

JEFFERSONIANA

Contributions from the Virginia Museum of Natural History

Number 31

April 2, 2025

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ISBN 1-884549-45-4 (online)

Virginia Museum of Natural History Scientific Publications Series

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RESEARCH ARTICLE

urn:lsid:zoobank.org:pub:8981AFD3-7902-461A-AC06-0135B1733099

The Groundwater Isopods of Virginia, Supplement I: Six New Species of Asellids (Isopoda: Asellidae)

Julian J. Lewis^{1, 2}, Salisa L. Lewis², William D. Orndorff³, Zenah Orndorff⁴, Florian Malard⁵, Lara Konecny-Dupré⁵, and Christophe Douady⁵

ABSTRACT

The purpose of this supplement was to present descriptions of six new species of asellid isopods as well as new records for other asellids inhabiting groundwater habitats of Virginia. Two species of *Lirceus* (*Hargerellus*) are described from southwestern Virginia, *Lirceus douadyi*, n. sp., known only from Quillin Spring, Scott County, and *Lirceus laurae*, n. sp., known only from Woodward Springs, Lee County. New records are provided for six other species of *Lirceus (Hargerellus)*, including the first records of *Lirceus hargeri* in Virginia and *Lirceus stygophilus* in Tennessee. Two new species of the *Caecidotea richardsonae* clade of cryptic species are described, *Caecidotea speleoconservata*, n. sp., from caves in the Cedars area of Lee County, and *Caecidotea malardi*, n. sp., from caves in Tazewell County. New records are presented for *Caecidotea ornatus*. *Conasellus larae*, n. sp., known only from Cohen Spring, Shenandoah County, is described and compared to *Conasellus laticaudatus* and a complex of similar species. *Pseudobaicalasellus novus*, n. sp., is described. It is endemic to caves in the New River drainage in Virginia, and *Pseudobaicalasellus incurvus*, from which the new species was split, is restricted to eastern Tennessee.

INTRODUCTION

The monographic revision of groundwater isopods of Lewis et al. (2023) was a synthesis of morphological taxonomy with molecular phylogenetics. A total of 53 species were discussed that occurred in Virginia or adjacent Appalachian states, including 24 species described as new to science (18 species of *Lirceus*, 3 *Conasellus*, 2 *Caecidotea* and 1 *Pseudobaicalasellus*). Each morphological species corresponded to a unique molecular operational taxonomic unit (MOTU) as delimited using the mitochondrial cytochrome oxidase subunit I (COI) gene. growing body of work on Virginia groundwater asellids and is focused on the description of six new species:

(1) two new species of *Lirceus* (*Hargerellus*) from springs in southwestern Virginia, with an expansion of the range of several species described by Lewis et al. (2023).

(2) two new species of the *Caecidotea richardsonae* clade of cryptic species from caves in Lee and Tazewell counties, Virginia.

(3) a new species from Cohen Spring, in Shenandoah County, belonging to the *Conasellus laticaudatus* species complex.

(4) a new species of Pseudobaicalasellus

This supplement to the monograph adds to the

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endemic to the New River drainage in Virginia, resulting from division of *Pseudobaicalasellus incurvus*, which is restricted herein to eastern Tennessee.

The monograph of Lewis et al. (2023) was shaped by molecular phylogenetics, and we adhered to the concept of one MOTU = one morphological species. Herein, we adapted to the idea that in MOTUs in which the isopods are so morphologically similar that they cannot be readily told apart, MOTUs constituting monophyletic clades could be combined to constitute a single morphospecies. This is a pragmatic approach, as some morphological species, e.g., *Caecidotea richardsonae*, with a range spanning over 300 km, are likely comprised of dozens of MOTUs, making it impractical to describe all of them morphologically as species.

Thus, some of the MOTUs that were identified, but not associated with species in the monograph (Lewis et al. 2023), are resolved here by a mixture of new species descriptions and combination with other morphospecies. For example, MOTU 439 from Quillin Spring, Scott County, Virginia is described herein as *Lirceus douady*, n. sp., while MOTU 444 from Big Spring (only 2 km west of Quillin Spring) is combined with *Lirceus clinchensis* (MOTU 445).

Regarding the members of the *Caecidotea richardsonae* species complex occurring in southwestern Virginia, we are carving the group into successively smaller pieces reflecting the known MOTUs. Most of the known Virginia populations are now accounted for with the description of two additional morphologically distinct species. As a matter of convenience, the populations of the complex occurring in the Maiden Spring Creek drainage upstream of Ward Cove (in Thompson Valley) are combined with *Caecidotea fisherorum*. This is done as a temporary act in view of the presence of small morphological differences in the Thompson Valley populations, as well as the fact that this might create a taxon that is not monophyletic.

MATERIALS AND METHODS

In general, all methods and procedures used

herein were a continuation of those utilized during preparation of the monograph of Lewis et al. (2023). A list of specimens used for molecular analyses with their corresponding species names, sampling codes, and accession numbers of DNA sequences in Genbank (National Center for Biotechnology Information) is presented in Appendix 1.

Family Asellidae Latreille, 1802

Genus Lirceus Rafinesque, 1820

Lirceus (Hargerellus) douadyi Lewis & Lewis, new species

urn:lsid:zoobank.org:act:24A7AD9E-C48F-49A8-B7A4-2F89A1B8BA8B

Figs. 1-4

Material examined: VIRGINIA: Scott County: Quillin Spring, 4.1 miles (6.6 km) N Gate City, J. Lewis, W. Orndorff, Z. Orndorff, 9 Jul 2018, 432 (VMNH112419.1-VMNH112419.6); same locality, J. Lewis, T. Malabad, K. K. Ficco, W. Orndorff, 24 Oct 2022, 335 (VMNH112420.1-VMNH112420.8) and a 6.7 mm 3 holotype (VMNH112418); same locality, J. Lewis, 21 Oct 2023, 232 (VMNH112421.1-VMNH112421.4); same locality, J. Lewis, F. Malard, 25 Apr 2024, 13(VMNH112422).

Besides the holotype, all specimens from the type-locality, Quillin Spring, are designated as paratypes, deposited in the Virginia Museum of Natural History, Martinsville, Virginia. Quillin Spring is located on the west side of Virginia state route 619, at N36.69695 W82.57732.

Material for molecular analysis: VIRGINIA: Scott County: Quillin Spring, 4.1 miles N Gate City, J. Lewis, W. Orndorff, Z. Orndorff, 9 Jul 2018, $3\Diamond^{\circ}$ (site code: QUILLISP).

Diagnosis: Of the three spring-dwelling species of *Lirceus* described from the Clinch River drainage in Virginia, each constitutes a distinct MOTU as delimited using the CO1 gene: *L. douadyi* MOTU



Figure 1. *Lirceus douadyi*, n. sp., head, antenna 1, antenna 2 peduncle and pereonites 1-3, from Quillin Spring, Scott County, Virginia (stacked photomicrograph by M. Milne and J. Lewis).

439, *L. stygophilus* MOTU 442, and *L. katarinae* MOTU 441(Lewis et al. 2023).

Lirceus douadyi is most similar morphologically to L. katarinae and L. stygophilus. Lirceus douadyi differs from L. katarinae by greater ornamentation along the mesial margin of the pleopod 2 protopodite (1 seta in L. douadyi versus 1-2 setae with many combspines present in L. katarinae), less setose pleopod 4 exopod (L. douadvi setae formula >40 -15 - 13, *L. katarinae* >50 - >30 - 15), and less setose pleopod 5 exopod (L. douadyi with no setae, L. katarinae with about 5 setae). L. douadyi differs from L. stygophilus by the absence of the lateral incisions of the head (present as a suture in L. stygophilus), less distinct post-mandibular lobes, less acute medial-lateral carinae, and fewer setae present along the mesial margin of the pleopod 2 protopodite (1 in L. douadyi versus 2-4 setae present in L. stygophilus). Lirceus douadvi is separated from L. clinchensis by the lack of prominent processes on the palmar margin of the pereopod 1 propodus.

Description: Length of males to 6.8 mm, females to 6.5 mm (ovigerous females 5.0 to 5.6

mm), body about 2.6X as long as wide. Eyes prominent and well formed, dorsal pigmentation brownish, darkest on anterior of head, posterior of head and anterior midline longitudinal part of pereonites lighter brown, with irregular pattern of mottled, lightly pigmented spots, lateral margins of pereonites somewhat lighter brown than midline, pleotelson with moderate brown granular stippled pigmentation.

Head anterior margin with medial-lateral carinae broadly rounded, about equal in height with medial carina, lateral margin entire, post-mandibular lobes mildly produced, lateral incisions not apparent. Lateral margins of head, pereonites, and pleotelson moderately setose and spinose. Antenna 1 slightly shorter than distal margin of penultimate article of antenna 2 peduncle, flagellum with 6 articles, with aesthetes on distal 4 articles. Antenna 2, flagellum with about 40 to 43 articles.

Pereopod 1 of male, propodus about 2.2X as long as wide, palmar margin undulating, with one elongate spine, medial process suggested by slightly rounded area; dactyl with stout subungual spine, flexor margin with 2-3 smaller spines and row of lower, broad spines. Female pereopod 1 propodus similar, about 2.2X as long as wide. Pereopod 4, carpus of male 2.2X as long as wide, carpus of female similar; dactyl flexor margin with stout subungual spine, plus 2 smaller stout spines in male, one small spine in female.

Pleotelson widest anteriorly, tapering distally, about as wide as long, caudomedial lobe broadly rounded, uropodal sinuses moderately pronounced. Pleopod 1, protopod mesial margin with 2 retinaculae; exopod about 2X longer than wide, 1.5X length of protopod, lateral and distolateral setae mostly longer than apical setae. Pleopod 2, protopod with 1 mesiodistal seta; exopod, proximal article without setae; distal article subovate, about 1.3X longer than proximal article, about 1.25X as long as wide, with about 12 elongate setae along margins; endopod tip cannula distinct, narrow, tapering distally to a blunt point, extending approximately parallel to the axis of the endopod, caudal margin of endopod scantly rugose, broadly rounded laterally; mesial process stalked, tip bent



Figure 2. *Lirceus douadyi*, n. sp., Quillin Spring, Scott County, Virginia, paratype male: (a) head, antenna 1, peduncle of antenna 2 (pigmentation omitted); (b) antenna 1 flagellum; (c) percopod 1, distal articles; (d) percopod 4; (e) same, dactylus; (f) uropod.



Figure 3. *Lirceus douadyi*, n. sp., Quillin Spring, Scott County, Virginia, paratype male: (a) pleopod 1; (b) pleopod 2; (c) same, endopodite tip; (d) pleopod 3; (e) pleopod 4; (f) pleopod 5.

anteriad; anterior process forming a shelf obscuring base of cannula, broadly rounded; lateral process broadly rounded, forming part of caudal margin of endopod, comprising almost half of the lateral side of the endopod. Pleopod 3 exopod, anterior surface sparsely setose, lateral and apical margins setose, setae along apical margin slightly longer. Pleopod 4 exopod, lateral margin setose, setae formula >40 – 15 - 13. Pleopod 5 exopod, proximolateral margin without setae.

Total length of male uropod to about 0.4X length of the pleotelson in ventral view, in dorsal view extending about 0.3X length of pleotelson; protopod flattened, about 0.67 of length extending beyond the margin of the pleotelson; exopod and endopod slightly flattened; exopod about 0.75X length of endopod; endopod about 1.6X longer than protopod.

Etymology: This species is named in honor of Professor Christophe Douady, molecular phylogeneticist, in recognition of his detection of this species and other new taxa among the cryptic species complex that constitutes the subgenus *Hargerellus*, along with his many other contributions to our knowledge of asellid isopods.

Habitat and range: *Lirceus douadyi* is known only from Quillin Spring, in Scott County, Virginia. It is a karst spring of modest proportions (Fig. 4), approximately 3 to 5 meters in width at the rise. Quillin Spring occurs between the Copper Creek Knobs that extend along the north side of Copper Creek, and Copper Ridge, which runs along the south side of the Clinch River.

Lirceus douadyi is rare and difficult to find. On two trips (7 June 2022, by J. Lewis, S. Lewis; 19 August 2022, by T. Malabad, K. K. Ficco, N.



Figure 4. Quillin Spring, Scott County, Virginia, is the type-locality and only known population of *Lirceus douadyi*. Florian Malard is shown standing at the origin of the spring, where the isopods are sometimes found clinging to the roof of the horizontal crevice that is the spring orifice. *Lirceus douadyi* was found on this occasion, 25 April 2024, on the underside of one of the larger moss-covered rocks shown on the bottom right side of the photograph. The emergent plant shown choking the spring stream on the left is Watercress, *Nasturtium officinale*, an exotic Eurasian species abundant in many springs in Virginia. *Lirceus douadyi* was never found on watercress, although some species, e.g., *Lirceus brachyurus*, commonly occur on the plant. (photo by J. Lewis).

Gustafson, K. Smith) the isopod could not be found. Of the isopods collected in the spring basin, most were taken from sticks or larger chunks of limestone within 10 meters of the rise. Subsequently, we started probing the roof of the spring orifice with a large sieve and found a few isopods in that manner.

Relationships: In the molecular phylogeny of Lewis et al. (2023), *L. douadyi* was designated MOTU 439. Five taxa, including *L. douadyi*, *L. stygophilus*, *L. katarinae*, *L. culveri*, in Scott County, Virginia and an undescribed species (MOTU 440) from a spring in Sullivan County, Tennessee comprised a relatively well-supported clade.

Lirceus (Hargerellus) laurae Lewis & Lewis, new species

urn:lsid:zoobank.org:act:3C57FF31-6736-4922-BF80-D52C26FEE43A

Figs. 5-7

Material examined: **VIRGINIA:** Lee County: Woodward Spring #2, 4.5 miles (7.2 km) SW Jonesboro, W. Orndorff, Z. Orndorff, 13 Aug 2020, 6♂5♀ (VMNH112424.1-VMNH112424.11); same locality, L. Young, S. L. Lewis, J. J. Lewis, W. Orndorff, 7 Jun 2021, 29∂♀ (VMNH112425.1-VMNH112425.29), and 18 holotype (VMNH112423); Woodward Spring #1, 4.5 miles SW Jonesboro, W. Orndorff, Z. Orndorff, 13 Aug 2020, 1° juvenile.

The holotype is a 6.8 mm \bigcirc collected from Woodward Spring #2 on 7 June 2021, the other specimens from this spring are designated as paratypes, deposited in the Virginia Museum of Natural History, Martinsville, Virginia. Woodward Spring #2 is located at N36.64416 W83.16768.

Material for molecular analysis: VIRGINIA: Lee County: Woodward Spring #2, 4.5 miles SW Jonesboro, W. Orndorff, Z. Orndorff, 13 Aug 2020, $3 \Diamond^{\circ} \uparrow$ (site code: WOODWASP)

Diagnosis: Among the spring-dwelling,

pigmented species of Virginia's lower Powell Valley in Lee County, in the geographic area downstream of Jonesville, *L. laurae* is separated from the four other species by the following characteristics: *L. laurae* lacks the yellow pigmentation on the head and pleotelson that is present in *L. powellensis*; *L. laurae* possesses a broadly rounded medial-lateral carinae of the head, which is high and subtriangular in *L. cedrus*; *L. laurae* lacks the post-mandibular lobes and lateral incision present in *L. zenahae*; and in *L. laurae*, the palmar margin of the propodus of pereopod 1 has a single low, rounded process, as opposed to the large processes present in *L. malabadi*.

Description: Length of males to 6.8 mm, females to 5.8 mm (ovigerous females from 4.8 to 5.8 mm), body about 2.5X as long as wide, sexual dimorphism moderate. Eyes prominent and well formed, dorsal pigmentation brown or grayish, darkest on anterior of head, posterior of head and anterior midline longitudinal part of pereonites lighter brown, with irregular pattern of mottled lightly pigmented spots, lateral margins of pereonites somewhat lighter brown than midline, pleotelson with midline lightly pigmented band, otherwise with moderate brown granular stippled pigmentation.

Head anterior margin with medial-lateral carinae broadly rounded, about equal in height with medial carina, lateral margin entire, post-mandibular lobes and lateral incisions not apparent. Lateral margins of head, pereonites, and pleotelson moderately setose and spinose. Antenna 1 slightly shorter than distal margin of penultimate article of antenna 2 peduncle, flagellum with 6-7 articles, with aesthetes on distal 3 articles. Antenna 2, flagellum with about 42 to 44 articles.

Pereopod 1 of male, propodus about 1.6X as long as wide, palmar margin with one large and one smaller stout proximal spines, medial process subtriangular, rounded apically; dactyl with stout subungual spine, plus a few smaller spines along flexor margin. Female pereopod 1 propodus about 2.1X as long as wide, sexual dimorphism apparent, palmar margin slightly concave with processes absent, comb spines in row along margin. Pereopod 4, carpus of male 2.3X as long as wide, carpus of female similar; dactyl flexor margin with stout subungual spine, plus 1 smaller stout spine.

Pleotelson widest anteriorly, tapering distally, about 1.1X wider than long, caudomedial lobe broadly rounded, uropodal sinuses moderately pronounced. Pleopod 1, protopod mesial margin with 1 retinaculum; exopod about 2X longer than wide, 1.2X length of protopod, lateral and distolateral setae longer than apical setae. Pleopod 2, protopod with 1 mesiodistal seta; exopod, proximal article without setae; distal article subovate, about 1.3X longer than proximal article, about 1.25X as long as wide, with about 10 elongate setae along margins; endopod tip, cannula distinct, narrow, tapering distally to a blunt point, extending approximately parallel to the axis of the endopod, caudal margin of endopod rugose, broadly rounded laterally; mesial process stalked, tip bent anteriad; anterior process forming a shelf obscuring base of cannula, broadly rounded; lateral



Figure 5. *Lirceus laurae*, n. sp., adult male holotype from Woodward Spring #2, Lee County, Virginia.

process broadly rounded, forming part of caudal margin of endopod, comprising almost half of the lateral side of the endopod. Pleopod 3 exopod, anterior surface sparsely setose, lateral and apical margins densely setose, setae along apical margin slightly longer. Pleopod 4 exopod, lateral margin setose, setae formula >30 - 8 - 7. Pleopod 5 exopod, proximolateral margin with 1 elongate seta.

Total length of male uropod to about 0.5X length of the pleotelson in ventral view, in dorsal view extending about 0.37X length of pleotelson; protopod flattened, about 0.5 of length extending beyond the margin of the pleotelson in largest adults, less in subadults; exopod and endopod slightly flattened; exopod about 0.8X length of endopod; endopod about 1.4X longer than protopod. In females all or most of the protopod is hidden by the margin of the pleotelson.

Etymology: This species is named in honor of Laura Young, Southwest Region Steward for the Virginia Natural Heritage Program, Department of Conservation and Recreation. She directed our attention to the presence of Woodward Springs and subsequently assisted in collecting specimens for the description of the species, along with assisting in the collection of isopods at many other sites.

Habitat and range: *Lirceus laurae* is known only from the type-locality at the Woodward Springs, which are found on the north side of the Powell River, in the region known as the Cedars. The primary habitat is Woodward Spring #2, located approximately 800 feet (250 meters) from the river, at an elevation of about 1300 feet (400 meters) above sea level. Flow from Woodward Spring #2 appears to be perennial. The isopods were found on sticks and gravel near the orifice of the spring.

Woodward Spring #1 is about 650 feet (200 meters) south-southwest of spring #2, at approximately the same elevation. Both springs emerge from limestone of Ordovician age. Woodward Spring #1 is ephemeral in nature and probably largely seasonal.

Relationships: From a geographic standpoint,



Figure 6. *Lirceus laurae*, n. sp., Woodward Spring #2, Lee County, Virginia, paratype male: (a) head, antenna 1, peduncle of antenna 2; (b) antenna 1 flagellum; (c) percopod 1, distal articles; (d) percopod 4; (e) same, dactylus; (f) uropod.



Figure 7. *Lirceus laurae*, n. sp., Woodward Spring #2, Lee County, Virginia, paratype male: (a) pleopod 1; (b) pleopod 2; (c) same, endopodite tip; (d) pleopod 3; (e) pleopod 4; (f) pleopod 5.

the Woodward Springs in which *Lirceus laurae* occurs are 2 miles (3.2 km) east of the Flanary Bridge Springs inhabited by *Lirceus cedrus*, another single site endemic. These springs receive groundwater flowing from the Cedars to the north. To the northeast Battle Creek, which receives the flow from Town Branch and Crockett Spring (inhabited by *L. powellensis*), is confluent with the Powell River. The Woodward Springs thus occur in an area isolated by surface and subterranean stream downcutting.

A preliminary phylogeny based on the mitochondrial 16S gene suggests that *Lirceus laurae* is most closely related to *Lirceus littonensis*, with which it shares a clade. *Lirceus laurae* is readily separated from *L. littonensis*, which is an eyeless, unpigmented stygobiontic species that also occurs in the Powell Valley in Lee County, Virginia.

Lirceus (Hargerellus) burnsi Lewis & Lewis

Material examined: TENNESSEE: Grainger County: Tate Spring, 3.4 m W Bean Station, J. Lewis, 29 Oct 2023, 53°

Habitat and range: The new locality listed above extends the range of *Lirceus burnsi* 3.0 miles (4.8 km) to the west of the previous limit of the distribution of the species at Rocky Spring, near Bean Station.

Lirceus (Hargerellus) clinchensis Lewis & Lewis

Material examined: VIRGINIA: Scott County: Big Spring, 4.5 m NNW Gate City, J. Lewis W. Orndorff, Z. Orndorff, 9 Jul 2018, 13; same locality, T. Malabad, K. Kosič Ficco, N. Gustafson, K. Smith, 18 Aug 2022, 233; Buck Spring, T. Malabad, K. Kosič Ficco, N. Gustafson, K. Smith, 18 Aug 2022, 13; Hale Spring, 6.5 m. NNE Gate City, J. Lewis, 21 Oct 2023, 336

Habitat and range: The population represented by MOTU 444 (Lewis et al. 2023) for the *Lirceus* population inhabiting Big Spring listed above is being combined with MOTU 445, *Lirceus* *clinchensis*, which encompasses the isopods found in several springs in northern Scott and Russell counties, Virginia (Fig. 8). This increases the range of *L. clinchensis* about 6.8 miles (11 km) to the south, bringing the total span of the range of the species to approximately 50 miles (80 km), which is a wide distribution for a *Hargerellus*. The addition of Hale Spring also extends the range of *Lirceus clinchensis* almost 5 miles (8 km) to the east.

Lirceus (Hargerellus) hargeri Hubricht & Mackin

Material examined: VIRGINIA: Scott County: Cate Branch, rocky stream next to Yuma Elementary School, J. Lewis, 21 Oct 2023, 173° ; Holston Springs, 1.4 m. WSW Weber City, J. Lewis, S. Lewis, 30 March 2023, 103° ; small stream in Cowan Branch Tunnel, 5.3 m. NNW Mt. Carmel, J. Lewis, 21 Oct 2023, 33° ;

Habitat and range: These are the first localities of *Lirceus hargeri* reported in Virginia, previously known only from springs in Hawkins County, Tennessee (Lewis et al. 2023). Despite extending the range of *Lirceus hargeri* into Virginia, the three new localities represent a relatively small range extension of about 4.3 miles (7.0 km) northward from Lee Spring, previously the most northerly known population (Fig. 8). The species is contained within the Holston River basin by Clinch Mountain.

Concerning the habitat preference of this species, it generally occurs in springs and spring streams. The origins of the two streams (Cate Branch and Cowan Branch Tunnel streams) above are unknown, but the characteristic watercress that usually grows in local spring streams was present, suggesting that their water emerges from springs.

Of note, the report of *Lirceus hargeri* from a well in Blackwell, Lee County, Virginia by Hubricht and Mackin (1949) remains a mystery. The community of Blackwell is in Washington (not Lee) County, Virginia, approximately 10 miles (16 km) NNE of Abingdon and there are no known species of *Hargerellus* in the vicinity. Another possibility is that this might involve an error on Hubricht's part for the Lee County community of Blackwater (there are other similar errors in Hubricht and Mackin 1949). If that is the case, the record would still be unlikely to represent a population of *Lirceus hargeri*, since Blackwater is well north of Clinch Mountain. The original vial of isopods can not be located in the Smithsonian collection with the rest of Hubricht's material, so until such time that it can be located, this record remains a puzzle.

Lirceus (Hargerellus) katarinae Lewis & Lewis

Material examined: VIRGINIA: Scott County: Carter Sisters Spring, 3.5 m. NW Rye Cove, J. Lewis, W. Orndorff, Z. Orndorff, 26 Oct 2022, $12 \bigcirc \bigcirc$; Mary Duff Spring, 1.2 m. S Duffield, J. Lewis, W. Orndorff, Z. Orndorff, 26 Oct 2022, $14 \bigcirc \bigcirc$; Roadside Spring Cave Spring, 7 m. ENE Duffield, J. Lewis, W. Orndorff, Z. Orndorff, 26 Oct 2022, $2 \bigcirc 5 \bigcirc$; Sparks Cave, 2.5 m. WSW Clinchport, T. Malabad, K. K. Ficco, E. Hollingsworth, L. Young, J. Hartley, C. Haynes, 26 Oct 2022, $34 \bigcirc \bigcirc$ (two vials). Habitat and range: With the added localities listed above, *L. katarinae* is now known from a range of about 18 km surrounding Rye Cove (Fig. 8).

Lirceus (Hargerellus) powellensis Lewis & Lewis

Material examined: VIRGINIA: Lee County: Cheek Spring, ESE Jonesville, J. Lewis, 24 Oct 2022, 1432; Sims Spring, 5.7 m SW Jonesville, J. R. Holsinger, 15-17 May 1990, 31322 (USNM 1687957); Sims Spring, west end of the Cedars, 6.8 m WSW Jonesville, C. A. Pague, 15 May 1990, 1332.

Habitat and range: The collections from Sims Spring are probably the same site, but the label information is sufficiently different that both are listed. The new localities lie within the range of this species described by Lewis et al. (2023) in Lee and Wise counties (Fig. 8).



Figure 8. Range map of species of *Lirceus* occurring in caves and springs in southwestern Virginia and extending into adjacent Tennessee.

Lirceus (Hargerellus) stygophilus Lewis & Lewis

Material examined: TENNESSEE: Sullivan County: Winegar Spring, 1.3 m. W Morrison City, J. Lewis, 21 Oct 2023, $29 \Diamond \bigcirc$; VIRGINIA: Scott County: Daniel Boone Cave Spring, 5 m. W Gate City, J. Lewis, W. Orndorff, 26 Oct 2022, $17 \Diamond \bigcirc$; same locality, J. Lewis, S. Lewis, 30 Mar 2023, $21 \Diamond \bigcirc$; Mazuelos Spring No. 1, L. Young, A. Mazuelos, 27 Apr 2022, $3 \Diamond$ juveniles.

Habitat and range: This species has the most unusual range of any species of Hargerellus, extending about 9 miles (14.5 km) from the typelocality at Speers Ferry Cave in Scott County, Virginia, to Winegar Spring, in the northwestern corner of Sullivan County, Tennessee (Fig. 8). The new records listed above are being interpreted as Lirceus stygophilus based on the results of sequences of the mitochondrial 16S gene, pending further sampling and analysis of populations in the region to further define the genetic and morphological boundaries of the species. Previously known only from the type-locality, when added to the new populations listed above, Lirceus stygophilus is known from both sides of Clinch Mountain. For example, the Mazuelos Spring is about 2 miles (3.2 km) due south on the south side of Clinch Mountain from Speers Ferry Cave, a range spanning a mountain barrier approximately 1,000 feet (over 300 meters) in height. This seemingly impossible feat for an aquatic invertebrate has a simple explanation. The North Fork of the Holston River has pirated the Moccasin Creek drainage from the Clinch River basin through the cleft in Clinch Mountain known as Moccasin Gap. In this manner the ancestor of Lirceus stygophilus and other members of its clade were able to invade from the Holston River Valley into the Clinch River Valley (or vice versa).

Of note, this is the first record of *Lirceus stygophilus* in Tennessee, albeit Winegar Spring is scarcely 1,000 feet (about 300 meters) south of the Virginia state line.

Lirceus (Hargerellus) zenahae Lewis & Lewis

Material examined: VIRGINIA: Lee County: Lesters Spring Cave, 0.2 m. upstream from SR833 bridge, T. Malabad, K.K. Ficco, W. Orndorff, J. Lewis, L. Young, J. Hartley, C. Haynes, 25 Oct 2022, 243° ; Sluice Cave, T. Malabad, K.K. Ficco, W. Orndorff, J. Lewis, L. Young, J. Hartley, C. Haynes, 25 Oct 2022, 143° .

Habitat and range: The new localities remain within the approximately 4 miles (6.5 km) linear range (Fig. 8) described by Lewis et al. (2023). All localities from which *L. zenahae* is known are on the north side of the Powell River, except Sluice Cave, which occurs on the south side of the river. The isopods occur in the entrance zone of Sluice Cave and its spring run.

Genus Caecidotea Packard, 1871

Caecidotea richardsonae clade

Caecidotea speleoconservata Lewis & Lewis, new species

urn:lsid:zoobank.org:act:C9C4E90C-A859-4A74-96EE-80FBD6EE3CA5

Figs. 9-11

Caecidotea richardsonae.—Holsinger and Culver 1988: 36 [in part].

Caecidotea ornatus.—Lewis et al. 2023: 72-76 [in part].

Material examined: VIRGINIA: Lee County: Gallohan Cave No. 1, T. Malabad, K. K. Ficco, 15 Dec 2021, 8 (VMNH112427.1-VMNH112427.8); 11 (VMNH112428.1-VMNH112428.11); same locality, perennial strand pool at end of entrance crawl, W. Orndorff, Z. Orndorff, 15 Dec 2021, 6 (11) (VMNH112429.1-VMNH112429.17); Gallohan Cave No. 2, T. Malabad, K. K. Ficco, 15 Dec 2021, 2 (VMNH112430.1-VMNH112430.9); 6 (3) (VMNH112431.1-VMNH112431.9); Gregorys Cave, J. R. Holsinger, 23 May 1966, 235° (USNM 230713); Thompson Cedar Cave, K. K. Ficco, F. Malard, J. Lewis, S. Lewis, 24 Apr 2024, 231° .

The holotype is a 14 mm \mathcal{E} (VMNH112426) collected from Gallohan Cave No. 2 on 15 December 2021; the other specimens from Gallohan Cave No. 1 and Gallohan Cave No. 2 are designated as paratypes, deposited in the Virginia Museum of Natural History, Martinsville, Virginia. The entrance to Gallohan Cave No. 2 is located at N36.625811 W83.255009.

Material for molecular analysis: VIRGINIA: Lee County: Gallohan Cave No. 1, T. Malabad, K. K. Ficco, 15 December 2021, 332 (site code: GALLOHCA).

Diagnosis: Caecidotea speleoconservata is readily separated from the other species of the *richardsonae* clade in Virginia: C. ornatus, C. fisherorum and C. malardi, by the uropods, which possess a massive protopod. This feature also separates C. speleoconservata from C. recurvata, with which it co-occurs in the type-locality. Each of these species of the *richardsonae* clade are distinct MOTUs as indicated by sequencing of the mitochondrial CO1 gene.

Description: Length of males to 14 mm, longest (ovigerous) females to about 12.5 mm; body about 2.2X as long as wide. Eyes and pigmentation absent. Head without post-mandibular lobes. Lateral margins of head, pereonites, and pleotelson moderately setose and spinose. Antenna 1 flagellum with up to 11 articles, with aesthetes on distal 7 articles. Antenna 2 long and fragile, broken from all specimens and loose in vial; peduncle distal article longest, about 1.6X length of penultimate article, flagellum very long, with up to at least 106 articles, reaching well beyond posterior margin of pleotelson. Mouthparts per the diagnosis of the genus.

Pereopod 1 of male, propodus elongate, about 2.2X as long as wide, palmar margin with about 12 stout spines between proximal edge and distal triangular process, with spine insertions forming a

corrugated appearance of small processes; dactyl flexor margin with row of about 16 stout spines. Pereopod 4, carpus of male elongate, 3.6X as long as wide, carpus of female 4.3X sexual dimorphism apparent; dactyl flexor margin with 2 small spines.

Pleotelson about 1.25X as long as wide, caudomedial margin broadly rounded, uropodal sinuses not produced. Pleopod 1, protopod mesial margin with 4 retinaculae; exopod about 2X longer than wide, with pronounced decurved distolateral lobe, 1.1X length of protopod, lateral setae longer than apical setae. Pleopod 2, protopod elongate, about 1.7X as long as wide, with 1 long proximolateral setae, and 4 short mesial setae; exopod, proximal article with 1 long seta; distal article subovate, elongate, about 2.4X as long as wide, about 2.5X longer than proximal article, apical margin with about 11 elongate plumose setae, 5 strongly appressed non-plumose setae along mesial margin; endopod tip, cannula beak-shaped, decurved and partially obscured in anterior aspect by lateral process; lateral process tubular, digitiform, slightly longer than cannula; mesial process beak-shaped, over-lying base of cannula. Pleopod 3 exopod, anterior surface moderately setose, apical margin with many setae, with 9 elongate plumose setae. Pleopod 4 exopod with single sigmoid false suture, marginal setae absent. Pleopod 5 exopod, without well-defined false sutures, marginal setae absent.

Uropods elongate, about 1.3X length of the pleotelson, brittle and detached from pleotelson in almost all specimens; protopod broad, massive, margin densely setose, 2.75X length of endopod; rami much thinner, exopod about 0.5X length of endopod; endopod about 0.3 the length of protopod.

Etymology: The name is a noun derived from the Latin spelaeum (cave) + conservatio (conservation). This species is an honorific named in recognition of the Cave Conservancy of the Virginias and their role in supporting this and many other avenues of cave and karst research. The suggested vernacular name is the Powell Valley cave isopod.

Habitat and range: According to Holsinger (1975), the type-locality, Gallohan Cave No. 2, is



Figure 9. *Caecidotea speleoconservata*, new species, from Gallohan Cave No. 2, Lee County, Virginia, holotype male: (a) antenna 1 flagellum, distal articles; (b) pereopod 1, carpus, propodus and dactylus; (c) pereopod 4; (d) same, distal end of propodus, dactylus; and (e) uropod.



Figure 10. *Caecidotea speleoconservata*, new species, from Gallohan Cave No. 2, Lee County, Virginia, holotype male: (a) pleopod 1; (b) pleopod 2; (c) same, endopodite tip; (d) pleopod 3; (e) pleopod 4; and (f) pleopod 5.

comprised of 1200 feet (365 meters) of surveyed passage in the upstream section of the Surgener-Gallohan Cave System. The water from Gallohan No. 2 flows through an impenetrable sump and then the stream continues in Gallohan Cave No. 1, which has 3,273 feet (1028 meters) of mapped passages. The water from these caves then flows into Surgener Cave, from which it exits and flows a short distance into the Powell River. Gregorys Cave is located about 2 km to the north of the typelocality and contains approximately 950 feet (290 meters) of mapped passages (Holsinger 1975). Thompson Cedar Cave is about 6 miles (9.7 km) ENE of the Surgener-Gallohan Cave System. That distance comprises the range of Caecidotea speleoconservata, all of which is in the region of the Cedars Natural Area in Lee County, Virginia (Fig. 13).

Relationships: *Caecidotea speleoconservata* conforms to the morphology of the *richardsonae* clade. All members of this group possess a male second pleopod endopodite tip that features an elongate beak-shaped cannula parallel to, and appressed with, a slightly longer digitiform lateral process. The thick, robust protopod and short endopod of the uropod separates this new species from all other members of the *richardsonae* clade. This feature is so prominent that it can be discerned in the field with the naked eye. It also serves to separate *Caecidotea speleoconservata* from *Caecidotea recurvata*, with which the species cooccurs.

We have obtained genetic sequencing of samples of populations of the *richardsonae* clade from eight caves in southwestern Virginia and Tennessee, and present molecular phylogenies of the mitochondrial 16S and CO1 genes (Fig. 13). General relationships have emerged from this analysis, but it is clear upon examination of the differences between the phylogenies that certain relationships remain unresolved, and some are poorly supported. This is a work in progress.

As a matter of nomenclatural convenience Corkscrew (Thompson Valley Cave System) and Bowen caves in Tazewell County are classified as



Figure 11. Comparison of uropod proportions of paratype males of *Caecidotea speleoconservata* from Gallohan Cave No. 2, Lee County, (left) and *Caecidotea malardi* from Stonley Cave, Tazewell County, Virginia (right). (stacked photomicrographs by M. Milne and J. Lewis).

Caecidotea fisherorum, while acknowledging that the Corkscrew population constitutes a separate MOTU, and there are recognizable differences in the gnathopod morphology of the Bowen Cave population that also separates it from *C. fisherorum*. Furthermore, this relationship in the phylogeny (Fig. 13) is poorly supported. This is a pragmatic approach for the moment while further sampling and sequencing is conducted in other caves in the northern part of the Maiden Creek drainage. Likewise, other populations of the *richardsonae* clade in Lee County, e.g., Young-Fugate Cave, remain specifically unclassified for the moment.

Caecidotea malardi Lewis & Lewis, new species

urn:lsid:zoobank.org:act:5B26FA06-EF3A-4BB2-9C55-34C128E55623

Figs. 14-15

Asellus richardsonae.—Steeves 1963: 478 [in part]. Caecidotea richardsonae.—Holsinger and Culver 1988: 36 [in part].

Caecidotea ornatus.—Lewis et al. 2023: 72-76 [in part].

Material examined: VIRGINIA: Tazewell County: Little River Cave, D.A. Hubbard, 22 Jun 1992, $3\overset{\circ}{\triangleleft}4\overset{\circ}{\downarrow}$; same locality, T. Malabad, K. Kosič Ficco, 29 Nov 2018, $2\overset{\circ}{\triangleleft}1\overset{\circ}{\downarrow}$; Lost Mill Cave No. 3, J. R. Holsinger, 28 May 1966, $3\overset{\circ}{\triangleleft}$, $3\overset{\circ}{\downarrow}$ (USNM 230711); Rosenbaums Water Cave, J. R. Holsinger, 2 Sep 1962, $2\overset{\circ}{\triangleleft}4\overset{\circ}{\downarrow}$ (USNM 230706); Stompbottom Cave, T. Malabad, K. Kosič Ficco, M. Ficco, 5 May 2021, $17\overset{\circ}{\triangleleft}^{\circ}$; Stonley Cave, J. Holsinger, 19 Aug 1962, $4\overset{\circ}{\triangleleft}5\overset{\circ}{\downarrow}$ (USNM 230707); same locality, T. Malabad, W. Orndorff, 10 Jan 2019, $4\overset{\circ}{\triangleleft}2\overset{\circ}{\downarrow}$; **Russell** County: Trooper Said Cave, W. Orndorff, 29 May 2008, $2\overset{\circ}{\triangleleft}1\overset{\circ}{\downarrow}$ (USNM 1431697).

The holotype is an 18.5 mm 3° (VMNH112432) collected in Stonley Cave on 10 January 2019, the other specimens from this locality are designated as paratypes deposited in the Virginia Museum of Natural History, Martinsville, Virginia. (VMNH112433.1-VMNH112433.6) and National Museum of Natural History, Washington, D.C. (USNM 230707). Stonley Cave is located on private property at N37.16721 W81.45445.

Material for molecular analysis: VIRGINIA: Tazewell County: Little River Cave (site code: LITTRICA), T. Malabad, K. Kosič Ficco, 29 Nov 2018 (sampling code: LITTRICA_201811), $2\stackrel{<}{}1^{\circ}$; Stonley Cave (site code: STONLECA), T. Malabad, W. Orndorff, 10 Jan 2019 (sampling code: STONLECA_201901), $1\stackrel{<math>}{}2^{\circ}$.

Diagnosis: *Caecidotea malardi* is one of the cryptic species of the *Caecidotea richardsonae* clade (Lewis et al. 2023) and shares the pleopod 2 endopodite tip process anatomy with a beak-shaped decurved cannula and elongate digitiform lateral process. The species is separated from other

asellids in eastern North America by the large spines present on the protopod of the male second pleopod. The palmar margin of the propodus of pereopod 1 possesses the largest processes of any species in this species complex. *Caecidotea malardi* is genetically distinct as a separate MOTU from other *richardsonae* clade in southwestern Virginia.

Description: Length of males to 18.5 mm, ovigerous females to about 11 mm; body vermiform, up to 9X as long as wide. Eyes absent, isopod appears white to the naked eye, vestigial pigmentation in the form of tiny threads of scattered magenta pigment visible under magnification under a dissecting microscope. Head without post-mandibular lobes. Lateral margins of head, pereonites, and pleotelson moderately setose and spinose. Antenna 1 flagellum with up to 14 articles, with aesthetes on distal 6-7 articles. Antenna 2 long and fragile, approximately equal in length to body; peduncle distal article longest, about 1.6X length of penultimate article, flagellum with up to 126 articles. Mouthparts per the diagnosis of the genus.

Pereopod 1 of male, propodus about 1.7X as long as wide, palmar margin with about 3 stout proximal spines, followed distad by large shouldered triangular process that slightly exceeds height of dactyl, and lower bicuspate process; dactyl flexor margin with a few small spines. Pereopod 4, carpus of male 3.9X as long as wide, carpus of female more elongate, 4.7X, sexual dimorphism apparent; dactyl flexor margin with 3 small spines.

Pleotelson about 1.3X as long as wide, caudomedial margin broadly rounded, uropodal sinuses not produced. Pleopod 1, protopod mesial margin with 3 retinaculae; exopod about 1.7X longer than wide, with pronounced decurved distolateral lobe, 1.3X length of protopod, lateral setae longer than apical setae. Pleopod 2, protopod elongate, about 1.3X as long as wide, with 5 robust spines along proximomesial margin; exopod, proximal article with 2 long plumose seta; distal article subovate, elongate, about 1.2X as long as wide, about 1.7X longer than proximal article, apical margin with about 15 elongate plumose setae; endopod tip, cannula beak-shaped, decurved and partially obscured in anterior aspect by lateral process; lateral process tubular, digitiform, slightly longer than cannula; mesial process beak-shaped, over-lying base of cannula. Pleopod 3 exopod, anterior surface sparsely setose, apical margin without elongate setae. Pleopod 4 exopod with single sigmoid false suture, marginal setae absent. Pleopod 5 exopod, with faint transverse false suture, marginal setae absent.

Uropods elongate, about 1.9-2.0X length of the pleotelson; protopod about 1.4X length of endopod; exopod about 0.2X length of endopod; endopod about 0.7x the length of protopod.

Etymology: This species is named in honor of Dr. Florian Malard, of the Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, Université Lyon-1, France, in recognition of his many contributions to our knowledge of asellid isopods.

Habitat and range: The type-locality, Stonley Cave, was described by Holsinger (1975) as one of the largest caves in Tazewell County, with over a mile (1.6 km) of surveyed passage. The range of *Caecidotea malardi* sensu stricto is limited to the type-locality, but from a more practical standpoint the species is combined herein with other populations of the *richardsonae* clade that occur in the upper reaches of the Clinch River basin. At least one of these, in Little River Cave, constitutes a distinct MOTU. Most of the material available for examination was comprised of specimens that were largely fragmental or subadults. At this juncture it appears that combining MOTUs is the best path forward in dealing with identification of these populations.

Thus, we are considering the range of *Caecidotea* malardi to be comprised of richardsonae clade populations in the Clinch River and upstream tributaries that occur west of Clinch Mountain and the Ward Cove/Maiden Spring basin inhabited by *Caecidotea fisherorum*. A sandstone ridge once formed a structural divide between the karst belts now inhabited by these two isopod species. This ridge, long known by geologists (Stevenson 1885), appears to have been the barrier that stemmed the divergence of *Caecidotea fisherorum* and *C.* malardi. Due to the intervening erosion cycles, the karst belts inhabited by these species are now continuous, but that was not always the case.

The range of Caecidotea malardi encompasses



Figure 12. Map of populations of the Caecidotea richardsonae species clade in southwestern Virginia discussed herein.

a region from Trooper Said Cave at the northern edge of Russell County through to Tazewell County in Stonley Cave (on the Bluestone River), finally to Rosenbaums Water Cave (approaching the Clinch headwaters). This comprises a geographic area (Fig. 12) extending approximately 35 miles (56 km).

Relationships: The relationship of the MOTUs of the *Caecidotearichardsonae* clade in southwestern Virginia are discussed above under *Caecidotea speleoconservata* (Fig. 13). Two MOTUs are combined herein to comprise *Caecidotea malardi*. Considering the specimens available from caves other than the type-locality, the longest are about half the length of the types and are probably all juveniles or subadults. In the pereopod 1 of those from Little River and Stompbottom caves, the palmar margin of the propodus has a subtriangular medial process, and the spines on mesial margin of pleopod 2 protopod are less robust.

Caecidotea fisherorum Lewis & Lewis

Material examined: VIRGINIA: Tazewell County: Bowens Cave, 4 miles S of Pounding Mill, J. R. Holsinger, 28 Jul 1963, $5\overline{\bigcirc}4\overline{\bigcirc}$; Corkscrew Cave, T. Malabad, K. K. Ficco, M. Ficco, A. Skowronski, T. Polson, 27 October 2018, $3\overline{\bigcirc}3\overline{\bigcirc}$.

Material for molecular analysis: VIRGINIA: Tazewell County: Corkscrew Cave (site code: CORKSCCA), T. Malabad et al. 27 Oct 2018 (sampling code: CORKSCCA_201910), 2∂1♀.

Variation: Examination of a more robust male (coiled, approximately 11mm in length) than that used for the description of *C. fisherorum* revealed the palmar margin on the pereopod 1 propodus was slightly flatter than illustrated (Fig. 49C, Lewis et al. 2023) and had 4 robust spines, rather than 3.

Habitat and range: *Caecidotea fisherorum* in the strict sense remains endemic to the caves of Ward Cove, Tazewell County (Lewis et al. 2023). As discussed above the Corkscrew Cave population constitutes a separate MOTU from *C. fisherorum*, but for the purposes of nomenclatural simplicity it is being lumped under *C. fisherorum* for the moment. Sequencing has not yet been performed on specimens from Bowen Cave. The Bowen Cave population was noteworthy in that one specimen possessed a small triangular process on the palmar margin of the propodus of the male first pereopod, which also separates it from *C. fisherorum* on a morphological basis.

Caecidotea ornatus Lewis & Lewis

Material examined: VIRGINIA: Scott County: Blair Cave, J. R. Holsinger, S. S. Taylor, 6 Nov 1966, $3^3 9^{\circ}$; Hortons Cave, 10 miles SW Clinchport, J. R. Holsinger, no date, $3^3 2^{\circ}$.

Habitat and range: The addition of the two localities above expands the range of the species to approximately 20 miles (32 km) across southern Scott County (Fig. 12). *Caecidotea ornatus* is endemic to caves in Clinch River Valley in the southwestern edge of Virginia.

Genus Conasellus Stämmer, 1932

Conasellus larae Lewis & Lewis, new species

urn:lsid:zoobank.org:act:3F8C0723-569C-4CD7-A85B-4ABC5C01BAA8

Figs. 16-18

Material examined: VIRGINIA: Shenandoah County: Cohen Spring, 0.7 miles S of Quicksburg, T. Malabad, K. Kosič Ficco, 26 May 2021, 213° (VMNH112435.1-VMNH112435.21); same locality, J. J. Lewis, S. L. Lewis, 23 June 2023, 1° (VMNH112436).

The holotype is an approximately 7.5 mm 3 (VMNH112434) collected from Cohen Spring; the other specimens from this locality are designated as paratypes, deposited in the Virginia Museum of Natural History, Martinsville, Virginia. Cohen Spring is located on private property at N38.683 W78.679.



Figure 13. Maximum-likelihood trees of *Caecidotea richardsonae* clade. A. 16S mitochondrial rRNA gene. B. mitochondrial cytochrome oxidase subunit I (COI) gene. Scale bars show the number of nucleotide substitutions per site. Numbers on the branches provide ALRT (approximate likelihood-ratio test) node supports. Information provided at the tip of branches are the localities of sequenced specimens with locality code (in capital letters) and sequenced specimen (spec.) number provided in bracket. Species within the *C. richardsonae* clade are shown on the right margin of the phylogenies.



Figure 14. *Caecidotea malardi*, new species, from Stonley Cave, Tazewell County, Virginia, holotype male: (a) antenna 1 flagellum, distal articles; (b) percopod 1, carpus, propodus and dactylus; (c) percopod 4; (d) same, distal end of propodus, dactylus; and (e) pleotelson and uropod.



Figure 15. *Caecidotea malardi*, new species, from Stonley Cave, Tazewell County, Virginia, holotype male: (a) pleopod 1; (b) pleopod 2; (c) same, large spines on mesial margin; (d) same, endopodite tip; (e) pleopod 3; (f) pleopod 4; and (g) pleopod 5.

Material for molecular analysis: VIRGINIA: Shenandoah County: Cohen Spring (site code: COHENSPR), T. Malabad, K. Kosič Ficco, 26 May 2021, 3⁽³⁾. (sampling code: COHENSPR).

Diagnosis: The male pleopod 2 endopodite tip of *Conasellus larae* most closely resembles that of *C. laticaudatus*, a species occurring in Louisiana (Williams, 1970). These species are separated by the appearance of the uropods, which in *C. laticaudatus* as the name of the species implies are wide and spatulate, while those of *C. larae* are much narrower.

Description: Length of males to about 8.2mm, longest female (ovigerous) to about 6.0 mm. Eyes large and distinct; pigmentation present, darkest on head, pereonites laterally mottled. Body short,



Figure 16. *Conasellus larae*, n. sp., head, antenna 1 and pereonite 1, ovigerous female from Cohen Spring, Shenandoah County, Virginia (stacked photomicrograph by M. Milne and J. Lewis).

compact, about 3.4X as long as wide. Antenna 1, flagellum to about 10 articles, distal 4 with aesthetascs. Antenna 2, distal article of peduncle about 1.3X longer than penultimate article; flagellum to about 61 articles, aesthetascs absent.

Pereopod 1, propodus about 1.35X as long as wide, palmar margin with 1-2 robust proximal spines on raised boss, large subtriangular medial process and lower, rounded distal process, with rows of marginal setae between proximal spines and medial process, and distal to medial process; dactylus flexor margin with small spines. Pereopod 4, carpus of male 1.3X as long as wide, dactylus with 1 moderate distal spine and 3 small spines along flexor margin; carpus of ovigerous female more slender, 2.2X as long as wide.

Pleotelson about as long as wide, lateral margins with dense, elongate setae; caudomedial well-produced, subtriangular, lobe uropodal sinuses not concave. Pleopod 1, longer than pleopod 2, protopod about 1.3X as long as wide, with 4-5 retinaculae along mesial margin, setae absent; exopod subrectangular, about 1.3X length of protopod, about 1.8X as long as wide, 2 proximomesial setae, lateral and apical margins with setae, longest non-plumose along distolateral margin. Pleopod 2, protopod subquadrate, 1.1X longer than wide, small retinaculum or spine on mesial margin, distomesial seta; exopod proximal article with small plumose setae along lateral margin, distal article subtriangular, 2.0X length proximal article, 1.5X as long as wide, 16 elongate plumose setae along margins; endopod shorter than exopod, basal apophysis prominent, basal spur short, apically rounded, tip without prominent processes adjacent to endopodial groove, cannula broad, about 2X as long as wide, extending parallel to axis of endopod, well beyond apex. Pleopod 3 exopod, anterior surface sparsely setose, about 8 prominent setae along proximolateral margin proximal to origin of transverse suture, about 11 setae along distolateral margin, apical margin with about 15 elongate plumose setae. Pleopod 4 exopod with 7 proximolateral setae, 2 false sutures, 1 faint, transverse, 1 distinct, forming mesiodistal oval. Pleopod 5 with 4 proximolateral setae, 2 faint



Figure 17. *Conasellus larae*, new species, from Cohen Spring, Shenandoah County, Virginia, paratype male: (a) antenna 1 flagellum, distal articles; (b) percopod 1, propodus and dactylus; (c) percopod 4; (d) same, distal end of propodus, dactylus; and (e) uropod.



Figure 18. *Conasellus larae*, new species, from Cohen Spring, Shenandoah County, Virginia, paratype male: (a) pleopod 1; (b) pleopod 2; (c) same, mesial margin; (d) same, endopodite tip; (e) pleopod 3; (f) pleopod 4; and (g) pleopod 5.

transverse false sutures discernible.

Uropods about 0.75X length of pleotelson, protopod flattened, 1.8X longer than wide; distal rami not broadly spatulate, exopod about 0.7X length of endopod, slightly expanded proximally, tapering distally; endopod slightly shorter or equal in length, slightly expanded towards midpoint, tapering distally.

Etymology: The name *larae* is a Latinized honorific for Lara Konecny-Dupré, who is recognized here for her role in performing the laboratory molecular genetic analysis of the hundreds of sequences reported in Lewis et al. (2023) as well as that presented herein and on-going work. The effort required to prepare this massive assemblage of sequencing is beyond words. These publications would not have been possible without her tireless, meticulous work.

Habitat and Range: Conasellus larae is known only from the type-locality, in the Appalachian Valley in Shenandoah County, Virginia. Cohen Spring is found below the entrance of Cohen Cave on the edge of the Shenandoah River. Although a stream is not present in Cohen Cave, which lies in the river bluff several meters above the Shenandoah River, the proximity of the spring to the cave suggests that the two are related.

Relationships: Conasellus larae is most closely related morphologically and genetically to an assemblage of species that possess a prominent cannula extending parallel to the axis from the tip of the male second pleopod endopodite tip, with other accessory processes absent. These species include C. communis (Say 1818), C. laticaudatus (Williams 1970), and C. foxi (Fleming 1972). Of these, the second pleopod morphology of C. larae most closely resembles that of C. laticaudatus, with both possessing relatively short cannulas. They are readily separated by the morphology of the uropods, with C. larae lacking the very broad distal rami of the uropods exhibited by C. laticaudatus. The pleopod 2 cannula of C. foxi illustrated by Fleming (1972) is about twice the length of that shown for

C. laticaudatus by Williams (1970). *Conasellus communis* is the least similar morphologically to the other members of this assemblage, with most specimens exhibiting a lateral shoulder on the male pleopod 2 endopodite tip that is not present in the other species.

Conasellus laticaudatus was described from specimens collected from a ditch in New Orleans, Louisiana, probably a man-made alteration of the bayous that originally constituted the waterways of southern Louisiana. The type-locality of C. laticaudatus is a lentic body of water as compared to the cold, lotic stream at Cohen Spring, located approximately 900 miles (1450 km) to the northeast. The type-locality of Conasellus foxi is in Pass Christian, Harrison County, Mississippi, with other localities cited from creeks in Natchitoches Parish, Louisiana and Ouachita County, Arkansas (Fleming 1972). Conasellus communis is known from many localities in northeastern U.S. and southeastern Canada, including one or more creeks, rivers, ponds, reservoirs, lakes and swamps (Williams 1970).

In researching the affinities of Conasellus larae, specimens from populations of C. laticaudatus from a variety of localities across the eastern U.S. were examined. Specimens present in the collections of the Illinois Natural History Survey (INHS) and the National Museum of Natural History (USNM) were available to compare the morphology of C. larae with related species (Fig. 19). None of these appeared to be conspecific with C. larae or C. *laticaudatus*, with some more closely resembling C. foxi, but all estimated to likely represent a complex of undescribed species. Specimens from the following populations identified as C. laticaudatus were examined: (1) Grantsburg Swamp, Johnson County, Illinois, in a vial labeled Asellus laticaudatus; (2) Little Princess Mine, California Diggings, Jo Daviess County, Illinois (USNM 230292) identified by Fleming (1972) as Asellus laticaudatus; (3) Jones Fall below Lake Roland Dam, 0.5 miles north of Baltimore city line, Baltimore County, Maryland (USNM 230171) identified by Thomas E. Bowman as Caecidotea laticaudata; and (4) Santee National Wildlife Refuge, Clarendon County, South Carolina reported by Biernbaum (1989).



Figure 19. Male pleopod 2 endopodite tip morphology of populations of the *Conasellus laticaudatus* species complex: (a) *Conasellus laticaudatus*, paratype from type-locality in New Orleans, Louisiana; (b) *C. laticaudatus*, Tangipahoe Parish, Louisiana; (c) *Conasellus* sp., Grantsburg Swamp, Johnson County, Illinois; (d) Little Princess Mine, Jo Daviess County, Illinois; (e) Jones Falls, Baltimore County, Maryland; (f) Mims Lake-Four Hole Swamp, Dorchester/Berkeley counties, South Carolina.

The specimens identified by Williams (1970) as *A. laticaudatus* from Louisville, Kentucky could not be located in the collection of the National Museum of Natural History. Reportedly collected from Beargrass Creek, this stream traverses metropolitan Louisville and was quite environmentally degraded at the time the original specimens were collected. We have made multiple attempts to recollect *C. laticaudatus* from Beargrass Creek, but these efforts have yielded only *Lirceus fontinalis*, perhaps reflecting the cleaner state of the creek as compared to the gross sewage pollution previously present.

A population was identified by Thomas E. Bowman as either *C. laticaudatus* or an undescribed species from a lake in Wapanocca National Wildlife Refuge, Crittenden County, Arkansas (Harp and Harp 1980). This collection (USNM 230373) was examined, but the specimen identified by Bowman could not be located. Multiple males from the collection were examined and all were *C. forbesi*. Wapanocca NWR was visited repeatedly by the senior authors and no *C. laticaudatus* specimens could be found, only *C. forbesi*. There is little doubt of Bowman's identification that a *laticaudatus* taxon exists there, but we have been unable to find it.

Sequencing of the mitochondrial 16S gene suggests that the closest relatives of *Conasellus larae* currently known to us are populations of undescribed species of *Conasellus* from a cypress swamp in Alachua County, Florida and a wetland near Jacksonville, Duval County, Florida.

Conasellus meriwetheri Lewis & Lewis

Material examined: VIRGINIA: City of Chesapeake: Sphagnum bog, chain ferry, North Ditch, Dismal Swamp, Robert Rose, 15 Nov 1985,



Figure 20. Localities of populations of the *Conasellus laticaudatus* species complex discussed in the text as reported by Williams (1970), Fleming (1972) and examined in museum collections.



Figure 21. *Conasellus meriwetheri* probably once occurred across the entire drainage area of the Great Dismal Swamp, which is now occupied by metropolitan area of Norfolk/Virginia Beach. All of the known localities are east of the low Suffolk Escarpment, which forms the western boundary of the swamp. The range of *Conasellus phreaticus* occurs in the uplands to the west and north of the range of *C. meriwetheri*.

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Habitat and Range: Conasellus meriwetheri is an inhabitant of shallow groundwater habitats, where the isopods occur in saturated soil interstices, as well as seeps and streams issuing from them. In the Dismal Swamp, which has been heavily impacted by human encroachment, the isopods are found in ditches draining the swamp. This species ranks among the largest asellid isopods in North America, with the longest specimen in the collection above measuring 26.3mm, despite the fact that *C. meriwetheri* inhabits interstitial microhabitats.

The new collection locality is within the narrow range of *Conasellus meriwetheri* on the south side of Chesapeake Bay in the Great Dismal Swamp area (Lewis et al. 2023). All the localities of this species are east of the Suffolk Scarp (Fig. 21), a ridge up to approximately 25 feet (8 meters) in height that rises above the swamplands at the edge of the coastal plain. In contrast, *Conasellus phreaticus* (Lewis and Holsinger 1985) is found in the uplands west of the escarpment.

Conasellus forbesi (Williams)

Material examined: VIRGINIA: Augusta County: Maple Flats, near Sherando, pond 2, K. A. Buhlmann, 21 Mar 1990, 633. WEST VIRGINIA: Mercer County: Speedway Roadside Park, W. Shear, 553.

Remarks: The records given here for *Conasellus forbesi*, *C. nodulus* and *C. scrupulosus* are from identification of material in the collection of the Virginia Museum of Natural History. These species were discussed by Lewis et al. (2023).

Conasellus nodulus (Williams)

Materialexamined:VIRGINIA:Northampton County:farm ditch on dirt road SWof Willis Wharf, J. W. Reid, 21 Mar 2008, 10191juv.

Conasellus scrupulosus (Williams)

Material examined: VIRGINIA: Henry County: Koehler, vernal pond beside Virginia 57, J. W. Reid, 26 Feb 2006, 13; Bath County: roadside pond by routes 39/42, 1 km W Rockbridge County line "Panther Gap", R. L. Hoffman, 27 Mar 2008, 532Q.

Genus *Pseudobaicalasellus* Henry & Magniez, 1968

Pseudobaicalasellus novus Lewis & Lewis, new species

urn:lsid:zoobank.org:act:1A9CE755-BA94-484E-AA5D-617E26C7393F

Figs. 22-24

Asellus incurvus.—Fleming 1972: 255.

Caecidotea incurva.—Henry et al. 1986: 447 [in part]; Holsinger and Culver 1988: 30-31, 35, 114, 116 [in part]; Lewis 2009b: 245, 254-255 [in part]; Holsinger et al. 2013: 46-47 [in part].

Pseudobaicalasellus incurvus.—Lewis et al. 2023: 15-16, 18-19, 26-28 [in part].

Material examined: VIRGINIA: Smyth County: Rowland Creek Cave, T. Malabad, K. Kosič Ficco, 10 Aug 2018, $5 \Diamond \bigcirc$. Wythe County: Bertha Cave, D. Hubbard, 3 Nov 1997, 17∂♀; Cave School Water Cave, T. Malabad, W. Orndorff, 16 Jul 2019, 235° ; Deep Spring Cave, W. Orndorff, E. Crowder, 7 Jul 2018, $2 \bigcirc 4 \bigcirc$; same locality, T. Malabad, K. Kosič Ficco, 21 Sep 2018, $1 \stackrel{?}{\bigcirc} 1 \stackrel{?}{\bigcirc};$ same locality, T. Malabad, A. Malabad, 7 Jun 2023, 9^{\uparrow}_{\circ} ; Early Cave, T. Malabad, K. Kosič Ficco, 7 Nov 2018, $1^{\circ}_{\circ}4^{\circ}_{\circ}$; same locality, T. Malabad, K. Kosič Ficco, R. Blackwell, 19 Feb 2020, $1 \stackrel{?}{\bigcirc} 3 \stackrel{?}{\ominus}$; Early Cave No. 2 (Early Pit), T. Malabad, K. Kosič Ficco, 7 Nov 2018, 232; Groseclose Cave No. 1, D. Hubbard, 10 Jul 2003, 4^{\bigcirc} ; Mockleys Cave, D. Hubbard, 29 Mar 1999, 1319; same locality, T. Malabad, K. Kosič Ficco, 20 Sep 2018, 2∂; Sam Six Cave, T. Malabad, K. Kosič Ficco, 19 Sep 2018,

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1319; Sinking Spring Cave No. 1, T. Malabad, K. Kosič Ficco, 21 Sep 2018, 2369 (VMNH112441.1-VMNH112441.8); same locality, collectors, 30 Nov 2021, 49 (VMNH112442.1-VMNH112442.4); same locality, T. Malabad, A. Malabad, 7 Jun 2023, 2039 (VMNH112438.1-VMNH112438.20), 2139 (VMNH112439.1-VMNH112439.21), 1939 (VMNH112440.1-VMNH112440.19).

The holotype is an approximately 11.0 mm ♂ (VMNH112437) collected from Sinking Spring Cave No. 1; the other specimens from Sinking Spring Cave No. 1 are designated as paratypes, deposited in the Virginia Museum of Natural History, Martinsville, Virginia. The entrance of Sinking Spring Cave No. 1 is located at N36.82972 W81.04041, on the lands of the U. S. Forest Service.

Material for molecular analysis: VIRGINIA: Smyth County: Rowland Creek Cave (site code: ROWLANCA), T. Malabad, K. Kosič Ficco, 10 Aug 2018 (sampling code: ROWLANCA 201808), 431 juvenile. Wythe County: Deep Spring Cave (site code: WYTHEVCA), W. Orndorff, E. Crowder, 7 Jul 2018 (sampling code: WYTHEVCA 201807), $2 \stackrel{?}{_{\sim}} 1 \stackrel{\circ}{_{\sim}} 2 \stackrel{\circ}{_{\sim}}$ with empty marsupium, 1 ovigerous $\stackrel{\circ}{_{\sim}}$; same locality (site code: WYTHEVCA), T. Malabad, K. Kosič Ficco, 21 Sep 2018 (sampling code: WYTHEVCA 201809), $1 \stackrel{<}{_{\bigcirc}} 1 \stackrel{\bigcirc}{_{\bigcirc}}$; Early Cave (site code: EARLYCAV), T. Malabad, K. Kosič Ficco, 7 Nov 2018 (sampling code: EARLYCAV 201811), $1 \stackrel{?}{\circ} 2 \stackrel{\circ}{\circ}$; same locality (site code: EARLYCAV), T. Malabad, K. Kosič Ficco, R. Blackwell, 19 Feb 2020 (sampling code: EARLYCAV 202002), $1 \stackrel{?}{\bigcirc} 3 \stackrel{?}{\bigcirc}$; Early Cave No. 2 (Early Pit) (site code: EARLYCA2), T. Malabad, K. Kosič Ficco, 7 Nov 2018(sampling code: EARLYCA2 201811), 132; Cave School Water Cave (site code: CASCHOCA), T. Malabad, W. Orndorff, 16 Jul 2019 (sampling code: CASCHOCA 201907), 2∂1♀.

Note that the same stream flows through the type-locality in Sinking Spring Cave No. 1 and Deep Spring Cave, from which the specimens for molecular analysis where collected. The two caves are separated by about 500 feet (150 meters) according to Holsinger (1975).

Diagnosis: Pseudobaicalasellus novus is most closely related to P. incurvus, with both species exhibiting apparent torsion of the male second pleopod endopodite, which has a helically spiraled appearance resembling a corkscrew, terminating in a stylet resembling other species in the genus. Pseudobaicalasellus novus is separated from P. incurvus populations in Tennessee by the structure of the second pleopod exopod, which in these species possesses an apparent intermediate article between the usual proximal and distal articles. In P. novus this medial article is barely more than a sliver that is not noticeable at lower magnifications. In the populations in Berry and Gregory caves this intermediate article is larger and relatively prominent. In P. novus the distal article of the exopod is placed on the lateral side of the medial article, with a shelf on the mesial side. In the P. incurvus populations the distal article occupies all or most of the medial article with little if any mesial shelf present.

Description: Longest male about 11.0 mm, longest female (ovigerous) 10.5 mm. Body elongate, about 5.3X as long as wide. Antenna 1, flagellum to about 7 articles, distal 5 with aesthetascs. Antenna 2, flagellum to about 71 articles, aesthetascs absent.

Pereopod 1, propodus about 2.4X as long as wide, palmar margin with 1-2 large proximal spines, sparsely setose, few comb spines present; dactylus flexor margin with 5 robust spines, increasing in size distally. Pereopod 4, carpus of male 3.3X as long as wide, dactylus with 1 small spine along flexor margin; carpus of female more slender, 3.7X as long as wide.

Pleotelson 1.4X as long as wide, caudomedial lobe broadly rounded, uropodal sinuses slightly concave. Pleopod 1, slightly longer than pleopod 2, protopod narrow, about 0.6X width of exopod, with 3-4 retinaculae along mesial margin, setae absent; exopod subovate, about 1.6X length of protopod, about 2.3X as long as wide, expanded laterally mid-length, broadly rounded, lateral and apical margins with longest 25 setae plumose, shorter nonplumose setae interspersed. Pleopod 2, protopod subquadrate, slightly longer than wide, elongate plumose seta on mesial margin; exopod proximal article with plumose lateral seta, distal article subtriangular, elongate, lateral margin straight, 3 short plumose setae proximolaterally, apex with 7 elongate plumose setae; endopod longer than exopod, distinctly spiral-shaped with endopodial groove twisting along axis, cannula a tapering stylet. Pleopod 3 exopod, anterior surface sparsely spinose, 4-5 prominent spines along distolateral margin, sparsely setose along apical margin. Pleopod 4 exopod without setae, faint sigmoid false sutures. Pleopod 5 without setae, 2 faint false sutures discernible.

Uropods subequal or equal to length of pleotelson, protopod slightly flattened, slightly shorter than exopod.

Etymology: The name *novus* was derived from the Latin word for "new", an adjective that refers to the occurrence of *Pseudobaicalasellus novus* in the New River drainage in southern Virginia.

Habitat and Range: The first record of *Pseudobaicalasellus novus* (as *Asellus incurvus*) was the report of the population in McMullin Cave, Smyth County, Virginia by Fleming (1972).

All but two of the known populations occur on the far eastern side of the Appalachian Valley and Ridge, along the edge of the Blue Ridge (Fig. 25). The populations are restricted to the New River basin or, in the case of McMullin Cave, in an adjacent area to the southwest that was once drained by the New River. These caves along the Blue Ridge are developed in the Shady dolomite, which is essentially the oldest non-metamorphosed carbonate rock in the state.

Relationships: Steeves and Holsinger (1968) designated Berry Cave, in Roane County, Tennessee, as the type-locality of *Asellus incurvus* and listed one other locality, Gregorys Cave in Cade's Cove, Blount County, Tennessee (type-specimens were placed by Steeves in the collection of the National Museum of Natural History). The illustrations in the original description were prepared from permanent slide-mounted appendages, which we examined and from which new illustrations were prepared of the male second pleopod from Berry and Gregorys caves (Fig. 23). In particular, the morphology of the second pleopod exopodite differed from that shown in the description of Steeves and Holsinger (1968) in showing a distinct suture dividing the exopodite into three apparent articles. Setae are present on the protopod of the Berry Cave specimen that are absent in those from Gregorys Cave.

Berry Cave was visited by W. Orndorff on 4 June 2023 and fresh material of *Pseudobaicalasellus incurvus* was collected for genetic analysis. Sequencing of the 16S gene revealed this Tennessee population was quite distinct from those occurring in Virginia, placed in a completely different clade. Permission to collect the isopod in Gregorys Cave for DNA analysis was denied by the National Park Service in Great Smoky Mountains National Park, due to the presence of bats in the cave during the winter. Thus, the relationship of that population to the others remains unknown.

Populations from Rowland Creek Cave (Smyth County) and Deep Spring Cave (Wythe County) were included in the molecular phylogeny of Lewis et al. (2023) and assigned to MOTU 62. We obtained 16S sequences from three other populations in Wythe County (Early Cave, Early Cave #2 and Cave School Water Cave). Based on analysis of the 16S gene, the population from Cave School Water Cave appears to diverge markedly from the other populations.

We suspect that based on the morphological and molecular genetic data in hand that four MOTUs and at least three morphological species are present among the populations examined: (1) Berry Cave, Roane County, Tennessee; (2) Gregorys Cave, Blount County, Tennessee; (3) Cave School Water Cave, Wythe County, Virginia; (4) other populations listed above from Smyth and Wythe counties, Virginia. Steeves (1969) discussed the zoogeography of *Asellus incurvus*, noting that the two populations known at the time (Berry and Gregory caves) were on opposite sides of the Appalachian Valley, separated by approximately 40 miles (64 km) including a six-mile band of noncavernous rocks. That is to say, a geologic situation that precludes dispersal of an obligate groundwater species. Steeves realized that it was unlikely that the two populations were conspecific, but at the time the molecular genetic tools now available for distinguishing species were unknown.

Pseudobaicalasellus species

Material examined: VIRGINIA: Washington County: Walker Mountain Saltpeter Cave, 6 miles NNE Blountville, D. A. Hubbard, 7 Oct 1996, $4 \stackrel{>}{\circ} 3 \stackrel{\bigcirc}{\circ}$ (USNM 239427).

Habitat and range: This population of *Pseudobaicalasellus* is known only from Walker Mountain Saltpeter Cave, near the base of Walker Mountain on its southeastern flank. Holsinger (1975) provided a location and brief description of the cave, which he reported was approximately 800 feet in length. Although there was no mention of a stream, he described the cave as wet and muddy in the back section. The streams in the vicinity flow into the South Fork of the Holston River in Tennessee.

Relationships: The vial containing this isopod was found in the collection of the National Museum of Natural History identified as *Caecidotea richardsonae*. That drew our attention as there are no known populations of that group of species in Washington County, Virginia. Examination revealed a *Pseudobaicalasellus* species. The male second pleopod endopodite tip possessed a relatively short, beak-shaped cannula similar to that illustrated by Steeves (1966) for *Asellus nortoni*.

Asellus (=Pseudobaicalasellus) nortoni was described from Cedar Creek Cave, Greene County, Tennessee (Steeves 1966). Steeves and Holsinger (1968) added localities from a cave in Carter County and a seep in Washington County, Tennessee (Fig. 25). They reported that the three known localities encompassed a range of 35 to 40 miles (approximately 60 km) along the eastern side of the Appalachian Valley. Walker Mountain Saltpeter Cave in Virginia lies about 22 miles (35 km) farther north of the known range of *P. nortoni*.

If the illustrations of *Pseudobaicalasellus* nortoni by Steeves (1966) are correct and from an undamaged specimen, then the population occurring in Walker Mountain Saltpeter Cave in Washington County, Virginia is an undescribed species. Steeves illustrated the pleopod 2 endopodite tip with a short thread-like stylet that he termed the mesial process, in addition to the cannula. Our concern is that experience has shown that when the fragile thread-like endopodite tip typical of many Pseudobaicalasellus species is placed under a glass coverslip (in the method employed by Steeves), the tip structures can break and spread in a manner that results in an appearance like that shown by Steeves (1966, Fig. 17). Resolution of the identity of the Walker Mountain Saltpeter Cave asellid will require careful examination of undissected specimens of P. nortoni.

ACKNOWLEDGMENTS

Major funding for the preparation of this manuscript was provided by a grant from the Cave Conservancy of the Virginias, kindly facilitated by Mr. Michael J. Ficco. Sample preparation and molecular work at the Université Lyon-1 were supported by funds from the French National Research Agency projects CONVERGENOMICS (ANR-15-CE32-0005) and EUR H2O'Lyon (ANR-17- EURE-0018).

The majority of specimens utilized in this monograph were deposited in the collection of the Virginia Museum of Natural History, facilitated by Dr. Kal Ivanov, Curator of Invertebrates, Dr. Jackson Means, Curator of Invertebrates, and Ms. Liberty Hightower, Research Technician. At the National Museum of Natural History, Smithsonian Institution we thank several people for facilitating our visits to work with the collection: Dr. Karen Osborn (Curator), Ms. Karen Reed (Museum Specialist), Mr. W. Moser (Collection Manager), Mr. Geoff Keel (Museum Specialist), Ms. Katie Ahlfeld (Museum Specialist), and Ms. Lisa Comer (Museum Specialist).

We wish to gratefully acknowledge the many



Figure 22. *Pseudobaicalasellus novus*, from Sinking Spring Cave No. 1, Wythe County, Virginia (revised from Lewis et al. 2023): (a) antenna 1, (b) same, tip of flagellum, (c) pleotelson and uropod (setation omitted on pleotelson), (d) percopod 1, propodus and dactylus, (e) percopod 4, (f) same, dactylus, (g) pleopod 1, (h) pleopod 2, (i) pleopod 3, (j) pleopod 4, and (k) pleopod 5.



Figure 23. *Pseudobaicalasellus incurvus*, pleopod 2: (a) paratype, Berry Cave, Roane County, Tennessee; (b) Gregorys Cave, Great Smoky Mountains National Park; (c and d) *Pseudobaicalasellus novus*, from Sinking Spring Cave No. 1, Wythe County, Virginia: pleopod 2 exopods.



Figure 24. *Pseudobaicalasellus novus,* n. sp., stacked photomicrograph of pleopod 2 of a paratype male from Sinking Spring Cave No. 1, Wythe County, Virginia (stacked photomicrograph by M. Milne and J. Lewis).

people who assisted with the field work in Virginia. In particular, Mr. Thomas Malabad, Dr. Katarina Kosič Ficco and Ms. Laura Young, of the Virginia Natural Heritage Program, collected countless isopods in many localities in Virginia and provided field assistance during the senior authors' visits to Virginia. This publication would not have been possible without them.

Most of the illustrations for this manuscript were finalized for publication by Dr. Zenah Orndorff -this was a burdensome task that requires special thanks. I also wish to thank Dr. Marc Milne at the University of Indianapolis for his support in preparing stacked photomicrographs.

We gratefully acknowledge support from the CNRS/IN2P3 Computing Center (Lyon/ Villeurbanne, France) for hosting the World Asellidae Datagase, which contains all molecular metadata related to the North American asellid specimens analyzed as part of this work. We thank the Université claude Bernard Lyon 1 Zoologie (UCBLZ) collection for storing the biological material used for molecular analysis. We thank

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Figure 25. Distribution of Pseudobaicalasellus taxa in southwestern Virginia and northeastern Tennessee. The dashed line and arrows indicate the hypothetical placement of an ancient drainage divide and the direction of movement of the basin.

Colin Issartel for his support in the preparation of Holsinger, J. R. 1975. Descriptions of Virginia samples for molecular analyses.

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Species name	Gene	Sampling code	Specimen molecular code	AN
Lirceus douadyi	16S	QUILLISP_201807	LIRhargeri_QUILLISP_201807_1	OR255746
Lirceus douadyi	16S	QUILLISP_201807	LIRhargeri_QUILLISP_201807_2	OR255744
Lirceus douadyi	16S	QUILLISP_201807	LIRhargeri_QUILLISP_201807_3	OR255745
Lirceus douadyi	28S	QUILLISP_201807	LIRhargeri_QUILLISP_201807_3	OR505757
Lirceus douadyi	FASTKD4	QUILLISP_201807	LIRhargeri_QUILLISP_201807_3	OR341931
Lirceus douadyi	FASTKD4	QUILLISP_201807	LIRhargeri_QUILLISP_201807_1	OR341932
Lirceus douadyi	COI	QUILLISP_201807	LIRhargeri_QUILLISP_201807_1	OR292069
Lirceus douadyi	COI	QUILLISP_201807	LIRhargeri_QUILLISP_201807_3	OR292070
Lirceus laurae	16S	WOODWASP_202008	LIRhargeri_WOODWASP_202008_1	PQ483704
Lirceus laurae	16S	WOODWASP_202008	LIRhargeri_WOODWASP_202008_2	PQ483705
Lirceus laurae	16S	WOODWASP_202008	LIRhargeri_WOODWASP_202008_3	PQ483706
Lirceus laurae	28S	WOODWASP_202008	LIRhargeri_WOODWASP_202008_2	PQ483727
Lirceus laurae	28S	WOODWASP_202008	LIRhargeri_WOODWASP_202008_1	PQ483728
Lirceus laurae	FASTKD4	WOODWASP_202008	LIRhargeri_WOODWASP_202008_1	PQ488525
Lirceus laurae	FASTKD4	WOODWASP_202008	LIRhargeri_WOODWASP_202008_2	PQ488526
Lirceus laurae	COI	WOODWASP_202008	LIRhargeri_WOODWASP_202008_1	PQ480068
Lirceus laurae	COI	WOODWASP_202008	LIRhargeri_WOODWASP_202008_2	PQ480069
Lirceus katarinae	16S	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_1	PQ483707
Lirceus katarinae	16S	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_2	PQ483708
Lirceus katarinae	16S	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_3	PQ483709
Lirceus katarinae	28S	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_1	PQ483729
Lirceus katarinae	FASTKD4	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_1	PQ488527
Lirceus katarinae	COI	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_1	PQ463697
Lirceus katarinae	COI	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_2	PQ480070
Lirceus katarinae	COI	CARSISSP_202210	LIRkatarinae_CARSISSP_202210_3	PQ480071
Lirceus katarinae	16S	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_1	PQ483710
Lirceus katarinae	16S	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_2	PQ483711
Lirceus katarinae	16S	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_3	PQ483712
Lirceus katarinae	28S	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_3	PQ483730
Lirceus katarinae	FASTKD4	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_3	PQ488528
Lirceus katarinae	COI	ROADCASP_202210	LIRkatarinae_ROADCASP_202210_3	PQ480072
Lirceus powellensis	16S	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_1	PQ483713
Lirceus powellensis	16S	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_2	PQ483714
Lirceus powellensis	16S	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_3	PQ483715
Lirceus powellensis	28S	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_2	PQ483731
Lirceus powellensis	28S	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_3	PQ483732
Lirceus powellensis	FASTKD4	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_2	PQ488529
Lirceus powellensis	FASTKD4	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_3	PQ488530
Lirceus powellensis	COI	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_1	PQ463698
Lirceus powellensis	COI	CHEEKSPR_202210	LIRpowellensis_CHEEKSPR_202210_3	PQ480073

Appendix 1. Specimens (specimen molecular code) used for molecular analyses with their corresponding species names, sampling codes, and accession numbers (AN) of DNA sequences.

Species name	Gene	Sampling code	Specimen molecular code	AN
Lirceus stygophilus	16S	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_1	PQ483716
Lirceus stygophilus	16S	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_2	PQ483717
Lirceus stygophilus	16S	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_3	PQ483718
Lirceus stygophilus	28S	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_1	PQ483733
Lirceus stygophilus	28S	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_2	PQ483734
Lirceus stygophilus	FASTKD4	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_1	PQ488531
Lirceus stygophilus	FASTKD4	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_2	PQ488532
Lirceus stygophilus	COI	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_1	PQ480074
Lirceus stygophilus	COI	DABOCASP_202210	LIRstygophilus_DABOCASP_202210_2	PQ463699
Lirceus stygophilus	16S	MAZUELSP_202204	LIRsp_MAZUELSP_202204_1	PQ483719
Lirceus stygophilus	16S	MAZUELSP_202204	LIRsp_MAZUELSP_202204_2	PQ483720
Lirceus stygophilus	16S	MAZUELSP_202204	LIRsp_MAZUELSP_202204_3	PQ483721
Lirceus stygophilus	28S	MAZUELSP_202204	LIRsp_MAZUELSP_202204_1	PQ483735
Lirceus stygophilus	28S	MAZUELSP_202204	LIRsp_MAZUELSP_202204_2	PQ483736
Lirceus stygophilus	FASTKD4	MAZUELSP_202204	LIRsp_MAZUELSP_202204_2	PQ488533
Lirceus stygophilus	FASTKD4	MAZUELSP_202204	LIRsp_MAZUELSP_202204_1	PQ488534
Lirceus stygophilus	COI	MAZUELSP_202204	LIRsp_MAZUELSP_202204_1	PQ463700
Lirceus stygophilus	COI	MAZUELSP_202204	LIRsp_MAZUELSP_202204_2	PQ463701
Caecidotea speleoconservata	16S	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_1	PQ483722
Caecidotea speleoconservata	16S	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_2	PQ483723
Caecidotea speleoconservata	28S	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_1	PQ483737
Caecidotea speleoconservata	28S	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_2	PQ483738
Caecidotea speleoconservata	FASTKD4	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_1	PQ488535
Caecidotea speleoconservata	FASTKD4	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_2	PQ488536
Caecidotea speleoconservata	COI	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_1	PQ480075
Caecidotea speleoconservata	COI	GALLOHCA_202112	CAEtriangularis_GALLOHCA_202112_2	PQ463702
Caecidotea malardi	16S	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_1	OP757834
Caecidotea malardi	16S	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_2	OP757836
Caecidotea malardi	16S	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_3	OP757835
Caecidotea malardi	28S	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_1	PQ483739
Caecidotea malardi	28S	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_2	PQ483740
Caecidotea malardi	FASTKD4	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_1	PQ488537
Caecidotea malardi	FASTKD4	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_2	PQ488538
Caecidotea malardi	COI	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_1	PQ463703
Caecidotea malardi	COI	LITTRICA_201811	CAErichardsonae_LITTRICA_201811_2	PQ463704
Caecidotea malardi	16S	STONLECA_201901	CAEnickajackensis_STONLECA_201901_1	OP757776
Caecidotea malardi	16S	STONLECA_201901	CAEnickajackensis_STONLECA_201901_2	OP757777
Caecidotea malardi	16S	STONLECA_201901	CAEnickajackensis_STONLECA_201901_3	OP757778
Caecidotea malardi	28S	STONLECA_201901	CAEnickajackensis_STONLECA_201901_1	PQ483741
Caecidotea malardi	28S	STONLECA_201901	CAEnickajackensis_STONLECA_201901_3	PQ483742
Caecidotea malardi	FASTKD4	STONLECA_201901	CAEnickajackensis_STONLECA_201901_1	PQ488539
Caecidotea malardi	FASTKD4	STONLECA_201901	CAEnickajackensis_STONLECA_201901_3	PQ488540

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Species name	Gene	Sampling code	Specimen molecular code	AN
Caecidotea malardi	COI	STONLECA_201901	CAEnickajackensis_STONLECA_201901_1	PQ463705
Caecidotea malardi	COI	STONLECA_201901	CAEnickajackensis_STONLECA_201901_3	PQ463706
Caecidotea fisherorum	16S	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_3	OP757833
Caecidotea fisherorum	16S	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_1ID	OP757831
Caecidotea fisherorum	16S	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_2	OP757832
Caecidotea fisherorum	28S	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_2	OP758030
Caecidotea fisherorum	28S	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_1ID	OP758029
Caecidotea fisherorum	FASTKD4	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_1ID	OP763130
Caecidotea fisherorum	FASTKD4	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_2	OP763131
Caecidotea fisherorum	COI	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_1ID	OP816968
Caecidotea fisherorum	COI	HUGHYOCA_201705	CAErichardsonae HUGHYOCA_201705_2	OP830422
Caecidotea fisherorum	16S	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_1	OP757828
Caecidotea fisherorum	16S	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_2	OP757829
Caecidotea fisherorum	16S	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_3	OP757830
Caecidotea fisherorum	28S	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_1	PQ483743
Caecidotea fisherorum	28S	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_2	PQ483744
Caecidotea fisherorum	FASTKD4	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_1	PQ488541
Caecidotea fisherorum	FASTKD4	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_2	PQ488542
Caecidotea fisherorum	COI	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_1	PQ463707
Caecidotea fisherorum	COI	CORKSCCA_201910	CAErichardsonae_CORKSCCA_201910_2	PQ463708
Caecidotea ornatus	16S	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_5	OP757774
Caecidotea ornatus	16S	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_6	OP757775
Caecidotea ornatus	28S	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_5	PQ483745
Caecidotea ornatus	28S	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_6	PQ483746
Caecidotea ornatus	FASTKD4	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_6	PQ488543
Caecidotea ornatus	FASTKD4	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_5	PQ488544
Caecidotea ornatus	COI	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_5	PQ463709
Caecidotea ornatus	COI	LANESCCA_201910	CAEnickajackensis_LANESCCA_201910_6	PQ463710
Caecidotea ornatus	16S	SFERRYCA_201904	CAErichardsonaeCF_SFERRYCA_201904_7	OP757837
Caecidotea ornatus	FASTKD4	SFERRYCA_201904	CAErichardsonaeCF_SFERRYCA_201904_7	PQ488545
Caecidotea ornatus	28S	SFERRYCA_201904	CAErichardsonaeCF_SFERRYCA_201904_7	PQ483747
Caecidotea ornatus	COI	SFERRYCA_201904	CAErichardsonaeCF_SFERRYCA_201904_7	PQ463711
Conasellus larae	16S	COHENSPR_202107	CAEsp_COHENSPR_202107_1	PQ483724
Conasellus larae	16S	COHENSPR_202107	CAEsp_COHENSPR_202107_2	PQ483725
Conasellus larae	16S	COHENSPR_202107	CAEsp_COHENSPR_202107_3	PQ483726
Conasellus larae	28S	COHENSPR_202107	CAEsp_COHENSPR_202107_1	PQ483748
Conasellus larae	28S	COHENSPR_202107	CAEsp_COHENSPR_202107_3	PQ483749
Conasellus larae	FASTKD4	COHENSPR_202107	CAEsp_COHENSPR_202107_1	PQ488546
Conasellus larae	FASTKD4	COHENSPR_202107	CAEsp_COHENSPR_202107_3	PQ488547
Conasellus larae	COI	COHENSPR_202107	CAEsp_COHENSPR_202107_1	PQ463712
Conasellus larae	COI	COHENSPR_202107	CAEsp_COHENSPR_202107_3	PQ463713
Pseudobaicalasellus novus	COI	ROWLANCA 201808	CAEincurva ROWLANCA 201808 1	OP830411

Species name	Gene	Sampling code	Specimen molecular code	AN
Pseudobaicalasellus novus	COI	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_3	OP816944
Pseudobaicalasellus novus	FASTKD4	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_1	OP763103
Pseudobaicalasellus novus	28S	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_1	OP758004
Pseudobaicalasellus novus	16S	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_1	OP757756
Pseudobaicalasellus novus	16S	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_2	OP757757
Pseudobaicalasellus novus	16S	ROWLANCA_201808	CAEincurva_ROWLANCA_201808_3	OP757758
Pseudobaicalasellus novus	16S	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_1	OP757759
Pseudobaicalasellus novus	16S	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_2	OP757760
Pseudobaicalasellus novus	16S	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_3	OP757761
Pseudobaicalasellus novus	16S	WYTHEVCA_201809	CAEincurva_WYTHEVCA_201809_4	OP757762
Pseudobaicalasellus novus	16S	WYTHEVCA_201809	CAEincurva_WYTHEVCA_201809_5	OP757763
Pseudobaicalasellus novus	28S	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_1	OP758005
Pseudobaicalasellus novus	FASTKD4	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_1	OP763104
Pseudobaicalasellus novus	COI	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_1	OP830412
Pseudobaicalasellus novus	COI	WYTHEVCA_201807	CAEincurva_WYTHEVCA_201807_3	OP816945
Pseudobaicalasellus novus	COI	WYTHEVCA_201809	CAEincurva_WYTHEVCA_201809_4	PQ480076
Pseudobaicalasellus novus	16S	EARLYCAV_201811	CAEincurva_EARLYCAV_201811_1	OP757750
Pseudobaicalasellus novus	16S	EARLYCAV_201811	CAEincurva_EARLYCAV_201811_2	OP757751
Pseudobaicalasellus novus	16S	EARLYCAV_201811	CAEincurva_EARLYCAV_201811_3	OP757752
Pseudobaicalasellus novus	16S	EARLYCAV_202002	CAEincurva_EARLYCAV_202002_4	OP757753
Pseudobaicalasellus novus	16S	EARLYCAV_202002	CAEincurva_EARLYCAV_202002_5	OP757754
Pseudobaicalasellus novus	16S	EARLYCAV_202002	CAEincurva_EARLYCAV_202002_6	OP757755
Pseudobaicalasellus novus	COI	EARLYCAV_201811	CAEincurva_EARLYCAV_201811_1	PQ480077
Pseudobaicalasellus novus	COI	EARLYCAV_202002	CAEincurva_EARLYCAV_202002_4	PQ463714
Pseudobaicalasellus novus	16S	EARLYCA2_201811	CAEincurva_EARLYCA2_201811_1	OP757747
Pseudobaicalasellus novus	16S	EARLYCA2_201811	CAEincurva_EARLYCA2_201811_2	OP757748
Pseudobaicalasellus novus	16S	EARLYCA2_201811	CAEincurva_EARLYCA2_201811_3	OP757749
Pseudobaicalasellus novus	COI	EARLYCA2_201811	CAEincurva_EARLYCA2_201811_1	PQ480078
Pseudobaicalasellus novus	16S	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_1	OP757744
Pseudobaicalasellus novus	16S	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_2	OP757745
Pseudobaicalasellus novus	16S	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_3	OP757746
Pseudobaicalasellus novus	28S	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_1	PQ483750
Pseudobaicalasellus novus	28S	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_3	PQ483751
Pseudobaicalasellus novus	FASTKD4	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_1	PQ488523
Pseudobaicalasellus novus	FASTKD4	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_3	PQ488524
Pseudobaicalasellus novus	COI	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_1	PQ480079
Pseudobaicalasellus novus	COI	CASCHOCA_201907	CAEincurva_CASCHOCA_201907_3	PQ463715

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