

Higher Level Phylogenetics  
of Erigonine Spiders  
(Araneae, Linyphiidae, Erigoninae)

GUSTAVO HORMIGA

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## ABSTRACT

Hormiga, Gustavo. Higher Level Phylogenetics of Erigonine Spiders (Araneae, Linyphiidae, Erigoninae). *Smithsonian Contributions to Zoology*, number 609, 160 pages, 48 figures, 79 plates, 2000.—This paper provides the first numerical cladistic analysis of erigonine phylogenetic relationships based on a sample of taxa. A total of 73 characters, most of them morphological, have been scored for 31 erigonine genera plus 12 outgroup taxa. The parsimony analysis of these data supports the monophyly of Erigoninae based on two synapomorphies: the male pedipalpal tibial apophysis and the loss of the female pedipalpal claw. The monophyly of Linyphiidae and of Linyphiidae plus Pimoidae also is supported. One of the largest clades within the erigonines is the “Distal Erigonines clade,” whose monophyly is supported by the loss of the taenidia in the tracheoles and the loss of the distal dorsal spine of tibia IV. The clade composed of Stemonyphantinae plus Mynogleninae is the sister group of Erigoninae. A number of relatively “basal” erigonine lineages, which have been classically regarded as “taxonomically problematic” or “transitional,” retain some plesiomorphic characters typical of other subfamilies, like the haplotracheate system or the taenidia in the tracheoles. The available data suggest that the cephalothoracic sulci and glands found in mynoglenines and erigonines are not homologous.

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# Higher Level Phylogenetics of Erigonine Spiders (Araneae, Linyphiidae, Erigoninae)

*Gustavo Hormiga*

## Introduction

The Erigoninae are a large group of small spiders within the araneoid family Linyphiidae. Their body size ranges from 1 to 6 mm, but most are about 2 mm (Roberts, 1995). In the United States they are called “dwarf spiders,” in England “money spiders,” and in German they are known under the common name of “Zwergspinnen.” In northern Europe alone there are more than 300 species of erigonines (Heimer and Nentwig, 1991; Roberts, 1993), which is about 25% of the total spider fauna. About 650 species and 122 genera of erigonines have been described for America north of Mexico (Buckle et al., 1994) so far. Erigonines are apparently the dominant spider group of the temperate and cold regions of the Northern Hemisphere. They also are present in the Southern Hemisphere but seem to be less diverse, although these faunas are still very poorly studied. New Zealand (Millidge, 1988b) and Australia (contra Wunderlich, 1995; see Platnick, 1997:419) seem to lack native erigonine species. Little is known about the biology of erigonines (but see Blest and Taylor, 1977; Blest, 1987; Bristowe, 1958; Lopez, 1976; Lopez and Emerit, 1981; Meijer, 1976; Nielsen, 1932; Schaible and Gack, 1987; Schaible et al., 1986; Schlegelmilch, 1974; Simon, 1894, and Wiehle, 1960). Many

species are leaf-litter dwellers and build tiny sheet webs, although these webs are rarely documented (but see Nielsen, 1932).

One of the most conspicuous characteristics of many species of erigonines is the presence in the males of a vast morphological diversity of cephalic modifications, including lobes and turrets, grooves, pits, and modified setae (Figures 32–35). In a few species the females grip the males with their cheliceral fangs by the pits or grooves during copulation and then proceed to feed on secretions produced by specialized prosomic glands of the male, by depositing “saliva” on them and then reingesting it (Bristowe, 1931; Schlegelmilch, 1974).

Arachnologists have long agreed that the Erigoninae are the largest group of the Linyphiidae, which in turn are the second most diverse spider family. Exactly what an erigonine is remains a matter of debate. Although the assignment of a large fraction of linyphiid genera to the subfamily Erigoninae seems uncontroversial to most authors, the position of many genera and the exact taxonomic limits of this subfamily remain a vexing question.

The Linyphiidae have a long taxonomic history, with some of the names dating from Clerck’s *Aranei Svecici* in 1757. The history of the taxonomy of the linyphiids has been summarized by Merrett (1963). More recent studies on the higher level systematics of the family (or parts of it) are those of Blest (1976, 1979), Hormiga (1994a, 1994b), Lehtinen and Saaristo (1970), Merrett (1963), Millidge (1977, 1983, 1984, 1985, 1986, 1988a, 1993b), van Helsdingen (1986), and Wunderlich (1986). Some of these groups are detailed in Appendix 2.

From Simon’s posthumous sixth tome of *Les Arachnides de France* (1926, 1929) until the late 1970s linyphiids were divided into two subfamilies, the Erigoninae and the Linyphiinae (but see Lehtinen, 1967). Wiehle (1956, 1960) recognized similar groups but treated them at the family level; he used the name Micryphantidae for the erigonines. The division into two groups (regardless of whether they were treated as subfamilies

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or families) seemed, at that time, to be quite clear cut, except for a number of genera that seemed to be intermediate between the linyphiines and the erigonines. Depending on what set of characters were taken into account, these so-called "transitional genera" would group in one subfamily or another. Merrett (1963) detailed many of these problems, mainly within the context provided by the male palp morphology of British linyphiids, although he was well aware of the fact that "palpal morphology is often liable to give misleading impressions of affinities if not considered in relation to other taxonomic characters." Merrett's (1963) study, however, divided the family into two main groups (linyphiines and erigonines). Lehtinen (1967:396) expressed serious doubts about the division of linyphiids into two groups and suggested that linyphiids had to be "radically reclassified according to all characters. Most probably there are more than two main groups, but the naming of them will be a difficult problem." Blest's (1976) study on the anatomy of the linyphiid tracheal system was an important step forward, and it suggested what is still regarded as one of the diagnostic synapomorphies of erigonines: the desmitracheate pattern, in which the median pair of the two pairs of tracheal trunks is extensively divided into many tracheoles that go into the prosoma (Lamy, 1902).

Until the late 1960s, most of the work on linyphiids had been done on the Holarctic fauna. The study of linyphiids from the southern hemisphere and the tropical regions had an important impact on the understanding of the family, starting with the addition of a third subfamily, the Mynogleninae (Lehtinen, 1967; Blest, 1979), a relatively small clade distributed in Africa (Holm, 1968), New Zealand (Blest and Taylor, 1977; Blest, 1979), and Tasmania and some southern Pacific islands (Hormiga, unpublished).

The single worker in modern times who has studied in most detail the higher level systematics of linyphiids has been A.F. Millidge. Millidge has attempted in several papers to identify the major lineages of linyphiids and to find the closest relatives of the family. Some of his results are summarized in Appendix 2. His hypotheses have changed as he added new data to the initial results. He started with the examination of the male palpal morphology (Millidge, 1977), followed with the epigynal and tracheal system morphology (Millidge, 1984), which he subsequently revised (1986), and concluded (so far) with his controversial opinions that linyphiids are not araneoids (Millidge, 1988a), which has been rebutted by several workers (Coddington, 1990a, 1990b; Hormiga, 1993, 1994a, 1994b; Peters and Kooor, 1991) as well as by the most exhaustive treatment of araneoid phylogenetics published to date (Griswold et al., 1998). In his most recent subfamilial classification, Millidge (1993b) recognized seven linyphiid subfamilies or groups (see Appendix 2): Mynogleninae, Dubiaraneinae (a new subfamily), Erigoninae, Linyphiinae, Micronetinae, Lepthyphantinae, and an admittedly artificial group of miscellaneous genera that includes most of the taxa that he had grouped in his 1984 classification under his "*Stemonyphantess* group." Mil-

lidge's (1993b) hypothesis was based mostly on epigynal characters, with some additional data from the tracheal system. Millidge did not address the poor fit between the extensively studied male palpal morphology (including his own 1977 hypothesis), and many other characters, and the new classification. Millidge did not justify why one character system is to be preferred over others to reconstruct the phylogeny of the group, or why the information from as many character systems as possible should not be used.

In my opinion four major problems afflict linyphiid systematics, especially at the genus level and above. First, cladistic research is virtually absent in linyphiid literature, and systematic problems above the genus level have received little attention. Second, when higher level problems have been treated, the "single-character system" approach has predominated, that is, authors have used data derived from a single character system (e.g., the morphology of the palp; Millidge, 1977) to group taxa, and they have excluded or ignored other equally valid character systems. Third, phenetic (overall similarity) and/or supposedly "evolutionary" criteria have been commonly used to delimit higher taxa. The goal of this approach apparently has been to maximize phenetic homogeneity within taxa by excluding offending "dissimilar taxa" from the group. For example, in his description of the monotypic erigonine genus *Miftengris* (known from a single male specimen), Eskov pointed out its close affinities to *Pelecopsis* Simon, but he justified the erection of the new genus on the basis of only a single difference, the "wide and irregularly curved embolus" (Eskov, 1993:52). This approach, which is common practice among some taxonomists, probably renders *Pelecopsis* paraphyletic and disregards monophyly, now almost universally acknowledged as mandatory in taxonomy. Similarly, the same author erected the monotypic erigonine genus *Okhotigone* Eskov on the basis of some minor differences with *Entelecara* Simon, despite admittedly sharing most of the features of latter genus (Eskov, 1993:55). Eskov is the author of more than 50 linyphiid genera (many of them monotypic), and one wonders how many of these genera will survive phylogenetic scrutiny. Simply put, monophyletic groups are real evolutionary entities, but paraphyletic and polyphyletic groups exist only in the taxonomist's imagination. Fourth, many new taxa have been established based upon studies of faunas or regions but which were outside a revisionary context. Such approach can potentially compromise the rigor of any systematic work by overlooking close relatives that live outside the study area or descriptions of the same taxa from different regions. These practices have resulted in an extraordinary number of monotypic genera in the Linyphiidae, particularly in the Erigoninae.

The present study tests the monophyly of the Erigoninae and provides a starting point to reconstruct, using numerical cladistic methods, the major lineages and their interrelationships within this subfamily. This work is based on a sample of linyphiid genera and outgroup taxa and uses data from character systems that have classically been used in linyphiid system-



atics, as well as some novel ones. This paper grows from my previous work on pimoids and linyphiids (Hormiga, 1994a, 1994b) in which, using the same approach, I studied the systematics of the sister group of linyphiids (Pimoidae) and began to explore its implications for the phylogeny of Linyphiidae. This work is explicitly designed to study erigonine phylogeny but does not attempt to study the interrelationships of linyphiid subfamilies; however, because the taxonomic sample includes representatives of the subfamilies currently accepted (except the somewhat controversial Dubiaraneinae, recently erected by Millidge (1993b); see "Taxon sampling"), it provides an opportunity to expand and test some of the most recent hypotheses, such as those of Wunderlich (1986) and Hormiga (1994b).

#### METHODS AND MATERIALS

**TAXON SAMPLING.**—I use an exemplar approach to sample erigonine diversity: characters are scored for a particular species, rather than using a ground plan for a given taxon. If possible, the type species is selected, and if the character information is correctly scored, the character data should not change regardless of any taxonomic changes in the genus because the type species goes, by definition, with the genus name. The risk exists that the character vector for the type and the genus ground plan may not be identical. One alternative is to postulate ground plans for taxa and to use those as "terminal taxa" in the analysis; however, to succeed, this second approach requires a comprehensive systematic knowledge of, and phylogenetic hypotheses for, the study taxa (see review by Yeates, 1995). Those requirements are scarcely met by the current taxonomic state of the linyphiids and the erigonines in particular. Results based on the analysis of reconstructed taxa are dependent upon the accuracy of the reconstruction. It seems then that, at least for the present study, the exemplar approach will be more fruitful and a more durable contribution given the nature of the problem. The exemplar approach also is commonly used in molecular systematics, where often nucleotide sequence data for a given taxon are the results of sequencing samples from a single species (and often a single individual).

Sampling the Erigoninae posed a special problem in this study because it was unclear initially how to define an erigonine. The currently accepted diagnostic characters (see Hormiga, 1994b, and references therein) are the presence of a tibial apophysis in the male pedipalp and a desmitracheate pattern in the tracheal system (an internal character that cannot be assessed without partially digesting the specimen). The only explicit and exhaustive (to date) assignment of all the linyphiid taxa to subfamilies was given in Brignoli's (1983) catalog. Unfortunately, Brignoli never specified the criteria he used to make these assignments, particularly for the old taxa that had not been studied since their original description. Brignoli listed approximately 300 valid linyphiid genera; more than 200 of those were in his Erigoninae. Many more genera have been added to the family in the past decade. Platnick (1993) listed

461 valid genera in the Linyphiidae, and his latest catalog (Platnick, 1997) included a total of 530 genera (a net increase of 71 linyphiid genera in four years). In the absence of a sound and widely accepted taxonomic scheme for the Erigoninae, I have decided to use the most finely grained classification available for the erigonine genera to guide taxon sampling. Millidge (1977) provided the most detailed classification of linyphiids, including erigonines, based on the male palpal morphology. Although Millidge (1984) abandoned many of the views that he held in the former paper, the 1977 monograph still partitioned linyphiid diversity, using one of the most informative character systems (male palpal morphology), which he scored for a large number of European taxa. The sixteen groups of Millidge (1977) (including one assemblage of miscellaneous genera), their composition, and the sample used in this study are given in Appendix 2. Except when specimens were not available, I selected at least two genera from each group, which allowed a test of the monophyly of those groups. Finally, because the current study is the first to investigate erigonine higher level systematics with quantitative analysis of objectively defined and sampled homology hypotheses (characters), where one begins may not be as important as to begin in the first place.

I selected the following species (listed in alphabetical order) as a taxonomic sample of the Erigoninae. Their character states are scored in the character matrix (Appendix 1). See Appendix 4 for specimens examined. *Araeoncus crassiceps* (Westring), *Asthenargus paganus* (Simon), *Ceratinops inflatus* (Emerton), *Diplocentria bidentata* (Emerton), *Diplocephalus cristatus* (Blackwall), *Dismodicus decemoculatus* Emerton, *Drepanotylus uncatus* (O.P.-Cambridge), *Entelecara acuminata* (Wider), *Erigone psychrophila* Thorell, *Gonatium rubens* (Blackwall), *Gongylidiellum vivum* (O.P.-Cambridge), *Gongylidium rufipes* (L.), *Grammonota pictilis* (O.P.-Cambridge), *Hilaira excisa* (O.P.-Cambridge), *Hybocoptus decollatus* (Simon), *Hyllyphantes graminicola* (Sundevall), *Islandiana princeps* Brændegaard, *Laminacauda plagiata* (Tullgren), *Leptorhoptrum robustum* (Westring), *Lophomma punctatum* (Blackwall), *Oedothorax gibbosus* (Blackwall), *Ostearius melanopygius* (O.P.-Cambridge), *Pelecopsis nemoralis* (Blackwall), *Savignia frontata* (Blackwall), *Sciastes truncatus* (Emerton), *Sisicus apertus* (Holm), *Tapinocyba praecox* (O.P.-Cambridge), *Tibioploides pacificus* Eskov and Marusik, *Tmeticus tolli* Kulczynski, *Typhochrestus digitatus* (O.P.-Cambridge), and *Walckenaeria directa* (O.P.-Cambridge).

The representatives of remaining linyphiid subfamilies are those used in Hormiga (1994b) (see Appendix 4 for specimens examined): *Linyphia triangularis* (Clerck) and *Microlinyphia dana* (Chamberlin and Ivie) (Linyphiinae, Linyphiini); *Bolyphantes luteolus* (Blackwall) and *Lepthyphantes tenuis* (Blackwall) (Linyphiinae, Micronetini); *Haplisis diloris* (Urquhart) and *Novafroneta vulgaris* Blest (Mynogleninae); and *Stemonyphantes blauveltae* Gertsch (Stemonyphantinae). Pimoids

are represented by *Pimoa altiocolata* (Keyserling) and *P. rupicola* (Simon).

My former analyses (Hormiga, 1993, 1994a, 1994b) had used Tetragnathidae and Araneidae as outgroups of linyphiids plus pimoids. Recent progress on the phylogeny of Araneoidea (Griswold et al., 1994, 1998) suggests that a large clade that includes the families Theridiidae, Nesticidae, Synotaxidae, and Cyatholipidae is the sister group of linyphiids plus pimoids. Based on those results, I have selected *Steatoda grossa* (C.L. Koch) (Theridiidae), *Theridiosoma gemmosum* (L. Koch) (Theridiosomatidae), and *Tetragnatha versicolor* Walckenaer (Tetragnathidae) as representative taxa of the closest lineages outside the linyphiid-pimoid clade.

**SPECIMEN PREPARATION AND STUDY.**—The methods of study follow those described in Hormiga (1994a), except in details listed below. Specimens (Appendix 4) were generally examined and illustrated using Leica Wild M10, Leica MZ-APO, and Wild M-5A stereoscopic microscopes with a Wild camera lucida. Further details were studied using Leitz Ortholux II, Olympus BH-2, and Leica DMRM compound microscopes and were illustrated using a drawing tube. The AMRAY 1810 and the Cambridge Stereoscan-100 of the Smithsonian Institution's Scanning Electron Microscope (SEM) Laboratory were used to create the scanning electron photomicrographs.

Female genitalia were excised and tissue was cleaned away using microscissors or fine, sharpened needles. The epigynum was then placed in methyl salicylate for examination under both the dissecting and the compound microscope. For examination with the compound microscope, the epigynum was temporarily mounted as described in Coddington (1983). Household bleach or a KOH solution was sometimes needed to dissolve nonchitinous tissues.

Male palps were first studied in 95% ethanol and then were transferred to methyl salicylate (Holm, 1979), temporarily mounted as described in Coddington (1983), and then illustrated. Most of the illustrations were done using the compound microscope, and at least ectal, mesal, and ventral views of the palp were drawn. Next the embolic division was excised by breaking the column (the membranous connection between the supratégulum and the radix). This procedure allowed detailed examination of the supratégulum and of the embolic division from many different angles. At least one illustration of the embolic division and of the rest of the dissected palp was then done.

Specimens examined with the SEM were first transferred to a vial with 70% ethanol and then cleaned ultrasonically for one to three minutes. The specimen was transferred to absolute ethanol and left overnight. Most of the specimens were air dried, and a few were submitted to critical point drying. The specimens were glued to round-headed rivets using an acetone solution of polyvinyl resin and then sputter coated (a carbon base coat followed by a gold-palladium coat) for examination using the SEM.

Spinneret spigot morphology was examined using the SEM. Methods of study and homology assessments follow those of Coddington (1989), although most abdomens were air-dried. In the few cases in which not enough specimens were available for SEM examination, I used a Leitz Ortholux II compound microscope with epi-illumination at  $\times 110$ .

All SEM images have been saved as 4 $\times$ 5 negatives (for archival purposes) and as graphic electronic files. Plates of SEM images were composed and labeled electronically using Adobe Photoshop® and Adobe Illustrator®. Left structures (e.g., palps, chelicerae, etc.) are depicted in the figures and plates, but in a few instances the right structure is used (unless otherwise noted in the figure legend, the images of right structures are reversed to facilitate comparisons).

**CLADISTIC ANALYSIS.**—I scored a total of 73 characters: 31 male and nine female genitalic characters, six spinneret spigot morphology characters, 25 somatic morphological characters, and two behavioral characters (see Appendix 1). Six of the characters are phylogenetically uninformative in the present context (characters 5, 12, 44–46, and 53) but have been retained in the matrix because of their importance for future studies of linyphiid and/or erigonine phylogeny; fourteen characters are multistate. The parsimony analyses were performed using the computer programs Hennig86 version 1.5 (Farris, 1988), NONA version 1.6 (Goloboff, 1993), and PAUP 3.1.1 (Swofford, 1993). MacClade version 3.0 (Maddison and Maddison, 1992) and Clados version 1.2 (Nixon, 1992) were used to study character optimizations on the cladograms. Ambiguous character optimizations were usually resolved so as to favor reversal or secondary loss over convergence (Farris optimization or ACCTRAN), otherwise the optimization scheme is discussed in the text. The fourteen multistate characters were treated as nonadditive (unordered or Fitch minimum mutation model; Fitch, 1971). The computer program PHAST (Goloboff, 1997) was used to calculate Bremer support indices (BS; "decay indices") (Bremer, 1988, 1995; Donoghue et al., 1992).

#### ABBREVIATIONS

Anatomical abbreviations used in the text and figures are as follows.

A	alveolus
AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALE	anterior lateral eye(s)
ALS	anterior lateral spinneret
AME	anterior median eye(s)
ARP	anterior radical process
AT	epigynal atrium
BH	basal haematodocha
CB	cymbium
CD	copulatory duct
CL	column
CO	copulatory opening
CY	cylindrical gland spigot(s)
DP	dorsal plate of the epigynum
DSA	distal supratégular apophysis

E	embolus
EA	embolic apophysis
ED	ejaculatory duct
EM	embolic membrane
F	fundus
FD	fertilization duct
FG	Fickert's gland
FL	flagelliform gland spigot(s)
LC	lamella characteristica
m	membrane (or membranous)
MA	median apophysis
MAP	major ampullate gland spigot(s)
mAP	minor ampullate gland spigot(s)
MSA	marginal supratregular apophysis
MTA	mynoglenine tegular apophysis
MTP	mynoglenine tegular process
P	paracymbium
pdp	pedipalpal
PEP	primoid embolic process
PI	piriform gland spigot(s)
PLE	posterior lateral eye(s)
PLS	posterior lateral spinneret
PME	posterior median eye(s)
PMS	posterior median spinneret
PT	protegulum
PTA	pedipalpal tibial apophysis
R	radix
S	spermatheca
SF	supratregular foramen
SPT	supratregulum
ST	subtegulum
T	tegulum
TA	terminal apophysis
TP	radical tailpiece
TS	tegular sac
VP	ventral plate of the epigynum

Institutional abbreviations used throughout are as follows.

AMNH	American Museum of Natural History, New York, USA
CAS	California Academy of Sciences, San Francisco, USA
IZUI	Institut für Zoologie der Universität, Innsbruck, Austria
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
OM	Otago Museum, Dunedin, New Zealand
UB	Universitat de Barcelona, Barcelona, Spain
USNM	Collections of the NMNH (including collections of the former United States National Museum)
UW	Burke Memorial Washington State Museum, Seattle, USA
ZMUC	Zoological Museum, University of Copenhagen, Denmark

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## Results

### CHARACTERS

This section details the characters used in the phylogeny reconstruction (Appendix 1), grouped by "character systems." When necessary for clarity, examples of taxa exhibiting a particular character state will be given in parentheses after the description of the state. The characters marked with an asterisk have been discussed in detail in Hormiga (1994a, 1994b) and will not be discussed herein unless new data or interpretations make it necessary.

#### *Male Palpal Morphology*

CHARACTER 1\*. Cymbium morphology: 0=smooth, 1=with a cymbial denticulate process. The presence of such a unique process on the cymbium is a synapomorphy of pimoids (Hormiga, 1993, 1994a).

CHARACTER 2. Cymbium size: 0=longer and wider than tibia and patella; 1=reduced relative to the size of the pedipal-

palp tibia and patella. In several linyphiids the size of the cymbium is clearly shorter than the pedipalpal tibia or patella, e.g., *Prinerigone vagans* (Audouin), *Tmeticus* spp., and *Leptorhoptum robustum* (Figure 19A,B). The apomorphic state (1) is interpreted as a result of a reduction of the cymbium, not as an increase of the size of the other pedipalpal segments; however, in the aforementioned taxa the male pedipalpal tibia (and sometimes the patella too) seem somewhat larger than in most linyphiids.

CHARACTER 3\*. Pimoid cymbial sclerite: 0=absent; 1=present. The presence of this sclerite is a synapomorphy of pimoids (Hormiga, 1993, 1994a).

CHARACTER 4\*. Paracymbium attachment: 0=integral (Hormiga et al., 1995, fig. 6E,H); 1=intersegmental (Figures 18A, 20B, 26A; Hormiga et al., 1995, fig. 5A,B); 2=articulated (Hormiga et al., 1995, fig. 7C-E).

CHARACTER 5. Paracymbium morphology: 0=linguiform and fused to pimoid cymbial sclerite (Hormiga, 1994a, figs. 15-17); 1=triangular (Hormiga, 1994a, figs. 128, 158, 303, 304); 2=*Stemonyphantes* type (Hormiga, 1994b, figs. 2A, 3C); 3=U- or J-shaped (Figures 1B, 5B, 23A; Hormiga et al., 1995, fig. 5A,B); 4=hook-shaped (Coddington, 1986, fig. 154); 5=straight and narrow (Hormiga et al., 1995, fig. 7C,D). The coding of this character has been slightly modified from that of Hormiga (1994b) to better fit the present selection of taxa.

CHARACTER 6\*. Paracymbium apophyses: 0=present (Hormiga, 1994b, fig. 13A); 1=absent (Figure 13B).

CHARACTER 7\*. Mynoglenine tegular apophysis: 0=absent; 1=present (Hormiga, 1994b, figs. 4A, 5A).

CHARACTER 8. Protegulum: 0=absent; 1=present (Figures 4A,C, 7A,B, 16A-C, 17A-C, 21A-C, 27A,B; Plates 15A-E, 22A-D, 40A,B, 58B,C,E, 62A-D). The protegulum (Holm, 1979:256) is a membranous, often sac-like, protuberance of the ectoapical part of the tegulum. Crosby and Bishop (1925:6) referred to it as the "anterior part of the bezel." Its function remains unknown. Holm (1984:140) suggested that the protegulum could have a mechano- and/or chemoreceptive function during copulation, in part because in the (artificially) expanded palp the protegulum is turned in the same direction as the embolus. Although this possibility remains untested, Huber (1993, 1995) has convincingly shown that artificial expansions very often provide an inaccurate picture of the spatial interrelationships of the palpal sclerites during copula. The protegulum is present in most erigonine spiders, but certainly not in all (e.g., *Laminacauda plagiata*, Plate 41A,B,E). Unfortunately, the majority of descriptive taxonomic papers are silent about this structure.

CHARACTER 9. Protegular papillae: 0=absent; 1=present (Plate 15D,E). As Holm (1979) noted for *Pelecopsis* species, the protegulum may bear a cluster of papillae. In some cases these papillae are large and conspicuous (e.g., *Sciastes truncatus*, Plate 58E,F) and can be seen with transmitted light microscopy at high magnification, but in other cases the papillae are

much smaller and can only be seen by using scanning electron microscopy.

CHARACTER 10. Tegular sac: 0=absent; 1=present (Figure 12C,D; Plate 30A-D). The tegular sac is a membranous sac on the ectal side of the tegulum, adjacent to the protegulum, the latter being in a more apical position. In the taxa so far examined, the tegular sac does not bear papillae. In *Gongylidium rufipes* the tegular sac is an elongate membranous structure, larger than the adjacent papillose protegulum (Plate 30D), whereas in *Tmeticus tolli* the sac is relatively small (Plate 67B-D). *Gonatium* species have a membranous projection (tegular apophysis in Millidge, 1981, figs. 1, 5) on the tegulum of varying length that, when long enough, closely follows the curve of the embolus. In *G. rubens* (Figure 10A,E; Plate 27A-C) this structure is a long membranous bag on the anteromesal region of the tegulum. The long and filiform embolus is partially hidden in a groove along the anterior margin of this bag. Although *G. rubens* lacks a protegulum, position and special similarity of the "bag" suggest that it is a tegular sac. In *Oedothorax gibbosus* the papillose protegulum (Figure 21A,B, Plate 49D) is prolonged into a membranous region without papillae that has been coded herein as a tegular sac. The tegular sac could be a homolog of what Holm (1979:256, figs. 66, 72, 74) designated as the "protegular basis" in some African species of *Pelecopsis*; unlike the protegulum and the tegular sac, the protegular basis of *Pelecopsis* is sclerotized, not membranous. Coding *Pelecopsis* as having a tegular sac (character 10) produces no topological changes in the minimal-length trees resulting from the parsimony analysis, but it increases tree length by one step. Holm (1979:256) also has suggested that the protegulum with its basis corresponds to "the tegular prominence (in the genus *Mynoglenes* (= *Haplinis*)) of Blest and Pomeroy (1978)." Coding the tegular process of *Haplinis* as a homolog of the protegulum (*Novafroneta* lacks the mynoglenine tegular process; Hormiga, 1994b) produces no topological changes in the minimal-length trees and requires one extra step (the origin of the protegulum in *Haplinis*).

CHARACTER 11. Suprattegulum: 0=absent; 1=present (Figures 9E, 17C, 20C, 22C). In the present taxonomic sample, the suprattegulum is present in all linyphiids except *Sisicus apertus* (Figure 26C). *Microbathyphantes* (= *Priscipalpus*) had been described as lacking a suprattegulum (Beatty et al., 1991), but Saaristo (1995:43) has subsequently shown that the suprattegulum is actually present.

CHARACTER 12. Suprattegulum: 0=continuous with tegulum (Figures 9E, 17C, 20C, 22C); 1=articulated (van Helsdingen, 1968, figs. 1, 22, 36; Hormiga, 1994b, fig. 2C). The articulated suprattegulum is an autapomorphy of *Stemonyphantes* (and thereby phylogenetically uninformative given the present taxonomic sample), but in the future it may help to identify the closest relatives of this enigmatic genus. Characters 11 and 12 were combined into a single character in Hormiga (1994b, character 13); keeping these two homology statements separate (the presence of a suprattegulum and its morphological condi-

tion) unambiguously preserves the presence of a supratregulum as a linyphiid synapomorphy.

CHARACTER 13. Distal supratregular apophysis (DSA): 0=absent; 1=present (Figures 2B, 6G). There is a remarkable range of variation in the morphology of the supratregulum; thus, establishing the homologies in some taxa can be difficult. The degree of sclerotization of the supratregulum itself is variable. The dorsal side usually is sclerotized, but in some cases the ventral side is either less sclerotized or often membranous (e.g., in *Ostearius melanopygius*, Figure 22A,C). In other cases the supratregulum is, overall, more sclerotized (e.g., in *Araeoncus crassiceps*, Figure 1E), leaving a small aperture through which the sperm duct runs to enter into the embolic division. I suggest the term “supratregular foramen” (SF) for this aperture that connects to the column (Figures 1E, 6G, 25D). I distinguish two types of supratregular apophyses for which I suggest the names “distal supratregular apophysis” (DSA) and “marginal supratregular apophysis” (MSA). The DSA is located, as its name suggests, distal to the supratregular foramen, and it is present in most linyphiids (Figures 2B, 6G). The often highly sclerotized DSA usually can be seen in an ectal view of the unexpanded palp (Figures 6A,B, 11B). The MSA is a tooth-like process near the supratregular foramen, on the distal margin of the supratregulum (Figures 2B, 6G). The MSA is usually hidden between the embolic division and the ventral side of the cymbium (Figures 6A,B, 15B,E, 20B,C). Both *Asthenargus paganus* (Figure 3E) and *Sciastes truncatus* (Figure 25D) have a supratregulum that is barely continued beyond the supratregular foramen and lacks the typical increased level of sclerotization found in most DSAs. For this reason they have been coded as lacking the typical DSA, although their phylogenetic position on the resulting cladograms suggests that this absence (or reduction) is secondary and that it has evolved in these two genera independently.

CHARACTER 14. Marginal supratregular apophysis (MSA): 0=absent; 1=present (Figures 1E, 2B, 9E). See description and discussion for character 13, above.

CHARACTER 15\*. Median apophysis: 0=present; 1=absent. The araneoid median apophysis is secondarily absent (lost) in linyphiids.

CHARACTER 16\*. Conductor: 0=present; 1=absent. The conductor is secondarily absent (lost) in linyphiids.

CHARACTER 17\*. Embolus length: 0=long (Figures 2C, 7D, 10F); 1=short (Figures 6F, 14E, 17D).

CHARACTER 18\*. Embolic membrane (“median membrane” of Saaristo and Tanasevitch, 1996:170): 0=absent; 1=present. The embolic membrane is an outgrowth of the column (Figures 5E, 17C, 18C, 22F, 25B) and is present in most linyphiids, including *Araeoncus humilis* (Blackwall) (Figure 2B,C) and *Diplocephalus cristatus* (Figure 6D,E) (cfr. Merrett, 1963, figs. 65, 66).

CHARACTER 19\*. Pimoid embolic process (PEP): 0=absent; 1=present. This structure is an autapomorphy of Pimoidae (Hormiga, 1994a).

CHARACTER 20\*. Radix: 0=absent; 1=present (Figures 18C, 20A,D, 30A,E,F). The araneid and the linyphiid radix are

not homologous sclerites (Hormiga, 1994b; Griswold et al., 1998; Scharff and Coddington, 1997).

CHARACTER 21. Radical tailpiece: 0=absent (Figures 15F, 16D); 1=present (Figures 13A, 18C, 19C, 30A).

CHARACTER 22. Radical tailpiece morphology: 0=straight (*Laminacauda plagiata*, Figure 18C); 1=spiraled (*Grammonota pictilis*, Figure 13F,H); 2=curved ectally (*Islandiana princeps*, Figure 17B); 3=curved mesally (*Leptorhoptrum robustum*, Figure 19C); 4=pointing anteriorly (*Erigone psychrophila*, Hormiga, 1994b, fig. 7A–D).

Crosby and Bishop (1928:5) used the term “scaphium” for the radix and referred to the radical tailpiece as the “mesal tooth of the scaphium” (“d” in their figure 3) (at least in the genera *Erigone*, *Eperigone*, and *Halorates*). In many erigonines the radix is prolonged toward the base of the cymbium. This was called the “tailpiece of the embolic division” by Crosby and Bishop (1925:6, fig. 4). Merrett (1963:350) referred to it as the “radical part,” of the (simple type of) embolic division. The posterior prolongation of the radix (i.e., the radical tailpiece, character 21) found in many erigonines is a potential homology, and it has been coded as such in the character matrix. Tailpiece morphology has been coded in character 22, and states 2, 3, and 4 of this character are autapomorphic in the present context. In *Gongylidiellum vivum* (Figure 11A,D,E) the radix is reduced to an enlargement at the base of the tegulum. The sclerite that Merrett (1963, fig. 78) identified as a radix in *G. vivum* (labeled “rp” in his figures) does not have the sperm duct going through it (Figure 11E) and has been coded herein as a lamella characteristica (character 27). Similarly, in *Asthenargus paganus* the sclerite labeled as radix by Merrett (1963, fig. 74) does not have the sperm duct going through it (Figure 3A,C,F,G) and has been reinterpreted herein as a lamella characteristica (character 27). *Hilaira excisa* (the type species of the genus) has an extremely reduced radix (to the point of not being clearly recognizable as such; Figure 14B,E) and has been coded as a “not applicable” for characters 21 and 22. I also have studied *H. vexatrix* (O.P.–Cambridge), which has a radix with a tailpiece (Figure 14K), but because the monophyly of the genus, as currently defined, might be questionable (Millidge, 1977:8), I have preferred to leave these two entries (characters 21 and 22) in the matrix as unresolved (coding *Hilaira* as having a radical tailpiece would not add any extra steps to the minimal-length trees).

CHARACTER 23. Anterior radical process (ARP): 0=absent; 1=present (*Typhochrestus digitatus*, Figure 30A–C; Plate 69A,B,D). The ARP is what Merrett (1963) called the “process of radical part (rpp).” In some erigonines there is more than one process in the radical part (e.g., *Islandiana princeps*, Figure 17D), or no process at all (e.g., *Leptorhoptrum robustum*, Figure 19C); therefore, I have introduced the term “anterior radical process” to designate this particular class of homologs. The ARP is adjacent to the embolus and points toward the distal end of the palp (Plate 69A,D). In some instances the ARP is a small protuberance on the radix (e.g., *Lophomma punctatum*, Figure 20A; Plate 46C). Crosby

and Bishop (1928:6, "b" in their figs. 67, 68, 70) referred to the ARP in *Erigone psychrophila* (Plate 25A) as the "median tooth of the scaphium."

CHARACTER 24\*. Column: 0=absent; 1=present. Recent progress in araneoid systematics (Hormiga et al., 1995; Scharff and Coddington, 1997; Griswold et al., 1998) suggests that the linyphiid column and the araneid distal haematodocha are not homologous structures; however, the column could be a homolog of the membrane that connects the tegulum to the embolus base in tetragnathids (Hormiga et al., 1995, figs. 9C, 10C, 13E-H). Although the linyphiid column and the tetragnathid embolus-tegulum membrane have been coded as homologous structures in the matrix of Appendix 1, they require independent origins in both lineages when optimized on the minimal-length cladograms that result from the parsimony analysis.

CHARACTER 25\*. Fickert's gland: 0=absent; 1=present (Hormiga, 1994b, fig. 14B).

CHARACTER 26\*. Terminal apophysis: 0=absent; 1=present (Hormiga, 1994b, fig. 8A-C). This character had been coded as present in *Erigone* in Hormiga (1993, 1994a, 1994b). Reexamination of this homology problem within a wider taxonomic context suggests that the radical process that I designated as "terminal apophysis" in *Erigone* (Hormiga, 1994b, fig. 7) is better interpreted as a homolog of the anterior radical process (character 23). In *Erigone*, Crosby and Bishop (1928) referred to what I have named the anterior radical process as the "median tooth of the scaphium" ("b" in their figs. 67, 68, 70). The linyphiid terminal apophysis is a sclerite (and not just an apophysis) attached to the mesal side of the radix, adjacent to the embolus, by means of a membrane (Merrett, 1963; Hormiga, 1994b, fig. 9A,B,D). The sclerotized radical process of *Erigone* is continuous with the radix, lacks a membranous connection, and is located ectally on the radix. The linyphiid terminal apophysis seems to be restricted to the Linyphiinae and is not homologous to the equally named sclerite in the Araneidae. The degree of complexity of the linyphiid terminal apophysis varies widely, and it has been illustrated by Blauvelt (1936), Merrett (1963), Saaristo (1971, 1973a, 1973b, 1975), and van Helsdingen (1969, 1970), among others. In sum, the erigonine taxa examined herein lack the terminal apophysis, which in the linyphiids is restricted to the Linyphiinae, and that the linyphiid terminal apophysis is not homologous to its homonym found in some members of the Araneidae.

CHARACTER 27\*. Lamella characteristica: 0=absent; 1=present (Figures 14B-E, 15A-C,F,G). The lamella characteristica attaches to the radix by means of a membrane and is best seen in ventral or mesoventral views of the palp. This radical sclerite is found in linyphiines and erigonines. Its relative size and morphology varies widely across taxa; it can be particularly large in the Linyphiini (e.g., Hormiga, 1994b, figs. 8-11).

CHARACTER 28\*. Male pedipalpal tibial apophysis: 0=absent; 1=present (Figures 1B, 3B,D, 9H, 16C, 23A). Most erigonines have one or more apophyses on the male pedipalpal tibia; these apophyses are usually retrolateral. It seems more appro-

priate to describe them as "tibial apophysis(es)" than as "retrolateral tibial apophysis(es)." Although typical of erigonines, tibial apophyses can be found in other groups of linyphiids (e.g., *Labulla thoracica* (Wider) or *Floronia bucculenta* (Clerck)). The ventral tibial process of *Stemonyphantes* (Hormiga, 1994b, fig. 2A,B) is not considered homologous to the erigonine pedipalpal tibial apophysis (Hormiga, 1994b:16). The morphological complexity, position, and degree of sclerotization of the erigonine tibial apophyses varies widely and characteristically, and for that reason it is one of the classical characters used in the taxonomy of this subfamily.

CHARACTER 29. Male pedipalpal patellar ventral apophysis: 0=absent; 1=present (*Tmeticus tolli*; Figure 29B). A conical ventral apophysis on the male pedipalpal patella is found in several erigonines. This character seems to be variable at lower taxonomic levels. For example, *Hylyphantes graminicola* has a ventral apophysis (Figure 16C), but it is absent in *H. nigrinus* (Simon) (Figure 16H).

CHARACTER 30\*. Number of prolateral trichobothria on male pedipalpal tibia: 0=two; 1=one; 2=none.

CHARACTER 31. Number of retrolateral trichobothria on male pedipalpal tibia: 0=two; 1=four; 2=three; 3=one. State 0 of characters 30 and 31 have been added to the original characters in Hormiga (1994b) to describe the present taxonomic sample.

#### Female Epigynal Morphology

CHARACTER 32. Scape of dorsal plate: 0=absent; 1=present (*Linyphia triangularis*, Plate 8D).

CHARACTER 33. Scape of ventral plate: 0=absent; 1=present (*Haplinis diloris*, Plate 4F).

CHARACTER 34. Ventral plate scape morphology: 0=straight; 1=sigmoid (*Lepthyphantes tenuis*, Plate 6D).

These three epigynal characters (32-34) are described in Millidge (1984). In the present context the scape of the dorsal plate is a synapomorphy of the Linyphiinae, with homoplasy in the mynogenine genus *Haplinis*. Ventral plate scapes are found in many, not closely related, linyphiid groups. A sigmoid scape in the ventral plate is found in many micronetine genera (Millidge, 1984:256). In the present context the sigmoid scape is a synapomorphy of the Micronetini.

CHARACTER 35. Bisection of the sclerotized ventral surface of the epigynum: 0=absent; 1=present (*Diplocephalus cristatus*, Figure 6t, Plate 21D). An epigynal ventral plate bisected longitudinally is found in several erigonines (Millidge, 1984:250). The current data suggests two independent origins within the erigonines of the epigynal bisection.

CHARACTER 36\*. Atrium: 0=absent; 1=present (Figure 13A; van Helsdingen, 1969, fig. 21). The atrium, termed "bursa copulatrix" by Blauvelt (1936:90), is a paired epigynal chamber formed by enlargements of the proximal end of the copulatory ducts and is located between the ventral and dorsal plates. This character is difficult to define objectively because it is not

clear how much enlargement of the copulatory ducts qualifies as an atrium. In the character matrix (Appendix 1), the atrium has been coded as present in the Linyphiini (*Linyphia* plus *Microlinyphia*), in the mynoglennine genus *Haplinis*, and in two erigonines, *Grammonota* (Figure 13A) and *Sisicus* (Figure 26F). In all the minimal-length trees resulting from the parsimony analysis, the atrium is a synapomorphy of Linyphiini and has evolved independently in the remaining taxa. In the linyphiines the atrium is perhaps more highly developed than in other taxa, forming a distinct chamber between the dorsal and ventral plates, with the dorsal plate constituting the floor of the atrium (Millidge, 1984:255).

CHARACTER 37. Copulatory duct: 0=separate from the fertilization duct (Figures 5H, 16G); 1=spirals around the fertilization duct (van Helsdingen, 1968, figs. 13, 14, 28, 29). Spiraling of the copulatory duct around the fertilization duct (Millidge, 1993b) is an apomorphic condition found in several linyphiids, including some erigonines, such as *Spirembolus* (Millidge, 1980). In the present context this apomorphy is restricted to *Microlinyphia* and *Stemonyphantes* and seems to have arisen independently.

CHARACTER 38. Copulatory duct encapsulation: 0=absent; 1=present (*Laminacauda plagiata*, Figure 18D–F). In many linyphiids the copulatory duct is partially enclosed in a capsule of varying morphology and degrees of sclerotization (Millidge, 1984:235; 1993b). This character is difficult to define objectively because there always seems to be some sclerotization of the ducts, as Millidge (1984:235) himself admitted: “Probably encapsulation defined in this way is never completely absent, since the [copulatory] duct at its point of entry to the spermatheca is always within the spermathecal capsule.” I have tried to reflect in my character coding the presence of a clearly sclerotized capsule around the copulatory duct.

CHARACTER 39. Spermathecae: 0=two (*Diplocentria bidentata*; Figure 5H); 1=four (*Ostearius melanopygius*, Figure 22G,H). The number of spermathecae seems to be variable at lower taxonomic levels. For example, some species of *Gonatum* have two pairs of spermathecae (e.g., *G. japonicum* Simon in Millidge, 1981, fig. 27), whereas the majority have one only pair. A similar situation also is found in *Tetragnatha* (Tetragnathidae), which are secondarily haplogyne (Levi, 1981; Scharff and Coddington, 1997; Griswold et al., 1998).

CHARACTER 40. Fertilization duct orientation (as it leaves the spermatheca): 0=posterior (Figures 7J, 13J, 15H); 1=mesal (Figures 2D,E, 5H, 9I); 2=anterior (Hormiga, 1994a, figs. 12, 35, 121, 140, 317). This character (Millidge, 1984:235) describes the trajectory of the fertilization ducts as they leave the spermathecae, viewed either dorsally or ventrally. Pimoids have fertilization ducts directed anteriorly (Hormiga, 1994a), which is rather rare among araneoid spiders but is common in other groups, such as salticids (C.E. Griswold, pers. comm., 1997). The presence of anteriorly directed fertilization ducts is another synapomorphy supporting the monophyly of Pimoidae and is interpreted as such herein for the first time. All the linyphiids stud-

ied herein have posteriorly directed fertilization ducts, with the exception of many erigonines (which can have them mesally oriented). *Steatoda grossa* (C.L. Koch) (Theridiidae) (Levi, 1957, fig. 83) and *Theridiosoma gemmosum* (L. Koch) (Theridiosomatidae) (Coddington, 1986, fig. 152) also have posteriorly directed fertilization ducts.

### Somatic Morphology

CHARACTER 41. Male cephalic region: 0=not raised (Figure 32A); 1=entirely raised (Figure 32B). Those linyphiids in which the cephalic region is not entirely raised have relatively low lateral eyes (close to the margin of the cephalothorax), which is the araneoid plesiomorphic condition. When the entire cephalic region is raised, the lateral eyes are raised higher (relative to the margin of the cephalothorax), which is the apomorphic condition.

CHARACTER 42. Male posterior median eye(s) (PME) cephalic lobe: 0=absent; 1=present (Figure 32F–H). This lobe carries the PME but not the other eyes.

CHARACTER 43. Male post-PME lobe: 0=absent; 1=present (Figures 32I,J, 33A). This cephalic lobe is posterior to the PME but does not carry the eyes.

CHARACTER 44. Male inter-AME–PME lobe: 0=absent; 1=present (Figure 33B,C). This lobe is between the anterior median eye(s) (AME), and the PME but does not carry either eye group.

CHARACTER 45. Male clypeal lobe: 0=absent; 1=present (Figure 33D–F). This lobe is located anywhere between the anterior edge of the AME and the anterior margin of the prosoma.

CHARACTER 46. Male AME lobe: 0=absent; 1=present (Figure 33G,H). This lobe is between the clypeus and the anterior margin of the PME and carries only the AME. It can be distinguished from an entirely raised cephalic region because the lateral eyes are low (close to the margin of the cephalothorax), and the AME are high and far from the lateral eyes.

Characters 41–46 attempt to describe the different types of linyphiid cephalic lobes. Three of these characters (44–46) are phylogenetically uninformative in the present taxonomic sample, but they have been left in the matrix because they probably will be informative with a different sample and because, with this set of characters, I have tried to cover the majority of cephalic lobes found in linyphiids. Given the diversity of linyphiids and our present taxonomic knowledge, the list of characters may very well increase in future studies. Examples of taxa exhibiting these different characters are given in Appendix 3. The conjunction test (Patterson, 1982) suggests that different types of lobes are different homologs and, therefore, different characters. These hypotheses are independent of the position of the lobes, regardless of the presence or absence of cuticular pores and/or setae, which have been coded as independent character evidence. The occurrence of two different types of lobes in a particular taxon suggests that, at least for the taxon in question, the lobes are not homologous. Of the 15 possible combinations

of cephalic lobes, taking two at a time, at least 13 exist in linyphiids (examples are given in Appendix 3). I have not found any instances of linyphiids presenting the combinations of characters 41 plus 44 or characters 44 plus 46. Given the astonishing diversity of cephalic modifications in linyphiids, it will be no surprise if the two missing combinations are found in the future.

CHARACTER 47\*. Subocular clypeal sulci: 0=absent; 1=present (Plates 4A–E, 11A–D, 78A). These types of sulci, located on the clypeus below the ALE, are found only in the Mynogleninae and are present in both sexes.

CHARACTER 48. Male lateral sulci: 0=absent; 1=present (Figures 32A, 35B,D; Plates 17A,B,E, 47A, 64A–D, 70A–D). These sulci are more or less elongated incisions on the lateral side of the prosoma of the males of many erigonine spiders.

CHARACTER 49. Male prosomal pits: 0=absent; 1=present (Figure 32A; Plates 17A,E, 64A,B). A prosomic pit is a more or less deep cavity located in the lateral side of the prosoma. It seems that it is possible to find taxa that have pits in the absence of lateral sulci (e.g., *Micrargus apertus* (O.P.–Cambridge); Roberts, 1993, fig. 38h) or lateral sulci without pits (e.g., *Typhochrestus digitatus*, Plate 70C).

CHARACTER 50. Male cephalic cuticular pores: 0=absent; 1=present (Plates 47F, 48D–F, 50C–E, 70E). Close examination of the cuticle of the prosoma shows that the presence of a few isolated pores (both in males and females) is common in linyphiids (Hormiga, unpublished); however, the presence of numerous pores in the prosoma, usually in the anterior part, is not as common, although these pores are not restricted to the erigonines. The males of the linyphiine genus *Bolyphantes* C.L. Koch have pores on the anterior part of the prosoma, including the clypeus (Blest and Taylor, 1977). I have examined *B. luteolus* (Blackwall) and found pores both in the male (Plate 2A–D) and the female (contra Blest and Taylor, 1977:491). The male has a higher density of pores than the female, some of them being clustered in groups of 10–12 pores. Hormiga (1999) has recently documented the presence of pore-bearing cephalothoracic sulci in several linyphiine spiders, including members of the genera *Bathyphantes* Menge, *Diplostyla* Emerton, *Kaestneria* Wiehle, *Porrhomma* Simon, and *Vesicapalpus* Millidge. I have examined 17 species of *Bathyphantes* and found that for both males and females (and, at least in *B. pallidus* (Banks), in subadults) the sulcus is on the anterior margin of the prosoma between the chelicera and the pedipalp. Examination of the pits of *B. pallidus* with scanning electron microscopy reveals that these pits closely resemble the clypeal sulci of mynoglennines (also present in males, females, and juveniles; Plates 4A–E, 11A–D, 78A). In *Bathyphantes* these pores cover more densely the dorsal part of the pit and, unlike in the mynoglennines, are not arranged in groups. In the erigonines (or in the linyphiids in general, for that matter) the distribution of pores fits the cladogram poorly. The pores are absent in what appear to be the basal lineages of erigonines, and their presence requires several independent origins. The occurrence of pores is not always as-

sociated with cephalic lobes and specializations (e.g., *Laminacauda plagiata*) and vice versa (e.g., *Hilaira excisa*).

CHARACTER 51\*. Tracheal system: 0=haplotracheate; 1=desmitracheate; 2=intermediate. The terms haplotracheate and desmitracheate are used sensu Millidge (1984:233) and refer to the morphology of the median tracheae (Lamy, 1902). Haplotracheate systems have simple unbranched median tracheae (Hormiga 1994b, fig. 15A), whereas desmitracheate systems are characterized by having the median tracheae branching into many small tracheoles (Hormiga 1994b, fig. 18A). State 2 (intermediate) characterizes the tracheal system first described by Blest (1976, fig. 1B) for *Allomengea scopigera* (Grube), in which the medial trunks divide into several branches. A similar tracheal pattern also has been described for *Laminacauda* (Millidge, 1985:26, 1986). I have studied the tracheal system of *Laminacauda plagiata*, *L. argentinensis* Millidge, and *L. diffusa* Millidge (*L. diffusa* also was studied by Millidge (1985)). All three, plus two additional species studied by Millidge (1985), have intermediate tracheal systems, but the morphology of the tracheae varies slightly (Figure 31C–G). In *L. plagiata* and *L. argentinensis* (Figure 31C–F) the lateral and medial trunks are approximately the same diameter and show very little branching. In *L. diffusa* (Figure 31G) the medial tracheal trunks are much more branched, and their diameter is about two times that of the lateral trunks. More species and individuals need to be studied to assess the range of morphological variation of the tracheal character in *Laminacauda*. In all of these *Laminacauda* species the tracheae have taenidia. In the only specimen of *Tibioploides pacificus* that I have been able to study (Figure 31A) at least one of the medial trunks was bifurcate, the lateral trunks were wider than the medial, and one of the lateral trunks had a small branch. This species has, therefore, been coded as being intermediate, but dissections of more specimens are needed to understand its tracheal morphology. In the present sample the intermediate tracheal system is restricted to only *Laminacauda* and *Tibioploides*, although it requires two independent origins on the cladogram: in the former genus as a simplification from desmitracheate (with taenidia) ancestors and in the latter genus as a modification from haplotracheate ancestors. The plesiomorphic haplotracheate morphology is retained in the erigonine genera *Asthenargus*, *Gongyliidiellum*, *Sisicus*, and *Ostearius*.

CHARACTER 52. Taenidia in tracheoles: 0=absent; 1=present. Presence of taenidia in the tracheal system of linyphiids (sensu Blest, 1976, pl. 1b) is the plesiomorphic condition that is retained in the basal lineages of erigonines. The loss of the taenidia in the tracheoles is a synapomorphy for a large clade of erigonines (informally referred to herein as “Distal Erigonines”).

CHARACTER 53. Male dorsal abdominal scutum: 0=absent; 1=present. Several erigonines have a dorsal scutum (a sclerotized plate) in the abdomen. In the present selection of taxa this



character state occurs only in *Pelecopsis*; thus, it is phylogenetically uninformative.

CHARACTER 54. Coxae IV-booklung stridulatory organ: 0=absent; 1=present (Figure 5G). A stridulatory organ consisting of a tooth in the fourth coxa and a file on the booklung plate is found in *Diplocentria bidentata* (Wiehle, 1960, fig. 787) and *Gongyliellum vivum* (Plate 29D–F). A similar organ also is present in *Rhaebothorax flaveolatus* (Dahl) (Wiehle, 1960, fig. 1138).

CHARACTER 55\*. Male chelicerae: 0=smooth; 1=with stridulatory striae (“pars stridens” in Starck, 1985) (Figure 29A–C).

CHARACTER 56. Cheliceral stridulatory striae: 0=ridged (*Lepthyphantes tenebricola* (Wider), Plate 5E); 1=scaly (*Oedothorax gibbosus*, Plate 49E); 2=imbricated (*Ceratinops inflatus*, Plate 16A,B). In many cases assessment of the absence of stridulatory striae requires scanning electron microscopy, even for relatively large species. For example, based on my own observations and those of van Helsdingen (1969:37) using a dissecting microscope, I (1994a, 1994b) scored *Linyphia triangularis* as lacking stridulatory striae. SEM examination of this species, however, shows that the stridulatory striae, although very subtle (rows of enlarged scales; Plate 7E,F), are indeed present. Most linyphiids have striae that are more or less long cuticular ridges (state 0), and that seems to be the plesiomorphic condition. In some linyphiids the striae are composed of rows of enlarged “scales” (state 1), whereas in others the striae are made out of “imbricated plates” similar to the ventral scales of snakes (state 2).

CHARACTER 57. Dorsal spur on male chelicerae: 0=absent; 1=present (*Gongyliellum vivum*, Plate 28F).

CHARACTER 58\*. Number of retrolateral teeth in female chelicerae: 0=three; 1=four or more; 2=two; 3=none; 4=one. States 3 and 4 have been added to the original coding of Hormiga (1994b).

CHARACTER 59\*. Female pedipalpal tarsus: 0=with claw (Hormiga, 1994b, fig. 19A,B); 1=without claw (Plates 60C, 63C).

CHARACTER 60\*. Leg autospasy at the patella-tibia junction: 0=absent; 1=present. Within Araneoidea patellar autospasy (Roth and Roth, 1984) is restricted to pimoids and linyphiids (Hormiga, 1993, 1994a, 1994b).

CHARACTER 61. Dorsal spines tibia I: 0=two or more; 1=one; 2=none.

CHARACTER 62. Dorsal spines tibia II: 0=two or more; 1=one; 2=one.

CHARACTER 63. Dorsal spines tibia III: 0=two or more; 1=one; 2=none.

CHARACTER 64\*. Dorsal spines tibia IV: 0=two or more; 1=one; 2=none.

CHARACTER 65\*. Trichobothrium of metatarsus IV: 0=present; 1=absent. Characters 61–65 are classical characters in linyphiid taxonomy and are commonly used in keys and species and generic delimitations (e.g., Locket and Millidge, 1953).

### Spinneret Spigot Morphology

CHARACTER 66\*. Aciniform spigots in female posterior median spinneret (PMS): 0=one or more (Plate 45C); 1=absent.

CHARACTER 67. PMS mAP nubbins: 0=none; 1=one. The absence of nubbins on the PMS is a synapomorphy of a large clade of araneoid families that includes linyphiids, pimoids, syntaxids, theridiids, and cyatholipids (Griswold et al., 1994, 1998).

CHARACTER 68\*. Posterior lateral spinneret (PLS) mesal cylindrical gland spigot base: 0=same size as the other base; 1=larger than the other cylindrical base (Plates 37D, 45D, 51E, 59D). The enlarged mesal cylindrical spigot base is a synapomorphy of pimoids plus linyphiids. Hormiga et al. (1995) reported homoplasy in this character in the tetragnathid genera *Glenognatha* Simon and *Pachygnatha* Sundevall.

CHARACTER 69\*. Aciniform spigots in female PLS: 0=more than one; 1=one; 2=absent. This character is phylogenetically uninformative for the present taxonomic sample.

CHARACTER 70. PLS aggregate gland spigots in male: 0=absent; 1=present (Plates 11E, 18D, 30F, 42D).

CHARACTER 71. PLS flagelliform gland spigots in male: 0=absent; 1=present (Plates 11E, 18D, 34F, 42D, 54D).

Most adult male araneoids lack the aggregate and flagelliform gland spigots on the PLS (PLS triad) and consequently cannot produce viscid sticky silk. In some linyphiids, the adult male retains the triad, including all the erigonines studied so far, except *Gongylidium rufipes* (Plate 30E,F) in which the flagelliform spigot is reduced to a nubbin in both the male and the female (both sexes have the pair of aggregate gland spigots). The triad also is present in the males of the two mynoglennines studied herein (*Haplinis* and *Novafrotoneta*, Plate 11E) and in *Stemonyphantes* (Plate 12F). Don Buckle (in litt., June 1994) reported the presence of sticky silk in the webs built by adult males of the erigonines *Diplocephalus cuneatus* (Emerton), *Erigone atra* Blackwall, *Soucron arenarium* (Emerton), *Halorates plumosa* (Emerton), *Pelecopsis moesta* (Banks), and *Centromerus sylvaticus* (Blackwall) (Micronetinae) and *Meioneta* sp. (Linyphiinae). Sticky silk production by adult males also has been reported from the erigonine *Masoncus pogonophilus* Cushing (Cushing, 1995).

### Behavior

CHARACTER 72\*. Male position during construction of spermweb: 0=above spermweb; 1=below spermweb.

CHARACTER 73\*. Male position during ejaculation: 0=above sperm web; 1=below spermweb.

Characters 72 and 73 (see Hormiga, 1994b, for references) are scored for only five taxa in the matrix, including representatives of all but one the linyphiid subfamilies in the sample. It is for this reason that, despite the many missing entries, these two characters are kept in the analysis. They also point to the study of mating behavior as a potential source of phylogeneti-

cally informative data in the Linyphiidae (van Helsdingen, 1983).

#### CLADISTIC ANALYSIS

Heuristic searches for minimal-length cladograms resulted in six most-parsimonious trees of 230 steps (consistency index (CI)=0.41, retention index (RI)=0.68), whose strict consensus cladogram (also 230 steps long, CI=0.41, RI=0.68) is shown in Figure 36. After the exclusion of the six phylogenetically uninformative characters, the CI and RI of these six minimal-length cladograms are 0.38 and 0.68, respectively, and the trees are 220 steps long.

When "m\*;bb\*;" is used in Hennig86, the program finds six trees of 230 steps. Hennig86's "t;bb\*;" fails to find optimal trees, finding 24 trees of 231 steps (CI=0.41, RI=0.68). PAUP (using 1,000 replicates of random addition, tree bisection-reconnection, and "MULPARS") finds the same six minimal-length cladograms as Hennig86. Using NONA's "mult\*500" (which uses 500 different addition-sequence replicates and swaps branches by tree bisection-reconnection) combined with "amb=" (a branch collapsing option that considers potential support by retaining those branches for which some states occurring in the set of possible states for the descendant node are absent in its ancestor or vice versa (Goloboff, 1993)) a total of six cladograms of 230 steps are found. These six trees differ from the those found by Hennig86 in that the linyphiines are left unresolved (a trichotomy) or resolved either as in Figure 37A or as in Figure 37C (but not as in Figure 37B). Using NONA's "mult\*500" combined with "amb=" (a stricter branch collapsing option that ignores potential support by collapsing branches that are not supported under every possible optimization) a single cladogram of 230 steps is found, which is topologically identical to the strict consensus cladogram of the six trees found by Hennig86 (Figure 36). The fact that the consensus tree has the same length as the set of minimum-length cladograms from which it was derived indicates that there is not unambiguous support for the conflicting groups in the data (Nixon and Carpenter, 1996:313).

Successive character weighting (Farris, 1969; Carpenter, 1988) was used to assess the internal consistency of the data and the cladistic reliability of the results (Carpenter et al., 1993). The initial cladograms were filtered for polytomies (i.e., polytomous trees were retained only if more highly resolved compatible trees did not exist) before calculating the new weights. The characters were reweighted in PAUP by the maximum value (best fit) of the rescaled consistency index (Farris, 1989) using a base weight of 1,000. Successive character weighting results in the same six minimal-length cladograms found by Hennig86 and PAUP (230 steps long under equal weights), and the results of the first round of character weighting are stable in successive iterations. The results of the Bremer support analysis (Figure 36), using PHAST under amb-, are

based on 32,759 trees up to four steps longer than the minimal-length cladograms.

#### Discussion

##### TREE CHOICE

The most-parsimonious cladograms for the present data set show two different areas of conflict, as seen in the strict consensus cladogram (Figure 36). The first involves the interrelationships of the linyphiines, and the second involves the placement of the relatively basal erigonine genera *Drepanotylus* and *Sciastes*. The first problem has three different resolutions (topologies) (Figure 37A–C), and the second has two; the combination of these two outcomes results in the six minimal-length cladograms that can be found with the described heuristic searches.

Only three of the six most-parsimonious cladograms are fully dichotomous; the remaining three have a trichotomy that involves *Drepanotylus*, *Sciastes*, and the Distal Erigonines. Fully dichotomous cladograms are more informative than less resolved trees, define more monophyletic groups, and, therefore, provide more testable hypotheses (Mickey and Platnick, 1989). The three minimal-length, fully dichotomous cladograms have *Drepanotylus* as a sister to *Sciastes* plus the Distal Erigonines (as depicted in Figure 38) and differ only in the interrelationships of the linyphiines; I prefer these three trees because of their higher information content and testability. No unambiguous character changes support any of these three linyphiine topologies, so character support has to be mapped on branches using some auxiliary criteria as follows:

First, characters 18 and 31 could support the monophyly of Micronetini plus the rest of linyphiids (excluding the Linyphiini) (Figure 37A). If character 18 (embolic membrane) is to provide such support, one must interpret the absence of the embolic membrane in *Microlinyphia* as ancestral and its presence in *Linyphia* as convergent with the embolic membranes of Micronetinae. This interpretation is unrealistic because most linyphiids have embolic membranes. It seems, therefore, that the absence of such a membrane in *Microlinyphia* is better interpreted as secondary (i.e., the membrane is lost) rather than ancestral. Character 31 (the number of retrolateral trichobothria in the male pedipalpal tibia) supports this branch if the ancestral condition for Linyphiinae is three trichobothria, as in *Linyphia*, most species of *Neriene* (van Helsdingen, 1969), and *Frontinellina frutetorum* (C.L. Koch) (van Helsdingen, 1970). Given the low fit of this character to any of the most-parsimonious cladograms (CI=0.27, RI=0.50), the support it offers is, at best, tenuous. Finally, depending upon where the changes of characters 18 and 31 are mapped, this branch could have no support at all (zero length).

Second, the branch supporting the monophyly of Linyphiini plus the rest of the linyphiids (excluding the Micronetini) (Figure 37B) is an artifact due to the way programs treat missing entries (Platnick et al., 1991; Coddington and Scharff, 1996;

Wilkinson, 1995). This branch either is supported by character 34 under Farris optimization or is of zero length. Character 34 refers to the distinctive sigmoid scape in the ventral plate of many Micronetini. The ventral plate scape is absent in most taxa, and the character is scored as not applicable in those instances. So the required change is only possible if the taxa outside the linyphiids (also scored as not applicable for this character) are assumed to have had the sigmoid scape, which is then lost in the linyphiids excluding the micronetines. Although technically possible, there is no evidence of ventral plate scapes outside linyphiids, so this optimization is very unlikely.

The third alternative is to have monophyletic Linyphiinae (Linyphiini plus Micronetini) as the sister to the rest of linyphiids (Figure 37C); this could potentially be supported by five character changes (characters 26, 27, 34, 72, 73). All of these changes are ambiguous in the strict sense; however, the ambiguity in characters 26 and 27 results, once more, from the taxa (outside the Linyphiidae) scored as not applicable. The presence of the terminal apophysis on the radix (character 26) is unique to linyphiines and has a perfect fit (no homoplasy) to the cladogram, but under Farris optimization the outgroups to linyphiids (which lack the radix, and therefore cannot be accurately scored for this character) are hypothesized to have this apophysis, which is subsequently lost in the rest of linyphiids. The presence of a lamella characteristica on the radix (character 27) is another synapomorphy of linyphiines, with homoplasy in several erigonines. The ambiguity in the optimization of this character is of the same nature as that in the terminal apophysis. I consider such ambiguity in these two characters an artifact of character coding. The sigmoid epigynal scape (character 34) has already been discussed above and provides evidence for the monophyly of Micronetini, not Linyphiini plus Micronetini. Finally, additional support for the monophyly of Linyphiinae could come from the two behavioral characters included in the matrix (characters 72 and 73); unfortunately data for these two characters are available for only a few species, and its optimizations are ambiguous. Nonetheless, *Microlinyphia*, *Linyphia*, and *Lepthyphantes* share the condition of being positioned above the web during construction of the spermweb and during ejaculation. If these two states represented the apomorphic condition, their presence in the linyphiines could provide additional support to the monophyly of Linyphiinae (node 36); this hypothesis has been mapped in Figure 39. In an undetermined species of *Tetragnatha* from Australia recorded in the documentary movie *Webs of Intrigue* (Roger Whittaker Films Pty Ltd., 1992; Australian Broadcasting Corporation, 1995), the male is positioned below the sperm web during ejaculation and when charging the pedipalps. On the basis of this observation, I have hypothesized that the position of the linyphiines above the web is apomorphic in this context; thus, the position of *Tetragnatha*, *Haplinis*, and *Erigone* below the web during ejaculation is a symplesiomorphy. This hypothesis has been depicted in the optimization of character 73 (and

72, although there is no information available for *Tetragnatha* for the latter character) in Figure 39.

It seems, therefore, that the best character support of any of these three equally parsimonious solutions of Linyphiinae relationships is that of the monophyletic Linyphiinae (Linyphiini plus Micronetini) (Figure 37C), which I prefer as a working hypothesis.

In sum, one of the six most-parsimonious cladograms (Figure 38) has been selected as a working hypothesis of erigonine relationships on the basis of being the most resolved cladogram for the erigonines with the most rational character support for the relationships of the linyphiines. This preferred topology has been diagnosed for the 230 character changes and is depicted in Figures 39 and 40. In the following discussion, node (clade) numbers make reference to Figures 38–40.

#### MONOPHYLY AND ERIGONINE CLADES

The monophyly of the subfamily Erigoninae (node 30) is unambiguously supported by the presence of one or more tibial apophyses in the male pedipalp (character 28; CI=0.50, RI=0.92) and the loss of the tarsal claw in the female pedipalp (character 59; CI=0.33, RI=0.78) (Bremer Support (BS)=1). Both characters are homoplasious for this taxonomic context but have relatively good fit to the cladogram, particularly the first. Most erigonine males have a pedipalpal tibial apophysis; among the present taxonomic sample the apophysis has been lost in *Leptorhoptrum* (Figure 19A,B). All the female erigonines examined lack the pedipalpal claw; this claw has been lost independently in other lineages, represented herein by *Lepthyphantes* and *Theridiosoma*. The desmitracheate system has been suggested as an erigonine synapomorphy (Blest, 1976; Millidge, 1986; Hormiga, 1994b), but increasing the taxonomic sample shows that the desmitracheate pattern evolved after the tibial apophysis and the loss of the pedipalpal claw. The classical diagnosis of Erigoninae as desmitracheate linyphiids (e.g., Blest, 1976) does not reflect the phylogenetic patterns reported herein (see below).

The erigonines are composed of two sister clades (Figure 38): a small clade of four genera (node 29) and a clade comprising the remaining erigonines (node 26). Node 29 includes the genera *Asthenargus*, *Gongylidiellum*, *Sisicus*, and *Tibioploides*. The monophyly of this lineage is unambiguously supported by a reduction in the number of retrolateral trichobothria in the male pedipalp to only one (character 31), although the reduction has occurred independently several times in the Erigoninae. This group is haplotracheate (character 51), except in the case of *Tibioploides*, which, as discussed previously, shows some branching in the medial trunks. The embolic division of the members of clade 29 has a radix without a tailpiece (character 21), a symplesiomorphy, and a lamella characteristica (character 27), except in *Tibioploides* where the lamella is absent.

The sister group to clade 29 contains the remaining erigonines in this study (node 26). The monophyly of this large lineage is unambiguously supported by three synapomorphies (BS=1): a short embolus (character 17), the presence of a radical tailpiece (character 21), and a change from posterior to mesally oriented fertilization ducts (character 40). All three characters are homoplasious and have a poor fit to the cladogram. A number of lineages are successively nested between the *Tibioploides* clade (node 29) and the Distal Erigonines (node 20). These taxa (from *Ostearius* through *Sciastes*, in Figure 39) are either haplotracheate (*Ostearius*) or desmitracheate with taenidia, except *Laminacauda*, which has an intermediate tracheal system with taenidia. The radical tailpiece (character 21) appears to have evolved in this region of the cladogram, at node 26, and is subsequently lost three times independently. The males of some of the members of this grade have post-PME cephalic lobes (*Hilaira* and *Drepanotylus*).

One of the largest erigonine clades is what I have informally named the Distal Erigonines (node 20, Figure 40), which includes 21 genera from the present sample (BS=2). Three character changes unambiguously support the monophyly of this clade: the loss of taenidia in the tracheoles (character 52), the presence of imbricated stridulatory striae in the chelicerae (character 56), and the presence of a single dorsal spine on tibia IV (i.e., loss of the distal spine, character 64). Character 52 has no homoplasy in any of the six minimal-length cladograms for this data set. The imbricated stridulatory striae (character 56) have evolved independently three times; this character has a poor fit (CI=0.25, RI=0.60). Character 64 has a good fit (CI=0.50, RI=0.89) but requires two parallel losses of the distal tibia IV spine (in *Theridiosoma* and in the *Asthenargus* plus *Gongylidiellum* clade). The Distal Erigonines are composed by two sister clades at nodes 19 and 13. Clade 19 (BS=1; Figure 40) includes genera such as *Typhochrestus*, *Diplocephalus*, and *Islandiana*, and its monophyly is unambiguously supported by the loss of the copulatory duct encapsulation (character 38; CI=0.17, RI=0.72). Within clade 19 the monophyly of *Araeonus*, *Savignia*, and *Diplocephalus* (node 15) is relatively well supported (BS=2) by the loss of the protegular papillae (character 9), a bisected epigynal plate (character 35; evolved in parallel at node 1), and the loss of the distal dorsal spine of tibia III (character 63). Clade 13 contains 14 genera (BS=1), including *Erigone* (which is the sister to the remaining taxa in the lineage), *Walckenaeria*, and *Pelecopsis*. The monophyly of this clade is supported by three synapomorphies: the presence of papillae on the protegulum (character 9; CI=0.17, RI=0.50), the presence of a ventral apophysis in the male pedipalpal patella (character 29, subsequently lost in most members of the clade; CI=0.33, RI=0), and the presence of a trichobothrium in the fourth metatarsus (character 65; CI=0.17, RI=0.71). Within clade 13 the monophyly of the lineage that includes, among others, genera such as *Grammonota*, *Pelecopsis*, *Ceratinops*, *Entelecara*, and *Dismodicus* (node 6) is relatively well supported (BS=2) by the presence of a lamella characteristica (charac-

ter 27, subsequently lost and re-evolved), posteriorly oriented fertilization ducts (character 40), cuticular pores in the male prosoma (character 50), and imbricated cheliceral stridulatory striae (character 56, which is subsequently modified into imbricated striae at node 3).

#### LINYPHIID MONOPHYLY AND SUBFAMILIAL RELATIONSHIPS

Nine synapomorphies support the monophyly of Linyphiidae (node 37, BS=4), six of which are unambiguously optimized on the cladogram of Figure 39: intersegmental paracymbium (character 4), presence of a suprategulum (character 11), loss of the araneoid median apophysis (character 15), loss of the araneoid conductor (character 16), presence of a radix (character 20), and presence of a membranous connection (the column) between the suprategulum and the embolic division (character 24). The optimization of the other three (characters 5, 18, 31) is ambiguous but nonetheless provides additional support: a U- or J-shaped paracymbium (character 5), the presence of an embolic membrane (character 18), and the presence of two retrolateral trichobothria on the male palpal tibia (character 31). Two of these synapomorphies are additions to those suggested by Hormiga (1994b): the suprategulum (which had been coded differently in my former study; see character descriptions) and the embolic membrane. Ambiguity in the optimization of the embolic membrane is artifactual, due to the presence of not applicable state codings in pimoids (because they lack the column they cannot be accurately coded for the embolic membrane, which is an outgrowth of the column). In sum, the monophyly of the Linyphiidae is well supported by numerous synapomorphies (BS=4), all of them derived from the male palpal morphology.

The linyphiid subfamilial relationships suggested by the preferred cladogram (Figure 37C) differ from those that I had hypothesized earlier (Hormiga, 1994b) (Figure 41B), as well as from those proposed by Wunderlich (1986) (Figure 41A). Nevertheless, the ingroup (i.e., Linyphiidae) network implied by the current results is the same as the ingroup network implied by Hormiga (1994b); in other words, only the position of the root within the linyphiids has changed from my former hypothesis (Figure 41D). The present data set differs from my former one in the sample of outgroup taxa and, obviously, in that the erigonines are now better represented. There are also a number of new characters added to this data set that were not used in Hormiga (1994b), as well as new character codings and interpretations. Recent research on the phylogeny of Araneoidea (Griswold et al., 1994, 1998) suggests that the sister group of linyphiids plus pimoids is a large clade that includes the families Theridiidae, Nesticidae, Synotaxidae, and Cyatholipidae. The phylogenetic relationships of these families can be represented in parenthetical notation as (((Theridiidae) (Nesticidae)) (Synotaxidae) (Cyatholipidae))). In my former analysis I had considered that Tetragnathidae and Araneidae were the two most likely candidates for the closest relatives of the linyphio-

ids (pimoids plus linyphiids). Accurate taxonomic representation of outgroups can be critical for assessing character polarities. The better sampling of the Erigoninae also has allowed me to modify some character interpretations, which in turn has resulted in differences in character codings in the data matrix (e.g., the terminal apophysis, character 26).

The most-parsimonious cladograms for the present data set offer three alternative topologies for the interrelationships of the linyphiid subfamilies (Figure 37A–C). None of these hypotheses is congruent with either Wunderlich's hypothesis (1986) (Figure 41A; it requires two extra steps for this data set) or my own cladogram (1994b) (Figure 41B; it requires one extra step for this data set). The six minimal-length trees for the present data set all have the erigonines as the sister group of stemonyphantines plus mynoglennines. I have already discussed my criteria for preferring the cladogram (for the present data) on which the Linyphiinae are monophyletic (Figures 37C, 41C), and I will center the following discussion around this preferred working hypothesis. In my 1994 study, the support for the monophyly of linyphiines plus erigonines was provided by the presence of the suprategulum continuous with the tegulum (in opposition to the articulated suprategulum of *Stemonyphantes*) and the presence of a terminal apophysis on the radix (Bremer support for Erigoninae plus Linyphiinae was 1); the optimization of the latter character change was ambiguous. Under my current interpretation, the suprategulum (character 11) is a synapomorphy of the Linyphiidae, and its membranous articulation (character 12) is an autapomorphy of *Stemonyphantes*; the terminal apophysis (character 26) is absent from the erigonines and is synapomorphic for the Linyphiinae. Two characters (not used in my 1994 study) unambiguously support the monophyly of a clade that includes the stemonyphantines, the mynoglennines, and the erigonines (Figure 38, node 33): the presence of both aggregate and flagelliform silk gland spigots in the PLS of adult males (characters 70 and 71, respectively; BS=1). These spigots are absent in the adult males of linyphiines, pimoids, and most araneoids but are present in some species of theridiosomatids (Coddington, pers. comm., 1995). Charles Griswold and I have examined the spinnerets of a Cameroonian species of the mynoglennine genus *Afroneta* Holm in which the adult males lack the triplet (which is present in the females of this particular species) that is present in the New Zealand mynoglennine males examined by me (*Novafroneta* and *Haplinis*, Plates 11E and 78B, respectively). Examination of more taxa within the mynoglennines and the linyphiines will be necessary to corroborate these two synapomorphies.

Unambiguous support for the monophyly of stemonyphantines plus mynoglennines (node 32) comes from the presence of a trichobothrium on the fourth tibia (character 65). In this data set the trichobothrium is ancestrally absent and evolves in parallel five times (at nodes 38, 65, 24, 13, 2); therefore, the character support for the monophyly of stemonyphantines plus mynoglennines is, at best, rather weak (BS=1). The monophyly of the Mynoglenninae is unambiguously supported by four synapo-

morphies (BS=2): the presence of the mynoglennine tegular apophysis (character 7), the loss of the suprategulum (character 11), and the presence of clypeal sulci (character 47) supplied by cytologically unusual glands (character 50; Blest and Taylor, 1977).

#### CHARACTERS AND EVOLUTIONARY TRENDS

The most-parsimonious cladograms resulting from the analysis of the present data allow us to study some of the evolutionary trends in the diversification of erigonines. As already discussed, most of the previous work on the higher-level systematics of linyphiids has emphasized one character system to the exclusion of others; at most, contrary evidence from other characters was discussed but not really allowed to influence the results. Not surprisingly, phylogenetic hypotheses changed as different character systems were considered. The lack of consilience among the different character systems has been known for a long time and has traditionally been explained as "noise" that obscured the "exact" limits of the family and the nature of its main lineages. I argue that what appeared to many as a lack of consilience is mostly just different rates of character evolution combined with confusion of primary and secondary absence, and therefore the phylogenetic pattern itself. To begin with, it is not clear to me why one should expect similar rates of character change for different character systems. Why should the distribution of a particular tracheal morphology change simultaneously with, for example, a particular type of embolic division? Setting aside this unwarranted constraint, it should not be surprising that different characters evolved at different times (i.e., at different nodes on the cladogram), resulting in a variety of character-state combinations. The notion that taxa are mosaics of relatively apomorphic and plesiomorphic character states is quite old; Hennig (1965, 1966, 1968) used the terms "heterobathmy of characters" (Takhtajan's *Heterobathmie der Merkmale*) or "specialization crossings" (*Spezialisationskreuzungen*) for this concept. Combinations such as a primitive tracheal system with an advanced palpal conformation are viewed as problematic by some (not cladistically oriented) spider systematists. These "combinations," however, are neither problematic nor conflicting, as they are the essence of phylogenetic patterns, that is, nested character hierarchies: "Heterobathmy of characters is therefore a precondition for the establishment of the phylogenetic relationship of species and hence a phylogenetic system" (Hennig, 1965:107).

The present study combines data from several character systems. The nature of some of these problems has been examined in some depth in Hormiga (1994b), so they are discussed here in only to the extent that the results suggest new interpretations.

MALE PALP.—The evolution of the extremely diverse morphology of the male copulatory organs has been a vexing problem for a long time. Merrett's (1963) detailed monograph documented the many difficulties in homologizing the sclerites of

male linyphiid palps. This precladistic study concluded that it was “probable that the simple erigonine type has evolved by reduction from the complex linyphiine type” (p. 465). In contrast, in his monograph on the same subject, Millidge (1977:50) assumed that the plesiomorphic palpal conformation was simple and that “regression from complex to more simple conformations” did not occur or was rare. Later Millidge (1984:261) reversed his views to hypothesize that “the primitive palp was relatively complex.” The use of “complex” and “simple” as palp characters should be avoided. Comparisons should instead be restricted to specific sclerites or other homologous structures. The terms “complex” and “simple” are used very loosely herein and only to mean whether one or more radical sclerites and/or apophyses are present and not to imply homology in any sense.

The present data show that male genitalic morphology (42% of the characters in the matrix), despite being homoplasious (their mean CI and RI are 0.59 and 0.76, respectively), provides evidence of monophyly in numerous instances. All linyphiids, except for a few reversals (such as *Microlinyphia*, *Hylyphantes*, or *Tapinocyba*), have an embolic membrane connected to the column (character 18). In the present data set the male pedipalpal tibial apophysis (character 28) is unique to erigonines (although lost or extremely reduced in *Leptorhoptrum robustum*, Figure 19A,B), so it presumably evolved at node 30 (Figure 39). Ancestrally, erigonine palps had a relatively simple embolic division: the radix lacks a tailpiece (character 21, Figure 42), and the lamella characteristica (character 27, Figure 44) and anterior radical process (character 23, Figure 43) are absent. The embolus may have been relatively long and filiform (character 17), although this character is highly homoplasious (CI=0.09, RI=0.50). *Hilaira excisa* differs from the other linyphiids examined herein by having an extremely reduced radix that is almost indistinguishable from the embolus (Figure 14B); an analogous condition is found in *Gongylidiellum vivum* (Figure 11E), where the radix is reduced to a subtle enlargement at the base of the embolus.

Complexity in the embolic division increases first with the evolution of the radical tailpiece (character 21, Figure 42) at node 26, which is subsequently lost three times (in *Drepanotylus*, *Hybocoptus*, and node 9). It appears that the plesiomorphic condition of the tailpiece morphology (character 22) is a more or less straight structure, directed posteriorly, which evolved into a number of different morphologies. The most parsimonious explanation suggests that the spiraled radical tailpiece (character 22, state 1), typical of genera such as *Grammonota* (Figure 13F), has evolved independently in the three instances that it is present in this matrix. The next step in the diversification of palpal morphology is the development of an anterior process on the radix (character 23, Figure 43); this radical process evolved at node 23 and is subsequently lost at node 11. The lamella characteristica (character 27, Figure 44) has evolved five times (four within the erigonines) and has been lost once (node 6). The optimization of this character suggests

that the lamella characteristica found in linyphiines is not homologous to its homonym in the erigonines. The protegulum (character 8, Figure 45), a characteristic feature of many erigonines, has evolved independently two times, at nodes 28 and 22. All the distal erigonines (with the exception of *Gonatium*, where the protegulum is secondarily absent) have a protegulum (Figure 45). The presence of protegular papillae seems to be rather homoplastic.

In sum, the overall pattern suggests a complex picture for the evolution of male palpal morphology, with numerous parallelisms and reversals, with complex embolic divisions having arisen more than once, and embolic divisions that can be either ancestrally simple or secondarily simplified to various degrees by reduction of the number of radical sclerites and processes found in the ancestors. Erigonine embolic divisions are plesiomorphically relatively simple, and some of the similarities between the complex embolic divisions of linyphiines and some erigonines (e.g., due to the presence of a lamella characteristica) are due to homoplasy.

**TRACHEAL SYSTEM.**—Since Blest’s (1976) influential study on the linyphiid tracheal system, the desmitracheate pattern (sensu Millidge, 1984) has been taken as a diagnostic feature for erigonines (e.g., Millidge, 1984, 1986). Yet a number of genera that had erigonine-like palps did not have the desmitracheate pattern but rather had the simpler haplotracheate pattern that is found in most araneoids. Once more the dilemma posed by this apparent incongruence was not due to a particular distribution of character states but to a failure by earlier authors to discriminate symplesiomorphy from synapomorphy.

Examination of all the character evidence under parsimony provides a coherent hypothesis for the evolution of the linyphiid tracheal system (Figure 46). The basal erigonine lineages (clade 28 and *Ostearius*) have the plesiomorphic haplotracheate system (character 51, state 0), which they share with the other linyphiid subfamilies as well as many other araneoids. The desmitracheate system (character 51, state 1) evolves at node 25. The basal desmitracheate erigonine lineages (and lineages basal to them) have the plesiomorphic type of tracheoles, that is, with taenidia (character 52, state 1). Taenidia are lost at node 20, the Distal Erigonines. This pattern fits all six minimal-length cladograms that result from the parsimony analysis of the present data, although there are a few instances of homoplasy. The intermediate tracheal morphology of *Laminacauda* and *Tibioploides* has already been discussed (see comments under character 51). In *Laminacauda* (Figure 31C–G) the intermediate condition seems to have evolved as a simplification from desmitracheate (with taenidia) ancestors. On the other hand, in *Tibioploides* (Figure 31A) the intermediate condition evolved as an elaboration of the morphology of haplotracheate ancestors (Figure 46). A few linyphiine genera, such as *Tennesseillum* and *Meioneta*, have convergently evolved a desmitracheate pattern (Hormiga, 1994b; Millidge, 1993b).

**CEPHALIC SPECIALIZATIONS.**—Perhaps one of the most distinctive characteristics of many species of erigonines are the

cephalic modifications found in the males (Figures 32–35). These modifications include cephalic lobes, lateral sulci (sometimes with pits), and glands that open through cuticular pores. The erigonine sulci (which are absent in the females) seem to play an active mechanical role during courtship (but data have been gathered for only a few species). The sulci are gripped by the female cheliceral fangs, as first noted by Bristowe (1931). During mating the females reportedly feed on secretions produced by the cephalic glands (see Hormiga (1994b) for references). The diversity of these structures is simply astonishing (see Appendix 3). Hormiga (1994b) summarized the available data on these cephalic specializations and tried to assess their cladistic content by congruence with the remaining characters. One of the questions discussed was whether the mynoglennine clypeal sulci and glands and the erigonine lateral sulci and glands were homologous structures, as had been suggested by several workers (Blest, 1979; Blest and Taylor, 1977; Millidge, 1993a). I concluded that although the nonhomology hypothesis was more parsimonious, the question could not be powerfully tested “until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands)” were studied (Hormiga, 1994b:34). Despite the appeal of this character system from many biological perspectives, there have been only a limited number of studies that have dealt with it (Blest, 1979; Blest and Taylor, 1977; Lopez, 1976; Lopez and Emerit, 1981; Schaible et al., 1986; Schaible and Gack, 1987); and the most comprehensive one remains unpublished (Schlegelmilch, 1974).

In this data set cuticular pores in the prosoma are scored conservatively (character 50). I assigned the same state to erigonines and mynoglennines despite the cytological differences found between their glands (Blest and Taylor, 1977); that is, I initially assumed that these two types of glands are homologous. The mynoglennine subocular sulci and the erigonine lateral sulci have been scored as two different characters (47 and 48, respectively). The results of the analysis suggest independent origins in erigonines and mynoglennines for both the sulci (Figure 47) and the cuticular pores (Figure 48), and by extension their associated glands. Recoding the sulci of erigonines and mynoglennines as two different states of the same transformation (i.e., treating the two types of sulci as homologous) produces no topological changes in the results. In other words, even if the sulci and glands found in erigonines and mynoglennines are treated as homologous, parsimony suggests that they have evolved independently from ancestors that lacked the sulci and the cuticular pores. The cuticular pores of the linyphiine *Bolyphantes* have also evolved independently. As previously discussed, other instances of homoplasy exist (e.g., the pore-bearing prosomal pits of *Bathyphantes*), and probably others remain to be discovered. Furthermore, within the Erigoninae the sulci have evolved independently at nodes 16 and 5 (see Figures 40, 47).

In the erigonines the male cephalothoracic cuticular pores (character 50, Figure 48) have five independent origins: in

*Laminacauda*, *Walckenaeria*, *Oedothorax*, and at nodes 17 and 6. The basal lineages of erigonines seem to lack the cuticular pores, although some of them, such as *Drepanotylus*, have post-PME cephalic lobes (character 43). The lateral pits (character 49) evolved at node 17 and are a synapomorphy for that clade; the same is true for lateral sulci (although there is one instance of parallelism in *Typhochrestus*). All taxa with sulci have cuticular pores (and presumably glands), but the distribution of pores across taxa is not restricted to those with sulci (e.g., *Laminacauda*).

The hypothesis for the evolution of male cephalic specializations presented herein should be treated with caution, mostly for two different reasons. First, this is an extremely complex character system requiring at least two additional types of data. Histological sections and cytological preparations are greatly needed to better understand the nature of these glands and the distribution and range of variation of types. Scoring for the presence or absence of cephalothoracic pores or fields of pores is only a beginning. Ethological data on the mating behaviors also are needed. Are these behaviors as diverse as the morphological cephalic specializations? Second, there is a potential problem with making inferences from the current data in that some of the results could be artifacts caused by sparse taxonomic sampling. This character system illustrates some of the potential problems of sparse sampling. The presumably monophyletic genus *Walckenaeria* has a fairly constant genitalic morphology (Millidge, 1983; Holm, 1984) but exhibits a remarkable variation in male cephalic morphology, including the presence/absence of lateral sulci, pits, and different types of lobes.

An elevated cephalic region in males (character 41) has independently evolved in *Bolyphantes*, *Araeoncus*, *Erigone*, and *Gonatium*. Cephalic lobes carrying the PMEs (character 42) are relatively common in erigonines, and in the present sample it has evolved in two clades, at nodes 14 (*Savignia* and *Diplocephalus*) and 4 (*Pelecopsis*, *Dismodicus*, etc.). The minimum-length cladogram suggests five independent origins for post-PME cephalic lobes (character 43) in erigonines: in *Hilaira*, *Drepanotylus*, *Typhochrestus* plus *Lophomma*, *Oedothorax*, and *Grammonota*. The lobes described by characters 44, 45, and 46 are autapomorphies of the genera *Walckenaeria*, *Dismodicus*, and *Diplocephalus*, respectively.

In sum, the evolution of the specializations of the male prosoma is a problem too large and complex to be understood with so little data at hand, especially in much detail at such a high taxonomic level. Nevertheless, these results suggest that the cephalic sulci and glands of erigonines and mynoglennines evolved independently and, therefore, are not homologous structures.

#### TESTING PREVIOUS HYPOTHESES OF ERIGONINE GROUPINGS

The erigonine clades defined by the preferred minimal-length cladogram (Figure 38) can be used to test how the exist-

ing hypotheses of erigonine groupings fit the data presented in this study.

Merrett (1963, 1965) divided the erigonines that he studied into three groups (see Appendix 2) on the basis of the form of the embolic division. He was explicitly doubtful, however, on whether the groups were truly significant but considered them "useful for descriptive and comparative purposes" (1963:457). Mapping Merrett's erigonine groups (Mioxeneae, Diplocephaleae, and Walckenaerinae) on the preferred cladogram (Figure 38) reveals that none of them are monophyletic, and that in fact the three groups are polyphyletic.

I have repeated the same test for Millidge's (1977) classification. In the present data set I had representatives of 14 of the 15 erigonine groups of Millidge's classification. I could not study specimens of the taxa included in his group 12 (*Erigonoplus* and *Cotyora*), which currently contains only one genus because the monotypic genus *Cotyora* (Simon, 1926) has been synonymized under *Erigonoplus* Simon, 1884 (Millidge, 1977:37). For Millidge's groups 6, 7, and 15 (see Appendix 2) I had only one genus per group, so I could not test their monophyly. Of the remaining 11 groups, groups 4, 11, and 13 (*Gongylidium*, *Savignia*, and *Entelecara* groups, respectively) are the only monophyletic assemblages. Groups 1, 2, 3, 5, 8, 9, 10, and 14 are polyphyletic. Although Millidge (1984) rejected his own 1977 hypothesis on the basis of other characters (mostly epigynal), neither he nor any other worker has advanced an alternative classification for the Erigoninae.

### Conclusions

This study provides an explicit phylogenetic hypothesis about the limits of the Erigoninae and its main lineages. Two synapomorphies, the male palpal tibial apophysis and the loss of the pedipalpal claw in the female, unambiguously support the monophyly of Erigoninae. Most of the traditionally problematic transitional genera are phylogenetically basal within Erigoninae and exhibit several plesiomorphic features (which

has been part of the source of the confusion about their placement). The monophyly of the Distal Erigonines, the largest clade of this subfamily, is supported by the loss of the taenidia in the tracheoles and the loss of the distal dorsal spine on tibia IV.

The available data suggest that the sulci and glands found in mynoglennines and erigonines are not homologous. Although the addition of new characters and more taxa has changed the subfamilial relationships from those suggested in Hormiga (1994b), the current hypothesis may change further as even more taxa and characters are added, as previously acknowledged (Hormiga, 1994b:4). Nevertheless, the cladogram in Figure 38 should be preferred over my former hypotheses because it is based on a broader taxonomic sample for one of the clades (Erigoninae), on more characters, and on a more accurate selection of araneoid outgroups.

Future studies on the phylogeny of the Linyphiidae should include a better representation of the taxa from the Southern Hemisphere and the tropical regions, whose linyphiid faunas are still largely unstudied. Advances in linyphiid systematics will require a strong focus on taxon-based revisionary work, rather than the too frequent isolated species descriptions or regionally based taxonomic studies. More importantly, in order to improve the chaotic state of affairs of linyphiid higher-level systematics many practicing arachnologists must abandon the systematic paradigm they currently embrace. Only by grouping taxa on the basis of shared derived features (regardless of the phenetic homogeneity of the resulting groups, to the dismay of some), so as to identify monophyletic groups, can such a goal be achieved. For large numbers of taxa and morphological characters this goal requires explicit homology statements in a taxon by character matrix and analysis using parsimony methods. This monograph begins to move linyphiid systematics in that direction, and provides a foundation from which to advance the reconstruction of the phylogenetic patterns of this large and diverse spider family.



# Appendix 1

## Characters and Taxon Codings

The character description format is presented as follows: "Character number. Character name: first state; second state; third state; etc." A "0" in the matrix codes for the first state, a "1" codes for the second state, etc. (abs = absent; pres = present; S = number of steps; CI = consistency index; RI = retention index; W = character weight applied in the successive character weighting analysis; see text for details). Erigoninae taxon abbreviations in the matrix are (in alphabetical order) as follows: *Araeoncus* (Ar), *Asthenargus* (As), *Ceratinops* (Ce), *Diplocentria* (Dt), *Diplocephalus* (Di), *Dismodicus* (Ds), *Drepanotylus* (Dr), *Entelecara* (En), *Erigone* (Er), *Gonatium* (Go), *Gongyliidiellum* (Ge), *Gongylidium* (Gi), *Grammonota* (Gr), *Hilaira* (Hi), *Hybocoptus* (Hb), *Hylyphantes* (Hy), *Islandiana* (Is), *Laminacauda* (Lm), *Leptorhoptrum* (Lr), *Lophomma* (Lo), *Oedothonax* (Oe), *Ostearius* (Os), *Pelecopsis* (Pe), *Savignia* (Sa), *Sciastes* (Sc), *Sisicus* (Si), *Tapinocyba* (Ta), *Tibioploides* (Ti), *Tmeticus* (Tm), *Typhochrestus* (Ty), and *Walckenaeria* (Wa). Outgroup abbreviations (in alphabetical order) are as follows: *Bolyphantes* (Bo), *Haplinis* (Ha), *Lepthyphantes* (Le), *Linyphia* (Li), *Microlinyphia* (Mi), *Novafroneta* (No), *Pimoa altiiculata* (al), *Pimoa rupicola* (ru), *Tetragnatha* (Te), *Theridiosoma* (Th), *Steatoda* (Sd), and *Stemonyphantes* (St).

	TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP	S	CI	RI	W
MALE PAPAL MORPHOLOGY					
01. Cymbium morphology: smooth; with CDP	ehduliioetaosiirscmriyoetsraireyimaorsnbeae	1	1.00	1.00	1000
02. Cymbium size: unmodified; reduced	00	2	0.50	0.00	0
03. Pimoid cymbial sclerite: abs; pres	0001100000000000000000000000000000000000	1	1.00	1.00	1000
04. Paracymbium attachment: integr; intrsgmnt; artic	20-00111111111111111111111111111111111111	2	1.00	1.00	1000
05. Paracymbium morphology: 0; 1; 2; 3; 4; 5	54-01333323333333333333333333333333333333	5	1.00	0/0	1000
06. Paracymbium apophyses: pres; abs	01-11110011111111111111111111111111111111	2	0.50	0.50	250
07. Mynoglenine tegular apophysis: abs; pres	0000000000110000000000000000000000000000	1	1.00	1.00	1000
08. Protegulum: abs; pres	000000000000110101000111111111111101111111	3	0.33	0.88	294
09. Protegular papillae: abs; pres	-----00-0-1---11111000011100-1100111	6	0.17	0.50	83
10. Tegular sac: abs; pres	00000000000000000000000000000000001011010000000	3	0.33	0.33	111
11. Supratégulum: abs; pres	00000111110010111111111111111111111111111111	3	0.33	0.71	238
12. Supratégulum: continuous with T; articulated	----00001--0-00000000000000000000000000000000	1	1.00	0/0	1000
13. Supratégular distal apophysis: abs; pres	----11111--0-11101111111111111111111111111111	2	0.50	0.00	0
14. Supratégular marginal apophysis: abs; pres	----0000--0-0000001101011101000000111101	3	0.33	0.81	273
15. Median apophysis: pres; abs	10000111111111111111111111111111111111111111	2	0.50	0.67	333
TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP					
	ehduliioetaosiirscmriyoetsraireyimaorsnbeae	S	CI	RI	W
16. Conductor: pres; abs	00000111111111111111111111111111111111111111	1	1.00	1.00	1000
17. Embolus length: long; short	0100000110001000111110111101110101000000111	11	0.09	0.50	45
18. Embolic membrane: abs; pres	000--011101111111110011111111111110111011101	7	0.14	0.33	48
19. Pimoid embolic process: abs; pres	000110000000000000000000000000000000000000	1	1.00	1.00	1000
20. Radix: abs; pres	00000111111111111111111111111111111111111111	1	1.00	1.00	1000
21. Radical tailpiece: abs; pres	----000000000001111-110111111000111110111	4	0.25	0.80	200
22. Radical tailpiece: 0; 1; 2; 3; 4	-----0000000000000000000000000000000000	6	0.67	0.00	0
23. Anterior radical process: abs; pres	----0000?00000101100110111111100010000000000	2	0.50	0.91	455
24. Column: abs; pres	10000111111111111111111111111111111111111111	2	0.50	0.67	333
25. Fickert's gland: abs; pres	000000011000000000000000000000000000000000	1	1.00	1.00	1000
26. Terminal apophysis: abs; pres	----11110000000000000000000000000000000000	1	1.00	1.00	1000
27. Lamella characteristic: abs; pres	----11110001100000010010000001110010011000	6	0.17	0.62	103
28. Male pedipalpal tibial apophysis: abs; pres	00000000000011111101111111111111111111111111	2	0.50	0.92	458
29. Male pdp patella ventral apophysis: abs; pres	0000000000000000000000000000010101000000000	3	0.33	0.00	0
30. Prolat trichobothria on male pedipalpal Ti: 2; 1; 0	0120011111011211110111111111111111111101?112	8	0.25	0.14	36
31. Retrolat trichobothria on male pedipalpal Ti: 2; 4; 3; 1	1332202000203330000200030003000000033003333	11	0.27	0.50	136

FEMALE EPIGYNAL MORPHOLOGY		TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP	S	CI	RI	W
32. Dorsal plate scape: abs; pres		ehduliietaosiirscmriyoetsraireyimaorsnbeae	2	0.50	0.50	250
33. Ventral plate scape: abs; pres		-000000110100100100000100000000000000000	5	0.20	0.20	40
34. Ventral plate scape: straight; sigmoid		-----11-0-----0-----0-----0-----0-----	1	1.00	1.00	1000
35. Epigynal bisection: abs; pres		-00000000000000000000000001110000000011000	2	0.50	0.75	375
36. Atrium: abs; pres		-0000110001001000000000000000000001000000	4	0.25	0.25	63
37. Copulatory duct: separate from FD; spirals around FD		-000010001000000000000000000000000000000	2	0.50	0.00	0
38. Copulatory duct encapsulation: abs; pres		-0000000001000010110010000001111110111111	6	0.17	0.72	120
39. Spermathecae: two; four		1000000000000001000000000000001000000000	3	0.33	0.00	0
40. Fertilization duct orientation: poster; mesal; anterior		-002200000000001101011100111110111110010100	9	0.22	0.61	136
SOMATIC MORPHOLOGY		TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP	S	CI	RI	W
41. Male cephalic region: not raised; entirely raised		ehduliietaosiirscmriyoetsraireyimaorsnbeae	4	0.25	0.00	0
42. Male PME cephalic lobe: abs; pres		00000001000000000000000010010000010000000	2	0.50	0.83	417
43. Male post-PME lobe: abs; pres		000000000000000000000000000000000100000	5	0.20	0.20	40
44. Male inter-AME-PME lobe: abs; pres		000000000000000000000000000000000000000	1	1.00	0/0	1000
45. Male clypeal lobe: abs; pres		000000000000000000000000000000000000000	1	1.00	0/0	1000
46. Male AME lobe: abs; pres		000000000000000000000000000000000000000	1	1.00	0/0	1000
47. Subocular clypeal sulci: abs; pres		000000000110000000000000000000000000000	1	1.00	1.00	1000
48. Male lateral sulci: abs; pres		0000000000000000000110000000000000011111	2	0.50	0.86	429
49. Male prosomal pits: abs; pres		000000000000000000000100000000000001111	2	0.50	0.83	417
50. Male cephalic cuticular pores: abs; pres		??000010011?00001?01100011101000101?1?11	7	0.14	0.60	86
51. Tracheal system: haplotr; desmitr; intermed		000000000000021012111011111111111111111	3	0.67	0.94	625
52. Taenidia in tracheoles: abs; pres		-----11-111100-0000000000000000000	1	1.00	1.00	1000
53. Male dorsal abdominal scutum: abs; pres		000000000000000000000000000000000000000	1	1.00	0/0	1000
54. Coxae IV-booklung stridulatory organ: abs; pres		00000000000000000000000110000000000000000	2	0.50	0.00	0
55. Male chelicerae: smooth; with stridulatory striae		00011111111?111111111111111111111111111	1	1.00	1.00	1000
56. Chelicerae stridulatory striae: ridged; scaly; imbricated		---?0110000?00000?0202222221111010?2?200	8	0.25	0.60	150
57. Dorsal spur on male chelicerae: abs; pres		1000000000000000100000010000001111000000000	5	0.20	0.33	67
58. Retrolateral teeth femal chelicerae: 3; 4 or >; 2; 0; 1		1432?111?111111111111111111111101000112	6	0.67	0.50	333
59. Female pedipalpal tarsus: with claw; without		010000001000111111111111111111111111111	3	0.33	0.78	259
60. Patella leg autospasy: abs; pres		000111111111111111111111111111111111111	1	1.00	1.00	1000
61. Dorsal spines tibia I: 2 or >; 1; 0		00000000000000000000000000000000011101112	3	0.67	0.80	533
62. Dorsal spines tibia II: 2 or >; 1; 0		00000000000000000000000000000000011101112	3	0.67	0.80	533
63. Dorsal spines tibia III: 2 or >; 1; 0		120000000000000000000001100111011111111112	7	0.29	1.72	206
64. Dorsal spines tibia IV: 2 or >; 1; 0		0100000000010000000111111111111111111112	4	0.50	0.89	444
65. Trichobothrium metatarsus IV: pres; abs		1110011110001111111001111111100000000011	6	0.17	0.71	118
SPINNERET SPIGOT MORPHOLOGY		TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP	S	CI	RI	W
66. Aciniform spigots in female PMS: >1; abs		ehduliietaosiirscmriyoetsraireyimaorsnbeae	2	0.50	0.50	250
67. PMS mAP nubbins: 0; 1		000110000100?000000000000000000000000000?	1	1.00	1.00	1000
68. PLS mesal CY spigot base: same size; enlarged		11000000000?00000?0000000000000000000000?	1	1.00	1.00	1000
69. Aciniform spigots in female PLS: >1; 1; abs		000111111111?11111111111111111111111111?	3	0.67	0.00	0
70. PLS AGs in male: abs; pres		00012000020000000000000000000000000000?	1	1.00	1.00	1000
71. PLS FL in male: abs; pres		000000001111111111111111111111101111?1?11	2	0.50	0.89	444
BEHAVIOR		TTSraMLBLSHNASTDOSLLHTLGDIASDEOHGTWGGDEHCTP	S	CI	RI	W
72. Male during construction spermweb: abv spweb; below		ehduliietaosiirscmriyoetsraireyimaorsnbeae	1	1.00	1.00	1000
73. Male during ejaculation: above spweb; below		????000?0?1????????????????1?????????????	1	1.00	1.00	1000

## Appendix 2

### Major Taxonomic Groupings for the Linyphiidae Proposed since 1963

(The genera sampled in this study are shown in bold characters under Millidge's (1977) classification.)

#### Classification according to Merrett (1963, 1965)

##### Family LINYPHIIDAE

##### Subfamily LINYPHIINAE

- Group A (Syedruleae): *Agyneta*, *Bolyphantes*, *Centromerita*, *Centromerus*, *Drapetisca*, *Floronia*, *Helophora?*, *Kaestneria*, *Lepthyphantes*, *Macrargus*, *Maro*, *Meioneta*, *Microneta*, *Oreonetides*, *Poeciloneta*, *Syedra*, *Syedra*, *Tapinopa*.
- Group B (Linyphieae): *Allomengea*, *Bathyphantes*, *Diplostyla*, *Labulla*, *Linyphia*, *Porrhomma*, *Stemonyphantes*, *Taranucus?*

##### Subfamily ERIGONINAE

- Group C (Mioxeneae): *Entelecara*, *Erigonidium*, *Gonatium*, *Gongylidium*, *Hilaira*, *Hybocoptus*, *Mioxena*, *Oedothorax*, *Scotargus*, *Tapinocyboides*, *Trematocephalus*.
- Group D (Diplocephaleae): *Acartauchenius*, *Araeoncus*, *Asthenargus*, *Aulacocyba*, *Collinsia*, *Dicymbium*, *Diplocentria*, *Diplocephalus*, *Donacochara*, *Eboria*, *Erigone*, *Erigonella*, *Glyphesis*, *Gongylidiellum*, *Halorates*, *Hillhousia*, *Jacksonella*, *Leptorhoptrum*, *Lophomma*, *Monocephalus*, *Notioscopus*, *Ostearius*, *Phaulothrix*, *Rhaebothorax*, *Savignia*, *Tapinocyba*, *Thyreosthenius*, *Tiso*, *Tmeticus*, *Trichoncus*, *Troxochrus*.
- Group E (Walckenaerinae): *Baryphyma*, *Caledonia*, *Ceratinella*, *Cnephalocotes*, *Dismodicus*, *Drepanotylus*, *Enidia*, *Evansia*, *Gnathonarium*, *Hypselistes*, *Lessertia*, *Maso*, *Mecopisthes*, *Metopobactrus*, *Micrargus*, *Minyriolus*, *Moebelia*, *Panamomops*, *Pelecopsis*, *Peponocranium*, *Perimones*, *Pocadicnemis*, *Praestigia*, *Saloca*, *Silometopus*, *Styloctetor*, *Typhochrestus*, *Walckenaeria*.

#### Classification according to Millidge (1977)

##### Subfamily ERIGONINAE

1. *Leptorhoptrum*/*Lophomma* Group: **Diplocentria**, "Gongylidiellum" *mediocre*, **Leptorhoptrum**, **Lophomma**, *Notioscopus*, *Tiso*, *Troxochrus*, *Zornella*.
2. *Drepanotylus* Group: **Drepanotylus**, **Tibiopoides**.
3. *Hilaira* Group: *Erigonidium*, **Hilaira**, *Hylyphantes*, *Phaulothrix*.
4. *Gongylidium* Group: **Gongylidium**, *Oedothorax*, *Trematocephalus*.

5. *Erigone* Group: *Anerigone*, "Centromerus" *quadridentatus*, *Collinsia*, "Collinsia" *hibernica*, *Eperigone*, **Erigone**, *Halorates*, **Islandiana**, *Milleriana*.
6. *Gongylidiellum* Group: **Gongylidiellum**.
7. *Mioxena* Group: *Heterotrichoncus*, *Mioxena*, **Sisicus**, *Tapinocyboides*, *Trichoncoides*, *Wiehlea*.
8. *Tapinocyba* Group: *Acartauchenius*, **Ceratinops**, *Conigerella*, *Latithorax*, *Mecynargus*, *Rhaebothorax*, **Tapinocyba**, *Thyreosthenius*, *Trachelocampius*, "Trichopterna" *thorelli*.
9. *Pelecopsis* Group: *Abacoproeces*, "Abacoproeces" *ascitus*, *Acanthophyma*, *Baryphyma*, *Caledonia*, *Ceratinella*, *Ceratinopsis*, *Cineta*, *Cnephalocotes*, *Cochlembolus*, **Dismodicus**, *Dresconella*, *Exechophysis*, **Gonatium**, **Grammonota**, *Hypomma*, *Hypselistes*, *Kratochviliella*, *Lasiargus*, *Lessertia*, *Lessertina*, *Lochkovia*, *Maso*, *Mecopisthes*, *Metopobactrus*, *Micrargus*, "Micrargus" *kaestneri*, *Microstrandia*, *Minicia*, *Minyrioloides*, *Minyriolus*, *Nematogmus*, *Panamomops*, *Panamomopsides*, **Pelecopsis**, *Peponocranium*, *Plaesianillus*, *Praestigia*, *Scotinotylus*, *Scotoneta*, *Silometopus*, *Trichoncus*, *Trichopterna*.
10. *Walckenaeria* Group: *Araeoncoides*, *Evansia*, *Moebelia*, *Perimones*, "Saloca," **Typhochrestus**, **Walckenaeria**.
11. *Savignia* Group:
  - 11i. *Savignia* Genus Group: *Alioranus*, **Araeoncus**, *Delorhipis*, *Diastanillus*, *Dicymbium*, **Diplocephalus**, *Erigonella*, *Glyphesis*, *Saloca*, **Savignia**.
  - 11ii. *Dactylopisthes* Genus Group: *Dactylopisthes*.
  - 11iii. Miscellaneous: *Aulacocyba*, *Janetschekia*, *Thaumatocnus*.
12. *Erigonoplus* Group: *Erigonoplus*, *Cotyora*.
13. *Entelecara* Group: **Entelecara**, **Hybocoptus**.
14. *Tmeticus* Group: *Donacochara*, *Eboria*, *Ostearius*, **Sciastes**, **Tmeticus**.
15. *Asthenargus* Group: **Asthenargus**, *Carorita*, *Jacksonella*, *Microcentria*, *Tibioplus*.
16. Doubtful Genera: *Caracladus*, *Gnathonarium*, *Hybauchenidium*, *Lessertina*, *Monocephalus*, *Pocadicnemis*.

##### Subfamily LINYPHIINAE

1. *Lepthyphantes* Group: **Bolyphantes**, *Centromerita*, *Centromerus*, *Drapetisca*, **Lepthyphantes**, *Poeciloneta*, *Sintula*, *Syedra*.

2. *Microneta* Group: *Agyneta*, *Meioneta*, *Microneta*, *Syedrula*, *Theonina*.
3. *Oreonetides* Group: *Floronia*, *Macrargus*, *Montetextrix*, *Oreonetides*, *Tapinopa*.
4. *Cresmatoneta* Group: *Cresmatoneta*, *Kaestneria*.
5. *Linyphia* Group: *Linyphia* (s. lat.), *Microlinyphia*.
6. *Porrhomma* Group: *Bathyphantes*, *Porrhomma*.
7. *Aphileta* Group: *Aphileta*, *Maro*, *Saaristoa*.
8. *Diplostyla*: *Diplostyla*.
9. Genera with erigonine conformations: *Allomengea*, *Helophora*, *Taranucus*.
10. *Stemonyphantes* and *Labulla*.

#### Classification according to Millidge (1984)

##### "EPIGYNAL GROUPS"

1. *Stemonyphantes* Group: *Caviphantes*, *Estrandia*, *Falklandoglenes*, *Frontinella*, *Frontinellina*, *Jalapyphantes*, *Linyphantes*, *Microlinyphia*, *Mioxena*, *Ostearius*, *Palaeohyphantes*, *Selenyphantes*, *Smermisia*, *Stemonyphantes*, *Tallusia*, *Taranucus*. (Millidge (1985) placed in this group the following genera: *Catacercus*, *Cautinella*, *Ctenophysis*, *Dubiaranea*, *Notholephyphantes*, *Notiohyphantes*, *Onychembolus*, *Ostearius*, *Patagoneta*.)
2. Subfamily Mynogleninae: *Afroneta*, *Cassafroneta*, *Haplunis*, *Hyperafroneta*, *Megafroneta*, *Metafroneta*, *Metamynoglenes*, *Novafroneta*, *Parafroneta*, *Poecilafroneta*, *Promynoglenes*, *Protoerigone*, *Pseudafroneta*, *Trachyneta*.
3. Subfamily Linyphiinae: *Australolinyphia*\*, *Bathyphantes*, *Cresmatoneta*, *Diplostyla*, *Kaestneria*, *Labulla*\*, *Laetesia*, *Laperousea*, *Lessertinella*, *Linyphia*, *Maro*, *Neriene*, *Pityohyphantes*, *Porrhomma*, *Sisicus*, *Wiehlea*\* (see redefinition in Millidge (1993b); \*= cfr. new composition).
4. Subfamily Drapetiscinae: *Allomengea*, *Aphileta*, *Arcuphantes*, *Asthenargus*, *Carorita*, *Doenitzius*, *Drapetisca*, *Fageiella*, *Helophora*, *Saaristoa*, *Simplicistilus*, *Sintula*, *Tibioplus*, *Typhlonyphia*, *Wubana*. (Millidge (1985) added to this group the genera *Neomaso*, *Rhabdogyna*, and *Valdiviella*.)
5. Subfamily Micronetinae: *Agyneta*, *Bolyphantes*, *Centromerita*, *Centromerus*, *Centrophantes*, *Floronia*, *Gnathantes*, *Labullula*, *Lepthyphantes*, *Locketidium*, *Macrargus*, *Metaleptyphantes*, *Oreonetides*, *Poeciloneta*, *Syedra*, *Tapinopa*, *Tennesseellum*, *Theonina*, *Troglohyphantes*.
6. Subfamily Erigoninae: *Abacoproeces*, *Acartauchenius*, *Alioranus*, *Araeonus*, *Aulacocyba*, *Baryphyma*, *Caledonia*,

*Caracladus*, *Ceraticelus*, *Ceratinella*, *Ceratinopsis*, *Cnephalocotes*, *Collinsia*, *Dicymbium*, *Diplocephalus*, *Dismodicus*, *Donacochara*, *Drepanotylus*, *Eboria*, *Elgonella*, *Emenista*, *Entelecara*, *Eridantes*, *Erigone*, *Erigonella*, *Erigonidium*, *Erigonoplus*, *Evansia*, *Exechophysis*, *Glyphesis*, *Gnathonargus*, *Gnathonarium*, *Gonatium*, *Gongylidiellum*, *Gongylidium*, *Grammonota*, *Halorates*, *Hilaira*, *Hybocoptus*, *Hypomma*, *Hypselistes*, *Islandiana*, *Lessertia*, *Lophomma*, *Maso*, *Mecopisthes*, *Metopobactrus*, *Microcyba*, *Milleriana*, *Minicia*, *Minyrioloides*, *Minyriolus*, *Moebelia*, *Monocephalus*, *Notioscopus*, *Oedothorax*, *Origanates*, *Panamomops*, *Pelecopsis*, *Peponocranium*, *Perimones*, *Phanetta*, *Phaulothrix*, *Pocadicnemis*, *Praestigia*, *Rhaebothorax*, *Saloca*, *Savignia*, *Sciastes*, *Scotynotilus*, *Scylaceus*, *Scytiella*, *Silometopus*, *Sisicottus*, *Souessoula*, *Spirembolus*, *Stajus*, *Strongyliceus*, *Tachygyna*, *Tapinocyba*, *Tapinocyboides*, *Thyreosthenius*, *Tiso*, *Tmeticus*, *Trematocephalus*, *Trichoncoides*, *Trichoncus*, *Trichopterna*, *Troxochrus*, *Tunagyna*, *Typhochrestus*, *Walckenaeria*, *Zornella*. (Note that Millidge (1985) placed *Sphecozone* here. Millidge (1986) reported a desmitracheate system in *Donacochara*, *Hilaira*, *Laminacauda*, *Leptorhoptrum*, and *Drepanotylus*, in addition to the nonerigonines *Tennesseellum* and *Meioneta*.)

#### Classification according to Millidge (1993b)

1. Subfamily Mynogleninae.
2. Subfamily Dubiaraneinae: *Dubiaranea*, *Notiohyphantes*.
3. Subfamily Erigoninae.
4. Subfamily Linyphiinae: In addition to taxa already included here by most older classifications, the following are added: *Cryptolinyphia*, *Frontinellina*, "*Linyphia*" *rita*, "*L.*" *catalina*, *Microlinyphia*, "*Neriene*" *limbata*, *Oilinyphia*. Millidge (1993b) excluded the following genera from this subfamily: *Australolinyphia*, *Labulla*, *Wiehlea*.
5. Subfamily Micronetinae: *Agyneta*, *Meioneta*, *Microneta*, *Syedrula*, *Tennesseellum*, *Theonina*.
6. Subfamily Lepthyphantinae: *Bolyphantes*, *Centromerita*, *Centromerus*, *Centrophantes*, *Floronia*, *Gnathantes*, *Labullula*, *Lepthyphantes*, *Locketidium*, *Macrargus*, *Metaleptyphantes*, *Oreonetides*, *Poeciloneta*, *Syedra*, *Tapinopa*, *Troglohyphantes*.
7. Miscellaneous genera: *Allomengea*, *Aphileta*, *Arcuphantes*, *Asthenargus*, *Doenitzius*, *Drapetisca*, *Fageiella*, *Helophora*, *Jacksonella*, *Laminacauda*, *Neomaso*, *Saaristoa*, *Sintula*, *Stemonyphantes*, *Typhlonyphia*, *Wubana*. (Drapetiscinae is heterogeneous and is no longer justifiable (Millidge, 1993b).)

## Appendix 3

### Examples of Linyphiid (Mostly Erigonines) Male Prosomic Morphology

(Illustration sources are given in parentheses. Character numbers refer to Appendix 1 (see text for details).)

1. Male cephalic region not raised (character 41, state 0):  
*Erigonoploides cardiratus* Eskov (Eskov, 1989, fig. 3.1).  
*Tapinocyba praecox* (O.P.-Cambridge) (Figure 32A; Roberts, 1993, fig. 31c).
2. Male cephalic region entirely raised (character 41, state 1):  
*Araeoncus crassiceps* (Westring) (Figure 32B; Roberts, 1993, fig. 41c).  
*Bolyphantus luteolus* (Blackwall) (Roberts, 1993, fig. 76a).  
*Caracladus aviculus* (L. Koch) (Figure 32B; Thaler, 1969, fig. 20).  
*Floronia bucculenta* (Clerck) (Roberts, 1993, fig. 72c).  
*Gonatium rubens* (Blackwall) (Figure 32D; Roberts, 1993, fig. 18a).  
*Hypselocara altissima* (Simon) (Figure 32E; Millidge, 1991, fig. 449).  
*Trematocephalus cristatus* (Wider) (Roberts, 1993, fig. 16g).  
*Tutaibo debilipes* Chamberlin (Millidge, 1991, fig. 669).
3. Male PME cephalic lobe (character 42):  
*Dactylopiastes mirabilis* Tanasevitch (Tanasevitch, 1989, fig. 128).  
*Dicornua hikosanensis* Oi (Oi, 1960, figs. 186, 187).  
*Entelacara acuminata* (Wider) (Figure 32F; Roberts, 1993, fig. 16a).  
*Entelacara flavipes* (Blackwall) (Roberts, 1993, fig. 16c).  
*Minicia kirghizica* Tanasevitch (Tanasevitch, 1989, fig. 128).  
*Trichopterna thorelli* (Westring) (Roberts, 1993, fig. 23e).  
*Walckenaeria capito* (Westring) (Roberts, 1993, fig. 9b).  
*Walckenaeria furcillata* (Menge) (Roberts, 1993, fig. 8j).  
*Walckenaeria gologolensis* Scharff (Figure 32H; Scharff, 1990, fig. 214).  
*Walckenaeria incisa* (O.P.-Cambridge) (Roberts, 1993, fig. 8f).  
*Walckenaeria mitrata* (Menge) (Figure 32G; Roberts, 1993, fig. 8h).  
*Walckenaeria nodosa* O.P.-Cambridge (Roberts, 1993, fig. 8d).  
*Walckenaeria stylifrons* (O.P.-Cambridge) (Roberts, 1993, fig. 8e).
4. Male post-PME lobe (character 43):  
*Dismodicus bifrons* (Blackwall) (Roberts, 1993, fig. 16h, Wiehle, 1960, fig. 523).  
*Hypomma bituberculatum* (Wider) (Roberts, 1993, fig. 16j).  
*Laminacauda tuberosa* Millidge (Figure 32i; Millidge, 1991, fig. 277).  
*Oedothorax apicatus* (Blackwall) (Roberts, 1993, fig. 23d).  
*Oedothorax gibbosus* (Blackwall) (Figure 32j; Roberts, 1993, fig. 21e,g).  
*Oedothorax retusus* (Westring) (Roberts, 1993, fig. 23c).  
*Scotinotylus majesticus* Millidge (Millidge, 1981, fig. 86).  
*Strandella quadrimaculata* Uyemara (Oi, 1960, fig. 201).  
*Thyreosthenius biovatus* (O.P.-Cambridge) (Roberts, 1993, fig. 38b).  
*Typhochrestus digitatus* (O.P.-Cambridge) (Roberts, 1993, fig. 41e).  
*Mitrager noordami* van Helsdingen (Figure 33A; van Helsdingen, 1985, fig. 1).
5. Male inter-AME-PME lobe (character 44):  
*Baryphyma duffeyi* (Millidge) (Figure 33B; Roberts, 1993, fig. 17f).  
*Diplocephalus connatus* Bertkau (Roberts, 1993, fig. 39k).  
*Minicia marginella* (Wider) (Wiehle, 1960, figs. 31, 32).  
*Walckenaeria clavicornis* (Emerton) (Roberts, 1993, fig. 8g).  
*Walckenaeria cuspidata* (Blackwall) (Roberts, 1993, fig. 8i).  
*Walckenaeria monoceros* (Wider) (Roberts, 1993, fig. 9d).  
*Walckenaeria kochi* (O.P.-Cambridge) (Figure 33C; Roberts, 1993, fig. 9f).  
*Walckenaeria unicornis* O.P.-Cambridge (Roberts, 1993, fig. 9c).
6. Male clypeal lobe (character 45):  
*Coreorgonal monoceros* (Simon) (Figure 33D; Millidge, 1981, figs. 147, 148).  
*Coreorgonal petulcus* (Millidge) (Millidge, 1981, fig. 146).  
*Floricomus pythonicus* Crosby and Bishop (Figure 33E; Bishop and Crosby 1935, fig. 26).  
*Floricomus littoralis* Chamberlin and Ivie (Chamberlin and Ivie, 1935, fig. 59).  
*Floricomus nasutus* Crosby and Bishop (Bishop and Crosby 1935, figs. 7, 8).  
*Gnathonargus unicornis* (Banks) (Figure 33F; Bishop and Crosby 1935, figs. 9, 10).  
*Goneatara platyrhinus* Crosby and Bishop (Crosby and Bishop, 1927, figs. 3, 4).  
*Glyphesis cottonae* (La Touche) (Roberts, 1993, fig. 39b).  
*Mecopisthes peusi* Wunderlich (Roberts, 1993, fig. 27f).  
*Panamomops sulcifrons* (Wider) (Roberts, 1993, fig. 41d).

7. Male AME lobe (character 46):  
*Savignia fronticornis* (Simon) (Figure 33G; Simon, 1894, figs. 669, 670).  
*Diplocephalus cristatus* (Blackwall) (Roberts, 1993, fig. 39g).  
*Diplocephalus foraminifer* (O.P.-Cambridge) (Figure 33H; Deltshv, 1985, fig. 6).  
*Praestigia kulczynskii* Eskov (Eskov, 1979, fig. 11).  
*Savignia frontata* (Blackwall) (Roberts, 1993, fig. 39f).  
*Savignia saitoi* Eskov (Eskov, 1988, fig. 67).  
*Spirembolus bilobatus* (Chamberlin and Ivie) (Millidge, 1980, figs. 178, 181).
8. Combined Characters.—The following are examples of combinations of the different types of cephalic modifications previously described. For example, "A" refers to taxa that exhibit the combination of types 3 (cephalic region entirely raised) plus 2 (PME cephalic lobe).

Prosomic modification type	Prosomic modification type				
	3	4	5	6	7
2	A	B	C	D	E
3	-	F	G	H	I
4	-	-	J	K	L
5	-	-	-	M	N
6	-	-	-	-	O

- A. Cephalic region entirely raised plus PME cephalic lobe:  
*Metopobacterus verticalis* Simon (Simon, 1894, fig. 659).  
*Walckenaeria capito* (Westring) (Figure 33i; Roberts, 1993, fig. 9b).
- B. Cephalic region entirely raised plus post-PME lobe:  
*Trematocephalus cristatus* (Wider) (Figure 33j; Roberts, 1993, fig. 16g).
- C. Cephalic region entirely raised plus inter-AME-PME lobe:  
 No examples found.
- D. Cephalic region entirely raised plus clypeal lobe:  
*Floricomus rostratus* (Emerton) (Figure 34A; Bishop and Crosby, 1935, figs. 29, 30).  
*Scotinotylus tianshanicus* Tanasevitch (Figure 34B; Tanasevitch, 1989, figs. 164, 165).
- E. Cephalic region entirely raised plus AME lobe:  
*Walckenaeria acuminata* Blackwall (Figure 34C; Roberts, 1993, fig. 9g).  
*Walckenaeria extraterrestris* Bosmans (Figure 34D; Bosmans and DeSmet, 1993, figs. 63, 64).
- F. PME cephalic lobe plus post-PME lobe:  
*Goneatara platyrhinus* Crosby and Bishop (Figure 34E; Crosby and Bishop, 1927, figs. 3, 4).
- G. PME cephalic lobe plus inter-AME-PME lobe:  
*Diplocephalus connatus* Bertkau (Figure 34F; Roberts, 1993, fig. 39k).  
*Walckenaeria furcillata* (Menge) (Figure 34G; Roberts, 1993, fig. 8j; Wiehle, 1960, fig. 310).  
*Callitrichia sellafrontis* Scharff (Figure 34H; Scharff, 1990, fig. 22).
- H. PME cephalic lobe plus clypeal lobe:  
*Trichopterna thorelli* (Westring) (Figure 34i; Roberts, 1993, fig. 23e).  
*Concavocephalus rubens* Eskov (Figure 34j; Eskov, 1989, fig. 1).
- I. PME cephalic lobe plus AME lobe:  
*Dactylopiastes mirabilis* Tanasevitch (Figure 35A; Tanasevitch, 1989, fig. 128).  
*Diplocephalus avernus* Denis (Denis, 1970, fig. 378).  
*Diplocephalus bicephalus* Simon (Simon, 1894, fig. 653).  
*Savignia birostrum* (Chamberlin and Ivie) (Figure 35B; Chamberlin and Ivie, 1947, figs. 17, 18).  
*Savignia borea* Eskov (Eskov, 1988, fig. 60).
- J. Inter-AME-PME lobe plus inter-AME-PME lobe:  
*Bursellia cameroonensis* Bosmans and Jocqué (Figure 35C; Bosmans and Jocqué, 1983, fig. 3A).  
*Scotinotylus majesticus* (Chamberlin and Ivie) (Figure 35D; Millidge, 1981, fig. 86).
- K. Post-PME lobe plus clypeal lobe:  
*Dismodicus bifrons* (Blackwall) (Figure 35E; Roberts, 1993, fig. 16h; Wiehle, 1960, fig. 523).
- L. Inter-AME-PME lobe plus AME lobe:  
*Minicia kirghizica* Tanasevitch (Figure 35F; Tanasevitch, 1985, fig. 6.1).  
*Spirembolus bilobatus* (Chamberlin and Ivie) (Figure 35G; Millidge, 1980, figs. 178, 179).
- M. Inter-AME-PME lobe plus clypeal lobe:  
*Savignia badzhalensis* Eskov (Figure 35H; Eskov, 1992, fig. 1).
- N. Inter-AME-PME lobe plus AME lobe:  
 No examples found.
- O. Clypeal lobe plus AME lobe:  
*Coreorgonal bicornis* (Emerton) (Figure 35I; Millidge, 1981, fig. 145).  
*Coreorgonal petulcus* (Millidge) (Figure 35J; Millidge, 1981, fig. 146).

## Appendix 4

### Material Examined

(Specimens are listed alphabetically by genus and species. Localities are given exactly as they appear on the museum specimen labels.)

#### LINYPHIIDAE

#### ERIGONINAE

- Araeoncus crassiceps* (Westring): England: Tennyson Moss Flint, 23.v.1965 (J.A.L. Cooke, AMNH).
- Araeoncus humilis* (Blackwall): England: Whiteford Burrows, 24.ix.1965 (J.A.L. Cooke, AMNH).
- Asthenargus paganus* (Simon): France: E. Simon Collection No. 282 (AMNH); Switzerland: Justital, Bernerberld (det. Schenkel, AMNH).
- Ceratinops inflatus* (Emerton): USA: California: Mendocino Co.: Caspar, 7.iii.1954 (J. Helfer, AMNH).
- Diplocentria bidentata* (Emerton): Russia: NE Siberia, Magadan Area, Ola River upper flow, 15–18.vii.1992 (Yu. M. Marusik, USNM); Russia: NE Siberia, Lankovaya river, 12–19.viii.1992 (Yu. M. Marusik, USNM).
- Diplocephalus cristatus* (Blackwall): England: Muckle Samnel. 3.i.1967 (J.A.L. Cooke, AMNH); Minster Lovell, Oxon, 13.v.1962 (J.A.L. Cooke, AMNH).
- Dismodicus decemoculatus* Emerton. Canada: The Pas, Manitoba, 1.vii.1917 (Emerton col & det, AMNH); USA: Alaska: Kobuk river between Shungnak and Kiana, 29.vi–16.vii.1948 (R.D. Hamilton, AMNH); New York, Ithaca, 16.v.1926 (Seely & Fletch, AMNH).
- Drepanotylus uncatulus* (O.P.-Cambridge): England: Surrey, 1979 (J.A. Murphy, AMNH).
- Entelecara acuminata* (Wider): Russia: Novotcherkask, Don. E40.N47 (Spassky coll. AMNH); Switzerland: Basel, 1946 (Schenkel coll., AMNH).
- Entelecara errata* (O.P.-Cambridge): England(?): Cairn Well Perth, 3059', 19-6-66 (J. Crooker, AMNH).
- Erigone psychrophila* Thorell: USA: Alaska: Pt. Barrow, 23.VI.1963 (R.F. Ashley, AMNH).
- Gonatium rubens* (Blackwall): England: Allerston forest, Yorks. [= Yorkshire], 10.2.1964 (AMNH).
- Gongylidiellum vivum* (O.P.-Cambridge): England: Surrey, 1979 (J.A. Murphy, AMNH).
- Gongylidium rufipes* (Sundevall): Denmark? (ZMUC).
- Grammonota pictilis* (O.P.-Cambridge): Canada: Nova Scotia, Knetville, 31.v.1957 (C. Dondale, AMNH).
- Hilaira excisa* (O.P.-Cambridge): England: Brecon, Beacon, 5.7.65 (J.A.L. Cooke, AMNH).
- Hilaira vexatrix* (O.P.-Cambridge): USA: Alaska: N slope Brgh Meade R. 60 mi [96 km] S Barrow, 20.viii.1978 (B. Vogel, AMNH).
- Hybocoptus decollatus* (Simon): Europe: No. 220, Simon collection (AMNH); J.E. Hull coll. (AMNH).
- Hylyphantes graminicola* (Sundevall): England: Surrey (J.A. Murphy, AMNH).
- Hylyphantes nigrinus* (Simon): Russia: Siberia: Sakhalin Is., Aniva Dist., Novoaleksandovka, vi.1990 (A.M. Basarukin, USNM).
- Islandiana cristata* Eskov: Russia: NE Siberia, Magadan Area, Ola river upper flow, 15–18.vii.1992 (Yu. M. Marusik, USNM).
- Islandiana princeps* Brændegaard: Greenland, 5.vii.1983 (P. Nielsen, ZMUC).
- Laminacauda argentinensis* Millidge: Argentina: Rio Negro, El Bolson, 25.vi.1992 (A. Kovacs, AMNH).
- Laminacauda diffusa* Millidge: Argentina: La Patiaia, Tierra del Fuego, 20–23.ii.1961 (B. Malkin, AMNH).
- Laminacauda plagiata* (Tullgren): Chile: Malleco, 3 km W Victoria, 100 m., mixed nothofagus forest, 13.xii.1984–12.ii.1985 (S. & J. Peck, AMNH).
- Leptorhoptrum robustum* (Westring): England: North Cumberland, 1979 (J.A. Murphy, AMNH).
- Lophomma punctatum* (Blackwall): England: Killhope haw., Durham, 2000', 15.vi.1966 (J.A.L. Cooke, AMNH).
- Oedothorax gibbosus* (Blackwall): England: Tentesmuir Dune; Marsh, 20.vi.1966 (J.A.L. Cooke, AMNH).
- Ostearius melanopygius* (O.P.-Cambridge): USA: Mass., Pepperell, 19.x.1963 (H.W. Levi, USNM); Hawaii: Maui, Makawao Dist., Poli Poli State Pk., 17.xii.1976 (V Roth & Schroepfer, CAS); Bolivia: Oruro, 12,500', 24.iii.1958 (F. Walsh, AMNH).
- Pelecopsis dorniana* Heimer: Russia: NE Siberia, Lankovaya River (Ola Riv. bassin [sic.]), 12–19.viii.1992 (Yu. M. Marusik, USNM).
- Pelecopsis nemoralis* (Blackwall): England: Whiteford Burrows, 8.iv.1966 (J.A.L. Cooke, AMNH); nr. Falstone, Northumberland, 15.viii.1965 (J.A.L. Cooke, AMNH).
- Pelecopsis parallela* (Wider): England: Capel Green, Suff., 12.ix.1960 (J.A.L. Cooke, AMNH).
- Savignia frontata* (Blackwall): England: Whiteford Burrows. Glam., 24.ix.1965; England, 4.x.1966 (J.A.L. Cooke, AMNH).
- Sciastes truncatus* (Emerton): Canada: NW Territories, MacKenzie: Stagg River camp, 12 mi [19.2 km] E Rae., 12.vi.ii.1965 (J. & W. Ivie, AMNH).
- Sisicus apertus* (Holm): USA: Alaska: Admiralty Is., vi.1963 (Sheppard, AMNH); Russia: NE Siberia, Lankovaya River

- (Ola Riv. bassin [sic.]), 18–19.viii.1992 (Yu. M. Marusik, USNM).
- Tapinocyba praecox* (O.P.-Cambridge): England: Surrey (J.A. Murphy, AMNH).
- Tibioploides pacificus* Eskov and Marusik: Russia: NE Siberia, 30 km NW Magadan, 3–7.vi.1991 (Marusik, AMNH).
- Tmeticus tolli* Kulczynski: Russia: NE Siberia, N Sakhalin, Okha dist Pil'tun Bay, 6.vi.1991 (AM Basaruki, USNM); Lankovava River (Ola Riv. bassin [sic.]), viii.1992 (Yu. M. Marusik, USNM).
- Typhochrestus digitatus* (O.P.-Cambridge): England: Whiteford Burrows, 29.ix.1965 (J.A.L. Cooke, AMNH).
- Walckenaeria acuminata* Blackwall: England: Wales, Dyfed, x. 1988 (K. Catley, AMNH).
- Walckenaeria directa* (O.P.-Cambridge): Canada: British Columbia: Terrace, III.1933 (Hippisley, AMNH).

## Other LINYPHIIDAE

- Afroneta* sp.: Cameroon: Northwest Province: Menchum Division, near Lake Oku, ca. 2150 m, 7–13.II.1992 (Griswold, Larcher, Scharff & Wanzie, USNM, CAS).
- Bathyphantes albiventris* (Banks): USA: Tennessee, Blount Co., nr. Cade's Cove, Rainbow cave, 8.viii.1981 (J. Coddington, USNM).
- Bathyphantes bishopi* Ivie: USA: North Carolina, Great Smoky Mtns. N. P., Clingman's Dome, 26.vii.1988 (USNM).
- Bathyphantes brevipes* (Emerton): St. Paul, det. K. Eskov, 4.i.1986 (USNM).
- Bathyphantes keeni* (Emerton): Canada: BC: Vancouver (USNM).
- Bathyphantes pallidus* (Banks): USA: Maryland: Prince George's Co.: Patuxent WRC, 2.vi.1994 (G. Hormiga, USNM).
- Bathyphantes* sp.: USA: Oregon, Coos Co., Shore Acres S. P., 0.5 mi [0.8 km] S of Botanical Garden, 16.vii.1990 (G. Hormiga & L. Garcia de Mendoza, USNM).
- Bolyphantes luteolus* (Blackwall): Spain: Huesca: Jaca, San Juan de la Peña, 19.XII.1977 (C. Pedrocchi-Renault et al., USNM).
- Diplostyla concolor* (Wider): USA: Mass., Barnstable Co., Quisset, 10.vi.1988 (R.L. Edwards, USNM).
- Haplisis diloris* (Urquhart): New Zealand: Fiordland Cascade, 16.i.1975 (A.D. Blest, OM).
- Lepthyphantes tenuis* (Blackwall): Spain: Huesca: Jaca, San Juan de la Peña, 8.VIII.1977 (C. Pedrocchi-Renault et al., USNM).
- Lepthyphantes tenebricola* (Wider): Sweden: Tullgarn, 14–15.vii.1995 (G. Hormiga, USNM).
- Linyphia triangularis* (Clerck): Germany: between Deutz and Siegen, 9.VIII.1964 (R. Crabill, USNM); France: Manche, Quettehou, 27.VII.1956 (USNM); Spain: Huesca, X.1986 (J.A. Coddington, USNM).
- Microlinyphia dana* (Chamberlin and Ivie): USA: Washington: Clallam Co.: Elwha river near Altaire campground, Olympic N.P., 2.VIII.1990 (G. Hormiga, USNM); Island Co.: Lake Pondilla, 16.VI.1987 (R. Crawford, UW).
- Novafroneta vulgaris* Blest: New Zealand: S of Brighton, 17.VII.1974 (A.D. Blest, OM).
- Stemonyphantes blauveltae* (Gertsch): USA: New York: Ithaca (USNM); Montana: Callaway Co.: Tucker Prairie, 22.III.1985 (J.C. Weaver, USNM).
- Vesicapalpus* sp.: Brazil: Rio de Janeiro, Teresopolis, P. N. Ser-  
ra dos Orgãos, 11.xi.1982 (L. Sorkin, AMNH).

## PIMOIDAE

- Pimoa altiocolata* (Keyserling): Canada: British Columbia: Wellington, Vancouver Is., 1–20.XI.1950 (R. Guppy, AMNH); USA: Washington: Nahcotta, 23.VIII.1955 (T. Kincaid, CAS); WA: Clark Co: N of Crawford Crossing, 25.x.1987 (R. Crawford, UW); Oregon: Lane Co.: Cape Perpetua, Cook Ridge Trail. Siuslaw Ntl. For., 14.VII.1990 (G. Hormiga, USNM); Mercer Lake N Rd., N of Florence, Siuslaw Ntl For, 14.viii.1990 (G. Hormiga, USNM); Canada: British Columbia: Wellington, Vancouver Is., 1–20.XI.1950 (R. Guppy, AMNH).
- Pimoa rupicola* (Simon): Italy: Alpi Apuane, 16.X.1975, 500 m (IZUI).

## THERIDIIDAE

- Steatoda grossa* (C.L. Koch): Switzerland: Bern, Gals, 16.vi.ii.1989 (J. Coddington, USNM).

## THERIDIOSOMATIDAE

- Theridiosoma gemmosum* (L. Koch): USA: Georgia: Rabun Co., Ellicott Rock Wilderness Area, 750–800 m., 2.vi.1993 (Bond, Dellinger, & Dobyns, USNM).

## TETRAGNATHIDAE

- Tetragnatha versicolor* Walckenaer: USA: California: Siskiyou Co.: Yreka-Sahasta River, 8 mi. [12.8 km] N of Yreka, 17.VIII.1964 (P.L. & U.F. Holt, USNM).



## Figures

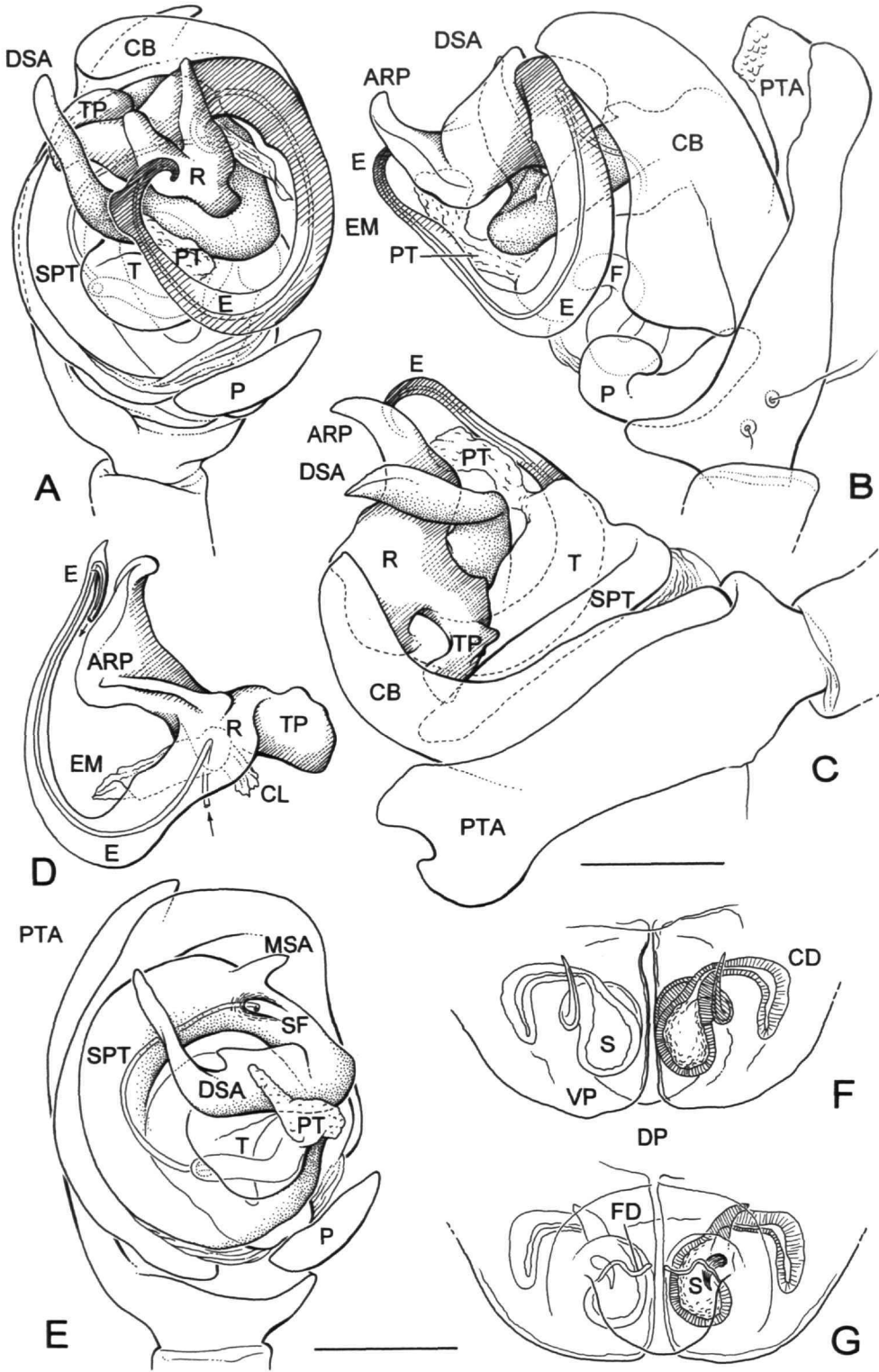


FIGURE 1.—*Araeoncus crassiceps*: A-E, male palp; F,G, epigynum. A, ventral; B, ectal; C, mesal; D, embolic division; E, ventral (embolic division removed); F, ventral; G, dorsal. (Scale bars=0.1 mm.)

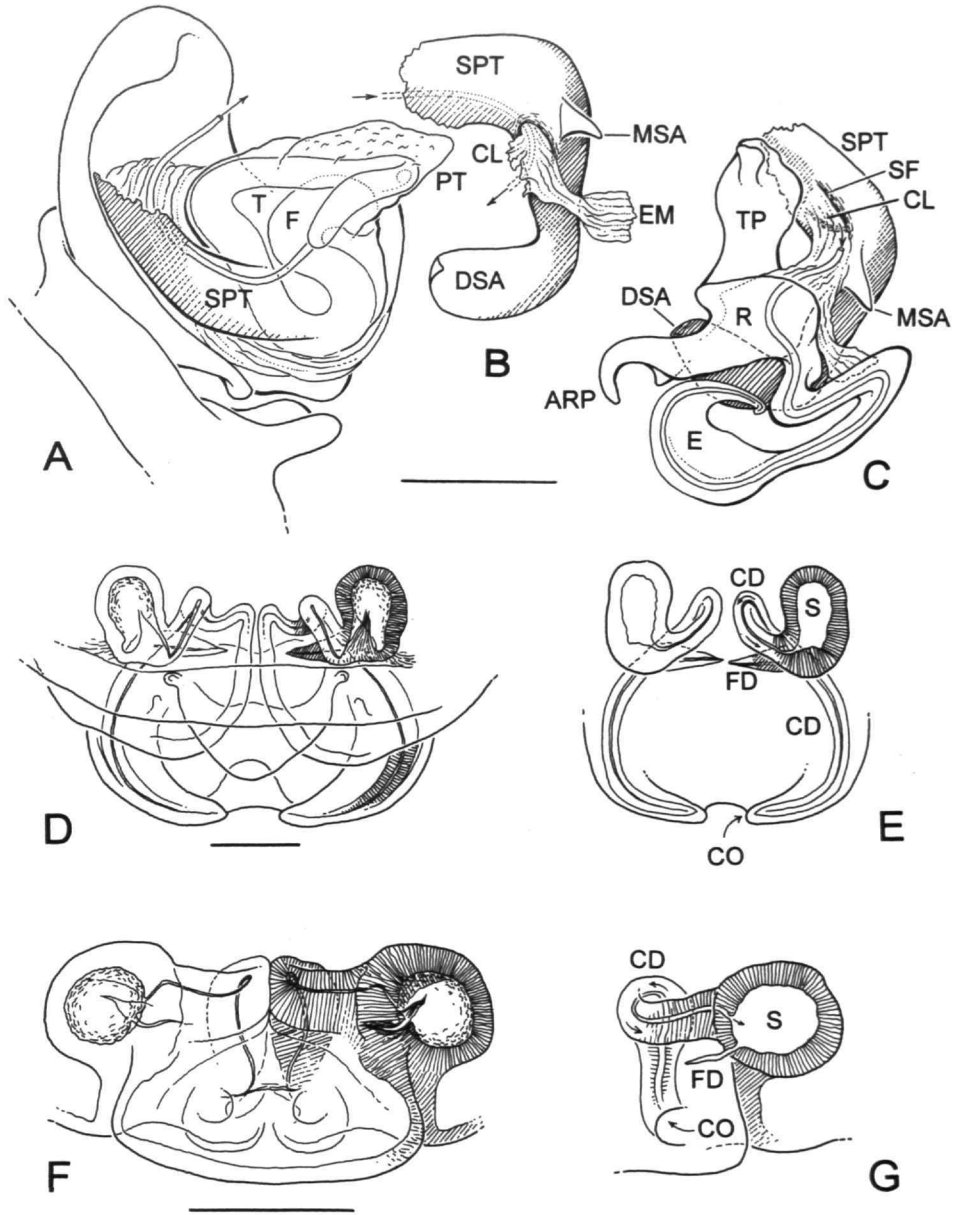


FIGURE 2.—*Araeoncus humilis* (A–C), *Erigone psychrophila* (D,E), and *Walckenaeria directa* (F,G): A–C, male palp; D–G epigynum. A, mesoventral (suprategulum removed); B, distal region of suprategulum; C, suprategulum (distal region) and embolic division; D, dorsal; E, same, schematic; F, dorsal; G, same, schematic. (Scale bars=0.1 mm.)

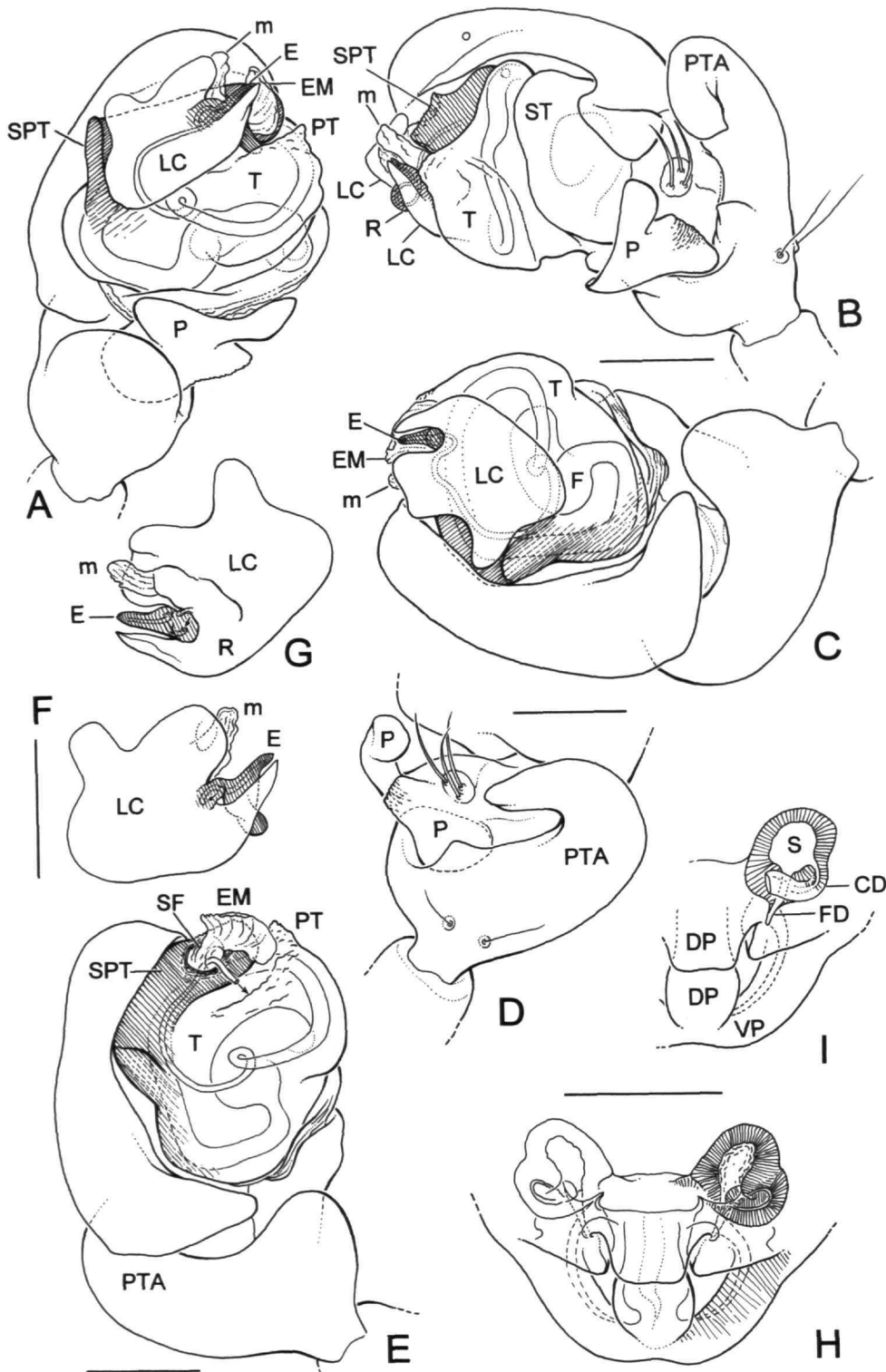


FIGURE 3.—*Asthenargus paganus*: A-G, male palp; H,I, epigynum. A, ventral; B, ectal; C, mesal; D, tibia and paracymbium, dorsoectal; E, ventral (embolic division removed); F, embolic division, ventral; G, same, dorsal; H, dorsal; I, schematic, dorsal. (Scale bars=0.1 mm.)

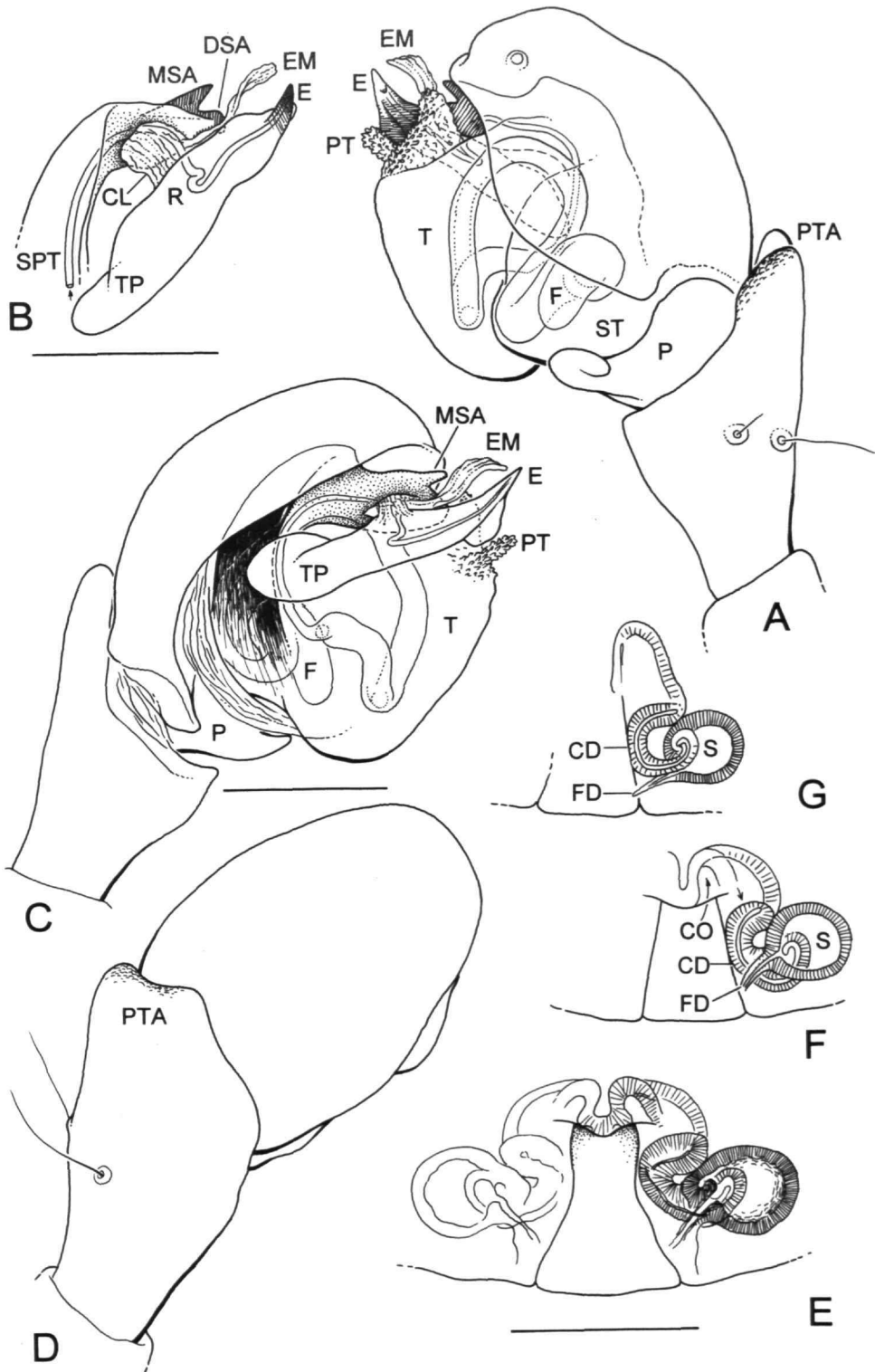


FIGURE 4.—*Ceratinops inflatus*: A–D, male palp; E–G, epigynum. A, ectal; B, embolic division and suprategulum (distal region); C, mesal; D, dorsal; E, ventral; F, schematic, ventral; G, schematic, dorsal. (Scale bars=0.1 mm.)

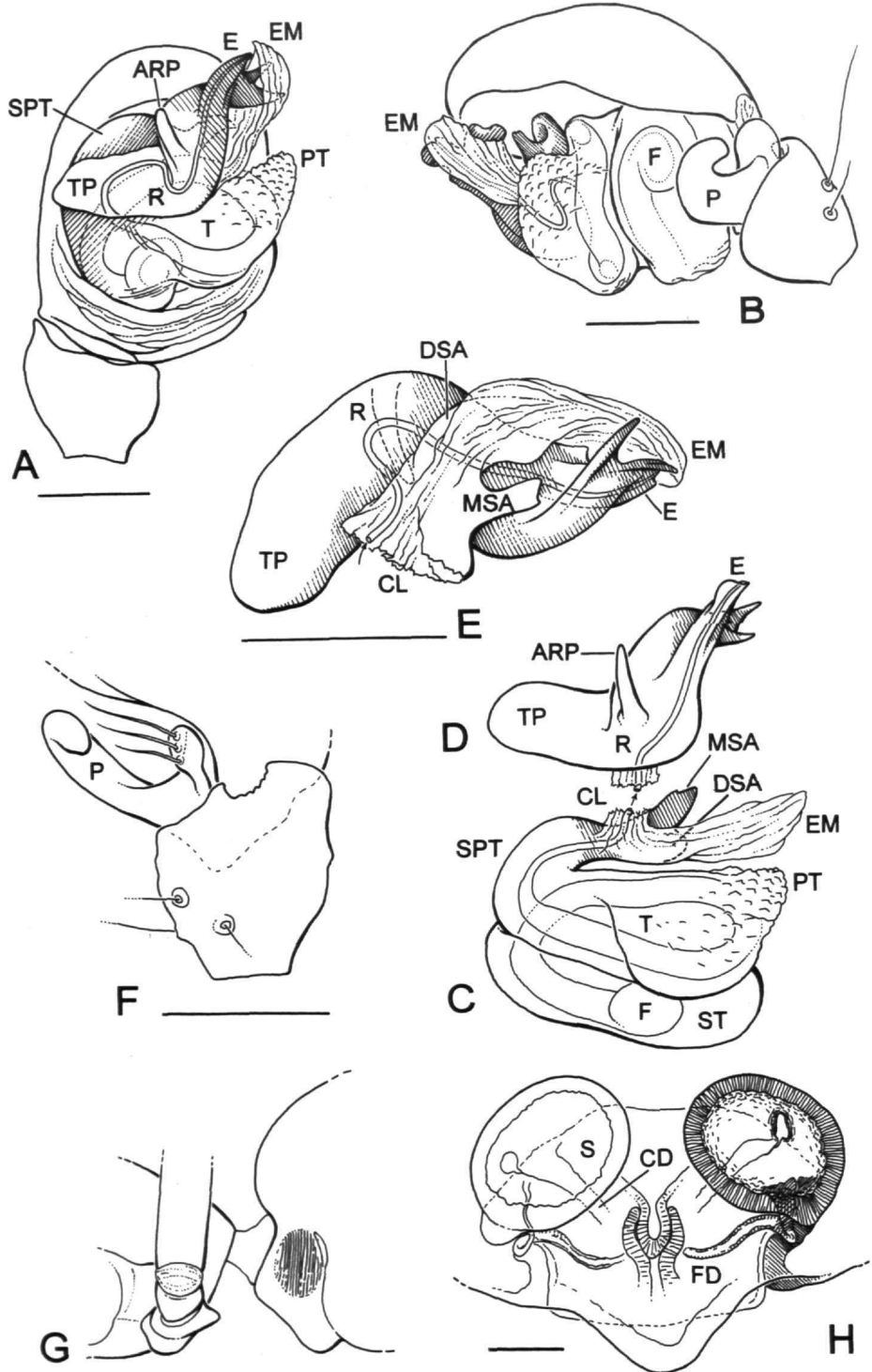


FIGURE 5.—*Diplocentria bidentata*: A–F, male palp; G, stridulatory organ; H, epigynum. A, ventral; B, ectal; C, schematic, embolic division removed; D, embolic division, schematic; E, embolic division; F, tibia and paracymbium, dorsal; G, male coxa IV–booklung plate stridulatory organ (redrawn from Wiehle, 1960, fig. 787); H, ventral. (Scale bars=0.1 mm.)

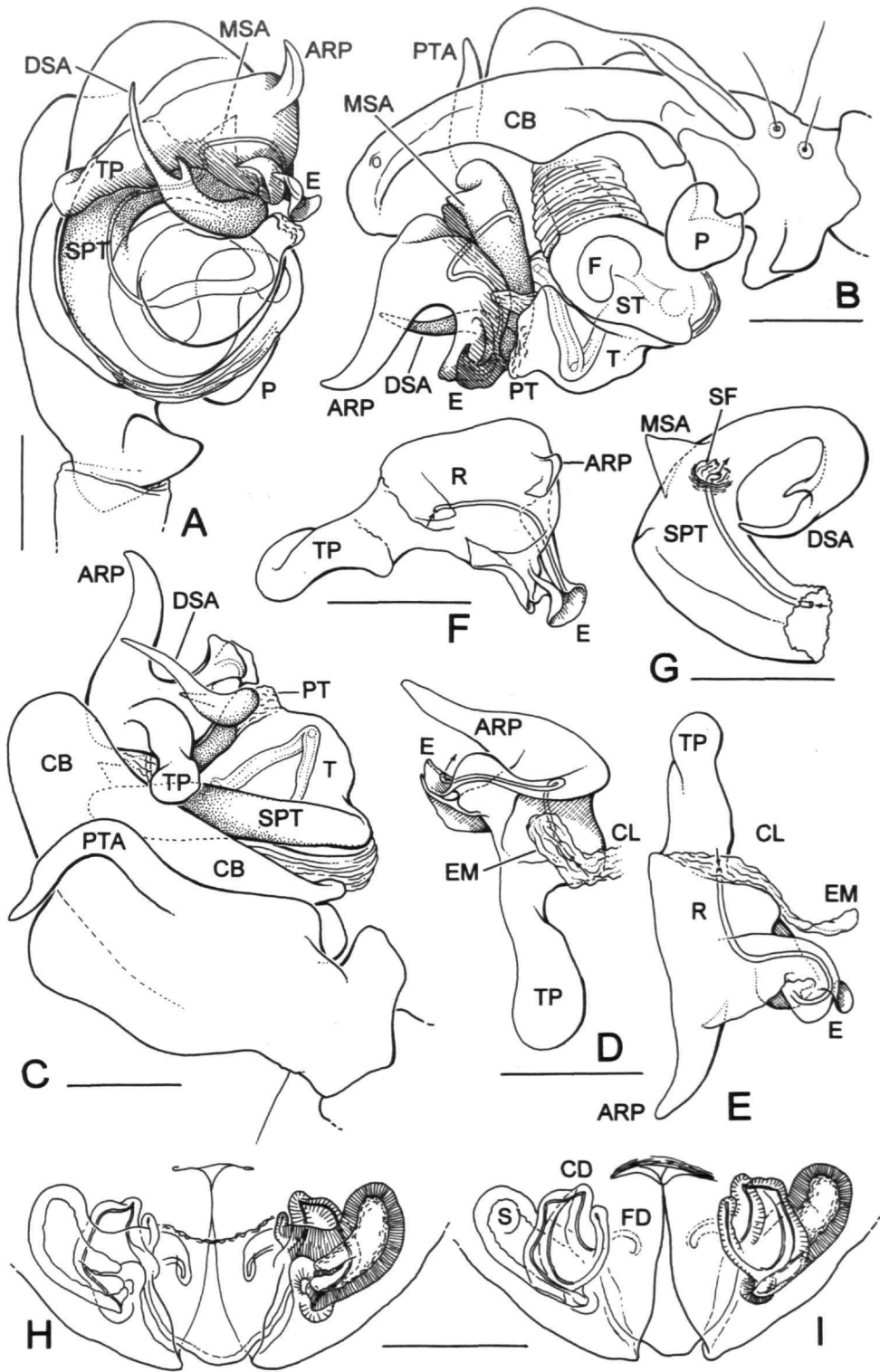


FIGURE 6.—*Diplocephalus cristatus*: A-G, male palp; H,I, epigynum. A, ventral; B, ectal; C, mesal; D, embolic division; E, same; F, same; G, supratégulum (distal end); H, dorsal; I, ventral. (Scale bars=0.1 mm.)

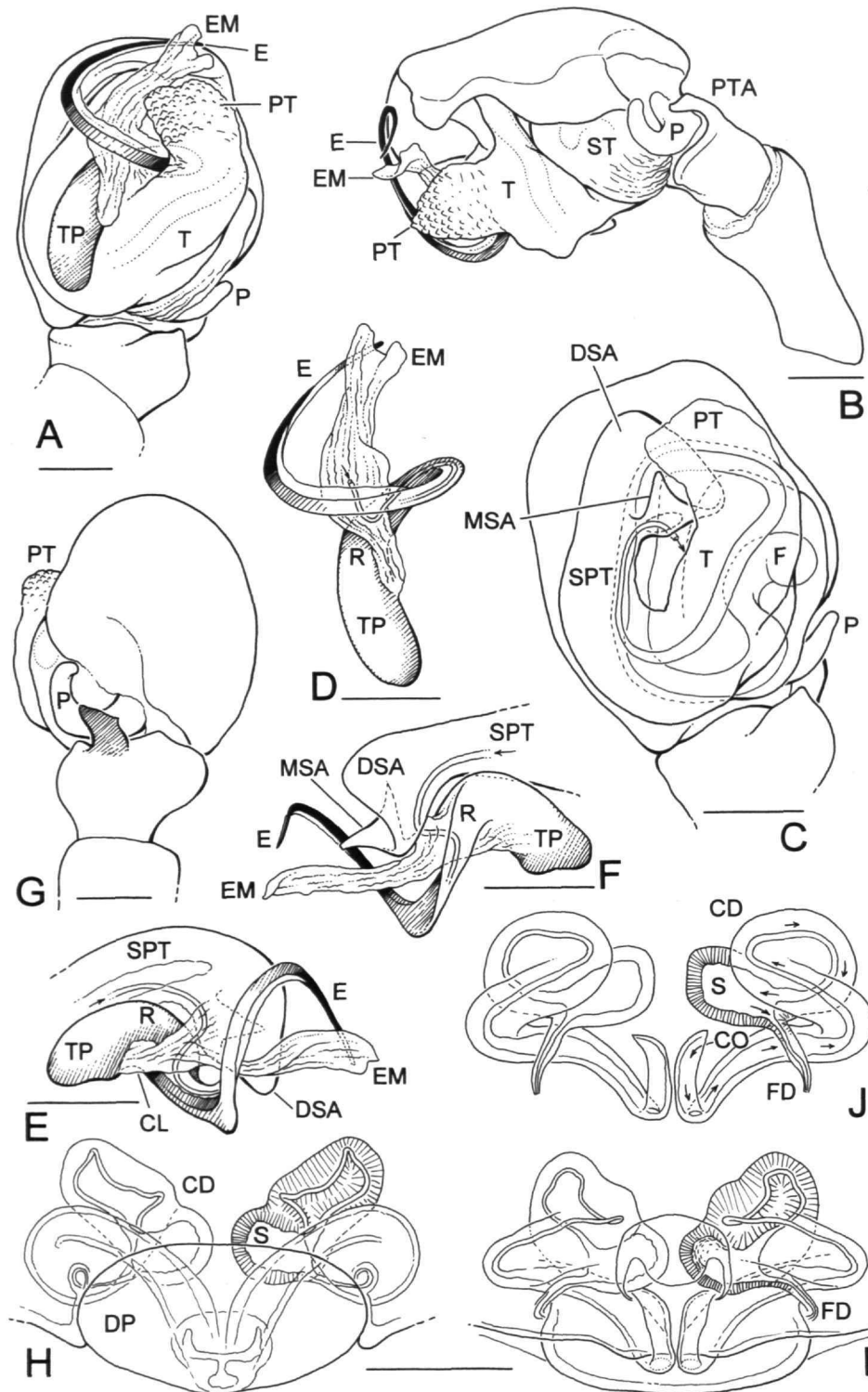


FIGURE 7.—*Dismodicus decemoculatus*: A–G, male palp; H–J, epigynum. A, ventral; B, ectal; C, ventral (embolic division removed); D, embolic division; E, embolic division and suprategulum (distal region), dorsal; F, same, ventral; G, dorsal; H, dorsal; I, ventral; J, schematic, ventral. (Scale bars=0.1 mm.)



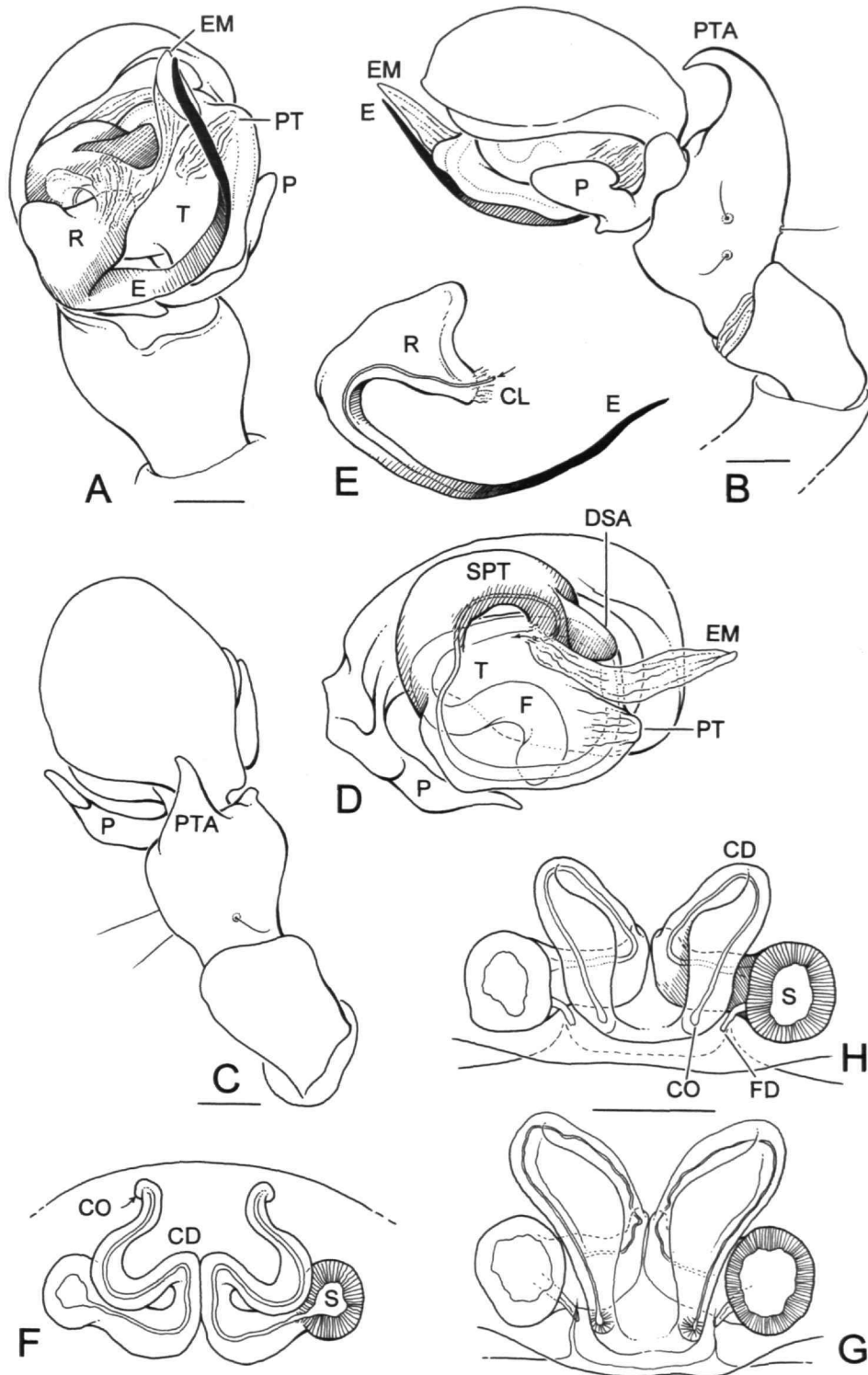


FIGURE 8.—*Drepanotylus uncatus*: A–E, male palp; F–H, epigynum. A, ventral; B, ectal; C, dorsal; D, ventral (embolic division removed); E, embolic division, ventral; F, schematic, anterior; G, ventral; H, same, schematic. (Scale bars=0.1 mm.)

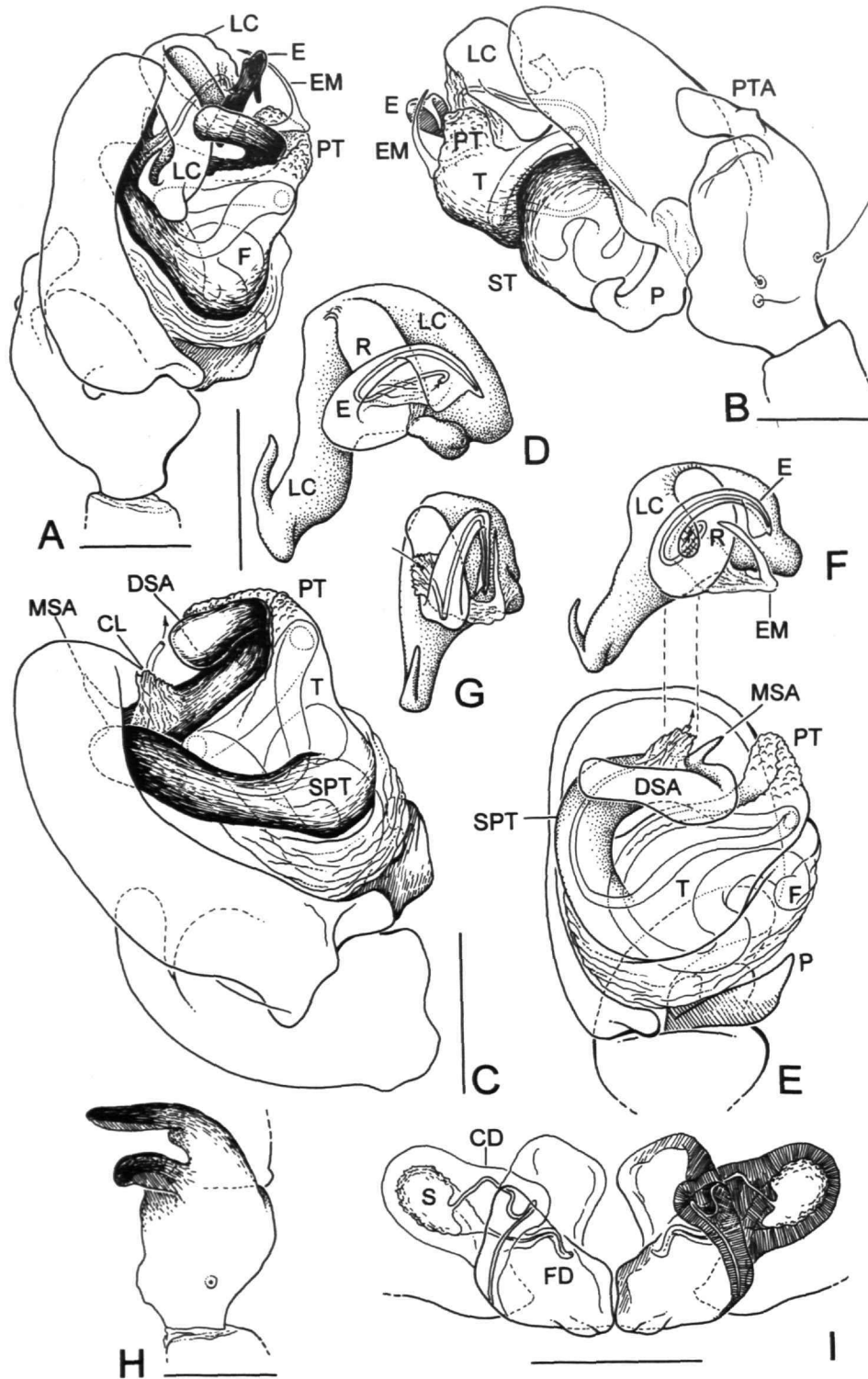


FIGURE 9.—*Entelecara acuminata*: A–H, male palp; I, epigynum. A, mesal; B, ectal; C, mesal (embolic division removed); D, embolic division; E, ventral, schematic (embolic division removed); F, embolic division, schematic, ventral; G, embolic division, mesal, schematic; H, tibia, dorsal; I, ventral. (Scale bars=0.1 mm.)

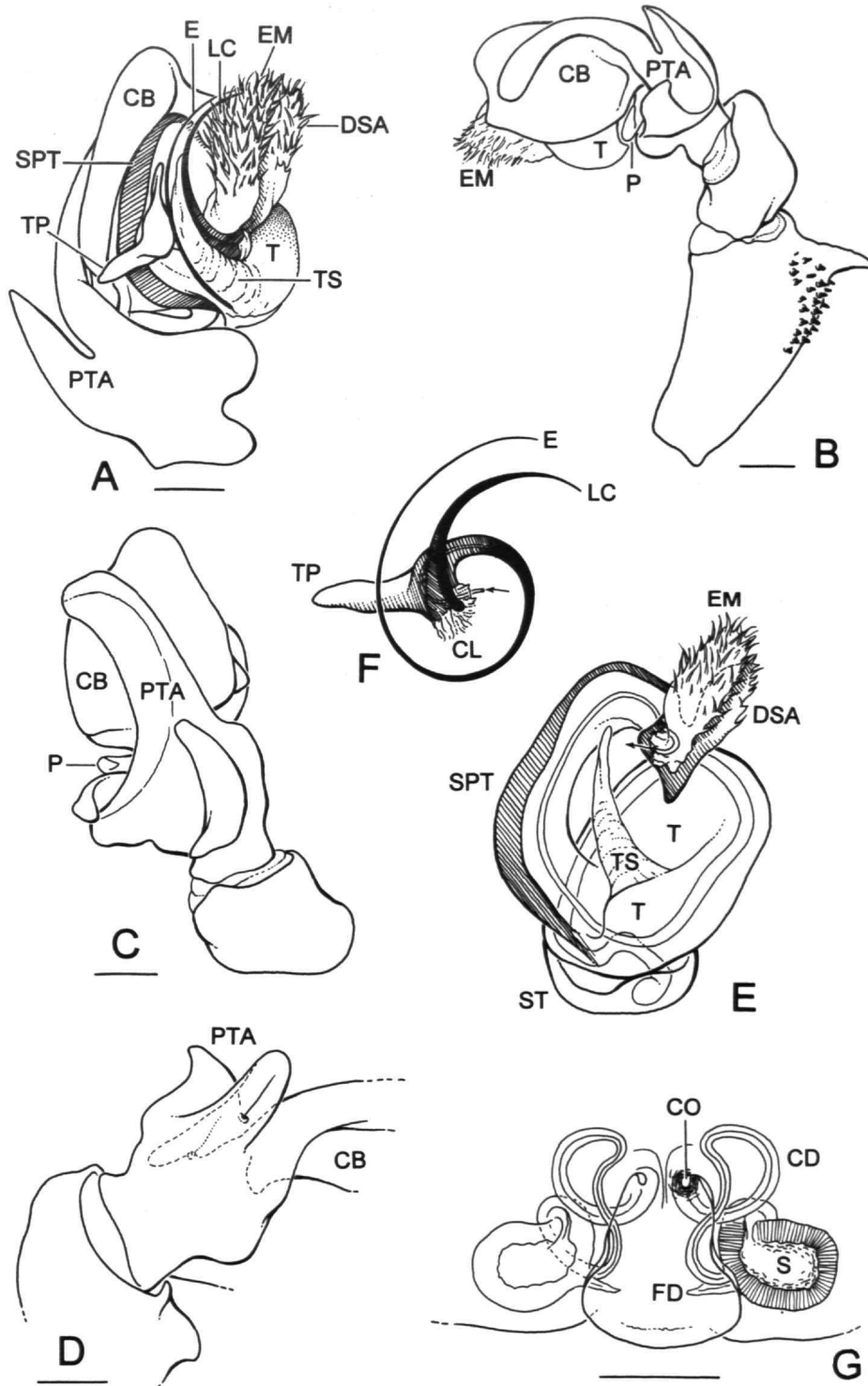


FIGURE 10.—*Gonatium rubens*: A–F, male palp; G, epigynum. A, mesal; B, ectal; C, dorsal; D, RTA, dorsoectal; E, ventral, schematic (embolic division removed); F, embolic division, schematic, ventral; G, ventral. (Scale bars=0.1 mm.)

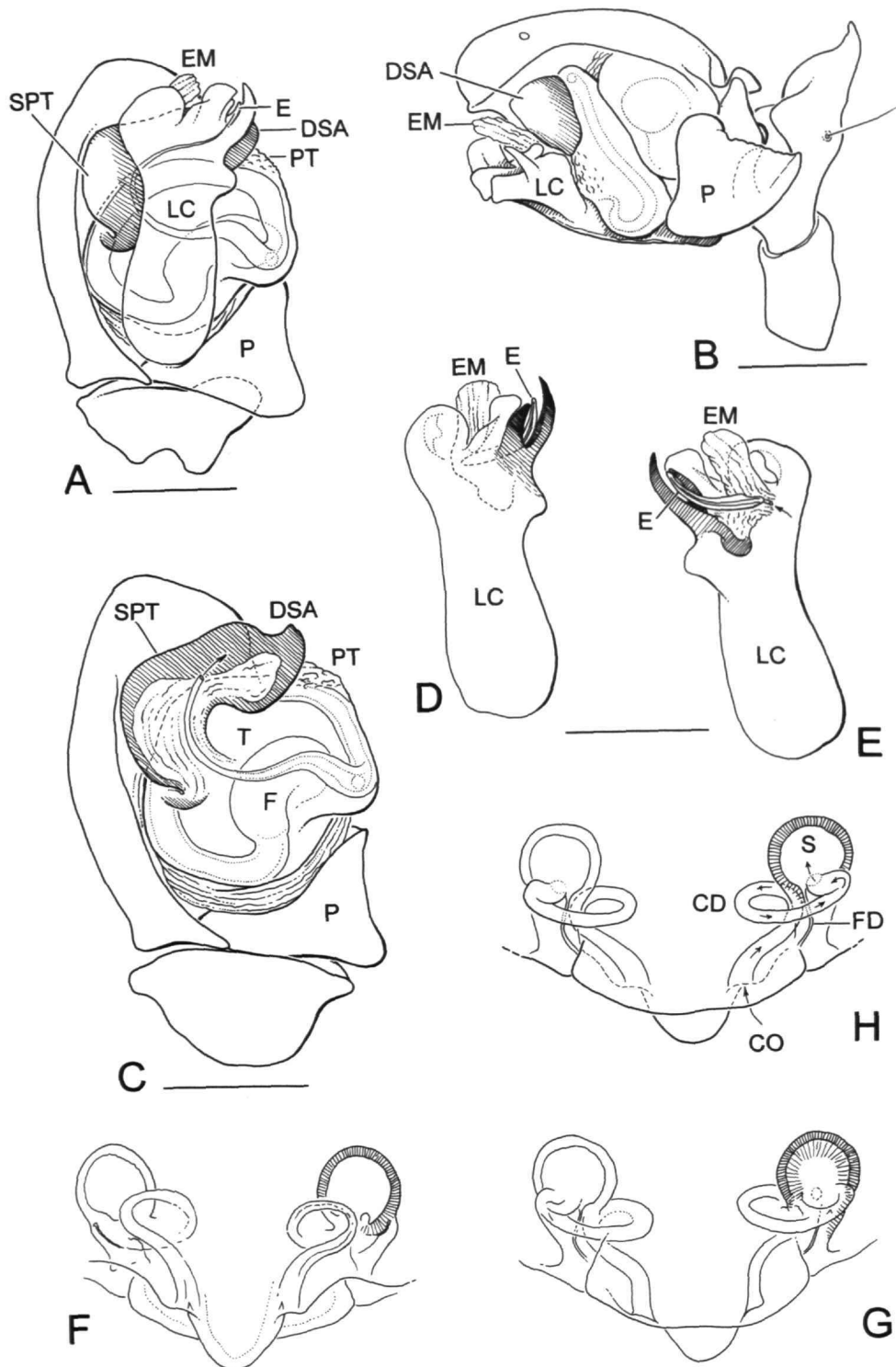


FIGURE 11.—*Gongyliidiellum vivum*: A–E, male palp; F–H, epigynum. A, ventral; B, ectal; C, ventral (embolic division removed); D, embolic division, ventral; E, same, dorsal; F, ventral; G, dorsal; H, schematic, dorsal. (Scale bars=0.1 mm.)

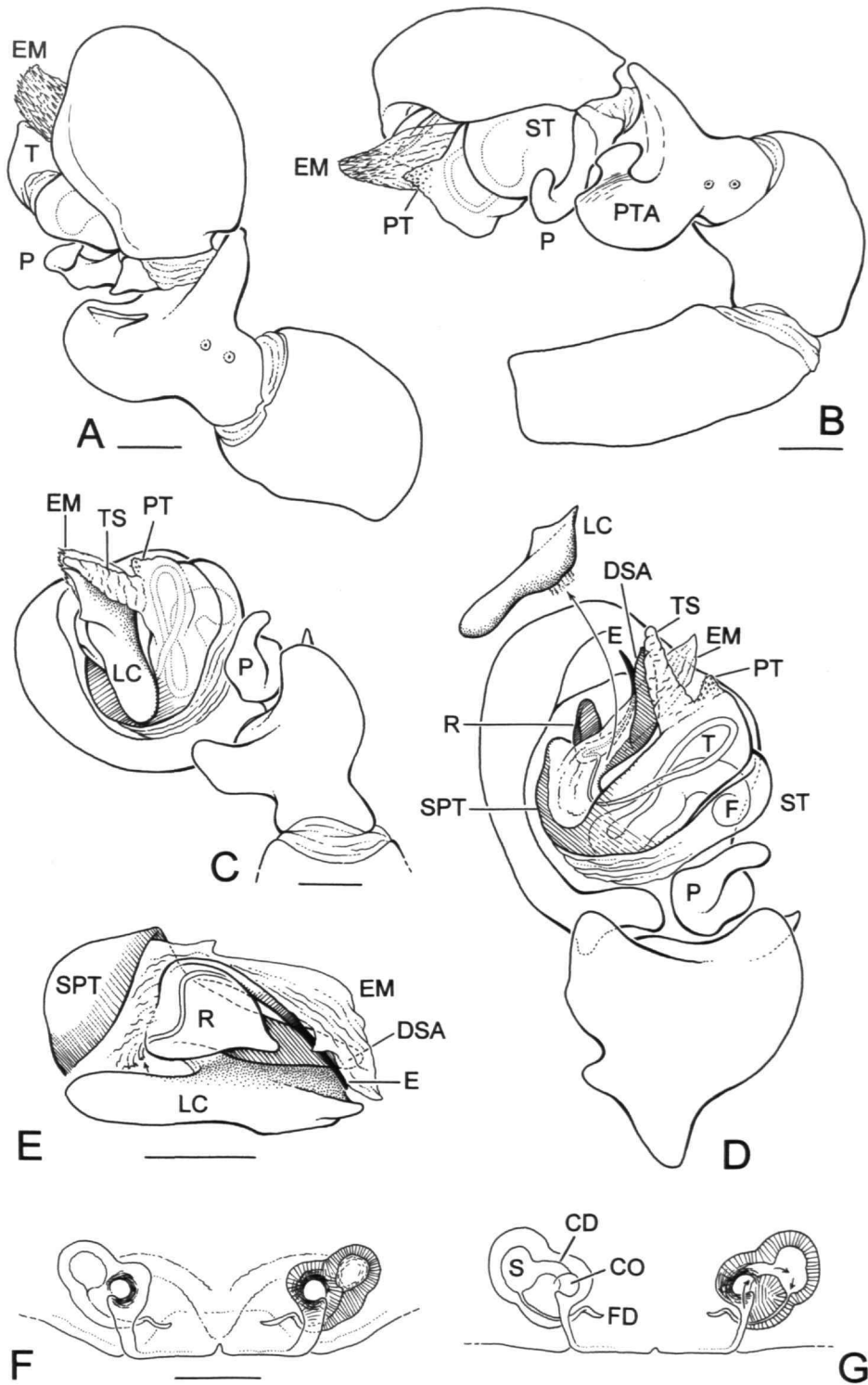


FIGURE 12.—*Gongylidium rufipes*: A–E, male palp; F,G, epigynum. A, dorsal; B, ectal; C, ventral; D, ventral, schematic (LC removed); E, embolic division and supralegulum (distal region); F, ventral; G, same, schematic. (Scale bars=0.1 mm.)

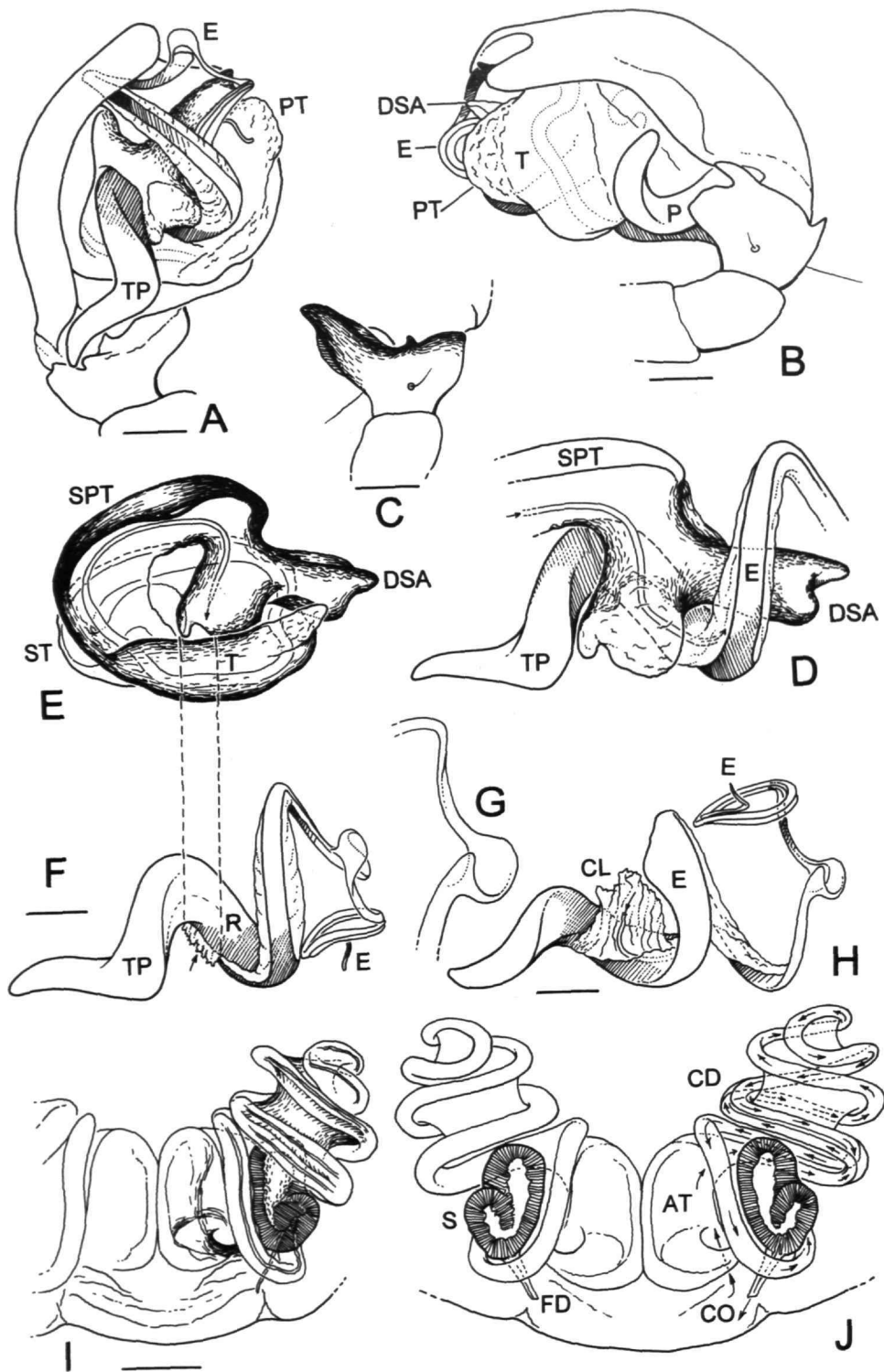


FIGURE 13.—*Grammonota pictilis*: A–H, male palp; I, J, epigynum. A, mesoventral; B, ectal; C, tibia, dorsal; D, embolic division and supratégulum (distal region); E, ventral (embolic division removed); F, embolic division, ventral; G, embolus, medial region; H, embolic division; I, dorsal; J, same, schematic. (Scale bars=0.1 mm.)

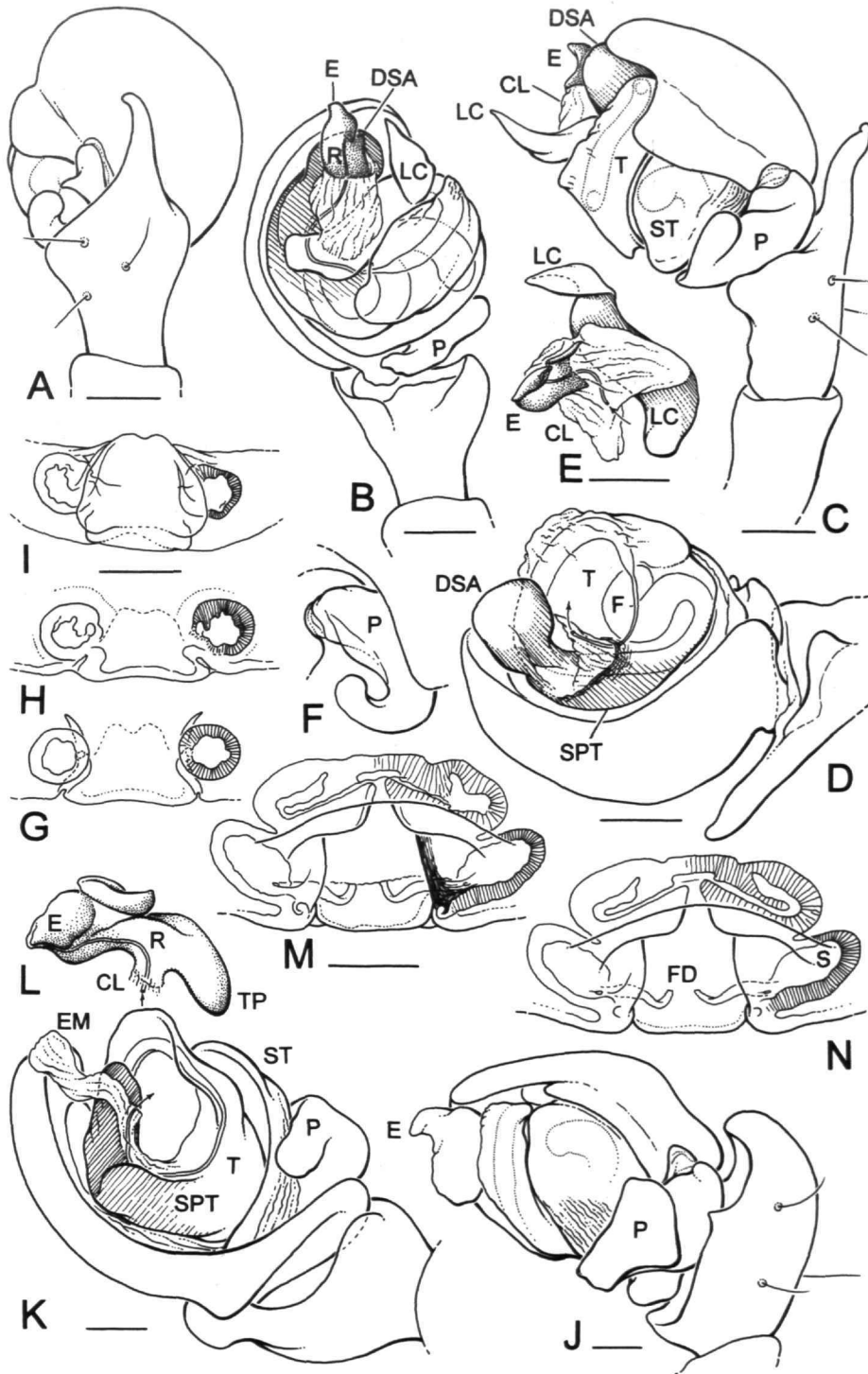


FIGURE 14.—*Hilaira excisa*: A-F, male palp; G-I, epigynum. A, dorsal; B, ventral; C, ectal; D, mesoventral (embolic division removed); E, embolic division, mesoventral; F, paracymbium, ectodorsal (schematic); G, ventral, schematic; H, ventral; I, dorsal. *Hilaira vexatrix*: J-L, male palp; M,N, epigynum. J, ectal; K, ventral (embolic division removed); L, embolic division, ventral; M, ventral; N, same, schematic. (Scale bars=0.1 mm.)

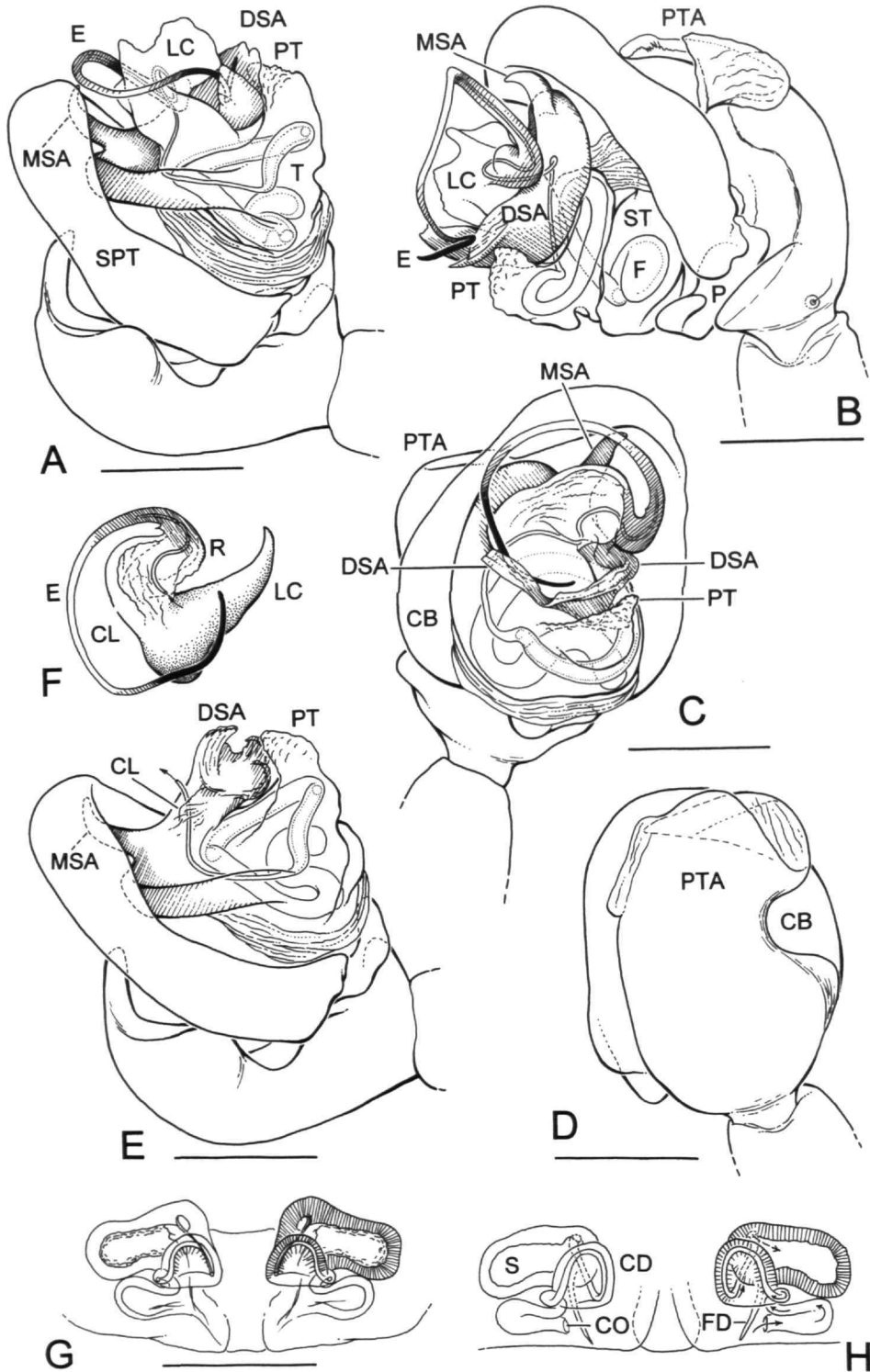


FIGURE 15.—*Hybocoptus decollatus*: A–F, male palp; G, H, epigynum. A, mesal; B, ectal; C, ventral; D, dorsal; E, mesal (embolic division removed; distal end of DSA broken off); F, embolic division, mesal; G, ventral; H, same, schematic. (Scale bars=0.1 mm.)



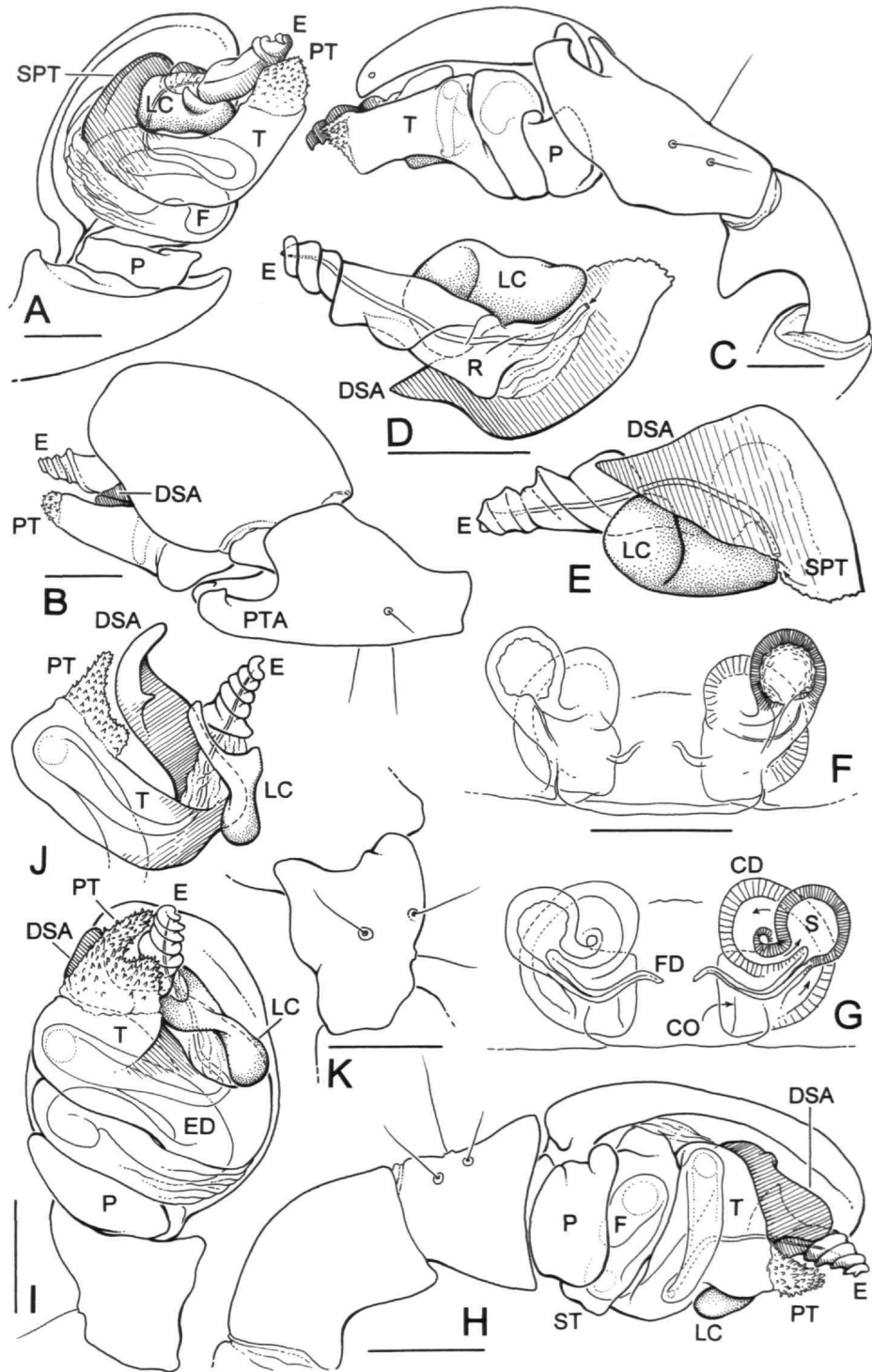


FIGURE 16.—*Hylyphantes graminicola*: A-E, male palp; F,G, epigynum. A, ventral; B, dorsal; C, ectal; D, embolic division and suprategulum (distal region), ventral; E, same, dorsal; F, dorsal; G, same, schematic. *Hylyphantes nigrinus*: H-K, male palp. H, ectal; I, ventral; J, tegulum and embolic division, schematic; K, tibia, dorsal. (Scale bars=0.1 mm.)

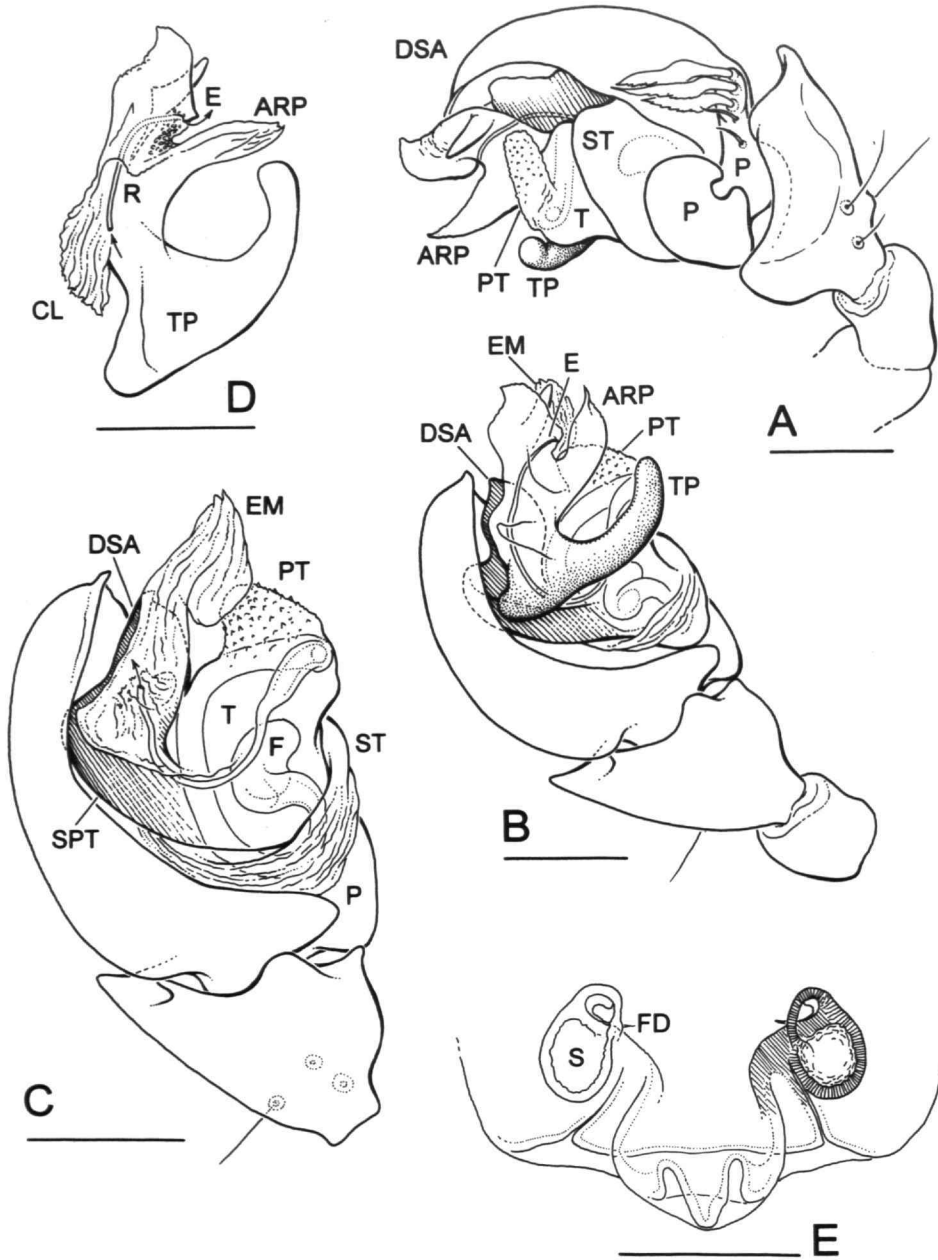


FIGURE 17.—*Islandiana princeps*: A–D, male palp; E, epigynum. A, ectal; B, mesoventral; C, mesoventral ventral (embolic division removed); D, embolic division, mesoventral; E, ventral. (Scale bars=0.1 mm.)

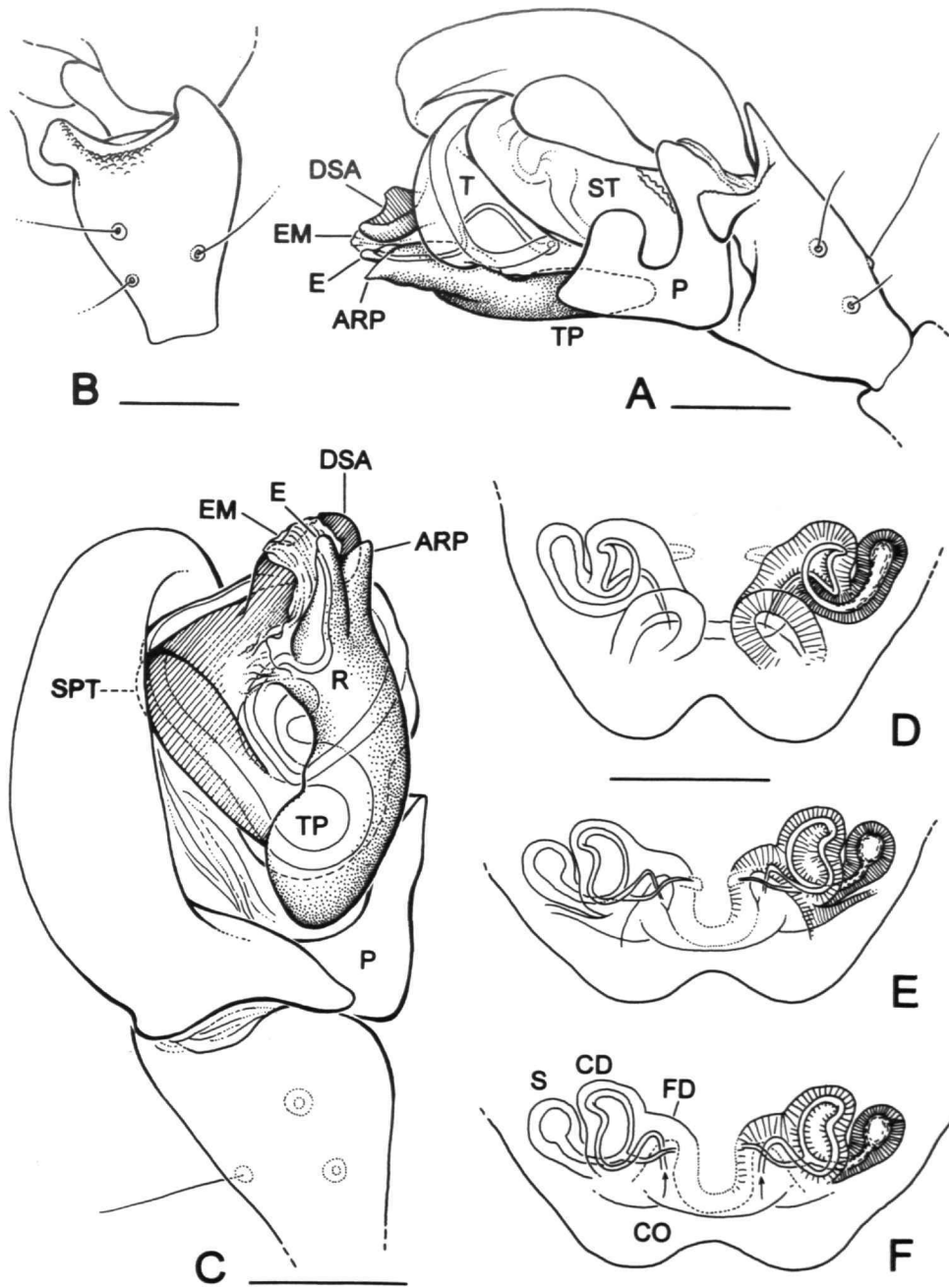


FIGURE 18.—*Laminacauda plagiata*: A–C, male palp; D–F, epigynum. A, ectal; B, tibia, dorsoectal; C, mesal; D, ventral; E, caudal; F, same, schematic. (Scale bars=0.1 mm.)

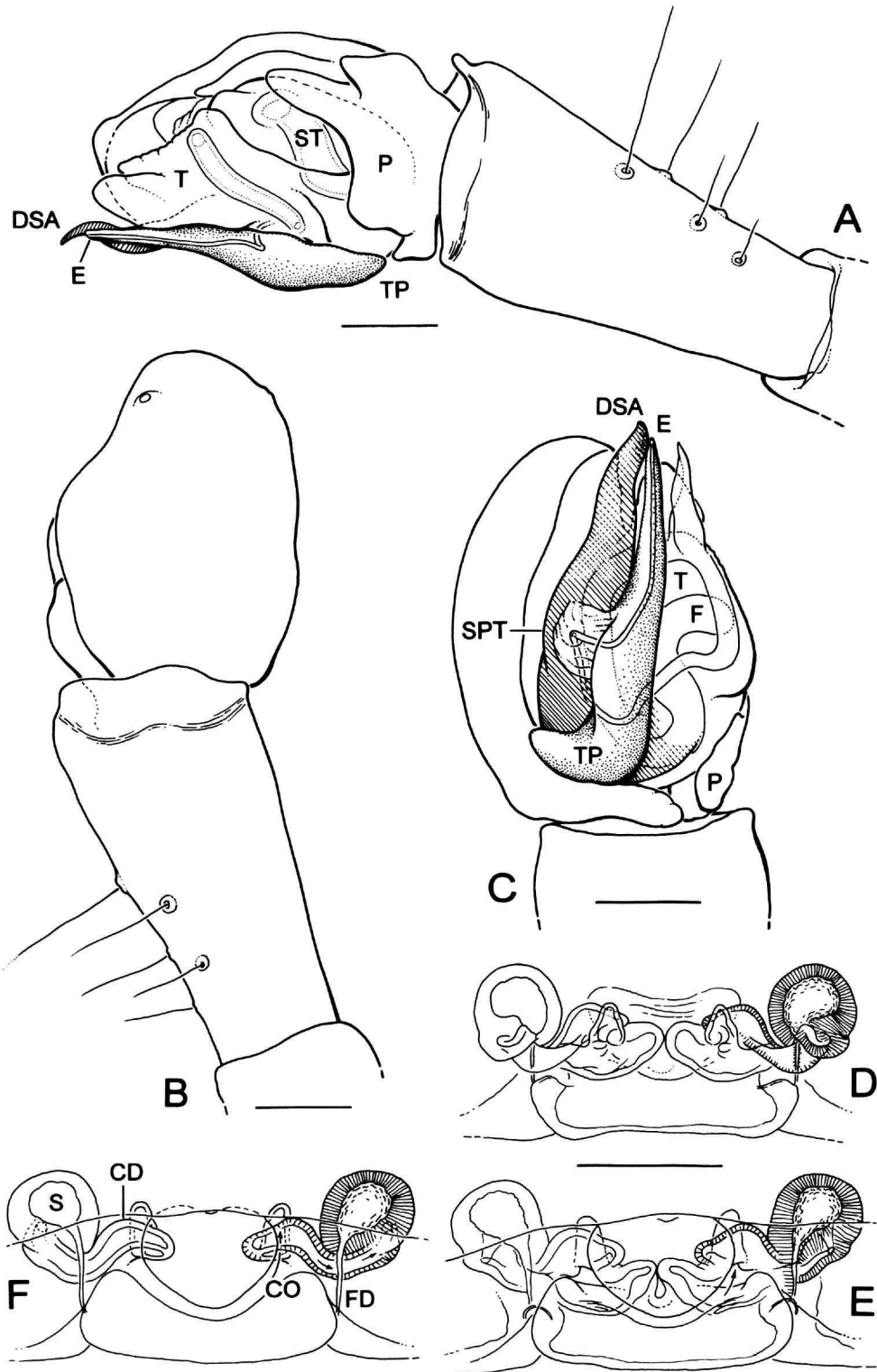


FIGURE 19.—*Leptorhoptrum robustum*: A–C, male palp; D–F, epigynum. A, ectal; B, dorsal; C, ectoventral; D, dorsal; E, ventral; F, schematic. (Scale bars=0.1 mm.)

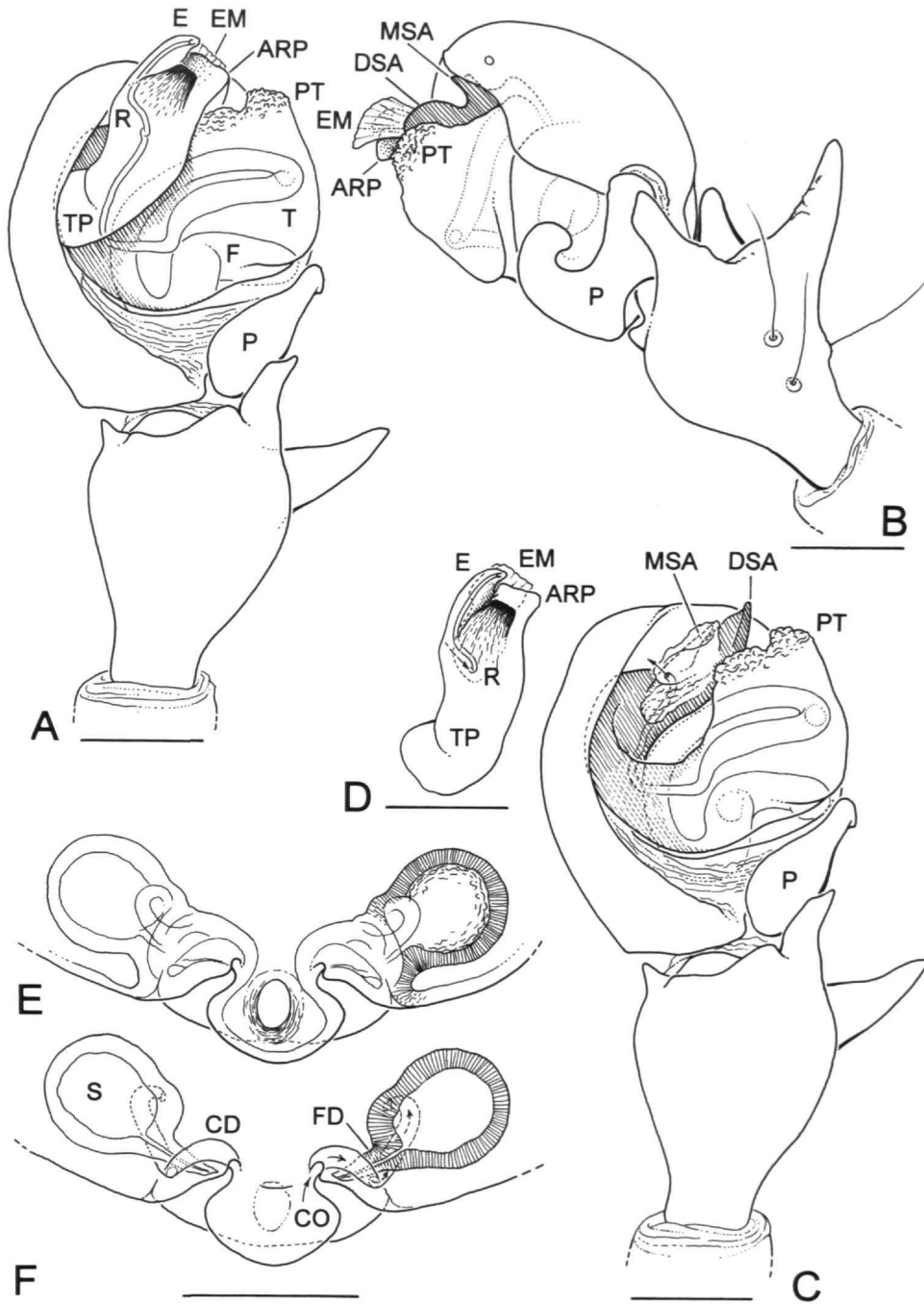


FIGURE 20.—*Lophomma punctatum*: A–D, male palp; E, F, epigynum. A, ventral; B, ectal; C, ventral (embolic division removed); D, embolic division, ventral; E, ventral; F, same, schematic. (Scale bars=0.1 mm.)

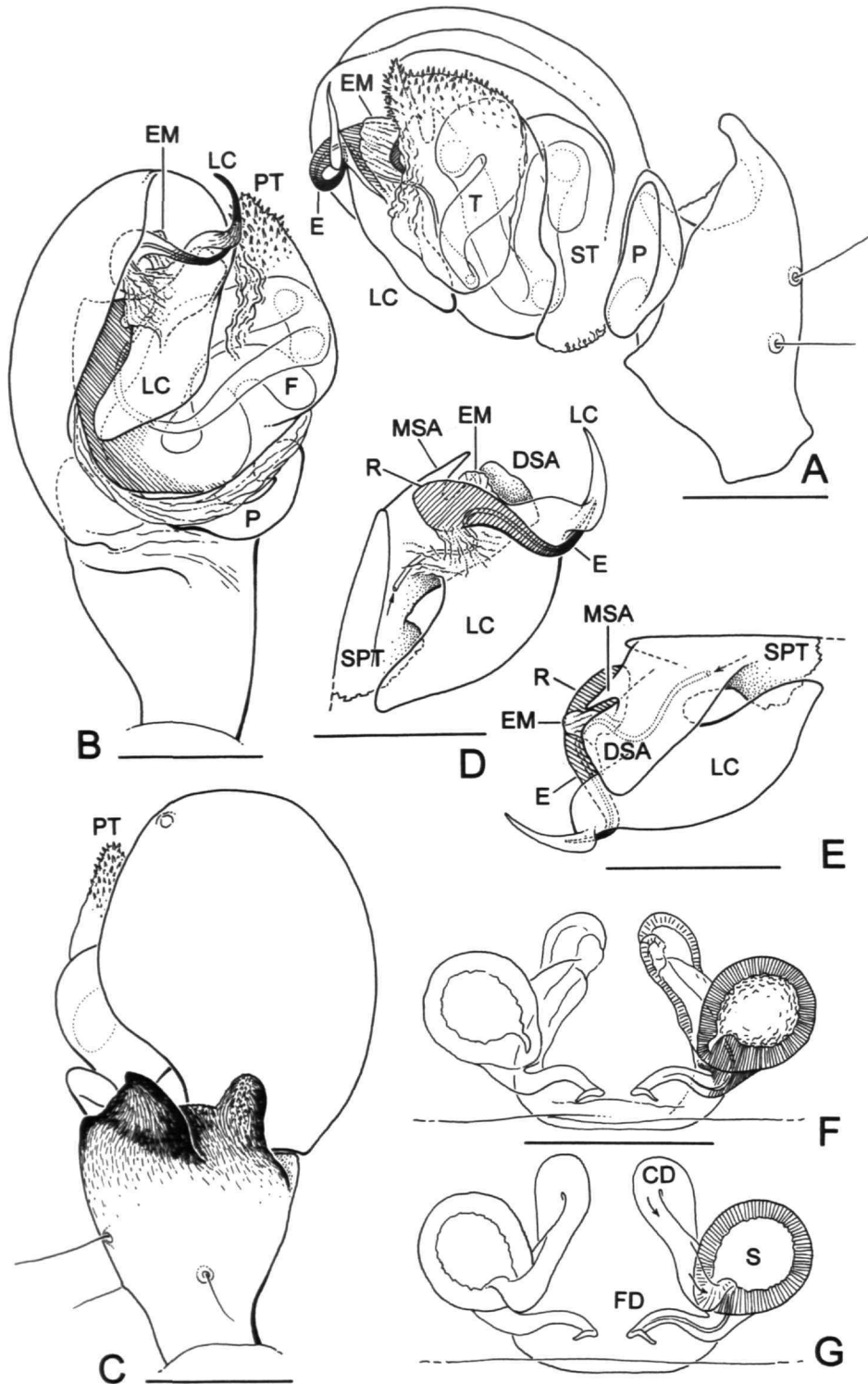


FIGURE 21.—*Oedothorax gibbosus*: A-E, male palp; F,G, epigynum. A, ectoventral; B, mesal; C, dorsal; D, embolic division and supralegulum (distal region), ventral; E, same, dorsal; F, dorsal; G, same, schematic. (Scale bars=0.1 mm.)

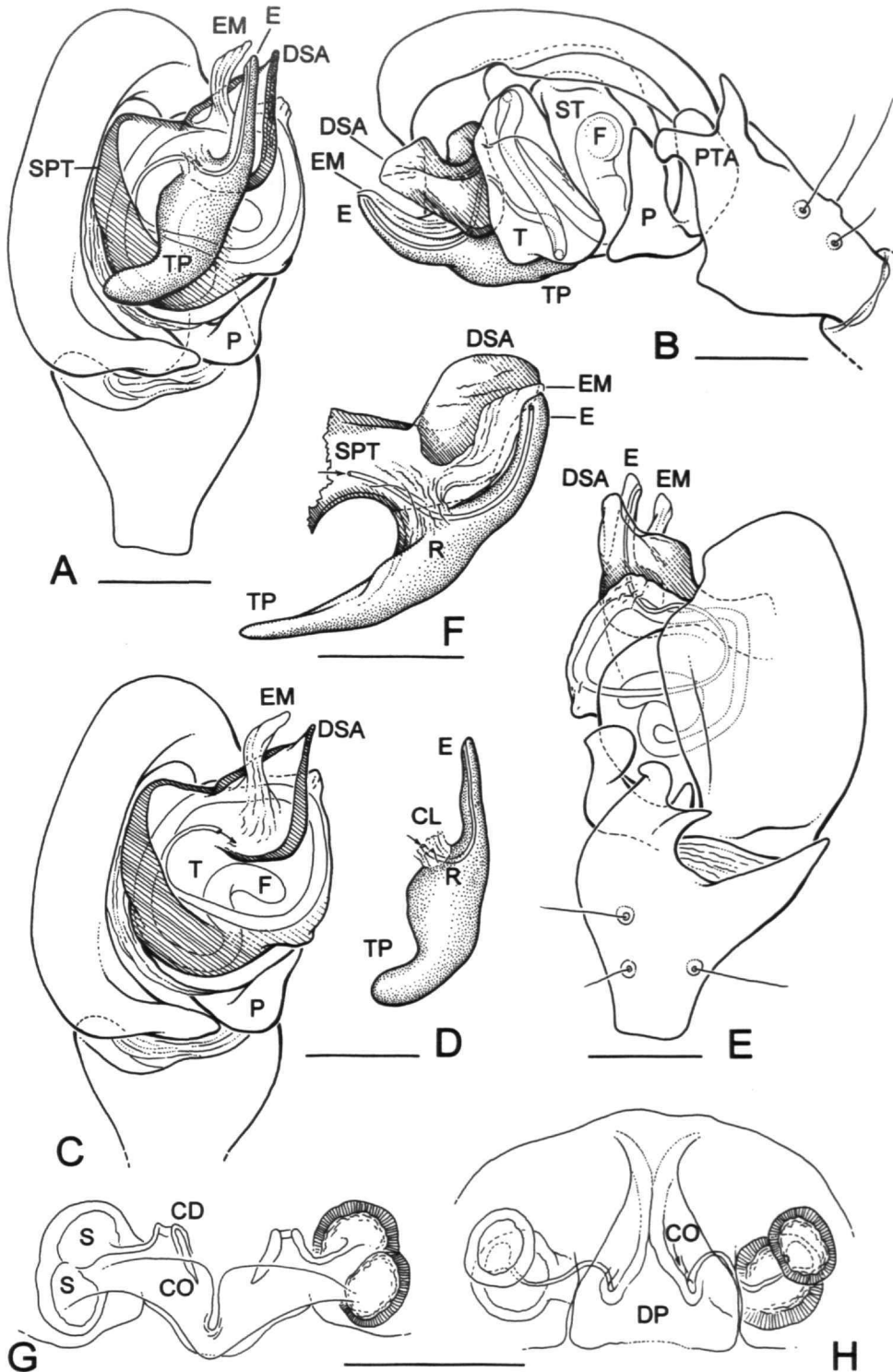


FIGURE 22.—*Ostearius melanopygius*: A–F, male palp; G,H, epigynum. A, mesoventral; B, ectal; C, mesoventral (embolic division removed); D, embolic division, mesoventral; E, dorsoectal; F, embolic division and suprategulum (distal region), mesal; G, ventral; H, dorsal. (Scale bars=0.1 mm.)

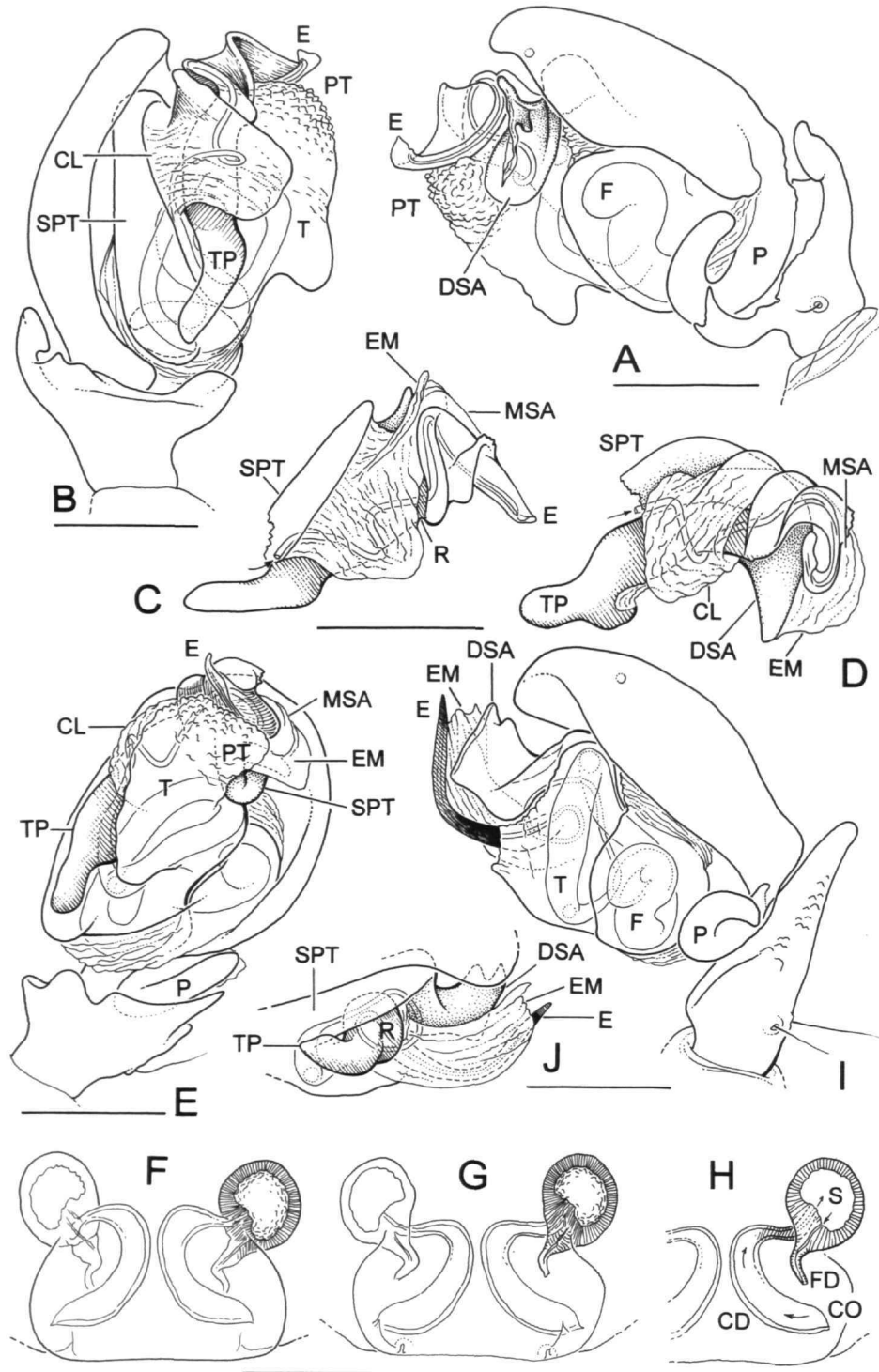


FIGURE 23.—*Pelecopsis nemoralis*: A–E, male palp; F–H, epigynum. A, ectal; B, mesal; C, embolic division and suprategulum (distal region), mesal; D, same, mesoapical; E, ventral; F, ventral; G, dorsal; H, same, schematic. *Pelecopsis parallela*: I, J, male palp. I, ectal; J, embolic division and suprategulum (distal region), mesal. (Scale bars=0.1 mm.)



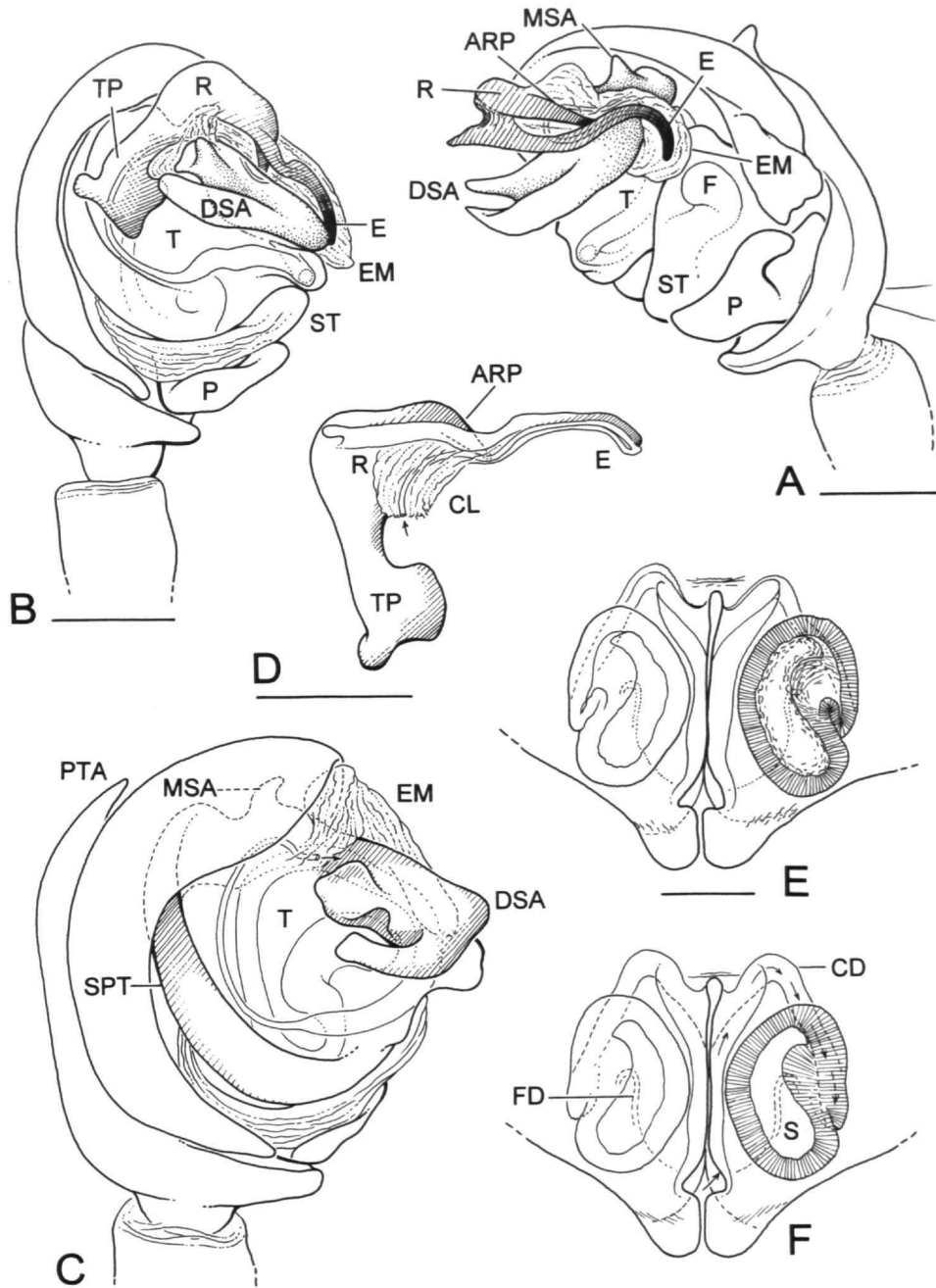


FIGURE 24.—*Savignia frontata*: A-D, male palp; E,F, epigynum. A, ectal; B, ventral; C, mesoventral (embolic division removed); D, embolic division, mesoventral; E, ventral; F, same, schematic. (Scale bars=0.1 mm.)

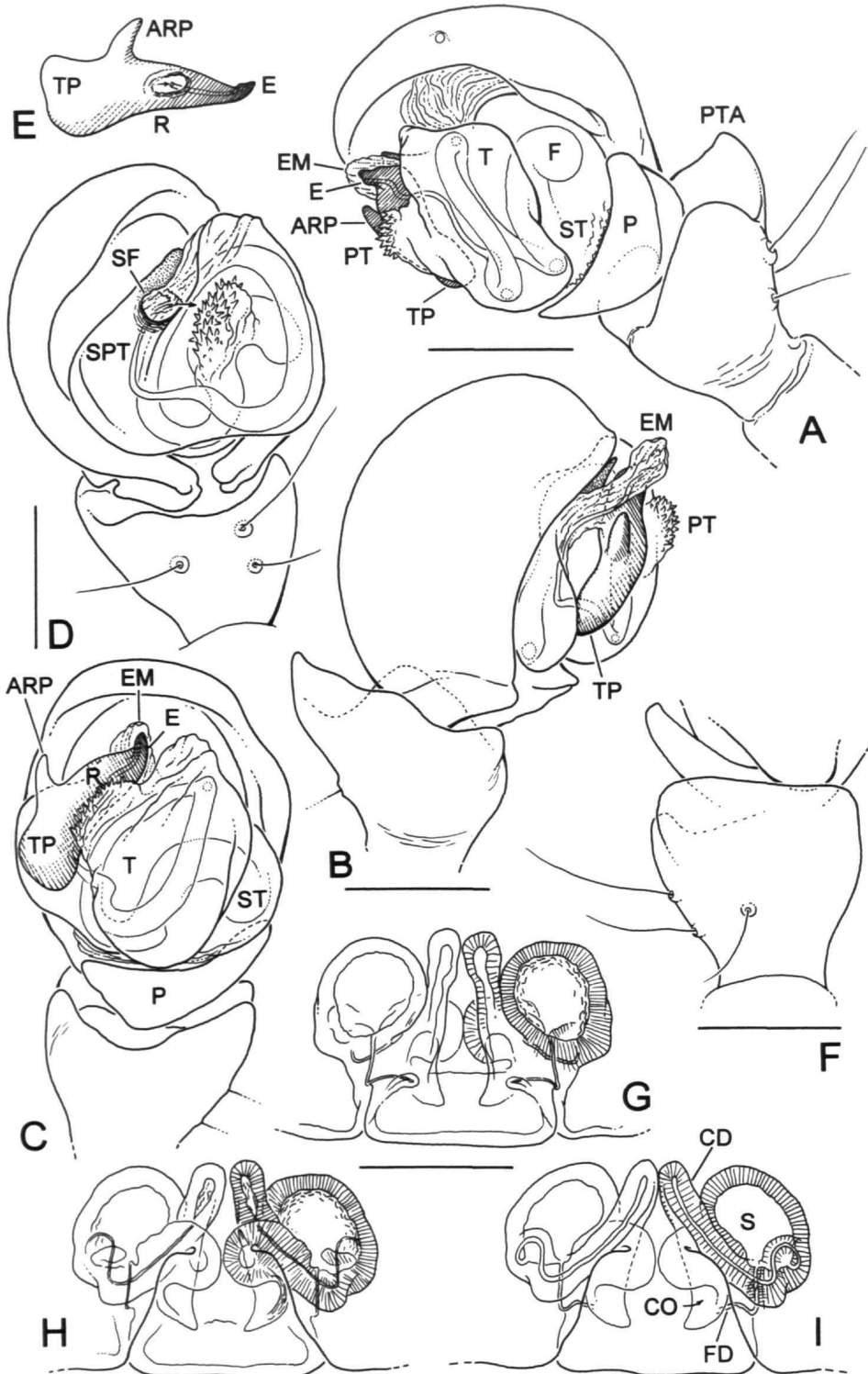


FIGURE 25.—*Sciastes truncatus*: A-F, male palp; G-I, epigynum. A, ectal; B, mesal; C, ventral; D, mesoventral (embolic division removed); E, embolic division, mesoventral; F, tibia, dorsal; G, dorsal; H, ventral; I, same, schematic. (Scale bars=0.1 mm.)

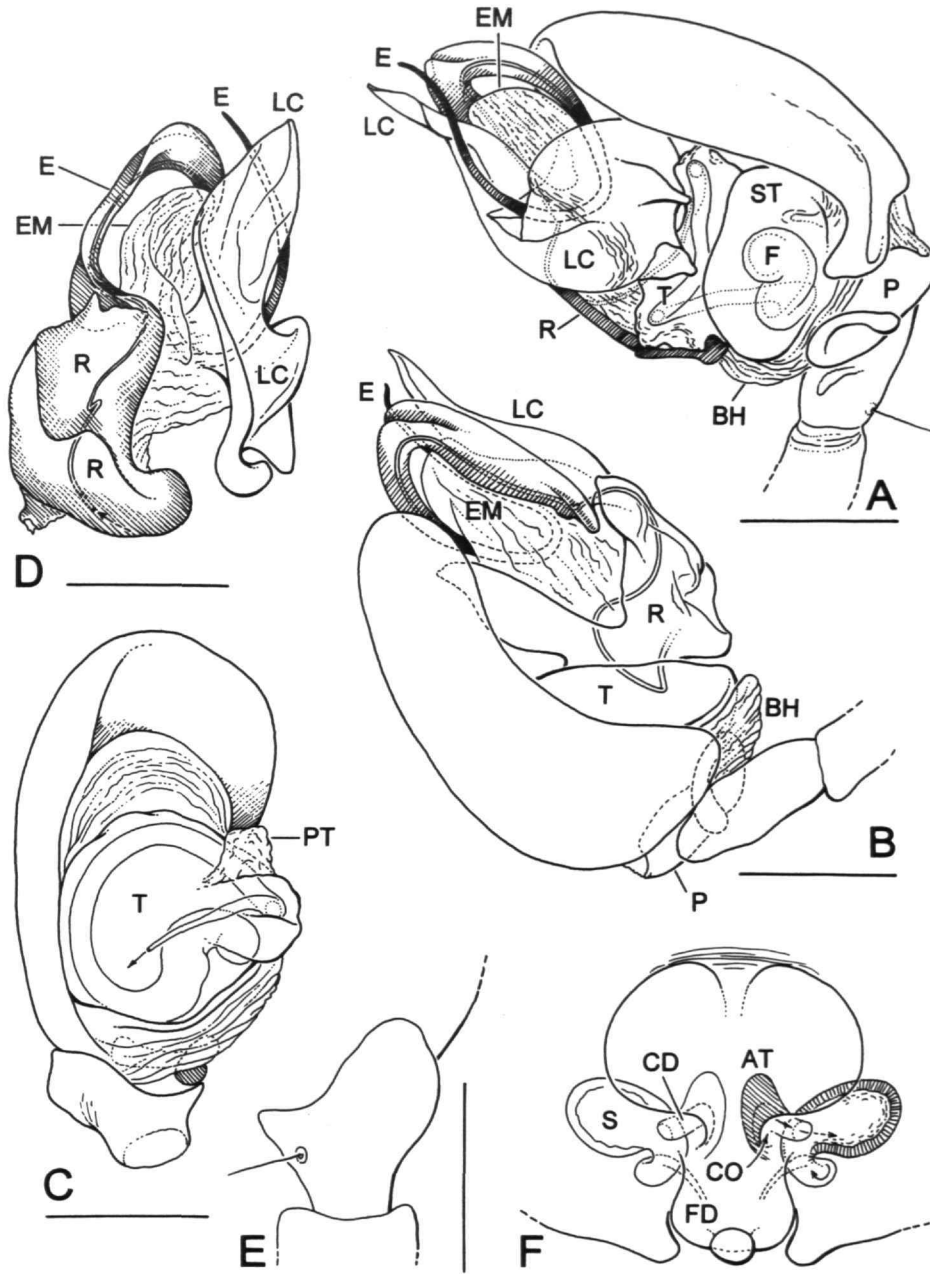


FIGURE 26.—*Sisicus apertus*: A–E, male palp; F, epigynum. A, ectal; B, mesal; C, ventral (embolic division removed); D, embolic division, ventral; E, tibia, dorsal; F, ventral, schematic. (Scale bars=0.1 mm.)

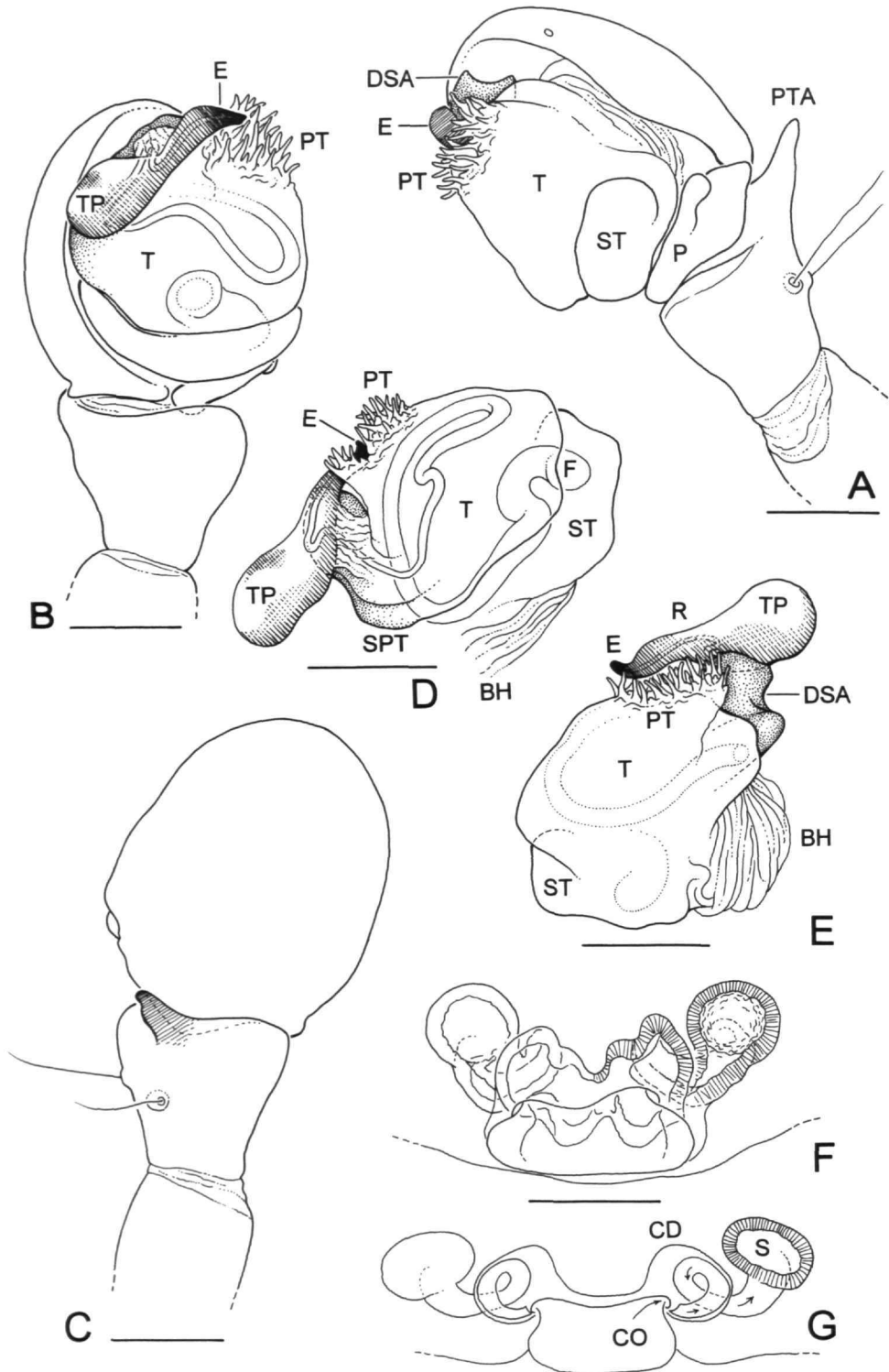


FIGURE 27.—*Tapinocyba praecox*: A-E, male palp; F,G, epigynum. A, ectal; B, ventral; C, dorsal; D, ventral; E, ectoventral; F, ventral; G, same, schematic. (Scale bars=0.1 mm.)

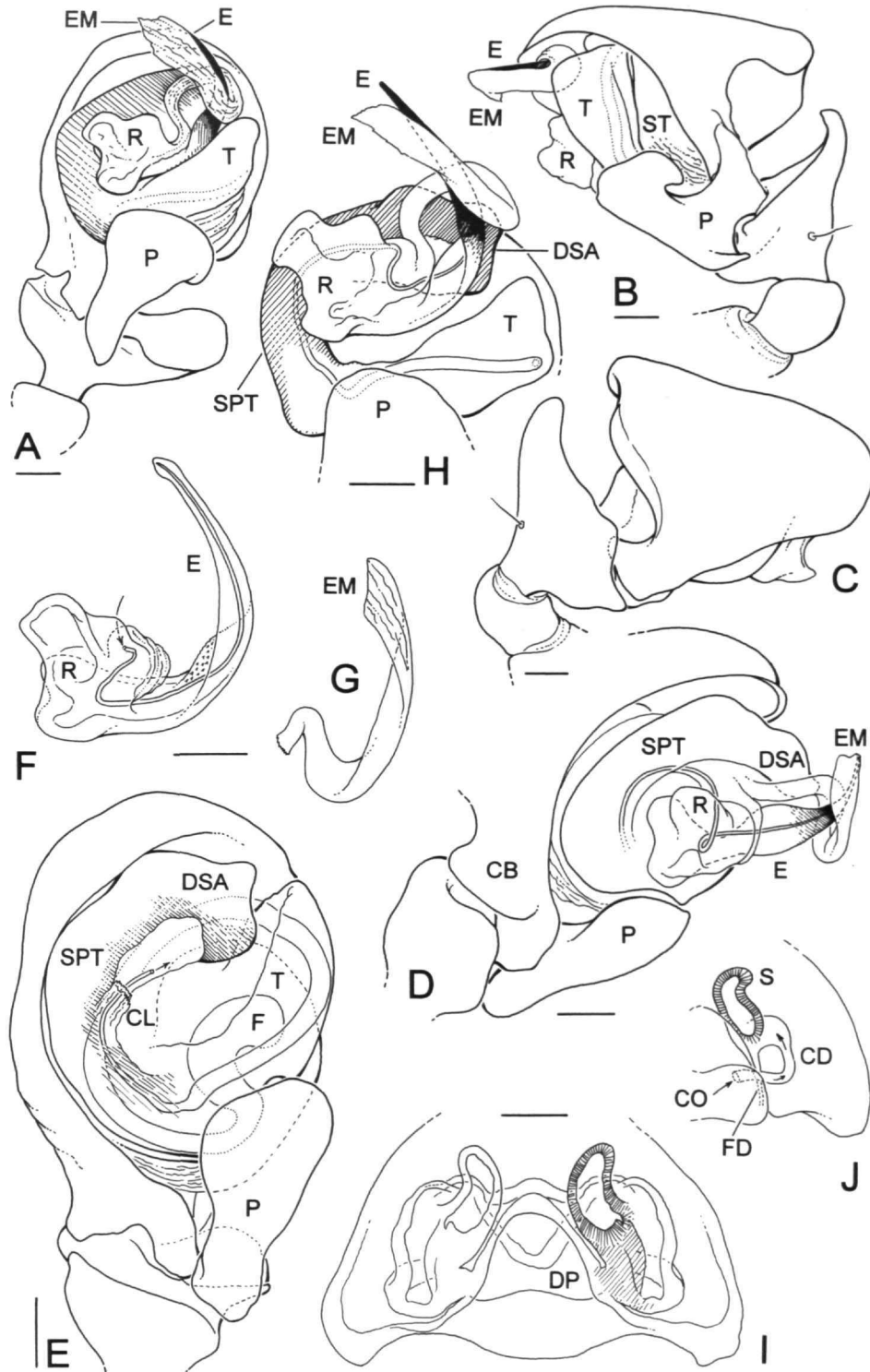


FIGURE 28.—*Tibioploides pacificus*: A–H, male palp; I, J, epigynum. A, ventral; B, ectal; C, mesal; D, mesoventral; E, ventral (embolic division removed); F, embolic division, ventral; G, embolic membrane; H, embolic division and suprategulum, ventral; I, ventral; J, caudal, schematic. (Scale bars=0.1 mm.)

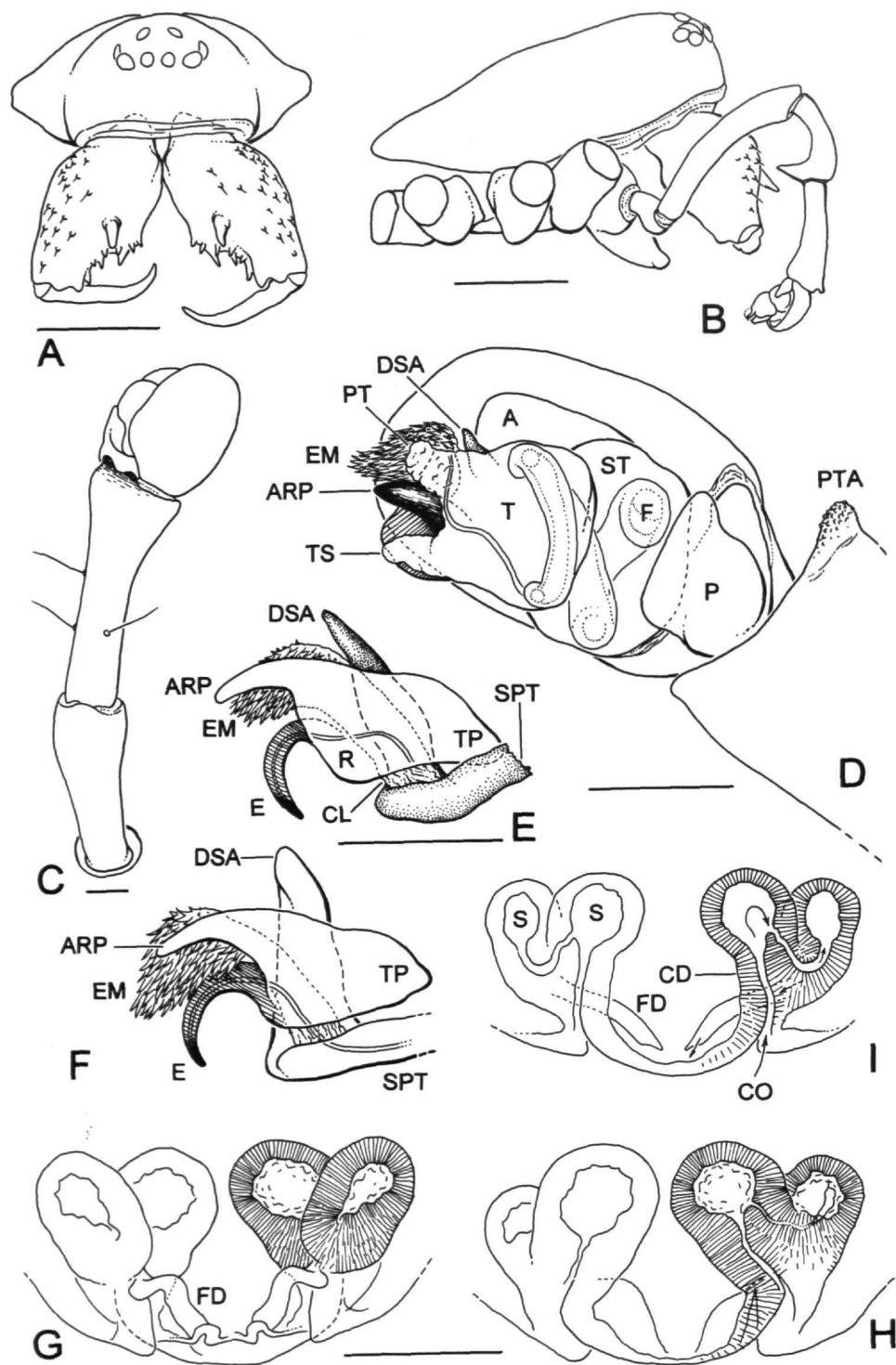


FIGURE 29.—*Tmeticus tolli*: A,B, male cephalothorax; C–F, male palp; G–I, epigynum. A, anterior; B, lateral; C, dorsal; D, ectoventral; E, embolic division and suprategulum (distal region); F, same, schematic; G, dorsal; H, ventral; I, same, schematic. (Scale bars=0.1 mm.)

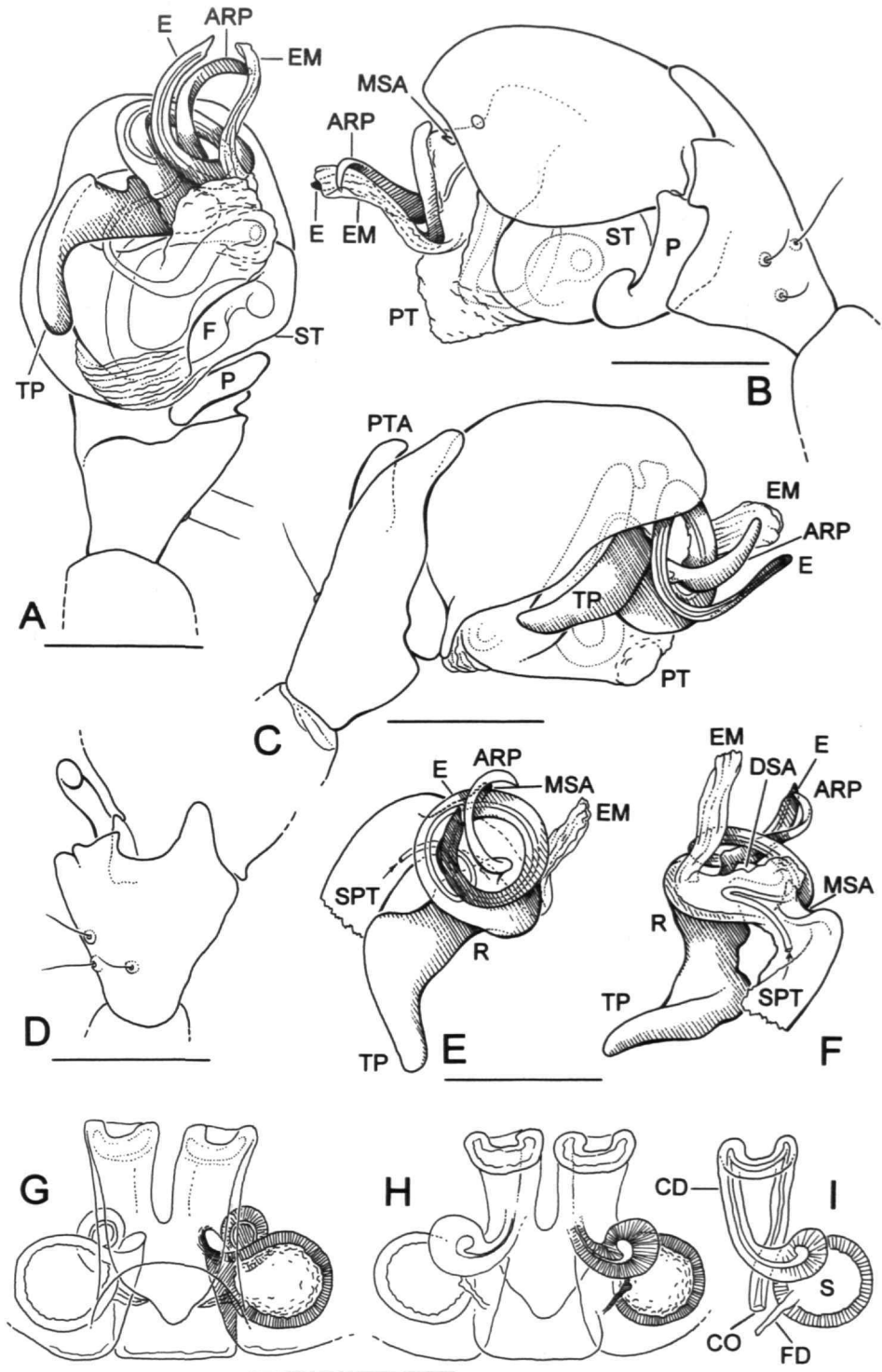


FIGURE 30.—*Typhochrestus digitatus*: A–F, male palp; G–I, epigynum. A, ventral; B, ectal; C, mesal; D, tibia, dorsal; E, embolic division and suprategulum (distal region), apicoventral; F, same, ectoventral; G, ventral; H, dorsal; I, spermatheca and ducts, dorsal, schematic. (Scale bars=0.1 mm.)

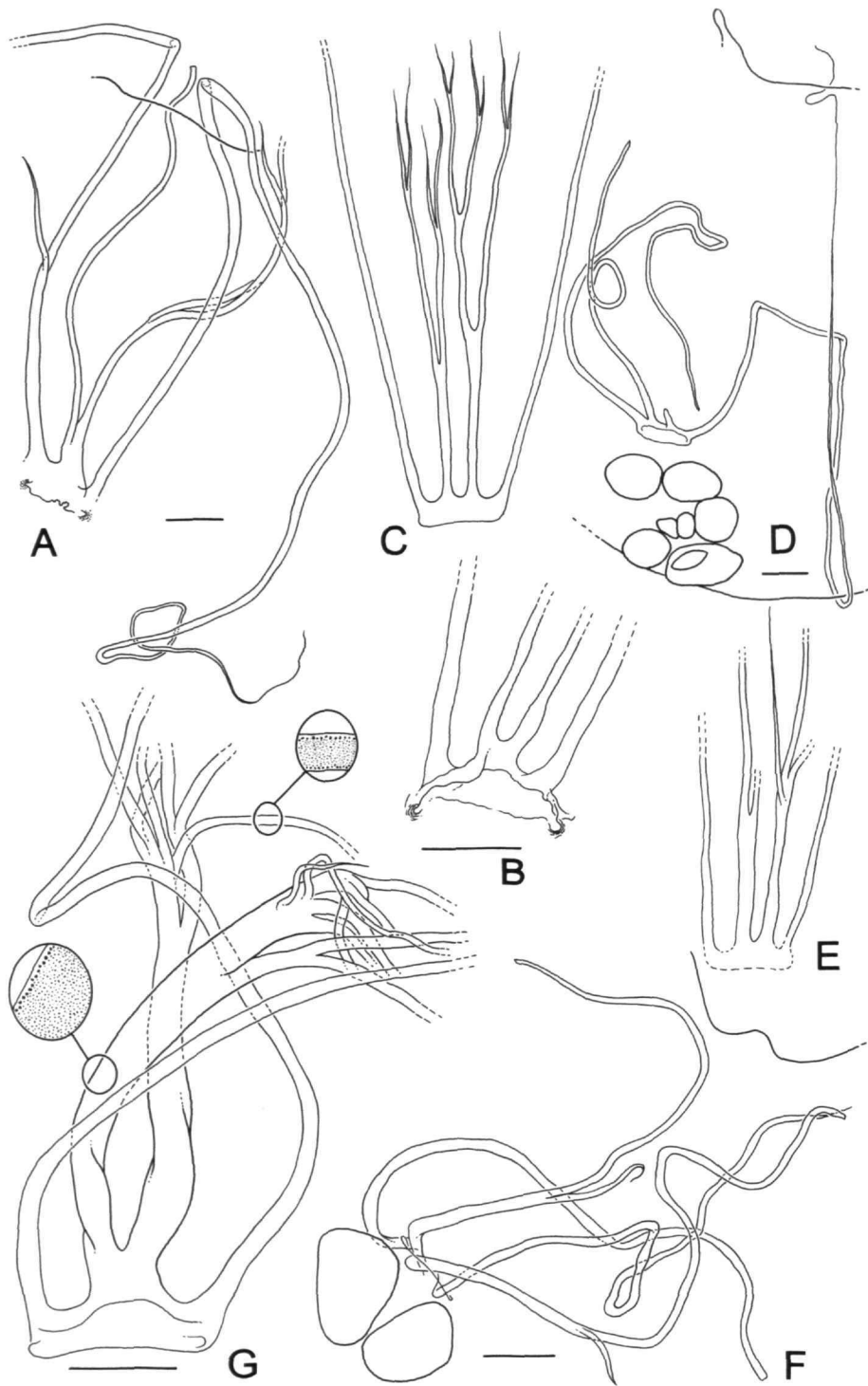


FIGURE 31.—Tracheal system morphology; taenidia not depicted, except in G. A, *Tibioploides pacificus*, female; B, *T. pacificus*, male; C, *Laminacauda argentinensis*, schematic; D, *L. plagiata*, male (right medial trunk is probably broken off at the base); E, *L. plagiata*, female, schematic; F, *L. plagiata*, female; G, *L. diffusa*, male (note that tracheoles are of varied diameters). (Scale bars=0.1 mm.)



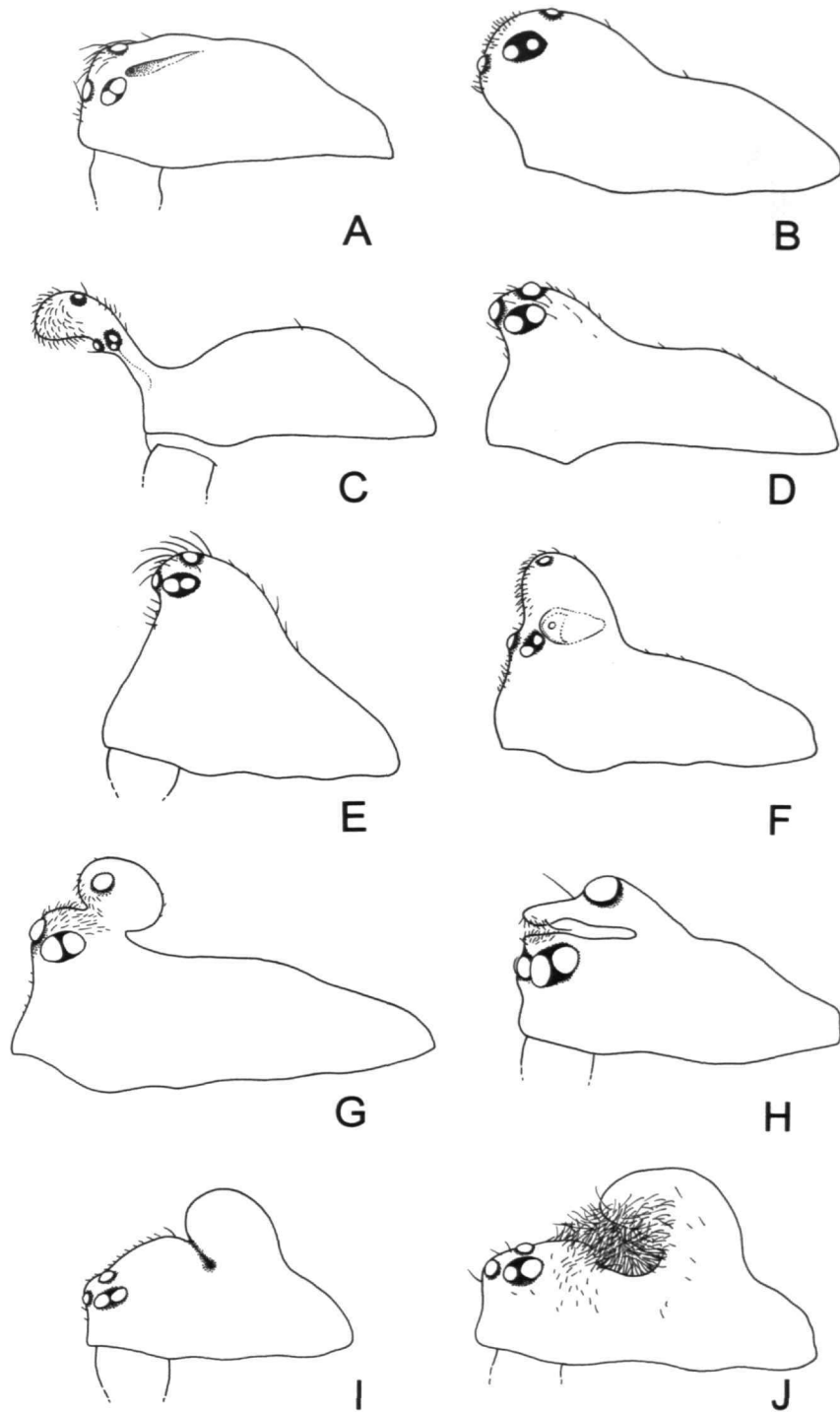


FIGURE 32.—Male cephalic morphology, lateral. A, *Tapinocyba praecox* (O.P.-Cambridge) (traced from SEM photograph); B, *Araeoncus crassiceps* (Westring) (Roberts, 1993, fig. 41C); C, *Caracladus aviculus* (L. Koch) (Thaler, 1969, fig. 20); D, *Gonatum rubens* (Blackwall) (Roberts, 1993, fig. 18A); E, *Hypselocara altissimum* (Simon) (Millidge, 1991, fig. 449); F, *Entelecara acuminata* (Wider) (Roberts, 1993, fig. 16a); G, *Walckenaeria mitrata* (Menge) (Roberts, 1993, fig. 8h); H, *Walckenaeria gologolensis* Scharff (Scharff, 1990, fig. 214); I, *Laminacauda tuberosa* Millidge (Millidge, 1991, fig. 277); J, *Oedothorax gibbosus* (Blackwall) (traced from SEM photograph).

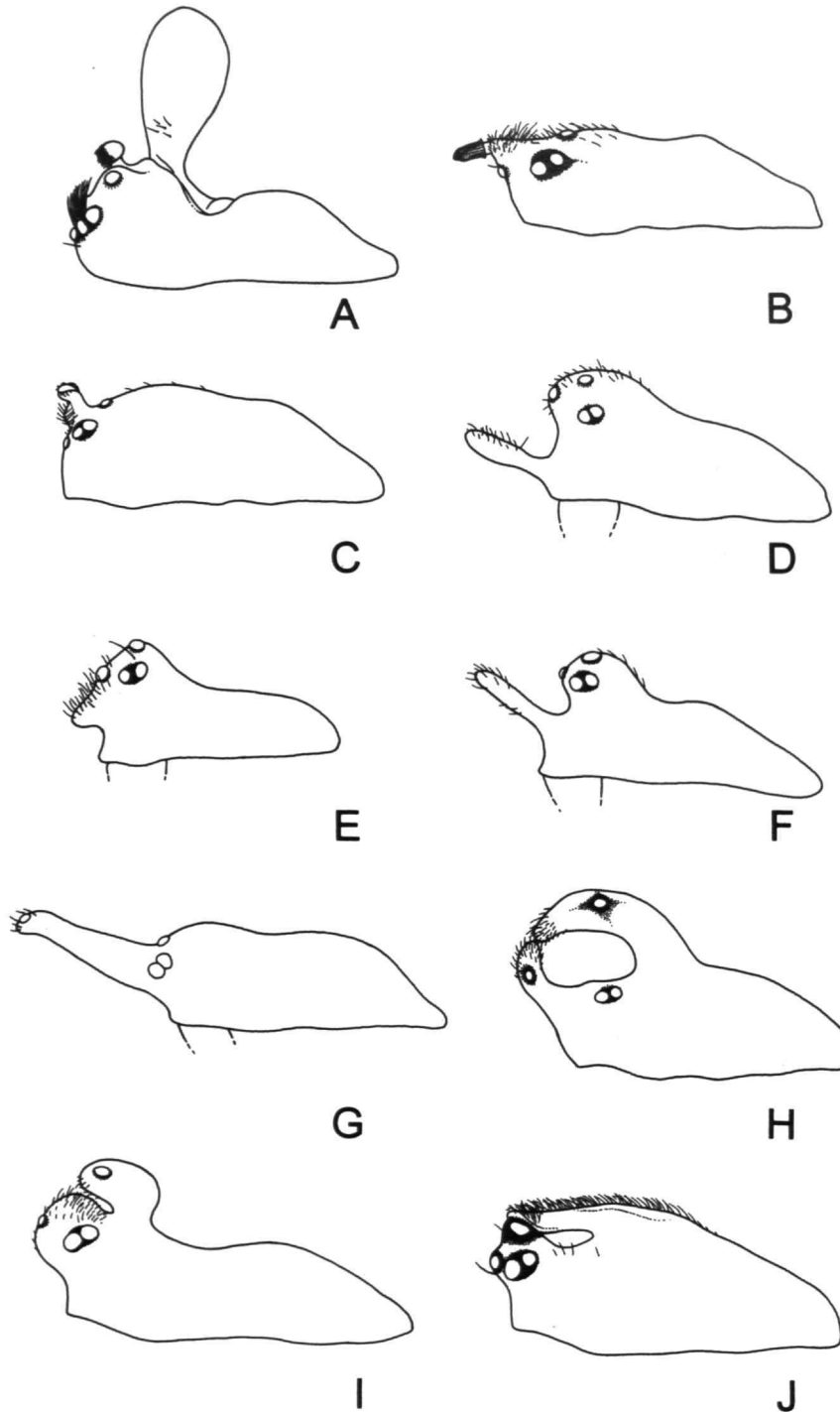


FIGURE 33.—Male cephalic morphology, lateral. A, *Mitrager noordami* van Helsdingen (van Helsdingen, 1985, fig. 1); B, *Baryphyma duffeyi* (Millidge) (Roberts, 1993, fig. 17b); C, *Walckenaeria kochi* (O.P.-Cambridge) (Roberts, 1993, fig. 9f); D, *Coreogona monoceros* (Simon) (Millidge, 1981, fig. 148); E, *Floricomus pythonicus* Crosby and Bishop (Bishop and Crosby, 1935, fig. 26); F, *Gnathonargus unicornis* (Banks) (Bishop and Crosby, 1935, fig. 9); G, *Savignia fronticornis* (Simon) (Simon, 1894, fig. 669); H, *Diplocephalus foraminifer* (O.P.-Cambridge) (Deltchev, 1985, fig. 6); I, *Walckenaeria capito* (Westring) (Roberts, 1993, fig. 9b); J, *Trematocephalus cristatus* (Wider) (Roberts, 1993, fig. 16g).

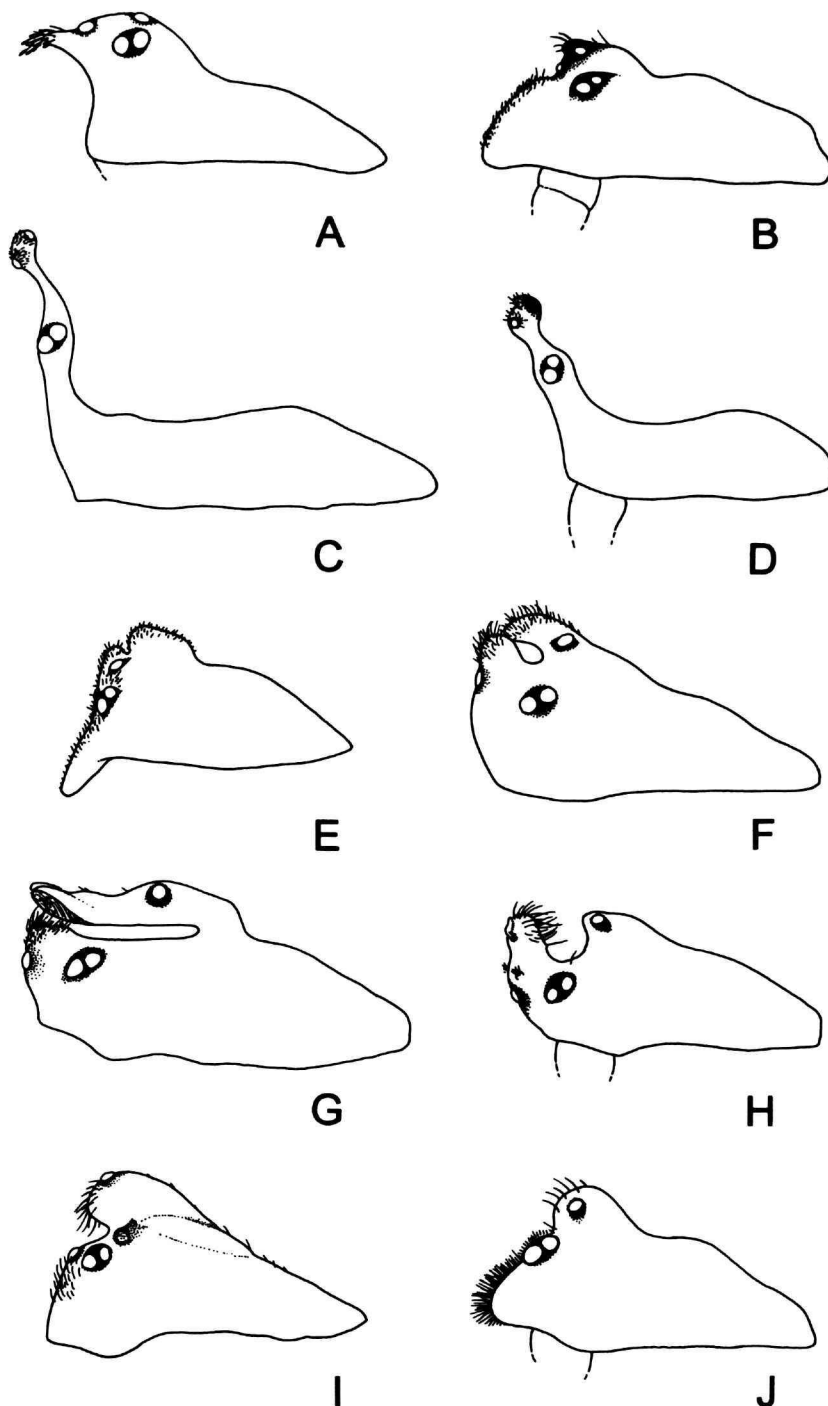


FIGURE 34.—Male cephalic morphology, lateral. A, *Floricomus rostratus* (Emerton) (Bishop and Crosby, 1935; fig. 30); B, *Scotinotylus tianshanicus* Tanasevitch (Tanasevitch, 1989, fig. 164); C, *Walckenaeria acuminata* Blackwall (Roberts, 1993, fig. 9g); D, *Walckenaeria extraterrestris* Bosmans (Bosmans and De Smet, 1993, fig. 63); E, *Goneatara platyrhinus* Crosby and Bishop (Crosby and Bishop, 1927, fig. 3); F, *Diplocephalus connatus* Bertkau (Roberts, 1993, fig. 39k); G, *Walckenaeria furcillata* (Menge) (Roberts, 1993, fig. 8j); H, *Callitrichia stellafrontis* Scharff (Scharff, 1990, fig. 22); I, *Trichopterna thorelli* (Westring) (Roberts, 1993, fig. 23e); J, *Concavocephalus rubens* Eskov (Eskov, 1989, fig. 1).

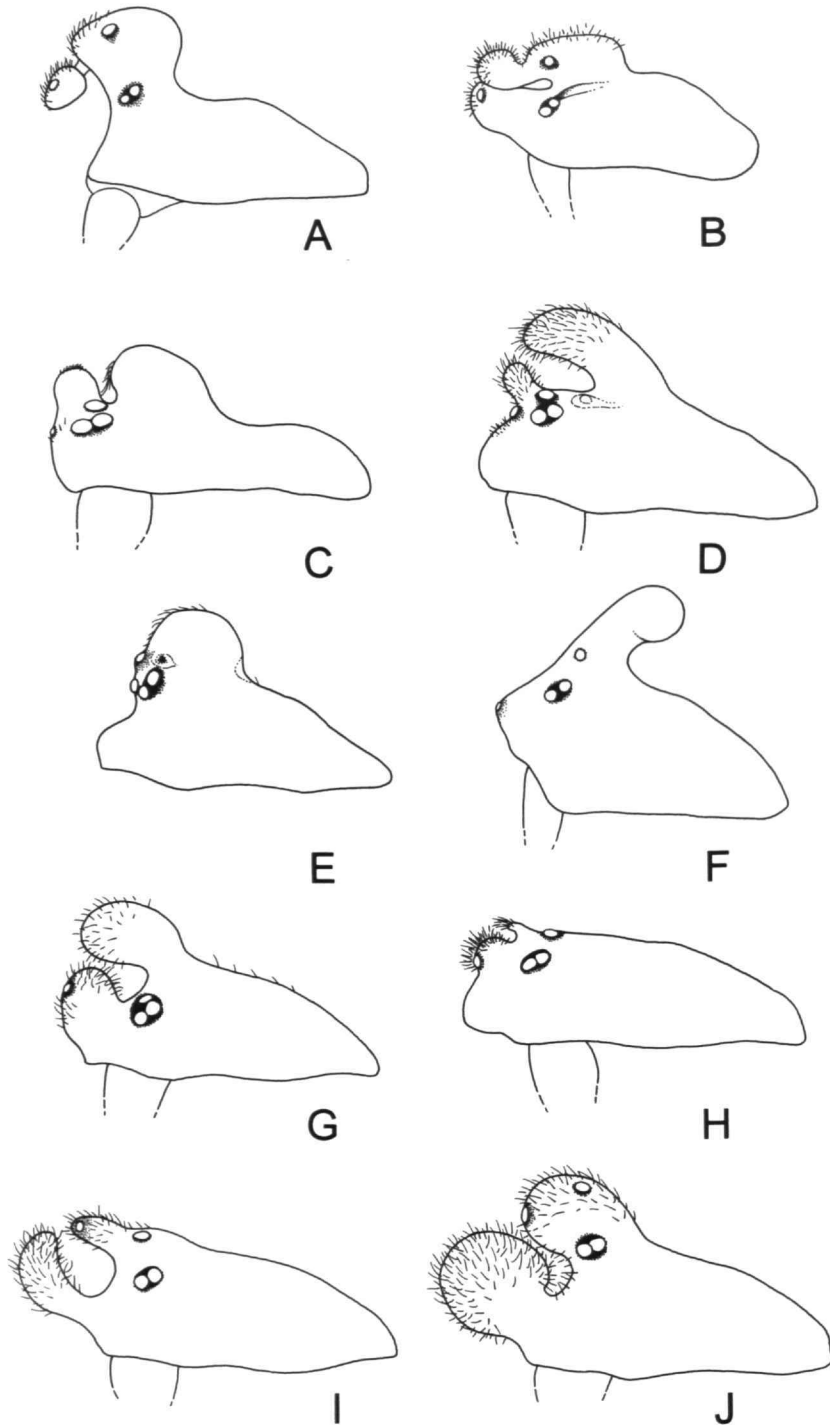


FIGURE 35.—Male cephalic morphology, lateral. A, *Dactylopiastes mirabilis* Tanasevitch (Tanasevitch, 1989, fig. 128); B, *Savignia birostrum* (Chamberlin and Ivie) (paratype); C, *Bursellia cameroonensis* Bosmans and Jocqué (Bosmans and Jocqué, 1983, fig. 3A); D, *Scotinotylus majesticus* (Chamberlin and Ivie) (Millidge, 1981, fig. 86); E, *Dismodicus bifrons* (Blackwall) (Roberts, 1993, fig. 16h); F, *Minicia kirghizica* Tanasevitch (Tanasevitch 1985, fig. 173); G, *Spirembolus bilobatus* (Chamberlin and Ivie) (Millidge, 1980, fig. 178); H, *Savignia badzhalsensis* Eskov (Eskov, 1992, fig. 1); I, *Coreogonol bicornis* (Emerton) (Millidge, 1981, fig. 145); J, *Coreogonol petalucis* (Millidge) (Millidge, 1981, fig. 146).

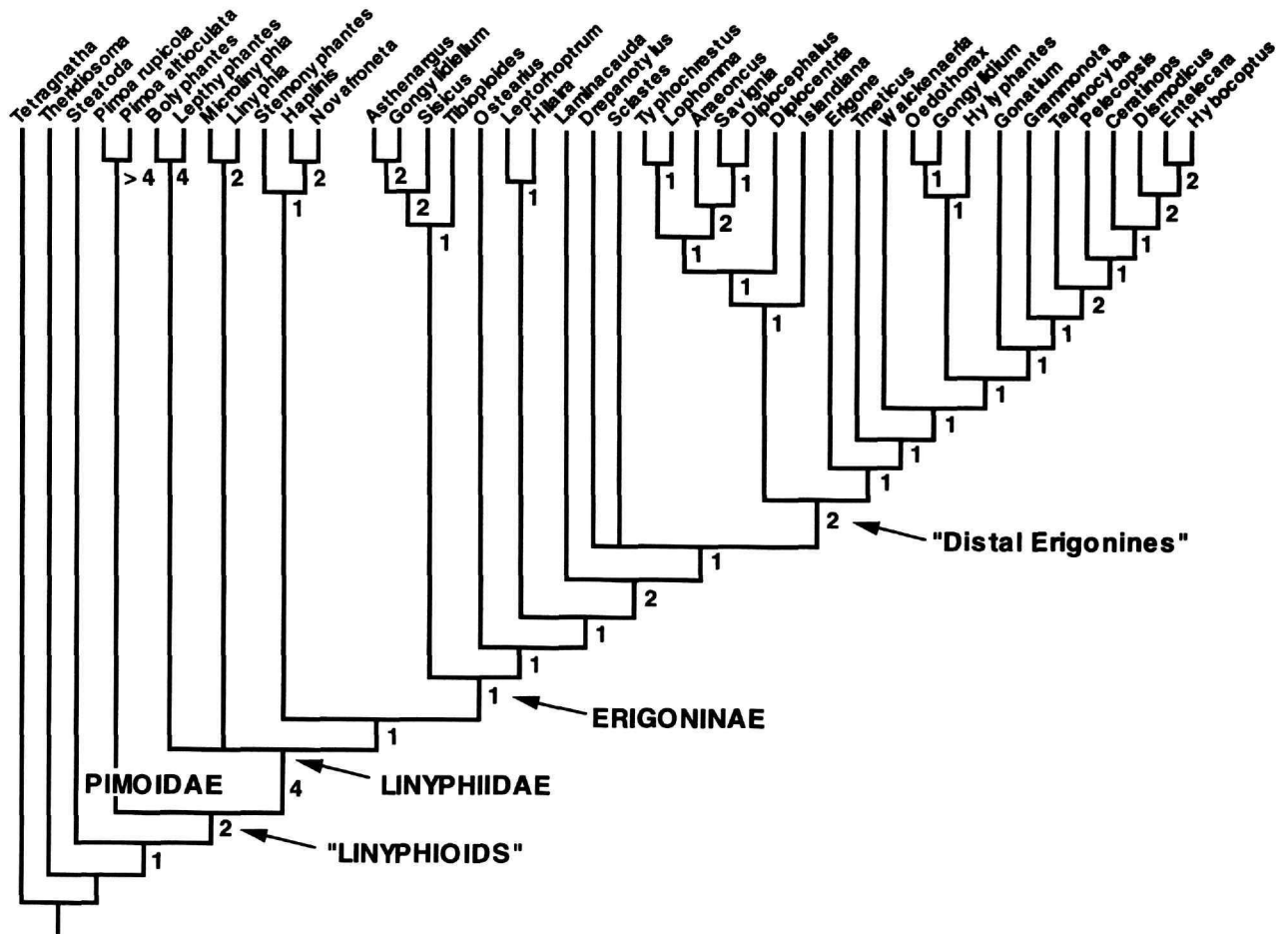


FIGURE 36.—Strict consensus cladogram of the six minimal-length trees that result from the parsimony analysis of the character data presented in Appendix 1 (length=230, consistency index=0.41, retention index=0.68). Numbers at nodes indicate Bremer support.

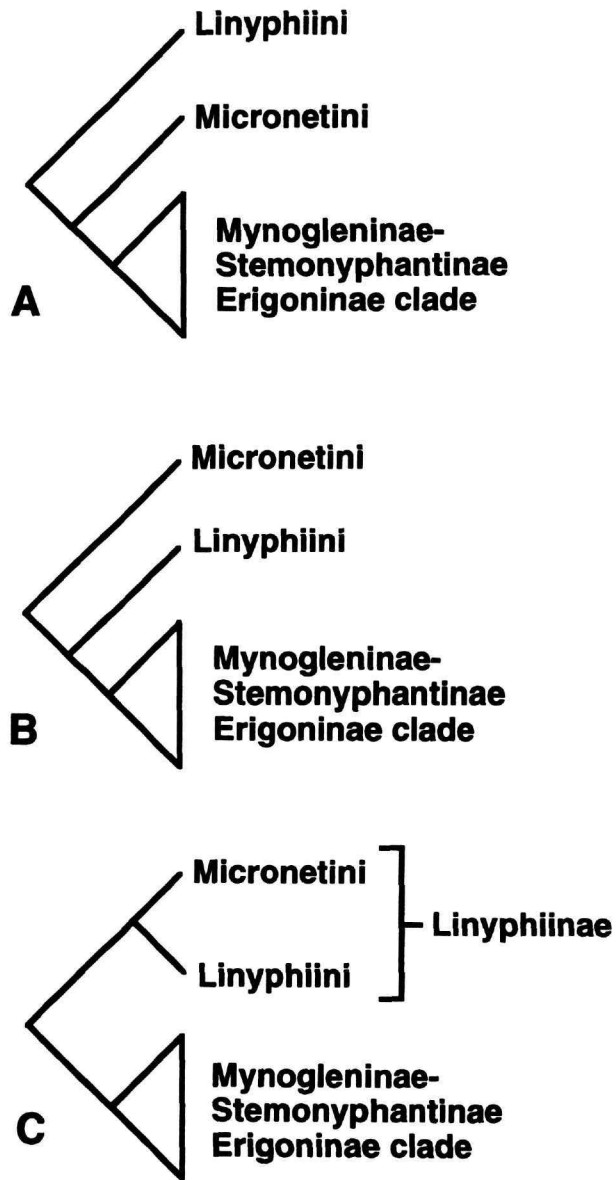


FIGURE 37.—The three minimal-length topologies for the interrelationships of the Linyphiini, Micronetini, and the clade of Mynogleninae, Stemonyphantinae, plus Erigoninae (see text for details).

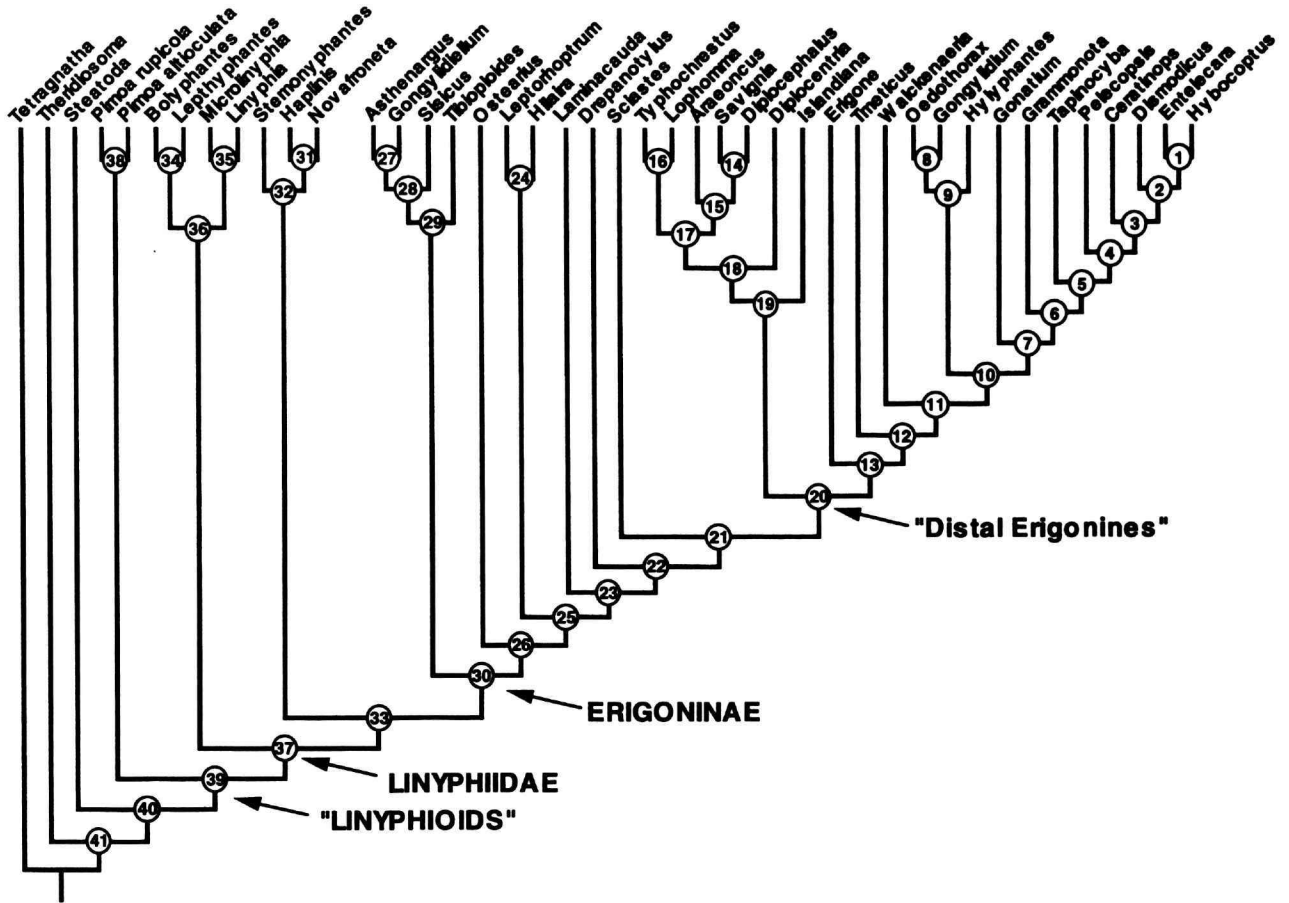


FIGURE 38.—Preferred minimal-length cladogram from parsimony analysis of the character data presented in Appendix 1 (length=230, consistency index=0.41, retention index=0.68; see text for more details).

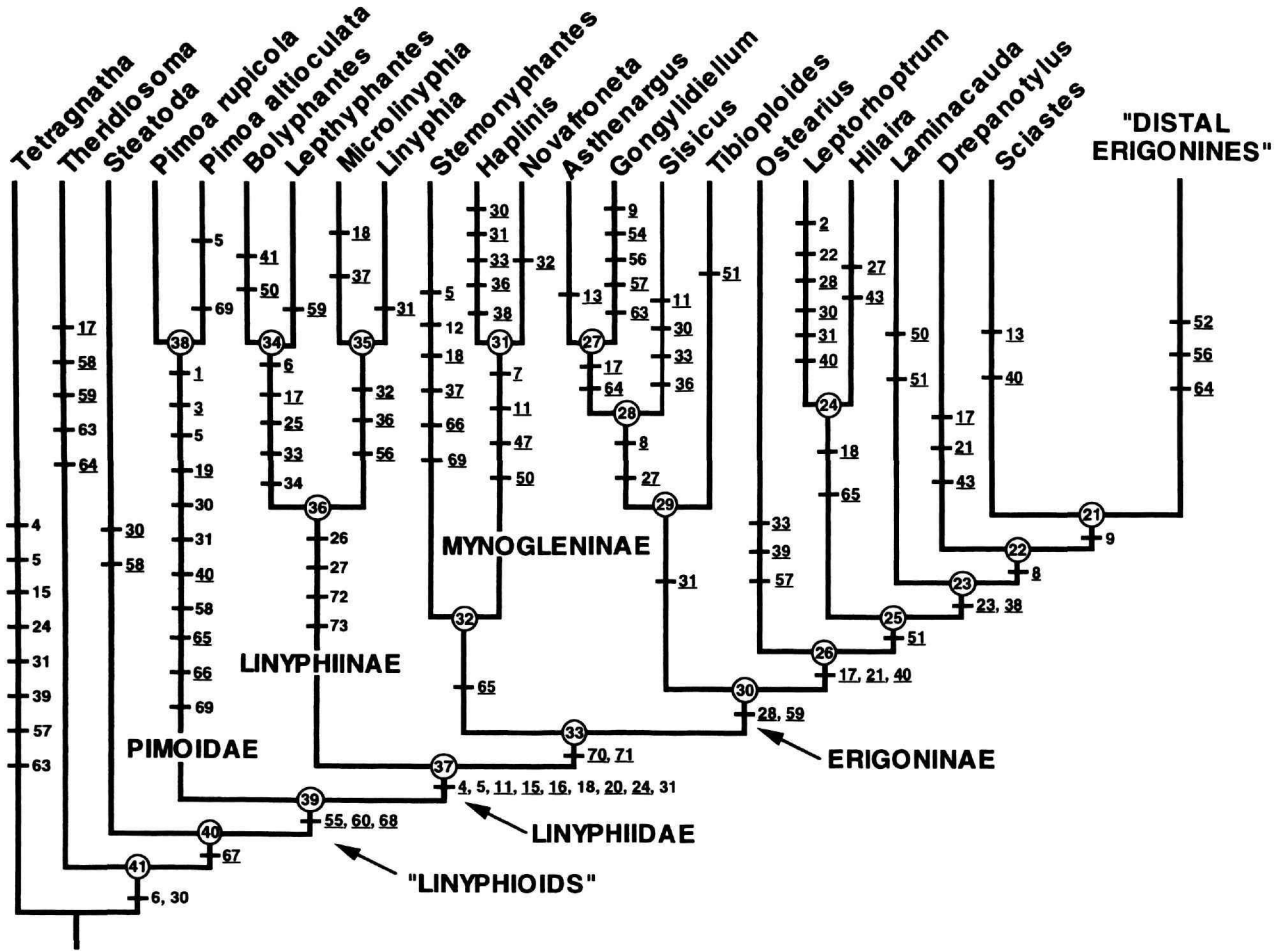


FIGURE 39.—Character optimizations for the preferred cladogram (length=230, consistency index=0.41, retention index=0.68; see text for more details). Underlined numbers denote unambiguous character-change optimizations.



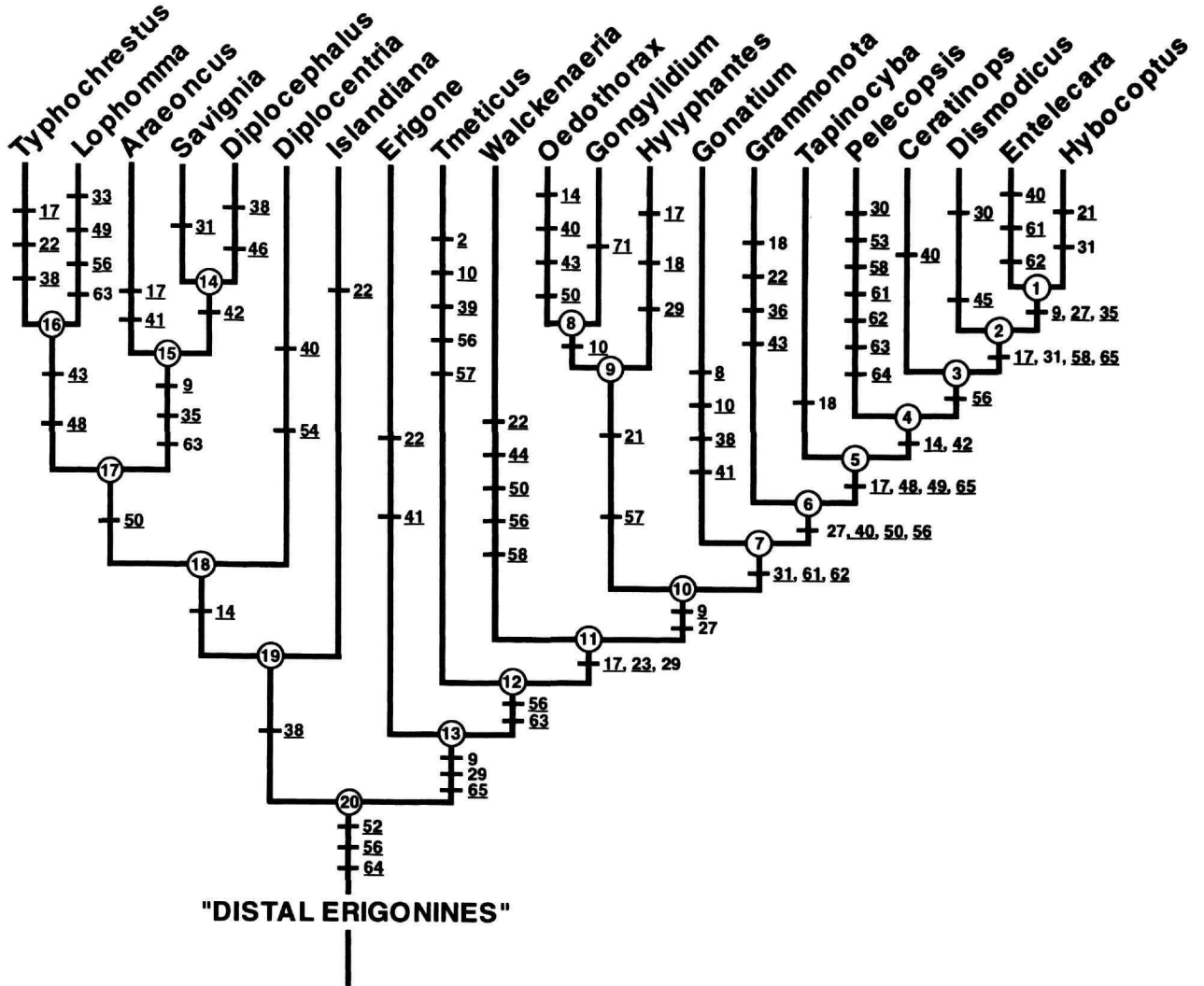


FIGURE 40.—Character optimizations for the preferred cladogram (length=230, consistency index=0.41, retention index=0.68; see text for more details). Underlined numbers denote unambiguous character-change optimizations.

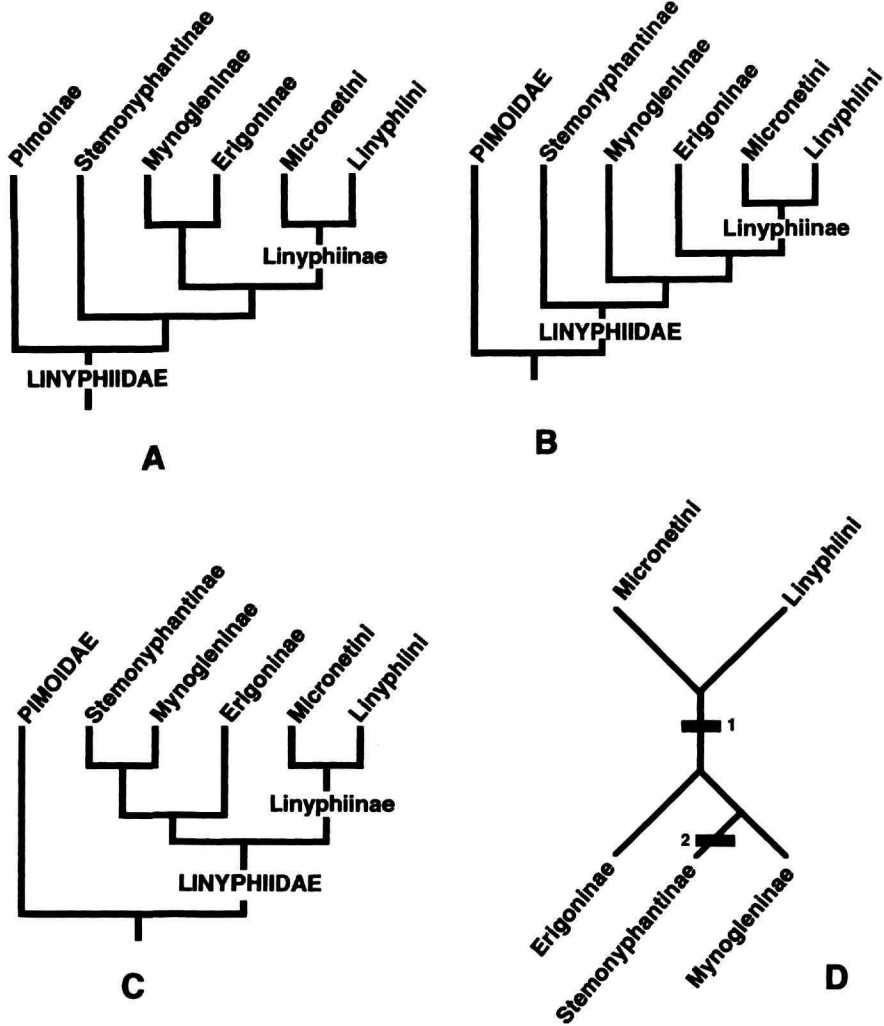


FIGURE 41.—Interrelationships of linyphiid subfamilies. A, Wunderlich (1986:106); B, Hormiga (1994b, fig. 32B); C, this study; D, unrooted topology of cladograms B (“root 2”) and C (“root 1”) (see text for more details).

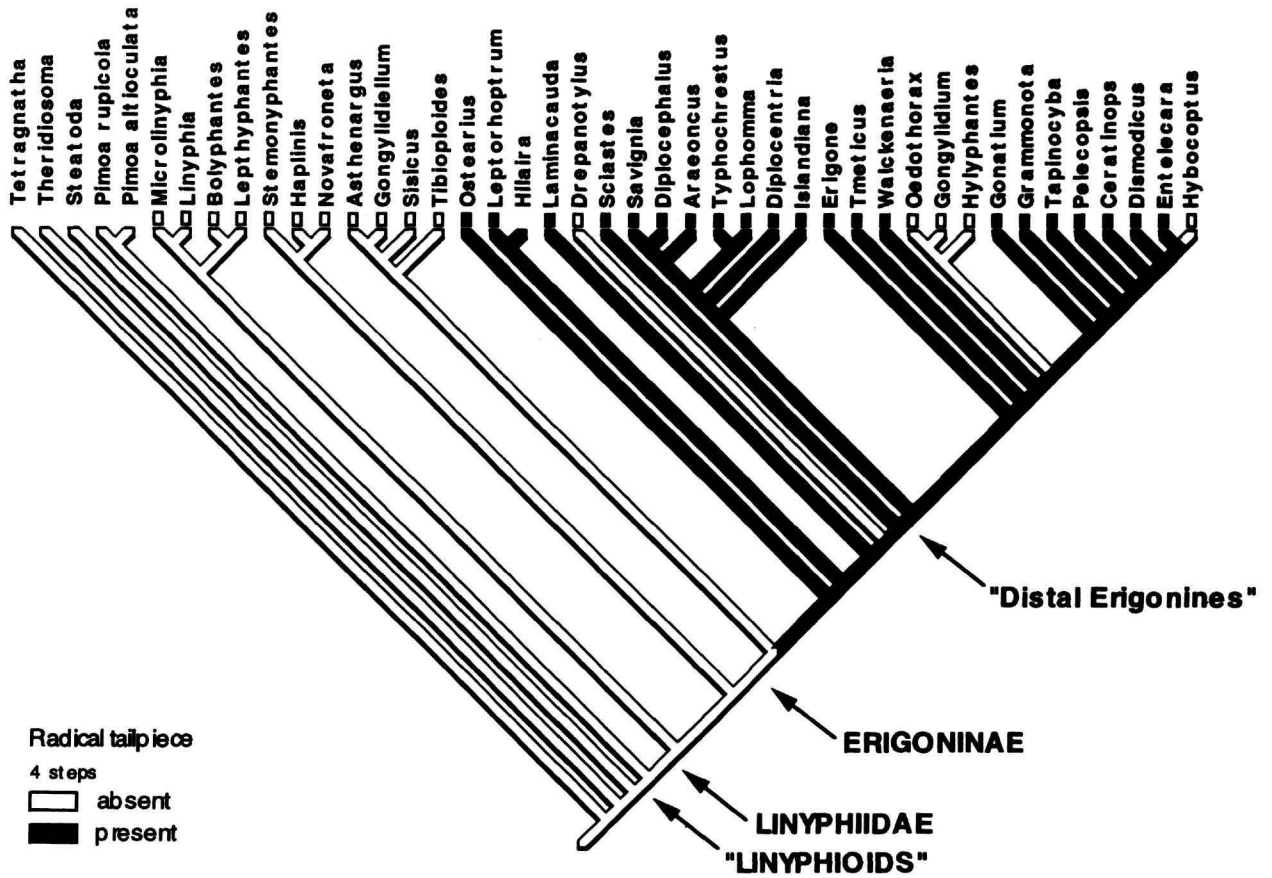


FIGURE 42.—Radical tailpiece (character 21) traced on the preferred cladogram.

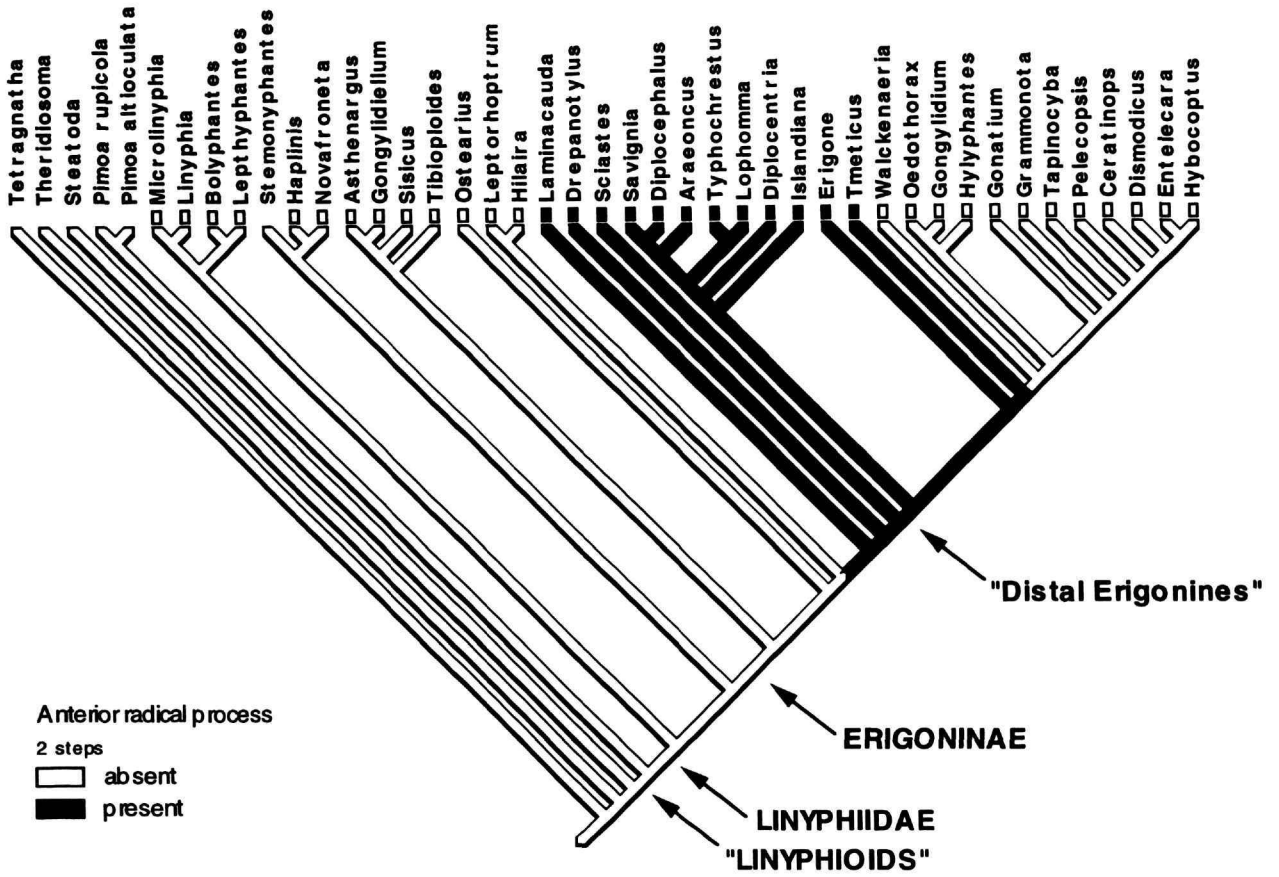


FIGURE 43.—Anterior radical process (character 23) traced on the preferred cladogram.

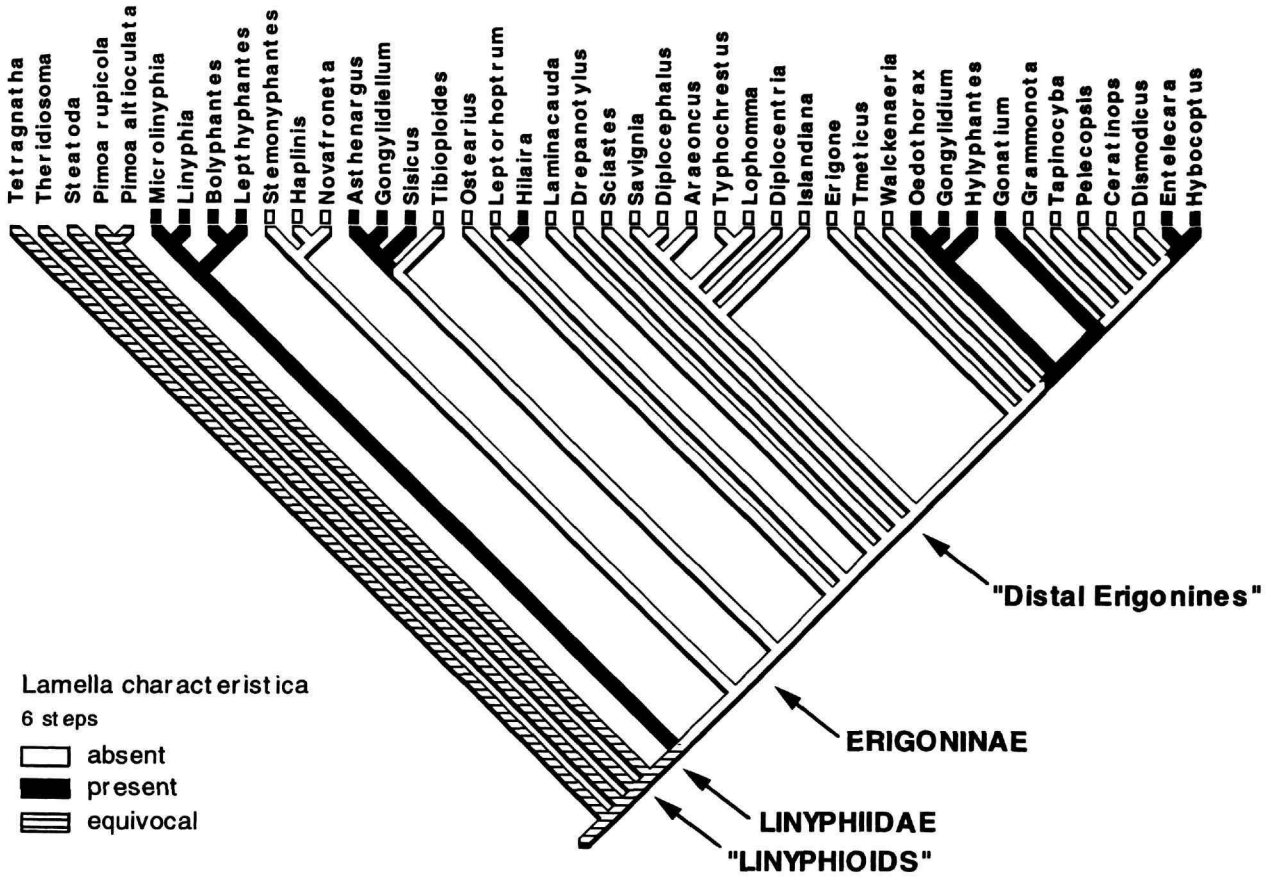


FIGURE 44.—Lamella characteristic (character 27) traced on the preferred cladogram.

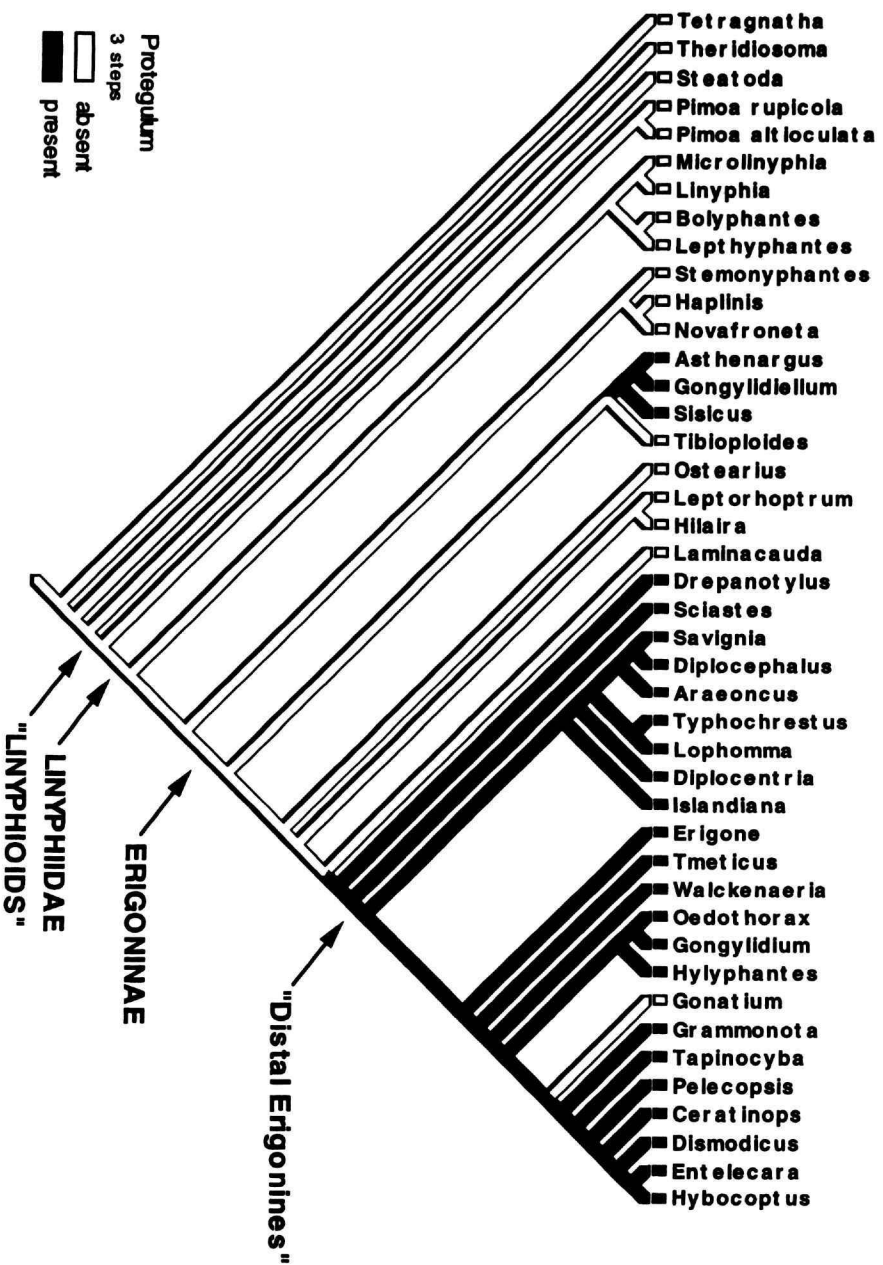


FIGURE 45.—Protegulum (character 8) traced on the preferred cladogram.

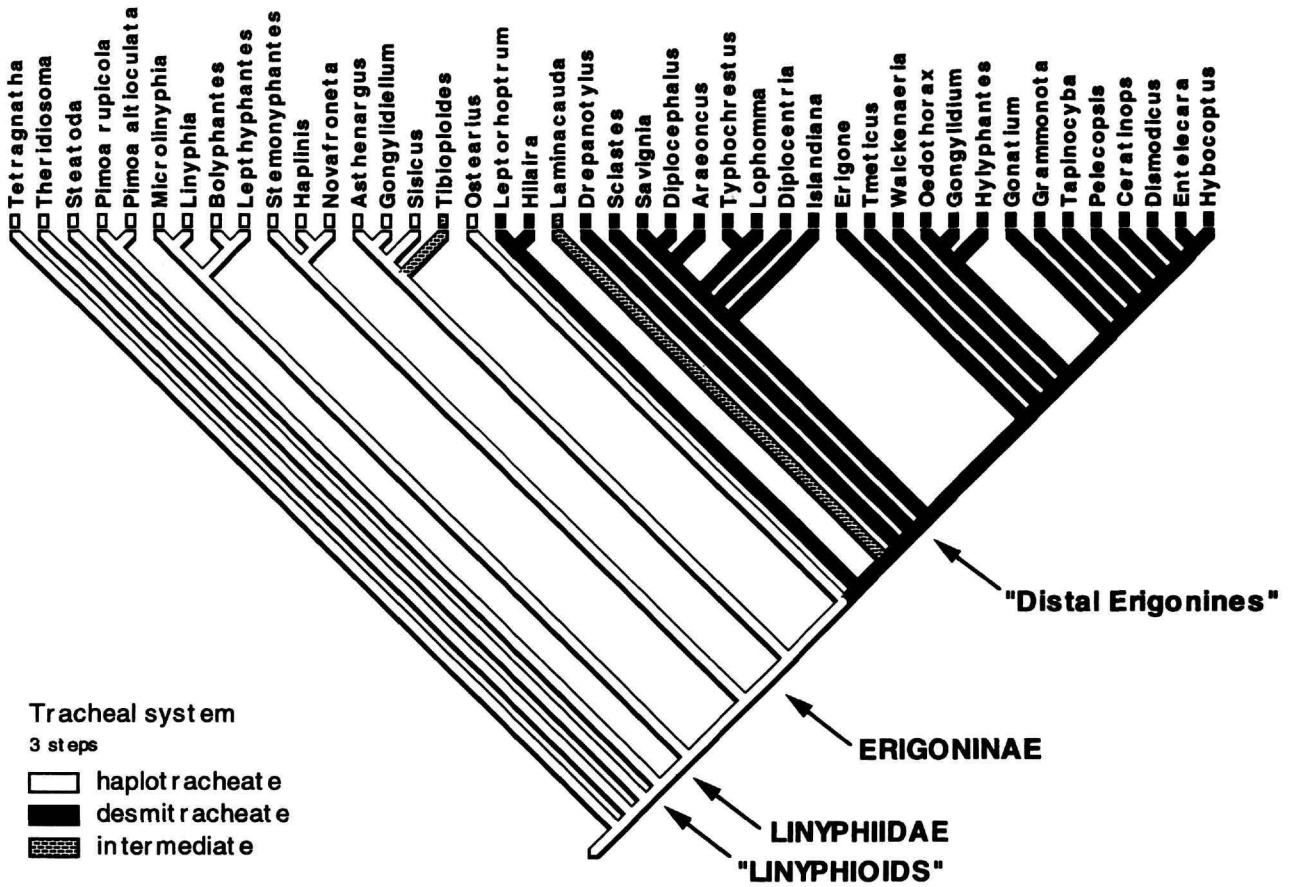


FIGURE 46.—Tracheal system (character 51) traced on the preferred cladogram.

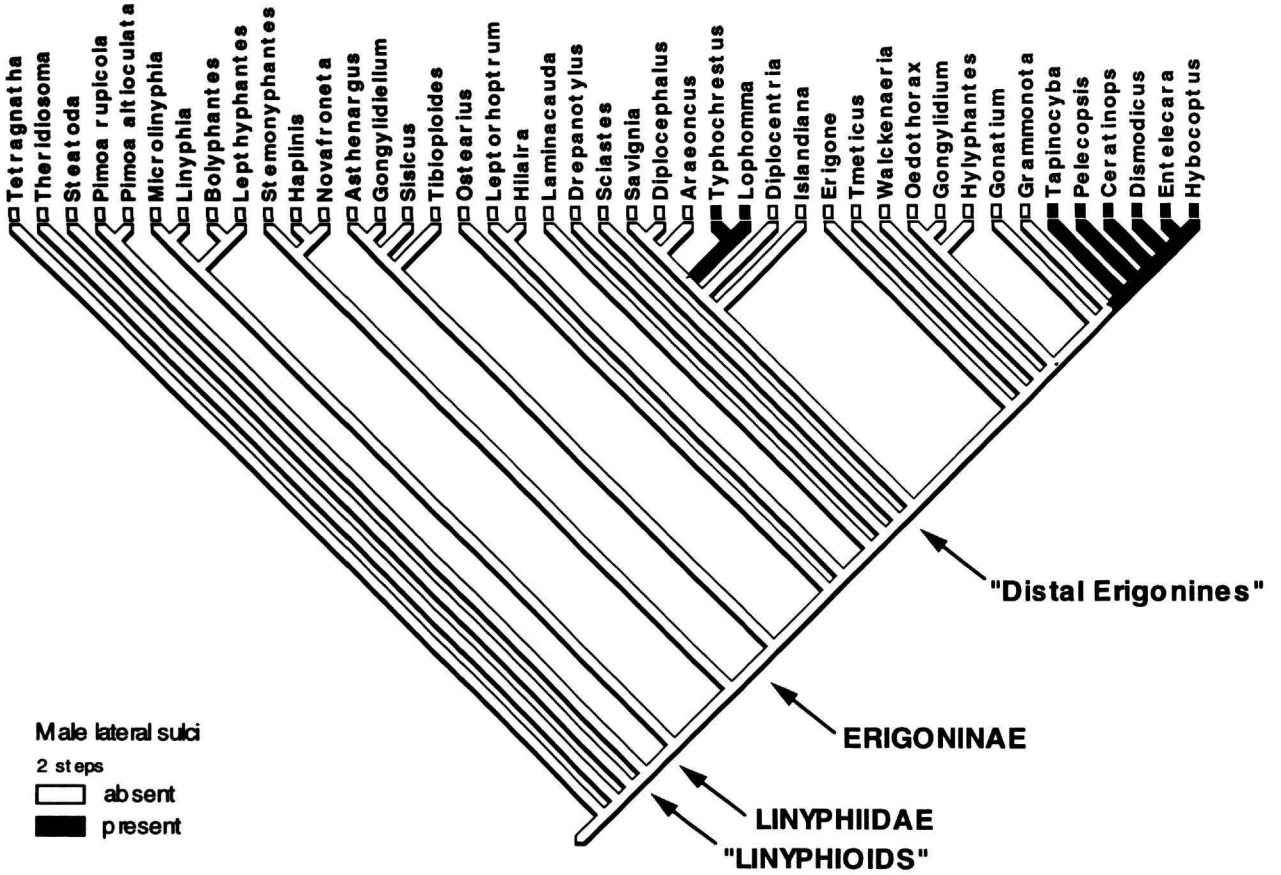


FIGURE 47.—Male lateral sulci (character 48) traced on the preferred cladogram.



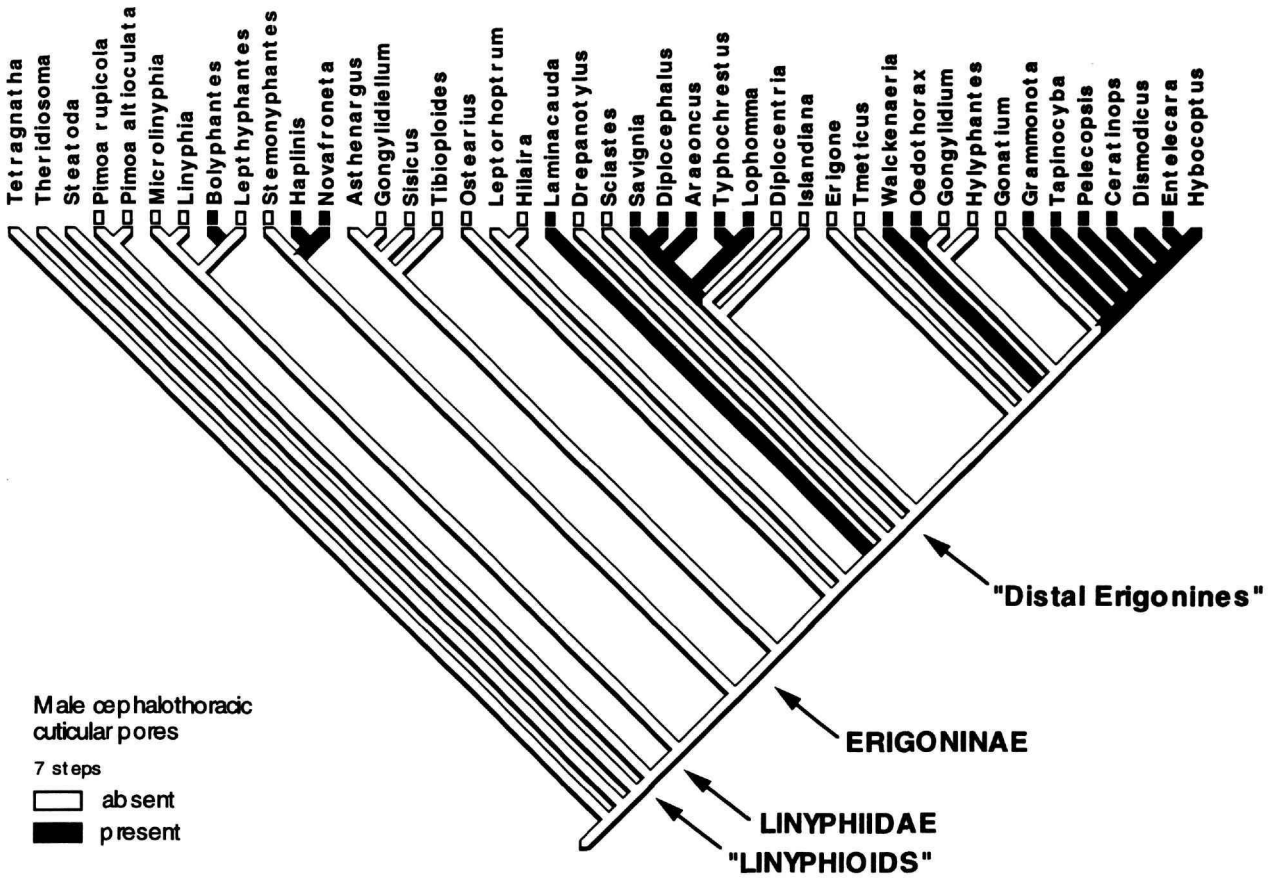


FIGURE 48.—Male cephalothoracic cuticular pores (character 50) traced on the preferred cladogram.



## Plates

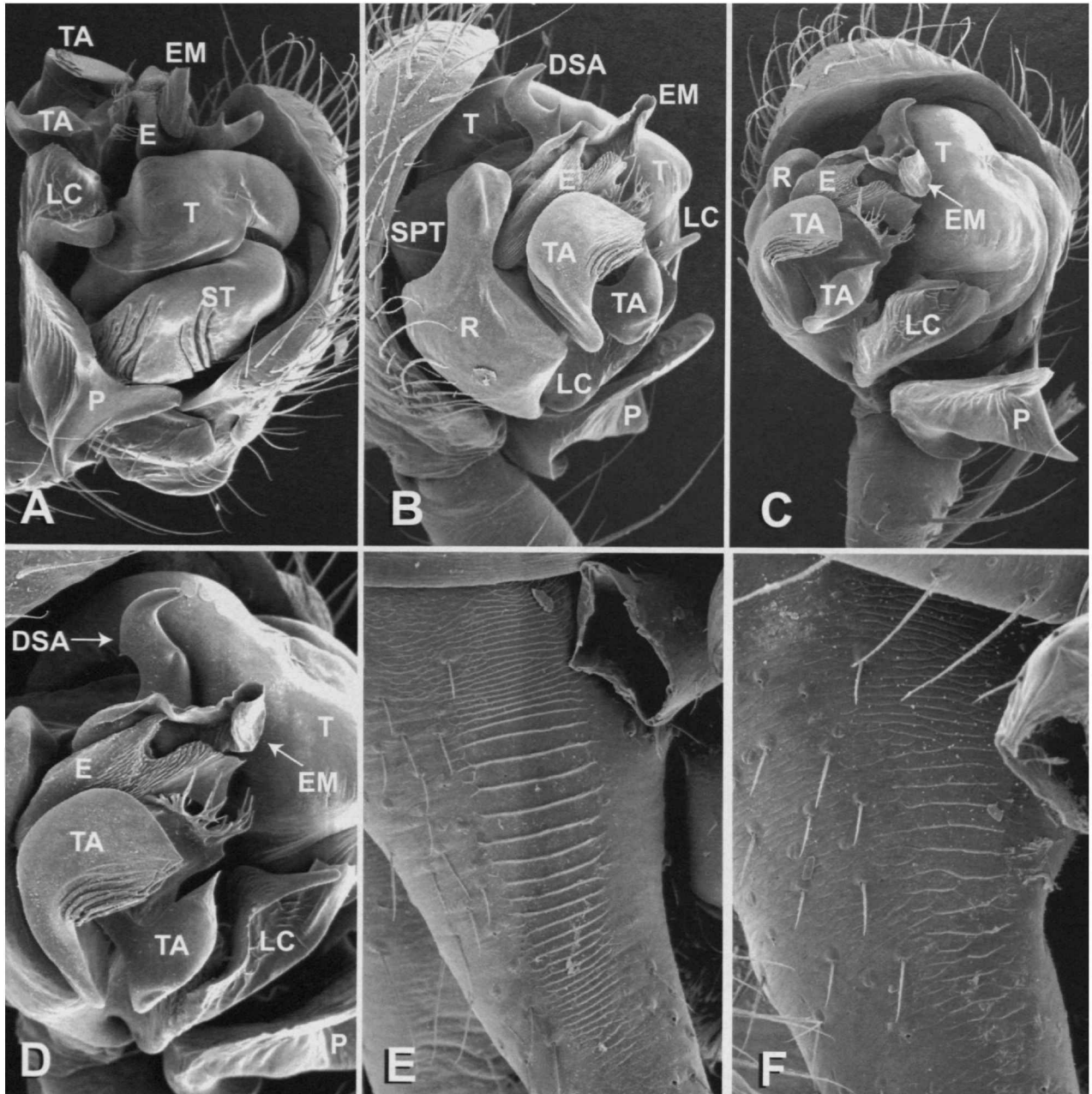


PLATE 1.—*Bolyphantes luteolus*: A–D, male palp (right); E, F, ectal side of chelicera. A, ectal; B, mesal; C, ventral; D, embolic division, ventral; E, male; F, female (right).

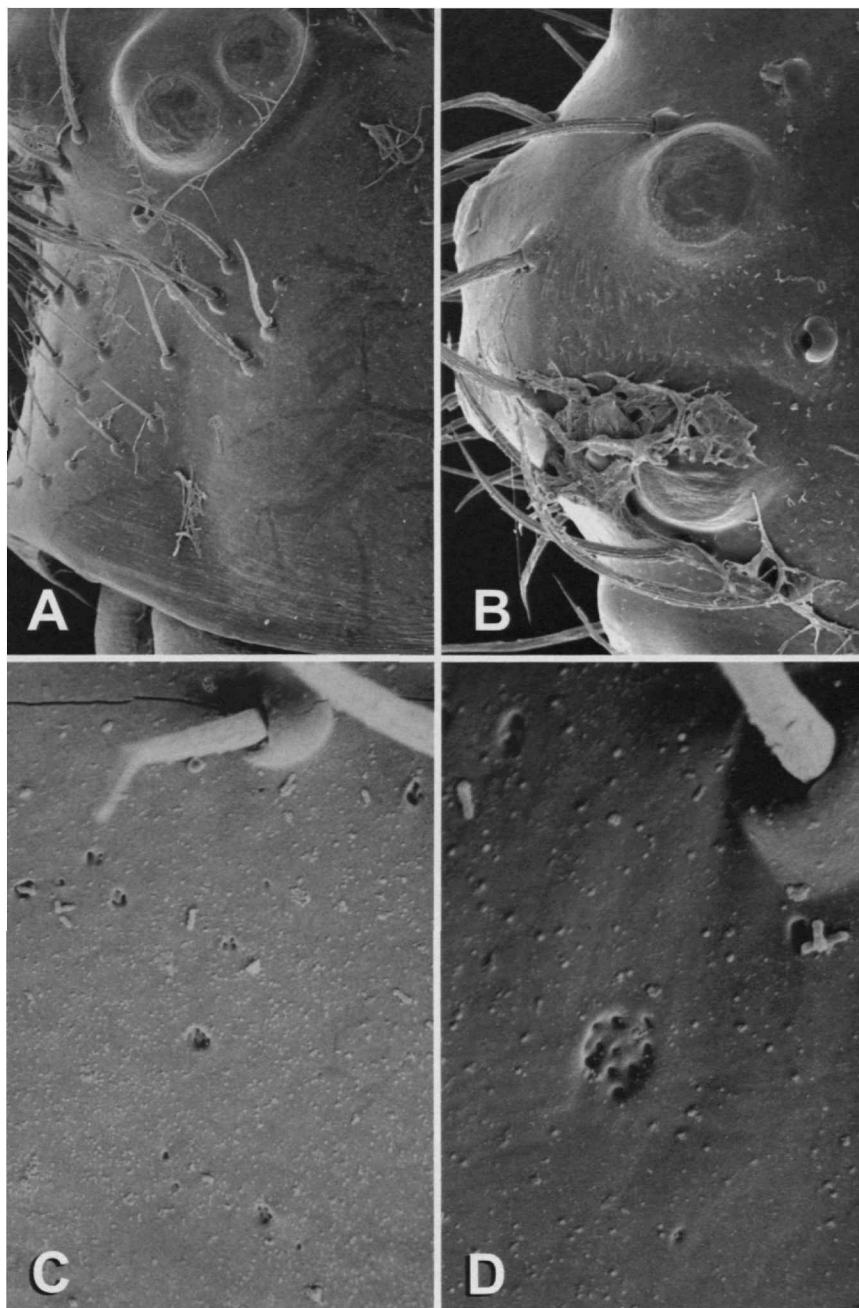


PLATE 2.—*Bolyphantes luteolus*: male prosoma. A, lateral; B, dorsal; C, cuticular pores (ventrad of lateral eyes); D, cuticular pores (clypeus).

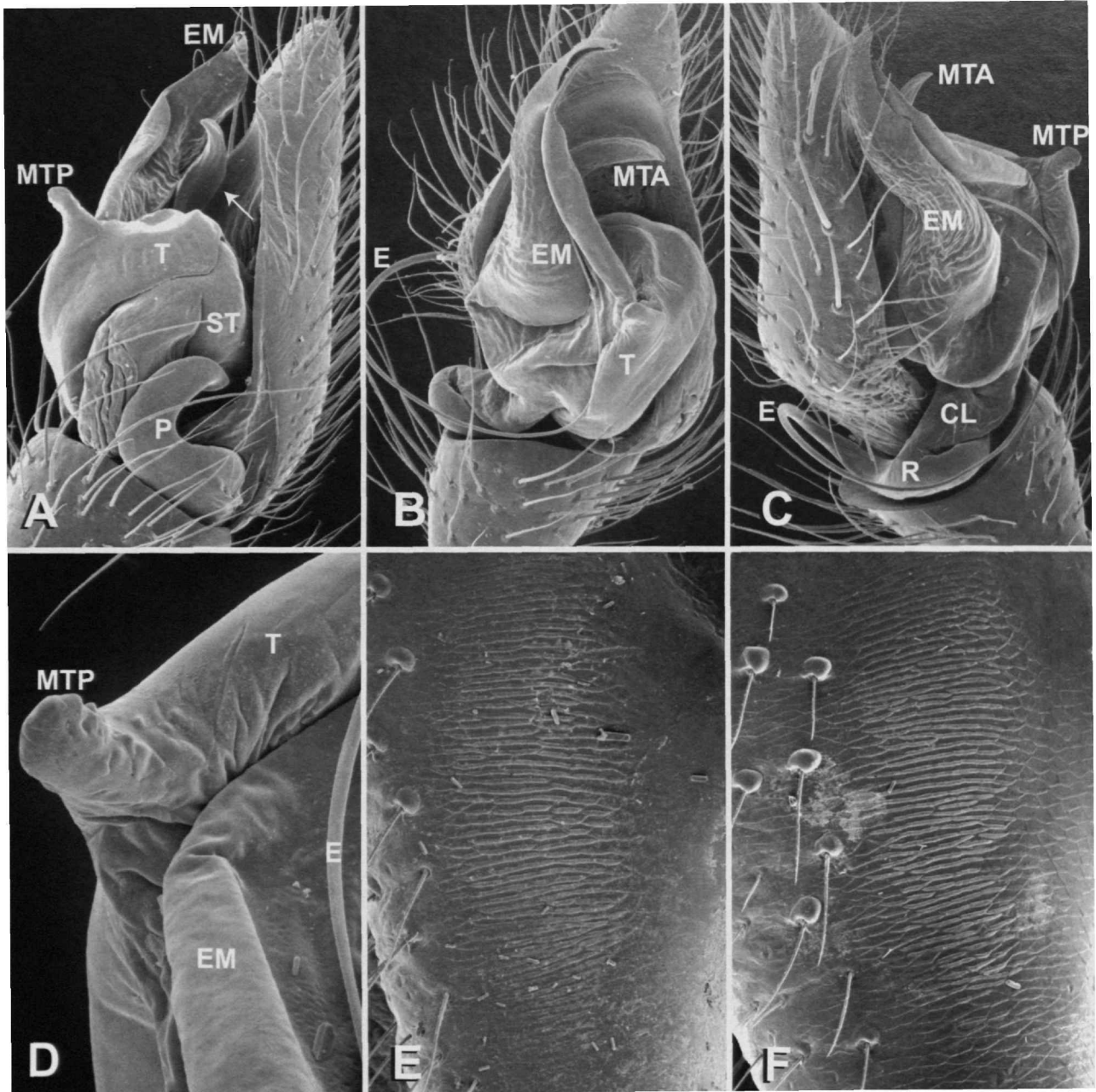


PLATE 3.—*Haplinis diloris*: A–D, male palp; E, F, ectal side of chelicera. A, ectal (arrow indicates mynoglennine tegular apophysis); B, ventral; C, mesal; D, tegulum, embolus and embolic membrane; E, male; F, female.

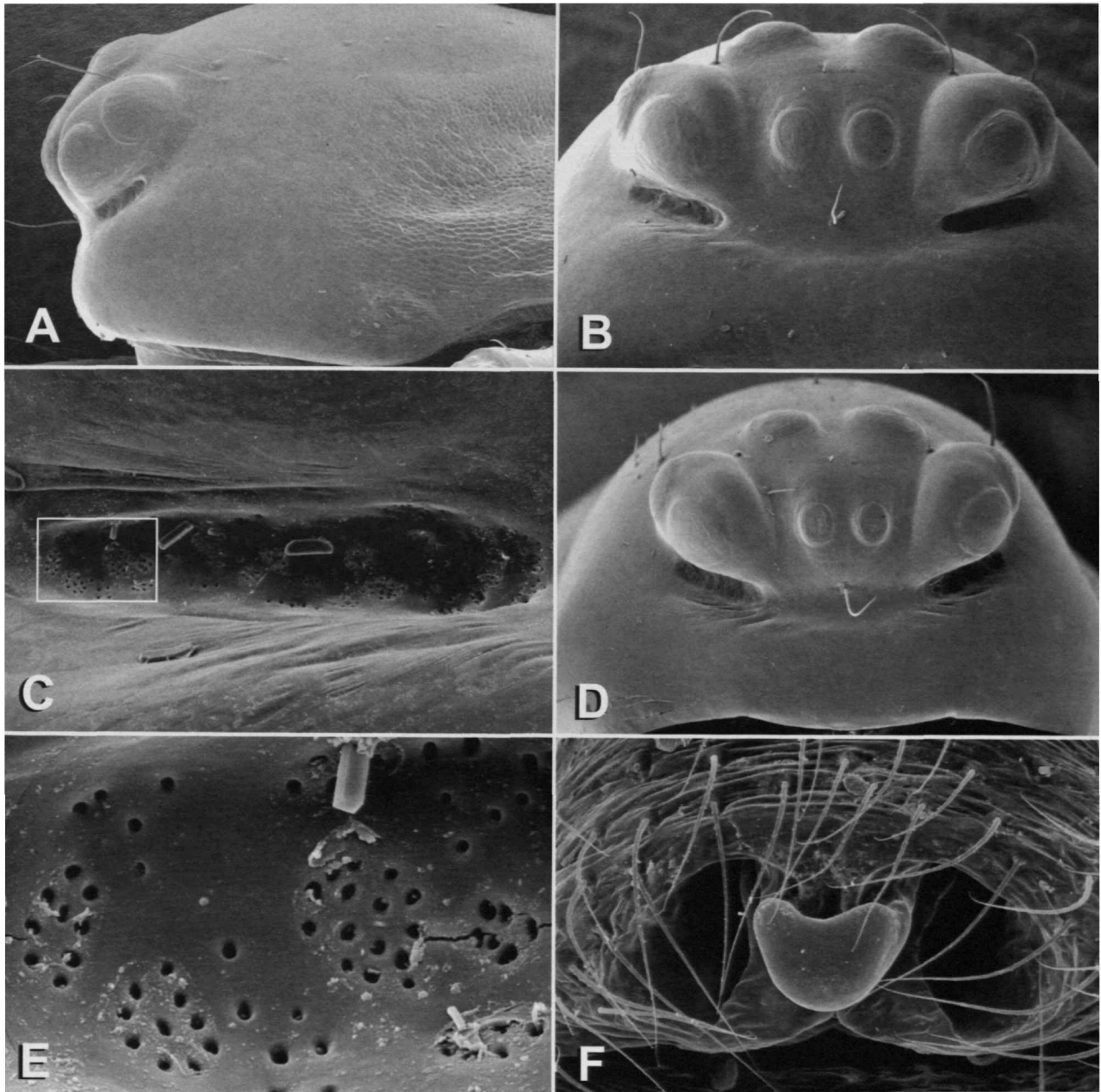


PLATE 4.—*Haplinis diloris*: A–E, prosoma; F, epigynum. A, male, lateral; B, male, frontal; C, male, sulcus; D, female, frontal; E, detail of figure C; F, posteroventral.

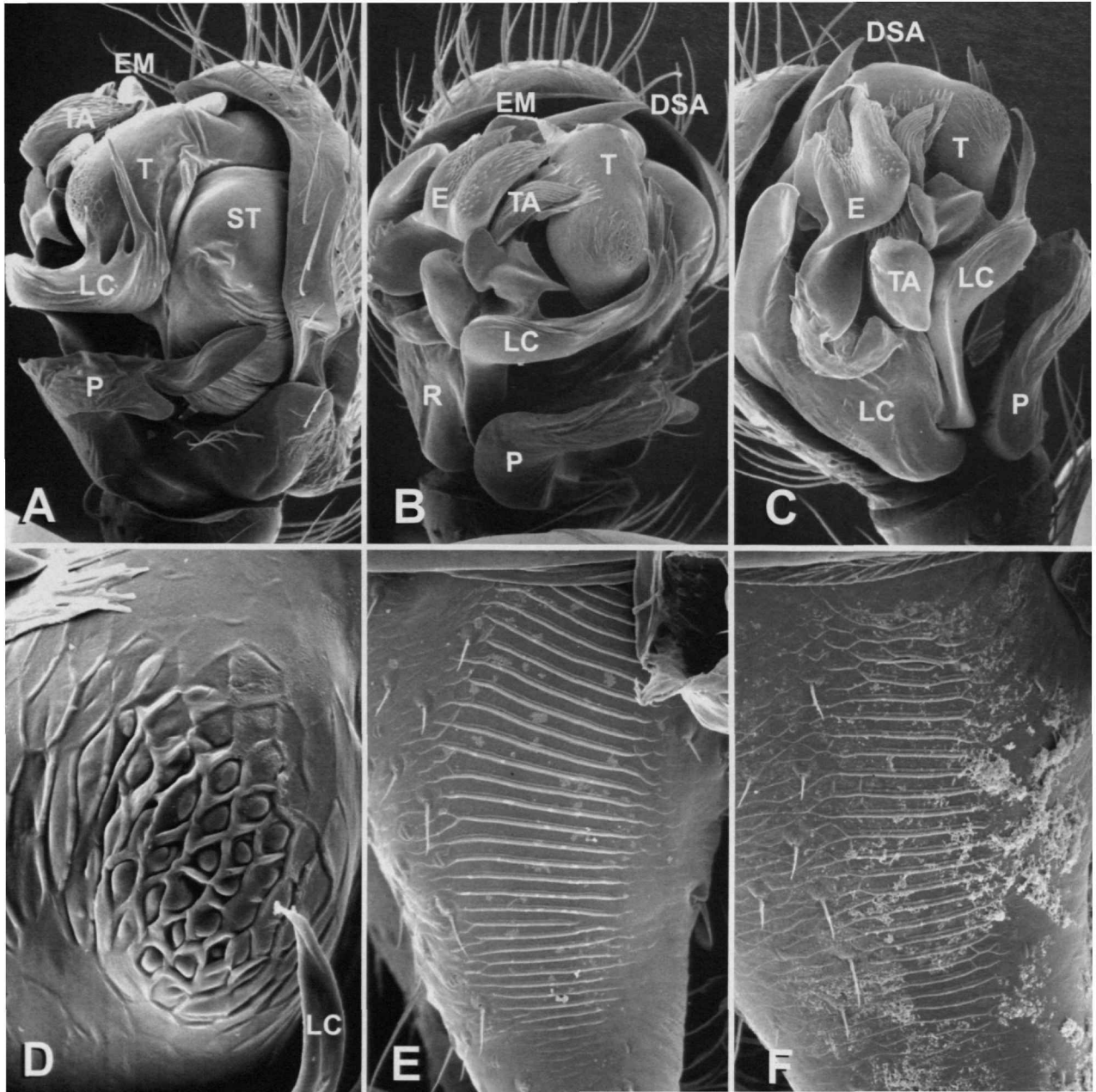


PLATE 5.—*Lephyphantes tenebricola*: A–D, male palp; E, F, ectal side of chelicera. A, ectal; B, ventral; C, mesal; D, tegulum; E, male; F, female.



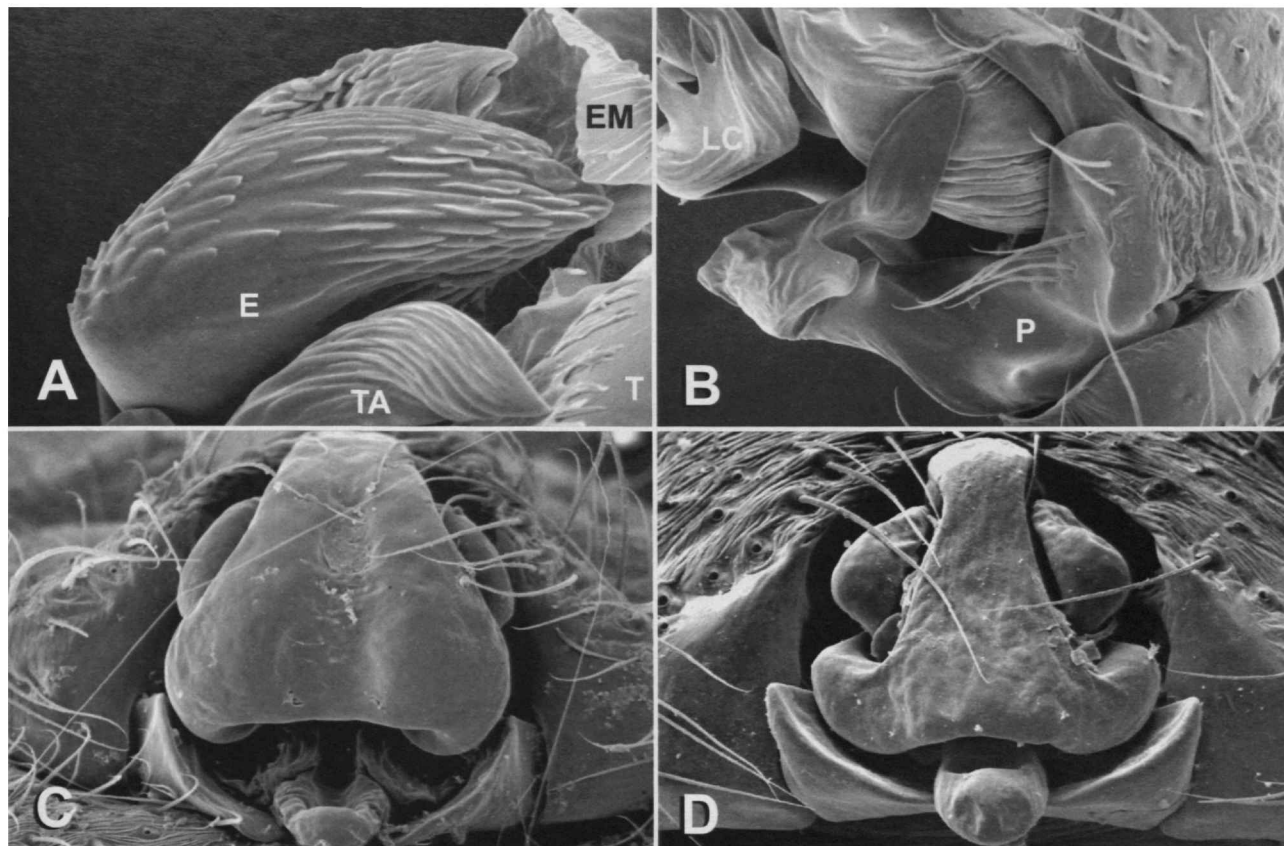


PLATE 6.—*Lepthyphantes tenebricola*: A, distal half of embolus, mesoventral; B, paracymbium, dorsoectal; C, epigynum, posteroventral. *Lepthyphantes tenuis*: D, epigynum, posteroventral.

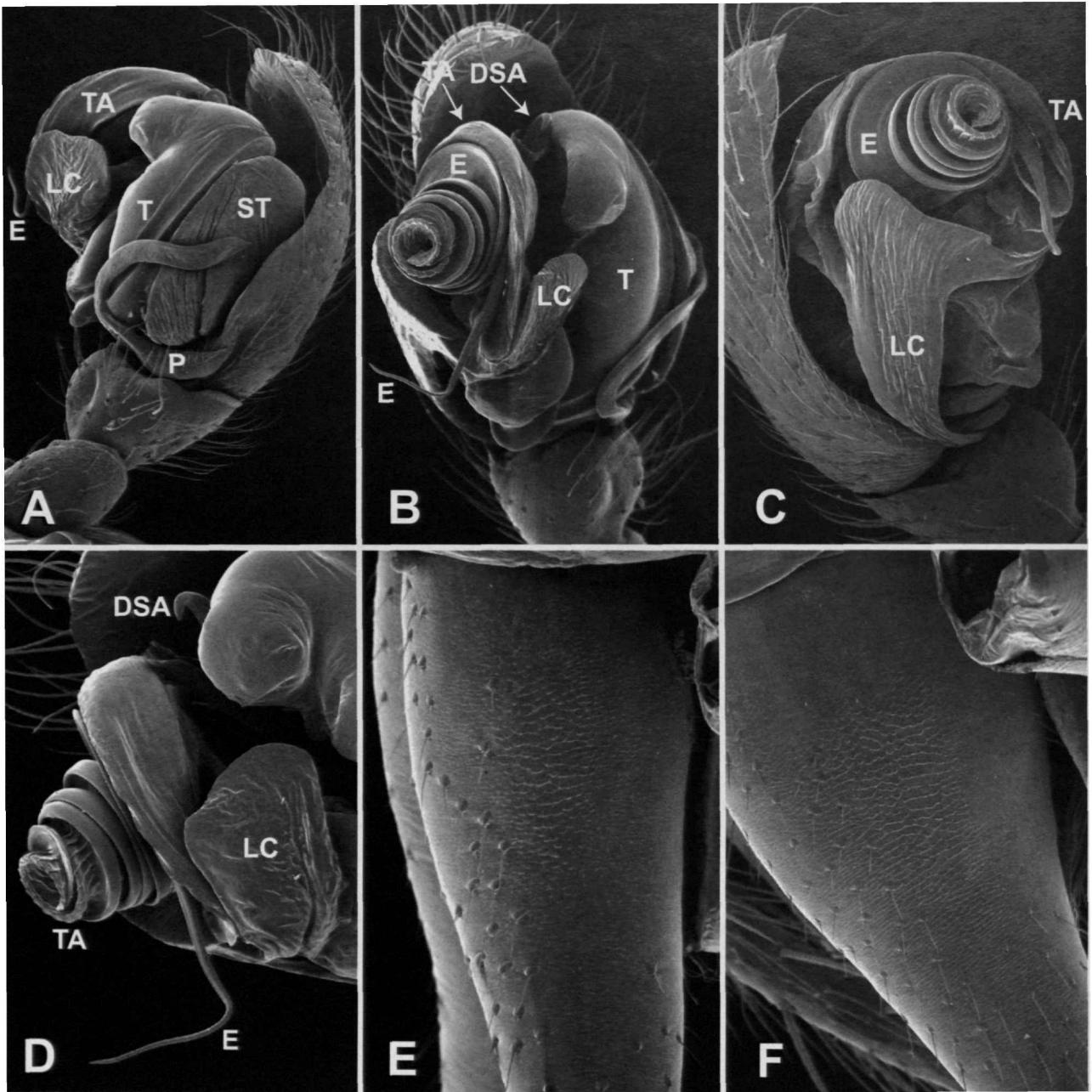


PLATE 7.—*Linyphia triangularis*: A–D, male palp; E, F, ectal side of chelicera. A, ectal; B, mesal; C, ventral; D, embolic division, ectoventral; E, male; F, female.

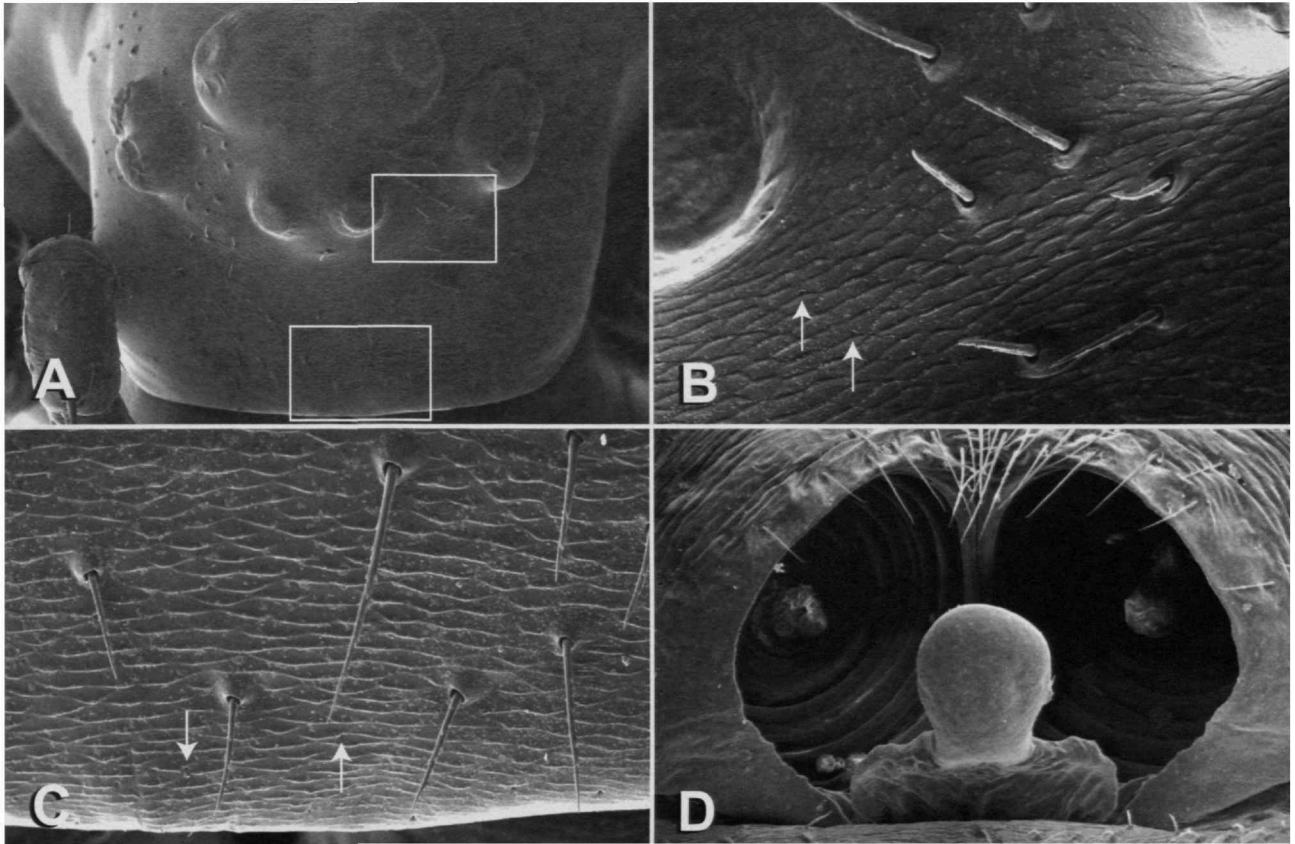


PLATE 8.—*Linyphia triangularis*: A–C, female prosoma; D, epigynum. A, frontal; B, cuticular pores, detail of A; C, cuticular pores, detail of A; D, posteroventral.

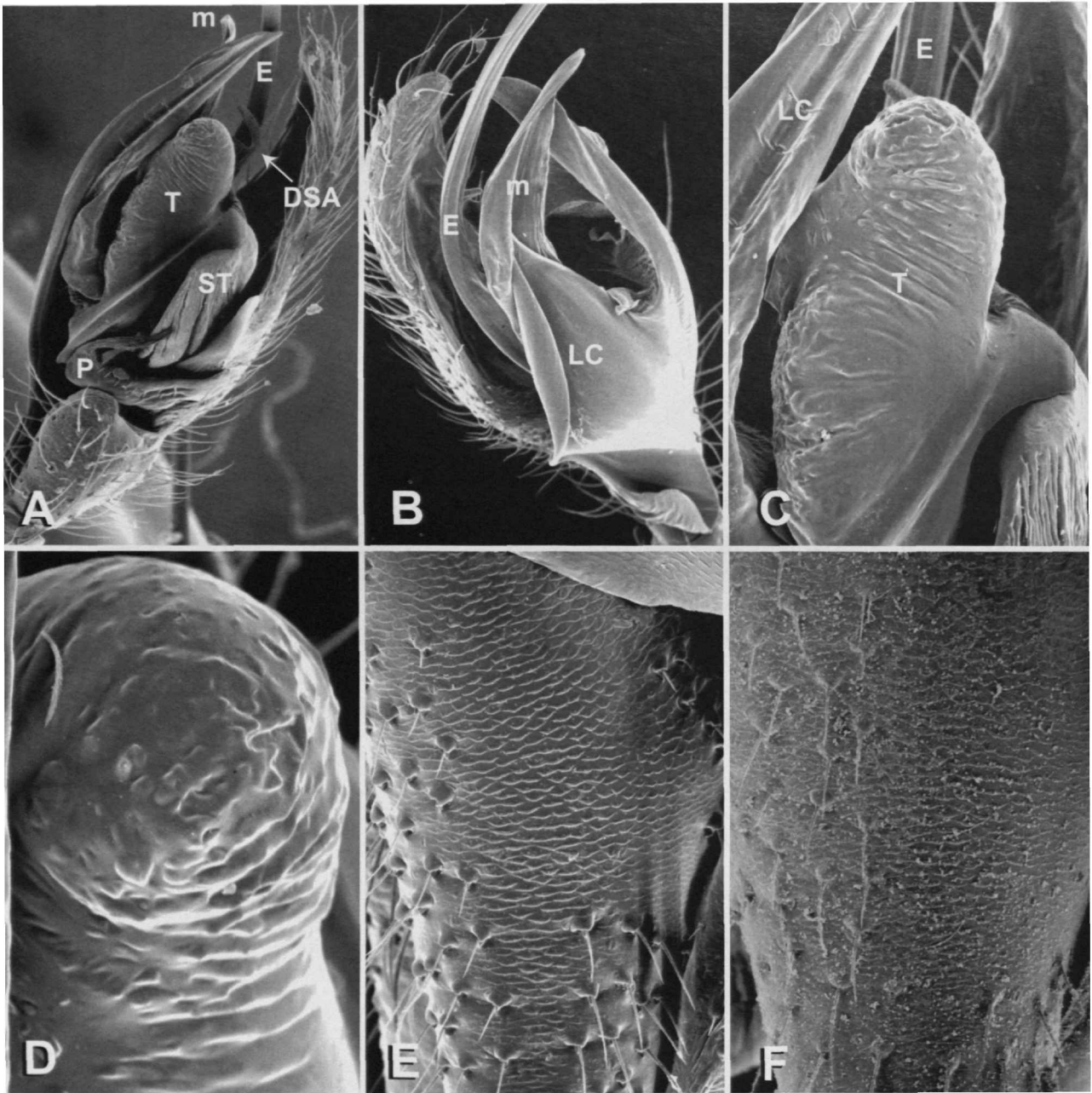


PLATE 9.—*Microlinyphia dana*: A–D, male palp (right); E, F, ectal side of chelicera. A, ectal; B, mesal; C, tegulum, ectal; D, tegulum, apical; E, male; F, female.

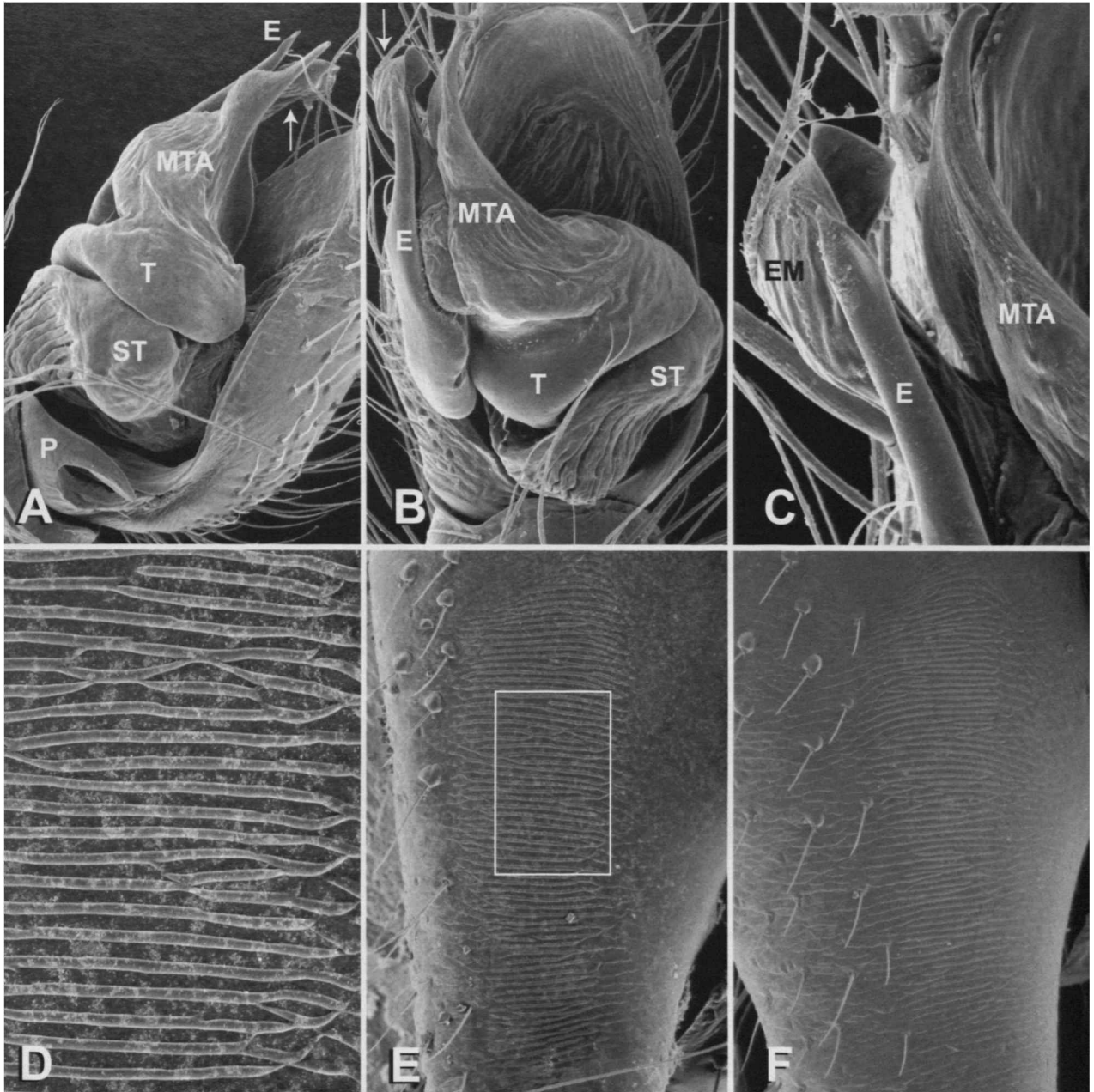


PLATE 10.—*Novafroneta vulgaris*: A–C, male palp; D–F, ectal side of chelicera. A, ectal (arrow indicates EM); B, ventral (arrow indicates EM); C, mesoventral; D, detail of E; E, male; F, female.

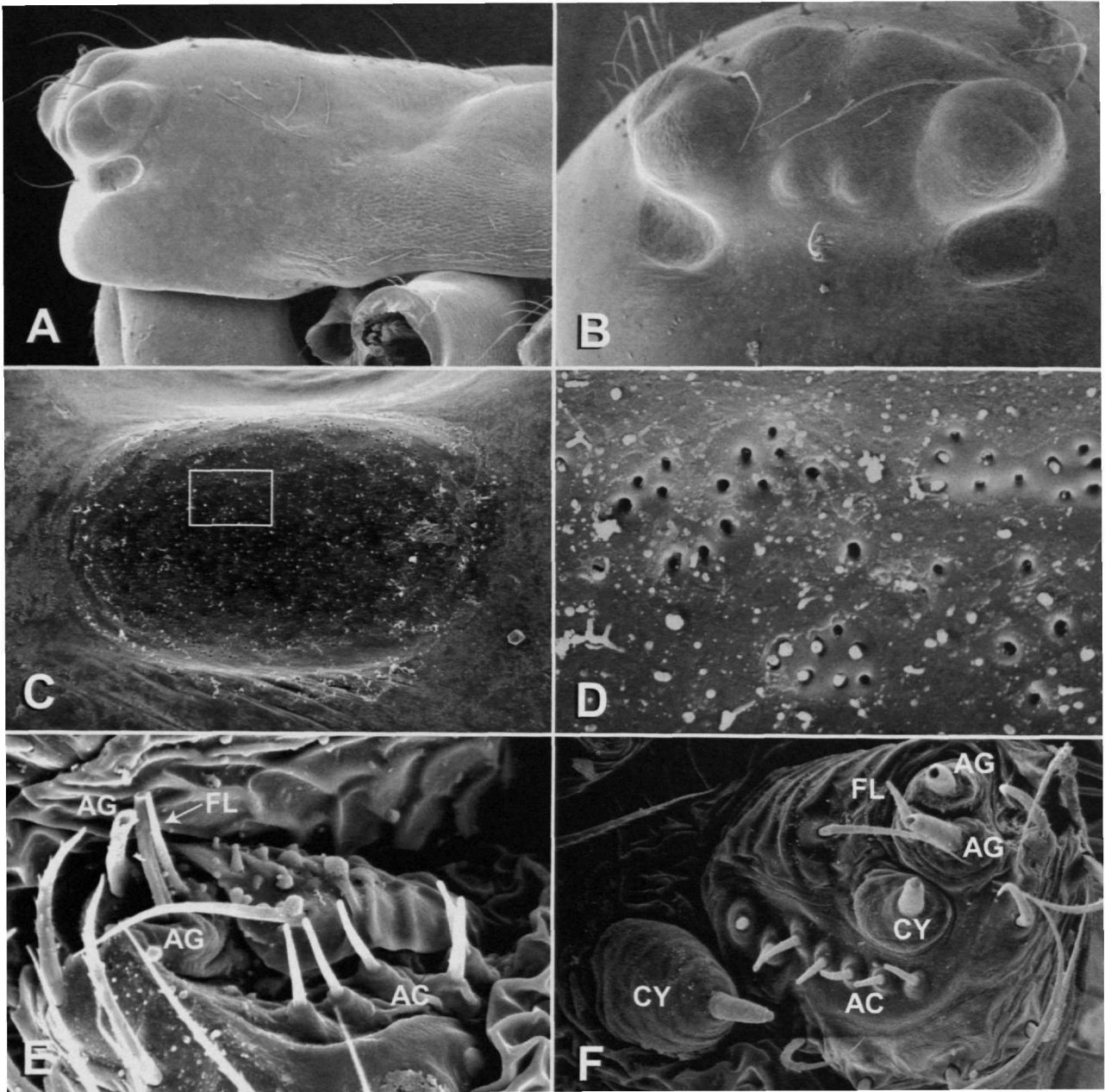


PLATE 11.—*Novafroneta vulgaris*: A–D, prosoma; E, F, PLS. A, male, lateral; B, female, frontal; C, female, clypeal sulcus; D, detail of C; E, male; F, female.

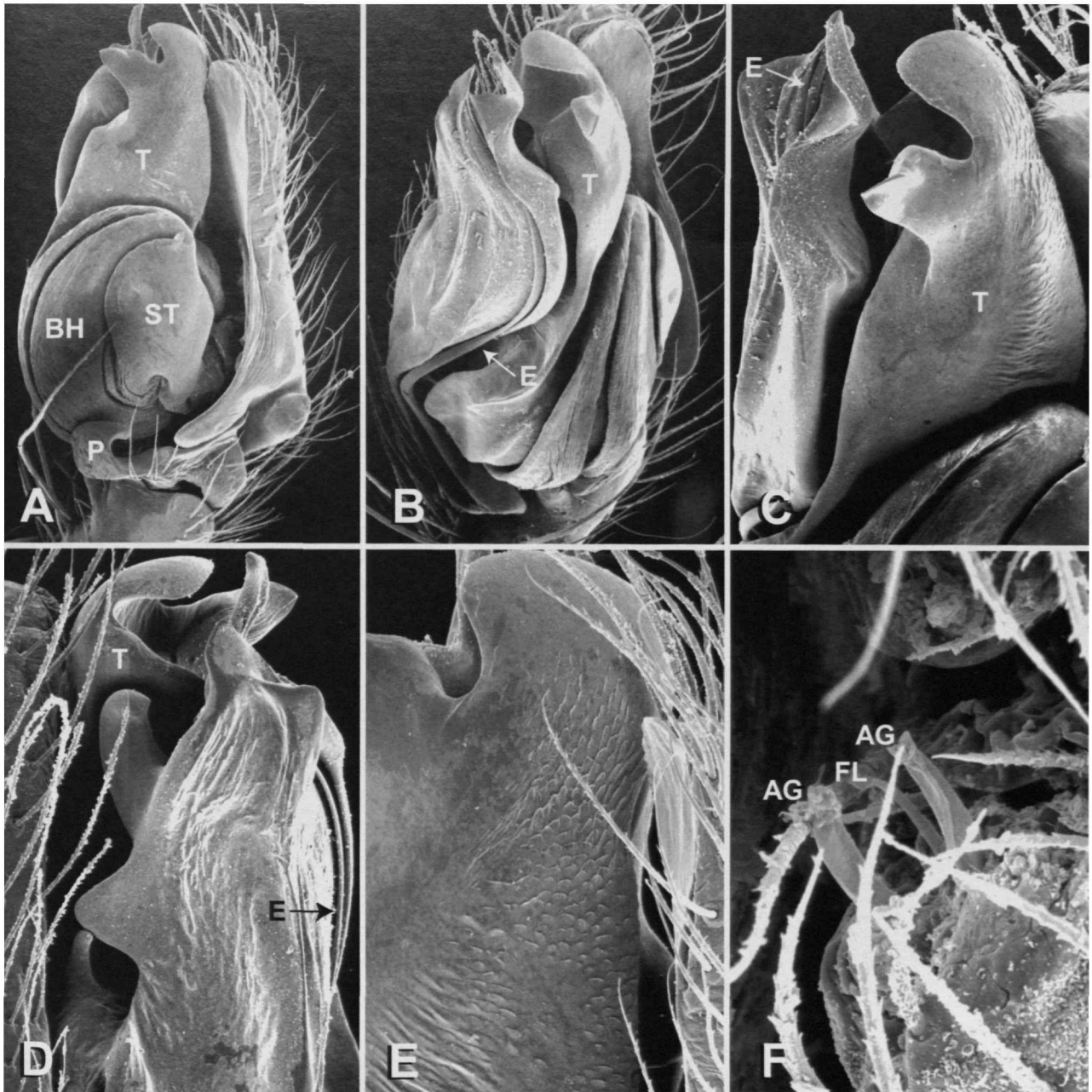


PLATE 12.—*Stemonyphantes blauveltae*: A–E, male palp (right); F, male PLS. A, ectal; B, ventral; C, tegulum and embolic division, ectoventral; D, mesoventral; E, tegular lobes; F, triad.

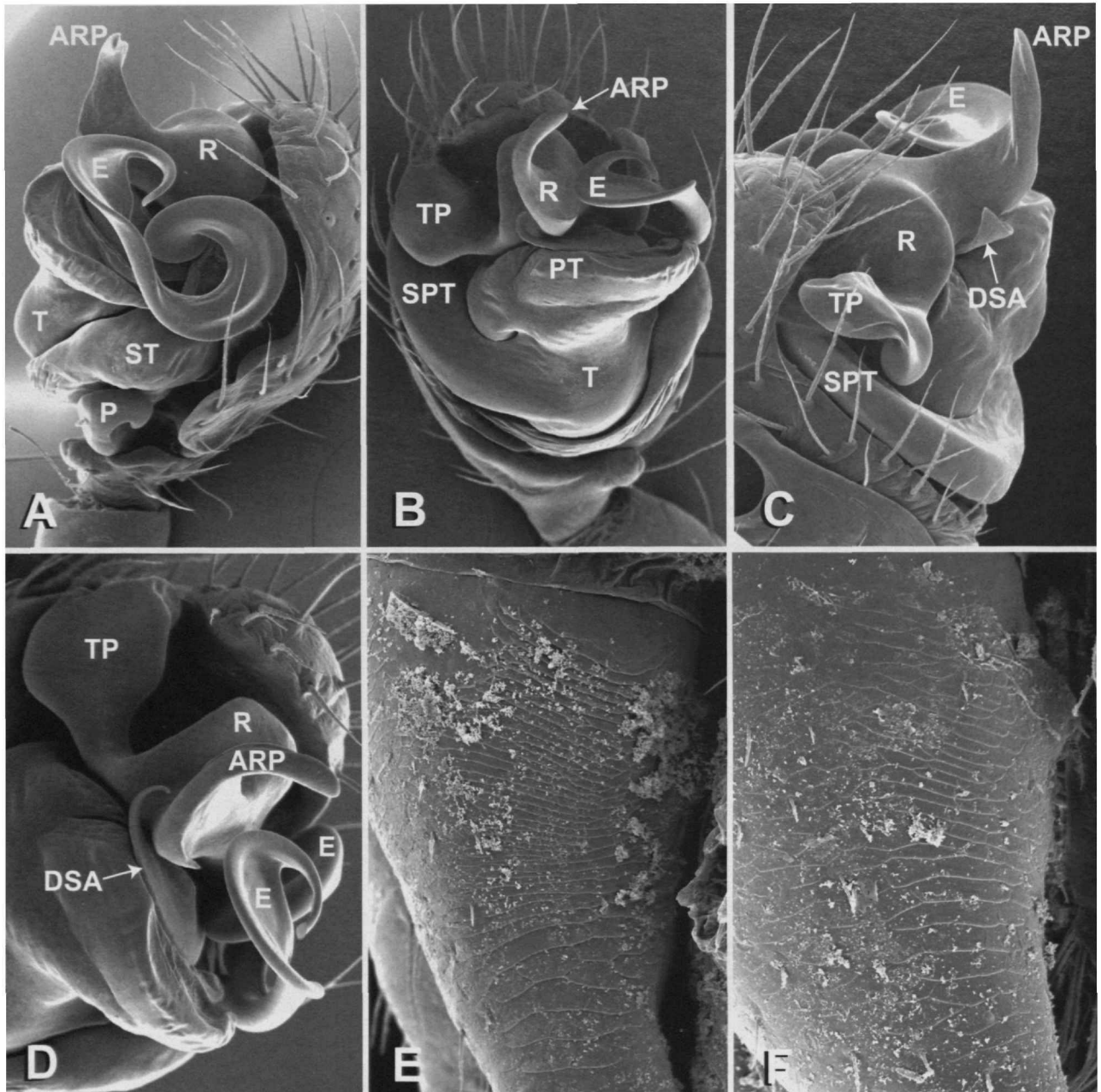


PLATE 13.—*Araeoncus humilis*: A–D, male palp (right); E, F, ectal side of chelicera. A, ectal; B, ventral; C, embolic division, mesal; D, mesoapical; E, male (right); F, female.



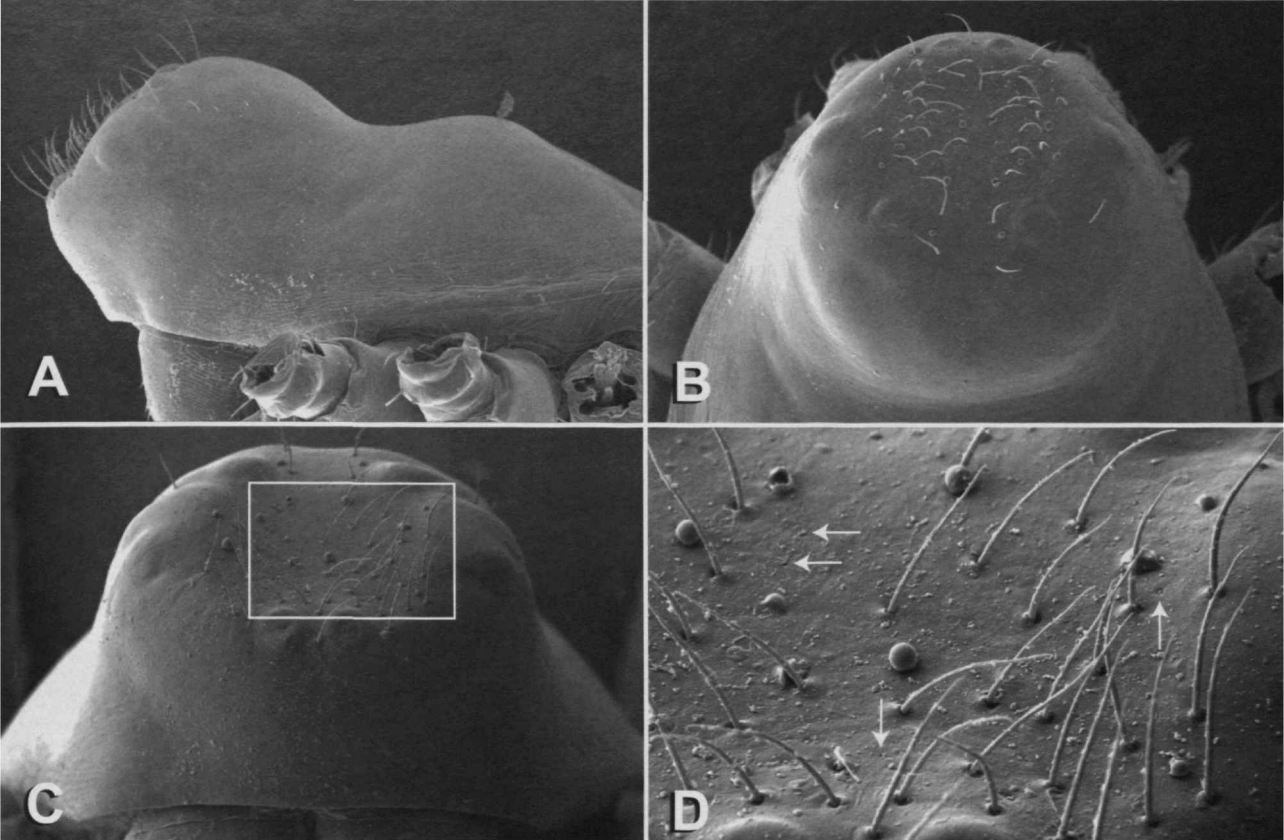


PLATE 14.—*Araeoncus humilis*: A–D, male prosoma. A, lateral; B, dorsal; C, frontal; D, detail of C.

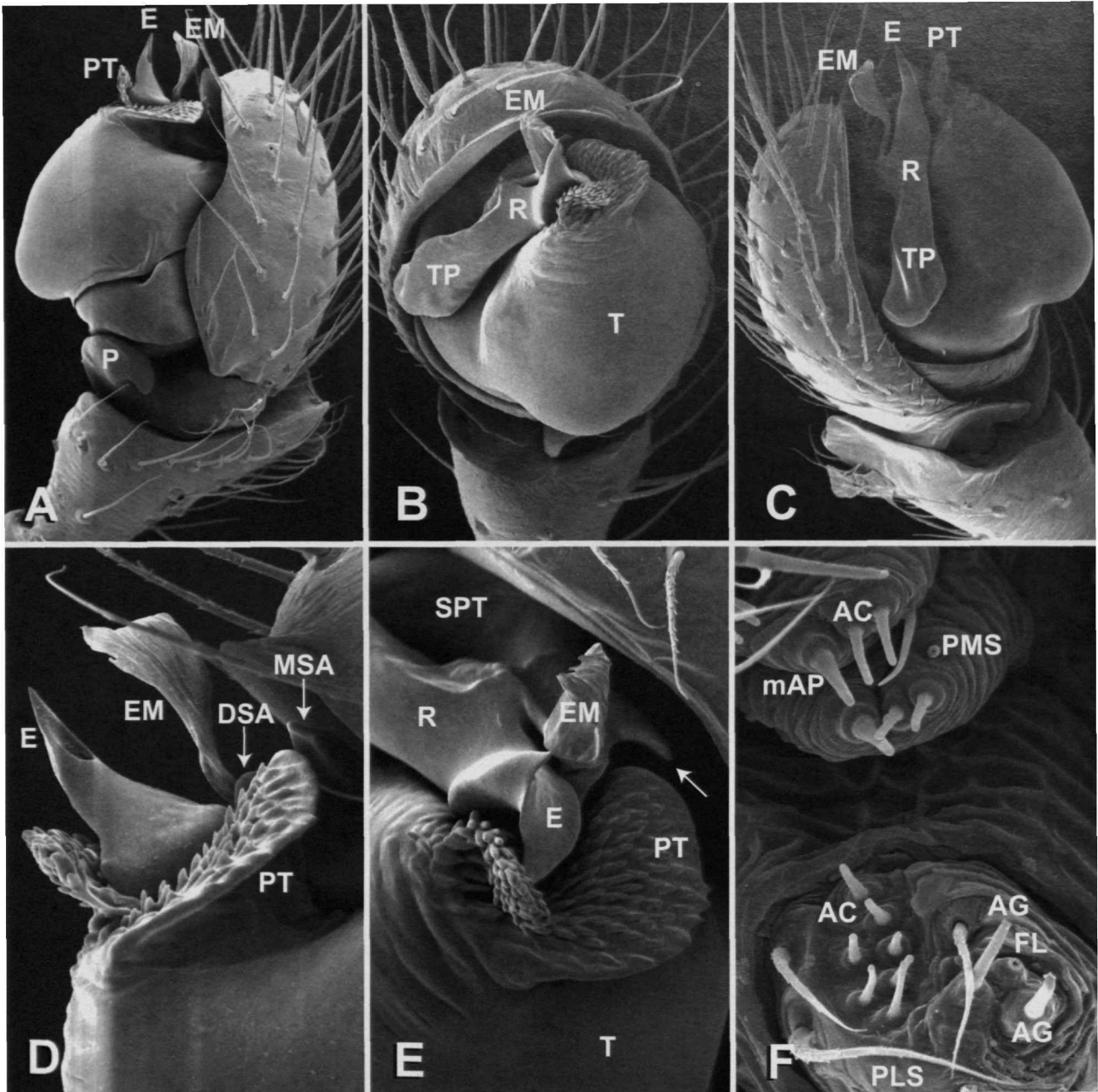


PLATE 15.—*Ceratinops inflatus*: A–E, male palp; F, male PMS and PLS. A, ectal; B, ventral; C, mesal; D, ectal; E, apical (arrow indicates MSA, DSA is only partially exposed between the E and the EM); F, triad (FL shaft is broken off).

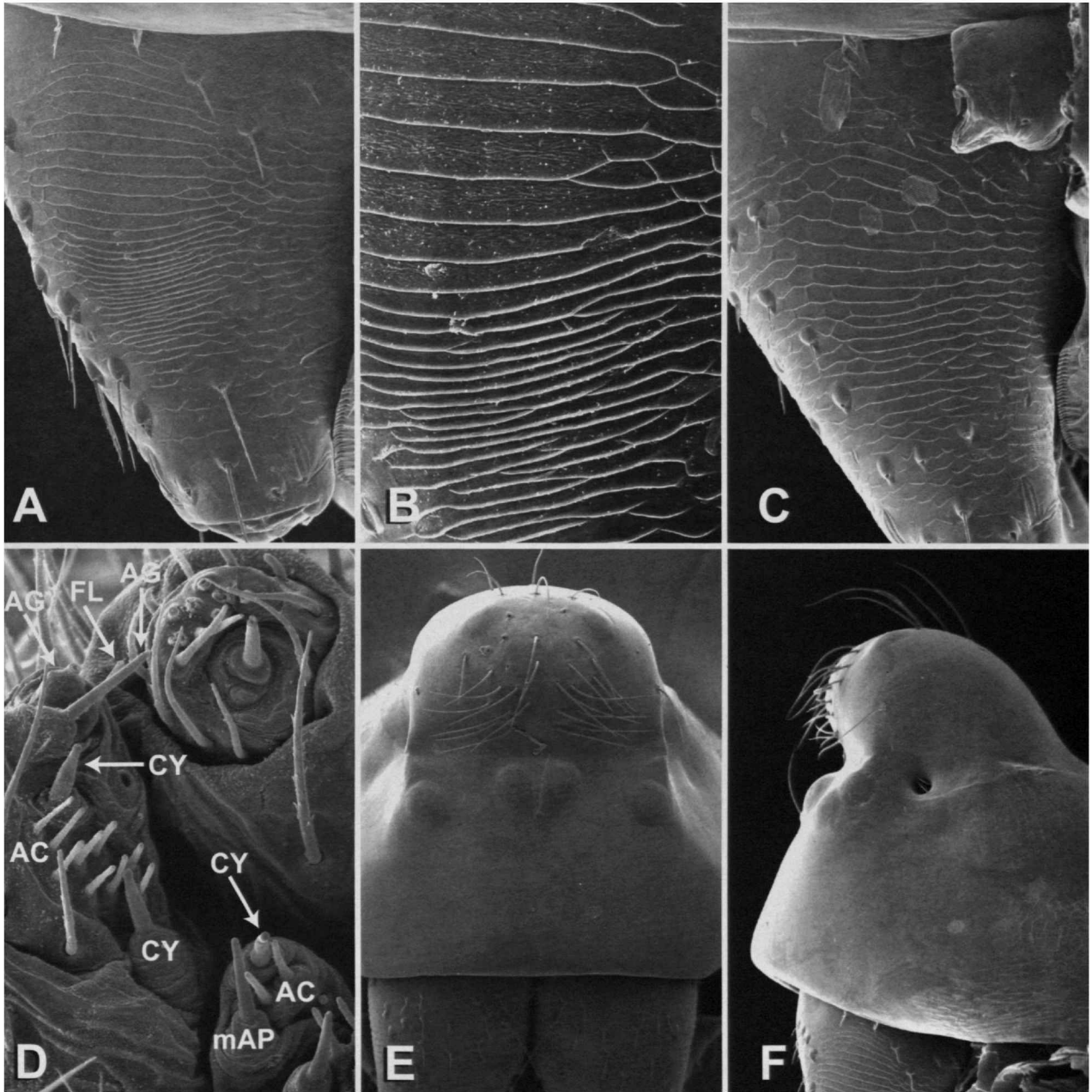


PLATE 16.—*Ceratinops inflatus*: A–C, ectal side of chelicera; D, female spinnerets (right); E,F, male prosoma. A, male; B, detail of A; C, female; D, arrows indicate CY (distal AG shaft is broken off); E, frontal; F, lateral.

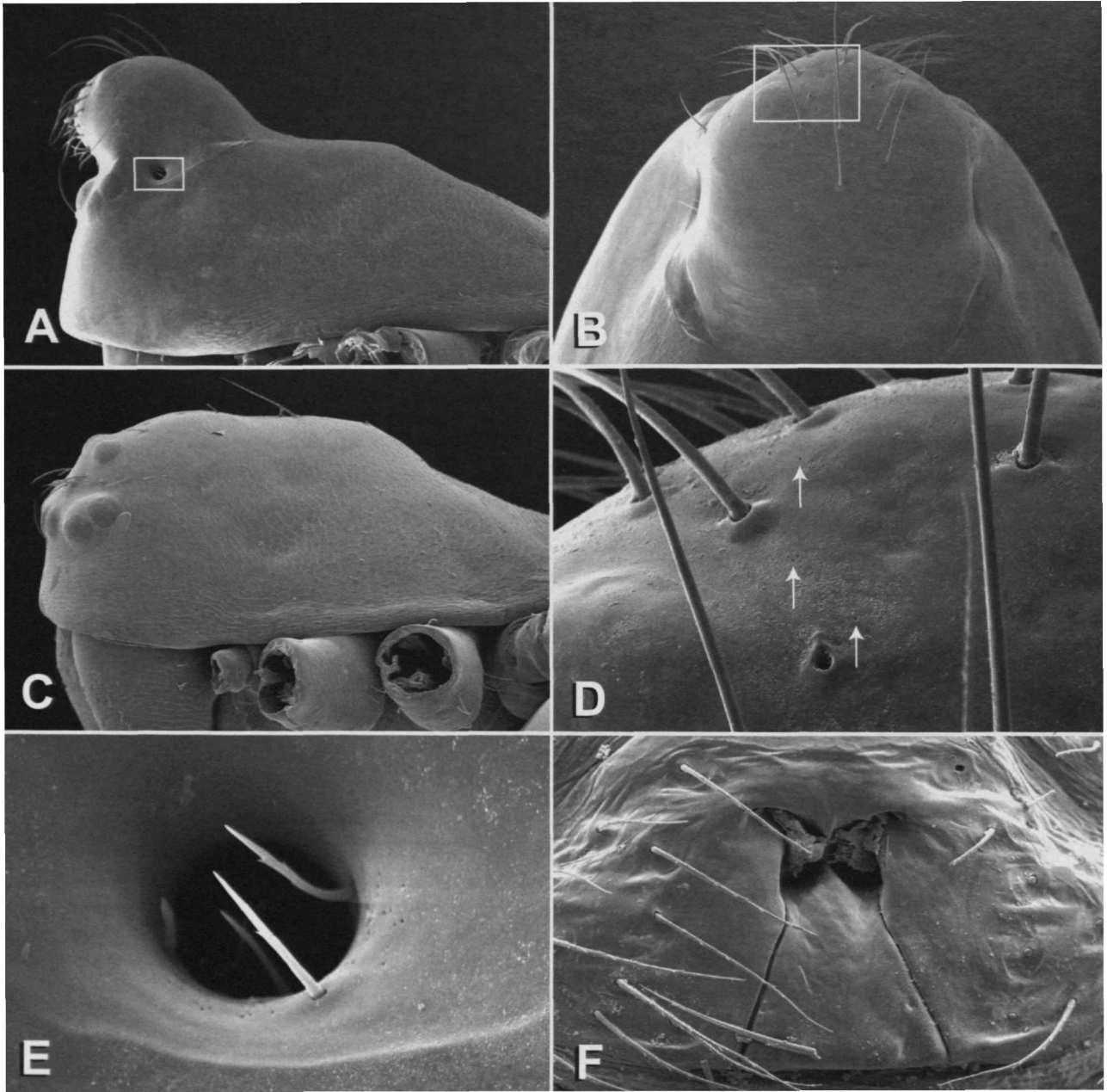


PLATE 17.—*Ceratinops inflatus*: A,B,D,E, male prosoma; C, female prosoma; F, epigynum. A, lateral; B, dorsal; C, lateral; D, detail of B; E, detail of A; F, ventral.

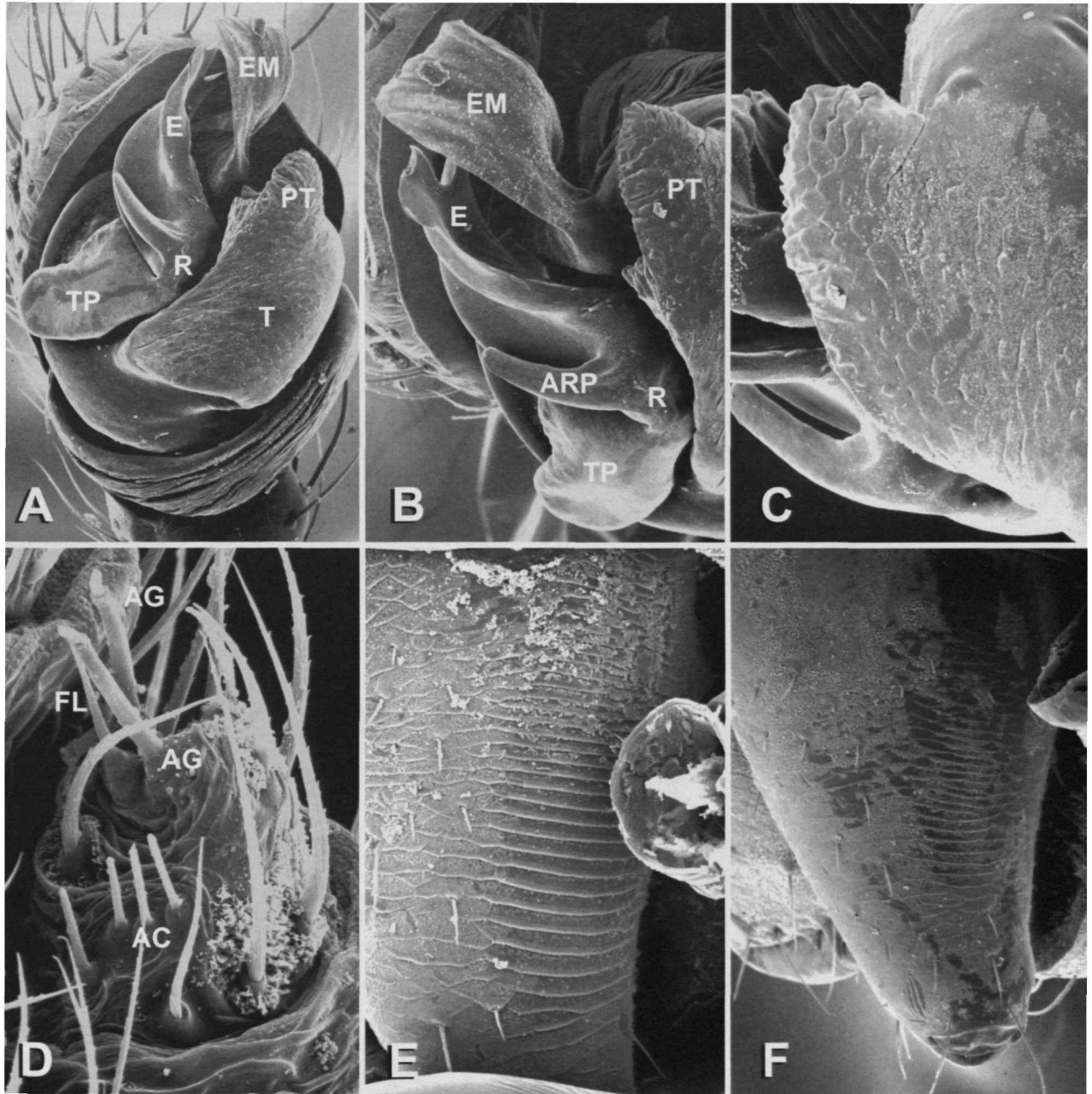


PLATE 18.—*Diplocentria bidentata*: A–C, male palp; D, male PLS; E,F, ectal side of chelicera. A, ventral; B, embolic division, ectal; C, protegulum, ectal; D, triad; E, male; F, female.

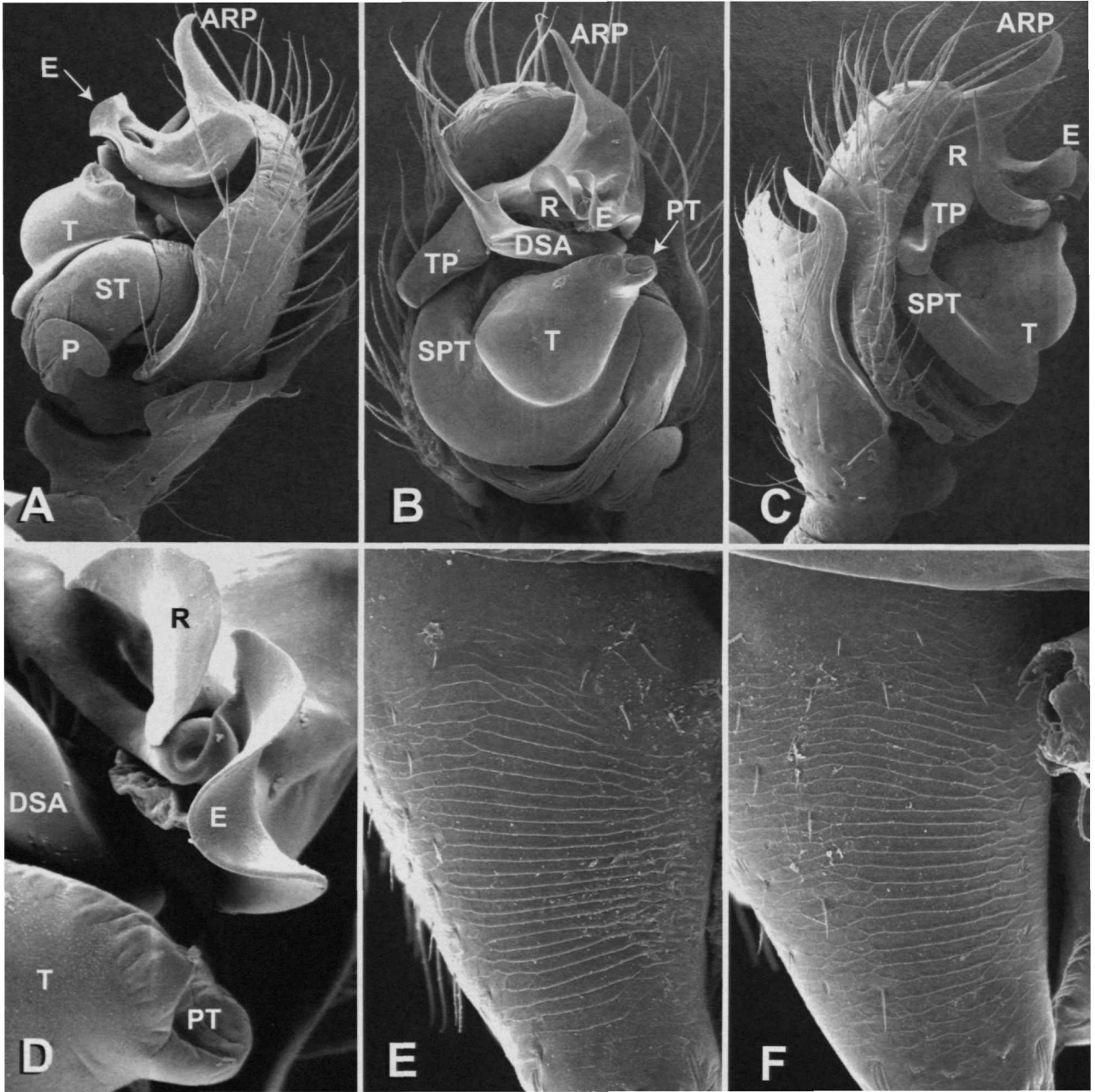


PLATE 19.—*Diplocephalus cristatus*: A–D, male palp; E, F, ectal side of chelicera. A, ectal; B, ventral; C, mesal; D, ventral; E, male; F, female.

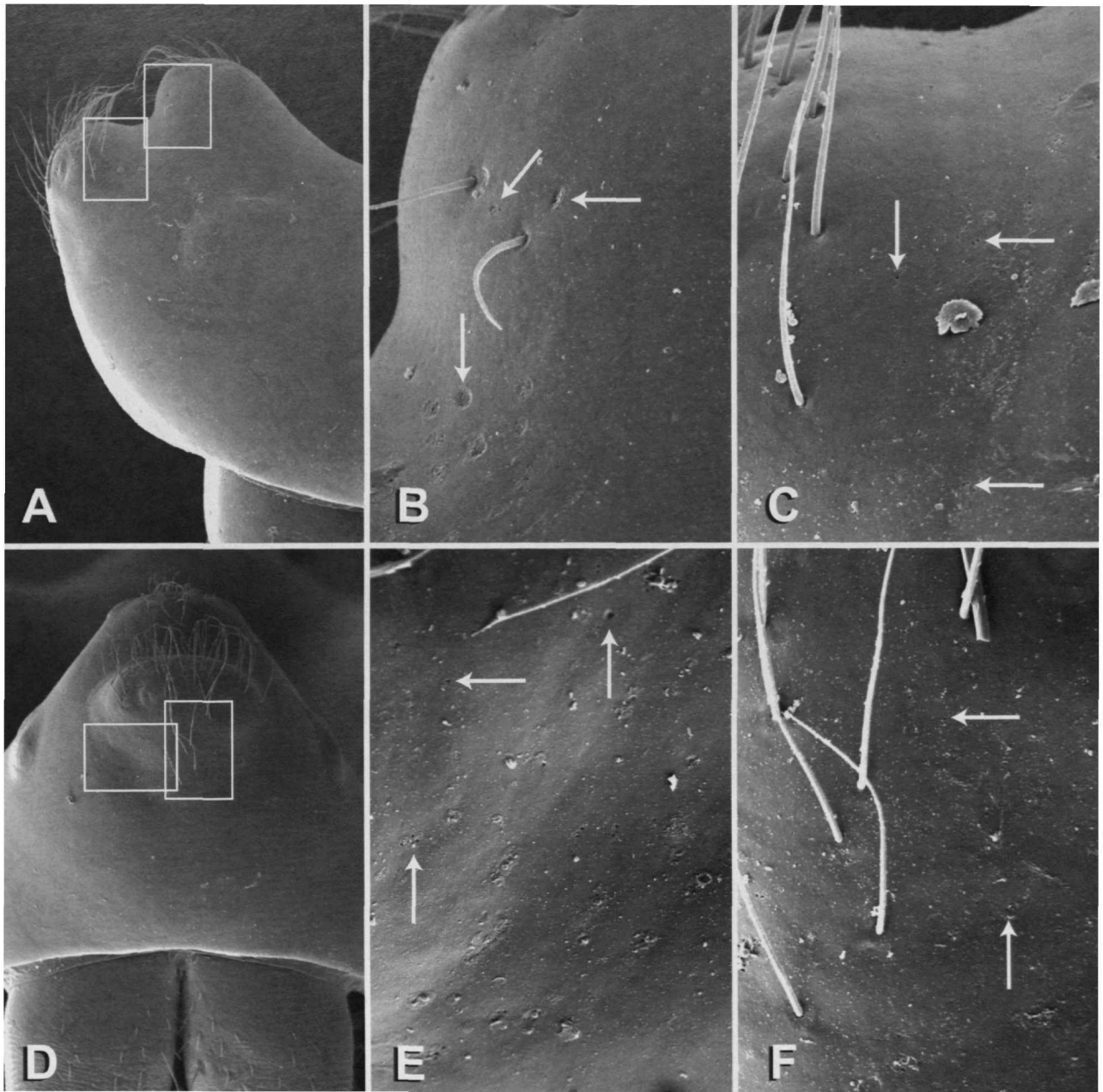


PLATE 20.—*Diplocephalus cristatus*: A-F, male prosoma. A, lateral; B,C, details of A; D, frontal; E,F, details of D.

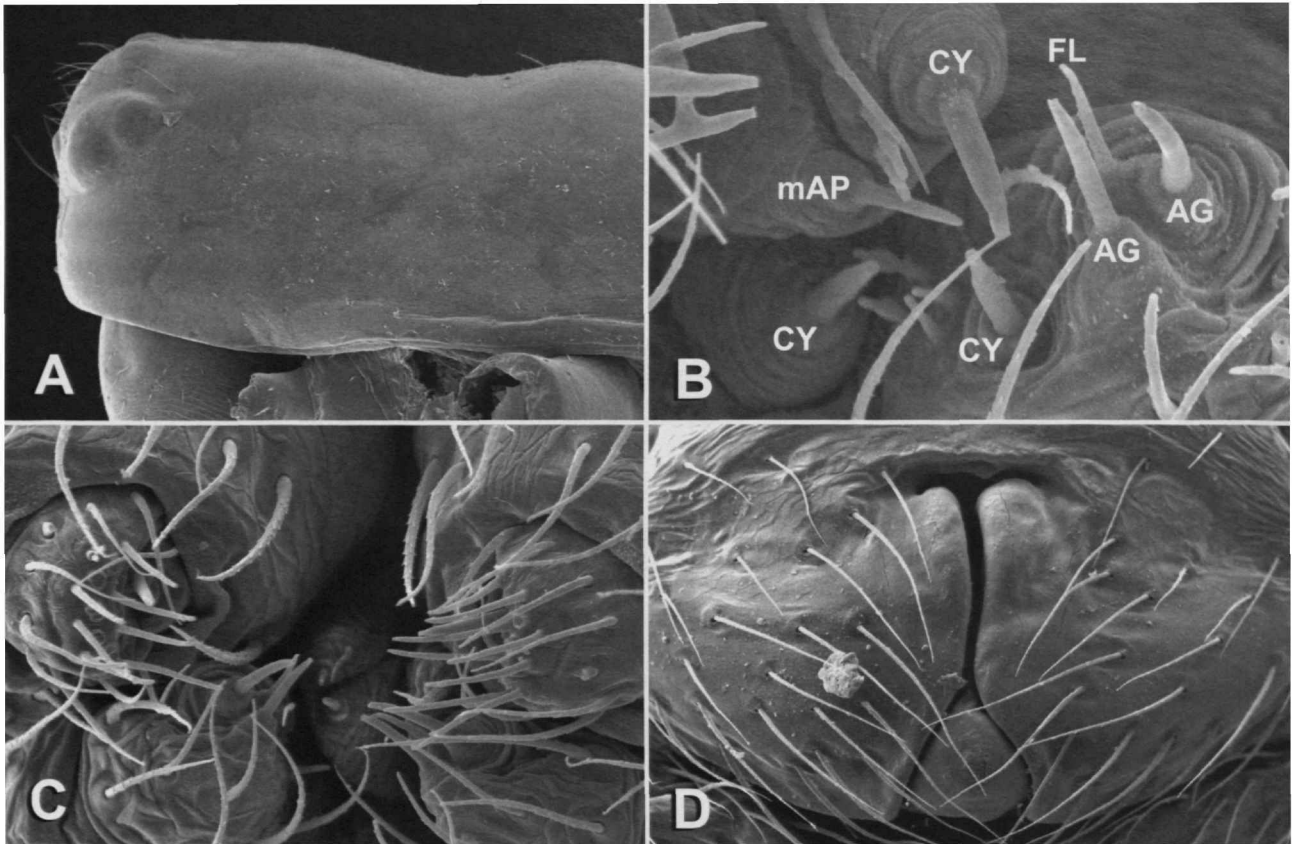


PLATE 21.—*Diplocephalus cristatus*: A, female prosoma, lateral; B, female PMS and PLS; C, male spinnerets; D, epigynum.



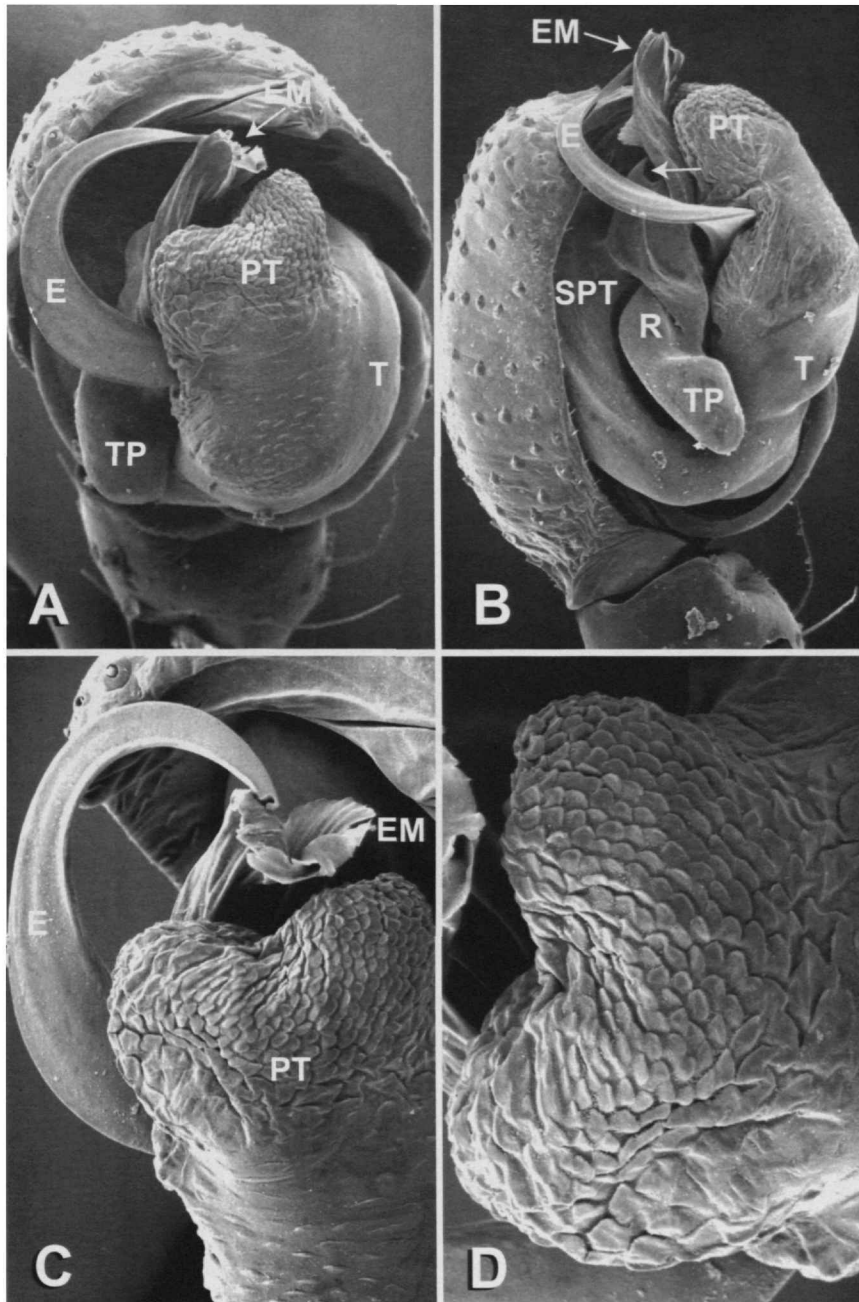


PLATE 22.—*Dismodicus decemoculatus*: A–D, male palp. A, ventral; B, mesal (arrow indicates MSA); C, mesoventral; D, protegulum, apicoventral.

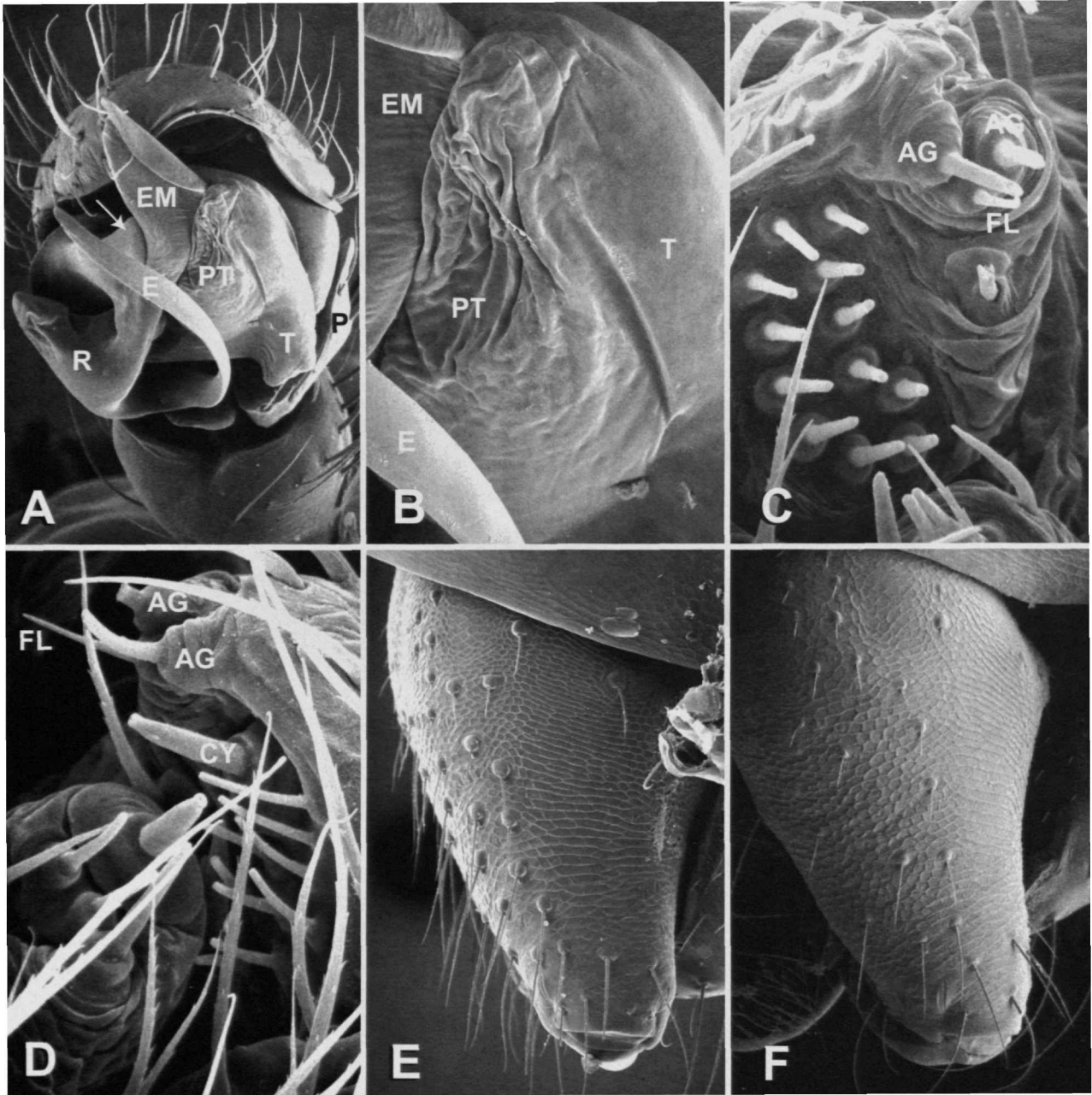


PLATE 23.—*Drepanotylus uncatus*: A,B, male palp; C,D, PLS; E,F, ectal side of chelicera. A, apicoventral (arrow indicates DSA); B, protegulum, apicoventral; C, male; D, female; E, male; F, female.

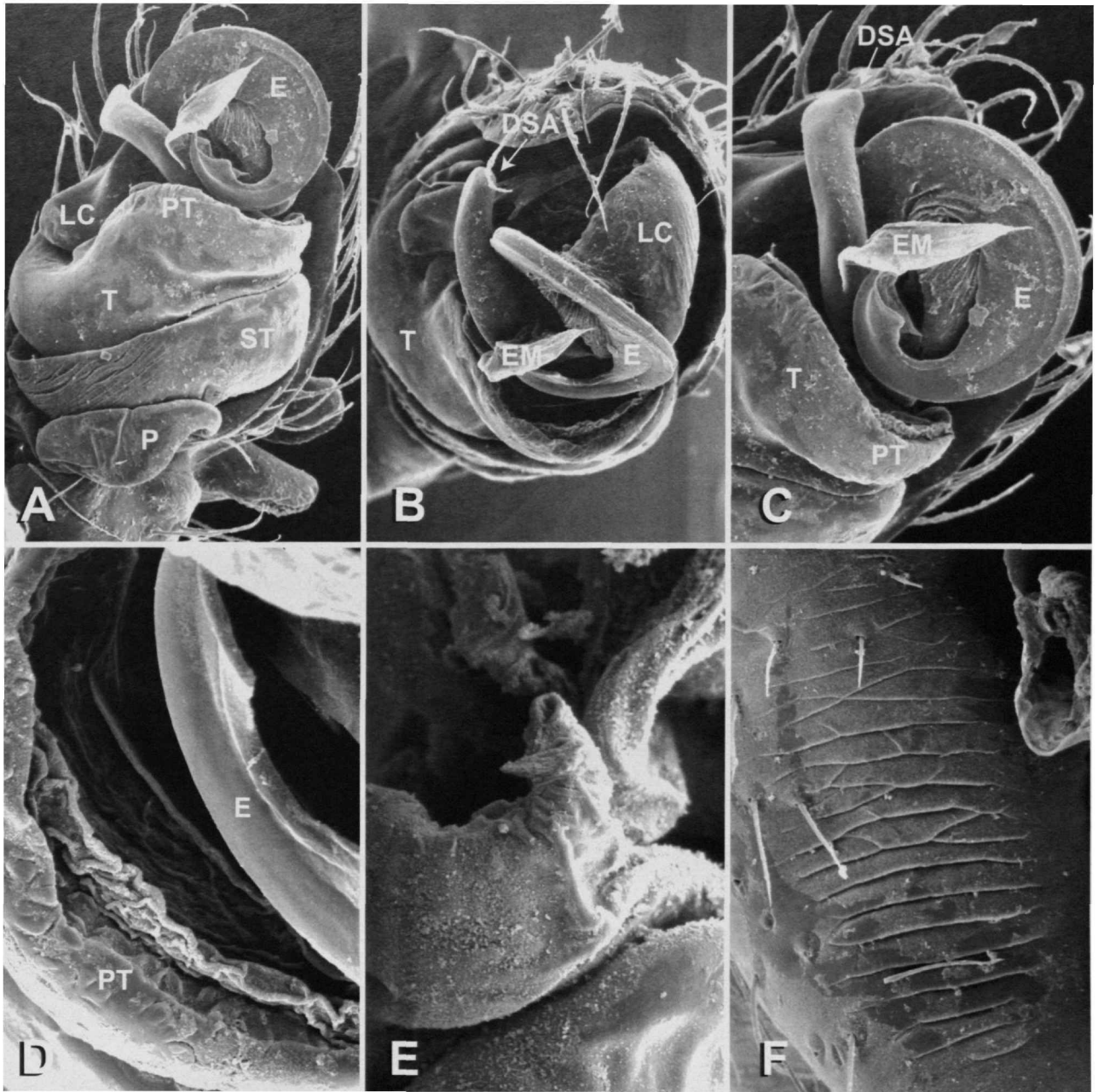


PLATE 24.—*Entelecara errata* (A–D,F): A, male palp, ectal; B, apical; C, embolic division, ventral; D, protegulum, apicoventral; F, ectal side of chelicera (right), male. *Entelecara acuminata*: E, protegulum (right), ectal.

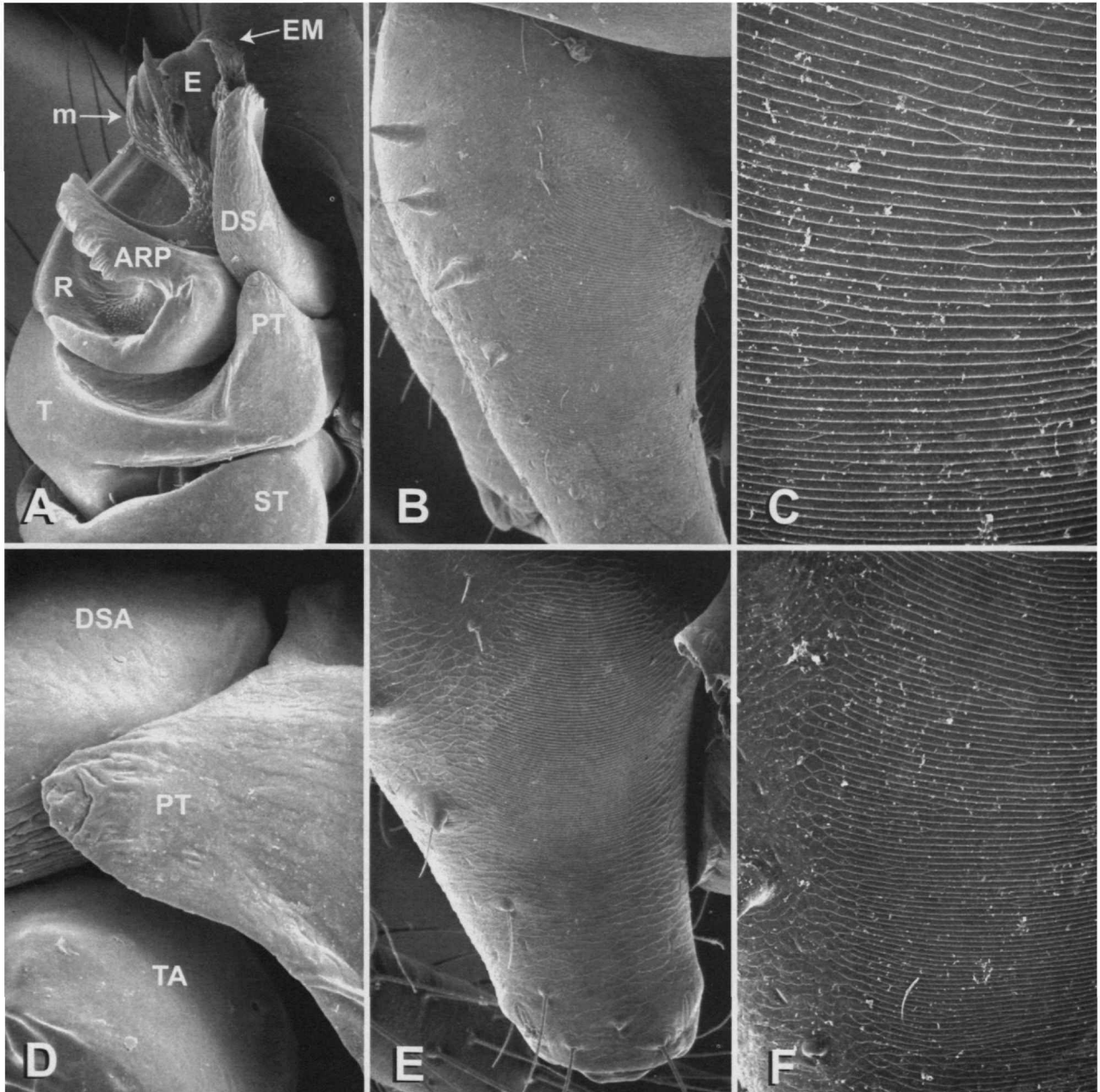


PLATE 25.—*Erigone psychrophila*: A,D, male palp; B,C,E,F, ectal side of chelicera. A, ventral; B, male; C, detail of B; D, protegulum, ventral; E, male; F, detail of E.

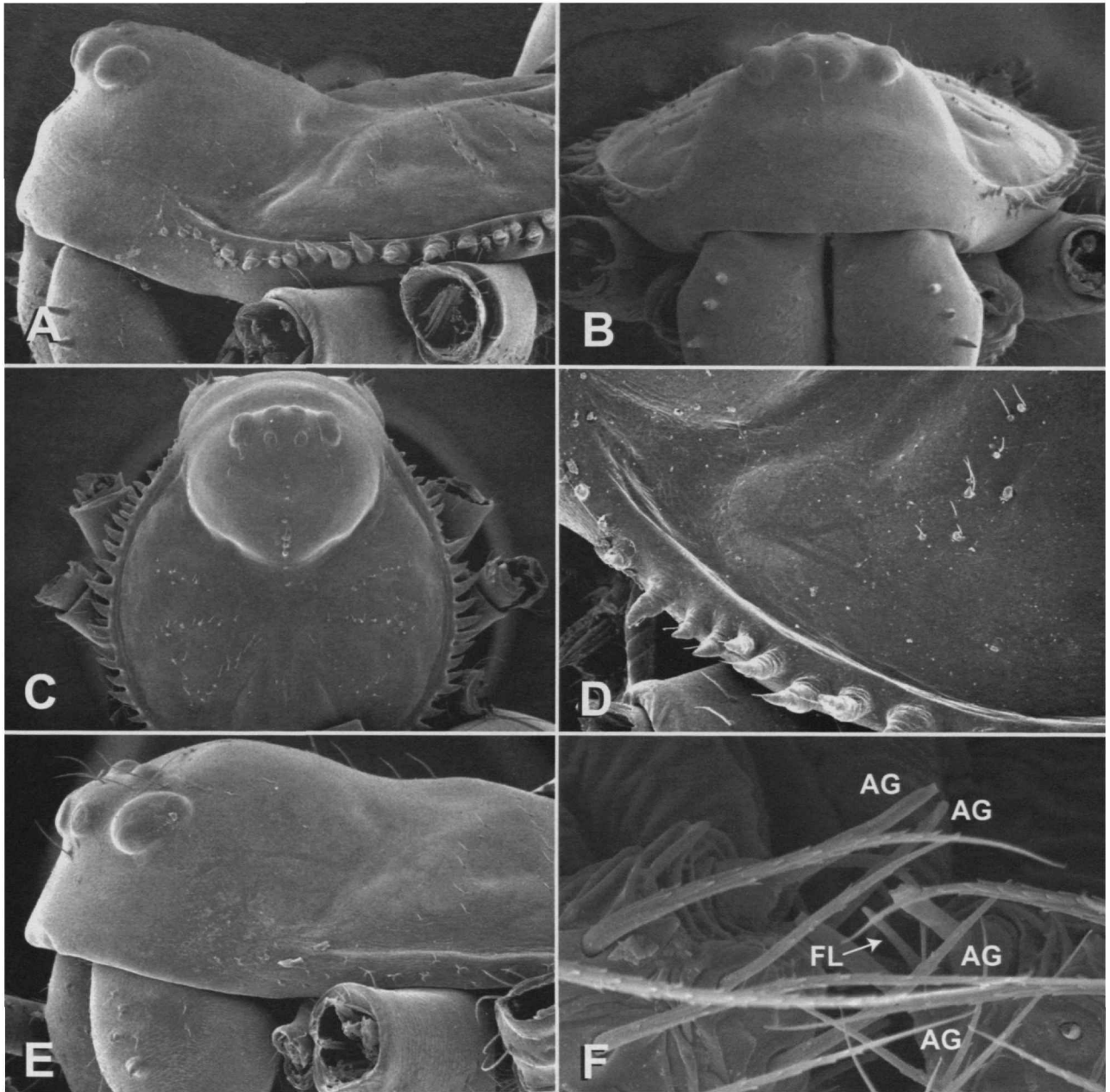


PLATE 26.—*Erigone psychrophila*: A–D, male prosoma; E, female prosoma; F, male PLS. A, lateral; B, frontal; C, dorsal; D, dorsolateral; E, lateral; F, detail of triad.

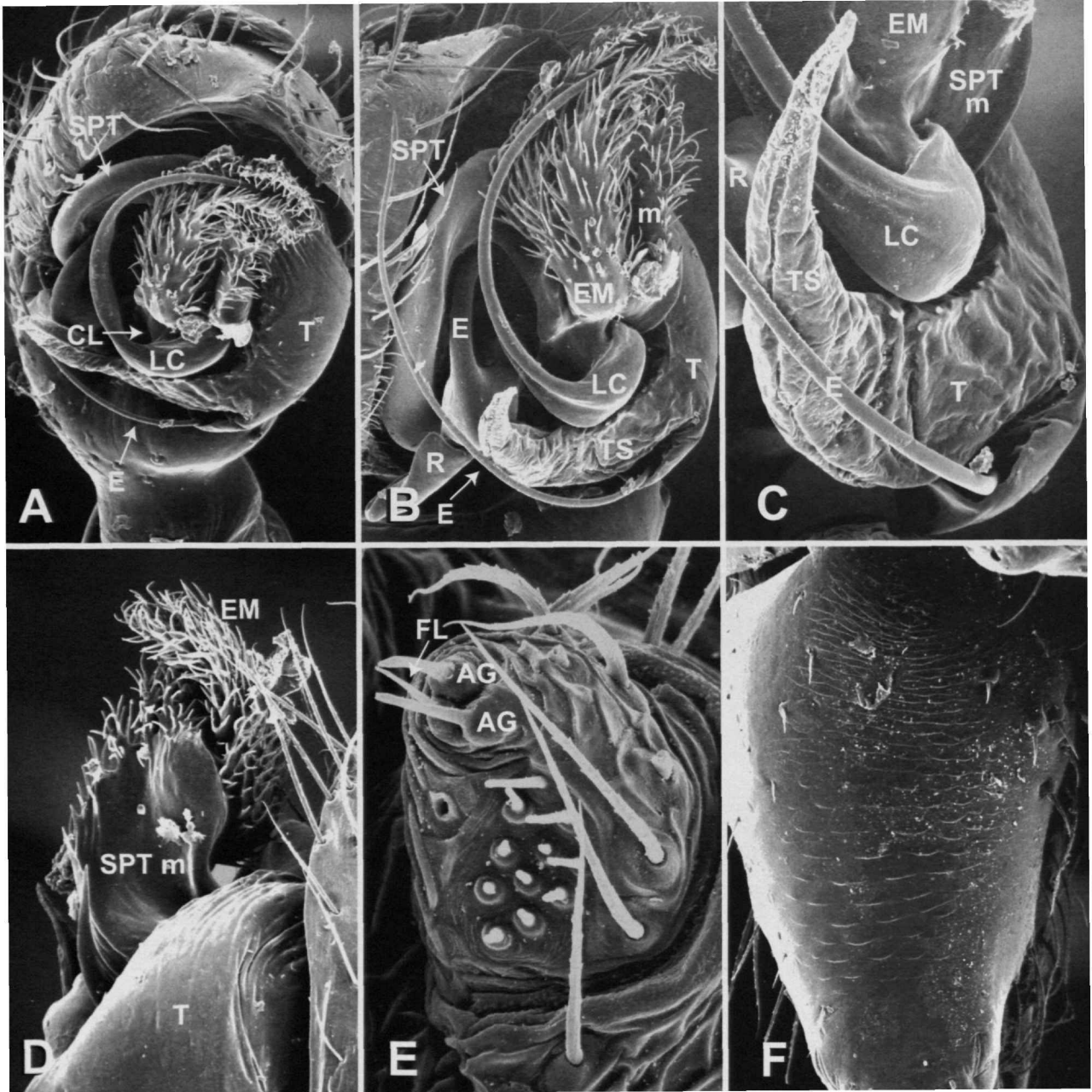


PLATE 27.—*Gonatium rubens*: A–D, male palp; E, male PLS; F, ectal side of chelicera (right). A, ventral; B, mesal; C, tegular sac; D, supratregular membrane and EM; E, detail of PLS; F, male.

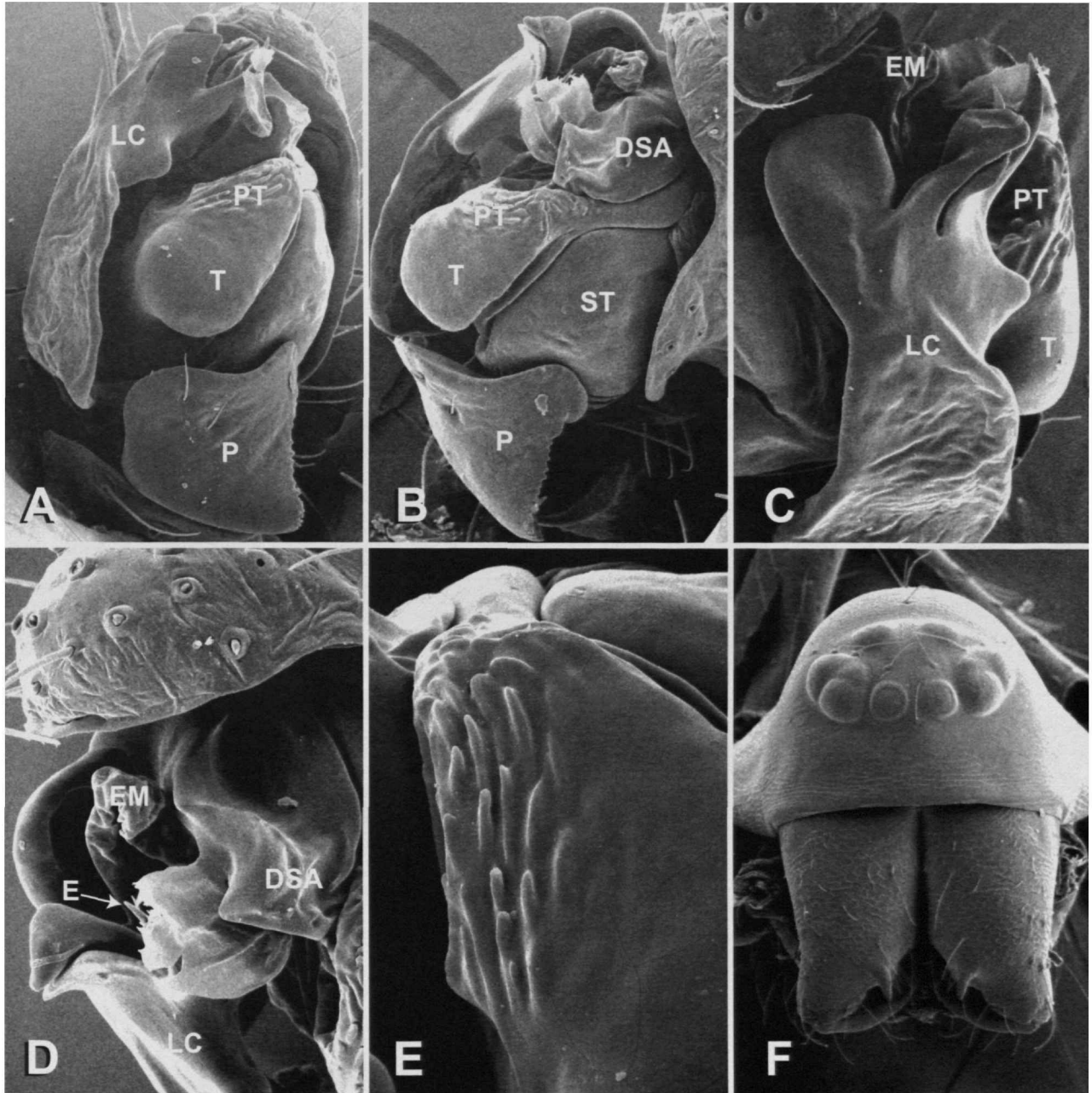


PLATE 28.—*Gongylidiellum vivum*: A–E, male palp (right); F, male prosoma. A, ventral; B, ectoapical; C, mesal; D, apical; E, protegulum, ventral; F, anterior.

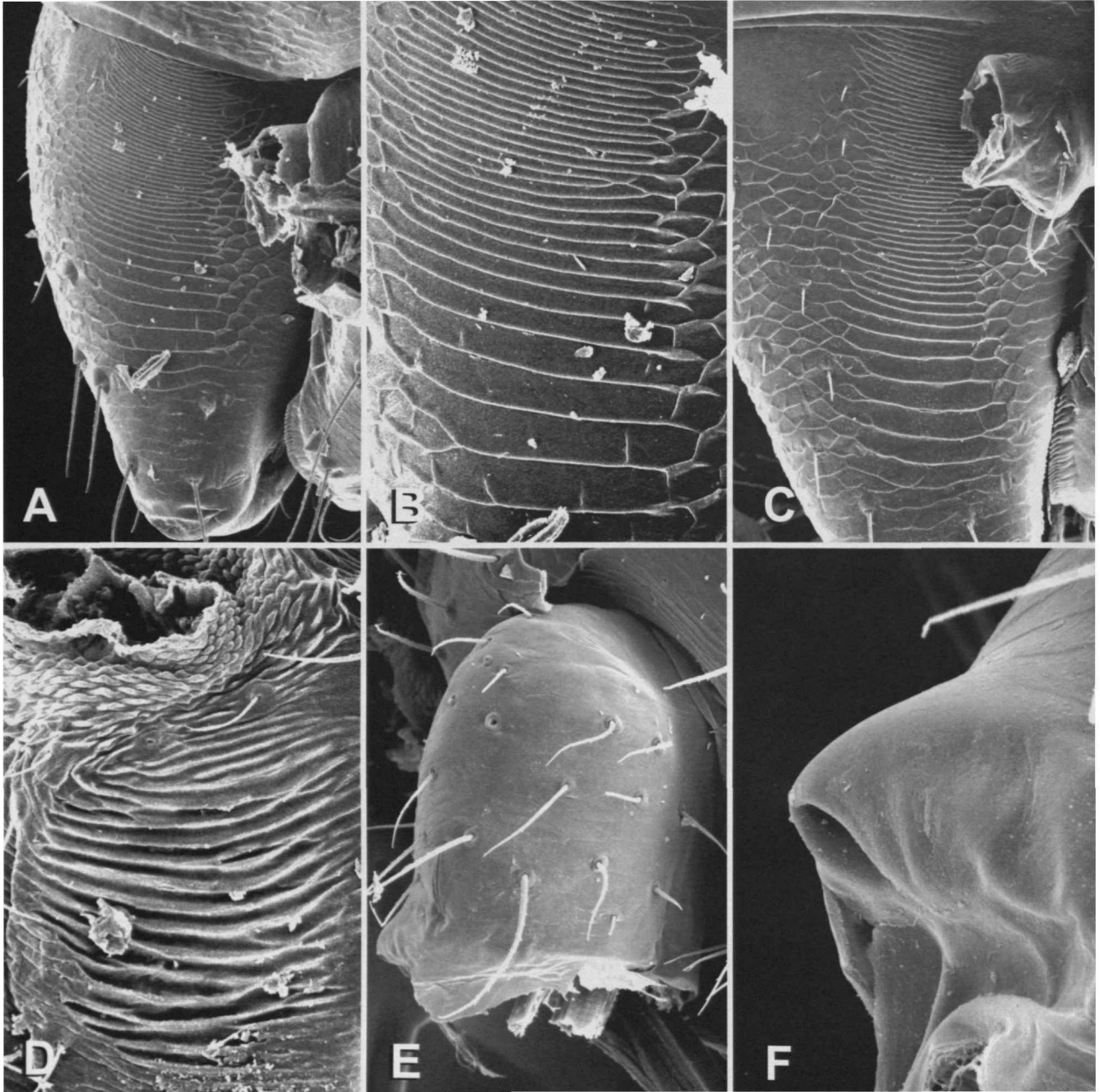


PLATE 29.—*Gongyldiellum vivum*: A–C, ectal side of chelicera; D,E, coxa IV-booklung stridulatory organ. A, male; B, detail of A; C, female; D, booklung cover, male; E, coxa IV, female; F, detail of coxal apophysis.



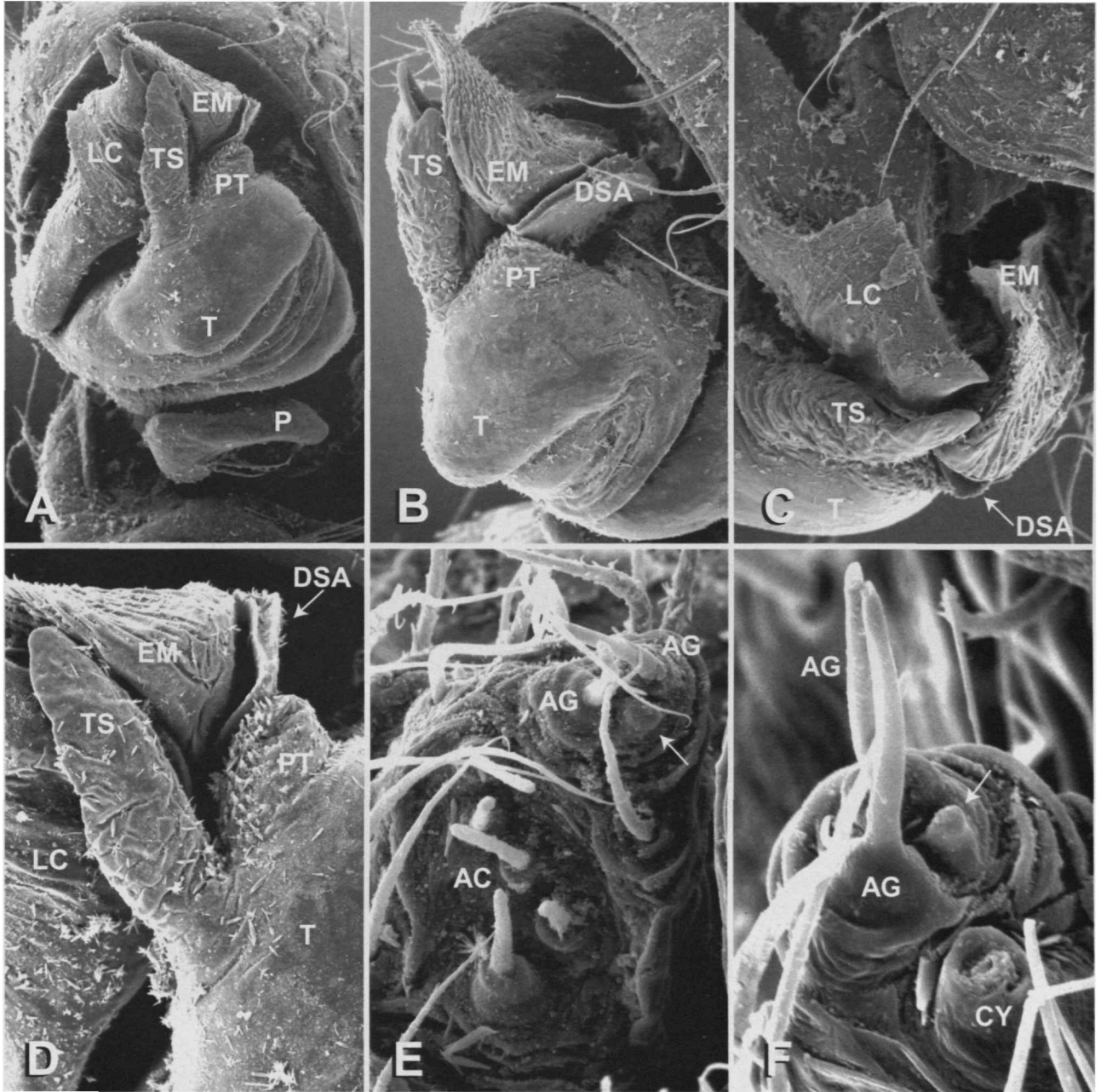


PLATE 30.—*Gongylidium rufipes*: A–D, male palp; E,F, PLS. A, ventral; B, ectoapical; C, apical; D, ventral; E, male (arrow indicates FL nubbin); F, female (CY spigot shaft is broken off).

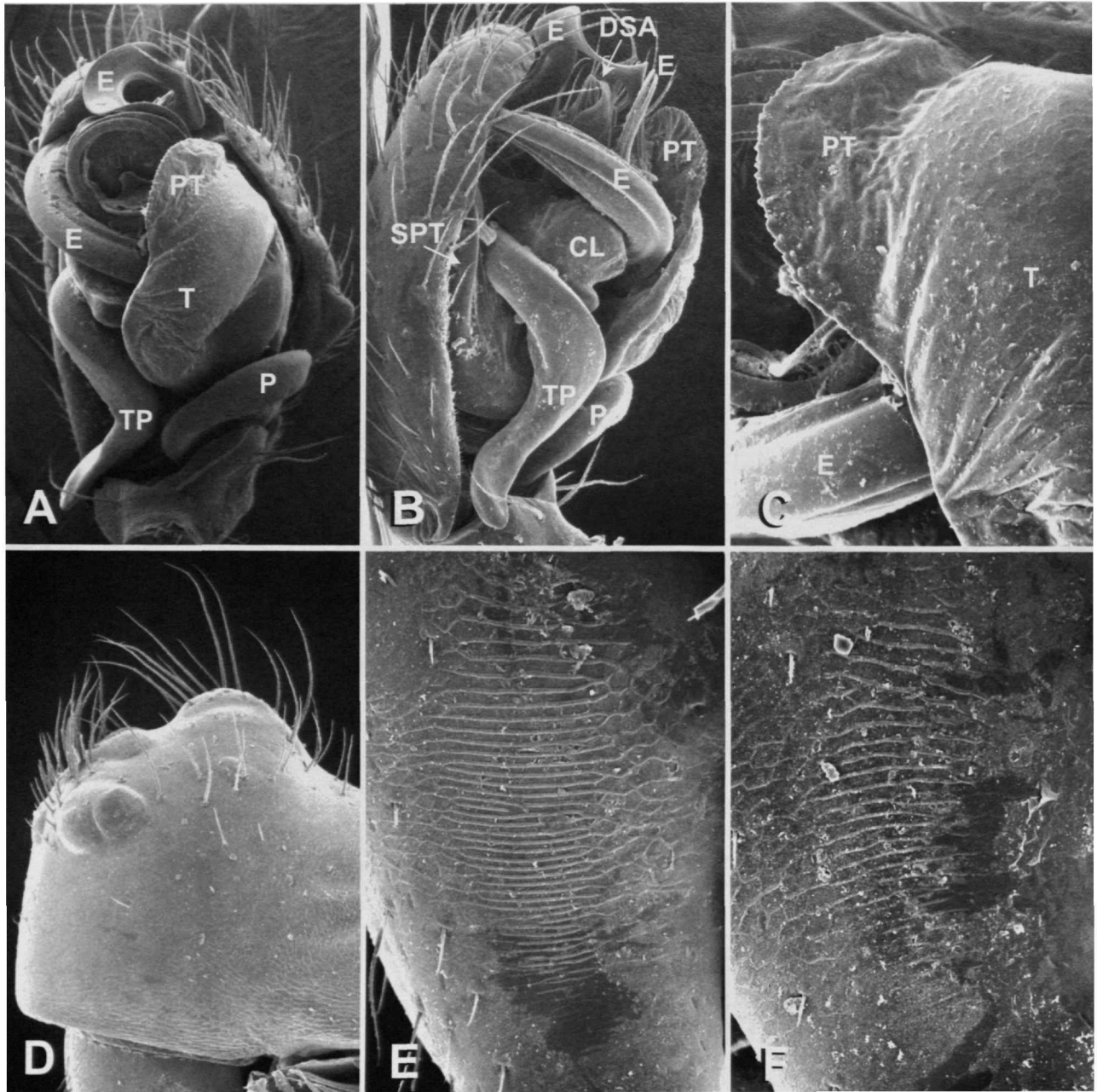


PLATE 31.—*Grammonota pictilis*: A–C, male palp; D, male prosoma; E, F, ectal side of chelicera. A, ventral; B, mesal; C, protegulum, ventral; D, lateral; E, male; F, female.

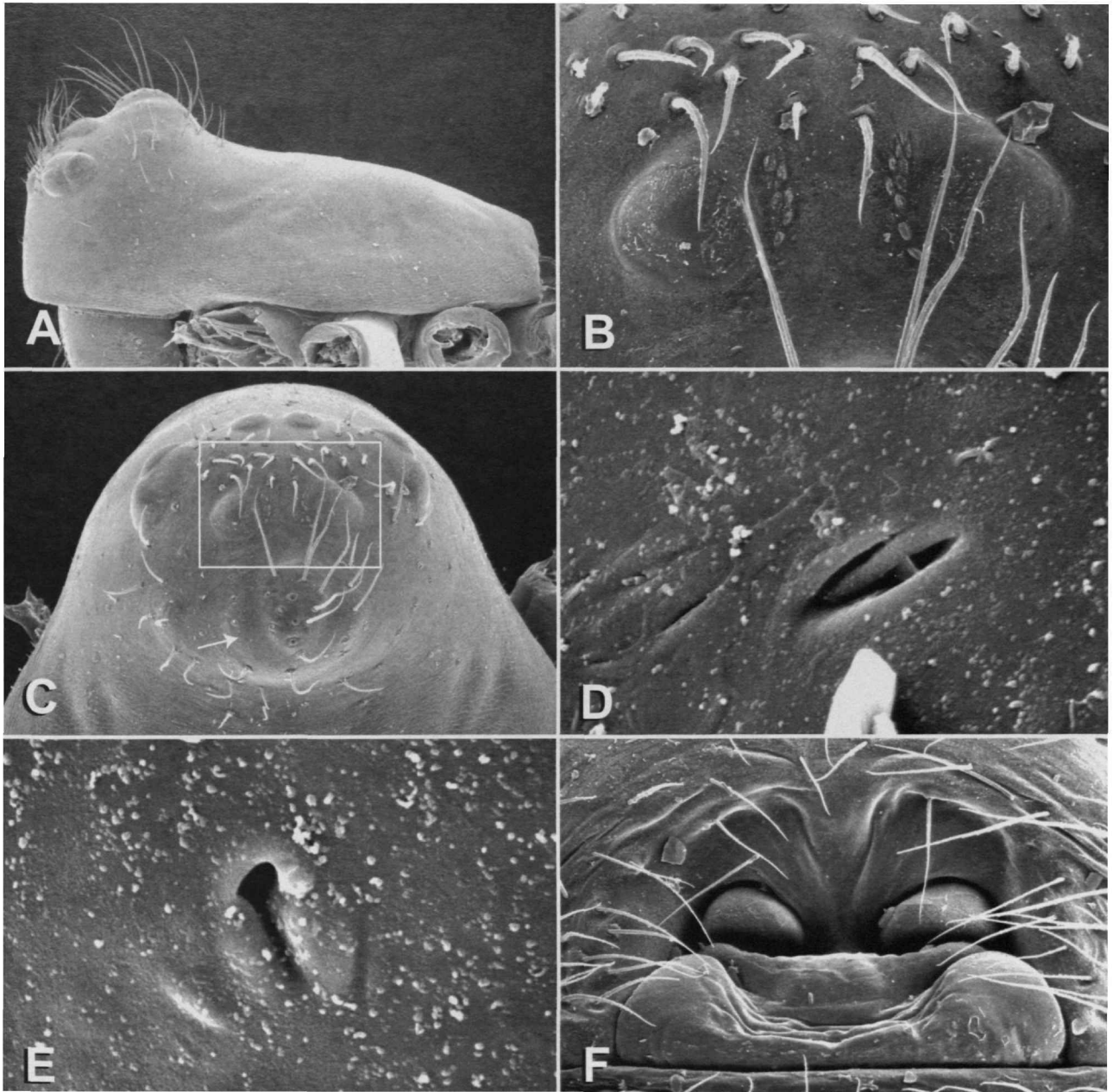


PLATE 32.—*Grammonota pictilis*: A–E, male prosoma; F, epigynum. A, lateral; B, PME, dorsal; C, cephalic region, dorsal (arrows indicate location of pores depicted in D and E); D, cuticular pore; E, cuticular pore; F, ventral.

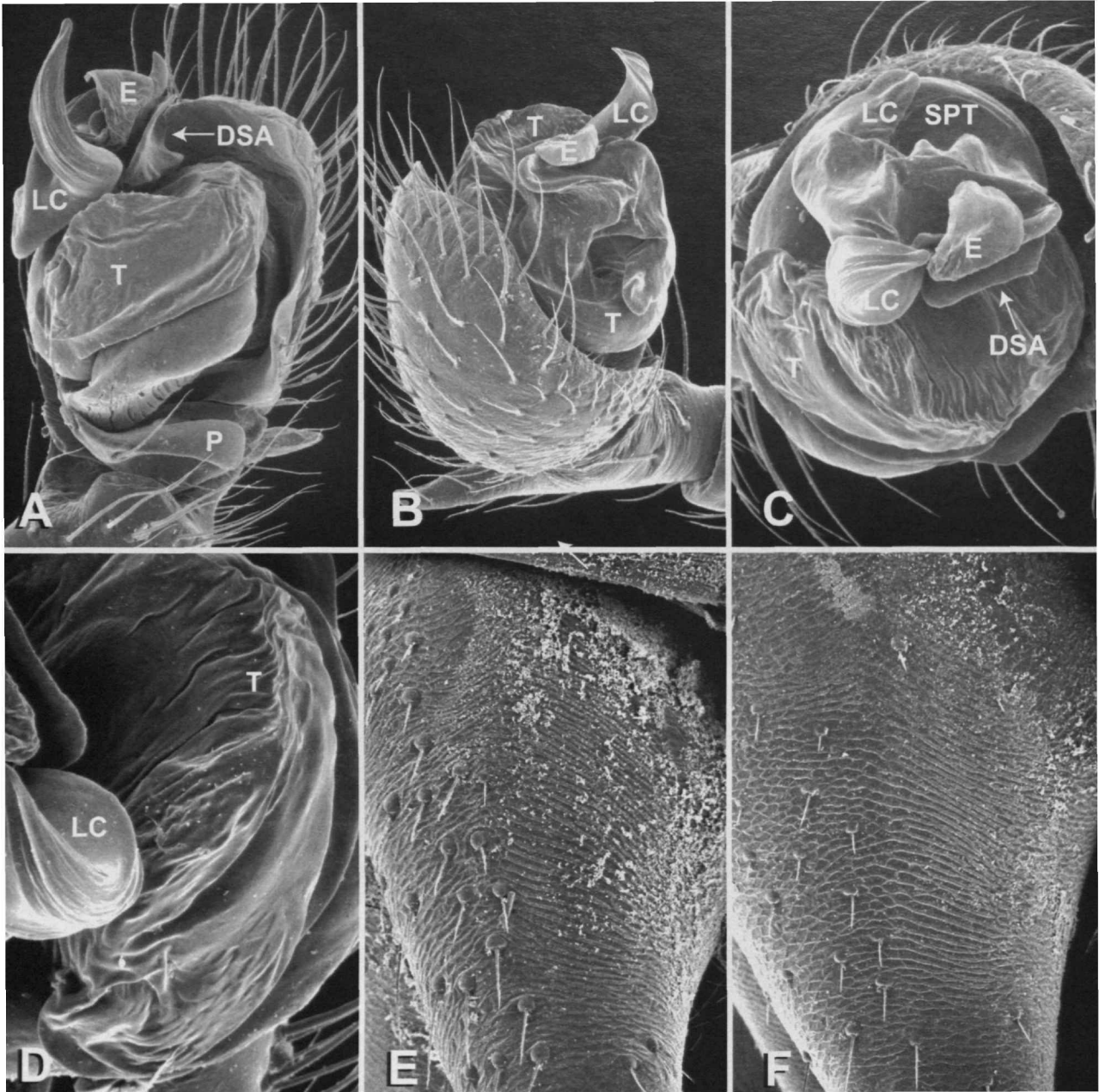


PLATE 33.—*Hilaira excisa*: A–D, male palp; E,F, ectal side of chelicera. A, ectoventral; B, mesoapical; C, apical; D, tegulum, apical; E, male (right); F, female.

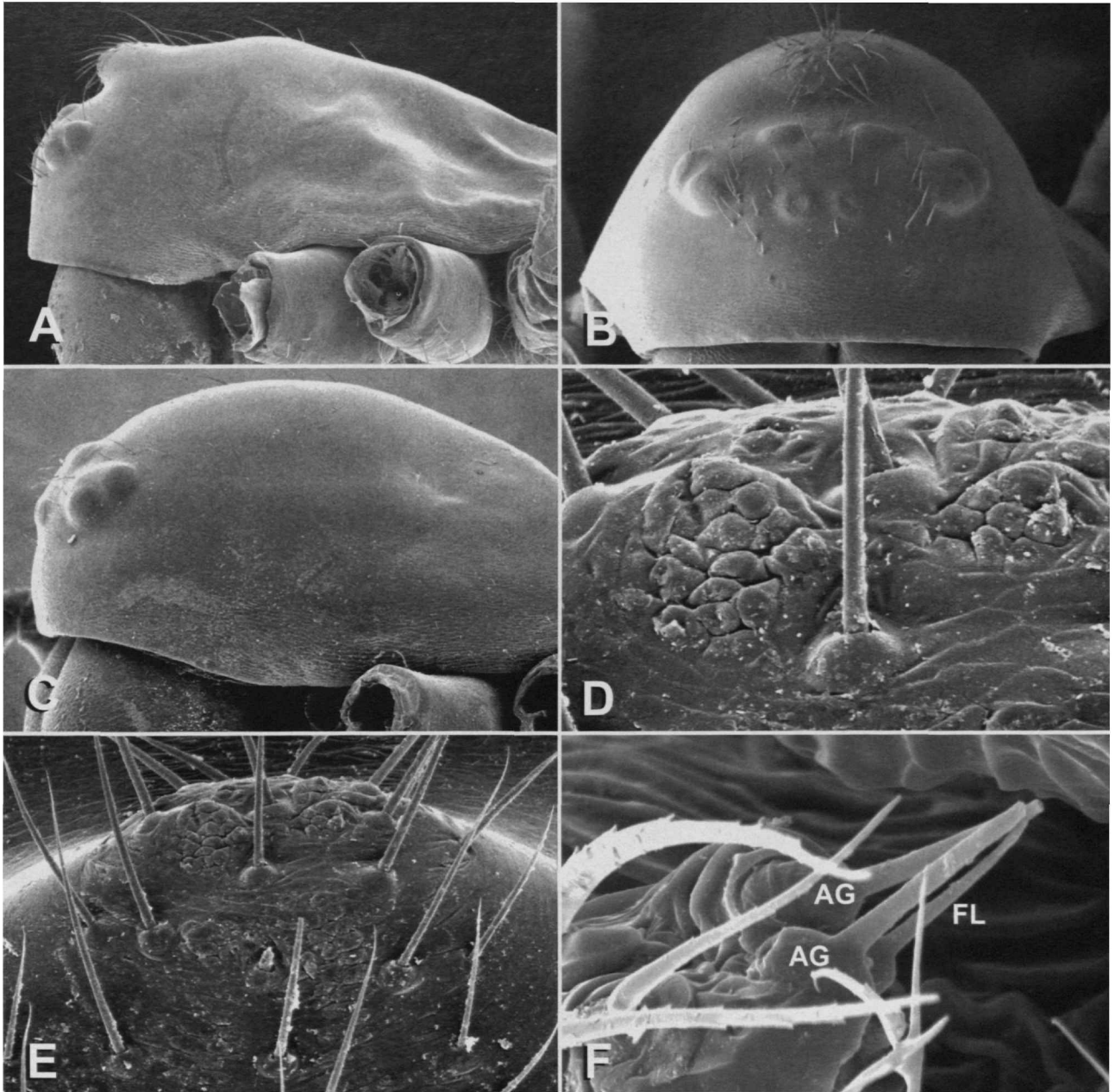


PLATE 34.—*Hilaira excisa*: A–E, prosoma; F, male PLS. A, male, lateral; B, male, frontal; C, female, lateral; D, detail of male frontal cephalic lobe; E, male frontal cephalic lobe; F, detail of PLS.

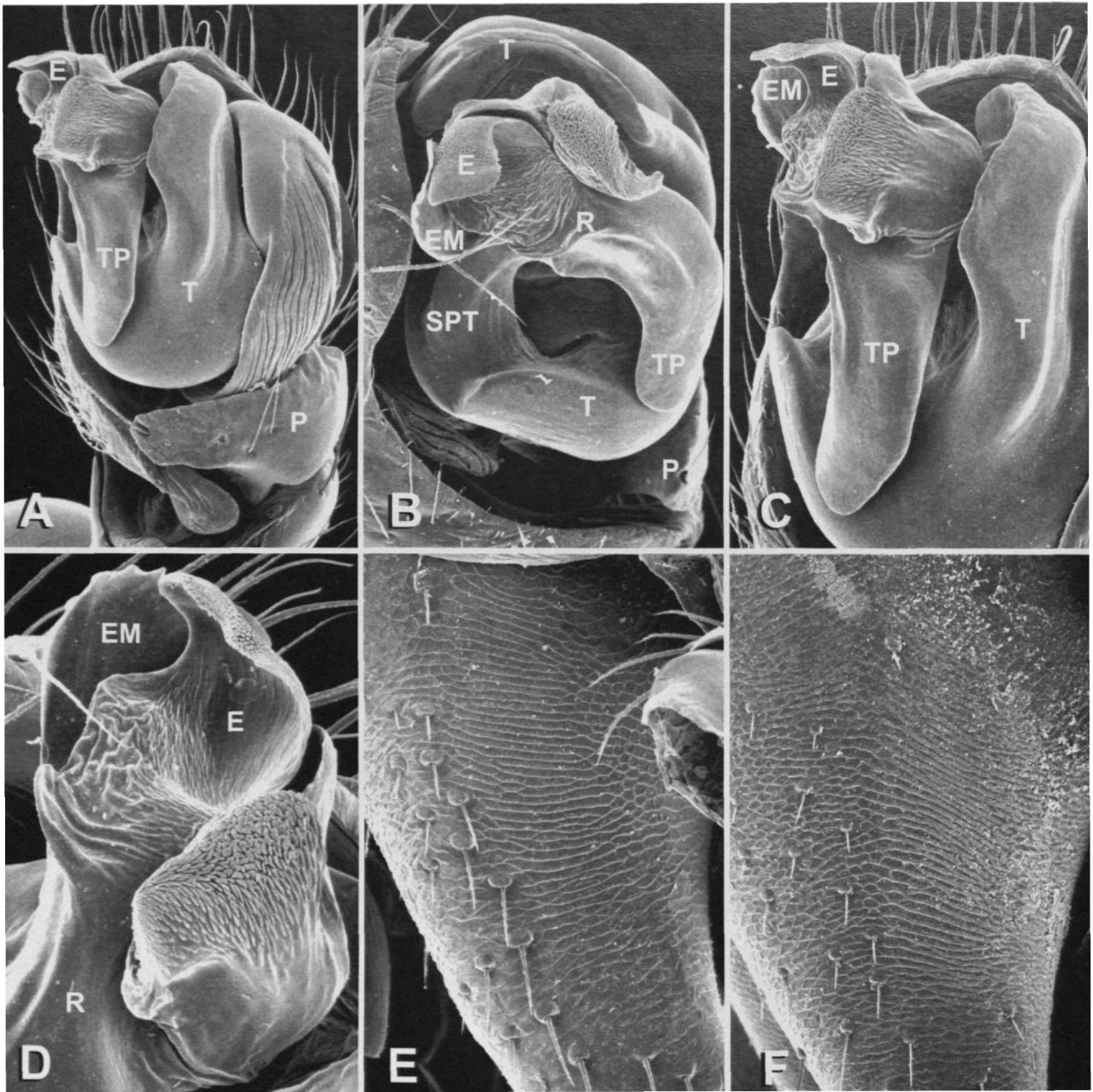


PLATE 35.—*Hilaira vexatrix*: A–D, male palp; E, F, ectal side of chelicera. A, ventral; B, mesoapical; C, embolic division, ventral; D, embolus, apical; E, male; F, female.

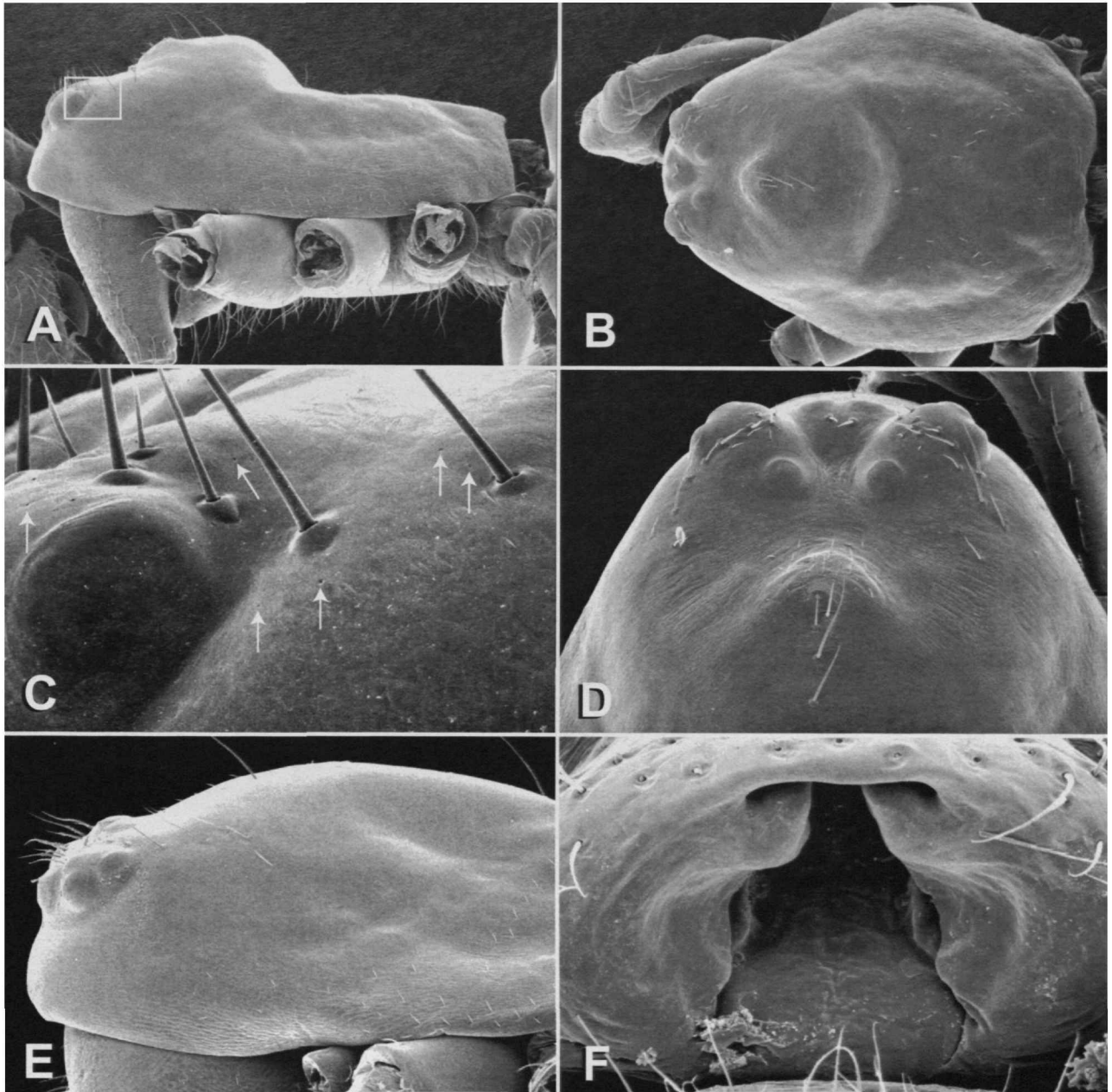


PLATE 36.—*Hilaïra vexatrix*: A–D, male prosoma; E, female prosoma; F, epigynum. A, lateral; B, dorsal; C, PLE region (arrows indicate cuticular pores); D, cephalic region, dorsal; E, lateral; F, caudal.

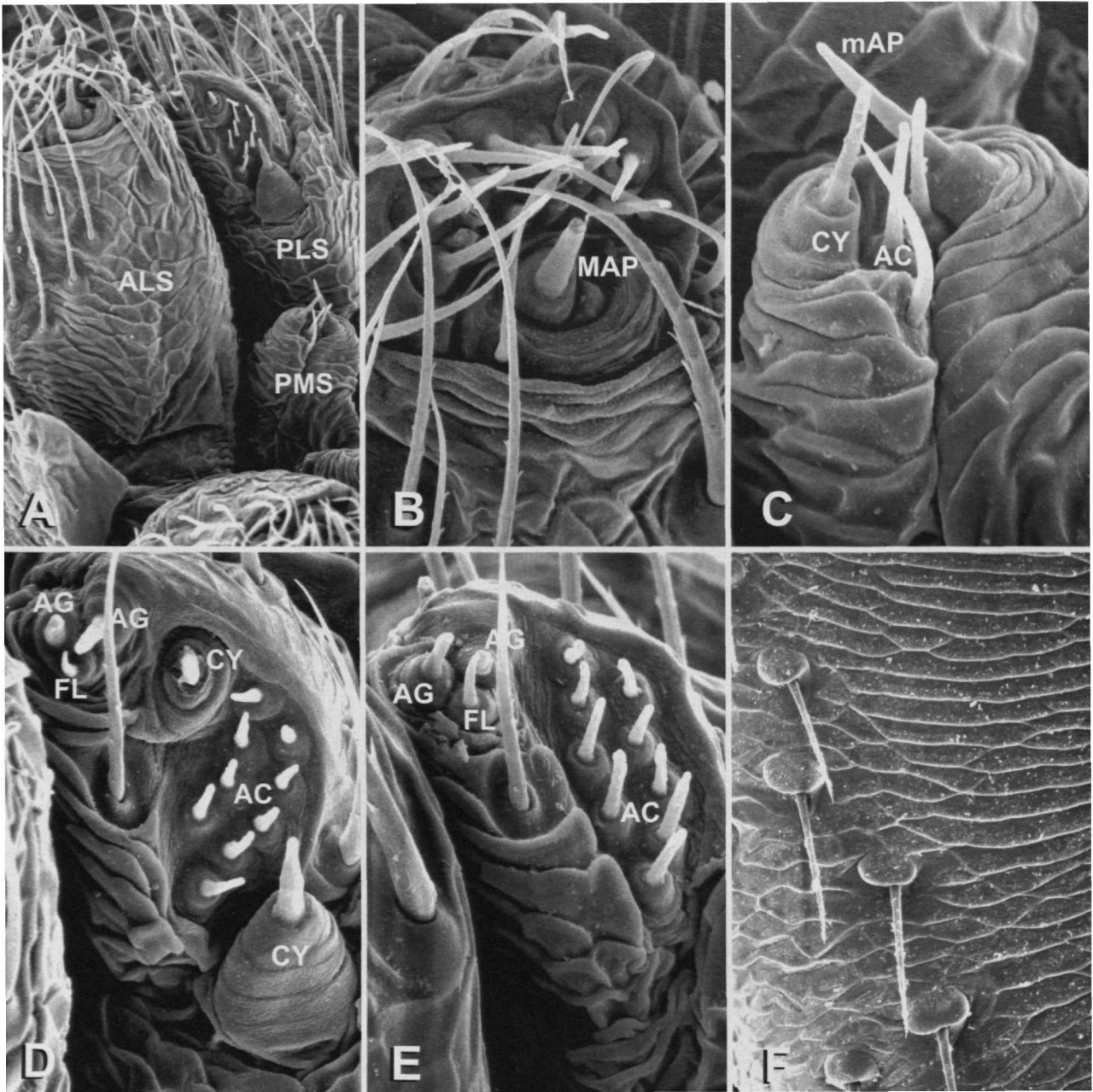


PLATE 37.—*Hilaira vexatrix*: A–E, spinnerets; F, ectal side of chelicera. A, female; B, ALS, female; C, PMS, female; D, PLS, female; E, PLS, male (right); F, male, detail of stridulatory striae.



PLATE 38.—*Hylyphantes nigrinus*: A–D, male palp; E,F, ectal side of chelicera. A, ventral; B, ectal; C, ventral; D, protegulum, apical; E, male; F, female.

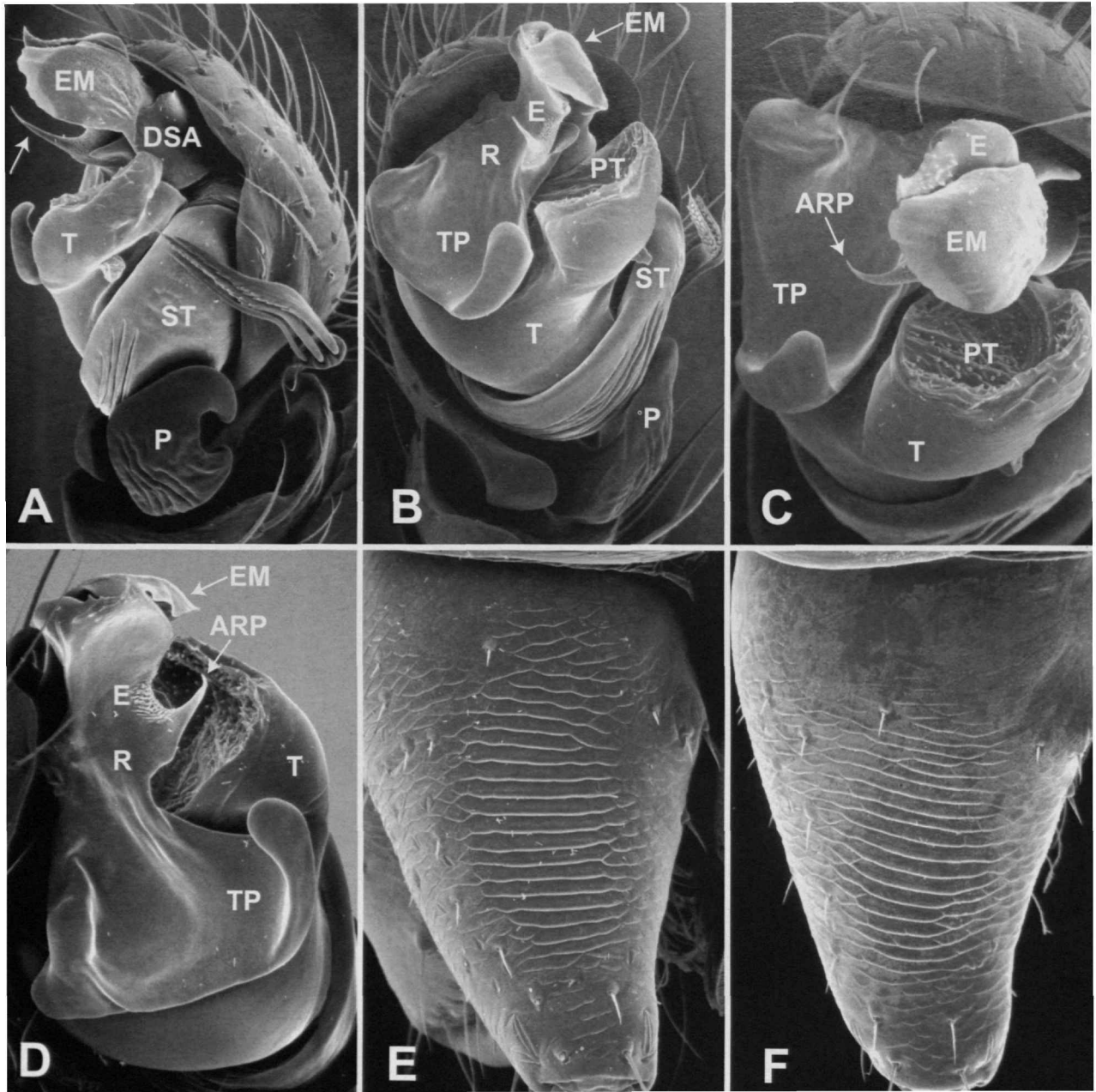


PLATE 39.—*Islandiana cristata*: A–D, male palp (right); E, F, ectal side of chelicera. A, ectal; B, ventral; C, apical; D, ectovenral; E, male; F, female.

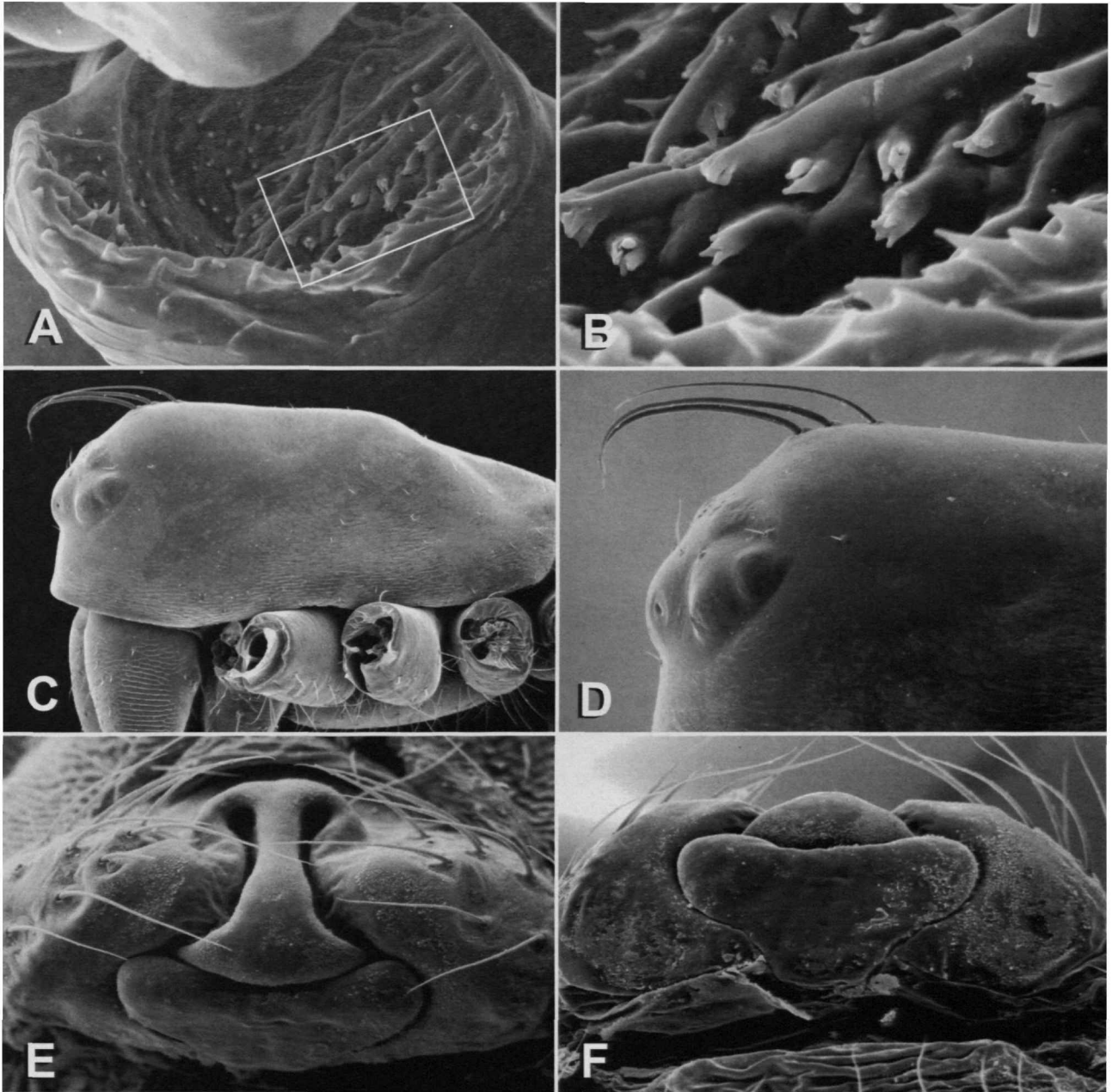


PLATE 40.—*Islandiana cristata*: A,B, male palp (right); C,D, male prosoma; E,F, epigynum. A, protegulum, apical; B, protegular papillae; C, lateral (right side, reversed); D, cephalic region, lateral; E, ventral; F, caudal.

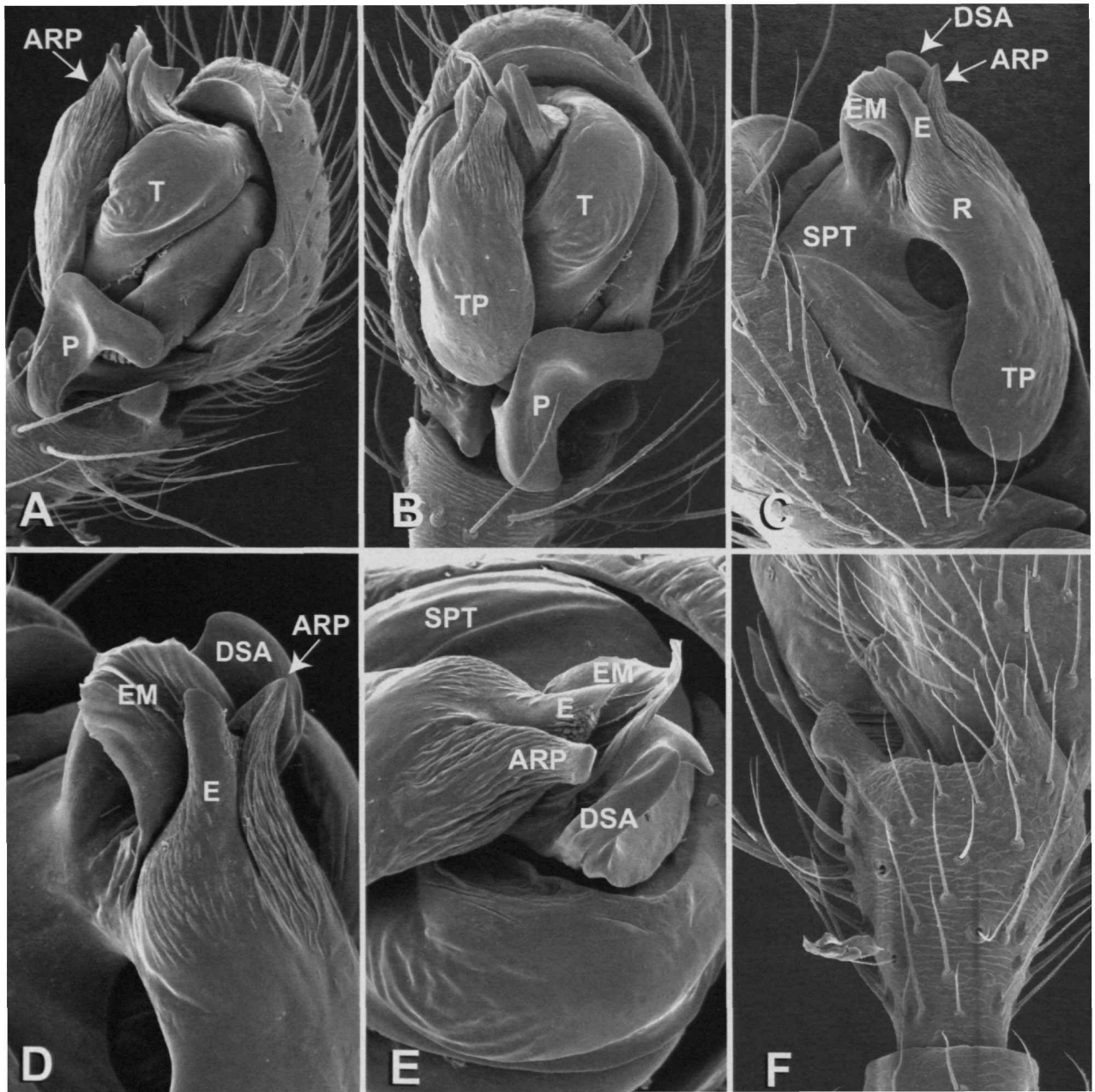


PLATE 41.—*Laminacauda plagiata*: A-F, male palp. A, ectal; B, ventral; C, mesal; D, mesoventral; E, apical; F, tibia, dorsal.

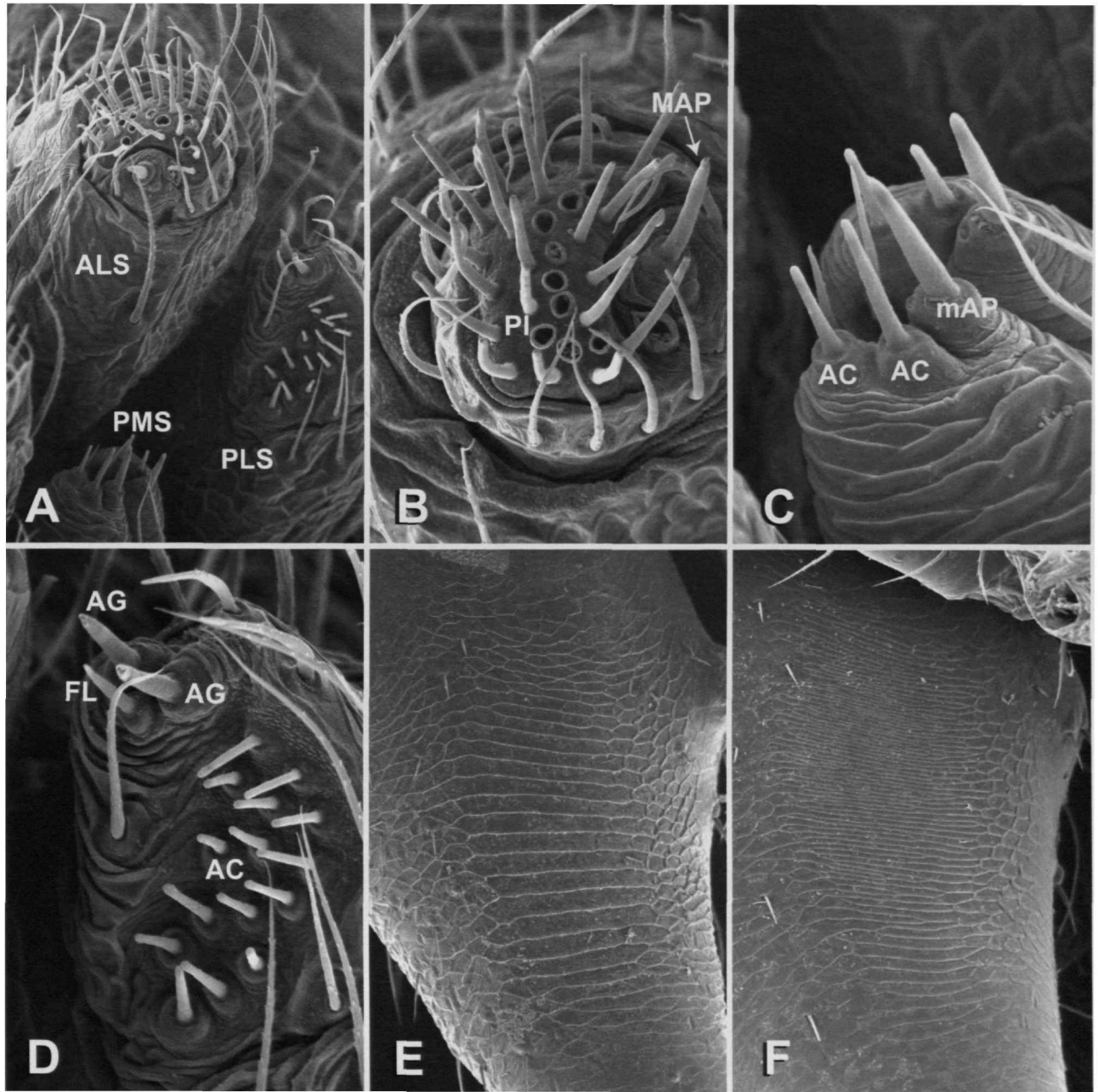


PLATE 42.—*Laminacauda plagiata*: A–D, male spinnerets; E, F, ectal side of chelicera. A, left spinnerets; B, ALS; C, PMS; D, PLS; E, male; F, female (right).

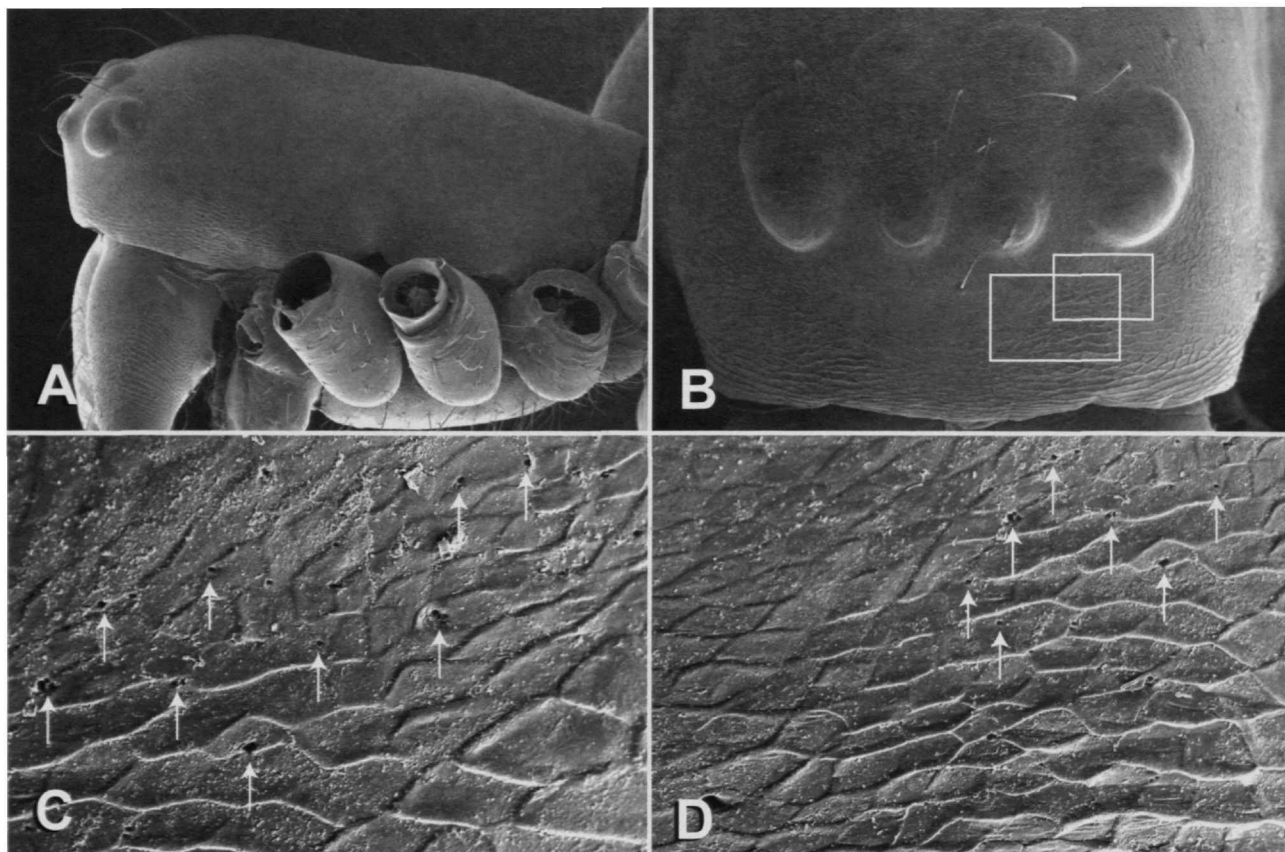


PLATE 43.—*Laminacauda plagiata*: A–D, male prosoma. A, lateral; B, frontal; C,D, clypeal cuticular pores (arrows).

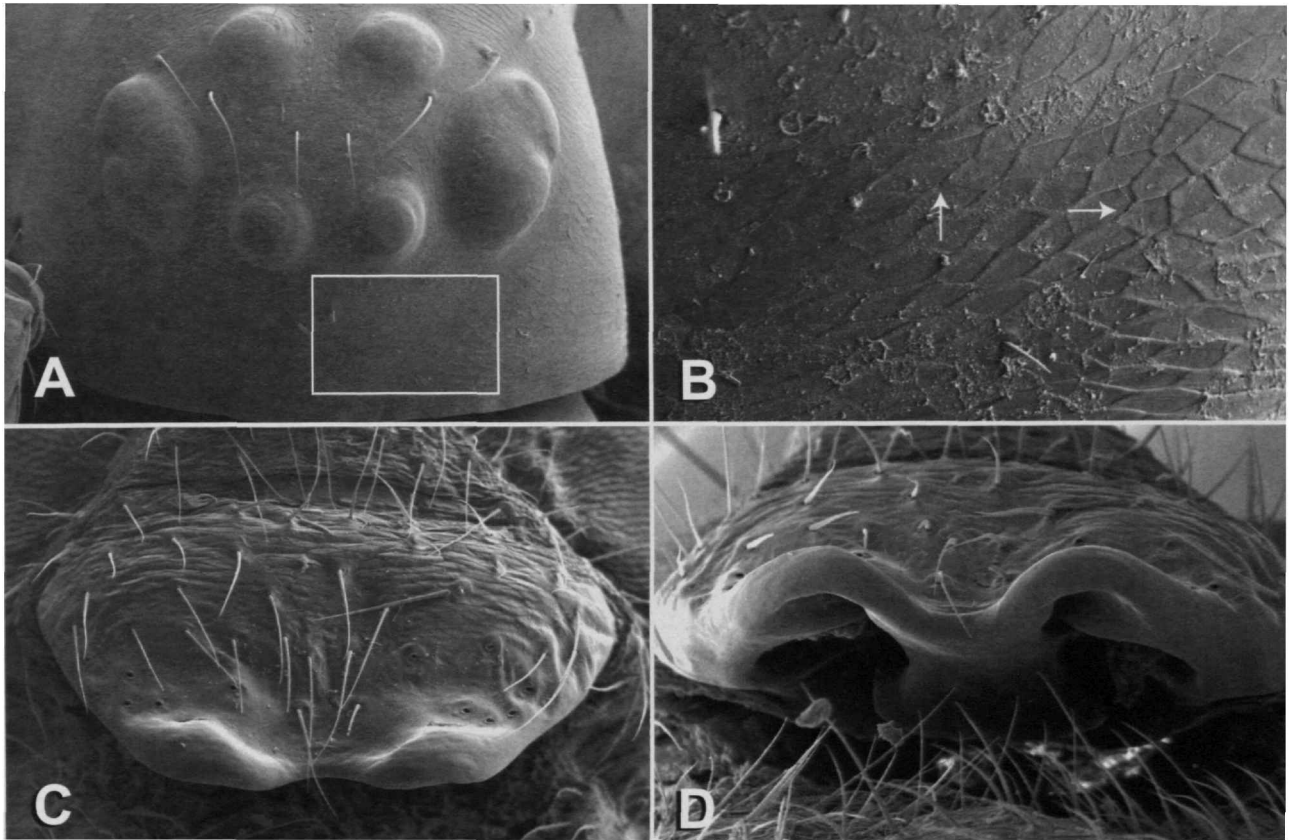


PLATE 44.—*Laminacauda plagiata*: A,B, female prosoma; C,D, epigynum. A, frontal; B, clypeal cuticular pores; C, ventral; D, caudal.

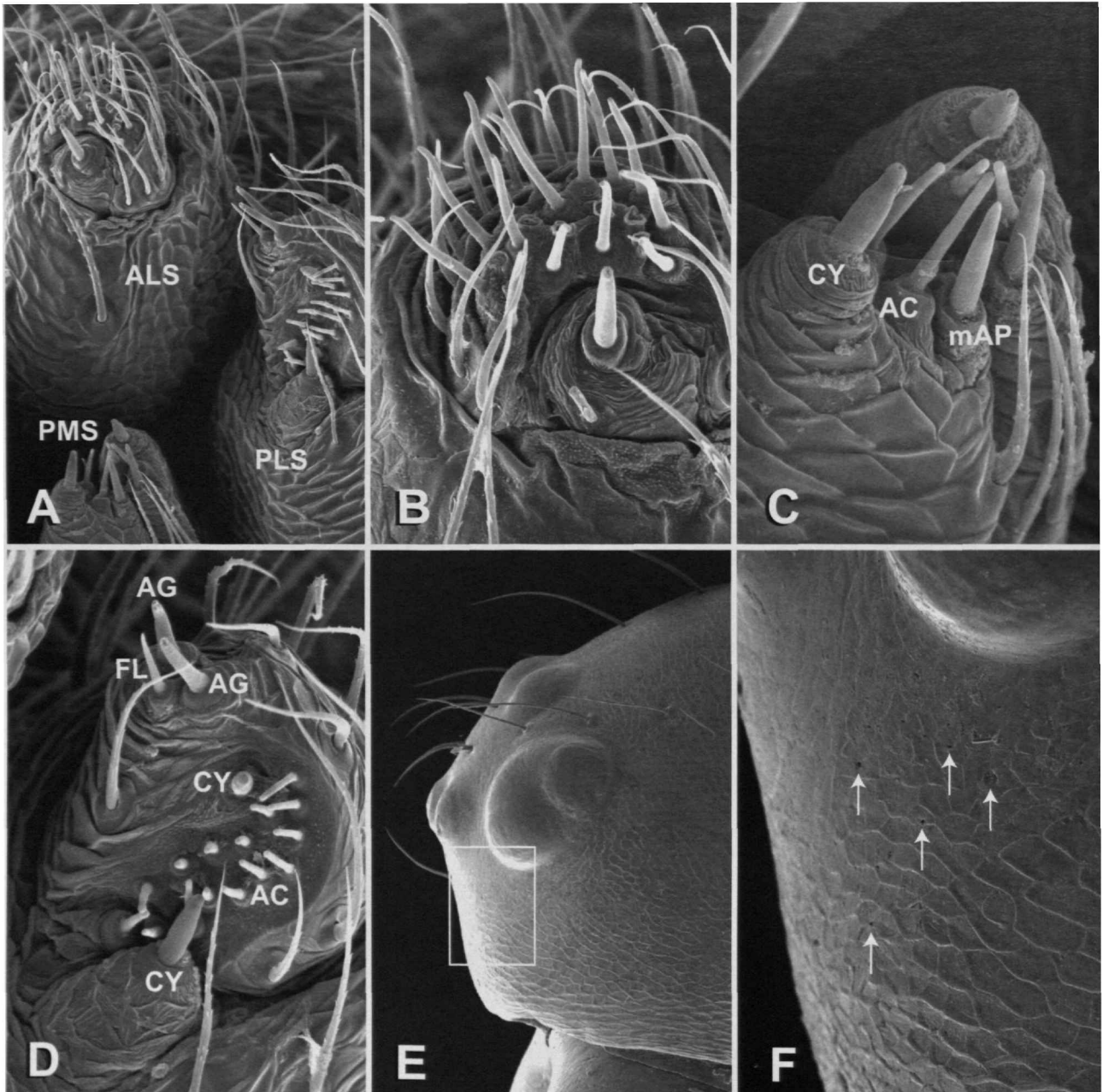


PLATE 45.—*Laminacauda plagiata*: A–D, female spinnerets; E,F, male prosoma. A, left spinneret group; B, ALS; C, PMS; D, PLS; E, cephalic region, lateral; F, detail of cuticular pores (arrows).



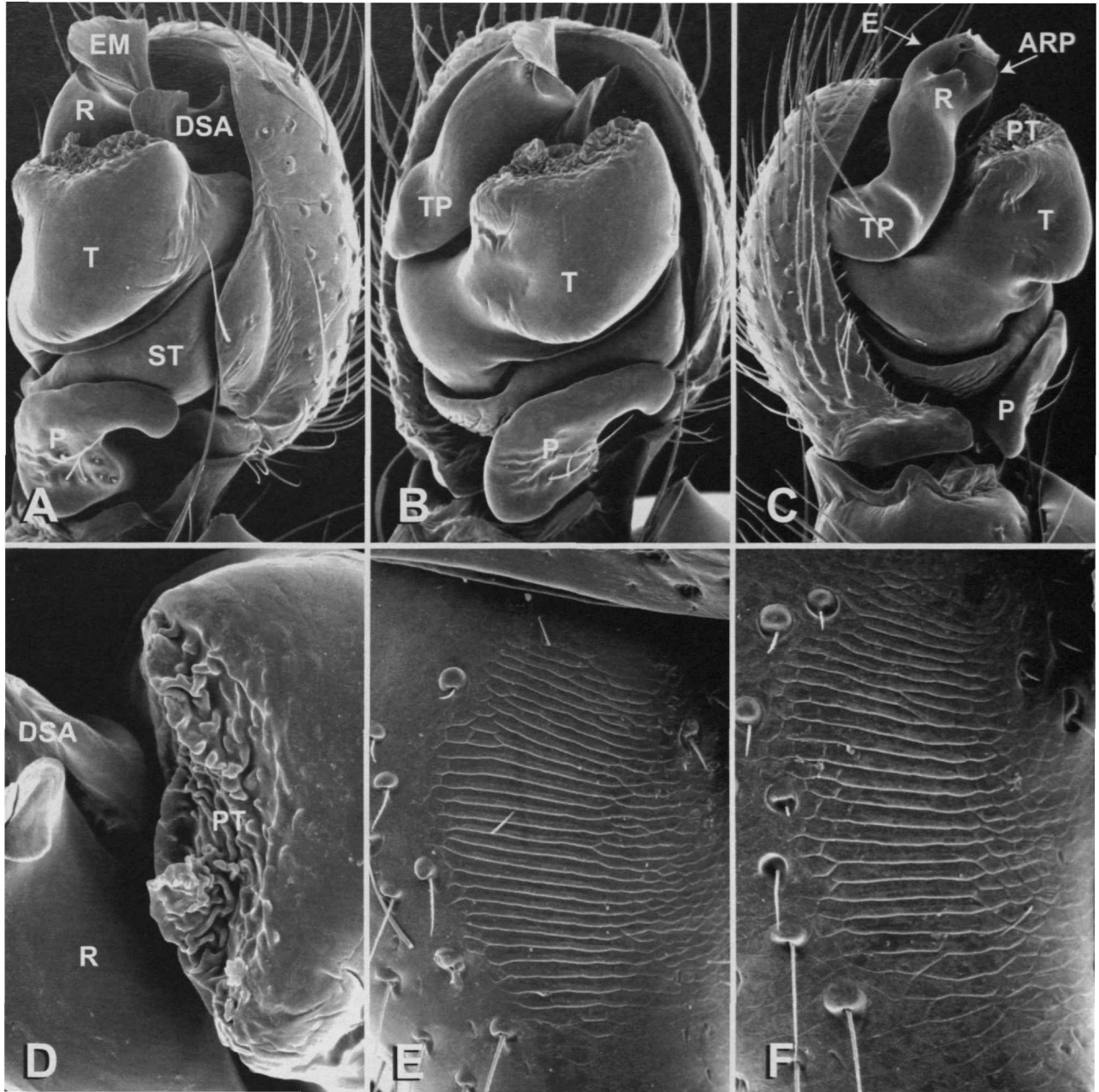


PLATE 46.—*Lophomma punctatum*: A–D, male palp; E,F, ectal side of chelicera. A, ectal; B, ventral; C, mesal; D, protegulum, ventral; E, male; F, female.

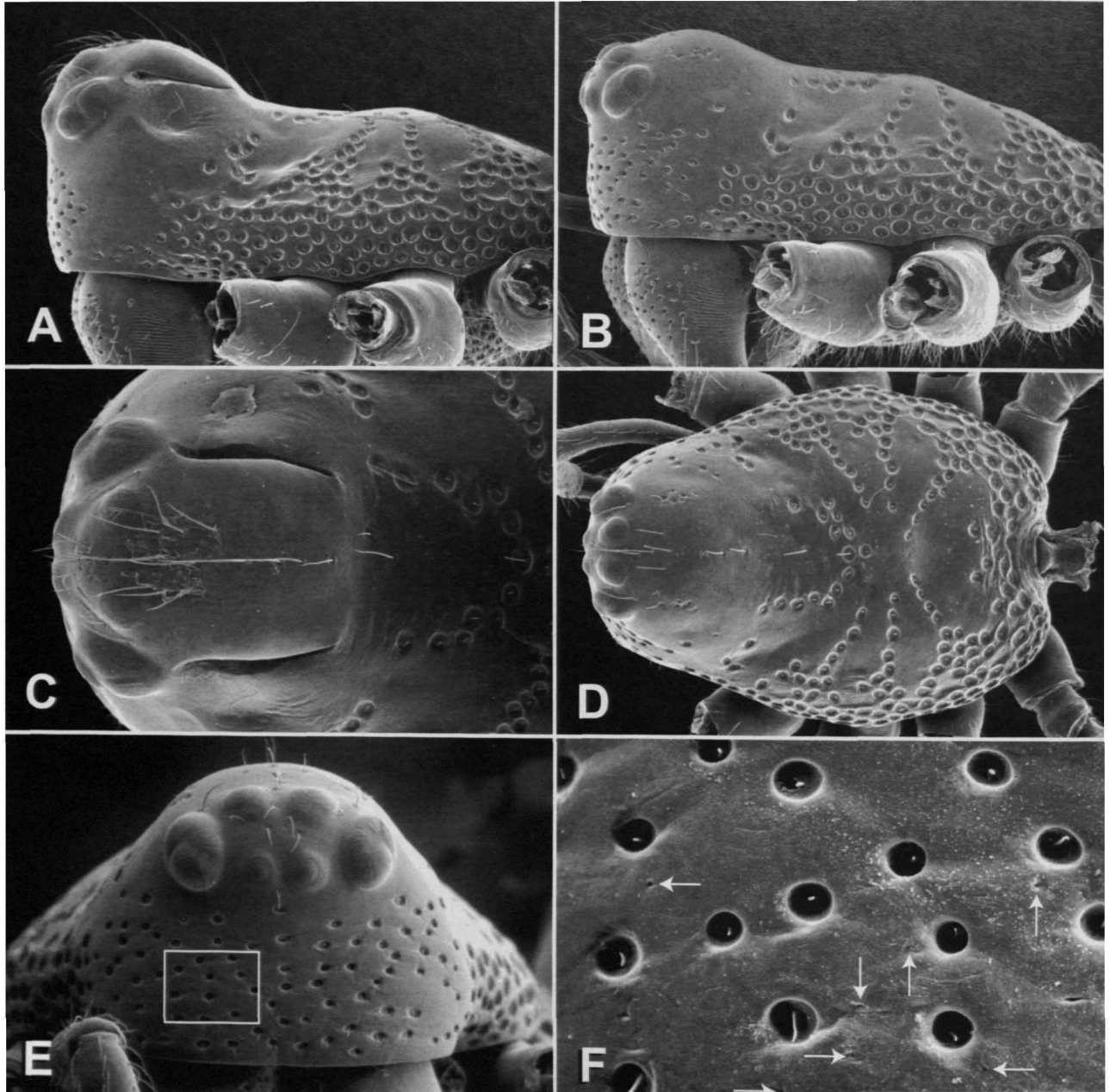


PLATE 47.—*Lophomma punctatum*: A,C, male; B,D-F, female. A,B, lateral; C,D, dorsal; E, frontal; F, detail of E (arrows indicate pores).

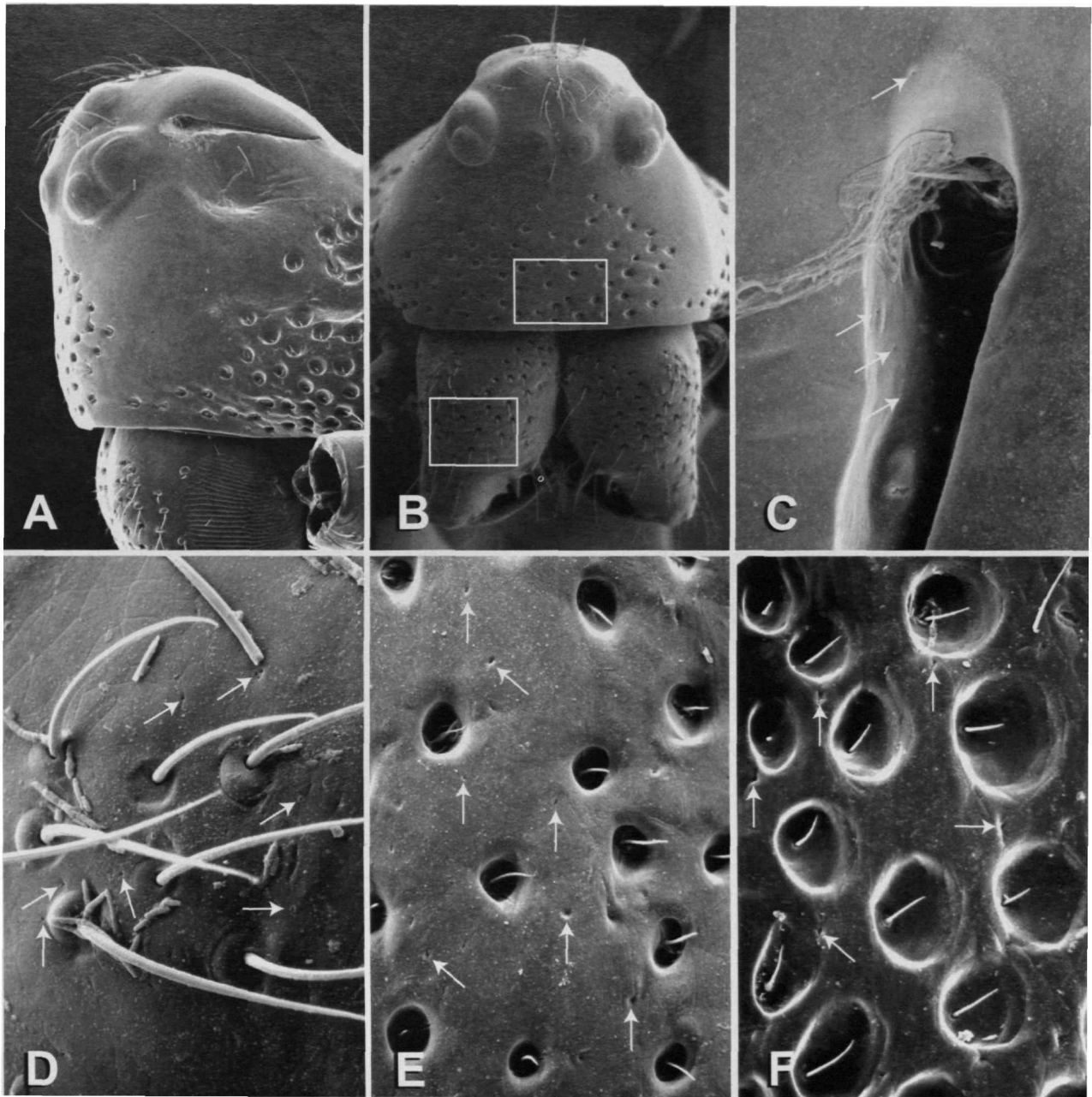


PLATE 48.—*Lophomma punctatum*: A-F, male prosoma. A, cephalic region, lateral; B, frontal; C, cephalothoracic sulcus; D, detail of AME-PME region, dorsal; E, clypeal cuticular pores; F, cheliceral cuticular pores (arrows indicate pores).

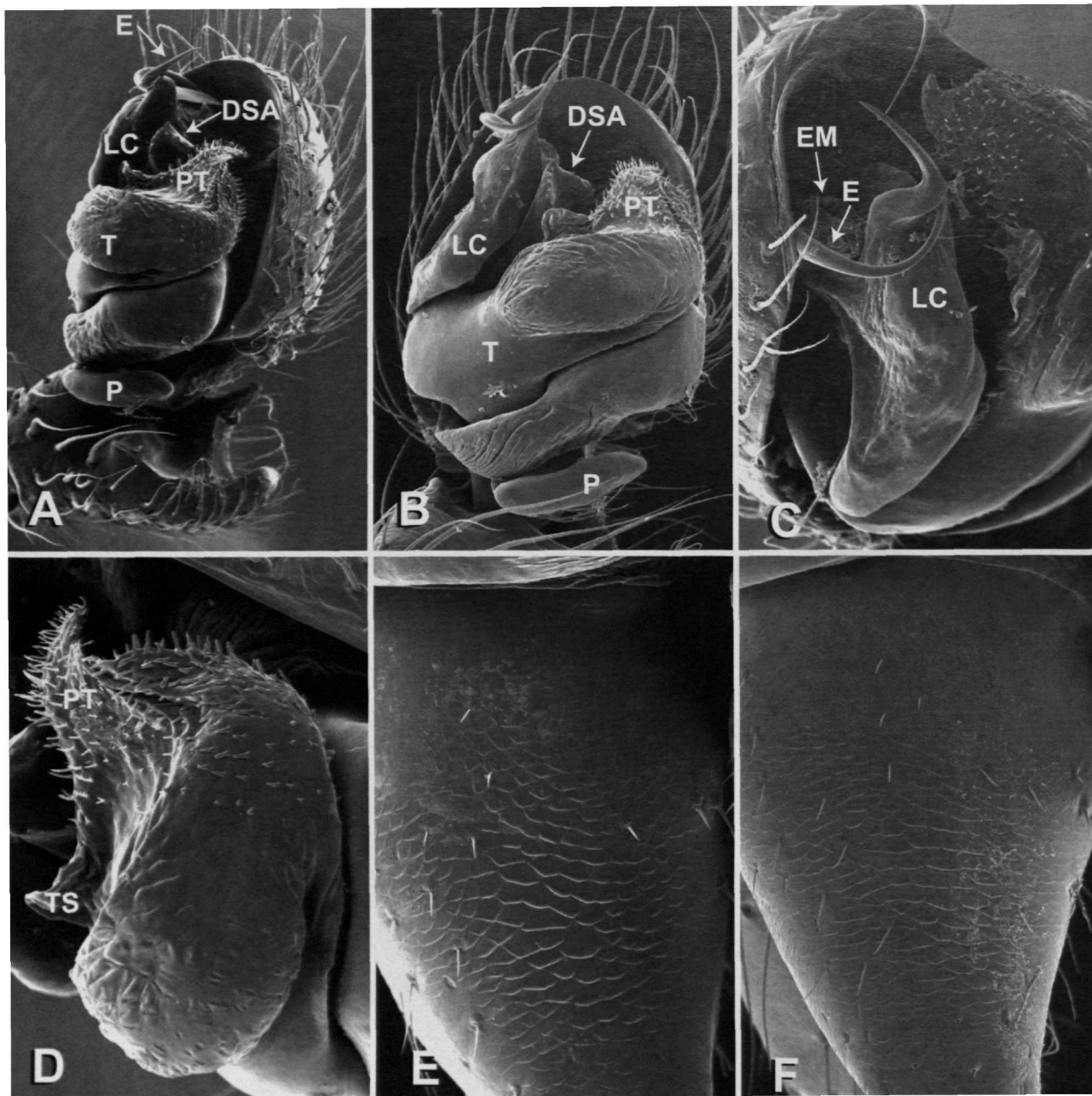


PLATE 49.—*Oedothorax gibbosus*: A–D, male palp; E,F, ectal side of chelicera. A, ectal (an insect scale can be seen between the E and the DSA); B, ventral; C, mesoapical; D, tegulum and protegulum, ectal; E, male; F, female.

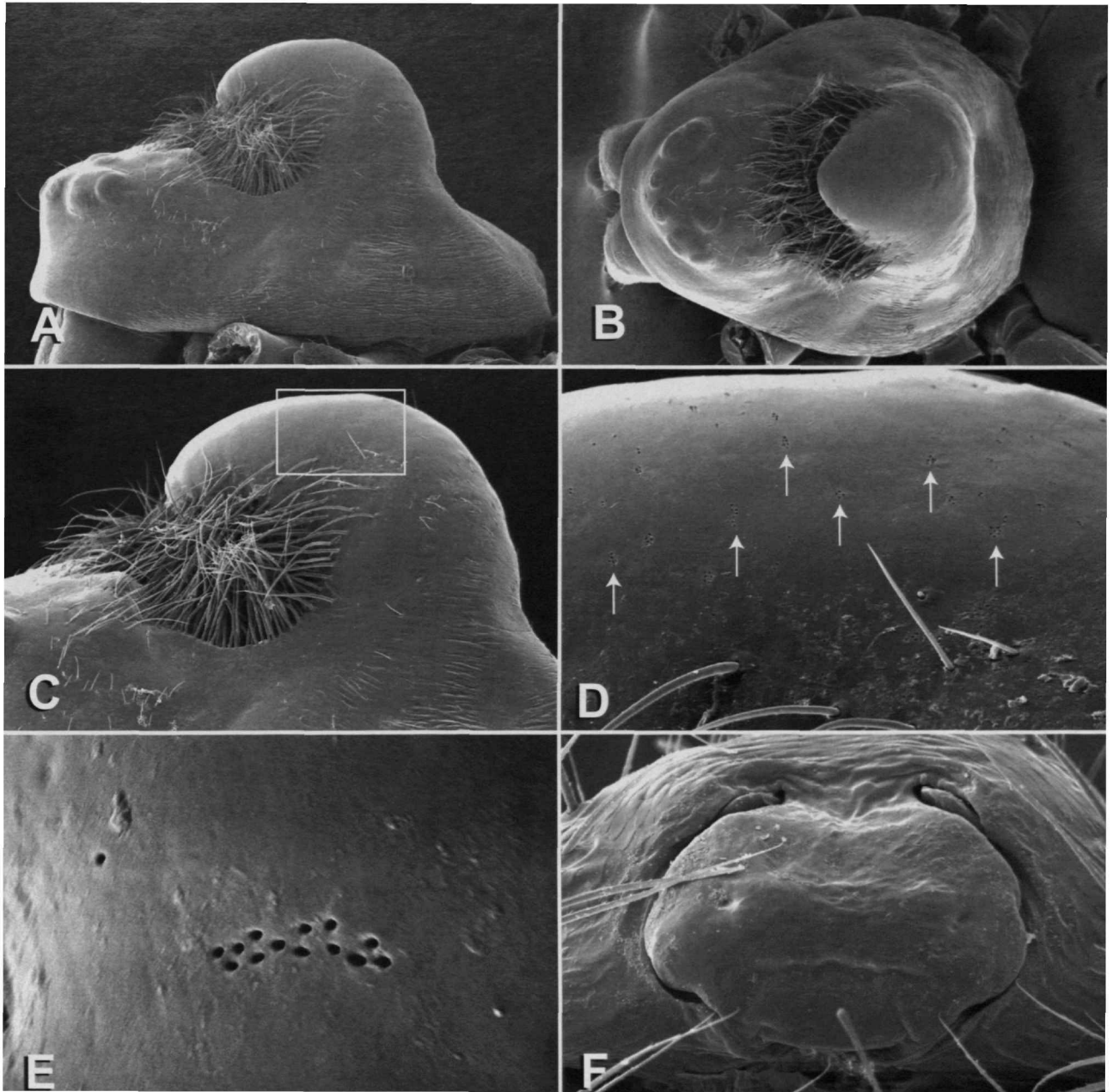


PLATE 50.—*Oedothorax gibbosus*: A–E, male prosoma; F, epigynum. A, lateral; B, dorsal; C, prosomic lobe, lateral; D, detail of C (arrows indicate pores); E, cuticular pores on prosomic lobe, dorsal; F, ventral.

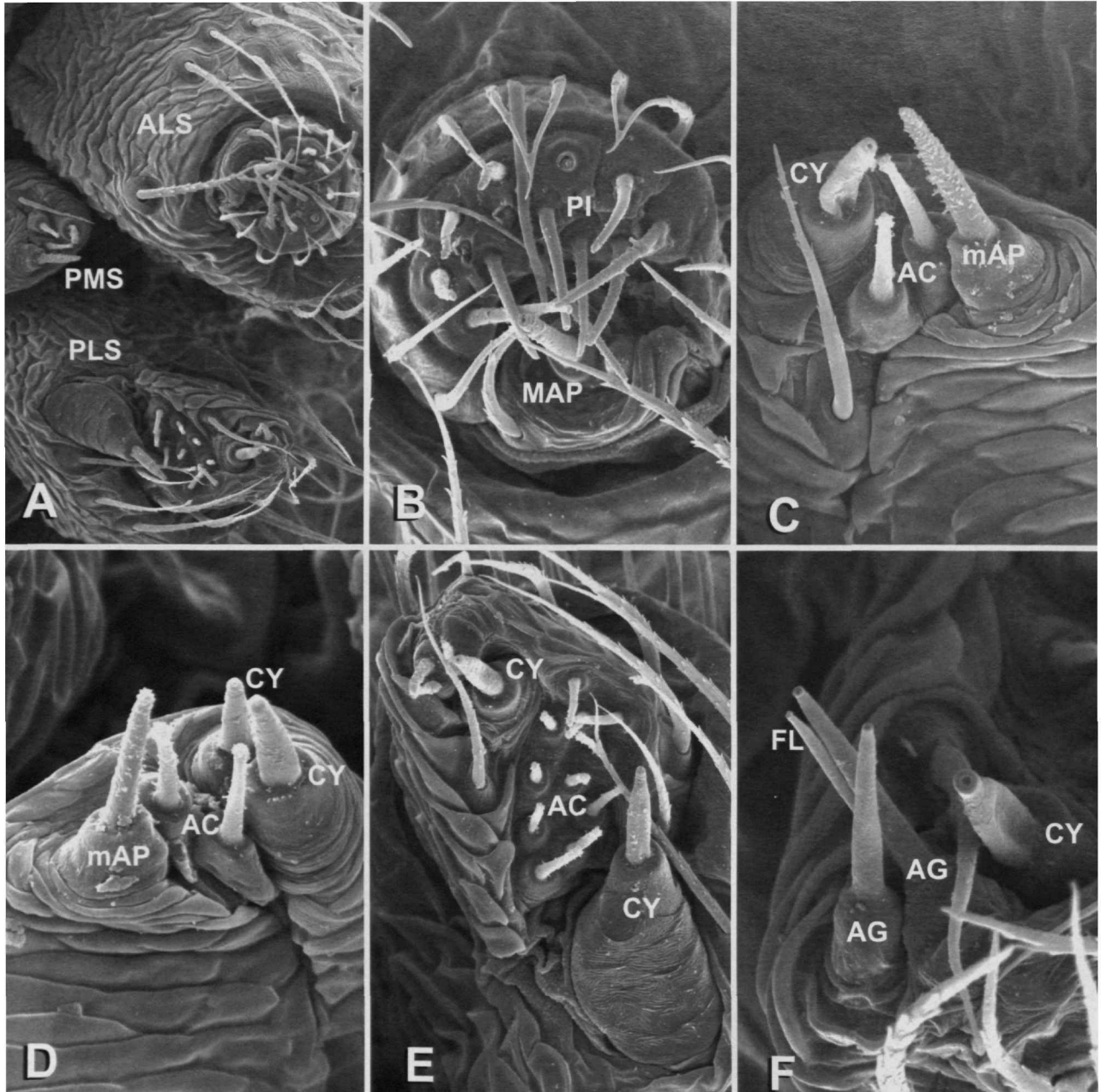


PLATE 51.—*Oedothorax gibbosus*: A–F, female spinnerets. A, left spinneret group; B, ALS; C, PMS; D, PMS (right, not reversed), showing two CY gland spigots; E, detail of PLS; F, PLS, detail of triad and distal CY.

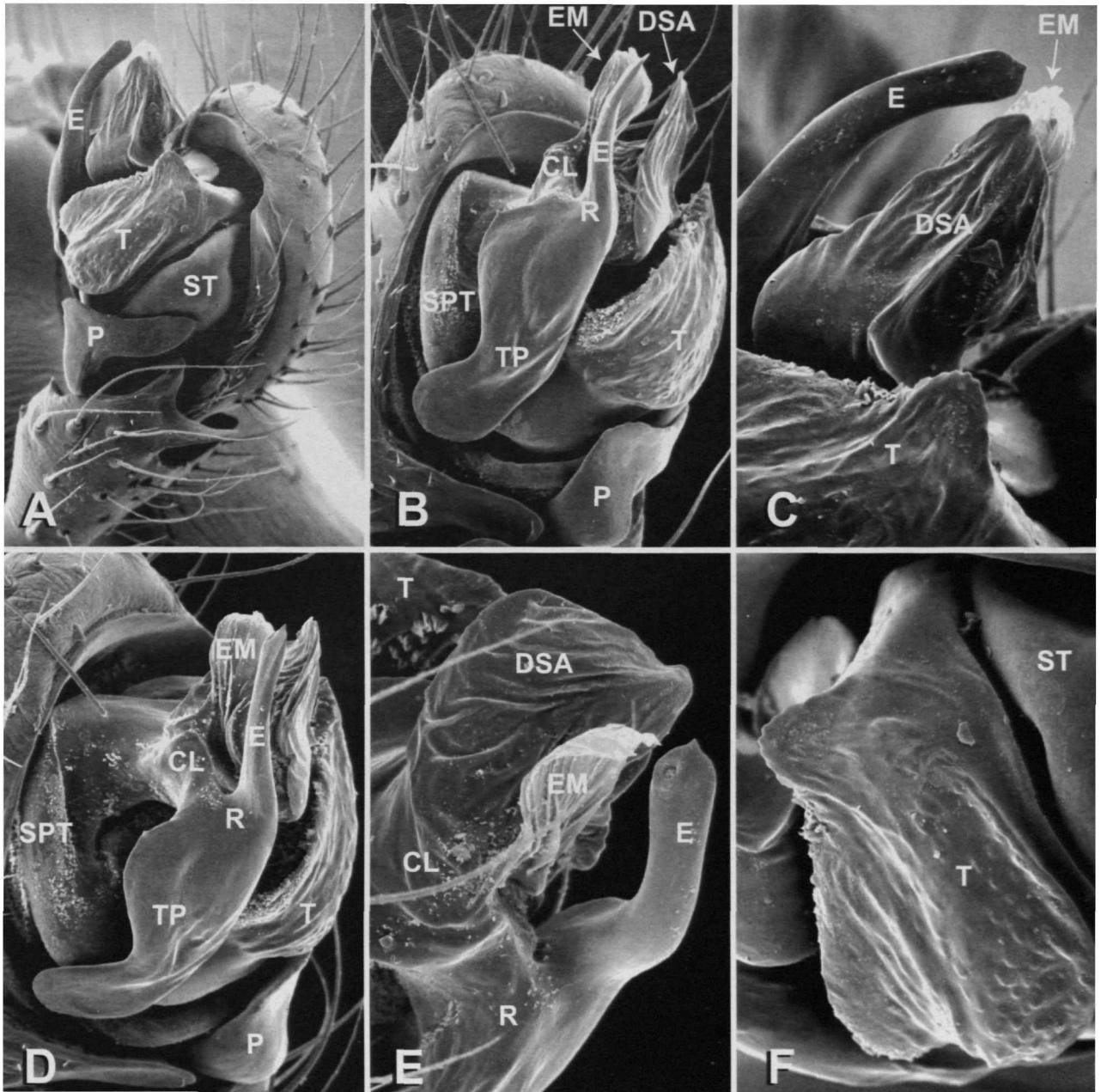


PLATE 52.—*Ostearius melanopygius*: A–F, male palp. A, ectal; B, ventral; C, ectal; D, embolic division, mesoventral; E, DSA and embolic division, mesal; F, tegulum, ectal.

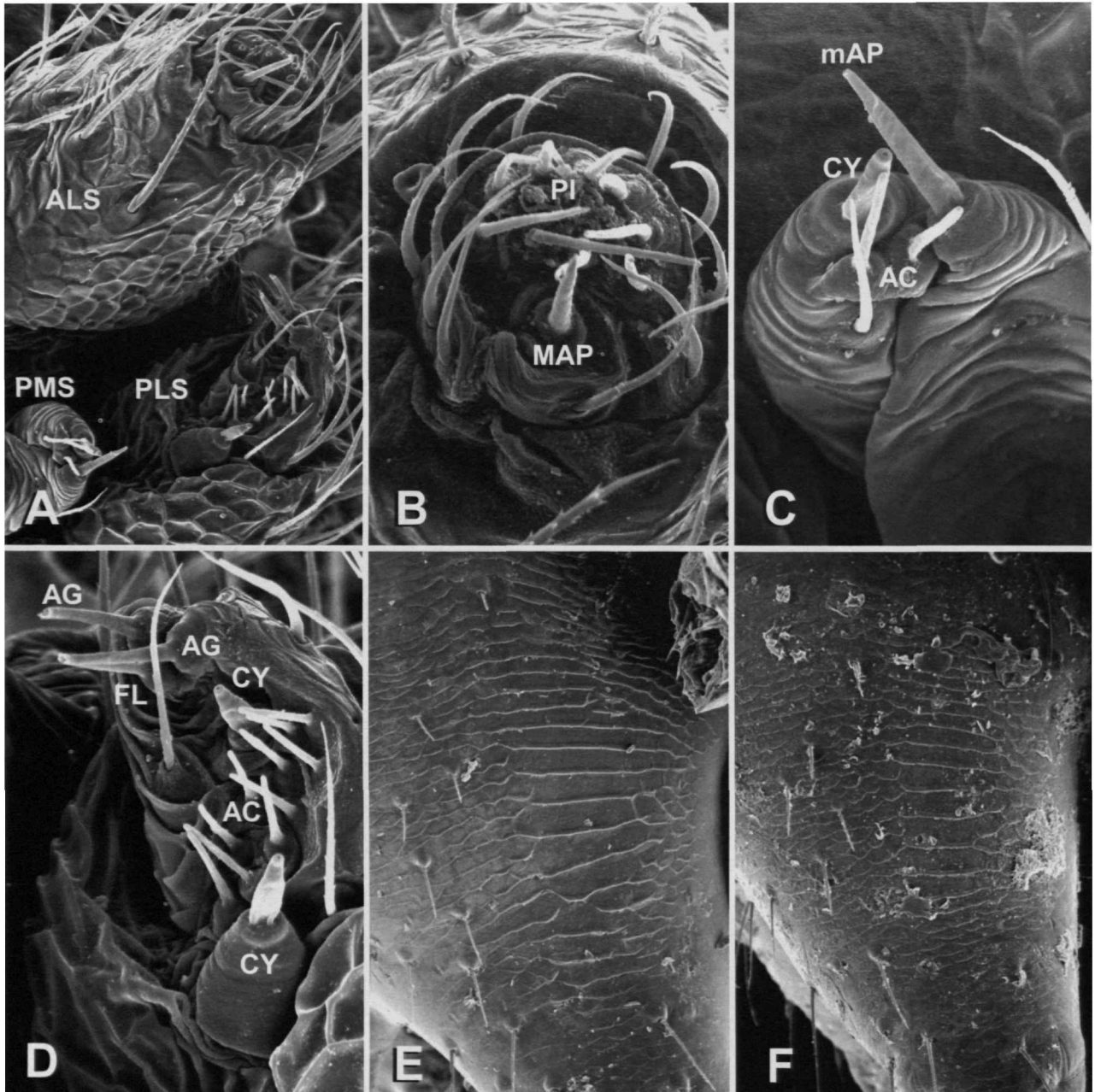


PLATE 53.—*Ostearius melanopygius*: A–D, female spinnerets; E,F, ectal side of chelicera. A, left spinneret group; B, ALS; C, PMS; D, PLS; E, male; F, female.



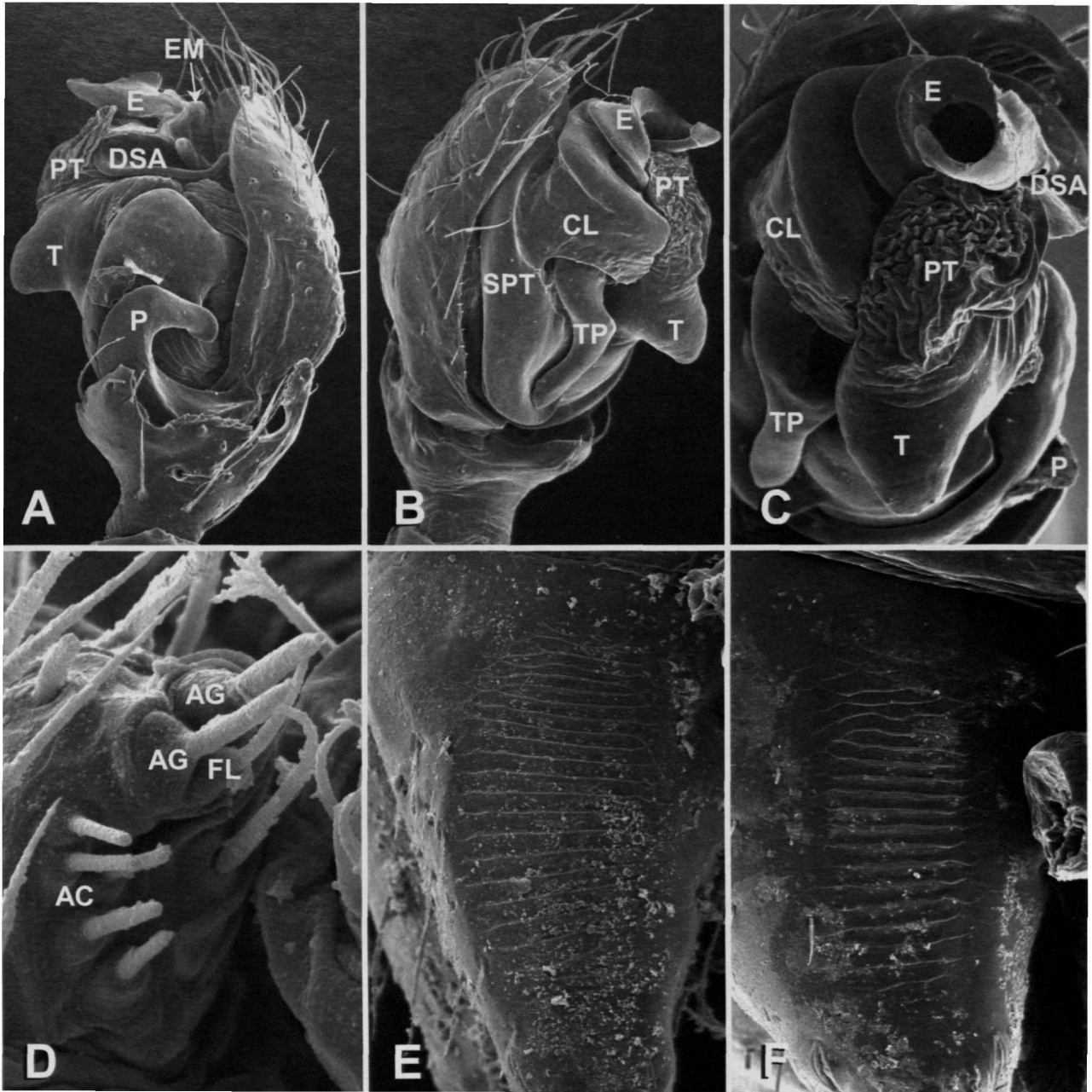


PLATE 54.—*Pelecopsis nemoralis*: A–C, male palp (right); D, male PLS (right, not reversed); E, F, ectal side of chelicera. A, ectal; B, mesal; C, mesoventral, apical view; D, detail of triad and AC field; E, male (right); F, female.

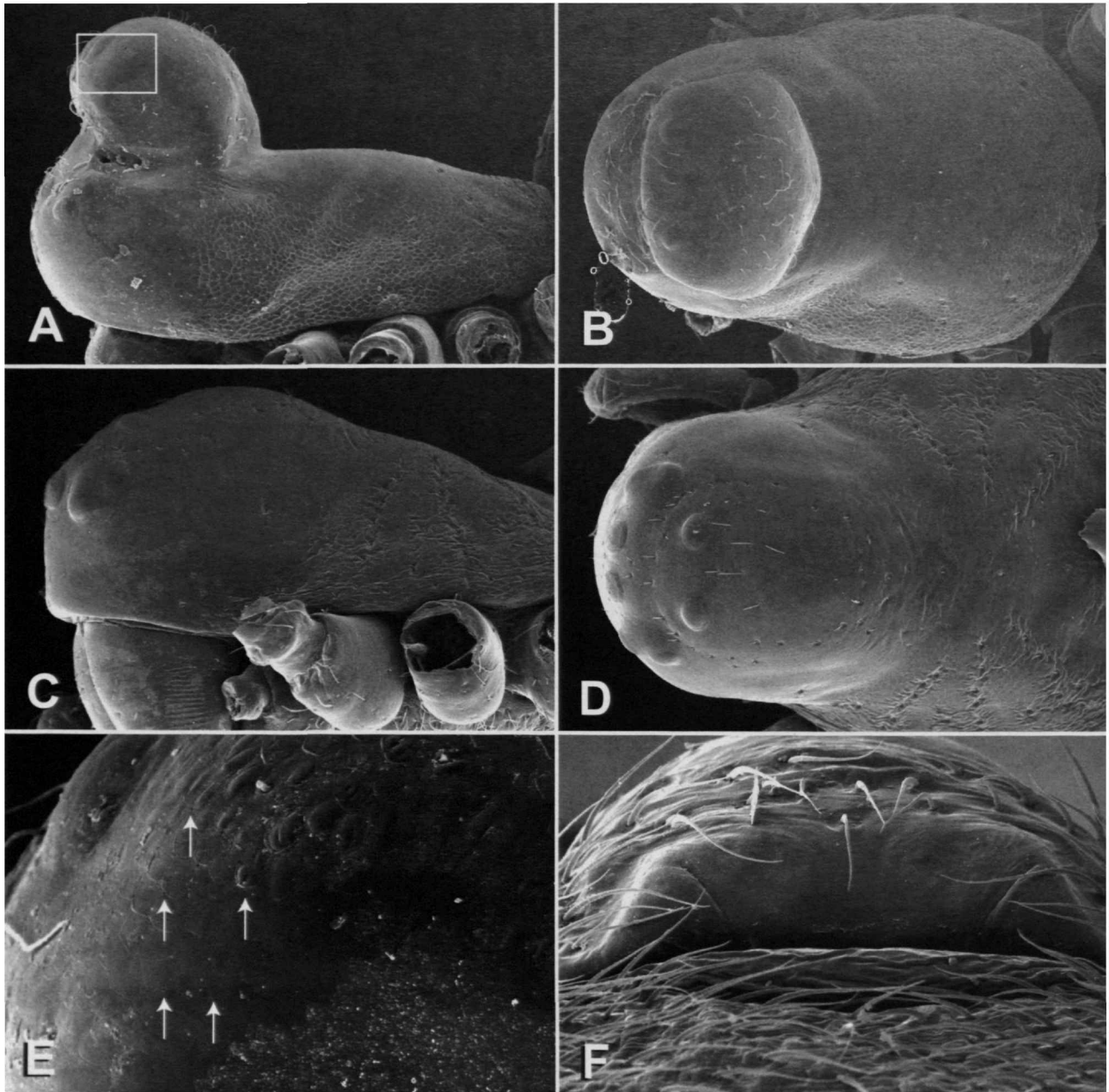


PLATE 55.—*Pelecopsis nemoralis*: A,B,E, male prosoma; C,D, female prosoma; F, epigynum. A, lateral; B, dorsal; C, lateral; D, dorsal; E, detail of A; F, caudal.

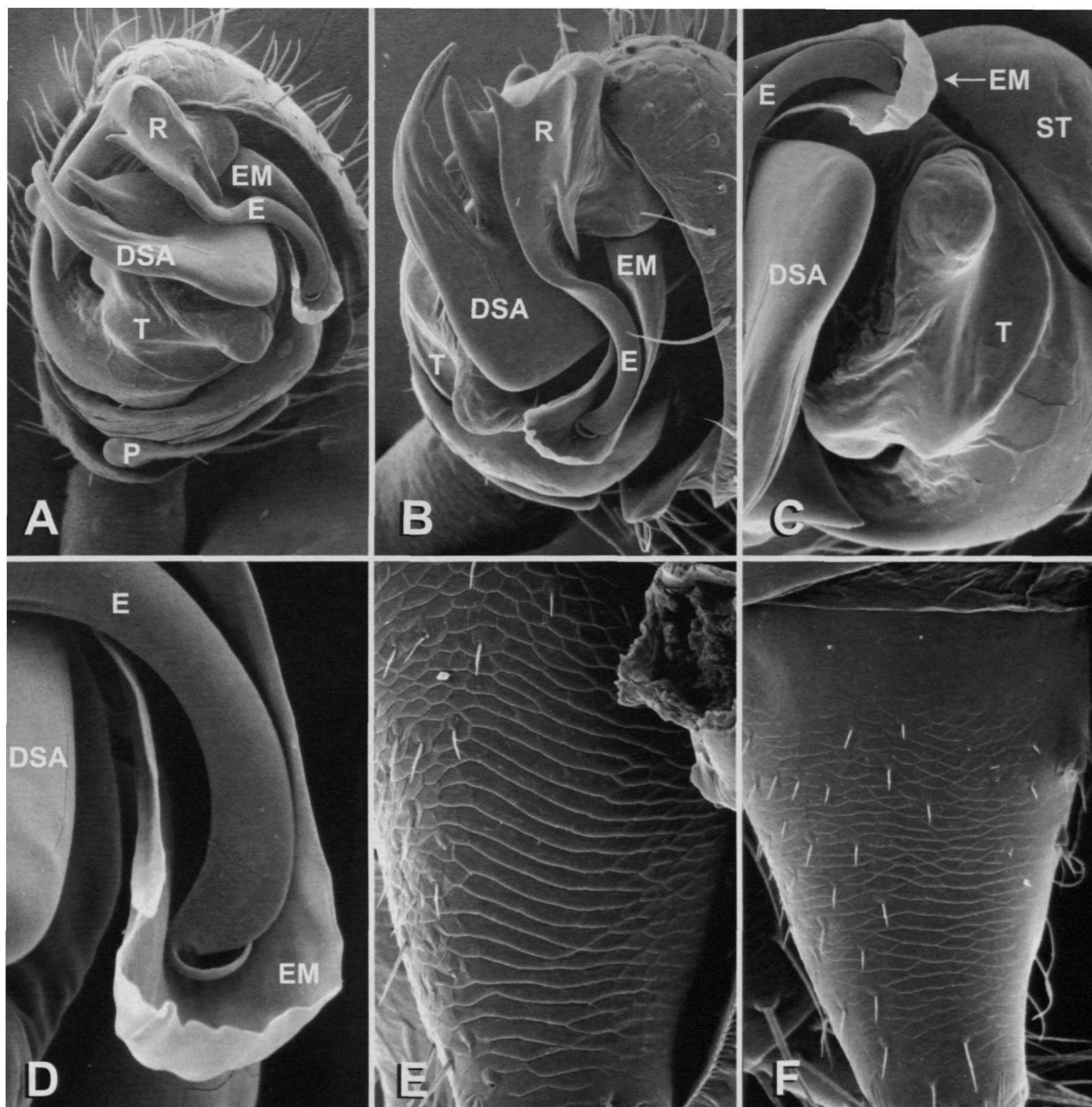


PLATE 56.—*Savignia frontata*: A–D, male palp; E,F, ectal side of chelicera. A, ventral; B, ectoapical; C, ectoven-tral; D, E AND EM, ventral; E, male; F, female.

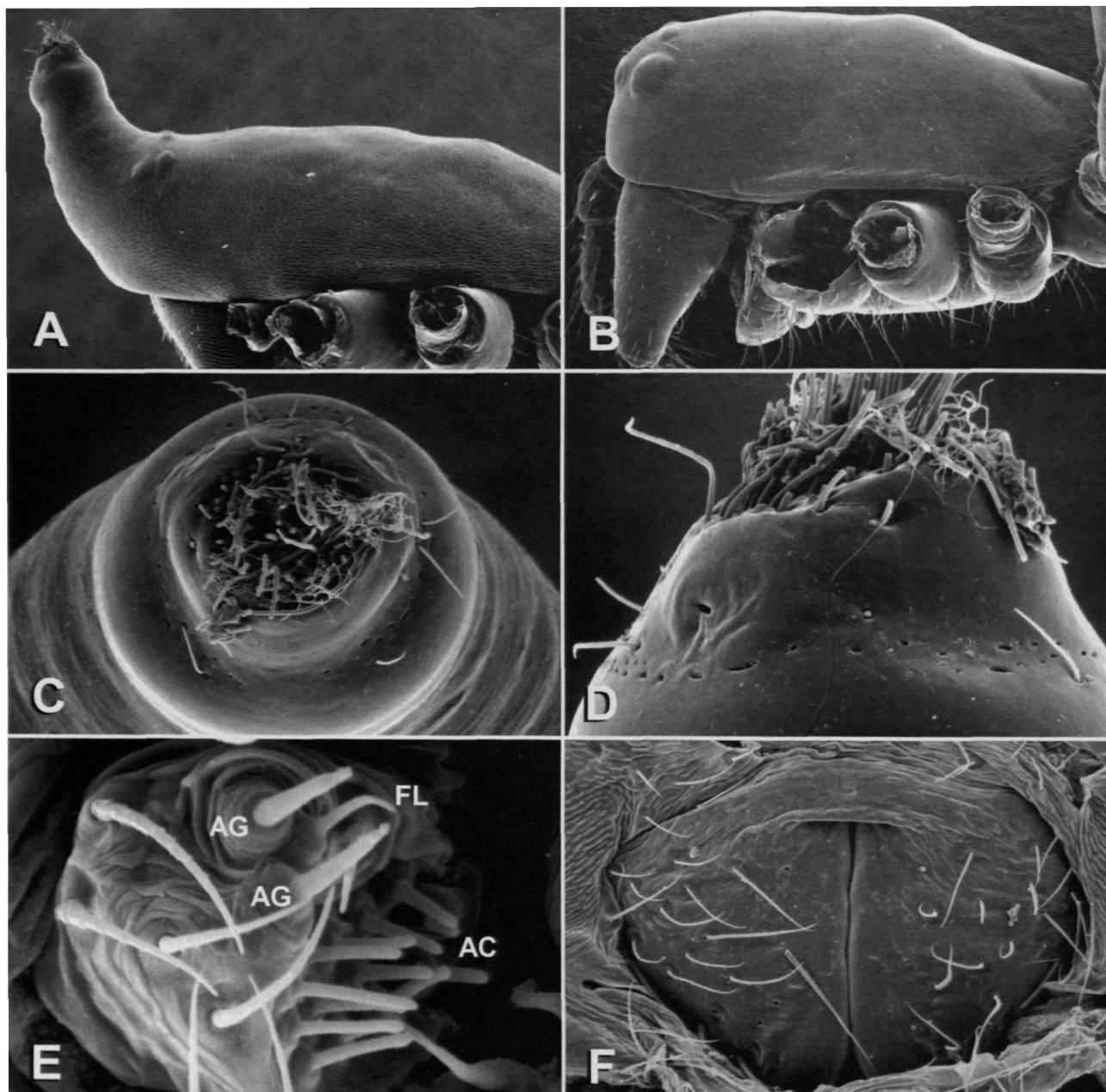


PLATE 57.—*Savignia frontata*: A,C,D, male prosoma; B, female prosoma; E, male PLS (right, not reversed); F, epigynum. A, lateral; B, lateral; C, cephalic lobe, dorsal; D, cephalic lobe, lateral; E, triad and AC field; F, ventral.

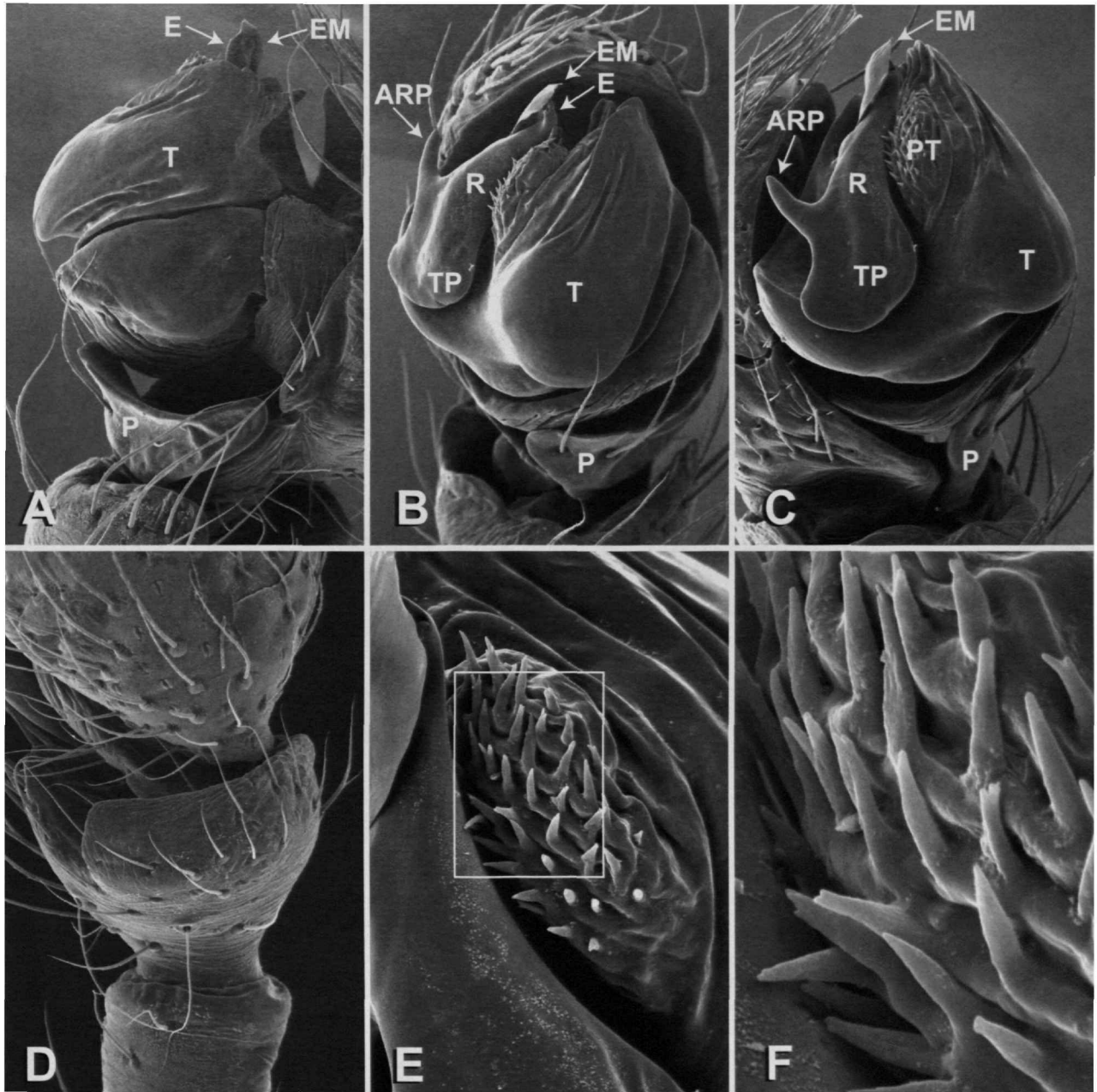


PLATE 58.—*Sciastes truncatus*: A–F, male palp. A, ectal; B, ventral; C, mesal; D, tibia, dorsal; E, protegulum, mesal; F, protegular papillae.

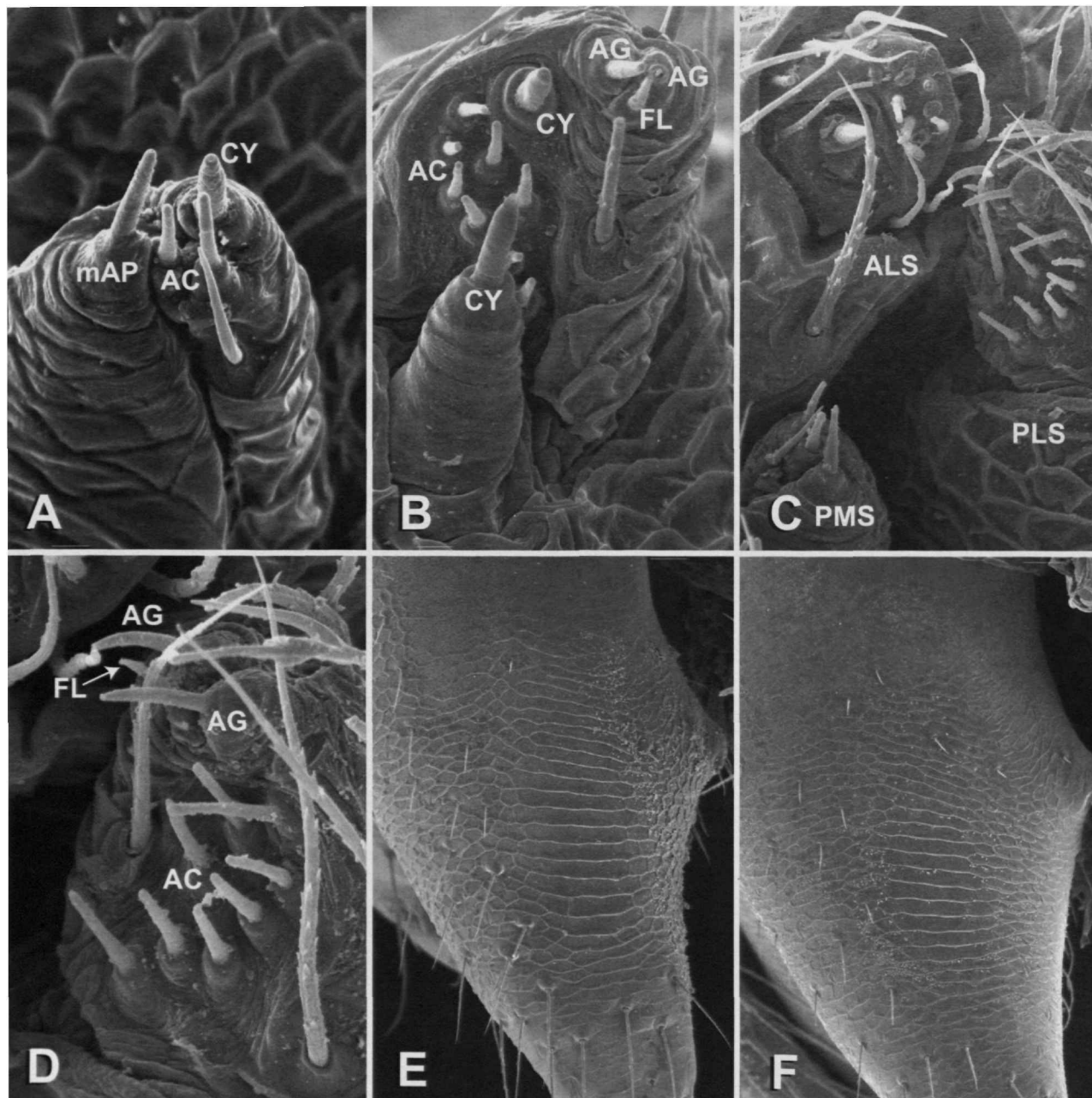


PLATE 59.—*Sciastes truncatus*: A,B, female spinnerets PLS (right, not reversed); C,D, male spinnerets; E,F, ectal side of chelicera. A, PMS; B, PLS (distal AG shaft broken off); C, left spinneret group; D, PLS; E, male; F, female.

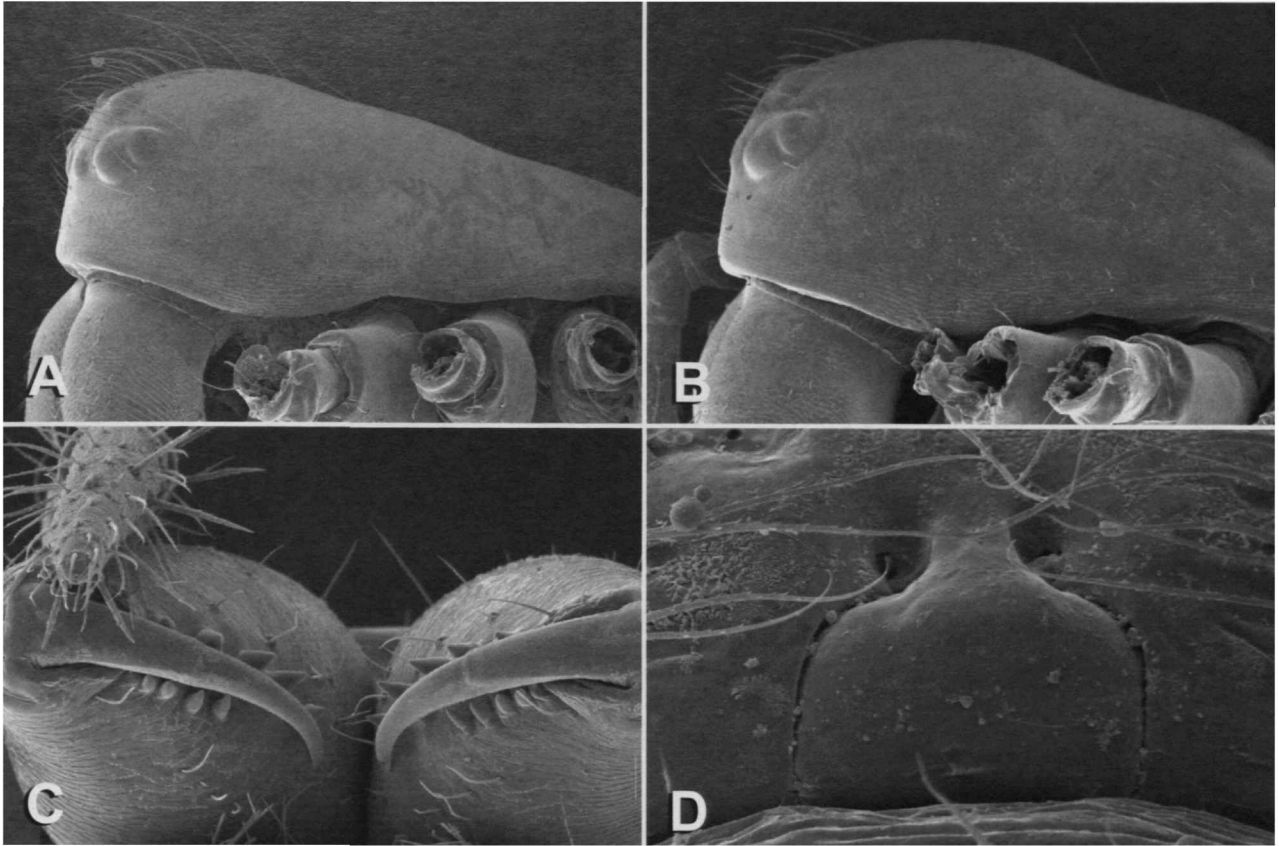


PLATE 60.—*Sciastes truncatus*: A, male; B–D, female. A,B, prosoma, lateral; C, chelicerae and pedipalpal tarsus, ventral; D, epigynum, ventral.

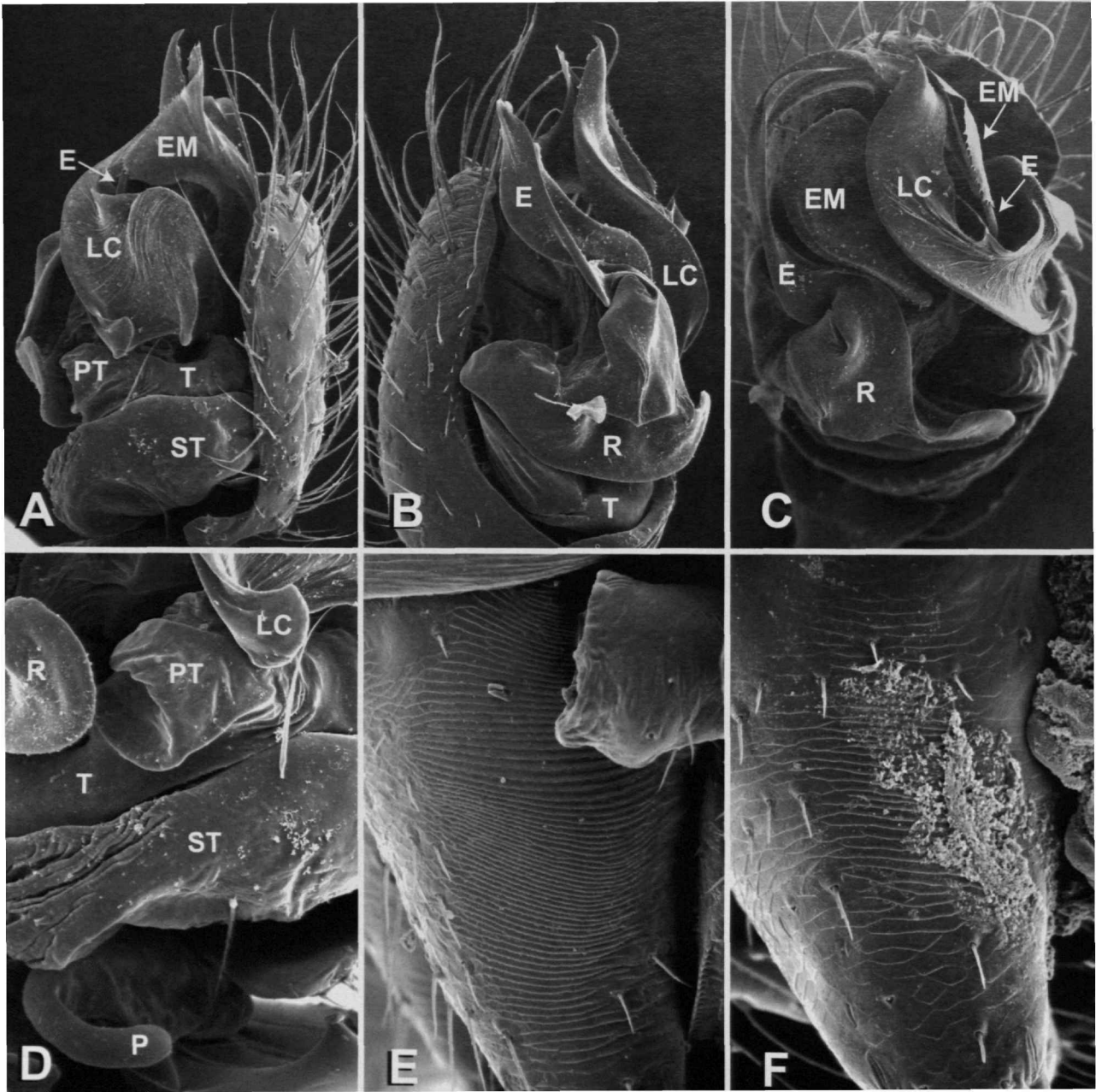


PLATE 61.—*Sisicus apertus*: A–D, male palp (right); E,F, ectal side of chelicera. A, ectal; B, mesal; C, ventral; D, ectoventral; E, male; F, female.



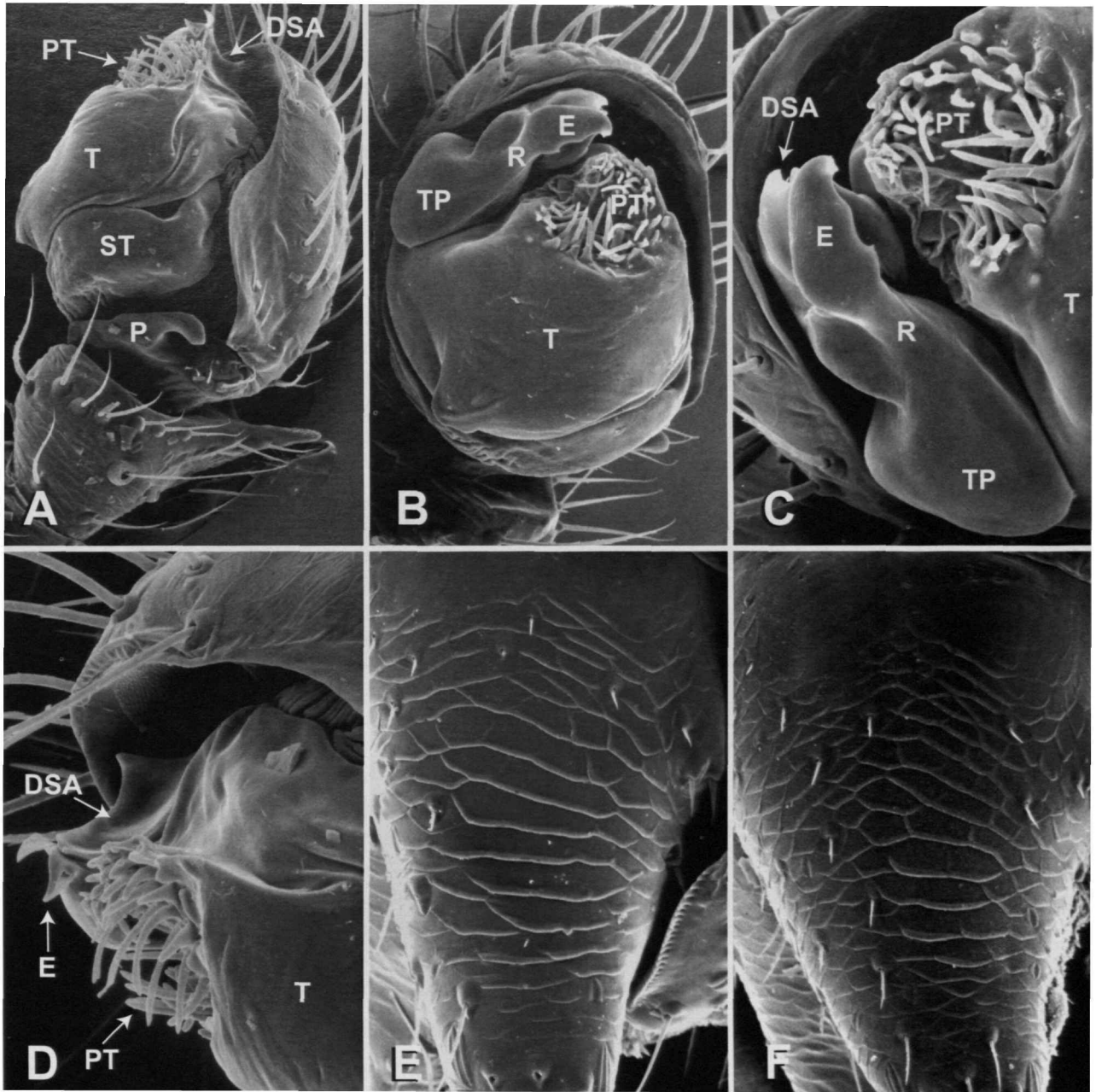


PLATE 62.—*Tapinocyba praecox*: A–D, male palp (right); E,F, ectal side of chelicera. A, ectal; B, ventral; C, mesoapical; D, ectoapical; E, male; F, female.

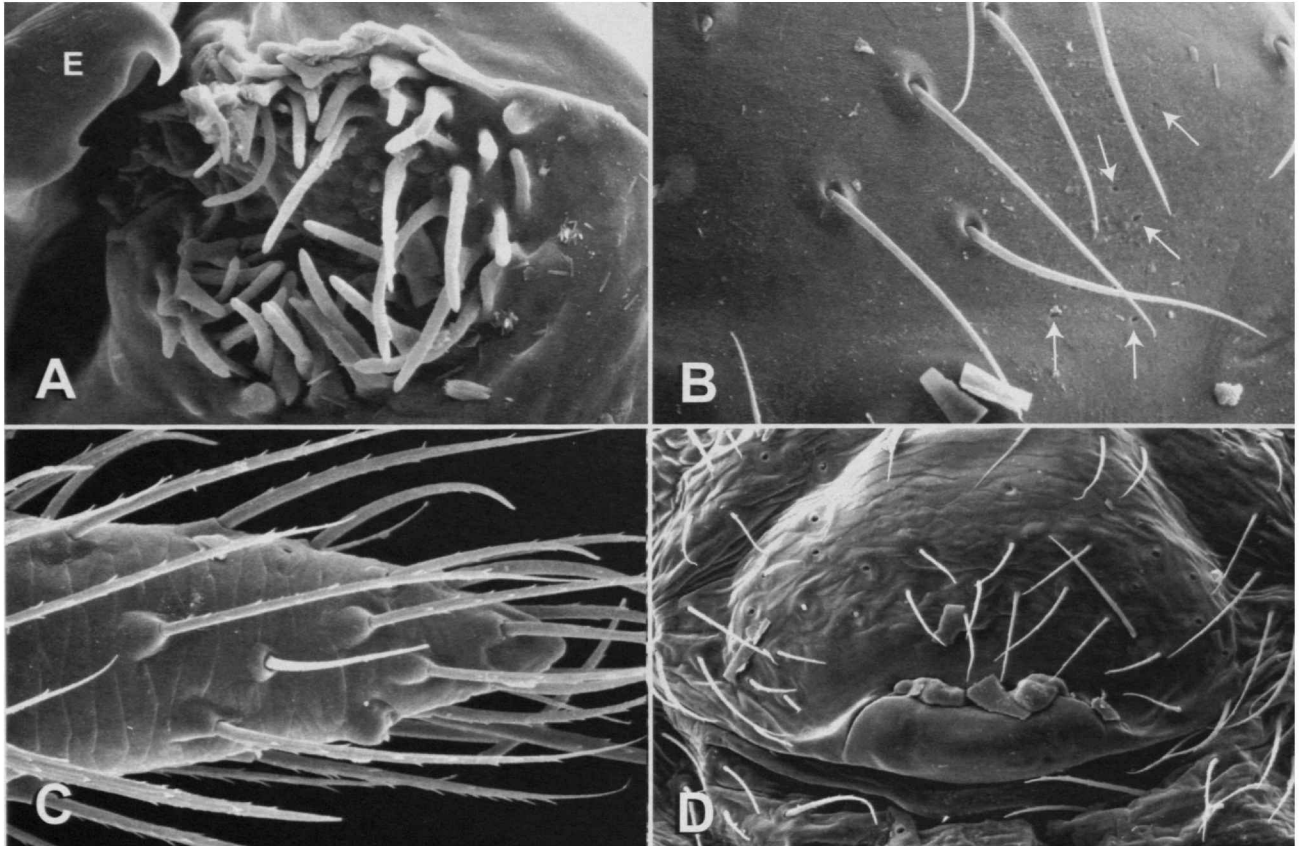
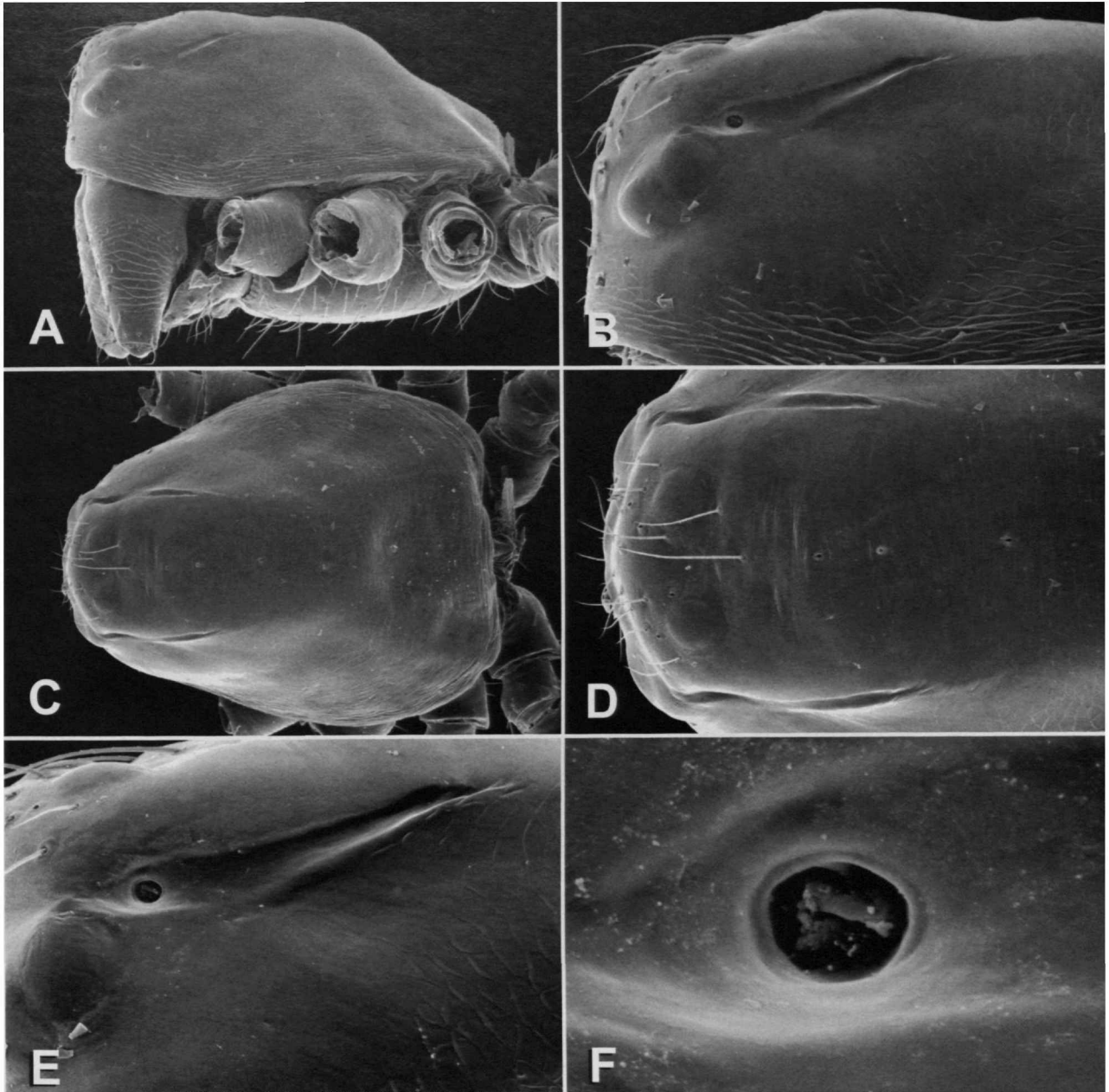


PLATE 63.—*Tapinocyba praecox*: A, protegular papillae (right); B, cuticular pores in male AME-PME region; C, female pedipalpal tarsus; D, epigynum, ventral.



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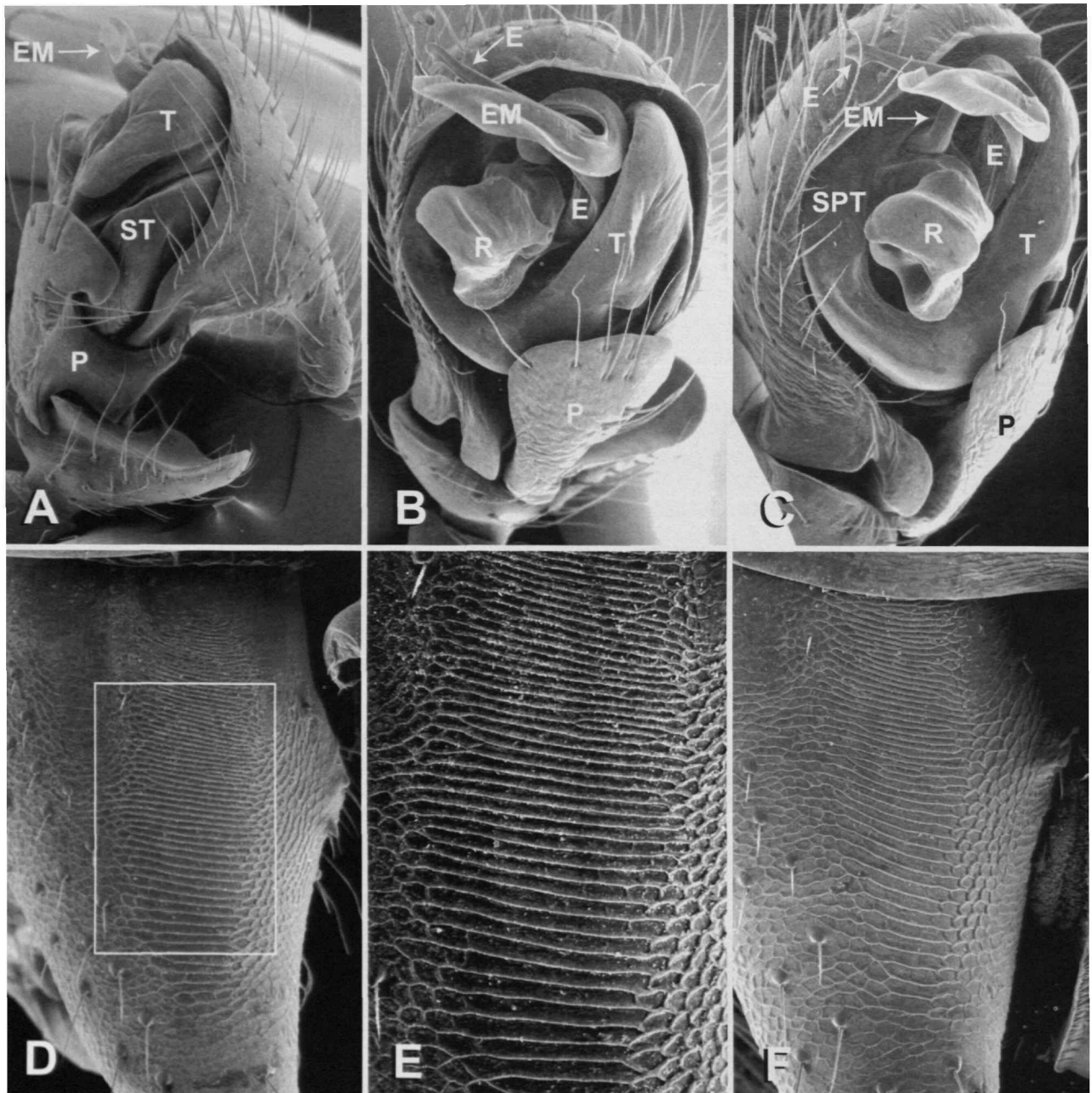


PLATE 65.—*Tibioploides pacificus*: A–C, male palp; D–F, ectal side of chelicera. A, ectal; B, ventral; C, mesoventral; D, male; E, detail of D; F, female.

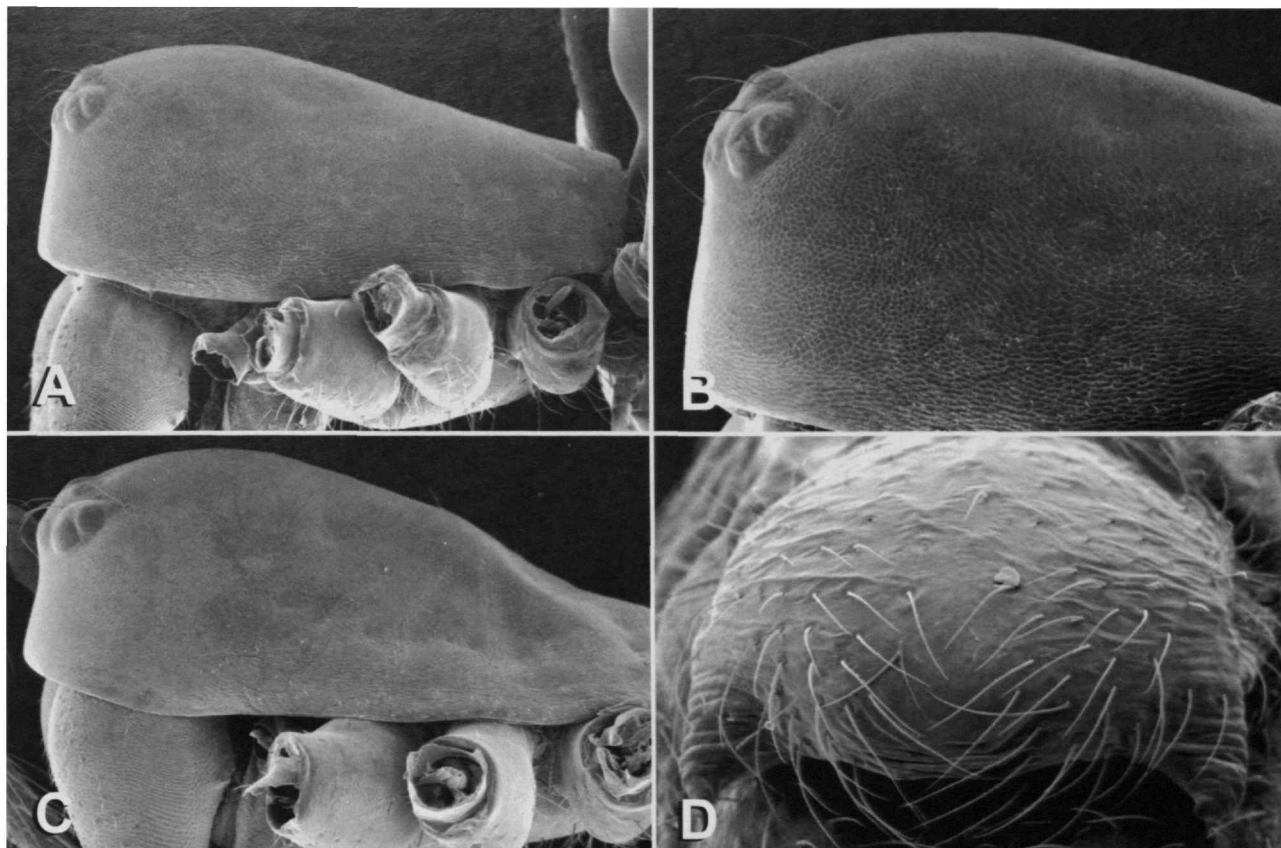


PLATE 66.—*Tibioplodes pacificus*: A,B, male prosoma; C, female prosoma; D, epigynum. A-C, lateral; D, ventral.

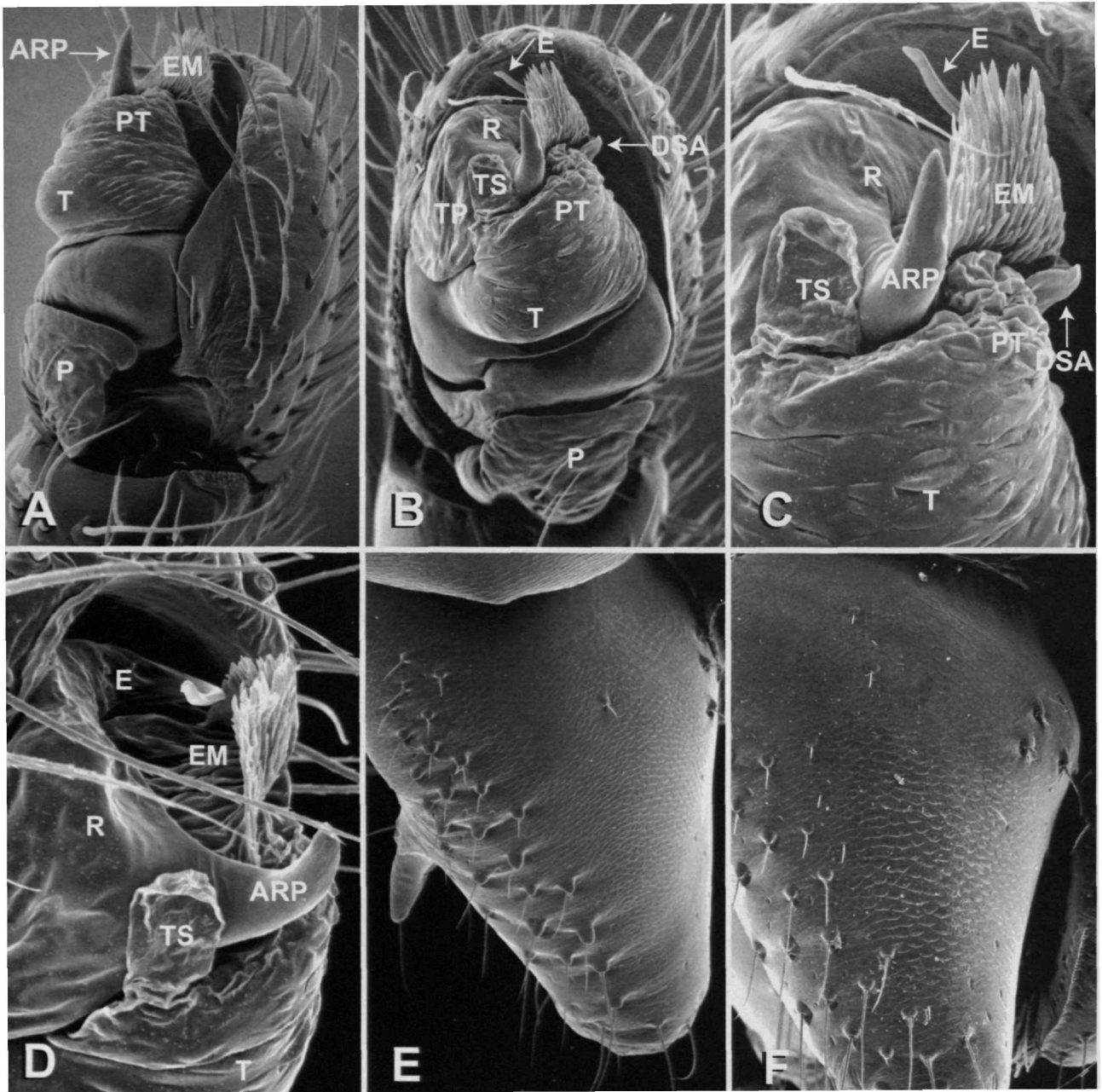


PLATE 67.—*Tmeticus tolli*: A–D, male palp; E, F, ectal side of chelicera. A, ectal; B, ventral; C, ventral; D, mesoapical; E, male; F, female.

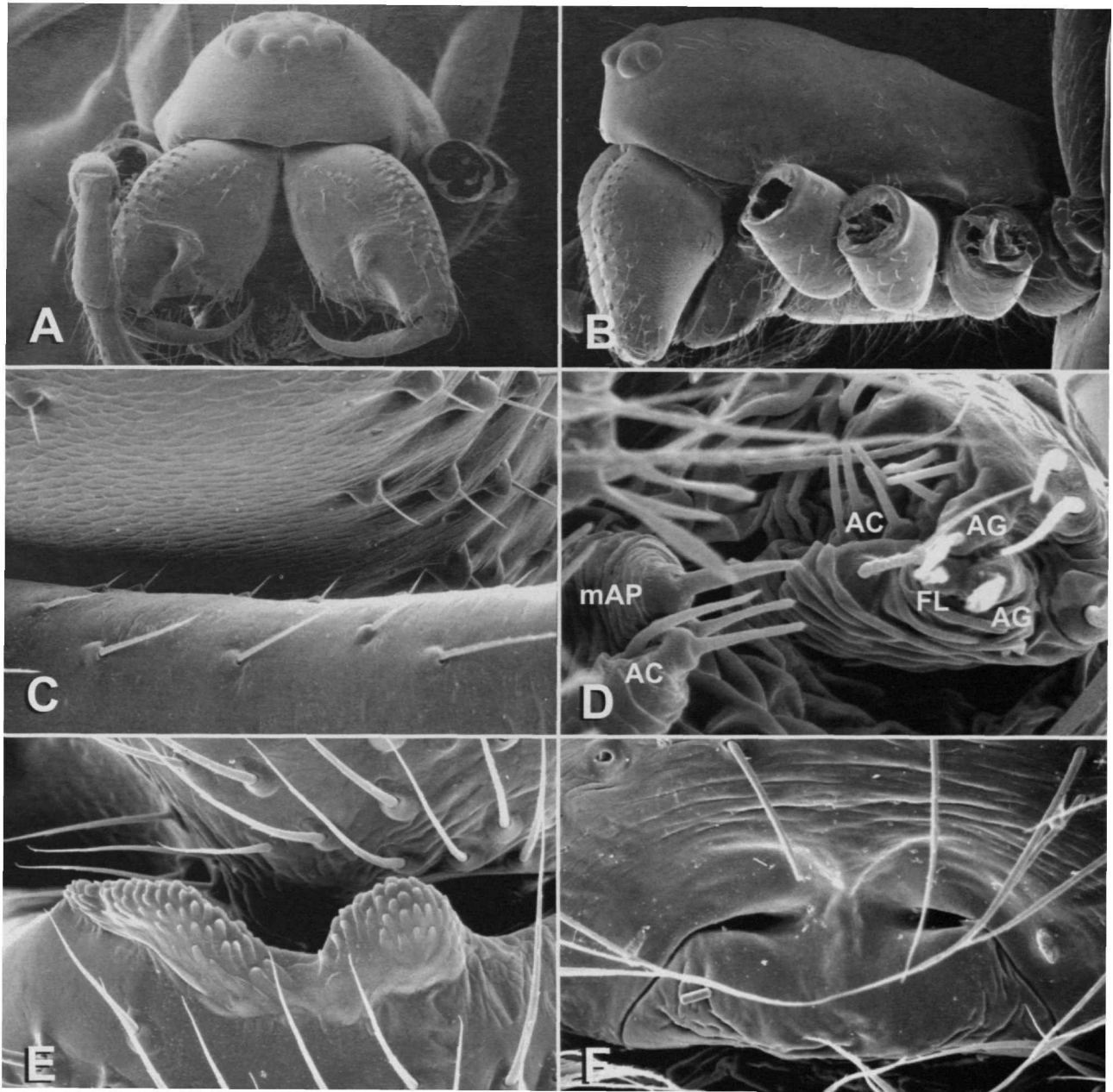


PLATE 68.—*Tmeticus tolli*: A, male prosoma, frontal; B, lateral; C, male stridulatory organ, detail of cheliceral striae and femoral plectra (enlarged setal basis); D, male PMS and PLS (right, not reversed); E, male tibial apophysis, dorsal; F, epigynum, ventral.

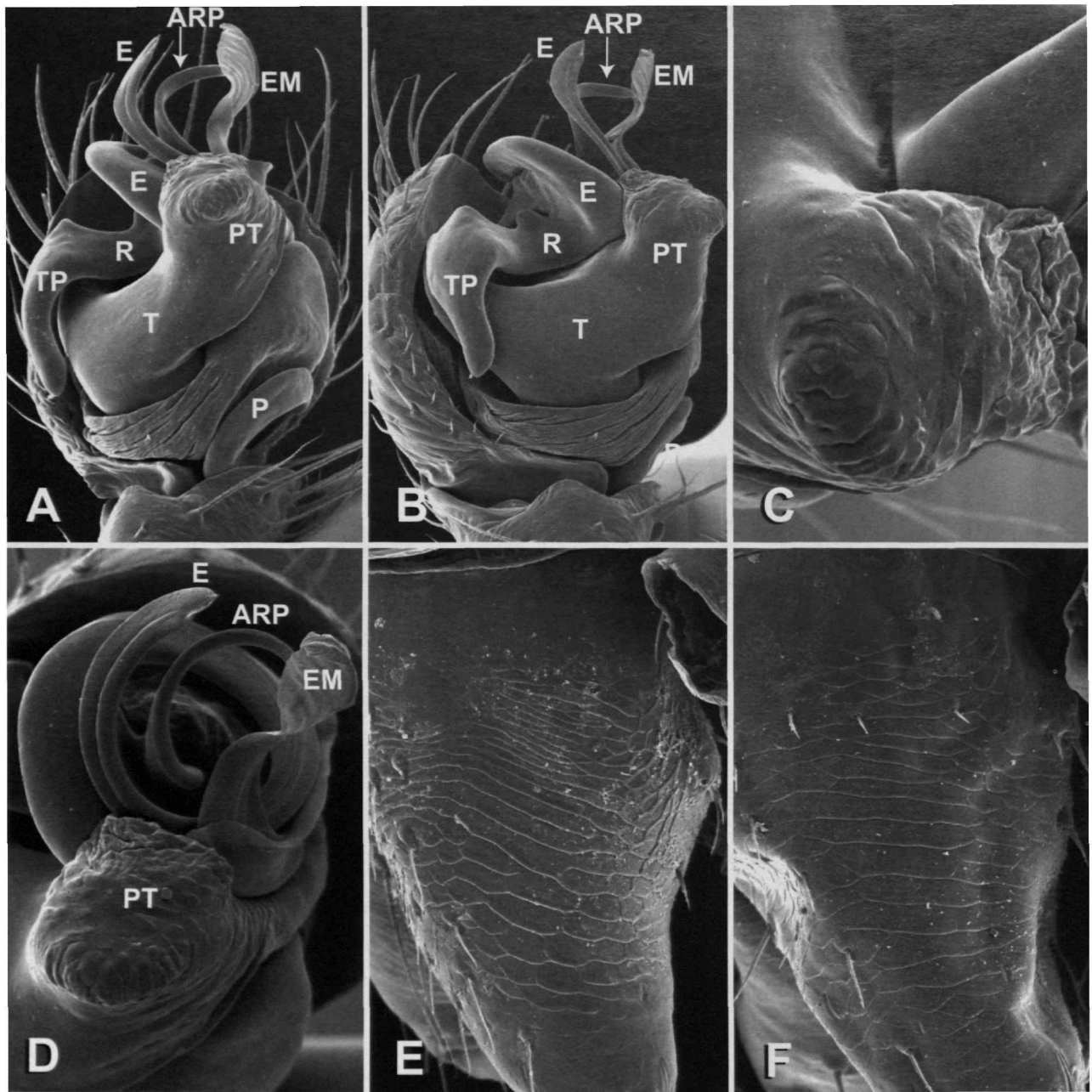


PLATE 69.—*Typhochrestus digitatus*: A–D, male palp; E, F, ectal side of chelicera. A, ventral; B, mesoventral; C, protegulum, apical; D, embolic division apical; E, male; F, female.



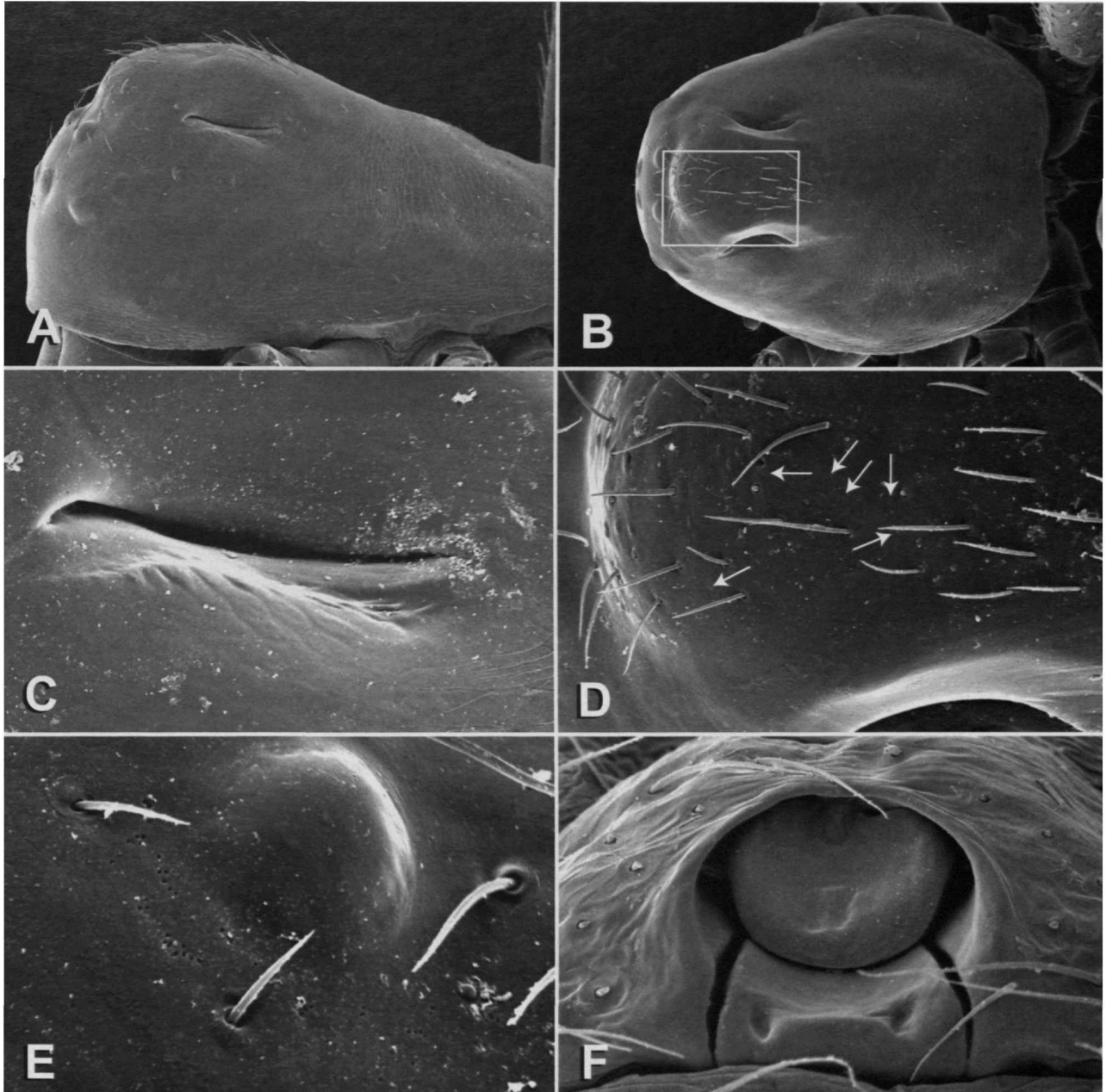


PLATE 70.—*Typhochrestus digitatus*: A–E, male prosoma; F, epigynum. A, lateral; B, dorsal; C, prosomic sulcus, lateral; D, dorsal (arrows indicate pores); E, PME; F, ventral.

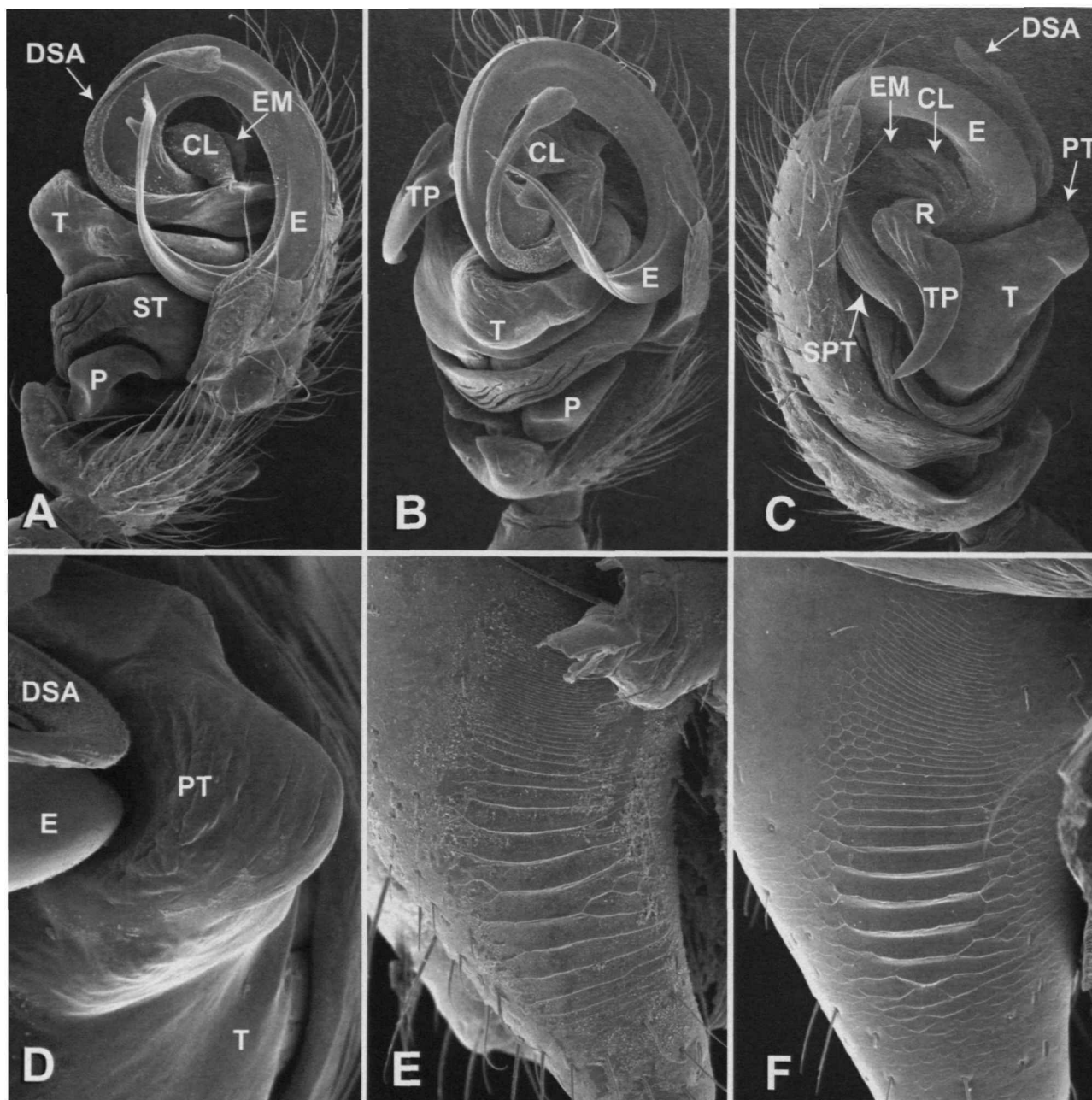


PLATE 71.—*Walckenaeria acuminata*: A–D, male palp; E, F, ectal side of chelicera. A, ectal; B, ventral; C, mesal; D, protogulum, apical; E, male; F, female.

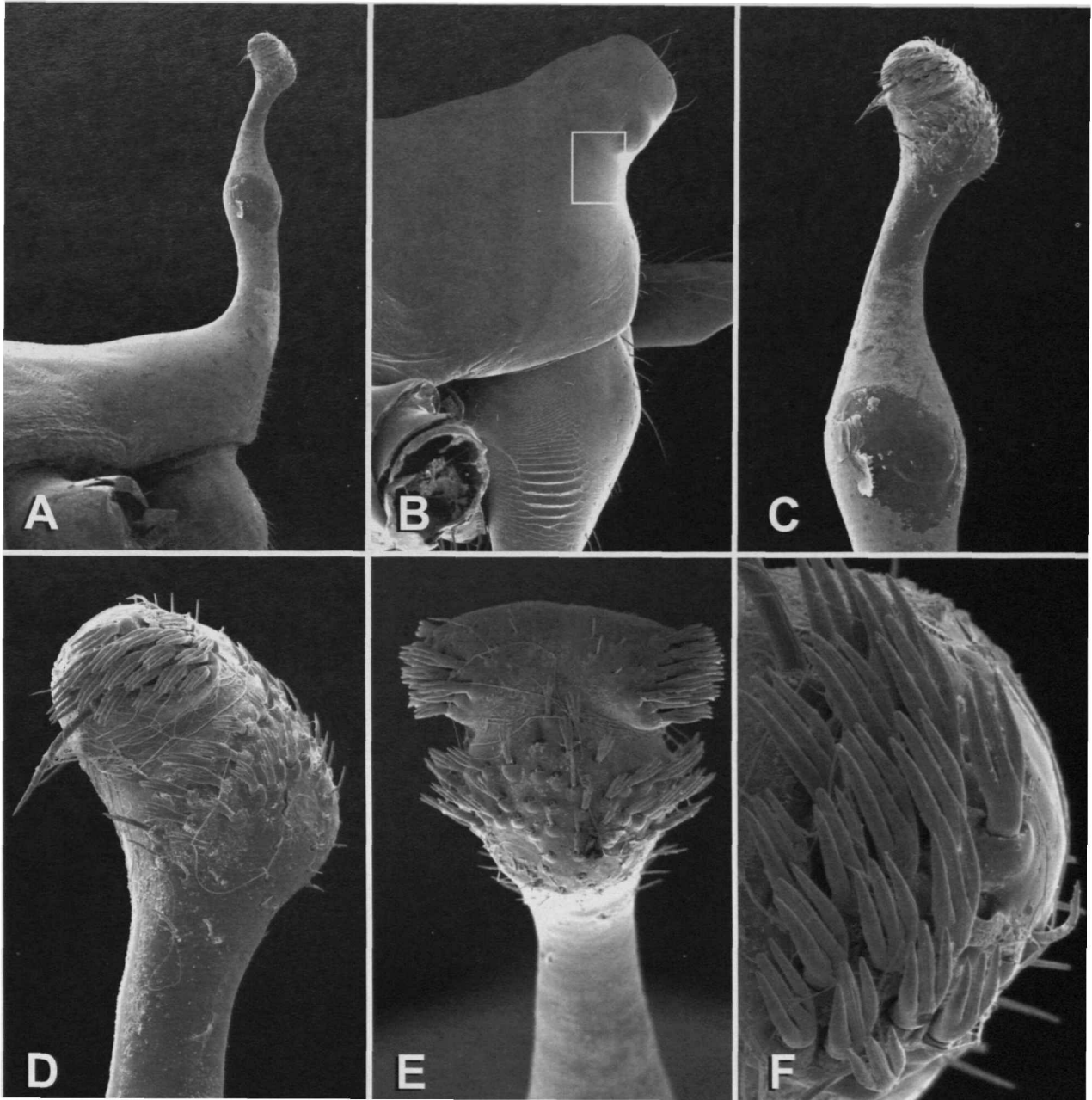


PLATE 72.—*Walckenaeria acuminata*: A,C–F, male prosoma; B, female prosoma. A, lateral; B, cephalic region, lateral; C, prosomic "turret," lateral; D, detail of distal end, lateral; E, same, frontal; F, detail of modified setae.

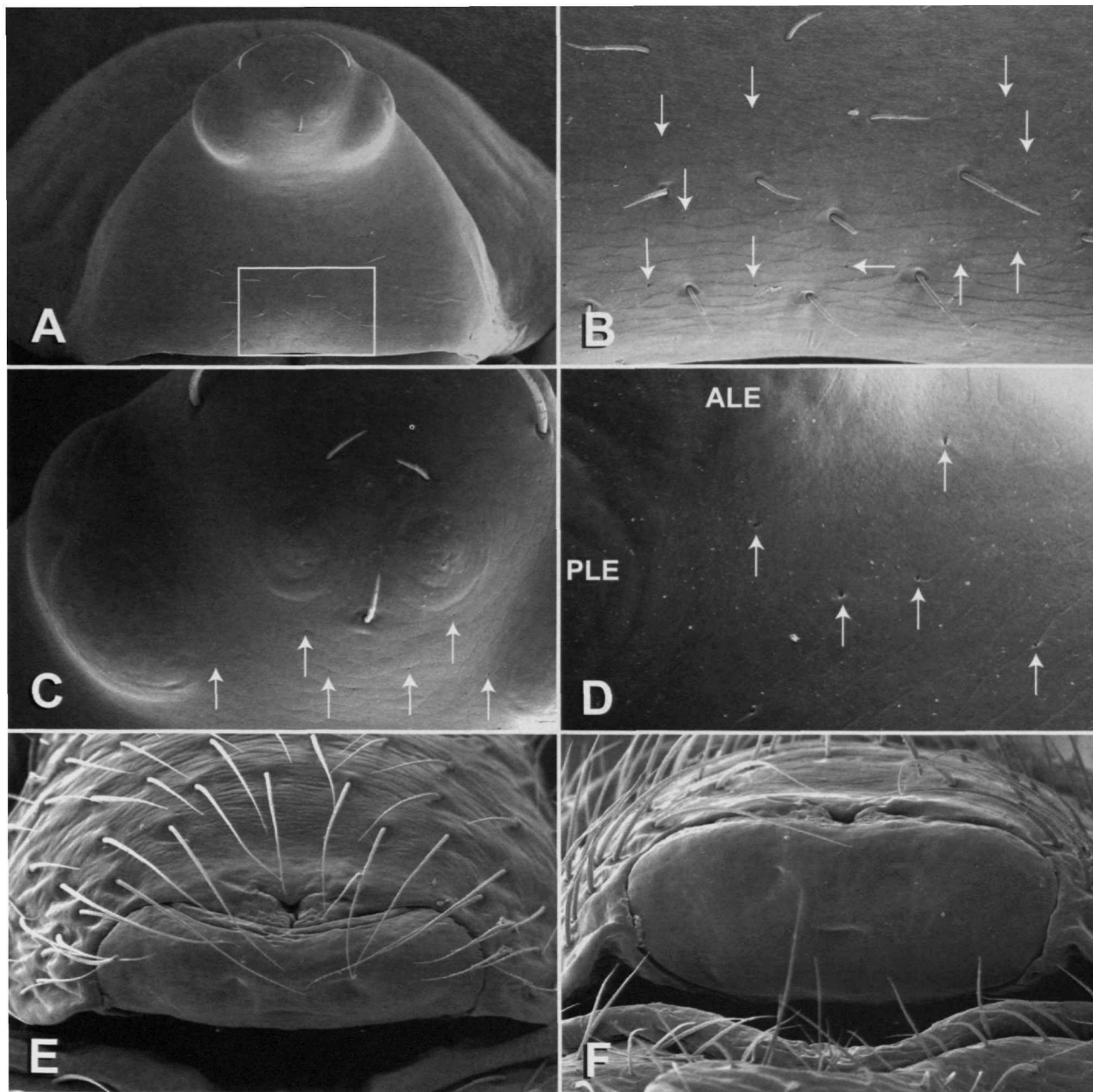


PLATE 73.—*Walckenaeria acuminata*: A–D, female prosoma; E, F, epigynum. A, frontal; B, clypeus, detail; C, eye region, frontal; D, detail of pores, ventrad of lateral eyes region; E, ventral; F, caudal.

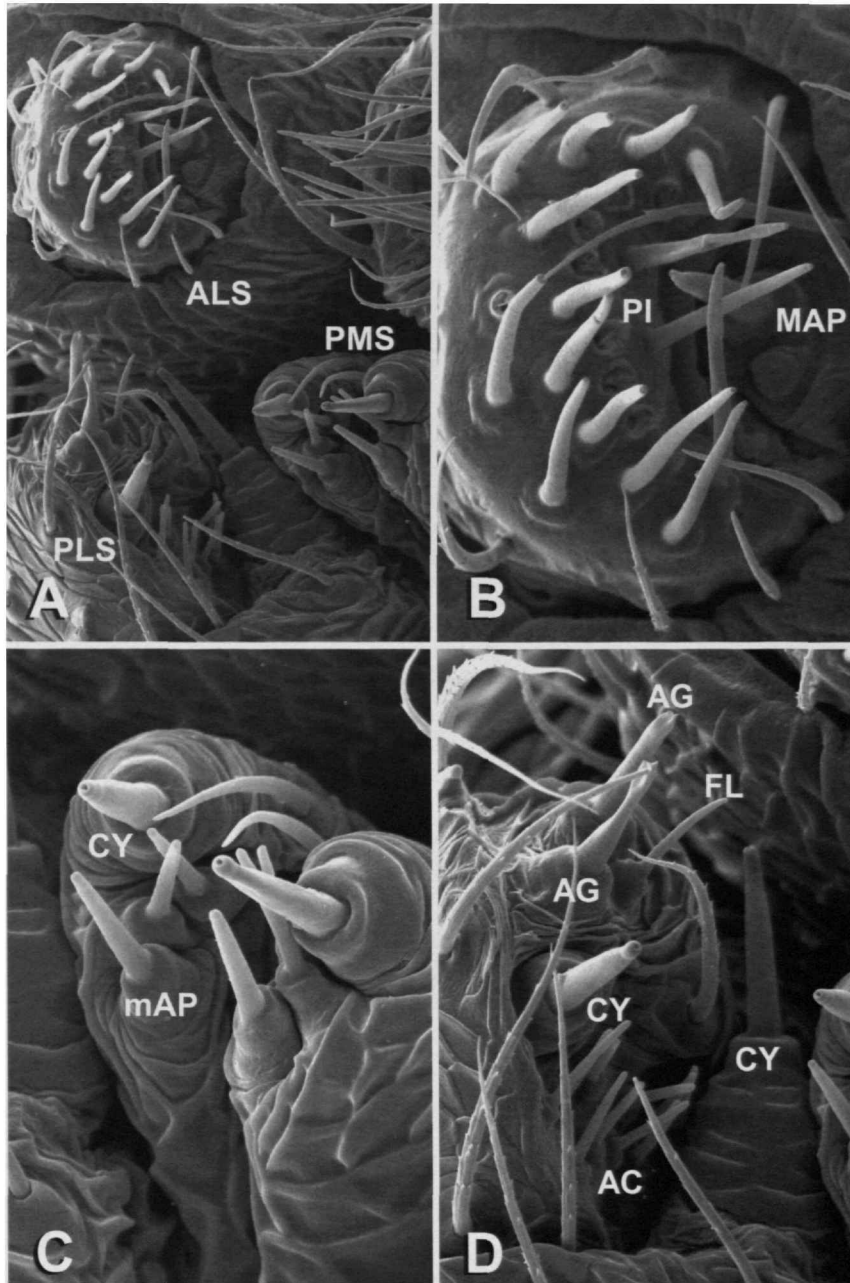


PLATE 74.—*Walckenaeria acuminata*: A–D, female spinnerets (right, not reversed). A, spinneret group; B, ALS; C, PMS; D, PLS.

PLATE 75.—*Walckenaeria directa*: A–D, male palp (right); E, ectal side of chelicera; F, PLS. A, apicoventral; B, ventral; C, embolic division, ectoventral; D, protegulum, ventral; E, male; F, male triad.

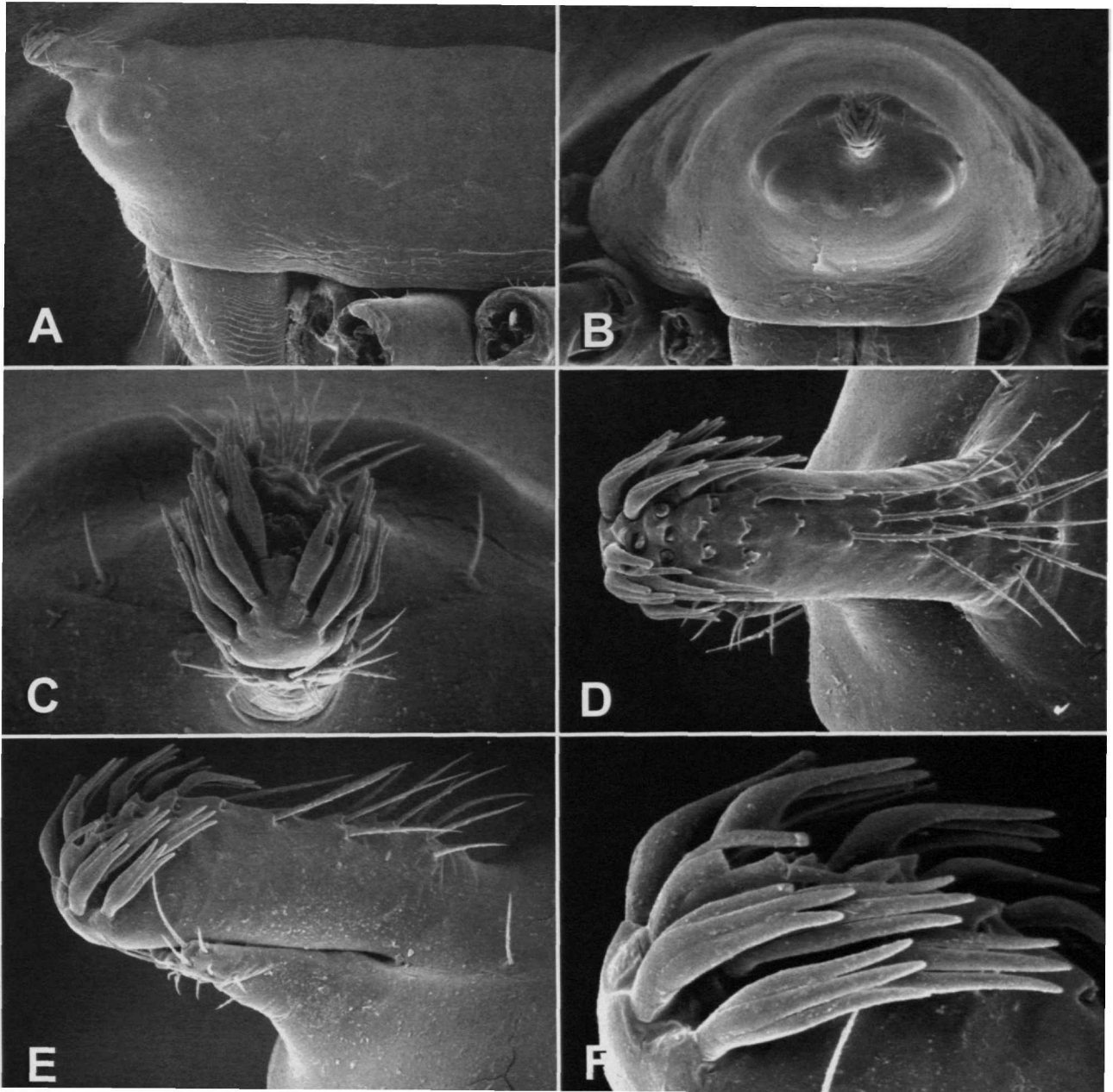


PLATE 76.—*Walckenaeria directa*: A–F, male prosoma. A, lateral; B, frontal; C, detail of cephalic lobe, frontal; D, same, dorsal; E, same, lateral; F, detail of modified setae.

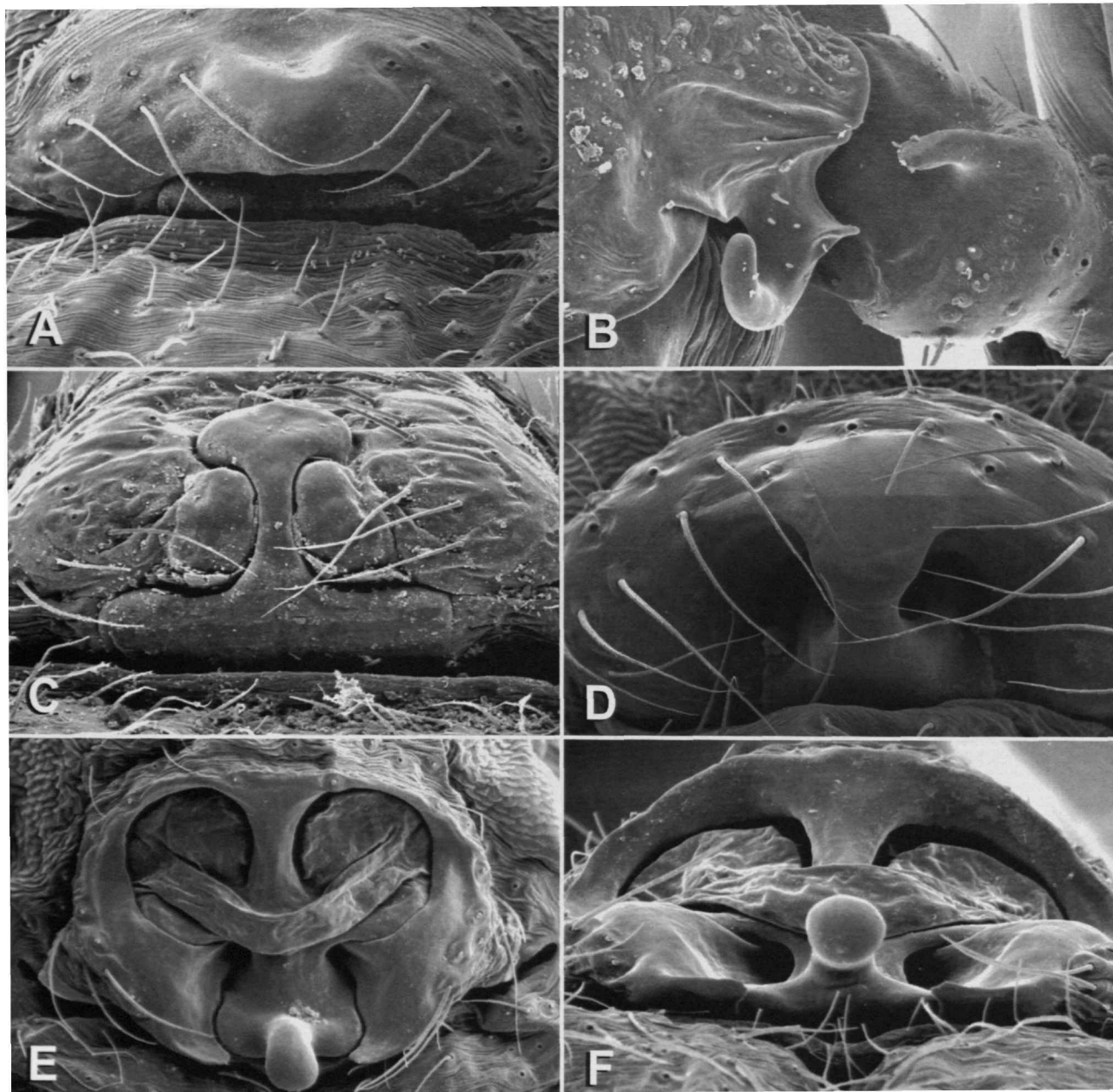


PLATE 77.—*Diplocentria bidentata*: A, epigynum, ventral. *Dismodicus decemoculatus*: B, paracymbium and tibial apophysis, ectal; C, epigynum, ventral. *Ostearius melanopygius*: D, epigynum, ventral. *Sisicus apertus*: E, epigynum, ventral; F, epigynum, caudal.



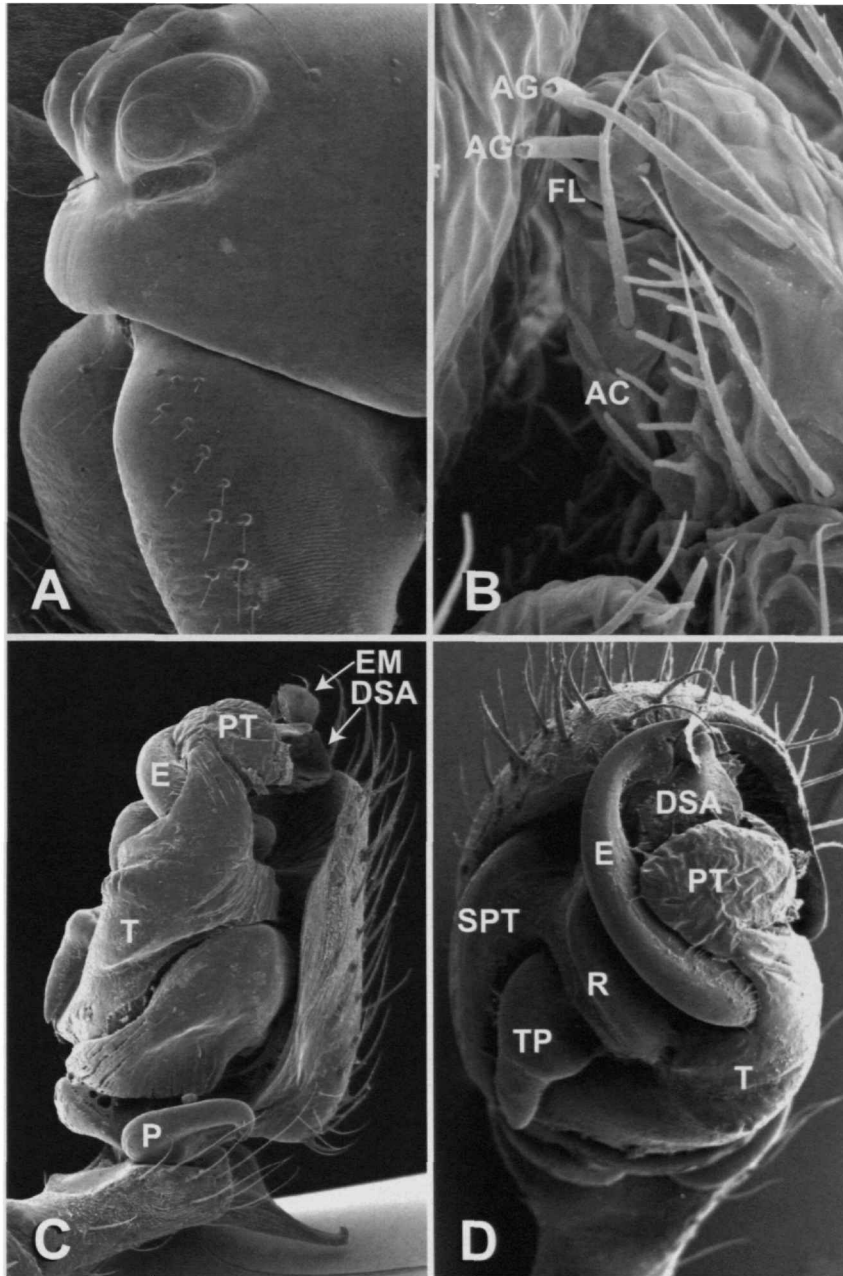


PLATE 78.—*Haplinis diloris*: A, male cephalic region, lateral; B, male PLS (right). *Pelecopsis dormiana*: C, male palp, ectal; D, same, ventral.

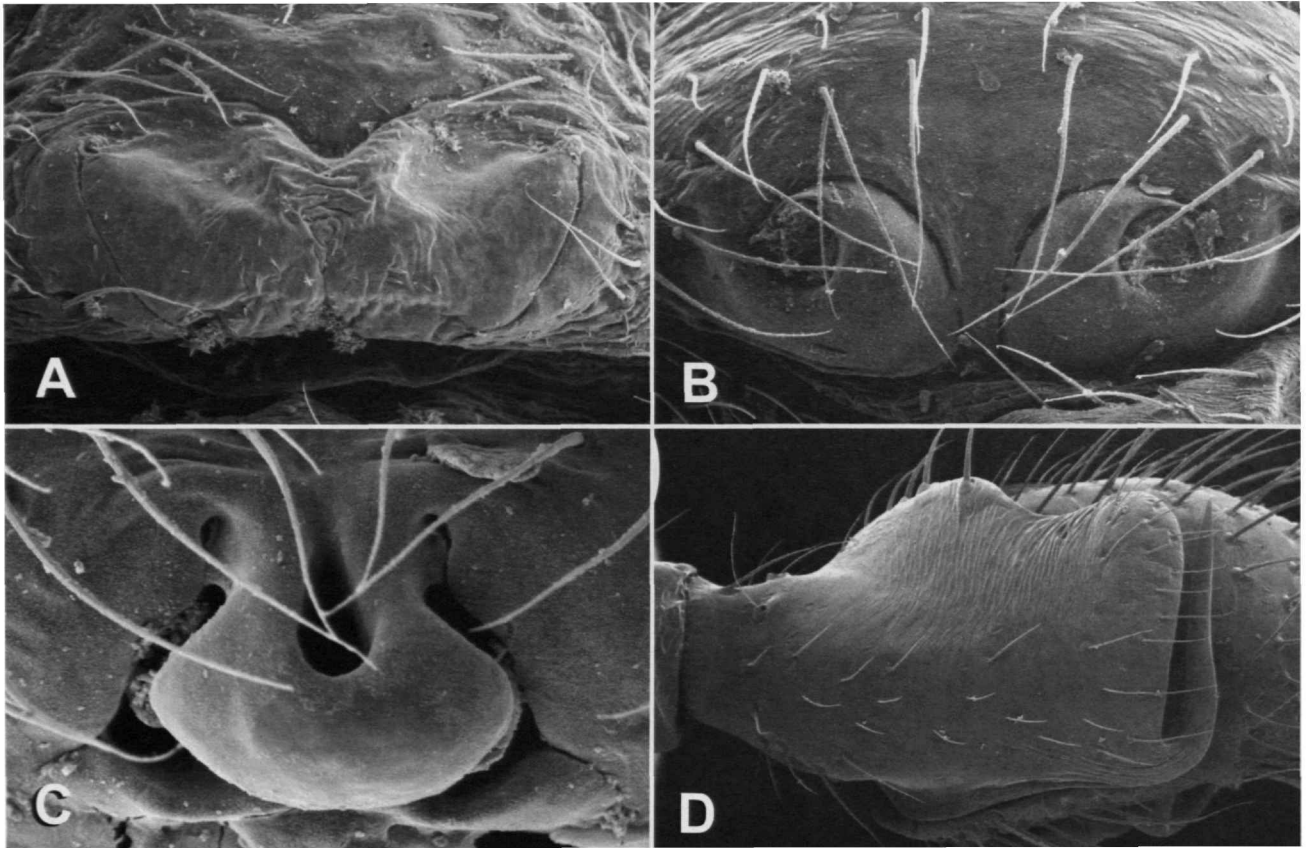


PLATE 79.—*Gongylidium rufipes*: A, epigynum, ventral. *Hylyphantes nigrinus*: B, epigynum, ventral. *Lophomma punctatum*: C, epigynum, ventral. *Diplocephalus cristatus*: D, male pedipalpal apophysis, dorsal.

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