



## The millipede family Striariidae Bollman, 1893. VI. Six new genera and thirteen new species from western North America (Diplopoda, Chordeumatida, Striarioidea)

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### Abstract

The following new genera and species of Striariidae are described from the states of California, Oregon and Washington: *Nototrisaria ornata* n. gen., n. sp., *Maraplia napa* n. gen., n. sp., *Maraplia chico* n. gen., n. sp., *Maraplia schusteri* n. gen., n. sp., *Lamparia curryensis* n. gen., n. sp., *Lamparia bentonensis* n. gen., n. sp., *Lamparia pratensis* n. gen., n. sp., *Lamparia millicoma* n. gen., n. sp., *Rampalia cheathamensis* n. gen., n. sp., *Plaramia arcata* n. gen., n. sp., *Plaramia johnsonae* n. gen., n. sp., *Ralampia complexa* n. gen., n. sp., and *Ralampia filamentosa* n. gen., n. sp.. The new species are all very small millipedes, 5.5 mm or less in length and with two or three ommatidia on each side of the head or blind. The majority have the sixth metazonal crest larger than the other crests and extended horizontally, so that the animals have the general appearance of having paranota. A new key to striariid genera is presented.

**Key words:** millipedes, California, Oregon, Washington

### Introduction

The North American endemic millipede family Striariidae has been the subject of five previous papers in this series (Shear 2020, 2021a, 2021b; Shear & Marek 2022; Shear *et al.* 2022). The Pacific Northwest of the continent, from San Francisco Bay in the south to Vancouver Island (Canada) in the north, has proven to be the center of diversity for the family, with an unexpected richness of new taxa (the genus *Amplaria* Chamberlin, 1941, also ranges south to Mt. Palomar in southern California). Although individuals in species of *Striaria* Bollman, 1888 and *Amplaria*, the only genera described prior to 2020 presently believed valid, can be considered as relatively medium-sized chordeumatidans at 12–25 mm in length (the largest chordeumatidans are only 30–35 mm long), much of the diversity now being described among striariids consists of quite small species, ranging from 3–5 mm long, and are some of the smallest known millipedes. Despite their small size, these species exhibit some of the same panoply of family characters and male secondary sexual modifications as their larger cousins. Further, they also display somatic characters that provoke interest, especially in the metazonal crests so characteristic of the family. In the genera *Stegostriaria* Shear & Marek, 2022 and *Kentrostriaria* Shear & Marek, 2022, the second crests on each side of the median sulcus are 4–6 times as high as the other crests. In *Nototrisaria ornata*, n. gen., n. sp., both the second and sixth crests are exaggerated (Figs 1–4), and in many of the other new species described here, the sixth crests expand laterally, giving the impression of moderate or pronounced paranota (*i.e.*, Figs 1, 17–20, 26, 27 etc.)—such that in the field they could be mistaken for small polydesmidans. Yet others have all crests approximately subequal. As we add more taxa to Striariidae, we will update our previously published keys; a new key to genera is presented below, and keys are provided for each of the multispecies genera described herein.

## Methods

Specimens were field-preserved in various solutions and later transferred to 70% ethanol. Morphological studies were done using an Olympus SZH stereomicroscope and an Olympus BX50 compound microscope equipped with Nomarski optics. Gonopods were temporarily mounted on microscope slides in glycerine for study up to 400X magnification and drawings were made from these slides using a drawing tube on the BX50. For scanning electron microscopy (SEM), specimens were first cleaned in an ultrasonic jewelry cleaner, then mounted on 12.7 mm diameter aluminum stubs using double-sided adhesive carbon discs and allowed to air-dry. These were sputter coated with a 40 nm thick layer of platinum and palladium, using a Leica EM ACE600 high vacuum sputter coater. SEM micrographs were taken with a FEI Quanta 600 FEG environmental scanning electron microscope. Photographs were edited and refined using GIMP, and plates were composed in InkScape. Age and poor preservation of some of the specimens made dissection and cleaning difficult, hence some SEM preparations were less suitable than others.

All of these species are very small, 5.5 mm long or less. Therefore in the generic diagnoses, the new genera are characterized in comparison only with similarly small species. *Amplaria* and *Striaria* species are 12–25 mm long, while *Stegostriaria* and *Kentrostriaria* species are 5–10 mm long.

We state explicitly that our species hypothesis is morphological. More broadly, we reason from the Biological Species Concept, which states that species are reproductively isolated populations. This concept predicts that species populations should not only be different, but also distinct; that is, there should be unbridged gaps in phenotypic characters between them. If these gaps are obvious (morphological) and consistent, this is evidence of species status. We also hold that a comparative diagnosis of a taxon is a testable hypothesis, subject to evaluation by other lines of evidence such as genetic sequencing, which we hope will be possible in the near future.

Type specimens are deposited as indicated with the species descriptions.

### Abbreviations of depositories:

CAS, California Academy of Sciences, San Francisco, California;

FMNH, Field Museum of Natural History, Chicago, Illinois;

FSCA, Florida State Collection of Arthropods, Gainesville, Florida.

The localities in the Materials Examined sections were transcribed from labels *ad verbatim* except the latitude and longitude, which in some cases were estimated from Google Earth and converted where applicable to decimal degrees for consistency. The precision of the coordinates is therefore according to the collector who recorded the coordinates or described the locality and may not be reflective of the actual value of a GPS instrument.

### Abbreviations used in the figures

<b>aac</b>	anterior angiocoxite
<b>c (numeral)</b>	numbered metazonite crests
<b>cc</b>	colpocoxite
<b>col</b>	collum
<b>cp</b>	coxal process
<b>cf</b>	coxal flask of legpair 3
<b>cx</b>	coxa of gonopods
<b>cx (numeral)</b>	coxa of numbered legpair
<b>cxp</b>	coxal process
<b>cxs</b>	coxosternum of legpair 9
<b>fc</b>	flagellocoxite
<b>L (numeral)</b>	numbered legpair
<b>lab</b>	labrum
<b>m</b>	mandibular stipes
<b>numerals</b>	ring numbers
<b>om</b>	ommatidium

<b>pac</b>	posterior angiocoxite
<b>pf (numeral)</b>	prefemur of numbered legpair
<b>pt7</b>	pleurotergite of ring 7
<b>s</b>	sternum of gonopods
<b>s (numeral)</b>	sternum of numbered legpair
<b>t (numeral)</b>	telopodite of numbered legpair
<b>tel</b>	telson
<b>To</b>	Tömösväry organ
<b>tp9</b>	process of telopodite 9
<b>vcp</b>	common pore of vasa deferential
<b>vd</b>	openings of vasa deferentia

## Taxonomy

### Family Striariidae Bollman, 1893

#### Key to genera of Striariidae

Names in bold italics are of genera described in this paper.

- 1a. Ninth legs of males with telopodites, coxae and sternum fused or free; gonopod flagellocoxites absent . . . . . Subfamily Trisariinae, 2.
- 1b. Ninth legs of males with all elements, or at least telopodites free; gonopod flagellocoxites present . . . . . Subfamily Striariinae, 4.
- 2a. Some crests of metazonites much larger than the others . . . . . 3.
- 2b. All metazonital crests similar in size . . . . . *Trisaria*.
- 3a. Sixth and second crests larger than others . . . . . *Nototrisaria n. gen.*
- 3b. Sixth crests not enlarged. . . . . *Stegostriaria*.
- 4a. On some rings, second and third crests of metazonites larger than others. . . . . *Kentrostriaria*.
- 4b. All crests subequal, or only sixth crests enlarged. . . . . 5.
- 5a. 10–25 mm long. . . . . 6.
- 5b. 5 mm long, or smaller. . . . . 7.
- 6a. Gonopod anterior angiocoxites with a distal crown of stout spines. . . . . *Striaria*.
- 6b. Gonopod anterior angiocoxites without such a crown of spines . . . . . *Amplaria*.
- 7a. Sixth crests of metazonites enlarged, paranota-like . . . . . 8.
- 7b. All metazonital crests similar in size . . . . . 10.
- 8a. Three ommatidia on each side of head . . . . . *Rampalia n. gen.*
- 8b. Two ommatidia on each side of head . . . . . 9.
- 9a. Gonopod anterior angiocoxites densely fimbriate on posterior surface. . . . . *Lamparia n. gen.*
- 9b. Gonopod anterior angiocoxites sigmoid. . . . . *Plaramia n. gen.*
- 10a. Gonopod anterior angiocoxites reflexed dorsally. . . . . *Maraplia n. gen.*
- 10b. Gonopod anterior angiocoxites not reflexed, gonopods compact . . . . . *Ralampia n. gen.*

### Subfamily Trisariinae Shear, 2020

**Note:** The diagnosis of this subfamily, it now appears, was too narrowly based on the type genus, *Trisaria* Shear, 2020. However, we do believe that the genera grouped in it represent a monophyletic taxon. Presently we rely on gonopod and ninth leg characters for a diagnosis (see key above) but when more genera and species of Striariidae available have been studied and described, we expect to compose a more detailed diagnosis. The new genus *Ralampia* is particularly difficult to place; the two species may or may not have a flagellocoxite and though there is a branch of the gonopod that resembles one, it is not sheathed. *Ralampia filamentosa n. gen., n. sp.*, has a lateral filamentous branch that appears similar to those seen in *Trisaria*. The ninth leg telopodites appear to be free. For the time being, however, we include this genus in Striariinae.

## Genus *Nototrisaria* Shear & Marek, new genus

**Type species:** *Nototrisaria ornata* Shear & Marek, new species

**Etymology:** The name of the genus combines *noto-* in reference to the enlarged, paranotum-like sixth crests (C6), and *Trisaria*, the name of a related genus in the subfamily. The name should be treated as feminine in gender.

**Diagnosis:** A genus of Trisariinae composed of a single small species, distinct from other small striariids in the highly ornate crests of the metazonites, with C1 on anterior rings consisting of anterior and posterior knobs but disappearing on posterior rings, C2 strongly exaggerated, and C6 expanded into paranota (see Figs 3, 4).

**Description:** As for the single species described below.

**Distribution:** Widely distributed in Washington State west of the Cascade Ranges, including Pacific, Jefferson, Whakiakum and Grays Harbor Counties.

**Note:** The genus has similarities to the previously described *Stegostriaria* Shear & Marek, 2022 in that C2 is elevated and larger than all the other crests. However, *Nototrisaria ornata* **n. gen., n. sp.**, also has C6 broadly extended, forming paranota, C1 is suppressed and missing posterior of the midbody rings, and there are no intercalary crests. The gonopods of *Nototrisaria* **n. gen.** are very different from those of *Stegostriaria dulcidormus* Shear & Marek, 2022, and the complicated, highly modified ninth legs of that species are unique and unlike the simpler ninth legs of *Nototrisaria ornata* **n. gen., n. sp.** *Stegostriaria dulcidormus* is known only from Linn and Tillamook Counties in Oregon, well to the south, although the intervening forests are not well-sampled.

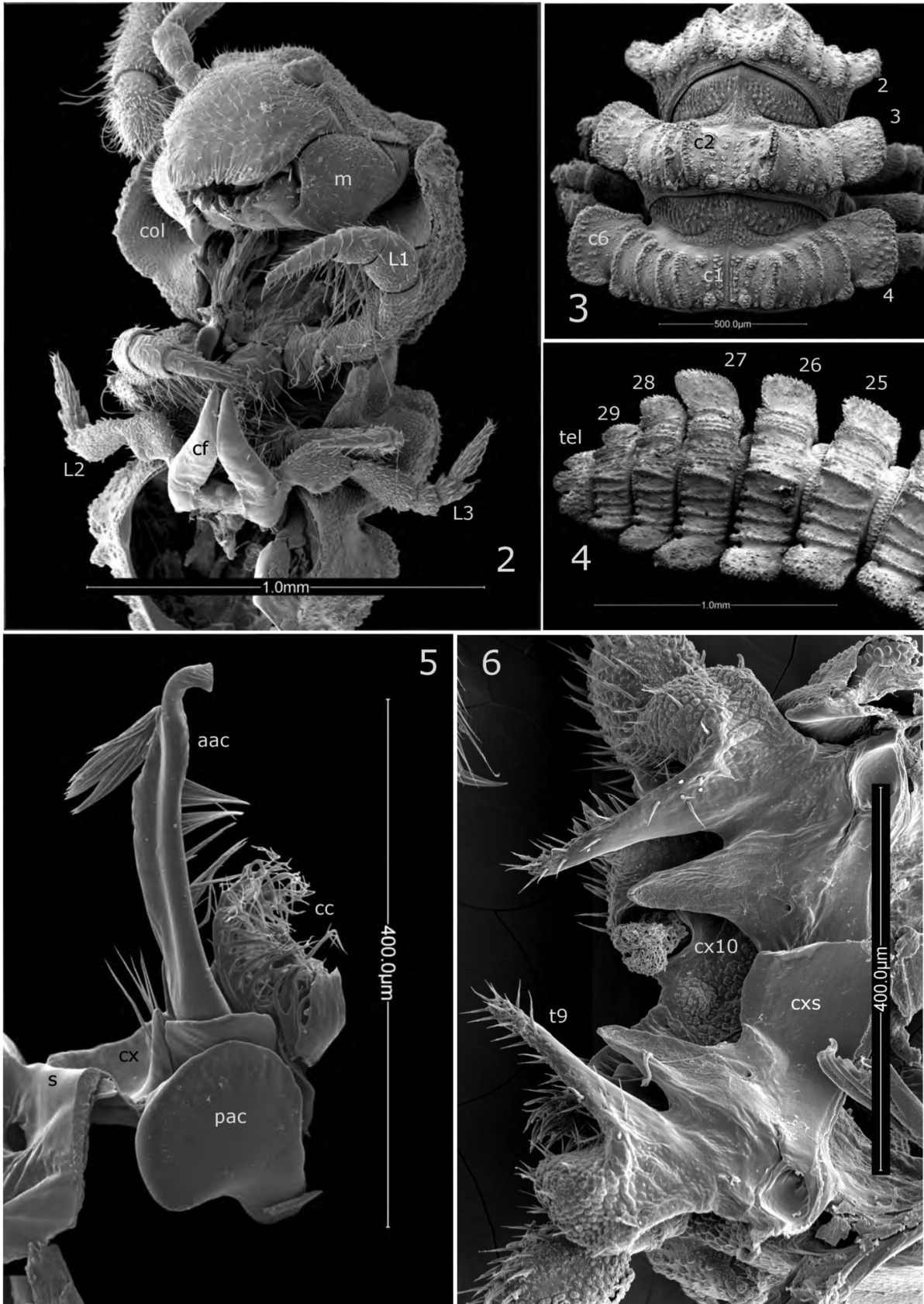
Despite the differences in the gonopods and ninth legs from species of *Trisaria*, the absence of a gonopod flagellocoxite and the fusion of all elements of the ninth legs, as well as an apparent comblike branch evidently fused to the anterior angiocoxite and a strongly fimbriate colpocoxite indicate that this genus and species are best placed in the subfamily Trisariinae.

### *Nototrisaria ornata* Shear & Marek, **n. sp.**

Figs 1–6, 49–51



**FIGURE 1.** *Nototrisaria ornata*, **n. gen., n. sp.**, live female in habitat. About 5.0 mm long. Photo by Bill Leonard.



**FIGURES 2–6.** *Nototrisaria ornata*, n. gen., n. sp. **2.** Anterior end of male, ventral view. **3.** Rings 2–4 of male, dorsal view. **4.** Posterior end of male, oblique view. **5.** Right gonopod, lateral view. **6.** Legpair 9 of male, anterior view. Abbreviations: **aac**, anterior angiocoxite; **col**, collum; **cc**, colpodoxite; **c1**, crest 1; **c6**, crest 6; **cxs**, coxosternite; **cx10**, coxa of leg 10; **L1**, leg 1; **L2**, leg 2; **L3**, leg 3; **m**, mandible; **numerals**, ring numbers; **pac**, posterior angiocoxite; **t9**, telopodite of leg 9.

**Types:** Male holotype and male paratype from 9.6 miles up Elochoman Valley Road from Rt. 4, Wahakiakum Co., Washington, 46.289633°N, -123.26485°W, 450' asl, collected 28 March 2004 by C. Richart, W. Leonard; male paratype from 11.7 mi up Elochoman Valley Road from Rt. 4, 450' asl, 46.316783°N, -123.2617°W, 28 March 2004, collected by C. Richart; male and female paratypes from Trap Creek, 1.1 mi S of SR6, Pacific Co. Washington, 46.5468°N, -123.6161°W, 180' asl, collected 11 January 2003 and 3 May 2003 by W. Leonard. Parts of a male paratype are mounted on SEM stub WS3-8. Types deposited in the CAS.

**Etymology:** The species name, a Latin adjective, refers to the ornate dorsum.

**Diagnosis:** As for the genus; see above.

**Description:** *Male paratype from Elochoman River Road.* Length, 5.5 mm, width 0.6 mm (includes paranota). Thirty postcephalic rings including telson.

Head (Fig. 2) densely setose, with sculpture of tiny, acute tubercles; labral corners rounded, without projecting hook. Ommatidia absent. Antennae short, robust. Mandibular stipes (Fig. 2, m) with sawtooth distal edge, acute apical projection. Color of live specimen white to pale yellow (Fig. 1).

Collum (Fig. 2, col) broadly expanded, with 10 subequal crests limited to posterior two-thirds; anterior third with pebbled sculpture. Anterior rings (Fig. 3) with C2 and C6 exaggerated, the latter expanded into prominent paranota with deep posterior notch; C1 reduced to a few knobs, absent on more posterior rings, C2 also progressively lower on midbody ring, exaggerated again on most posterior 6–8 rings (Fig. 4). Metazonal setae not observed, probably absent. Limbus serrate.

Telson without crests, lobes deeply incised (Fig. 4).

First legpair crassate (Fig. 2, L1), larger than legpairs 2 and 3 (Fig. 2, L2, L3), postfemora and tibia set with long, stiff setae, tarsus with comb. Legpair 2 relatively small, similar to postgonopodal legs. Legpair 3 with prominent, broad, slightly sigmoidal coxal flasks bearing curled setae on anterior surface (Fig. 2, cf); prefemora expanded, flattened. Legpairs 4–6 strongly crassate. Legpair 7 similar to pairs 4–6, but with large, flattened coxal plates covering bases of gonopods.

Gonopods in mesal view (Figs 5, 50) with anterior angiocoxites erect, narrow, hooked and expanded at tip; posterior edge with continuous fimbriate lamina, lamina ends in long distal projection; tuft of strong, thin cuticular projections subapically (aac, Figs 5, 49, 50). Posterior angiocoxites as broad, rounded plate (pac, Figs 5, 50). Flagellocoxites absent. Colpocoxite (cc, Figs 5, 49, 50) developed as compact mass of finely divided, sinuous fimbriae with small posterior portion unmodified, sclerotized.

Ninth legpair (Figs 6, 51) strongly reduced, sternum (s9), coxae (cx) and telopodites (t9) fused; coxal part with blunt triangular process (cp), telopodite part with long, finger-like basal process bearing acute setae.

Tenth leg with enlarged, glandular coxae (Fig 6, cx10).

*Female paratype* similar to male in nonsexual characters, but exaggerated crests significantly lower. A living female specimen is depicted in Fig. 1.

**Distribution:** As for the genus. The Grays Harbor County record (WASHINGTON: Grays Harbor Co.: Canyon River, 47.303517°N, -121.508167°W, 1500' asl, 12 December 2004, W. P. Leonard) is based on a female that strongly resembles the females from other localities.

## Subfamily Striariinae Bollman, 1893

The genera and species described below in this subfamily have a number of characters in common: two or three ommatidia on each side of the head, rounded corners of the labra of males without labral hooks, much enlarged male first legs with needle setae, and mesal indentations in the male second coxae, creating what appears as a common pore for the vas deferens of each side.

## Genus *Maraplia* Shear & Mark, new genus

**Type species:** *Maraplia napa* Shear & Marek, new species

**Etymology:** The genus name is an arbitrary combination of letters, an anagram of the related genus name *Amplaria* forming a Latin neologism to be treated as feminine in gender.

**Diagnosis:** A genus of the subfamily Striariinae by virtue of having gonopods with a flagellocoxite and ninth legs with free telopodites. The gonopod flagellocoxite, while sheathed in a process from the posterior angiocoxite, is unusually short and stout, unlike other members of this subfamily. The anterior angiocoxites are erect (extending posteriorly) in other genera of striariines, but in species of *Maraplia* n. gen., they are reflexed anteriorly and dorsally. The gonopod coxae have prominent distal processes. The ninth legs are unique in that the telopodites have a long, mesodistal apophysis that is tipped with ensiform setae.

**Description:** Small striariines, 4.5 mm or less in length. Twenty-eight (Fig. 7) or 30 postcephalic rings, including telson. Two ommatidia on each side of head. Head (Figs 8, 12) densely setose, with small tubercles. Labral hook lacking (Fig. 12, lab). Mandibular stipes (Fig. 12, m) with serrate margin, blunt triangular process. Collum with crests limited to posterior region, anterior region separated from posterior with distinct sulcus so that anterior region appears somewhat like a hat brim, studded with small tubercles. Metazonal crests (Figs 7, 15) subequal, C6 sometimes a little larger; metazonal setae long, acute. Telson (Fig. 15, tel) with lobes very shallowly demarcated, sulci shallow. Legpair 1 larger than legpairs 2 or 3, femora (Fig. 12, fl) and tibiae with long, needle-like setae, tarsus with comb. Legpair 2 with short telopodites, vas deferens openings in coxae facing mesally, coxae notched so that when appressed, a single pore is formed (Fig. 11, vcp). Legpair 3 with relatively short or long flasks (Fig. 13, cf), heavily set with raised cuticular scales. Legpairs 4–7 crassate, legpair 7 with small coxal lobes.

Gonopods (Figs 10, 14, 52, 53, 55, 56, 58, 59) small; gonopod sternum massive, quadrate (Fig. 14, s). Coxa setose, with obvious distolateral process of varying form. Anterior angiocoxites short or long, deflexed anteriodorsally. Posterior angiocoxites with posterior process forming partial sheath for flagellocoxites. Flagellocoxites short, robust, curved near tip. Colpocoxites variable, but evidently moved anteriomesally, fimbriate or botrydial anteriorly.

Ninth legs (Figs 10, 14, 54, 57, 60) with coxosternite and free telopodites. Coxosternite with one or two processes on each side, probably one from sternal portion, one from coxal part. Telopodite small (Figs 10, 14, 60, t9), with pebbled sculpture and setae; long apophysis extends mesally, with dense group of ensiform setae. Telopodite locks into deep notch in ventrolateral margin of pleurotergite 7 (Fig. 14, t9, pt7).

Tenth leg with coxal pores, coxae enlarged.

**Included species:** In addition to the type, *Maraplia schusteri* Shear & Marek, n. sp., and *M. chico* Shear & Marek, n. sp.

**Distribution:** Northern California, including the counties of Napa, Lake, and Butte.

**Note:** The gonopods of these species are difficult to interpret in terms of the usual scheme adopted for other striariid genera and the various divisions may not be homologous to those with the same name in those previously described. In fact it may be that the subfamily distinctions are breaking down somewhat, but with numbers of new taxa yet to be described, we are holding onto the two subfamilies until a more complete picture of striariid diversity is achieved.

### Key to species of *Maraplia* based on males

- 1a. Gonopod coxal process broad, plate-like, not divided, flagellocoxite distinctly hooked, Anterior part of posterior angiocoxite botrydial . . . . . *M. napa*, n. sp.
- 1b. Not as above . . . . . 2.
- 2a. Gonopod anterior angiocoxite long, evenly curved . . . . . *M. schusteri*, n. sp.
- 2b. Gonopod anterior angiocoxite short, sharply reflexed . . . . . *M. chico*, n. sp.

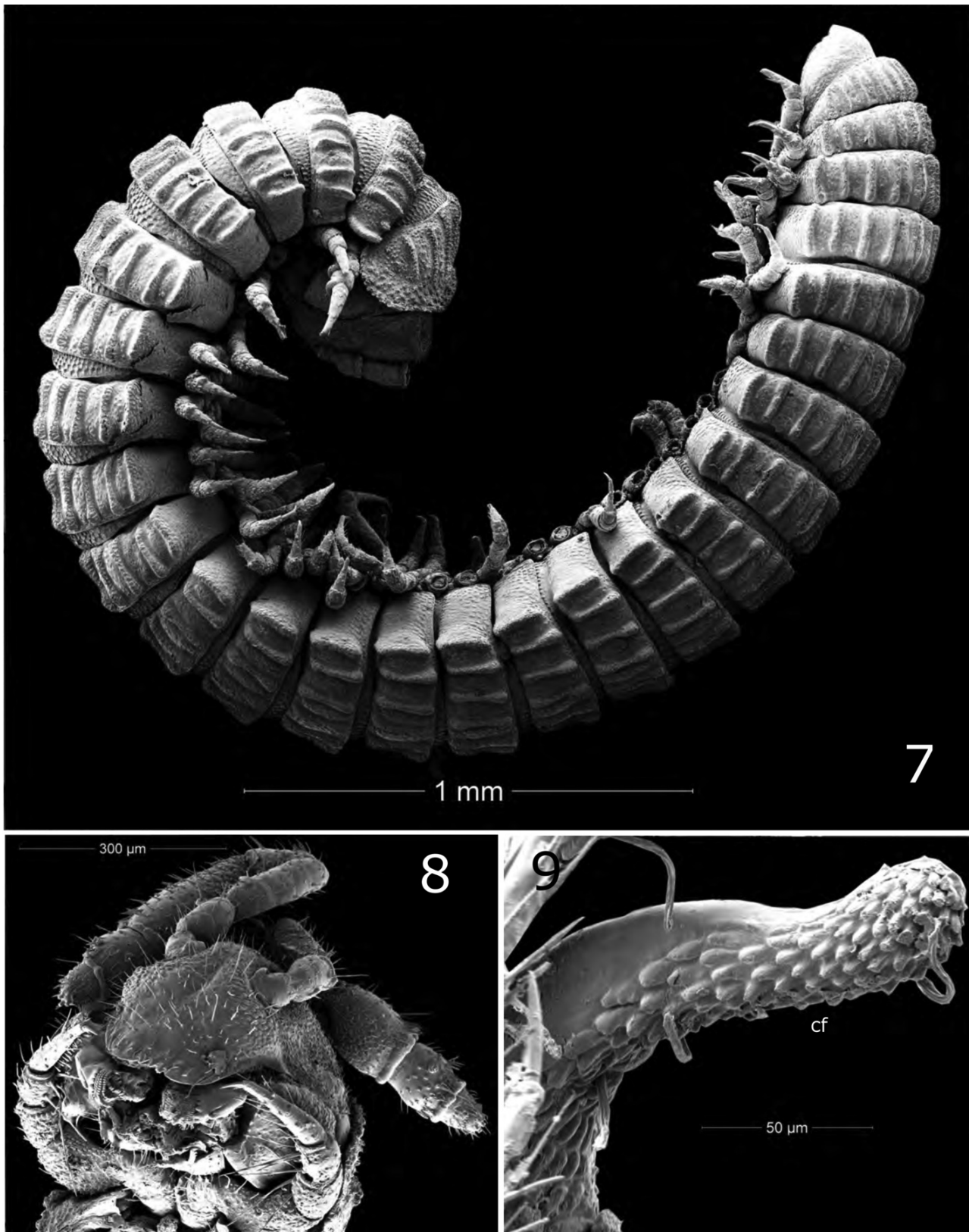
### *Maraplia napa* Shear & Marek, n. sp.

Figs 7–9, 52–54

**Types:** Male holotype and 3 female paratypes from 1 mi SW of Oakville, Berlese of laurel litter (sample 79–17), Napa Co., California, 38.4245°N, -122.4123°W, 235' asl, collected 29 April 1979 by D. S. Chandler; male paratype from the same locality, but Berlese of general forest litter (sample 79–18); two male and one female paratypes from 9 mi S of Middletown, Berlese of litter along a stream (sample 79–8), Lake Co., California, 38.6426°N, -122.5295°W, 1720' asl, 29 April 1979, D. S. Chandler. The Lake County male and female paratypes are mounted on SEM stub WS35-6. All specimens deposited in FMNH.

**Etymology:** The species name is a noun in apposition referring to the type locality in Napa County.

**Diagnosis:** Distinct from the two other species of the genus in the form of the gonopods; most easily seen is the broad, platelike coxal process and the relatively long, hooked flagellocoxite, as well as the curious botrydial branch of the posterior angiocoxite.



**FIGURES 7–9.** *Maraplia napa*, n. gen., n. sp. 7. Female, lateral view. 8. Head and first legpair of male, ventral view. 9. Coxal flask of leg 3 of male, lateral view. Abbreviation: cf, coxal flask of leg 3.



**Description:** *Male paratype*. Length, about 4.5 mm, width 0.4 mm. Twenty-eight postcephalic rings including telson. Two black ommatidia on each side of head. Color white. Other characters as described for the genus. Third coxae flasks (Fig. 9, cf) short, reaching only to fourth coxae when reflexed posteriorly.

Gonopods (Figs 52, 53) small, compact. In lateral view, coxa with about 10 setae, coxal process (Fig. 53, cp) broad, flattened, distally recurved. Anterior angiocoxite sharply deflexed, unbranched (Figs 52, 53, aac). Posterior angiocoxite in mesal view with two branches, one of which sheaths a thick, blunt, hooked flagellocoxite, anterior branch developed as curious botrydial structure of numerous rounded lobes on short stalks. Colpocoxite (Figs 52, 53, cc) shifted anteriomesally, posterior part swollen, finely tuberculate-fimbriate.

Ninth legs (Fig. 54) with single, apically bifurcate process from coxosternum (Fig. 54, cp), telopodite fungiform, bearing mesal process (Fig. 54, t9) set with as many as 10–12 ensiform setae (these setae may or may not spring from sockets).

Tenth leg coxae slightly enlarged, with glandular openings.

*Female paratype* similar to male in nonsexual characters but some females may have 30 rings. A 28-ring female is depicted in Fig. 7.

**Distribution:** Presently known only from Napa and Lake Counties, California, but probably more widely distributed in the region, given the distance between these localities.

**Note:** The function of the botrydial part of the posterior angiocoxite defies speculation. At first it appeared as if this might be part of a spermatophore, but after ultrasonic cleaning, which would dislodge or disintegrate a spermatophore, the structure, found on all the males, remained unchanged.

### ***Maraplia schusteri* Shear & Marek, n. sp.**

Figs 10, 11, 55–57

**Types:** Male holotype and two male paratypes from near Stringtown Hill, NE of Oroville, Butte Co., California, 39.5219°N, -121.3909°W, 1440' asl, collected 9 February 1956 by R. O. Schuster. Types deposited in FSCA. Parts of holotype and one paratype on SEM stub WS35-4.

**Etymology:** The species is named for entomologist Robert O. Schuster (1927–1989).

**Diagnosis:** Distinct from the two other species of *Maraplia* n. gen. in the form of the gonopods. *Maraplia schusteri* n. sp., has long, thin, and evenly curved angiocoxites, rather than the sharply deflexed, relatively short anterior angiocoxites seen in the other species (Figs 10, 55, 56, aac). The coxal process is not flattened and platelike but narrower and distinctly bifid (Fig. 55, cp).

**Description:** *Male holotype*. Length 3.5 mm, width about 0.32 mm. Two black ommatidia on each side of head. Color white. Sixth crests about twice height of C5, as short paranota. Telson lobes obscure. Other characters as for genus.

Gonopods (Figs 10, 55, 56) small, compact. In lateral view, coxa (Fig. 55, cx) with about 6 or 7 setae, coxal process narrow, distally bifid, anterior branch longer, posterior branch slightly recurved (Fig. 55, cp). Anterior angiocoxite (Figs 10, 55, 56, aac) narrow, long, evenly curved, apically acute, with smaller basal triangular tooth. Posterior angiocoxite strongly reduced to single blunt rod, apparently not sheathing the very short, straight flagellocoxite. Colpocoxite (Figs 55, 56, cc) shifted anteriomesally, with anterior branch densely fimbriate, posterior part swollen, with a few small, fine triangular fimbriae. Ninth legs (Fig. 57) with mesal coxosternal process low, triangular (Fig. 57, cp), telopodite fungiform (Figs 10, 57, t9), bearing mesal process set with 6 or 7 ensiform setae and second curved, roughly triangular posterior process. Tenth leg coxae slightly enlarged, with glandular openings.

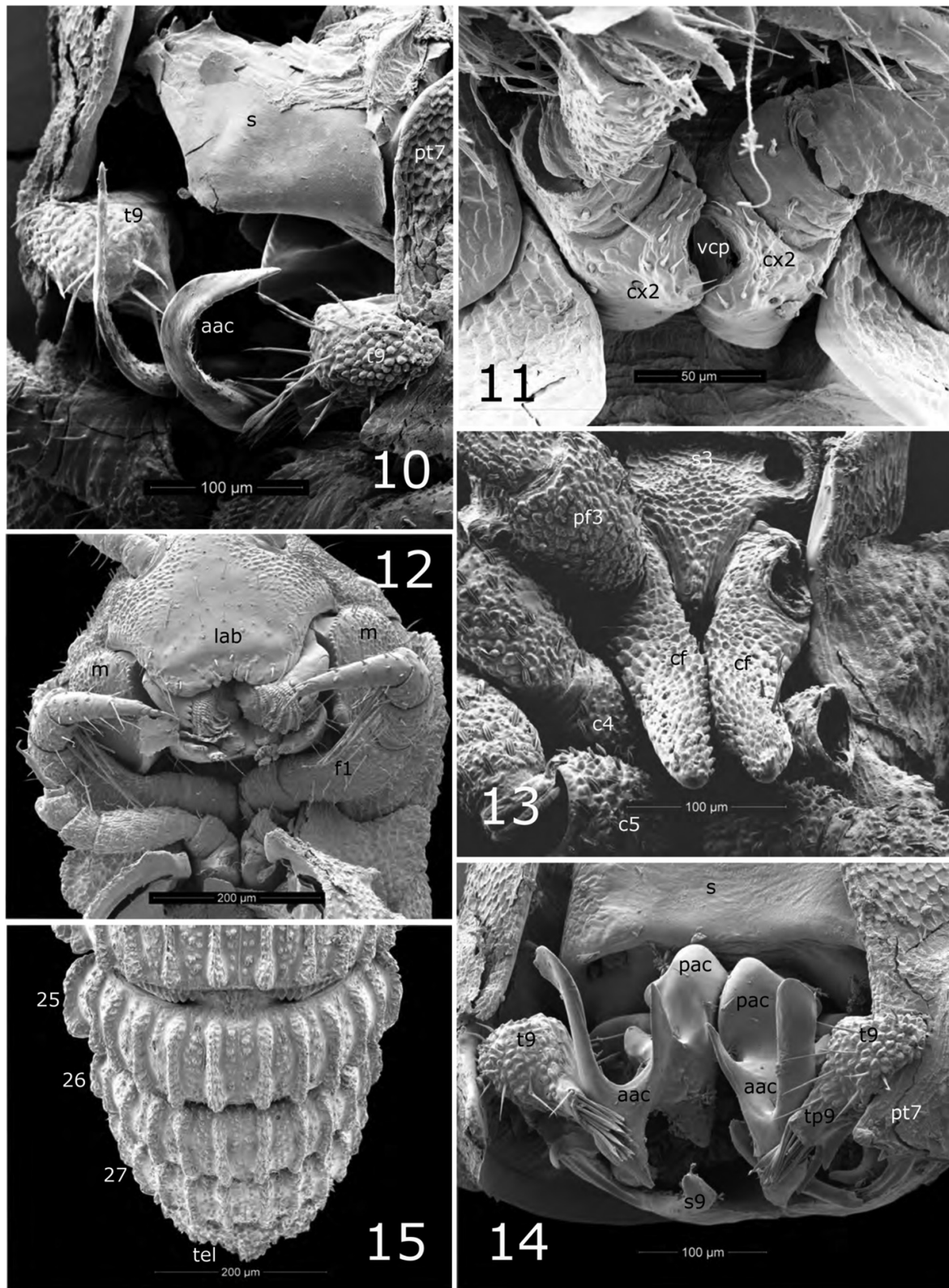
Females not collected.

**Distribution:** Presently known only from Butte County, California.

### ***Maraplia chico*, Shear & Marek, n. sp.**

Figs 12–15, 58–60

**Types:** Male holotype from West Branch of Feather River, Butte Co., California, 39.8290°N, 121.7734°W, 1600' asl, sifting oak and grape litter (sample #81-291), collected 13 April 1981 by D. S. Chandler; Male paratype (SEM stub WS35-7)



**FIGURES 10–15.** Striariid millipedes. **Figs 10, 11.** *Maraplia schusteri*, n. gen., n. sp. **10.** Gonopods, legpair 9 and paratergite 7, oblique lateral view. **11.** Coxae of legpair 2, ventral view. **Figs 12–15.** *Maraplia chico*, n. gen., n. sp. **12.** Head and first two legpairs, ventral view. **13.** Coxal flasks of legpair 3, ventral view. **14.** Gonopods, ventral view. **15.** Posterior end of male, dorsal view. Abbreviations: **aac**, anterior angiocoxite; **c4**, coxa of leg 4; **c5**, coxa of leg 5; **cf**, coxal flask of leg 3; **cx2**, coxa of leg 2; **f1**, femur of leg 1; **lab**, labrum; **m**, mandible; **numerals**, ring numbers; **pac**, posterior angiocoxite; **pf**, prefemur of leg 3; **pt7**, paratergite of ring 7; **s**, gonopod sternum; **t9**, telopodite of ninth leg; **tp9**, telopodite process; **vcp**, common opening of vas deferens.

from same locality, but collected sifting laurel litter; two male paratypes from 4 mi SE of Chico, Butte Co., California, sifting elderberry and oak litter (sample 79-12), 39.6877°N, -121.7734°W, 200' asl, collected 24 February 1979 by D. S. Chandler. All specimens deposited in FMNH.

**Etymology:** The species epithet is a noun in apposition, after one of the paratype localities near the town of Chico, California.

**Diagnosis:** Differs from *M. napa n. sp.*, in having males with 30 rings and from *M. schusteri, n. sp.*, in the much shorter, sharply deflexed anterior angiocoxites of the gonopods (Figs 58, 59, aac).

**Description:** *Male paratype.* Length, about 3.5 mm, width 0.35 mm. Thirty postcephalic rings including telson. Two black ommatidia on each side of head. Color white. Telson lobes obscure (Fig. 15, tel). Other characters as described for the genus. Third coxae flasks (Fig. 13, cf) short, reaching only to fourth coxae when reflexed posteriorly.

Gonopods (Figs 14, 58, 59) small, compact. In lateral view, coxa (Fig. 58, cx) with about 6 or 7 setae. Coxal process broad, with deep, semicircular apical notch separating a curved, narrow anterior part from more broad, less curved posterior part. Anterior angiocoxite sharply deflexed (Figs 14, 58, 59, aac), with two branches. Posterior angiocoxite in lateral view (Fig. 58, pac) with two branches, one of which sheaths a thick, blunt, short, gently curved flagellocoxite (Fig 58, fc). Colpocoxite (Figs 58, 59, cc) shifted anteriomesally, with anterior branch densely fimbriate, posterior part swollen, with a few small, fine triangular fimbriae. Ninth legs (Fig. 60) with lateral coxosternal processes (Fig. 60, cp) broad at bases, with two branches, mesal branch hamate, lateral branch slightly curved, acute; sternal part with median knob, telopodite fungiform (Figs 14, 60, t9), bearing mesal process set with 6 or 7 ensiform setae (these setae appear socketed in SEM view).

Tenth leg coxae slightly enlarged, with glandular openings.

Females not collected.

**Distribution:** Presently known only from Butte County, California.

## Genus *Lamparia* Shear & Marek, new genus

**Type species:** *Lamparia bentonensis* Shear & Marek, new species

**Etymology:** The genus name is an arbitrary combination of letters, an anagram of the related genus name *Amplaria* forming a Latin neologism to be treated as feminine in gender.

**Diagnosis:** A genus of the subfamily Striariinae by virtue of having gonopods with a flagellocoxite and ninth legs with free telopodites. The gonopod flagellocoxite is small and thin. The anterior angiocoxites are erect (extending posteriorly) as in most other genera of striariines, and a key feature is the many fine cuticular processes extending from their posterior surfaces. The ninth legs are distinctive for each of the three included species.

**Description:** Small striariines, 3.5–5.2 mm long. Thirty postcephalic rings, including telson. Two ommatidia (Fig. 16, om). Head densely setose, with small tubercles. Labral hook lacking. Mandibular stipes with serrate margin, acute triangular process (Fig. 16, m). Collum with crests limited to posterior region, studded with small tubercles. C1–C5 subequal, C6 larger, giving appearance of small or broad paranota; metazonal setae not observed, either absent or strongly reduced and concealed by cerotegument. Telson with lobes very shallowly demarcated or nearly indiscernable, sulci shallow. Legpair 1 larger than legpairs 2 or 3, femora and tibiae with long, needle-like setae, tarsus with comb. Legpair 2 with short telopodites, vas deferens openings in coxae facing mesally, coxae notched so that when appressed, a single pore is formed. Legpair 3 with long flasks, reaching sixth or seventh coxae when extended posteriorly, heavily set with raised cuticular scales, few contorted setae. Legpairs 4–7 crassate, legpair 7 lacking coxal lobes.

Gonopods small; gonopod sternum massive, quadrate. Coxa sparsely setose, with obvious distolateral process of varying form. Anterior angiocoxites long, not deflexed, hooked or knobbed distally, posterior surface set with fine fimbriae. Posterior angiocoxites with small posterior process forming partial sheath for flagellocoxites, larger and various anterior processes. Flagellocoxites small, thin, slightly curved. Colpocoxites variable, poorly sclerotized, saclike, set with many triangular fimbriae.

Ninth legs with coxosternite and free telopodites. Coxosternite with two processes from coxal part, sternal part sometimes expanded, with central knob. Telopodite large, with pebbled sculpture and setae, with deep notch (sometimes toothed) to accommodate gonopods. Telopodite locks into deep notch in ventrolateral margin of pleurotergite 7.

Tenth legs with coxal pores, coxae slightly enlarged.

**Included species:** In addition to the type, *Lamparia curryensis* Shear & Marek, **n. sp.**, *L. pratensis* Shear & Marek, **n. sp.** *L. millicoma* Shear & Marek, **n. sp.**

**Distribution:** Southwestern Oregon, including the counties of Douglas, Coos and Benton, and Del Norte County, California.

### Key to species of *Lamparia* based on males

- 1a. Anterior angiocoxites of gonopods with distinct terminal knob; coxosternal process of ninth legs flattened, plate-like . . . . .2.
- 1b. Anterior angiocoxites of gonopods not knobbed, blunt, slightly curved distally; coxosternal processes of ninth leg otherwise . . . . .3.
- 2a. Coxosternal processes of ninth legs long, apically expanded (Fig. 51) . . . . . *L. curryensis*.
- 2b. Coxosternal processes of ninth legs short, not apically expanded (Fig. 65) . . . . . *L. bentonensis*.
- 3a. Coxosternal processes of ninth legs subtriangular . . . . . *L. pratensis*.
- 3b. Coxosternal processes of ninth legs long, hooked; sternal portion expanded . . . . . *L. millicoma*.

### *Lamparia curryensis* Shear & Marek, **n. sp.**

Figs 16–19, 49–51

**Types:** Male holotype from NE of Brookings Curry Co., Oregon, north bend of Chetco River Road, 0.6 mi NW of entrance to Alfred A. Loeb State Park, Redwood Nature Trail, 135' asl, 42.1187°N, -124.1959°W, collected 4 January 2011 by C. Richart *et al*; male and female paratypes from 13 mi W, 5 mi N of Brookings, T39S, R14W, S5 (42.1239°N, -124.0141°W), 2000' asl, collected 12 February 1972 by E. M. Benedict. All material deposited in CAS; male holotype is on SEM stub WS35-13.

**Etymology:** The species epithet refers to Curry County, Oregon, which includes both known collection localities for this species.

**Diagnosis:** Obviously close to *L. bentonensis*, **n. sp.**, but distinct in details of the gonopods (compare Figs 61, 62 with Figs 63, 64) and in the much longer coxosternal process of the ninth legs (Fig. 19, cp). The sixth crests of this species are nearly twice as high as those of *L. bentonensis* **n. sp.** (compare Figs 17, 18 with Figs 20, 21).

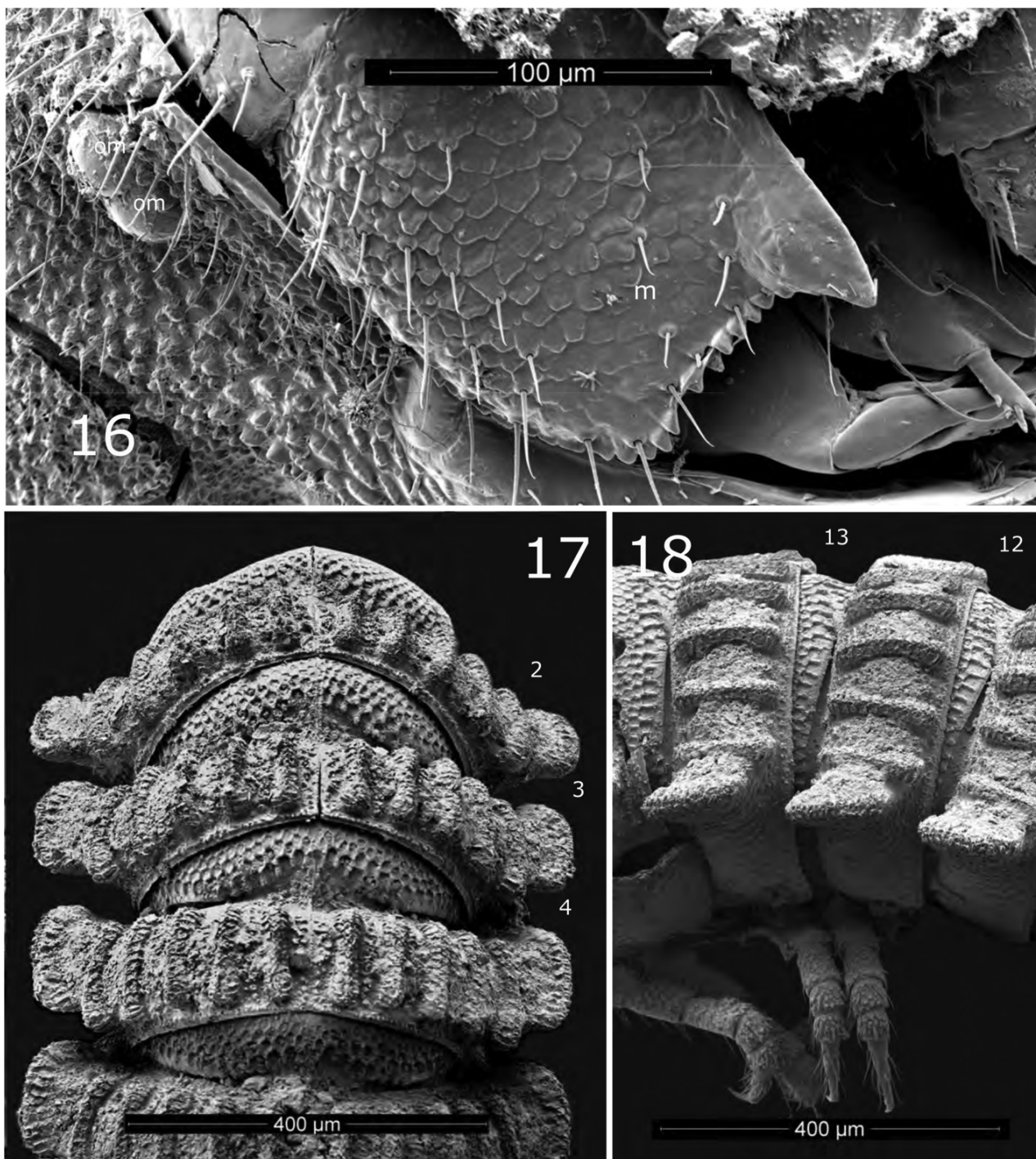
**Description:** *Male holotype.* Length, 4.8 mm, width 0.48 mm. Two black ommatidia on each side of head (Fig. 16, om). Sixth crests well extended as broad paranota (Figs 17, 18). Telson lobes nearly completely suppressed. Metazonital setae not seen, absent or concealed by heavy cerotegument. Color white to pale tan, faintly suffused pale purplish brown. Flasks of third coxae long, when extended posteriorly reaching to anterior margin of seventh coxae. Other characters as described for genus.

Gonopods (Figs 19, 61, 62) moderately large. Coxae with 3 setae, bulbous (Fig. 61, cx). Anterior angiocoxites narrow, erect, with flattened, bulbous tip, posterior surface finely fimbriate from base to just below bulbous tip (Figs 19, 61, 62, aac). Posterior angiocoxite complex (Fig. 62, pac) with two branches. Flagellocoxite possibly not sheathed. Two flagellocoxites, each narrow, slightly curved, comparatively short (Figs 61, 62, fc). Colpocoxite large and bulbous, shifted anteriomesally, densely set with triangular, fine cuticular teeth (Fig. 62, cc). Ninth legs with coxosternum. Coxosternal processes (Fig. 19, cp) flattened, elongate, distally slightly expanded. Telopodites (Fig. 19, tp) free, apically flattened, mesally curved anteriorly, with sawtooth edges, interlocking with gonopods, laterally fitting into shallow indentations in ventrolateral edges of seventh ring. Tenth coxae not much swollen, gland openings anteriodorsal.

*Female paratypes* similar to males in nonsexual characters.

**Distribution:** Presently known from two nearby localities in Curry Co., Oregon.

**Note:** Additional collecting is required to establish the distribution of this species and the following one. They are evidently closely related and may in fact be variants of a single species.



FIGURES 16–18. *Lamparia curryensis*, n. gen., n. sp. 16. Mandibular stipes and ommatidia of male, lateral view. 17. Rings 2–4 of male, dorsal view. 18. Rings 12 and 13 of male, lateral view. Abbreviations: **om**, ommatidium; **m**, mandible; **numerals**, ring numbers.

***Lamparia bentonensis* Shear & Marek, n. sp.**

Figs 20–25, 63–65

**Types:** Male holotype and male and female paratypes from Clemens Park, Seely Creek Road, 0.3 mi from SR34, north fork of Alsea River, Benton Co., Oregon, 400' asl, 44.4092°N, -123.5678°W, collected 4 December 2005 by W. Leonard and C. Richart. Male and female paratypes from localities along Wells Creek Road, Benton Co., Oregon as follows: at SR34, 44.4707°N, -123.4797°W, collected 29 November 2004 by W. Leonard; 0.6 mi W of SR34,

44.4722°N, -123.4794°W, collected 25 February 2005 by W. Leonard, C. Richart; 0.7 mi from SR34, 6.3 mi from SR20, 44.4686°N, -123.4941°W, 1100' asl, collected 9 December 2005 by W. Leonard, C. Richart.

**Etymology:** The species epithet refers to Benton County, Oregon, which includes all known collection localities for this species.

**Diagnosis:** Very similar to *L. curryensis*, **n. sp.**, but distinct in details of the gonopods (compare Figs 63, 64 with Figs 61, 62) and in the shorter coxosternal processes of the ninth legs (Fig. 64, cp). The sixth crests of this species (Fig. 21) are only about half the height of those of *L. curryensis* **n. sp.**.

**Description:** *Male paratype from Clemens Park.* Length, 5.1 mm, width 0.6 mm. Two ommatidia on each side of head. Sixth crests well extended as small paranota (Figs 20, 21). Telson lobes nearly completely suppressed (Fig 22, tel). Color white, suffused light purplish brown. Second coxae with common opening for vas deferens (Fig. 23). Flasks of third coxae long, when extended posteriorly reaching to anterior margin of seventh coxae (Fig. 25, cf). Other characters as described for genus.

Gonopods (Figs 24, 63, 64) moderately large. Coxae with 5–6 setae, elongate. Anterior angiocoxites (Figs 24, 63, 63, aac) narrow, erect, with flattened, bulbous tip, posterior surface finely fimbriate from base to just below bulbous tip. Posterior angiocoxite complex (Figs 63, 64, pac) with three branches, one of which sheaths flagellocoxite. Flagellocoxite (possibly 2 of these) narrow, slightly curved, comparatively short (Fig. 63, fc). Colpocoxite (Fig. 64, cc) small, densely set with triangular, fine cuticular teeth. Ninth legs (Fig. 65) with coxosternum. Coxosternal processes (Figs 24, 65, cp) flattened, drawn out laterally to points. Telopodites (Figs 24, 65, t9) free, apically flattened, mesally curved anteriorly, with sawtooth edges, interlocking with gonopods, laterally fitting into deep indentations in ventrolateral edges of seventh ring (Fig. 24). Tenth coxae not much swollen, gland openings anteriodorsal.

*Female paratypes* similar to males in nonsexual characters.

**Distribution:** Presently limited to Benton Co., Oregon.

**Note:** Initially we thought this species and the preceding were the same, but careful examination of the gonopods at 400X under the compound microscope and a study of SEM photographs of the ninth legs showed that they are clearly distinct.

### ***Lamparia pratensis* Shear & Marek, n. sp.**

Figs 26–29, 66–68

**Types:** Male holotype from Grassy Flat Campground, Rt. 199, 5 mi by road E of Gasquet, Del Norte Co., California, 41.8564°N, -123.8890°W, 700' asl, collected 25 March 1976 by A. K. Johnson. The specimen is mounted on SEM stub WS35-10, deposited in FMNH.

**Etymology:** The species epithet is a Latin adjective, meaning “of the meadow,” and refers to Grassy Flats, the type locality.

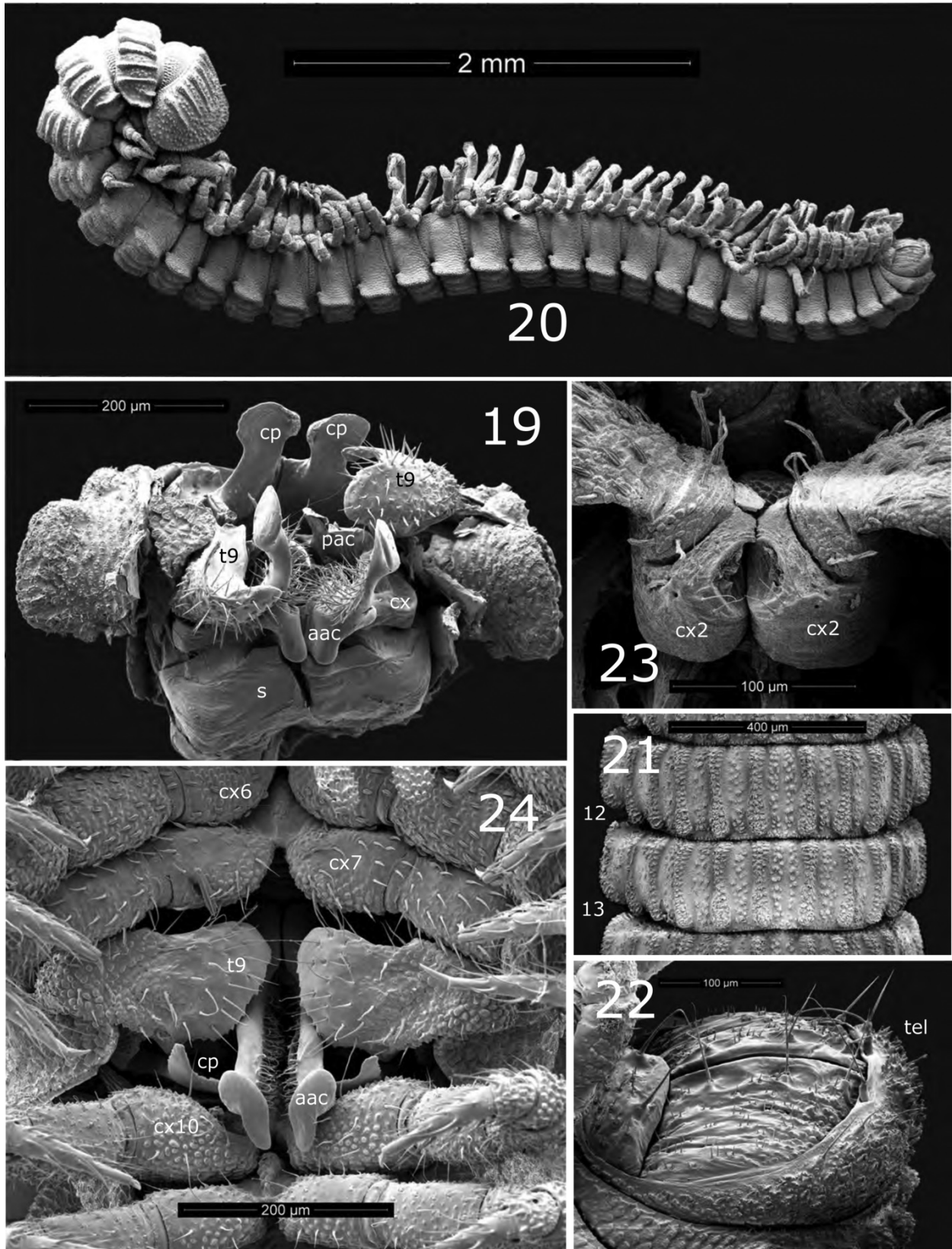
**Diagnosis:** Very similar to the *L. millicoma* **n. sp.**, but distinct in the form of the ninth legs, which lack the expanded coxosternum, the median coxosternal knob, and the curved coxosternal process. Instead, there is a smaller triangular coxosternal process (compare Figs 68 and 71).

**Description:** *Male holotype.* Length, 5.0 mm, width 0.45 mm. Two black ommatidia on each side of head. Sixth crests well extended as broad paranota (Figs 26, 27). Telson lobes nearly completely suppressed (Fig. 29, tel). Metazonital setae not seen, absent or concealed by heavy cerotegument. Color after long preservation medium brown. Flasks of third coxae short, when extended posteriorly reaching only to anterior margin of fifth coxae. Other characters as described for genus.

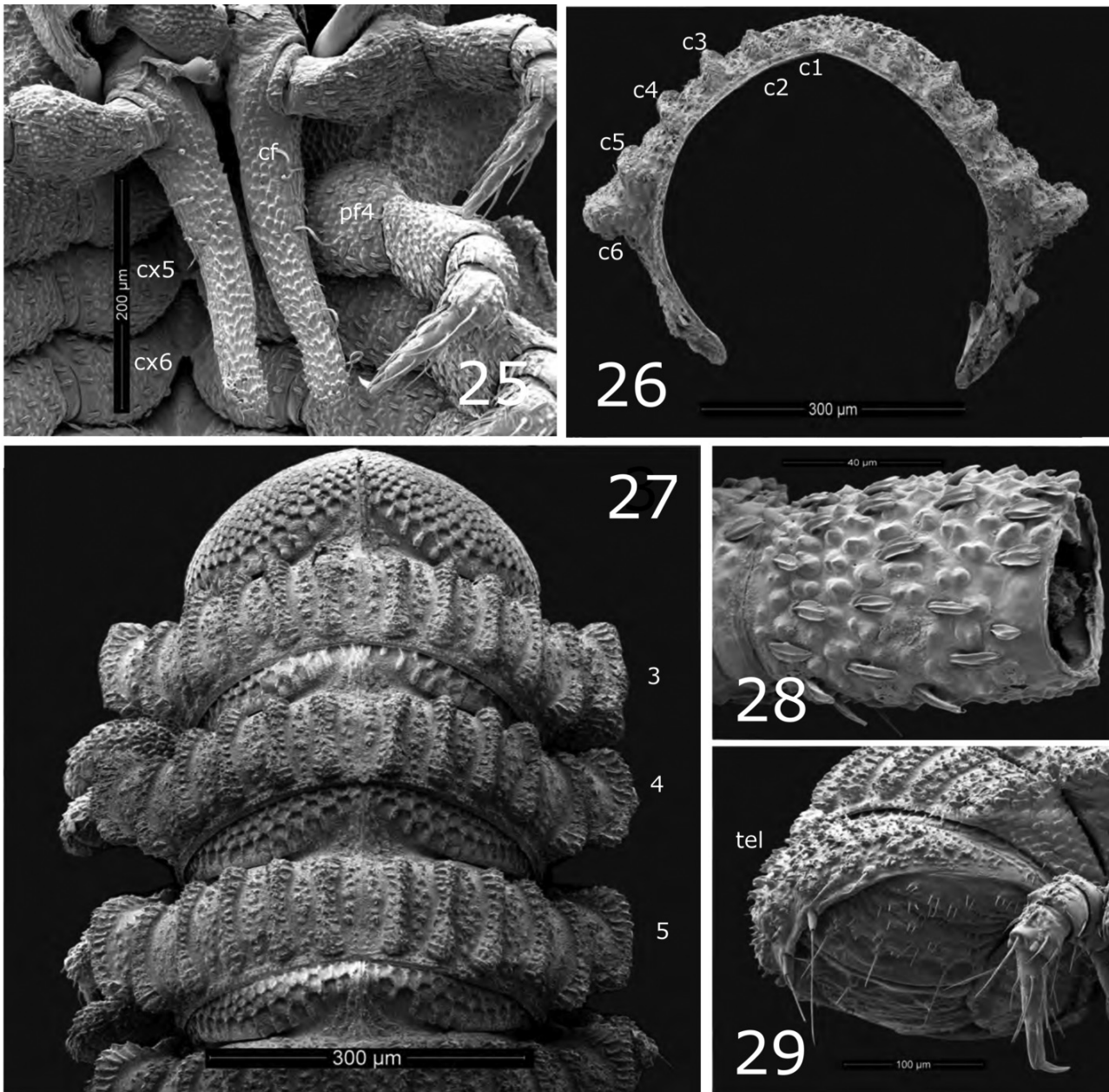
Gonopods (Figs 66, 67) moderately large. Coxae with 3 setae, bulbous, with acute angle distally (Fig. 66, cx). Anterior angiocoxites narrow, erect, with slightly expanded, curved tip, posterior and anterior surface finely fimbriate from base to about half length of coxite (Figs 66, 67, aac). Posterior angiocoxite much reduced; flagellocoxite not sheathed. Flagellocoxite (Figs 66, 67, fc) single, thin, short. Colpocoxite bulbous, shifted anteriomesally, set with a few triangular, fine cuticular teeth (Fig. 67, cc). Ninth legs (Fig. 68) with coxosternum. Coxosternal processes flattened, long, bluntly triangular (Fig. 68, cp), arising near midline. Telopodites (Fig. 68, cp) free, rounded, with projecting posterior lobe. Tenth coxae not much swollen, gland openings anteriodorsal.

Females not collected.

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



**FIGURES 19–24.** Striariid millipedes. **19.** Gonopod, ninth legs, and ring 7 of *Lamparia curryensis*, n. gen., n. sp., anteroventral view. **Figs 20–24.** *Lamparia bentonensis*, n. gen., n. sp. **20.** Female, lateral view. **21.** Rings 12 and 13 of male, dorsal view. **22.** Telson, paraproct and epiproct, ventral view. **23.** Coxae of legpair 2, ventral view. **24.** Legpairs 6–10 and gonopods, ventral view. Abbreviations: **aac**, anterior angiocoxites; **cp**, coxal process; **cx2**, coxa of leg 2; **cx6**, coxa of leg 6; **cx7**, coxa of leg 7; **cx10**, coxa of leg 10; **pac**, posterior angiocoxite; **tel**, telson; **t9**, telopodite of leg 9.



**FIGURES 25–29.** Striariid millipedes. **25.** Coxae of legpairs 3–6 of male *Lamparia bentonensis*, **n. gen., n. sp.**, ventral view. **Figs 26–29.** *Lamparia pratensis*, **n. gen., n. sp.** **26.** Ring 14 of male, posterior view. **27.** Rings 3–5 of male, dorsal view. **28.** Prefemur of leg 3 of male, lateral view. **29.** Telson and paraprocts of male, lateral view. Abbreviations: **cf**, cosal flask of leg 3; **cx5**, coxa of leg 5; **cx6**, coxa of leg 6; **c1–6**, crests 1 to 6, respectively, **numerals**, ring numbers; **pf4**, prefemur of leg 4; **tel**, telson.

***Lamparia millicoma* Shear & Marek, n. sp.**

Figs 30–32, 69–71

**Types:** Male holotype and female paratype from 11 mi E, 4 mi N of Allegany Douglas Co., Oregon, Berlese of myrtle and rhododendron litter, Weyerhauser Millicoma Tree Farm, company road 5000, T24S, R9W, S18 (43.4862°N, -123.8177°W) 1055' asl, collected 20 November 1971 by E. M. Benedict. Male and female paratypes from 8 mi E, 2 mi S of Allegany, Coos Co., Oregon, Berlese of *Pseudotsuga* bark on clear-cut slope, Weyerhauser Millicoma Tree Farm, company road 5000, T25S, R10W (43.3936°N, -123.8705°W), 1450' asl, S15, collected 20 November 1971 by E. M. Benedict; 11 mi E, 4 mi S of Allegany, Douglas Co., Oregon, Berlese of hemlock duff and moss,



Weyerhaeuser Millicoma Tree Farm, company road 6040, T25S, R9W, S31 (43.3740°N, -123.8106°W), 850' asl, collected 21 November 1971 by E. M. Benedict. All material deposited in CAS.

**Etymology:** The species epithet is a noun in apposition, referring to the Weyerhaeuser Millicoma Tree Farm.

**Diagnosis:** Distinct from *L. curryensis*, **n. sp.** and *L. bentonensis*, **n. sp.** in not having a knob at the tip of the gonopod anterior angiocoxite and in the reduced posterior angiocoxite (Figs 69, 70). From the related *Lamparia pratensis* **n. sp.**, separable by the form of the ninth legs of males of that species, which have a median sternal knob and a long, curved coxosternal process that parallels the elongate telopodite (compare Figs 68 and 71).

**Description:** *Male holotype.* Length, 4.7 mm, width 0.48 mm. Two black ommatidia on each side of head. Sixth crests well extended as broad paranota (Figs 26, 27). Telson lobes nearly completely suppressed. Metazonal setae not seen, absent or concealed by heavy cerotegument. Color white to pale tan, faintly suffused pale purplish brown. Flasks of third coxae short, when extended posteriorly reaching only to anterior margin of fifth coxae (Fig. 30, cf). Other characters as described for genus.

Gonopods (Figs 39, 69, 70) moderately large. Coxae (Fig. 69) with 3 setae, bulbous. Anterior angiocoxites (Figs 31, 69, 70, aac) narrow, erect, with slightly expanded, curved tip, posterior surface finely fimbriate from base to about half length of coxite. Posterior angiocoxite (Fig. 31, pac) much reduced; flagellocoxite not sheathed. Flagellocoxite single, thin, short (Figs 31, 69, fc). Colpocoxite large and bulbous, shifted anteriomesally, set with a few triangular, fine cuticular teeth (Figs 69, 70, cc). Ninth legs with coxosternum (Fig. 71). Telopodites (Fig. 71, t9) free, apically flattened, mesally curved anteriorly, interlocking with gonopods, laterally fitting into deep indentations in ventrolateral edges of seventh ring. Telopodite processes (Fig. 71, tp9) flattened, long, sharply curved, mesally elongate, tips crossing in midline. Tenth coxae not much swollen, gland openings anteriodorsal.

*Female paratypes* similar to males in nonsexual characters.

**Distribution:** Found in the vicinity of Allegany, Oregon. The small village of Allegany is in Coos Co., but near the border with Douglas Co.

**Note:** This species is very similar to *L. pratensis* **n. sp.**, but has very different male ninth legs. The more basal segments of the legs bear the modified setae characteristic of striariids (Fig. 28). The female genitalia are complex (Fig. 32) but their taxonomic value has not been assessed. It would appear that they are not exactly symmetrical when left and right are compared.

## ***Rampalia* Shear & Marek, new genus**

**Type species:** *Rampalia cheathamensis* Shear & Marek, **n. sp.**

**Etymology:** The genus name is an arbitrary combination of letters, an anagram of the related genus name *Amplaria* forming a Latin neologism to be treated as feminine in gender.

**Diagnosis:** A genus of the subfamily Striariinae by virtue of having gonopods with a flagellocoxite and ninth legs with free telopodites. The gonopod flagellocoxite is inconspicuous. The anterior angiocoxites are erect and fused, a character unique in the family, while the posterior angiocoxites appear to be reduced to just a sheath for the single, small flagellocoxite. The ninth legs are distinctive in the bifurcate coxosternal process and the rather small, elongate telopodites bearing a subterminal lobe.

**Description:** See the description of the single known species, below.

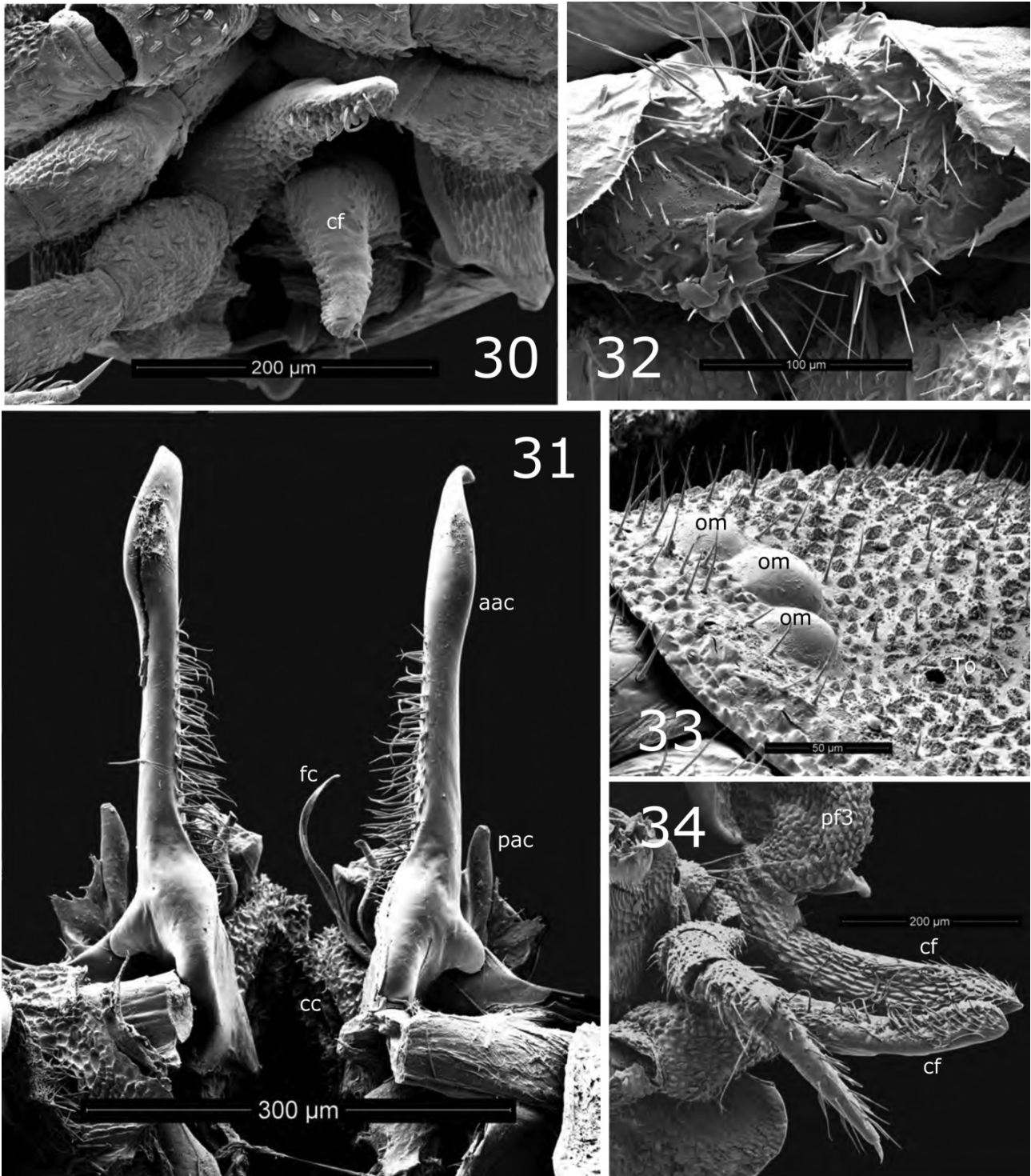
**Included species:** Only the type species.

**Distribution:** Humboldt County, California.

## ***Rampalia cheathamensis* Shear & Marek, **n. sp.****

Figs 33–36, 72–75

**Types:** Male holotype and paratype from Owen R. Cheatham Redwood Grove, along Rt. 36 and Van Duzen River, 40.4829°N, -123.9630°W, 270' asl, Humboldt Co., California, collected 18 December 1977 by A. K. Johnson. Parts of male paratype on SEM stub WS35-5. Deposited in FSCA. Male paratype from Along Rt. 101, 1.5 mi by road south of Scotia, 40.4626°N, -124.0871°W, 120' asl, Humboldt Co., California, collected 3 January 1977 by A. K. Johnson, deposited in FSCA.



**FIGURES 30–34.** Striariid millipedes. **Figs 30–32.** *Lamparia millicoma*, n. gen., n. sp. **30.** Coxal flasks of legpair 3 of male, ventral view. **31.** Gonopods, anterior view. **32.** Female genitalia, ventral view **Figs 33, 34.** *Rampalia cheathamensis*, n. gen., n. sp. **33.** Ommatidia and Tömösváry organ of male, lateral view. **34.** Legpair 3 of male, lateral view. Abbreviations: **aac**, anterior antiocoxite; **cc**, colpocoxite; **cf**, coxal flasks of leg 3; **fc**, flagellocoxite; **om**, ommatidium; **pac**, posterior angiocoxite; **pf3**, prefemur of leg 3; **To**, Tömösváry organ.

**Etymology:** The name is derived from the type locality.

**Diagnosis:** As for the genus, see above.

**Description:** *Male holotype.* 30 rings. Length, 5.0 mm, width 0.45 mm. Three black ommatidia on each side of head (Fig. 33, om). Sixth crests well extended as broad paranota. Telson lobes clearly divided. Metazonital setae not

seen, absent or concealed by heavy cerotegument. Color after long preservation pale whitish tan with slight purplish brown markings on crests. First legs enlarged, with needle-like setae. Second legpair smaller, when coxae apposite, appearing to have common seminal opening. Flasks of third coxae long (Fig. 34, cf), when extended posteriorly reaching to posterior margin of sixth coxae; telopodites with broad, flattened prefemora (Fig. 34, pf3). Fourth through sixth legs encrassate, podomeres flattened, with prominent characteristic modified setae. Seventh coxae with large, flattened lobes covering bases of gonopods (Fig. 35, cx7). Other characters as described for genus.

Gonopods (Figs 36, 72, 73) moderately large. Sternum massive, short (Fig. 36, s). Coxae (Figs 72, 72, cx) with 3–4 setae on mesal side, 2 setae laterally, extended into long, twisted and apically flattened processes bearing short, recurved subterminal branch (Figs 72, 73, cp). Anterior angiocoxites projecting anteriorly between coxae, fused in midline, simple (Figs 36, 72, 73, aac). Posterior angiocoxites reduced to sheath for single flagellocoxite (Fig. 72, fc) Colpocoxites (Fig. 73, cc) pushed anteriorly, with many small finger-like extensions. Ninth legs with median, apically bifurcate coxosternal process (Figs 74, 75, csp); telopodites free, small, narrow, with subapical lobe densely setose in posterior view, fitting into locking notch in pleurotergite 7 (Fig. 36, pt7). Tenth coxae not much swollen, gland openings anteriodorsal.

Females not collected.

**Distribution:** Known only from two localities in Humboldt Co., California.

**Note:** The gonopods of this species presented difficulties in interpretation and we cannot be entirely sure that the homologies we have suggested are correct. Alternatively, the fused median structure we have called the anterior angiocoxites could be a process from the sternum, but Fig. 36 shows them quite separate from the sternum and basically as a double structure. The coxal processes in this interpretation might be the anterior angiocoxites, but they are continuous with the coxae and the coxal setae are set more distally than we have seen in other striariids. The collection of additional material and further study with SEM should resolve the question. The unique ninth legs seem to set this species well apart from the others described here.

## ***Plaramia* Shear & Marek, new genus**

**Type species:** *Plaramia arcata* Shear & Marek, n. sp.

**Etymology:** The genus name is an arbitrary combination of letters, an anagram of the related genus name *Amplaria* forming a Latin neologism to be treated as feminine in gender.

**Diagnosis:** The flagellocoxites are long, thin and largely concealed in this genus and the ninth leg telopodites are free. Thus we place the genus in Striariinae. Three of the striariine genera described in this paper have their metazonal crests all roughly subequal and not paranota-like. The two species of *Plaramia*, n. gen., differ from those of *Maraplia*, n. gen., in that the gonopod anterior angiocoxites are erect and sinuously curved, rather than reflexed anteriorly and either short or if long, curved in an arc. In *Ralampia*, n. gen., the gonopods are quite compact, and the colpocoxites have long, erect, branched, stiff fimbriae distally.

**Description:** Small striariines, about 3–4 mm long (Fig. 46). Thirty postcephalic rings, including telson. Two ommatidia on each side of head (Fig. 45, om). Head (Fig. 37) densely setose, with small tubercles. Labral hook lacking. Mandibular stipes with serrate margin, acute triangular process. Collum with crests limited to posterior region, studded with small tubercles. Metazonal crests 1–5 subequal (Fig. 41), crest 6 slightly elevated as paranota (though variably so; Fig. 46); metazonal setae long, with brush-like tips. Telson with lobes very shallowly demarcated or nearly indiscernible, sulci shallow. Legpair 1 (Fig. 37, L1) larger than legpairs 2 or 3, femora and tibiae with long, needle-like setae, tarsus with comb. Legpair 2 with short telopodites, vas deferens openings in coxae facing mesally, coxae notched so that when appressed, a single pore is formed. Legpair 3 with relatively short flasks (Figs 38, 48, cf), reaching fifth coxae when extended posteriorly, heavily set with raised cuticular scales, few contorted setae. Legpairs 4–7 crassate, legpair 7 lacking coxal lobes.

Gonopod sternum large, broader than long (Fig 43, s). Coxa with 4–6 setae, coxal process absent. Anterior angiocoxites long, not deflexed, sinuously curved or with hooked termination (Figs 42, 43, 72, 73). Posterior angiocoxites small, inconspicuous, forming short sheath for flagellocoxites. Flagellocoxites single, long, thin, concealed by angiocoxites. Colpocoxites large, sac-like, seemingly well sclerotized, with fine longitudinal ridges but lacking fimbriae. Ninth legs (Figs 44, 78) with coxosternite and free telopodites. Coxosternite with two processes

from coxal part, sternal part sometimes expanded, with central knob. Telopodite large, variable, with pebbled sculpture and setae, with deep notch to accommodate gonopods. Telopodite locks into deep notch in ventrolateral margin of pleurotergite 7.

Tenth legs with coxal pores, coxae slightly enlarged.

**Distribution:** Humboldt Co., California.

### Key to species of *Plaramia*, based on males

- 1a. Gonopod anterior angiocoxite slightly curved; 9th leg telopodite not excavate . . . . . *P. arcata*, n. sp.
- 1b. Gonopod anterior angiocoxite strongly sigmoidially curved, tip as a definite hook, 9<sup>th</sup> leg telopodite strongly excavate with a deep notch mesally . . . . . *P. johnsonae*, n. sp.

### *Plaramia arcata* Shear & Marek, n. sp.

Figs 37–40, 76–78

**Types:** Male holotype, 2 male paratypes and female paratype from the north side of Jolly Giant Canyon, Arcata Community Forest, 40.8759°N, -124.0681°W, 400–600' asl, collected 21 February 1978 by A. K. Johnson; two male paratypes from Arcata Community Forest, 40.8699°N, -124.0725°W, collected 31 March 2011 by C. Richart *et al.*; two male paratypes (parts of these are on SEM stub WS35-3) from along Jacoby Road and Kilpatrick Quarry Road, 100–200' asl, T5N, R1E, Sec 14 (40.8279°N, -124.0390°W) collected 24 November 1977 by A. K. Johnson; six male and two female paratypes from behind Humboldt State University campus, Arcata Community Forest, 40.8748°N, -124.0506°W, 200–700' asl, collected 1 April 1979 by A. K. Johnson. All material deposited in FSCA.

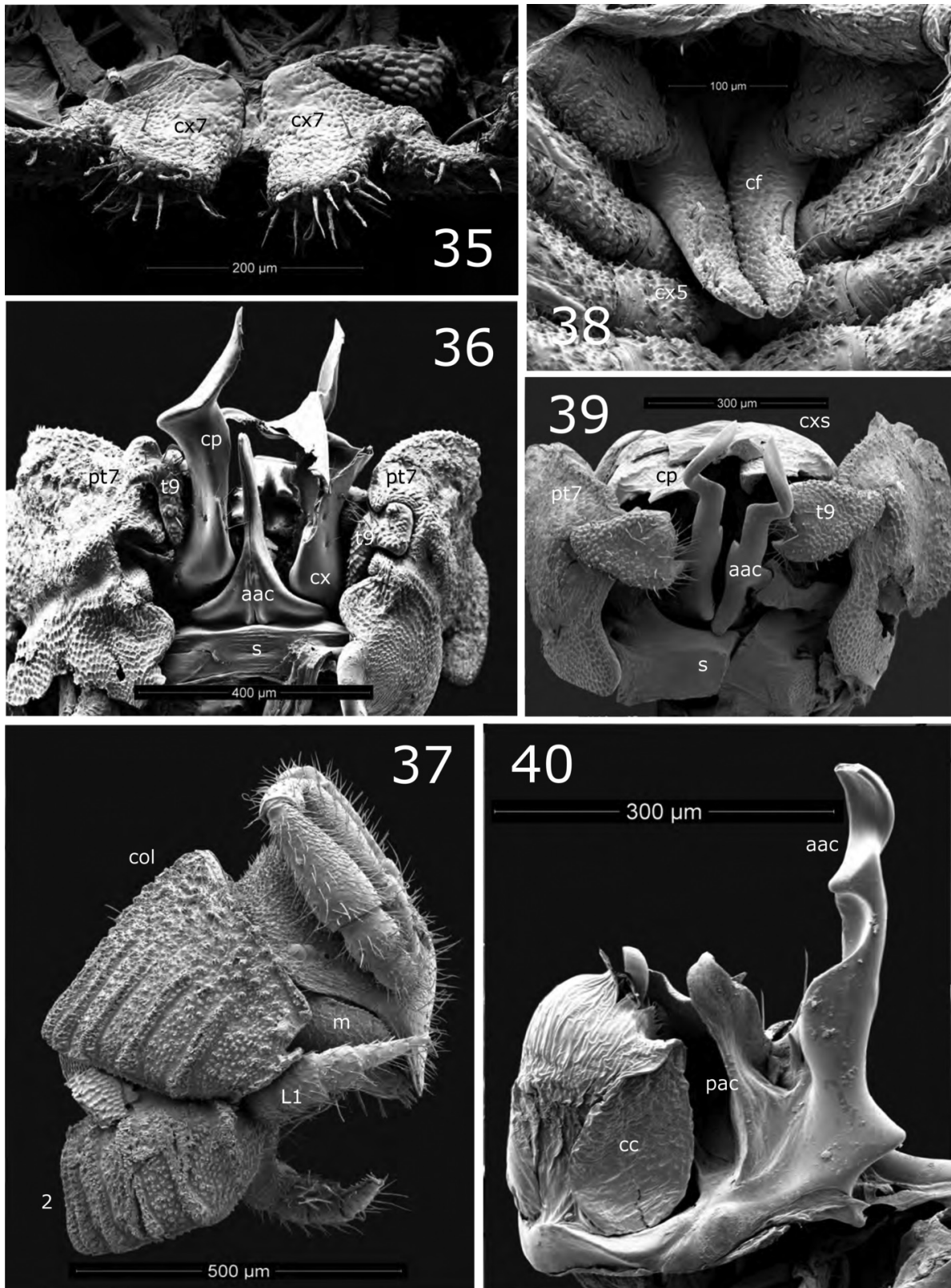
**Etymology:** The name is derived from the type locality, Arcata Community Forest, and is a noun in apposition.

**Diagnosis:** The two species of this genus are closely similar, but *Plaramia arcata*, n. sp., can be distinguished from *P. johnsonae*, n. sp., by details of the gonopods and ninth legs. The gonopods of the latter species have more curved anterior angiocoxites than the former, with a hooked termination, and the ninth leg telopodites are deeply notched. C6 of this species are very prominent, they are less so in *P. johnsonae*, but this difference can only really be seen in comparison.

**Description:** *Male holotype.* Length 3.8 mm, width 0.4 mm; 30 rings. Two black ommatidia on each side of head (Fig. 37). C6 moderately extended as paranota. Telson lobes shallowly divided, nearly obscure. Metazonal setae obvious only on anterior rings, relatively short, acute. Color after long preservation pale yellowish tan. First legs enlarged (Fig. 37, L1), with needle-like setae. Second legpair smaller, when coxae apposite, appearing to have common seminal opening. Flasks of third coxae short (Fig. 38, cf), when extended posteriorly reaching to anterior margin of fifth coxae; telopodites with broad, flattened prefemora. Fourth through sixth legs encrassate, podomeres flattened, with prominent characteristic modified setae. Seventh coxae lacking lobes. Gonopods (Figs 39, 40, 76, 77) moderately large. Sternum massive, short. Coxae with 3 or 4 setae on lateral side, extended into short, triangular process (Fig. 76, cx). Anterior angiocoxites curved laterally, then mesally, without branches, slightly flattened at tip (Figs 40, 76, 77, aac). Posterior angiocoxites small, low, with two processes; reduced to sheath for single flagellocoxite (Fig. 77, fc). Single flagellocoxite long, thin, evenly curved, possibly movable (there may be a basal articulation). Ninth legs (Fig. 78) with broad, plate-like coxosternal process (Fig. 77, cpx); telopodites (Fig. 39, 77, t9) free, large, flattened, notched on mesal surface to embrace gonopod anterior angiocoxites, laterally fitting tightly into notch in seventh pleurotergite (Fig. 39). Tenth coxae not much swollen, gland openings anteriodorsal.

Females similar to males in nonsexual characters.

**Distribution:** Known only from Arcata Community Forest, Humboldt Co. California.

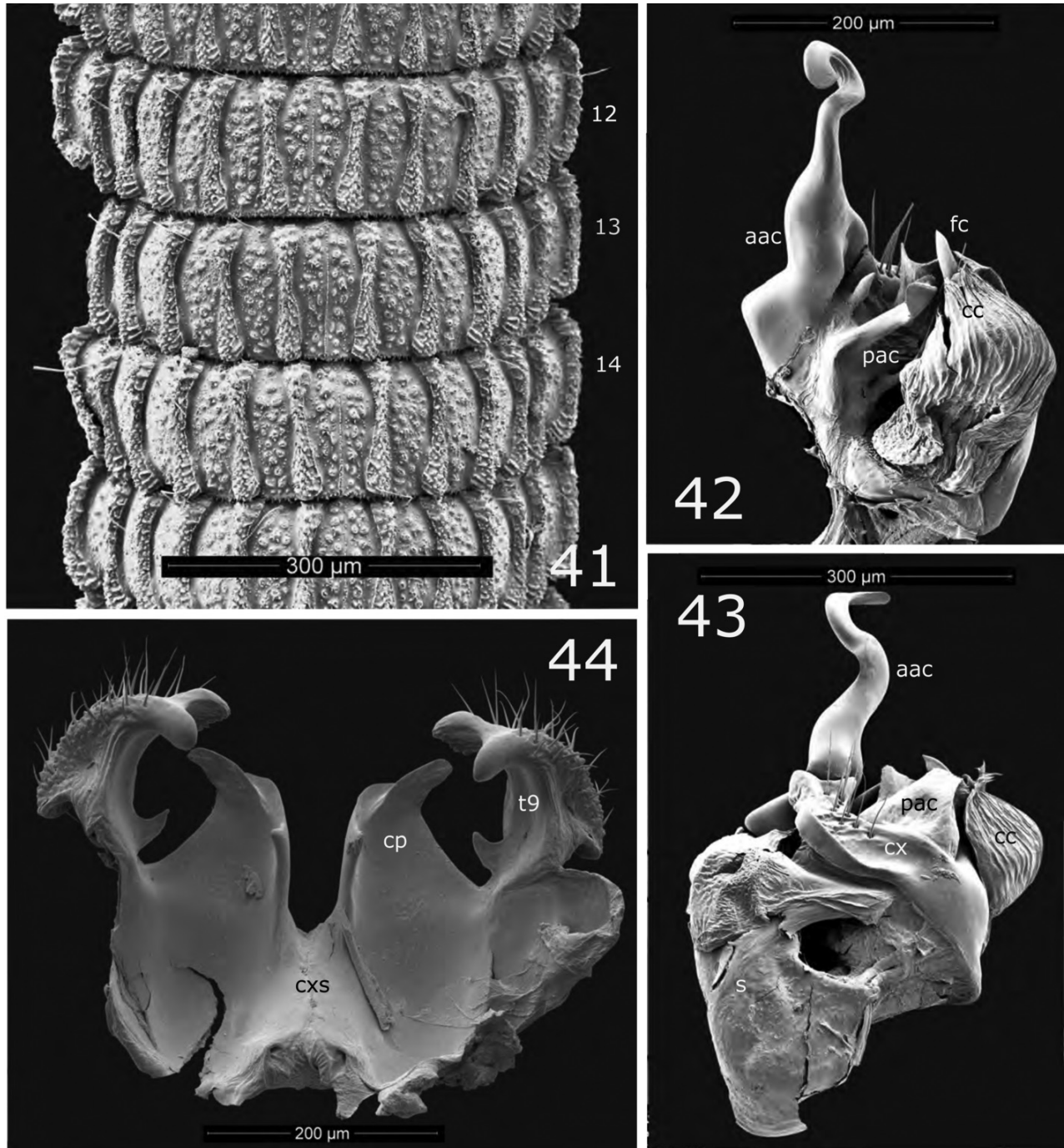


**FIGURES 35–40.** Striariid millipedes. **Figs 35, 36.** *Rampalia cheathamensis*, n. gen., n. sp. **35.** Coxae of male legpair 7, ventral view. **36.** Gonopods, anteroventral view. **Figs 37–40.** *Plaramia arcata*, n. gen., n. sp. **37.** Head, collum and ring 2 of male, lateral view. **38.** Legpair 3 coxae of male, ventral view. **39.** Gonopods, ventral view. **40.** Right gonopod, mesal view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cf**, coxal flask of leg 3; **col**, collum; **cp**, coxal process; **cx**, gonopod coxa; **cxs**, coxosternite of leg 9; **cx5**, coxa of leg 5; **cx7**, coxa of leg 7; **L1**, leg 1; **m**, mandible; **s**, sternum of gonopods; **t9**, telopodite of leg 9; **2**, ring 2.

*Plaramia johnsonae* Shear & Marek, n. sp.

Figs 41–44.

**Types:** Male holotype, female paratypes from Lady Bird Johnson Grove, Redwood National Park, 2.6 mi from US101 on Bald Hills Road, Humboldt Co., California, 41.3084°N, -124.0181°W, 1308' asl, collected 21 December 2006 by C. Richart and A. Fusek. Parts of the male holotype are mounted on SEM stub WS35-16. Deposited in CAS.



**FIGURES 41–44.** *Plaramia johnsonae*, n. gen., n. sp. **41.** Rings 12–14 of male. **42.** Right gonopod, lateral view. **43.** Right gonopod, mesal view. **44.** Legpair 9 of male, anterior view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cp**, coxal process; **cx**, gonopod coxa; **cxs**, coxosternite of legs 9; **fc**, flagellocoxite; **numerals**, ring numbers; **s**, gonopod sternum; **t9**, telopodite of ninth leg.

**Etymology:** The name honors the late First Lady of the United States, Lady Bird Johnson (1912–2007), a firm supporter of biodiversity conservation.

**Diagnosis:** See the diagnosis of *Plaramia arcata* n. sp., above.

**Description:** *Male holotype.* Length 3.5 mm, width 0.36 mm; 30 rings. Two black ommatidia on each side of head. C6 moderately extended as paranota (Fig. 41); less so than in the preceding species. Telson lobes hardly discernable. Metazonital setae of moderate length, with brushy tips. Color (fresh specimens) pale gray, crests accentuated with brownish purple. First legs enlarged, with needle-like setae. Second legpair smaller, when coxae apposite, appearing to have common seminal opening. Flasks of third coxae short, when extended posteriorly reaching to anterior margin of fifth coxae; telopodites with broad, flattened prefemora. Fourth through sixth legs encrassate, podomeres flattened, with prominent characteristic modified setae. Seventh coxae lacking lobes.

Gonopods (Fig. 42, 43) moderately large. Sternum (Fig. 43, s) massive, long. Coxae (Fig. 43, cx) with about 8 setae on lateral side, coxal process absent. Anterior angiocoxites (Figs 42, 43, aac) sigmoidially curved, apical curve results in hook-like termination, slightly flattened at tip. Posterior angiocoxites small, low, with two processes; reduced to flagellocoxite sheath (Figs 42, 43, pac). Flagellocoxite not observed, but presumed to be long, thin, evenly curved, possibly movable as in the preceding species. Colpocoxites large, inflated, sclerotized, striated (Figs 42, 43, cc). Ninth legs (Fig. 44) with broad, plate-like, curved coxosternal processes (Fig. 44, cp); telopodites free, large, flattened, notched on mesal surface to embrace gonopod anterior angiocoxites, laterally fitting tightly into notch in seventh pleurotergite. Tenth coxae not much swollen, gland openings anteriodorsal.

Females similar to males in nonsexual characters.

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

## ***Ralampia* Shear & Marek, new genus**

**Type species:** *Ralampia complexa* Shear & Marek, n. sp.

**Etymology:** The genus name is an arbitrary combination of letters, an anagram of the related genus name *Amplaria* forming a Latin neologism to be treated as feminine in gender.

**Diagnosis:** Three of the striariine genera described in this paper have their metazonital crests all roughly subequal and the sixth crests not especially paranota-like. In *Ralampia*, n. gen., the gonopods are quite small and compact, the short anterior angiocoxites are reflexed posteriorly and the colpocoxites have long, erect, branched, stiff fimbriae distally. The two species of *Plaramia*, n. gen., differ from those of *Maraplia*, n. gen., in that the gonopod anterior angiocoxites are erect and sinuously curved, rather than reflexed anteriorly and either short or if long, curved in an arc.

**Description:** Small striariines, about 5 mm long. Thirty postcephalic rings, including telson (Fig. 46). Two ommatidia on each side of head (Fig. 45, om). Head densely setose, with small tubercles. Labral hook lacking. Mandibular stipes with serrate margin, acute triangular process. Collum with crests limited to posterior region, studded with small tubercles. C6 nearly subequal with C1–5, but oriented horizontally (Fig. 46); metazonital setae short, with brush-like tips. Telson with lobes very shallowly demarcated or nearly indiscernable, sulci shallow. Legpair 1 (Fig. 47) larger than legpairs 2 or 3, femora and tibiae with long, needle-like setae, tarsus with comb. Legpair 2 with short telopodites, vas deferens openings in coxae facing mesally, coxae notched so that when appressed, a single pore is formed. Legpair 3 (Fig. 48) with relatively short flasks, barely reaching fifth coxae when extended posteriorly, heavily set with raised cuticular scales, few contorted setae. Legpairs 4–7 crassate, legpair 7 lacking coxal lobes.

Gonopods small, compact (Figs 79–82). Gonopod sternum large, broader than long. Coxa evidently lacking setae or with 3–4 setae, coxal processes short, quadrate (Figs 79, 81, cp). Anterior angiocoxites short, somewhat decurved posteriorly, with lateral flange (Figs 79–82, aac). Posterior angiocoxites with several branches (Fig. 80, pac), at least one of which appears like flagellocoxite. Flagellocoxites not observed. Colpocoxites oblong, with distal fimbria or crown of branched lamellae (Figs 80, 82, cc).

Ninth legs (Fig. 83) with coxosternite and free telopodites. Coxosternite with short, blunt, but complex process. Telopodite large, mesally elongate, with pebbled sculpture and setae, with deep notch to accommodate gonopods. Telopodite locks into deep notch in ventrolateral margin of pleurotergite 7.

Tenth legs with coxal pores, coxae slightly enlarged.

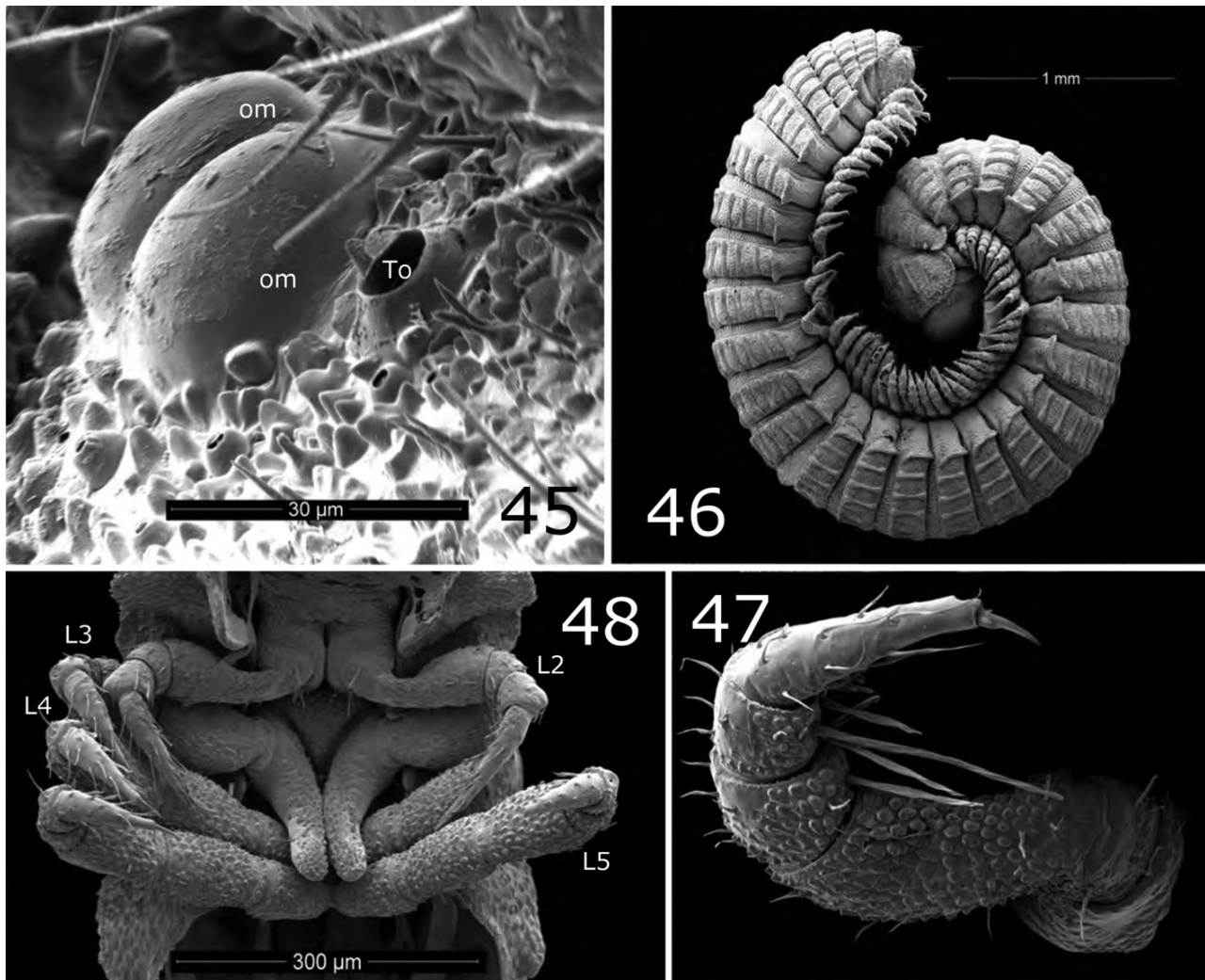
**Distribution:** Del Norte Co., California, and Curry Co., Oregon.

**Note:** This genus is the most problematical of those described here. We cannot be certain that the two species are congeneric, but place them here based on the overall similarity of the small, compact gonopods and the body form. If a single gonopod feature uniting them is required, we can point to the elongate colpocoxites with long, apical fimbriae. However, there are differences in gonopod details—for example, *Ralampia filamentosa*, **n. sp.**, has a gonopod branch divided into many long filaments that is absent in *R. complexa*, **n. sp.**, while the latter has numerous complicated branches that seem to arise from the posterior angiocoxite region. In neither species could the presence of a flagellocoxite be confirmed, though both have what appear to be posterior angiocoxite branches that look like flagellocoxites. But these are not sheathed. The probable absence of flagellocoxites would argue for placement in Trisariinae, but because we cannot be sure of that, and because the ninth leg telopodites are free, we retain them in Striariinae. Fresh material suitable for more detailed study is required to resolve the difficulties in *Ralampia*, **n. gen.**

***Ralampia complexa* Shear & Marek, n. sp.**

Figs 45, 79, 80

**Types:** Male holotype and male and female paratypes from Patrick Creek Campground on Rt. 199, 7 mi by road ENE of Gasquet, 41.8718°N, -123.8456°W, 990' asl, Del Norte Co., California, collected 22 December 1977 by A. R. Johnson. Parts of the holotype and paratypes are mounted on SEM stub WS35-9. All materials deposited in FSCA.

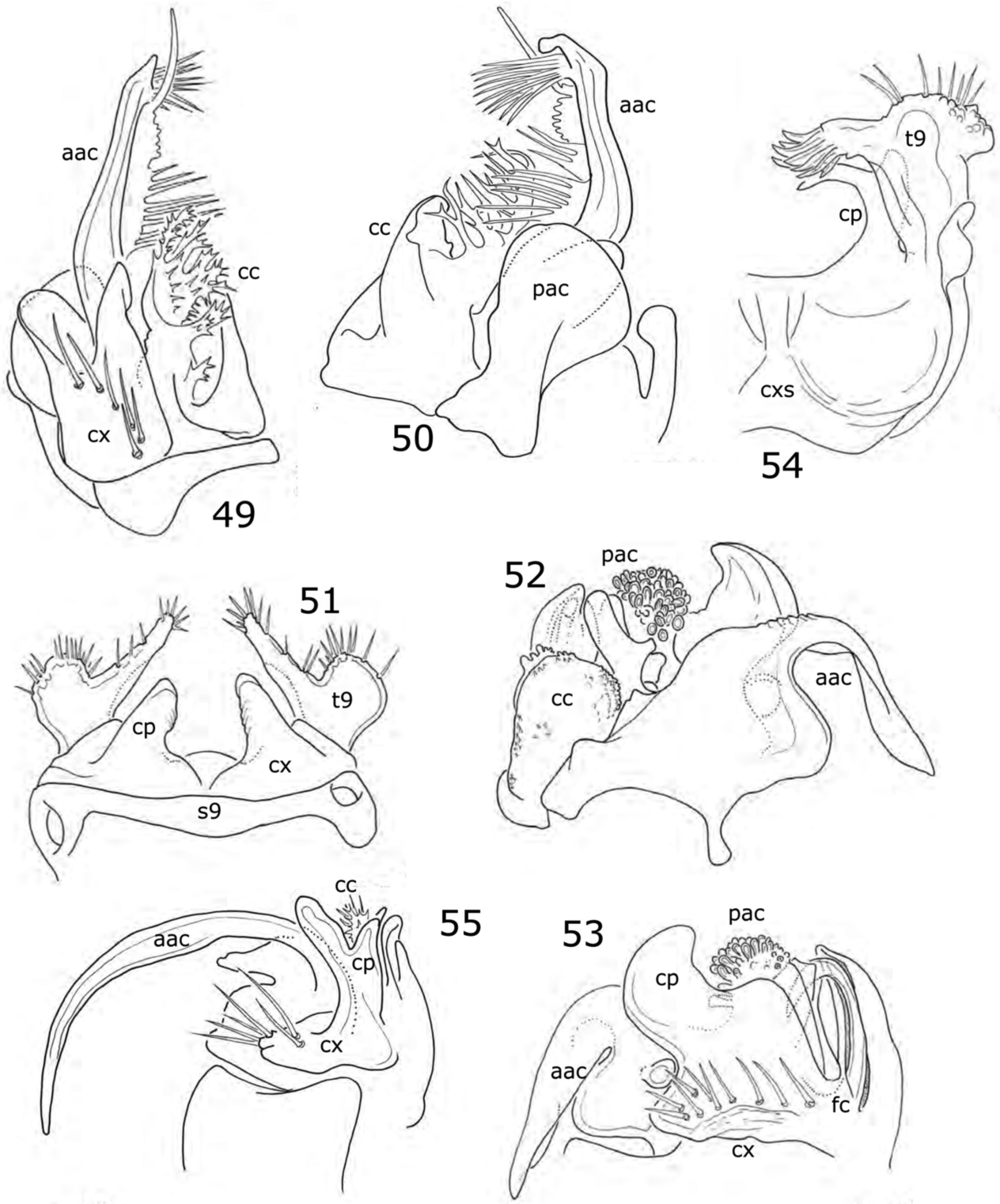


**FIGURES 45–48.** Striariid millipedes. **Fig. 45.** Ommatidia and Tömösváry organ of *Ralampia complexa*, **n. gen., n. sp.** **Figs 46–48.** *Ralampia filamentosa*, **n. gen., n. sp.** **46.** Female, lateral view. **47.** Right leg 1 of male, posterior view. **48.** Legpairs 2–5 of male, ventral view. Abbreviations: **L2–5**, legs 2–5, respectively; **om**, ommatidium; **To**, Tömösváry organ.

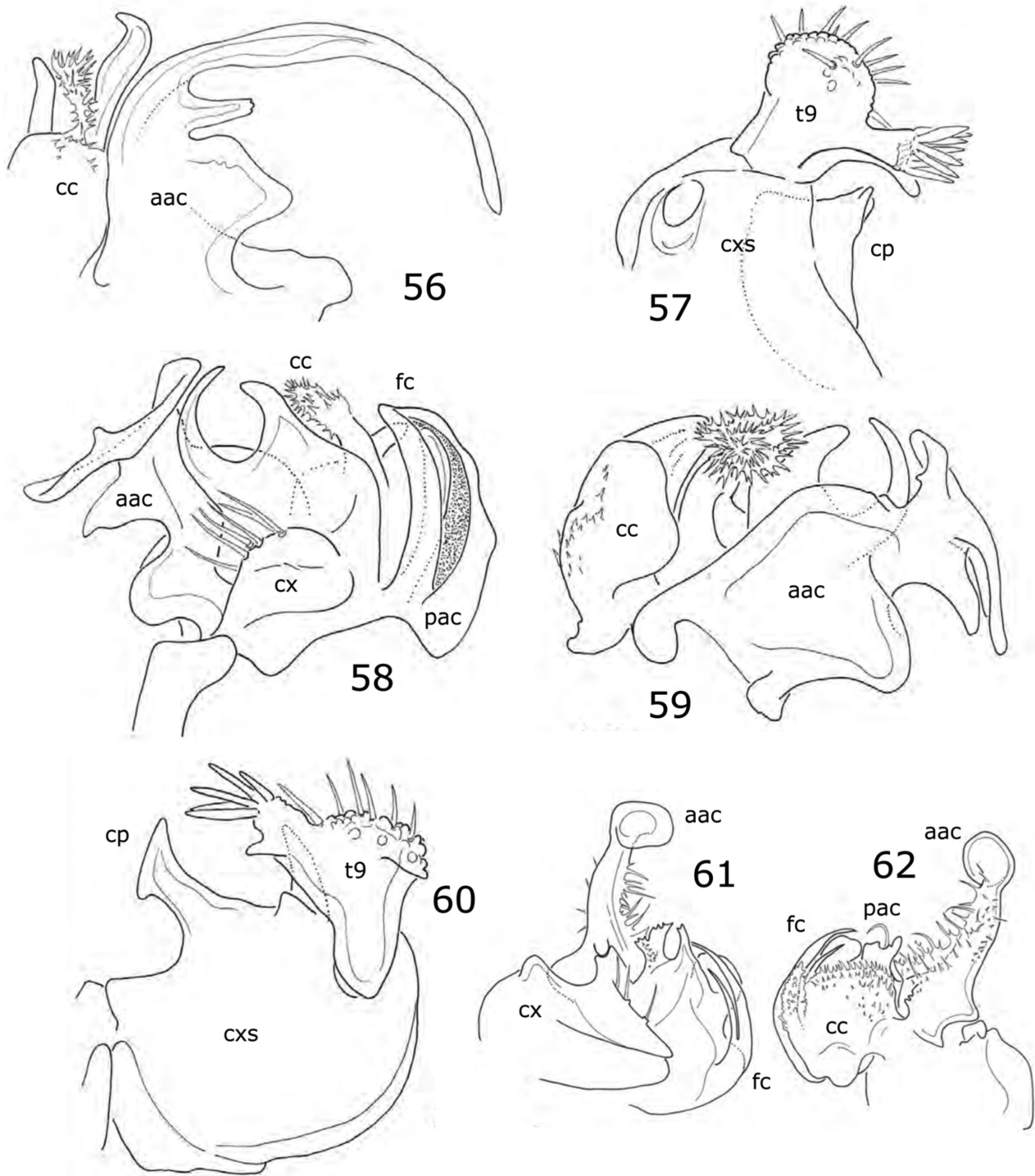


**Etymology:** The species name, an adjective, refers to the complicated gonopods.

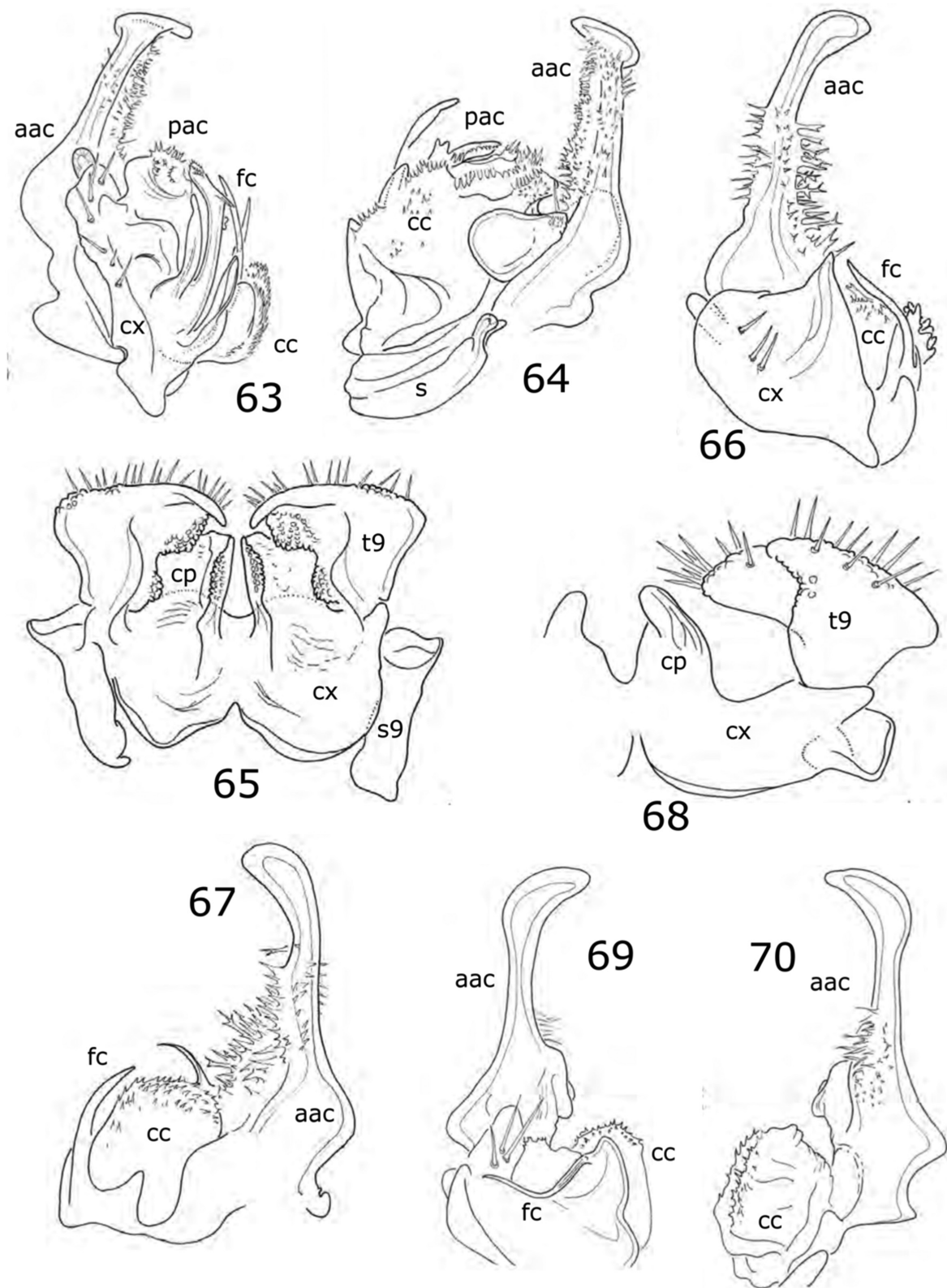
**Diagnosis:** Distinct from *Ralampia filamentosa*, n. sp., in lacking a multifilamentous lateral branch of the gonopods.



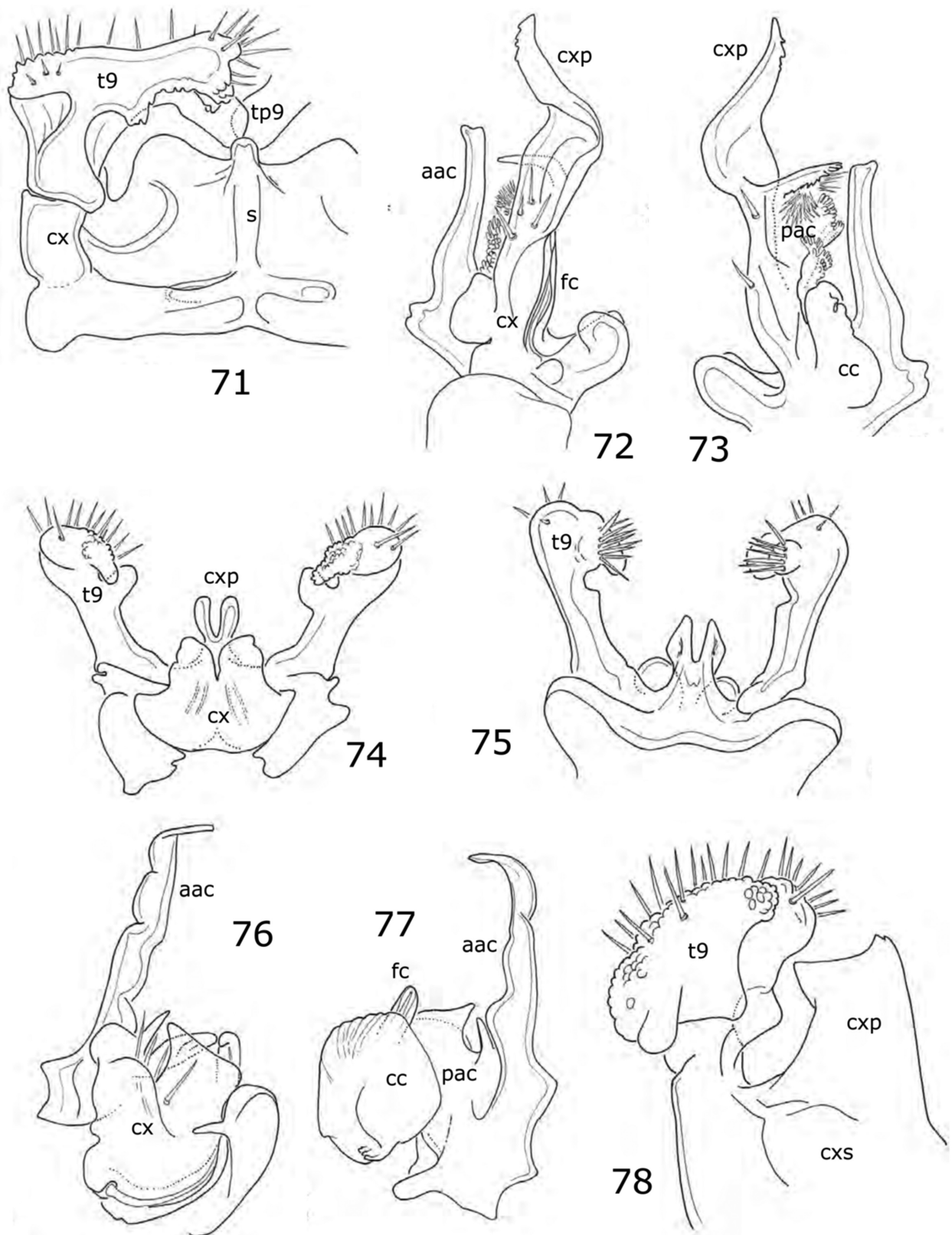
**FIGURES 49–55.** Striariid millipedes. **Figs 49–51.** *Nototrisaria ornata*, n. gen., n. sp., right gonopod, lateral view. **50.** Same, mesal view. **51.** Legpair 9 of male, anterior view. **Figs 52–54.** *Maraplia napa*, n. gen., n. sp. **52.** Right gonopod, mesal view. **53.** Right gonopod, lateral view. **54.** Right leg 9 of male, posterior view. **55.** Right gonopod of *Maraplia schusteri*, n. gen., n. sp., lateral view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cp**, coxal process; **cx**, gonopod coxa; **fc**, flagellocoxite; **pac**, posterior angiocoxite; **s9**, sternum of ninth legs; **t9**, telopodite of ninth leg.



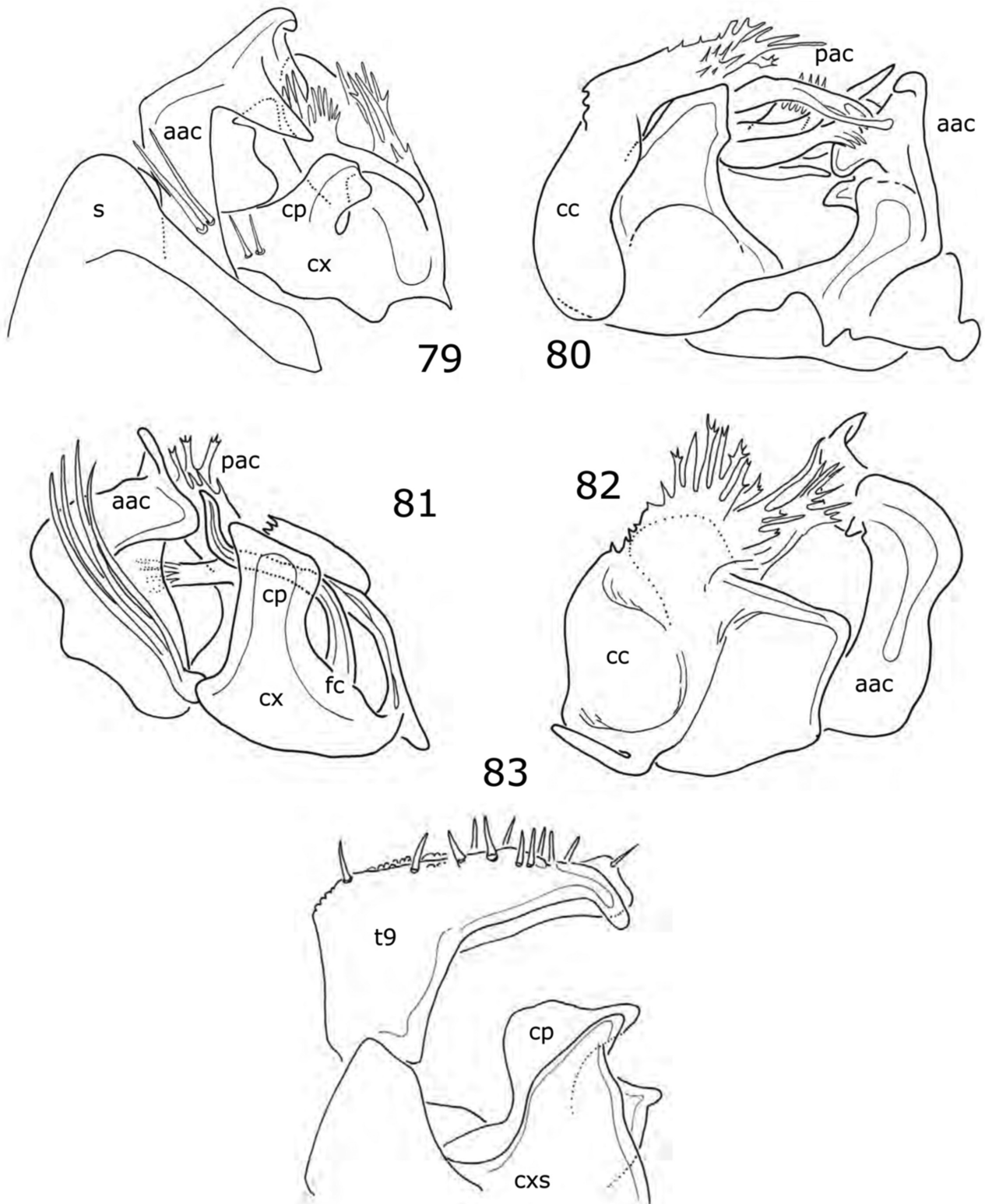
**FIGURES 56–62.** Striariid millipedes. **Figs 56, 57.** *Maraplia schusteri*, n. gen., n. sp. **56.** Right gonopod, mesal view. **57.** Right leg 9 of male, anterior view. **Figs 58–60.** *Maraplia chico*, n. gen., n. sp. **58.** Right gonopod, lateral view. **59.** Right gonopod, mesal view. **60.** Right leg 9 of male, posterior view. **Figs 61, 62.** *Lamparia curryensis*, n. gen., n. sp. **61.** Right gonopod, lateral view. **62.** Right gonopod, mesal view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cp**, coxal process; **cx**, gonopod coxa; **cxs**, coxosternite of legs 9; **fc**, flagellocoxite; **pac**, posterior angiocoxite; **s9**, sternum of ninth legs; **t9**, telopodite of ninth leg.



**FIGURES 63–70.** Striariid millipedes. **Figs 63–65.** *Lamparia bentonensis*, n. gen., n. sp. **63.** Right gonopod, lateral view. **64.** Right gonopod, mesal view. **65.** Male legpair 9, posterior view. **Figs 66–68.** *Lamparia pratensis*, n. gen. n. sp. **66.** Right gonopod, lateral view. **67.** Right gonopod, mesal view. **68.** Male right leg 9, posterior view. **Figs 69, 70.** *Lamparia millicoma*, n. gen., n. sp. **69.** Right gonopod, lateral view. **70.** Right gonopod, mesal view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cp**, coxal process; **cx**, gonopod coxa; **fc**, flagellocoxite; **pac**, posterior angiocoxite; **s9**, sternum of ninth legs; **t9**, telopodite of ninth leg.



**FIGURES 71–78.** Striariid millipedes. **71.** Right leg 9 of male *Lamparia millicoma*, n. gen., n.sp., anterior view. **Figs 72–75.** *Rampalia cheathamensis*, n. gen. n. sp. **72.** Right gonopod, lateral view. **73.** Right gonopod, mesal view. **74.** Male ninth legpair, anterior view. **75.** Male ninth legpair, posterior view. **Figs 76–78.** *Plaramia arcata*, n. gen., n. sp. **76.** Right gonopod, lateral view. **77.** Right gonopod, mesal view. **78.** Left leg 9 of male, anterior view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cxp**, coxal process; **cx**, gonopod coxa; **fc**, flagellocoxite; **pac**, posterior angiocoxite; **t9**, telopodite of ninth leg.



**FIGURES 79–83.** Striariid millipedes. **Figs 79, 80.** *Rampalia complexa*, n. gen., n. sp. **79.** Right gonopod, lateral view. **80.** Right gonopod, mesal view. **Figs 81–83.** *Rampalia filamentosa*, n. gen., n. sp. **81.** Right gonopod, lateral view. **82.** Right gonopod, mesal view. **83.** Left leg 9 of male, anterior view. Abbreviations: **aac**, anterior angiocoxite; **cc**, colpocoxite; **cp**, coxal process; **cx**, gonopod coxa; **cxs**, coxosternum of ninth legs; **fc**, flagellocoxite; **pac**, posterior angiocoxite; **s9**, sternum of ninth legs; **t9**, telopodite of ninth leg.

**Description:** *Male holotype.* Length 5.0 mm, width 0.38 mm; 30 rings. Two black ommatidia on each side of head (Fig. 45, om). All crests subequal, but C6 oriented horizontally.

Telson lobes hardly discernable. Metazonal setae of moderate length, with brushy tips. Color white after long preservation. First legs enlarged, with needle-like setae. Second legpair smaller, when coxae apposite, appearing to have common seminal opening. Flasks of third coxae short, scarcely reaching fourth coxae; telopodites with broad, flattened prefemora. Fourth through sixth legs encrassate, podomeres flattened, with prominent characteristic modified setae. Seventh coxae lacking lobes.

Gonopods (Figs 79, 80) small, compact. Sternum massive, long (Fig. 79, s). Coxae with 4 setae on lateral side, coxal process (Fig. 79, cp) small, narrow, quadrate. Anterior angiocoxites short (Figs 79, 80 aac), apically divided, with sharp posterior bend midlength. Posterior angiocoxites (Fig. 80, pac) with complex group of branches. Flagellocoxite not observed, likely absent. Colpocoxites oblong, flattened, with long apical fimbriae (Fig. 80, cc). Ninth legs with broad coxosternal processes, telopodites free, large, flattened, notched on mesal surface to embrace gonopod anterior angiocoxites, laterally fitting tightly into notch in seventh pleurotergite. Tenth coxae not much swollen, gland openings anteriodorsal.

Females similar to males in nonsexual characters.

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

### ***Ralampia filamentosa* Shear & Marek, n. sp.**

Figs 81–83

**Types:** Male holotype and male and female paratypes from 4 mi S of Pistol River on US 101, T38S/R14W/S32, 42.2329°N, -124.3860°W, 200' asl, collected 12 February 1972 by E. M. Benedict. Parts of holotype and paratypes mounted on SEM stub WS35-9. All material deposited in CAS.

**Etymology:** The species name, an adjective, refers to the filamentous branches of the male gonopods.

**Diagnosis:** This species may be separated from the foregoing by the presence of a lateral filamentous branch of the gonopod.

**Description:** *Male holotype.* Length, 5.0 mm, with 0.40 mm. 30 rings. Male secondary sexual characters as described for *R. complexa*, n. sp., above.

Gonopods (Figs 81, 82) small, compact. Coxal setae not observed; coxal process erect, quadrate (Fig. 81, cp). Filamentous branch arises basolaterally, divides into four long, thin, acute filaments. Anterior angiocoxites blocky (Figs 81, 82 aac), sharply bent posteriorly along midlength. Posterior angiocoxites with at least two branches, one of which is long, curved, and resembles flagellocoxite (Fig. 81, pac, fc). Colpocoxites (Fig. 82, cc) large, inflated, with crown of stiff, sometimes branched, narrow cuticular lamellae. Ninth leg as in Fig 83. Tenth coxae not much swollen, gland openings anteriodorsal.

Females similar to males in nonsexual characters.

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

## **Discussion**

We described six new genera and 13 new species of millipedes in the family Striariidae. These new small-bodied (3–5 mm long) taxa are from the Pacific Northwest of North America. The Sierra Nevada Range (California) is where early taxa were described, e.g., *Amplaria* Chamberlin, 1941, but now the Pacific Northwest has proven to be the center of diversity for the family, with an unexpected richness of new small-bodied taxa. These new genera and new species, and those described earlier in a series of five articles led by the first author, have challenged long-held morphology-based limits of their subfamilies and the other higher-level taxon boundaries. Some taxa are so morphologically divergent, with highly exaggerated metazonal crests (*Kentrostriaria*, *Stegostriaria*, and *Notostriaria*) and other features, that these new taxa themselves have significantly expanded the limits of the family. In contrast, species of the eastern U.S. genus, *Striaria*, is notably more conservative in its somatic morphology. *Striaria* is critically understudied, and would make a good subject of inquiry by a student of myriapodology. A synthesis combining western and eastern taxa of this North American family, with careful collecting in the Pacific

Northwest hotspot, would be similarly beneficial to undertake. Compared to other North American families with well-known species diversity, such as Xystodesmidae (Polydesmida), a molecular phylogeny-based classification system of Striariidae awaits this current phase of accelerated genus and species description

## Acknowledgements

We are especially thankful to Bill Leonard, Casey Richart and the late Ellen Benedict who collected much of the material reported on here, and to curators Petra Sierwald (FMNH) and G. B. Edwards (FSCA; since retired) for loans of specimens. We also thank two anonymous reviewers for their comments on the manuscript. Virginia Tech's NFCL (ICTAS) provided access to scanning electron microscopy supported by a grant from the National Science Foundation of the United States (#1916368) to Paul Marek at Virginia Tech and Michael Caterino at Clemson University.

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