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Revalidation of the milliped genus *Amplaria* Chamberlin 1941 (Diplopoda, Chordeumatida, Striariidae), and description of two new species from caves in Sequoia and Kings Canyon National Parks, California

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Abstract

The milliped genus *Amplaria* Chamberlin 1941 was synonymized with *Striaria* Bollman 1888 by Hoffman (1980). Examination of a much wider range of materials of nominal *Striaria* species both from eastern North America and the Pacific coastal states shows that some species occurring from California to Washington (state) represent a distinct phyletic line, for which *Amplaria* Chamberlin 1941 is the oldest available generic name. *Speostriaria* Causey 1960 is a synonym of *Amplaria.* *Amplaria muiri* **n. sp.** and *A. adamsi* **n. sp.** are two new, recently discovered species from caves in Sequoia and Kings Canyon National Parks, California. Illustrations are provided of a specimen that may represent the type species, *Amplaria eutypa* (Chamberlin) 1953.

Key words: caves, U. S. A. National Parks, troglobionts, troglophiles, Sierra Nevada Mountains, *Speostriaria, Striaria, Vaferia*

Intoduction

The milliped family Striariidae, endemic to the United States and the southwestern corner of Canada, has remained somewhat enigmatic since Bollman established it as a subfamily in 1893, for his species *Striaria granulosa,* described from Jefferson Co., Tennessee (Bollman 1888). The striariids are perhaps the most unusual and deviating members of the entire order Chordeumatida (Figs. 24–27). They are very heavily sclerotized, with thick cuticle often covered by a waxy secretion, and have a hood-like collum, which partially conceals the head. The metazonites of the trunk diplosegments each bear 12 longitudinal crests, and the epiproct is distinctly trilobed. The typical segmental setae of the Chordeumatida are strongly reduced and, it would seem, entirely absent in some species. The gonopods of males are often inordinately complex, even for chordeumatids, and the pregonopodal legs of males may have an extensive suite of secondary sexual modifications.

Striariids are not common in collections. In eastern North America, species seem more likely to be associated with drier habitats than other millipeds, occupying places where millipeds are not generally searched for, and this may in part account for the low numbers of specimens in collections. However, recent intensive collecting (see below) reveals that striariids are an important and abundant part of the milliped fauna of western North America and are found there in both dry and moist habitats.

In 1895, Cook raised Striariinae to full family status, and later (Cook 1899) published a more detailed account, in which he added two additional species: *S. columbiana* from the Washington, DC, area, and *S. californica* from Marin Co., California, establishing the presence of the family in western North America. Over

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the next 70 years, eleven additional species were added to the family, often without careful attention to those that had been described previously.

At the generic level, Chamberlin (1941) added a new genus, *Amplaria*, based on *Amplaria eutypa* Chamberlin 1941, from Eldorado Co., California. Only female specimens of this species were available, and Chamberlin based the distinction between *Amplaria* and *Striaria* on the presence of 12 crests on the collum in *Amplaria*, not 10, as was thought to occur in *Striaria* species. Causey (1958) pointed out that both 10 and 12 collum crests can occur in species of *Striaria,* (the lateralmost crest on each side of the collum may be suppressed to varying degrees) but continued to recognize *Amplaria* on the basis of its fewer ocelli and a deep transverse groove on the collum (ocellus number, however, also varies within *Striaria*, and the groove on the collum occurs generally in species throughout the family, while being quite variable in its expression in *Amplaria* species). Causey then named a new genus, *Vaferia* Causey 1958, based on *Striaria imberbis* Loomis 1936, from San Luis Obispo Co., California; this genus was set up because *imberbis* is supposedly "anteriorly flattened" and lacked the modified mentum of male *Striaria*. However, the status of this generic name remains questionable, because an examination of the type material of *imberbis* shows that the anterior part of the body is not really perceptibly flattened, and numbers of new taxa of striariids, distinct from *imberbis,* lack the modified mentum in males. Determination of the actual generic placement of *Vaferia imberbis* must wait for more material from southern California; at this time the type locality of this species represents the farthest south record for the family in western North America.

A careful reading of Causey's 1958 paper, a general review of all striariids known at the time, shows that not a single male specimen was examined, nor were types of previously described species.

Causey (1960) later established the genus *Speostriaria* for *Striaria shastae* Causey 1958 from Samwel Cave in Shasta Co., California; she described males and presented accurate gonopod drawings that were the first complete gonopod illustrations to be published for the entire family. Causey's description of this species sets a high standard for subsequent work and is in stark contrast to her own previous work on striariids and that by Chamberlin (see below).

Exactly where Striariidae fits in the classification scheme has been the subject of controversy. Cook (1899), struck by the many unusual characters of the few species available to him, considered Striarioidea to be a suborder coordinate with Lysiopetaloidea and Chordeumoidea (*recte*: Chordeumatoidea) in his Order Coelochaeta. This arrangement was retained by Chamberlin and Hoffman (1958) in their North American checklist, but they used Chordeumida (*recte*: Chordeumatida) as the name for the order previously called Coelochaeta by Cook. However, Causey (1952, 1958) found the arguments unconvincing, and pointed out that the somatic peculiarities could be seen as adaptive to the particular situation and behavior of the family members, and that, like the chordeumatidans, striariids had six metatergal setae and lacked repugnatorial pores. Hoffman (1979, 1999) accepted the placement of striariids in Chordeumatida, with Callipodida (= Lysiopetaloidea) as a separate order, but still maintained subordinal status (now under Chordeumatida) for the family Striariidae alone, based on the gonopores of males opening from the second coxae as membranous tubes. WAS favored an intermediate view (Shear 1972, 2000), retaining Striariidea as a suborder, but including two superfamilies, Striarioidea Bollman 1888 and Caseyoidea Verhoeff 1909. In this arrangement Striarioidea includes the families Striariidae Bollman 1888, Rhiscosomididae Silvestri 1909 and Apterouridae Loomis 1966, while Caseyoidea includes Caseyidae Verhoeff 1909 and Urochordeumatidae Silvestri 1909.

In 2000, terrestrial mollusk researcher William Leonard of Olympia, Washington, began sending WAS abundant collections of millipeds from the Pacific Northwest of North America. Included in these collections were many new taxa of striariids, including a wide array of species that must eventually be placed in new genera, tribes and subfamilies. These materials will be the subject of a series of later papers, but among them were forms that lacked the tubular extensions of the seminal pore, having it opening flush with the coxal surface on either the anterior or posterior side, laying to rest once and for all the "unique" nature of that character and its use to justify a suborder for Striariidae alone. (Further, scanning electron microscopy has shown that in at least some polydesmids, including the very common eastern US species *Pseudopolydesmus serratus*, the male gonoducts are also produced into membranous tubes.) We are now more convinced than ever that common features of the gonopods and of the modifications of male ninth legs and pregonopodal legs link the families WAS included in Striariidea in 2000.

During this same period, residues from Berlese funnel collections made over many years and deposited in the Field Museum, Chicago, were sorted for millipeds. Still more striariids, primarily from the western states, were obtained. Found in both the Leonard collections and those in the Field Museum were a group of species with clear and consistent differences in the gonopods and other characters from the *Striaria* species of eastern North America, and representing a compact and distinct phyletic line, ranging from the Sierra Nevada Mountains and the San Francisco Bay area of California north to southern Oregon and on to the southern reaches of the Puget Sound region in Washington, as well as isolated occurrences in Idaho and probably Montana. *Amplaria* is the oldest available name for this genus-level taxon.

The two new *Amplaria* species described below were taken during a survey of cave life carried out in Sequoia and Kings Canyon National Parks, California, under the direction of JKK. They are being described here because it is important, for conservation purposes, to give them names as soon as possible.

Taxonomy

Amplaria Chamberlin

Amplaria Chamberlin 1941, p. 9. *Type species*: *Amplaria eutypa* Chamberlin 1941 (by monotypy).

Speostriaria Causey 1960, p. 26. *Type species*: *Striaria shastae* Causey 1958 (by monotypy). **NEW SUBJECTIVE SYNONYMY.**

Diagnosis: Distinct from *Striaria* in the simpler gonopods. In *Striaria*, the anterior angiocoxites of the gonopods are sharply angled posteriorly about two-thirds of their length from the base, with distinct transverse rugae at the angle, and terminate in multiple acute spines; the angle and rugae are absent from *Amplaria*, and the terminations of the anterior angiocoxites are simple, usually lobe-like. The posterior angiocoxites of *Amplaria* species are clearly bifid, with an anterior branch serving to sheath the flagellocoxites; no such anterior sheathing branch is found in *Striaria* species. Although a complete survey has not been taken, *Amplaria* species appear to have a special type of seta on the legs that is not found in *Striaria*. These setae (Fig. 14) are flattened, curved, and appressed to the leg surface; dorsally they flare into a leaflike shape, and ventrally are divided into many cylindrical filaments. Leg setae in *Striaria* species are much simpler, appearing as straight, blunt-tipped rods with parallel-grooved shafts. The functional significance of neither setal type is understood.

Description: Striariids of moderate to large size (12–25 mm long). Males: head robust, antennae short, distinctly angled; 2–7 poorly developed and pigmented ocelli irregularly arranged on each side of head; mentum with distinct sigmoid spine at each distal angle (Fig. 12). Mandibles with ventral carina on basal article (Fig. 12). Collum broad, hoodlike; poorly developed transverse groove separates uncrested, rebordered anterior third from posterior two-thirds, anterior median part slightly projecting, roughened with small acute tubercles, posterior section with 12 longitudinal crests, the lateralmost partly suppressed. Trunk segments with 12 longitudinal crests on metazonites, segmental setae located between, not on, crests, usually aciculate. Fourth prozonite with long medial extension on each side, passing between the bases of legpairs three and four. Seventh segment distinctly enlarged. Epiproct three-lobed.

First legs with combs of long, stout, modified setae (Figs. 5, 6) on tibiae and tarsi. Second legs with seminal openings from posterior surfaces of coxae, with or without extended membranous rims, trochanters with heavily setose ventral processes (Fig. 4). Third legs with swollen coxae drawn out into flask-shaped structures, telopodites articulating basolaterally; prefemora slender (Fig. 13). Legpairs 4–7 enlarged, more robust than postgonopodal legs, prefemora and femora dorsoventrally flattened. Gonopods (Figs. 1–3, 7–11, 17–22):

sternum distinct, well-sclerotized. Gonopod coxae separate and articulated laterally with sternum, with two pairs of angiocoxites, the anterior pair appressed in the midline, straight, with simple lobed terminations, bearing basally three flagellocoxites; the posterior angiocoxite pair larger, sigmoid, with bulky posterior branch, thinner anterior branch sheathing flagellocoxites. Colpocoxites poorly sclerotized, with large lobe extending anterolateral to angiocoxites, smaller posterior lobe often with short, scale-like fimbriae. Ninth legs (Figs. 15, 16) much reduced; sternum deeply bowl-like, receiving at rest the gonopods; coxae short, cylindrical, with gland pore near base, with or without mesal terminal apophysis; telopodites condensed to single article, flattened, heavily sclerotized, setose-tuberculate. Coxae of tenth legs enlarged, bearing coxal gland openings. Coxae eleven unmodified.

Female: similar to male but usually smaller, lacking secondary sexual modifications of the legs; collum shorter, with rounded posterior angles. Segments two and three with distinct ventral marginal carinae. Segment seven not enlarged.

Included species: Amplaria eutypa Chamberlin, 1941, *A. eldora* (Chamberlin) 1953, *A. nazinta* (Chamberlin)1910, *A. shastae* (Causey)1958, *A. muiri* **n. sp.**, and *A. adamsi* **n. sp.** (both are described below).

At this time, a key to species would be impractical due to the confusion surrounding *eutypa* and *eldora*, and the absence in collections of males of *nazinta* (and *Striaria californica*, see below).

Distribution: From the southern Sierra Nevada and San Francisco Bay areas of California north to Shasta Co., California, coastal southwestern Oregon and the southern end of Puget Sound, Washington; at least one species in north-central Idaho, possibly in far western Montana. The San Francisco Bay area records and elements of the distribution north of Shasta Co., California, and in Idaho are based on undescribed species.

Remarks: Striaria causeyae Chamberlin 1940, from North Carolina, was placed in *Amplaria* by Chamberlin and Hoffman (1958); examination of the holotype male in the United States National Museum of Natural History (USNM) shows it to be a typical *Striaria* species.

Amplaria eutypa is unfortunately based on a female. The vial containing the syntypes (USNM) holds parts of two or perhaps three animals, the anterior end of one, posterior end of another, and a second posterior end that may or may not belong to the anterior end. The identity of this species, from nine miles north of Placerville, El Dorado Co., California, cannot be ascertained with certainty until males are collected at or near the type locality. *Amplaria eldora*, discussed below, is also from near Placerville, collected in Crystal Cosumnes Cave. It is possible these two species are synonyms; *eutypa* is the senior name. The synonymy cannot be established until the collection of males of both species from their respective type localities. However, a male from Grapevine Cave (in nearby Calaveras County) was seen by Chamberlin (1953b) and determined by him as *A. eldora*. Its gonopods conform to our concept of *Amplaria.* Admittedly this is a tenuous chain of logic: *eldora* may be a synonym of *eutypa,* and a male purported to be *eldora* (but not from the type locality) has gonopods that are like those of the two new species described below, therefore we apply the name *Amplaria*, type species *A. eutypa*, to the whole group. However, in all the material from the Sierra Nevada and the foothills region to the west WAS has seen so far, only one genus is represented, so we think it unlikely that *eutypa* does not belong to it.

Amplaria shastae is a very large species, the largest known striariid, found in caves in Shasta Co., California. Males and females have been well-described and illustrated by Causey (1958, 1960) and by Shear (1969). Examination of topotypical specimens makes it clear that despite the inordinate size (25 mm), the gonopods are those of an *Amplaria* species. Long legs and antennae, depigmentation, and reduced ocelli, together with gigantism, strongly mark *A. shastae* as a troglobiont. The case is less clear in the two new species described below, which may be at best troglophilic.

Amplaria nazinta, described as a *Striaria* by Chamberlin in 1910 from Portland, Oregon, and placed in *Amplaria* by Chamberlin (1941), may or may not belong in the genus; the holotype, a female, has evidently been lost. WAS has seen specimens of several species of striariid from the Portland area but at this point none of them seem to fit the description of *nazinta*.

Cook's (1899) *Striaria californica* (type locality, Sausalito, Marin County, California) is another candidate for membership in *Amplaria*, but there are other striariid genera, as yet unnamed, in the San Francisco Bay area, and in the absence of males a definite generic assignment is not yet possible. The female holotype (USNM) is in bad condition, having been pinned and dried before being transferred to alcohol. If, as we suspect, *Striaria nana* Loomis 1936 and *Striaria carmela* Chamberlin 1947 are both junior synonyms of *S. californica* (they are certainly synonyms of each other, based on an examination of the types [USNM]; *nana* is the senior name), it indeed belongs to an undiagnosed genus. Males of *nana* lack the curved labral spines, the seminal ducts open flush on the surfaces of the second coxae, and the leg setae, while basically leaflike as in *Amplaria*, do not have the bunches of filaments and are instead drawn out distally into a long, thin extension. The gonopods of this genus do not have the anterior sheathing branch on the posterior angiocoxite division, and in that detail resemble *Striaria* species.

Amplaria eldora **(Chamberlin)**
Figs. 1, 2

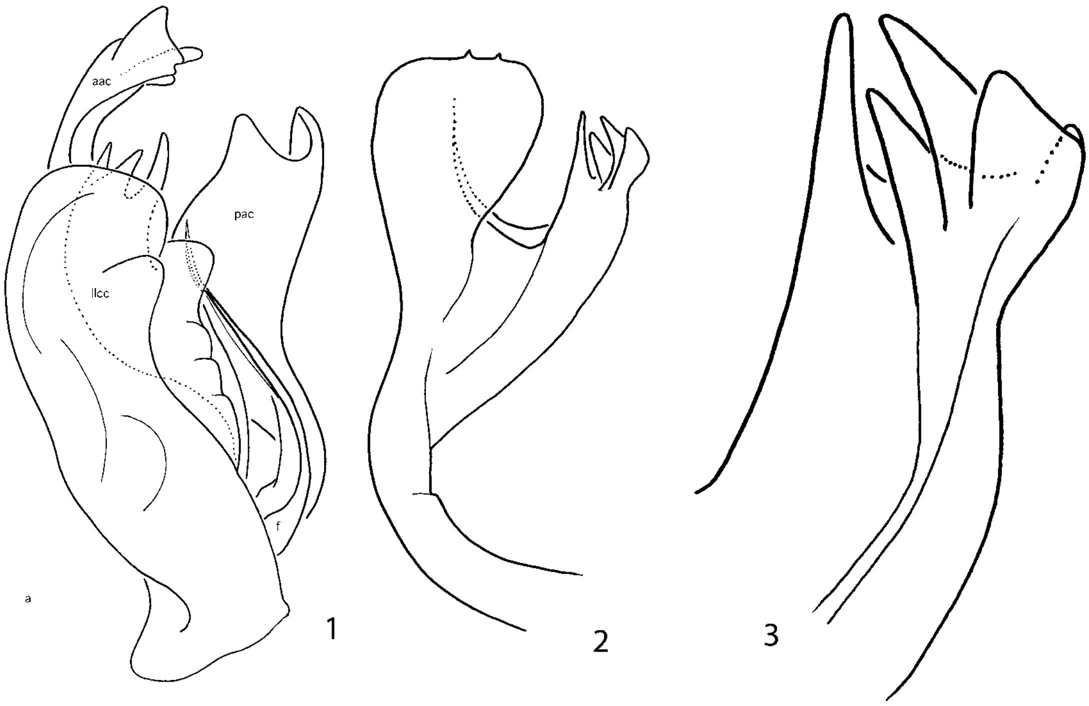
Types: Three female syntypes from Crystal Cosumnes Cave, Eldorado Co., California, collected by A. Lang and G. Lange, 2 February 1952, whereabouts unknown.

Notes: Chamberlin (1953a) did not formally designate a holotype from among the three females available to him, and these specimens cannot be located; they are not in the USNM, where type material Chamberlin retained in his personal collection is now deposited. The specimens were part of a collection made by Edward Danehy and others in 1950 and 1951, and sent to Chamberlin for identification. The USNM does contain a vial labeled "*Striaria eldora* Chamberlin, PARATYPE." This single male specimen is from Grapevine Cave, Calaveras Co., California, and was collected 17 April 1951 by E. Jacobus. Morley Hardaker, of Davis, California, kindly provided us with information about Crystal Cosumnes Cave and Grapevine Cave:

"Crystal Cosumnes cave is near the little town of Fairplay in El Dorado County, and is located above the Middle Fork of the Cosumnes River…at about 2000 feet elevation….Grapevine Cave is about 36 air miles in a southerly direction and located about 3 miles east of the little town of Vallecito in Calaveras County. It is in a karst area high above and on the north side of the Stanislaus….Unlike Crystal Cosumnes its passages are maybe 20 to 30 feet below the surface, and many of its ceilings contain tree roots, some up to a couple feet in length. Grapevine is one of our richer caves in containing cave fauna. Millipedes and salamanders are commonly found here. I have personally seen millipedes in both caves on most trips."

In a later paper, Chamberlin (1953b) mentioned this Grapevine Cave collection without specifying the sex or number of specimens, or designating the specimen as a type of any sort, so the museum labeling of it as a paratype has no formal standing. It would be a particularly maddening aspect of Chamberlin's often capricious work if he had a male available but chose to describe the species from females. And why did he decide to describe two of the species from the Danehy collection separately (Chamberlin 1953a), then just a few months later mix the descriptions of two more, plus more records of the first two, into a paper that was fundamentally about material from Honduras (Chamberlin 1953b)? Furthermore, in a checklist published in 1958, only five years after reporting the male *eldora* specimen from Grapevine Cave, Chamberlin stated that *eldora* was "known only from the type locality (Chamberlin and Hoffman 1958)." Chamberlin's (1953) sketchy description of female *eldora* could apply to almost any species of medium-sized striariid, and so is of no help in determining the identity of this specimen. Until males from Crystal Cosumnes Cave appear, no harm is done by considering the Grapevine Cave male to be *Amplaria eldora*. However, as stated above, it remains to be proven that *eldora* is a junior synonym of *eutypa*, though we strongly suspect that it is.

The gonopods of the Grapevine Cave male are illustrated in figs. 1 and 2; unfortunately the specimen was in poor condition, but the distal parts of the gonopods are clearly distinct from other species now placed in *Amplaria*.



FIGURES 1–3. *Amplaria eldora,* Grapevine Cave specimen, male. 1. Right gonopod, lateral view; **aac**, anterior angiocoxite; **pac**, posterior angiocoxite; **llcc**, lateral lobe of colpocoxite; **f**, flagellocoxite. 2. Posterior angiocoxite of right gonopod, mesal view. 3. Tip of sheathing branch of posterior angiocoxite, mesal view.

Amplaria muiri, n. sp.
Figs. 4–15, 24, 26, 27

Types: Male holotype and female and male paratypes from Crystal Cave, Sequoia National Park, Tulare Co., California, collected 15 July 2003 by Jean Krejca, V. Loftin and S. Fryer, deposited in Field Museum of Natural History, Chicago (FMNH).

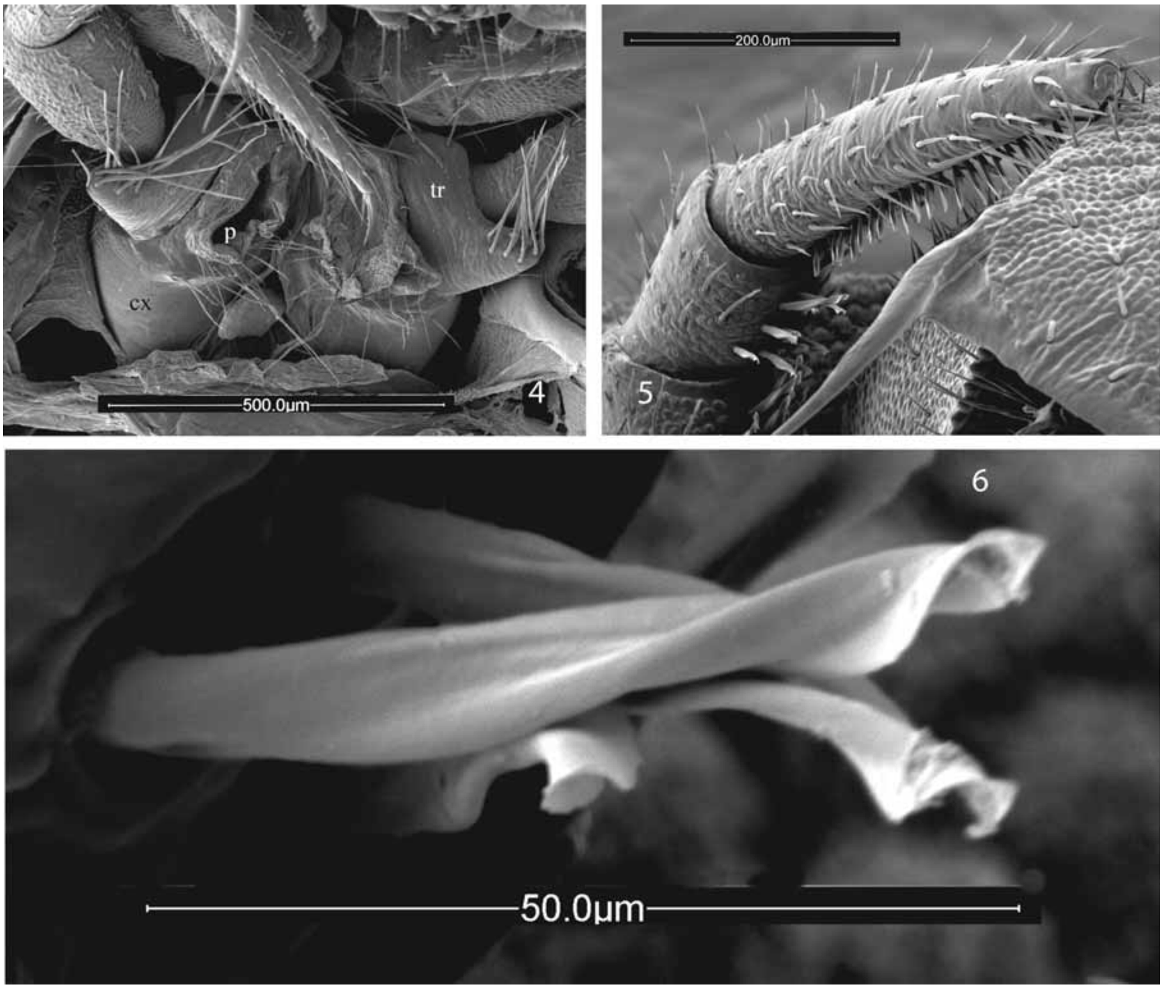
Diagnosis: Distinct from the nearby *A. adamsi,* **n. sp.**, in the larger size, fewer ocelli, paler pigmentation, and details of the gonopods as illustrated.

Etymology: After John Muir, famous naturalist of the late nineteeth and early twentieth century, whose name is forever connected with the Sierra Nevada, which he called “the Range of Light.”

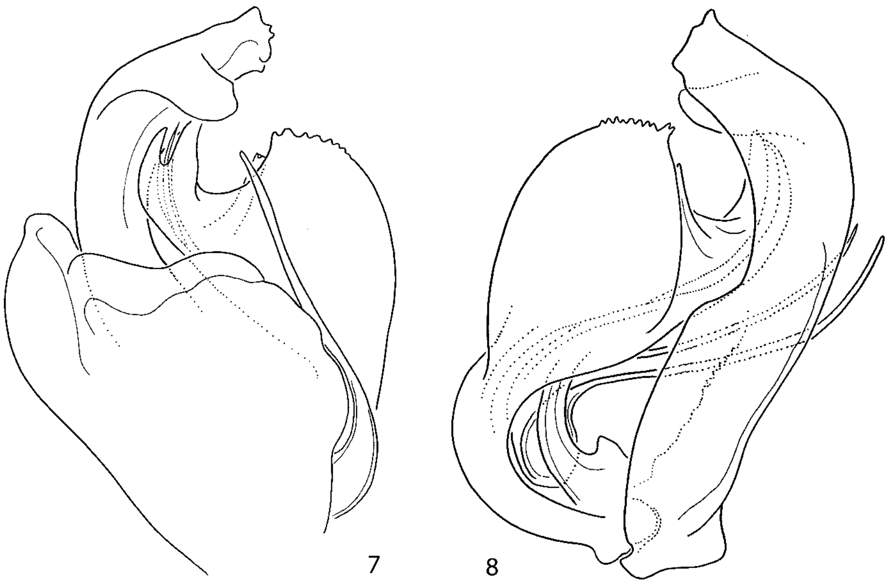
Description: Male. Length, 16.5 mm, width, 1.2 mm. Three, four or five small, irregularly shaped black ocelli in one or two rows. Crest 6 (lateralmost) of collum incomplete, obscure; more prominent on metazonites 2, 3, complete on metazonite 4. Segmental setae of collum to metazonite 5 aciculate, twice as long as intercrest distance, becoming shorter from metazonite 6 posterior, blunt, subclavate, as long as intercrest distance or shorter. Epiproct broad, spatulate. Color of most specimens yellowish white (Figs. 24, 26, 27), few have slight reticulate pattern of pale purplish brown on posterior margins of metazonites 24–29 and epiproct; legs and antennae white. Secondary sexual modifications as described for genus.

Gonopods (Figs. 7–11) robust, anterior angiocoxites appressed in midline, apically with three unequal teeth, deltoid lateral branch sharply, evenly curved; posterior angiocoxites with flagellar sheathing branch stout, apically flaring, posterior branch inflated, with curved, toothed ridge. Colpocoxites typical of genus (note: poorly sclerotized lateral lobe of colpocoxite collapses in SEM preparation). Legpair 9 as in Fig. 15.

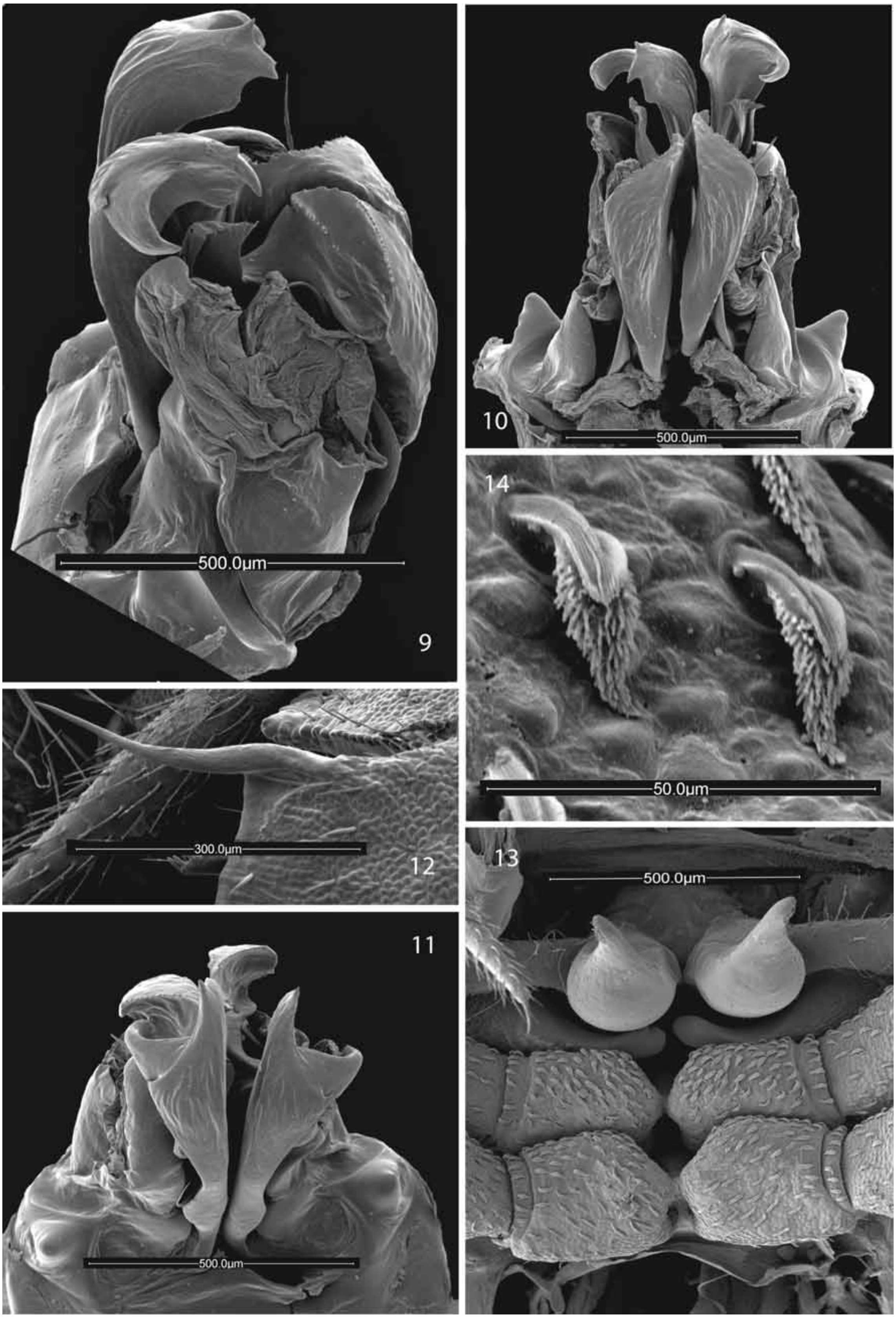
Female: length, 15.2 mm, width, 1.0 mm. Except for secondary sexual characters, much as male.



FIGURES 4–6. *Amplaria muiri*, **n. sp.**, male, scanning electron micrographs. 4. Coxae and trochanters of second legs of male, ventral view; **p**, seminal pore; **cx**, coxa; **tr**, trochanter. 5. Tibia and tarsus of first leg of male, showing modified setae on ventral surface, posterior view. 6. Modified setae from ventral surface of tibia.

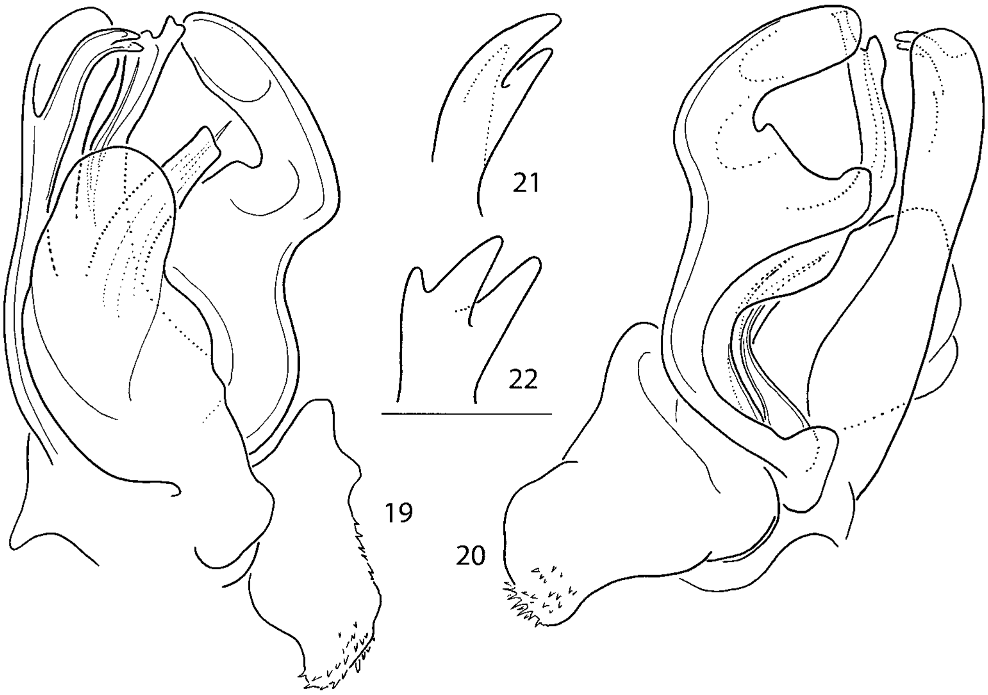


FIGURES 7, 8. *Amplaria muiri*, **n. sp.**, male. 7. Right gonopod, lateral view. 8. Right gonopod, mesal view.



FIGURES 9–14. *Amplaria muiri,* **n. sp.**, male, scanning electron micrographs. 9. Gonopods, ventrolateral view; posterior to the right. 10. Gonopods, posterior view. 11. Gonopods, ventroposterior view. 12. Spine at corner of mentum and modified mandibular stipes, anterior view, ventral to the left. 13. Coxae of legpairs 3–5, anterior at the top. 14. Modified setae from coxa of leg 3.

FIGURES 15–18. New species of *Amplaria*, males, scanning electron micrographs. 15. *A. muiri*, ninth legpair, anterior view. 16–18. *A. adamsi*, **n. sp.** 16. Ninth legpair, anterior view. 17. Left gonopod, mesal view. 18. Right gonopod, lateral view.



FIGURES 19–22. *Amplaria adamsi*, **n. sp.** 19. Right gonopod, lateral view. 20. Right gonopod, mesal view. 21. Tip of internal branch of anterior angiocoxite, lateral view. 22. Same, anterior view.

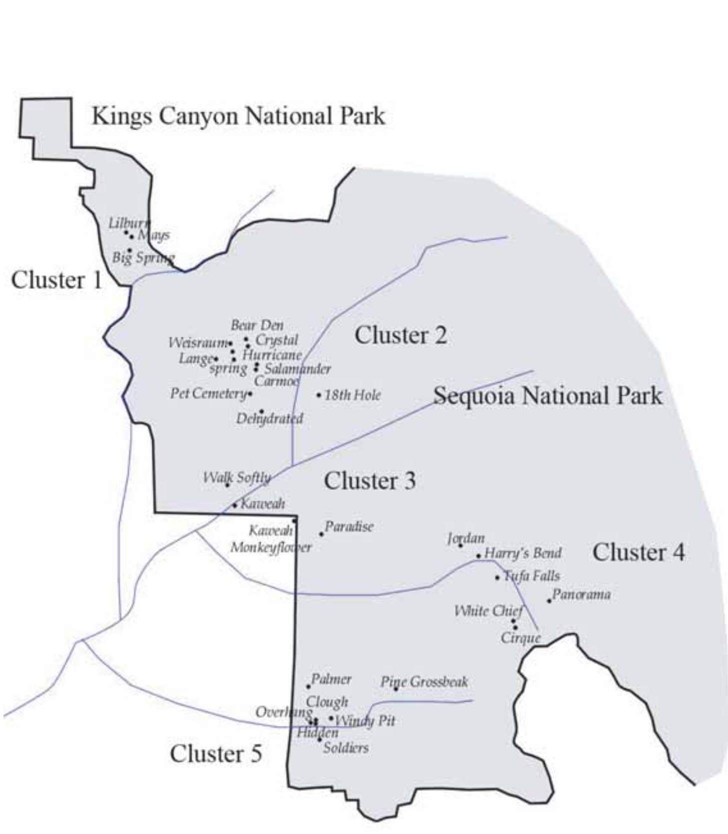


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FIGURE 23. Map of parts of Sequoia and Kings Canyon National Parks, Tulare Co., California, showing locations of caves studied in 2003–2004 by JKK and associates. Note that some of the cave names are shortened for ease of viewing on the map, typically the word "Cave" is left off. See text for the full names of caves in which *Amplaria* specimens were collected.

TABLE 1. Collection localities for species of Amplaria in Sequoia and Kings Canyon National Parks. Cave names have been abbreviated; full names are given in the text.

Cave	Date	Collectors	Collection number	Species	Notes
Hidden	15-Nov-03	J. Krejca, V. Loftin	JKK-302-B1	*Amplaria adamsi*	male
Overhang	29-Apr-04	J. Krejca, P. Sprouse	JKK-22-C9	*Amplaria adamsi*	juvenile
Overhang	29-Apr-04	J. Krejca, P. Sprouse	JKK-25-C6	*Amplaria adamsi*	female
Overhang	29-Apr-04	J. Krejca, P. Sprouse	JKK-24-C4	*Amplaria adamsi*	male
Bear Den	17-Jul-03	J. Krejca, V. Loftin, S. Fryer	JKK-33-A3	*Amplaria muiri*	male
Bear Den	18-Jul-03	J. Krejca, V. Loftin, S. Fryer, C. Walck	JKK-333-A1	*Amplaria muiri*	2 males, female
Bear Den	1-May-04	J. Krejca, J. Snow, A. Snow, P Sprouse	JKK-43-C2	*Amplaria muiri*	2 penultimate instar males
Bear Den	1-May-04	J. Krejca, J. Snow, A. Snow, P Sprouse	JKK-40-C6	*Amplaria muiri*	5 males, 3 females
Carmoe Crevice	18-Nov-03	J. Krejca, V. Loftin	JKK-331-B2	*Amplaria muiri*	2 females, 4 juveniles
Carmoe Crevice	18-Nov-03	J. Krejca, V. Loftin	JKK-335-B1	*Amplaria muiri*	2 males, female, juvenile
Carmoe Crevice	18-Nov-03	J. Krejca, V. Loftin	JKK-330-B1	*Amplaria muiri*	3 males
Carmoe Crevice	5-Jul-04	J. Krejca, A. Gluesenkamp	JKK-1-D1	*Amplaria muiri*	2 males, female
Clough	19-Nov-03	J. Krejca, V. Loftin	JKK-341-B1	*Amplaria adamsi*	penultimate male
Clough	19-Nov-03	J. Krejca, V. Loftin	JKK-340-B9	*Amplaria adamsi*	2 males, 2 females
Clough	27-Apr-04	J. Krejca, P. Sprouse et al	JKK-3-C11	*Amplaria adamsi*	2 females
Clough	27-Apr-04	J. Krejca, P. Sprouse et al	JKK-2-C7	*Amplaria adamsi*	female
Clough	27-Apr-04	J. Krejca, P. Sprouse et al	JKK-1-C14	*Amplaria adamsi*	juvenile
Crystal	15-Jul-03	J. Krejca, V. Loftin, S. Fryer	JKK-003-A1	*Amplaria muiri*	15 specimens, type series
Crystal	15-Jul-03	J. Krejca, V. Loftin, S. Fryer, D. Boiano	JKK-005-A2	*Amplaria muiri*	male, female
Crystal	17-Jul-03	J. Krejca, V. Loftin	JKK-021-A1	*Amplaria muiri*	3 males, females
Crystal	17-Jul-03	J. Krejca, V. Loftin	JKK-027-A2	*Amplaria muiri*	5 females
Hurricane Crawl	16-Jul-03	J. Krejca, S. Fryer, A. Snow, V. Loftin	JKK-17-A5	*Amplaria muiri*	very small juvenile
Hurricane Crawl	16-Jul-03	J. Krejca, S. Fryer, A. Snow, V. Loftin	JKK-18-A3	*Amplaria muiri*	female
Hurricane Crawl	16-Jul-03	J. Krejca, S. Fryer, A. Snow, V. Loftin	JKK-10-A1	*Amplaria muiri*	female
Hurricane Crawl	9-Jul-04	J. Krejca, A. Gluesenkamp et al	JKK-47-D2	*Amplaria muiri*	2 males, female
Hurricane Crawl	9-Jul-04	J. Krejca, A. Gluesenkamp et al	JKK-47-D3	*Amplaria muiri*	very small juvenile
Hurricane Crawl	9-Jul-04	J. Krejca, A. Gluesenkamp et al	JKK-44-D2	*Amplaria muiri*	2 males, 2 females

to be contineud.

TABLE 1. (continued)

Cave	Date	Collectors	Collection number	Species	Notes
Lange	6-May-04	J. Krejca, V. Sprouse, S. Fryer, C. Walck	JKK-90-C16	*Amplaria muiri*	very small juvenile
Lange	5-Jun-04	J. Krejca, P. Sprouse et al	JKK-94-C1	*Amplaria muiri*	3 males, 2 females
Pet Cemetery	11-May-04	J. Krejca, S. Fryer, A. Snow, P Sprouse	JKK-1323-C1	*Amplaria muiri*	female
Pet Cemetery	11-May-04	J. Krejca, S. Fryer, A. Snow, P Sprouse	JKK-122-C9	*Amplaria muiri*	3 males, 2 females
Pet Cemetery	11-May-04	J. Krejca, S. Fryer, A. Snow, P Sprouse	JKK-123-C1	*Amplaria muiri*	3 females
Pet Cemetery	11-May-04	J. Krejca, S. Fryer, A. Snow, P Sprouse	JKK-120-C14	*Amplaria muiri*	male, female
Lilburn	15-May-04	J. Krejca, S. Fryer, A. Snow, D. Boiano	JKK-201-C5	*Amplaria sp.*	juvenile
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-113-C8	*Amplaria sp.*	female
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-110-C5	*Amplaria sp.*	juvenile
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-115-C9	*Amplaria sp.*	female
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-114-C3	*Amplaria sp.*	very small juvenile
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-114-C3	*Amplaria sp.*	juvenile
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-115-C9	*Amplaria sp.*	female
Weisraum	10-May-04	J. Krejca, P. Sprouse et al	JKK-114-C16	*Amplaria sp.*	2 females
Windy Pit	4-May-04	J. Krejca, S. Fryer, A. Snow, P Sprouse	JKK-72-C5	*Amplaria sp.*	Smallpigmented individual; immature,probably adamsi

Distribution; See Table 1 and fig. 23.

Habitat, abundance and life history: Eighty-four specimens from Bear Den Cave, Carmoe Crevice, Crystal Cave, Hurricane Crawl Cave, Lange Cave, and Pet Cemetery Cave were positively identified, and another nine immature and female specimens from Lilburn Cave and Weisraum Cave were tentatively identified (Table 1), and the following data are based on those 93 individuals. Air temperatures were recorded for 75 of those collections and the average air temperature where specimens were collected was 10.4 deg C (range = 8.3 to 12.5 deg C). Substrates were recorded for 37 of those collections: 43% (16/37) were found on a silt floor, 24% (9/37) were found on a dead small mammal, 16% (6/37) were found on roots, 11% (4/37) were found on calcite, and 5% (2/37) were found under a rock. Of those 37 collections, 73% (27/37) were associated with some kind of energy source, including fungus, roots, a dead mammal or bait on a pitfall trap. For all 93 specimens, the average distance they were found into the cave was 80 m (range = 0 to 166 m). Also on average one *A. muiri* was found per 7 linear meters of cave passage (range = 1 m to 48 m). For 82 specimens with records of search effort, on average 18 person minutes were spent to find one millipede (range = 4 to 98 person minutes).

On two occasions *Amplaria muiri* were observed mating (Fig. 27). On 15 July 2003, two individuals in the Whitewash Canyon section of Crystal Cave were observed mating on a fluffy sandy silt floor. On 13 October 2006, two individuals in the passage below the rope drop of Carmoe Crevice were observed mating on a gravel floor. A third individual was nearby and probably involved, as it was seen curled up so that its mouth was near its gonopods. Also on 13 October 2006, an unusual abundance of individuals were seen feeding on the seed of a California Bay Laurel, *Umbellularia californica*. Approximately thirty individuals were seen within 5 meters of the food item, and this abundance of prey also probably attracted a potential predator, the salamander *Ensatina eschscholtzii* (Fig. 26).

Methods for habitat, abundance and life history: Temperatures were measured using an alcohol thermometer, and they were measured at locations in the same area of the cave the specimen was taken from, but not always exactly at that spot. Distances into the cave were calculated from survey stations measured during cave mapping, and these represent actual line of travel through the cave, not a straight line distance to the entrance that may be impossible to follow because it is through bedrock. The distance each organism was found into the cave was calculated for the search area the specimen was found in. The search area is bound by two survey stations, and if the closest survey station to the entrance is 10 meters into the cave and the farthest one is 20 m into the cave, the distance that specimen was found from the entrance is calculated at 15 m into the cave. The range that individual was found at is 10 to 20 m from the entrance. The distance between these two stations is an approximate measure of search area, in this case 10 linear meters of passage. In the cases of two long caves, Crystal Cave and Hurricane Crawl Cave, the distances were estimated based on personal experience in the cave. The search time was calculated as person minutes spent in that area, and this time also includes searching for non-millipede taxa, and time to collect specimens and record data. Furthermore, not every millipede seen was collected and these data are based on collected specimens, so the data may slightly overestimate rarity.

Notes: The caves of Sequoia National Park and Kings Canyon National Park, explored by JKK and her associates during a survey of cave fauna for the National Park Service, occur in five distinct clusters (Fig. 23), which we have arbitrarily numbered 1–5 from north to south. *Amplaria muiri* has only been found in the caves of cluster 2. Unidentifiable striariids (males were not collected) were found in Lilburn Cave in cluster 1; these could also be *A. muiri.* As shown in Table 1, millipeds attributable to *A. muiri* were collected in Bear Den Cave, Carmoe Crevice, Crystal Cave, Hurricane Crawl Cave, Lange Cave, Pet Cemetery Cave and Weisraum Cave. Males were not available from the last listed of these caves, but geography makes a good case that the specimens taken in Weisraum Cave are *A. muiri*. Specimens from Hurricane Crawl Cave and Weisraum Cave were moderately well-pigmented, but those from the other caves were pale yellowish white. Because no attempt was made to collect extensively in the forest litter and soil near the caves or elsewhere in the parks, it is not possible to say if *A. muiri* is cave-limited. The legs and antennae are not inordinately long, and while at the large end of the size spectrum of *Amplaria* species (except for the giant *A. shastae*), a convincing picture of troglobiosis is not presented. The pale populations may represent permanent cave residents (troglophiles) but still may be in reproductive contact with surface populations.

***Amplaria adamsi*, n. sp.**

Figs. 16–22, 25

Types: Male holotype from Hidden Cave, Sequoia National Park, Tulare Co., California, collected 15 November 2003 by Jean Krejca and V. Loftin (FMNH); male and female paratypes from Overhang Cave, Sequoia National Park, Tulare Co., California, collected 29 April 2004 by J. Krejca and P. Sprouse (FMNH).

Diagnosis: This species is smaller, more darkly pigmented (Fig. 25), and has more ocelli than *A. muiri;* details of the gonopods are also different.

Etymology: After the late Ansel Adams, an extraordinary photographer whose finest pictures depict the Sierra Nevada.

Description: Male: length, 12.0 mm, width, 0.89 mm. Structure much as in *A. muiri*, but with 5–7 small, irregular, depigmented ocelli. Metazonites with reticulate pattern of purplish brown, darker pigment along posterior borders of metazonites, edges of crests. Legs and antennae light tan to yellowish white. Secondary sexual modifications as described for genus.

FIGURES 24–26. 24. *Amplaria muiri* in Lange Cave. 25. *Amplaria adamsii* in Clough Cave. 26. *Amplaria muiri* ecology in Carmoe Crevice. To the right is an individual of the salamander *Ensatina eschscholtzii*, found near a large group of *Amplaria muiri* that were feeding on the seed of a California Bay Laurel (left). The salamander was not observed eating the millipeds, but likely preys on them.

FIGURE 27. *Amplaria muiri* mating in Carmoe Crevice. Male above and slightly to the right; note use of encrassate anterior legs of male in clasping female.

Gonopods (Figs. 17–22) robust, anterior angiocoxites appressed in midline, apically only gently curved, with even margin lacking teeth, broad, thin lateral branch not much curved, with teeth as shown in Figs. 21, 22; posterior angiocoxites with flagellar sheathing branch long, accessory process extending a little beyond tip of sheathing groove, posterior branch narrow, geniculate, evenly rounded apically. Colpocoxites typical of genus (note: poorly sclerotized lateral lobe of colpocoxite collapses in SEM preparation). Legpair 9 as in Fig. 16.

Female: length, 12.0 mm, width, 0.81 mm. Similar to male in nonsexual characters.

Distribution: See Table 1 and fig. 23.

Habitat and abundance: Thirteen specimens from Hidden Cave, Overhang Cave and Clough Cave were positively identified, and another immature specimen from Windy Pit was tentatively identified (Table 1), and the following data are based on those 14 individuals. Air temperatures were recorded for 10 of those collections and the average air temperature where specimens were collected was 11.2 deg C (range = 8 to 15.3 deg C). Substrates were recorded for 13 of those collections, and 54% (7/13) were found under a rock on the floor, 15% (2/13) were found on a gravel floor, and 8% (1/13) were found on each of these substrates: under woody debris, on a silt floor, on ringtail scat, and on a calcite wall. Of those 13 collections, 62% (8/13) were associated with some kind of energy source, including woody debris, bat guano, ringtail scat, roots, and moldy applesauce. For all fourteen specimens, the average distance they were found into the cave was 74 m (range =

0 to 153 m). On average one *A. adamsi* was found per 25 linear meters of cave passage (range = 10 m to 70 m), and 54 person minutes of search effort (range = 16 to 154 person minutes).

Methods for habitat and abundance: The same methods were used for this species as for *Amplaria muiri*, above.

Notes: Amplaria adamsi has been collected in caves of Cluster 5, namely Clough, Hidden, Overhang, and Windy Pit Caves (Table 1, Fig. 23). Males were not taken in Windy Pit Cave, but it seems unlikely that cave harbors a different species. Noticeably smaller than *A. muiri* and consistently pigmented, with 5–7 pale ocelli, *A. adamsi* is at best a troglophile, and surface collecting in suitable habitats would undoubtedly turn it up. Having described these two species, it should be noted that all the caves named on the map (Fig. 23) were visited, many repeatedly, so the absence of strirariids from a given cave is important. Collectors noted, however, that repeat visits continued to produce new species records and that the fauna were sparse and infrequently detected, suggesting that continued search efforts may yield more localities. These two species might be quite local, but in the absence of extensive surface collecting, full distribution of either species has not been established.

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