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The millipede family Striariidae Bollman, 1893. IV. *Amplaria oedipus*, n. sp., with a secondary sexual modification of males unique among millipedes (Diplopoda, Chordeumatida, Striarioidea)

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Abstract

A new species, *Amplaria oedipus*, is described from Oregon, USA. Males of the new species have greatly inflated pyriform tarsi on the 5th and 6th legpairs, which is a secondary sexual modification previously not known from any other millipede.

Key words: new species, Oregon

Introduction

The millipede family Striariidae Bollman, 1893 is endemic to North America, occurring both in the southern Appalachian Mountains of the eastern United States, and from southern California north to southern British Columbia (unpublished records), including the U.S. states of California, Oregon, Washington and Idaho. Members of the family show a unique morphology, with a hood-like collum, crested metazonites and a trilobed telson (*pygidium* in most previously published accounts of millipedes; we write *telson* to use a more universal terminology in arthropods). *Amplaria* Chamberlin, 1941 is the most frequently encountered genus in the western distribution of the family, found in all states where striariids are present. Previous papers in this series (Shear & Krejca 2007, Shear *et al.* 2017, Shear 2020, 2021a, 2021b) have resulted in an improved understanding of diversity in this genus, which presently consists of 18 species (including the one described here; see below for a key and list), two of them highly adapted troglobionts.

Amplaria species males have an extensive suite of secondary sexual modifications, which occur in varying combinations in the 18 species, including labral spurs, acute projections of the mandibular stipes, specialized setae of the first legpair, various morphologies of the basal podomeres of the second legpair, long flask-like extensions of the third coxae (which often have reduced telopodites), and enlargement and flattening of legpairs 4–7, as well as gonopods developed from the eighth legpair and strongly reduced ninth legs, consisting only of a coxa (or coxosternum) and single telopodite article. The new species described below shows an additional modification previously not seen elsewhere in the order Diplopoda: the tarsi of the fifth and sixth legpairs are enormously swollen and pyriform (Figs 3, 6, 7). This is so distinctive that a new genus was briefly contemplated, but studies of other characters, especially the gonopods, convinced us that the species was best accommodated in *Amplaria*.

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Methods

Specimens were field-preserved in 90% isopropanol 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 mounted on 12.7 mm diameter aluminum stubs, using double-sided carbon discs. 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.

Type specimens are deposited in the collection of the California Academy of Sciences, San Francisco, California, USA, along with the SEM stub, WS36-15, to be deposited later.

Abbreviations used in the figures

aac	anterior angiocoxite
c (numeral)	numbered metazonite crests
ср	coxal process
cf	coxal flask of legpair 3
cx	coxa
cx (numeral)	coxa of numbered legpair
fc	flagellocoxite
lab	labrum
lcc	lateral lobe of colpocoxite
lh	labral hook
ms	mandibular stipes
numerals	ring numbers
numerals pac	ring numbers posterior angiocoxite
numerals pac pcc	ring numbers posterior angiocoxite posterior lobe of colpocoxite
numerals pac pcc pf (numeral)	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair
numerals pac pcc pf (numeral) s	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods
numerals pac pcc pf (numeral) s s (numeral)	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods sternum of numbered legpair
numerals pac pcc pf (numeral) s s (numeral) t (numeral)	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods sternum of numbered legpair tarsus of numbered legpair
numerals pac pcc pf (numeral) s s (numeral) t (numeral) tel	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods sternum of numbered legpair tarsus of numbered legpair telson
numerals pac pcc pf (numeral) s s (numeral) t (numeral) tel tr2	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods sternum of numbered legpair tarsus of numbered legpair telson trochanter of legpair 2
numerals pac pcc pf (numeral) s s (numeral) t (numeral) tel tr2 trp	ring numbers posterior angiocoxite posterior lobe of colpocoxite prefemur of numbered legpair sternum of gonopods sternum of numbered legpair tarsus of numbered legpair telson trochanter of legpair 2 trochanter process

Taxonomy

Family Striariidae Bollman, 1893

Subfamily Striariinae Bollman, 1893

Genus Amplaria Chamberlin, 1941

For synonymy and a detailed discussion of the genus, see Shear (2020, 2021a).

Amplaria oedipus Shear, Nosler & Marek, new species

Figs 1-13.

Types: Male holotype and female paratype from Cape Mountain, near Florence, 44.0947°, -124.0756°, Lane Co., Oregon, collected 18 September 2021 by Phil Nosler; male paratype from same locality but 44.0954°, -124.9766, collected 25 September 2019 by Phil Nosler.

Parts of male paratype on SEM stub WS36-15. All specimens deposited in California Academy of Sciences.

Diagnosis: This species cannot be confused with any other, due to the unique modification of the tarsi of male legpairs 5 and 6, which are enormously swollen and pyriform (Figs 3, 6, 7).

Etymology: The species epithet is a noun in apposition, a Greek proper name. Oedipus is a well-known figure from Greek mythology and the subject of two tragedies by Sophocles. The name Oedipus means "swollen foot" and is therefore appropriate for this unusual species.

Description: *Male holotype.* Body with 30 rings (including telson). Length, about 12 mm, width 1.2 mm at midbody. Ocularium with 12 or 13 ommatidia. Labrum (**lab**, Fig. 1) with acute spines (**lh**, Fig. 1) at distal corners. Mandibular stipes (**ms**, Fig. 1) lacking projections, rimmed with rounded teeth. Collum white, with 10 low crests, sixth crest on each side vaguely noticeable. Metazonite ornamentation (Fig. 2) typical of the family, with 12 crests, prominent and equal, wider spacing between crests 2 and 3, and 4 and 5 on each side. Rings with two longitudinal bands of purplish brown pigment; crests 2 and 3 of each side within these pigmented bands thereby making crests appear with darker pigment. Segmental setae short, distally with a brush of small spinules. Telson (**tel**, Fig. 2) slightly elongated, 3-lobed. Cerotegument lacking in all specimens so far examined.

Legpair 1 white, reduced, smallest of all legs (Fig. 1), needle-like setae lacking, but femora with flattened specialized setae. Tarsi of legpair 1 (**t1**, Fig. 1) with comb setae. Remaining legpairs with purplish brown pigment. Legpair 2 (Figs 1, 4) with *vasa deferentia* (**vd**, Fig. 4) opening from unmodified coxae (**cx2**, Fig. 4); with rounded, bulging trochanters (**tr2**, Fig. 4) with short processes bearing modified setae (**trp**, Fig. 4); and with enlarged, flattened prefemora (**pf2**, Fig. 4). Legpair 3 (Figs 3, 5) with short, curved coxal flasks (**cf**, Fig. 5) distally with curled setae; and with telopodites not enlarged but femora flattened, lower surface with evenly scattered small tubercles (Fig. 3). Postcoxal bars of ring 3 long, distally expanded, meeting or crossing in midline. Legpairs 4–7 (Fig. 3) much enlarged, with flattened femora; legpairs 5 and 6 with greatly swollen pyriform tarsi (**t5**, **t6**, Figs 3, 6, 7) about 0.5 mm long and 0.4 mm in diameter, tapering proximally to articulation with tibiae and tapering distally at tarsungulum (Fig. 7), but nearly spherical in distal view (Fig. 6). Legpair 7 without coxal lobes covering bases of gonopods (Fig. 3).

Gonopods (Figs 8–10, 12, 13) with structure typical of *Amplaria*. Anterior angiocoxites (**aac**, Figs 8, 10, 12, 13) slightly curved, distally hook-like, with small, bifurcate posterior distal process (Fig. 9). Posterior angiocoxites (**pac**, Figs 8–10, 12, 13) about half the length of the anterior angiocoxites, long, projecting anterior branch sheaths at least 3 flagellocoxites (**fc**, Figs 8, 13). Posterior lobes of colpocoxites (**pcc**, Figs 8, 13) with finely spiculate surface. Lateral lobes of colpocoxite (**lcc**) large. Ninth legpair (Fig. 11) with mesally hooked coxal process (**cp**, Fig. 11), telopodite setose, flattened, mesally with recess receiving coxal process. Telopodites fitting into shallow depressions in ventrolateral margins of seventh diplotergite. Tenth leg coxae with coxal glands.

Female paratype. Similar to male but with smaller collum, less projecting pygidium and lacking the greatly inflated tarsi on the 5th and 6th legpairs, and other male secondary sexual modifications.

Distribution: Known only from Cape Mountain, Lane Co., Oregon.

Notes: Collections were made by hand in early fall to late spring. Most searches were made along the main trail to the peak of Cape Mountain (accessed from the parking lot at Dry Lake Horse Camp). All specimens were collected from the vicinity of the peak. Litter and soil were examined, as well as the undersides of logs, rocks, and bark. Specimens were fixed in 90% isopropanol and preserved in 70-80% ethanol.

The habitat at this location is a Sitka Spruce (*Picea sitchensis* (Bong.) Carrière) forest. In Oregon, this is a unique ecosystem found only in very close proximity to the Pacific coast, where the climate is mild and wet (Franklin and Dyrness 1988); Cape Mountain lies approximately 5 km from the coast. Sitka Spruce is the dominant conifer in this habitat, and is supplemented by Western Red Cedar (*Thuja plicata* Donn ex D. Don) and Red Alder (*Alnus rubra* Bong.) in disturbed areas. The undergrowth consists of dense Salal (*Gaultheria shallon* Pursh), Western Sword-fern (*Polystichum munitum* (Kaulf.) C. Presl), Salmonberry (*Rubus spectabilis* Pursh), Red Elderberry (*Sambucus racemosa* Linnaeus), Evergreen Huckleberry (*Vaccinium ovatum* Pursh), and Red Huckleberry (*Vaccinium parvifolium* Sm. in Rees).



FIGURES 1 and 2. *Amplaria oedipus* n. sp., male paratype. Fig. 1. Head and anterior legs, ventral view; lab, labrum; lh, labral hook; ms, mandibular stipes; pf1, prefemur of first leg; pf2, prefemur of second leg; t1, tarsus of first leg. Fig. 2. Rings 26–29 and telson; numerals, ring numbers; c (numerals), crest numbers of right side of ring 26; tel, telson.



FIGURES 3–7. *Amplaria oedipus*, n. sp., male paratype. Fig. 3. Legpairs 3–7, ventral view; cx3, third leg coxa; pf(numeral), prefemora of legs 4-7; t(numeral), greatly inflated tarsi of legs 5, 6. Fig. 4. Bases of legpair 2, ventral view; cx2, coxa of second leg; pf2, prefemur of leg 2; tr2, trochanter of second leg; trp, trochanteral process; vd, opening of vas deferens. Fig. 5. Bases of legpair 3; cf, coxal flask of third leg; cx3, coxa of third leg; s3, sternum of third leg. Fig. 6. Greatly inflated tarsus of left fifth leg, distal view; t5, tarsus of fifth leg. Fig. 7. Greatly inflated tarsus of right sixth leg, lateral view; t6, tarsus of sixth leg.

Amplaria oedipus was always found at or near the litter surface. The male paratype was found underneath a small, broken branch which also supported platydesmid and rhiscosomid millipedes. The male holotype and female paratype were found in leaf litter. *Amplaria oedipus* was found in places rich with other chordeumatidan families, including Caseyidae, Tingupidae, and Conotylidae.



FIGURES 8–11. *Amplaria oedipus*, n. sp., male paratype. Fig. 8. Gonopods, posterior view; aac, anterior angiocoxite; cx, gonopod coxa; fc, flagellocoxite; lcc, lateral lobe of colpocoxite; pac, posterior angiocoxite; pcc, posterior lobe of colpocoxite. The lateral lobe of the colpocoxite has collapsed due to drying for SEM. Fig. 9. Tip of left anterior angiocoxite, mesal view. Fig. 10. Tips of right anterior and posterior angiocoxites, posterior view; aac, anterior angiocoxite; fc, flagellocoxite; pac, posterior angiocoxite. Fig. 11. Left leg 9, anterior view; cp, coxal process; cx9, coxa of leg 9.



FIGURES 12, 13. *Amplaria oedipus*, n. sp., male holotype. Fig. 12. Right gonopod, lateral view; aac, anterior angiocoxite; pac, posterior angiocoxite; lcc, lateral lobe of colpocoxite. Fig. 13. Right gonopod, mesal view; aac, anterior angiocoxite; fc, flagellocoxite; pcc, posterior lobe of colpocoxite; pac, posterior angiocoxite. Without scale.

When the first male was collected by PN and sent to WS for identification we suspected the strange tarsi might have been due to a parasite, such as a nematode or a fly larva. However, dissection of one of the tarsi revealed neither, just amorphous tissue. Also, why would a parasitic attack be limited to just those tarsi? Another consideration was that a random mutation may have occurred in the single male. The collection by PN of another male with the exact same greatly inflated tarsi on the 5th and 6th legpairs spoke against both the parasite and mutation hypotheses. We therefore think that the evidence at hand supports our conclusion that the modifications are normal for the mature males of this species. In our experience, such a tarsal condition is not known from any other species of the class Diplopoda, though enlarged other podomeres (usually the prefemora) are not unusual. Aside from the enlarged tarsi, *A. oedipus* is a typical species of *Amplaria*.

The unique nature of this modification recalls the eastern North American species *Pseudotremia peponocranium* Shear, 2011 (Cleidogonidae) which differs from all other members of its genus in having a large, swollen, quadrate projection on the front of the head in both males and females (Shear 2011: 15, figs 34, 35).

A single male and two female *Amplaria* of another, undescribed species were collected at a lower elevation on Cape Mountain (44.0910°N, -124.0737°W). The gonopods of this species, to be described later, are similar but distinct from those of *A. oedipus* and the male lacks the enlarged tarsi.

Key to species of Amplaria

Key based on males. Amplaria eutypa and A. eldora are not included (both descriptions based on females only).

1a.	Tarsi 5 and 6 of males pyriform, much enlarged
1b.	Tarsi 5 and 6 of males similar to other tarsi
2a.	Eveless with troglobiotic adaptations 3.
2b	Ommatidia present not troglobiotic 4
3a.	Length 25 mm or greater
3b.	Length about 12 mm
4a.	First legs of males with long, needle-like setae
4b.	First legs of males without long, needle-like setae.
5a.	Coxae and trochanters of legs 2 separate, not fusedstaceyi.
5b.	Coxae and trochanters of legs 2 fused
6a.	Third coxal flasks separate, but tightly appressed in midline
6b.	Third coxal flasks basally fused
7a.	Four or fewer ommatidia
7b.	Seven to 9 ommatidia
8a.	Telson elongate, flattened
8b.	Telson not elongate, not flattened
9a.	Metatergal crests posteriorly elevated arcata.
9b.	Metatergal crests moderately developed, not elevated
10a.	Length 16–17 mm
10b.	Length 9–12mm
11a.	Thirteen to 15 ommatidia
11b.	5 or fewer ommatidia
12a.	Coxae of legpairs 4 and 5 depressed, finely setose
12b.	Coxae of legpairs 4 and 5 not depressed
13a.	Process of second trochanter very short or apparently absent
13b.	Process of second trochanter of moderate length
14a.	Gonopod anterior angiocoxite simple, scoop-like
14b.	Gonopod anterior angiocoxite with lateral branch
15a.	Coxal flasks of legpair 3 long, gradually taperedumatilla.
15b.	Coxal flasks of legpair 3 short, basally swollenadamsi.

List of species

Species	Type Locality
adamsii Shear & Krejca, 2007	CALIFORNIA: Tulare Co., Hidden Cave, Sequoia National Park
arcata Shear, 2021a	CALIFORNIA: Humboldt Co., Prairie Creek Redwoods State Park, 41.3730°, -124.0139°
baughi Shear, 2021a	IDAHO: Idaho Co., O'Hara Campground, 46.0852°, -115.5174°
cervus Shear, 2021a	CALIFORNIA: Humboldt Co., 6 mi N of Loleta, 40.6991°, -124.1168°
crawfordi Shear, 2021a	WASHINGTON: King Co., Thornton Creek, 47.698°, -122.279°
eldora (Chamberlin, 1953)	CALIFORNIA: Eldorado Co., Crystal Cosumnes Cave
eutypa (Chamberlin, 1941)	CALIFORNIA: Eldorado Co., 9 miles N of Placerville
flucticulus Shear, 2021a	CALIFORNIA: Amador Co., Rippled Cave, 38.4386°, -120.7255°
fontinalis Shear, 2021a	WASHINGTON: Skamania Co., Spring Creek Hatchery, 45.7280°, -121.5445°
imberbis (Loomis, 1936)	CALIFORNIA: San Luis Obispo Co., south of Atascodero
mendocino Shear, 2021a	CALIFORNIA: Mendocino Co., Usal Road, 39.7910°123.8290°
muiri Shear & Krejca, 2007	CALIFORNIA: Tulare Co., Crystal Cave, Sequoia National Park
nazinta (Chamberlin, 1910)	OREGON: Multnomah Co., Powell Butte Park, 45.4888°, -122.5131° (neotype)
oedipus n. sp.	OREGON: Lane Co., Cape Mountain, 44.0947°, -124.0756°
rykkenae Shear, 2021a	OREGON: Linn Co., Willamette National Forest, 44.4131°, -122.2619°
shastae (Causey, 1958)	CALIFORNIA: Shasta Co., Samwel Cave
staceyi Shear, 2021a	CALIFORNIA: San Diego Co., Palomar Mountain State Park, 33.3435°, -116.9072°
umatilla Shear, 2021a	OREGON: Umatilla Co., Umatilla National Forest, 49.9801°, -118.0523°

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