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FRESHWATER ISOPODS OF THE GENUS *LIRCEUS* FROM CAVES AND SPRINGS OF THE INTERIOR HIGHLANDS, USA, WITH DESCRIPTION OF THREE NEW SPECIES (ISOPODA: ASELLIDAE)

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ABSTRACT

Eleven species of the freshwater isopod genus *Lirceus* occur in the Interior Highlands, a region of the south-central United States comprised of the Ozark and Ouachita physiographic provinces. As part of research on the morphology and molecular genetics of eastern North American asellid isopods, three new species of *Lirceus* were discovered in the Interior Highlands. *Lirceus slayorum*, n. sp., is described from Greathouse Spring, Washington County, Arkansas and occurs in caves and springs associated with the Ozark Springfield Plateau. *Lirceus ozarkensis*, n. sp., is described from Maxey Cave, Pulaski County, Missouri and was originally identified in 1949 by Hubricht and Mackin as a subspecies of *Lirceus hoppinae*. In actuality, *L. ozarkensis* is quite distinct from *L. hoppinae*, and occurs allopatrically in caves and springs of the southern Ozark Salem Plateau in southern Missouri. *Lirceus robisoni*, n. sp., is described from Abernathy Spring, Polk County, Arkansas and is found in only a few springs in a narrow area of the Ouachita Mountains in western Arkansas. Eight other species of *Lirceus* occur in the Interior Highlands, most of which are confined to springs and caves. New localities are presented and the ranges of the species are established. Illustrations of the genital pleopods demonstrate a common theme across the species of the Interior Highlands, with all possessing a sperm-transfer cannula arising adjacent to a variously papillate or dentate digitiform lateral process, and nestled under a dominant broadly rounded or subtriangular apex. Within this morphological template, some of the Ozark species, like *Lirceus bidentatus*, are among the most anatomically bizarre in North America.

INTRODUCTION

The isopod crustaceans of the genus *Lirceus* generally prefer cool, lotic waters and thus gravitate toward the groundwaters of caves, springs, and seeps. The region known as the Interior Highlands (Fig. 1), comprised of the Ozark and Ouachita physiographic provinces (Hunt, 1967), abounds in these habitats. The first *Lirceus* discovered in the Ozarks was described as *Asellus hoppinae* (Faxon, 1889). The species was discovered in a cave in Jasper County, Missouri by the remarkable Ruth Hoppin, who was also attributed with discovery of the Ozark cavefish *Troglichthys rosae*. Subsequently, Mackin and Hubricht (1938), described *Mancasellus ouachitaensis* from streams in the Ouachita Mountains of eastern Oklahoma, and documented *Asellus hoppinae* (Faxon) from several new sites in the Ozarks of northern Arkansas. Included in the publication of the new species by Mackin and Hubricht (1938) were descriptions and illustrations of the male second (genital) pleopod endopodite tip. By that point in time, it had been recognized that description of the male genitalia of isopods of the Family Asellidae was crucial in any characterization of a new species (Racovitza, 1920).

The largest contribution to the literature concerning *Lirceus* in the Interior Highlands was the monograph by Hubricht and Mackin (1949), who described five new species from the region.

It was their belief that *Asellus hoppinae* was a widespread species in the Interior Highlands, which was transferred to the genus *Lirceus,* with description of three subspecies: (1) *Lirceus hoppinae hoppinae*, occurring in southwestern Missouri and northwestern Arkansas; (2) *L. h. ouachitaensis* received *Mancasellus ouachitaensis*, in eastern Oklahoma; and (3) *L. h. ozarkensis* for populations in southcentral Missouri. All records of *Asellus hoppinae* from Mackin and Hubricht (1938) were assigned to *Lirceus bicuspidatus*, a new species described by Hubricht and Mackin (1949). The other species described by Hubricht and Mackin (1949) from the Interior Highlands were *Lirceus megapodus, L. bidentatus, L. trilobus* and *L. garmani*.

For reasons that now elude us, Hubricht and Mackin (1949) did not include the morphology of the male second (genital) pleopod in their species descriptions. This was problematic, as none of the species described by Hubricht and Mackin (1949) could be recognized or identified, and distribution patterns were impossible to ascertain for *Lirceus* species. Thus, this important group of isopods became a morass of unidentifiable species.

The purpose of this paper is to describe three new species of *Lirceus*, plus supplement the work of Hubricht and Mackin (1949) with illustrations of the male second pleopod endopodite for species of the Interior Highlands. This characterization of the species now allows accurate identification and delimitation of the ranges. This paper is a companion

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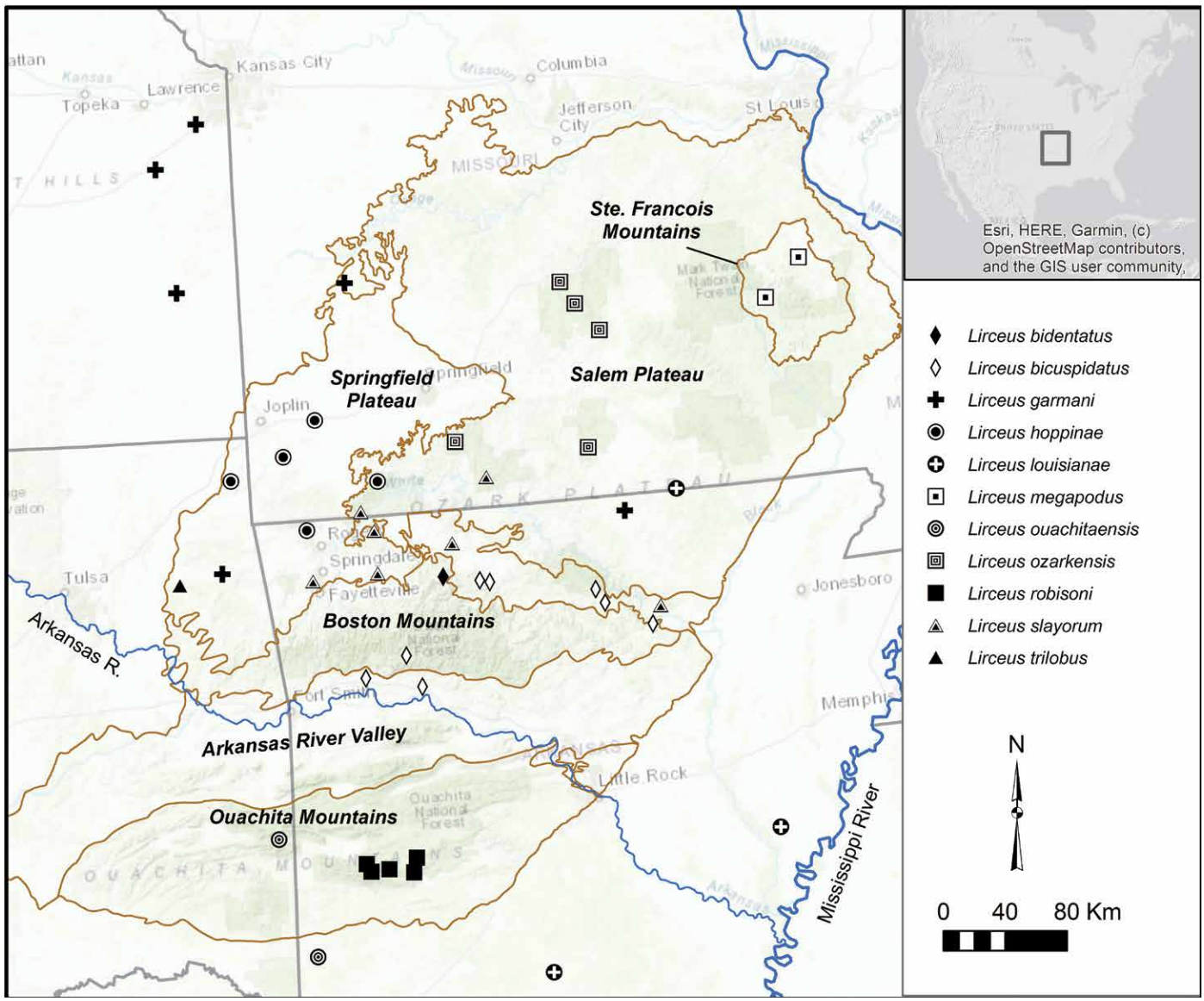

Figure 1. Map of occurrence of *Lirceus* species in the Interior Highlands.

to a monograph of the groundwater isopods of Virginia and the surrounding Appalachian region (Lewis, et al., 2023). Molecular phylogenetic analysis of the asellids of eastern North America, which is included in the Virginia monograph, confirms the status of the genus *Lirceus* as a monophyletic group. Fresh material was collected for all Interior Highland species except *Lirceus trilobus,* and molecular analysis demonstrated divergence greater than 0.16 substitution per site in the mitochondrial cytochrome oxidase 1 gene, as measured by patristic distances (Douady, C.J. and Malard, F., unpublished data). Thus, not only are all taxa herein morphologically distinct species, the molecular genetic analysis strongly supports these species (Lefébure et al., 2006).

MATERIALS AND METHODS

Specimens for this research were obtained from several sources, the richest of which was the collection of the National Museum of Natural History (USNM), Smithsonian Institution, maintained at the Smithsonian Museum Support Center in Suitland, Maryland. There we found the type specimens and other material collected by Leslie Hubricht and utilized in the monograph of Hubricht and Mackin (1949). The type specimens of *Lirceus hoppinae* were obtained on loan from the Museum of Comparative Zoology, Harvard University, in Cambridge, Massachusetts.

Other specimens were contributed by Henry W. Robison (Professor Emeritus, Southern Arkansas University), Michael Slay (The Nature Conservancy), Michael Sutton (Cave Research Foundation), and collections of the authors. All new material was placed in the collection of the Smithsonian Institution.

The precision of some cave-associated localities is restricted per state cave surveys (National Speleological Society internal organizations) to county level to protect the security of cave entrance location information. Where distances were included in localities, the collection vial label information was copied verbatim for clarity in future retrieval of the specimens, with the English system if measurement retained when used by the collector ("mile" was abbreviated as "mi.").

The isopods were examined using a Leica stereo dissecting microscope, with appendages for illustration removed and placed in temporary glycerin mounts on glass microscope slides. These were then placed on a Leica compound microscope with an optical drawing tube, with which pencil drawings were prepared. The drawings were then inked, scanned, and placed into plates with Adobe Illustrator.

DNA sequencing of the asellid species of the Interior Highlands discussed herein was conducted as part of the extensive molecular phylogenetic work presented by Lewis et al. (2023), and detailed procedures are included there. Inferences presented here are from sequencing of the mitochondrial 16S and CO1 genes, plus nuclear Fast2 and 28S rDNA genes. The sequences were deposited in Genbank (National Center for Biotechnology Information (NCBI), National Institutes of Health (NIH)) and accession numbers are presented with the new species descriptions. The molecular phylogeny of the *Lirceus* species of the Interior Highlands is included in Lewis, et al. (Fig. 8, 2023), including references to the molecular operational taxonomic units (MOTUs).

Figure 2. S. L. Lewis using a dipnet to collect the type series of *Lirceus slayorum* from organic debris in the spring run of Greathouse Springs, Washington Co., Arkansas.

SYSTEMATICS

Lirceus Rafinesque, 1820

Lirceus slayorum, new species

Lirceus hoppinae ozarkensis.—Hubricht and Mackin, 1949: 344 [Bear Creek Springs record]

Lirceus hoppinae sensu latu.—Graening, et al., 2007: 9 [in part]

Material examined: ARKANSAS: Benton Co.: Electric Springs, 1.2 mi. NE Rogers, M. E. Slay, C. M. Slay, 12 Nov 2004, 1♂1♀; Boone Co.: Bear Creek Springs, J. J. Lewis, S. L. Lewis, 18 Jun 2016, 11♂♀; Carroll Co.: Sweet Spring, on Spring Street, Eureka Springs, J. J. Lewis, S. L. Lewis, 17 Oct 2017, 1♂; same locality and collectors, 19 Oct 2017, 2♀; Independence Co.: Spring Mill Run (Big Spring), 6.2 mi. NW Batesville, J. J. Lewis, S. L. Lewis, 11 May 2022; Madison Co.: Withrow Springs, 4.9 mi. N Huntsville, J. J. Lewis, S. L. Lewis, 18 Jun 2016, 1♀. Washington Co.: Greathouse Springs, 5.7 mi. NNW Fayetteville, J. J. Lewis, S. L. Lewis, 16 Jun 2016, 60♂♀; same locality, M. E. Slay, 7 Aug 2018, 42♂♀. MISSOURI: Barry Co.: spring branch below entrance of Twilight Joint Cave, M. Sutton, 25 Aug 2001, 1♂1♀; Taney Co.: Spring Cave, stream in entrance zone, M. Sutton, 11 Dec 2004, 1♂.

Type material: Holotype ♂ (USNM 1508058) and 59♂♀ paratypes (USNM 1436126) collected 16 June 2016, and 42♂♀ paratypes (USNM 1607414) collected 7 August 2018, from Greathouse Springs, Washington Co., Arkansas (Figs. 1 and 2) located at N36.13951 W94.19803, deposited in the collection of the Smithsonian Institution. Genbank (NCBI) accession numbers of material sequenced from the type-locality at Greathouse Springs are 16S: OX383329, OX383330, OX383331; CO1: OX383323, OX383324; 28S: OX383342, OX383343; Fast2: OX383337, OX383338.

Diagnosis: Separated from its geographic neighbors by its 1-merous mandibular palp, which is 3-merous in *L. hoppinae* and *L. bicuspidatus*. The pleopod 2 endopodite tip of *L. slayorum* and *L. hoppinae* possesses a subtriangular caudal

process in both species, but the cannula in *L. slayorum* is short and emerges from the center of the space between the mesial and lateral processes, while it is longer and emerges from the side of the lateral process in *L. hoppinae*. The closest genetic relative of *L. slayorum* (indicated as MOTU 452 *Lirceus* undescribed species by Lewis, et al., Figure 8, 2023) is *L. hoppinae*.

Description: Length to 8.0 mm, body 2.8× as long as wide, grayish-brown pigmentation dorsally, darkest on anterior of head, head and pereonites with stippled appearance along lateral margins, otherwise with mottled pattern darkest along midline, pleotelson with stippled, granular appearance (Fig. 3). Head with distinct eyes, lateral margins entire, incisions not apparent in dorsal view, lateral incision suture line visible in ventral view. Antenna 1 flagellum of 7 articles, reaching to distal margin of penultimate article of antenna 2, distal five articles with one aesthetasc each. Mandibular palp 1-merous with apical seta (Fig. 4).

Figure 3. Living specimen of *Lirceus slayorum*, length approximately 8 mm, from Greathouse Springs, Washington Co., Arkansas illustrating dorsal pigmentation pattern and relative proportions of appendages (photo by Michael Slay, The Nature Conservancy).

Pereopod 1, propodus about 1.6× as long as wide, palmar margin with stout proximal spine, medial process large, subtriangular, apically blunt, distal process low, broadly rounded; dactylus, flexor margin weakly spinose, 3−4 larger spines distally, decreasing in size proximally.

Pleotelson broader proximally, tapering distally, about 1.1× wider than long; caudomedial lobe modestly produced, broadly rounded, uropodal sinuses present. Pleopod 1, protopod with 4−5 retinaculae, exopod about 1.3× longer than protopod, about 0.67× as wide as long, setae longest on lateral margin, decreasing in length then increasing at apex. Pleopod 2, protopod with single seta on distal-mesial margin; exopod, proximal article without setae; distal article subtriangular, relatively elongate, about 1.4× as long as wide, apex blunt, about 11 elongate setae along lateral and apical margins; endopod tip subtriangular, tapering to a rounded caudal process, cannula small but distinct, cylindrical, extending from bowl formed between base of lateral and mesial processes, base of cannula obscured by lateral dentate/papillate curved digitiform process, mesial process with a short knob at base, main process a broad lobe slightly longer than lateral process. Pleopod 3, exopod with many setae along lateral and apical margins, longest distolaterally, shortest setae along apical margin, anterior surface sparsely setose with smaller setae. Pleopod 4, exopod with sigmoid suture with weak lines dividing lateral and apical margins into four parts; proximal section with 15 setae, mesial section with 18 setae, distolateral section with 7 setae, apical margin without setae. Pleopod 5, exopod with 4 proximolateral setae proximal to weak lateral false suture.

Uropods equal or slightly longer than pleotelson, protopod flattened, exopod and endopod slightly flattened; endopod equal in length to protopod, exopod about 0.75× length of endopod.

Etymology: This species is named in honor of Christy Melhart Slay (The Sustainability Consortium) and Michael Slay (The Nature Conservancy), in recognition of their dedication to environmental conservation and sustainability. Suggested vernacular name is Slays' spring isopod.

Habitat and range: This species is endemic to the karst of the Ozark Springfield Plain in northern Arkansas and the adjacent part of the southwestern Salem Plateau in Missouri, spanning a range of about 140 miles (225 km). Preliminary analysis of the 16S mitochondrial gene of a sample from the eastern edge of the range (Independence County) suggests that population is an undescribed cryptic species included here within the morphospecies *L. slayorum*.

At Greathouse Spring (Fig. 2) the isopods were abundant on rocks and sticks in the spring run along Arkansas State Highway 112. Elsewhere *L. slayorum* occurs in cave entrances and springs, where it typically inhabits stream gravels and the undersides of stones

***Lirceus ozarkensis* Hubricht and Mackin, 1949, new status, new species**

Lirceus hoppinae ozarkensis Hubricht and Mackin, 1949: 336, 344; Williams, 1972: 14.

Material examined: MISSOURI: Christian Co.: Cascade Spring Cave, M. Sutton, 19 Feb 2000, 2♂; Rattlesnake Cave, M. Sutton, 19 Feb 2000, 1♂; Ozark Co.: Bat Cave, M. Sutton, 20 Sep 2003, 1♂; same locality and collector, 6 Mar 2004, 1♂; Pulaski Co.: stream at mouth of Maxey Cave, 2 mi. N Hanna, L. Hubricht, 8 Oct 1939, 78♂♀; Fort Leonard Wood: Sand Boil Spring, M. E. Slay, S. Taylor, 12 May 2004, 5♂ 1 juvenile; *Lirceus* Shelter, M. E. Slay, S. Taylor, 13 May 2004, 2♂2♀; Defile Spring, S. Taylor, M. E. Slay, V. R. Block, 19 Apr 2003, 5♂2♀; Kerr Cave, S. Taylor, V. R. Block, 26 Mar 2003,

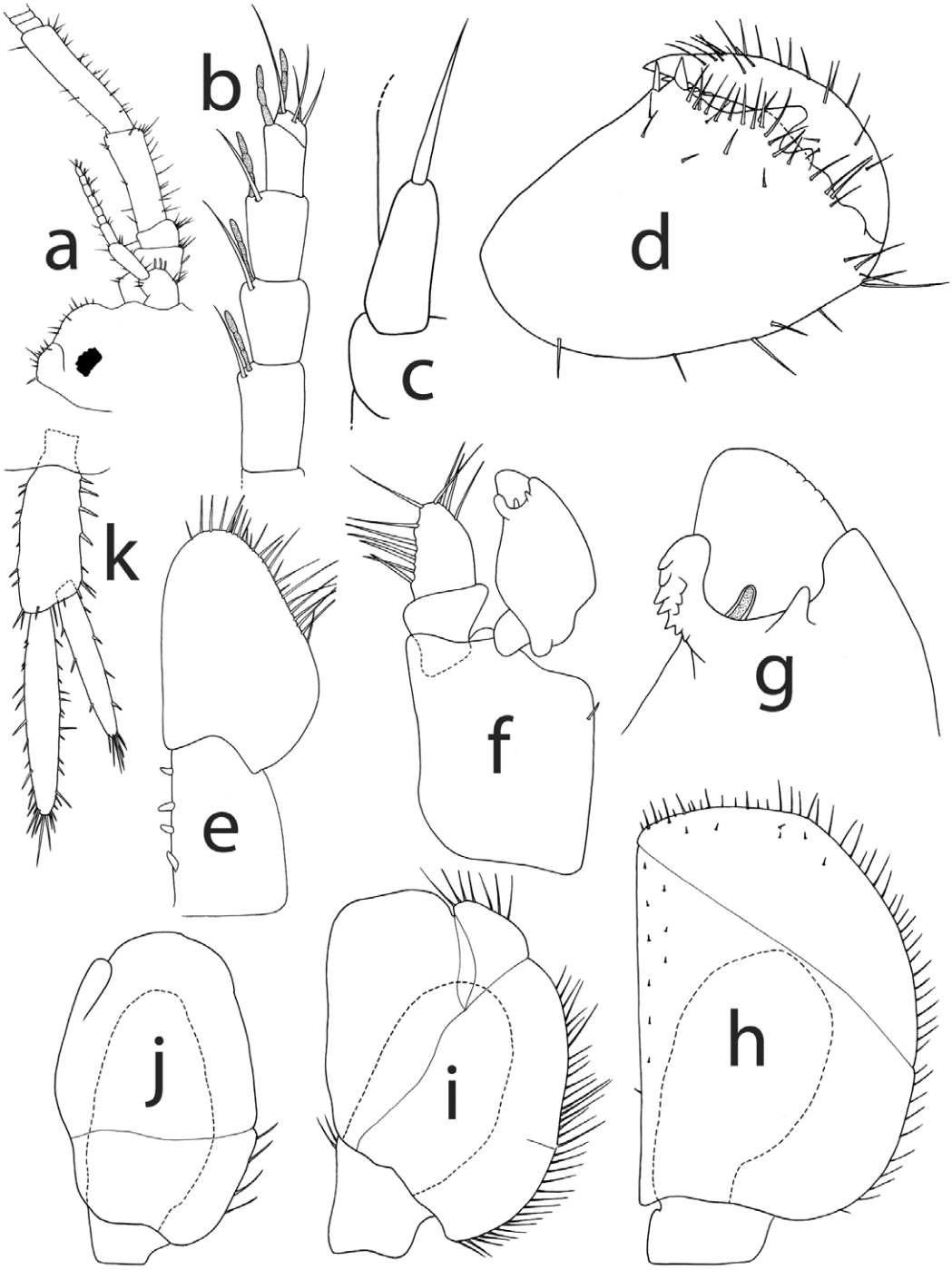

Figure 4. *Lirceus slayorum*, n. sp., Greathouse Springs, Washington Co., Arkansas: (a) head, antenna 1, antenna 2 peduncle (pigmentation omitted), (b) antenna 1 distal articles, (c) mandibular palp, (d) pereopod 1, propodus and dactylus, (e) pleopod 1, (f) pleopod 2, (g) pleopod 2 endopodite tip, (h) pleopod 3, (i) pleopod 4, (j) pleopod 5 and (k) uropod.

1♂3♀; Texas Co.: Bat Cave, from spring mouth of cave, L. Hubricht, 5 Jul 1940, 12♂♀; Boiling Springs, 5.5 mi. ENE Success, J. J. Lewis, S. L. Lewis, 14 Oct 2017, 12♂♀.

Type material: Syntypes 78♂♀ specimens (USNM 1254684) from Maxey Cave, Pulaski Co., Missouri, deposited in the Smithsonian Institution by Hubricht and Mackin (1949). The specimens from the type-locality were believed to be a subspecies of *Lirceus hoppinae* by Hubricht and Mackin (1949), however our analysis revealed that neither the morphology nor genetics were conspecific with that species. The subspecies is elevated to the status of new species. Genbank (NCBI) accession numbers of material sequenced from Boiling Springs, Texas County, Missouri, are 16S: OX383334; CO1: OX383325, OX383326; 28S: OX383344, OX383345; Fast2: OX383339, OX383340.

Diagnosis: This species is distinguished from *L. hoppinae* by the apex of the male second pleopod endopod, which is broadly rounded in *L. ozarkensis*, but subtriangular in *L. hoppinae*. The mandibular palp of *L. ozarkensis* possesses 1 article, whereas it is 3-merous in *L. hoppinae* and *L. bicuspidatus*, the allopatric neighbors in southwestern Missouri and adjacent Arkansas. *Lirceus slayorum* also has a 1-merous mandibular palp, but is separable by its pleopod 1 with retinaculae, which are absent in *L. ozarkensis*. The closest genetic relative of *L. ozarkensis* (indicated as MOTU 368 *Lirceus* undescribed species by Lewis, et al., Figure 8, 2023) is *L. louisianae. Lirceus ozarkensis* is readily separated from *L. louisianae* by the latter's lack of a mandibular palp.

Description: Length to 19 mm, body 2.6× as long as wide, pigmentation darkest on anterior part of head, pereonites with brown mid-line stripe, mottled light areas on either side blending into darker gray area on margins, pleotelson with stippled pattern of relatively large blotches of grayish pigment. Head with eyes distinct, lateral incisions prominent. Man-

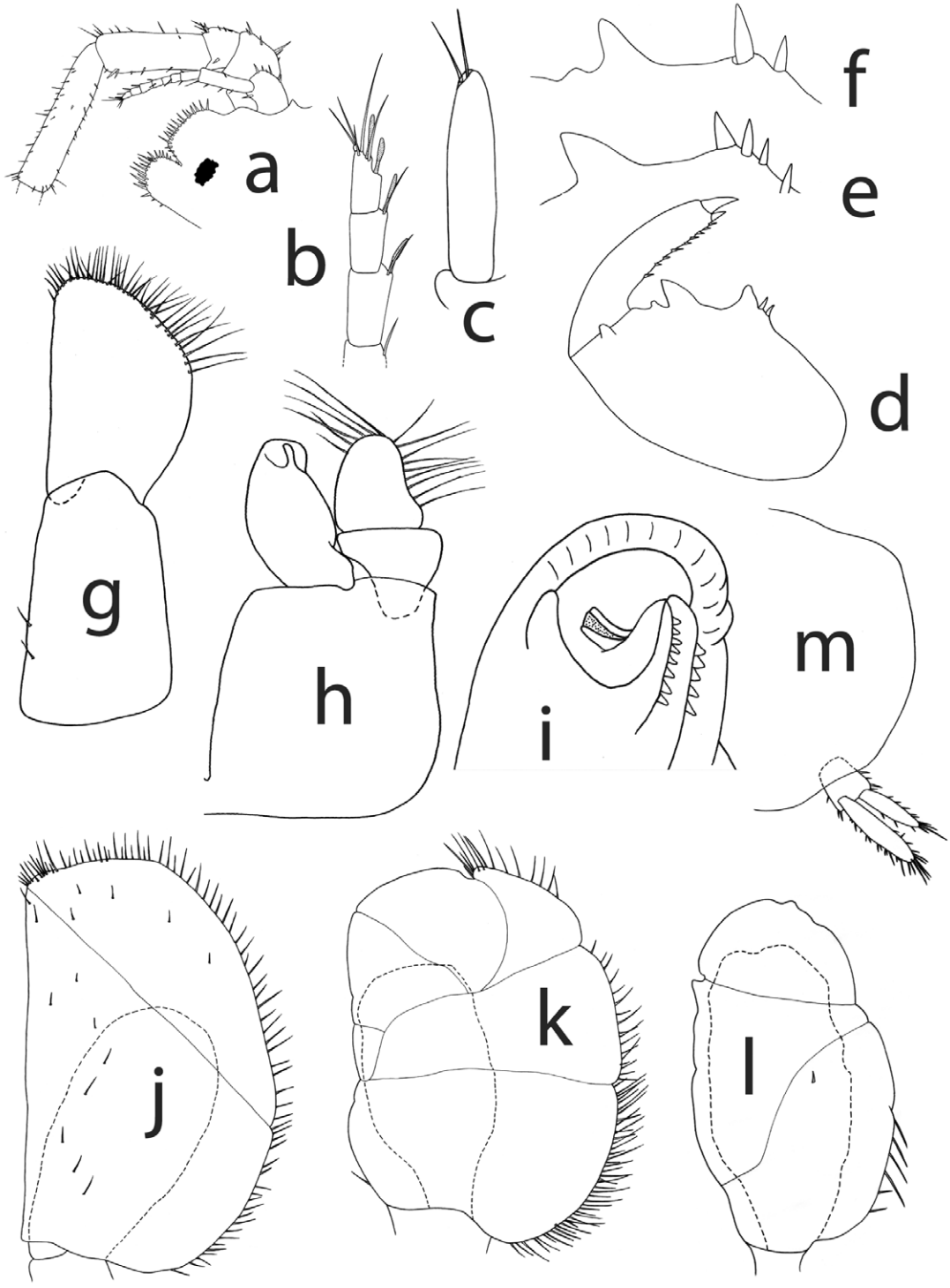

Figure 5. *Lirceus ozarkensis*, n. sp., Maxey Cave, Pulaski Co., Missouri: (a) head, antenna 1, antenna 2 peduncle (pigmentation omitted); (b) antenna 1 distal articles; (c) mandibular palp; (d) pereopod 1, propodus and dactylus (setation omitted); (e) same, palmar margin; (f) same, palmar margin; (g) pleopod 1; (h) pleopod 2; (i) same, endopodite tip; (j) pleopod 3; (k) pleopod 4; (l) pleopod 5, and (m) pleotelson and uropod.

dibular palp 1-merous. Antenna 1 flagellum of 6−7 articles, reaching to distal margin of penultimate article of antenna 2, distal four articles each bearing one aesthetasc (Fig. 5).

Pereopod 1, propodus about 1.6× as long as wide, palmar margin with proximal spine or subtriangular process, separated by wide cleft from subtriangular medial process ranging from about the same height in individuals with proximal spine or slightly higher if proximal process is present, separated by u-shaped cleft from low distal rounded knob; dactylus, flexor margin with 9−10 small spines increasing in size distally.

Pleotelson widest proximally, tapering distally, about 0.8× as long as wide, caudomedial lobe broadly rounded, uropodal sinuses modestly developed. Pleopod 1, protopod without retinaculae, exopod about 0.9× length of protopod, distolateral marginal setae decreasing in length distally. Pleopod 2, exopod distal article subovate, 1.4× as long as wide, apex broadly rounded, about 17 elongate setae along margin; endopod apex broadly rounded, rugose laterally; cannula distinct, slightly conical, tapering slightly distally, extending variably from perpendicular to obliquely to the axis of the endopod, arising from mesial wall of lateral process; lateral process relatively large, obstructing cannula in anterior aspect, dentate along medial and lateral margins; mesial process digitiform. Pleopod 3, exopod with many setae along lateral and apical margins, anterior surface sparsely setose with smaller setae. Pleopod 4, exopod with weak, difficult to discern false suture lines dividing lateral and apical margins into four parts; proximal section with >40 setae,

Figure 6. Panoramic photo (collage of 5 images) of Abernathy Spring, Polk County, Arkansas. The water emerges from a 30-inch diameter pipe in the upper right of the photo (red arrow). Approximately three meters of the spring downstream from the orifice the substrate is monopolized by a microbial mat, which is then replaced by a variety of emergent green plants in which the isopods occur. An 8-inch sieve and plastic containers are present in the lower right side of the photo for scale.

mesial section with 17 setae, distolateral section with 14 setae, apical margin without setae. Pleopod 5, exopod with 6 proximolateral setae proximal to weak sigmoid false suture and second distal transverse false suture.

Uropods up to 0.7× length of pleotelson; protopod flattened, endopod up to 1.4× longer than protopod.

Etymology: The name of this species refers to its occurrence in the Ozark Plateaus. Suggested vernacular name is the Ozark spring isopod.

Habitat and range: Lirceus ozarkensis occurs in southcentral Missouri in the western part of the Ozark Salem Plateau (Fig. 1). Hubricht and Mackin (1949) presented records from Laclede and Maries counties that remain unconfirmed, but seem reasonable. The type-locality was commercialized under the name Inca Cave, then acquired by the Missouri Department of Conservation in 2011 and designated Great Spirit Cave Conservation Area.

This species is known from springs and the entrance zone of caves. At Boiling Springs, Texas County, we found *Lirceus ozarkensis* in the entrance of a mostly water-filled cave by digging about 15 cm below the surface into gravel interstices. In this subsurface habitat *L. ozarkensis* was found with the stygobiontic species *Caecidotea salemensis* and *C. antricola*.

***Lirceus robisoni*, new species**

Lirceus ouachitaensis.—Lewis, 1983: 152.

Material examined: ARKANSAS: Montgomery Co.: Collier Springs, 5.2 mi. ENE Norman, H. W. Robison, 16 Jun 1979, 30♂♀; same locality and collector, 24 Aug 2018, 26♂♀; Ida Sublette Spring, Caddo Gap, H. W. Robison, 24 Aug 2018, 32♂♀; small rocky stream adjacent to parking area for Little Missouri Falls, 21.5 mi. ESE Mena, J. J. Lewis, S. L. Lewis, 13 May 2022, 2♂5♀; unnamed spring at Arkansas Game and Fish Commission boat launch on Caddo River, in Caddo Gap, H. W. Robison, 24 Aug 2018, 11♂♀; Polk Co.: Abernathy Spring, H. W. Robison, 21 Dec 2018, 17♂♀; same locality and collector, 23 Aug 2018, 4♂♀; same locality and collector, 16 Jun 1979, 100+♂♀; same locality, J. J. Lewis, S. L. Lewis, 13 May 2022, 44♂♀; Boxx Spring, on Forest Road 73, 1.2 mi. from state highway 8, H. W. Robison, 23 Aug 2018 7♂6♀; same locality and collector, 21 Dec 2018, 36♂♀.

Type material: Holotype ♂ (USNM 1607404), 17♂♀ paratypes (USNM 1607405; USNM 1608025), and 44♂♀ paratypes (USNM 1593460), from Abernathy Spring, 0.8 mi. west of the Polk-Montgomery Co. line, on the north side of Highway 8 (N34.46816 W93.94798), were deposited in the collection of the Smithsonian Institution. Genbank (NCBI) accession numbers for material sequenced from the type-locality at Abernathy Spring are 16S: OX383335, OX383336; CO1: OX383327, OX383328; 28S: OX383346; Fast2: OX383341.

Diagnosis: An eyed and pigmented species most closely related to *L. bicuspidatus*, from which *L. robisoni* is separated by the male second pleopod endopodite tip with the cannula extending parallel to the axis of the endopodite, and well beyond the margin of the tip, whereas in *L. bicuspidatus* the cannula extends obliquely and is nested among the endopodite tip processes. In *L. robisoni* the palmar margin of pereopod 1 has rounded processes, in large specimens with a shoulder on the medial process (Fig. 8), but not distinctly bi-cuspate as in *L. bicuspidatus*. The closest genetic relative of *L. robisoni* (indicated as MOTU 417 *Lirceus* undescribed species by Lewis, et al., Figure 8, 2023) is *L. bicuspidatus*.

Figure 7. Photo of a living *Lirceus robisoni*, approximately 9 mm in length, from Abernathy Spring, Polk County, Arkansas, illustrating the dorsal pigmentation pattern and proportions of the habitus and appendages.

Description: Length of males to 13.5 mm, ovigerous females to 6.6 mm, body 2.8× as long as wide; dorsal pigmentation darkest on anterior of head (Fig. 7), anterior and lateral margins of head and pereonites unmottled, central and posterior parts of head with mottling, pereonites with moderately pigmented longitudinal midline band with adjacent mottling, margins pigmented, but unmottled, pleotelson darkest in midline, stippled in appearance without pattern. Head with eyes prominent; lateral incisions closed, post-mandibular lobe not apparent, margin of head appears entire. Antenna 1 reaching to distal margin of penultimate article of antenna 2, flagellum of 6 articles, distal 4 each with one aesthetasc. Mandibular palp 3-merous (Fig. 8).

Pereopod 1, propodus about 1.6× as long as wide, palmar margin with prominent proximal spine or process and 1−2 smaller spines, medial process large, rounded or with shoulder in large specimens, separated by U-shaped cleft from lower rounded process; dactylus with subungual spine about half the length of unguis, smaller spines decreasing in size along flexor margin.

Pleotelson subtrapezoidal (Figs. 7 and 9), about 0.8× as long as wide, tapering posteriorly, caudomedial lobe broadly rounded, uropodal sinuses moderately produced. Pleopod 1 longer than pleopod 2, protopod with

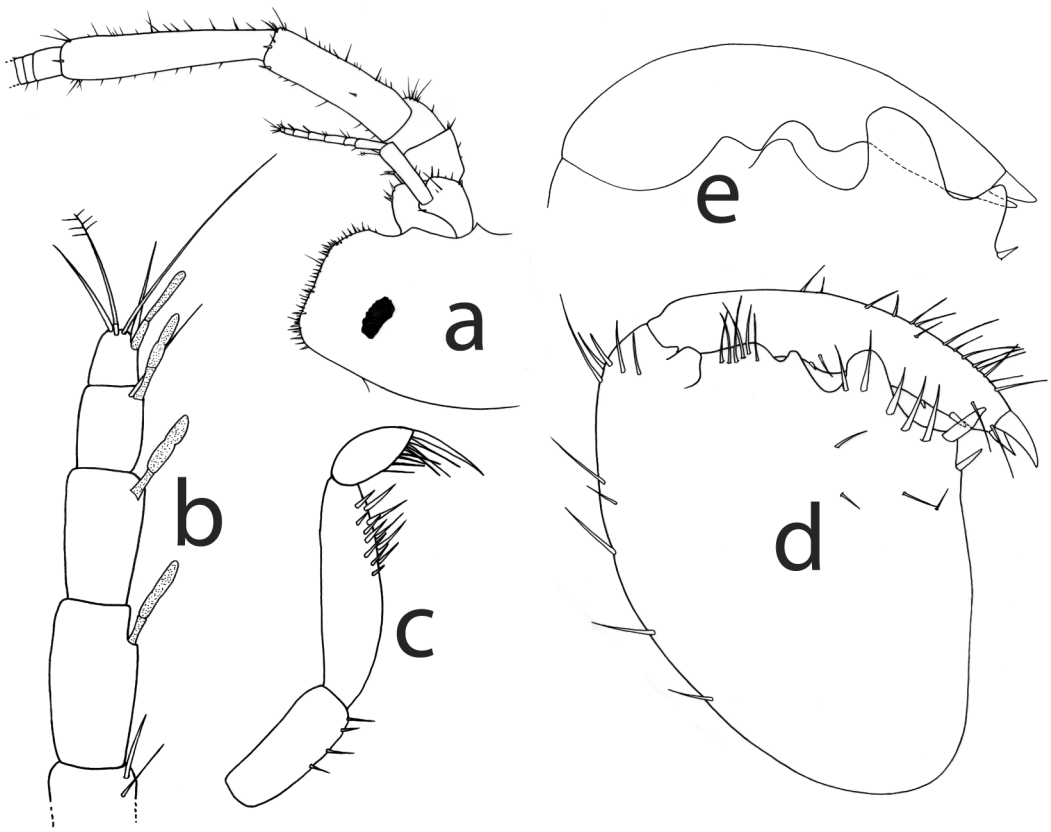

Figure 8. *Lirceus robisoni*, n. sp., Abernathy Spring, Polk Co., Arkansas: (a) head, antenna 1, antenna 2 peduncle (pigmentation omitted); (b) antenna 1 distal articles; (c) mandibular palp; (d) pereopod 1, propodus and dactylus (e) same, palmar margin of different specimen (setation omitted).

3 retinacula, exopod about 1.2× length of protopod, 0.6× as wide as long, setae longest on distolateral margin, decreasing in length slightly at apex (Fig. 9). Pleopod 2, protopod without setae, minute spines along distomesial margin; exopod proximal article without setae, distal article subovate, apex rounded, about 1.5× as long as wide, distal-lateral and apical margins with about 14 elongate setae; endopod, widest medially, tip cannula distinct, cylindrical, extending beyond margin of caudal process approximately parallel to the axis of the endopod; caudal process broadly rounded; lateral process extending diagonally, densely papillate/denticulate. Pleopod 3, exopod with many setae along lateral and apical margins, anterior surface sparsely setose with smaller setae. Pleopod 4, exopod with weak sigmoid false suture dividing lateral and apical margins into four parts; proximal section with >40 setae, mesial section with >20 setae, distolateral section with 13 setae, apical margin without setae. Pleopod 5, exopod with 2 mediolateral setae proximal to weak sigmoid false suture.

Uropods to 0.5× length of pleotelson, protopod flattened, mostly visible beyond margin of pleotelson in dorsal view, exopod and endopod slightly flattened; endopod about 1.5× length of protopod, exopod 0.9× length of endopod.

Etymology: Named in honor of Dr. Henry W. Robison, Professor Emeritus at Southern Arkansas University, collector of the type series of this species, as well as previously discovering *Caecidotea fonticulus* at Abernathy Spring (Lewis, 1983). Suggested vernacular name is Robison's spring isopod.

Habitat and range: Lirceus robisoni is known from six localities in the Ouachita Mountains on the north side of the Caddo Mountains, in Polk and Montgomery counties, Arkansas. Five of the localities are springs, along with one small (possibly spring-fed) stream. At the type-locality, the waters of Abernathy Spring emerge from the fractured Bigfork chert formation at the faulted contact with the underlying Womble shale (both Ordovician). A 30-inch (76 cm) diameter vertical pipe provides a well-like situation historically used as a domestic drinking water supply. Abernathy Spring discharges approximately 30 gallons per minute (Arkansas Geological Survey, 1937) at 16 °C (Wagner and Steele, 1980). McAllister (2020) described the site as a mineral spring, with iron (ferrous) carbonate the primary chemical constituent.

We visited Abernathy Spring on 13 May 2022. At that time the substrate for about the first three meters downstream from the spring orifice was covered with a thick, brownish-orange flocculent microbial mat that was not inhabited by isopods (Fig. 6). Beyond that point emergent plants filled the spring run and *L. robisoni* was common on the vegetation. The substrate was comprised of gravels in which were found both *L. robisoni* and the endemic stygobiontic *Caecidotea fonticulus* (Lewis, 1983).

***Lirceus hoppinae* (Faxon, 1889)**

Asellus hoppinae Faxon, 1889: 232, 237−238, plate II.—Mackin and Hubricht, 1938: 632.

Asellus incisus.—Van Name, 1936: 464−465

Mancasellus incises.—Mackin, 1940: 17.

Lirceus hoppinae hoppinae.—Hubricht and Mackin, 1949: 336, 343, 349; Williams, 1970: 73; 1972: 14.

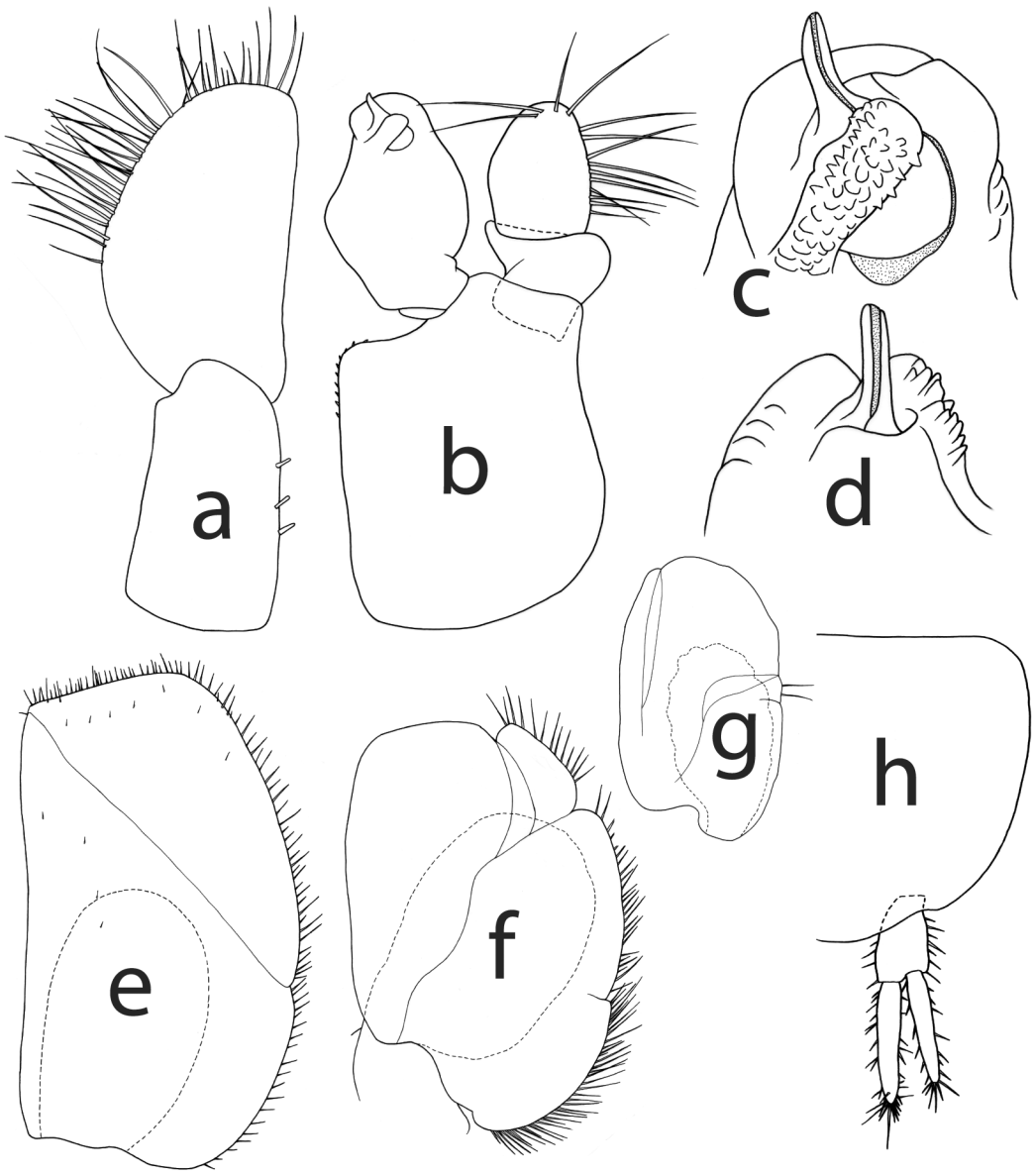

Figure 9. *Lirceus robisoni*, n. sp., Abernathy Spring, Polk Co., Arkansas: (a) pleopod 1; (b) pleopod 2; (c) pleopod 2 endopodite tip; (d) same, rotated laterad; (e) pleopod 3; (f) pleopod 4; (g) pleopod 5; (h) pleotelson and uropod.

Lirceus hoppinae.—Pennak, 1978: 446; Graening, et al, 2011: 61, 159.

Lirceus hoppinae sensu latu.—Graening, et al., 2007: 3, 9 [in part].

Material examined: ARKANSAS: Benton Co.: Big Spring, Bella Vista, L. Hubricht, 7 May 1940, 40♂♀. MISSOURI: Barry Co.: Mushroom Rock Cave, M. Sutton, 10 May 2002, 1♂1♀; spring near Dogwood Blossom Cave, M. Sutton, 11 Mar 2019, 1♂; Hidden Salamander Cave, M. Sutton, 2 Dec 2019, 1♀; Wet Foot Cave, M. Sutton, 2 Dec 2019, 1♂1♀; spring near Cobblestrewn Cave, M. Sutton, 2 Dec 2018, 1♀; Jasper Co.: Day's Cave, Sarcoxie, in mud under stones, R. Hoppin, date unknown, 4♂; same locality, L. Hubricht, 22 May 1942, 75♂♀; Newton Co.: Hearrell Spring, Neosho National Fish Hatchery, J. J. Lewis, S. L. Lewis, 16 Oct 2017, 20♂♀; Big Spring, Neosho, J. J. Lewis, S. L. Lewis, 16 Oct 2017, 1♂ 5♀; spring 1.4 mi. N of Tipton Ford, L. Hubricht, 9 May 1940, 58♂♀. OKLAHOMA: Ottawa Co.: Schifflet Cave, G. Graening, D. Fenolio, 6 Dec 2003, 4♂; Cave Springs Ranch Cave, G. Graening, D. Fenolio, 14 Dec 2003, 4♂.

Type material: Syntypes 4♂ (Faxon, 1889) collected by Ruth Hoppin from Day's Cave, Jasper Co., Missouri (N37.06988 W94.11871), in the collection of the Museum of Comparative Zoology (MCZ 4203), Harvard University, Cambridge, Massachusetts.

Diagnosis: The 3-merous mandibular palp separates the species from *L. slayorum*, with 1-merous mandibular palp. The pleopod 2 endopodite of *L. hoppinae* (Fig. 10a, b) has a prominent subtriangular caudal process with the elongate cannula extending at an oblique angle from the base of the papillate lateral process. In *L. slayorum* the cannula is shorter and nestled between lateral and mesial processes.

Habitat and range: The range of this species is restricted from that envisioned by Hubricht and Mackin (1949) as encompassed by three subspecies of *Lirceus hoppinae* to a smaller region of southwestern Missouri, northwestern Arkansas, and adjacent Oklahoma, corresponding to a portion of the Ozark Springfield Plateau (Fig. 1). The isopods inhabit springs and caves, usually near the entrance. The type-locality, Day's Cave (also known as Dowler or Sarcoxie cave) is in the Sarcoxie Cave and Spring Preserve owned by the Ozark Land Trust.

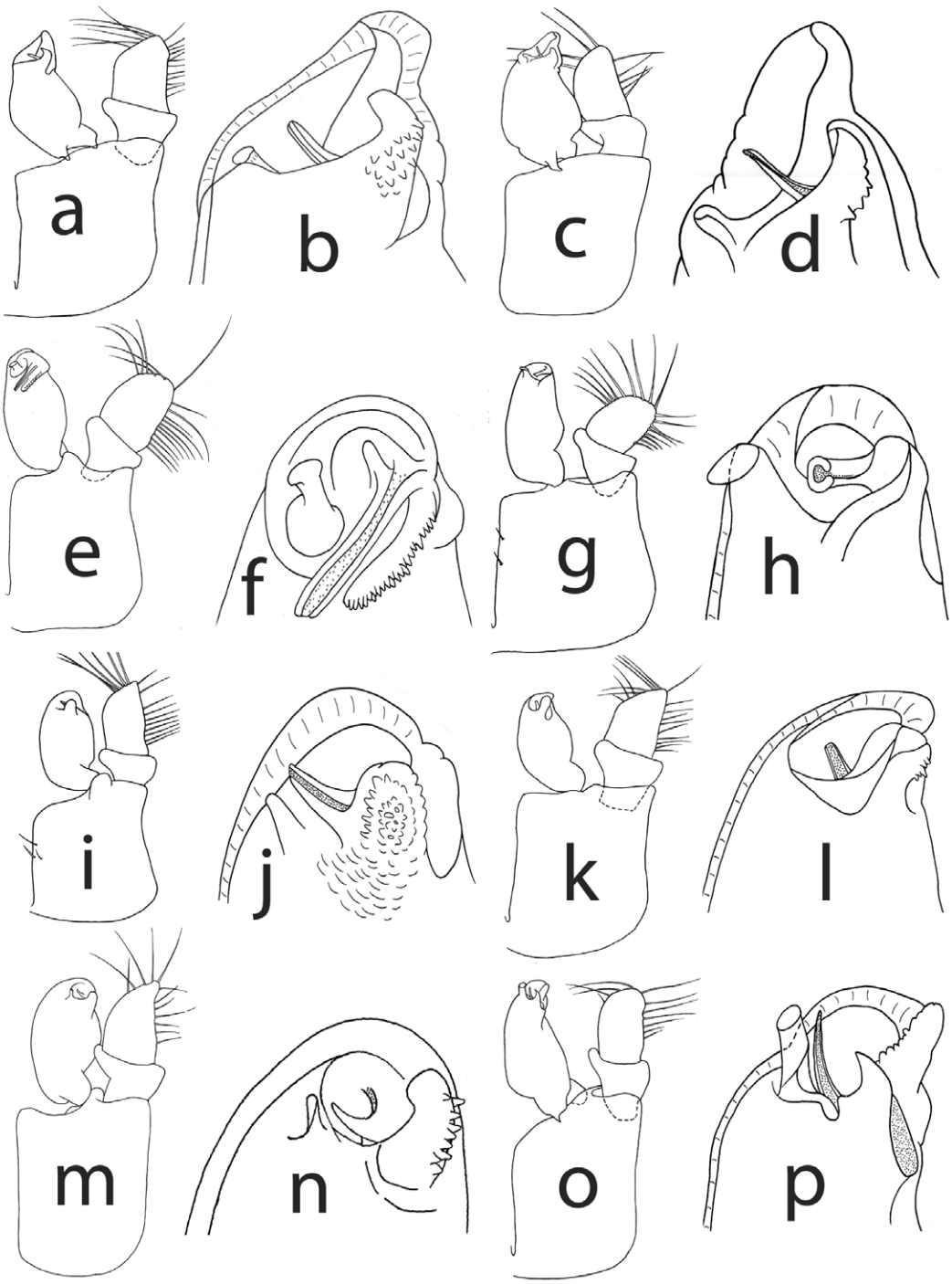

Figure 10. Pleopod 2 and endopodite tip of *Lirceus* species: (a-b) *L. hoppinae,* Day's Cave, Jasper Co., Missouri ; (c-d) *L. ouachitaensis*, tributary of Kiamichi River, Leflore Co., Oklahoma; (e-f) *L. bidentatus*, seep on Osage Creek, Boone County, Arkansas; (g-h) *L. megapodus*, spring 4 mi. NW of Hogan, Iron County, Missouri; (i-j) *L. bicuspidatus*, spring behind college chapel, Clarksville, Johnson County, Arkansas; (k-l) *L. garmani*, temporary stream, Cedar County, Missouri; (m-n) *L. louisianae*, seeps 0.6 mi. S of Junction City, Claiborne Parish, Louisiana; (o-p) *L. trilobus*, spring 3.2 mi. S Locust Grove, Mayes County, Oklahoma.

***Lirceus ouachitaensis* (Mackin and Hubricht, 1938)**

Mancasellus ouachitaensis Mackin and Hubricht, 1938: 632−633.

Lirceus hoppinae ouachitaensis.—Hubricht and Mackin, 1949: 337, 344; Williams, 1972: 14.

Lirceus ouachitaensis.— Graening, et al., 2007: 3, 9−10 [in part]; Graening, et. al, 2011: 159.

Material examined: ARKANSAS: Sevier Co.: Walnut Spring, 1.7 mi. ENE Horatio, off Arkansas State Highway 24, H. W. Robison, 19 Aug 2018, 6♂1♀. OKLAHOMA: Leflore Co.: tributary of Kiamichi River, Ouachita National Forest, J. G. Mackin, 30 Mar 1935, 21♂♀.

Type material: Syntypes 10♂♀ (USNM 108819) and 21♂♀ (USNM 108820) from a tributary of the Kiamichi River, near Big Cedar, LeFlore Co., Oklahoma, deposited in the Smithsonian Institution (Mackin and Hubricht, 1938).

Diagnosis: Distinct from other species of the Ouachitas by the absence of a mandibular palp. The pleopod 2 endopodite is narrow, subtriangular, cannula narrow, mesial process a short knob (Fig. 10c, d). This taxon was considered a subspecies of *Lirceus hoppinae* by Hubricht and Mackin (1949), but is morphologically and genetically distinct.

Habitat and range: Lirceus ouachitaensis occurs in the Ouachita Mountains in western Arkansas and eastern Oklahoma, where it occurs in creeks and springs. Hubricht and Mackin (1949) listed tributary streams in Latimer and Pushmataha counties (Fig. 1).

***Lirceus bidentatus* Hubricht and Mackin, 1949**

Lirceus bidentatus Hubricht and Mackin, 1949: 336, 344−345, 349; Williams, 1972: 14; Robison and Smith, 1982: 53; Robison and Allen, 1995: 47−48; Graening, et al. 2007: 2−3, 8; Robison, et al., 2008: 92; Graening, et al., 2011: 72, 159.

Material examined: ARKANSAS: Boone Co.: seepage area, Osage Creek at bridge, 1 mi. W Compton, M. E. Slay, C. Slay, 7 Mar 2009, 26♂♀; small seeps, 9 mi. SW Harrison, L. Hubricht, 8 Apr 1939, 18♂♀. Newton Co.: Hutchinson Waterfall Cave, 2.2 mi. ESE Compton, M. E. Slay, C. Bitting, C. M. Slay, 29 Dec 2004, 1♂2♀; Tight-N-Twisty Cave, 1.8 mi. ENE Compton, M. E. Slay, C. Brickey, 11 Dec 2004, 1♂.

Type material: Syntypes 18 ♂♀ (USNM 108813) from small seeps 9 mi. SW of Harrison, Boone Co., Arkansas (Hubricht and Mackin, 1949) deposited in the Smithsonian Institution.

Diagnosis: The extremely long, tubular cannula of the male second pleopod endopodite is unique in the genus (Fig. 10e, f), as well as bizarre and unmatched among other North American asellids.

Habitat and range: This species is endemic to a small area of northern Arkansas in the Boston Mountains, with a range of less than 5 kilometers. *Lirceus bidentatus* occurs in seeps, springs, and cave entrances.

***Lirceus megapodus* Hubricht and Mackin, 1949**

Lirceus megapodus Hubricht and Mackin, 1949: 337, 342−343, 348; Williams, 1972: 15.

Material examined: MISSOURI: Iron Co.: small spring 2 mi. N of Belleview, L. Hubricht, 29 Sep 1940, 54♂♀; spring 4 mi. NW of Hogan, L. Hubricht, 18 Jan 1942, 217♂♀; St. Francois Co.: Rock Spring, 1.5 mi. NE Doe Run, J. J. Lewis, S. L. Lewis, 10 Jun 2016, 1♂3♀.

Type material: Syntypes 217♂♀ (USNM 1254685) from a spring 4 mi. NW of Hogan, Iron Co., Missouri (Hubricht and Mackin, 1949) deposited in the Smithsonian Institution.

Diagnosis: Characterized by the enormous pereopod 1 propodus of adult males, which separates *Lirceus megapodus* from other species in the genus, as well as the elongate, laterally projecting tubular cannula of the second pleopod endopodite (Fig. 10g, h). The absence of retinaculae on the protopod of pleopod 1 is unusual, shared with *L. ozarkensis*. The molecular phylogeny of Lewis, et al., (Fig. 8, 2023) suggests that *L. megapodus* differs from other *Lirceus* of the Interior Highlands at the subgenus level.

Habitat and range: This species is endemic to the St. Francois Mountains in southeastern Missouri (Hubricht and Mackin, 1949), where it inhabits seeps and springs emerging from fissures in granitic bedrock (Fig. 1).

***Lirceus bicuspidatus* Hubricht and Mackin, 1949**

Lirceus bicuspidatus Hubricht and Mackin, 1949: 336, 345, 349; Williams, 1972: 14; Robison and Smith, 1982: 53; Robison and Allen, 1995: 47; Graening, et al. 2007: 2−3, 8; Robison, et al., 2008: 87, 92; Graening, et al., 2011: 72, 159.

Lirceus n. sp.—McDaniel and Smith, 1976: 58.

Material examined: ARKANSAS: Franklin Co.: creek at bridge on highway 21, no. 1, M. E. Slay, 26 Feb 2009, 23♂♀; Independence Co.: Foushee Cave Spring Run, M. E. Slay, 11 Mar 2010, 4♂2♀; same locality, M. E. Slay, J. Baxter, 25 Feb 2020, 6♂2♀; Foushee Cave, M. E. Slay, 14 Jun 2011, 15♂♀; same locality, M. E. Slay, J. Baxter, 25 Feb 2020, 3♂8♀; Johnson Co.: Bull Creek Flats Spring, 15 mi. NNW Clarksville, L. D. Leeds, 28 Dec 2020, 19♂♀; small creek W of the College Chapel, Clarksville, L. Hubricht, 28 Apr 1938, 86♂♀; Spadra Branch 1, M. E. Slay, 26 Feb 2009, 38♂♀; spring west of chapel, University of Ozarks, M. E. Slay, 4 Apr 2009, 22♂♀; same locality and collector, 26 Feb 2009, 29♂♀; Newton Co.: Dear Buster Cave, W. Baker, 28 May 2006, 2♂1♀; NW41bb Cave, W. Baker, 4 Mar 2006, 1♂1♀; seep at hillside cabin at Lost Valley Canoe and Cabin, M. E. Slay, C. M. Slay, 11 Nov 2003, 7♂2♀; Spring below collapsed cave, Yardelle, 18 Oct 2017, J. J. Lewis, S. L. Lewis, 5♂♀; Steel Creek Cave, G. O. Graening, D. Fenolio, 12 Dec 2004, 1♂1 juvenile; spring below Whitely School in Buffalo River Valley, M. E. Slay, 11 Nov 2008, 5♂2♀; Searcy Co.: spring on Kelly Creek, M. E. Slay, 25 Feb 2008, 3♂3♀; spring at mouth of Great Hurricane Cave, L. Hubricht, 22 Oct 1939, 42♂♀; West Spring Hollow, M. E. Slay, 25 Feb 2008, 3♂4♀, 1 juvenile; Stone Co.: Barkshed picnic area spring, M. E. Slay, 8 Mar 2010, 11♂3♀, 1 juvenile; Big Spring, M. E. Slay, K. Furr, 9 Mar 2010, 4♂10♀; Blanchard Springs Caverns spring run, M. E. Slay, 23 Aug 2008, 2♂2♀ +fragments; Branscum Spring, M. E. Slay, K. Furr, 9 Mar 2010, 8♂2♀; Mountain View, city park spring, M. E. Slay, 10 Mar 2010, 2♂1♀, 1 juvenile; Mountain View, city park stream, M. E. Slay, 10 Mar 2010, 16♂♀; Tarwater Spring, M. E. Slay, 11 Mar 2010, 1♂1♀; Mountain View, spring in stone amphitheater in city park, J. J. Lewis, S. L. Lewis, 14 May 2022, 17♂♀; unspecified site 2.5 mi. N Mountain View, on Arkansas 9, V. R. McDaniel, 29 Nov 1974, 9 juveniles.

Type material: Syntypes 78♂♀ (USNM 108871) from a small stream west of the college chapel, Clarksville, Johnson Co., Arkansas (Hubricht and Mackin, 1949) deposited in the collection of the Smithsonian Institution. This site is an intermittent spring about 100 meters west of the Munger-Wilson Memorial Chapel on the campus of the University of the Ozarks, located at N35.4775 W93.4689.

Diagnosis: This is the only Ozark *Lirceus* with two bicuspate processes on the palmar margin of pereopod 1 propodus. It is further separated from other Ozark species by the combination of the fused lateral incisions of the head, 3-merous mandibular palp and male pleopod 2 endopodite tip with prominent cannula terminating within the margin of the broadly rounded caudal process (Fig. 10i, j).

Habitat and range: The range of this species is restricted herein to the Boston Mountains of northern Arkansas, about half the area reported by Hubricht and Mackin (1949), who included the Ouachita Mountains (now identified as *L. robisoni*). Preliminary data from sequencing of the mitochondrial 16S gene suggests that this remains a simplification, i.e., *L. bicuspidatus* is a morphospecies comprised of multiple cryptic undescribed species not readily separable by features of the male pleopod endopodite tip. One of these is a troglomorphic population in Foushee Cave, Independence County, Arkansas (Fig. 11).

Lirceus bicuspidatus is an inhabitant of springs, spring-fed streams and caves. At the type-locality, the isopods are common when the water table is sufficiently high for the spring to flow. During dry times of the year the spring disappears, along with the isopods, which presumably retreat into the groundwater.

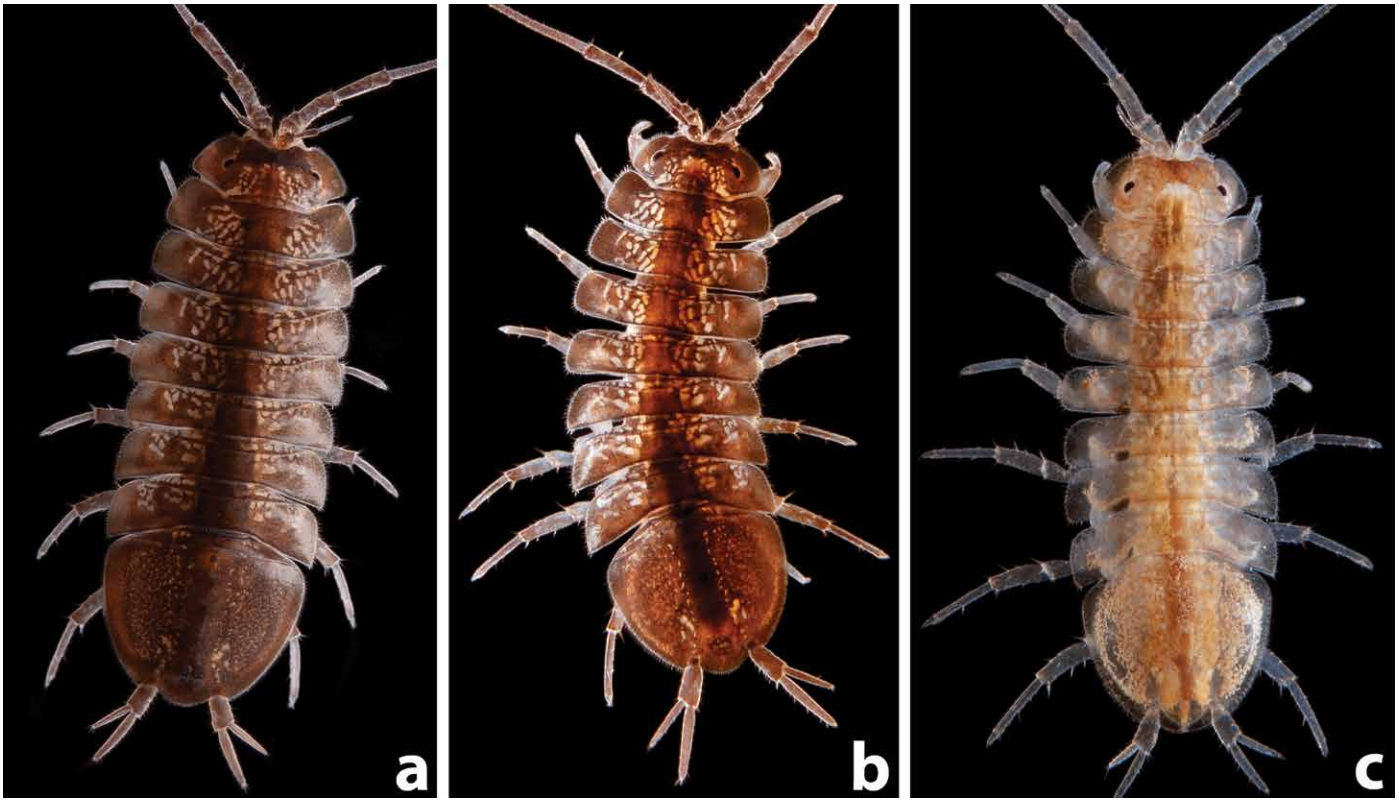

Figure 11. Dorsal pigmentation patterns in Arkansas *Lirceus bicuspidatus* populations: (a) type-locality at Clarksville, Johnson County; (b) Foushee Cave Spring, Independence County; (c) Foushee Cave. (photos by Michael Slay, The Nature Conservancy).

Lirceus garmani Hubricht and Mackin, 1949

Lirceus garmani Hubricht and Mackin, 1949: 337, 345−346; Black, 1971: 7; Williams, 1972: 14. Schultz, 1973: 349−364; Nickol, 1985: 326; Pennak, 1978: 446; Graening, et al., 2007: 3, 8−9; Graening, et al., 2011:159.

Mancasellus macrourus.—Fleming, 1938:310−313; Mackin and Hubricht, 1938: 632 [in part].

Lirceus germani.—Bass, 1994: 7.

Material examined: ARKANSAS: Fulton Co.: sluggish stream in roadside ditch next to Arkansas State Highway 62, 0.6 mi. SSE Flint Spring, J. J. Lewis, S. L. Lewis, 18 Jun 2016, 1♂ 5 juveniles. KANSAS: Bourbon Co.: seep 2.3 mi. S Bronson, L. Hubricht, 17 May 1942, 10♂♀; seep 2.2 mi. E Uniontown, L. Hubricht, 17 May 1942, 16♂♀; Franklin Co.: abandoned well, Wheeler Farm, 5.0 mi. SSE Ottawa, L. Hubricht, 31 Aug 1941, 2♀; spring on Dunkak Farm, 1.5 mi. NW Lane, L. Hubricht, 31 Aug 1941, 44♂♀; Johnson Co.: small temporary stream 1 mi. NE Clare, L. Hubricht, 31 Aug 1941, 14♂♀. MISSOURI: Cedar Co.: temporary stream 3.6 mi. E Cedar Springs, L. Hubricht, 17 May 1942, 42♂♀. OKLAHOMA: Mayes Co.: spring at girl scout camp, 3.2 mi. S Locust Grove, L. Hubricht, 22 May 1940, 15♂♀; Locust Grove spring, J. C. Stout, G. O. Graening, D. Fenolio, 21 Jan 2006, 4♂3♀; spring 3.7 mi. W Locust Grove, L. Hubricht, 31 Aug 1941, 64♂♀; stream in roadside park 0.5 mi. E Locust Grove, upstream of pipe spring, J. J. Lewis, S. L. Lewis, 12 Jun 2016, 12♂♀.

Type material: Syntypes 42♂♀ (USNM 1254682) from a temporary stream 3.6 mi. east of Cedar Springs, Cedar Co., Missouri (Hubricht and Mackin, 1949) deposited in the collection of the Smithsonian Institution.

Diagnosis: Lirceus garmani is separated from other Ozark *Lirceus* by the male second pleopod endopodite that appears two-lobed distolaterally, and the pereopod 1 propodus processes that descend in size distad (Fig. 10k, l).

Habitat and range: This species appears to have a broader range of acceptable habitats than other *Lirceus* occurring in the Interior Highlands. *Lirceus garmani* is primarily known from the Osage Plains region in eastern Kansas, eastern Oklahoma, and western Missouri, with sporadic records in northern Arkansas. The species occurs in springs, seeps, small creeks, and ponds. Black (1971) reported an occurrence in a cave. The Illinois record (Page, 1974) is an error.

***Lirceus louisianae* (Mackin and Hubricht, 1938)**

Mancasellus louisianae Mackin and Hubricht, 1938: 634.

Lirceus louisianae.—Hubricht and Mackin, 1949: 337, 342, 348; Williams, 1972: 15; Graening, et al., 2007: 3, 9; Patrick, 2003: 41; Pennak, 1978: 446.

Material examined: ALABAMA: Greene Co.: roadside ditch 0.8 mi. N Boligee, L. Hubricht, 11 Feb 1962, 13♂♀. ARKANSAS: Fulton Co.: Mammoth Spring, impounded lake below spring, J. J. Lewis, S. L. Lewis, 18 Jun 2016, 19♂♀; Ouachita Co.: Scale Springs, 14.2 mi. NE Camden, H. W. Robison, 23 Jul 2022, 3♂1♀. Phillips Co.: slough 0.5 mi. S Turner, L. Hubricht, 7 Apr 1941, 14♂♀. FLORIDA: Walton Co.: spring 1.5 mi. NE Grayton Beach, under stones, W. Farmer, 27 Dec 2016, 18♂♀. LOUISIANA: Claiborne Parish: seeps 0.6 mi. SE Junction City, L. Hubricht, 8 Apr 1941, 40♂♀; Natchitoches Parish: dead leaves in small creek below an artificial pond, 2 mi. S Saline, L. Hubricht, 19 Apr 1936, 2♂3♀. MISSISSIPPI: Oktibbeha Co.: ditch 6.8 mi. SW junction of state routes 25 and 12, on SR 25, W.G. Anding, 26 Feb 1968, 9♂♀. TEXAS: Nacogdoches Co.: permanent seep area, Nacogdoches, D.C. Rudolph, J.A. Matos, 16 Feb 1980, 3♂1♀.

Type material: Syntypes, 2♂ (USNM 74843), 3♀ (USNM 108807) from a small creek below an artificial pond, 2 mi. S of Saline, Natchitoches Parish, Louisiana (Mackin and Hubricht, 1939), deposited in the Smithsonian Institution.

Diagnosis: This species is separable from other *Lirceus* by a combination of characters: the triangular distal article of the exopod of the second pleopod and coiled appearance of the endopodite tip cannula arising from the papillate lateral process (Fig. 10m, n). In the Interior Highlands, *Lirceus louisianae* is readily separated from *L. bicuspidatus* and *L. ozarkensis* by its lack of a mandibular palp.

Habitat and range: The range of *Lirceus louisianae* is expanded herein from that of Hubricht and Mackin (1949) to encompass the lower Mississippi River drainage, from Louisiana to northern Arkansas, west to Texas and east to the panhandle region of western Florida. Records listed above include the first reports from Texas, Mississippi and Florida. Hubricht and Mackin (1949) included southern Illinois based on specimens from two localities in Union County. These specimens were examined and were not conspecific with *L. louisianae*. The discovery of *L. louisianae* in Mammoth Spring, Arkansas is the first report of this species from the Interior Highlands.

This species occurs in springs, seeps, small creeks, sloughs, and ditches. At Mammoth Spring, Arkansas, we found *L. louisianae* inhabiting gravels about 100 meters downstream from the rise pool.

***Lirceus trilobus* Hubricht and Mackin, 1949**

Lirceus trilobus Hubricht and Mackin, 1949: 336, 346, 349; Williams, 1972: 15; Graening, et al., 2007: 2−3, 10; Graening, et al, 2011: 159.

Material examined: OKLAHOMA: Mayes Co.: spring 3.2 mi. S Locust Grove, L. Hubricht, 22 May 1940, 29♂♀.

Type material: Syntypes 29♂♀ designated as woodland pools at a girl scout camp 3.2 mi. south of Locust Grove, Mayes Co., Oklahoma (Hubricht and Mackin, 1949) deposited in the Smithsonian Institution.

In jars of uncatalogued *Lirceus* from Oklahoma in the collection of the Smithsonian Institution we found two vials labeled “spring 3.2 mi. S of Locust Grove”. Each vial contained a different species. This locality was cited by Hubricht and Mackin (1949) for *L. garmani*. In the second vial, the uncatalogued collection was a distinct species that matches the description for *L. trilobus,* now catalogued as USNM 1254708. No vial with a label matching the wording of the type-locality provided by Hubricht and Mackin (1949) was found among Hubricht’s specimens in the Smithsonian collection. The actual collection site of the type specimens of *Lirceus trilobus* remains a mystery. Perhaps a labelling error occurred and the habitat was indeed a woodland pool, but at this point this question seems unlikely to be resolved. The property on which the type-locality of *L. trilobus* is located, Camp Scott, was closed after the murder of three girl scouts in 1977. We attempted to visit the type-locality, but were unable to gain access.

Diagnosis: The male second pleopod endopodite tip is unlike any other species of *Lirceus* in the Interior Highlands, and it is among the most complex of any species in the genus, with a narrow, elongate cannula extending parallel to the axis of the endopod surrounded by 3 anterior processes and caudal process (Fig. 10o, p)

Habitat and range: Lirceus trilobus is known only from the type-locality, in eastern Oklahoma.

SUMMARY AND CONCLUSIONS

During the course of this investigation, we examined 1825 specimens collected from 43 springs, 7 seeps, 18 caves, 1 well, and 14 small streams (including creeks and ditches). Every species, except *Lirceus louisianae*, occurred predominantly in cool-water habitats (springs, seeps and caves). With the description of 3 new species, there are now 11 species of *Lirceus* recognized from the Interior Highlands. Diversity undoubtedly remains underestimated by this number, e.g., with several populations of the morphospecies *L. bicuspidatus* (including one stygobiontic species) remaining to be described.

Hubricht and Mackin (1949) asserted that the genital pleopods were "so similar in different species that they were, with one exception [*Lirceus bidentatus*], useless as a means of separation". We found similarities in the morphology of the male second (genital) pleopod endopodite tips of the Interior Highlands *Lirceus*, including a lateral process that was digitiform, and usually papillate or dentate, along with a dominant broadly rounded or subtriangular apex. That said, there were many differences in the appearance of the genital pleopods, including great variation in the shape and length of the sperm transfer cannula, as well as the shape and proportions of the exopodites. These morphological differences are consistent with molecular phylogenetic evidence that strongly supported the diversity of the *Lirceus* fauna (Lewis, et al., 2023).

From a conservation standpoint, two species are extremely rare and vulnerable: *Lirceus trilobus*, known only from the type-locality; and *L. bidentatus*, known from a few sites within a range of less than five kilometers. Two spring inhabitants, *L. robisoni* and *L. megapodus*, are recorded from only a few localities confined to small ranges.

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