS, 575 \times , 500 \times .



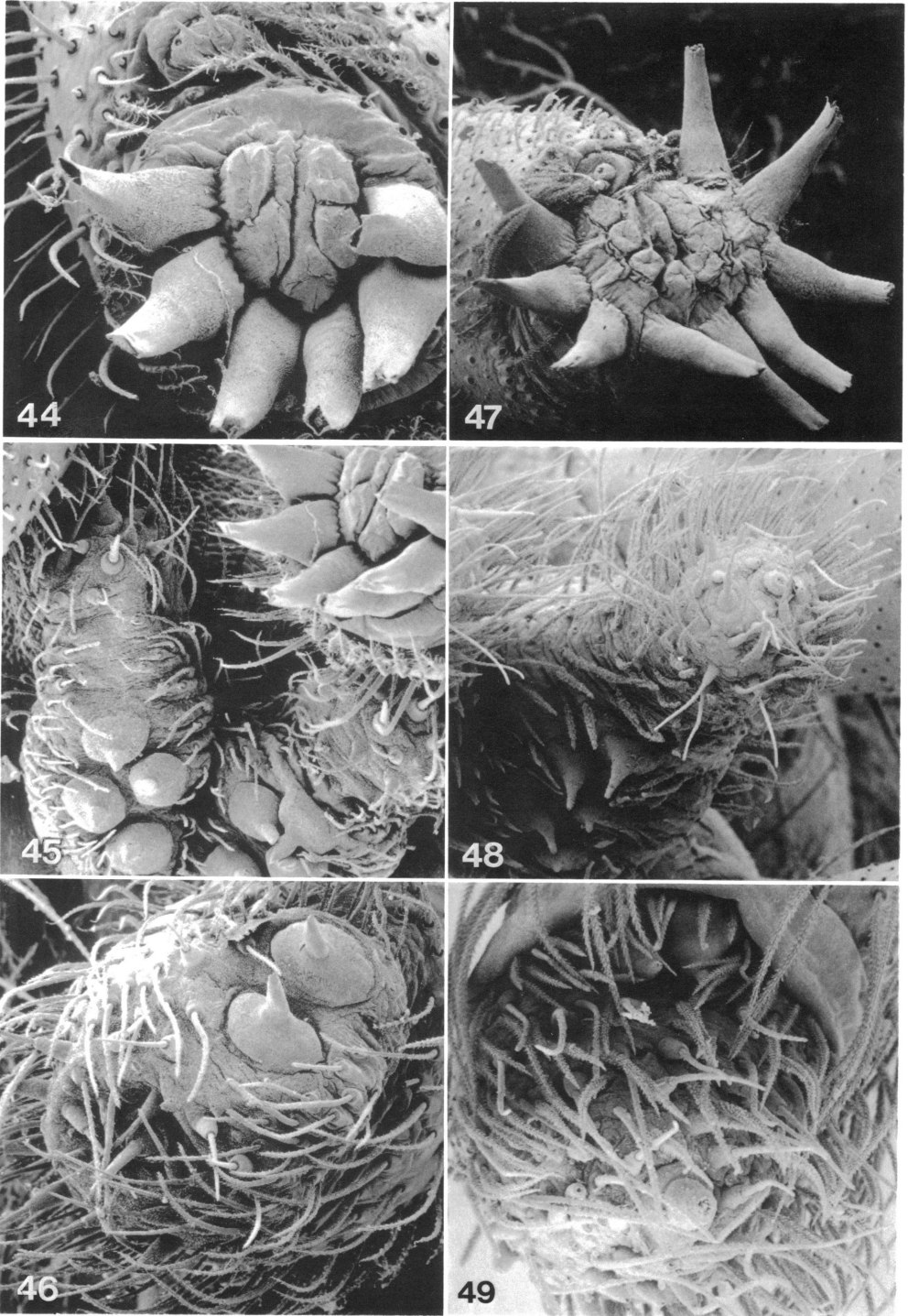
Figs. 26–31. Spinnerets of Echeminae (Gnaphosidae). 26–28. *Echemoides tofo* Platnick and Shadab. 29–31. *Scopoides naturalisticum* (Chamberlin). 26, 29. ALS, 176 \times , 542 \times . 27, 30. PMS, 414 \times , 284 \times . 28, 31. PLS, 340 \times , 378 \times .



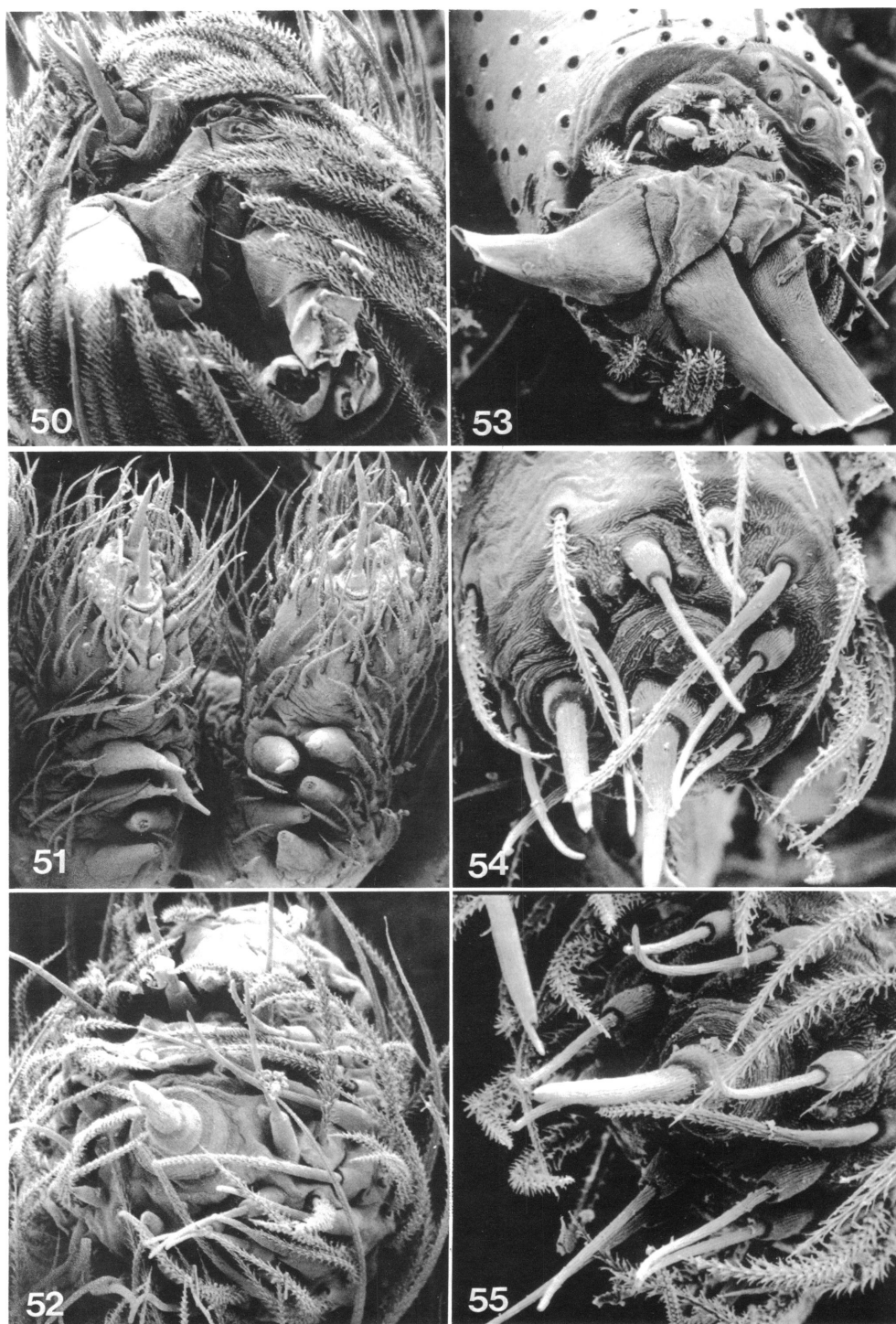
Figs. 32-37. Spinnerets of Echeminae and Zelotinae (Gnaphosidae). 32-34. *Zimiromus muchmorei* Platnick and Shadab. 35-37. *Camillina elegans* (Bryant). 32, 35. ALS, 617 \times , 662 \times . 33, 36. PMS, 438 \times , 725 \times . 34, 37. PLS, 876 \times , 880 \times .



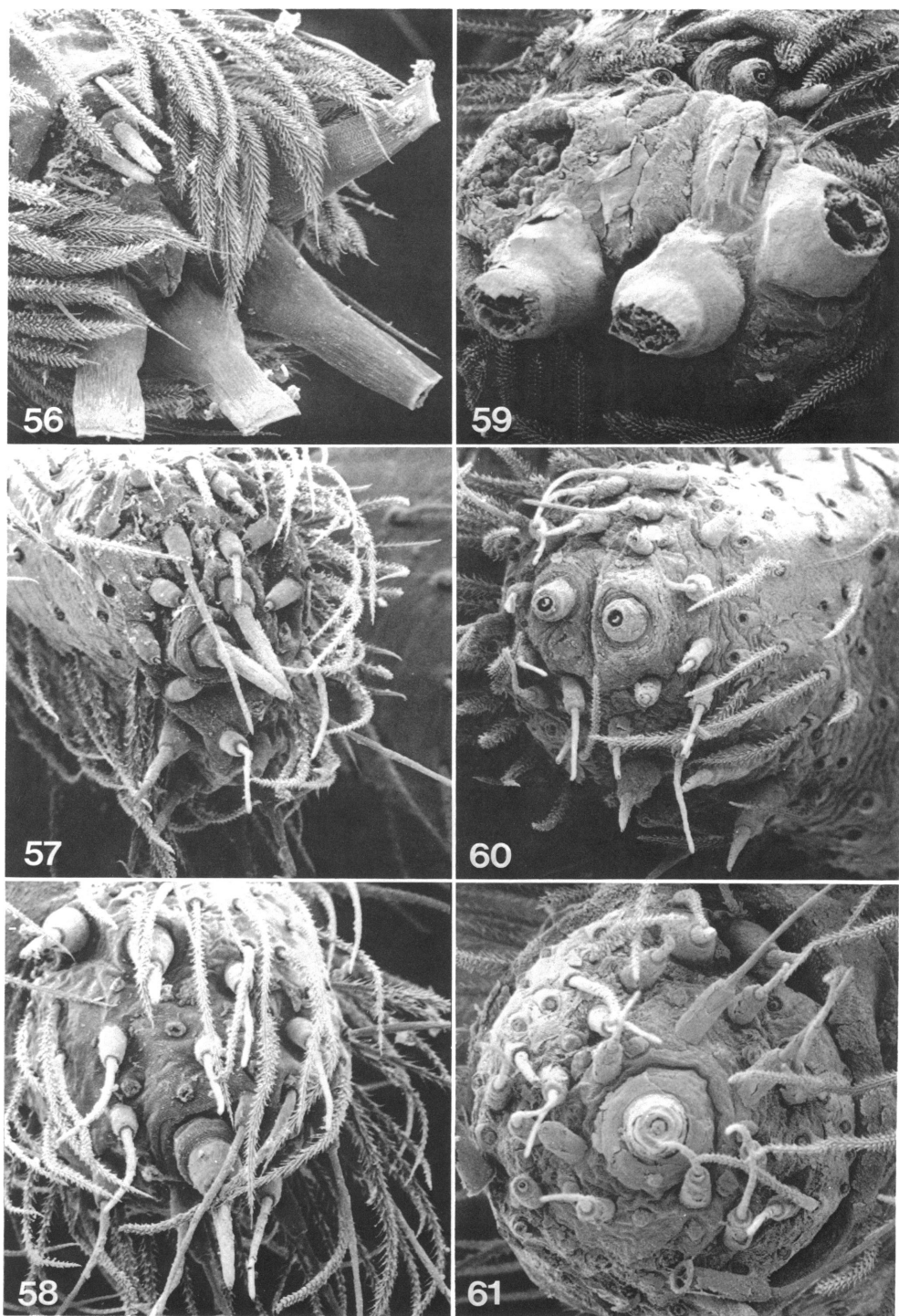
Figs. 38–43. Spinnerets of Zelotinae (Gnaphosidae). 38–40. *Drassyllus depressus* (Emerton). 41–43. *Urozelotes rusticus* (L. Koch). 38, 41. ALS, 569 \times , 288 \times . 39, 42. PMS, 602 \times , 438 \times . 40, 43. PLS, 761 \times , 500 \times .



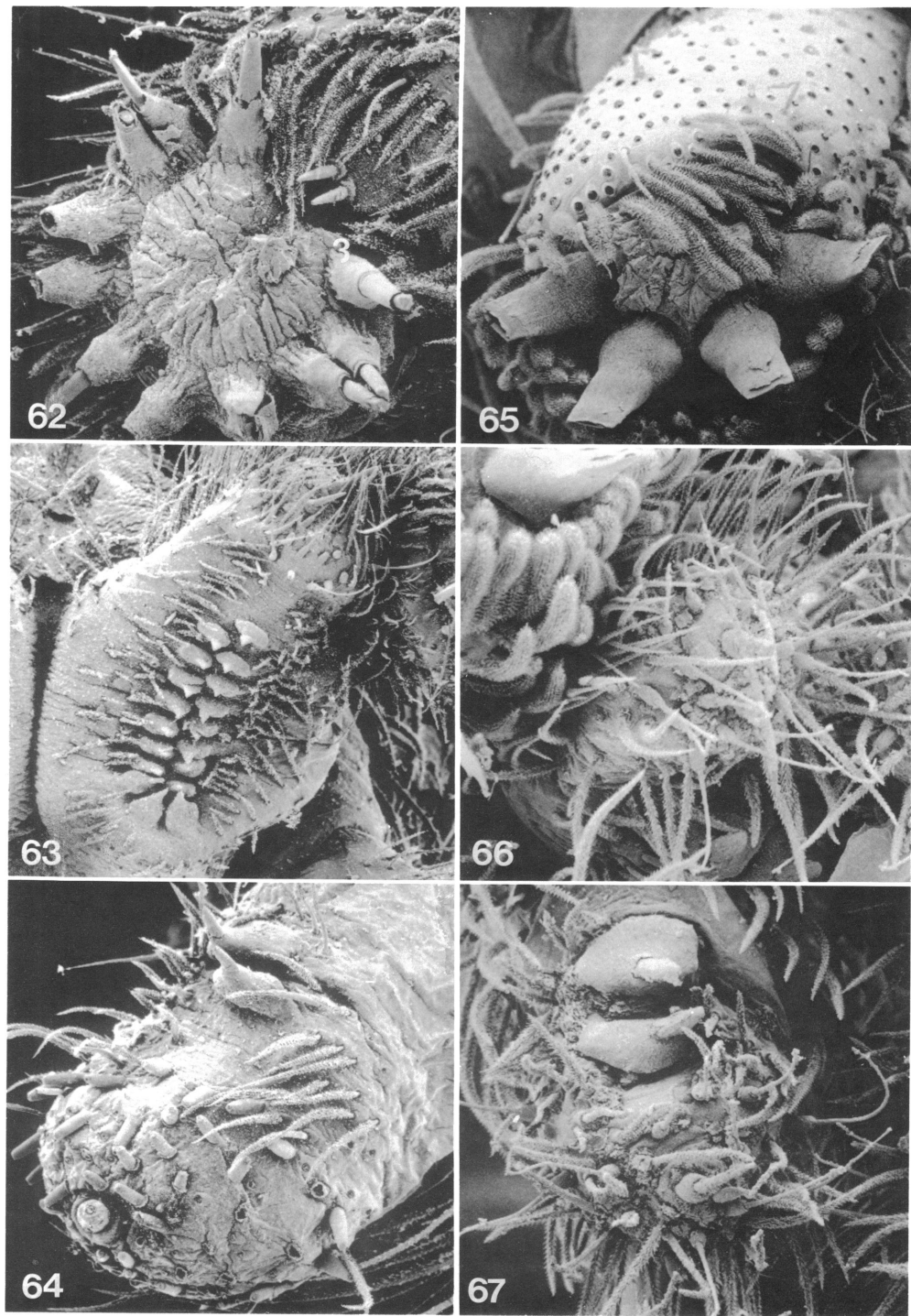
Figs. 44–49. Spinnerets of Zelotinae and Herpyllinae (Gnaphosidae). 44–46. *Zelotes fratris* Chamberlin. 47–49. *Herpyllus ecclesiasticus* Hentz. 44, 47. ALS, 400 \times , 166 \times . 45, 48. PMS, 249 \times , 200 \times . 46, 49. PLS, 362 \times , 388 \times .



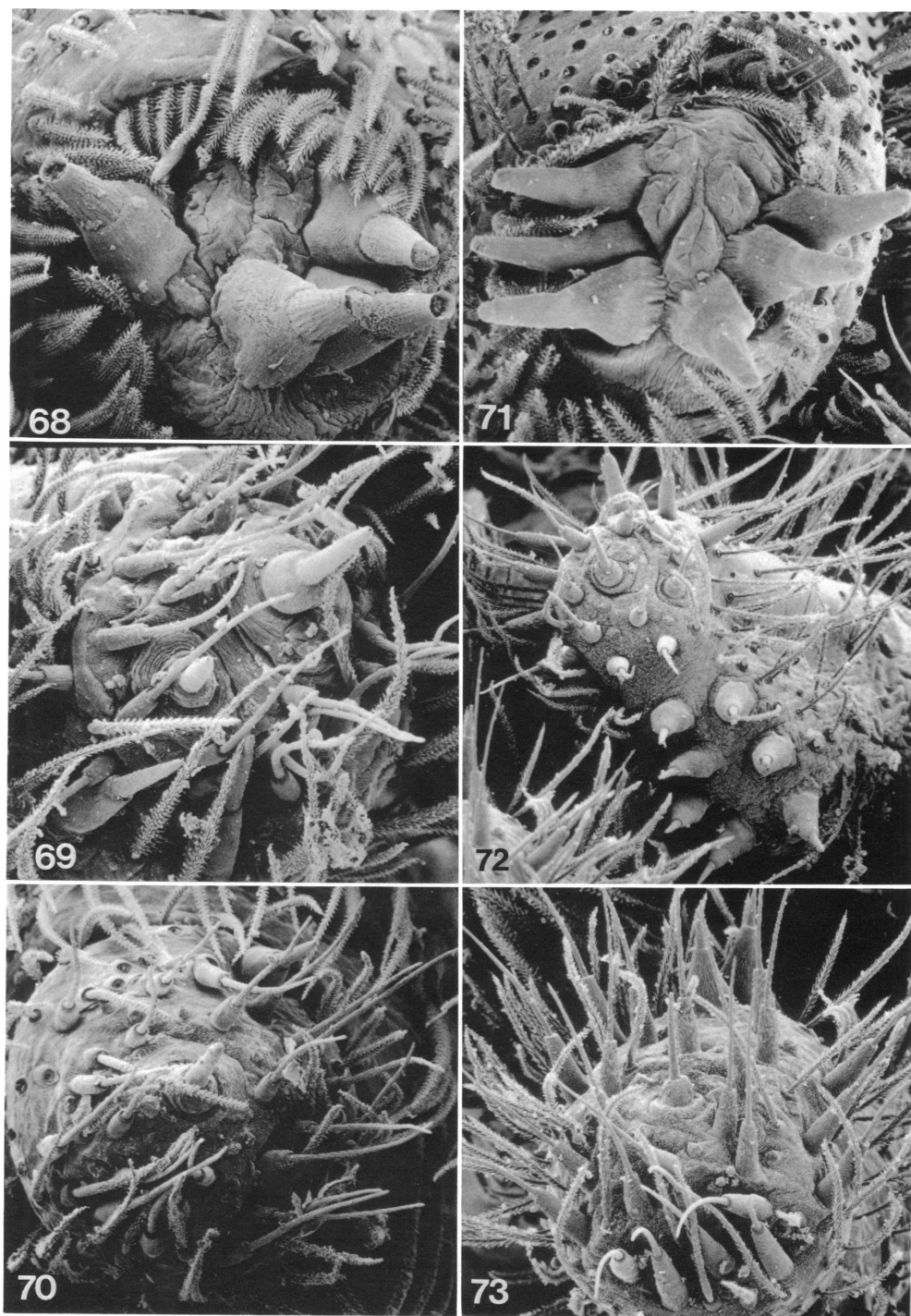
Figs. 50–55. Spinnerets of Herpyllinae (Gnaphosidae). 50–52. *Cesonia bilineata* (Hentz), female. 53–55. Same, male. 50, 53. ALS, 500 \times , 560 \times . 51, 54. PMS, 252 \times , 1089 \times . 52, 55. PLS, 563 \times , 1114 \times .



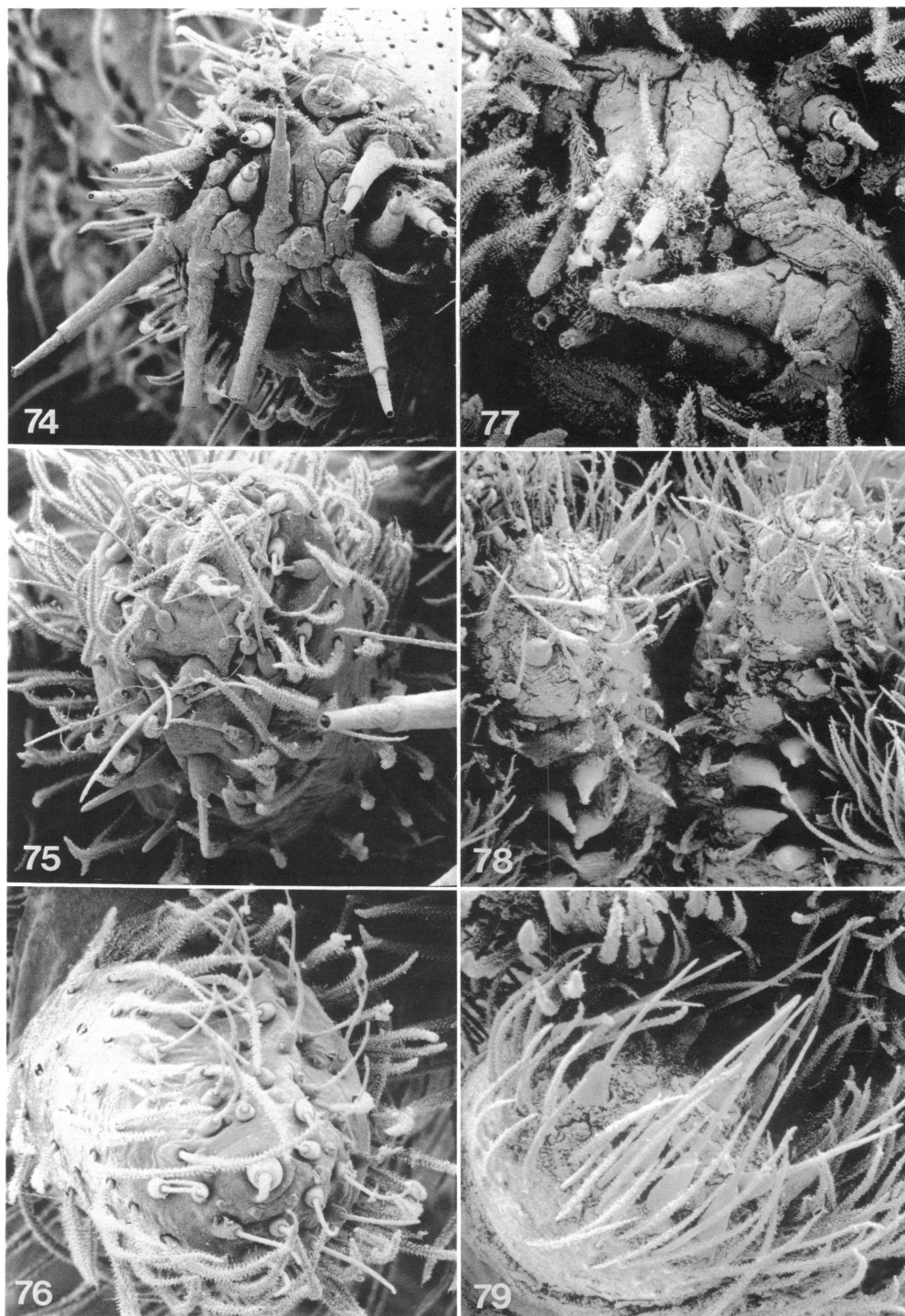
Figs. 56–61. Spinnerets of Herpyllinae (Gnaphosidae). 56–58. *Nodocion floridanus* (Banks). 59–61. *Sergiolus minutus* (Banks). 56, 59. ALS, 454 \times , 644 \times . 57, 60. PMS, 563 \times , 560 \times . 58, 61. PLS, 602 \times , 716 \times .



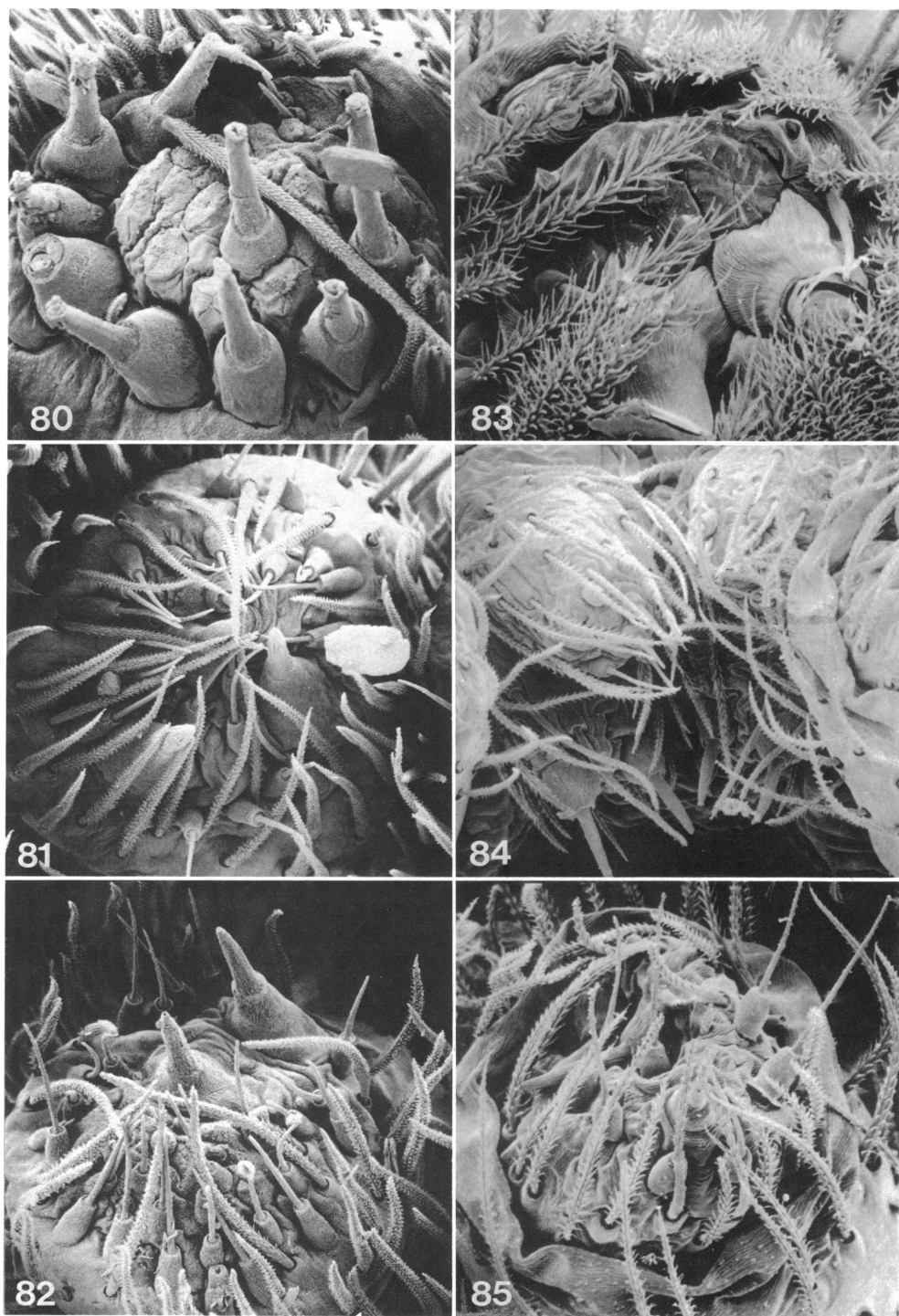
Figs. 62–67. Spinnerets of Drassodinae (Gnaphosidae). 62–64. *Apodrassodes araucanius* (Chamberlin). 65–67. *Apopyllus silvestrii* (Simon). 62, 65. ALS, 231×, 292×. 63, 66. PMS, 131×, 386×. 64, 67. PLS, 252×, 500×.



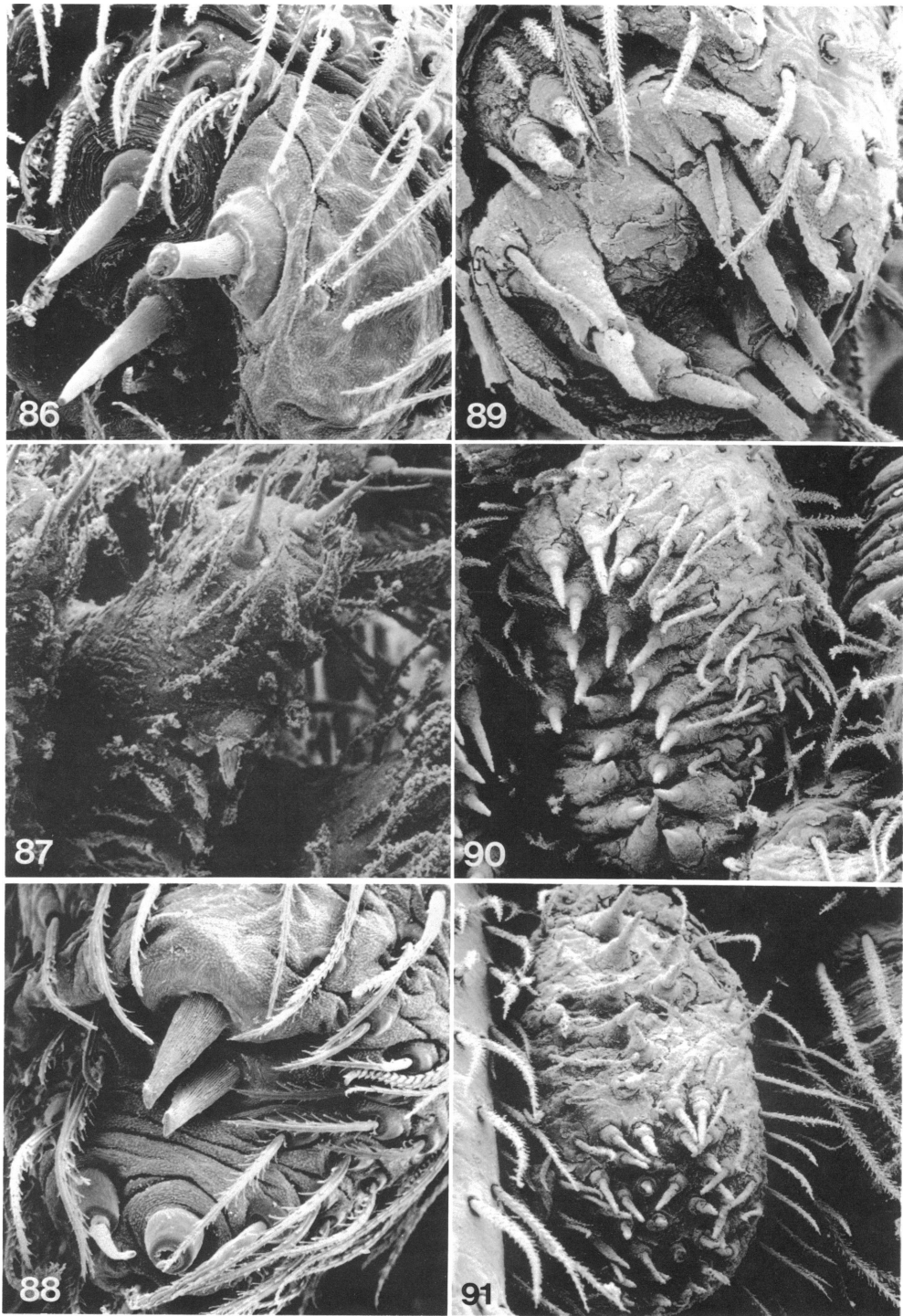
Figs. 68–73. Spinnerets of Drassodinae (Gnaphosidae). 68–70. *Drassodes saccatus* (Emerton). 71–73. *Haplodrassus signifer* (C. L. Koch). 68, 71. ALS, 500 \times , 398 \times . 69, 72. PMS, 617 \times , 344 \times . 70, 73. PLS, 500 \times , 430 \times .



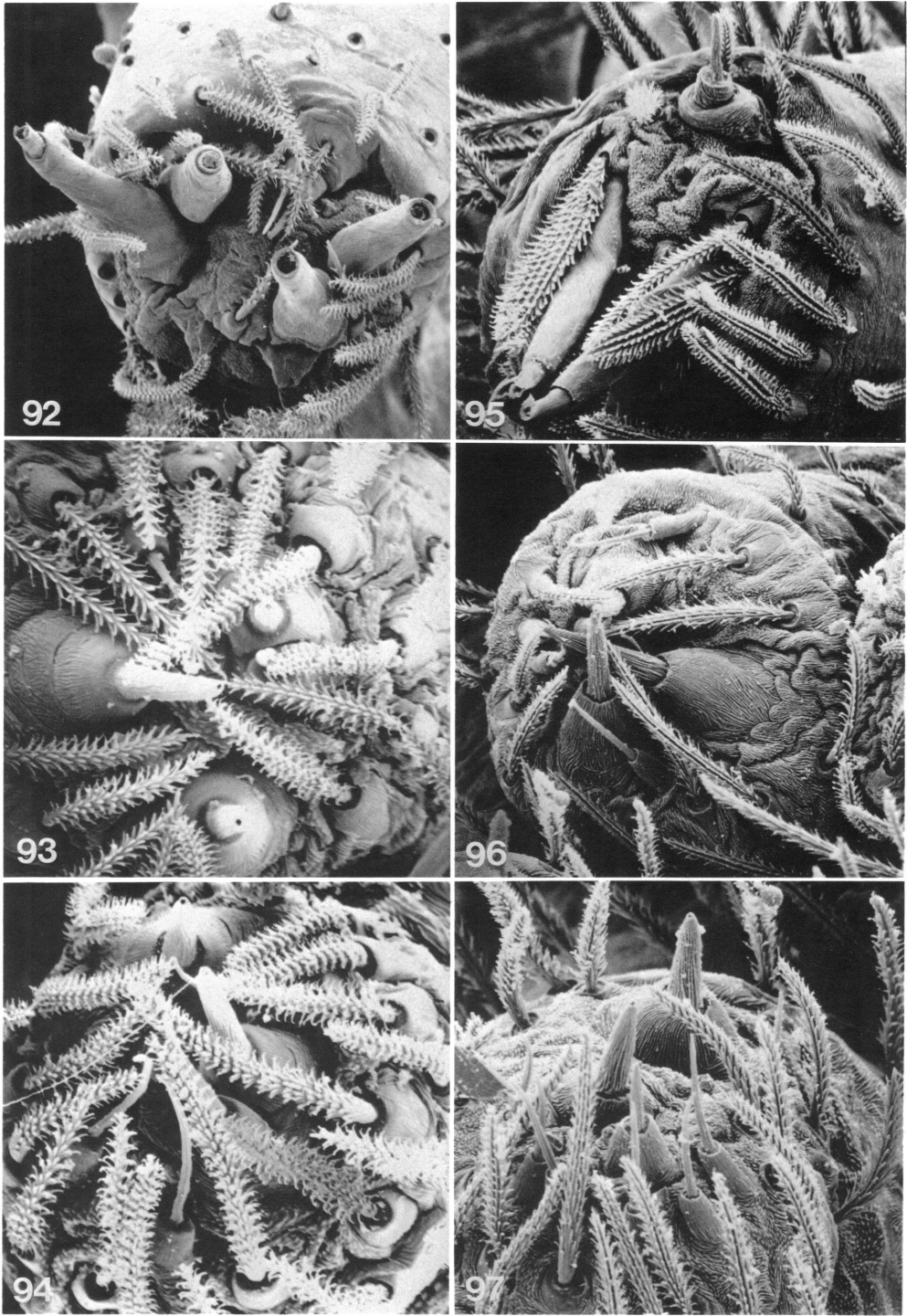
Figs. 74–79. Spinnerets of Drassodinae (Gnaphosidae). 74–76. *Hypodrassodes* sp. 77–79. *Orodrassus coloradensis* (Emerton). 74, 77. ALS, 262 \times , 406 \times . 75, 78. PMS, 500 \times , 201 \times . 76, 79. PLS, 500 \times , 310 \times .



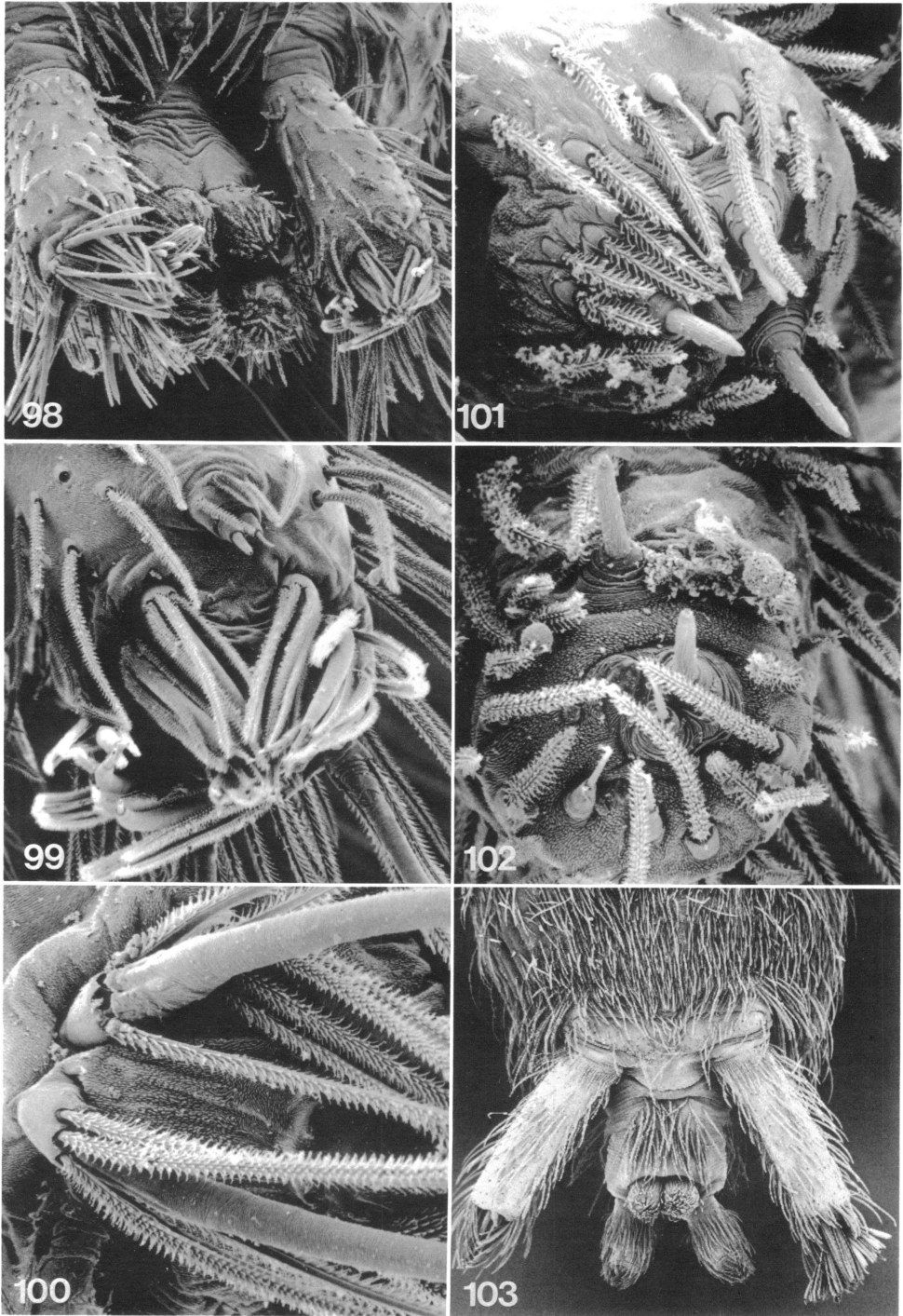
Figs. 80–85. Spinnerets of Drassodinae (Gnaphosidae). 80–82. *Rachodrassus exlineae* Platnick and Shadab. 83–85. *Synaphosus syntheticus* (Chamberlin). 80, 83. ALS, 500 \times , 1094 \times . 81, 84. PMS, 644 \times , 758 \times . 82, 85. PLS, 662 \times , 1000 \times .



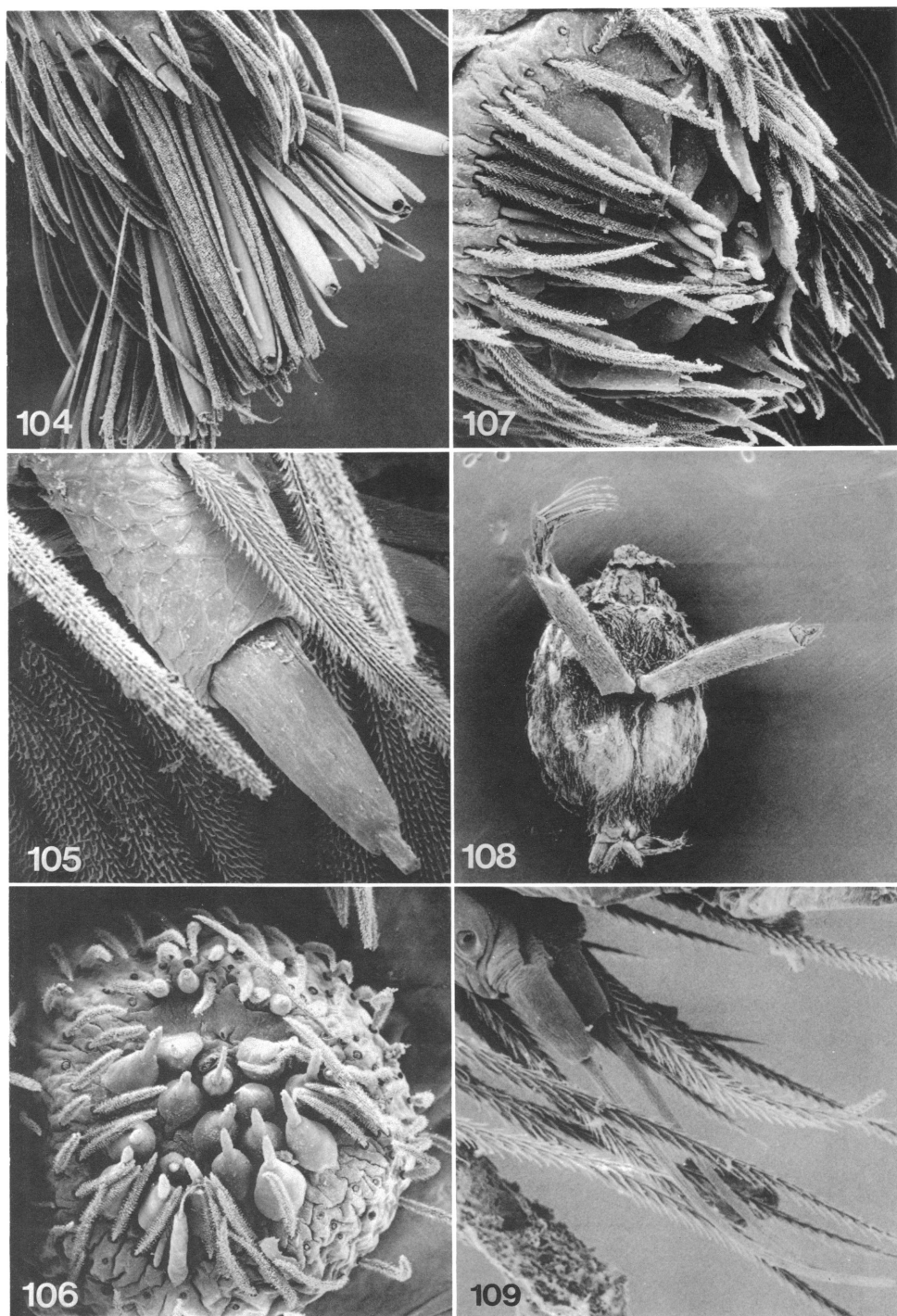
Figs. 86–91. Spinnerets of Gnaphosidae. 86, 88. *Micaria aenea* Thorell. 87. *M. pulicaria* (Sundevall). 89–91. *Vectius niger* (Simon). 86, 89. ALS, 1234 \times , 710 \times . 87, 90. PMS, 650 \times , 446 \times . 88, 91. PLS, 1149 \times , 446 \times .



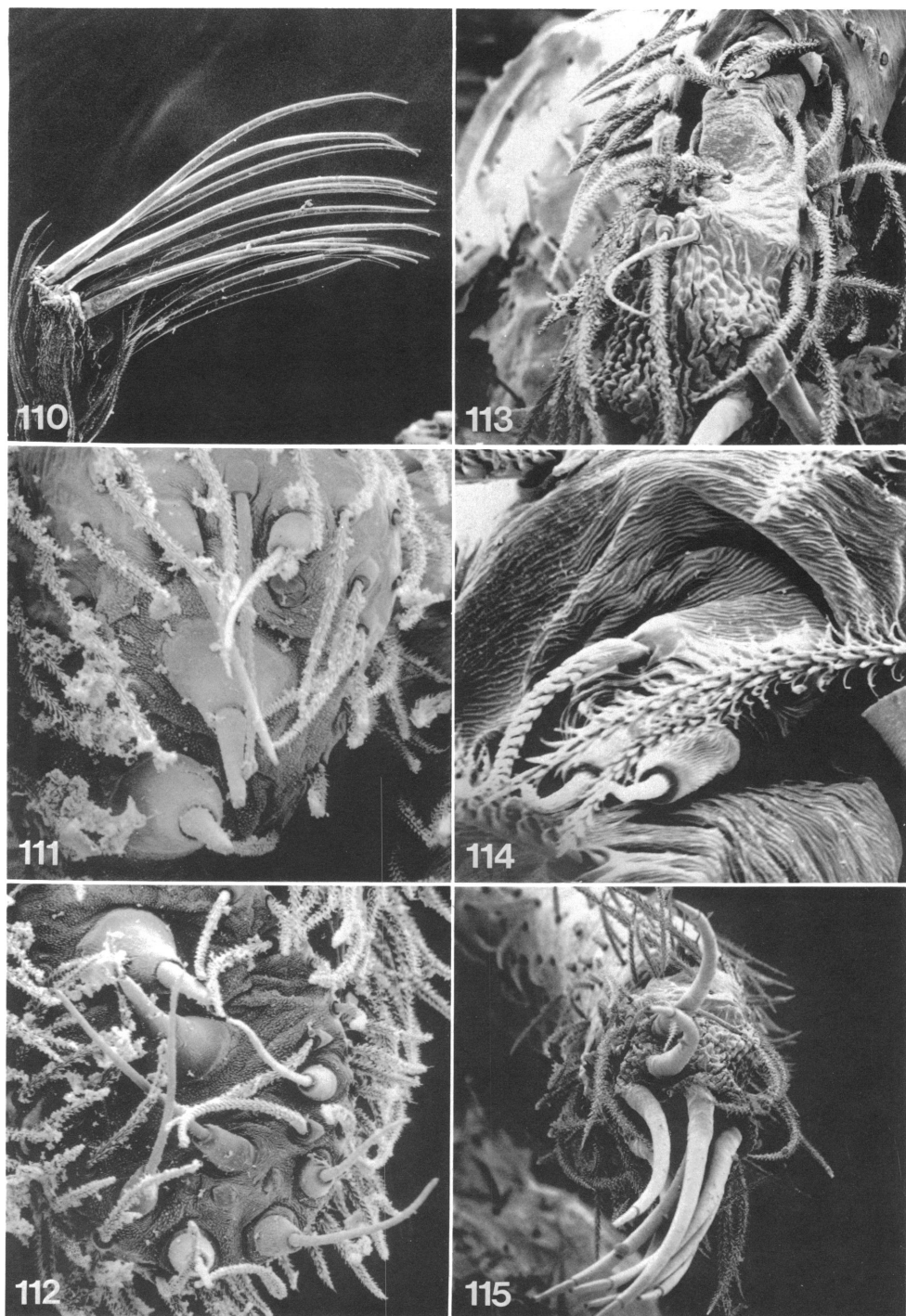
Figs. 92–97. Spinnerets of Anagraphidinae (Prodidomidae). 92–94. *Tivodrassus farias* Platnick and Shadab. 95–97. *Tricongius amazonicus* Platnick and Höfer. 92, 95. ALS, 832×, 1000×. 93, 96. PMS, 2000×, 1164×. 94, 97. PLS, 2000×, 1585×.



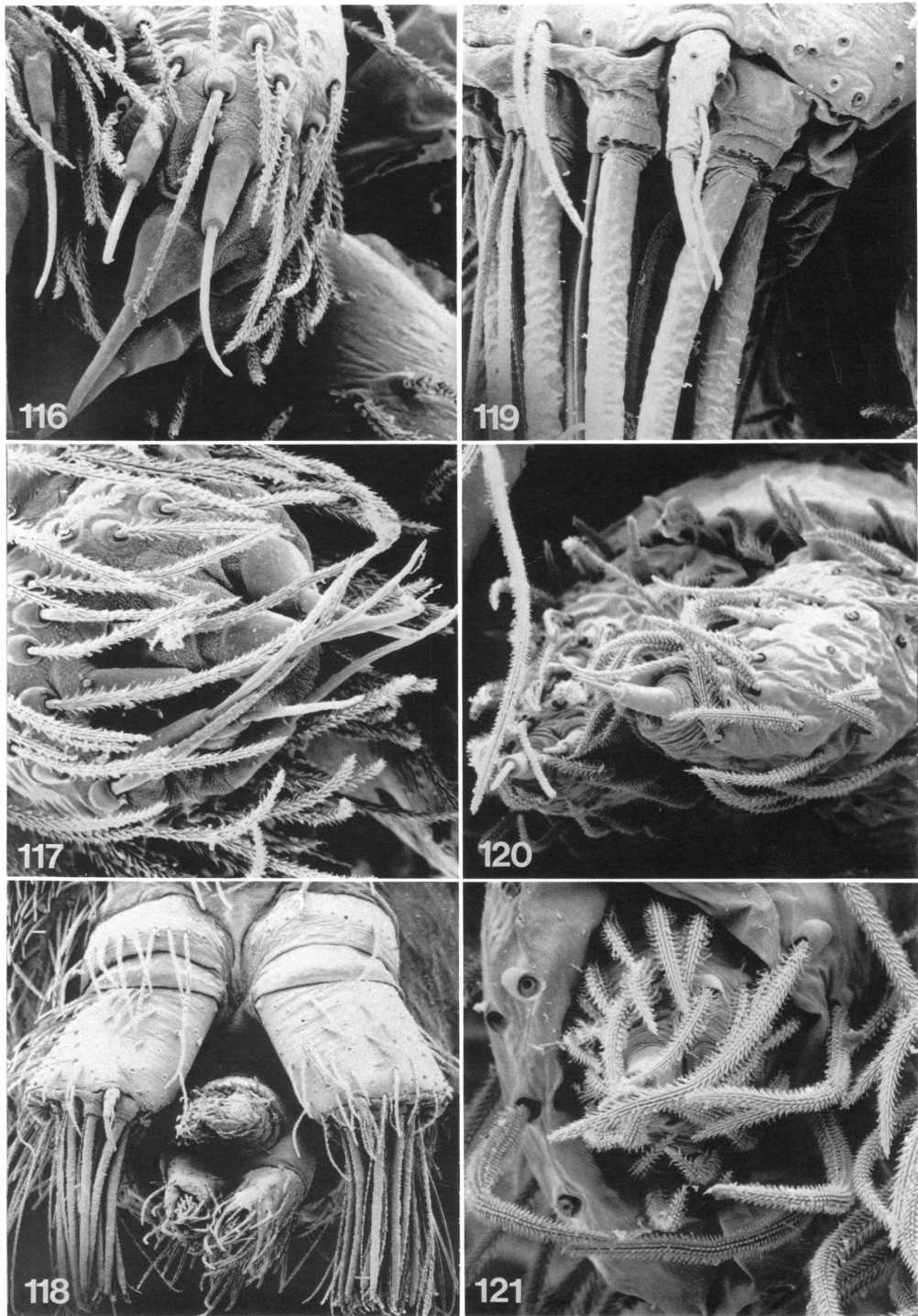
Figs. 98–103. Spinnerets of Anagraphidinae (Prodidomidae). 98–102. *Lygromma dybasi* Platnick and Shadab. 103. *Theuma* sp. 98, 103. Spinneret group, showing slight anterior advancement of ALS, 200 \times , 35 \times . 99. ALS, 581 \times . 100. Base of piriform gland spigot on ALS, 1144 \times . 101. PMS, 1219 \times . 102. PLS, 1273 \times .



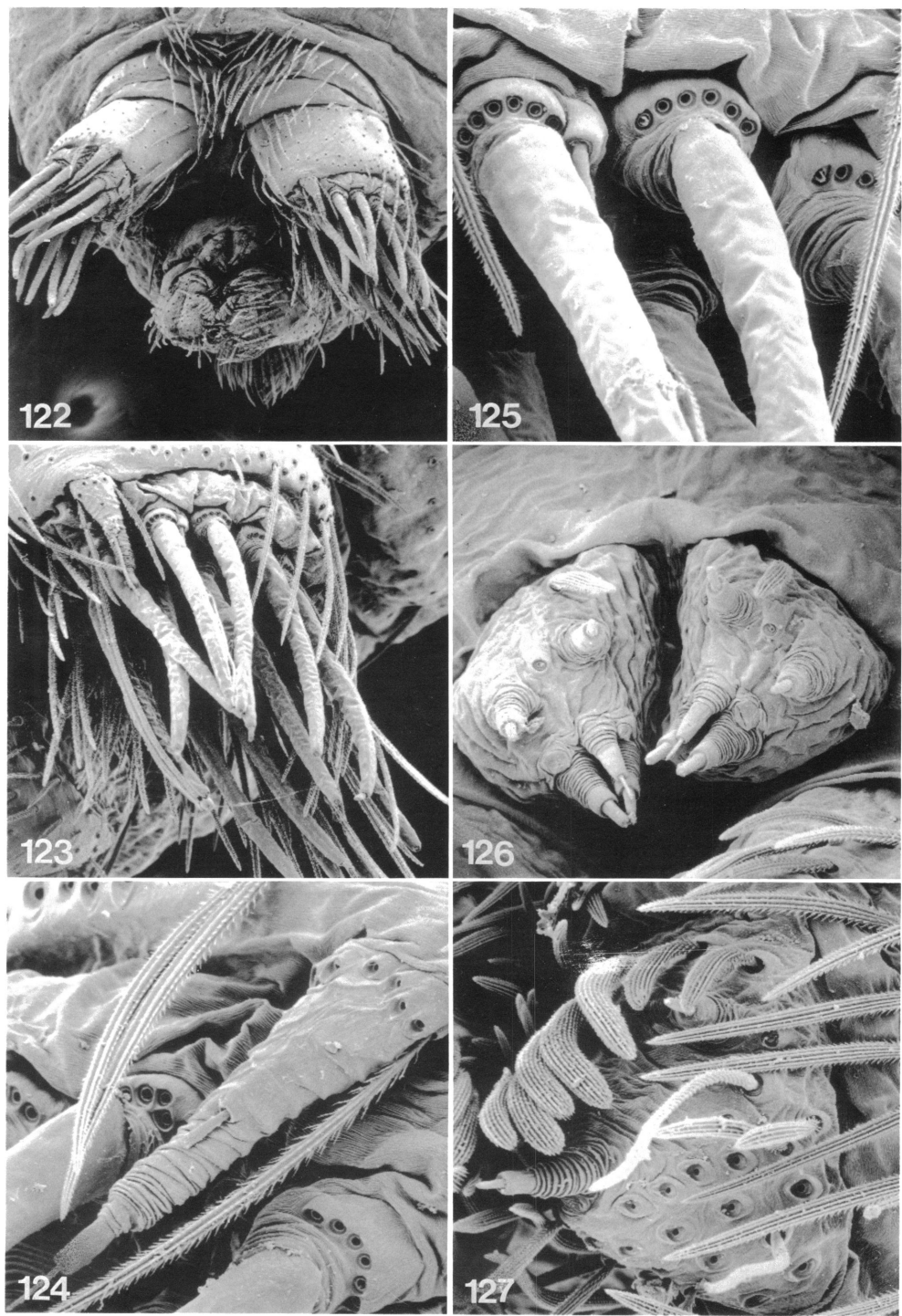
Figs. 104–109. Spinnerets of Anagraphidinae and Molycriniinae (Prodidomidae). 104–107. *Theuma* sp. 108, 109. *Molycrnia mammosa* O. P.-Cambridge. **104.** ALS, 170 \times . **105, 109.** Major ampullate gland spigots on ALS, 1000 \times , 1124 \times . **106.** PMS, 406 \times . **107.** PLS, 500 \times . **108.** Spinneret group, showing great anterior advancement of ALS, 31 \times .



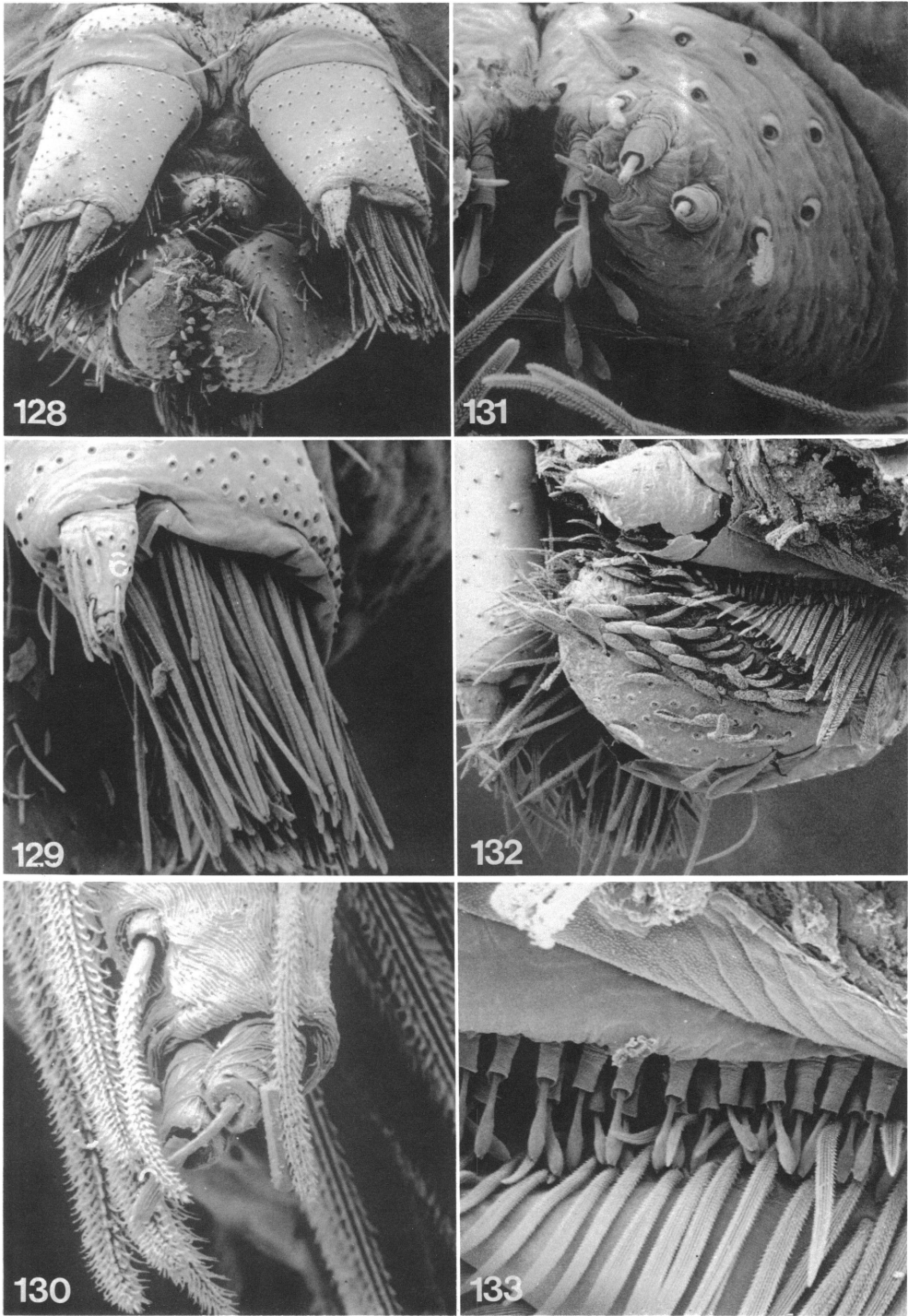
Figs. 110–115. Spinnerets of Molycriniinae (Prodidomidae). 110–112. *Molycrnia mammosa* O. P.-Cambridge. 113–115. *Myandra* sp. 110. ALS, 146 \times . 111. PMS, 888 \times . 112. PLS, 749 \times . 113. Proximal portion of ALS tip, showing great separation of major ampullate gland spigots from piriform gland spigots, 452 \times . 114. ALS major ampullate gland spigots, 2000 \times . 115. ALS piriform gland spigots, 328 \times .



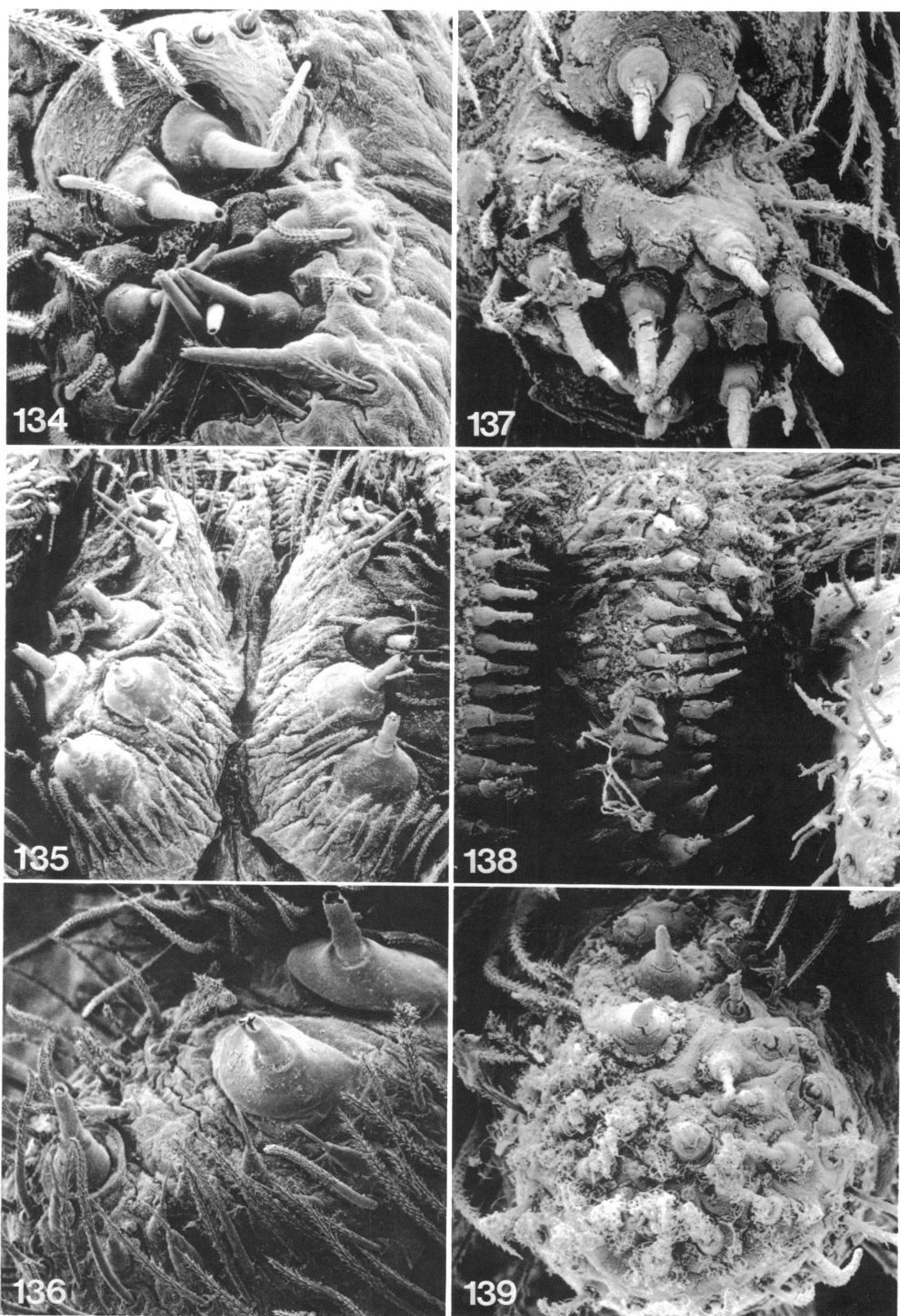
Figs. 116–121. Spinnerets of Molycriinae and Prodidominae (Prodidomidae). 116, 117. *Myandra* sp. 118–121. *Zimirina* sp. **116, 120.** PMS, 1000 \times , 686 \times . **117, 121.** PLS, 1054 \times , 1000 \times . **118.** Spinneret group, showing slight anterior advancement of ALS, 124 \times . **119.** ALS, 500 \times .



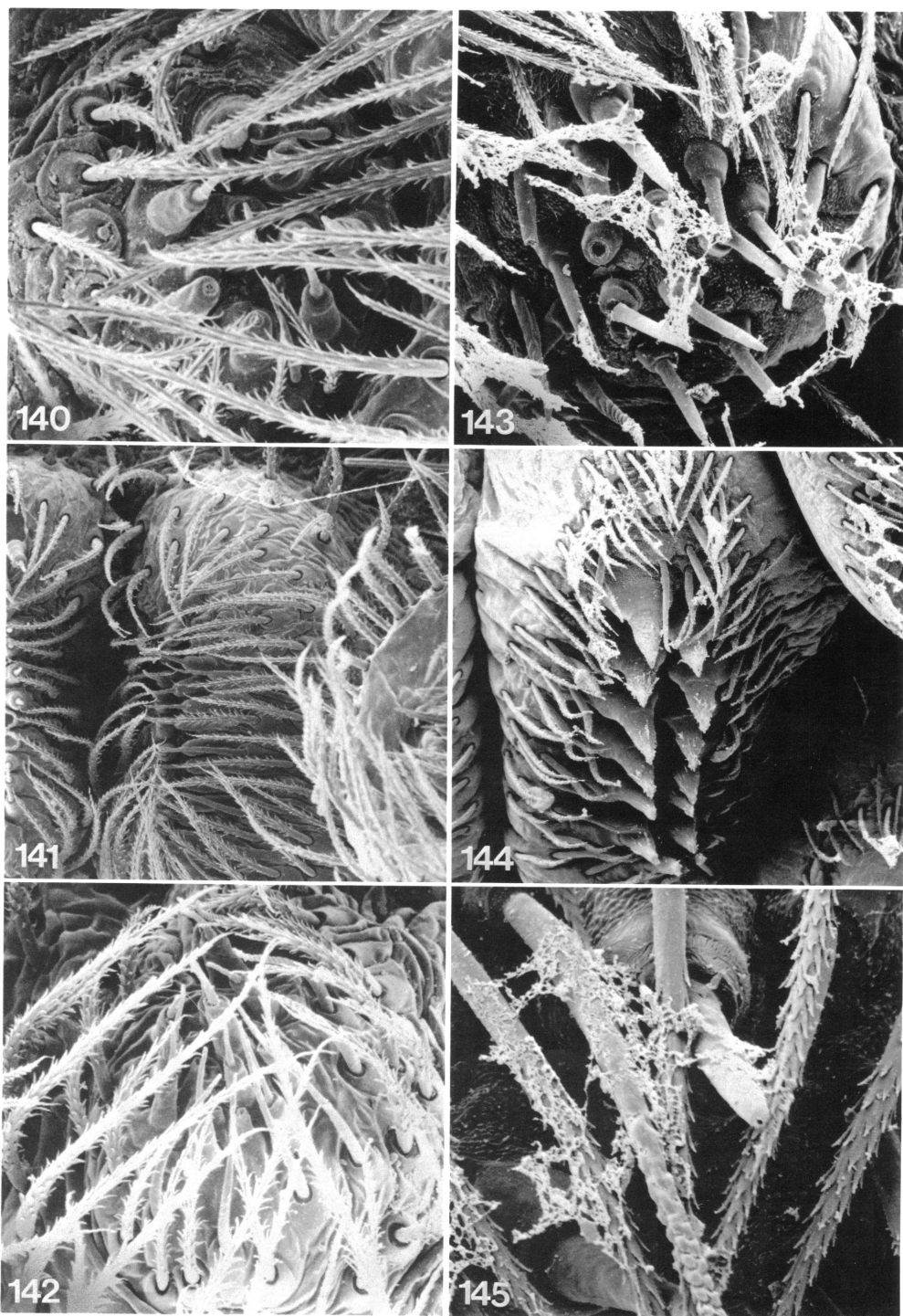
Figs. 122–127. Spinnerets of Prodidominae (Prodidomidae): *Neozimiris pubescens* (Banks). 122. Spinneret group, showing slight anterior advancement of ALS, 120×. 123. ALS, 286×. 124. ALS major ampullate gland spigot, 1000×. 125. Base of ALS piriform gland spigot, 1000×. 126. PMS, 816×. 127. PLS, 1000×.



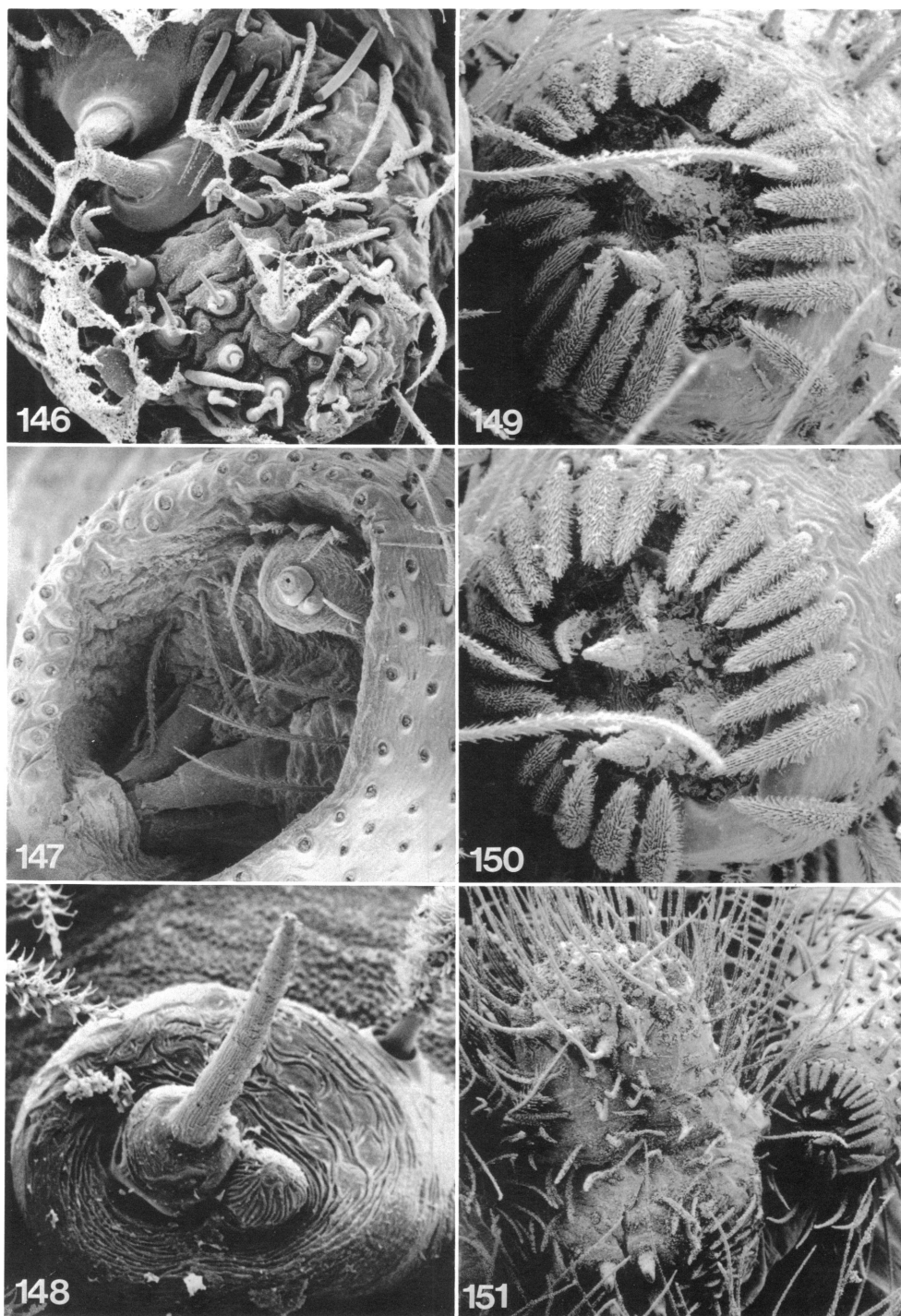
Figs. 128–133. Spinnerets of Prodidominae (Prodidomidae): *Prodidomus dalmasi* Berland. 128. Spinneret group, showing slight anterior advancement of ALS, 131×. 129. ALS, 332×. 130. ALS major ampullate gland spigot, 2000×. 131. PMS, 1000×. 132. PMS and PLS, lateral view, 249×. 133. Same, 1000×.



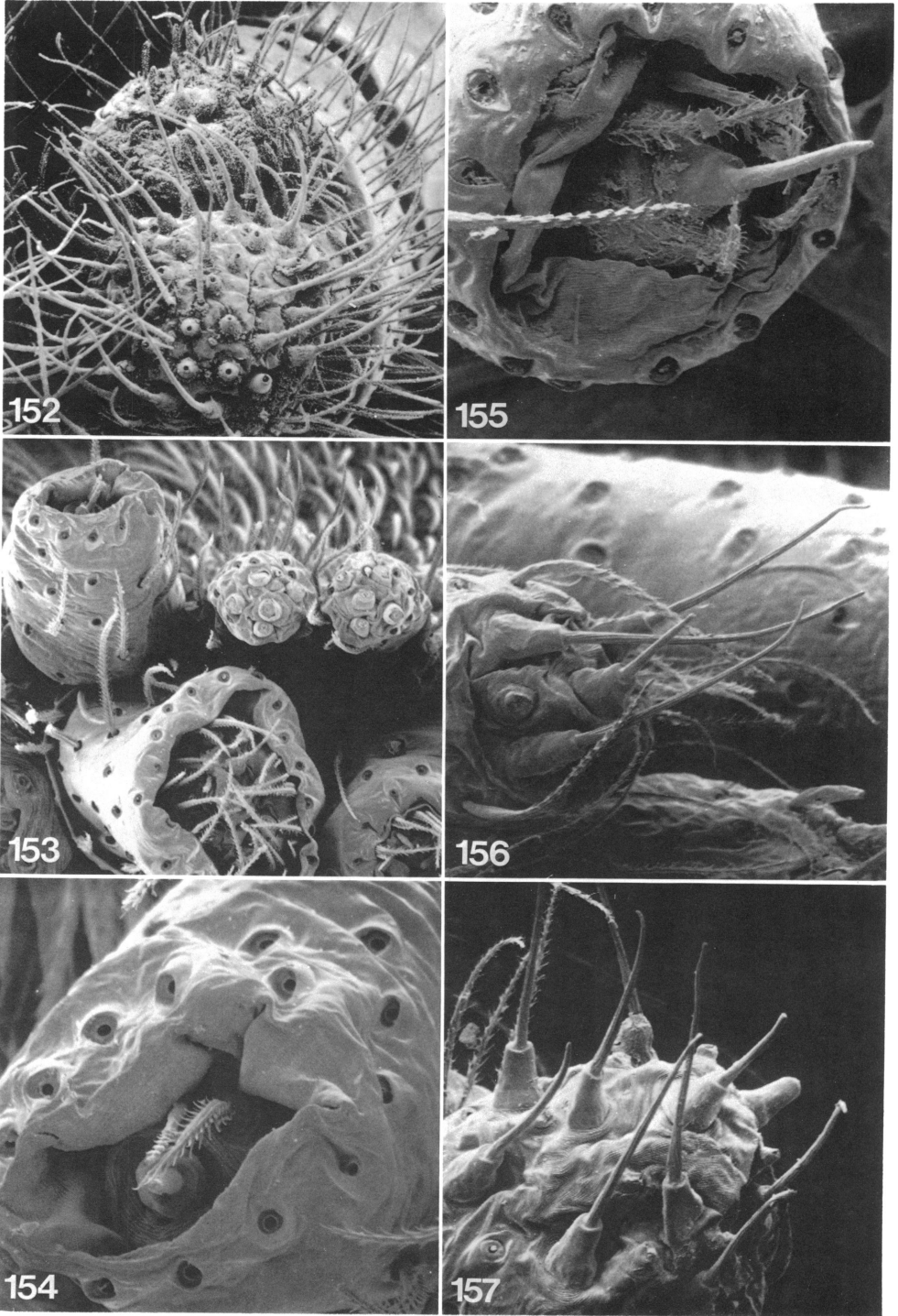
Figs. 134–139. Spinnerets of Trochanteriidae. 134–136. *Platyoides walteri* (Karsch). 137–139. *Doliomalus cimicoides* (Nicolet). 134, 137. ALS, 698 \times , 536 \times . 135, 138. PMS, 258 \times , 320 \times . 136, 139. PLS, 462 \times , 629 \times .



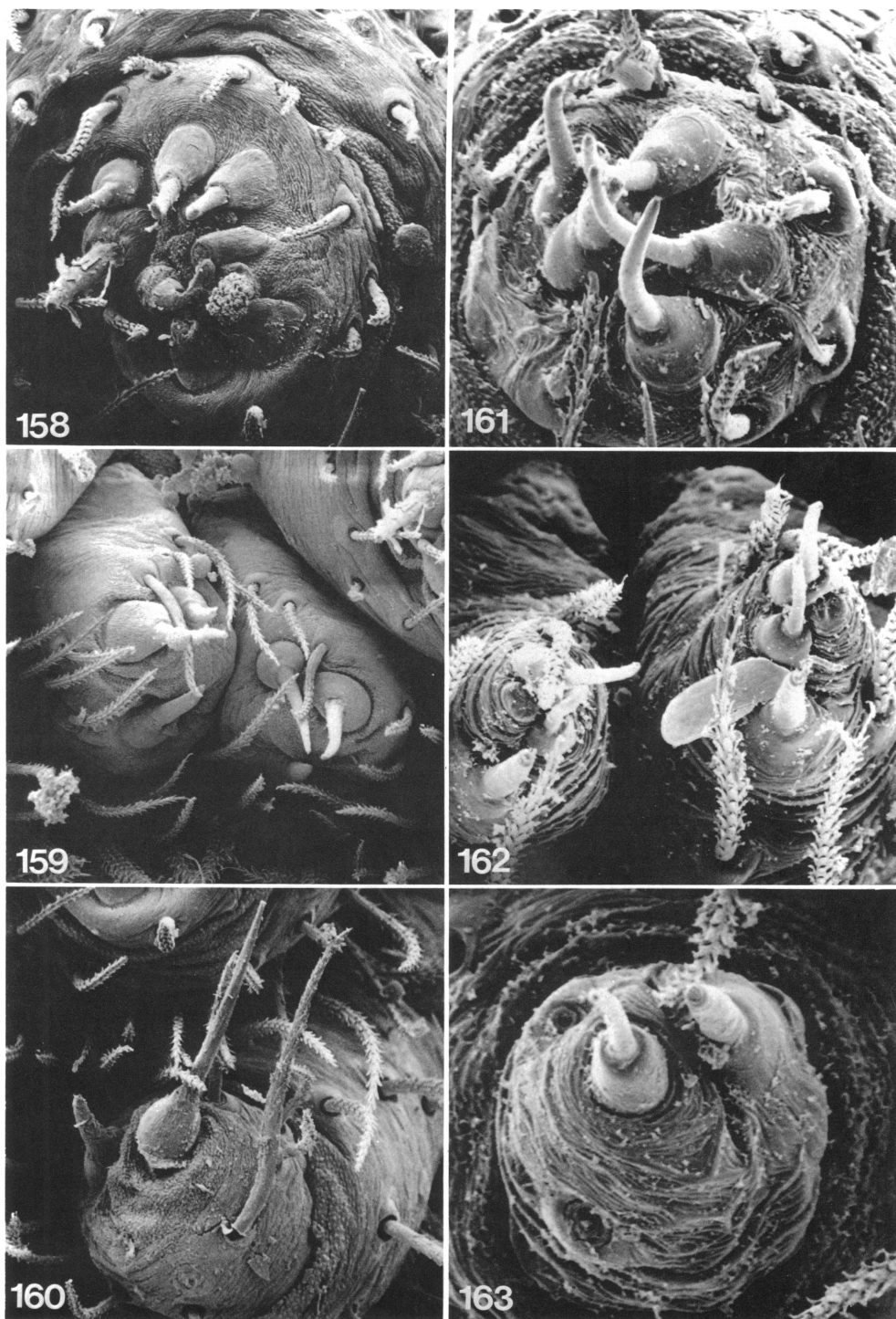
Figs. 140–145. Spinnerets of Trochanteriidae. 140–142. *Plator* sp., penultimate female. 143–145. *Rebilus* sp. 140, 143. ALS, 1000 \times , 832 \times . 141, 144. PMS, 500 \times , 286 \times . 142. PLS, 1144 \times . 145. Distal spigots from PMS, 1872 \times .



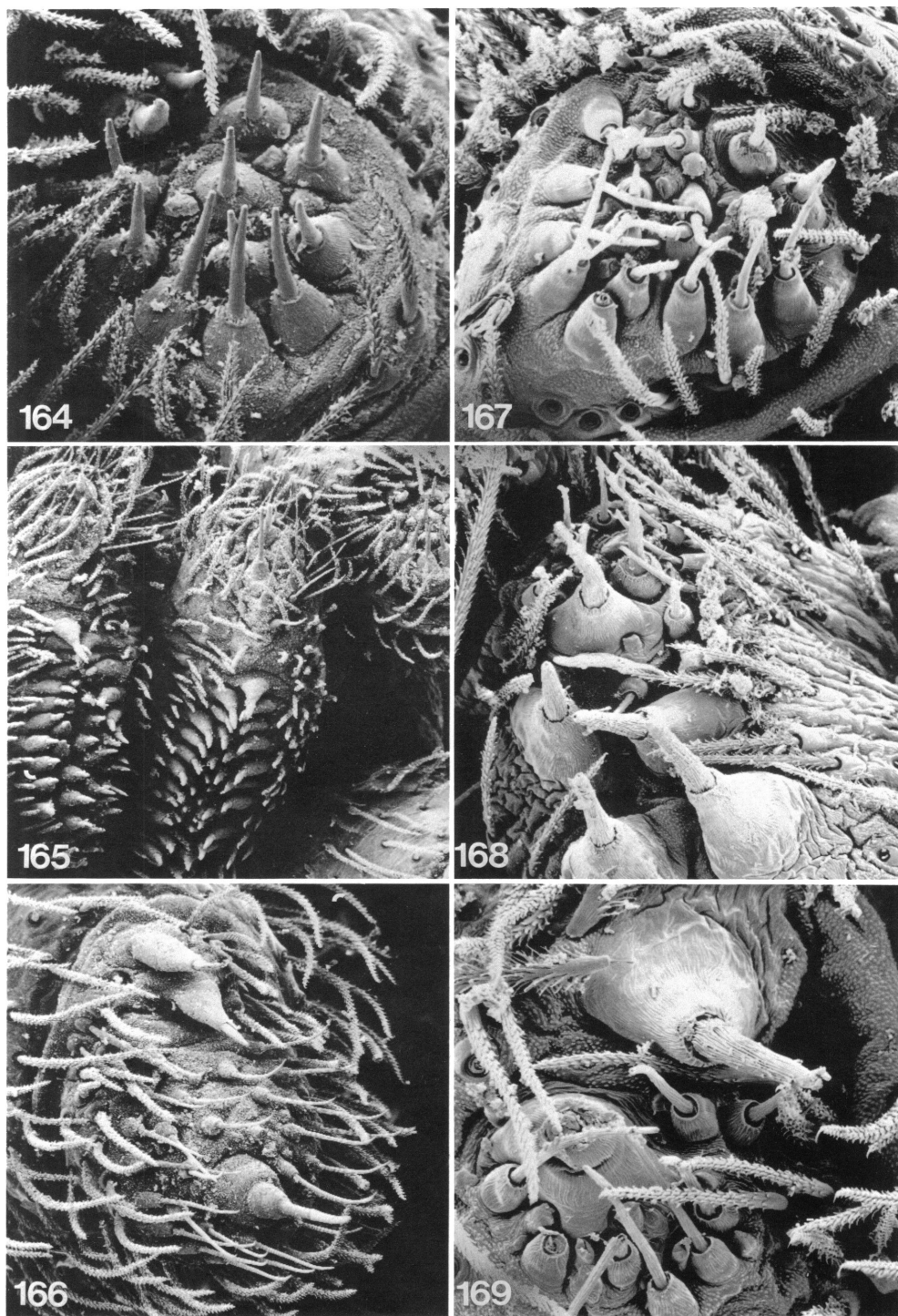
Figs. 146–151. Spinnerets of Trochanteriidae, Gnaphosidae, and Ammoxenidae. 146. *Rebilus* sp. 147. *Hemicloea* sp. 148. *Hypodrassodes* sp. 149–151. *Ammoxenus psammodromus* Simon. **146.** PLS, 498 \times . **147, 149, 150.** ALS, 530 \times , 776 \times , 812 \times . **148.** ALS major ampullate gland spigots, 2000 \times . **151.** PMS, 222 \times .



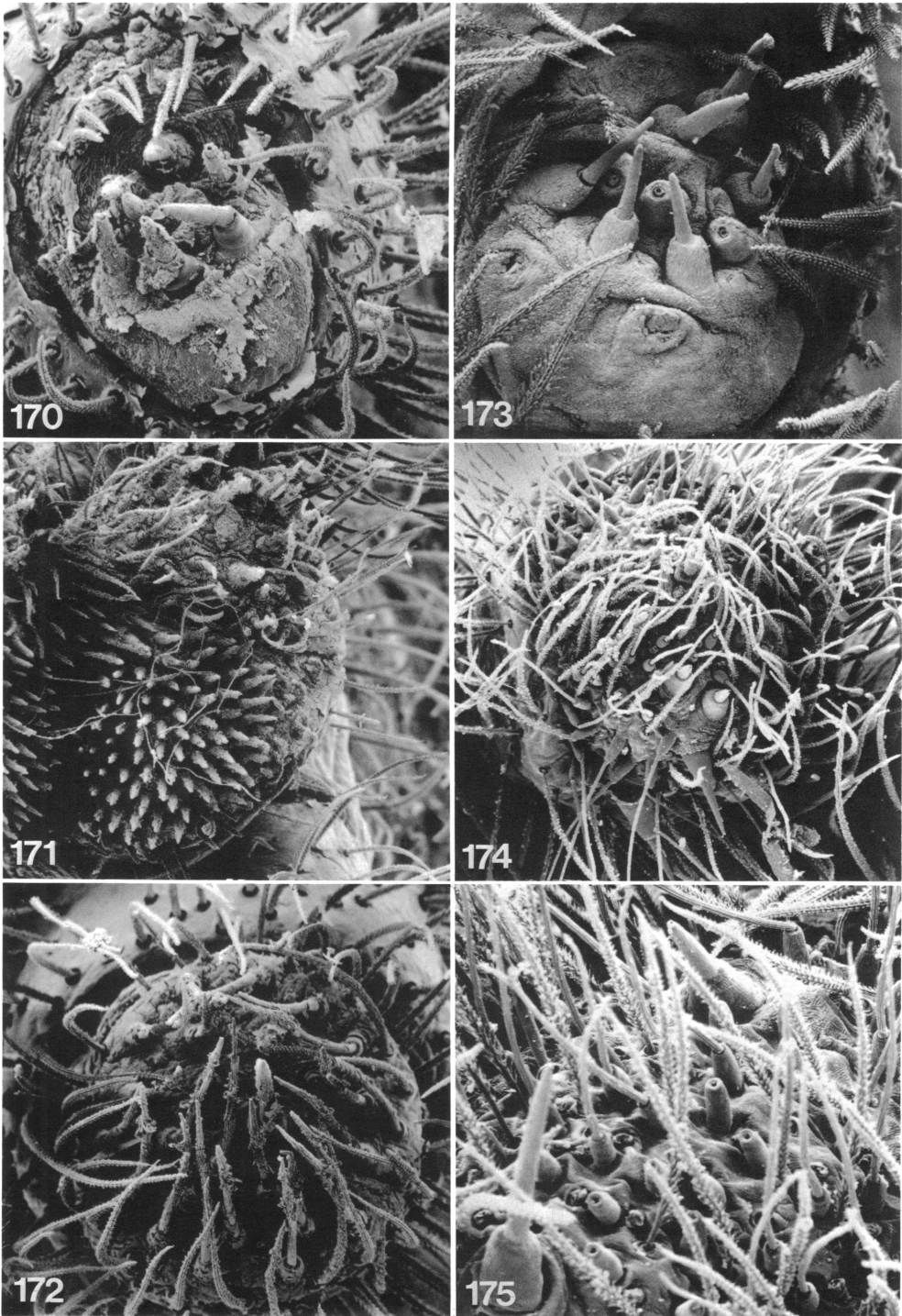
Figs. 152–157. Spinnerets of Ammoxenidae. 152. *Ammoxenus psammodromus* Simon. 153–157. Undescribed African genus. 152, 157. PLS, 238 \times , 1000 \times . 153. Spinneret group, 554 \times . 154, 155. ALS, 1641 \times , 1464 \times . 156. PMS, 1049 \times .



Figs. 158–163. Spinnerets of Gallieniellidae. 158–160. *Gallieniella mygaloides* Millot. 161–163. *Legendrena angavokely* Platnick. **158, 161.** ALS, 1000 \times , 2246 \times . **159, 162.** PMS, 749 \times , 2000 \times . **160, 163.** PLS, 892 \times , 2846 \times .



Figs. 164–169. Spinnerets of Gallieniellidae. 164–166. *Drassodella septemmaculata* (Strand). 167–169. Undescribed Australian genus. **164, 167.** ALS, 1000 \times , 1000 \times . **165, 168.** PMS, 298 \times , 788 \times . **166, 169.** PLS, 500 \times , 1259 \times .



Figs. 170–175. Spinnerets of Cithaeronidae and Lamponidae. 170–172. *Cithaeron delimbatus* Strand. 173–175. *Lampona* sp. 170, 173. ALS, 662 \times , 796 \times . 171, 174. PMS, 330 \times , 334 \times . 172, 175. PLS, 545 \times , 749 \times .

that these enormous spigots are gained successively as the spiders mature and the spinnerets become larger.

The PMS of female gnaphosids are unusual in shape; the spinning field is not confined to the distal tip of the spinneret, but extends along the distal half of the posterior surface of the spinneret as well. These spinnerets are typically bent forward, at almost a 90° angle, so that all the spigots face posteroventrally, and are often deeply constricted at about half their length (as in figs. 12, 21); as a result, the most anterior edge of these spinnerets bears the most distal, rather than the most proximal, spigots. The PMS and PLS each bear three types of spigots; all three spigot types differ from those on the ALS, but occur on both the PMS and PLS.

The proximal portion of the spinning field of the PMS is occupied by several large spigots, often arranged in two parallel rows. Apstein (1889) characterized these as mammiliform spigots (an apt description of their appearance in the zelotine gnaphosids Apstein examined; see figs. 45, 46), and thought they served the ampullate glands. Apparently homologous spigots (usually two in number) occur proximally on the PLS; in every case examined, these PLS spigots conform in all morphological details to those on the PMS. Because these spigots are apparently absent in males, they are here presumed to serve the cylindrical (rather than ampullate) glands.

The distal portion of the PMS and PLS spinning fields includes several small spigots with long shafts, apparently homologous to spigots serving the aciniform glands in other spiders (Coddington, 1989), as well as one or two spigots with shorter, wider shafts. They may serve the minor ampullate glands, although those glands have not previously been reported to open on the PLS as well as the PMS.

PHYLOGENETIC CONTEXT THE INGROUP

Members of the superfamily Gnaphosoidea have been recognized by the combined presence of irregularly shaped and flattened posterior median eyes, obliquely depressed endites, and heavily sclerotized ALS (Platnick, 1984b, 1985). All three of these putative synapomorphies show some limited homo-

plasy outside the superfamily, but apparently not in any of the same taxa. Similarly modified posterior median eyes occur in some quite distantly related spiders, such as the palpimanid genus *Diaphorocellus*, but also appear in the genus *Rhaeboctesis* (originally described as a liocranine; see comments below under Prodidomidae). Similarly depressed endites have been noted in some phrurolithine genera (Platnick and Ubick, 1989), whereas similarly sclerotized ALS occur most notably in some male (but not female) clubionines.

Shear (1986: 417) indicated that "In some publications, the family Gnaphosidae is placed in its own superfamily, together with a few small satellite families probably better included in Gnaphosidae itself." Shear's suggested lumping of all these taxa into a single family would ignore the differences in spinneret morphology discussed below, would obscure the status of the smaller families as relatively plesiomorphic phylogenetic relicts (often with austral distributions), and would contravene a century of literature in which most of the members of the smaller, more plesiomorphic families were accurately separated from true Gnaphosidae.

At the other end of the spectrum, Roewer (1942, 1955a) recognized three superfamilies (listed adjacently within his "Subcohors Dionycha") for these taxa, placing Ammoxenidae in its own superfamily (Ammoxeniformia) and grouping the Cithaeronidae and Homalonychidae together in his Homalonychiformia. The latter family contains the single genus *Homalonychus*; although the relationships of that genus are enigmatic, there seems to be no basis for associating it with gnaphosoids.

THE OUTGROUP

The only explicit hypothesis of an outgroup for Gnaphosoidea in the modern literature seems to have been put forward in an unpublished thesis by Penniman (1985), where a group including just the corinnines, castianeirines, trachelines, and phrurolithines was placed as the sister group of the Gnaphosidae (representatives of the other gnaphosoid families were not examined or considered by Penniman). These groups were united by the occurrence of sexually dimorphic PMS; fe-

males have "laterally compressed to subtriangular" PMS, whereas males (and more distantly related taxa) have "slender, conical, or cylindrical" PMS. Clubionines and anyphaenids were placed as the closest relatives of these groups, united with them by the presence of "precoxal triangles" (sclerotized extensions of the sternal margin).

THE TAXA EXAMINED

As currently construed, the superfamily Gnaphosoidea contains over 2200 described species assigned to about 150 genera and six families (Ammoxenidae, Cithaeronidae, Gallieniellidae, Gnaphosidae, Platoridae, and Trochanteriidae). For this survey, representatives of 50 gnaphosoid genera were chosen as exemplars of the known taxonomic diversity of these families; scanning electron micrographs of their spinnerets are presented here (figs. 2–175). The taxa examined, their previous systematic position, and the figure numbers of their spinneret micrographs are listed in table 1.

Based on Penniman's hypothesis, the sister group of the Gnaphosoidea presumably consists of some of the taxa formerly amalgamated in the family Clubionidae, constituting another 2200 described species currently assigned to about 215 genera and seven families (Anyphaenidae, Clubionidae, Corinnidae, Liocranidae, Miturgidae, Tengellidae, and Zoridae). Spinnerets of representatives of some 25 of these genera have been examined to date, and constitute the outgroup taxa referred to below. Because some of those taxa show more extensive sexual dimorphism in spinneret morphology than has been noted in any gnaphosoid to date (and will therefore require micrographs of both sexes for full documentation), and because a wide variety of other cribellate and hunting spider taxa will need to be examined to place those results in a phylogenetic context, micrographs for the outgroup taxa will be presented in a subsequent paper.

VARIATION AMONG GNAPHOSOIDS THE FAMILY GNAPHOSIDAE

The variation detected among gnaphosoids in spinneret morphology suggests that the family Gnaphosidae needs to be relimited.

Typical gnaphosids are immediately recognizable, even under light microscopy, by the modifications of the spigots on the ALS; the piriform gland spigots are enormously enlarged, so that they are several times the size of the other spigots, or of piriform gland spigots in most of the outgroup genera. These modified piriform gland spigots typically have a widened base, a widened, longitudinally ridged shaft, and a slitlike opening (as in figs. 5, 23). Even in those gnaphosids where the piriform gland spigots are not as wide as usual, the size disparity between them and the other spigots remains obvious (see figs. 62, 74).

The family is therefore redefined here to include just those genera with this type of piriform gland spigot modification. As a result, the subfamilies Molycriniinae, Prodidominae, and Anagraphidinae, and the genera *Drassodella*, *Rebilus*, and *Lampona*, are excluded from the Gnaphosidae (see below), and the genera *Vectius* and *Bobineus*, previously included in the families Platoridae and Cithaeronidae, respectively, are transferred into the family (see the discussion under Trochanteriidae below).

The only homoplasy observed in this character to date occurs outside the superfamily. Males of the genera *Clubiona* and *Clubionoides*, for example, have piriform gland spigots resembling those of gnaphosids in their degree of enlargement. In those clubionine genera, however, females have normal, unmodified piriform gland spigots, and the modifications in males are therefore unlikely to be homologous to the feature in Gnaphosidae, where both sexes have the enlarged spigots. It is of interest that the ALS of male *Clubiona* and *Clubionoides* also resemble those of gnaphosids in being cylindrical (rather than conical, as in clubionine females) and heavily sclerotized (although they are subcontiguous rather than widely separated). It may be that the ALS tip must be enlarged and heavily sclerotized in order to support enlarged piriform gland spigots.

Variation within the Gnaphosidae is seen most obviously in the actual numbers of each spigot type present. There are usually two major ampullate gland spigots, but (as in other groups of spiders), one of those spigots may be reduced to a nubbin (*Hypodrassodes*, fig. 148). The number of piriform gland spigots

varies within genera (different species of *Gnaphosa*, for example, have from four to eight), and may be closely correlated with body size and/or the number of instars prior to maturity. In other genera the number may reach as high as 11 (*Apodrossodes*, fig. 62) or as low as two (*Callilepis*, fig. 20). The genus *Micaria* is anomalous (and possibly neotenic) in having only one piriform gland spigot, and in having that spigot only slightly larger than the major ampullate gland spigots (fig. 86); although *Micaria* has been placed outside the Gnaphosidae in some classifications, its single piriform gland spigot is widened and hence unlike those of the phrurolithine taxa with which the genus has sometimes been associated.

One feature of the piriform gland spigots that may prove to be more informative than mere number is the nature of the separation of the base and shaft. In outgroup taxa and some gnaphosids, the shaft is clearly separated from the base (as in figs. 23, 68), presumably reflecting the origin of the spigots as modified setae, but in many gnaphosids the shaft is fully fused to the base. The examined members of the subfamilies Gnaphosinae (figs. 2, 14) and Zelotinae (figs. 38, 44), for example, all show the apomorphic fusion.

Among the genera examined, those showing the smallest degree of piriform gland spigot widening are members of the "Drassodinae." That group also includes the only genera examined in which some of the piriform gland spigots are still situated in the middle, rather than exclusively around the edge, of the spinneret tip (figs. 74, 80). The "Drassodinae" is thus almost certainly a para- or polyphyletic assemblage of relatively plesiomorphic gnaphosids.

The number of cylindrical gland spigots on the PMS also varies extensively; within the genus *Gnaphosa* alone, for example, a range of 3 to 10 has been observed, and smaller species again seem to have the smallest numbers (for example, *Upognampa* and *Synaphosus*, with only two, figs. 18, 84). When several cylindrical gland spigots occur, they are typically arranged in two striking, parallel rows (for example, *Apodrossodes*, fig. 63), an arrangement that also occurs outside the family (see fig. 138).

THE FAMILY PRODIDOMIDAE

As traditionally construed, this family contained genera with several conspicuous autapomorphies, including a strongly procurved posterior eye row, enlarged and divergent chelicerae, unarmed superior tarsal claws, and widened ALS. Platnick and Shadab (1976b), in the course of a revision of genera traditionally placed in the Prodidomidae and Anagraphidinae (Gnaphosidae), noted several features shared by these groups and therefore reduced the prodidomids to subfamilial status within the Gnaphosidae. The results presented here suggest that these groups, along with the subfamily Molycriinae (classically placed in the Clubionidae but considered a subfamily of Prodidomidae by Lehtinen, 1967) are indeed closely related, but that they do not belong to the Gnaphosidae.

Prodidomines (including the zimirine genera sometimes recognized as a subgroup or sister group of more typical prodidomines), molycriines, and anagraphidines do not have the type of enlarged and widened piriform gland spigots described above. Those spigots instead show a different sort of modification; their bases are extremely elongated, becoming several times longer than the shaft, and are closely associated with highly plumose setae (figs. 95, 99, 115, 123) that generally originate on the spinneret tip rather than the tube itself. As the oldest family-group name among the many that are available for these taxa is Prodidomidae, that family is here revalidated and expanded to include the anagraphidines and molycriines.

The members of all three subfamilies have the ALS more anteriorly placed than in typical gnaphosids. Within the Anagraphidinae, this anterior displacement is most pronounced in *Theuma* (fig. 103, admittedly not greatly different from the situation in those gnaphosids, such as *Pterotracha* and *Scopoides*, with relatively long ALS). The displacement reaches its maximum in the prodidomine genus *Zimiris* and in all the members of the Molycriinae, where the ALS originate near the anterior, rather than posterior, end of the abdomen (fig. 108). Similarly anteriorly originating and elongate ALS occur in

an undescribed genus from Namibia that seems not to be a prodidomine and will therefore be either the first anagraphidine with this extreme form of the character, the first molycrine found outside of Australia, or the first known member of a fourth subfamily.

Members of all three subfamilies have the plate bearing the major ampullate gland spigots shifted proximally and widely separated from the piriform gland spigots (for an extreme example, see *Myandra*, fig. 113). In some cases, such as the anagraphidine genera *Tivodrassus* (fig. 92) and *Theuma* (figs. 104, 105), and the prodidomine genus *Neozimiris* (figs. 123, 124), the plate has even fused with the distal margin of the ALS tube. This fusion is not unique to the group, however (see the gnaphosine genus *Pterotricha*, fig. 11).

The highly plumose setae on the ALS tip may simply originate near the elongated piriform gland spigots (*Tricongius*, fig. 95; *Tivodrassus*, fig. 92; *Myandra*, fig. 113), or may share a common origin with those spigots (*Lygromma*, fig. 100). In the prodidomines, there may be enough of these setae associated with the base of each piriform gland spigot to give that base a "wagon wheel" appearance when the setae fall off (*Neozimiris*, figs. 123–125; *Zimirina*, fig. 119).

The prodidomines seem to share a peculiar minor ampullate gland spigot morphology, where the shaft is reduced to a needlelike extension of the base (figs. 120, 126, 131); in *Zimirina* (fig. 119) the major ampullate gland spigot is similarly shaped. In *Prodidomus*, the PMS and PLS are highly modified; the PMS bear posterior rows of modified setae or spigots that interdigitate with elongate setae on the anterior edge of the PLS (figs. 132, 133). In the molycrines, the minor ampullate gland spigots are differently modified, with greatly elongated shafts that are even longer than the shafts of the aciniform gland spigots (figs. 111, 112).

As delimited, the family includes some 27 genera, although some are poorly known and of dubious validity and placement. The Anagraphidinae includes *Anagraphis*, *Anagrina*, *Encoptarthria*, *Lygromma* (see Platnick and Shadab, 1976b), *Lygrommatoides*, *Oltacloea* (see Platnick, 1986b), *Theuma*, *Theumella*, *Tivodrassus* (see Platnick and Shadab, 1976a),

and *Tricongius* (see Platnick and Höfer, 1990). The African liocranine genus *Rhaeboctesis* was transferred to the Anagraphidinae by Lehtinen (1967), but neither males nor females kindly made available by John Murphy have piriform gland spigots like those of other anagraphidines; the placement of this genus will be reexamined when a wider variety of "clubionoid" spinneret morphologies can be documented. The Molycrinae includes *Cryptoeirithus* (listed as a prodidomine by Roewer, 1955a, and Brignoli, 1983, but correctly identified as a molycrine by Dalmás, 1918, and Cooke, 1964), *Honunius*, *Molycrion*, and *Myandra*, all from Australia; three other genera were listed as molycrines by Roewer (1955a), but *Sphingius* was placed as a corinnine by both Lehtinen (1967) and Reiskind (1969), and *Ceryerda* and *Jacaena* do not appear to be molycrines and are retained in the Gnaphosidae until they can be revised (both genera may be misplaced in that family as well). The Prodidominae includes *Achalaicola* (transferred from the Micariinae by Reiskind, 1969), *Austrodomus*, *Caudalia*, *Eleleis*, *Hyltonia*, *Katumba*, *Neozimiris* (see Platnick and Shadab, 1976b), *Plutonodomus*, *Prodida*, *Prodidomus*, *Purcelliana*, *Zimirina*, and *Zimiris*.

THE FAMILY TROCHANTERIIDAE

Several genera of gnaphosoids are extremely flattened and apparently adapted to life under bark and in crevices, and their interrelationships have long been obscure. A classically recognized family, the Platoridae, has traditionally been construed to contain three of these flattened genera (*Plator* from southern Asia, *Doliomalus* from Chile, and *Vectius* from tropical South America), but no synapomorphies supporting this grouping have been recognized (see Platnick, 1976a, 1976b, 1984a). Other flattened genera have been assigned to the Australasian gnaphosid subfamily Hemicleiinae. The oldest family-group name available for any of these flattened forms is Trochanteriidae, and two genera sometimes considered hemicleiines (*Platyoides* from Africa and *Trochanteria* from South America) have been assigned to the Trochanteriidae in recent revisions (Platnick,

1985, 1986a). A third (and only slightly flattened) non-Australian genus listed as a hemicloetine by Roewer (1955a), *Oltacloea*, was transferred to the Anagraphidinae by Platnick (1986b). Wunderlich (1987) considered all the extremely flattened forms to be members of a single monophyletic group (erroneously called Hemicloetineae), but spinneret morphology indicates that both his hypothesis and the more traditional arrangement are unacceptable.

Two features of the ALS are relevant here, piriform gland spigot morphology and the presence or absence of a sclerotized subdistal ring on the ALS tip. This ring, which is separated from the distal rim of the ALS tube by unsclerotized cuticle, apparently represents the remnants of a separate distal segment. The feature is unfortunately not apparent in scanning electron micrographs, but is easily seen with light microscopy. It occurs in all the taxa listed in table 1 (except those genera here assigned to the Gnaphosidae and Prodidomidae) and in all the relevant outgroup genera examined to date.

Of the flattened genera examined here, *Vectius* (fig. 89) and *Hemicloea* (fig. 147) have the enlarged piriform gland spigots typical of Gnaphosidae, and lack a sclerotized ring on the ALS; *Vectius* is therefore here transferred from the Platoridae to the Gnaphosidae. However, *Rebilus* (fig. 143), *Platyoides* (fig. 134), and *Doliomalus* (fig. 137) definitely have plesiomorphic piriform gland spigots and retain the ALS ring, and the same seems to be true for *Plator* (only a penultimate female was available for SEM examination, fig. 140, but light microscopic examination of an adult female also revealed no enlarged piriform gland spigots). Thus it seems clear that there are at least two groups of greatly flattened gnaphosoids; until additional evidence indicates otherwise, it is most parsimonious to accept the suite of modifications associated with the flattened habitus (including laterigrade leg rotation) as having originated only twice. The Hemicloetineae are therefore here retained in the Gnaphosidae, but *Rebilus*, *Doliomalus*, and *Plator* are here placed, along with *Trochanteria* and *Platyoides*, in the Trochanteriidae; Platoridae is considered a junior synonym of that name. The elongated fourth trochanters characteristic of *Trochanteria* and

Platyoides do not occur in *Plator* or *Doliomalus*, but do occur in some (as yet unidentified) Australian trochanteriids.

The Australian genera *Corimaethes*, *Hemicloetina*, and *Pyrnus* are retained in the Hemicloetineae until that fauna can be revised. The Argentine genus *Xenoplectus* was placed as a hemicloetine by its authors (Schiapelli and Gerschman, 1958) but not, for unexplained reasons, by Brignoli (1983); it is not a hemicloetine (and may even be misplaced as a gnaphosid).

THE FAMILY AMMOXENIDAE

As currently limited, this family includes only the genus *Ammoxenus*, from South Africa, Botswana, and Namibia. The relationships of this genus have been enigmatic. In their recent revision, Dippenaar and Meyer (1980: 42) indicated that "The species of *Ammoxenus* resemble those of Zodariidae in size, colour and appearance, but their relationship with the other families of Araneae is difficult to determine because of their adaptations to life in sandy areas." Benoit (1972: 180), in an earlier revision, also indicated that "La recherche de la parenté de cette famille est rendue malaisée et plutôt spéculative par la présence de nombreuses adaptations à la vie dans les sables et les dunes du désert," but instead cited similarities with the Hersiliidae (in carapace form, eyes concentrated on an ocular tubercle, an inclined clypeus and endites, reduced fangs, sternal form, and the separated ALS).

Lehtinen has argued for the extreme isolation of ammxenids from other araneomorphs, indicating that "The pattern of spinnerets . . . in Ammxenidae and Caponiidae is similar to that in [the mygalomorph superfamily] Atypoidea" (Lehtinen, 1978: 260), and that the ammxenid "pattern of spinnerets cannot be compared with that of any classical Labidognath spiders" (Lehtinen, 1980: 496). It is difficult to see any basis for these startling conclusions, although similar comments were made by Petrunkevitch (1933: 321), who mistook the constricted portion of the PMS for a distal segment and therefore thought the ALS and PMS had exchanged positions, creating an arrangement "different from that in all other spiders."

Such comments notwithstanding, the spinnerets of *Ammoxenus* are gnaphosid-like in appearance and show no special similarities to those of *Atypus* or any other mygalomorph. The ALS are cylindrical, extremely widely separated, and heavily sclerotized; the PMS are clearly bent anteriorly, and even have a deep constriction as in many gnaphosids (fig. 151); and the PLS have two proximal cylindrical gland spigots (fig. 152) agreeing in morphology with those occurring proximally on the PMS.

The ALS of *Ammoxenus* are anomalous, however, in that they do not appear to have any piriform gland spigots (figs. 149, 150), and are completely separated by the PMS, which are anteriorly advanced (fig. 151). The same appears to be true for an apparently related genus from southern Africa (figs. 153–157), resembling *Ammoxenus* in digging adaptations, that will be described elsewhere (Platnick and Griffin, in prep.).

The apparent loss of piriform gland spigots makes it difficult to determine the relationships of these genera to other gnaphosoids. The cylindrical, widely separated ALS indicate that they could conceivably represent highly autapomorphic gnaphosids or prodidomids; the ALS are actually more widely separated in ammoxenids than in the members of either of those groups. As indicated above, the PMS of *Ammoxenus* are very gnaphosid-like, but that is not true of the undescribed African genus (fig. 153). Moreover, ammoxenids appear to retain the subterminal sclerotized ring on the ALS, and their traditional placement outside the Gnaphosidae or Prodidomidae therefore seems to be correct.

THE FAMILY GALLIENIELLIDAE

As currently limited, this family includes just two genera, *Gallieniella* and *Legendrena*, known only from Madagascar and the Comoro Islands (Platnick, 1984b). These spiders are most notable for the elongated, desid-like chelicerae of males (Platnick, 1984b: figs. 1–4, 33–36). It is now apparent, however, that the family in fact has a wide, austral distribution. Over recent years, Charles Griswold and Rudy Jocqué encountered females from southern Africa that seemed to be possible

members of the family. Recent pitfall samples including males have now allowed these spiders to be identified as members of the genus *Drassodella*. In describing *Drassodella* as a gnaphosid, Hewitt (1916: 209) expressed uncertainty about its relationships:

This name is proposed for the reception of a species which cannot be referred to any of the genera included by M. Simon in the family Drassidae [= Gnaphosidae], and, but for the fact that the maxillae are strongly impressed, the species might with some propriety be referred to the family Clubionidae. The labium is much shorter than that of other Drassidae known from South Africa (except the anomalous genus *Titus* O. P. Camb.), and the inferior spinners are not widely separated although not actually contiguous.

The piriform gland spigots of *Drassodella* are plesiomorphic in morphology (fig. 164) and clearly exclude the genus from the Gnaphosidae. The elongated chelicerae of males as well as the closely spaced, conical ALS retaining a sclerotized subdistal ring agree instead with those features in *Gallieniella* and *Legendrena*. *Drassodella* is therefore here transferred from the Gnaphosidae to the Gallieniellidae.

During a visit to the Queensland Museum, Brisbane, during 1987, specimens of another, apparently undescribed genus with similar cheliceral and spinneret morphology were encountered (see figs. 167–169). A description of this eastern Australian genus of gallieniellids is in preparation, and the family also appears to be represented in Western Australia (Mark Harvey, personal commun.).

THE FAMILY CITHAERONIDAE

This little-known family was classically construed to include only the genus *Cithaeron*, found from western Africa to Malaysia. Roewer (1955b) added a second genus, *Bobineus*, to the family, based on a new Iranian species, *Bobineus loeffleri*. Through the courtesy of Manfred Grasshoff of the Forschungsinstitut Senckenberg, I have been able to examine the male holotype of that species; it has the cheliceral keel synapomorphic for the gnaphosid subfamily Gnaphosinae, and the greatly elongated ALS characteristic of the gnaphosine genus *Pterotricha*, and *Bobineus* is here transferred to the Gnaphosidae and placed as a junior synonym of *Pterotricha*.

The familial status of this group seems to be warranted; although clearly a gnaphosoid, *Cithaeron* has unmodified piriform gland spigots (fig. 170), and again differs from true Gnaphosidae in retaining a sclerotized ring on the ALS tip. The PMS are highly modified; instead of the large cylindrical gland spigots found in other gnaphosoids and many outgroup genera, the posterior portion of the PMS is covered with numerous small spigots (fig. 171). The only other gnaphosoid examined to date that approaches this condition is *Drassodella* (fig. 165), which has multiple rows of cylindrical gland spigots. It is possible that the arrangement in *Cithaeron* is merely a generic feature, as an unidentified female from India (in the American Museum of Natural History) that may prove to belong to a second cithaeronid genus has numerous large cylindrical gland spigots, arranged in two parallel rows, on the PMS.

THE FAMILY LAMPONIDAE

The genus *Lampona* is widely known, primarily because one species, *Lampona cylindrata* (L. Koch), which is widespread in southern Australia, Tasmania, and New Zealand, is also synanthropic, will enter the webs of other spiders and prey upon them, and has been implicated in human envenomations. Although the genus has classically been placed in its own tribe or subfamily within the Gnaphosidae, the palpal endites of *Lampona* show little evidence of an oblique depression. The ALS have normal, unmodified piriform gland spigots (fig. 173), and apparently retain (at least plesiomorphically) the sclerotized ring on their tip, and the genus therefore seems not to be a true gnaphosid. *Lampona* appears to be the only described genus in a complex, involving numerous undescribed Australian genera, that is currently being revised by Russell Moran, who concurs that the group does not belong to the Gnaphosidae, and deserves familial status.

FAMILIAL INTERRELATIONSHIPS

Spinneret morphology may provide an additional synapomorphy linking the seven gnaphosoid families delimited above. If the spigots referred to here as minor ampullate gland spigots do indeed serve those glands, their presence on the PLS as well as the PMS

may be unique to gnaphosoids; in other spiders, the minor ampullate glands have been reported to open only on the PMS (Kovoor, 1977, 1987; Coddington, 1989). Even if the association with minor ampullate glands proves to be incorrect, at least some females of all seven families have three spigot types shared by the PMS and PLS, a clearly anomalous feature for ecribellate spiders; see figures 51, 52, 54, 55 (Gnaphosidae), 126, 127 (Prodidomidae), 135, 136 (Trochanteriidae), 156, 157 (Ammoxenidae), 165, 166 (Gallieniellidae), 171, 172 (Cithaeronidae), and 174, 175 (Lamponidae).

Among those families, the Gnaphosidae and Prodidomidae may be sister groups, united by the loss of the sclerotized ring on the ALS tip that occurs in the members of the other five gnaphosoid families as well as all the relevant outgroup genera examined. The loss of the sclerotized ring may be functionally related to the increase in piriform gland spigot width or length in those two families.

One classical character may also be informative at the familial level, namely the wide separation of the ALS. Those spinnerets are separated (at their base) by their diameter or more in all true Gnaphosidae. Among the Prodidomidae, the anagraphidines also have widely separated ALS. Many prodidomines and molycrines have ALS separated by less than their diameter, but that seems to be a secondary condition, caused by an increase in ALS width in those taxa, and hence not homologous with the closely spaced but much narrower ALS found in Gallieniellidae, Cithaeronidae, and the outgroup taxa (with the exception of some *Drassinella*). Ammoxenids and (to a much lesser degree) lamponids resemble gnaphosids and prodidomids in this character, and hence may be the closest relatives of that clade. The feature varies within the Trochanteriidae; *Doliomalus*, *Plator*, and *Rebilus* have widely separated ALS, but *Platyoides* and *Trochanteria* do not. A cladistic analysis of trochanteriid genera will be necessary to determine the most parsimonious groundplan state for that family.

NOTES ON OUTGROUPS

The most obvious difference among the outgroup genera thus far surveyed is the ap-

parent absence of cylindrical gland spigots on the PMS and PLS of at least some genera currently assigned to the Clubionidae, Anyphaenidae, and Miturgidae. The absence of cylindrical glands was recorded in the Clubionidae (as well as the Filistatidae, Scytodidae, Pholcidae, Dysderidae, Segestriidae, and Salticidae) by Kovoov (1987). However, in the other outgroup taxa examined to date, including all the phrurolithine, liocranine, corinnine, castianeirine, and tracheline genera examined, these spigots do occur, and in essentially the same form as within the Gnaphosoidea. Determining the polarity of this feature will require documentation of cylindrical gland spigot morphology in more distantly related outgroups.

Much work remains to be done before homologies of spigot types across all araneomorphs will become clear. Further studies, particularly of cylindrical gland spigots in cribellate taxa and their closest relatives, will be necessary to determine the generality of the differences in spinneret morphology detected between gnaphosoids and other araneomorphs, and their phylogenetic and systematic significance.

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