

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 2855, pp. 1-16, figs. 1-62  
September 18, 1986

## On the Tibial and Patellar Glands, Relationships, and American Genera of the Spider Family Leptonetidae (Arachnida, Araneae)

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### ABSTRACT

Middorsal tibial integumentary glands opening on cuticular plates, previously known only in telemid spiders, are newly reported in leptonetids; their presence suggests that the Telemidae and Leptonetidae are sister groups. Species of the leptonetid subfamily Archoleonetinae Gertsch share a unique form of tibial cuticular plate that corroborates the monophyly of that group, even though it was originally based only on a plesiomorphy (retention of the normal eye pattern). Apparently homologous cuticular plates also occur on the patellae of most leptonetids examined; differences in patellar plate structure corroborate both Brignoli's hypothesis that several genera exist within the American leptonetid fauna and his delimitation of the genus *Neoleoneta* Brignoli. Congruence between patellar plate structure and

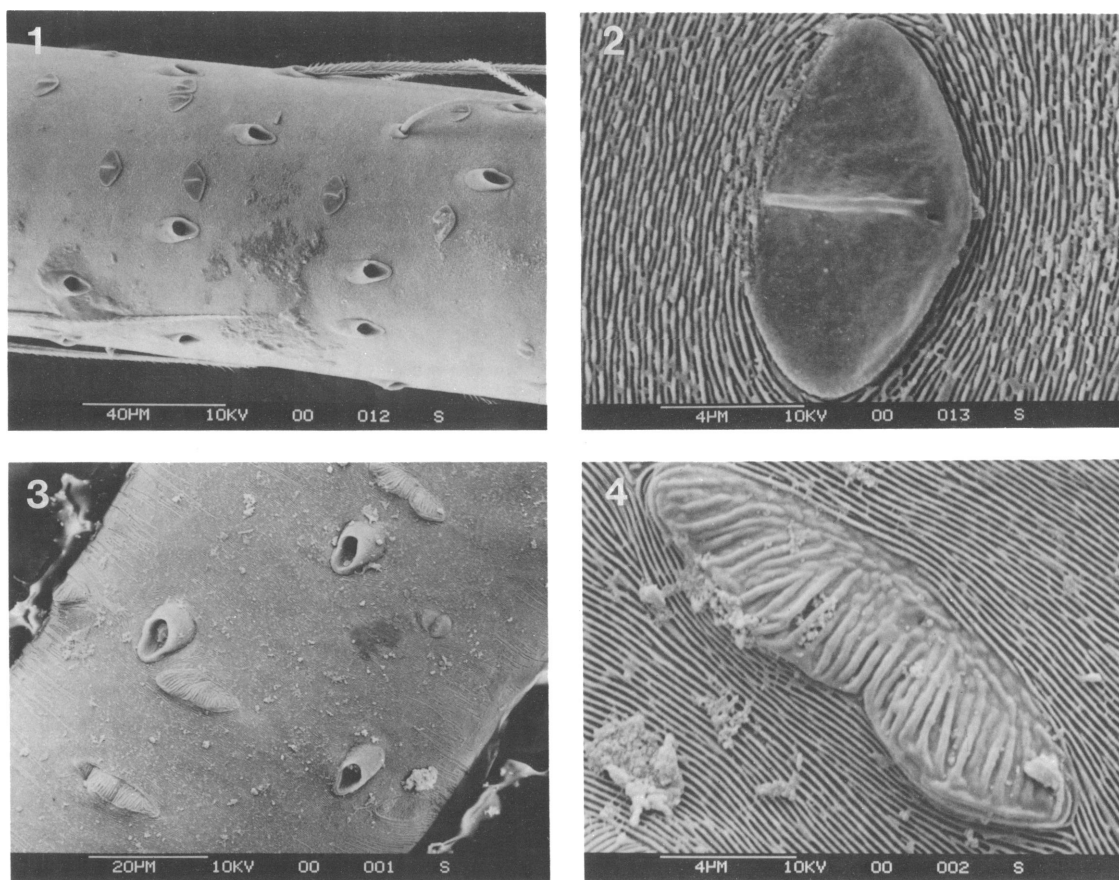
genitalic features supports the establishment of two additional genera: *Appaleptoneta*, described for the Appalachian species *Leptoneta silvicultrix* Crosby and Bishop (type species), *L. coma* Barrows, *L. gertschi* Barrows, *L. fiskei* Gertsch, *L. jonesi* Gertsch, *L. credula* Gertsch, and *L. barrowsi* Gertsch, and *Calileptoneta*, described for the California and Oregon species *L. oasa* Gertsch (type species), *L. noyoana* Gertsch, *L. wapiti* Gertsch, *L. helferi* Gertsch, and *L. californica* Banks. Two remaining American species not assigned to *Archoleoneta*, *Neoleoneta*, *Appaleptoneta*, or *Calileptoneta* (*L. sandra* Gertsch and *L. brunnea* Gertsch) each have peculiar patellar plates and genitalia, and may prove to be more closely related to Mediterranean or east Asian genera than to other American taxa.

### INTRODUCTION

Leptonetids are small spiders, about a dozen genera of which have been found in de-

tritrus and caves in the Mediterranean area, eastern Asia, and North America. Although

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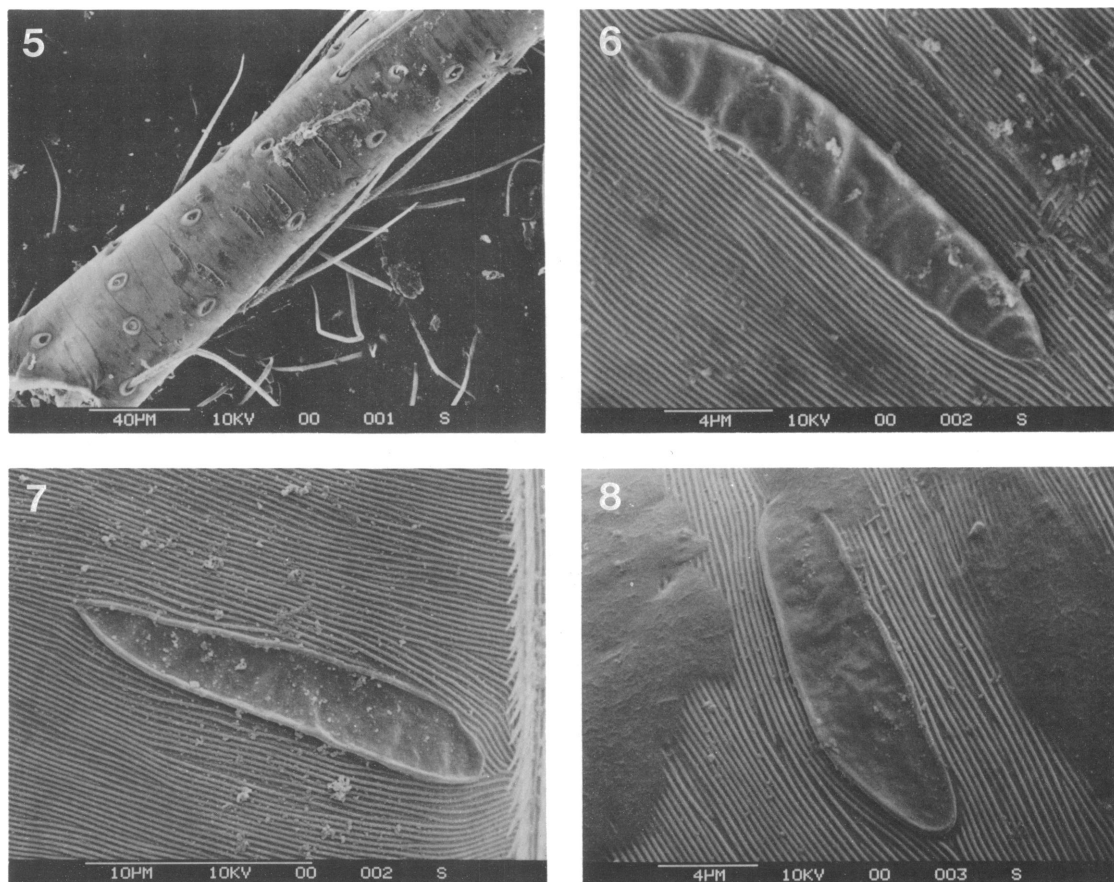


Figs. 1–4. Cuticular plates of leptonetid tibial glands. 1, 2. *Falcileptoneta striata* (Oi), female, leg I. 3, 4. “*Leptoneta*” *sandra* Gertsch, female, leg I.

they have traditionally been considered “haplogyne” spiders, their relationships have never been cladistically resolved. Early workers, such as Fage (1913) and Simon (1914), treated leptonetids and telemids as subfamilies within a single family, but the two groups have been separated at least since the time of Petrunkevitch (1923). Brignoli (1979a), who has contributed much to our knowledge of the group, could find “no synapomorphies shared by the Leptonetidae and any other haplogyne family,” and suggested that they should be placed in a superfamily of their own.

The American leptonetid fauna was reviewed by Gertsch (1974), who recognized only two genera. Three new species were placed in the new genus *Archoleptoneta* and assigned to a subfamily of their own, the Ar-

choleptonetinae, on the basis of their retention of a normal eye arrangement, an obviously plesiomorphic feature (the remaining genera, constituting the Leptonetinae, are characterized by a unique eye arrangement in which two of the posterior eyes have retreated posteriorly on the carapace). The remaining 41 American species recognized by Gertsch (1974) were placed in the type genus *Leptoneta*, originally described from the Mediterranean region. This generic classification has been controversial, because Gertsch (1974) did not accept the genus *Neoleptoneta*, proposed by Brignoli (1972) for several Mexican species originally described in *Leptoneta* by Gertsch (1971). Brignoli (1977) objected strenuously to Gertsch’s synonymy of both *Neoleptoneta* and the Mediterranean genus *Paraleptoneta* Fage (1913).



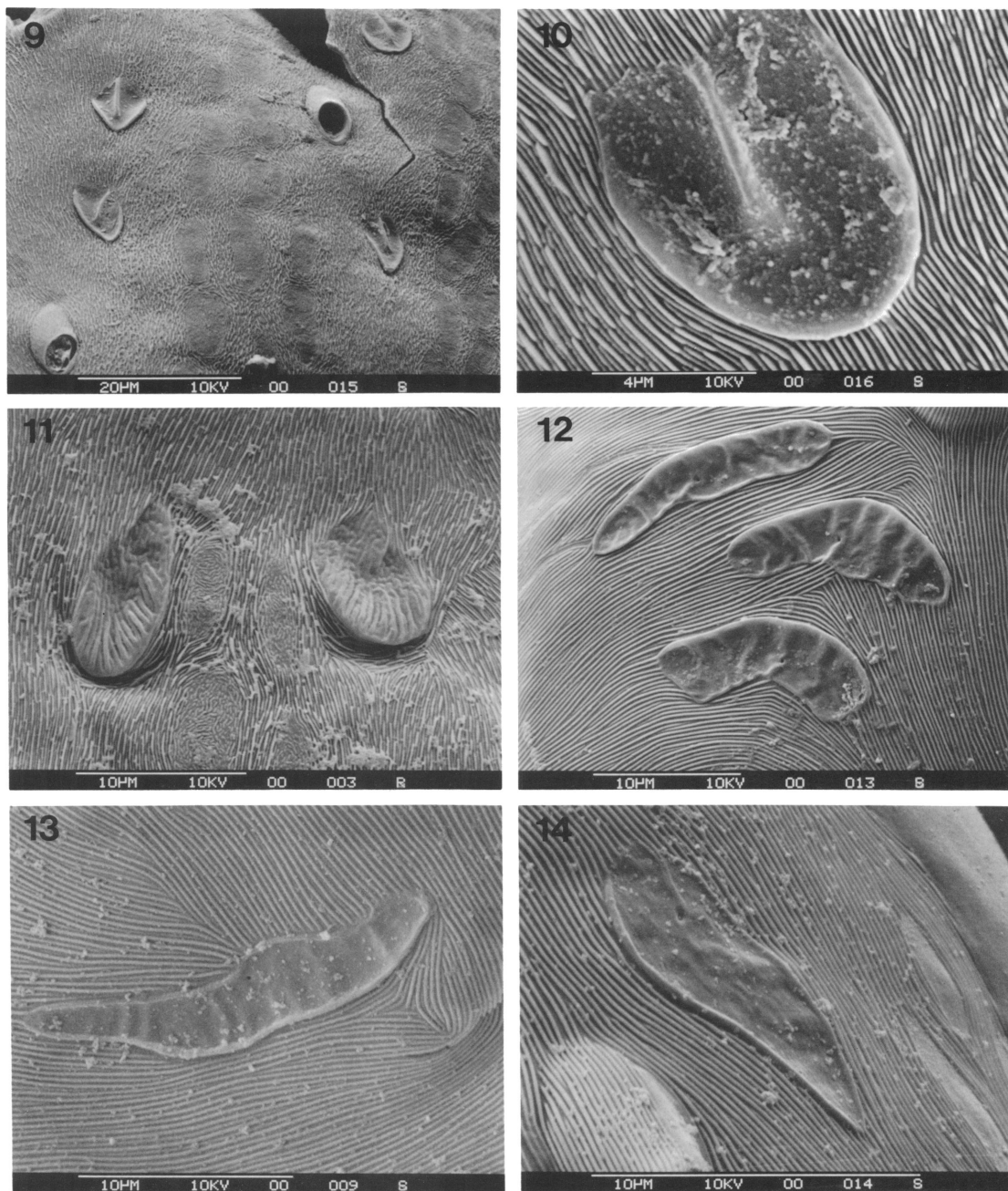
Figs. 5–8. Cuticular plates of leptonetid tibial glands. 5, 6. *Archoleptoneta schusteri* Gertsch, female, leg II. 7. *A. garza* Gertsch, female, leg II. 8. *A. obscura* Gertsch, female, leg II.

with *Leptoneta*, and argued that “the American species should be grouped in 4–5 genera” rather than lumped into *Leptoneta*.

In a fascinating series of recent papers, Emerit (1981, 1984, in press) and Emerit and Juberthie (1983) have reported on the discovery, in the haplogyne family Telemidae, of middorsal tibial integumentary glands, a feature previously unknown in any other spiders. These multicellular glands occur on the tibia of each leg (but not the pedipalps) in both sexes, and may produce a repugnatorial secretion. Two types of cuticular modifications are associated with the glands. In the genera *Telesa* and *Usofila*, the tibiae each bear a row of as many as 22 oval, pore-bearing plates, whereas in the genera *Apneumonnella*, *Seychellia*, *Cangodermes*, and *Jocquella*, the normally striated cuticle is interrupted

by a series of smooth, transversely oriented, pore-bearing furrows that presumably help disperse the secretion.

Emerit (1981) found no trace of tibial glands in one European leptonetid, *Leptoneta microphthalmia* Simon. Recently, while investigating the trichobothria of leptonetids, it became apparent that seemingly homologous cuticular plates do nonetheless occur in some other species of leptonetids. Communication of this discovery to Dr. R. R. Forster of the Otago Museum, Dunedin, New Zealand, elicited the response that he had found similar structures in leptonetids, but on the patellae rather than the tibiae! Hence this paper, which presents a survey of the occurrence and taxonomic implications of the tibial and patellar plates of available leptonetid species.

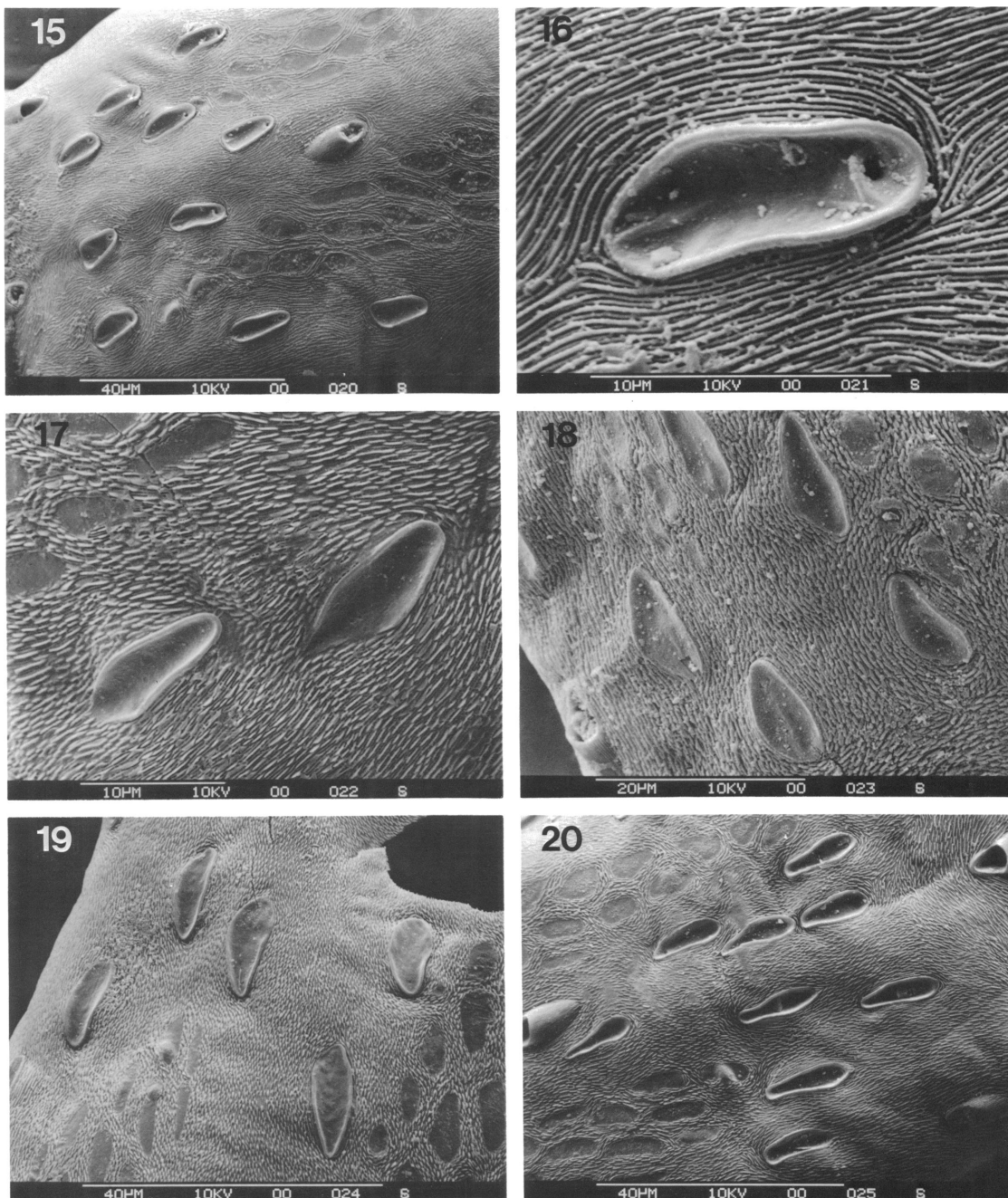


Figs. 9–14. Cuticular plates on patellae of the leptonetid species known to have tibial glands. 9, 10. *Falcileptoneta striata* (Oi), female, leg II. 11. “*Leptoneta*” *sandra* Gertsch, female, leg I. 12. *Archoleptoneta schusteri* Gertsch, female, leg II. 13. *A. garza* Gertsch, female, leg II. 14. *A. obscura* Gertsch, female, leg IV.

I thank Drs. P. M. Brignoli, M. Emerit, R. R. Forster, W. J. Gertsch, W. P. Maddison, and R. J. Raven for their comments and sug-

gestions; Dr. Emerit was especially generous in making his forthcoming paper available in manuscript form. Specimens of two Japanese

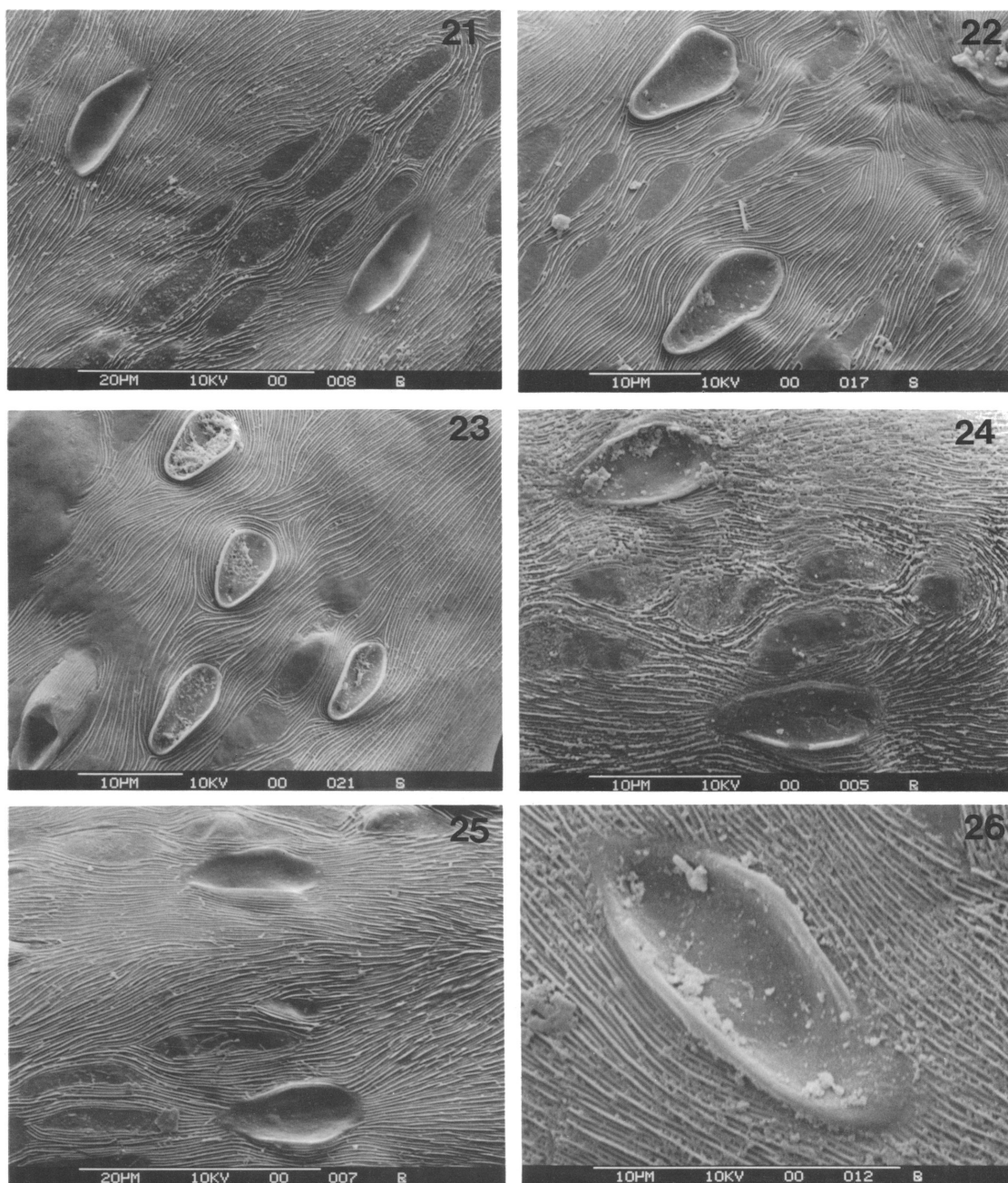




Figs. 15–20. Cuticular plates on patellae of Mediterranean *Leptoneta* species. **15, 16.** *L. infuscatissima* Simon, male, leg III. **17.** *L. abeillei* Simon, male, leg II. **18.** *L. olivacea* Simon, female, leg IV. **19.** *L. trabucensis* Simon, male, leg III. **20.** *L. vittata* Fage, female, leg III.

leptonetid species were kindly donated by Drs. T. Yaginuma and K. Nishikawa of Ohtemon-Gakuin University. Assistance with the scanning electron microscope was provided by

Ms. Lauren Duffy of the American Museum of Natural History. This project was supported by grant BSR-8406225 from the National Science Foundation.

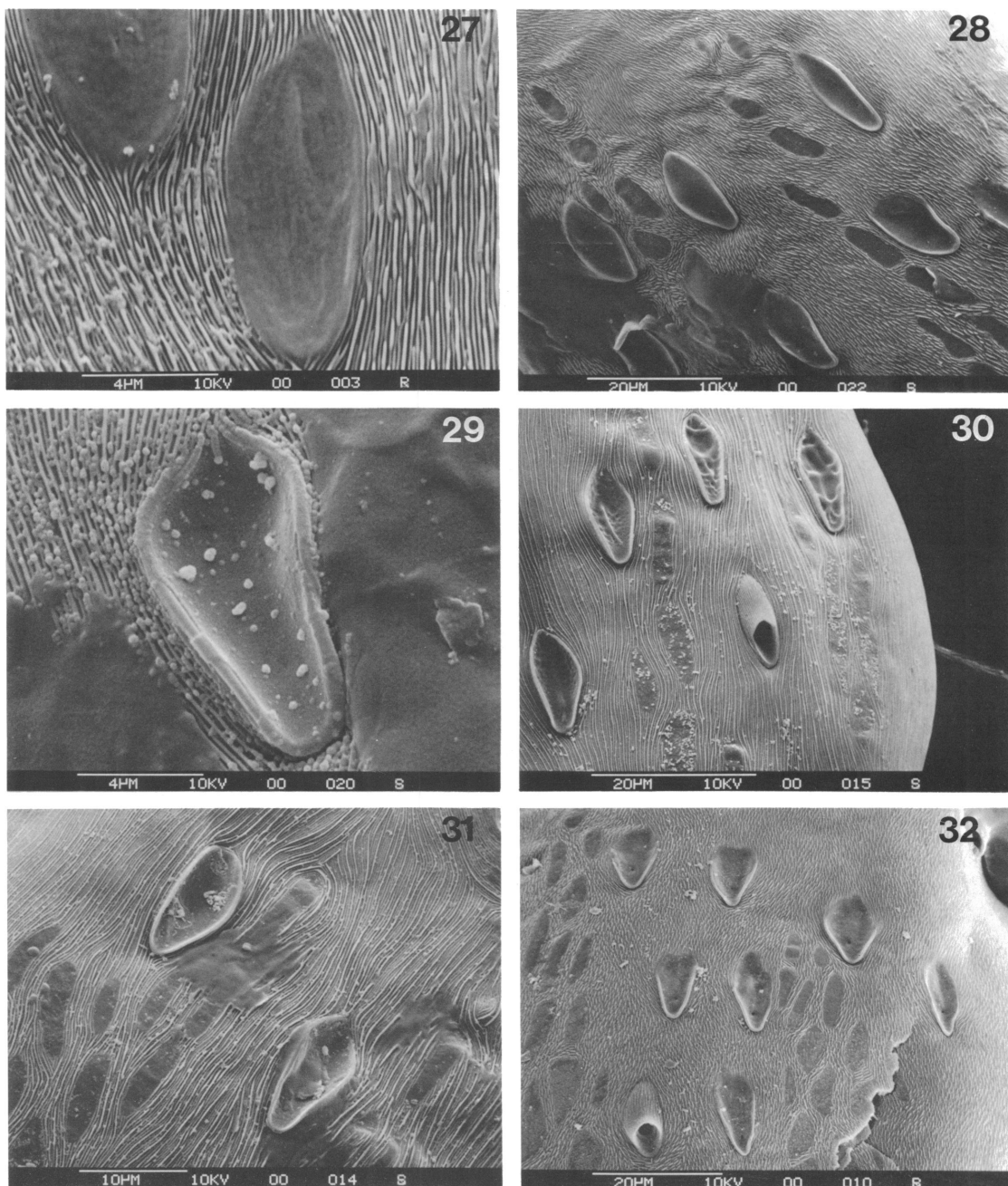


Figs. 21–26. Cuticular plates on patellae of *Neoleptoneta* species. 21. *N. alabama* (Gertsch), female, leg I. 22. *N. anopica* (Gertsch), female, leg II. 23. *N. apachea* (Gertsch), male, leg III. 24. *N. archeri* (Gertsch), male, leg II. 25. *N. arkansa* (Gertsch), female, leg IV. 26. *N. blanda* (Gertsch), female, leg I.

#### TIBIAL GLANDS AND FAMILIAL RELATIONSHIPS

Examination of the tibiae of representatives of each of the 44 American leptonetid

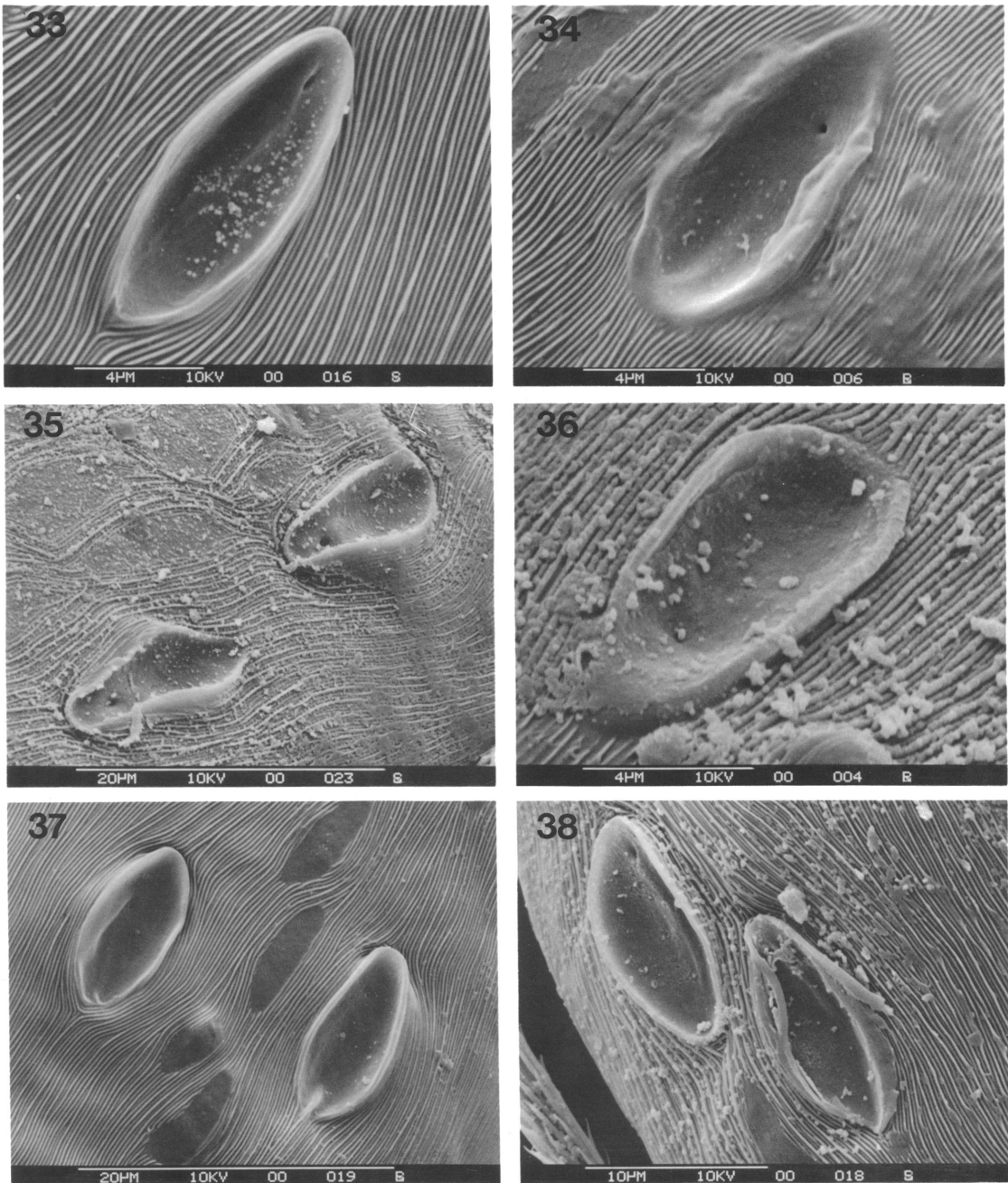
species treated by Gertsch (1974), except for *Neoleptoneta anopica* (Gertsch), indicates that cuticular plates occur in four of them. Access to Old World leptonetid material has been



Figs. 27–32. Cuticular plates on patellae of *Neoleptoneta* species. 27. *N. bonita* (Gertsch), male, leg IV. 28. *N. capilla* (Gertsch), male, leg I. 29. *N. chisea* (Gertsch), female, leg II. 30. *N. coeca* (Chamberlin and Ivie), female, leg III. 31. *N. concinna* Gertsch, male, leg II. 32. *N. delicata* (Gertsch), male, leg III.

much more restricted, but I have been able to confirm Emerit's (1981) indication that *Leptoneta microphthalmia* Simon lacks the tibial plates. The same is also true for specimens of five other Mediterranean *Leptoneta*

species (*L. abeillei* Simon, *L. infusca minos* Simon, *L. olivacea* Simon, *L. trabucensis* Simon, and *L. vittata* Fage), and for the Japanese species *Masirana akiyoshiensis* (Oi). However, cuticular plates are present on the



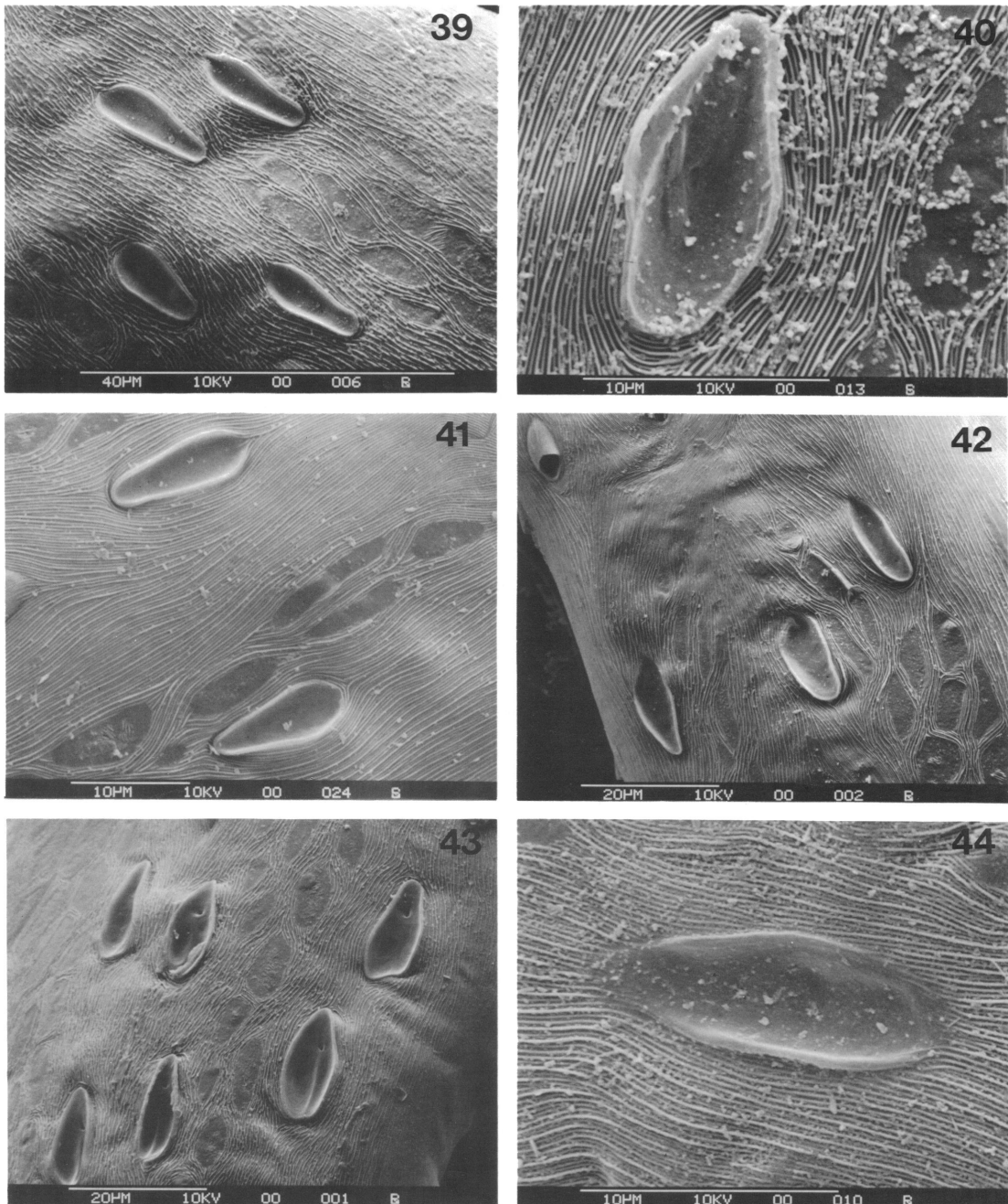
Figs. 33–38. Cuticular plates on patellae of *Neoleptoneta* species. 33. *N. devia* (Gertsch), female, leg II. 34. *N. georgia* (Gertsch), female, leg II. 35. *N. isolata* (Gertsch), male, leg I. 36. *N. iviei* (Gertsch), female, leg IV. 37. *N. limpida* (Gertsch), female, leg II. 38. *N. microps* (Gertsch), female, leg II.

tibiae of the Japanese species *Falcileptoneta striata* (Oi); these are of particular interest because of their similarity to those of *Telema* (compare figs. 1 and 2 with Emerit, 1981, pl.

2, figs. 2, 4; Emerit and Juberthie, 1983, pl. 1; and Emerit, 1984, fig. A).

Two rather different types of tibial plates are found among the American leptonetids



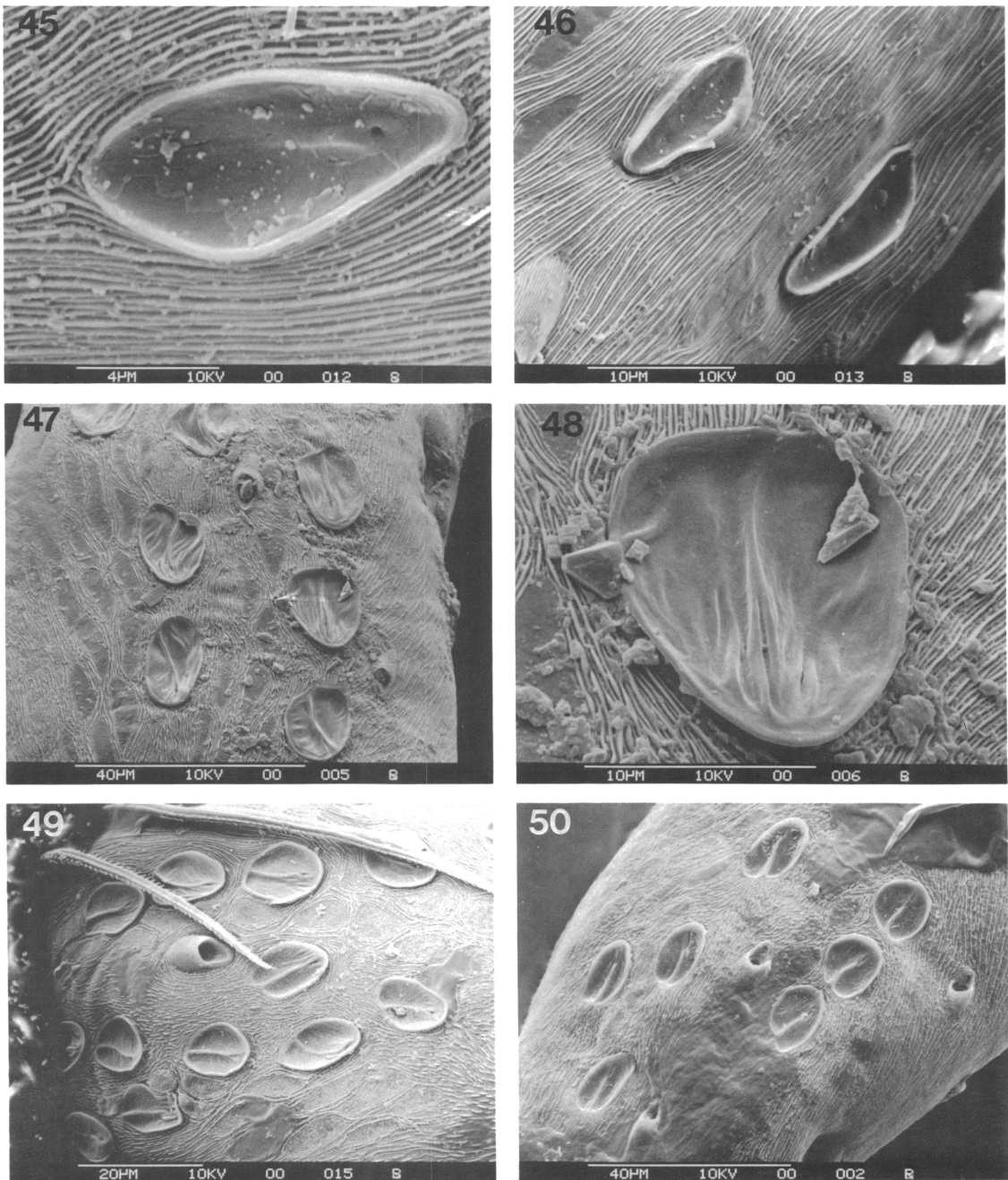


Figs. 39–44. Cuticular plates on patellae of *Neoleptoneta* species. 39. *N. modica* (Gertsch), male, leg III. 40. *N. myopica* (Gertsch), female, leg I. 41. *N. pecki* (Gertsch), male, leg II. 42. *N. rainesi* (Gertsch), male, leg II. 43. *N. reclusa* (Gertsch), male, leg II. 44. *N. serena* (Gertsch), female, leg I.

examined. In “*Leptoneta*” *sandra* Gertsch of southern West Virginia and adjacent Virginia, the plates are wider and wing-shaped, resembling those of the telemid genus *Usofila*

in bearing numerous raised striations that are set at right angles to the normal cuticular striations and surround a median pore (compare figs. 3 and 4 with Emerit, 1984, figs. E,



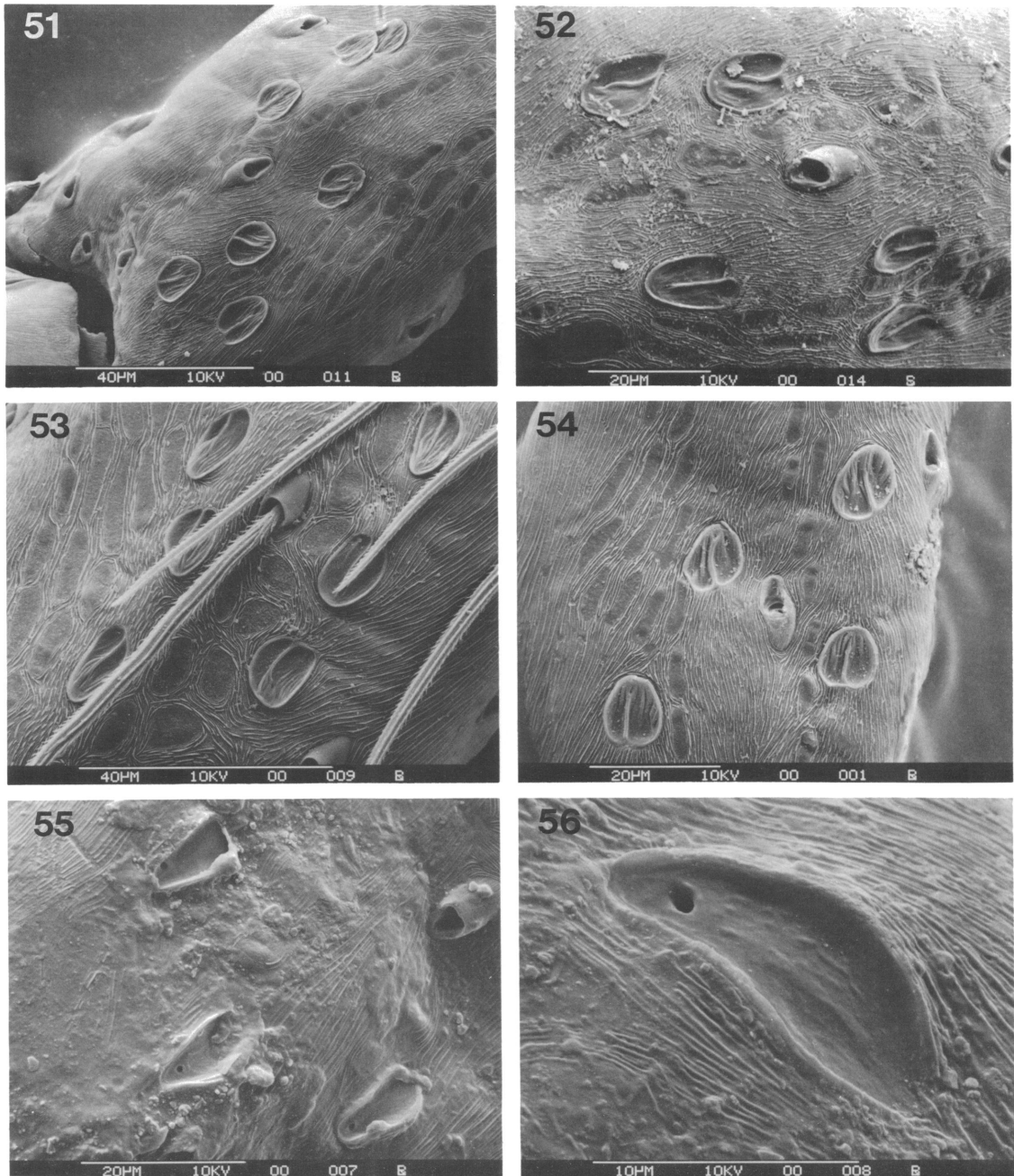


Figs. 45–50. Cuticular plates on patellae of *Neoleptoneta* and *Appaleptoneta* species. 45. *N. uvaldea* (Gertsch), female, leg II. 46. *N. valverdae* (Gertsch), female, leg III. 47, 48. *A. gertschi* (Barrows), female, leg II. 49. *A. barrowsi* (Gertsch), female, leg III. 50. *A. coma* (Gertsch), female, leg I.

F; and Emerit, in press, figs. A, B). In the three species of the genus *Archoleptoneta* recognized by Gertsch (1974), the plates are even

wider, are shaped like a peapod, and have at most only a few slight elevations (figs. 5–8).

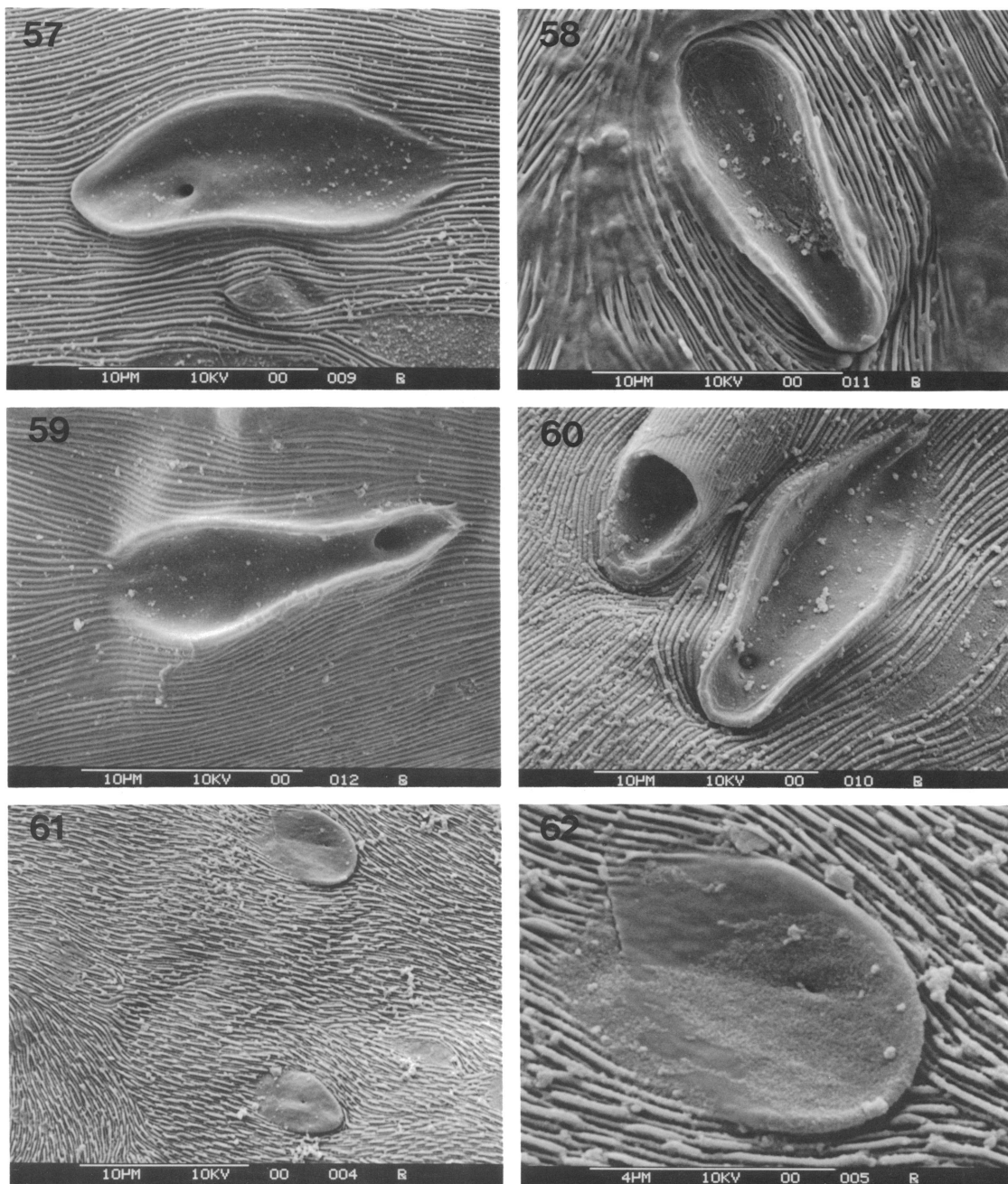
In evaluating the phylogenetic significance



Figs. 51–56. Cuticular plates on patellae of *Appaleptoneta* and *Calileptoneta* species. 51. *A. credula* (Gertsch), female, leg I. 52. *A. fiskei* (Gertsch), female, leg II. 53. *A. jonesi* (Gertsch), male, leg I. 54. *A. silvicultrix* (Crosby and Bishop), female, leg I. 55, 56. *C. californica* (Banks), female, leg II.

of the tibial glands, the primary question to be answered concerns the plesiomorphic condition within the Leptonetidae. There seems to be little doubt that *Archoleptoneta* repre-

sents the sister group of all other leptonetids, as Gertsch (1974) implied when he established the subfamily Archoleptonetinae to contain it. Although the normal eye pattern



Figs. 57–62. Cuticular plates on patellae of *Calileptoneta* and “*Leptoneta*” species. 57. *C. helferi* (Gertsch), male, leg III. 58. *C. noyoana* (Gertsch), male, leg II. 59. *C. oasa* (Gertsch), male, leg II. 60. *C. wapiti* (Gertsch), female, leg III. 61, 62. “*L.*” *brunnea* Gertsch, male, leg III.

of *Archoleptoneta* is clearly plesiomorphic, the unique type of tibial cuticular plate possessed by its species argues that the Archoleptonetinae is indeed a monophyletic group.

Given that tibial glands occur in *Archoleptoneta* and in at least two genera of the Leptonetinae, it may well be that the presence of the glands is plesiomorphic for the family

(this hypothesis gains much support from the patellar features discussed below). If so, then the glands are (based on our current knowledge of their distribution) a synapomorphy uniting the Leptonetidae and Telemidae. Hence, they may provide decisive evidence against classifications (such as that of Levi, 1982) which have allocated leptonetids and telemids to different superfamilies; these allocations, it should be noted, have not been based on any claimed synapomorphies.

If correct, this hypothesis may require some changes in the ideas on telemids put forth by Emerit (in press). In particular, Emerit suggested (1) that there are two lineages within the telemids, corresponding to the two groups of genera defined by differences in the form of the cuticular plates mentioned above, and (2) that the type of oval cuticular plate found in *Telema* and *Usofila* is derived, relative to the furrows found in the other four genera. Of course, if the second hypothesis is correct, then only the grouping of *Telema* and *Usofila* is cladistically supported by the character. But Emerit's polarity judgment seems to have been derived (so to speak) only from functional considerations, and the similarity between the cuticular plates of *Telema* and *Falcileptoneta* documented above suggests that the oval plate may in fact be plesiomorphic for both the Telemidae and Leptonetidae.

On the other hand, many species of leptonetines seem to lack tibial glands, and it is possible that the distribution of glands within that subfamily may be such that their occurrences must parsimoniously be considered parallelisms. To answer the question, of course, we need a broad-based survey of the Old World species of leptonetids, to see how widely the glands occur; hopefully this paper may stimulate workers with wider access to Mediterranean and eastern Asian taxa to undertake such a survey. There is additional evidence relevant to the question, however, from leptonetid patellae.

#### PATELLAR GLANDS AND GENERIC RELATIONSHIPS

In each of the five leptonetid species in which tibial cuticular plates have been found, similar cuticular plates appear on the patellae (figs. 9–14). There seems little doubt that these

patellar plates are homologous to those on the tibiae, for in each case the form of the patellar plates corresponds to the structure of the tibial ones: for *Falcileptoneta striata*, compare figures 1 and 2 with figures 9 and 10; for "*Leptoneta*" *sandra* compare figures 3 and 4 with figure 11; and for the three species of *Archoleptoneta*, compare figures 5–8 with figures 12–14.

Interestingly, the species of leptonetids that lack tibial cuticular plates generally do, nevertheless, have patellar plates. Representatives of each of the 44 American leptonetid species treated by Gertsch (1974) were examined, except for *Neoleptoneta furtiva* (Gertsch), and all of them have patellar plates. As with the tibial plates, they occur in both sexes and are usually present on each leg (although the number of plates is sometimes reduced on legs I and II, and occasionally plates are entirely lacking on patellae I).

Of the Old World leptonetids examined, two seem to lack patellar plates: the Japanese species *Masirana akiyoshiensis* and the Mediterranean species *Leptoneta microphthalma*. However, the five other Mediterranean *Leptoneta* species mentioned above do each have patellar plates (figs. 15–20). These are different in structure from the tibial plates of any known leptonetids or telemids, but occur in precisely the same position on the patella (proximally on the dorsal surface) as do the patellar plates in those species which have both the tibial and patellar structures (in *Archoleptoneta*, cuticular plates occur distally on the patella as well). There seems to be no reason to doubt that they too are homologous, although it would be good to have histological confirmation of this. It should be noted that patellar plates have not been recorded in any telemids, and attempts to locate them in one American species, *Usofila oregona* Chamberlain and Ivie, have been unsuccessful.

The structure of the patellar plates does vary among the American species, however, and is therefore relevant to the controversies about their generic classification noted above. Prior to Brignoli's (1972) study, all American leptonetids had been assigned to *Leptoneta* itself. Brignoli established *Neoleptoneta* for six species described by Gertsch (1971) from Mexico, separating it from other genera by,

among other features, the presence in males of a spine-bearing retrodorsal apophysis on the palpal tibia. Subsequently, Brignoli (1977) described an additional species from Oaxaca and transferred 21 further species into *Neoleptoneta*, and later (1979b) he added a further new species from New Mexico.

Examination of representatives of each of the 29 species currently assigned to *Neoleptoneta*, except for *N. caliginosa* Brignoli, *N. furtiva* (Gertsch), and *N. novaegalleciae* Brignoli, indicates that all share a characteristic patellar plate structure (figs. 21–40) much more similar to that of Mediterranean *Leptoneta* than to that of Japanese *Falcileptoneta*. As all other American leptonetids examined have patellar plates readily distinguishable from those of *Neoleptoneta*, Brignoli's (1977) delimitation of the genus seems to be correct. That delimitation, however, left a total of 14 American species unplaced in either *Archoleptoneta* or *Neoleptoneta*.

The most conspicuously different type of patellar plate is found in a group of seven Appalachian species (figs. 47–54) in which the plates are rounded, rather than triangular, and bear a large, longitudinal median ridge as well as several smaller parallel ridges. According to Brignoli (1977),

Somewhat related seem to be the following "*Leptoneta*": *silvicultrix* CROSBY and BISHOP 1925, *coma* BARROWS, 1940, *gertschi* BARROWS, 1940, *jonesi* GERTSCH, 1974, *credula* GERTSCH, 1974, *barrowsi* GERTSCH, 1974 and possibly *fiskei* GERTSCH, 1974. These species have a pedipalp considerably different from that of the *Neoleptoneta*, with a specialized femur and tarsus (not the tibia), a complicated bulbus and coiled spermathecae, of a structure evidently different from those of the *Neoleptoneta*. This group of "truly" Appalachian forms, should be united in a separate genus. Without material, I prefer to abstain from this.

The seven species associated by Brignoli on the basis of these genitalic features are precisely those united by the rounded and ridged patellar plates, and they are therefore assigned below to the new genus *Appaleptoneta*.

Similarly, the five species known from California and Oregon also share a distinctive form of patellar structure (figs. 55–60) in

which an extremely large pore occurs near the narrowed tip of a sinuous plate. According to Brignoli (1977),

In a separate genus, near to *Falcileptoneta*, should belong three species from California, "*L.*" *oasa* GERTSCH, 1974, "*L.*" *wapiti* GERTSCH, 1974 and "*L.*" *noyoana* GERTSCH, 1974; still to another genus, evidently different from all known, belong "*L.*" *californica* BANKS, 1904 (= *L. sylvia* CHAMBERLIN and IVIE, 1942) and "*L.*" *helferi* GERTSCH, 1974.

The latter two species are almost certainly sister taxa; they share a bizarre proximal prolongation of the palpal bulb that is unique among spiders (see Gertsch, 1974, figs. 144, 146, 148). However, the patellar plates of these two species conform fully to those of the other three California species, and there seems to be a genitalic synapomorphy uniting the five species as well. This is a distinctive lobe situated on the prolateral side of the palpal tarsus of males (see Gertsch, 1974, figs. 135–137, 139, 141, 144, and 145). The lobe is very conspicuous in four of these species; in "*L.*" *helferi*, the lobe appears reduced but may have become fused, at least partially, to the palpal bulb (the lobe is obvious, however, in its sister species, "*L.*" *californica*, and hence may be considered plesiomorphically present for the pair). All five species are therefore assigned below to the new genus *Calileptoneta*.

Brignoli (1977) was unable to place the two remaining American species:

Somewhat problematical are two species superficially similar to the European *Paraleptoneta*: "*L.*" *sandra* GERTSCH, 1974 from Virginia and West Virginia and "*L.*" *brunnea* GERTSCH, 1974 from Hidalgo (Mexico) . . . . These species are very similar, also for the ♀ genitalia to the Japanese *Sarutana* (see KOBAYASHI, 1973).

Each of these species has an apparently unique type of patellar plate. Those of "*L.*" *sandra* (fig. 11) have been discussed above. Those of "*L.*" *brunnea* are simple, triangular, flattened elevations bearing a small, subcentral pore (figs. 61, 62). In the absence of a detailed survey of the patellar plates of Old World leptonetids, the plate structure provides no additional evidence about the relationships of these two species, which are here considered Leptonetidae incertae sedis.



## SYNOPSIS OF AMERICAN LEPTONETIDAE

### *Archoleptoneta* Gertsch (1974)

TYPE SPECIES: *Archoleptoneta schusteri* Gertsch (1974).

DIAGNOSIS: Specimens of *Archoleptoneta* can be readily separated from all other leptonetids by having the eyes in a single group (Gertsch, 1974, figs. 128, 129) and by the elongated, peapod-shaped tibial and patellar gland plates (figs. 5–8, 12–14; not checked in *A. arganoi*).

INCLUDED SPECIES: *A. schusteri* Gertsch (1974); *A. garza* Gertsch (1974); *A. obscura* Gertsch (1974); and *A. arganoi* (Brignoli, 1974).

DISTRIBUTION: California, Texas, and Chiapas, Mexico.

### *Neoleptoneta* Brignoli (1972)

TYPE SPECIES: *Leptoneta capilla* Gertsch (1971).

DIAGNOSIS: Specimens can be distinguished from those of the other American genera by the presence of a spine-bearing retrodorsal apophysis on the palpal tibia of males (as in Gertsch, 1974, figs. 65–72) and by the triangular patellar gland plates bearing a small pore (figs. 21–40; not checked in *N. caliginosa*, *N. furtiva*, and *N. novaegalleciae*).

INCLUDED SPECIES: See Brignoli (1983, pp. 199–201) for a listing of the 29 included species.

DISTRIBUTION: Arizona east to Georgia and south to Oaxaca, Mexico.

### *Appaleptoneta*, new genus

TYPE SPECIES: *Leptoneta silvicultrix* Crosby and Bishop (1925).

ETYMOLOGY: The generic name is a contraction of Appalachian *Leptoneta* and is feminine in gender.

DIAGNOSIS: Specimens can be distinguished from those of the other American genera by the shape of the male palpal tarsus, which is transversely constricted, with a short distal portion bearing a retrolateral lobe armed with a spine or modified setae (as in Gertsch, 1974, figs. 22–32), and by the rounded patellar gland plates bearing parallel ridges (figs. 47–54).

INCLUDED SPECIES: *A. silvicultrix* (Crosby and Bishop, 1925), new combination; *A. coma* (Barrows, 1940), new combination; *A. gertschi* (Barrows, 1940), new combination; *A. fiskei* (Gertsch, 1974), new combination; *A. jonesi* (Gertsch, 1974), new combination; *A. credula* (Gertsch, 1974), new combination; and *A. barrowsi* (Gertsch, 1974), new combination.

DISTRIBUTION: Virginia, Tennessee, North Carolina, South Carolina, Georgia, and Alabama.

### *Calileptoneta*, new genus

TYPE SPECIES: *Leptoneta oasa* Gertsch (1974).

ETYMOLOGY: The generic name is a contraction of Californian *Leptoneta* and is feminine in gender.

DIAGNOSIS: Specimens can be distinguished from those of the other American genera by the presence of a prolateral lobe on the male palpal tarsus (as in Gertsch, 1974, figs. 135–137; reduced in *C. helferi*) and by the sinuous patellar gland plates bearing very large pores (figs. 55–60).

INCLUDED SPECIES: *C. oasa* (Gertsch, 1974), new combination; *C. noyoana* (Gertsch, 1974), new combination; *C. wapiti* (Gertsch, 1974), new combination; *C. helferi* (Gertsch, 1974), new combination; and *C. californica* (Banks, 1904), new combination.

DISTRIBUTION: California and Oregon.

### Leptonetidae incertae sedis

1. "*Leptoneta*" *sandra* Gertsch (1974), from West Virginia and Virginia.
2. "*Leptoneta*" *brunnea* Gertsch (1974), from Hidalgo, Mexico.

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