WILLIAM A. SHEAR

The Milliped Family Conotylidae
(Diplopoda, Chordeumida)
Revision of the Genus Taiyutyla,
With Notes on Recently Proposed Taxa
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ABSTRACT

The millipede family Conotylidae Cook is divided into four subfamilies: Conotylinae Cook, Austrotylinae (new), Lophominae Loomis and Schmitt, and Macromastinae Loomis and Schmitt, the last originally proposed as an independent family. A key to the subfamilies and their included genera is presented. The genus Taiyunyla (Conotylinae) is revised, and nine new species are described: clatsop, benedictae, simplex, trifurca, prefemorata, variata, millioma, lewisi, and clarki. Conotyla extorris Shear is transferred to Taiyunyla. New observations and illustrations are presented of the gonopods of Macromastus marginandus Loomis and Schmitt; the gonopod appears to have one less articulation than the original authors observed. Troglotyla skamania Causey is transferred to Lophomus (Lophominae). Corypus cochlearis Loomis and Schmitt is transferred from the Conotylinae to the Austrotylinae. Brunsonia complexipes Loomis and Schmitt is synonymized with Conotyla albertaina Chamberlin. Three nomina dubia in the Conotylidae [Cookella leibergi (Cook and Collins), Zygolota phana Chamberlin, and “Trichopetalum” glomeratum Harger] are discussed. Endopus parvipes Loomis and Schmitt and Orthogmus oculatus Loomis and Schmitt, described in the family Trichopetalidae, were based upon immature conotylids; their status cannot be settled without mature material from the type localities.

INTRODUCTION

My 1971 revision of the millipede family Conotylidae was, as stated then, based on relatively few specimens from scattered localities. Since the publication of that paper, additional specimens and data have accumulated to the point that it has now become possible to issue a series of supplements to that original work. This third paper on the Conotylidae (see Shear 1971, 1974) deals with the western North American fauna. In 1972, in the context of a reclassification of the New World Chordeumida, I added the family name Idagonidae Buckett and Gardner to the synonymy of the Conotylidae, and the evidence for that placement is to be found in that paper. Loomis and Schmitt (1971) described several new chordeumids related to or included in the family Conotylidae from western Montana. I have at last been able to borrow type material of

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these forms and have suggested below some changes in the taxonomic positions of some of them.

Perhaps most significantly, hundreds of collections of millipedes made by Berlese extraction in Oregon and Washington by Mrs. Ellen M. Benedict have come into my hands. This material now makes possible a comprehensive restudy of the genus *Taiyutyla*, apparently endemic to the Pacific Northwest, west of the continental divide. *Taiyutyla* was established by Chamberlin in 1952 for *T. corvallis* Chamberlin, from Oregon. Hoffman (1961) studied some topotypical material, verified the validity of the genus as distinct from *Conotyla*, and suggested that *Conotyla jonesi* Chamberlin, described in 1951 from Oregon, was a possible synonym. Chamberlin retained the holotype of *T. corvallis* in his personal collection; the holotype of *C. jonesi* was to go to the British Columbia Provincial Museum, but they never received it. Neither could be located when I requested they be loaned in 1970.

*Bollmanella* was based by Chamberlin (1941) on the single species *B. oregona* Chamberlin, in a confusing series of paragraphs in which generic and specific diagnoses actually contradicted each other. In 1970, I borrowed the male holotype of *B. oregona* from the Chamberlin collection, through the courtesy of Mr. Thomas Lorenz, who was then in charge of it. *Bollmanella oregona* proved to be a distinctive conotyloid, and the material received from the Benedict collection added several additional species to the genus, which includes species related to, but readily distinguished from, species of *Taiyutyla* by the presence of a coxal flagellum on the posterior gonopods, uniform pregonopodal leg modifications, and generally smaller size (Shear, 1974). No species of *Bollmanella* are known as yet from California.

I express thanks to Mrs. Ellen M. Benedict, Portland State University, Portland, Oregon, for sending me the crucially important Berlese collections on which most of this and several subsequent papers will be based. I thank Dr. Ralph Crabbill, National Museum of Natural History, Smithsonian Institution, Washington, D.C., for the loan of type material.

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**ABBREVIATIONS**

AMNH, the American Museum of Natural History
USNM, National Museum of Natural History, Smithsonian Institution
PWAS, Personal Collection of William A. Shear

**GONOPOD STRUCTURE AND FUNCTION**

The structure of the gonopods of the genera treated below is typical of conotyloid millipedes. The anterior gonopods consist of single pieces representing a fusion of the coxa and telopodite of each leg, firmly articulated with a well-developed, chitinized, bandlike sternum that in some species extends along the lateral side of the gonopod, a tendency most clearly developed in species of *Austrotyla*. The posterior gonopods consist of three segments, of which the distal two are essentially similar in all known species, differing only in their proportions in some species populations. The basal, coxal segment bears colpocoxites of various forms that are crucial in species determinations. In species of *Taiyutyla*, the colpocoxites are simple or are apically bifurcate and may bear fimbriate regions or branches, or patches of tiny microsetae, about midway in their length. There is no articulate coxal flagellum present; in size the colpocoxites approximate the anterior gonopods. In related *Bollmanella* species (Shear, 1974), the posterior gonopod sternum is more strongly developed and in several species extends as a prominent T-shaped process between the coxae of the posterior gonopods. There is a basal coxal flagellum which, however, is not articulated, as it is in species of *Lophomus*. The main branch of the colpocoxite may be complex, and carries on its posterior surface a sheathing structure in which the coxal flagellum usually lies.

In both genera, the gonopods are positioned in the same way, a form shared by species of *Conotyla* and *Idagona*, although *Idagona* is quite aberrant. The gonopod complex is pushed posteriad so that the gonopods are nearly parallel to the long axis of the body. In this position, the tips of the anterior gonopods reach only to the middle of the posterior gonopod colpocoxites,
and are usually curved laterad and posteriad so that they pass lateral to the colpocoxites, forming on each side a sort of forceps-like arrangement (Shear, 1971).

The secondary sexual modifications of males of the western genera are essentially similar. Some of the pregonopodal legs are crassate and curved mesiad, and in species of Taiyutyla, posterioriomesial processes on some or all the femora are present. In species of Bollmanella, leg pairs three and four are enlarged, but the legs subsequently decrease in size so that pair seven is of nearly normal size. Only small femoral knobs appear on pairs three and four, if at all. My observations on the mating of Conotyla blakei in New England suggest that these are adaptations for grasping the head, antennae, and anterior segments of the female during copulation. The tenth and eleventh pairs of legs, just posterior to the gonopod complex, are also modified, and in the same way in all species of Conotyla, Taiyutyla, and Bollmanella. The tenth coxae are enlarged and bear an eversible gland; the trochanters are enlarged mesially in most species. The eleventh coxae and trochanters are usually essentially unmodified, but there is a long basal process on the eleventh prefemur in many species, which extends dorsomesiad nearly to the sternum. The functional significance of the eleventh leg modifications is not clear, but it does seem certain that the tenth coxal glands are used by the males to form spermatophores. Having available for the first time a large series of preserved male conotylids, I was able to verify a few sketchy observations about gonopod function made on living animals. Prior to or during mating, male conotylids probably flex the body so that the penes, opening through the coxae of the second legs, insert into the tenth coxal glands (perhaps the processes of the eleventh prefemora act as guides in this process) and therein discharge sperm. The glands add a secretion, in alcohol yellow-brown and hard, which forms up the sperm into spermatophores. Immediately before or during mating, the glands are extruded and the spermatophores are picked up by the forceps-like action of the anterior gonopods working against the posterior gonopod colpocoxites. I have found preserved males with extruded, spermatophore-tipped glands, and with spermatophores grasped in this fashion by the gonopods, always at the point where the tips of the anterior gonopods cross lateral to the posterior gonopod colpocoxites. Probably the gonopods force the spermatophores into the cyphopods of the female. In some Taiyutyla, Bollmanella, and Conotyla species there is an obvious recessed glandular area in the coxal region of the anterior gonopods, with a channel that opens near the gonopod tip. Perhaps the apparatus produces a lubricating substance that aids in spermatophore transfer. The functional significance of the flagellum in species of Bollmanella and Lophomus remains obscure.

Unfortunately, it is difficult to draw any functional parallels in the female genitalia. These structures in conotylids show few differences between species, and, as yet, I have been unable to discover anything about them that would be taxonomically useful. The lack of nonsexual differences between species thus renders isolated female specimens virtually unidentifiable.

EVOLUTIONARY RELATIONSHIPS

Gonopod structure, as described above and in an earlier paper (Shear, 1971), clearly relates the genera Conotyla, Taiyutyla, Plumatyla, and Bollmanella. However, the gonopods of Austrotyla species appear to be simpler and more reduced, and obviously do not form a forceps-like structure. Further, pregonopodal leg modifications show significant interspecies and intraspecies differences in Conotyla and Taiyutyla, and are stabilized in Austrotyla (all known species having femoral lobes on legs three and four). I consider this to be a specialization, and thus the species of Austrotyla seem to me to be derivative. Achimenides pectinatus may be further specialization of the basic austrotyline stock. For the same reasons, Bollmanella, with stabilized pregonopodal leg modifications and more complicated gonopods, can be considered a specialized derivative of a Taiyutyla-like ancestor. The two western species of Conotyla, C. albertana and C. atrolineata, seem in many ways to link Conotyla and Taiyutyla.

These relationships should be recognized by establishing subfamilies. Loomis and Schmitt (1971) divided the Conotylidae into two subfamilies: Lophominae, including only their new species Lophomus laxus (treated at length below), and the Conotylinae, including every-
thing else. Although they designated this second subfamily name as "new," the original proposal of the family level name Conotylidae by Cook in 1895, according to the rules of nomenclature, covered the establishment of a corresponding subfamily. Also, a subfamily Conotylinae had been proposed in 1913 by Verhoeff. Verhoeff also set up the subfamily names Eudigoninae and Japanosomatinae, but these names for exotic forms probably do not apply to any North American types and can be placed outside the scope of this paper, although from Verhoeff's 1913 illustrations of Japanosoma scabrum, it does not appear to be very much unlike Conotyla and Taiyutyla. Loomis and Schmitt (1971) also seemed unaware of my proposal (Shear, 1971) of the family name Adritylidae for the very distinct species Adrityla humerosa, and included Adrityla in their concept of Conotylinae.

Moreover, Loomis and Schmitt's system suggests that Lophomus laxus represents a sister-group of all other conotylids, although clearly it was not their intent to do so. I recognize the subfamily as constituted by them, but do not believe that it should be set off in such a way as to indicate a complete divergence for all other conotylids. The question of sister-groups in the Conotylidae cannot be properly dealt with until the Asian and South American genera mentioned above can be studied.

Now, with a more or less complete knowledge of the range of species to be found in the Conotylidae in North America, a more useful division into subfamilies can be carried out.

KEY TO SUBFAMILIES AND GENERA OF THE CONOTYLIDAE

1. Posterior colpocoxites of male gonopods consisting of long, thin structure partially sheathed at base by sternal process (fig. 32); body with paranota prominent, flat, and rimmed ............... Subfamily Macromastinae Loomis and Schmitt, Genus Macromastus Loomis and Schmitt. Posterior colpocoxites more complex, not as above ............... 2

2. Posterior colpocoxites of male gonopods with an articulated basal flagellum (figs. 34, 37) ............... Subfamily Lophominiae Loomis and Schmitt, gen-

nus Lophomus Loomis and Schmitt. Gonopods not as above. ............... 3

3. Anterior gonopods flattened, more or less platelike, usually larger than posterior gonopod colpocoxites, with lateral sternal processes at least partially fused to lateral regions of anterior gonopods ............... Subfamily Austrotylinae, new. 4

Anterior gonopods not flattened, more or less complex, with a number of branches and processes, usually smaller than posterior gonopod colpocoxites; without lateral sternal process ............... Subfamily Conotylinae Cook, 7

4. Posterior gonopod telopodites absent; ice caves in Idaho. ............... Idagona Buckett and Gardner Posterior gonopods with telopodites ....... 5

5. Anterior gonopods basally fused; anterior gonopod sternum divided; Wisconsin, Illinois, and Iowa, mostly in caves ............... Achemenides Shear. Anterior gonopods not fused; anterior gonopod sternum entire. ............... 6

6. Anterior gonopods larger than posterior gonopod colpocoxites; Wisconsin, Illinois, Missouri, Rocky Mountains from Alberta to Chihuahua. ............... Austrotyla Causey. Anterior gonopods smaller than posterior gonopod colpocoxites (fig. 42); Montana ............... Corypus Loomis and Schmitt.

7. Troglobitic species; ocelli reduced in number to about 10; anterior and posterior gonopods both two-branched; California ............... Plumatyla Shear. Pigmented species; not troglobitic; more than 10 ocelli; anterior and posterior gonopods not both two-branched. ............... 8

8. Posterior gonopod colpocoxites with unarticulated flagellum at least partially sheathed by another branch of coxite; animals 7 mm. or less in length; Oregon and Washington ............... Bolimanella Chamberlin. Posterior gonopod colpocoxites without such a branch; animals usually more than 7 mm. long ............... 9

9. Anterior gonopods subequal to posterior gonopod colpocoxites; anterior gonopod sternum heavily sclerotized; posterior gonopod colpocoxites frequently complexly branched; central California north to Washington and thence east to Montana in the region of the Continental Divide ............... Taiyutyla Chamberlin. Anterior gonopods smaller than posterior gon-
opod colpocoxites, usually not complexly branched; Maine south to North Carolina, west to Indiana, Rocky Mountains of Alberta and British Columbia. . . . . . . . Conotyla Cook and Collins.

FAMILY CONOTYLIDAE COOK


Synonymy. A diagnosis and description of the family is given in Shear (1971, 1972) and needs no emendation here to include Macromastus marginandus Loomis and Schmitt, the type species of the type genus of the family Macromastidae. Loomis and Schmitt (1971) named this family because M. marginandus seemed to them to be "unusually large," bore prominent, flat paranota, and had an extra segment in the posterior gonopod telopodites. The somatic modifications alone do not justify separating this species at the family level; the development of the paranota is very nearly equal in Lophomus laxus, another species they described in the same paper. The extra segment in the posterior gonopods appears to be a mistaken observation: I could not discern the joint clearly depicted by Loomis and Schmitt in their illustration (1971, p. 127, fig. 29; compare my fig. 33).

SUBFAMILY CONOTYLINAE COOK

Conotylinae, Loomis and Schmitt, 1971, p. 121, in part (including only Conotyla and Taiyutyla, of the genera mentioned; type genus, Conotyla Cook and Collins).

Diagnosis. Conotylid millipedes with 30 segments and undivided mentum. Anterior gonopods simple, acuminated, or with two branches, erect or clasping posterior gonopod colpocoxites. Posterior gonopod colpocoxites simple or complexly branched, upright; posterior gonopod telopodites present, two-segmented.

Included genera. Conotyla, Taiyutyla, Bollmanella, Plumatyla.

Discussion. This subfamily at first appears heterogeneous, but all the genera are clearly related by species with intermediate gonopod types. Conotyla species appear most divergent from the basic type, as I suggested earlier (Shear 1972), through the reduction of the anterior gonopods. However, Conotyla bollmani is strikingly like a simplified Taiyutyla species, except that the anterior gonopods firmly clasp the posterior. Taiyutyla, Bollmanella, and Plumatyla are difficult to keep separate. The picture is confused by the troglobitic adaptations shown in Plumatyla species, and the development in them of two branches of the anterior gonopods. The anterior gonopod sterna in P. humerosa actually resemble those of Austrotyla species! Species of Bollmanella are generally smaller than those of Taiyutyla, and bear an unarticulated, sheathed flagelliform branch on the posterior gonopod. They also have stabilized pregonopodal leg modifications, but otherwise there seems to be a fair amount of continuity in gonopod pattern.

CONOTYLA COOK AND COLLINS

Conotyla Cook and Collins, 1895, p. 70 (type species by original designation C. fischerti Cook and Collins): Shear, 1971, p. 64, 1972, p. 271.

Proconotyla Verhoef, 1932, p. 501 (type species by original designation and monotypy P. blakei Verhoef).


Synonymy. The genus is diagnosed, described, and discussed in detail in my earlier papers (Shear, 1971, 1972). Having gonopods identical to an earlier described species, Brunsonia complexipes is a synonym of Conotyla albertana Chamberlin; the records given by Loomis and Schmitt (1971) extend the range of this common species south into Montana. I have hundreds of specimens from the Maligne Range, Alberta, and the species seems to be found quite frequently in treeless areas as well as forests, at high elevations.

Species of Conotyla in the northeastern United States are scattered, and most are known only from a few specimens. My 1971 key relied heavily on pregonopodal leg modification, but as
more new material accumulates, variation is apparent. However, it will be some years before enough new specimens are collected to fully assess the extent of the variation.

**TAIYUTYLA CHAMBERLIN**

* Taiyutyla Chamberlin 1952, p. 1 (type species *T. corvallis* Chamberlin by original designation).


The genus is adequately diagnosed and described in my 1971 revision, which, however, included only three species. The discovery of additional species included some that lack apophyses on the third and fourth legs of the males, and which bear a coxal depression, or pocket, posteriorly on the posterior gonopods.

Species of *Taiyutyla* are distributed through the Coast Ranges of the Pacific Northwest from San Francisco Bay to the Columbia River, with one species (previously misplaced in *Conotyla*) known from interior California and one from Western Montana. The lack of records north of the Columbia River is almost certainly due only to the lack of collections from Washington state. Because of the numerous species probably remaining to be discovered, I present no key at this time. All the species can quickly be distinguished from one another by comparison of the illustrations given here, and in my earlier paper (Shear, 1971).

* Taiyutyla extorris (Shear)  
  new combination

*Conotyla extorris* Shear, 1971, p. 70-71, figs. 22, 23.

I described this species in *Conotyla* in 1971 because it seemed to me to combine features of *Conotyla* and *Taiyutyla*, but appeared to fit best in *Conotyla*. A better knowledge of the range of species belonging to *Taiyutyla* has made me change my mind; this generic assignment of *extorris* is also more palatable zoogeographically, although the species still is out of the range of the genus to some degree, and is unusual in having unmodified pregonopodal legs. Only the male holotype is known, from one mile south of Grass Valley, Nevada Co., California; it is in the Museum of Comparative Zoology.

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**Taiyutyla corvallis** Chamberlin  

* Taiyutyla corvallis Chamberlin 1952, p. 1, figs. 1, 2. Shear, 1971, p. 87, figs. 8, 59, 60.

This, the type species of the genus, is known only from Corvallis, Oregon. Despite extensive sampling in that region by E. M. Benedict, no additional material has turned up, and I can add nothing to my 1971 account.

* Taiyutyla napa* Shear  

* Taiyutyla napa* Shear 1971, p. 87-88, figs. 63, 64.

This species is known only from Mt. St. Helena, Napa Co., California. I have nothing to add to my 1971 description.

* Taiyutyla francisca* Shear  

* Taiyutyla francisca* Shear, 1971, p. 88, figs. 61, 62.

This species is known from Inverness, Marin Co., California. Nothing additional concerning it has come to my attention.

* Taiyutyla clatsop*, new species  

Figures 1, 2

*Types*. Male holotype and female paratype from 700 ft. elev., 5 mi. N and 7 mi. W of Elsie (T5N/R9W), Clatsop Co., Oregon, collected March 15, 1972, by E. M. Benedict, deposited in AMNH.

*Etymology*. The species epithet is a noun in apposition referring to the type locality.

*Diagnosis*. None of the other species have the pregonopodal legs without femoral knobs, except for leg 7. The posterior gonopod colpocoxites somewhat resemble those of *T. prefemorata* and related species (*T. lewisi*, *T. clarki*, etc.) but are narrower (fig. 1) and bear a pair of flagelliform branches basally.

*Male*. 6.0 mm. long; antennal segment three 0.41 mm. long. Eighteen pigmented ocelli in three rows form triangular eyepatch. Pigmentation very light tan, mottled slightly darker. Segments of typical conotylid form. Legpairs three to seven much enlarged, pairs three and four the largest, size decreasing five through seven, but pair seven still larger than postgonopodal legs.
Small blunt knobs basal on femora of legs seven; pregonopodal femora otherwise unmodified. Anterior gonopods (fig. 2) slightly curved posteriad, passing lateral to midpoint of posterior gonopod colpocoxites, with lateral T-shaped branch and complex termination including microsetae as shown. Posterior gonopods with telopodite articles short and subequal, colpocoxites strongly curved posteriad, with two flagelliform basal branches, small terminal fimbriate area, divided tip (fig. 1).

**Distribution.** Known only from type locality.

Notes: The types were collected from duff and loose bark around the base of a sitka spruce. The relationships of this species are somewhat obscure, but it serves at least superficially to link species of *Bollmanella* and *Taiyutyla*, due to the small size and the unsheathed flagelliform branches of the posterior gonopod. However, the species lacks the typical pregonopodal leg modifications of *Bollmanella* species. Within *Taiyutyla*, *T. clatsop* is distant from most of the other species, but may be related to *T. trifurca*, considering the peculiar posterior gonopods of that species.

**Taiyutyla benedictae**, new species

**Figures 3-5**

**Types.** Male holotype, male and female paratypes 4100 ft. elev., 17 mi. NE of McKenzie Bridge on Highway 242, Lane Co., Oregon, collected October 16, 1971, by E. M. Benedict, deposited in AMNH.

**Etymology.** The species epithet honors the collector, E. M. Benedict.

**Diagnosis.** The peculiar posterior gonopods (fig. 4) and the form of the posterior gonopod sternum (fig. 3) set this species apart from all others.

**Male.** 9.3 mm. long; third antennal segment 0.53 mm. long. Twenty pigmented ocelli in three or four rows form triangular eyepatches. Pigmentation light tan, mottled darker, shaded darker on head and antennae. Legpairs one and two reduced in size, pairs three and five enlarged, pair six nearly normal, pair seven of normal size. Legpairs three and four with large, capitate, basal femoral knobs. Anterior gonopods (fig. 5) very simple, acuminated, curved posteriad, with definite basal pit and gland channel. Posterior gonopods with telopodite articles large, distal article largest; colpocoxites (fig. 4) with broad, posterior membranous area, short lateral branch, and double termination with lateral prong very long and coiled, mesal prong sharply hooked.

**Female.** Length, 9.9 mm. Third antennal segment 0.45 mm. long. Body stouter than in male, pigmentation slightly darker. No sexual characters of taxonomic value.

**Distribution.** Known only from type locality.

Notes: The types were taken from conifer duff and rotted wood. Like *T. clatsop*, this species might have been placed in *Bollmanella*, but is larger than any species of that genus and lacks the sheathed flagelliform branch of the posterior gonopods.

**Taiyutyla simplex**, new species

**Figures 6-8**

**Types.** Male holotype and male and female paratypes 400 ft. elev., 3.2 mi. NE of Scottsburg (T22S/R9W/Sec. 5), Douglas Co., Oregon, collected December 11, 1971, by E. M. Benedict, deposited in AMNH.

**Etymology.** The species epithet is an adjective referring to the form of the gonopods.

**Diagnosis.** The simple gonopods relate this species to *corvallis*, from which it may be distinguished by the form of the posterior gonopod colpocoxites, which in *simplex* are not apically bifurcate.

**Male.** Length, 11.6 mm.; third antennal article 0.55 mm. long. Twenty-two ocelli in four rows in triangular eyepatch. Pigmentation light brown, heavily mottled darker purplish brown on all segments and head; antennae dark brown. Legpairs one and two reduced in size; pairs three and four somewhat enlarged, pairs five, six, and seven of nearly normal size. Legpairs three and four with moderately developed mesal knobs on femora. Anterior gonopods (fig. 6) broad, flat, simple, blade-like, but with a complex arrangement of specialized flattened setae and microsetae on apical branch (fig. 8). Posterior gonopods (fig. 7) with distal telopodite article about twice as long as basal; colpocoxide simple, curved slightly posteriad.

**Female.** Length, 11.9 mm., third antennal
segment 0.52 mm. long. Color and general appearance as in male, but body somewhat stouter.


Notes: This species is most commonly associated with duff and litter from deciduous trees, such as bigleaf maple. At the Millicoma Tree Farm, it was collected in the riparian zone of Fall Creek; at that point and at Elliott State Forest, *T. simplex* is syntopic with *T. millicoma*. The latter is much more common at both sites. *Bolmanella oregona* Chamberlin was also collected there.

**Taiyutyla trifurca**, new species

**Figures 9-11**


**Etymology.** The species epithet is an adjective referring to the three-branched condition of the posterior gonopod colpocoxites.

**Diagnosis.** No other species of *Taiyutyla* has the gonopod colpocoxites three-branched as in figure 10.

**Male.** 9.5 mm. Antennal segment three 0.49 mm. long. Ocelli 20 in four rows form triangular eyepatch. Pigmentation off-white, lightly marked pale tan. Legpairs one and two reduced in size, pairs three to seven enlarged, pair three only slightly the largest; pairs five and six with small basal femoral knobs, pair seven with large distal femoral hook (fig. 9). Anterior gonopods (fig. 11) relatively small and subequal; colpocoxites three-branched, lateral branch broad, apically laciniate, with lateral group of microsetae, middle branch flagelliform, mesial branch apically broadened, spatulate.

**Female.** Unknown.


Notes: The types came from a Berlese sample of conifer and vine maple duff; at Paradise Park a male was taken from moss and hemlock duff. The Paradise Park male has small basal femoral knobs on legpairs three and four as well as on five and six, but those on the latter two pairs are larger. The male from Clackamas County resembles the types, but has the lobe of legpair seven smaller and definitely fungiform.

**Taiyutyla curtata** Loomis and Schmitt

**Figures 12, 13**

**Taiyutyla curtata** Loomis and Schmitt, 1971, p. 125, figs. 19-21 (male holotype from Leigh Lake Campground, Lincoln Co., Montana, 3600 ft. elev., collected June 14, 1949, no collector given, deposited in USNM, examined).

**Diagnosis.** The only *Taiyutyla* known from Montana. Clearly related to *T. trifurca* (see above) but differing in the form of the posterior gonopod colpocoxites (fig. 12).

**Male.** Length 9.8 mm.; antennal segment three 0.47 mm. long. Ocelli 22 in four rows forming triangular eyepatch. Pigmentation faded from long preservation, pale. Legpairs one and two reduced; pairs three to seven enlarged, decreasing in size posteriorly, pair seven still larger than postgonopodal legs. Legpair five with large mesial femoral knobs, smaller knobs on pair four. Anterior gonopods (fig. 13) acuminate, curved, with small triangular lateral branch. Posterior gonopod colpocoxites (fig. 12) with three branches as shown.

**Female.** Unknown.

**Distribution.** Known only from the type locality.
Notes: This species is outside the known range of other Taiyutyla species, and suggests that an exploration of eastern Washington and northern Idaho might turn up more species.

_Taiyutyla prefemorata_, new species

_Figures 14, 15_

_Types_. Male holotype and male and female paratypes 1000 ft. elev., Canyonville Co. Park, 2 mi. E of Canyonville on Highway 227 (T30S/R5E), Douglas Co., Oregon, collected November 6, 1971, by E. M. Benedict, deposited in AMNH.

_Etymology_. The species epithet is an adjective referring to the knobs on the prefemora of the male pregonopodal legs.

_Diagnosis_. The knobs of the prefemora of the pregonopodal legs clearly relate this species and the following, _T. millicoma_. The present species has such knobs on legpairs five and six; they are reduced to low swellings on these legs in _T. millicoma_.

_Male_. Length, 10.8 mm. Antennal segment three 0.54 mm. long. Nineteen ocelli in three rows plus single ventral ocellus form triangular eyepatch. Pigmentation medium brown marked dark purplish brown. Legpairs one and two much reduced; pairs three to seven enlarged and subequal. Legpairs three to seven with large basal femoral knobs, largest on pairs three and four; prefemoral distal knobs on pairs five to seven increasing in size posteriad. Anterior gonopod tip (fig. 15) with apical spine above posterior fimbriate area; lateral margin roughened. Posterior gonopod colpocoxite (fig. 14) apically bifurcate, turned mesial, with posterior branch bearing microsetae.

_Female_. Length 11.1 mm. Antennal segment three 0.51 mm. long. Pigmentation as in male. No sexual characters of taxonomic value.


Notes: This species seems to be definitely associated with dust and litter from deciduous trees, having been collected from alder, black cottonwood, live oak, and maple litter and dust at various localities. Together with _T. millicoma, variata, lewisi_, and _clarki_, this species forms a group of related species marked by an apical spine on the anterior gonopod colpocoxite (except in _clarki_) usually bent laterad at a right angle, and a fimbriate or setose posterior branch. All are from the Douglas and Lane county areas.

_Taiyutyla millicoma_, new species

_Figures 16-18_

_Types_. Male holotype, male and female paratypes 1200 ft. elev., 14 mi. E and 2 mi. S of Allegany on Weyerhauser Millicoma Tree Farm Company Rd. 6000 (T25S/R9W/Sec. 16), Coos Co., Oregon, collected Nov. 21, 1971, by E. M. Benedict, deposited in AMNH.

_Etymology_. The species epithet is a noun in apposition referring to the type locality.

_Diagnosis_. Clearly related to _prefemorata_, but lacking the large prefemoral knobs, which appear in this species as low swellings. The femoral knobs found on legpairs five and six of _prefemorata_ are absent in most _millicoma_ males (see Notes below).

_Male_. Length, 10.8 mm.; antennal segment three 0.60 mm. long; ocelli 22 in four rows forming triangular eyepatch. Pigmentation light tan, mottled darker purplish brown. First two legpairs reduced in size; pairs three through seven uniformly larger. Small prefemoral knobs on leg pairs three to seven, smallest on legpairs five and six; large capitate or fungiform knobs (fig. 17) on femora of legpairs three, four, and seven. Anterior gonopods (fig. 18) typical of this group, flattened, acuminate, slightly curved posteriad, with basal depression and gland channel, bearing apical spine. Posterior gonopod colpocoxites (fig. 16) likewise typical, but apical branches widely
separated and sharply curved, posterior branch lobelike, with ornaments of fine cuticle, not microsetae. Posterior gonopod sternum with three teeth between gonopods.

**Female.** Length, 10.5 mm. Antennal segment three 0.53 mm. long. Pigmentation as in male.


Notes: This species has been taken in Berlese samples of hemlock duff, moss, duff from *Rhododendron*, myrtle, bigleaf maple, red alder, and black cottonwood, and from rotted wood. At the type locality and at Elliott State Forest, *Taiyutyla* (fig. 19) with apex broadly flared mesial, short curved terminal spine. Posterior gonopod colpoxites (fig. 20) typical of group, apex deeply divided and curved laterad, posterior branch relatively short and slender, with basal group of microsetae.

**Females. Unknown.**


Notes: At the type locality this species was taken from a Berlese sample of white alder and willow litter. The O'Brien specimens show some clear differences from the types in the posterior gonopods (fig. 21) and in the pregonopodal leg modifications, in which femoral knobs appear on legpairs six and seven, being large and hooklike on the latter. Legpairs three, four, and five lack femoral knobs.

**Taiyutyla variata**, new species

**Figures** 19-22

**Types.** Male holotype and male paratypes 1660 ft. elev., Buckley Co. Park Rest Area, 3.5 mi. S of Ruch on the Upper Applegate River, 2.5 mi. from Highway 238 (T38S/R3W/Sec. 15), Jackson Co., Oregon, collected November 13, 1971, by E. M. Benedict, deposited in AMNH.

**Etymology.** The species epithet honors Capt. Meriwether Lewis, noted explorer of the Pacific Northwest in the early nineteenth-century.

**Diagnosis.** Similar to and related to the preceding three species and *T. clarki*, but distinct in the longer apical spine of the anterior gonopods (figs. 24, 25).

**Male.** Length, 11.5 mm. Antennal segment three 0.62 mm. long. Ocelli 24 in four rows, plus single ocellus. Pigmentation medium brown, marked darker brown especially on anterior segments; the darkest pigmented *Taiyutyla* species. Legpairs one and two reduced; legpairs three to seven enlarged. Legpairs four to six with
moderate femoral knobs mesial, knobs very strong on femora of legpair seven. Anterior gonopods (fig. 25) strongly curved posteriad, with long apical spine (fig. 24). Posterior gonopod colpocoxites typical of group (fig. 23), very similar to those of *T. variata* from Buckley Park.

**Female.** 11.0 mm. long, antennal segment three 0.57 mm. long. Pigmentation as in male.


Notes: This species has been collected from Berlese samples of pine and oak duff, moss, red alder litter, fungal mycelia, rotted wood, and rotted ponderosa pine bark chips. Consistent with its widespread distribution, there is some variation in the pregonopodal leg modifications. A male from the Benton Co. line has a heavy basal knob on femora seven and very low distal swellings on femora three to six. Males from Clatskanie have a smaller knob on seven but large mesial knobs on five and six; femora three and four are unmodified, and the legs themselves are of nearly normal size. Specimens from Mason Co., Washington, resemble the Clatskanie males closely. The Glenbrook males are like the Benton Co. ones, but the knob of femur seven is truly enormous, whereas knobs are absent from femora three to six.

**Taiyutyla clarki,** new species

**Figures 26-28**

**Types.** Male holotype from 1700 ft. elev., Boulder Flat Campground, 3 mi. E, 10 miles S of Steamboat (T26S/R2E/Sec. 13), Douglas Co., Oregon, collected October 30, 1971, by E. M. Benedict, deposited in AMNH.

**Etymology.** The species epithet honors Capt. William Clark, who, with Meriwether Lewis, led the first American expedition to the mouth of the Columbia River overland from St. Louis, Missouri.

**Diagnosis.** Distinct from the preceding four species in the undivided tip of the posterior gonopod colpocoxites.

**Male.** Length, 9.2 mm. Antennal segment three 0.50 mm. long. Ocelli 19 in three rows, forming triangular eyepatch. Pigmentation pale tan, anterior segments marked slightly darker. Legpairs one and two reduced in size, pairs three to seven enlarged but decreasing in size posteriad, with pair three the largest. Large, mesial hooked knobs on femora three and four; knobs weaker and basal on femora five and six; femora of legpair seven unmodified. Anterior gonopods (figs. 27, 28) with apical spine somewhat broadened, gonopod termination complex. Posterior gonopod colpocoxites (fig. 26) with apex turned laterad at 90 degree angle, but not divided: posterior branch rotated mesiad, divided.

**Female.** Unknown.


Notes: This species has been taken from Berlese samples of moss and of red alder and vine maple duff. Although *T. clarki* is clearly related to the preceding four species, it differs from them in size, and in the undivided apex of the posterior gonopod colpocoxite.

**SUBFAMILY MACROMASTINAE**

**LOOMIS AND SCHMITT; new status**


**Diagnosis.** Thirty-segmented conotylids with undivided mentum. Anterior gonopods with two subequal branches (fig. 29), deeply grooved on anterior face; anterior gonopod sternum extend-
The nonsexual characters of this species are fully described by Loomis and Schmitt (1971), who thought the species distinctive enough to warrant the designation of its own family. However, such a designation is unjustified, in my opinion. The body form is not very divergent from other conotylids, and the general gonopod plan is well within the conotylid range. The anterior gonopods (fig. 29) consist of a single piece, although a posterior view shows some indication of a separate coxal region found in a few other conotylids. The anterior gonopod sternum is not triangular, as stated by Loomis and Schmitt (1971), but is mesially bandlike and laterally extends up the sides of the gonopods (fig. 29, dotted line) as in *Austrotyla*. The colpocoxites of the posterior gonopods are simple and rodlike or spinelike (fig. 32), and are basally sheathed by a process from the sternum (fig. 31). I could not detect the division in the coxal segment as shown by Loomis and Schmitt (1971), although the gonopod was slightly twisted at that point. I examined the gonopod temporarily mounted on a microscope slide in glycerine; perhaps the illustration provided by Loomis and Schmitt was made at low magnification. The holotype had just molted (data from holotype label) and thus

*Macromastus marginandus* Loomis and Schmitt

*Figures 29-32*


Some diagrams are shown of the right posterior gonopod outlook. A right posterior gonopod colpocoxite, posterior view. A right anterior gonopod, lateral view. The apex of a right anterior gonopod, posterior view. These diagrams show the parts of the gonopod from different angles.

various parts of the body might have been liable to distortion upon preservation.

Because the posterior gonopod colpocoxites are the simplest of all known conotylids, and the coxa is apically cylindrical and setose, *Macro-
mastus marginandus* seems to suggest a primitive type. Another character that may also be primitive (that is, more like *Heterochordeuma* species) is the lack of pregonopodal leg modifications of any great nature. Legpairs three to seven are enlarged. Loomis and Schmitt detected no femoral modifications, but I found small, perforate, fungiform knobs on femora five and six (fig. 30).

**SUBFAMILY LOPHOMINAE**

**LOMIS AND SCHMITT**


**Diagnosis.** Thirty-segmented conotylids with undivided mentum. Anterior gonopods with two unequal branches, the inner, anterior branch the smaller; right and left gonopods sometimes fused at base; anterior gonopod sternum extending laterad and ventrad along lateral sides of gonopods. Posterior gonopods with large, posteriorly curved, simple colpocoxite, bearing at base an anteromesial articulated flagellum (figs. 23, 39).

**Included Genus.** *Lophomus.*

**LOPHOMUS LOOMIS AND SCHMITT**


*Troglotyla* Causey 1972, p. 27 (type species *Troglotyla skamania* Causey, by monotypy). New subjective synonymy.

**Synonymy.** This genus may be diagnosed by the same characters as the subfamily. A side-by-side examination of the type species of *Lophomus* and of *Troglotyla* revealed no differences significant enough to warrant recognizing both genera. In particular, the presence of an articulated coxal flagellum on the anteromesial face of the posterior gonopod colpocoxite provides evidence for synonymizing the two names.

*Lophomus laxus* Loomis and Schmitt

Figures 36, 37, 39


The nonsexual characters of this species have been fully described by Loomis and Schmitt (1971). The anterior gonopods of the holotype (fig. 37) consist of two branches, the inner smaller and covered with fine microsetae; the sternum goes up the lateral side of the gonopods as in the austrotylines. The posterior gonopods (figs. 36, 39) have an articulated coxal flagellum. The anterior surface was not depicted by Loomis and Schmitt (1971), but they showed the flagellum (by means of a dotted line, their fig. 25) as not being articulated. An articulated flagellum probably has an entirely different origin than an unarticulated one, the latter simply appearing as a branch of the colpocoxite, as in *Bollmanella* (Shear, 1974), the former a parallel development of the coxal solenite found in most polydesmoid families. The anterior male legs have knobs proximal on femora four and five. Legpair 11 is also strongly modified, with a large process, slightly sinuous, projecting from the prefemur. Similar modifications may be found in a few *Taiyutyla* species. However, the coxae of legpairs 12 and 13 are also ventrally pointed in *L. laxus.*

*Lophomus skamania* (Causey), new combination

Figures 34, 35, 38

*Troglotyla skamania* Causey, 1972, p. 27 (male holotype from Dead Horse Cave, 1 mi. NW of Trout Lake, Skamania Co., Washington, deposited in USNM, examined).

This species differs from *L. laxus* in having the anterior gonopods fused mesially and in the reduction of the anterior branch (fig. 34). The posterior gonopod colpocoxites are not as complex as in *L. laxus* (fig. 33), but bear the same type of articulated flagellum, and the first telopodite segment is much larger than the second, as in *L. laxus.* The femora of legpair four bear small knobs proximally; femora five are unmodified. The coxae of legpair seven (fig. 35)
have mesial hooks which are sharply curved anteriad. Eleventh leg modifications are like those in *L. laxus*, but less extreme.

Although probably a troglobite, this species is not a highly evolved one, as Causey (1972) suggested. It has also been recorded from a cave locality in Klickitat County, Washington.

**SUBFAMILY AUSTROTYLINAE**

new subfamily

**Type Genus.** *Austrotyla* Causey, 1961.

**Diagnosis.** Typical 30-segmented conotylids with undivided mentum. Anterior gonopods much larger than posterior gonopod colpocoxites (except in *Corpus*), flattened, with mesoposterior branch. Posterior gonopod colpocoxites relatively small, simple, cupped anteriad around basal branch of anterior gonopods, or entire gonopod (*Corpus*).

**Included genera.** *Austrotyla*, *Corpus*, *Idagona*, *Achemenides*.

**AUSTROTYLA CAUSEY**

*Austrotyla* Causey, 1961, p. 260 (type species *Conotyla specus* Loomis, by original designation).

*Sonoratyla* Hoffman, 1961, p. 369 (type species *Conotyla montivaga* Loomis, by original designation).

*Corpus montani* Loomis and Schmitt

Figure 40

*Corpus montani* Loomis and Schmitt, 1971, p. 122 fig. 12 (male holotype from Missoula Co., Montana, junction of Clark Fork and Deep Creek, deposited in USNM, examined).

This species is clearly related to, but distinct from, *A. borealis* Shear, from Alberta. The anterior gonopods were not to be found in the holo-

**CORYPS LOOMIS AND SCHMITT**


This genus is distinct from *Austrotyla*, to which it obviously is closely related, in the proportions of the gonopods. In *Corpus* the posterior gonopod colpocoxites are larger than the anterior gonopods, while in *Austrotyla* the reverse is true.

*Corpus cochlearis* Loomis and Schmitt

Figures 41, 42


Because of the proportions of the gonopods, this species could be considered the most primitive of the autrotylines, as it is most like the *Taiyutyla* plan. However, femora three and four are modified in typical autrotyline fashion, and the posterior gonopod colpocoxites (fig. 42) are cupped anteriad, receiving the posterior branch (fig. 41) of the anterior gonopods.

**NOMINA DUBIA AND OBLITA**

The status of the generic name *Cookella* and its type species *C. leibergi* (Cook and Collins) remains unsettled (Shear, 1971). The type was reported to be a female by Cook and Collins (1895), from Lake Pend d’Oreille, Idaho, and was deposited in the USNM, but could not be
located in that collection. According to Cook and Collins (1895), the mentum was divided, and on that statement Chamberlin (1941) erected the generic name *Cookella*, without ever seeing specimens. In 1971, I called the original observation of the mentum “mistaken,” but had no evidence for doing so and withdrew the statement. However, it is unlikely that a species with typical conotylid body form would not have the typical undivided mentum of a conotylid. Until additional specimens from the type locality are available, the status of the name *Cookella leibergi* is in doubt.

*Zygotyla phana* Chamberlin was described from Blue River, British Columbia, on the basis of a single immature male. The type has probably been lost, never having reached the designated depository, the British Columbia Provincial Museum. I am fairly sure it is a junior synonym of *Conotyla atrolineata* (Bollman), since this is the only conotylid to appear in several large collections from British Columbia.

“*Trichopetalum* glomeratum” Harger is probably a species of *Taiyutyla* or *Bollmanella*. The type is no longer in existence (it was from the John Day Valley, Oregon), and the description (Harger, 1872) is too vague to be of any use in placing the species. The name has not appeared in print since 1895, except in lists, and should probably be considered a *nomen oblitum*.

Loomis and Schmitt (1971) described two monotypic new genera, *Endopus* (type species *E. parvipes* Loomis and Schmitt) and *Orthogmus* (type species *O. oculatus* Loomis and Schmitt) in the family Trichopetalidae. However, the type species of both of the genera have undivided menta, which excludes them from the Trichopetalidae. I examined the holotypes of the two type species (USNM), and though they represent two different species, they are certainly not trichopetalids but immature male conotylids, lacking one molt of maturity (both holotypes have 28 body segments). It will probably prove impossible to synonymize these names properly, except by an arbitrary assignment, unless mature material can be gathered from the type localities. On the basis of the descriptions and distribution data given by Loomis and Schmitt (1971), I suggest that *E. parvipes* is a junior synonym of *Conotyla albertaina* Chamberlin, which Loomis and Schmitt redescribed in the same paper (from adults) as *Brunsonia complexipes*.

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