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The Milliped Family Tingupidae (Diplopoda, Chordeumatida, Brannerioidea)

WILLIAM A. SHEAR[1]

ABSTRACT

The Tingupidae, a family of small, litter and soil-dwelling millipeds, is reviewed and seven new species of *Tingupa* from western North America are described and illustrated (*eldorado, sinuosa, causeyae, auricula, clatskanie, benedictae,* and *tillamook*). The species *Buotus carolinus* is placed in the Tingupidae; it was described as a polyzoniid. It is suggested that *Tingupa utahensis* and *T. arizonica* may be isolated populations of the same species; new records for *T. pallida* from Arkansas caves are given. The evolutionary relationships and biogeography of the family are briefly discussed.

INTRODUCTION

The milliped family Tingupidae is made up of a dozen or so species of small to minute millipeds with (in many cases) reduced segment numbers. Aside from the single known species of *Branneria* (Branneriidae), the family includes the smallest known North American chordeumatid species. These small creatures are almost always collected by means of Berlese or Tullgren funnels, or by sharp-eyed cave biologists used to spotting tiny, unpigmented animals. One species (*Tingupa pallida* Loomis) is found in caves in Missouri, Arkansas, and Illinois; the other species in the family are inhabitants of the leaf litter, almost always in moist, cool, heavily forested regions. The family is not known to occur outside of North America, and even here its distribution is scattered. The Appalachians, with their rich, nearly perpetually moist litter, have but one species of tingupid, *Buotus carolinus,* and this species seems to be quite rare, though widespread. The occurrence of *T. pallida* in Ozark region caves has already been mentioned, and *Tingupa utahensis* is found at high elevations in the litter of the montane forests of Utah and Arizona. Aside from a single California species and one fragmentary female from Washington state, all the other species are known from coastal Oregon, where one presumes conditions are ideal for them: deep humus and litter that in many localities never dries out or freezes. But because tingupids are hard to collect

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without special effort, it seems to me unlikely that we have found all the species, and I am sure that the distribution of the family will be further extended into the states of California and Washington.

The first tingupid species, *Tingupa utahensis,* was described by Chamberlin in 1910 from Mill Creek Canyon in Salt Lake County, Utah. *Tingupa monterea,* described from California by Chamberlin in the same paper, has been shown to be a species of *Rhiscosomides* (Shear, 1973). Twenty-nine years later, in 1939, Loomis described *Tingupa pallida* from Missouri caves, and in 1966, a third species, *T. arizonica,* was discovered in the Santa Catalina Mountains of Arizona (Loomis, 1966).

At the same time as he described *T. arizonica,* Loomis recognized that the genus *Tingupa* could no longer be accommodated in the family Rhiscosomididae, and duly established the family Tingupidae, with *Tingupa* as the type and only genus. In 1972, I reviewed what was then known of the family and provided new illustrations of the three species so far assigned to it.

It remained only for Rowland Shelley to discover that once again, Chamberlin had made a gross error in his description of a new milliped species. *Buotus carolinus* Chamberlin was originally described (Chamberlin, 1940) as a member of the order Polyzoniida, from specimens taken by Nell Causey in the Duke Forest, Durham County, North Carolina. When the type specimen was finally rediscovered by Shelley (1975), he was astonished to find it to be a typical chordeumatid and obviously a member of the Tingupidae. Earlier, I had reported on Richard Hoffman's collection of tingupids in Montgomery County, Virginia (Shear, 1972). More material has now been collected from Virginia and West Virginia which includes male specimens and leaves no doubt about the correctness of Shelley's assignment. The proper placement of *Buotus* adds a second genus to the family Tingupidae.

Again, as in my previous studies of millipeds from the Pacific Northwest, I have to express my deep appreciation to Dr. E. M. Benedict, of Portland State University, for allowing me to sort millipeds from the Berlese samples taken by her as a part of her faunal survey of west coast Pseudoscorpionida. Particularly in the present family, virtually all the western United States material available of small, soil and litter-dwelling millipeds comes from her work. Dr. Richard Hoffman and Dr. Rowland Shelley also have my thanks for their efforts in regard to *Buotus carolinus,* and their helpful comments on this species. Mr. Rod Crawford of the Burke Memorial Museum, Seattle, Washington, lent me a fragmentary *Tingupa* collected in the state of Washington. Dr. Norman Platnick read the manuscript and I thank him for his comments.

For the past seven years, my taxonomic studies in Diplopoda and Arachnida have been generously supported by the Faculty Research Committee of Hampden-Sydney College. This rare commitment to research by a small, liberal arts college is unusual and deserves recognition.

ABBREVIATIONS

AMNH, American Museum of Natural History, New York, New York.
MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts.
WAS, Personal collection of William A. Shear, Hampden-Sydney, Virginia.
RLH, Personal collection of Richard L. Hoffman, Radford, Virginia.

TAXONOMIC CHARACTERS

Surprisingly, most very small millipeds have extraordinarily complex male gonopods, and it is these structures that provide the prime taxonomic characters for the differentiation of species. The patterns of gonopod structure in turn allow species to be grouped as genera, and genera to be grouped into families. At levels above the family, nonsexual characters such as body segments and antennae become valuable.

The gonopods of tingupids must be studied at high magnification under a compound microscope in order to fully appreciate the

wealth of features available for comparison. The best method seems to be to mount them temporarily in glycerine so that they can be put back into the vial in which the remainder of the specimen is stored. The anterior coxites of the gonopods of most species differ strikingly and provide good points for recognition that can sometimes be picked out without putting the gonopods on a slide. The patterns of setation and spination as well as the overall shape of the coxites are the most important features. The gonopod telopodites are much more uniform, especially the lobate, glandular portions, which can show considerable variation within a population, perhaps depending on the reproductive condition of the male. The two- or three-branched section of the telopodite does present some distinct features, however, particularly in the form of the middle, or *B,* branch, and in the degree of fusion of the branches. These correlate well with coxite form and allow the recognition of related species. The posterior gonopods are less useful. As in the Cleidogonoidea (Shear, 1972), these "gonopods" evidently do not really function as such. They are simply legs that have become reduced in size to get them out of the way of the functional anterior gonopods, formed from the leg pair just ahead of them. In some cleidogonoid species, a secondary function of locking the retracted anterior gonopods into place seems to have developed, but this is not the case in the brannerioids (Tingupidae, Branneriidae) where these appendages have simply become very small and indeed are often closely appressed to the bases of the functional gonopods. In *Tingupa,* however, the degree of reduction, expressed in the length of the second article, is somewhat useful for distinguishing species. The presence in *Buotus* of a well-developed coxite on the posterior gonopod is an important distinguishing feature of that genus.

The female genitalia of all millipeds are simpler and present far fewer features of taxonomic use. In *Tingupa,* I was not able to utilize the female genitalia to separate species; females must be associated with males in order to be identified.

GONOPOD STRUCTURE AND FUNCTION

The gonopod structure of the Brannerioidea, and the Tingupidae in particular, has already been discussed (Shear, 1972). The anterior gonopods are the functional pair. They are so greatly reduced and modified that they are no longer recognizable as having been derived from legs, but a study of the pattern of muscularization allows the recognition of two divisions on each side. In *Tingupa,* the gonopod coxae articulate solidly with a cuplike sternum whose form is relatively constant from species to species. The coxal bases are bulbous and rugose (fig. 24) and bear groups of short, stout setae. The coxal portion on each side is divided into inner and outer coxites, and all four of these pieces are contiguous across the front of the gonopod, forming a plate. Rows of setae are present on each coxite and their number and pattern of distribution may be of taxonomic use. Distally, each coxite bears a group of setae or spines often no longer movable and present as long extensions of the coxite tips; the form of these provides for quick recognition of species. In some species, one or the other of the coxites on each side has been somewhat modified. Most frequently the outer coxite of each side has been reduced in size (fig. 4) and displaced laterally by the expanded inner coxites, so that the coxite shield tends to envelop the telopodite divisions laterally.

The telopodite division itself consists of two parts: a posterior, lobular branch containing glandular tissue, and an anterior set of two or three sclerotized processes (fig. 25). The basic number of these processes or branches seems to be three, with a tendency existing for the two smaller, more anterior branches to fuse to one another. Branch *A* is anteriormost and smallest, and is usually recognizable by a distal mass of cuticular fimbriae that range, in the various species, from feathery, branched structures to stout hooks. Branch *B* is likewise simpler and shorter, except in *T. clatskanie* (fig. 9); usually it bears a distal series of ridges with a

distinct spiral arrangement. Except in *T. clatskanie,* neither of these branches appears tubular. Branch *C,* however, is tubular and generally much longer, so that it protrudes even above the tips of the coxites. It appears to bear a subterminal pore, beyond which the branch attenuates rapidly and is elaborately curved.

The posterior gonopods appear as a pair of much reduced legs (figs. 6, 10, 16). The coxa of each bears a small membranous lamella posteriorly and a row of partially fused, very fine setae anteriorly. The telopodites are small and are flexed dorsally out of the way. The gonopods of *Buotus carolinus* are roughly similar; the differences will be noted under the discussion of that genus.

Leg pairs 10 and 11 are unmodified, but the coxae have gland pores which originate from very large basal glands. Likewise, the pregonopodal leg modifications met with so often in chordeumatid millipeds are absent in the tingupids.

Fortunately I was able to find, in a single collection of *T. benedictae,* a male evidently in preparation for immediate mating. Each of the coxal gland pores of leg pairs 10 and 11 has extruded a long, curved, ribbon-like structure that appears to be a spermatophore (fig. 8). If these objects are indeed such, it seems likely by analogy with other, albeit unrelated, millipeds (Shear, 1976) that *Tingupa* species males flex the body to bring the penes (short extensions of the second coxae) in contact with the glandular pores of these legs, where a secretion that forms the spermatophores is added to the sperm, which are then transferred mechanically by the gonopods. How that latter step might occur in *Tingupa* is not known. It is possible that the glandular lobe of the telopodite elaborates a secretion that is extruded through telopodite branch *A,* and which lubricates the spermatophores for insertion into the valves of the female genitalia. An alternative hypothesis might suggest instead that the production of a pheromone is involved.

RELATIONSHIPS OF THE TINGUPIDAE

In my 1972 monograph, I grouped the chordeumatid milliped families of North America into superfamilies. Recently (Shear, 1979), I was able to extend this classification to encompass the east Asian fauna as well. The affinities that exist between the Asian and North American faunas suggest a derivation of the most characteristic chordeumatid millipeds of these areas from an original circum-Pacific fauna, probably a very ancient one. The European chordeumatids appear to be a much more highly specialized group of families, startlingly diverse considering the relative land areas.

However, the members of the superfamily Brannerioidea (Branneriidae and Tingupidae) do show, in the general pattern of gonopod structure, some similarities to the European families Orobainosomatidae, Brachychaetumatidae, and Xystrosomatidae as illustrated by Brolemann (1935). The functional gonopods in both families come from the eighth leg pair, and have strongly modified coxal and telopodite divisions, with the coxae as a complex anterior shield. On the other hand, these European families have articulated gonopod flagella which are not found in the brannerioids. But among the North American superfamilies, the brannerioids most closely resemble in gonopod plan the Striarioidea, a group which, like them, is most abundant and diverse on the west coast of North America, and in which such flagella are found.[2] More distantly related are the Cleidogonoidea, a group which I have postulated (Shear, 1972) has reached its greatest diversification in Mexico and the Appalachian Mountains, while incorporating as an outlying element the Entomobielziidae of Nepal and eastern Europe.

As so often happens, additional information and careful study from the species level has somewhat clouded the picture rather than clarifying it. It now seems tenable that the European fauna contains elements which may indeed be close to some North Ameri-

[2] In his recent monograph Richard Hoffman (1979) has not recognized the superfamily Striarioidea as I set it up in 1972. He puts Rhiscosomididae and Apterouridae in Brannerioidea (with several European families) and leaves Caseyidae and Urochordeumidae as families of uncertain status. Striariidae alone is raised to the rank of suborder, as suggested by Cook in 1899.

can families (Hoffman, 1979) and that the striking and obvious circum-Pacific distribution of the well-studied Heterochordeumatoidea (Shear, 1972, 1976, 1979) has diverted us from fully understanding this.

Without being able to delineate membership, I think we are starting to see the outlines of three major evolutionary lines within the order Chordeumida. One of these would include (broadly taken) the heterochordeumatoids, with a circum-Pacific distribution. The second group, chiefly American, but with suggestions of European affinities, would include the Cleidogonoidea and some as yet unspecified European groups. The third group, the largest and most diverse, would cover the European families grouped by Brolemann as "Craspedosomidi," plus the Brannerioidea and Striarioidea of North America. It is to this latter line that the Tingupidae belong.

As indicated by their placement in the Brannerioidea, the tingupids are closest to the branneriids; indeed, it may be necessary to combine the two families at some later date. The structure of the gonopods, diplosegments, and antennae, as illustrated by me in 1972, all suggest this relationship. The Branneriidae includes only a single species widely distributed in the southeastern United States.

TAXONOMY

TINGUPIDAE LOOMIS

Tingupidae Loomis, 1966, p. 227. Shear, 1972, p. 264. Hoffman, 1979, p. 135.

TYPE GENUS: *Tingupa* Chamberlin, 1910.

DIAGNOSIS: Members of no other family of small chordeumid millipeds have the pattern of sculpture found in the tingupids, with short, acute ridges running longitudinally, and scattered over the dorsal surface (fig. 2). In the related Branneriidae, the tegumental sculpture is in the form of irregular bumps and the segmental setae are flat and broad, not subcylindrical and acute as they are in the tingupids; branneriid gonopods have a telopodite flagellum that interlocks with processes from the coxites. In the Rhiscosomididae, which Hoffman (1979) has placed in the Brannerioidea, the collum is wider than the head and the body sculpture is in the form of numerous small, acute tubercles.

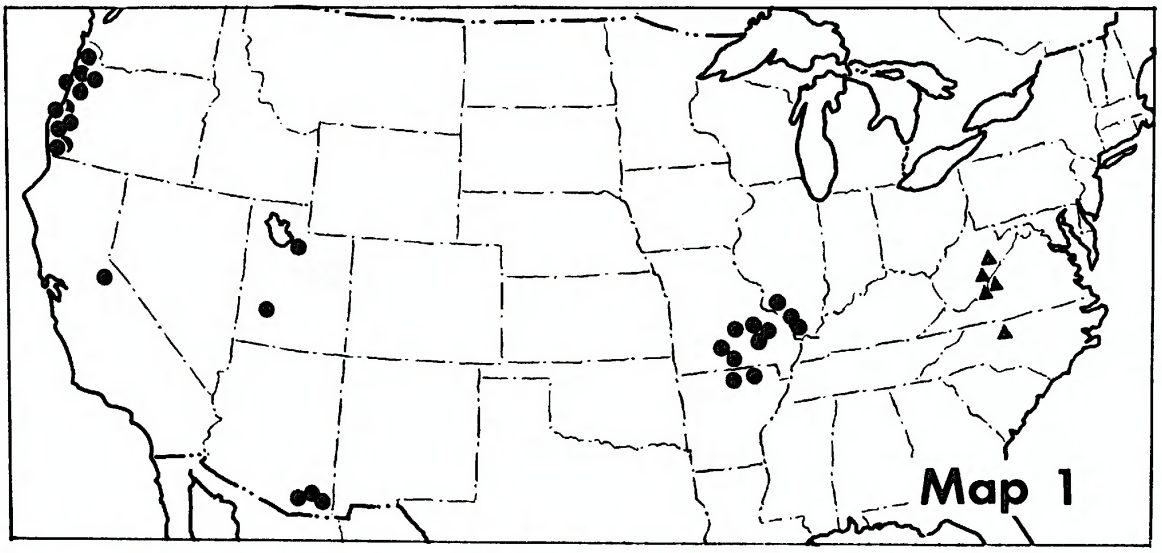
DESCRIPTION: Twenty-six, 28, or 30 segments. Mentum divided. Head wider than collum, antennae short, clavate; ocelli present or absent, if absent their place taken by single, deep-lying black spots (*Buotus carolinus*). Postcollum trunk segments with pronounced paranota (fig. 1) horizontal or slightly deflected ventrad, segmental setae present, normal; dorsum with heavy sculpturing of short, acute, scattered longitudinal ridges (fig. 2). Epiproct squared off to subacute, with two spinnerets. Pregonopodal legs of males not modified, sometimes slightly more crassate than following legs. Anterior gonopods functional, with two divisions; coxal division with mesal and lateral coxites or with single coxite, with or without terminal setae. Telopodite division with one or more acute branches; in one genus (*Tingupa*) with large, lobelike part filled by glandular tissue. Posterior gonopods with one or two postcoxal segments; coxa bears either anterior group of modified setae and posterior transparent lamella or long, spatulate coxite. Coxae of tenth and eleventh legs with coxal glands used in making spermatophore.

INCLUDED GENERA: *Tingupa* Chamberlin, 1910; *Buotus* Chamberlin, 1940.

DISTRIBUTION: See map 1. Mountains along the Virginia-West Virginia border, North Carolina piedmont; caves in Missouri, Illinois (epigean localities?), and Arkansas; Rocky Mountains in northern and southern Utah and southeastern Arizona; Eldorado Co., California; Oregon in the Coast Ranges; Washington (?). The "immature *Tingupa*" I cited from Marin Co., California, in 1972 turned out to be *Rhiscosomides*.

KEY TO MALES

1. With 26 segments (females with 28); ocelli replaced by single deep-lying spot of black pigment; posterior gonopods with long, spatulate coxite (fig. 33); North Carolina, Virginia, West Virginia ..... *Buotus carolinus*
   With 28 or 30 segments; 4–17 ocelli present ..... *Tingupa*, 2
2. With 30 segments; caves in Missouri, Illinois, and Arkansas ..... *T. pallida*



MAP 1. Distribution of the family Tingupidae in North America. Dots, records of *Tingupa* spp. Triangles, records of *Buotus carolinus*.

With 28 segments 3
3. Lacking pigment except under ocelli 4
Body with some tan, brown, or purplish pigment 6
4. Less than 2.5 mm. in length; 7–8 ocelli on each side; Oregon ..... *T. sinuosa*
More than 3.0 mm. long; no more than 5–6 ocelli 5
5. Maximum width more than 0.6 mm.; inner coxites of anterior gonopods with long, curved spines (fig. 11); Oregon ..... *T. clatskanie*
Maximum width less than 0.5 mm.; inner coxites with 3 small terminal spines (fig. 12); Oregon ..... *T. tillamook*
6. Ocelli 5 or less on each side; slightly more than 3 mm. long; Oregon ..... *T. causeyae*
Ocelli 10 or more on each side; more than 3.5 mm. long 7
7. Inner coxite of anterior gonopod much the largest, with single apicolateral spine (figs. 3, 4, 5); Oregon ..... *T. benedictae*
Inner coxite of anterior gonopod not as above 8
8. Inner coxite with mesal flange, projecting slightly posteriorly (fig. 29); telopodite branches fused (female with 28 segments); California ..... *T. eldorado*
Inner coxite without median flange; telopodite branches not fused (female with 30 segments) 9
9. Slightly more than 4 mm. long; outer coxite of anterior gonopods with single, large, sinuous spine (fig. 17); Oregon ..... *T. auricula*
More than 6 mm. long; coxites with small spines; Utah and Arizona .... *T. utahensis* and *T. arizonica*

TINGUPA CHAMBERLIN

Tingupa Chamberlin, 1910, p. 328 (type species *T. utahensis*, by original designation). Loomis, 1939, p. 185; 1943, p. 387. Chamberlin and Hoffman, 1958, p. 106. Shear, 1969, p. 141; 1972, p. 265. Hoffman, 1979, p. 135.

DIAGNOSIS: Distinct from *Buotus* in lacking a spatulate coxite on the posterior gonopod, having ocelli, and in being absent from the Appalachian region.

DESCRIPTION: With the characters of the family, and as follows. Twenty-eight or 30 segments. Ocelli present. Anterior gonopods of male with inner and outer coxites; telopodites with two divisions, one lobular, anteriormost with two or three attenuate branches. Posterior gonopods with two postcoxal segments, coxa with posterior transparent lamella, anterior group of modified setae.

DISTRIBUTION: As given for the family,

but absent from North Carolina, Virginia and West Virginia.

NOTES: Four species groups can be recognized in *Tingupa,* two of which contain only single species. The *utahensis* group consists of the two (?) Rocky Mountain species, *utahensis* and *arizonica,* large, pigmented forms with 28-segmented males and 30-segmented females; the *benedictae* group of species occurs in Oregon and includes some with 28-segmented females, all males with three telopodite branches; *T. eldorado* should be recognized as a group in its own right because of the fused telopodite branches and increased pilosity of the head; *T. pallida* likewise stands alone, with 30-segmented males and females.

A detailed cladistic analysis cannot be carried out at this time because of the obviously incomplete nature of our knowledge of the diversity of species, but it does seem that, as the classification would indicate, Branneriidae is the sister-group of the Tingupidae, and *Buotus* of *Tingupa. Buotus* is specialized in the reduced segment number and simplified anterior gonopods, but primitive in the retention of a large coxite on the posterior gonopods. Within *Tingupa,* I think *T. pallida* alone is the sister-group of all the other species, which have specialized at least to the extent of having 28-segmented males. This trend toward the reduction of segment number is shown by some species having 30-segmented females, whereas others have 28-segmented females. The sequence seems to be 30 ♂/30 ♀, 28 ♂/30 ♀, 28 ♂/28 ♀, 26 ♂/28 ♀ (*Buotus*). The relationships of the Oregon species remain to be worked out; it is difficult to make polarity judgments about the details of gonopod construction with little else to go on.

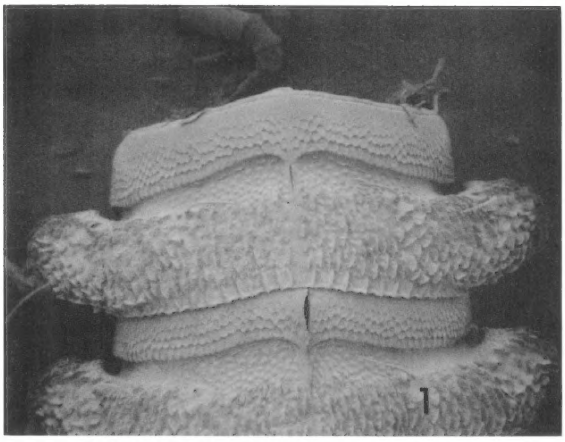
The rough model above is consistent with an origin for the family in the Appalachians, where *Branneria* and *Buotus* still occur. *Tingupa pallida,* with 30-segmented males and generalized gonopods, is probably closest to the primitive stock of *Tingupa.* Segment number is reduced and gonopods become more specialized as one moves west, so that in coastal Oregon we see a complex of species which seem to be of relatively recent origin invading a variety of microhabitats, differentiating largely on the basis of size and gonopod specialization in several directions. It is likely that the speciation events among them are related to Pleistocene glacial conditions; it is almost certain that the present troglobitic habit of *T. pallida* is since it shows little general adaptation to troglobiosis.

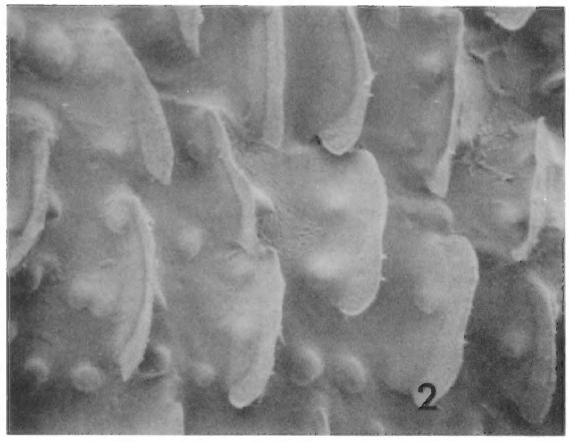
Tingupa utahensis Chamberlin

Tingupa utahensis Chamberlin, 1910, p. 238, pl. 33, figs. 3–8. Chamberlin and Hoffman, 1958, p. 106. Shear, 1972, p. 265, figs. 459–464.
Tingupa utahensis australis Chamberlin, 1925, p. 62. Chamberlin and Hoffman, 1958, p. 106.

TYPES: Of *utahensis,* types of unspecified sex collected in Mill Creek Canyon, Salt Lake County, Utah, presumed lost; female holotype of subsp. *australis* from "the canyon," Cedar City, Iron County, Utah, deposited in MCZ, examined.

For my 1972 discussion, I examined material of *utahensis* in the Museum of Comparative Zoology, collected by Chamberlin at the type locality in 1924. There is little to distinguish this species from the following, except for distance and the absence of intervening records. Comparing my 1972 illustrations, it can be seen that the difference between *utahensis* and *arizonica* is not nearly as great as that between Oregon species that are geographically close. The isolation of submesic forests at higher elevations in the American Southwest is probably recent. During Pleistocene glacial maxima, these forests extended to lower elevations and may have covered broad areas (Gleason and Cronquist, 1964; Hunt, 1974). There are examples from other components of the soil and litter (millipeds, Shear, 1971; opilionids, Briggs, 1971; burrowing spiders, Coyle, 1974, etc.) with broad distributions of relict populations isolated for perhaps less than 15,000 years. However, without records from suitable habitats in the great expanse between the known localities, I think it premature to synonymize *arizonica* with *utahensis.* There doesn't seem to be any reason





FIGS. 1, 2. Scanning electron micrographs of *Tingupa benedictae* female. 1. Diplosegment 10 and part of 11, 90×. 2. Sculpturing of metazonite of diplosegment 10, 950×.

to recognize the subspecies *T. u. australis,* based on a single female.

Tingupa arizonica Loomis

Tingupa arizonica Loomis, 1966, p. 228, figs. 14–16. Shear, 1972, p. 265, figs. 465–468.

TYPE: Male holotype from Mt. Lemmon (8000 ft. elev.), Santa Catalina Mtns., Pima County, Arizona, collected May 30, 1930 by H. F. Loomis, deposited in USNM, not examined.

In 1972, I studied specimens from the type locality and additional material from a Graham County locality mentioned by Loomis (1966) in his original description. I have now seen a female collected at Rustler's Park, near Portal, Cochise County, Arizona (AMNH). The distribution of this species as we now know it seems to be in the mountain ranges of Pima, Graham, and Cochise counties in southern Arizona. Loomis (1966) collected the types from beneath the bark of fallen pines.

Tingupa pallida Loomis

Tingupa pallida Loomis, 1939, p. 185, figs. 12a–c; 1943, p. 387, fig. 7. Chamberlin and Hoffman, 1958, p. 106. Shear, 1969, p. 141, fig. 9; 1972, p. 265, figs. 469–472. Peck and Lewis, 1978, p. 49.

TYPES: Male holotype from River Cave, near Hahatunka, Camden County, Missouri, collected June 8, 1938, by Kenneth Dearolf, deposited in MCZ, examined.

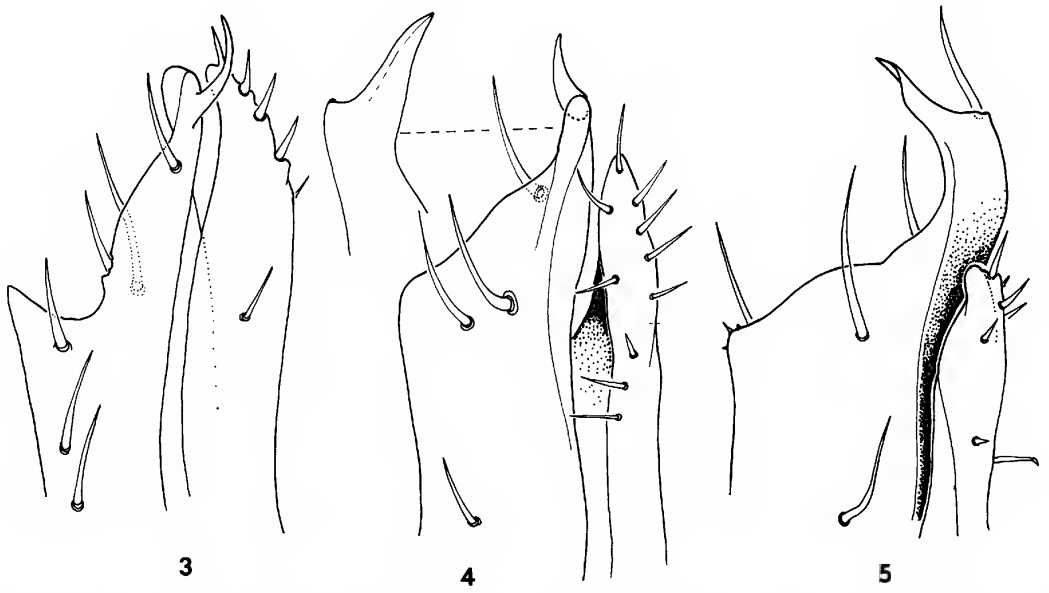
Loomis (1939) has described in detail the nonsexual characters of this species. In 1969, I published additional data on distribution, and in 1972 illustrated the gonopods. Recently, Peck and Lewis (1978) have reviewed what is known of the species' distribution in Missouri and Illinois; it seems to be the most common cave diplopod in the region.

However, *T. pallida* has not been reported previously from Arkansas. The late Dr. Nell Causey sent me the following specimens from caves in the northern part of that state. ARKANSAS: *Randolph Co.:* Mansell Cave, May 1, 1970, D. E. Barnett, 2 ♀♀ (WAS). *Sharpe Co.:* Martin Creek Cave, January 24, 1970, D. E. Barnett, 5 ♀♀ (WAS).

Tingupa benedictae, new species
Figures 1–8

TYPES: Male holotype and male and female paratypes from 4.5 mi. E of Wells Creek Ranger Station, Oregon, 300 ft. elev. (T22S/R9W/Sec. 15), collected December 11, 1971 by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet honors Dr. Ellen M. Benedict, Portland State Uni-



FIGS. 3–5. *Tingupa benedictae,* new species, figure 3. Tips of right anterior gonopod coxites, anterior view, specimen from Wells Creek. 4. Same, specimen from Blaine. 5. Same, specimen from Clatskanie.

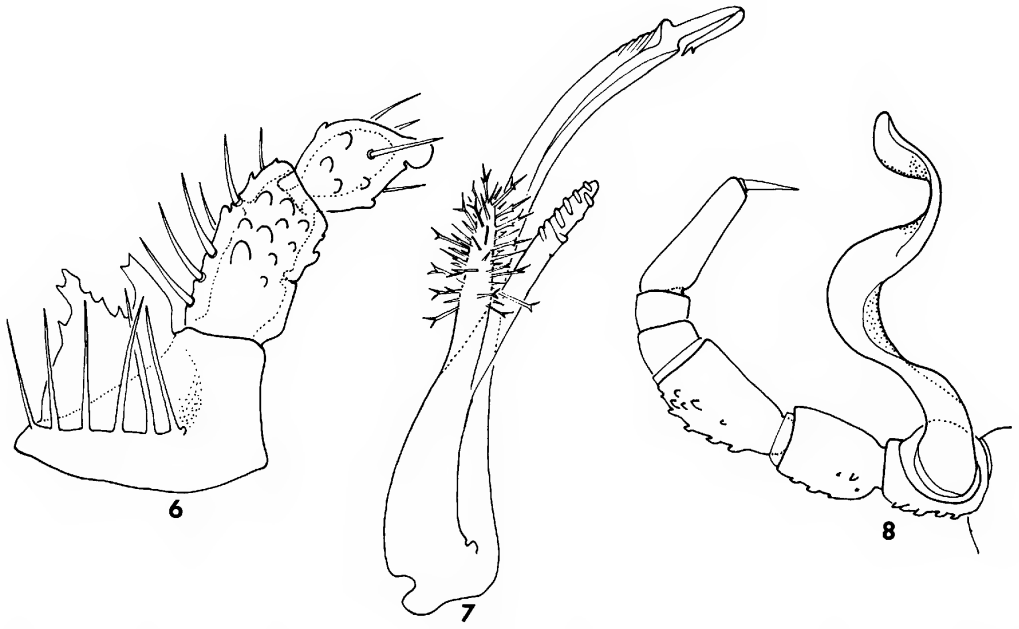
versity, Portland, Oregon, in thanks for most of the specimens on which this study was based.

DIAGNOSIS: The inner coxites of the anterior gonopods are much broadened and platelike, with a twisted apical lamella (figs. 3, 4, 5), while the outer coxites are much reduced; this combination of gonopod characters will separate *benedictae* from the other species. Also, *benedictae* is nearly 2 mm. longer than any of the other Oregon pigmented species, falling in the size range of *utahensis* and *arizonica*. Neither of the last two species is found in Oregon.

MALE: Twenty-eight segments. Length, 5.7 mm., greatest width, 0.74 mm. Antennal segment three 0.26 mm. long, 0.07 mm. wide. Ocelli 11 on each side in a three-rowed triangular patch (rows with 5, 4, 2 ocelli dorsal to ventral); small unpigmented lens at ventral apex of patch. Body from (fig. 1) typical. Color dark gray-purple with light tan midline, group of tan spots near each paranotal base; venter light tan, legs and antennae mottled darker gray-purple. Anterior gonopods with inner coxites broadened, tightly appressed in midline, with some variation in shape as illustrated (figs. 3, 4, 5), but in general flattened, laterally drawn out to twisted apical lamella bearing single seta or unarticulated spine. Outer coxites reduced in size, with few small apical setae, displaced laterad so that in some examples they are actually on the sides of the gonopod complex (figs. 4, 5). Telopodites (fig. 7) with usual three free branches, branch *A* with fimbriae rather scattered, acute, branched. Posterior gonopods as usual, but with somewhat better developed posterior coxal lamella than in other species; prefemur only about one-fourth longer than terminal segment, terminal segments with apical knob (fig. 6).

FEMALE: Twenty-eight segments. Length, 6.6 mm., greatest width 0.82 mm. Antennal segment three 0.26 mm. long, 0.07 mm. wide. Ocelli 13 in subtriangular patch (rows of 1, 6, 4, 2, dorsal to ventral); single unpigmented lens rudiment at ventral apex of eye-patch.

DISTRIBUTION: All collections by E. M. Benedict. OREGON: *Clatsop Co.:* 3 mi. SE of Olney on Ore. Rt. 202, T7N, R8W, Sec. 20, elev. 400 ft., March 27, 1971, ♂; 6 mi. SE of North Fork of Klaskanne River, T7N,



FIGS. 6–8. *Tingupa benedictae,* new species. 6. Right posterior gonopod, anterior view. 7. Branches of left anterior gonopod telopodite, mesal view. 8. Left leg 10, anterior view, with spermatophore extruded from coxal gland.

R8W, Sec. ?, elev. 800 ft., November 27, 1971, ♂. *Columbia Co.:* 3 mi. SW of Clatskanie, T7N, R4W, Sec. 7, elev. 300 ft., January 8, 1972, ♂, 3 ♀♀. *Curry Co.:* 13 mi. E of Gold Beach on Agness road, T36S, R13W, Sec. 3, elev. 600 ft., March 10, 1972, ♀. *Douglas Co.:* 1 mi. S, 2 mi. W of Ash, T23S, R10W, Sec. 20, elev. 1100 ft., December 11, 1971, ♂. *Lincoln Co.:* 1.4 mi. W of Nashville, T10S, R8W, Sec. 25, elev. 600 ft., December 20, 1971, ♂, 3 ♀♀. *Tillamook Co.:* 4 mi. SE of Blaine, T4S, R8W, elev. 500 ft., March 15, 1972, 2 ♂♂, 2 ♀♀; as above but 7 mi. SE of Blaine, 2 ♂♂, 4 ♀♀ (all WAS).

NOTES: The form of the inner coxite of the anterior gonopods and its size relation to the posterior coxite shows considerable variation; this is illustrated in figures 3–5.

This species is sympatric with *clatskanie* and *tillamook* at their type localities. It has been found with *sinuosa* at several places, and in the vicinity of Ash, Oregon, *benedictae, sinuosa,* and *causeyae* probably all occur together.

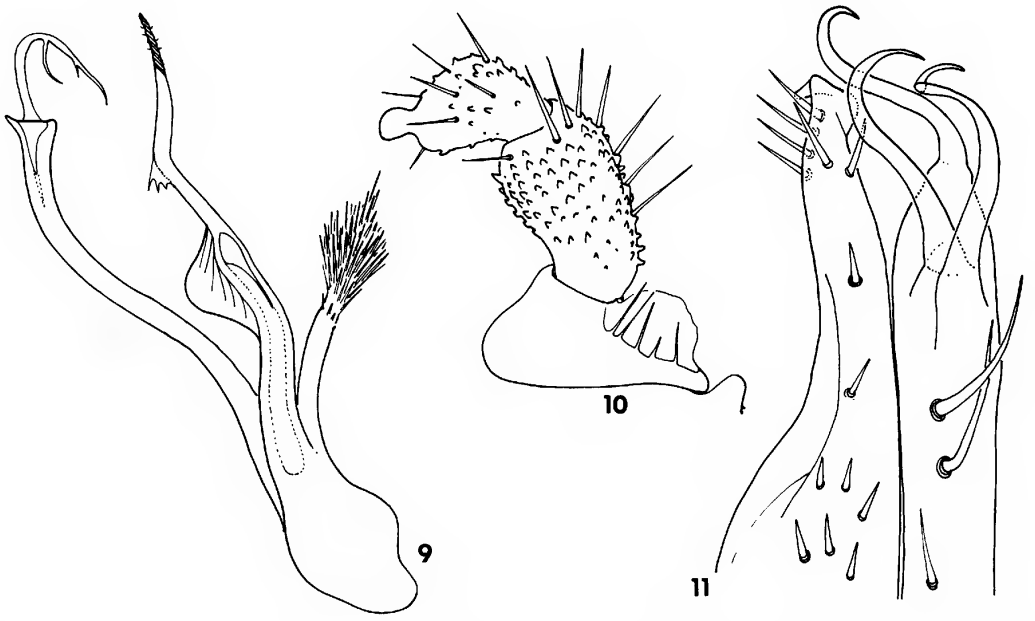
Tingupa clatskanie, new species
Figures 9–11

TYPES: Male holotype and female paratypes from 3 mi. southwest of Clatskanie (T7N/R4W/Sec. 7), Columbia Co., Oregon, collected January 8, 1972, by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet is a noun in apposition making reference to the type locality.

DIAGNOSIS: This species is not closely related to the others; the very large, sinuous spines on the inner coxite of the anterior gonopod are unique (fig. 11). In somatic characters, *clatskanie* resembles *tillamook*. Both are small (3.3–4.5 mm. long), white, and have a reduced number (4–6) of poorly pigmented ocelli, but the gonopod anatomy is distinct. Females of *tillamook* are unknown, however.

MALE: Twenty-eight segments. Length, 4.5 mm., greatest width, 0.68 mm. Antennal segment three 0.13 mm. long, 0.06 mm.



FIGS. 9–11. *Tingupa clatskanie*, new species. 9. Branches of left anterior gonopod telopodite, mesal view. 10. Left posterior gonopod, anterior view. 11. Tips of left anterior gonopod coxites, anterior view.

wide. Ocelli 4–5, variable in size and shape, poorly pigmented, arranged in two irregular rows. Body form typical. Completely unpigmented. Anterior gonopods with outer coxite conspicuously narrowed apically, with a few small subterminal setae; tip flattened, curved, slightly deflected posteriorly. Inner coxite not narrowed, slightly shorter, bearing three large, S-shaped spines, two subapical, one apical (fig. 11). Telopodite with three branches free; *A* with closely packed cuticular fimbriae; *B* longer than in other species, with evident pore midway in length near broad, thin flange, second smaller flange at deflection point nearly ⅔ distal; *C* as usual (fig. 9). Posterior gonopods with prefemur substantially shortened, only slightly longer than distal segment, which bears a distinct apical knob (fig. 10).

FEMALE: Thirty segments. Total length, 5.2 mm., greatest width 0.85 mm. Antennal segment three 0.21 mm. long, 0.07 mm. wide. Ocelli 6, small, poorly pigmented, in two irregular rows (4, 2). Body form typical Completely unpigmented.

DISTRIBUTION: Known only from the type collection.

NOTES: At the type locality, this species is sympatric with *T. benedictae*.

Tingupa tillamook, new species

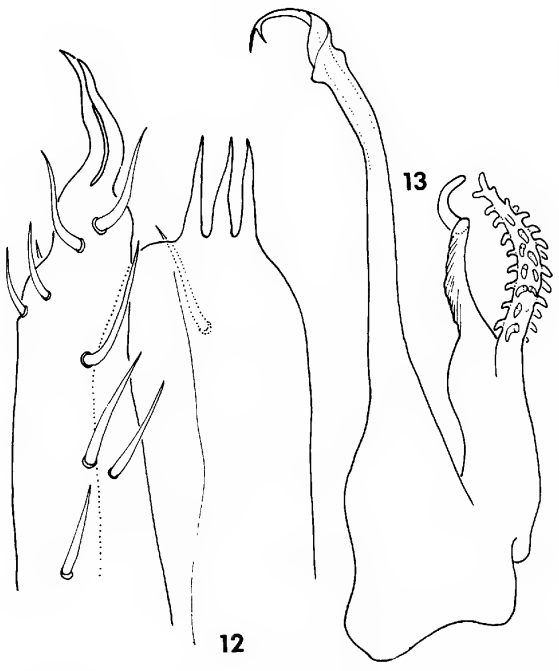
Figures 12, 13

TYPES: Male holotype from 4 mi. SE Blaine (T4S/R8W/Sec. ?), 500 ft. elev., Tillamook County, Oregon, collected March 15, 1972 by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet is a noun in apposition, after the type locality.

DIAGNOSIS: This species is close to *causeyae*, but differs from it in lacking pigment, and in the details of the apices of the anterior gonopod coxites.

MALE: Twenty-eight segments. Length, 3.3 mm., greatest width, 0.49 mm. Antennae missing from holotype. Ocelli 4, lightly pigmented, 3 in vertical row, 1 adjacent to ventralmost in row (1, 1, 2). Body form typical. Pigment entirely lacking. Outer coxite of an-



FIGS. 12, 13. *Tingupa tillamook,* new species. 12. Tips of right anterior gonopod coxites, posterior view. 13. Branches of left anterior gonopod telopodite, lateroposterior view.

terior gonopods narrower than inner, slightly longer, with two sinuous apical spines and scattered setae; inner coxite quite broad, with three small, straight apical spines (fig. 12). Telopodite (fig. 13) nearly as in *causeyae,* but branches *A* and *B* fused for part of their length. Posterior gonopods as in *causeyae.*

FEMALE: Unknown.

DISTRIBUTION: Known only from the type locality.

NOTES: For the present this species seems fully distinct from *causeyae,* but may later prove to be a subspecies of that variable form.

Tingupa causeyae, new species
Figures 14–16

TYPES: Male holotype from 0.6 mi. S of Ferguson Rd. on Turnbow Lane, 4.5 mi. NW Cheshire (T15S/R5W/Sec. ?), Lane County, Oregon, collected December 4, 1971, by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet honors the late Dr. Nell Bevel Causey, in recognition of her contributions to our knowledge of North American millipeds.

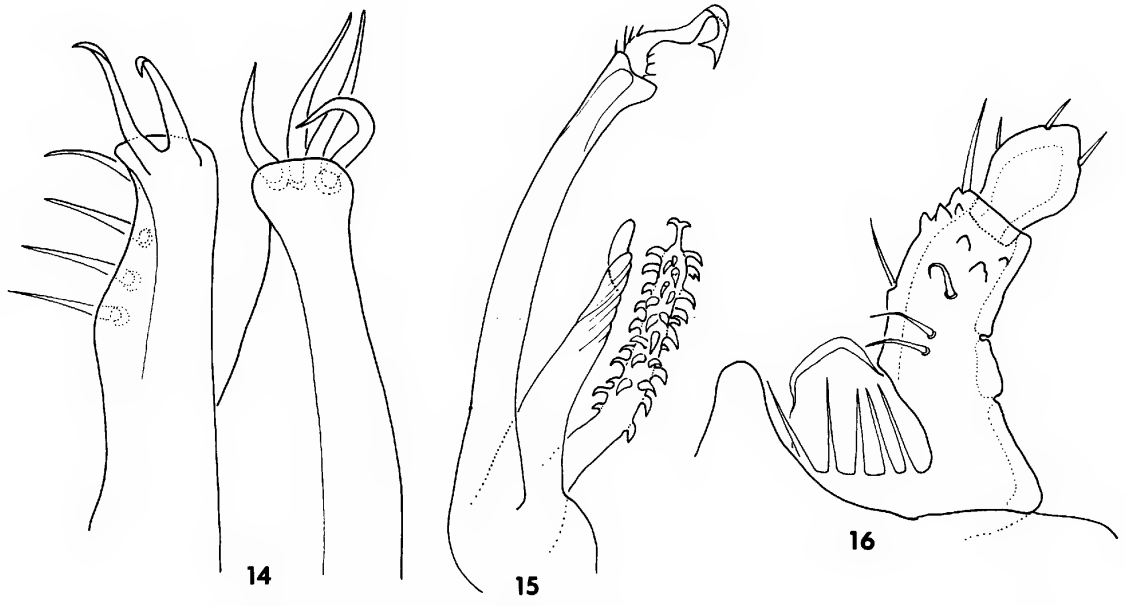
DIAGNOSIS: This species resembles *arizonica* and *utahensis,* but occurs only in Oregon and has recurved hooks on branch *C* of the anterior gonopod telopodites. Both the latter species are more than 5 mm. long. *Tingupa causeyae* may be separated from *T. tillamook* by the lack of pigment in *tillamook.*

MALE: Twenty-eight segments. Length, 3.23 mm., greatest width, 0.51 mm. Antennal segment three 0.14 mm. long, 0.04 mm. wide. Ocelli 5, black, in a right-angled row, 3 dorsal and 2 ventral (3, 1, 1). Body form typical. Brown-tan overall, with darker reticulate pattern of purplish brown on anterior segments; light center stripe on all segments, light tan oval areas at paranotal bases. Anterior gonopods with outer coxite at first narrowed, then slightly expanded apically, with two hooked apical spines (but see Notes below), row of 3–4 lateral setae (fig. 14); inner coxite in anterior view narrower than outer, but with broad lateral flange extending posteriorly, with 4 apical spines variously curved (fig. 14). Telopodite with three branches free; branch *A* stout, cuticular fimbriae as retrorse hooks; *B* as usual, apically twisted; *C* typical (fig. 15). Posterior gonopods with prefemur twice length of distal segment, nonetheless short and stout, distal segment without knob, posterior lamella well-developed (fig. 16).

FEMALE: Unknown.

DISTRIBUTION: All collections by E. M. Benedict. OREGON: *Benton Co.:* 0.5 mi. NW Glenbrook on South Fork Alsea River Access Road (T14S/R6W/Sec. 28), elev. 600 ft., December 4, 1971, ♂. *Coos Co.:* 14 mi. E, 2 mi. S of Allegany, Weyerhauser Millicoma Tree Farm, Company Road 6000 (T25S/R9W/Sec. 16), November 21, 1971, 3 ♂♂. *Douglas Co.:* 11 mi. E, 5 mi. S of Allegany, Weyerhauser Millicoma Tree Farm, Company Road 6040 (T25S/R9W/Sec. 31), November 21, 1971, ♂; Elliot State Forest, 1 mi. S, 2.5 mi. W of Ash, elev. 1200 ft., December 11, 1971, ♂♂ (all WAS).

NOTES: Variation in this species is con-



FIGS. 14–16. *Tingupa causeyae,* new species. 14. Tips of right anterior gonopod coxites, anterior view. 15. Branches of left anterior gonopod telopodite, lateral view. 16. Right posterior gonopod, anterior view.

centrated in the outer coxites of the anterior gonopods; in males from the Millicoma Tree Farm and from the Elliot State Forest, the apical spines were absent. It is possible that they might have been broken off, but there was no sign they had ever been present.

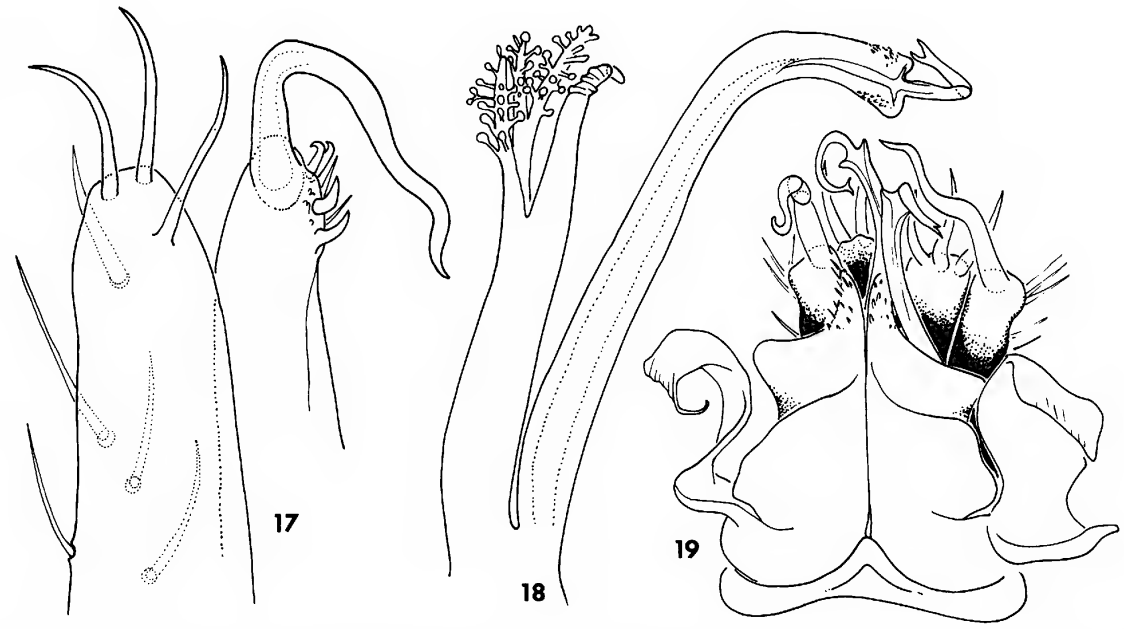
Tingupa auricula, new species
Figures 17–20

TYPES: Male holotype and male and female paratypes from 4 mi. SE of Olney (T17N/R8W/Sec. ?), elev. 600 ft., Clatsop County, Oregon, collected November 27, 1971 by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet is an adjective referring to the earlike extensions of the anterior gonopods.

DIAGNOSIS: This species has several distinctive features not shared by others. The terminal spine of the outer coxite of the anterior gonopod is very large and decurved (fig. 17), and the telopodites have branches *A* and *B* partly fused; *A* is frequently multiple. The earlike extensions are not present in all specimens since they are probably easily broken off.

MALE: Twenty-eight segments. Length, 4.2 mm., greatest width, 0.6 mm. Antennal segment three 0.17 mm. long, 0.04 mm. wide. Ocelli 12, well-formed, black, in triangular patch. Body form typical. Color light tan, heavily mottled darker purplish brown on trunk, head and antennae, with light areas at paranotal bases extending onto paranota anterior to segment 10, light areas are smaller and eventually disappear on posterior segments; legs white. Anterior gonopods (fig. 19) often with auriculate extensions from telopodite lobes. Outer coxites (fig. 17) not much narrowed distally, with lateral group of small subterminal spines and setae, single terminal spine very large, sharply curved posteriorly and dorsally; inner coxites with terminal spines somewhat reduced, coxites broader than outer ones. Telopodites (fig. 18) with branches *A* and *B* basally fused, branch A frequently multiple, with fimbriae club-shaped; branch *C* typical. Posterior gono-



FIGS. 17–19. *Tingupa auricula,* new species. 17. Tips of right anterior gonopod coxites, anterior view. 18. Branches of right anterior gonopod telopodite, lateral view. 19. Anterior gonopods, posteriolateral view.

pods (fig. 20) with prefemur four to five times longer than terminal article; terminal article with nipple-like knob; coxal lamella low, rounded, coxal setae evidently reduced.

FEMALE: Thirty segments. Length, 6.0 mm., greatest width 1.5 mm. Antennal segment three 0.24 mm. long, 0.09 mm. wide. Ocelli 16–17, well-formed, black, in triangular patch. Color and nonsexual characters as in male.

DISTRIBUTION: All collections by E. M. Benedict. OREGON: *Clatsop Co.:* 5 mi. N, 7 mi. W of Elsie, T5N, R9W, elev. 700 ft., March 15, 1972, 2 ♂♂, 2 ♀♀. *Coos Co.:* 0.25 mi. N of Boundary Campground, T32S, R11W, Sec. 6, elev. 300 ft., February 19, 1972, ♂, 3 ♀♀. *Douglas Co.:* Elliot State Forest, 1 mi. S, 2.5 mi. W of Ash, T23S, R10W, Sec. 27, elev. 1200 ft., December 11, 1971, ♂, ♀. *Lincoln Co.:* 0.6 mi. NW of Elk City, Yaquina River, T11S, R10W, Sec. 10, elev. 200 ft., December 20, 1971, ♂, 3 ♀♀ (all WAS).

Tingupa sinuosa, new species
Figures 21–24

TYPES: Male holotype, female paratype and male and female paratypes from 6 mi. S, 1 mi. E of Oakridge (T22S/R3E/Sec. 10), elev. 1500 ft., Lane County, Oregon, collected March 4, 1972 by E. M. Benedict, deposited in AMNH.

ETYMOLOGY: The species epithet, an adjective, refers to the form of the terminal spines of the outer coxites of the anterior gonopod.

DIAGNOSIS: This species may be distinguished from *tillamook* and *causeyae* by the more numerous ocelli, which are well-pigmented and arranged in a triangular patch rather than an L-shaped row.

MALE: Twenty-eight segments. Length, 2.1 mm., greatest width, 0.56 mm. Antennal segment three 0.13 mm. long, 0.05 mm. wide. Ocelli 7 or 8 (9 in some specimens), black, well-formed, in triangular patch. Body form typical. Color entirely white. Anterior

gonopods (fig. 24) variable; outer coxite always with two terminal spines sinuously curved, with as few as two (Gold Beach, fig. 21) and as many as four (Estep Creek, fig. 22) subterminal setae. Inner coxite narrower, with two straight terminal spines. Telopodites with branch *A* reduced, perhaps absent in some specimens, *B* with some variation (cf. figs. 23, 25), *C* typical. Posterior gonopods (fig. 26) with prominent coxal lamella, prefemur little less than twice as long as terminal article.

FEMALE: Twenty-eight segments. Length, 3.6 mm., greatest width, 0.64 mm. Antennal segment three 0.17 mm. long, 0.07 mm. wide. Ocelli 8 or 9, black, in triangular patch more compact than male. Color white.

DISTRIBUTION: All collections by E. M. Benedict. OREGON: *Curry Co.:* 13 mi. E of Gold Beach on road to Agness, T36S, R13W, Sec. 3, elev. 600 ft., March 10, 1972, ♂, 3 ♀♀; 14 mi. E of Gold Beach, same data, 10 ♂♂, 14 ♀♀; 5 mi. N of Brookings, T40S, R14W, Sec. 13, elev. 900 ft., February 12, 1972, ♂, ♀. *Douglas Co.:* 1 mi. S, 2 mi. W of Ash, T23S, R10W, Sec. 27, elev. 500 ft., December 11, 1971, 2 ♂, ♀. *Lane Co.:* 4 mi.

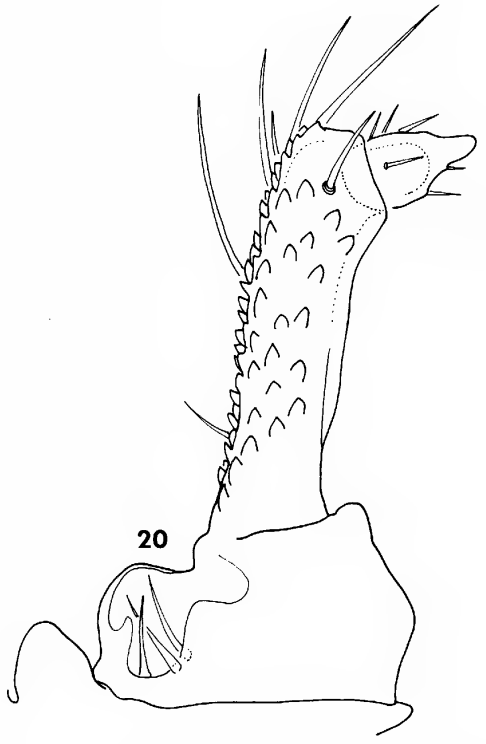
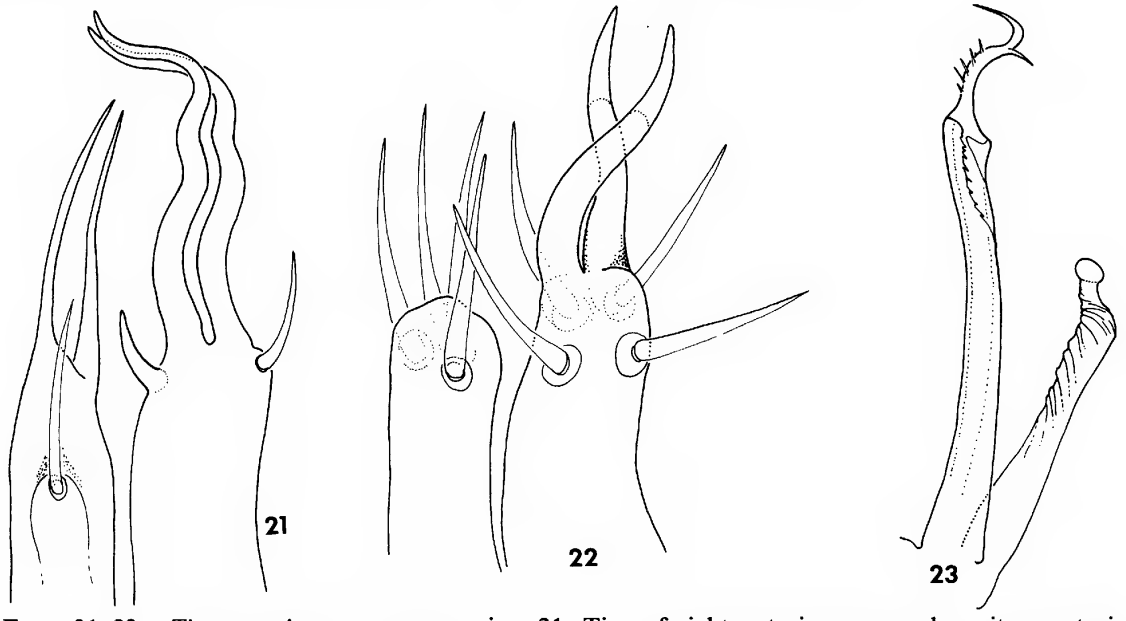


FIG. 20. Right posterior gonopod of *Tingupa auricula,* anterior view.



FIGS. 21–23. *Tingupa sinuosa,* new species. 21. Tips of right anterior gonopod coxites, anterior view, specimen from Gold Beach. 22. Same, specimen from Estep Creek. 23. Branches of right anterior gonopod telopodite, lateral view, specimen from Gold Beach.

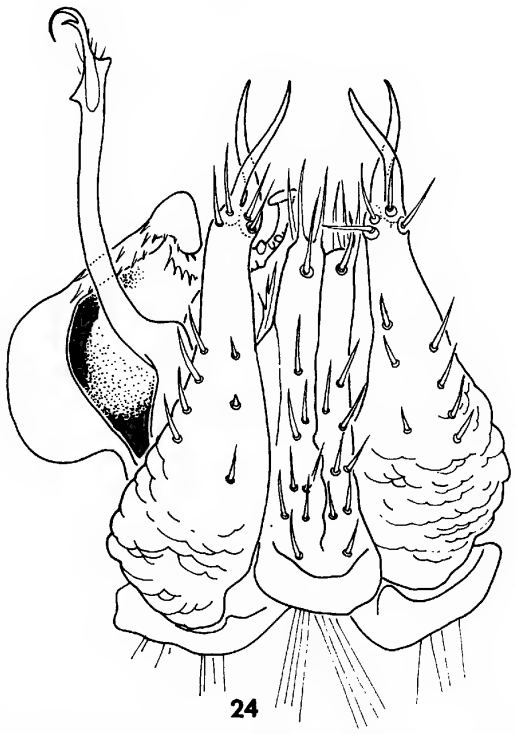


FIG. 24. Anterior gonopods of *Tingupa sinuosa*, anteriolateral view.

N, 13 mi. E of Lowell, T18S, R2E, Sec. 25, elev. 1200 ft., ♂; Dolly Varden Campground, T18S, R2E, Sec. 21, March 4, 1972, ♂, ♀; 0.3 mi. S of Estep Creek, 12 mi. S of Oakridge, TweS, R3E, Sec. 21, elev. 1800 ft., March 4, 1972, 3 ♂♂, 5 ♀♀ (all WAS).

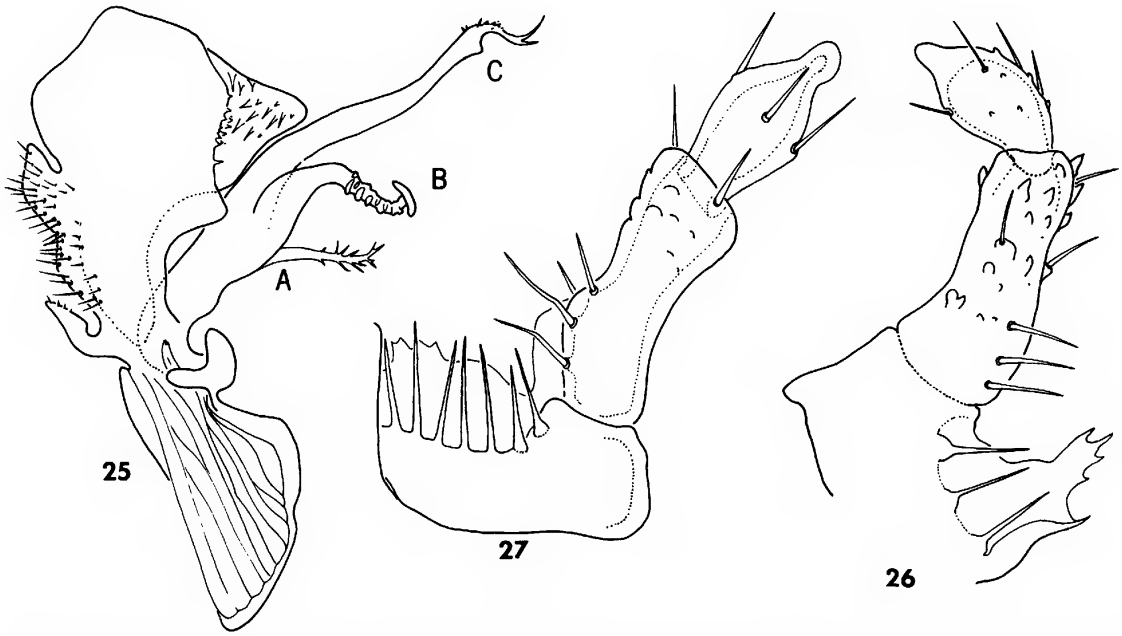
NOTES: This species shows considerable variation in the gonopods, and I originally thought two species were involved, representing the extremes of variation shown in figures 21 and 22. However, the appearance of intermediate forms, particularly the male from Dolly Varden Campground, caused me to decide to treat the populations as representing a single, variable species.

Tingupa eldorado, new species
Figures 27–29

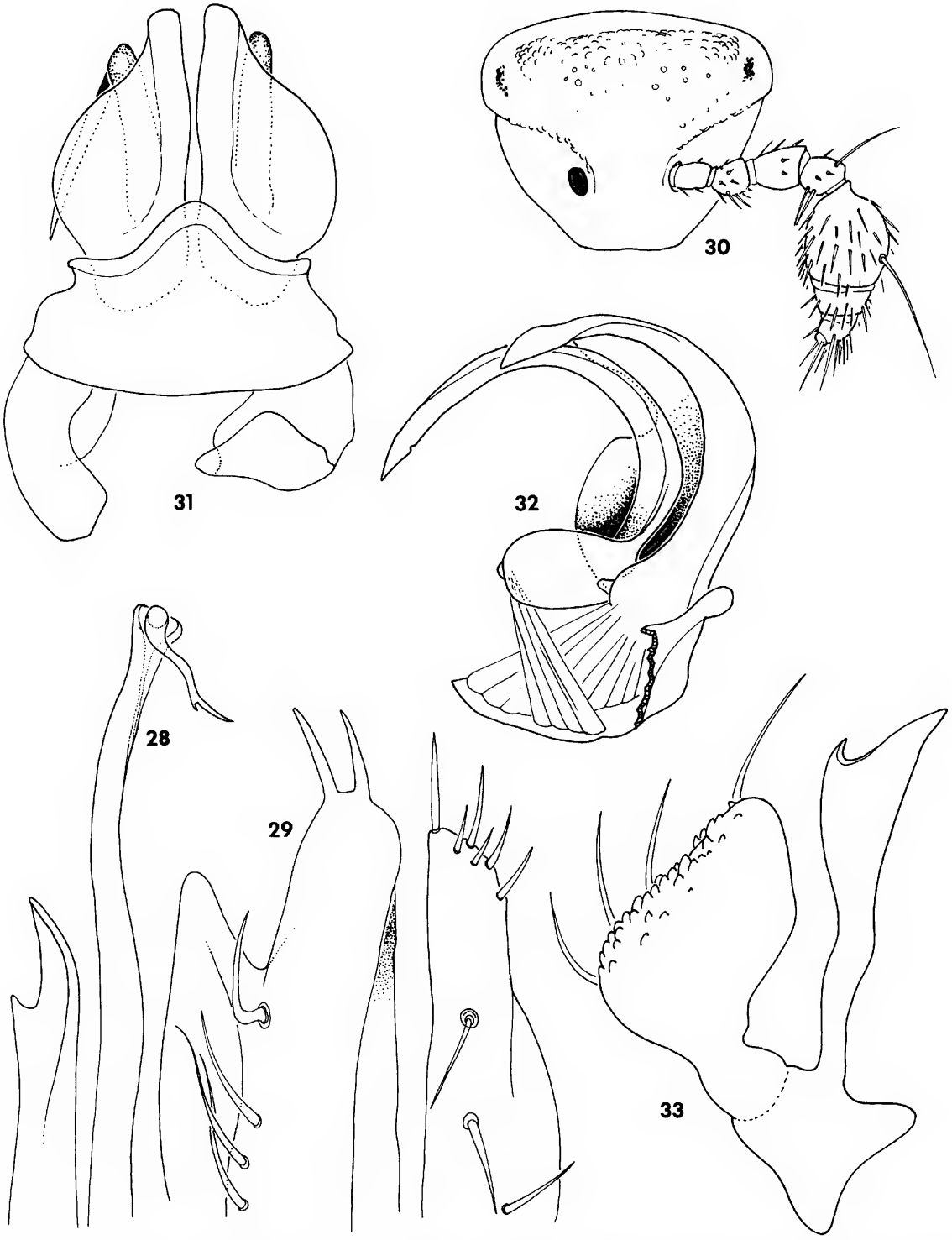
TYPES: Male holotype, male and female paratypes from Riverton, Eldorado County, California, collected February 22, 1958 by R. Schuster, deposited in AMNH.

ETYMOLOGY: The species epithet is a noun in apposition and refers to the type locality.

DIAGNOSIS: This species is distinct from all others in the fusion of the telopodite



FIGS. 25–27. *Tingupa sinuosa* and *T. eldorado*, new species. 25, 26. *T. sinuosa*. 25. Right anterior gonopod telopodite, mesal view. 26. Left posterior gonopod, anterior view. 27. Right posterior gonopod of *T. eldorado*, anterior view.



FIGS. 28–33. *Tingupa eldorado,* new species, and *Buotus carolinus*. 28, 29. *T. eldorado*. 28. Right anterior gonopod telopodite branches, anterior view. 29. Tips of coxites of right anterior gonopods, anterior view. 30–33. *B. carolinus*. 30. Head and left antenna, anterior view. 31. Anterior gonopods, anterior view. 32. Right anterior gonopods, mesal view. 33. Left posterior gonopod, posterior view.

branches of the anterior gonopod and the presence of a large median flange on the inner coxite.

MALE: Twenty-eight segments. Length, 3.6 mm., greatest width, 0.58 mm. Antennal segment three 0.17 mm. long, 0.05 mm. wide. Eleven dark brown ocelli arranged in triangular patch of three rows. Body form typical. Color white to cream with light tan mottlings on head and anterior third of trunk. Segmental setae somewhat longer than usual, head and front more densely hairy than in other species. Anterior gonopods with outer coxite narrower than inner, lacking spines, with few small, weak terminal setae (fig. 29); inner coxite with two small terminal spines, large median flange (fig. 29). Telopodite branches (fig. 28) with *C* as usual, *A* and *B* evidently fused to form a single, massive branch. Posterior gonopods (fig. 27) typical, coxal setae more numerous than usual.

FEMALE: Twenty-eight segments. Length, 5.1 mm., greatest width, 0.64 mm. Antennal segment three 0.19 mm. long, 0.06 mm. wide. Eight ocelli in triangular patch. Color and nonsexual characters as in male.

DISTRIBUTION: Known only from type locality.

BUOTUS CHAMBERLIN

Buotus Chamberlin, 1940, p. 58 (types species *B. carolinus* Chamberlin by original designation; genus misplaced in Polyzoniida). Chamberlin and Hoffman, 1958, p. 186. Shelley, 1975, p. 382; 1978, p. 52. Hoffman, 1979, p. 135.

DIAGNOSIS: Distinct from *Tingupa* in that males are 26-segmented, lack ocelli and have a long coxite on the posterior gonopod.

DESCRIPTION: With the characters of the family, and as follows. Males with 26 segments, females with 28. Ocelli absent. Anterior gonopods of male with only one coxite; telopodites with one division consisting of a curved acute rod. Posterior gonopod with one postcoxal segment (proximal or prefemoral segment evidently fused to coxa), coxa with long, spatulate coxite.

DISTRIBUTION: Montane region along the border of Virginia and West Virginia; North Carolina piedmont (reported by Chamberlin, 1940).

Buotus carolinus Chamberlin
Figures 30–33

Buotus carolinus Chamberlin, 1940, p. 58. Chamberlin and Hoffman, 1958, p. 186. Shelley, 1975, p. 382; 1978, p. 52. Hoffman, 1979, pp. 126, 135.

TYPES: Female holotype from Duke Forest, Durham County, North Carolina, collected December 10, 1940 by N. B. Causey, deposited in Chamberlin collection (currently on loan to RLH from United States National Museum), examined.

MALE: Twenty-six segments. Length, 3.0 mm., greatest width, 0.42 mm. Ocelli absent; but a single, deep-lying spot of black pigment present on each side of head (fig. 30). Antennae (fig. 30) very strongly clavate, fifth segment much the largest, with laterodistal seta. General body form typical of family, with usual sculpture; segmental setae reduced. Color entirely white but for pigment spots on head. Anterior gonopods (fig. 31) with inner and outer coxites not distinct, single coxite present basally flared on each side, rapidly attenuate distally, sharply curved posteriorly, then dorsally (fig. 32). Telopodite (fig. 32) simple, not branched, lobular portion absent, curved in one-half circle, distally acute. Posterior gonopod (fig. 33) with long coxite, single lobe-like telopodite branch.

FEMALE: Twenty-eight segments. Length, 3.3 mm., greatest width 0.44 mm. Structure and coloration as in male.

DISTRIBUTION: VIRGINIA: *Giles Co.:* Potts Mtn. at head of Little Stony Creek, elev. 3600 ft., June 3, 1977, R. L. Hoffman, ♂, ♀ (RLH); Brush Mtn. 2 mi. W of Blacksburg, March 5, 1961, R. L. Hoffman, 3 ♀♀ (RLH). *Montgomery Co.:* Brush Mtn., 1 mi. W of Blacksburg, March 20, 1976, R. Hoffman, W. Shear, R. Shelley, ♂, 2 ♀♀ (WAS). WEST VIRGINIA: *Pendleton Co.:* 5 mi. S of Witmer, elev. 3000 ft., July 8, 1971, S. B. Peck, 2 ♀♀ (WAS). *Pocahontas Co.:* Hills Creek Falls Scenic Area, above middle falls on flood plain, June 19, 1971, W. Shear, 5 ♀♀ (WAS).

NOTES: Shelley (1978) and Hoffman (1979) have described the nomenclatorial tangle surrounding this species, which Chamberlin (1940) had originally described as a polyzoniid.

The species has been collected from leaf litter in mixed deciduous forests. On Brush Mountain, the litter was composed mostly of oak leaves on an exposed, rather dry hillside; at Hills Creek Falls, specimens came from birch, beech and hemlock litter in the narrow, moist floodplain of Hills Creek nearly halfway down the steep-sided gorge. The Witmer material came from a berlese sample of mixed deciduous litter.

LITERATURE CITED

Briggs, Thomas
1971. The harvestmen of the family Triaenonychidae in North America. Occas. Papers, California Acad. Sci., vol. 90, pp. 1–43, figs. 1–44.

Brolemann, Henry W.
1935. Myriapodes diplopodes (Chilognathes I). Faune de France, vol. 29, pp. 1–369, figs. 1–748.

Chamberlin, Ralph Vary
1910. Diplopoda from the western states. Ann. Ent. Soc. Amer., vol. 3, pp. 233–262, pl. 30–43.
1925. Notes on some centipeds and millipeds from Utah. Pan-Pacific Entomol., vol. 2, pp. 55–63.
1940. On some chilopods and diplopods from North Carolina. Can. Entomol., vol. 72, pp. 56–59.

Chamberlin, Ralph Vary, and Richard L. Hoffman
1958. Checklist of the millipeds of North America. U.S. Natl. Mus. Bull. No. 212, pp. 1–236.

Cook, Orator F.
1899. The diplopod family Striariidae. Proc. U.S. Natl. Mus., vol. 21, pp. 667–676, pls. 53–54.

Coyle, Frederick A.
1974. Systematics of the trapdoor spider genus *Aliatypus* (Araneae: Antrodiaetidae). Psyche, vol. 81, pp. 431–500, figs. 1–194.

Gleason, Henry A., and Arthur Cronquist
1964. The natural geography of plants. Columbia Univ. Press, New York, 420 pp.

Hoffman, Richard L.
1979. Classification of the Diplopoda. Mus. d'Hist. Nat., Geneva, 237 pp.

Hunt, Charles B.
1974. Natural regions of the United States and Canada. Freeman, San Francisco, 725 pp.

Loomis, Harold F.
1939. The millipeds collected in Appalachian caves by Mr. Kenneth Dearolf. Bull. Mus. Comp. Zool., vol. 86, pp. 165–193, figs. 1–14.
1943. New cave and epigean millipeds of the United States, with notes on some established species. *Ibid.*, vol. 92, pp. 371–410, figs. 1–18.
1966. Two new families and other North American Diplopoda of the suborder Chordeumidea. Proc. Biol. Soc. Washington, vol. 79, pp. 221–230, figs. 1–19.

Peck, Stewart Blaine, and Julian J. Lewis
1978. Zoogeography and evolution of the subterranean invertebrate faunas of Illinois and southeastern Missouri. Nat. Speleol. Soc. Bull., vol. 40, pp. 39–63, figs. 1–6.

Shear, William A.
1969. A synopsis of the cave millipeds of the United States. Psyche, vol. 76, pp. 126–143, figs. 1–22.
1971. The milliped family Conotylidae in North America, with the proposal of the new family Adritylidae (Diplopoda, Chordeumida). Bull. Mus. Comp. Zool., vol. 141, pp. 55–96, figs. 1–81.
1972. Studies in the milliped order Chordeumida (Diplopoda): a revision of the family Cleidogonidae and a reclassification of the order in the New World. *Ibid.*, vol. 144, pp. 151–352, figs. 1–538.
1973. The milliped family Rhiscosomididae (Diplopoda: Chordeumida: Striarioidea). Psyche, vol. 80, pp. 189–203, figs. 1–16.
1976. The milliped family Conotylidae (Diplopoda, Chordeumida): revision of the genus *Taiyutyla*, with notes on recently proposed taxa. Amer. Mus. Novitates, no. 2000, pp. 1–22, figs. 1–42.
1979. Diplopoda from the Nepal Himalayas. Chordeumida with comments on the Asian chordeumid fauna. Senckenbergiana Biol., vol. 60, pp. 115–130, figs. 1–23.

Shelley, Rowland M.
1975. Two new diplopods of the genus *Polyzonium* from North Carolina, with records of established species (Polyzoniida: Polyzoniidae). Proc. Biol. Soc. Washington, vol. 88, pp. 179–188, figs. 1–10.
1978. Millipeds of the eastern piedmont region of North Carolina, U.S.A. (Diplopoda). Jour. Nat. Hist., vol. 12, pp. 37–79, figs. 1–72.