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A Cladistic Analysis of the Opilionid Superfamily Ischyropsalidoidea, with Descriptions of the New Family Ceratolasmatidae, the New Genus *Acuclavella,* and Four New Species

WILLIAM A. SHEAR[1]

ABSTRACT

A cladistic analysis of the opilionid superfamily Ischyropsalidoidea revealed three groups of genera, each probably monophyletic, and recognized here as families. The family Ischyropsalididae Simon is redefined to include only the genus *Ischyropsalis,* the family Sabaconidae Dresco is expanded to include *Sabacon* (=*Tomicomerus,* new synonymy) and *Taracus,* and the family Ceratolasmatidae is described as new for the genera *Ceratolasma, Hesperonemastoma, Crosbycus,* and *Acuclavella,* new genus. *Acuclavella* consists of four new species from Idaho and Washington: *cosmetoides, shoshone, merickeli,* and *quattuor. Crosbycus dasycnemus* (Crosby) is redescribed and illustrated, and new distribution records are given.

INTRODUCTION

The opilionid family Ischyropsalididae has been problematical for opilionologists for many years, with a piecemeal approach being taken to the inclusion or exclusion of various taxa in the family. Originally proposed by Simon (1879) to cover the genera *Ischyropsalis, Sabacon,* and *Taracus,* the family was readily recognized (Hansen and Sorensen, 1904), but nothing substantial was done regarding its composition or relationships until Martens (1969) revised the type genus, disposing of a vast plethora of extraneous species names proposed by Roewer (1950). For the first time, Martens' work allowed some clear insights into the true nature of this taxon. For example, he established that *Ceratolasma tri-*

[1] Research Associate, Department of Entomology, American Museum of Natural History; Professor of Biology, Hampden-Sydney College, Hampden-Sydney, Virginia 23943.

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cantha, originally described by Goodnight and Goodnight (1942) as a trogulid (on the mistaken assumption it was related to *Ortholasma,* now known to be a nemastomatid, but at that time considered a trogulid also), was in fact related at some level to *Ischyropsalis,* while *Taracus* and *Sabacon* were more distantly so. A nonconforming element of the family was removed when Martens and Suzuki (1966) showed that *Nipponopsalis* was in fact allied in some way to the trogulids. Later, Gruber (1978) and Shear and Gruber (1983) placed *Ruaxphilos petrunkevitchou* Goodnight and Goodnight (1945) in the synonymy of *Ortholasma bolivari,* an ortholasmatine nemastomatid.

Dresco (1970) suggested a monotypic family for *Sabacon,* and this proposal was accepted by Martens (1983), who characteristically provided much better evidence for the idea in his revision of European *Sabacon.* However, Martens did not include *Taracus.*

Gruber (1970) showed that the North American species described by several authors in *Nemastoma* were not even members of Nemastomatidae but related to *Ischyropsalis*; he gave them the new (unfortunate) name *Hesperonemastoma.* In several publications, Gruber (1970) and Martens (1976, 1978) presented evidence for including *Crosbycus* in the ischyropsalidid assemblage; Martens persistently suggested a monotypic new family for it, but has never actually used the name "Crosbycidae."

In two important papers, Martens (1976) and Martens et al. (1981) used, among other characters, details of the penes and ovipositors to produce a widely accepted cladogram of the order Opiliones. It was not unexpected that their analysis led to a dismemberment of the old "tribe" Dyspnoi, in which Ischyropsalididae had been allied with Nemastomatidae, Dicranolasmatidae, Nipponopsalididae, and Trogulidae. Martens raised the taxon to superfamily level and placed it close to the superfamilies Phalangioidea and Caddoidea.

However, as Gruber (1978) had pointed out, the single family Ischyropsalididae is one of the most heterogeneous taxa in Opiliones. He decried the solution of monotypic families for each genus, which, considering the Sabaconidae of Dresco, and Martens' suggestion of a family for *Crosbycus* alone, he saw in the future.

Work with *Sabacon, Crosbycus, Ceratolasma,* and *Hesperonemastoma* had suggested to me that there might be a solution to the evident difficulties in the taxonomy of this family, and when evidence became available a few years ago of an exciting new genus from Idaho and Washington related to *Ceratolasma,* I resolved to try to make some sense of relationships in the Ischyropsalidoidea.

Acknowledgments

I thank, first of all, Frank Merickel of the University of Idaho for his generosity in providing specimens of *Acuclavella* and notes on their habits. He was referred to me by my colleague in American opilionid taxonomy, James C. Cokendolpher (Texas Tech University). I had first been made aware of the existence of this new genus by Rod Crawford of the Burke Memorial Museum, Seattle, who sent a single female specimen from Lewis County, Washington. The scanning electron micrographs illustrating this paper were taken at the Virginia-Maryland College of Veterinary Medicine, through the kindness of Brent Opell. Additional specimens of ischyropsalidoids were provided by Cokendolpher, by Jochen Martens (Johannes-Gutenberg-Universität, Mainz), and by Nobuo Tsurusaki, Hokkaido University, Japan. Jürgen Gruber (Natural History Museum, Vienna [VM]) very kindly turned over to me his voluminous notes on *Crosbycus dasycnemus,* and commented extensively on an earlier draft of this paper, as did Martens, Cokendolpher, and Norman Platnick of the American Museum of Natural History. Material for study came from my own collection and that of the American Museum of Natural History (AMNH; Norman Platnick), the Field Museum of Natural History (FMNH; Henry Dybas and John Kethley), the Burke Memorial Museum of the University of Washington (BMM; Rod Crawford), the Museum of Comparative Zoology at Harvard University (MCZ; H. W. Levi), and the personal collection of James C. Cokendolpher (JCC).

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FAMILIES OF ISCHYROPSALIDOIDEA

The superfamily Ischyropsalidoidea has been defined by Martens (1976) and by Martens et al. (1981) on the basis of characters of the genitalia and palpi. The ovipositor has secondarily lost its segmentation (retaining vestiges of segmentation in the musculature), and the palpal claw is vestigial or absent. In this study, I add to these characters the presence of unique sensory cones on the metapeltidial midline. The superfamily corresponds roughly in extent to the old "family," the history of which was reviewed to 1976 by Gruber (1978). According to the analysis of Martens, the sister group of Ischyropsalidoidea is Caddoidea + Phalangioidea. Uniting these three taxa are two synapomorphies: one muscle in the penis and plumose setae (figs. 2–9) on the palpi. This latter character, previously thought to occur primarily, if not exclusively, in the Ischyropsalidoidea, has been verified for a number of species of Phalangioidea (Tsurusaki, personal commun.; Cokendolpher, personal commun.; unpublished data) and Caddoidea (see fig. 5). However, such setae may be synapomorphic for Opiliones as a whole, since scanning electron microscopy of the major palpal setae of some Laniatores has revealed minute tubular ducts like those illustrated here. A more comprehensive survey of seta types in Opiliones is needed.

How many families of Ischyropsalidoidea should there be? Dresco (1970) suggested two: Ischyropsalididae and a monotypic Sabaconidae. This idea has been criticized and rejected by Shear (1975) and Gruber (1978), but lately accepted by Martens (1976, 1978, 1981), who has also called for the establishment of a monotypic family based on *Crosbycus.*

While Dresco's arguments for a monotypic family based on *Sabacon* were not convincing (Shear, 1975), Martens (1981) has drawn attention to the unusual penis muscle in *Sabacon.* The muscle actually lies outside the shaft of the penis, originating on the two arms of a fork extending from the base of the shaft and inserting by means of a long tendon on the base of the glans. The penis, as in many other ischyropsalidoids, phalangioids, and nemastomatoids, bends at the base of the glans and the base of the stylus when this muscle contracts. According to Martens this arrangement of the penial muscle and "weitere Merkmale, die hier nicht diskutiert werden" justify a monotypic family for *Sabacon.* The additional characters are not given. As Martens pointed out, at least one genus in each of the families Phalangiidae and Nemastomatidae have a very similar arrangement, and just as importantly, there are at least two other apomorphies (dense distribution of plumose setae on the tibia and tarsus of the palp, with the tarsus curved back on the tibia; presence of a deep slot in the carapace between the chelicerae) shared by *Sabacon* and *Taracus,* and *Taracus* does not have the penis muscle as in *Sabacon.* I therefore regard the form of the penis in *Sabacon* as an autapomorphy only for the genus.

My cladistic analysis (fig. 1) shows that *Sabacon* and *Taracus,* taken together, are the sister group of all the other Ischyropsalidoidea. On this basis I have decided to recognize a family Sabaconidae, which includes these two genera.

Similarly, *Ischyropsalis* (with its isolated position in central and western Europe) is shown to be the sister group of the remaining genera. I choose to incorporate this situation in the classification by limiting the family Ischyropsalididae only to the genus *Ischyropsalis,* and recognizing a family Ceratolasmatidae which includes four genera. The type genus was selected because there is still some ambiguity about the position of *Crosbycus,* and *Ceratolasma* is the next oldest name in the group. The revised classification is as follows:

Superfamily Ischyropsalidoidea Simon
- Family Ischyropsalididae Simon
  - *Ischyropsalis* C. L. Koch
- Family Ceratolasmatidae, new
  - *Ceratolasma* Goodnight and Goodnight
  - *Acuclavella,* new
  - *Crosbycus* Roewer
  - *Hesperonemastoma* Gruber
- Family Sabaconidae Dresco
  - *Sabacon* Simon
  - *Taracus* Simon

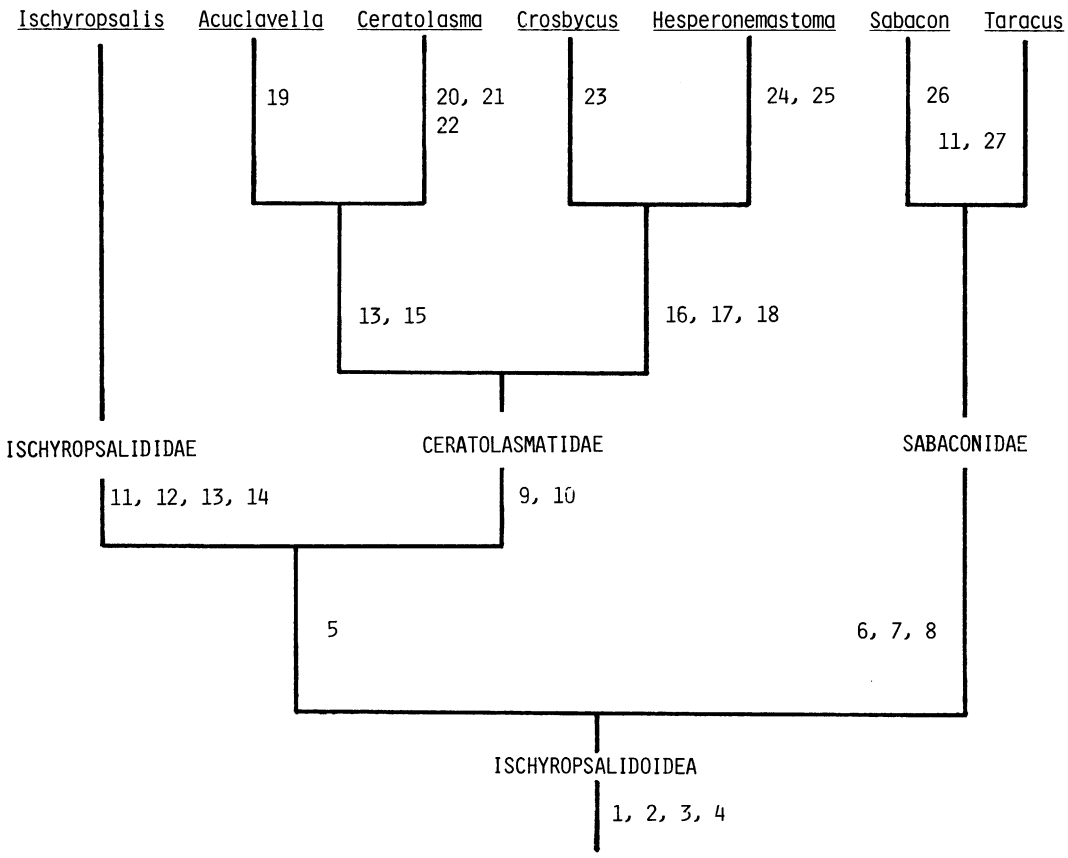


FIG. 1. Cladogram of families and genera of the superfamily Ischyropsalidoidea.

THE GENERA OF ISCHYROPSALIDOIDEA

The larger genera within the superfamily Ischyropsalidoidea are well defined. However, the monotypic genera *Ceratolasma, Crosbycus,* and *Tomicomerus* present certain problems. Placing the species concerned in monotypic genera implies that they are the sister groups of all the other species included in the most closely related genus or group of genera.

Ceratolasma tricantha as a species has at least two significant autapomorphies: troguloid facies and the presence of a palpal/cheliceral stridulatory apparatus. These are not found in any other ischyropsalidid species. Interestingly, these characters coexist with a number of significant plesiomorphic features: the simple penis, endites on all coxae, and a large sternum and labium (Gruber, 1978).

Acuclavella is the closest relative of *Ceratolasma,* as shown by my cladistic analysis. At present the species of this genus are grouped together on the basis of the cuticular microsculpture of large, rounded warts. The penis shows slight torsion in the stylus, but this may not be a consistent difference. The plesiomorphic characters mentioned above for *Ceratolasma* are also found in *Acuclavella* (and *Ischyropsalis*). The question to be answered here is whether or not *Acuclavella* and *Ceratolasma* should be merged. Possible characters to unite them could be the ornamentation of the leg femora (also found in *Hesperonemastoma*), the dorsal ornamentation, and the extended eye tubercle, but *C. tricantha* is, in fact, strikingly different from the species of *Acuclavella.* In my opinion, the single species included in *Ceratolasma* is indeed the sister group of the rest of the species, and the information retrieval aspects of the

TABLE 1
Characters for Cladistic Analysis of Ischyropsalidoidea

Characters	Plesiomorphic	Apomorphic
1. Metapeltidial sensory cones	Absent	Present
2. Ovipositor	Segmented	Segmentation lost
3. Palpal claw	Large	Reduced or absent
4. Cheliceral glands of males	Absent	Present
5. Genital operculum	No suture	With suture
6. Palpus	Gracile	Tibia and tarsus enlarged
7. Front of carapace	Not indented	Deep slot in midline
8. Sclerotization	Heavy	Reduced
9. Legs	With setae and microtrichia	With raised scalelike tubercles
10. Abdominal scutum	Without spikes	With spikes
11. Chelicerae	Normal size	Enlarged and spiny
12. Metapeltidial sensory cones	2	More than 2
13. Plumose setae of palpus	Present	Lost
14. Seminal receptacles	4	More than 4
15. Eye tubercle	Rounded, low	With median spike
16. Cheliceral glands of males	Present	Lost
17. Metapeltidial sensory cones	Present	Reduced or lost
18. Microsculpture of scutum	Small acute denticles	Anvil-shaped tubercles
19. Microsculpture of scutum	Small acute denticles	Large, round warts
20. Troguloid facies	Absent	Present
21. Stridulatory mechanism	None	Cheliceral/palpal
22. Spikes of abdominal scutum	Erect, acute	Recumbent, blunt
23. Macrosetae of legs	Erect	Recumbent, sinuous
24. Scutum	Parvum	Magnum
25. Palpal femora of males	Without glands	With glands
26. Muscles of penis	In truncus	Not in truncus
27. Metapeltidial sensory cones	2	1

classification are better served by retaining both names.

Crosbycus dasycnemus is likewise difficult to place. Some clear affinities with *Hesperonemastoma* are seen in the presence of anvil-shaped tubercles as cuticular macrosculpture (fig. 17) and in the evident loss of the metapeltidial sensory spines (fig. 30). Unlike *Ischyropsalis, Ceratolasma,* and *Acuclavella,* the palpi of *Crosbycus* and *Hesperonemastoma* have plumose hairs (figs. 6, 8). Evidence might be garnered concerning the relationships of *C. dasycnemus* if males were present, since the penes of *Hesperonemastoma* species are highly apomorphic—but this species is almost certainly parthenogenetic. Of the perhaps 100 specimens in collections, all are females, and the ovipositors lack seminal receptacles (fig. 41). The microsculpture and setation of the legs of *C. dasycnemus* are unique (fig. 12). The species of *Hesperonemastoma* are the closest relatives of *Crosbycus dasycnemus,* but again, that species is extraordinarily different from them, and again, I argue that this information is best conveyed by maintaining the genus *Crosbycus* for this single species.

The case of *Tomicomerus,* however, is different. The included species, *T. bryanti,* is known at this time from a single mangled male specimen. In my 1975 revision, I considered *Tomicomerus* intermediate between *Taracus* and *Sabacon.* A careful reexamination of the data I collected at that time, together with more information about the range of species in *Sabacon* (Suzuki, 1974; Martens, 1972, 1983; Cokendolpher, 1984), has convinced me that there are no striking autapomorphies in this species that could justify (as in the above cases) the retention of a monotypic genus by suggesting that *T. bryanti* is the sister group of all other *Sabacon.* Accordingly, I now consider *Tomicomerus* a synonym of *Sabacon.*

EVOLUTION AND RELATIONSHIPS

Discussion of Characters

In the following discussion, I have again taken up the principles set forth in Shear and Gruber (1983) for the determination of polarity in transformation series in opilionid groups, namely: (1) occurrence in outgroups speaks for plesiomorphy, (2) less differentiated, more homonomously patterned characters are plesiomorphic, (3) states resembling those in juveniles are plesiomorphic, (4) characters known to be consistently correlated with others known to be apomorphic are likely also to be apomorphic, and (5) correlations between morphological and ecological or distributional characters should be used cautiously.

I have accepted the arguments of Martens (1976, 1981) and Martens et al. (1981) that the immediate outgroup of Ischyropsalidoidea is Phalangioidea and Caddoidea.

List of Characters

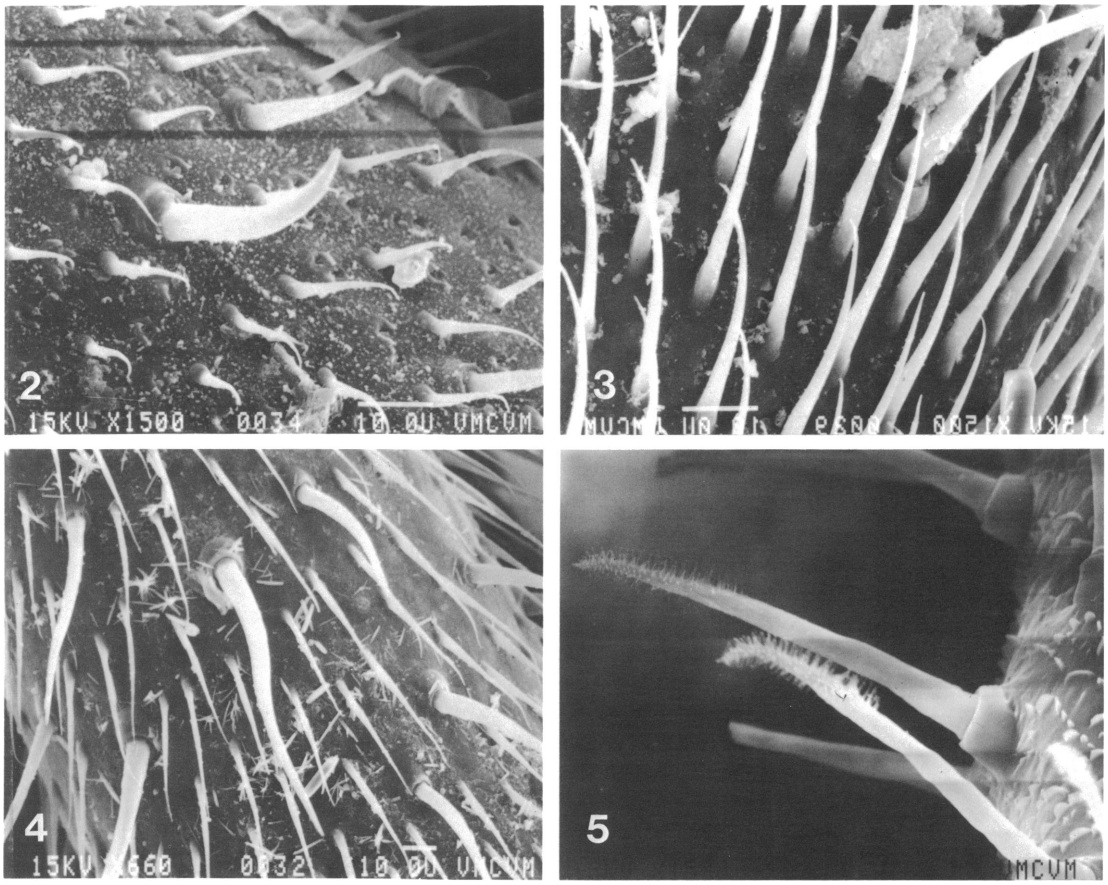
The numbering of the characters below is the same as in table 1 and in figure 1.

Metapeltidial Sensory Cones. These unique sense organs, the function of which can only be guessed at (Juberthie et al., 1981), are found only in the Ischyropsalidoidea and constitute an unequivocal synapomorphy for the group (character 1). In *Crosbycus* and *Hesperonemastoma,* these organs have been lost, or are in the process of being lost (character 16). In *Hesperonemastoma modestum,* examination under high magnification shows a pair of depressions on either side of the midline of the metapeltidium; these are probably the reduced sensory cones. There is no trace of these structures in *Crosbycus dasycnemus* (fig. 38). Two additional apomorphic modifications also occur; in *Taracus* species, the number of cones is reduced to one (character 27), and in most *Ischyropsalis* species, multiple cones occur (character 12). However, it would require an ultrastructural examination to prove that the midline metapeltidial structures in *Ischyropsalis* are all sensory cones.

Ovipositor. According to Martens et al. (1981), the ovipositor of ischyropsalidoids is secondarily unsegmented (character 2), in contrast to the Phalangioidea, Caddoidea, and Cyphophthalmi, where segmentation has been retained. The basal number of seminal receptacles for opilionids is not known, but is probably two or four (Martens et al., 1981). In any case, by outgroup comparison, the presence in many species of *Ischyropsalis* of more than four is apomorphic (character 14).

Palpal Characters. The palpal claw of all ischyropsalidoids has been reduced to a small nubbin or entirely lost (character 3); this is apomorphic by outgroup comparison, as well as by the presence of claws on the serially homologous legs. The plumose setae of the palpi (figs. 2–9) are plesiomorphic for the superfamily (synapomorphic for Ischyropsalidoidea and its sister group), so their loss, which has taken place twice (character 13) is apomorphic. In Sabaconidae, a key synapomorphy (because it makes the palpi even less like legs) is the very dense distribution of plumose setae, the swollen tibia and tarsus, and the tarsus reflexed on the mesal surface of the tibia. I regard this suite of adaptations as functionally linked, even though the function is not known (character 6). In the genus *Hesperonemastoma,* males have the secondary sexual character of a swollen palpal femur, with a gland (character 25); this is a synapomorphy for the genus found nowhere else in the superfamily, though there is a parallel development in males of *Ortholasma* (Nemastomatidae; Shear and Gruber, 1983). This character has not been used in the analysis, but both *Crosbycus* and *Hesperonemastoma* have palpi nearly as long as the first legs.

Chelicerae. The presence of cheliceral glands (Martens and Schawaller, 1977) in males (character 4) is apomorphic by outgroup comparison. In *Hesperonemastoma,* these glands have been lost (character 16), probably to be replaced functionally by the palpal glands. Greatly enlarged, spiny chelicerae have been developed twice in the superfamily (*Ischyropsalis* and *Taracus,* character 11), as has happened sporadically in virtually every opilionid superfamily. I regard this as parallelism here, since no other synapomorphies suggest a sister-group relationship between *Ischyropsalis* and *Taracus.* In particular, the pattern of cheliceral muscle origins on the carapace is quite different, since

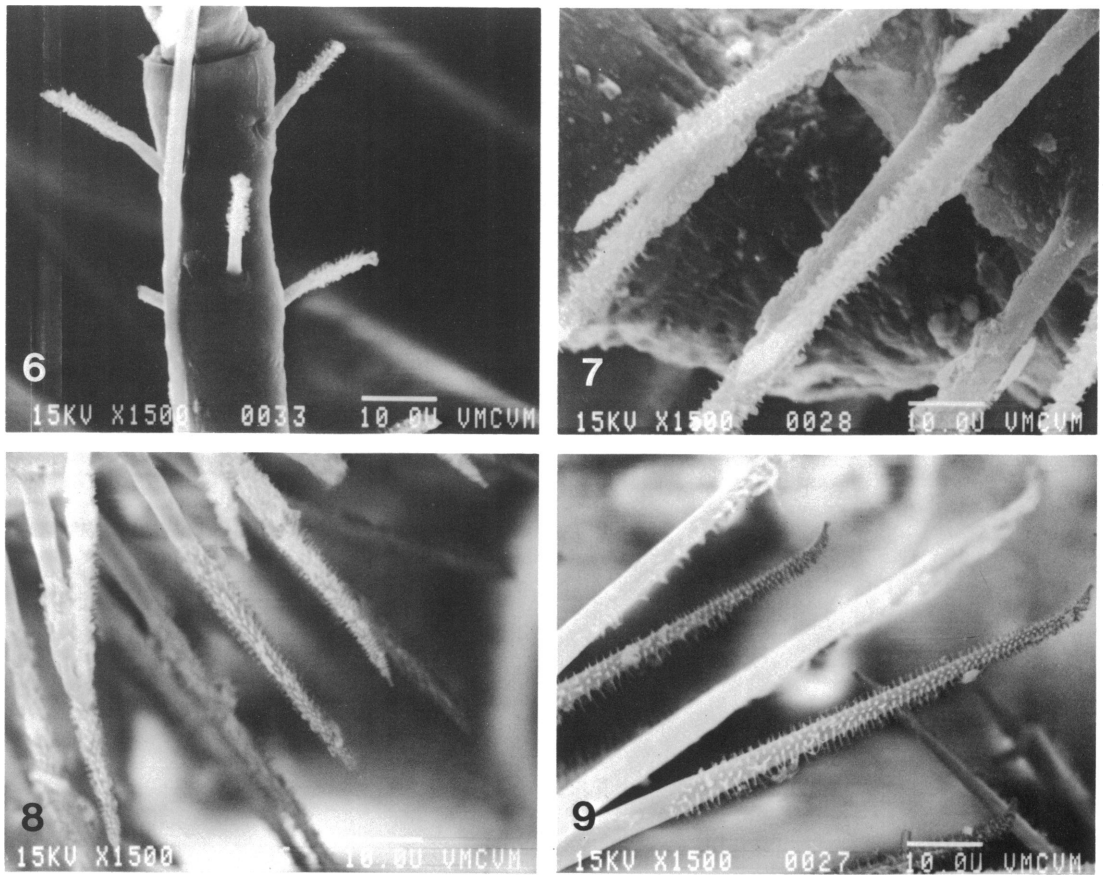


FIGS. 2–5. Scanning electron micrographs of parts of palpal tibiae. All bars = 10 μm. **2.** *Acuclavella merickeli* (distal to lower right, ×975). **3.** *Ceratolasma tricantha* (distal to upper right, ×975). **4.** *Ischyropsalis hellwigi* (distal to lower right, ×430). **5.** *Acropsopilio chomulae* (distal above, ×975).

in *Ischyropsalis* the big muscles operating the basal article of the chelicera originate behind the eye tubercle, whereas in *Taracus* these muscles originate on either side of it. In *Ceratolasma,* the chelicera is part of a unique cheliceral/palpal stridulating mechanism (character 21; see Gruber, 1969, 1978).

Genital Operculum. By outgroup comparison, a suture (partial or complete) setting off the genital operculum from the second abdominal sternite is apomorphic (character 5).

Sclerotization and Ornamentation of Dorsum. Outgroup comparison at a basic level in the cladogram of Martens et al. (1981) forces one to the conclusion that heavy sclerotization of the body is an apomorphy only at the level of the order Opiliones as a whole, and therefore a reduction in sclerotization should be regarded as apomorphic wherever it occurs. Here, it is regarded as a synapomorphy for Sabaconidae (character 8), where it is especially significant in affecting the carapace and metapeltidium in many species (Shear, 1975; Martens, 1983). Reduction of sclerotization to a much lesser degree, and primarily in the abdomen, is found in some species of *Ischyropsalis* (Martens, 1969). An additional synapomorphy for Sabaconidae is the slot in the frontal midline of the carapace extending in most species nearly to the eye tubercle (character 7). On the other hand, fusion of the carapace and abdominal scutum (scutum magnum) is clearly an alternative synapomorphy (by principle 4 above, only in *Hesperonemastoma*; character 24). Having serially arranged, paired spikes on the scutum

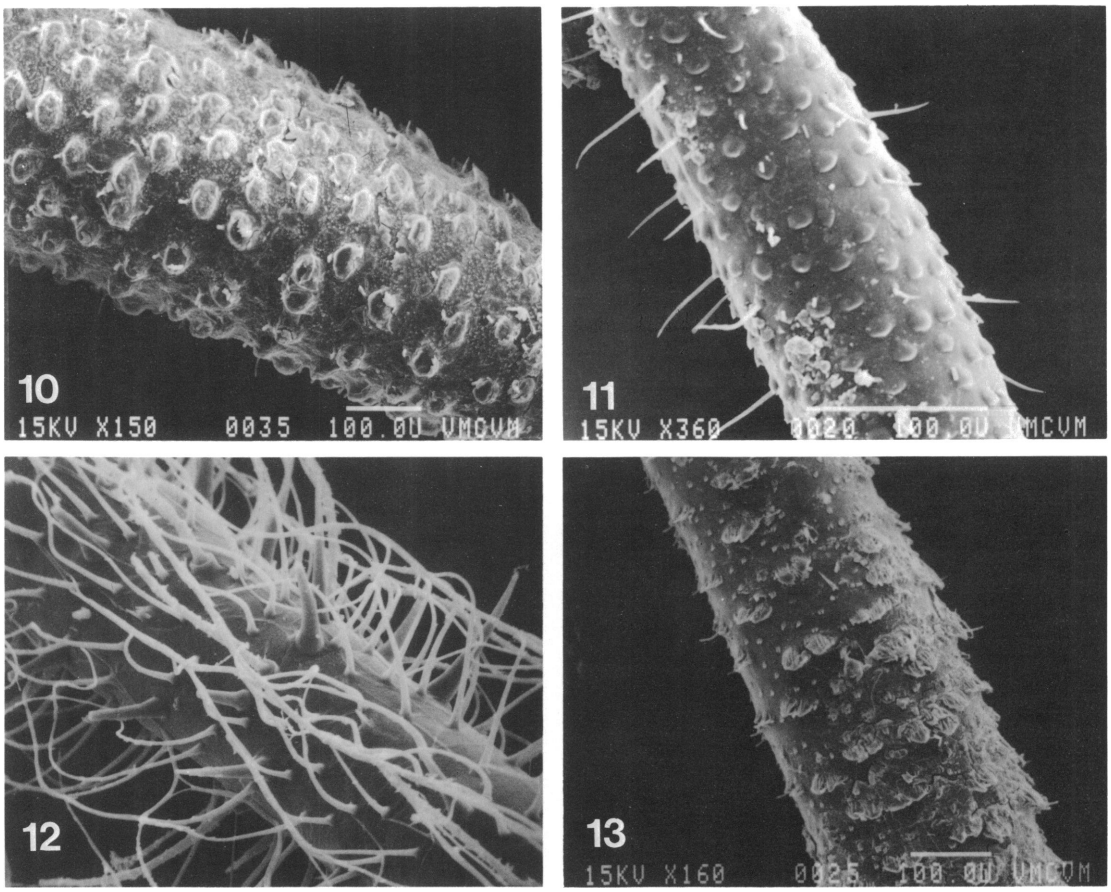


FIGS. 6–9. Scanning electron micrographs of parts of palpal tibiae. All ×990, bars = 10 μm. **6.** *Crosbycus dasycnemus* (distal above). **7.** *Taracus pallipes* (distal to upper left). **8.** *Hesperonemastoma modestum* (distal to lower left). **9.** *Sabacon occidentalis* (distal to lower right).

is synapomorphic for Ceratolasmatidae, by outgroup comparison (character 19); acute in *Hesperonemastoma* and *Acuclavella,* these are blunt, somewhat recumbent cones in *Ceratolasma* (character 22). In the heavily sclerotized species, small, acute thorns on the sclerites appear to be the plesiomorphic form of sculpture. In *Acuclavella* these become quite large, rounded warts (character 19), and in *Crosbycus* and *Hesperonemastoma* appear as anvil-shaped tubercles (figs. 17, 38; character 18), a parallelism with Nemastomatidae.

Eye Tubercle. Apomorphic by outgroup comparison, *Acuclavella* and *Ceratolasma* carry a forward-slanting spike on the eye tubercle (character 15). In *Ceratolasma* this spike extends virtually horizontally forward and becomes a part of the typical troguloid facies, contributing to the camerostome (character 20; see Gruber, 1978, and Shear and Gruber, 1983, for a discussion of the troguloid facies).

Legs. Legs ornamented with microtrichia and ordinary micro- and macrosetae (figs. 14–16) are plesiomorphic by principle 2 above; ornamentation of raised scalelike tubercles subtending setal bases (figs. 10, 11, 13) is apomorphic (character 9). *Crosbycus* has unique procumbent, curly hairs on the femora, patellae, and tibiae of the legs (fig. 12; character 23). Martens (1983) has illustrated a pattern of raised scales on the femora of some species of *Sabacon,* but these raised scales do not subtend setae and are clearly a different development.



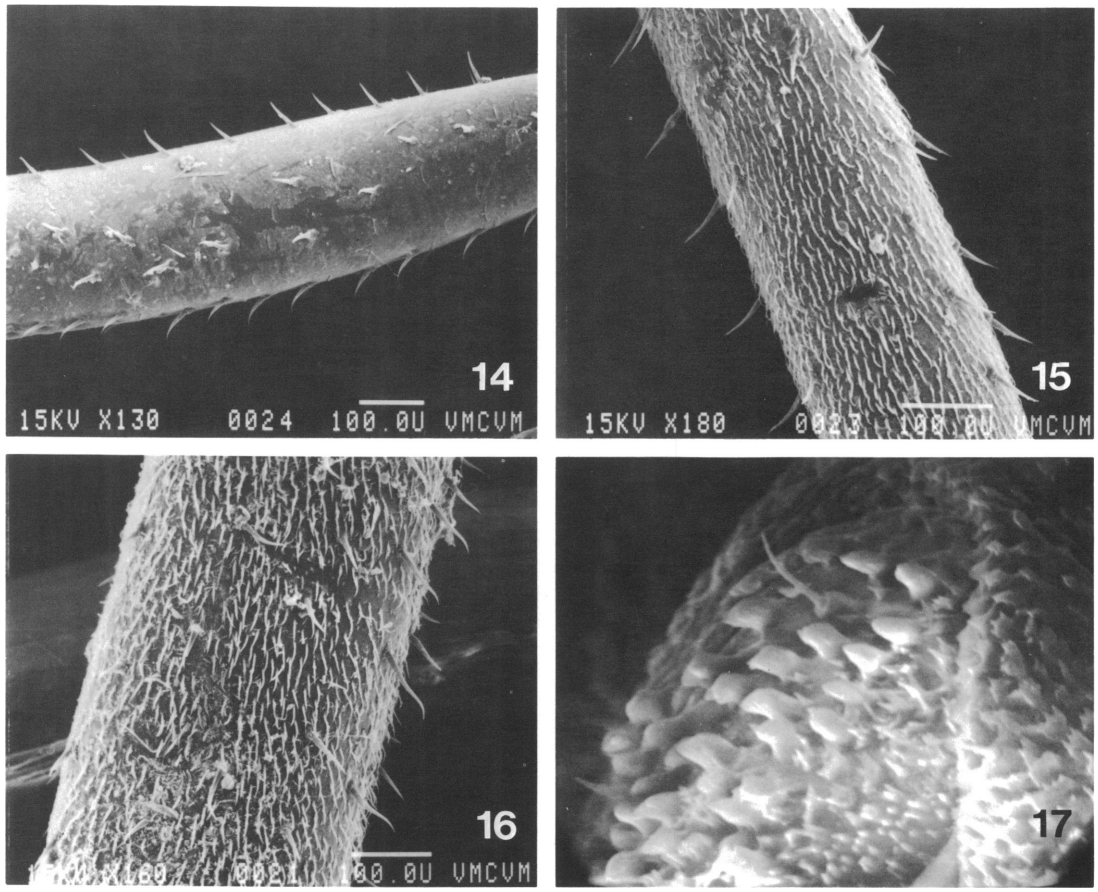
FIGS. 10–13. Scanning electron micrographs of parts of second leg femora. All bars = 100 μm, except for figure 12, where bar = 10 μm. **10.** *Acuclavella merickeli* (distal to upper left, ×100). **11.** *Hesperonemastoma modestum* (distal to lower right, ×235). **12.** *Crosbycus dasycnemus* (distal to upper left, ×225). **13.** *Ceratolasma tricantha* (distal to lower right, ×105).

CLADISTIC ANALYSIS

The relationships of the ischyropsalidoid families and genera are illustrated in figure 1; the character numbers refer to those found in table 1. The base of the cladogram is, unfortunately, only weakly resolved by regarding the suture of the genital operculum as synapomorphic for Ischyropsalididae and Ceratolasmatidae. The suggestion of Martens (1969) and Gruber (1978) that *Ceratolasma* is the closest relative of *Ischyropsalis* is not borne out by this analysis; the characters suggested as supporting the relationship have turned out to be plesiomorphies (form of sternum and endites, simple penis).

For reasons already discussed in the section on families, the family Sabaconidae is accepted, but expanded to include *Taracus*. *Tomicomerus* is regarded as a synonym of *Sabacon*.

Crosbycus and *Hesperonemastoma* remain difficult elements. Each has a large number of autapomorphies, and in *Crosbycus,* these are coupled with substantial numbers of primitive characters. However, if they are indeed ischyropsalidoids (as indicated for at least *Hesperonemastoma* by the single penis muscle and secondarily unsegmented ovipositor), they belong in the cladogram as shown. Martens (1976, 1981) has repeatedly suggested a monotypic family for *Crosbycus* but has never formally used the name "Crosbycidae." Because of my uneasiness about



FIGS. 14–17. Scanning electron micrographs. All bars = 100 μm. 14–16. Parts of second leg femora. **14.** *Taracus pallipes* (distal to left, ×85). **15.** *Sabacon occidentalis* (distal to lower right, ×120). **16.** *Ischyropsalis hellwigi* (distal below, ×105). **17.** Anal operculum of *Crosbycus dasycnemus,* showing ornamentation of anvil-shaped tubercles on heavily sclerotized parts and trifid scales on membranous parts (×300).

the position of the genus, and a prudent wish to base the family name on the oldest generic name other than *Crosbycus,* I have decided to call the family Ceratolasmatidae.

DIAGNOSES OF TAXA

The literature citations given below for described taxa are not meant to be exhaustive, but include the original proposal and subsequent substantive discussions.

SUPERFAMILY ISCHYROPSALIDOIDEA SIMON

Ischyropsalidae Simon, 1879, p. 265. Roewer, 1923, p. 680. Comstock, 1913, p. 80. Ischyropsalidoidea Martens, 1976, p. 64; 1978, p. 186. Gruber, 1978, p. 107. Martens, Hoheisel, and Götze, 1981, p. 37.

TYPE GENUS: *Ischyropsalis* C. L. Koch, 1839.

DIAGNOSIS: Palpatorid opilionids with single muscle in penis; ovipositor secondarily unsegmented, with common canal for cement glands; metapeltidium with one or more sensory cones of unknown function (these lost in some genera); males with cheliceral or palpal glands probably producing sex pheromone (this well documented for *Ischyropsalis*; see Martens, 1969); palpi usually with plumose setae, lacking claw.

INCLUDED FAMILIES: Ischyropsalididae Simon; Ceratolasmatidae, new; and Sabaconidae Dresco.

DISTRIBUTION: Southwestern, central, and southeastern Europe; central Asia, the Himalayas, and Siberia; Japan; western North America from southern Alaska to San Francisco Bay; in the inland mountains of central Idaho and western Montana, the Sierra Nevada, and the Rockies from Alberta to Utah, New Mexico, and Arizona; sporadic in Mississippi River drainage from Minnesota and Michigan to Mississippi; Appalachian Mountains from New Hampshire to Georgia.

FAMILY ISCHYROPSALIDIDAE SIMON

Ischyropsalidae Simon, 1879, p. 265. Roewer, 1923, p. 680 (in part). Martens, 1969, p. 133; 1978, p. 186; Martens, Hoheisel, and Götze, 1981, p. 37. Shear, 1975, p. 7. Gruber, 1978, p. 107.

TYPE GENUS: *Ischyropsalis* C. L. Koch, 1839.

DIAGNOSIS: Ischyropsalidoidea with greatly enlarged spiny chelicerae; carapace heavily sclerotized, with strip of cuticle extending between chelicerae; sclerotization of abdomen variable; eye tubercle deeply grooved; genital operculum separated from second abdominal sternite by suture; palpi without plumose setae; legs without cuticular sculpture (fig. 16); penis basally broad, muscle in truncus, stylus usually deflexed; ovipositor with 4 to 12 seminal receptacles.

INCLUDED GENUS: *Ischyropsalis* C. L. Koch. The genus (type species *I. kollari* C. L. Koch) is diagnosed, and all known species described, in the revision by Martens (1969).

DISTRIBUTION: Central Europe and the Pyrenees.

FAMILY SABACONIDAE DRESCO

Ischyropsali[di]dae, Roewer, 1923, p. 680 (in part). Comstock, 1913, p. 80 (in part). Shear, 1975, p. 7 (in part). Suzuki, 1974, p. 83 (in part).

Sabaconidae Dresco, 1970, p. 1210. Martens, 1978, p. 225; 1983, p. 269.

TYPE GENUS: *Sabacon* Simon, 1879.

DIAGNOSIS: Ischyropsalidoids with generally reduced sclerotization, sternum and labium scarcely sclerotic at all; anterior midline of carapace deeply indented to form slot reaching from margin to eye tubercle; one or two metapeltidial sensory cones; genital operculum not set off by suture; chelicerae normal or greatly enlarged, spiny, with or without gland in males; palpi with tibia and tarsus slightly or greatly inflated, very densely set with plumose setae of uniform length ("bottle-brush" palpi), tarsus with narrow basal stem, reflexed against asetose area on median surface of tibia. Legs lacking cuticular sculpture.

INCLUDED GENERA: *Sabacon* Simon, *Taracus* Simon. *Sabacon* (type species *S. paradoxum* Simon) has been the subject of revisions by Suzuki (1974, Japanese species), Shear (1975, American species), and Martens (1972, Himalayan species; 1983, European species). The best diagnosis is in Martens (1983). *Taracus* has never been given a comparative diagnosis in the context of the superfamily, and this is done below.

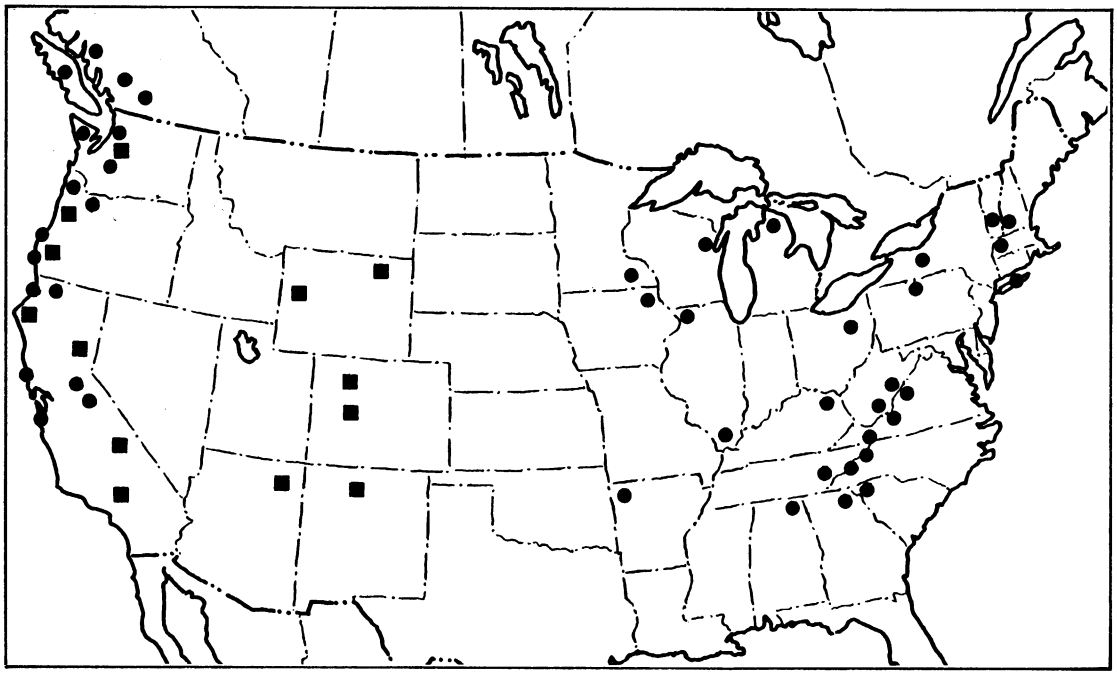
DISTRIBUTION: For *Sabacon* only, see the map in Martens (1983, p. 267); Pacific coast of North America from southern Alaska to south of San Francisco Bay; Sierra Nevada Mountains; Appalachians from New Hampshire to North Carolina (isolated records from Ohio, Illinois, Minnesota, Iowa, Wisconsin, Michigan, and Arkansas); Pyrenees and French and Italian Alps; Himalayas; Tunguska and Altai, Siberia; Korea, Manchuria, and Primorje (USSR); Japan. For *Taracus*, see below.

Taracus Simon, 1879

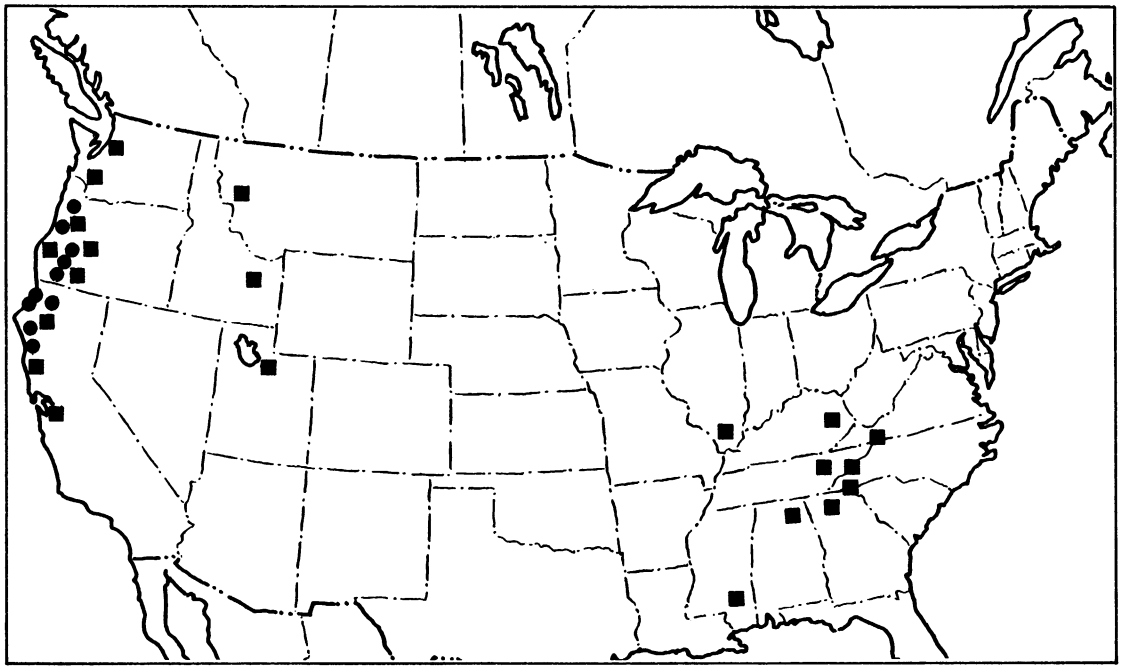
Taracus Simon, 1879, p. 277. Comstock, 1913, p. 81. Roewer, 1923, p. 693; 1950, p. 52. Shear, 1975, p. 8.

TYPE SPECIES: *T. packardi* Simon, 1879.

DIAGNOSIS: Sabaconids with greatly enlarged, spiny chelicerae lacking gland in males; labrum flat; metapeltidium usually not sclerotized, metapeltidial sensory cone single, in median line; abdomen not sclerotized, or with small sclerotized patches, to scutum laminatum; sternum reduced to two small plates with single setae; palpi long, slender, with distal teeth on patella in males; legs without microtrichia on femora (fig. 14); penis with



MAP 1. Part of North America, showing distribution of *Sabacon* species (circles) and *Taracus* species (squares). *Sabacon* also occurs in southern Alaska.



MAP 2. Part of North America, showing distribution of *Hesperonemastoma* species (squares) and *Ceratolasma tricantha* (circles).

muscle in truncus; ovipositor slightly longer than wide.

DISTRIBUTION: Seven of the eight described species (*packardi, spinosus, pallipes, silvestrii, gertschi, nigripes,* and *malkini*) are limited to western North America, but their exact distribution remains uncertain without a revisionary treatment. The range includes, however, most of montane California, western Oregon and Washington, central Colorado (Utah?), northern New Mexico, and northwestern Arizona. A single species, *T. birsteini,* was described by Ljovushkin (1971) from Primorsky Krai, near Vladivostok in Siberia.

FAMILY CERATOLASMATIDAE, NEW

Ischyropsalidae, Goodnight and Goodnight, 1945, p. 5 (in part). Gruber, 1970, p. 130 (in part); 1978, p. 105 (in part).
Ischyropsalididae, Martens, 1978, p. 187 (in part).
Nemastomatidae, Banks, 1894, p. 51; 1901, p. 677 (in part). Roewer, 1923, p. 650 (in part); 1951, p. 95 (in part).

TYPE GENUS: *Ceratolasma* Goodnight and Goodnight, 1942.

DIAGNOSIS: Ischyropsalidoids with very heavy sclerotization, scutum parvum to magnum; metapeltidium not separate sclerite, with two sensory cones or none; carapace and scutum heavily ornamented with microsculpture of warts, fine denticles, or anvil-shaped tubercles; macrosculpture of rows or pairs of tubercles on scutum, these sometimes very high and acute, or blunt and appressed (*Ceratolasma*), or absent (*Crosbycus*); genital operculum with suture; labium and sternum usually well sclerotized; chelicerae with or without (*Hesperonemastoma*) gland in males, not enlarged; palpi long, with (*Crosbycus, Hesperonemastoma*), or short, without (*Ceratolasma, Acuclavella*) plumose setae; legs with microsculpture of apically notched, distally raised, scalelike tubercles subtending small blunt setae, or acute spikes, macrosetae, and recumbent hairs; penis with muscle in truncus; ovipositor about as long as wide, or longer than wide, two or four seminal receptacles.

INCLUDED GENERA: *Ceratolasma* Goodnight and Goodnight (see diagnosis in Gruber, 1978), *Crosbycus* Roewer (diagnosis below), *Hesperonemastoma* Gruber (see diagnosis in Gruber, 1970), *Acuclavella,* new.

DISTRIBUTION: North America, from southern British Columbia to central California (?); central Idaho; western Montana; Mississippi Valley from southern Illinois to northern Mississippi; southern Appalachians from southwestern Virginia to northern Georgia and Alabama.

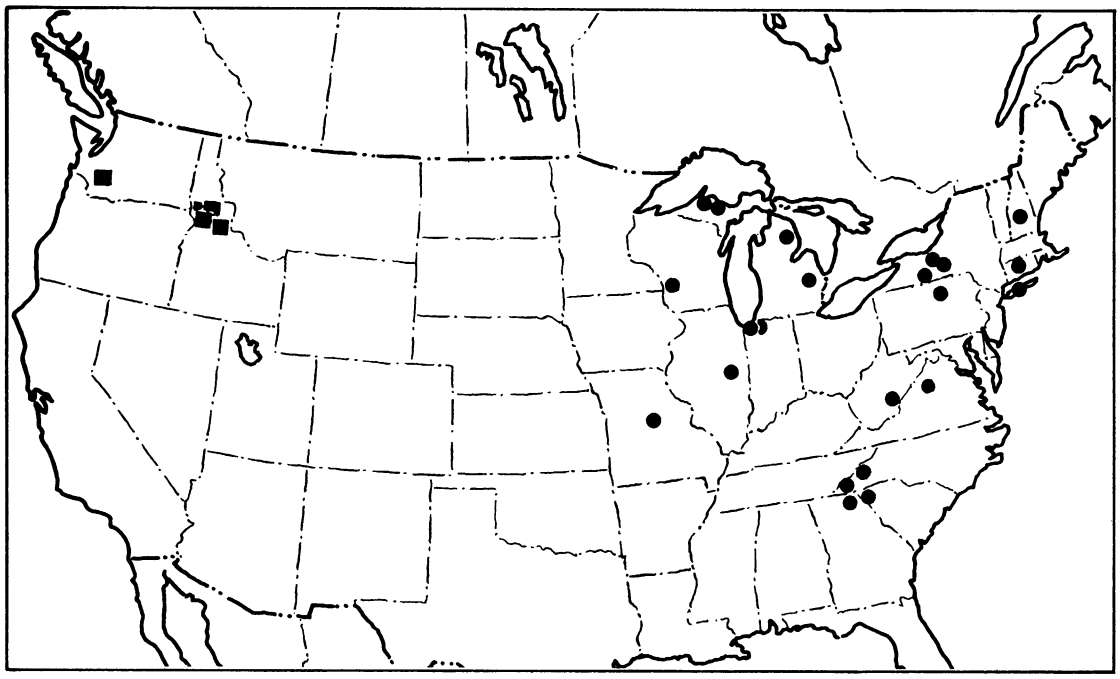
Acuclavella, new genus

TYPE SPECIES: *Acuclavella cosmetoides,* n. sp.

ETYMOLOGY: The genus name is a Latin neologism—"acute little spines"—and should be treated as feminine.

DIAGNOSIS: Closest to *Ceratolasma,* but differing in lacking lateral anterior extensions of carapace and in erect, acute (rather than procumbent, blunt) spine of the eye tubercle, and in bearing large, pointed spines on some abdominal scute areas (*Ceratolasma* has small bumps on areas 2 and 3 and large blunt spines on area 4).

DESCRIPTION: Heavily sclerotized, black or dark brown opilionids of medium size with sclerotized parts of cuticle ornamented with distinctive hemispheric warts. Carapace with suture immediately behind eye tubercle, separating propeltidium from mesopeltidium. Metapeltidium ("second thoracic tergite") set off by distinct cuticular fold but not by a suture. Metapeltidium with median pair of prominent blunt spines (probably sense organs; see Juberthie et al., 1981). Abdomen with scutum parvum, first five abdominal tergites fused, last three free. Ninth tergite divided; tenth forms anal operculum. All abdominal sternites free. Genital operculum sexually dimorphic, clearly delineated by transverse furrow that forms membranous suture at lateral ends. All coxae with endites. Sternum broader than long, larger than labium. Chelicerae and palpi short, chelicerae of males with raised, setose glandular region on basal article. Vestiture of palpi microtrichia and ordinary setae; claw remnant short, very small. Legs moderately long, microsculpture of femora, patellae, and tibiae scattered, distally elevated scales infrequently bi-



MAP 3. Part of North America, showing distribution of *Crosbycus dasycnemus* (circles) and species of *Acuclavella* (squares).

lobed and subtending short setae. Metatarsi not divided; typical microsculpture limited at most to basal third, remainder with setae and microtrichia. Tarsi with many segments. Penis very simple, distally tapering, glans with sparse microsetae, stylus distinctively twisted in some species. Ovipositor short, with small apical setae groups, four typical seminal receptacles.

DISTRIBUTION: Idaho, Washington.

NOTES: *Ceratolasma tricantha* (Gruber, 1978) is more specialized than *Acuclavella* species in a number of obvious ways. It has assumed the troguloid facies (Shear and Gruber, 1983) characteristic of soil-dwelling opilionids of many unrelated genera and families, with the profoundly flattened body and typical modifications of the carapace and anterior appendages to produce a camerostome. The cuticular sculpture of the body is well adapted for the trapping of small soil particles, a function evidently augmented by an adhesive secretion. In addition, there exists an unusual chelicera/palpus stridulatory mechanism.

Acuclavella species, on the other hand, have a robustly convex dorsum with high, sharp spines on the scute, as well as an erect spine on the eye tubercle. There is no impression of flattening and no suggestion of a camerostome; the surface of the cuticle is not adapted to trap and hold soil particles. There is no stridulatory mechanism. I regard the cuticular microsculpture of large, hemispherical warts as synapomorphic for *Acuclavella* species. However, having an eye tubercle spine at all is a synapomorphy for the two genera.

After due consideration, I have decided to describe four species in this genus. Although each population (except for *A. merickeli* at Meadow Creek) is represented by a very small sample of one to four animals, the distinctions in the dorsal armature seem consistent within the samples (including Meadow Creek), and there are between-sample differences in size and proportions. Obviously, further sampling for this genus in Idaho is required to clarify the status of the various populations.

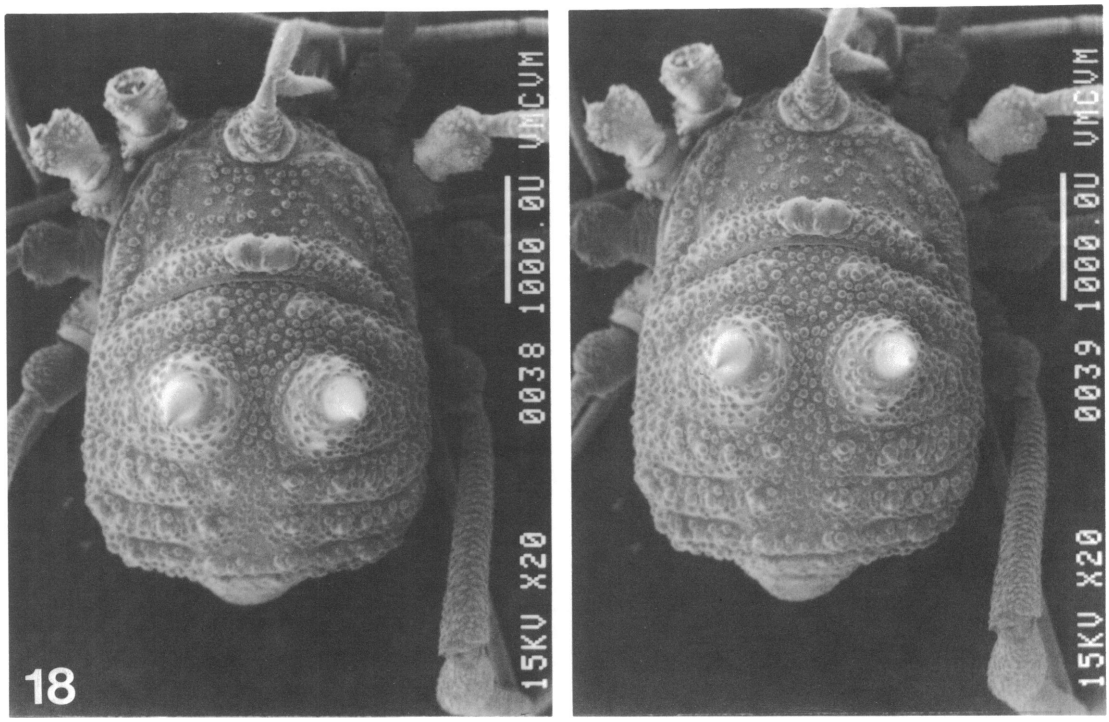


FIG. 18. Stereo-pair scanning electron micrograph of *Acuclavella merickeli* female (×16).

KEY TO *ACUCLAVELLA* SPECIES

1. Dorsum of abdomen with prominent acute spines 2
   Without such spines, but paired, low, rounded tubercles on all five dorsal areas ..... females of *shoshone*
2. A single pair of abdominal spines, on area 2 ..... *merickeli*
   More than one pair of abdominal spines .. 3
3. Abdominal spines on area 1 4
   No spines on area 1, paired spines on areas 2, 3, and 4 ..... *cosmetoides*
4. Four pairs of abdominal spines (on areas 1–4) ..... males of *shoshone*
   Two pairs of abdominal spines (on areas 1 and 2) ..... females of *quattuor*

Acuclavella cosmetoides, new species
Figures 19–24, 30, 33, 34, 37

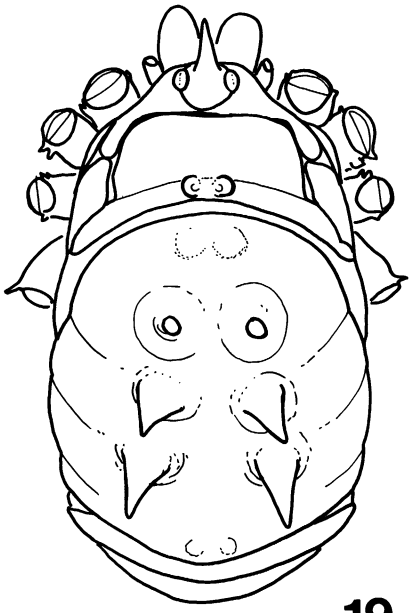
TYPES: Male holotype and female paratype (AMNH) from Pierce, Clearwater Co., Idaho (August 29, 1959; W. J. Gertsch and V. Roth).

ETYMOLOGY: The species name is an adjective pointing out the resemblance of this species to members of the tropical opilionid family Cosmetidae.

DIAGNOSIS: Easily distinguished from the other species by three pairs of acute spines on the abdominal scutum.

DESCRIPTION OF MALE HOLOTYPE: Body (fig. 23) highly arched, convex dorsally, somewhat rectangular in general outline, only slightly longer than wide. Nearly all of body heavily sclerotized, black, with densely scattered warts; body without pilosity. Total length 4.42 mm; carapace length in midline 1.35 mm, greatest carapace width 2.86 mm; length of scutum in midline 2.47 mm, greatest width of scutum 3.04 mm.

Eye tubercle (fig. 30) at edge of carapace, oval at base, prolonged into sharp, conical spine standing 1.04 mm above carapace. Eyes small, dark brown, on rounded basal part of tubercle. Carapace surface evenly curved, posterior margin arcuate; mesopeltidium (first thoracic tergite) probably fully incorporated, but its side-pieces free, entirely dorsal. Metapeltidium (second thoracic tergite) incorporated but clearly delimited by deep fold; sensory cones very prominent, paramedian in position, with shiny brown tips. Ozopores not visible from above, opening in mem-



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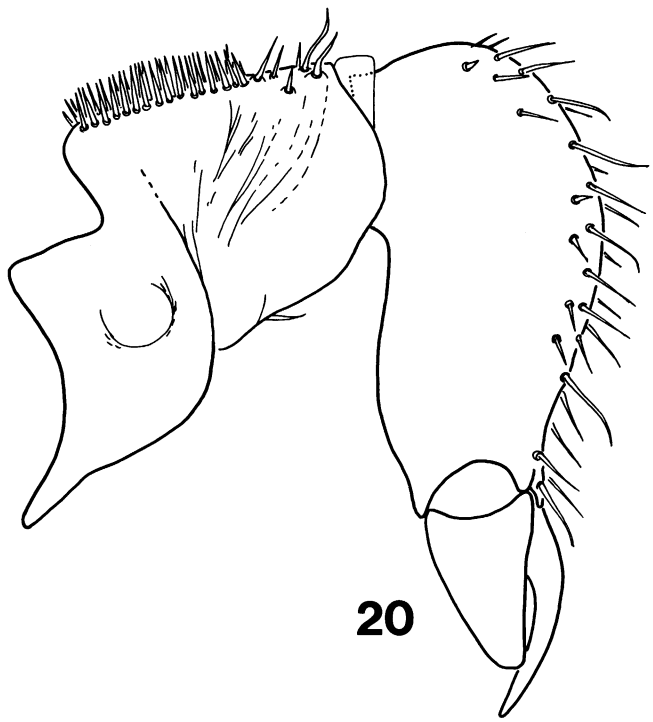

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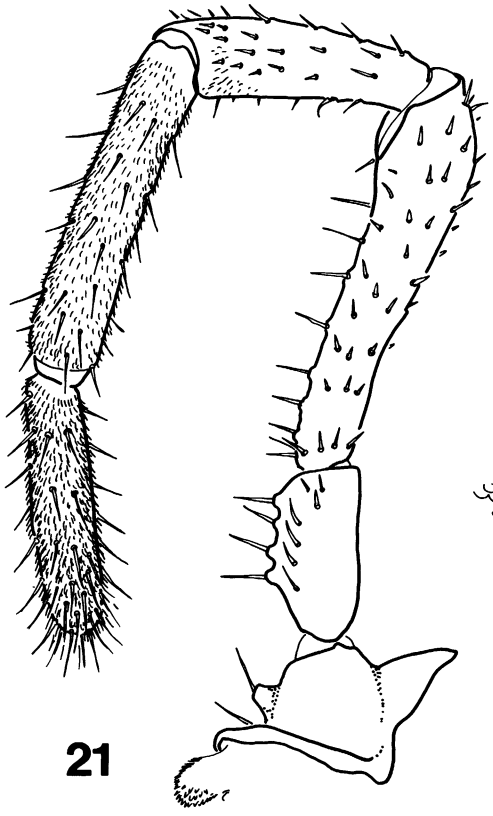

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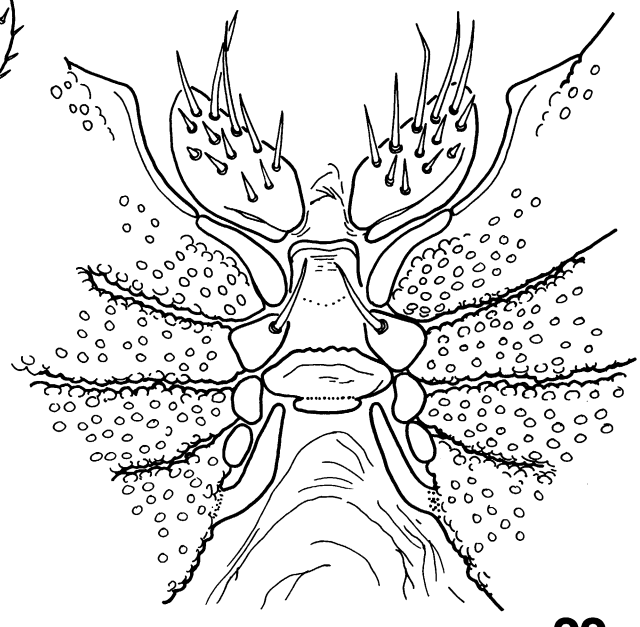

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brane between carapace and first and second leg coxae.

Scutum of opisthosoma well-arched, nearly square in outline when seen dorsally. All areas with paired tubercles; on area 1 paired small bunches of slightly enlarged cuticular warts, on areas 2, 3, and 4, tubercles enormously enlarged to form smooth, shining spikes with acute tips rising from swollen, nearly circular bases with same warty sculpture as the scutum surface. Spikes subequal in size, but those of area 3 slightly smaller than others. Area 5 with widely separated small tubercles; these barely noticeable on free abdominal tergites.

Sclerites of anal region typical, like those of *Ceratolasma tricantha.* Abdominal sternites narrow, not modified, with typical sculpture. Spiracles not visible. Genital operculum tongue-shaped, separated from second abdominal sternite by faintly indicated incomplete suture. Distal margin rebordered, glossy. Prosomal sternum 0.09 mm long, 0.13 mm wide, brown, without setae. Labium weakly sclerotized, longer than wide, without setae. All leg coxae with endites, those of legs III and IV smallest. Endites of leg II about twice their size, with single setae. Endites of legs I with free sclerite, oval, brown, setose (fig. 22). Palpal endites free, with large sclerotized and membranous parts.

Chelicerae (fig. 20) black, surface smooth, shining. Basal article 1.09 mm long, 0.65 mm wide, dorsally with oval, slightly raised glandular area densely set with amber setae. In holotype, this area capped with hardened glandular secretion. Palp (fig. 21) with dimensions given in table 2. Coxae black, ventrally with three seta-bearing tubercles. Trochanter very dark brown with ventral row of four seta-bearing tubercles. Remaining segments light yellow-brown except as noted. Patella with diffuse darker band on middle third, bearing small setae and few microtrichia distally. Tibia very faintly darkened distally, with scattered ordinary setae and dense cover of microtrichia. Tarsus slightly and uniformly darker than tibia, with setae and dense microtrichia; claw rudiment very small.

TABLE 2

Lengths of Appendage Segments in Holotype Male *Acuclavella cosmetoides*

(Measurements are in millimeters.)

Segment	Palpus	Legs 1	2	3	4
Trochanter	0.52	0.52	0.73	0.52	0.74
Femur	0.78	2.21	3.17	2.00	2.86
Patella	0.65	0.91	1.04	1.04	1.04
Tibia	0.73	1.66	2.39	1.69	2.24
Metatarsus	—	2.34	3.77	2.42	3.72
Tarsus	0.73	2.63	4.94	—	4.16

Legs with segments long, cylindrical, with microsculpture of evenly spaced, low, flat tubercles made scalelike by raised distal margin, widely scattered small setae usually in notch on distal margin of tubercle. All leg segments black except metatarsi and tarsi, these bright brown; metatarsi and tarsi lack tubercles, densely clothed in microsetae. Metatarsi not divided, tarsi divided with longer basal segment and many short distal ones; distitarsus of three segments. Claws single, evenly curved, black, not toothed.

Penis (figs. 33, 34) 2.5 mm long, widest (0.13 mm) at base of shaft. Shaft evenly tapered, broadening slightly at glans. Dorsal glans plate with scattered small setae, stylus spirally twisted, well set off from body of glans.

DESCRIPTION OF FEMALE PARATYPE: Similar in nearly all respects to male, differing in dimensions and in secondary sexual characters (fig. 24). Total length 5.2 mm. Midline lengths: carapace 1.48 mm, metapeltidium 0.26 mm, scute 3.30 mm. Widths: carapace 2.6 mm, scute 3.56 mm (greatest width of body). Eye tubercle spike 1.10 mm above surface of carapace.

Sternum 0.13 mm long, 0.31 mm wide. Chelicerae with basal article lacking glandular area found in male, 1.3 mm long, 0.52 mm wide; distal article 1.3 mm long, 0.44

←

FIGS. 19–22. *Acuclavella cosmetoides.* **19.** Male, dorsal view. **20.** Right male chelicera, lateral view. **21.** Right male palpus, mesal view. **22.** Anterior ventral surface of male, ventral view, genital operculum removed.

TABLE 3
Lengths of Appendage Segments in Paratype Female *Acuclavella cosmetoides*
(Measurements are in millimeters.)

Segment	Palpus	Legs 1	2	3	4
Trochanter	0.52	0.62	0.65	0.52	0.73
Femur	0.94	2.03	2.83	1.79	2.60
Patella	0.65	1.04	1.25	0.96	1.09
Tibia	0.78	1.38	2.08	1.30	1.95
Metatarsus	—	1.82	3.17	2.18	3.27
Tarsus	0.68	2.13	4.16	2.60	2.70

mm wide. Lengths of palpal and leg segments given in table 3.

Ovipositor (fig. 37) blunt, short, unsegmented, symmetrical, with apical tufts of setae.

DISTRIBUTION: Known only from the type locality.

Acuclavella shoshone, new species
Figures 27, 28, 35

TYPES: Male holotype and two female paratypes (AMNH) from Hobo Cedar Grove, Shoshone Co., Idaho (July 20–29, 1984; F. W. Merickel).

ETYMOLOGY: The species name is a noun in apposition referring to Shoshone County.

DIAGNOSIS: Easily distinguished from the other species by four pairs of spines on the abdominal dorsum in males, and four low tubercles in the same position in females.

DESCRIPTION OF MALE HOLOTYPE: Body (fig. 27) not so highly arched as in type species, convex dorsally, more or less oval in general outline, significantly longer than wide (length/width = 1.62). Nearly all of body heavily sclerotized, black, with densely scattered small warts; body without pilosity. Total length 4.37 mm; carapace length in midline 1.30 mm, greatest carapace width 2.47 mm; length of scutum in midline 2.50 mm, greatest width of scutum 2.70 mm.

Eye tubercle at edge of carapace, oval at base, prolonged into sharp, conical, forward-tilted spine standing 0.91 mm above carapace. Eyes small, dark brown, on rounded basal part of tubercle. Features of carapace as in *A. cosmetoides.*

Scutum of opisthosoma rounded anteriorly, posterior margin nearly square when seen dorsally. All areas with paired tubercles, on areas 1–4, enlarged to form smooth shining spikes with acute tips, rising from nearly circular, swollen, warty bases; spikes of areas 1 and 4 smallest, subequal, those of areas 2 and 3 nearly twice as large, subequal. Area 5 with paired clusters of four to six slightly larger cuticular warts; free tergites without any trace of paired tubercles.

Anal region, spiracles, and genital operculum as in *A. cosmetoides.* Prosomal sternum 0.13 mm long, 0.31 mm wide, brown, without setae. Labium weakly sclerotized, longer than wide, without setae. Endites as in *A. cosmetoides.*

Chelicerae black, surface smooth, shining. Basal article 1.17 mm long, 0.55 mm wide, dorsally with oval, slightly depressed, rimmed glandular area densely set with amber setae. Gland area not as stongly raised posteriorly as in *A. cosmetoides.* Palp with dimensions given in table 4. Coxae black, ventrally with two seta-bearing tubercles. Trochanter very dark brown with ventral row of four seta-bearing tubercles. Otherwise palpi as in *A. cosmetoides.*

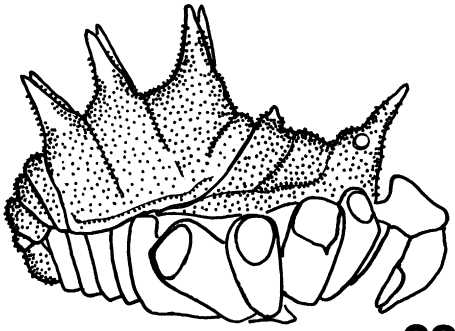
Structure and color of legs as in *A. cosmetoides*; lengths of segments given in table 4.

Penis (fig. 35) 3.25 mm long, widest (0.13 mm) at base of shaft. Shaft evenly tapered, not broadening at glans. Dorsal glans plate with very few small setae, stylus straight, not perceptibly set off from glans.

DESCRIPTION OF FEMALE PARATYPE: Similar in nearly all respects to male, differing in dimensions, in secondary sexual characters, and in dorsal ornamentation (fig. 28). Scute

→

FIGS. 23–30. Structure of *Acuclavella* species. 23–29. Lateral view of body. **23.** *A. cosmetoides* male. **24.** *A. cosmetoides* female. **25.** *A. merickeli* male. **26.** *A. merickeli* female. **27.** *A. shoshone* male. **28.** *A. shoshone* female. **29.** *A. quattuor* female. **30.** Eye tubercle of *A. cosmetoides* male, subdorsal view. Figures 23–29 are not all drawn to the same scale.



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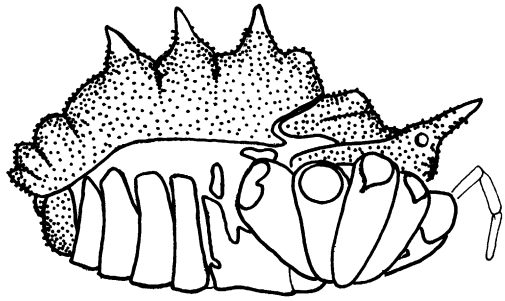

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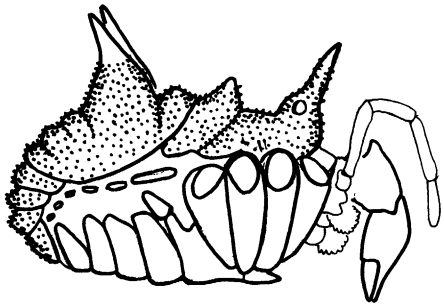

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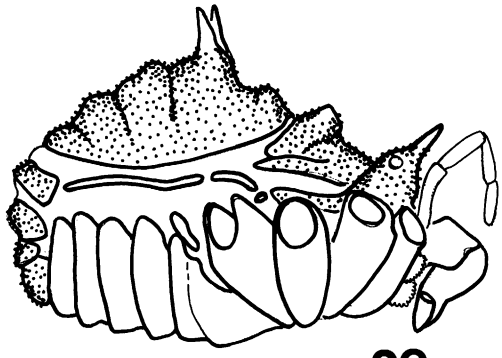

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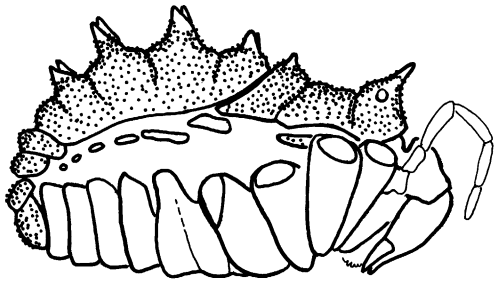

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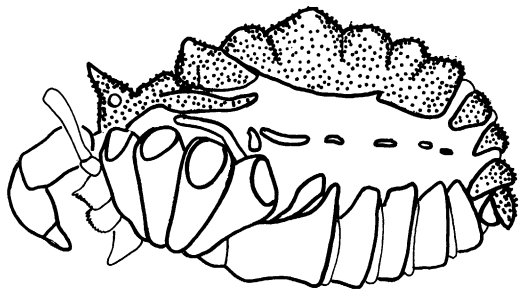

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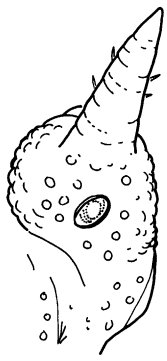

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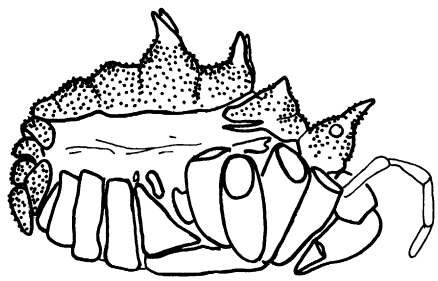

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TABLE 4
Lengths of Appendage Segments in Holotype Male *Acuclavella shoshone*
(Measurements are in millimeters.)

Segment	Palpus	Legs 1	2	3	4
Trochanter	0.55	—	—	—	—
Femur	0.91	2.34	3.17	2.03	2.73
Patella	0.70	0.88	1.17	0.96	1.17
Tibia	0.86	1.69	2.16	1.56	1.95
Metatarsus	—	2.35	3.64	2.60	3.80
Tarsus	0.73	2.50	4.55	2.76	3.64

TABLE 5
Lengths of Appendage Segments in Paratype Female *Acuclavella shoshone*
(Measurements are in millimeters.)

Segment	Palpus	Legs 1	2	3	4
Trochanter	0.65	0.57	0.73	0.55	0.68
Femur	0.91	1.95	2.86	2.08	2.60
Patella	0.70	0.83	1.35	0.90	1.09
Tibia	0.78	1.43	2.18	2.08	1.56
Metatarsus	—	2.34	3.77	2.47	4.47
Tarsus	0.78	2.60	4.29	2.81	3.00

areas lacking characteristic spikes; these replaced by low, warty tubercles largest on area 2, slightly smaller on area 1; those on areas 3 and 4 about half size of tubercles of area 2. Area 5 with very small bumps at very margin of scute; first free tergite similar; no bumps on second free tergite.

Total length 5.2 mm. Midline lengths: carapace 1.69 mm, scute 3.33 mm. Widths: carapace 2.6 mm, scute 3.38 mm (greatest width of body). Eye tubercle spike 0.68 mm above surface of carapace.

Sternum 0.10 mm long, 0.31 mm wide. Chelicerae with basal article lacking glandular area found in male, 1.3 mm long, 0.54 mm wide; distal article 1.43 mm long, 0.56 mm wide. Lengths of palpal and leg segments given in table 5.

Ovipositor as in *A. cosmetoides*.

DISTRIBUTION: Known only from the type locality.

Acuclavella merickeli, new species
Figures 2, 10, 18, 25, 26, 31, 32, 36

TYPES: Male holotype, three male and four female paratypes (AMNH) from Meadow Creek, 20 miles east-southeast of Lowell, Idaho Co., Idaho (August 18, 1984; F. W. Merickel). Three female paratypes (WAS) from same locality (May 17, 1983, May 20, 1984; F. W. Merickel), and one additional female paratype (JCC) from same locality (collection undated; F. W. Merickel).

ETYMOLOGY: The species name honors Frank W. Merickel; with only three exceptions he has collected all the known specimens of *Acuclavella* species.

DIAGNOSIS: Easily distinguished from the other species by having only a single pair of prominent dorsal spikes in both males and females, and these on area 2.

DESCRIPTION OF MALE HOLOTYPE: Body (fig. 25) not so highly arched as in *A. cosmetoides*, convex dorsally, rounded anteriorly, but appearing squared off posteriorly; longer than wide (length/width = 1.52). Nearly all of body heavily sclerotized, black, with densely scattered warts. Total length 4.16 mm; carapace length in midline 1.40 mm, greatest carapace width 2.60 mm; length of scutum in midline 2.60 mm, greatest width of scutum 2.73 mm.

Eye tubercle at edge of carapace, oval at base, prolonged into sharp, conical, forward-tilted spine standing 1.06 mm above carapace. Eyes small, dark brown, on rounded basal part of tubercle. Features of carapace as in *A. cosmetoides*. Metapeltidial sensory cones unusually large, much larger than in other species.

Scutum of opisthosoma rounded anteriorly, posterior margin nearly square when seen dorsally, lateral margins convex. All areas with paired tubercles, on area 1, as small bunches of slightly enlarged cuticular warts, smaller than sensory cones of metapeltidium. Area 2 with enormously enlarged, shining spikes curving slightly posteriad, bases prominently warty. On areas 3–5, tubercles scarcely discernible bunches of warts; tubercles not distinct on free tergites.

Anal region, spiracles, and genital operculum as in *A. cosmetoides*. Prosomal sternum 0.10 mm long, 0.26 mm wide, brown, without setae. Labium well sclerotized,

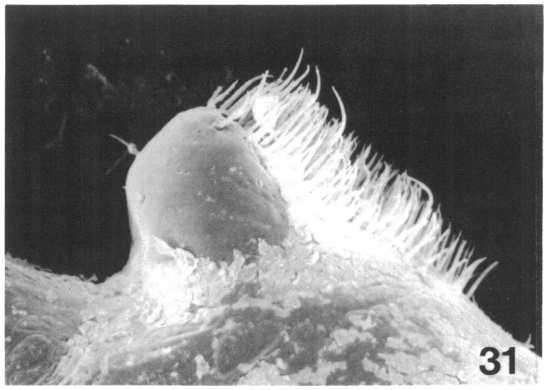


FIG. 31. Scanning electron micrograph of cheliceral gland mound of male *Acuclavella merickeli*; lateral view, ×120.

slightly wider than long, without setae. Endites as in *A. cosmetoides*.

Chelicerae medium brown, surface smooth, shining. Basal article 1.13 mm long, 0.57 mm wide, dorsally with oval, slightly depressed, rimmed glandular area (fig. 31) densely set with amber setae. Gland area not more strongly raised posteriorly than in *A. cosmetoides*. Palp with dimensions given in table 6. Coxa dark brown, ventrally with two seta-bearing tubercles. Trochanter brown with ventral row of four seta-bearing tubercles. Remaining segments pale yellow, but tarsus shaded darker distally.

Structure and color of legs as in *A. cosmetoides*; lengths of segments given in table 6.

Penis (figs. 32, 36) 2.34 mm long, widest (0.09 mm) at base of shaft. Shaft evenly tapered, not broadening at glans. Dorsal glans plate with rows of small setae, stylus spirally curved, well set off from glans, lacking subapical tooth.

DESCRIPTION OF FEMALE PARATYPE: Similar in nearly all respects to male, differing in dimensions, in secondary sexual characters, and in dorsal ornamentation (figs. 18, 26). Sensory cones smaller, rounder than in male. Spikes of area 2 smaller, less acute than in male; tubercles of areas 3–5 hardly detectable; free tergites without tubercles.

Total length 5.15 mm. Midline lengths: carapace 1.22 mm, scute 3.38 mm. Widths: carapace 2.9 mm, scute 3.51 mm (greatest width of body). Eye tubercle spike 0.94 mm above surface of carapace.

TABLE 6

Lengths of Appendage Segments in Holotype Male *Acuclavella merickeli*

(Measurements are in millimeters.)

Segment	Palpus	Legs			
		1	2	3	4
Trochanter	0.52	0.65	0.73	0.65	0.70
Femur	0.96	2.08	3.43	2.08	2.83
Patella	0.68	1.04	1.09	0.91	1.09
Tibia	0.83	1.48	2.34	1.51	2.08
Metatarsus	—	2.29	3.77	2.55	3.74
Tarsus	0.73	2.73	4.68	2.80	3.77

Sternum 0.31 mm long, 0.18 mm wide. Chelicerae with basal article lacking glandular area found in male, 1.35 mm long, 0.54 mm wide; distal article 1.4 mm long, 0.56 mm wide. Lengths of palpal and leg segments given in table 7.

Ovipositor as in *A. cosmetoides*.

DISTRIBUTION: WASHINGTON: *Lewis Co.:* 2.3 mi NE of Mossyrock, waterfall on Corn Creek, September 3, 1974 (R. Crawford), female (BMM).

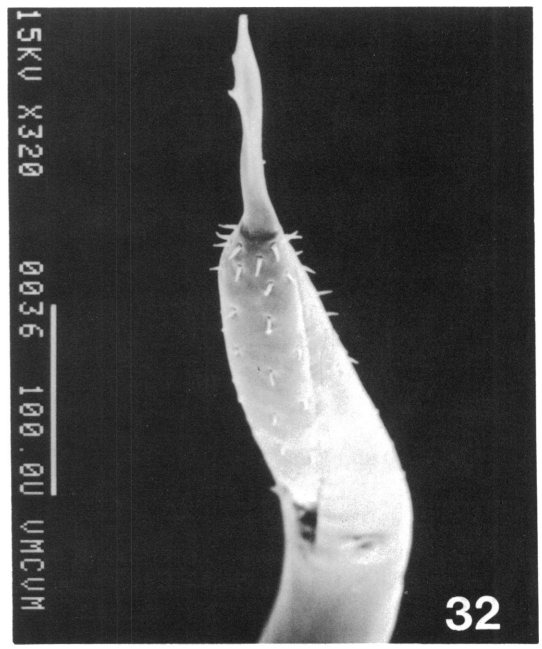


FIG. 32. Scanning electron micrograph of glans penis of *Acuclavella merickeli*; lateral view, dorsal is to the left (×250).

TABLE 7
Lengths of Appendage Segments in Paratype Female *Acuclavella merickeli*
(Measurements are in millimeters.)

Segment	Palpus	Legs			
		1	2	3	4
Trochanter	0.57	0.65	0.72	0.65	0.68
Femur	0.96	1.90	3.00	1.95	2.73
Patella	0.78	1.04	1.04	0.86	1.04
Tibia	0.83	1.38	2.18	1.43	1.95
Metatarsus	—	2.16	3.64	2.44	3.67
Tarsus	0.73	2.47	4.32	2.66	3.51

NOTES: As with the other species, this one is evidently quite cryptic, with only a few specimens having been taken until the type collection was made in fall of 1984.

Regarding this collection, Mr. Merickel wrote me: "All these were collected next to a small creek, on bare, moist ground. Two of these, probably a pair, were discovered quite accidentally while I was washing dishes and I suspect they were disturbed out of hiding. Thinking that they might be nocturnal, I returned to the same place that night and sure enough was able to pick up six more walking along the [stream] bank. A number of other situations were examined, including moist logs and mossy areas, but to no avail." The previous specimens from Meadow Creek came from Berlese samples of litter taken near the same stream.

The specimen from Lewis Co., Washington, was found under wet rocks near a waterfall. While very distant from the type locality, this specimen is very similar in all respects to the material from Idaho, and so is included here.

Acuclavella quattuor, new species

Figure 29

TYPE: Female holotype (AMNH) from 10 miles east of Slate Creek, Idaho Co., Idaho (May 10–21, 1983; F. W. Merickel and J. B. Johnson).

ETYMOLOGY: The species name is an adjective referring to the four prominent spikes on the dorsum of the abdomen.

DIAGNOSIS: Easily distinguished from the other species by having two pairs of spikes on the scutum, on areas 1 and 2.

DESCRIPTION OF FEMALE HOLOTYPE: Body (fig. 29) highly arched, convex dorsally, broader posteriorly, longer than wide (length/width = 1.35). Nearly all of body heavily sclerotized, dark brown, with densely scattered, small, black warts; body without pilosity. Total length 5.04 mm; carapace length in midline 1.30 mm, greatest carapace width 2.86 mm; length of scutum in midline 3.38 mm, greatest width of scutum 3.74 mm.

Eye tubercle at edge of carapace, oval at base, prolonged into sharp, conical, forward-tilted spine standing 1.09 mm above carapace. Eyes small, dark brown, on rounded basal part of tubercle. Features of carapace as in *A. cosmetoides.*

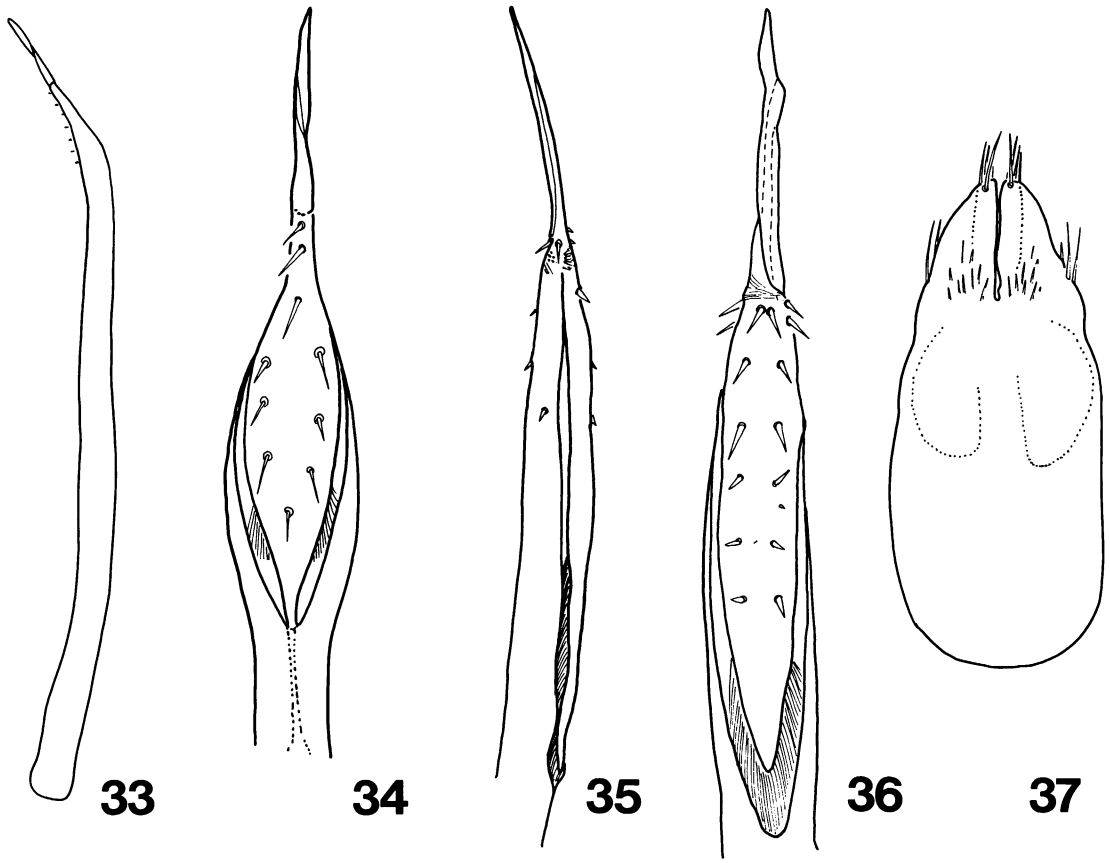
Scutum of opisthosoma rounded, narrower anteriorly, posterior margin broadly squared off when seen dorsally. All areas with paired tubercles; on area 1, large spikes situated at anterior edge of scute on either side of midline. On area 2, spikes about 25 percent larger, about twice as far apart. Areas 3 and 4 have small, raised, warty knobs paired near the midline, with three noticeably enlarged clusters of warts lateral to them in row on each side; on area 5 only clusters homologous to spikes visible; free tergites without tubercles, warts irregularly distributed.

Anal region, spiracles, and genital operculum as in *A. cosmetoides.* Prosomal sternum 0.13 mm long, 0.34 mm wide, brown, without setae. Labium weakly sclerotized, about as long as wide, without setae. Endites as in *A. cosmetoides.*

Chelicerae light brown, surface smooth, shining. Basal article 1.19 mm long, 0.57 mm wide. Palp with dimensions given in table 8. Coxa yellowish, ventrally with two seta-bearing tubercles. Trochanter light brown with ventral row of four seta-bearing tubercles. Femur white. Patella very light brown, bearing small setae and microtrichia distally. Tibia white, with denser setae and microtrichia. Tarsus darkened distally, claw rudiment absent.

Structure and color of legs as in *A. cosmetoides*; lengths of segments given in table 8.

Ovipositor as in *A. cosmetoides.*



FIGS. 33–37. Genitalia of *Acuclavella* species. 33, 34. *A. cosmetoides.* **33.** Penis, lateral view. **34.** Glans penis, dorsal view. **35.** Glans penis of *A. shoshone,* lateral view. **36.** Glans penis of *A. merickeli,* dorsal view. **37.** Ovipositor of *A. cosmetoides,* dorsal view.

DISTRIBUTION: Known only from the type locality.

NOTES: The holotype specimen was taken from a cantharidin trap.

Crosbycus Roewer, 1914

Crosbycus Roewer, 1914, p. 168. See additional citations below.

TYPE SPECIES: *Nemastoma dasycnemum* Crosby (1911).

DIAGNOSIS, ETC.: The only known species is discussed below.

NOTES: Giltay (1932), Roewer (1951), and Loksa (1962) all described additional *Crosbycus* species from Europe. Rambla (1968) and Gruber and Martens (1968) demonstrated that all these names were based on juvenile nemastomatids. An additional American species was also described by Roewer in 1951: *Crosbycus goodnighti,* from Fountain Cave, Augusta Co., Virginia (no date or collector's name given). Unfortunately, the vial containing the types could not be located at the Senckenberg Museum. As Rambla (1968) pointed out, the illustrations and the descrip-

TABLE 8
Lengths of Appendage Segments in Holotype Female *Acuclavella quattuor*
(Measurements are in millimeters.)

		Legs			
Segment	Palpus	1	2	3	4
Trochanter	0.57	0.60	0.73	0.58	0.73
Femur	0.94	2.18	3.25	2.21	2.73
Patella	0.78	0.86	1.09	1.04	1.00
Tibia	0.89	1.56	2.13	1.43	1.98
Metatarsus	—	2.34	3.54	2.60	3.80
Tarsus	0.70	2.65	4.16	2.99	3.77

tion leave little doubt that this, too, is a juvenile nemastomatid. The only nemastomatid in eastern North America is *Nemastoma bimaculatum,* a European species that obviously has been imported and has established itself. (I found a large number of specimens in the collection of the AMNH that had been taken in Toronto in 1945 and 1946 by W. Ivie and T. B. Kurata; the species was reported from Montreal by LeSage, 1978.) In western North America and Mexico are the very distinctive ortholasmatine nemastomatids (Shear and Gruber, 1983). Fountain Cave is well known to biospeleologists (Holsinger, 1964, 1975; personal commun.), and no opilionids answering the description of *C. goodnighti* have been taken there or in the vicinity.

The specimens Roewer used must somehow have gotten mislabeled. Clearly *Crosbycus goodnighti,* whatever it might be, or from whence it might have come, is not a *Crosbycus.*

Crosbycus dasycnemus (Crosby)

Figures 6, 12, 17, 38–41

Nemastoma dasycnemum Crosby, 1911, p. 20. Comstock, 1912, p. 78.

Crosbycus dasycnemum, Roewer, 1914, p. 168; 1919, p. 160.

Crosbycus dasycnemus, Roewer, 1923, p. 678; 1951, p. 151. Crosby, Wolfe, and Bishop, 1928, p. 1074. Comstock, 1940, p. 78. Bishop, 1949, p. 172. Levi and Levi, 1952, p. 165. Edgar, 1966, p. 356. Rambla, 1968, p. 70. Gruber, 1970, p. 129. Suzuki and Kunita, 1972, p. 89. Suzuki et al., 1977, p. 126. Martens, 1976, p. 66; 1978, p. 186.

TYPE: Female holotype (Cornell Colection, AMNH) from Columbia, Boone Co., Missouri, examined.

DESCRIPTION: Female (fig. 38) from Dune Acres, Porter Co., Indiana. General color dark brown, with unsclerotized areas white. Legs yellowish. Total length, 0.89 mm. Carapace 0.17 mm long, 0.41 mm wide; abdominal scutum 0.49 mm wide. Carapace arcuate, slightly indented in midline, with clusters of small, acute to anvil-shaped, black denticles generally distributed anteriorly in two groups on either side eye tubercle. Eye tubercle 0.09 mm wide, rounded, at margin of carapace, with posteriomedian group of black denticles. Metapeltidium fully incorporated into carapace, marked by distinct fold of cuticle; without sensory cones, with densely scattered black denticles. Scutum nearly square, anterior and posterior margins convex, lateral margins nearly parallel, with five areas (evidently incorporating five tergites). First three areas not distinct, marked by densely and evenly scattered black denticles; areas 4 and 5 oval, 4–5 times wide than long, densely set with black denticles. (In some specimens, area 5 partially separated by white membrane from remainder of scutum.) Free tergites and anal operculum with same dense scattering of denticles.

Sclerotized parts of ventral surface with scattered denticles and densely set, thin, tridentate microscales in irregular rows (fig. 17). Genital operculum very broad, set off by complete, straight suture, with scattered setae. Sternum and labium not sclerotized. All coxae with large, prominent endites, as in figure 39. Labrum with long, distinctive median projection.

Chelicerae brown, not enlarged. Basal article without gland.

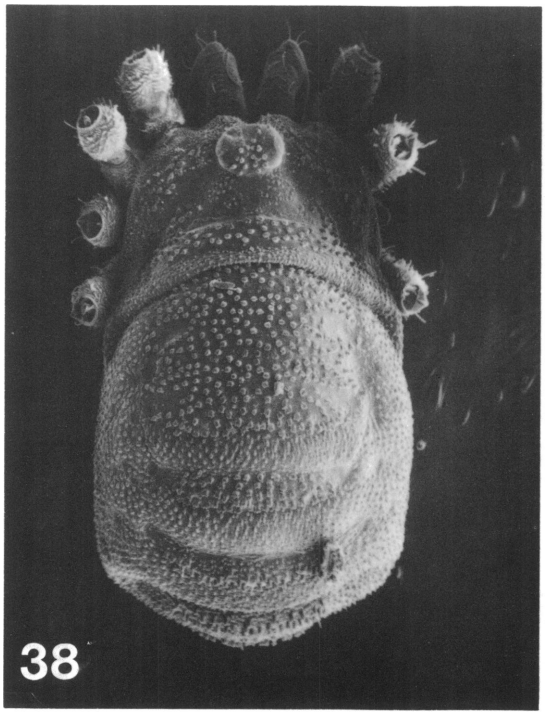
Palpus (fig. 40) with dimensions as in table 9, extremely long and thin, nearly as long as first and third legs. Trochanter, femur, and patella with few ordinary setae, as in figure 40; tibia and tarsus with plumose setae (fig. 6), becoming more dense towards tip of tarsus, claw rudiment completely absent.

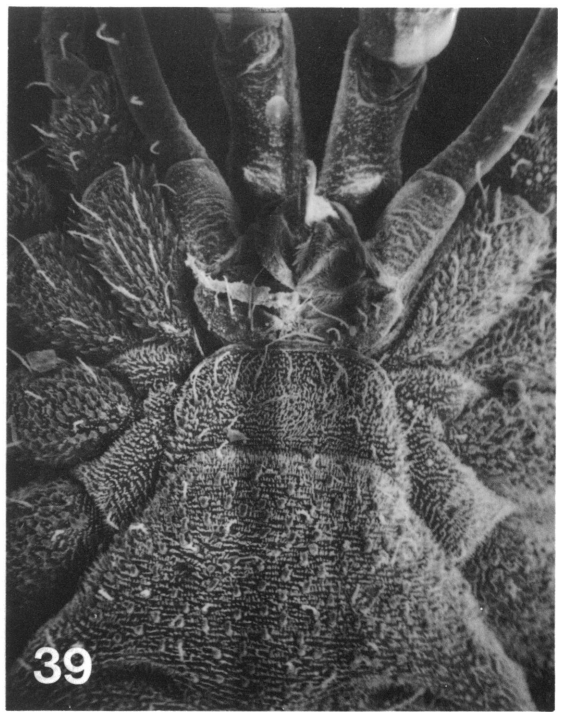
Dimensions of legs as in table 9. Femora, patellae, and tibiae with complex ornamentation consisting of large, socketed setae, unsocketed spikes projecting perpendicular to segment axis, and unsocketed curly hairs, procumbent distad, seemingly densely interwoven (fig. 12). Tarsi consisting of single basitarsal segment, two distitarsal segments on first legs, three on legs 2–4, claws untoothed.

Ovipositor (fig. 41) very short, two to three times longer than wide, apically bifurcate, each furca with two dorsal, two ventral, and one apical seta. Seminal receptacles not detected, probably absent.

Males unknown, probably do not exist.

DISTRIBUTION: NEW HAMPSHIRE: *Sullivan Co.:* Meriden, June 28, 1967 (W. B. Muchmore), 3 ff (VM). NEW YORK: *Monroe Co.:* Powder Mills Park, May 2, 1965, Apr. 16, 1966 (W. B. Muchmore), 2 ff (VM).





FIGS. 38, 39. Scanning electron micrographs of female *Crosbycus dasycnemus*. **38.** Body, dorsal view (×82). **39.** Anterior ventral surface, ventral view (×160).

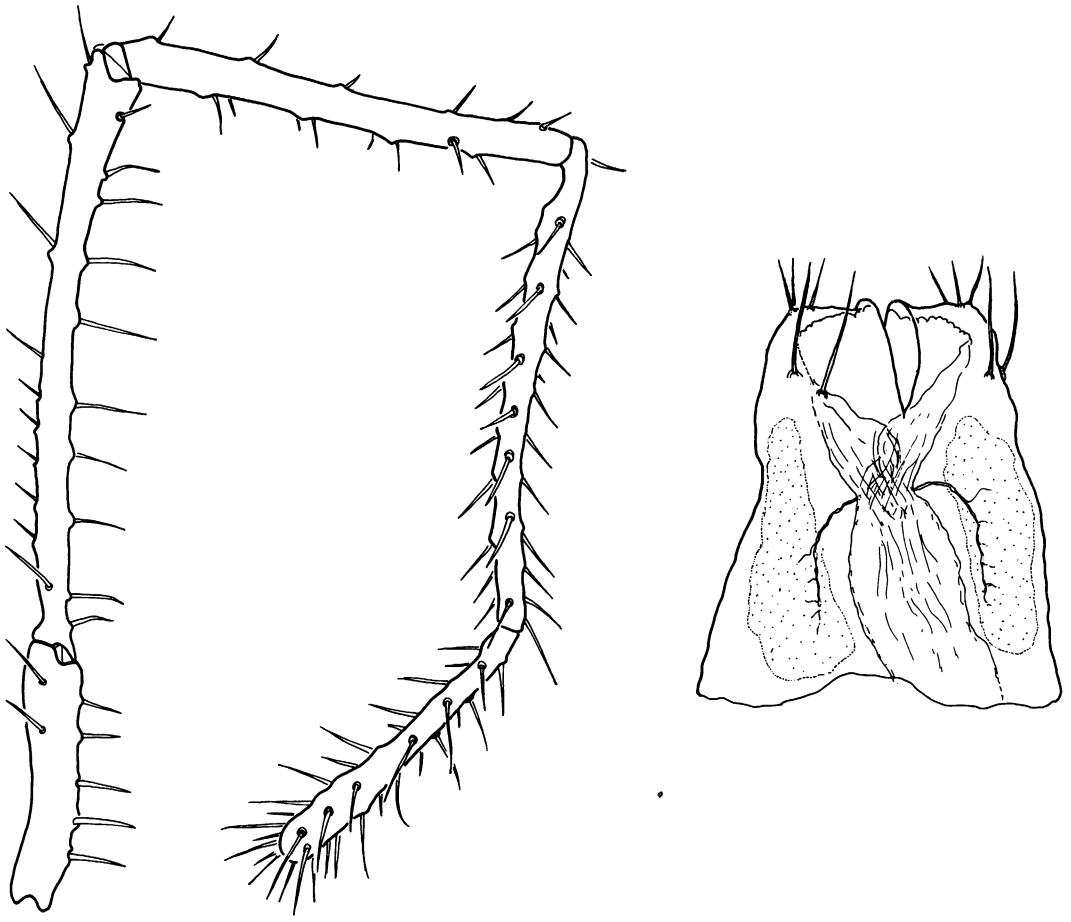
Steuben Co.: Stoney Brook State Park, Aug. 1, 1957, 1 f (AMNH). *Suffolk Co.:* Montauk Point, from sphagnum, June 25, 1927 (vial empty but containing a Crosby determination label; AMNH). *Tompkins Co.:* Connecticut Hill, Sept. 8, 1935 (C. R. Crosby), 1 f (AMNH); Freeville, Oct. 12, 1924, 1 f (AMNH). *Wayne Co.:* Zurich Bog, Apr. 26, 1970 (W. B. Muchmore), 2 ff (VM). *Yates Co.:* Keuka Lake, July 3, 1926, 1 f; Sept. 24, 1920, 1 f (AMNH). PENNSYLVANIA: *Lycoming Co.:* near Williamsport, Sept. 18, 1969 (W. B. Muchmore), 1 f (VM). WISCONSIN: *Vernon Co.:* 5 mi N Viola, mixed hardwood litter, Sept. 2, 1954 (H. W. Levi), 1 f (MCZ). MINNESOTA: *Hennepin Co.:* Lake Minnetonka, Aug. 28, 1924 (C. Fletcher) (two empty vials with Crosby determination labels, AMNH). MICHIGAN: *Alger Co.:* Shelter Bay, 6 mi W Au Train, July 16, 1953 (H. Dybas), 1 f (FMNH). *Alpena Co.:* T30N, R7E, Sec. 5, beech-maple forest, July 16–20, 1969 (G. V. Manley), 2 ff (MSU). *Leelanau Co.:* near Empire, June 7, 1946 (C. Goodnight), 1 f (AMNH). *LaPeer Co.:* Bog 4 mi E Columbiaville, July 25, 1963 (W. Suter, R. Graves), 2 ff (FMNH). *Marquette Co.:* 15 mi S Ishpenning (Green Hills Area), Aug. 10, 1956 (H. Dybas), 2 ff (FMNH). INDIANA: *Porter Co.:* Dune Acres, Apr. 12, 1949 (H. Dybas), 2 ff (FMNH); 1 mi SW McCool, Oct. 4, 1952 (H. Dybas), 2 ff (FMNH). ILLINOIS: *Champaign Co.:* Urbana, Oct. 4, 1925 (V. G. Smith), 1 f (AMNH). WEST VIRGINIA: *Pocahontas Co.:* Hills Creek Falls Scenic Area,

TABLE 9

Lengths of Appendage Segments in Female *Crosbycus dasycnemus* from Dune Acres, Porter Co., Indiana

(Measurements are in millimeters.)

		Legs			
Segment	Palpus	1	2	3	4
Trochanter	0.26	—	—	—	—
Femur	0.50	0.52	0.68	0.47	0.64
Patella	0.41	0.13	0.14	0.13	0.14
Tibia	0.43	0.39	0.71	0.43	0.64
Metatarsus	—	0.37	0.59	0.39	0.52
Tarsus	0.27	0.38	0.63	0.43	0.50



FIGS. 40, 41. *Crosbycus dasycnemus* female. **40.** Left palpus, mesal view. **41.** Ovipositor, ventral view. Note lack of seminal receptacles. Drawing courtesy of Jürgen Gruber.

above Middle Falls, June 19, 1971 (W. Shear), 2 ff (WAS). VIRGINIA: *Shenandoah National Park:* Big Meadows (3500 ft), July 2, 1963 (W. B. Muchmore), 2 ff (VM). *Giles Co.:* Mountain Lake, July 2 and 12, 1970 (W. B. Muchmore), 5 ff (VM). NORTH CAROLINA: *Buncombe Co.:* Craggie Pinnacle on Blue Ridge Parkway (5640 ft), July 14, 1977 (J. D. Pittillo), 2 ff (WAS). *Macon Co.:* 5 mi NE Highlands, ericaceous litter, Oct. 25, 1969 (W. Shear), 2 ff (WAS); Wayah Bald Summit (5300 ft) June 21, 1963 (W. B. Muchmore), 1 f (VM). *Watauga Co.:* Grandfather Mountain, Fork Creek (4080 ft), *Rhododendron* litter, May 16, 1977 (J. D. Pittillo) 1 f (WAS). SOUTH CAROLINA: *Oconee Co.:* Stumphouse Mt., 4 mi NW Walhalla, Apr. 4, 1929 (C. R. Crosby), 1 f (AMNH). GEORGIA: *Rabun Co.:* Chatooga River bank, 1.5 mi NE jct GA 28 and Jeep Road, June 1, 1975 (L. Driskill), 2 ff (WAS).

NOTES: As Bishop (1949) pointed out, less well-sclerotized specimens may appear to have tergites 4 and 5 not incorporated in the abdominal scutum. From an examination of a series of specimens it seems likely that with age (within the adult instar) additional sclerotization or additional deposition of pigment leads to the typical scutum parvum. In all the specimens examined for this study, as well as those in the Vienna Museum studied by Gruber, no males were found. Using light

microscopy at high magnifications, no seminal receptacles could be detected in the ovipositors. This strongly suggests that the species is parthenogenetic, but relatively few specimens are available, and males might be highly seasonal. Likewise, there are no juvenile specimens in collections, suggesting that a different habitat might be occupied early in life. Prey probably consists of even tinier mites, collembolans, and myriapods.

In North America, *C. dasycnemus* is found in boreal regions, high mountains, or in cool microhabitats. In the midwestern states, collection labels suggest an association with mosses, particularly sphagnum. From West Virginia south, the species occurs in the mountains, at moderate to higher elevations, but evidently not in coniferous forests (collection labels mention beech and maple), and often near streams. Usually taken in Berlese samples, this animal would be very difficult to spot during hand sorting, especially if it were slow-moving or tonically immobile. In no case is there a record of how much litter was sorted, but only two collections contained more than one or two individuals. Specimens may be overlooked in the field or misfiled in museums because of their resemblance to mites, just as *Opilioacarus* (an opilionid-like mite) can often be found in museums' opilionid collections.

The wide distribution of this species includes Japan (Suzuki et al., 1977), as well as the North American localities listed above. The Japanese specimens were compared by Suzuki with North American ones and are virtually identical; likewise there is no detectable variation over the range of the species in North America. Other opilionid species and genera have a similar discontinuous distribution: *Caddo agilis, C. pepperella,* and *Acropsopilio boopis* (Caddidae), *Dendrolasma* (Nemastomatidae), and *Paranonychus brunneus* (= *Mustsunonychus fuscus* Suzuki; Paranonychidae). The connection seems to be between eastern North America and southern Japan, and western North America and northern Japan. For three of the disjunct species, males are not known (*C. pepperella, A. boopis, C. dasycnemus*), and for a fourth (*C. agilis*), single males have been found just once in Japan (Suzuki and Tsurusaki, 1983) and just once in North America (Gruber, 1974). For a further discussion of the biogeographical situation, see Suzuki et al. (1977), and Shear and Gruber (1983).

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