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The female and emended male description of the USA Interior Highlands endemic *Allocapnia oribata* Poulton & Stewart, 1987 (Plecoptera: Capniidae)

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Abstract

The female of *Allocapnia oribata* Poulton & Stewart, 1987 is newly associated by tree- and genetic distance-based phylogenetic methods using the mitochondrial cytochrome c oxidase subunit I gene barcode fragment sequence data. The first description of the female and an emended description of the male of *A. oribata* are presented. Supporting data includes color images, scanning electron micrographs, and genetic analysis of DNA barcodes. Corrections to the holotype and paratype localities are presented with the help of B.C. Poulton. Additional notes on the phylogeny and endemism of *Allocapnia* Claassen, 1928 are provided.

Key words: Plecoptera, Capniidae, *Allocapnia*, taxonomy, phylogeny, endemism

Introduction

The winter stonefly genus *Allocapnia* Claassen, 1928 is the second most speciose stonefly genus in the eastern Nearctic with 47 recognized species, trailing only *Isoptera* Banks, 1906a which has 64 described taxa (DeWalt *et al.* 2024). Ricker & Ross (1971) proposed 10 species groups for the 38 species known at that time. There have been 10 new species described, one new synonym proposed, and two reviews of group characteristics and membership between 1980 and 2012 (DeWalt *et al.* 2024). Grubbs & Sheldon (2008) reviewed the *A. mystica* Frison, 1929 group using Scanning Electron Microscopy (SEM), resulting in the description of *A. muskogee* Grubbs & Sheldon (2008). Stark & Kondratieff (2012) also studied the male morphology of three species groups with SEM, prompting a taxonomic update with the removal of *A. minima* (Barnston, 1848) from the *A. forbesi* Frison, 1929 group and subsequent transfer into its own newly-proposed species group. Ross & Ricker (1971) previously defined three groups to contain only one species each: *A. illinoensis* Frison, 1935, *A. jeanae* Ross, 1964, and *A. virginiana* Frison, 1942. The placement of these species into well-defined groups was impeded by distinct morphology and complicated by unclear evolutionary relationships between species. Poulton & Stewart (1987) recognized the potential placement of *A. oribata* Poulton & Stewart, 1987 within the *A. recta* (Claassen, 1924) group based on the architecture of the dorsal limb of the epiproct and the eighth abdominal tergite but acknowledged the uncertainty of the current species group placement.

The male of *A. oribata* was described from the eastern Boston Mountains in northern Arkansas. In a survey of the Interior Highlands stonefly fauna, Poulton & Stewart (1987) noted that the known distribution of *A. oribata* only included two 4th order streams in adjacent Searcy and Van Buren counties. The female is presently unknown. Recent collections of unassociated females alongside males of this apparent endemic to the Boston Mountains prompted a study to associate the sexes, describe the female morphology, and assess the species group placement of *A. oribata* using DNA barcoding, a molecular technique that has been commonly used with insects (Johanson 2007), including stoneflies (e.g., Mynott *et al.* 2011; Grubbs *et al.* 2020, 2023). Herein, we describe the female and provide an emended

description of the male *A. oribata* supported by color images, SEM photomicrographs, and maximum likelihood (ML) and pairwise genetic distance-based analyses based on mitochondrial cytochrome c oxidase subunit I (COI) barcode fragment data (Hebert *et al.* 2003). We also present the first partial molecular-based phylogenetic treatment for *Allocapnia*. Additionally, we provide ancillary details on the holotype and paratype locations of *A. oribata*.

Material and methods

Field sampling

Adult *Allocapnia* specimens were collected by hand-picking with forceps from riparian vegetation and structures. Specimens were immediately preserved in 95% ethanol. Coordinate data (WGS 84) were taken *in situ* using a handheld GPS unit. Museum specimens examined without associated coordinate data were georeferenced using Acme Mapper 2.2 (mapper.acme.com) to the lowest discernible geographic resolution possible from the locality description and are indicated by brackets. Morphological terminology followed that of Ross & Ricker (1971). The holotype male of *A. oribata* is deposited in the United States National Museum, Washington, D.C., USA (USNM). All other specimens reviewed are stored at the Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (BYUC), C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado (CSUIC), Illinois Natural History Survey, University of Illinois, Urbana, Illinois (INHS), and the Phillip N. Hogan Collection (PHNC). Collection data were mapped using ArcGIS Pro 3.3.1 (ESRI, 2024).

Microscopy

Adult male terminalia of *A. oribata* were prepared for SEM via serial dehydration in 95% and 100% ethanol for 10 minutes each, then in hexamethyldisilazane for 30 minutes minimum until fully dry. Dehydrated terminalia were attached to aluminum stubs with double-stick tape and sputter-coated with gold-palladium in an Emscope SC500. Coated specimens were examined at Western Kentucky University (WKU) using a Jeol JSM-6510LV SEM and digital images were captured with an IXRF system. Multiple digital micrographs of *Allocapnia* adults in ethanol were taken at different focal depths and then stacked using a Keyence VHX-7100 series digital microscope.

Molecular Analyses

Two legs and attached thoracic tissue per individual from three females and two males of *A. oribata*, two males of *A. perplexa* Ross & Ricker, 1971, and four males of *A. wrayi* Ross, 1964 were sent to the Canada Centre for DNA Barcoding (CCDB) at the University of Guelph, Ontario, Canada, to sequence the barcode fragment of COI. Several additional high-quality sequences of 12 widespread species of *Allocapnia* were obtained from the Barcode of Life Data System (BOLD) (Ratnasingham & Hebert 2007) (Supplementary Table 1). Sequences for two additional species of Nearctic Capniidae, *Capnura manitoba* (Claassen, 1924), and *Paracapnia angulata* Hanson, 1961, were also obtained from BOLD to serve as outgroup taxa (Supplementary Table 1). Sequences received from BOLD and CCDB were assembled and aligned using MUSCLE in MEGA 11 (Tamura *et al.* 2021).

Table 1. Maximum intraspecific and minimum interspecific (vs. *A. oribata* only) genetic distance values (%) of mtCOI sequences from 14 Nearctic Capniidae species. n = number of sequences per species, OG = outgroup species.

Species	n	Intraspecific	Interspecific
		Maximum	Minimum
<i>Allocapnia oribata</i>	5	1.39	
<i>Allocapnia forbesi</i>	2	2.65	8.26
<i>Allocapnia granulata</i>	7	0.46	4.41
<i>Allocapnia illinoensis</i>	3	0.15	7.42
<i>Allocapnia minima</i>	7	1.39	11.62
<i>Allocapnia nivicola</i>	3	0.15	11.25
<i>Allocapnia perplexa</i>	2	0.31	9.85
<i>Allocapnia pygmaea</i>	8	1.23	11.06
<i>Allocapnia recta</i>	5	0.31	4.25
<i>Allocapnia rickeri</i>	6	0.46	10.19
<i>Allocapnia vivipara</i>	6	1.23	5.73

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Table 1. (Continued)

Species	n	Intraspecific	Interspecific
		Maximum	Minimum
<i>Allocapnia wrayi</i>	4	0.92	4.58
<i>Capnura manitoba</i> (OG)	2	0.31	13.21
<i>Paracapnia angulata</i> (OG)	3	1.70	19.65

Gene sequence data were analyzed using tree- and genetic distance-based phylogenetic methods. A Maximum Likelihood analysis was performed using the General Time Reversible (GTR) model in MEGA 11 (Tamura *et al.* 2021), with gamma distribution and invariant sites, complete deletion for gaps, all codons, and 999 bootstrap replicates. Trees were manipulated for optimal visualization with text overlaid in Adobe Illustrator version 26.3.1. Pairwise divergence values were calculated in MEGA 11 using the Kimura two-parameter model of nucleotide substitution with the complete codon position deletion option. We focused on two measures: (a) maximum intraspecific values for males vs. putative females of *A. oribata* and (b) minimum interspecific values for *A. oribata* vs. all other Capniidae species included in this paper.

Results

Allocapnia malverna Ross, 1964

Gulf Snowfly

<https://plecoptera.speciesfile.org/otus/892702/overview>

(Figs. 1, 5A)

Allocapnia malverna Ross, 1964: 170. Holotype male: (INHS, examined), USA, Arkansas, Hot Springs County, Tenmile Creek, south of Malvern, [34.26062, -92.88567 ±100 m], (INHS Plecoptera 1330).

Allocapnia malverna Ross & Ricker, 1971: 22. ♂, ♀.

Allocapnia malverna Szczytko & Stewart, 1977: 345. ♂, ♀.

Allocapnia malverna Poulton & Stewart, 1991: 18. ♂, ♀.

Allocapnia malverna Grubbs & Sheldon, 2008: 65. ♂ SEM.

Distribution. USA: AR, LA, OK, TX (DeWalt *et al.* 2024) (Fig. 9A).

Material examined. USA, **ARKANSAS, Hot Springs Co.**, Tenmile Creek, south of Malvern, [34.26062, -92.88567 ±100 m], 5 February 1961, H.H. Ross & J.A. Ross, 1♂, (holotype; INHS; INHS Plecoptera 1330). Same collection information, 1♂, (paratype; INHS; INHS Plecoptera 9428). **Dallas Co.**, Browns Creek [Hall Creek], Highway 8, 4.5 miles west of Princeton, [33.98981, -92.70234 ±10 m], 4 February 1984, B.C. Poulton, 6♂, (INHS; INHS Insect Collection 930186). Brushy Creek, Highway 128, 0.5 miles east of Sparkman, [33.91613, -92.83549 ±10 m], 4 February 1984, B.C. Poulton, 1♂, 8 nymphs, (INHS; INHS Insect Collection 930187). East Tulip Creek, Highway 8 at Princeton, [33.98179, -92.63025 ±10 m], 4 February 1984, B.C. Poulton, 52♂, 10♀, (INHS; INHS Insect Collection 930189). **Nevada Co.**, Sandy Creek, Highway 19, 0.5 miles east Laneburg, [33.68464, -93.33778 ±10 m], 4 February 1984, B.C. Poulton, 8♂, 1♀, nymphs, (INHS; INHS Insect Collection 930191). **LOUISIANA, Lasalle Parish**, 15 miles southwest Jena, [31.52529, -92.30919 ±1,000 m], 4 January 1968, H.H. Ross & J.A. Ross, 1♀, (allotype; INHS; INHS Plecoptera 1331). Earl Creek, Whitehall, [31.61823, -92.03256 ±100 m], 2 January 1970, H.H. Ross, 4♂, 2♀, (INHS; INHS Plecoptera 9431). **Natchitoches Parish**, Winn Creek, [31.69223, -93.30966 ±100 m], 5 February 1972, K.W. Stewart, Rhame, & B.P. Stark, 12♂, 3♀, (INHS; INHS Insect Collection 795208). **Vernon Parish**, Leesville, [31.14158, -93.25809 ±1,000 m], 2 January 1970, H.H. Ross, 6♂, 1♀, (INHS; INHS Plecoptera 9432). **OKLAHOMA, Bryan Co.**, Sulphur Creek, [33.94672, -96.04946 ±1000m], 31 January 1972, B.P. Stark, 1♂, 1♀, (BYUC; BYUC Arthropod Collection 4537).

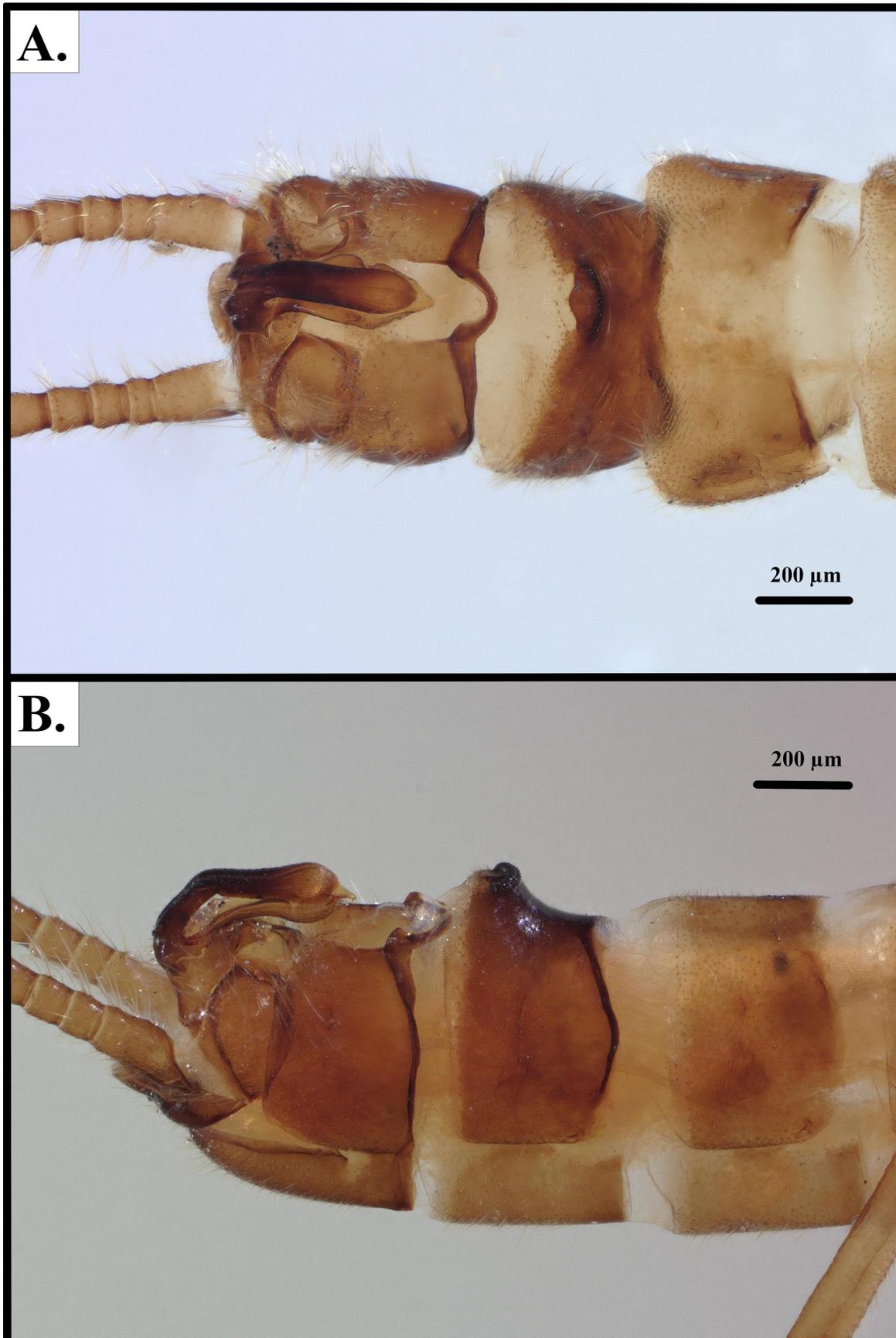


Figure 1. *Allocapnia malverna* terminalia. **A**, adult male, dorsal view, USA, Arkansas, East Tulip Creek, (INHS Insect Collection 930189); **B**, adult male, lateral view, USA, Louisiana, Vernon Parish, (INHS Plecoptera 9432).

***Allocapnia mohri* Ross & Ricker, 1964**

Ouachita Snowfly

<https://plecoptera.speciesfile.org/otus/892703/overview>

(Figs. 2, 5B)

Allocapnia mohri Ross & Ricker, 1964: 91. Holotype male: (INHS, examined), USA, Oklahoma, LeFlore County, two miles south of Summit, [35.63878, -95.43231 ±1,000 m], (INHS Plecoptera 1332).

Allocapnia mohri Ross & Ricker, 1971: 23. ♂, ♀.

Allocapnia mohri Poulton & Stewart, 1991: 18. ♂, ♀.

Allocapnia mohri Grubbs & Sheldon, 2008: 65. ♂ SEM.

Distribution. USA: AR, MO, OK. (DeWalt *et al.* 2024) (Fig. 9A)

Material examined. USA, ARKANSAS, Hot Springs Co., Reyburn Creek, Highway 67, 3 miles north of Gifford, [34.41204, -92.73346 ±10 m], January 12, 1986, B.C. Poulton, 8♂, 1♀, 11 nymphs, 2 exuvia, (INHS; INHS Insect Collection 1531659). Logan Co., Lick Creek, AR-109, 35.10886, -93.84313 ±10 m, 14 March 2022, P.N. Hogan, 5♂, 3♀, (PNHC; PNH-067-22). Scott Co., Brush Creek, AR-28, [34.83801, -93.78629 ±10 m], 29 December 2008, B.P. Stark, 1♂, 1♀, (INHS; INHS Insect Collection 1531654). Van Buren Co., Peyton Creek, Highway 65, 3 miles north of Dennard, [35.78802, -92.53969 ±10 m] January 17, 1999, B.P. Stark, 31♂, (INHS; INHS Insect Collection 1531658). Washington Co., West Fork White River, 0.5 miles north of Brentwood, at rest stop, [35.86629, -94.11874 ±10 m], 25 November 1995, C.R. Nelson & family, 84♂, 27♀, 1 nymph, (INHS; INHS Insect Collection 1531653). Yell Co., Turner Branch, Highway 314, 3 miles east Onyx, [34.86607, -93.36255 ±10 m], 6 January 1999, B.P. Stark, 4♂, (INHS; INHS Insect Collection 1531626). Gafford Creek, AR-28, [34.89791, -93.61269 ±10 m], 6 January 1999, B.P. Stark, 2♂, (INHS; INHS Insect Collection 1531655). MISSOURI, Iron Co., Mina Sauk Falls, Taum Sauk State Park, 37.56268, -90.73964 ±10 m, 11 January 2023, P.N. Hogan, 22♂, 9♀, (PNHC; PNH-2023-011-01). OKLAHOMA, Haskell Co., Eaton Creek, OK-82, [35.08502, -95.11733 ±10 m], 28 December 2006, B.P. Stark & J. Stark, 4♂, 2♀, (INHS; INHS Insect Collection 1531656). LeFlore Co., two miles south of Summit, [35.63878, -95.43231 ±1,000 m], 11 February 1961, H.H. Ross & J.A. Ross, 1♂, (holotype, INHS; INHS Plecoptera 1332). Same information, 1♀, (allotype, INHS; INHS Plecoptera 1333). Tributary to Big Creek, ~100' west Big Creek Road, US-270, [34.71483, -94.56004 ±10 m], 2 January 2016, B.P. Stark, 5♂, (INHS; INHS Insect Collection 1531627). Big Creek, off US-270, 34.70601, -94.51203 ±10, 29 December 2023, P.N. Hogan, 21♂, 27♀, (PNHC; PNH-2023-280). Kiamichi River, OK-259, 34.63732, -94.65366 ±10 m, 29 December 2023, P.N. Hogan, 2♂, 2♀, (PNHC; PNH-2023-285).

***Allocapnia oribata* Poulton & Stewart, 1987**

Bowed Snowfly

<https://plecoptera.speciesfile.org/otus/892692/overview>

(Figs. 3–4, 5C)

Allocapnia oribata Poulton & Stewart 1987: 296. Holotype male: (USNM, unexamined), USA, Arkansas, Searcy Co., Middle Fork Little Red River, US-65 at Leslie, [35.8165, -92.5496 ±10 m], (USNM 103849).

Allocapnia oribata Poulton & Stewart, 1991: 19. ♂.

Distribution. USA: AR (DeWalt *et al.* 2024) (Figs. 7, 9B)

Material examined. USA, ARKANSAS, Searcy Co., Middle Fork Little Red River, Leslie, US-65 bridge, 35.8165, -92.5496, 4 January 1997, B.P. Stark & S. Tucker, 2♂, 2♀, (CSUIC; CSU ENT 5000175). Same location, 1 January 2024, P.N. Hogan & M.A.X. Finley, 3♂, (PNHC; PNH-2024-002). Peyton Creek, South of Leslie, [35.7880, -92.5398, ±1000 m], 12 February 1967, P.H. Freytag, 1♂, (INHS; INHS Plecoptera 1318). Van Buren Co., Archey Creek, Archey Creek, County Route 166, 7 km northeast of Rupert, [35.6886, -92.6501, ±10 m], 6 January 1985, B.C. Poulton, 1♂, (paratype; INHS; INHS Insect Collection 930232). Same location, 3 January 1997, B.P. Stark &

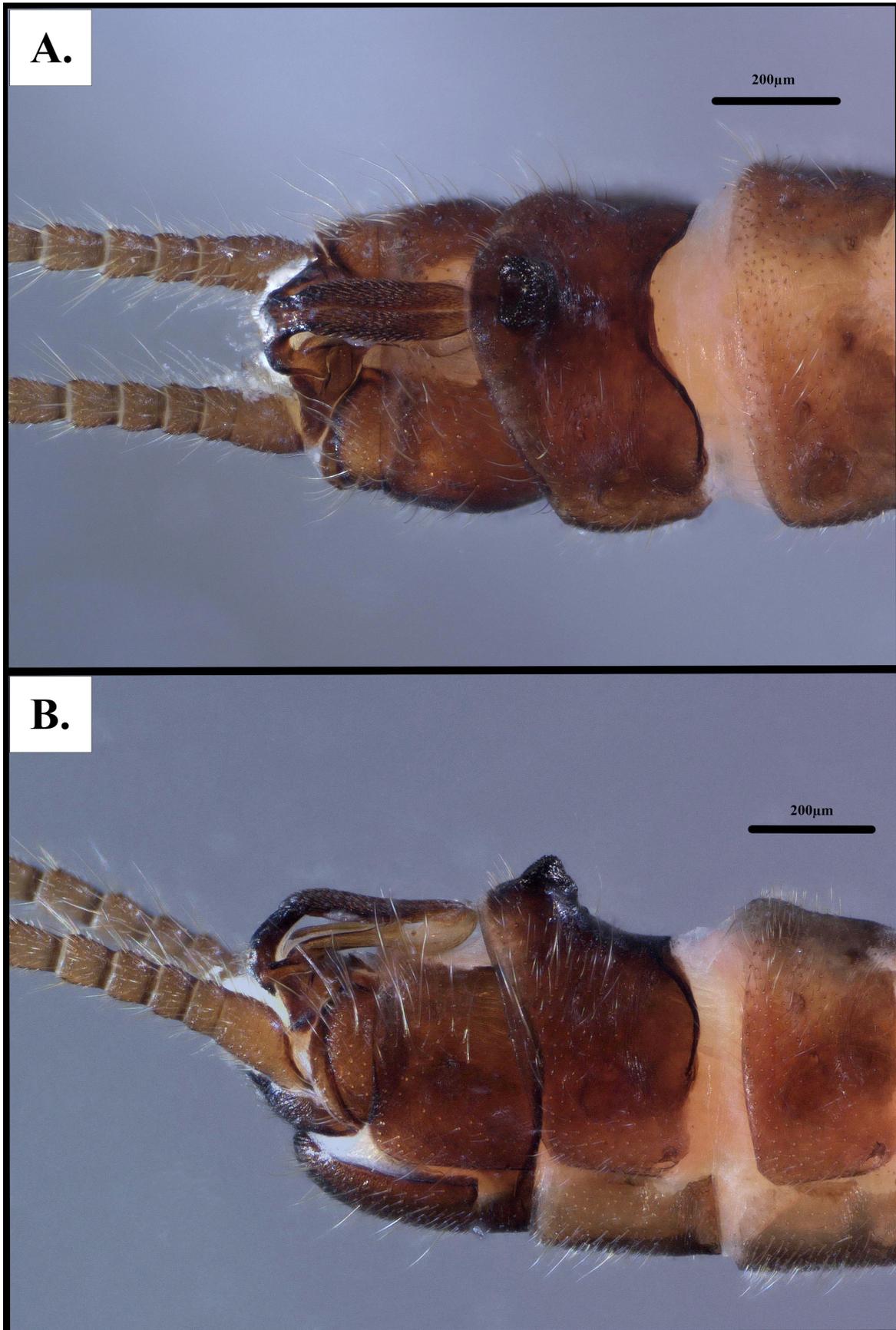


Figure 2. *Allocapnia mohri* terminalia, USA, Oklahoma, Big Creek, (PNH-2023-280). **A**, adult male, dorsal view; **B**, adult male, lateral view.

S. Tucker, 3♂, (INHS; INHS Insect Collection 1531625). Same location, 7 February 2003, B.C. Kondratieff, R. Zuellig, Schmidt, 2♂, (CSUIC; CSU ENT 5000176). Same location, 1 January 2024, P.N. Hogan & M.A.X. Finley, 3♂, (PNHC; PNH-2024-001). South Fork Little Red River, Highway 95 bridge, [35.5486, -92.5856, ±10 m], 20 February 1994, B.C. Poulton & H.W. Robinson, 3♂, 4♀, (INHS; INHS Insect Collection 930233). **Yell Co.**, Dutch Creek, Moss Creek Road, 34.9998, -93.5145, 14 March 2022, P.N. Hogan, 1♂, 3♀, (PNHC; PNH-055-22). Kitchen Branch of Dutch Creek, AR-80, 34.9883, -93.5617, 14 March 2022, P.N. Hogan, 12♂, 8♀, (PNHC; PNH-056-22).

Morphology

Adult male. Body length 4.5–5.3 mm (n = 6) (Fig. 3A). Male wing brachypterous, moderately well developed for the genus, extending from the 5th sternite to nearly 8th abdominal dorsal process (Fig. 3A). Forewing length 2.3–3.2 mm (n = 6). Hindwing length 1.9–2.5 mm (n = 3). General body color typical of the genus, tawny to dark brown in life, light brown in aged specimens preserved in ethanol. Wings hyaline with medium to dark brown veins. Head triocellate with a well-defined occipital suture connecting the posterior two ocelli. Head approximately the same length as the pronotum. Head length 0.64–0.72 mm (n = 2). Pronotum length 0.62–0.75 mm (n = 3). Antennae and palpi light brown. Antennae with 14 flagellomeres. Thorax tawny to dark brown with rugosities present dorsally, concentrated medially. Abdomen length 2.4–2.8 mm (n = 3). Cerci 16 segmented.

Terminalia: The male epiproct is bipartite, divided into an upper and lower limb. In lateral view, epiproct upper limb slightly longer than the lower limb (Figs. 4A). Apex of the apical segment broadly convex but with apical face slightly concave (Fig. 4B). Apical segment limb approximately two-thirds the length of the proximal segment with apical segment length 340–385 µm (n = 2) and proximal segment length 290–322 µm (n = 2) (Fig. 4A). Lower epiproct limb length 540 µm (n = 1). The 7th tergite is unmodified. The 8th tergite is uplifted dorsally to a single tuberculate process on the posterior half of the segment. The apex of the 8th tergum dorsal process is a narrow, scaly ridge in lateral view (Fig. 4C) and slightly sinuous in dorsal view (Fig. 4D). In posterior view, the dorsal process is conical with a rounded apex (fig. 3, Poulton & Stewart 1987).

Adult female. Body length 5.5–6.0 mm (n = 3). Macropterous, forewing length 4.5–5.5 mm (n = 3). Female wing length variable, reaching the 7th sternum or extending past the apex of the abdomen (Fig. 3B). General habitus coloration similar to males.

Terminalia: The 1st through 8th abdominal tergites are sclerotized laterally but have a broad membranous area medially, occupying ½ the width of the tergite. The 9th and 10th abdominal tergites are fully sclerotized. The 7th and 8th abdominal sterna are not fused, separated completely by a membrane (Fig. 5C). The 8th sternum is darkly sclerotized medially, with lateral sides lightly sclerotized; the apex is broadly convex with a posterior, median point (Fig. 5C).

Larva. Unknown.

Egg. Unknown.

Differential Diagnosis

Poulton & Stewart (1987, their figs. 1–3) described and depicted the morphology of the adult male terminalia in lateral (fig. 1), dorsal (fig. 2), and posterior views (fig. 3). These same figures were carried forward into Poulton & Stewart (1991, their figs. 58, 71, 92). Males of *A. oribata* are most easily distinguished from other members of *Allocapnia* by the shape and length of the upper epiproct limb and the sculpturing of the elevated dorsal process on the 8th abdominal segment. The transverse ridge of the dorsal process lacks a mesal cleft present in members of the *A. mystica* group, rather forming a single arcuate undivided bar in the posterior aspect typical of the *A. recta* group. Males of *A. oribata* bear the most morphological similarity to *A. malverna*, but can be distinguished by the structure of the apical section of the epiproct upper limb and the shape of the tuberculate ridge on the dorsal process. The apical segment of the upper limb of *A. malverna* is expanded at the tip leading to a bulbous appearance (Fig. 1B). In *A. oribata*, the apical segment is expanded ventrally with an apical concavity caudally, leading to an angular appearance (Fig. 4B). The remaining regional member of the *A. recta* group, *A. mohri*, is distinguished from both *A. oribata* and *A. malverna* by its dorsally flattened and laterally expanded epiproct upper limb visible in both dorsal (Fig. 2A) and lateral aspects (Fig. 2B). The tuberculate ridge on the dorsal process of *A. mohri* is crescent-shaped in dorsal view (Fig. 2A), while in both *A. malverna* and *A. oribata* it is slightly sinuous to linear (Figs. 1A, 4D). Viewed in posterior aspect, the transverse ridge of *A. oribata* is conical with a rounded apex, whereas the ridge is subtruncate in *A. malverna*. Females cannot be reliably distinguished from several regional congeners.

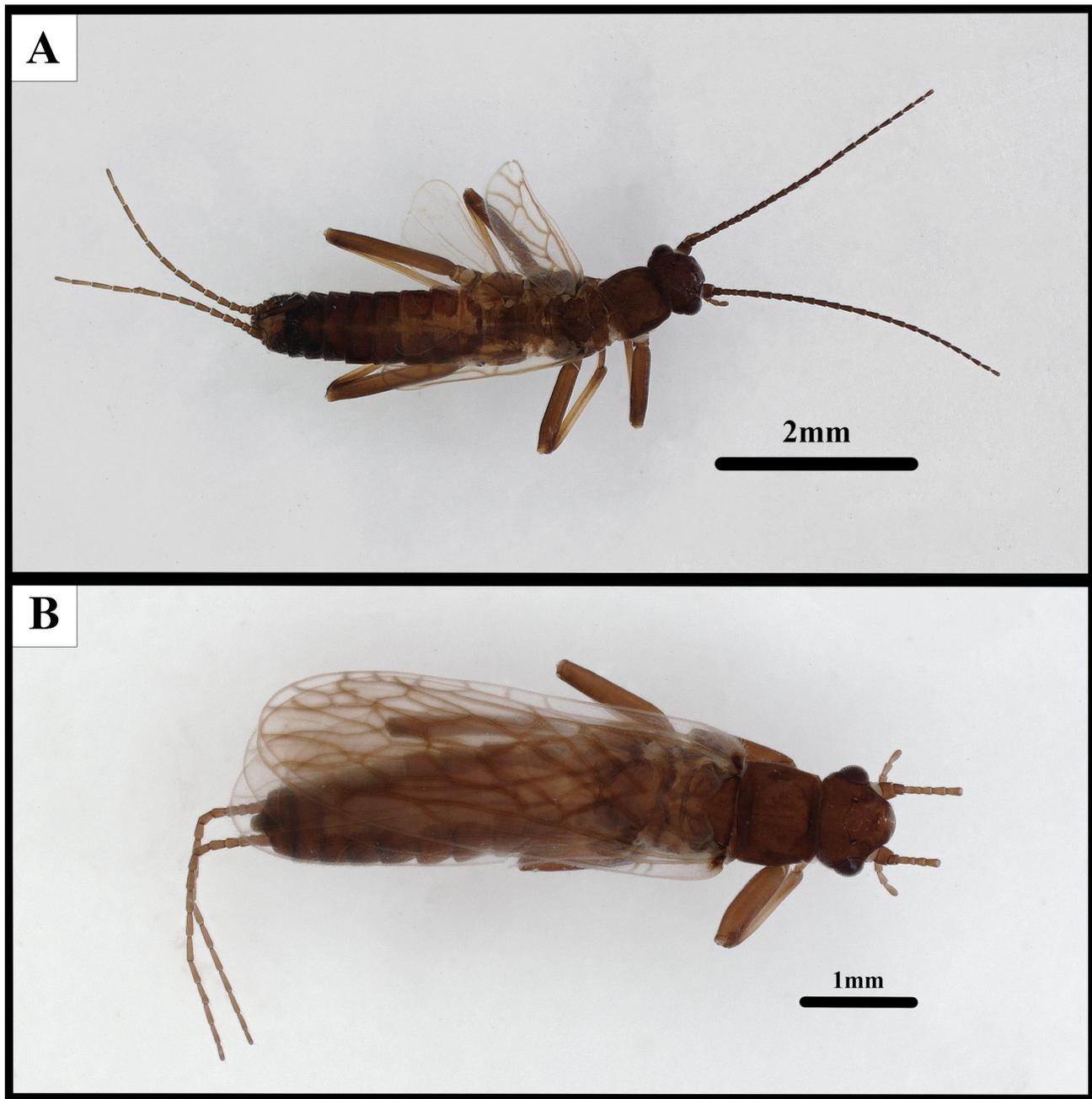


Figure 3. *Allocapnia oribata* adults, USA, Arkansas, Kitchen Branch of Dutch Creek, (PNH-056-22). **A**, adult male, dorsal view; **B**, adult female, dorsal view.

Systematics

A total of 63 *mtCOI* sequences from 14 species were analyzed from a combination of BOLD ($n = 54$) and new data ($n = 11$) (Supplementary Table 1). *Allocapnia oribata* females grouped with males with 100% nodal support (Fig. 7) and the maximum intraspecific distance was only 1.39% (Table 1), providing robust evidence for the association of the females as described above with males. *Allocapnia oribata* was nested in a broader clade with *A. granulata* (Claassen, 1924), *A. recta*, and *A. wrayi* with high nodal support (100%; Fig. 6). Minimum interspecific distance vs. the three species noted above were only 4.41%, 4.25%, and 4.58%, respectively (Table 1). The greatest minimum interspecific divergence for *A. oribata* from the 12 sequenced *Allocapnia* species was with *A. minima* (11.62%; Table 1). Overall, there were two larger *Allocapnia* clades, but each with weak nodal support ($< 40\%$; Fig. 6) potentially as a result of incomplete taxon sampling with only 12/47 (26%) species included. Individually, six of the other 11 *Allocapnia* species sequenced showed strong bootstrap support $\geq 99\%$. Only one *Allocapnia* species sampled, *A. granulata*, received poor bootstrap support as a single clade (67%).

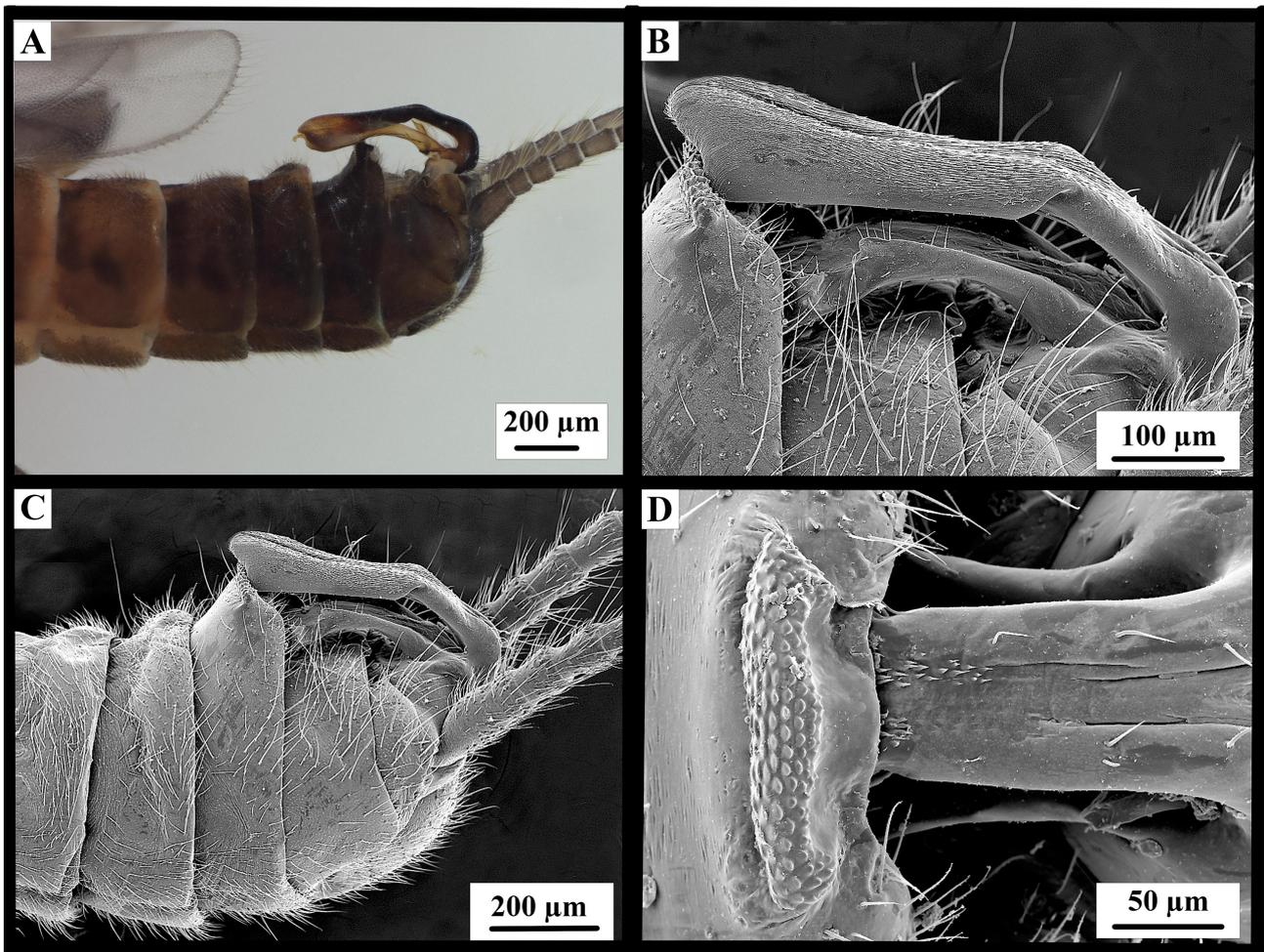


Figure 4. *Allocapnia oribata* adult terminalia. **A**, adult male, lateral view, USA, Arkansas, Archey Creek, (PNH-2024-001); **B**, adult male, lateral view, USA, Arkansas, Dutch Creek, (PNH-055-22); **C**, adult male, dorsal view, USA, Arkansas, Dutch Creek (PNH-055-22), **D**, USA, Arkansas, Dutch Creek, (PNH-055-22).

Comments

We were able to resolve both localities presented in Poulton & Stewart (1987). They reported the holotype male from “Searcy Co., Middle Fork Little Red River, Hwy 65 @ Shirley.” All of these geographic entities exist but not in that specific combination. Shirley is located in adjacent Van Buren Co. but not along US-65. Similarly, the Middle Fork of the Little Red River flows under US-65 in Searcy Co. but the closest town is Leslie. The paratype location was reported as “Van Buren Co., Archey Creek, Hwy 254, 12.1 km NE Rupert.” A contradiction between topographic maps of the period and today led to the reporting of Highway 254, rather than the County Route 166 bridge. Upon discussing these inconsistencies with B.C. Poulton, the following corrections to the holotype and paratype locations are presented:

Holotype: Searcy Co., Middle Fork Little Red River, US-65 at Leslie, [35.8165, -92.5496 ±10 m], 6 January 1985, B.C. Poulton, 1♂ (USNM 103849).

Paratype: Van Buren Co., Archey Creek, County Route 166, 7 km northeast of Rupert, [35.6886, -92.6501, ±10 m], 6 January 1985, B.C. Poulton, 1♂, (INHS Insect Collection 930232).

The definitive association of type material to a single locality, with high geographic precision, is paramount to beginning to decipher the ecological needs for species described as new to science. This is especially important for species that are considered rare, imperiled, and with a small known geographic range. *Allocapnia oribata* has been listed as a Species of Greatest Conservation Need (SGCN) in the Arkansas Wildlife Action Plan (Fowler 2015), with a S1 rank as “Critically imperiled in Arkansas”. A priority SGCN score of 80 (out of 100) has been assigned to *A. oribata*, further indicating high need for conservation.

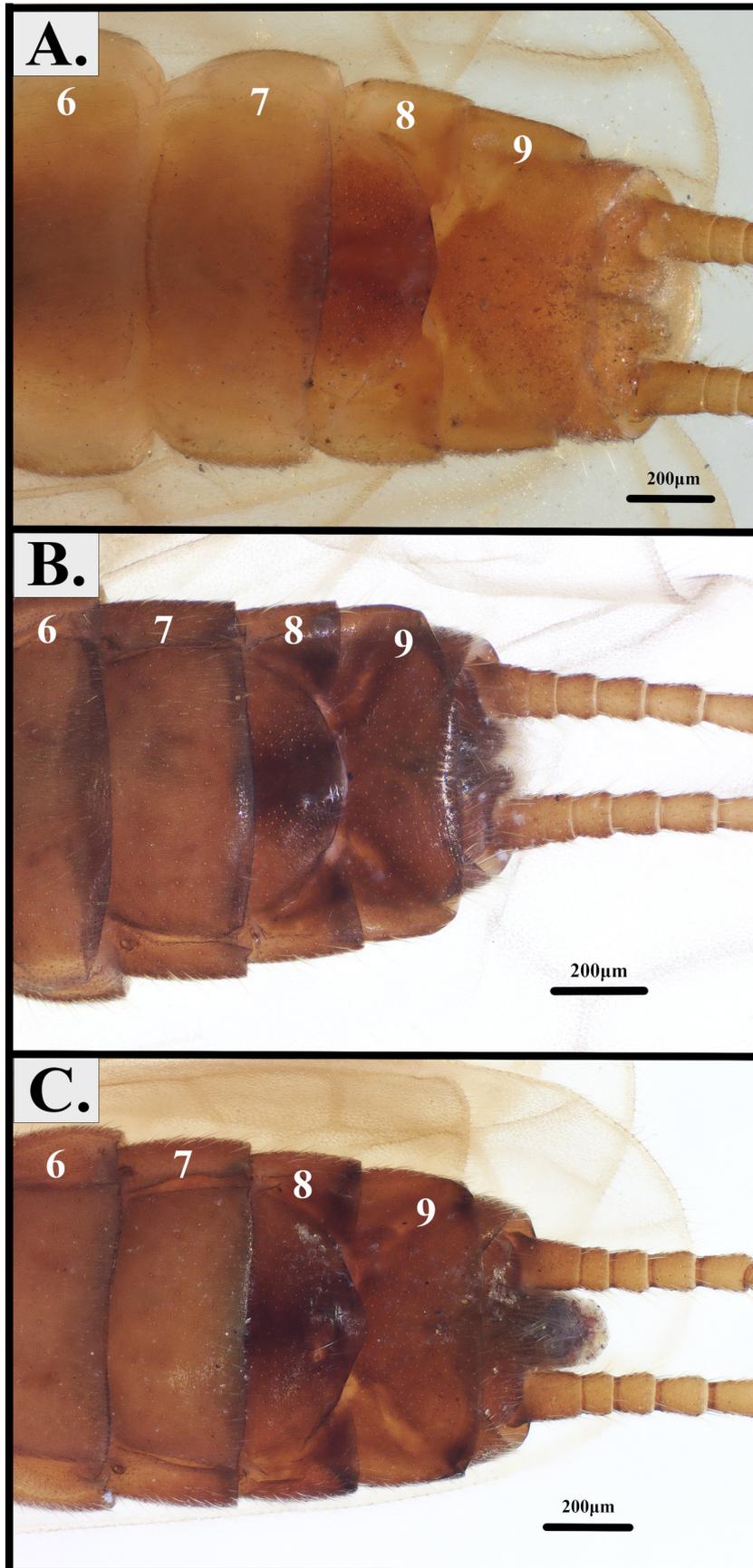


Figure 5. *Allocapnia* species adult female terminalia, ventral view. **A.** *A. malverna*, USA, Louisiana, Vernon Parish, (INHS Plecoptera 9432); **B.** *A. mohri*, USA, Oklahoma, Big Creek, (PNH-2023-280); **C.** *A. oribata*, USA, Arkansas, Dutch Creek, (PNH-055-22).

Biological notes

Allocapnia oribata occurs in at least two US EPA Level III ecoregions, Arkansas Valley (37) and Boston Mountains (38), and two USGS Hydrologic Unit Code 8 (HUC8) watersheds (Fig 7). The holotype and paratype localities are 4th-order streams, draining 115 km² and 67 km², respectively. The new locations reported herein are from a drainage of a similar size, encompassing 174 km², but also a 1st-order tributary draining only 2 km² located approximately 1 km away. Both the holotype (Fig 8A, Fig. 8B) and paratype locality (Fig. 8C, Fig. 8D) have coarse gravel substrates intermixed with cobble and boulders. The 2022 collections of *A. oribata* extend the known period of adult presence from early January to mid-March and the reported distribution southward to the northern Ouachita Mountains (Fig. 7). Other stoneflies collected at these locations consisted of *A. granulata*, *A. mohri*, *Strophopteryx fasciata* (Burmeister, 1839), and *Taeniopteryx burksi* Ricker & Ross, 1968.

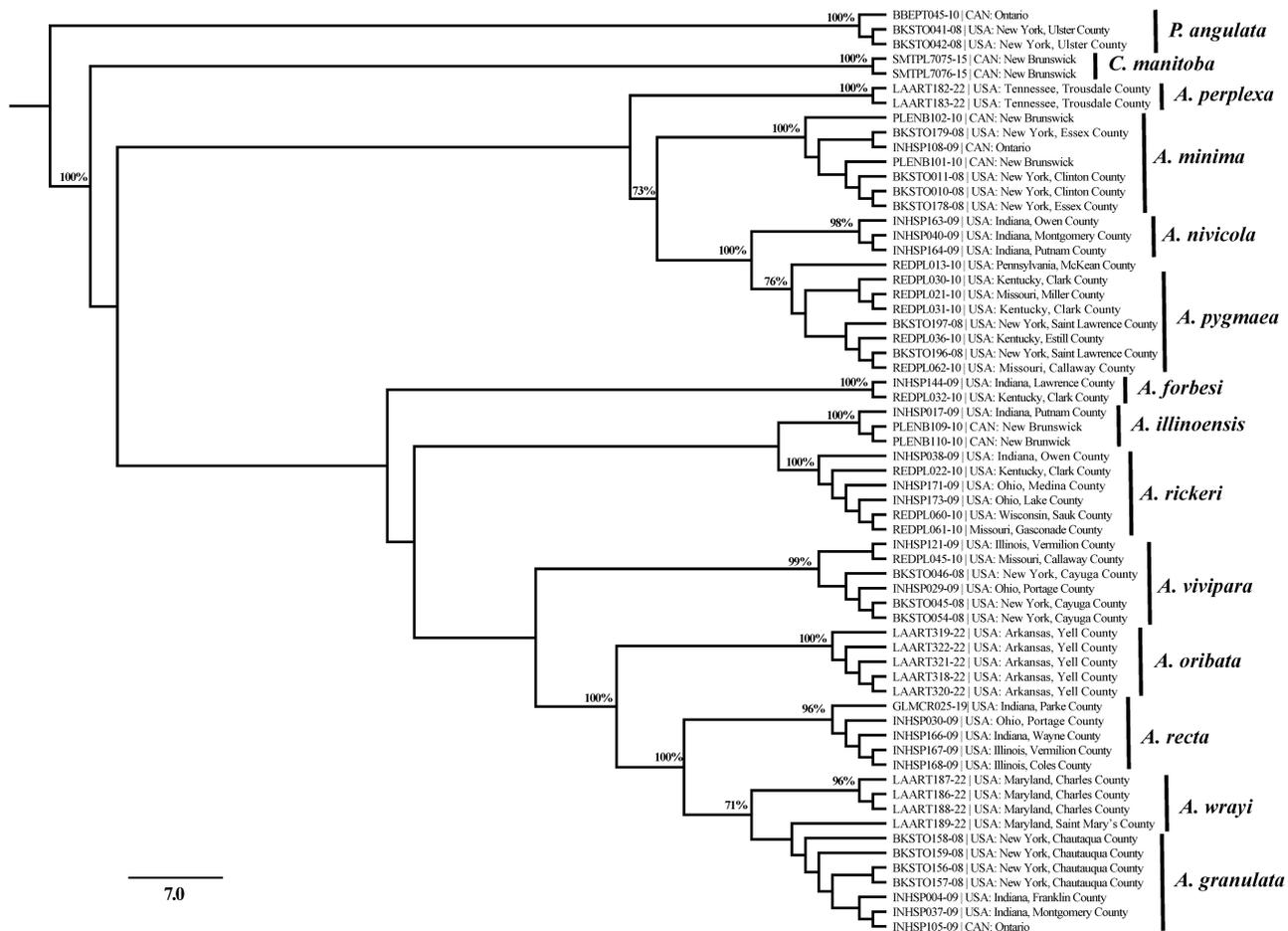


Figure 6. Maximum Likelihood analysis tree for twelve *Allocapnia* species. *Capnura manitoba* and *Paracapnia angulata* are outgroup species. Tips are labeled with specimen BOLD IDs. Country abbreviations, state, and county if applicable are included at tips. Nodes with ≥ 70% bootstrap support are noted.

Discussion

Systematics

Poulton and Stewart (1991) suggested that *A. oribata* may be a member of the *A. recta* (Claassen, 1923) group (Ross & Ricker 1971). The diagnostic characteristics that Ross & Ricker (1971) defined for this group were males lacking a dorsal process on the 7th abdominal segment and having a raised dorsal process on the 8th abdominal segment that is either incised posteriorly or arcuate. With females, the 7th and 8th abdominal sternites are not fused and the 8th sternite lacks modifications.

Couplet 29 in Ross & Ricker (1971) for adult females ends in a dichotomous “polytomy”, with four species (seven total) included for each choice. All seven species corresponded to the five (*A. loshada* Ricker, 1952, *A. malverna*, *A. mohri*, *A. polemistis* Ross & Ricker, 1971, *A. recta*) and two (*A. mystica* Frison, 1929, *A. wrayi*) presently-valid species

that were the original members of the *A. recta* and *A. mystica* species groups, respectively. The only dichotomy noted in couplet 29 was whether the 8th sternum was apically concave or convex. *Allocapnia mohri* was placed in each choice due to variation across specimens in the 8th sternum displaying both characters, further muddling the placement of this species in the *A. recta* group. Alternatively, the females determined as *A. mohri* with an apically convex 8th sternum could have referred to a different species.

Allocapnia oribata is easily differentiated from the upper half of couplet 29 in Ross & Ricker (1971), which includes *A. loshada*, *A. mohri*, *A. polemisticus*, and *A. recta*. The 8th sternum for all four species is concave, albeit with (Fig. 5A, figs. 53, 55 in Ross & Ricker (1971)) or without (Fig. 5B, fig. 54 in Ross & Ricker (1971)) a slight medial projection. Although the 8th sternum of *A. oribata* also bears a small medial projection (Fig. 5C), the general convex outline is distinct from the four species noted above.

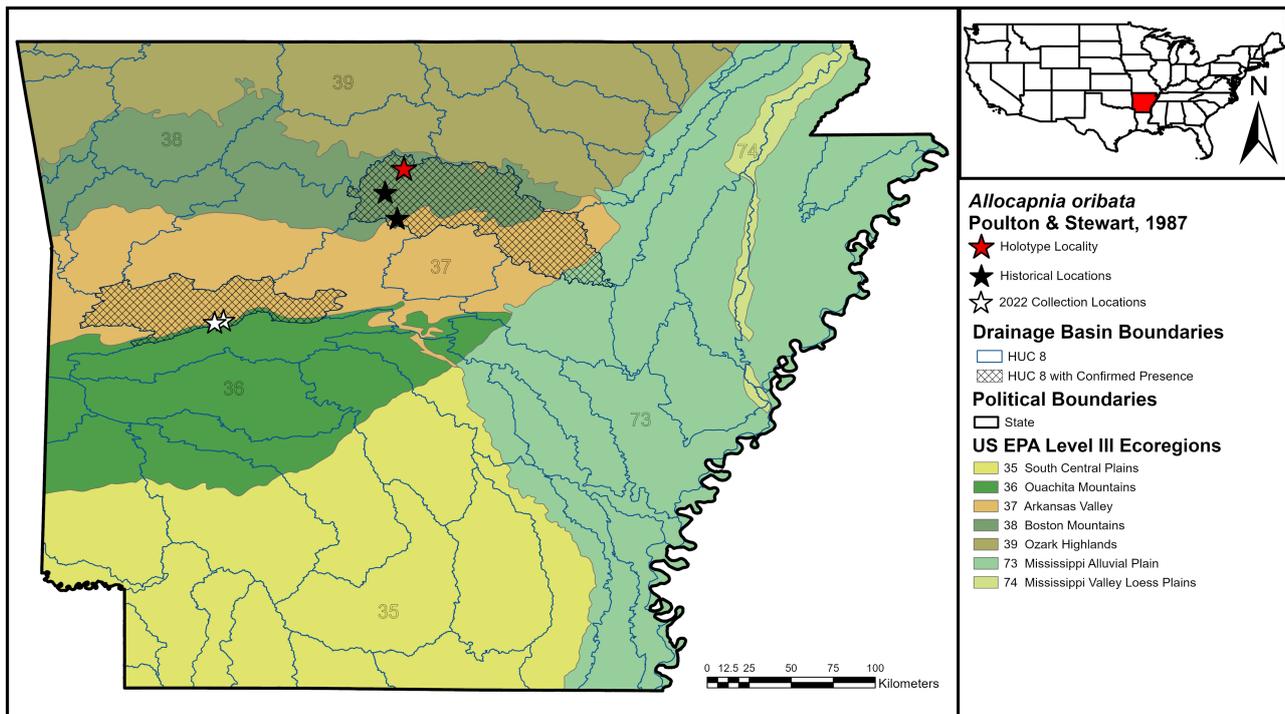


Figure 7. Updated distribution map for *Allocapnia oribata* in Arkansas, USA. United States Geological Survey Hydrologic Unit Code 8 (HUC8) watersheds with confirmed presence are distinguished from other watersheds in the state.

Since 1971, five species have been described and placed into the *A. mystica* (*A. muskogee* Grubbs & Sheldon, 2008) or *A. recta* (*A. sano* Grubbs, 2006, *A. sequatchie* Kondratieff & Kirchner, 2000, *A. starki* Kondratieff & Kirchner, 2000, *A. tsalagi* Grubbs, 2008) species groups. Females of all five species have an apically-convex 8th sternum, further exacerbating the difficulty in objectively differentiating between females based solely on morphology. As of yet, no distinguishing characters have been identified to reliably separate females of the *A. recta* and *A. mystica* groups with apically-convex 8th sterna, with the exception of geographic location. The three Ozark members of the *A. recta* group (*A. malverna*, *A. mohri*, and *A. oribata*) are morphologically similar, suggesting common ancestral origins and close relationships. The upper limb of the epiproct of *A. mohri* is thin, resembling *A. recta*, however, the apical segment of the upper epiproct of both *A. malverna* and *A. oribata* are expanded at the tip. Poulton and Stewart (1991) further separated *A. malverna* and *A. oribata* by shapes of the dorsal process, as the former is flattened and the latter pointed in the posterior aspect. An apparent endemic to the Cumberland Plateau, *A. tsalagi*, is morphologically similar to both *A. malverna* and *A. oribata*. A detailed diagnosis, in addition to SEM imagery of *A. malverna* and *A. tsalagi*, is found in Grubbs (2008). Although the dorsal process of *A. oribata* (Fig. 4D) is more sinuous than arcuate (see figs. 1A, 2A–B in Grubbs 2008), there is enough similarity to suggest a close evolutionary history amongst the four species.

Females of *A. oribata* were grouped with males both with strong (100%) nodal support (Fig. 6) and a low maximum (1.39%) intraspecific divergence value (Table 1). Zhou *et al.* (2011) suggested that a maximum standard threshold of 2% divergence is common within the orders Ephemeroptera, Plecoptera, and Trichoptera. However, there is variability in the reported intraspecific divergence for stoneflies when using barcode data which limits the application of a single genetic distance threshold across taxa (Gill *et al.* 2015a). The majority of intraspecific divergence values for stoneflies range from 0–6% (Mynott *et al.* 2011; Boumans & Baumann 2012; Gill *et al.* 2015a, Gill *et al.* 2015b;

Metzger *et al.* 2022), however, values as high as 15% have been recorded for Neotropical *Kempnyia* Klapálek, 1914 (Avelino-Capistrano 2014) and 19% for Nearctic *Leuctra* Stephens, 1836 (Metzger *et al.* 2022). In studies reporting high intraspecific values within taxa without clear diagnostic morphological characters, the possibility of a cryptic species or historic isolation should be considered (Hebert *et al.* 2004; Elbrecht *et al.* 2014). Maximum intraspecific pairwise distances obtained from the 14 species presented herein show less variation, from 0.15–2.65%. This range is comparable to other molecular studies of stoneflies associating life stages or unidentified females (Mynott *et al.* 2011; Mynott 2015). South *et al.* (2019) found comparable intraspecific genetic distance values, 0–2.4%, in their study that included Interior Highland *Perlesta* Banks, 1906b. The degree of variation between intraspecific divergence values has been attributed to geographic isolation, resulting from the poor dispersal capabilities of stoneflies (Boumans & Baumann 2012). Gill *et al.* (2015a) found that comparing the maximum intraspecific divergence to the minimum interspecific divergence of the most related species was reliable in the delimitation of western Nearctic *Isoperla* species.

Although our taxon sampling was incomplete, there are two additional results that are worth noting. First, the strong nodal support for *A. nivicola* (Fitch, 1847) + *A. pygmaea* provides partial support for the *A. pygmaea* group as proposed by Ross & Ricker (1971) and supported by Stark & Kondratieff (2012). There have been no proposed additions since the original inclusion of the two species noted above plus *A. aurora* Ricker, 1952, *A. indianae* Ross & Ricker, 1964, *A. ohioensis* Ricker, 1952, and *A. smithi* Ross & Ricker, 1971. Second, Ross & Ricker (1971) tentatively placed *A. perplexa* into the *A. rickeri* group on the basis of the long proximal segment and short apical segment of the epiproct upper limb in males and the well-defined line of fusion of the female sternites 7 and 8. However, *A. perplexa* was not grouped with *A. rickeri* here, suggesting that the evolutionary affinities of the former species lie elsewhere in the genus.



Figure 8. Holotype and paratype locations for *Allocapnia oribata* (photo credit: P.N. Hogan, 1 January 2024). **A**, upstream view of holotype location at Middle Fork Little Red River, Highway 65, Searcy County, Arkansas. **B**, downstream view of holotype location. **C**, upstream view of paratype location, Archey Creek, CR-166, Van Buren County, Arkansas. **D**, downstream view of paratype location.

Endemism

Endemism is common within the North American Interior Highlands (Allen 1990; Zollner *et al.* 2005), particularly in the Ozark and Ouachita Mountains. Vicariance events stemming from glacial advances and retreats of the Pleistocene ice sheets isolated high-gradient lotic habitats and resulted in current patterns of regional endemism found among freshwater taxa (Strange & Burr 1997). Within the Ozark and Ouachita Mountains, aquatic insects with restricted dispersal capabilities exhibit varying degrees of endemism, with distributions ranging from single river systems to metapopulations across the region (Allen 1990). Biogeographical hypotheses posited suggest colonization of this region by aquatic insects from progenitor species in the Appalachian Mountains, with dispersal and subsequent isolation following glaciation events of the Pleistocene (Ross 1956; Ross & Ricker 1971; Pessino *et al.* 2014).

Regional-scale endemism is especially prevalent amongst *Allocapnia*, with approximately 16 of the 47 species (34%) known only from small geographic ranges (Table 2). Although distributional knowledge for several of these species is likely deficient, all 16 species are known from historically unglaciated landscapes (Grubbs 2021). In addition to *A. oribata*, six additional species—*A. jeanae*, *A. mohri*, *A. ozarkana* Ross 1964, *A. peltooides* Ross & Ricker, 1964, *A. sandersoni* Ricker, 1952, and *A. warreni* Ross & Yamamoto, 1967, are endemic to the Interior Highlands region. Except for *A. mohri*, six (including *A. oribata*) species have restricted distributions (Fig. 9). There are three notable examples. First, *A. ozarkana* has only been recovered from the southern Ozark Plateau and adjacent Boston Mountains (Poulton & Stewart 1991) (Fig. 9B). Second, *A. warreni* is still known only from the type locality (Ross & Ricker 1971), a third-order stream in the Ozark Plateau that has undergone considerable degradation (Fig. 9C). Third, the distribution of *A. peltooides* only spans the Ouachita Mountains and Arkansas River Valley in both Arkansas and Oklahoma (Poulton & Stewart 1991) (Fig. 9C).

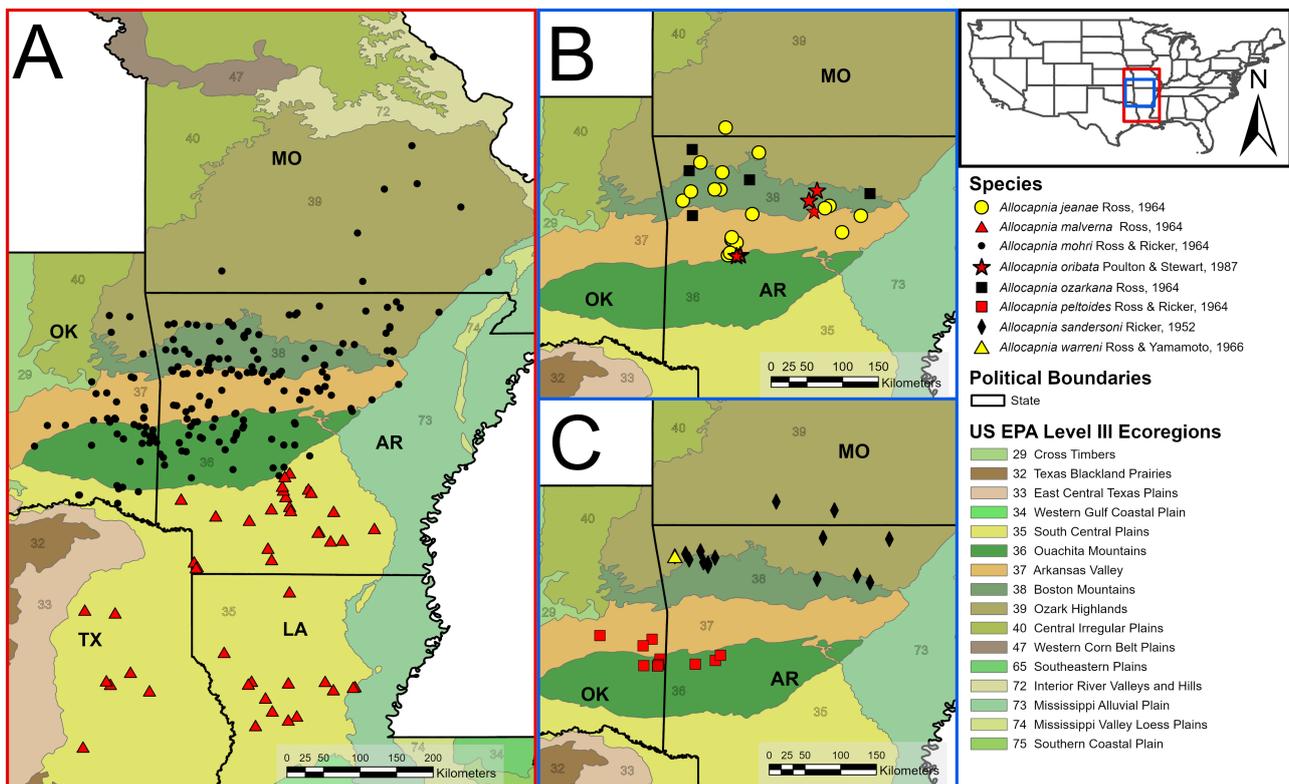


Figure 9. Distribution map for *Allocapnia* species endemic to the South Central Plains and Interior Highlands, USA. **A**, *A. mohri* and *A. malverna*; **B**, *A. jeanae*, *A. oribata*, and *A. ozarkana*; **C**, *A. peltooides*, *A. sandersoni*, and *A. warreni*.

Conclusions

Although a partial phylogeny is presented herein for the Nearctic endemic *Allocapnia*, taxon sampling was purposely limited to focus mainly on resolving the identity of the female of *A. oribata* and placing the species within a defined species group. The placement of *A. oribata* confidently within the morphology-based *A. recta* group, however, was inconclusive. Although *A. oribata* grouped with *A. recta* in a larger clade, this also included *A. wrayi* and *A. granulata*

populations from four USA states. A complete sampling of *Allocapnia*, especially for species with broad geographic ranges (e.g. *A. granulata*, *A. rickeri*), is needed to assess the validity of all 11 presently recognized morphology-based species groups as proposed by Ross & Ricker (1971) and Stark & Kondratieff (2012).

Table 2. Regionally endemic species of *Allocapnia* Claassen, 1928. States are abbreviated as follows: Alabama (AL), Arkansas (AR), Georgia (GA), Kentucky (KY), Maryland (MD), Mississippi (MS), Oklahoma (OK), Tennessee (TN), and West Virginia (WV). United States Environmental Protection Agency Level III Ecoregion codes that encompass the distribution of each species are provided. Citations are provided for additional distribution records exclusive of original species descriptions.

Species	States	Level III Ecoregions	Citations
<i>A. brooksi</i> Ross, 1964	TN	67	Kirchner et al. 2002
<i>A. cunninghami</i> Ross & Ricker, 1971	KY, TN	71	Kirchner et al. 2002; Stark & Kondratieff 2012; Grubbs 2021
<i>A. frumi</i> Kirchner, 1982	MD, WV	67, 69	Stark & Kondratieff 2012; Hogan & Grubbs 2022
<i>A. menawa</i> Grubbs & Sheldon, 2008	AL	67	
<i>A. muskogee</i> Grubbs & Sheldon, 2008	AL, GA	67	Verdone et al. 2017
<i>A. oribata</i> Poulton & Stewart, 1987	AR	37, 38	
<i>A. ozarkana</i> Ross, 1964	AR	37, 38, 39	Stark & Kondratieff 2012
<i>A. peltoides</i> Ross & Ricker, 1964	AR, OK	36, 37	
<i>A. perplexa</i> Ross & Ricker, 1971	TN	71	Kirchner et al. 2002, Stark & Kondratieff 2012
<i>A. polemistis</i> Ross & Ricker, 1971	AL, MS	65, 71	Stark et al. 2000; Nations et al. 2007
<i>A. sano</i> Grubbs, 2006	AL	68	
<i>A. sequatchie</i> Kondratieff & Kirchner, 2000	TN	68	
<i>A. tennesa</i> Ross & Ricker, 1964	AL, TN	71	
<i>A. tsalagi</i> Grubbs, 2008	AL, GA	68	Verdone et al. 2017
<i>A. unzickeri</i> Ross & Yamamoto, 1966	GA, TN	68	Grubbs & Sheldon 2008
<i>A. warreni</i> Ross & Yamamoto, 1966	AR	39	

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