ZooKeys 1096: 1–16 (2022)
doi: 10.3897/zookeys.1096.80773
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Revision of rove beetle genus *Bolitogyrus* Chevrolat (Staphylininae, Cyrtoquediini). Supplement 1

Adam J. Brunke[1]

1 *Agriculture and Agri-Food Canada, Canadian National Collection of Insects, Arachnids and Nematodes, 960 Carling Avenue, Ottawa, Ontario, Canada*

Corresponding author: A. J. Brunke (adam.j.brunke@gmail.com)

Academic editor: Zi-Wei Yin | Received 18 January 2022 | Accepted 1 February 2022 | Published 14 April 2022

http://zoobank.org/A69E5D47-3BD0-42AC-8394-C6D79D8E2699

Citation: Brunke AJ (2022) Revision of rove beetle genus *Bolitogyrus* Chevrolat (Staphylininae, Cyrtoquediini). Supplement 1. ZooKeys 1096: 1–16. https://doi.org/10.3897/zookeys.1096.80773

Abstract

Bolitogyrus is a moderately diverse genus of 78 species that are widely disjunct in the subtropical and tropical forests of the Neotropical and Oriental regions. Following recent revisions of both the Neotropical and Oriental species, this study provides new distributional data, a revised species concept for *Bolitogyrus strigifrons* (Wendeler) **sensu nov.**, and the description of *B. pseudostrigifrons* **sp. nov.** and *B. nigropolitoides* **sp. nov.**, bringing the total number of *Bolitogyrus* species to 80. Several keys are updated to reflect the newly available data and new species.

Keywords

Neotropical, new species, Oriental, Staphylinidae, taxonomy

Introduction

Bolitogyrus Chevrolat (Staphylininae, Cyrtoquediini) is an uncommonly collected genus of predatory rove beetles. Its 78 extant species are specialists of humid microhabitats on and in fungusy deadwood within the forests of the Neotropical and Oriental regions (Brunke and Solodovnikov 2014; Brunke 2017). Twenty-eight species are distributed from Mexico to Ecuador (Brunke and Solodovnikov 2014), while the 50 Oriental species are distributed west of Wallace's Line, from the Himalayan region and southwest India, east to Taiwan (Brunke 2017). Briefly widespread across the northern hemisphere during one of the short early Eocene hyperthermals, the range of *Bolitogyrus* shortly thereafter diverged into two lineages and further contracted southward to refugia as global climate polarized and temperate biomes emerged at higher latitudes during the Eocene–Oligocene transition (Brunke et al. 2017). Eocene fossils of the genus have revealed critical evidence of its past distribution in the Western Palaearctic (Baltic amber: *Bolitogyrus fragmentus* Brunke, Żyła & Solodovnikov) and North America (Green River Formation: undescribed taxon) (Brunke et al. 2017, 2019).

As a supplement to previous taxonomic revisions, the present work aims to publish new specimen data, refine concepts of described species, and describe two new species.

Materials and methods

Depositories

cShi Personal collection of Y. Shibata, deposited at the Museum of Nature and Science, Toshiba, Japan (S. Nomura);

cSmet Personal collection of A. Smetana, deposited at the Museum of Nature and Science, Toshiba, Japan (S. Nomura);

CMN Canadian Museum of Nature, Ottawa, Ontario, Canada (R. Anderson);

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada;

IRSNB Institut royal des Sciences Naturelles de Belgique, Brussels, Belgium (Y.Gérard, T. Struyve);

NHMD Natural History Museum of Denmark, University of Copenhagen, Denmark (A. Solodovnikov, J. Pedersen);

NMPC National Museum Prague, Prague, Czech Republic (J. Hájek);

ROM Royal Ontario Museum Collection, Toronto, Ontario, Canada (B. Hubley);

SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (S. Blank);

SEMC Snow Entomological Collection, Biodiversity Institute, Kansas, USA (Z. Falin).

Specimen data

Type label data are given verbatim, with labels separated by "/" and comments indicated in square brackets. Non-type label data were standardized to improve clarity. Specimens were georeferenced using Google Earth or Google Maps.

Microscopy, illustration, and photography

All specimens were examined dry using a Nikon SMZ25 stereomicroscope. Genitalia and terminal segments of the abdomen were dissected and placed in glycerin filled vials, pinned with their respective specimens. Line illustrations were made from standard images and then digitally inked in Adobe Illustrator CC-2021. All imaging, including photomontage was accomplished using a motorized Nikon SMZ25 microscope and NIS Elements BR v. 4.5. Photos were post-processed in Adobe Photoshop CC-2021.

Measurements and character variability

All measurements were made using a live measurement module within NIS Elements BR v. 4.5. Measurements were taken as listed below, but only proportional (HW/HL, PW/PL, EW/EL, PW/HW) and forebody measurements were stated directly in descriptions. Total body length is generally difficult to standardize for Staphylinidae and was not measured due to the contractile nature of the abdomen.

HL	Head Length, at middle, from the anterior margin of frons to the nuchal ridge;
HW	Head Width, the greatest width, including the eyes;
PL	Pronotum Length, at middle;
PW	Pronotum Width, greatest width;
EL	Elytral Length, greatest length taken from level of the anterior most large, lateral macroseta to apex of elytra. EL approximates the length of the elytra not covered by the pronotum and therefore contributing to the forebody length;
EW	Elytral Width, greatest width;
ESut	Elytral Suture, apex of the scutellum to the apex of the elytra
Forebody	HL + PL + EL.

Taxonomy

Staphylininae Latreille, 1802
Cyrtoquediini Brunke & Solodovnikov, 2016

Bolitogyrus Chevrolat, 1842

Bolitogyrus Chevrolat, 1842: 641. Type species *Quedius buphthalmus* Erichson, 1840: 534, fixed by monotypy. Brunke and Solodovnikov 2014 (revision of Neotropical species); Cai et al. 2015 (Chinese species); Brunke 2017 (revision of Oriental species); Brunke et al. 2017 (biogeography, fossils); Brunke et al. 2019 (Baltic amber fossil); for extensive reference list, see Brunke and Solodovnikov 2014

Neotropical species

Buphthalmus group

Bolitogyrus costaricensis (Wendeler, 1927)

Cyrtothorax costaricensis Wendeler, 1927: 8
Cyrtothorax nevermanni Scheerpeltz, 1974: 181 (in key)
Bolitogyrus costaricensis (Wendeler): Brunke and Solodovnikov 2014 (redescription)

Non-type material. Nicaragua: Matagalpa Dept.: 6 km N Matagalpa, Selva Negra, 12°9'54"N, 85°4'36"W, 1300 m, montane forest, beating, 19–22.V.2002, R. Anderson (5, CMN).

Bolitogyrus erythrurus (Kraatz, 1858)

Fig. 1A–C

Cyrtothorax erythrurus Kraatz, 1858: 368
Bolitogyrus erythrurus (Kraatz): Brunke and Solodovnikov 2014 (redescription)

Type material. ***Syntype*** (1 female, SDEI): Nov. Gren. [green label script] / Coll. Kraatz [white label, printed] / erythrurus [green label, script] / Syntypus [red label, printed] / Syntype ♀, Cyrtothorax erythrurus Kraatz, 1858, det A. Brunke 2013 [red printed label].

Non-type material. Country unknown: "Nova Grenada" [handwritten label], erythrurus Kr. [handwritten label], "R. I. Sc. N. B.", "17.479", "Coll. et det. A. Fauvel" (1 female, IRSNB).

Comments. Kraatz (1858) described *B. erythrurus* based on an unknown number of specimens from "Nova Grenada" [= Panama + Colombia]. Brunke and Solodovnikov (2014) were able to examine one female syntype from the Kraatz collection (SDEI) and redescribed the species based on this and several other, more recently collected single female specimens from medium elevations (1300–1350 m) in southern Puntarenas, Costa Rica and adjacent Chiriquí, Panama. However, the non-syntype females differed from the syntype in coloration, with the former group possessing a bluish forebody and brassy-green elytra (Fig. 1A), and the latter a brassy-green forebody and bluish elytra (Fig. 1B). The legs of the syntype also appeared darker and less clearly bicolored than the non-syntypes and most species of the genus (Fig. 1B), though this was thought to be due to age or discoloration from a killing agent (Brunke and Solodovnikov 2014). The above specimen from IRSNB (Fig. 1C), also collected from "Nova Grenada", corresponds closely with the syntype in coloration, including the faintly but clearly bicolored legs with a paler area in the basal third of the femur. This raises the possibility that *B. erythrurus* was originally described from present-day Colombia rather than Panama and may not be conspecific with the specimens previously examined from Central America. This hypothesis is further supported by an image taken by D. Hoyos Velasquez of a live specimen from La Tebaida, Quindío, Colombia (mid-elevation, northern Andes), matching the coloration of specimens from "Nova Grenada" and posted on various social media websites (e.g., https://www.facebook.com/groups/491915904153407/posts/2464208683590776). This image represents the first definitive evidence of the Buphthalmus group in South America. A more accurate species concept for *B. erythrurus* is badly needed but will not be possible without the study of male specimens from both Central and South America.

Although the specimen from IRSNB is quite old and collected from "Nova Grenada", it is not considered to be a syntype of *Cyrtothorax erythrurus* as the labels are different from that of the syntype deposited in the Kraatz collection (Brunke and Solodovnikov 2014).

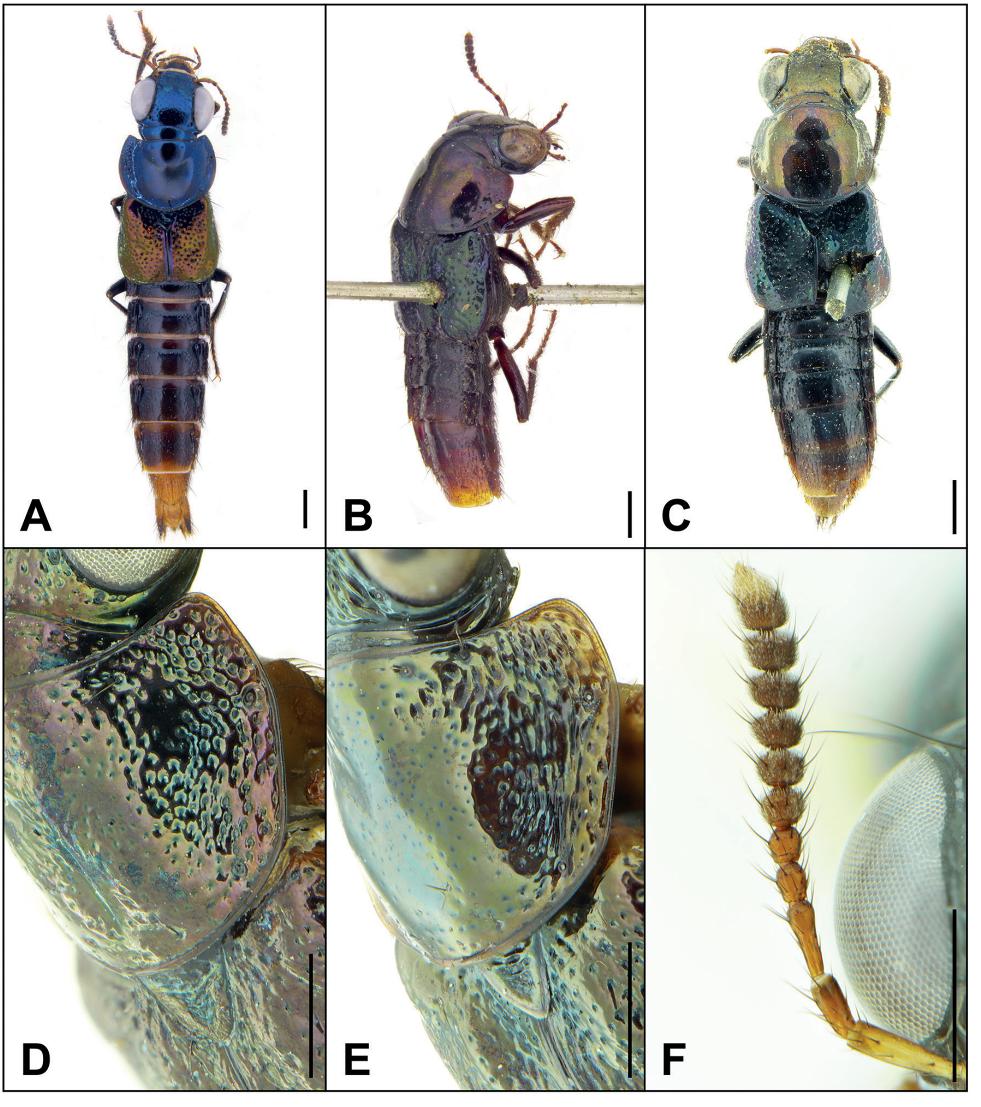

Figure 1. A–C habitus of *Bolitogyrus erythrurus* (Kraatz) **A** non-type, Panama **B** syntype, "Nova Grenada" **C** non-type, "Nova Grenada" **D, E** pronotum, lateral view **D** *B. viridescens* Brunke **E** *B. pseudostrigifrons* Brunke **F** antenna of *B. nigropolitoides* Brunke. Scale bars: 1 mm (**A, B**); 0.5 mm (**D–F**).

Bolitogyrus sallei (Kraatz, 1858)

Cyrtothorax sallei Kraatz, 1858: 367
Bolitogyrus sallei (Kraatz): Brunke and Solodovnikov 2014 (resurrection, redescription)

Non-type material. Mexico: Veracruz: "Jalappa" [= Xalapa] (1, NMPC).

Comment. Only two distant localities were previously known for this species: Chapulhuacán (Hidalgo) and Córdoba (Veracruz) (Brunke and Solodovnikov 2014).

Bolitogyrus salvini (Sharp, 1884)

Cyrtothorax salvini Sharp, 1884: 341
Bolitogyrus salvini (Sharp): Brunke and Solodovnikov 2014 (redescription; three morphotypes)

Non-type material. Guatemala: Suchitepéquez: Volcán Atitlán, Ref. El Quetzal, 1670 m, 14.55067, –91.19235, 3–6.VI.2015, Z.H. Falin & F. Carrillo, ex. FIT [flight intercept trap], cloud forest (1 male, SEMC).

Comment. The above specimen perfectly corresponds to *B. salvini* morphotype I of Brunke and Solodovnikov (2014): forebody with greenish metallic reflections, disc of head without impunctate area, frontal impression weak, basal segments of abdomen reddish, apex of abdomen pale, parameral arms with dense peg setae. The only other known specimens of morphotype I are the male and female types from El Zapote, Guatemala, also in the Sierra Madre mountain range. The close morphological consistency of the non-type male with the type series suggests that the concept of *B. salvini* should be restricted to morphotype I alone. However, formal changes, including the possible description of new species corresponding to morphotypes II and III, should wait until the unknown male of morphotype II is studied.

Bullatus lineage

Strigifrons group

Revised key to the Strigifrons group

1 Base of head with a pair of large, glossy protuberances, creating expansive impunctate areas (fig. 6A in Brunke and Solodovnikov 2014); Guatemala .... ***B. silex* Brunke**
– Base of head with small, well separated protuberances that may or may not be entirely obscured by sculpture; Mexico.......... **2**
2 Head with small, shining, protuberances generally lacking sculpture; pronotum laterally without strigose sculpture forming longitudinal channels (Fig. 1D); abdominal tergite VI without median impunctate area ....***B. viridescens* Brunke**
– Head with small protuberances, almost entirely obscured by sculpture; pronotum laterally with strigose sculpture forming longitudinal channels (Fig. 1E); abdominal tergite VI with median impunctate area.......... **3**
3 Elytra with extensive strigose sculpture, not limited to lateral patch; abdominal tergite VII with median impunctate area; paramere longer than median lobe and with peg setae arranged in a simple, well-aligned marginal row at each side (Fig. 2E); apex of median lobe in ventral view narrower and more strongly converging to apex (Fig. 2C) .... ***B. strigifrons* (Wendeler), sensu nov.**
– Elytra with strigose sculpture limited to lateral patch; abdominal tergite VII without median impunctate area; paramere shorter than median lobe and with peg

setae arranged in loosely organized marginal row, often with doubled punctures (Fig. 2F); apex of median lobe in ventral view broader and more weakly converging to apex (Fig. 2D)................................ ***B. pseudostrigifrons* Brunke, sp. nov.**

Bolitogyrus pseudostrigifrons Brunke, sp. nov.

http://zoobank.org/CC047B84-4978-4F62-8C1F-ACD9DBE8A307

Figs 1E, 2B, D, F

Bolitogyrus strigifrons (Wendeler): Brunke and Solodovnikov, 2014 (misidentification, in part)

Type locality. Tlanchinol, 43 km SW Huejutla de Reyes, Hidalgo, Mexico.

Type material. ***Holotype*** (male, CNC): Mex: Hdgo., Tlanchinol, 43 km SW Huejutla, 14.VI.–4.VIII.1983, S.&J. Peck, 1500 m, cloud forest FIT [typed label] / *Bolitogyrus pseudostrigifrons* Brunke, des. Brunke, 2021 [red label].

Paratypes (4, CNC; 1 UAEH): same data as holotype (2 males, 2 females, CNC); **Hidalgo:** Zacualtipán, Camino a Sto. Domingo [trail to Santo Domingo], 20°38'00.7"N, 98°34'00.5"W, 1830 m, Bosque mixto? o mesofilo? [=mixed? or cloud forest?] pert. [=disturbed], en troncos podridos [in rotten logs], 16.VIII.2003, J. Asiain y J. Márquez (1 male, UAEH).

Etymology. The species epithet refers to the similarity to its sister species, *B. strigifrons* (Wendeler).

Diagnosis. Within the Strigifrons group (for diagnosis, see Brunke and Solodovnikov (2014)): strigulose sculpture of elytra present but restricted to small lateral patch; posterior protuberances of head not creating expansive impunctate areas; abdominal tergite VI (but not VII) with disc impunctate medially. *Bolitogyrus pseudostrigifrons* is most similar to *B. strigifrons* but can be easily recognized externally by the lack of an impunctate medial area on tergite VII and the strigulose sculpture on the elytra limited to a lateral patch. The paramere is also markedly different (Fig. 2F), with the overall shape expanded subapically and with disorganized, marginal rows of peg setae that are often doubled; it is also shorter than the median lobe, while it is longer in *B. strigifrons*. Additionally, the apex of the median lobe in ventral view is broader and less strongly convergent (Fig. 2D).

Description. Measurements ♂ (n = 4): HW/HL 1.54–1.60; PW/PL 1.42–1.56; EW/EL 1.20–1.35; PW/HW 1.11–1.13; ESut/PL 0.82–0.90; forebody length 3.26–3.58 mm.

Measurements ♀ (n = 2): HW/HL 1.50–1.55; PW/PL 1.46–1.50; EW/EL 1.32–1.44; PW/HW 1.10; ESut/PL 0.82–0.88; forebody length 3.26–3.37 mm.

As in the description of *B. strigifrons* given by Brunke and Solodovnikov (2014) except: head distinctly more transverse (*B. strigifrons*, HW/HL = 1.38); elytra with strigose microsculpture confined to lateral patch; tergite VII without clear impunctate medial area; aedeagus with paramere distinctly shorter than median lobe; median lobe in ventral view broader, less strongly convergent to apex (Fig. 2D); median lobe in

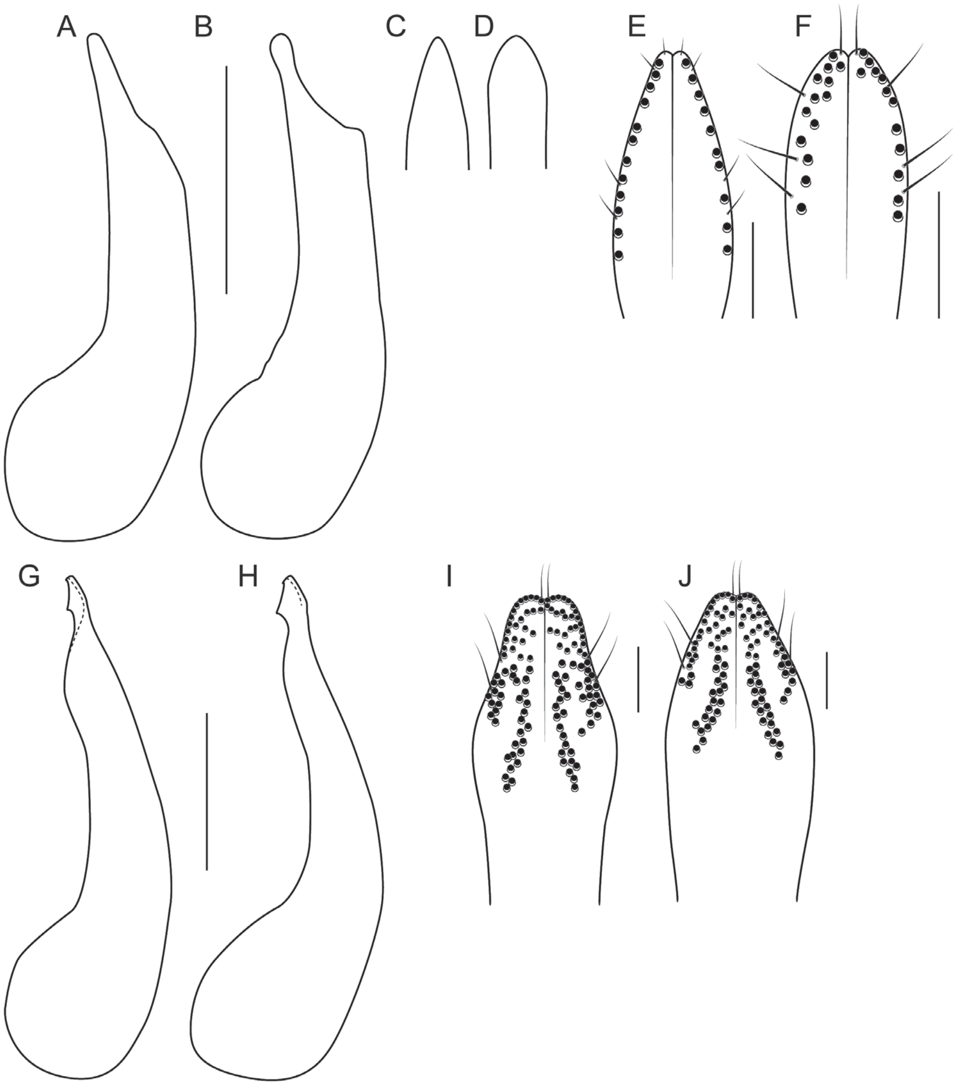

Figure 2. Male genitalia **A, C, E** *Bolitogyrus strigifrons* (Wendeler) **B, D, F** *B. pseudostrigifrons* Brunke **G, I** *B. nigropolitus* Smetana **H, J** *B. nigropolitoides* **A, B, G, H** median lobe in lateral and **C, D** ventral view. **E, F, I, J** inner face of paramere, apex. Scale bars: 0.5 mm (**A–D, G, H**); 0.1 mm (**E, F, I, J**).

lateral view with apex slightly swollen, knob-like (Fig. 2B); paramere spoon-shaped, apical part broadest subapically, with marginal row of peg setae disorganized and with several setae in row doubled (Fig. 2F), parameral setae thicker and longer.

Distribution. This species is known from two rather close localities in Hidalgo, Mexico.

Bionomics. Specimens were collected in cloud forests (1500–1830 m), using an FIT and from a rotten log.

Comments. In Brunke and Solodovnikov (2014), the only non-type specimen of *B. strigifrons* available (male from Hidalgo, listed as a paratype above) had the tip of the paramere missing. Although there were some external differences with the holotype that were noted, a conservative approach was taken, and they were treated as conspecific. A newly available series of specimens from Hidalgo (CNC), in good condition, revealed that two species are involved that differ both externally and in male genitalia. This is the species figured in Brunke and Solodovnikov (2014) as *B. strigifrons* (fig. 6F, 13E).

Bolitogyrus strigifrons (Wendeler, 1928), sensu nov.

Fig. 2A, C, E

Cyrtothorax strigifrons Wendeler, 1928: 34
Bolitogyrus strigifrons (Wendeler): Brunke and Solodovnikov 2014 (redescription; misidentification of *B. pseudostrigifrons*, in part)

Type material. Holotype, examined for Brunke and Solodovnikov (2014), images used for comparison.

Diagnosis. Within the Strigifrons group (for diagnosis, see Brunke and Solodovnikov (2014)): strigulose sculpture of elytra present and more expansive, not restricted to small lateral patch; posterior protuberances of head not creating expansive impunctate areas; abdominal tergites VI–VII with disc impunctate medially. *Bolitogyrus strigifrons* is most similar to *B. pseudostrigifrons* but can be easily recognized externally by the impunctate medial area on tergite VII and the more expansive strigulose sculpture on the elytra. The paramere is also markedly different (Fig. 2E), with the overall shape evenly narrowed to the apex and with simple, organized marginal rows of peg setae; it is also longer than the median lobe. Additionally, the median lobe in ventral view is more strongly convergent to a narrower apex (Fig. 2C)

Distribution. In its revised sense, *B. strigifrons* is known only from the holotype male, collected from an imprecise locality in Veracruz state, Mexico (“Jalapa”).

Comments. At the moment, sister species *B. pseudostrigifrons* (Hidalgo) and *B. strigifrons* (Veracruz) appear to be broadly allopatric but more collecting is needed in Veracruz and Puebla states at medium elevations to verify this.

Bolitogyrus viridescens Brunke, 2014

Bolitogyrus viridescens Brunke in Brunke and Solodovnikov 2014: 73

Non-type material. Mexico: Veracruz: “Jalapa”, Georg Heine (1 female, NMPC); Aguita Fria, 1.3 km SWW of Rancho Viejo (W of Xalapa), 19°31.3'N, 96°59.5'W, 1510 m, 9.IX.2016, Alvarado, Arriaga, Fikáček and Seidel lgt., sifting of thin layer of leaf litter, sparse riverside forest with emergent, large *Platanus* and dense understory (1 female, NHMD).

Comment. *Bolitogyrus viridescens* was previously known only from a single imprecise locality: ~9 km E Teziutlán. Although this locality was listed as from Puebla state on the labels of the type series (Brunke and Solodovnikov 2014), 9 km E of Teziutlán must be just over the border in neighboring Veracruz state. Based on the detailed record from Aguita Fria, *B. viridescens* is probably sympatric with *B. strigifrons*, and both are recorded from the general area around the city of Xalapa.

Neotropical species incertae sedis

Bolitogyrus newtoni Brunke, 2014

Bolitogyrus newtoni Brunke in Brunke and Solodovnikov 2014: 78

Non-type material. Guatemala: Suchitepéqez: Volcan Atitlán, Ref. El Quetzal, 1670 m, 14.55067, −91.19235, 6–10.VI.2015, Z.H. Falin & F. Carrillo, ex. FIT, cloud forest (1, SEMC); same except 10–13.VI.2015 (2, SEMC); same except 13–16.VI.2015 (1, SEMC).

Comments. The above material, more than doubling the number of known specimens, was collected by FIT very close to the locality of one paratype and indicate that this species readily disperses through flight.

Oriental species

Electus group

Revised key to the Electus group

Upon study of one paratype of *B. cyanipennis* (cSmet), it was discovered that this species can also have a darker abdomen, with only the apical margins of the tergites paler. The key below is emended below to accommodate for this color dimorphism.

1 Pronotum dark reddish brown to bright orange, contrasting with dark head; elytra bright metallic green to blue; abdomen bicolored red and black, or at least with tergites distinctly paler apically **2**

– Pronotum dark, concolorous with head; elytra with only faint metallic reflection; abdomen entirely dark, elytra dark **3**

2 Paramere with constricted stem, exposing median lobe in parameral view; apex of median lobe obtuse in parameral view; northeastern Sichuan, northern Chongqing and southern Shaanxi, China .... ***B. kitawakii* Smetana & Zheng**

– Paramere vaguely constricted, not exposing median lobe in parameral view; apex of median lobe acute in parameral view; north-central Sichuan, China .... ***B. cyanipennis* (Zheng)**

3 Head with deeply impressed punctures, many punctures confluent, forming rows; Hubei and Guizhou, China.. **4**
– Head with regular, non-impressed punctures, most punctures clearly separated, Sichuan and Yunnan, China, Laos and Vietnam **5**
4 Paramere with peg setae medially, on projected ridge; peg setae with median group extended clearly basad of marginal group; median lobe in lateral view without subapical teeth; Hubei, China..................................***B. metallicus* Cai et al.**
– Paramere without projected ridge; peg setae with median group extended to no more than just behind level of marginal group; median lobe in lateral view with small subapical teeth; Guizhou, China ....***B. nigerrimus* Yuan et al.**
5 Hind tibia in lateral view with at least distal half distinctly paler than darkened portion of femur; paramere with median rows of peg setae extended far basad of marginal rows (Fig. 2I, J); median lobe in lateral view subparallel in middle portion (Fig. 2G, H) **6**
– Hind tibia in lateral view entirely dark, as dark as darkened portion of femur; paramere with median rows of peg setae, if present, extended only just basad of marginal rows; median lobe in lateral view gradually widening basad from subapex 7
6 Antennomere 5 elongate, 6 very weakly transverse; paramere shorter than median lobe, apex of median lobe visible in parameral view; paramere with wide subapical part angulate and then narrowed to broader, more truncate apex (Fig. 2I); median lobe in lateral view with large subapical expansion (Fig. 2G); Sichuan, China..... ....***B. nigropolitus* Smetana**
– Antennomere 5 subquadrate, 6 distinctly transverse (Fig. 1F); paramere slightly longer than median lobe, apex of median lobe not visible in parameral view; paramere with wide subapical part broadly rounded to narrower apex (Fig. 2J); median lobe in lateral view with only slight subapical expansion (Fig. 2H); northern Vietnam...***B. nigropolitoides* Brunke, sp. nov.**
7 Antennomeres 7–10 relatively elongate: 6 quadrate and 7 weakly transverse; paramere with attenuate apex **8**
– Antennomeres 7–10 relatively transverse: 6 weakly, and 7 distinctly transverse; paramere with evenly converging sides **9**
8 Apex of median lobe in lateral view forming a more elongate triangle; paramere in lateral view with broad lateral projection; Central Yunnan, China, east of the Salween River.. ***B. electus* Smetana & Zheng**
– Apex of median lobe in lateral view forming a shorter triangle; paramere in lateral view with sharp lateral projection; Western Yunnan, China, west of the Salween River ....***B. uncus* Cai et al.**
9 Peg setae absent from broad oval shaped area along middle of paramere; median lobe in lateral view without expansion basad of subapical tooth; Western Yunnan, China, west of the Salween River, possibly adjacent Myanmar .... ***B. huanghaoi* Hu et al.**
– Peg setae absent from only narrow strip along middle of paramere; median lobe in lateral view with distinct expansion basad of subapical tooth; southeast Yunnan, China, and northern Laos and Vietnam (possibly northern Thailand)................ ....***B. confusus* Brunke**

Bolitogyrus confusus Brunke, 2017

Bolitogyrus confusus Brunke, 2017: 18
Bolitogyrus electus Smetana & Zheng, 2000: Hu et al. 2011 (misidentification)

Non-type material. Vietnam: Lai Châu: Hoàng Liên Nat. Pk., Tram Ton Pass 22.348, 103.775, 1948 m, subtropical forest, fungusy wood, beating, 23.VI.2017, R. Schuh (1 male, 1 female, CNC).

Comment. Newly recorded from Vietnam and known elsewhere from southern Yunnan, China and northern Laos. The above specimens fill in a distribution gap between the southern Chinese and Laos localities. *Bolitogyrus confusus* may also occur in northern Thailand. The specimens were collected by beating wooden trail posts that had weathered, cracked, and become fungusy in the constant humidity.

Bolitogyrus huanghaoi Hu et al., 2011

Bolitogyrus huanghaoi Hu et al., 2011: 60
Bolitogyrus huanghaoi Hu et al.: Brunke 2017 (redescription)

Non-type material. China: Yunnan: 1.8 km W Zizi vill., 2.VII.2016, 25°44.7'N, 98°33.6'E, 2005 m, from large dead tree stumps, J. Hajek and J. Ruzicka (1 female, NMPC).

Comments. Although this specimen is a single female, the transverse antennomeres and its locality west of the Salween River (“Nujiang” in China) allow for a determination to *B. huanghaoi*. The specimen represents only the third record for this species, just west (~13 km) of the type locality. Another single female is known from just over the border in Myanmar (Brunke and Solodovnikov 2014).

Bolitogyrus uncus Cai et al., 2015

Bolitogyrus uncus Cai et al., 2015: 472
Bolitogyrus uncus Cai et al.: Brunke et al. 2017 (redescription)

Non-type material. China: Yunnan: Gaoligong mts, 2200–2500 m, 24.57, 98.45, 8–16.V.1995, O. Semela (5, cShi).

Comments. The female paratype of sister species *B. electus*, collected from Gaoligongshan, was considered of doubtful identity by Brunke (2017) based on it being a western outlier from the main distribution of that species. A series of males and females from the same locality indicate that this female paratype is really *B. uncus* and that these two species are probably separated allopatrically by the Salween River valley (“Nujiang” in China).

Bolitogyrus nigropolitoides Brunke, sp. nov.

http://zoobank.org/E2752AD1-20AB-49C7-ADBB-86EEFA76FDCE
Figs 1F, 2H, J

Type locality. Phia Oac National Park, Cao Bang, Vietnam.

Type material. ***Holotype*** (male, CNC): Vietnam, Cao Bang, Phia Oac Nat. Park, summit rd., behind upper FIT, 22°36'21.60"N, 105°52'19.20"E, 1600 m, mat. secondary forest, fogging standing dead tree w/ orange fungus, 7–17.V.2019, A. Brunke & H. Schillhammer, CNC1898850 [typed label] / *Bolitogyrus nigropolitoides* Brunke, des. Brunke, 2021 [red label]

Etymology. The species epithet refers to the similar species *B. nigropolitus* from Sichuan, China.

Diagnosis. Within the Electus group (for diagnosis, see Brunke and Solodovnikov 2014): abdomen entirely dark; head without deeply impressed punctures; lateral face of hind tibia bicolored, distal half distinctly paler than darkened part of hind femur; antennomere 5 subquadrate, 6 distinctly transverse (Fig. 1F); paramere slightly longer than median lobe, in ventral view median lobe not visible; paramere with apical part broadly rounded to apex (Fig. 2J); median lobe in lateral view with smaller subapical expansion (Fig. 2H).

Description. Measurements ♂ (n = 1): HW/HL 1.30; PW/PL 1.17; EW/EL 1.12; ESut/PL 0.85; PW/HW 1.09; forebody length 4.5 mm.

Very similar to *Bolitogyrus nigropolitus* (Fig. 2G, 2I) except: antennae shorter, antennomere 5 subquadrate, 6 distinctly transverse (Fig. 1F); pronotum slightly less transverse; elytral slightly longer; paramere slightly longer than median lobe, in ventral view median lobe not visible with paramere in situ; paramere with apical part broadly rounded to narrower apex (Fig. 2J); median lobe in lateral view with subapical expansion much smaller (Fig. 2H).

Distribution. This species is known only from Phia Oac National Park in northern Vietnam, though it likely occurs at similar elevations in neighboring Yunnan, China and elsewhere in northern Vietnam east of the Red River.

Bionomics. The holotype was pyrethrin-fogged from a dead standing tree, bearing orange-fungal fruiting bodies.

Caesareus group

Bolitogyrus sp.

Non-type material. Indonesia: Sumatra: Aceh, G. Leuser Nat. Pk., Ketambe Res. Sta., 3°41'N, 97°39'E, primary rainforest, malaise trap, 350 m, XII.1989, IIS 89001B, D.C. Darling, 1 female (ROM).

Comments. The above single female specimen is similar to *B. proximus* but could also represent an undescribed species. The genus is newly reported from the island of Sumatra, where it is undoubtedly diverse but extremely poorly sampled.

Vulneratus group

Bolitogyrus flavus Yuan et al., 2007

Bolitogyrus flavus Yuan et al., 2007: 148
Bolitogyrus flavus Yuan et al.: Brunke 2017 (redescription)

Non-type material. Vietnam: Hoa Bihn: "Tonkin", de Cooman (1, NMPC).

Bolitogyrus depressus Cai et al., 2015

Bolitogyrus depressus Cai et al., 2015: 454
Bolitogyrus depressus Cai et al.: Brunke 2017 (redescription)

Non-type material. China: Guangdong: Nanling Nat. Reserve, Dadongshan, 18–21.IV.2013, border of mixed forest, 24°56.0'N, 112°42.9'E, 690 m, J. Hajek and J. Ruzicka (1, NMPC); **Guangxi:** Longsheng Hot Spring, forested river valley, wet rocks, 25°53.6'N, 110°12.4'E, 360 m, 11–14.IV.2013, M. Fikacek, J.Hajek, J. Ruzicka (2, NMPC).

Comments. This species is newly reported from Guangxi, indicating that it is probably very broadly distributed in the low forested hills of southeastern China. The specimens from wet rocks in a forested river valley probably dropped when disturbed from overhanging coarse woody debris.

Bolitogyrus tumidus Brunke, 2017

Bolitogyrus tumidus Brunke, 2017: 55

Non-type material. Laos: Hua Phan: 20°13'9–19"N, 103°59'54–104°0'3"E, 1480–1510 m, Phou Pane Mt. [= Mt. Phu Phan], 22.IV.–14.V.2008, Vit. Kuban (3, NMPC).

Bolitogyrus himalayicus Brunke, 2017

Bolitogyrus himalayicus Brunke, 2017: 66
Bolitogyrus vulneratus Fauvel, 1878: Smetana 1988 (misidentification of *B. himalayicus*)

Non-type material. Nepal: Prov. No. 1: Khandbari, Arun Valley, at Num bridge, 1050 m, 22.IV.1984, Smetana and Löbl (1 male, cSmet).

Comments. *Bolitogyrus himalayicus* is here newly reported from Nepal. The above specimen is substantially larger than the holotype and was collected at a higher elevation (200 m versus 1000 m), but its aedeagal morphology corresponds perfectly. This specimen also represents the only record of the genus from Nepal and was previously reported by Smetana (1988) under the name *B. vulneratus*. The couplets from the key in Brunke (2017) should be modified as follows:

30 Paramere with subbasal expansion in lateral view; Garo Hills, Meghalaya, India . ... ***B. concavus* Brunke**
– Paramere without subbasal expansion in lateral view; Khasi Hills, Meghalaya, and Himalaya of Nepal and West Bengal, India **31**
31 Apex of the median lobe in parameral view with single toothed carina; paramere with peg setae arranged in disorganized marginal row, apex with dense group; Himalaya of Nepal and West Bengal, India .... ***B. himalayicus* Brunke**
– Apex of median lobe in parameral view with double-toothed carina; paramere with peg setae in sparse, single marginal row; Khasi Hills, Meghalaya, India .... ***B. nanus* Brunke**

Acknowledgements

I would like to thank the curators listed in Materials and methods for making specimens under their care available for study. I would also like to thank Hong Thai Pham (Vietnam National Museum of Nature) for his assistance with fieldwork in Vietnam in 2017 and 2019. This study received financial support from A-base funding from the Government of Canada (Agriculture and Agri-food Canada: Systematics of Beneficial Arthropods – J-002276). Two reviewers are thanked for their input, which improved the manuscript.

References

Brunke AJ (2017) A revision of the Oriental species of *Bolitogyrus* Chevrolat (Coleoptera, Staphylinidae, Staphylininae). ZooKeys 664: 1–97. https://doi.org/10.3897/zookeys.664.11881

Brunke A, Solodovnikov A (2014) A revision of the Neotropical species of *Bolitogyrus* Chevrolat, a geographically disjunct lineage of Staphylinini (Coleoptera, Staphylinidae). ZooKeys 423: 1–113. https://doi.org/10.3897/zookeys.423.7536

Brunke A, Chatzimanolis S, Metscher BD, Wolf-Schwenninger K, Solodovnikov A (2017) Dispersal of thermophilic beetles across the intercontinental Arctic forest belt during the early Eocene. Scientific Reports 7: e12972. https://doi.org/10.1038/s41598-017-13207-4

Brunke AJ, Żyła D, Yamamoto S, Solodovnikov A (2019) Baltic amber Staphylinini (Coleoptera: Staphylinidae: Staphylininae): a rove beetle fauna on the eve of our modern climate. Zoological Journal of the Linnaean Society 187(1): 166–197. https://doi.org/10.1093/zoolinnean/zlz021

Cai Y-P, Zhao Z-Y, Zhou H-Z (2015) Taxonomy of the genus *Bolitogyrus* Chevrolat (Coleoptera: Staphylinidae: Staphylinini: Quediina) from China with description of seven new species. Zootaxa 3955: 451–486. https://doi.org/10.11646/zootaxa.3955.4.1

Chevrolat A (1842) *Bolitogyrus*. In: D'Orbigny C (Ed.) Dictionnaire Universel d'Histoire Naturelle. Bureau Principal de Éditeurs, Paris, 641 pp.

Erichson WF (1840) Genera et species Staphylinorum insectorum coleopterorum familiae F.H. Morin, Berlin 1: 401–954. https://doi.org/10.5962/bhl.title.59644

Hu J-Y, Liu T-T, Li L-Z (2011) New and Little-Known Species of the Genus *Bolitogyrus* Chevrolat from China (Coleoptera: Staphylinidae: Staphylininae). Journal of the Kansas Entomological Society 84: 58–63. https://doi.org/10.2317/JKES101003.1

Kraatz G (1858) Einige neue und ausgezeichnete Staphylinen-Gattungen. Berliner Entomologische Zeitschrift 2(3-4): 361–368. https://doi.org/10.1002/mmnd.18580020310

Scheerpeltz O (1974) Studien an den Arten der Gattung *Cyrtothorax* Kraatz mit Beschreibung neuer Arten sowie einer Dichotomik aller bis heute bekannt gewordenen Arten dieser Gattung (Coleoptera, Staphylinindae, Staphylininae, Quediini). Reichenbachia 15: 175–192.

Sharp D (1884) Staphylinidae. Biologia Centrali-Americana Insecta Coleoptera. Taylor and Francis, London 1(2): 313–392.

Smetana A (1988) Revision of the tribes Quediini and Atanygnathinini. Part II. The Himalayan region (Coleoptera: Staphylinidae). Quaestiones Entomologicae 24: 163–464.

Wendeler H (1927) Neue exotische Staphyliniden (Col.). Neue Beiträge zru systematischen Insektenkunde 4: 2–9.

Wendeler H (1928) Neue exotische Staphyliniden. Neue Beiträge zur systematischen Insektenkunde 4: 32–35. https://doi.org/10.1002/mmnd.48019280403

Yuan X, Zhao M-J, Li L-Z, Hayashi Y (2007) Contributions to the knowledge of the genus *Bolitogyrus* (Coleoptera: Staphylinidae) of China. Entomological Review of Japan 62: 145–155.

ZooKeys 1096: 17–118 (2022)
doi: 10.3897/zookeys.1096.73485
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A revision of the *wilsoni* species group in the millipede genus *Nannaria* Chamberlin, 1918 (Diplopoda, Polydesmida, Xystodesmidae)

Derek A. Hennen[1], Jackson C. Means[1], Paul E. Marek[1]

1 *Virginia Polytechnic Institute and State University, Department of Entomology, Price Hall, 170 Drillfield Drive, Blacksburg, Virginia, USA*

Corresponding author: Derek A. Hennen (dhennen@vt.edu)

Academic editor: Nesrine Akkari | Received 25 August 2021 | Accepted 18 February 2022 | Published 15 April 2022

http://zoobank.org/DC44FD3E-BB71-451E-B784-6A5A991A3327

Citation: Hennen DA, Means JC, Marek PE (2022) A revision of the *wilsoni* species group in the millipede genus *Nannaria* Chamberlin, 1918 (Diplopoda, Polydesmida, Xystodesmidae). ZooKeys 1096: 17–118. https://doi.org/10.3897/zookeys.1096.73485

Abstract

Although many new species of the millipede genus *Nannaria* Chamberlin, 1918 have been known from museum collections for over half a century, a systematic revision has not been undertaken until recently. There are two species groups in the genus: the *minor* species group and the *wilsoni* species group. In this study, the *wilsoni* species group was investigated. Specimens were collected from throughout its distribution in the Appalachian Mountains of the eastern United States and used for a multi-gene molecular phylogeny. The phylogenetic tree recovered *Nannaria* and the two species groups as monophyletic, with *Oenomaea pulchella* as its sister group. Seventeen new species were described, bringing the composition of the *wilsoni* species group to 24 species, more than tripling its known diversity, and increasing the total number of described *Nannaria* species to 78. The genus now has the greatest number of species in the family Xystodesmidae. Museum holdings of *Nannaria* were catalogued, and a total of 1,835 records used to produce a distribution map of the species group. Live photographs, illustrations of diagnostic characters, ecological notes, and conservation statuses are given. The *wilsoni* species group is restricted to the Appalachian region, unlike the widely-distributed *minor* species group (known throughout eastern North America), and has a distinct gap in its distribution in northeastern Tennessee and adjacent northwestern North Carolina. The *wilsoni* species group seems to be adapted to mesic microhabitats in middle to high elevation forests in eastern North America. New species are expected to be discovered in the southern Appalachian Mountains.

Keywords

Appalachia, Diplopoda, Nannariini, phylogeography, taxonomy

Introduction

Millipedes in the family Xystodesmidae encompass a large component of the diplopod fauna in the deciduous forests of the Holarctic, with 539 currently known species (Marek et al. 2014; Means et al. 2021a, b; Mikhaljova 2021). Many species in the family are strikingly aposematic, with bold hues of yellow, orange, and red that are paired with black, thereby advertising their toxic chemical defenses of hydrogen cyanide and benzaldehyde (Marek and Bond 2009; Marek et al. 2018). While all members of the family are chemically defended, a few groups within the family do not appear to rely heavily on chemical defense and aposematism as a main form of defense. This is exemplified by the genus *Nannaria* Chamberlin, 1918, an assemblage of small-bodied (15–38 mm long) millipedes distributed in eastern North America. They are typically chestnut brown to black with a bimaculate pattern of orange to red, or white spots; uncommonly they may also have stripes.

The small size and comparatively subdued colors are atypical for xystodesmids, and previous authors have termed *Nannaria* as non-aposematic due to these traits, but speculated *Nannaria* may be mimicking colorless juveniles of aposematic xystodesmids (Whitehead and Shelley 1992). Additionally, *Nannaria* do not exhibit as much diurnal surface-level activity, traits typically associated with aposematic organisms, as other xystodesmids do, such as the apheloriine species *Apheloria polychroma* (Marek et al. 2018). More commonly, *Nannaria* species are collected under forest detritus such as dead leaves and stones, or with passive trapping methods such as pitfall traps. They are difficult to deliberately collect through traditional methods of collecting xystodesmid millipedes (Hennen and Shelley 2015; Means et al. 2015). Part of this difficulty stems from their behavior: individuals tend to remain buried in the soil, even as adults. They either stay completely beneath the surface, or with only a portion of their body exposed above the soil.

The distribution of *Nannaria* extends from Arkansas and Missouri east through northern Mississippi to central North Carolina, and north to New York. Within that distribution, the region with the highest number of *Nannaria* species is the Appalachian Mountains of eastern North America. *Nannaria* is classified in the tribe Nannariini, which also includes the monotypic genus *Oenomaea* Hoffman, 1964, known from eastern Tennessee, northern Alabama, and northern Georgia. A recent molecular phylogenetic analysis of Xystodesmidae showed that the Nannariini was sister to a clade composed of the former families Euryuridae and Eurymerodesmidae (now tribes Euryurini and Eurymerodesmini) within the Xystodesmidae (Means et al. 2021a). This study showed that *Oenomaea pulchella* (Bollman, 1889) was sister to *Nannaria*, which was composed of two monophyletic species groups: the *minor* species group and the *wilsoni* species group. Means et al. (2021b), with additional species sampling within the genus, confirmed the monophyly of these species groups, and described 35 new species of the *minor* species group.

Despite the small size and cryptic behavior of *Nannaria*, millipede workers have described 62 species of Nannariini in two genera: *Nannaria* and *Oenomaea* (Marek et al.

2014; Hennen and Shelley 2015; Means et al. 2021a, b). The first species of *Nannaria* was described in 1847 by C. L. Koch, as *Fontaria oblonga* (C. L. Koch, 1847), with its type locality simply stated as Pennsylvania (Koch 1847). Two more species were described in the late 1800s (McNeill 1887; Bollman 1888), but the genus *Nannaria* had not been erected until the early 20th century, with *Nannaria minor* (Chamberlin, 1918) designated as the type species (Chamberlin 1918). Later papers by Chamberlin (1928, 1940, 1947, 1949), Williams and Hefner (1928), Causey (1942, 1950a, b), Hoffman (1948, 1949a, b, 1950), Loomis and Hoffman (1948), Shelley (1975), Hennen and Shelley (2015), and Means et al. (2021a, b) added more species and characters to define the Nannariini. Previous species included in *Nannaria* have been transferred to other genera such as *Boraria* Chamberlin, 1943; *Howellaria* Hoffman, 1950; *Stenodesmus* De Saussure, 1859; and the genera *Castanaria* Causey, 1950 and *Mimuloria* Chamberlin, 1928, the latter two of which were later synonymized with *Nannaria*. The monophyly of the *minor* and *wilsoni* species groups in the tribe has been tested using molecular phylogenetics in Means et al. (2021a, b). However, the monophyly and phylogenetic placement of the tribe Nannariini has never been rigorously tested using molecular phylogenetics until recently (Marek and Bond 2006; Means et al. 2021a, b). The tribe Nannariini is diagnosed by the following main characters: sterna with lateral triangular spines; males with twisted, spatulate pre-gonopodal claws; gonopods with straight or curving acropodites; and a stout, long prefemoral process (Hoffman 1964; Hennen and Shelley 2015; Means et al. 2021b: figs 2, 8). For a detailed summary of the taxonomic history and diagnostic characters of the Nannariini, see Means et al. (2021b).

Previous authors have indicated that many undescribed species, and possibly even genera, remain to be found in the tribe (Hoffman 1999; Hennen and Shelley 2015; Marek et al. 2018), and this has been supported in a recent study of the *minor* species group, in which 35 new species of the genus were named (Means et al. 2021b). However, the *wilsoni* species group has not been investigated, and new species have been uncovered by examination of material in museum collections. Upon study of material from the Virginia Museum of Natural History amassed by Richard Hoffman and museum staff during decades of field collecting and molecular phylogenetics conducted over the past decade, two main clades within the genus were uncovered (Means et al. 2021a, b). One group, whose gonopod morphology was relatively simple, was referred to as the *Nannaria minor* species group, based on *N. minor*, the oldest name in the group (Means et al. 2021a, b). The second group, whose gonopod morphology was more complex due to the twists and additional processes on the acropodite branch, was labeled the *Nannaria wilsoni* species group, based on the species *N. wilsoni* Hoffman, 1949. The *Nannaria minor* species group (hereafter referred to as the "*minor* species group") is more widespread in eastern North America, found across the entire generic range, while the *Nannaria wilsoni* species group (hereafter "*wilsoni* species group") is restricted to the Appalachian Mountains, where it occupies two separated distributions, a northern and a southern portion.

Previous work on the *wilsoni* species group has been mostly limited to species descriptions. The first described species from the group was *N. scutellaria* (Causey 1942), followed by *N. morrisoni* (Hoffman 1948), *N. shenandoa* (Hoffman 1949a), *N. ericacea* and *N. wilsoni* (Hoffman 1949b), *N. austricola* (Hoffman 1950), and most recently, *N. aenigma* (Means et al. 2021a). The discovery of the *wilsoni* species group as a distinct clade from the *minor* species group was only recently proposed and supported by genetic evidence (Means et al. 2021a, b). The gonopod differences between species now included in the *wilsoni* and *minor* groups were vaguely noted by past workers (Hoffman 1948, 1949a; Hennen and Shelley 2015), but were not investigated further. The only notable non-taxonomic study on the *wilsoni* species group is a comparative morphological study of the gonopods of 17 specimens of *N. scutellaria* by Causey (1950), in which a variation in the angle of the acropodite tip and the number and shape of the distal projections of the acropodite were documented by the author.

With the discovery of 52 undescribed species in the two groups, the ambitious goal of describing them all was split between two projects. The species of the *minor* species group were treated in a first revision (Means et al. 2021b), while the species of the *wilsoni* species group are treated here. The aims of this study are to: (1) confirm the monophyly of the *wilsoni* species group using molecular phylogenetics, (2) describe new species of this species group, and (3) provide full taxonomic accounts for each species in the species group, including natural history notes and an investigation of the ecology of the species.

Materials and methods

Field collection

Nannaria specimens were collected by raking leaf litter and digging at/beneath the soil-litter interface in deciduous forest habitats throughout the eastern United States, according to the methods described in Means et al. (2015). Millipedes were collected with the goal of preserving material for both genetic and morphological analysis. Efforts were made to collect samples of all described species and any undescribed species represented in museum collections. *Nannaria* holdings from the Virginia Museum of Natural History (**VMNH**, Martinsville, Virginia), Virginia Tech Insect Collection (**VTEC**, Blacksburg, Virginia) and the North Carolina Museum of Natural Sciences (**NCSM**, Raleigh, North Carolina) were examined and georeferenced, if geographical coordinates were not originally provided, with the program GEOLocate (Rios 2018). Uncertainty estimates for the georeferenced coordinates were included as the most inclusive error radius that encompassed the recorded locality for each specimen. Natural history specimens were then databased with catalogue numbers beginning with the prefix NAN (e.g., NAN0001). The preceding museum material represented the bulk of *Nannaria* holdings worldwide, and provided locality data for putative new species. With this museum material, further *Nannaria* specimen records from the Symbiota Collections of Arthropods Network (**SCAN**) database (https://scan-bugs.org/) were acquired, including those from the National Parks Service's Great Smoky Mountains

National Park natural history collection (**GRSM**) and the Museum of Comparative Zoology, Harvard University (**MCZ**). All *wilsoni* species group specimens and records used for this study are listed in Suppl. material 1.

Sampling sites were selected based on the historical natural history collections material, with a focus on unsampled areas within the generic distribution. Field collecting took place in seven states: Georgia, Kentucky, North Carolina, South Carolina, Tennessee, West Virginia, and Virginia. Additional states in the eastern United States were visited, but yielded no specimens of the *wilsoni* species group. Scientific collecting permits were acquired for collecting and are listed in the acknowledgements section.

Morphological investigation

After field collection of specimens, millipedes were processed using the workflow described by Means et al. (2021b). Millipedes were photographed on a moss background in the laboratory with a Canon EOS 6D camera and a 50-mm lens. They were then given a catalog number with the prefix MPE (e.g., MPE02123). Twenty-four legs were removed from the right side of the body and preserved in RNAlater or 100% ethanol and stored in a -80 °C freezer in the VTEC (https://www.collection.ento.vt.edu) for molecular analysis. The rest of the body was preserved in 70% isopropanol for morphological analysis and deposited in the VTEC. Measurements for the following six characters were taken from a male specimen of each species using a Leica M125 stereomicroscope, after Marek (2010), and all following measurements are given in millimeters: body length (**BL**), collum width (**CW**), intergenal width (**IW**), interantennal socket width (**ISW**), body ring 10 width (**B10W**), and body ring 10 height (**B10H**). Morphological coding and scoring of taxonomic characters for species descriptions and diagnoses was accomplished using the program Mesquite (Maddison and Maddison 2010) to produce a matrix of qualitative male and female exoskeletal and genitalic characters for species diagnosis, description, and comparison (Suppl. material 2 and 3). A total of 54 qualitative morphological characters (21 male external morphology characters, 25 gonopodal characters, eight cyphopodal characters) were scored for all species in the *wilsoni* species group, incorporating seven new and 47 previously-used taxonomic characters in morphological studies of Xystodesmidae (Marek and Bond 2006; Means et al. 2021a, b). The left gonopod of each species was photographed with a Canon 6D camera with a 65 mm Canon MP-E macro lens mounted on a Passport II Portable Digital Imaging System (Canon, Tokyo, Japan; Visionary Digital, Charlottesville, USA). Photographs were focus stacked with the program Helicon Focus Pro v.6.7.1 (HeliconSoft, Kharkiv, Ukraine), and the composite image was outlined in Adobe Illustrator CS6. Distribution maps were made using the program SimpleMappr (Shorthouse 2010) and Adobe Illustrator CS6. Type specimens of each new species were deposited in the Field Museum of Natural History (**FMNH**), the North Carolina Museum of Natural Sciences (**NCSM**), the Virginia Tech Insect Collection (**VTEC**), and the Virginia Museum of Natural History (**VMNH**). Type repositories for previously-described species include the Smithsonian Institution, National Museum of

Natural History (**USNM**, Washington, D.C.), the Academy of Natural Sciences of Drexel University (**ANSP**, Philadelphia, Pennsylvania), and the Florida State Collection of Arthropods (**FSCA**, Gainesville, Florida).

For species description, we used a morphology based species delimitation criterion that species are diagnosable from others by a combination of unique characteristics. Under this criterion, a total of 17 new species were identified, in addition to the seven species already described in the *wilsoni* species group. Species delimitation followed criteria in Marek (2010) and Means et al. (2021a, b), and using the morphological data (i.e., comparison of gonopod shape), new species hypotheses were proposed.

Phylogenetic inference

A phylogenetic tree of the genus *Nannaria*, including specimens of both the *minor* and *wilsoni* species groups, was estimated from two mitochondrial (16S, CO1) and four nuclear (28S, EF1a, fbox, and RPB1) gene regions using primers developed by Means et al. (2021b). Amplification procedures for the newly developed primers are available in Suppl. material 4, and procedures for previously developed primers can be found in Means and Marek (2017). Outgroup species were selected from other Nannariini genera (*O. pulchella*) and from the tribes most closely related to Nannariini, the Eurymerodesmini and Euryurini. Terminals of the genera *Eurymerodesmus* Brölemann, 1900 and *Euryurus* C. L. Koch, 1847 were used to root the tree. Genomic DNA was extracted from millipede legs and purified with a Qiagen DNeasy kit according to the manufacturer's instructions. The DNA was then amplified via polymerase chain reaction and sequenced with a Sanger protocol, as in Means and Marek (2017) and Means et al. (2021b). Chromatograms were trimmed, bases called, and overlapping fragments assembled into contiguous sequences with the program Mesquite using phred and phrap in the Chromaseq module (Maddison and Maddison 2010; Ewing et al. 1998). The program PRANK (Probabilistic Alignment Kit, Löytynoja and Goldman 2005) was used for sequence alignment using the default gap opening and extension probabilities. Aligned sequences from PRANK were subsequently partitioned by gene and codon position (in protein coding genes) and by intron and exon boundaries (EF1a, RPB1) in Mesquite and then concatenated, following methods in Means et al. (2021b). IQ-TREE 2 (Version 2.0.6, Minh et al. 2020; Chernomor et al. 2016) was then used to estimate a phylogeny under maximum likelihood (ML) as an optimality criterion with 1,000 bootstrap pseudoreplicates. Node support values were inferred based on bootstrap sampling, and node support values greater than 70 were considered to be well-supported. ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the best-fit model with edge-linked-proportional partition models. IQ-TREE 2 was also used to measure nucleotide frequencies and base composition and to perform a $\chi 2$-test for compositional heterogeneity for each gene alignment using only nannariine taxa, with a null hypothesis of homogeneity. To compare separate gene histories, individual gene trees were also estimated in IQ-TREE2 using the same methods as for the concatenated tree.

Results

Field collection

In total, 1,835 *Nannaria* specimens and their specimen-level label records in the *wilsoni* group were examined for this study. Of these, 374 specimens were recently collected (i.e., between 2003 and 2019) and were deposited in the VTEC. Based on the field collections conducted, *Nannaria* specimens often exhibited a patchy distribution, with only a few individuals in each encounter. In this sense, it is unclear if this was a true reflection of their supposed low abundance compared to other syntopic millipedes, or a result of their comparatively cryptic habits (compared to other large xystodesmid millipedes). Their cryptic body coloration and burrowing behavior resulted in specimens being difficult to regularly collect, and when found, were most often partly buried in the soil, with only a small portion of their dorsum exposed above the soil. Due to this difficulty, sampling strategies were subsequently adjusted, with field collectors' focus shifting towards habitats with abundant hemlock (*Tsuga* spp.) and rhododendron (*Rhododendron* spp.), as these plants provide shady, moist microhabitats in their understory (Rohr et al. 2009). Preference was also given to riparian habitats, which also tended to have cool, moist soil that *Nannaria* seemed to prefer. In addition to hemlock and rhododendron, the most commonly encountered plant species include: oaks (*Quercus* spp.), maples (*Acer* spp.), tuliptree (*Liriodendron tulipifera*), pawpaw (*Asimina triloba*), witch hazel (*Hamamelis* spp.), birches (*Betula* spp.), American beech (*Fagus grandifolia*), dogwoods (*Cornus* spp.), black cherry (*Prunus serotina*), hickories (*Carya* spp.), and sassafras (*Sassafras albidum*). An example of typical habitat for the *wilsoni* group is in Fig. 1, and descriptive habitat information for each specimen is given in Suppl. material 1.

The *wilsoni* species group is restricted to the Appalachian region of the eastern United States, within the following U.S. Level III ecoregions (Omernik and Griffith 2014): Blue Ridge, Ridge and Valley, Southwestern Appalachians, Central Appalachians, and Western Allegheny Plateau (Fig. 2). The distribution of the *wilsoni* species group is split into two separate sections: the central Appalachians portion (West Virginia, Virginia, and Kentucky) and the southern Appalachians portion (North Carolina, South Carolina, Tennessee, and Georgia). There is a 140 km gap in the distribution in northeastern Tennessee and adjacent northwestern North Carolina. This gap was initially considered an artifact of collecting bias, but concerted collecting trips to this area revealed only *minor* group species, indicating that this is a true gap in the distribution.

Species of the *wilsoni* group are sympatric with the *minor* group throughout most of the *wilsoni* group's distribution, except for northern Georgia and adjacent southwestern North Carolina. Outlying records of the *wilsoni* group in east-central Tennessee, eastern Kentucky, and northeastern West Virginia indicate that the *wilsoni* group likely has a larger distribution than is currently known, however these areas are poorly-collected for *Nannaria*.

Figure 1. Typical habitat of species in the *Nannaria wilsoni* group. This photograph shows a representative mesic forest during early fall, with a leaf litter layer comprised of tuliptree (*Liriodendron tulipifera*), hemlock (*Tsuga* sp.), alder (*Alnus* sp.), ironwood (*Carpinus caroliniana*), and rhododendron (*Rhododendron* sp.). Henderson County, North Carolina.

Molecular phylogenetics

Our phylogenetic analysis used a concatenated supermatrix which included six genes from 204 taxa and had a total length of 4,651 bp. Gene boundaries are as follows: 16S (1–845), COI (846–1,403), EF1a (1,404–2,098), 28S (2,099–3,193), RPB1 (3,194–4,254), fbox (4,255–4,651). These six genes were subdivided by ModelFinder into eight partitions. Of the 4,651 characters, 2,939 were constant, 691 were parsimony uninformative, and 1,021 were parsimony informative. Partition one contained 16S with TVM+F+I+G4 as its best-fit model, and had 351 parsimony informative characters. Partition two contained the first codon position of COI with TIM3+F+I+G4 as its best-fit model, and had 35 parsimony informative characters. Partition three contained the second codon position of COI and the first and second codon positions of RPB1 with TPM2+F+R3 as its best-fit model, and had 73 parsimony informative characters. Partition four contained the third codon position of COI with TIM3+F+I+G4 as its best-fit model, and had 166 parsimony informative characters. Partition five contained the first and second codon positions of both fbox and EF1a with TIM3e+R3 as its best-fit model, and had 19 parsimony informative characters. Partition six contained

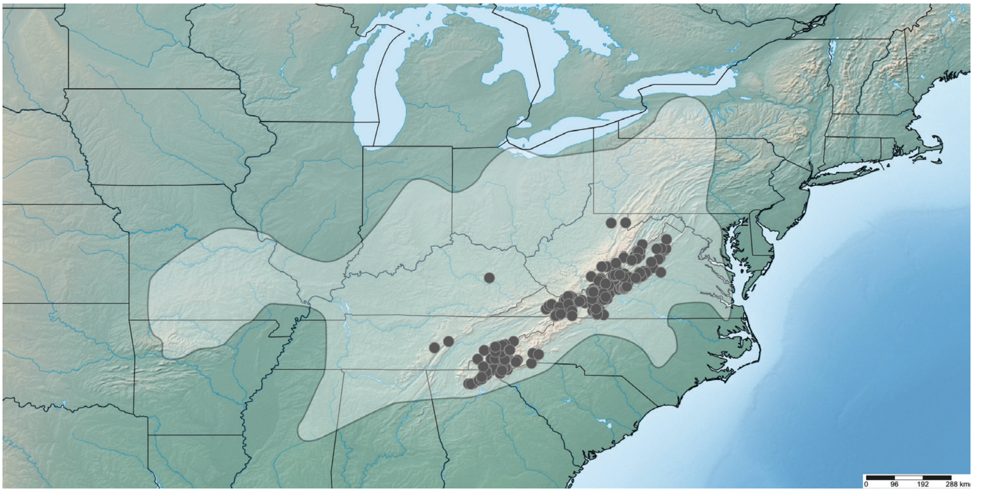

Figure 2. Distribution of the *Nannaria wilsoni* species group. *Nannaria wilsoni* species group specimens are indicated by black dots within the *Nannaria* generic distribution (white shaded region). Biogeographical cluster 1 (Central Appalachian Mountains Species Cluster) are the cluster of dots primarily in Virginia, and Biogeographical cluster 2 (Southern Appalachian Mountains Species Cluster) are those primarily in western North Carolina.

the third codon positions of both fbox and EF1a with TIM+F+R2 as its best-fit model, and had 95 parsimony informative characters. Partition seven contained the third codon position and intron of RPB1 and the intron of EF1a with HKY+F+R3 as its best-fit model, and had 219 parsimony informative characters. Partition eight contained 28S with TVM+F+R3 as its best-fit model, and had 63 parsimony informative characters. The observed mean base pair composition for the concatenated matrix was $A = 0.238$, $C = 0.193$, $G = 0.263$, and $T = 0.306$. Nucleotide base frequencies for 16S were $A = 0.28$, $C = 0.07$, $G = 0.23$, $T = 0.43$ and average gap/ambiguity was 16.09%. Nucleotide base frequencies for COI were $A = 0.20$, $C = 0.14$, $G = 0.24$, $T = 0.42$ and average gap/ambiguity was 2.11%. Nucleotide base frequencies for EF1a were $A = 0.26$, $C = 0.23$, $G = 0.26$, $T = 0.26$ and average gap/ambiguity was 22.98%. Nucleotide base frequencies for 28S were $A = 0.15$, $C = 0.29$, $G = 0.36$, $T = 0.21$ and average gap/ambiguity was 7.45%. Nucleotide base frequencies for RPB1 were $A = 0.31$, $C = 0.17$, $G = 0.23$, $T = 0.29$ and average gap/ambiguity was 8.36%. Nucleotide base frequencies for fbox were $A = 0.23$, $C = 0.27$, $G = 0.28$, $T = 0.23$ and average gap/ambiguity was 0.23%. No taxa were found to have failed the $\chi 2$ test for stationarity ($P > 0.05$, $df = 3$), and nucleotide frequency was found to be homogenous for each gene region for all taxa tested. Mean uncorrected percent difference of COI sequences between *Nannaria* species in the *wilsoni* group is 9.97% (maximum: 19.54%, minimum: 0%, standard deviation: 3.11%). The aligned sequences used in the phylogenetic analysis have been deposited in GenBank, and a complete list of sequences and associated accession numbers are given in Suppl. material 5.

The estimation of the phylogenetic history here tested recovered Nannariini as monophyletic, with the monophyletic genus *Nannaria* split into the two clades: *wilsoni* and *minor* species groups (Suppl. material 6).

Both of the *Nannaria* species groups were recovered as monophyletic (bootstrap support = 79), and *O. pulchella* was sister to *Nannaria* (bootstrap support = 100). In each of the individual gene trees, the two species groups were only recovered as monophyletic and well-supported with bootstrap values > 70 in the EF1a tree (Suppl. material 7). Within the *wilsoni* group (Fig. 3), individual species clades were generally well-supported with bootstrap values > 70, though many species from the Southern

Figure 3. Maximum likelihood phylogeny of the *Nannaria wilsoni* species group. Phylogeny estimated from the gene regions 16S, COI, EF1a, 28S, RPB1, and fbox. Branches colored by species identity. Bootstrap support values > 70 indicated by asterisks (*).

Appalachian Mountains had lower bootstrap support. Higher-level relationships within the clade, however, were not strongly supported, with an average bootstrap support of 45. Average bootstrap support within the *wilsoni* group clade was 68, and 49 of 95 nodes had bootstrap support > 70. Species from the southern portion of the distribution were generally a paraphyletic grade in the phylogeny.

Taxonomy

The following species accounts include 17 new species and seven previously described species, bringing the total number of species in the *wilsoni* group to 24. Gonopod illustrations in anterior and magnified posterior views for each species are given in Fig. 4, along with a labeled diagram of a representative gonopod. Species are listed in alphabetical order. In each diagnosis, the treated species is compared with other species in the *wilsoni* group that are geographically close and/or morphologically similar. The descriptions are included in a scored morphological matrix to facilitate straightforward species comparison (Suppl. material 2 and 3). Photographs of live specimens (when available) and gonopod illustrations in anterior, medial, and posterior views are given for each species in Figs 5–50. A key to species based on male specimens is provided after the species accounts.

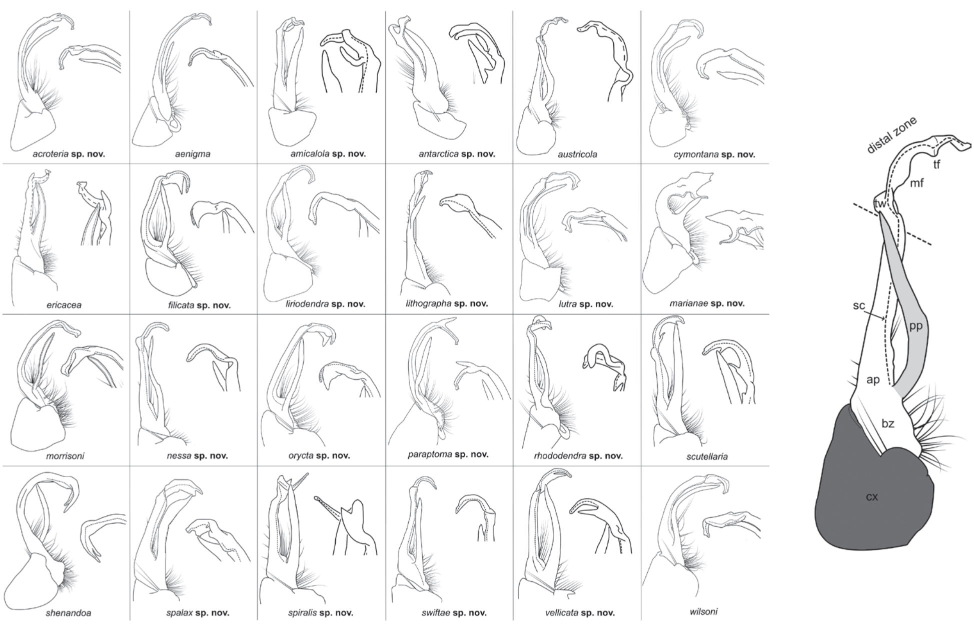

Figure 4. *Nannaria wilsoni* species group left male acropodites: (left) anterior view and (right) magnified posterior view. At right, *N. austricola* gonopod diagram, anterior view, color-coded by region: coxa (dark grey), prefemur (light grey), and acropodite (white). A dashed line indicates the beginning of the distal zone region of the acropodite. Abbreviations: **ap**, acropodite; **bz**, basal zone; **cx**, coxa; **mf**, acropodite medial flange; **pp**, prefemoral process; **sc**, seminal canal; **tf**, acropodite tip medial flange; **tw**, anterior bend twist.

Morphological terms used in the species descriptions and diagnoses follow the precedent set by previous xystodesmid workers (e.g., Marek 2010; Means and Marek 2017, Means et al. 2021b). The gonopod terminology is defined here for clarity (Fig. 4). The coxa (**cx**) is the most proximal part of the gonopod to the body of the millipede, and is typically rounded, with a basal coxal apodeme for muscle attachment. On the mesal side of the gonopod is the cannula, a thin, hooked tube that connects to the base of the acropodite and forms the beginning of the seminal canal. The acropodite (**ap**) is the main gonopod branch and is large and falcate in the *wilsoni* species group. It may be entire or bifurcate distally, with various twists and modified flanges. At its base between the coxa (**cx**) and prefemoral process attachment, is the basal zone (**bz**), which may have a lateral bulge. The prefemoral process (**pp**) is the secondary branch of the gonopod and typically attaches at the base of the acropodite, and varies in form from acicular to curved. Medial to the prefemoral process is the seminal canal (**sc**), which begins at the tapered terminal apex of the cannula. The seminal canal is a thin, open groove within the acropodite that winds its way to the tip of the acropodite. In a few taxa, there is a quadrate basomedial process posterior to the seminal canal at the base of the acropodite (Fig. 44A). The anterior bend of the gonopod marks the beginning of the distal zone of the gonopod, and is where the acropodite curves. The anterior bend in the *wilsoni* species group typically has a twist (**tw**), which can be weak (a slightly helical twist) to strong (a concave pinch or crimping of the acropodite). Immediately after the anterior bend is the medial flange (**mf**) of the acropodite, a structure on the medial side of the gonopod that can be variously modified into several different shapes. Distal to the medial flange is the acropodite tip medial flange (**tf**), which can also take a multitude of forms, and is separated from the medial flange by its location closer to the tip of the acropodite than to the anterior bend. The acropodite tip lateral flange is a modified flange distally on the lateral side of the gonopod, immediately before the tip.

Nannaria taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Infraclass Helminthomorpha Pocock, 1887
Order Polydesmida Leach, 1815
Family Xystodesmidae Cook, 1895
Subfamily Rhysodesminae Brolemann, 1916

Tribe *Nannariini* Hoffman, 1964

Tribe diagnosis. The genera *Nannaria* and *Oenomaea* (tribe Nannariini) can be separated from closely related genera by the following combination of characters. The tribe Nannariini have triangular sternal projections laterally on the sterna, while non-Nannariini lack lateral sternal projections but may have rounded sternal lobes (as in *Pleuroloma* Rafinesque, 1820) or “scooped out” sterna (as in *Gyalosteth-*

us Hoffman, 1965) or unmodified sterna (as in Apheloriini). Males with pregonopodal claws twisted and spatulate; non-Nannariini males with pregonopodal claws simple, bisinuate (Means et al. 2021a: fig. 16H). Gonopods with straight or gently curving acropodites and long prefemoral processes; gonopods never with circular or sigmoid acropodites as in *Apheloria* Chamberlin, 1921 or *Sigmoria* Chamberlin, 1939, and gonopods without small, hooked prefemoral processes as in *Apheloria*, and never lacking a prefemoral process completely as in some Apheloriini. Size small to moderate (body length 15–38 mm). Dorsum chestnut brown to black with orange to red, or sometimes white, paranotal spots, sometimes with orange to red stripes connecting the spots.

Genus *Nannaria* Chamberlin, 1918

Vernacular name: The Twisted-Claw Millipedes

Nannaria Chamberlin, 1918: 124. Attems 1938: 199. Chamberlin and Hoffman 1958: 39. Hoffman 1964: 33. Jeekel 1971: 274. Hoffman 1980: 159. Hoffman 1999: 365 (349 in pdf version). Shelley et al. 2000: 113. Hennen and Shelley 2015: 16. Means et al. 2021a: 16. Means et al. 2021b: 18.
Mimuloria Chamberlin, 1928: 155. Chamberlin and Hoffman 1958: 37. Hoffman 1964: 33. Jeekel 1971: 273. Hennen and Shelley 2015: 5. Means et al. 2021a: S65.
Castanaria Causey, 1950c: 1. Chamberlin and Hoffman 1958: 37.

Type species. *Nannaria minor* Chamberlin, 1918, by original designation. Taxa included: 78, see Table 1.

Taxa included in the *wilsoni* species group

Nannaria acroteria sp. nov.
Nannaria aenigma Means, Hennen, & Marek, 2021
Nannaria amicalola sp. nov.
Nannaria antarctica sp. nov.
Nannaria austricola Hoffman, 1950
Nannaria cymontana sp. nov.
Nannaria ericacea Hoffman, 1949
Nannaria filicata sp. nov.
Nannaria liriodendra sp. nov.
Nannaria lithographa sp. nov.
Nannaria lutra sp. nov.
Nannaria marianae sp. nov.
Nannaria morrisoni Hoffman, 1948
Nannaria nessa sp. nov.
Nannaria orycta sp. nov.
Nannaria paraptoma sp. nov.

Table 1. List of all *Nannaria* species. Species are listed in alphabetical order, with species group listed alongside each species.

No.	Species	Species group
1	*N. acroteria* sp. nov.	*wilsoni* group
2	*N. aenigma* Means, Hennen & Marek, 2021	*wilsoni* group
3	*N. alpina* Means, Hennen & Marek, 2021	*minor* group
4	*N. ambulatrix* Means, Hennen & Marek, 2021	*minor* group
5	*N. amicalola* sp. nov.	*wilsoni* group
6	*N. antarctica* sp. nov.	*wilsoni* group
7	*N. asta* Means, Hennen & Marek, 2021	*minor* group
8	*N. austricola* Hoffman, 1950	*wilsoni* group
9	*N. blackmountainensis* Means, Hennen & Marek, 2021	*minor* group
10	*N. bobmareki* Means, Hennen & Marek, 2021	*minor* group
11	*N. botrydium* Means, Hennen & Marek, 2021	*minor* group
12	*N. breweri* Means, Hennen & Marek, 2021	*minor* group
13	*N. castanea* (McNeill, 1887)	*minor* group
14	*N. castra* Means, Hennen & Marek, 2021	*minor* group
15	*N. caverna* Means, Hennen & Marek, 2021	*minor* group
16	*N. cingulata* Means, Hennen & Marek, 2021	*minor* group
17	*N. conservata* Chamberlin, 1940	*minor* group
18	*N. cryomaia* Means, Hennen & Marek, 2021	*minor* group
19	*N. cymontana* sp. nov.	*wilsoni* group
20	*N. daptria* Means, Hennen & Marek, 2021	*minor* group
21	*N. davidcauseyi* Causey, 1950	*minor* group
22	*N. dilatata* (Hennen & Shelley, 2015)	*minor* group
23	*N. domestica* Shelley, 1975	*minor* group
24	*N. equalis* Chamberlin, 1949	*minor* group
25	*N. ericacea* Hoffman, 1949	*wilsoni* group
26	*N. filicata* sp. nov.	*wilsoni* group
27	*N. fowleri* Chamberlin, 1947	*minor* group
28	*N. fracta* Means, Hennen & Marek, 2021	*minor* group
29	*N. fritzae* Means, Hennen & Marek, 2021	*minor* group
30	*N. hardeni* Means, Hennen & Marek, 2021	*minor* group
31	*N. hippopotamus* Means, Hennen & Marek, 2021	*minor* group
32	*N. hokie* Means, Hennen, & Marek, 2021	*minor* group
33	*N. honeytreetrailensis* Means, Hennen & Marek, 2021	*minor* group
34	*N. ignis* Means, Hennen & Marek, 2021	*minor* group
35	*N. kassoni* Means, Hennen & Marek, 2021	*minor* group
36	*N. komela* Means, Hennen & Marek, 2021	*minor* group
37	*N. laminata* Hoffman, 1949	*minor* group
38	*N. liriodendra* sp. nov.	*wilsoni* group
39	*N. lithographa* sp. nov.	*wilsoni* group
40	*N. lutra* sp. nov.	*wilsoni* group
41	*N. marianae* sp. nov.	*wilsoni* group
42	*N. mcelroyorum* Means, Hennen & Marek, 2021	*minor* group
43	*N. minor* Chamberlin, 1918	*minor* group
44	*N. missouriensis* Chamberlin, 1928	*minor* group
45	*N. monsdomia* Means, Hennen & Marek, 2021	*minor* group
46	*N. morrisoni* Hoffman, 1948	*wilsoni* group
47	*N. nessa* sp. nov.	*wilsoni* group
48	*N. oblonga* (Koch, 1847)	*minor* group
49	*N. ohionis* Loomis & Hoffman, 1948	*minor* group
50	*N. orycta* sp. nov.	*wilsoni* group
51	*N. paraptoma* sp. nov.	*wilsoni* group
52	*N. paupertas* Means, Hennen & Marek, 2021	*minor* group
53	*N. piccolia* Means, Hennen & Marek, 2021	*minor* group

No.	Species	Species group
54	*N. rhododendra* sp. nov.	*wilsoni* group
55	*N. rhysodesmoides* (Hennen & Shelley, 2015)	*minor* group
56	*N. rutherfordensis* Shelley, 1975	*minor* group
57	*N. scholastica* Means, Hennen & Marek, 2021	*minor* group
58	*N. scutellaria* Causey, 1942	*wilsoni* group
59	*N. serpens* Means, Hennen & Marek, 2021	*minor* group
60	*N. sheari* Means, Hennen & Marek, 2021	*minor* group
61	*N. shenandoa* Hoffman, 1949	*wilsoni* group
62	*N. sigmoidea* (Hennen & Shelley, 2015)	*minor* group
63	*N. simplex* Hoffman, 1949	*minor* group
64	*N. solenas* Means, Hennen & Marek, 2021	*minor* group
65	*N. spalax* sp. nov.	*wilsoni* group
66	*N. spiralis* sp. nov.	*wilsoni* group
67	*N. spruilli* Means, Hennen & Marek, 2021	*minor* group
68	*N. stellapolis* Means, Hennen & Marek, 2021	*minor* group
69	*N. stellaradix* Means, Hennen & Marek, 2021	*minor* group
70	*N. suprema* Means, Hennen & Marek, 2021	*minor* group
71	*N. swiftae* sp. nov.	*wilsoni* group
72	*N. tasskelsoae* Means, Hennen & Marek, 2021	*minor* group
73	*N. tennesseensis* (Bollman, 1888)	*minor* group
74	*N. tenuis* Means, Hennen & Marek, 2021	*minor* group
75	*N. terricola* (Williams & Hefner, 1928)	*minor* group
76	*N. tsuga* Means, Hennen & Marek, 2021	*minor* group
77	*N. vellicata* sp. nov.	*wilsoni* group
78	*N. wilsoni* Hoffman, 1949	*wilsoni* group

Nannaria rhododendra sp. nov.
Nannaria scutellaria Causey, 1942
Nannaria shenandoa Hoffman, 1949
Nannaria spalax sp. nov.
Nannaria spiralis sp. nov.
Nannaria swiftae sp. nov.
Nannaria vellicata sp. nov.
Nannaria wilsoni Hoffman, 1949

Genus diagnosis. See diagnosis in Means et al. (2021b).

Nannaria wilsoni species-group diagnosis. The *minor* species group and *wilsoni* species group can be separated by the following characters: Acropodite setae extending to at most halfway up length of acropodite (except in *N. lithographa* sp. nov.), and not reaching distal zone as in the *minor* species group. Anterior bend of acropodite typically with a gently curving or abrupt helical twist, not absent as in the *minor* species group. Prefemoral process arising from the base of the acropodite, or rarely, from the side of the acropodite, but never from an acropodite shelf as in the *minor* species group. Females often with cyphopod receptacle modified or enlarged; the cyphopod receptacle is unmodified in the *minor* species group. Female 2nd leg coxae laterally expanded, partly or entirely covering cyphopod aperture, female 2nd leg coxae not expanded in the *minor* species group.

Nannaria wilsoni species group

***Nannaria acroteria* sp. nov.**
http://zoobank.org/0E1B503C-4F84-48B2-8EA1-81FDD44D91CD
Vernacular name: The Fork Mountain Twisted-Claw Millipede
Figs 5, 6

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Giles County, Kire, Jefferson National Forest, in gully beside North Fork Mountain Rd; 37.4493°N, -80.5201°W, ± 6m; elev. 876 m; 27 April 2017; D. A. Hennen, J. C. Means, P. E. Marek, P. Shorter, V. Wong leg.; gully with small stream, litter moderately moist, rhododendron, oak, maple, mountain laurel, some pine, rocky, with large logs; VTEC, MPE02500. ***Paratypes*:** United States – **Virginia** • 2 ♀♀; same collection data as for holotype; VTEC, MPE02564, MPE02567. **Non type material:** United States – **West Virginia** • 1 ♂; Greenbrier County, SW end of Kate's Mtn. summit Picnic Area; 37.7638°N, -80.302°W, ± 3000m; 24 June 1967; W. A. Shear leg.; VMNH, NAN0025 • 2 specimens; Greenbrier County, Greenbrier State Forest, along 3 mi. of Young's Nature Trail; 37.7394°N, -80.3336°W; 28 August 1973; W. A. Shear leg.; VMNH, NAN0029 • 1 ♂; Greenbrier County, Kate's Mtn. summit; 37.7638°N, -80.302°W, ± 3000m; 10 April 1969; W. A. Shear leg.; VMNH, NAN0032 • 2 specimens; Greenbrier County, 8.5 miles W of Lewisburg; 37.8156°N, -80.5913°W, ± 5000m; 23 September 1949; J. P. E. Morrison leg.; VMNH, NAN0422 • 1 ♀; Monroe County, CR-6/2, 0.25 rd km S Greenbrier Co.; 7.6882°N, -80.3644°W;

Figure 5. *Nannaria acroteria* sp. nov., in situ, male holotype (MPE02500) from Giles County, Virginia.

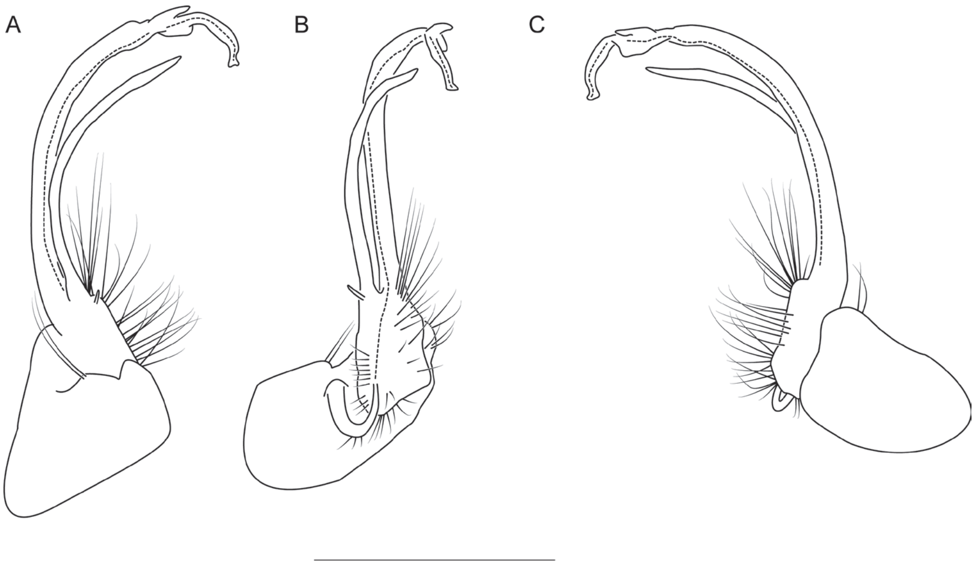

Figure 6. Left gonopod of *Nannaria acroteria* sp. nov. male holotype (MPE02500, Giles County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

elev. 816.5 m; 18 July 2005; P. E. Marek, C. Spruill leg.; VTEC, SPC000674. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria acroteria* sp. nov. can be separated from the geographically close and morphologically similar species *N. lutra* sp. nov. and *N. aenigma* by the following characters. Prefemoral process sinuous and strongly curving, rather than acicular or slightly curving as in *N. aenigma*. Acropodite dorsal projection triangular, rather than rounded as in *N. lutra* sp. nov. Acropodite tip lateral flange absent, rather than bilobed as in *N. lutra* sp. nov. Additionally, *Nannaria acroteria* sp. nov. has a triangular process at the base of its prefemoral process, which is absent in the other two species.

Description. Suppl. material 2. Based on holotype (♂) MPE02500 and paratype (♀) MPE02564.

Measurements: Taken from holotype (♂) MPE02500: BL = 27.80, CW = 3.96, IW = 2.76, ISW = 0.81, B10W = 4.75, B10H = 2.68. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 5). **Gonopods**. Male gonopod acropodite arc gradually curving (Fig. 6A–C). Acropodite with smoothly undulating twist at anterior bend (Fig. 6C), and acropodite medial flange lobed and with a medium-sized dorsal, triangular tooth (Fig. 6C). Acropodite tip medial and lateral flange both absent. Acropodite tip entire, directed ventrally (Fig. 6B). Prefemoral process sinuous (Fig. 6A) and curving medially (Fig. 6B). Prefemoral process tip directed medially, length almost as long as acropodite. Prefemoral process beset at base with a short, thin triangular process (Fig. 6A, B). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. No notable variation observed.

Distribution. Only known from the type locality in Giles County, Virginia and nearby localities in Greenbrier and Monroe counties, West Virginia (Fig. 51).

Ecological notes. The type locality is a rocky mesic mixed forest with oak, maple, rhododendron, mountain laurel, and pine, bisected by a stream. The elevation of the type locality is 876 m.

Etymology. This species is named for the small projection at the base of the prefemoral process, a unique trait within the *wilsoni* species group. The specific name is a feminine adjective derived from the Latin *acroterium*, meaning a small pedestal or projection.

***Nannaria aenigma* Means, Hennen & Marek, 2021**
Vernacular name: The New River Twisted-Claw Millipede
Figs 7, 8

Nannaria aenigma Means, Hennen & Marek in Means et al., 2021a: 16, S65, figs 3, 5S, T, 14.

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Smyth County, Sugar Grove: Raccoon Branch Wilderness Campground, Jefferson National Forest, Raccoon Branch Trail; 36.7454°N, -81.4259°W, ±7 m; elev. 858 m; 5 May 2017; D. A. Hennen leg.; moist deciduous leaf litter of rhododendron and eastern hemlock; VTEC, MPE02632. ***Paratype*:** United States – **Virginia** • 1 ♀; same collection data as for holotype; VTEC, MPE02633. **Non type material:** United States – **Virginia** • 1 ♂; Bland County, Burkes Garden, SW Garden Mtn., NE facing slope; 37.0783°N, -81.4152°W, ± 5000m; 30 June 1967; W. A. Shear leg.; VMNH, NAN0028 • 1 specimen; Bland County, west slope Walker Mtn along Va. Hy. 738; 37.1015°N, -80.8836°W, ± 3000m; 17 March 1989; R. L. Hoffman leg.; VMNH, NAN0421 • 1 specimen; Bland County, west side of Little Walker Mtn., 2 mi. S of

Figure 7. *Nannaria aenigma,* in situ, male holotype (MPE02632) from Smyth County, Virginia.

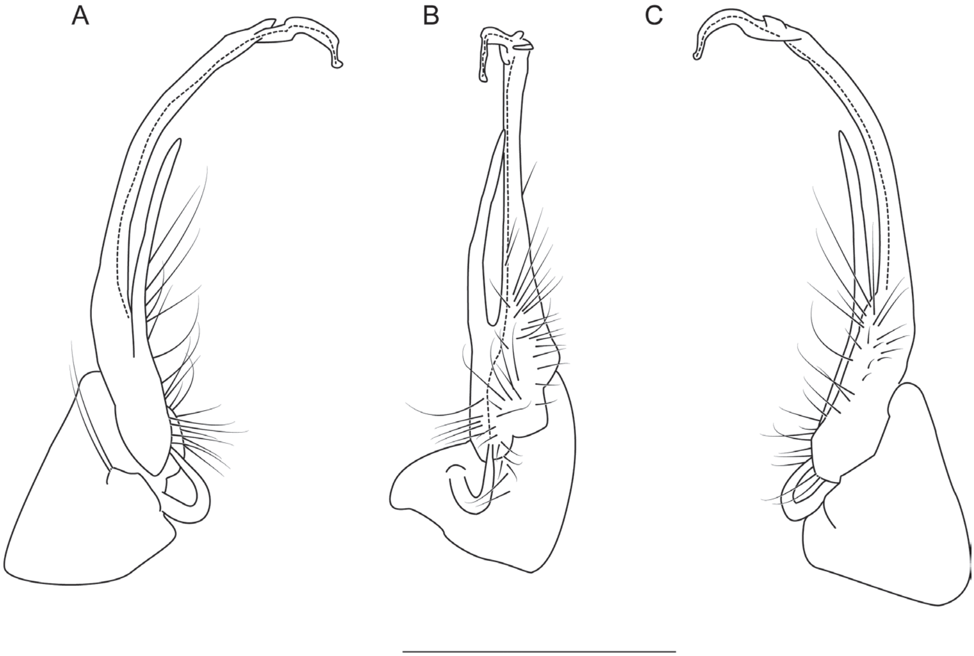

Figure 8. Left gonopod of *Nannaria aenigma* holotype (MPE02632, Smyth County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Long Spur; 37.0638°N, -80.9481°W, ± 3000m; 31 March 1967; R. L. Hoffman, Gardner leg.; VMNH, NAN0425 • 1 ♂; Bland County, Rt 42 roadside picnic area for AT just S of Possum Creek; 36.9859°N, -81.4076°W, ± 12m; elev. 827 m; 13 October 2014; P. E. Marek leg.; VTEC, MPE00002 • 2 ♂♂; Bland County, VA-Rt 623 3km North Jct w/ Va 42 in Burke's Garden Wilderness Area in Garden Mtn, 5.7 km WxNW of Walker Mtn; 37.0593°N, -81.2906°W, ± 7m; elev. 951 m; 14 October 2014; P. E. Marek, E. Francis, J. C. Means, T. McCoy leg.; VTEC, MPE00006, MPE00007 • 2 ♂♂; Bland County, 1 km N of jct with Rt. 42, on roadside, 6.6 km south of Burkes Garden; 37.0393°N, -81.3477°W, ± 3m; elev. 891 m; 14 May 2014; J. C. Means, P. E. Marek, E. Francis leg.; VTEC, MPE00018, MPE00019 • 3 ♂♂ and 1 ♀; Bland County, Ceres, off rt. 622, halfway up mountain, dry streambed; 36.9199°N, -81.4448°W, ± 4m; elev. 915 m; 10 June 2015; J. C. Means, P. Shorter leg.; VTEC, MPE00551, MPE00552, MPE00581, MPE00582 • 2 ♀♀; Bland County, side of rt. 717 pull off, in gorge up dry creek bed; 37.0093°N, -81.1674°W, ± 4m; elev. 762 m; 10 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE00583, MPE00584 • 1 ♂; Bland County, 3.15 air km W Hicksville, south slope of Rich Mountain; 37.1924°N, -81.1703°W; elev. 788 m; 21 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01008 • 1 ♂; Bland County, 1.4 air km SSW Carnot, north slope of Little Walker Mountain; 37.0306°N, -81.1035°W, ± 3m; elev. 802 m; 21 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01033 • 2 ♂♂; Bland County, 0.7

air km S Carnot, along CR 603 north slope of Little Walker Mountain; 37.0346°N, -81.0945°W, ± 2m; elev. 800 m; 21 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01040, MPE01041 • 2 ♂♂; Bland County, 1.2 air km SSW Carnot, nr intersection of Little Walker Creek and powerline; 37.0329°N, -81.1041°W, ± 3m; elev. 755 m; 21 March 2016; P. E. Marek, J. C. Means, A. Prewitt; VTEC, MPE01044, MPE01045 • 1 ♂; Bland County, 1.1 air km SSW Carnot, north of Little Walker Creek; 37.0352°N, -81.1055°W, ± 3m; elev. 804 m; 28 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01055 • 1 ♂; Bland County, 1.3 air km W Carnot, north of CR 717 on south slope Walker Mountain; 37.0391°N, -81.1114°W, ± 2m; elev. 871 m; 28 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01057 • 1 ♂; Bland County, 1.9 air km WNW Carnot, crest of Walker Mountain; 37.0466°N, -81.1159°W, ± 3m; elev. 1168 m; 30 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01059 • 3 ♂♂; Bland County, 2.0 air km WNW Carnot, crest of Walker Mountain; 37.0493°N, -81.1161°W, ± 2m; elev. 1118 m; 30 March 2016; P. E. Marek, J. C. Means, A. Prewitt leg.; VTEC, MPE01060, MPE01061, MPE01062 • 4 ♂♂; Bland County, 1.8 km WNW Carnot, next to rock face along Walker Mountain road; 37.0478°N, -81.1155°W, ± 4m; elev. 1184 m; 17 May 2016; P. Shorter, D. A. Hennen, D. Krall, A. Prewitt leg.; VTEC, MPE01197, MPE01199, MPE01200, MPE01201 • 1 ♂ and 3 ♀♀; Bland County, 1.8 km WNW Carnot, down steep hill along Walker Mountain road; 37.0478°N, -81.116°W, ± 5m; elev. 1178 m; 17 May 2016; P. L. Shorter, D. A. Hennen, A. Prewitt, D. Krall leg.; VTEC, MPE01205, MPE01203, MPE01204, MPE01206 • 1 ♂; Bland County, 2.4 km W Carnot, along Walker Mountain Road; 37.043°N, -81.1227°W, ± 5m; elev. 1131 m; 17 May 2016; P. Shorter, D. A. Hennen, D. Krall, A. Prewitt leg.; VTEC, MPE01216 • 1 ♂; Bland County, 3.2 km SW Hicksville, beside Grapefield Rd at forest access road; 37.1845°N, -81.1691°W; elev. 690 m; 23 May 2016; P. Shorter, V. Wong, D. Krall leg.; VTEC, MPE01419 • 2 ♂♂; Bland County, 1.2 km SSW Carnot, nr intersection of Little Walker Creek and powerline; 37.0329°N, -81.1043°W, ± 5m; elev. 813 m; 17 May 2016; D. A. Hennen, P. L. Shorter, D. Krall, A. Prewitt leg.; VTEC, MPE03701, MPE03702 • 1 ♂; Bland County, CR623, 2.8 rd km N Sharon Springs, S slope of Brushy Mtn; 37.0549°N, -81.2989°W; elev. 887 m; 26 May 2004; P. E. Marek leg.; VTEC, SPC000304 • 2 ♂♂; Bland County, Garden Mountain Quad, CR623, 2.8 rd km N Sharon Springs, S slope of Brushy Mountain; 37.0594°N, -81.2989°W; elev. 862 m; 14 May 2005; D. Beamer, M. Beamer leg.; VTEC, SPC000550, SPC000551 • 1 ♂; Grayson County, Lewis Fork, Fox Cr., Lewis Fork Trail; 36.682°N, -81.5159°W; 27 May 1984; Baumann, Nelson leg.; NCSM, NAN0478 • 1 specimen; Grayson County, Mount Rogers, beech-maple zone; 36.6597°N, -81.5447°W, ± 2000m; 19 May 1975; Douglas Ogle leg.; VMNH, NAN0420 • 1 specimen; Grayson County, W of Independence; 36.6296°N, -81.1715°W, ± 3000m; 18 June 1950; R. L. Hoffman leg.; VMNH, NAN0430 • 4 specimens; Pulaski County, Draper Mtn. above Pulaski; 37.0188°N, -80.7823°W, ± 3000m; 4 October 1959; R. L. Hoffman, R. Crabill leg.; VMNH, NAN0419 • 1 ♂ and 1♀; Pulaski County, off of 738, north side of Brush Mtn. range

(Croy Mtn. or Little Walker); 37.1018°N, -80.8867°W; elev. 678 m; 10 May 2015; J. C. Means leg.; VTEC, MPE00350, MPE00392 • 2 ♂♂ and 1 ♀; Pulaski County, gully off rt 641 gravel rd.; 37.073°N, -80.873°W; elev. 671 m; 13 May 2015; J. C. Means leg.; VTEC, MPE00409, MPE00416, MPE00412 • 1 ♀; Pulaski County, north side of Draper Mtn.; 37.0252°N, -80.7752°W, ± 2m; elev. 740 m; 28 July 2015; P. E. Marek, J. C. Means, V. Wong, P. Shorter leg.; VTEC, MPE00759 • 1 ♀; Pulaski County, in gully next to private drive off Case Knife Road; 37.0332°N, -80.8087°W, ± 3m; elev. 639 m; 28 July 2015; P. E. Marek, P. Shorter, J. C. Means, V. Wong leg.; VTEC, MPE00762 • 2 ♂♂ and 2 ♀♀; Pulaski County, VA-650; 37.0248°N, -80.7842°W, ± 7m; elev. 667 m; 1 October 2015; V. Wong, P. E. Marek leg.; VTEC, MPE00857, MPE00858, MPE00856, MPE00859 • 1 specimen; Russell County, SE side of Beartown Mountain; 36.9244°N, -81.8786°W, ± 2000m; 23 April 2003; A. C. Chazal, C. S. Hobson, et al. leg.; VMNH, NAN0412 • 1 specimen; Russell County, Clinch Mtn., 1 mile SE of Repass; 36.9759°N, -81.7932°W, ± 1000m; elev. 1128 m; 5 July 1962; R. L. Hoffman leg.; VMNH, NAN0418 • 1 ♀; Smyth County, Sugar Grove: Raccoon Branch Wilderness campground, near beginning of Raccoon Branch Trail by campsite 8; 36.7462°N, -81.4247°W, ± 6m; elev. 855 m; 5 May 2017; D. A. Hennen leg.; VTEC, MPE02635 • 2 specimens; Smyth County, Grindstone Camp Area, 4.5 mi. W of Troutdale; 36.6875°N, -81.5423°W, ± 500m; 24 May 1975; R. L. Hoffman leg.; VMNH, NAN0411 • 1 specimen; Smyth County, Big Branch north slope of Whitetop Mtn; 36.658°N, -81.599°W, ± 1000m; 3 May 1992; K. A. Buhlmann leg.; VMNH, NAN0414 • 1 specimen; Smyth County, Va. Hy. 600, halfway between Konnarock and Elk Garden; 36.6582°N, -81.5884°W, ± 2000m; elev. 1219 m; 10 May 1982; R. L. Hoffman, et al. leg.; VMNH, NAN0417 • 1 specimen; Smyth County, Big Walker Mtn. W of Hungry Mother State Park; 36.8927°N, -81.559°W, ± 3000m; 9 September 1956; R. L. Hoffman leg.; VMNH, NAN0423 • 3 specimens; Smyth County, NW slope of Iron Mtn., 7 mi. SE of Chilhowie; 36.7012°N, -81.6133°W, ± 3000m; 4 May 1964; R. L. Hoffman leg.; VMNH, NAN0424 • 1 ♂; Smyth County, Mt Rogers Nat'l Rec Area, FR 84; 36.7067°N, -81.6028°W, ± 2m; elev. 1138 m; 25 June 2014; J. C. Means, P. E. Marek, E. Francis leg.; VTEC, MPE00072 • 1 ♂ and 7 ♀♀; Smyth County, Side of road (VA-16) on west slope of Big Walker Mtn, ca. 3 mi W of Hungry Mother State Park; 36.9112°N, -81.5317°W, ± 6m; elev. 1054 m; 9 September 2014; J. C. Means leg.; VTEC, MPE00172, MPE00168, MPE00170, MPE00171, MPE00173, MPE00175, MPE00176, MPE00177 • 2 ♂♂; Smyth County, south of Laurel Bed Lake, off Tumbling Creek Rd.; 36.9384°N, -81.8118°W, ± 8m; elev. 956 m; 13 June 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE01680, MPE01683 • 1 specimen; Tazewell County, River Mtn. summit, NW, above Bluefield; 37.223°N, -81.2479°W, ± 5000m; 17 April 1973; C. J. Chapman leg.; VMNH, NAN0030 • 7 specimens; Tazewell County, Burkes Garden, crest of Garden Mtn at Rt. 623; 37.1222°N, -81.3647°W, ± 3000m; elev. 1158 m; 14 April 1965; Radford College herpetology class leg.; VMNH, NAN0318 • 4 specimens; Tazewell County, East River Mtn.; 37.2125°N, -81.2979°W, ± 3000m; 11 September 1955; R. L. Hoffman leg.; VMNH, NAN0416 • 2 ♂♂ and 1 ♀; Tazewell County, Reese Bowen's property, down by Indian Creek; 37.0148°N, -81.41°W, ± 2m; elev. 735 m; 28 October 2014; J. C. Means, R. Bowen leg.; VTEC, MPE00256, MPE00268, MPE00267 • 1 specimen; Washington County, 2 mi SE of Taylors Valley; 36.6146°N, -81.6827°W, ± 3000m; 7 May 1972; R. L. Hoffman, L. S. Knight leg.; VMNH, NAN0426 • 5 specimens; Washington County, 4 miles SW of Konnarock; 36.6306°N, -81.6647°W, ± 3000m; 28 April 1951; L. Hubricht leg.; VMNH, NAN0429 • 1 ♂; Washington County, south of Laurel Bed Lake, on Laurel Bed Road, pull off on road; 36.9477°N, -81.8242°W, ± 9m; elev. 1047 m; 13 June 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE01648 • 1 ♀; Washington County, south of Laurel Bed Lake, off Tumbling Creek Rd.; 36.9384°N, -81.8118°W, ± 8m; elev. 956 m; 13 June 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE01681 • 1 ♂; Washington County, Hayter's Gap, pull off along Brumley Gap Rd (CR 689) before Dublin Ln.; 36.8304°N, -81.9593°W, ± 9m; elev. 587 m; 8 June 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE02106 • 2 specimens; Wythe County, Gullion Fork Wildlife Management Area, w. of Blackfork; 36.9816°N, -81.2829°W, ± 3000m; 1 September 1964; D. E. Marvin, et al. leg.; VMNH, NAN0427 • 1 specimen; Wythe County, 3 mi. S of Speedwell on U.S. Hy. 52, W side of Iron Mtn.; 36.7702°N, -81.1717°W, ± 5000m; 13 July 1962; R. L. Hoffman leg.; VMNH, NAN0428 • 1 ♂; Wythe County, Seven Sisters Campground; 37.0195°N, -81.1355°W, ± 3m; elev. 788 m; 10 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE00576 • 4 ♀♀; Wythe County, off Oriole Dr.; 37.016°N, -81.2436°W, ± 4m; elev. 804 m; 16 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE00649, MPE00650, MPE00652, MPE00653 • 1 ♂; Wythe County, off rt. 686 side of road near Deer Trail Campground, marshland; 37.0223°N, -81.2048°W, ± 3m; elev. 729 m; 16 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE00658 • 2 ♂♂; Wythe County, Crawfish Valley, channel Rock Hollow trail 1 mile from Strawberry Rd. end; 36.9526°N, -81.3247°W; 24 March 2017; C. W. Harden leg.; VTEC, MPE02415, MPE02423 • 5 ♂♂; Wythe County, Crawfish Valley, Channel Rock, follow trail about 1.5 miles from Strawberry Rd. end; 36.9585°N, -81.3189°W; 24 March 2017; C. W. Harden leg.; VTEC, MPE02417, MPE02418, MPE02425, MPE02426, MPE02427 • 2 ♂♂ and 3 ♀♀; Wythe County, side of Oriole Rd. in moist creek bed; 37.0157°N, -81.246°W, ± 5m; elev. 780 m; 11 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE03709, MPE03723, MPE03724, MPE03725, MPE03726. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria aenigma* can be separated from the geographically close and morphologically similar species *N. acroteria* sp. nov. and *N. wilsoni* by the following characters. Acropodite medial flange with a dorsal median projection, rather than lacking a projection as in *N. wilsoni*. Prefemoral process acicular or slightly curving, length 3/4 or less the length of the acropodite, rather than having a sinuous and strongly curving prefemoral process with length greater than 3/4 the length of the acropodite, as in *N. acroteria* sp. nov. and *N. wilsoni*.

Description. Suppl. material 2. Based on holotype (♂) MPE02632 and paratype (♀) MPE02633.

Measurements: Taken from holotype (♂) MPE02632: BL = 31.95, CW = 4.20, IW = 2.79, ISW = 0.88, B10W = 5.19, B10H = 3.01. **Color.** Tergites with two paranotal white spots, collum outlined in white, and tergites with background black (Fig. 7). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 8A). Acropodite with smoothly-undulating helical twist at anterior bend (Fig. 8C). Acropodite medial flange laminate, with a dorsal triangular tooth (Fig. 8C) and acropodite tip lacking medial and lateral flanges. Acropodite tip entire, slightly constricted distally (Fig. 8A–C); directed caudally (Fig. 8B). Prefemoral process acicular, straight, with only a slight curve (Fig. 8A–C). Prefemoral process tip directed cephalically (Fig. 8A). Prefemoral process length about half that of the acropodite. **Cyphopods.** Female cyphopod receptacle triangular.

Variation. The dorsal triangular tooth process on the gonopod acropodite varies in size and shape, but is generally triangular. The acropodite tip is sometimes more elaborately lobed before the distal constriction in some specimens. The prefemoral process varies in its length, sometimes being almost as long as the acropodite. *Nannaria aenigma* varies in color as well, with some specimens having pink to red paranotal spots instead of white.

Distribution. *Nannaria aenigma* is distributed throughout southwest Virginia, and is known from the following counties: Bland, Grayson, Pulaski, Russell, Smyth, Tazewell, Washington, and Wythe (Fig. 51). In the eastern portion of its distribution, it is limited by the course of the New River. It may eventually be found in West Virginia, Tennessee, and North Carolina, as some of its locality records are very near the borders of these states.

Ecological notes. This species has been found in mesic deciduous forest habitats, as well as ericaceous hemlock-rhododendron coves, and at elevations ranging from 587 m to 1219 m.

Etymology. The specific name is a noun in apposition, derived from the Latin *aenigma*, for something obscure or a riddle. This is in reference to the question-mark like shape of the acropodite (Means et al. 2021a).

Nannaria amicalola **sp. nov.**

http://zoobank.org/7220D2E8-34A9-4105-B7E6-49386E99AAEC
Vernacular name: The Tumbling Waters Twisted-Claw Millipede
Figs 9, 10

Nannaria sp. nov. 'Amicolola': Means et al. 2021b: 85.

Material examined. Type material: ***Holotype*****:** United States – **Georgia** • ♂; Dawson County, 6 miles W of Amicalola Falls; 34.5681°N, -84.3140°W, ±5000m; 6 November 1960; L. Hubricht leg.; ex ravine; VMNH, NAN0319. ***Paratypes*****:** United States – **Georgia** • 1 ♀; same collection data as for holotype; VMNH, NAN0671 • 2 ♀♀; Lumpkin County, 3.5 km NW Nimblewill on Nimblewill Gap Rd/FS 28-2,

Figure 9. *Nannaria amicalola* sp. nov., in situ, female paratype (MPE01230) from Lumpkin County, Georgia.

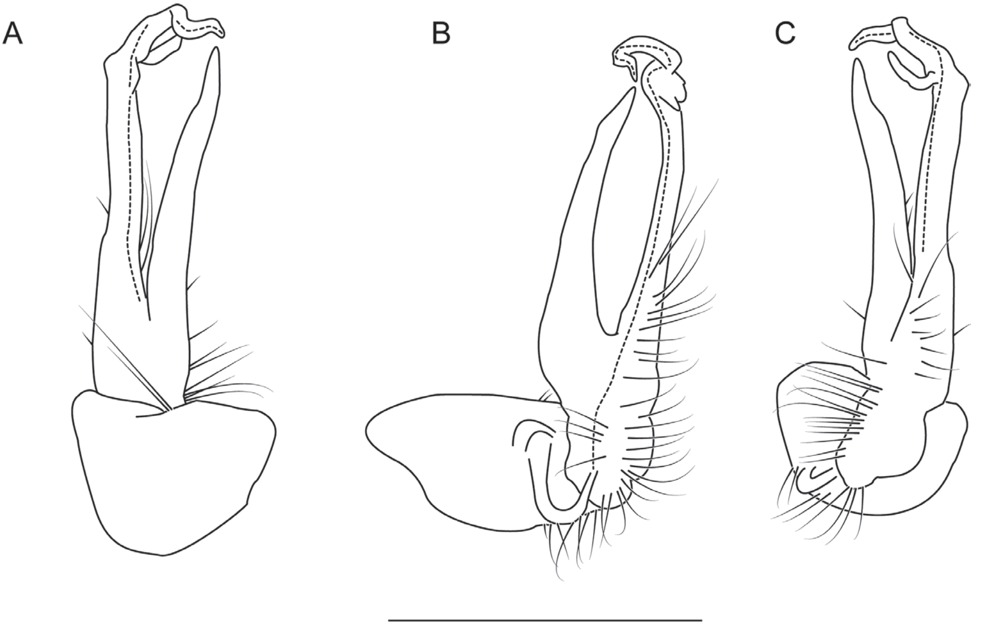

Figure 10. Left gonopod of *Nannaria amicalola* sp. nov. holotype male (NAN0319, Dawson County, GA) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

before road crosses Chester Creek, on short path to Nimblewill Creek; 34.5753°N, -84.1757°W; elev. 590 m; 24 May 2016; J. C. Means, D. A. Hennen leg.; ex rhododendron, maple, oak, hemlock gully with lots of poison ivy, moist litter; VTEC, MPE01230, MPE01280. **Non type material:** United States – **Georgia** • 1 ♀; Dawson County, Amicalola Falls State Park; 34.5611°N, -84.2474°W; 16 April 1978; R. M. Shelley, R. T. Ashton leg.; NCSM, NAN0473. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria amicalola* sp. nov. can be separated from the geographically close and morphologically similar species *N. antarctica* sp. nov. and *N. rhododendra* sp. nov. by the following characters. Acropodite anterior bend acutely bent, rather than slightly twisted as in *N. rhododendra* sp. nov. Acropodite medial flange long and hooked, curving cephalically rather than lobed and sinuous as in *N. rhododendra* sp. nov. Acropodite tip entire, not bifurcate as in *N. antarctica* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) NAN0319 and paratype (♀) MPE01230.

Measurements: Taken from holotype (♂) NAN0319: BL = 24.40, CW = 3.56, IW = 2.82, ISW = 0.96, B10W = 4.70, B10H = 3.00. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 9). **Gonopods.** Acropodite arc straight, with abrupt bend distally (Fig. 10A–C). Acropodite with acute twist at anterior bend (Fig. 10A), acropodite medial flange tooth-like, long, and hooked, curving cephalically (Fig. 10C). Acropodite tip medial and lateral flanges absent. Acropodite tip entire, curving and directed ventrally (Fig. 10B). Prefemoral process laminate, very wide at base (Fig. 10B); straight, tapering to tip with a slight curve, with tip directed cephalically (Fig. 10A). **Cyphopods.** Female cyphopod receptacle enlarged into a triangular hood, covering cyphopod valves.

Variation. No noticeable variation was observed.

Distribution. *Nannaria amicalola* sp. nov. is only known from Dawson and Lumpkin counties in northern Georgia (Fig. 52).

Ecological notes. This species inhabits ravines and riparian areas with a mix of moist oak, maple, hemlock, and rhododendron forest.

Etymology. This species is named for nearby Amicalola Falls State Park, which itself is named after the Cherokee expression *amo* and *kalola* for "tumbling waters." The specific name is a noun in apposition.

***Nannaria antarctica* sp. nov.**

http://zoobank.org/A076437D-7513-42E4-84FD-EF177B248FCF
Vernacular name: The Chilled Twisted-Claw Millipede
Figs 11, 12

Material examined. Type material: *Holotype*: United States – **North Carolina** • ♂; Macon County, 9.79 mi WSW of Franklin, at scenic view spot along US 64 beside Poplar Cove Creek; 35.1241°N, -83.5392°W, ±10m; elev. 1082 m; 26 October 2017; D. A. Hennen, J. C. Means leg.; steep hillside with moist dark crumbly soil in tuliptree, buckeye, birch, cherry woods beside mountain steam; VTEC, MPE03311. ***Paratypes*:** United States – **Georgia** • 3 ♂♂ and 3 ♀♀; Towns Coun-

Figure 11. *Nannaria antarctica* sp. nov., in situ, male paratype (MPE03317) from Towns County, Georgia.

ty, 9.5 air mi. (15.3 km) NNW of Helen: Enota Mountain Retreat, off Georgia State Route 180, trail by primitive campground, above Henson Creek; 34.8364°N, -83.7710°W, ±13m; elev. 787 m; 25 October 2017; D. A. Hennen, J. C. Means leg.; moist deciduous woods with crumbly, dark soil, rhododendron, hemlock, tuliptree forest; VTEC, MPE03317; VMNH, MPE03380; FMNH, MPE03382; VTEC, MPE03378; VMNH, MPE03379; FMNH, MPE03381. **Non type material:** United States – **Georgia** • 1 ♂; Dawson County, 6 miles W of Amicalola Falls; 34.5681°N, -84.314°W, ± 4000m; 6 November 1960; L. Hubricht leg.; VMNH, NAN0672 • 8 ♂♂; Towns County, 17 miles NW Clayton, Burnt Cabin Br.; 34.989°N, -83.5586°W; 30 September 1994; G. Wharton leg.; NCSM, NAN0187, NAN0188, NAN0481 • 6 ♂♂ and 2 ♀♀; Towns County, 9.5 air miles (15.3 km) NNW of Helen: Enota Mountain Retreat, off Georgia State Route 180, trail by primitive campground, above Henson Creek; 34.8364°N, -83.771°W, ± 13m; elev. 787 m; 25 October 2017; D. A. Hennen, J. C. Means leg.; VTEC, MPE03377, MPE03384, MPE03385, MPE03386, MPE03388, MPE03389, MPE03383, MPE03387 • 1 ♀; Union County, Blairsville: Vogel State Park, Trahlyta Falls Trail; 34.7701°N, -83.9163°W, ± 12m; elev. 697 m; 14 October 2018; D. A. Hennen leg.; VTEC, MPE04608; **North Carolina** • 3 ♂♂ and 3 ♀♀; Macon County, trail from deep gap to top Standing Ind. Mtn.; 35.0355°N, -83.538°W; 16 August 1977; A. L. Braswell, M. Baranksi leg.; NCSM, NAN0524 • 2 ♂♂; Macon County, Coweeta Hydrologic Station; 35.0598°N, -83.4302°W; 16 June 1978; Lee Reynolds leg.; NCSM, NAN0555 • 7 ♂♂ and 3 ♀♀; same collection data as for preceding; 29 August 1977; NCSM, NAN0557 • 9 ♂♂ and 2 ♀♀; same

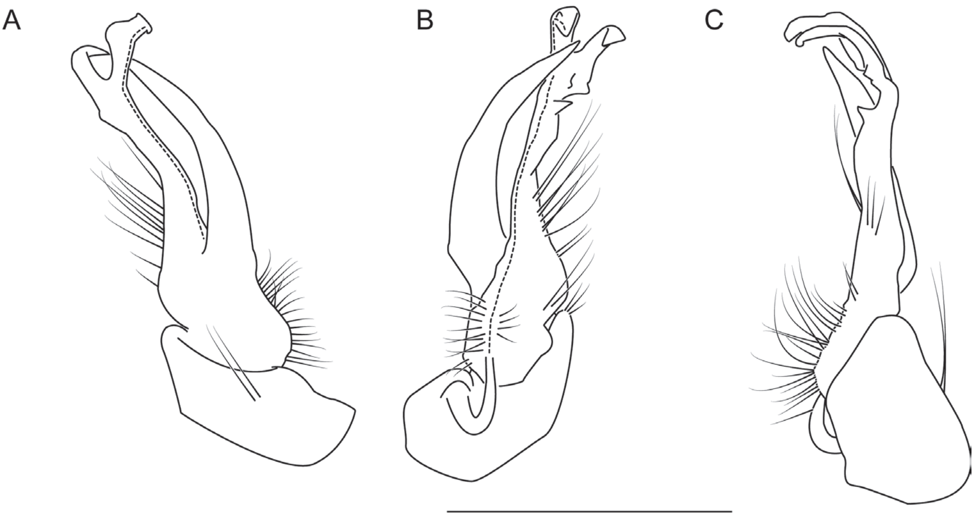

Figure 12. Left gonopod of *Nannaria antarctica* sp. nov. male holotype (MPE03311, Towns County, Georgia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

collection data as for preceding; 20 October 1977; NCSM, NAN0559, NAN0569, NAN0577, NAN0594 • 5 ♂♂ and 7 ♀♀; same collection data as for preceding; 14 September 1977; NCSM, NAN0561, NAN0562 • 2 ♂♂ and 1 ♀; same collection data as for preceding; 7 April 1977; NCSM, NAN0563 • 8 ♂♂ and 7 ♀♀; same collection data as for preceding; 29 September 1977; NCSM, NAN0565, NAN0574, NAN0589 • 6 ♂♂ and 8 ♀♀; same collection data as for preceding; 27 October 1977; NCSM, NAN0566, NAN0580, NAN0593, NAN0634 • 10 ♂♂ and 9 ♀♀; same collection data as for preceding; 22 September 1977; NCSM, NAN0568, NAN0570, NAN0571 • 10 ♂♂ and 7 ♀♀; same collection data as for preceding; 13 October 1977; NCSM, NAN0573, NAN0588, NAN0596, NAN0598 • 2 ♂♂ and 1 ♀; same collection data as for preceding; 2 June 1978; NCSM, NAN0575, NAN0638 • 6 ♂♂ and 3 ♀♀; same collection data as for preceding; 21 April 1978; NCSM, NAN0576, NAN0625 • 5 ♂♂; same collection data as for preceding; 7 April 1978; NCSM, NAN0578, NAN0613 • 70 ♂♂ and 76 ♀♀; same collection data as for preceding; 3 November 1977; NCSM, NAN0581, NAN0582, NAN0584, NAN0600, NAN0628, NAN0629 • 88 ♂♂ and 81 ♀♀; same collection data as for preceding; 10 November 1977; NCSM, NAN0585, NAN0590, NAN0626, NAN0627, NAN0640 • 6 ♂♂ and 3 ♀♀; same collection data as for preceding; 17 November 1977; NCSM, NAN0592, NAN0642 • 4 ♂♂; same collection data as for preceding; 6 October 1977; NCSM, NAN0597, NAN0606 • 9 ♂♂ and 3 ♀♀; same collection data as for preceding; 26 May 1978; NCSM, NAN0599, NAN0607, NAN0614 • 12 ♂♂ and 5 ♀♀; same collection data as for preceding; 28 April 1978; NCSM, NAN0608, NAN0615, NAN0620, NAN0639 • 2 ♂♂ and 1 ♀; same collection data as for preceding; 14 April 1977; NCSM, NAN0609 • 14 ♂♂ and 5 ♀♀; same collection data as for preceding; 31 March 1978; NCSM, NAN0610, NAN0624, NAN0630, NAN0632, NAN0635, NAN0637 • 4 ♂♂ and 3 ♀♀; same collection data as for preceding; 9 June 1978; NCSM, NAN0611 • 20 ♂♂ and 6 ♀♀; same collection data as for preceding; 5 May 1978; NCSM, NAN0612, NAN0616, NAN0617, NAN0619, NAN0636 • 4 ♂♂ and 5 ♀♀; same collection data as for preceding; 6 September 1978; NCSM, NAN0618 • 6 ♂♂ and 3 ♀♀; same collection data as for preceding; 14 April 1978; NCSM, NAN0622, NAN0631 • 1 ♂; Macon County, Coweeta Hydro. Lab. Coldspring Gap; 35.0214°N, -83.4482°W, ± 1000m; elev. 1189 m; 17 April to 28 May 1994; J. Laerm, et al. leg.; VMNH, NAN0312 • 7 ♂♂ and 3 ♀♀; Macon County, Nr. Wine Spring Cr., burn; 35.1921°N, -83.6394°W, ± 5000m; 13 August 1996; J. Laerm, et al. leg.; VMNH, NAN0313 • 19 specimens; Macon County, Nr. Wine Spring Cr., control-C3; 35.1921°N, -83.6394°W, ± 5000m; 16 June 1995; J. Laerm, et al. leg.; VMNH, NAN0315 • 13 specimens; Macon County, Coweeta Hydrologic Laboratory, nr Norton; 35.0598°N, -83.4302°W, ± 2000m; elev. 991 m; 17 September 1964; M. R. Steeves leg.; VMNH, NAN0362 • 1 ♂; Macon County, Nantahala Mtns, Coweeta Hydrologic Lab, Watershed 14; 35.0546°N, -83.432°W; elev. 690 m; 25 September 2004; ECU TABC leg.; VTEC, SPC000367. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria antarctica* sp. nov. can be separated from the geographically close and morphologically similar species *N. austricola* and *N. rhododendra* sp. nov. by the following characters. Acropodite with a strong twist at anterior bend, rather than a slightly-twisted helix as in *N. rhododendra* sp. nov. Acropodite bifurcate, rather than entire as in *N. austricola*.

Description. Suppl. material 2. Based on holotype (♂) MPE03311 and paratype (♀) MPE03378.

Measurements: Taken from holotype (♂) MPE03311: BL = 23.50, CW = 3.20, IW = 2.48, ISW = 0.78, B10W = 3.92, B10H = 2.32. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 11). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 12A–C). Acropodite with acute twist at anterior bend, appearing somewhat scooped and folded (Fig. 12C). Acropodite medial flange tooth-like, ending in a sharp point (Fig. 12C). Acropodite tip medial flange laminate, long and curving, terminating in a distal sharp point (Fig. 12A, B). Acropodite tip lateral flange lobed, and with a short tooth-like projection dorsally (Fig. 12A). Tip of acropodite bifurcate, each branch hooked at tip and directed medially (Fig. 12B). Prefemoral process sinuously tapered and quite thick at base (Fig. 12B), curving laterally (Fig. 12A). Prefemoral process crossing acropodite ventrolaterally (Fig. 12A), and with tip directed medially. **Cyphopods.** Female cyphopod receptacle in the shape of a finger-like projection, curving over cyphopod valves and tapering distally.

Variation. No noticeable variation observed.

Distribution. *Nannaria antarctica* sp. nov. is known from Dawson and Towns counties, Georgia, and Macon County, North Carolina (Fig. 52).

Ecological notes. This species has been collected in typical *wilsoni* species group habitat: mesic deciduous forest (oak, maple, tuliptree, birch, cherry, buckeye) and rhododendron and hemlock coves. It ranges in elevation from 690 m to 1189 m.

Etymology. This species is named for the extreme cold temperatures experienced by DAH and JCM while collecting this species. The specific name is a feminine adjective in the nominative case, derived from the Greek *antarktikos*, meaning southern, and refers to the currently frozen continent at Earth's South Pole.

Nannaria austricola Hoffman, 1950

Vernacular name: The Highlands Twisted-Claw Millipede
Fig. 13

Nannaria austricola Hoffman, 1950: 26, pl. 8, figs 26, 27. Chamberlin and Hoffman 1958: 40. Wray 1967: 152. Hoffman 1999: 365 (350 in pdf version). Shelley 2000: 196. Marek and Bond 2006: 721. Means et al. 2021a: S65. Means et al 2021b: 9, fig. 4D.

Type material. ***Holotype*:** United States – **North Carolina •** ♀; Macon County, Highlands, Satulah Mountain; 35.036°N, -83.191°W, ±2000m; 26 July 1949; R. L. Hoffman leg.; USNM Entomology, no. 1879; (non vidi). Habitat at the type locality was a "dense, wet rhododendron thicket edging a small swift stream" (Hoffman 1950).

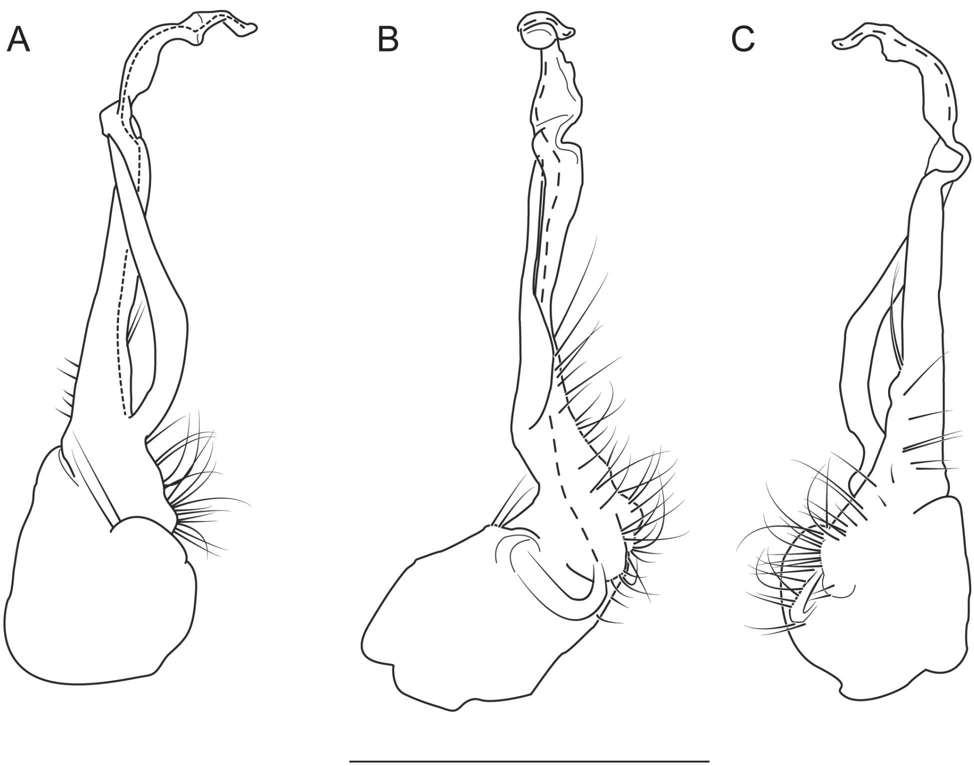

Figure 13. Left gonopod of *Nannaria austricola* (NAN0072, Macon County, North Carolina) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Material examined. Non type material: United States – **Georgia** • 1 ♀; Rabun County, Glade Mtn.; 34.9966°N, -83.1341°W, ± 5000m; 27 July 1949; R. L. Hoffman leg.; VMNH, NAN0075; **North Carolina** • 3 ♂♂ and 1 ♀; Macon County, 5 miles NW of Highlands; 35.1038°N, -83.2594°W, ±5000m; 9 July 1958; R. L. Hoffman leg.; VMNH, NAN0072 • 1 ♂; Macon County, 2.25 mi NW Highlands, along US 64 at Bridal Veil Falls; 35.072°N, -83.2293°W; 4 April 1980; A. L. Braswell leg.; NCSM, NAN0474 • 2 ♀♀; Macon County, Highlands; 35.0525°N, -83.1969°W, ± 4322m; 1 to 2 June 1954; VMNH, NAN0071 • 2 specimens; Macon County, Highlands, Bowery Road; 35.0571°N, -83.1705°W, ± 3000m; 16 July 1962; A. Van Pelt leg.; VMNH, NAN0076 • 2 ♂♂; Macon County, Coweeta Hydrologic Station; 35.0597°N, -83.4305°W; 7 October 1977; Lee Reynolds leg.; NCSM, NAN0503, NAN0587 • 4 ♂♂; Macon County, Coweeta Hydrologic Station; 35.0598°N, -83.4302°W; 13 October 1978; Lee Reynolds leg.; NCSM, NAN0572 • 2 ♂♂; same collection data as for preceding; 20 October 1977; NCSM, NAN0583 • 1 ♂; same collection data as for preceding; 6 October 1977; NCSM, NAN0586 • 2 ♂♂; same collection data as for preceding; 3 November 1977; NCSM, NAN0595 • 4 ♂♂; same collection data as for preceding; 13 October 1977; NCSM, NAN0602 • 1 ♂ and 1 ♀; same collection data as for preceding; 26 May 1978; NCSM, NAN0623 • 1 ♂; same collection data as for preceding; 28 April 1978; NCSM, NAN0633 • 5 ♂♂ and 7 ♀♀; Macon County, Coweeta Hydro. Lab. Ball Creek Cove; 35.0595°N, -83.4288°W, ± 2000m; elev. 1311 m; 17 April to 28 May 1994; J. Laerm, et al. leg.; VMNH, NAN0291 • 1 ♂; Macon County, Coweeta Hydro. Lab. Drymans Fork Cove; 35.0433°N, -83.4275°W, ± 3000m; elev. 1311 m; 17 April to 23 July 1994; J. Laerm, et al. leg.; VMNH, NAN0311 • 4 ♂♂; Macon County, Coweeta Hydro. Lab. Coldspring Gap; 35.0214°N, -83.4482°W, ± 1000m; elev. 1189 m; 17 April to 28 May 1994; J. Laerm, et al. leg.; VMNH, NAN0312 • 1 ♂; Macon County, Nr. Wine Spring Cr., control-C3; 5.1921°N, -83.6394°W, ± 5000m; 16 June 1995; J. Laerm, et al. leg.; VMNH, NAN0314 • 1 ♂ and 1 ♀; Macon County, Nantahala Mtns, Coweeta Hydrologic Lab, Watershed 2; 35.0633°N, -83.4368°W; elev. 690 m; 24 September 2004; ECU TABC leg.; VTEC, SPC000352, SPC000353. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria austricola* can be separated from the geographically close and morphologically similar species *N. antarctica* sp. nov., *N. nessa* sp. nov., and *N. scutellaria* by the following characters. Acropodite entire, not bifurcate as in *N. antarctica* sp. nov. Acropodite medial flange lobed, not acuminate and tapering as in *N. scutellaria*. Acropodite tip medial flange lobed, rather than absent as in *N. nessa* sp. nov. Prefemoral process without a notch on medial side, which is present in *N. nessa* sp. nov.

Description. Suppl. material 2. Based on (♂) and (♀) specimens from lot NAN0072.

Measurements: Taken from (♂) specimen NAN0072: BL = 22.70, CW = 3.10, IW = 2.48, ISW = 0.75, B10W = 4.10, B10H = 2.40. **Color.** Tergites with two paranotal pink spots, collum outlined in pink, and tergites with background olive-brown.

Gonopods. Male gonopod acropodite arc straight, with an abrupt bend distally (Fig. 13A–C). Acropodite with acute twist at anterior bend, appearing crimped and folded (Fig. 13C). Acropodite medial flange lobed (Fig. 13C), acropodite tip lateral flange absent. Acropodite tip entire, directed medially (Fig. 13B). Prefemoral process sinuous, thicker at base and tapering distally, curving laterally and crossing acropodite dorsolaterally (Fig. 13A). Prefemoral process tip directed cephalically (Fig. 13A). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. Acropodite medial flange size varies from narrow to wide.

Distribution. *Nannaria austricola* is only known from Macon County, North Carolina and adjacent Rabun County, Georgia (Fig. 52).

Ecological notes. The type specimen was collected in a rhododendron thicket near a stream (Hoffman 1950) on Satulah Mountain in the town of Highlands, North Carolina. Elevation notes on the labels of other specimens range from 690 meters to 1311 meters, and may indicate that *N. austricola* is restricted to cool, high elevation habitats.

Etymology. The specific epithet derives from the Latin word *australis*, meaning "of the south," and was named for being the most southern species of *Nannaria* known at the time (Hoffman 1950).

Nannaria cymontana **sp. nov.**
http://zoobank.org/46B272E0-9D49-48D6-B172-33415A9C7640
Vernacular name: The Blue Ridge Twisted-Claw Millipede
Figs 14, 15

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Floyd County, bottomland in Rocky Knob Recreation Area near Rock Castle Creek; 36.7856°N, -80.3726°W, ±2m; elev. 830 m; 27 May 2015; J. C. Means, A. Chazal leg.; ex forest with ferns, yam, witch-hazel, oak, magnolia, maple; VTEC, MPE00460. ***Paratypes*:** United States – **Virginia** • 1 ♂; Floyd County, Rocky Knob Picnic Area, on hill edge by side of road; 36.8132°N, -80.3495°W, ±3m; elev. 970 m; 18 September 2015; J. C. Means, P. E. Marek, K. Lawler, P. Shorter, V. Wong leg.; much undergrowth in chestnut oak woods; VTEC, MPE00822. • 4 ♂♂; Floyd County, Rocky Knob Park; 36.8195°N, -80.3422°W, ±3000m; 3 July 1947; R. L. Hoffman leg.; VMNH, NAN0279. **Non type material:** United States – **Virginia** • 5 ♂♂ and 2 ♀♀; Carroll County, Blacksnake Meadery, bottomland near creek at entrance; 36.776°N, -80.5446°W; 14 September 2014; J. C. Means leg.; VTEC, MPE00200, MPE00205, MPE00209, MPE00218, MPE00220, MPE00206, MPE00207 • 1 specimen; Floyd County, Buffalo Mtn.; 36.7869°N, -80.4509°W, ± 3000m; elev. 1067 m; 5 October 1997; VMNH survey leg.; VMNH, NAN0086 • 1 ♂; Floyd County, Buffalo Mountain, pitfall site on north slope; 36.7958°N, -80.4772°W, ± 3000m; elev. 1067 m; 19 August to 1 October 1992; VMNH survey leg.; VMNH, NAN0281 • 1 ♂; Floyd County, Buffalo Mtn.; 36.7958°N, -80.4772°W, ± 3000m; elev. 1067 m; 24 October 1958; R. L. Hoffman leg.; VMNH, NAN0282 • 1 ♂; Floyd County, Willis Ridge, w

Figure 14. *Nannaria cymontana* sp. nov., in situ, male holotype (MPE00460) from Floyd County, Virginia.

of Floyd, Rt. 892; 36.9328°N, -80.4046°W, ± 3000m; 17 June 1990; J. M. Anderson, R. L. Hoffman leg.; VMNH, NAN0283 • 1 ♂; Floyd County, Willis Ridge, ca. 4 mi. west of Floyd CH; 36.9328°N, -80.4046°W, ± 3000m; elev. 914 m; 5 September 1982; R. L. Hoffman leg.; VMNH, NAN0284 • 1 ♂; Floyd County, Felker's property Rt 726; 36.8008°N, -80.3988°W, ± 10000m; 3 June 1995; J. M. Anderson leg.; VMNH, NAN0285 • 1 ♂; Floyd County, Mile 176, Blue Ridge Parkway; 36.7501°N, -80.4047°W, ± 3000m; 6 June 1976; R. L. Hoffman leg.; VMNH, NAN0287 • 3 specimens; Floyd County, 2 mi. SW of Copper Valley; 36.9703°N, -80.5426°W, ± 5000m; 15 October 1974; R. L. Hoffman leg.; VMNH, NAN0288 • 2 specimens; Floyd County, Chestnut Creek Natural Area Preserve, off Rt. 771, 4 km SE of Willis; 36.8373°N, -80.4421°W, ± 4000m; 15 October 2007; S. M. Roble, R. L. Hoffman leg.; VMNH, NAN0290 • 1 ♂ and 2 ♀♀; Floyd County, Blue Ridge Parkway mile post 174.3, private gravel drive crossing Laurel Creek; 36.7716°N, -80.4047°W; elev. 916 m; 24 June 2014; P. E. Marek, E. Francis, J. C. Means leg.; VTEC, MPE00071, MPE00057, MPE00060 • 1 ♂; Floyd County, hardwood opening in rhododendron forest off Blue Ridge Pkwy south of Mabry Mill; 36.7448°N, -80.3994°W, ± 2m; elev. 923 m; 26 May 2015; J. C. Means, P. E. Marek, A. Chazal, P. L. Shorter leg.; VTEC, MPE00450 • 1 ♀; Floyd County, off Buffalo Mtn. Road intersection with Blue Ridge Pkwy; 36.7724°N, -80.4054°W, ± 3m; elev. 912 m; 26 May 2015; J. C. Means, P. E. Marek, A. Chazal, P. L. Shorter leg.; VTEC, MPE00452 • 1 ♂; Floyd County, 2 km north of Mabry Mill on Blue Ridge Parkway; 36.7678°N, -80.4049°W, ± 2m; elev. 913 m; 27 May 2015; J. C. Means, A. Chazal leg.; VTEC, MPE00476 • 1 ♂; Floyd County, 0.8 km SW Mabry Mill; 36.7437°N, -80.4097°W, ± 4m; elev. 961 m; 27 May 2015; J. C. Means leg.; VTEC, MPE00488 • 1 ♂; Floyd County, right side of gravel road off Blue

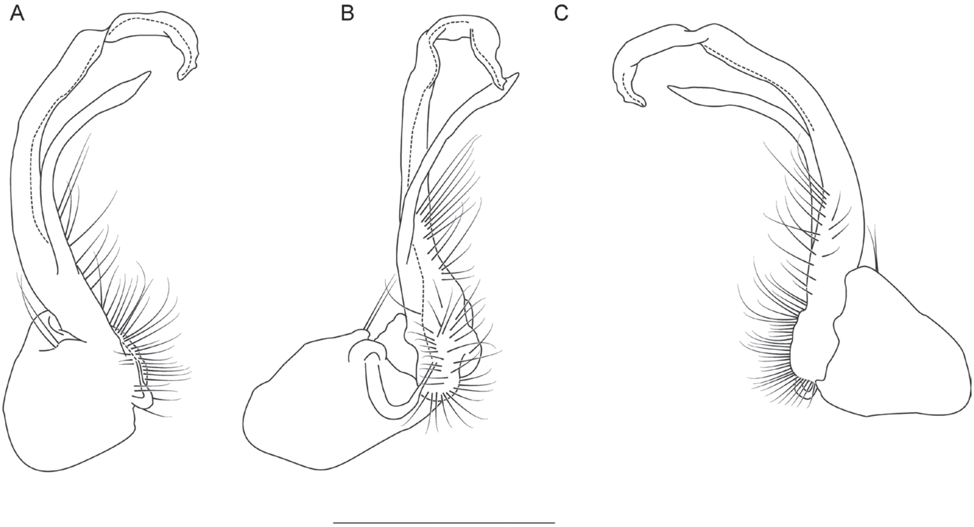

Figure 15. Left gonopod of *Nannaria cymontana* sp. nov., male holotype (MPE00460, Floyd County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Ridge Pkwy. in a marshy area between two streams; 36.7796°N, -80.3984°W, ± 3m; elev. 937 m; 30 June 2015; J. C. Means, P. L. Shorter leg.; VTEC, MPE00720 • 2 ♂♂; Floyd County, Rocky Knob Recreation Area; 36.7848°N, -80.3733°W; 19 September 2015; J. C. Means, P. E. Marek leg.; VTEC, MPE00826, MPE03707 • 3 ♂♂ and 1 ♀; Floyd County, 3.5 km NNE Mabry Mill, gully behind farm off Blue Ridge Parkway, on small island in creek; 36.7825°N, -80.3997°W; elev. 945 m; 26 April 2017; J. C. Means, P. L. Shorter leg.; VTEC, MPE02513, MPE02514, MPE03670, MPE02504 • 1 ♂; Floyd County, 3.7 km NNE Mabry Mill; 36.7836°N, -80.4°W; elev. 975 m; 26 April 2017; J. C. Means, P. L. Shorter leg.; VTEC, MPE02524 • 1 ♂; Floyd County, Rhododendron/oak forest behind Mabry Mill off Blue Ridge Parkway; 36.7505°N, -80.405°W; elev. 869 m; 26 April 2017; J. C. Means, P. L. Shorter leg.; VTEC, MPE02542 • 1 ♂; Floyd County, 3.5 km NNE Mabry Mill, slight clearing by rhododendron cove on Laurel Creek by Blue Ridge Parkway; 36.7805°N, -80.395°W; elev. 918 m; 4 May 2017; J. C. Means, P. L. Shorter leg.; VTEC, MPE02628 • 1 ♂; Montgomery County, Trail to Bottom Creek at end of VA. Rt 637; 37.1161°N, -80.2051°W, ± 1000m; 6 May 1990; R. L. Hoffman leg.; VMNH, NAN0304 • 3 ♂♂; Montgomery County, Riner: in wetland below lake; 36.9662°N, -80.4179°W; elev. 773 m; 17 October 2014; J. C. Means leg.; VTEC, MPE00234, MPE00243, MPE00245 • 5 specimens; Patrick County, Pinnacles of Dan; 36.6738°N, -80.4388°W, ± 1807m; 15 October 1950; L. Hubricht leg.; VMNH, NAN0277 • 4 specimens; Patrick County, along Laurel Creek, MP 174.5, Blue Ridge Parkway; 36.7676°N, -80.4062°W, ± 3000m; 20 May 1983; R. L. Hoffman leg.; VMNH, NAN0278 • 2 specimens; Patrick County, Below Townes Dam, Pinnacles of Dan; 36.6859°N, -80.4308°W, ± 3000m; 22 April 1972; R. L. Hoffman leg.; VMNH, NAN0280 • 1 specimen; Patrick County, 1.5 miles NW of Patrick Springs; 36.6571°N, -80.2142°W, ± 3000m; 16 November 1952; L. Hubricht leg.; VMNH, NAN0286 • 1 specimen; Patrick County, Pinnacles of Dan, 4 miles SW of Vesta; 36.6756°N, -80.4092°W, ± 5000m; 19 April 1957; R. L. Hoffman leg.; VMNH, NAN0289 • 3 ♂♂; Patrick County, Rock Castle Creek, Rock Castle Gorge Trail, Rocky Knob Recreation Center; 36.7858°N, -80.3717°W, ± 7m; elev. 839 m; 21 September 2015; J. C. Means, P. E. Marek leg.; VTEC, MPE00828, MPE00829, MPE00831 • 1 ♂; Patrick County, Pinnacles of Dan area, top of gated road leading to Townes Reservoir, Lower Dam Rd., SW of Meadows of Dan; 36.6866°N, -80.4415°W, ± 5m; elev. 842 m; 5 June 2016; D. A. Hennen leg.; VTEC, MPE02059 • 3 ♂♂; Roanoke County, Bradshaw Creek, ca. 5 miles N of LaFayette; 37.2991°N, -80.2238°W, ± 5000m; 1 March 1957; R. L. Hoffman leg.; VMNH, NAN0303 • 3 ♂♂ and 1 ♀; Roanoke County, Poor Mtn.; 37.1975°N, -80.1525°W, ± 2000m; 15 October 1956; R. L. Hoffman leg.; VMNH, NAN0305 • 1 ♂ and 2 ♀♀; Roanoke County, Side of road & gully off Blue Ridge Parkway, Poor Mountain view pull off; 37.1369°N, -80.1108°W; elev. 899 m; 26 April 2017; J. C. Means, P. L. Shorter leg.; VTEC, MPE02495. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria cymontana* sp. nov. can be separated from the geographically close and morphologically similar species *N. ericacea*, *N. lutra* sp. nov., and *N. wilsoni* by the following characters. Acropodite arc gradually curving, not straight with an abrupt bend at tip as in *N. ericacea*. Acropodite medial flange lacking a dorsal median projection, not with a rounded projection as in *N. lutra* sp. nov. Acropodite medial flange small rather than large and laminate as in *N. wilsoni*, acropodite tip lateral flange sharp instead of rounded as in *N. wilsoni*, and prefemoral process tip spear-shaped, not gradually tapered as in *N. wilsoni*.

Description. Suppl. material 2. Based on holotype (♂) MPE00460 and paratype (♀) MPE00452.

Measurements: Taken from holotype (♂) MPE00460: BL = 27.60, CW = 3.72, IW = 2.70, ISW = 0.99, B10W = 4.60, B10H = 2.85. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 14). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 15A–C). Acropodite gently twisted at anterior bend (Fig. 15A). Acropodite medial flange slightly lobed (Fig. 15C). Acropodite tip medial flange absent, acropodite tip lateral flange slightly bilobed, both projections rounded and small (Fig. 15A). Acropodite tip blunt, entire, directed ventrally (Fig. 15B). Prefemoral process sinuous and slightly spear-shaped distally, with tip directed medially (Fig. 15A). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. The size of the acropodite tip lateral flanges differs slightly among specimens, ranging from small to medium-sized.

Distribution. Known from the following Virginia counties: Carroll, Floyd, Montgomery, Patrick, and Roanoke (Fig. 51).

Ecological notes. This species has been collected most often from rhododendron cove habitats, but is also sometimes found in mesic mixed forests.

Etymology. This species is named for its type locality, the Blue Ridge Parkway, an invaluable stretch of protected land which provides recreation for millions of people a year and conserves over 370 km^2 of natural habitat. The word *cymontana* is a feminine adjective, a combination of the Latin *cymatilis* meaning blue and *montanus* meaning "of mountains."

Nannaria ericacea Hoffman, 1949

Vernacular name: The Heathland Twisted-Claw Millipede
Figs 16, 17

Nannaria ericacea Hoffman, 1949b: 381, figs 9, –10. Chamberlin and Hoffman 1958: 40. Hoffman 1999: 366 (351 in pdf version). Means et al. 2021a: 4, 5, S67, fig. 3. Means et al 2021b: 6, 9, figs 2, 4F.

Type material. ***Holotype*:** United States – **Virginia** • ♂; Alleghany County, McGraw Gap, 3 miles [4.8 km] northwest of Clifton Forge; 37.858°N, - 79.864°W, ±1000m; 13 April 1947; R. L. Hoffman leg.; USNM Entomology, no. 1784; (non vidi). ***Paratypes*:** United States – **Virginia** • 1 ♂; same collection data as for holotype; 1 June 1948; VMNH, NAN0366 (vidi) • 1 ♂ and 1 ♀; same collection data as for holotype; 27 April 1947; VMNH, NAN0367 (vidi). Hoffman (1949b) indicated that he collected "several topoparatypes" for his personal collection from the type locality and listed three specimens with his personal collection codes "RLH Nos. 4-2747-1, 5-1847-1c, and 6-147-1a." The VMNH specimens included here, NAN0366 and NAN0367, represent these specimens. The jar that contains these specimens is labeled "PARATYPE" and the vials each have labels reading "TOPOPARATYPES."

Material examined. Non type material: United States – **Virginia** • 1 ♂; Alleghany County, Pott's Mtn. Pond; 37.602°N, -80.1385°W, ± 5000m; elev. 1097 m; 2 January

Figure 16. *Nannaria ericacea,* in situ, male (MPE02263) from Roanoke County, Virginia.

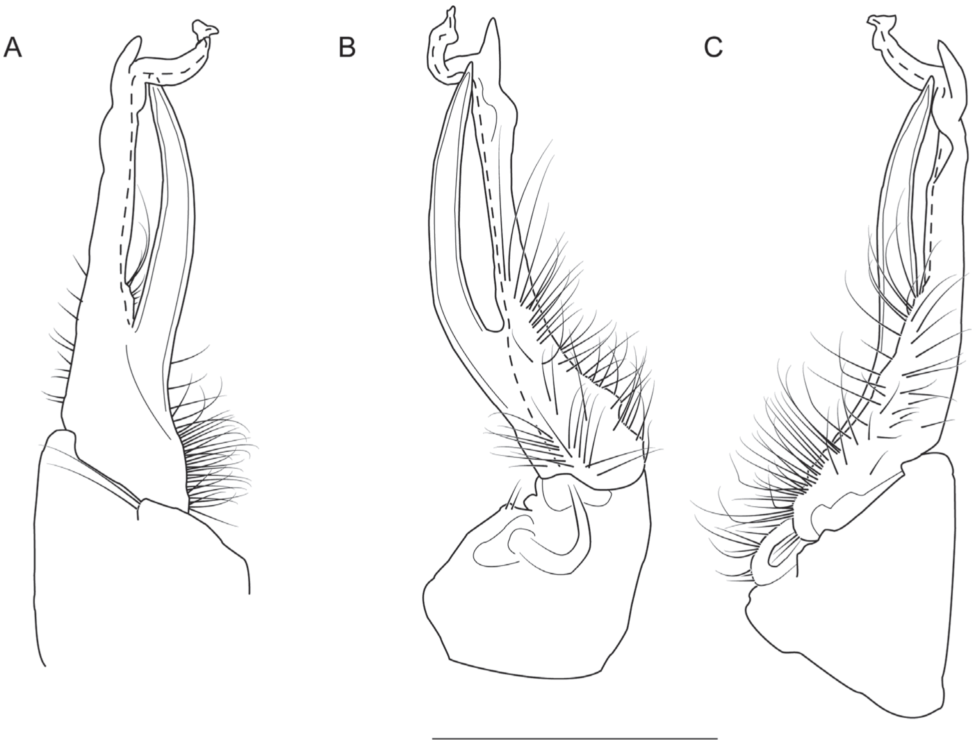

Figure 17. Left gonopod of *Nannaria ericacea* (MPE02263, Roanoke County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

1954; R. L. Hoffman leg.; VMNH, NAN0441 • 2 specimens; Alleghany County, Top of Little Mtn, east of Natural Well on FS 342; 37.9223°N, -79.9134°W, ± 3000m; 30 January 2002; M. W. Donahue leg.; VMNH, NAN0446 • 50 specimens; Bath County, Douthat State Park; 37.8967°N, -79.8022°W; 13 September 1988; R. M. Shelley leg.; NCSM, NAN0465 • 2 ♂♂; Bath County, 5.4 km NW Warm Springs, Meadow Lane Farm; 38.0792°N, -79.8358°W; elev. 577 m; 8 April 2017; J. C. Means leg.; VTEC, MPE02434, MPE03672 • 1 specimen; Botetourt County, Roaring Run DF site, ca. 7 mi. NW Eagle Rock; 37.7079°N, -79.8933°W, ± 2000m; 22 August to 21 September 1996; M. W. Donahue, R. S. Hocan leg.; VMNH, NAN0436 • 1 specimen; same collection data as for preceding; 22 September to 26 October 1996; VMNH, NAN0438 • 1 ♂; Botetourt County, Jefferson National Forest, along forest road just north of Blackhorse Gap; 37.4256°N, -79.7578°W; elev. 727 m; 11 June 2017; C. W. Harden leg.; VTEC, MPE02861 • 1 specimen; Craig County, West side Johns Creek Mountain near Maggie; 37.3982°N, -80.3865°W, ± 5000m; 20 April 1976; R. L. Hoffman, et fils leg.; VMNH, NAN0443 • 2 specimens; Craig County, Barbours Creek, NW of Newcastle; 37.5536°N, -80.0576°W, ± 5000m; June 1947; R. L. Hoffman leg.; VMNH, NAN0447 • 2 ♂♂; Craig County, Appalachian Trail parking lot near Caldwell Fields campground. Side of stream, off 621; 37.3795°N,

-80.2503°W; elev. 490 m; 13 June 2018; J. C. Means leg.; VTEC, MPE04304, MPE04309 • 1 ♂ and 1 ♀; Giles County, 4 miles N Pembroke, Cascades Recreation Area, Jefferson National Forest; 37.3535°N, -80.5994°W; 3 August 1981; R. M. Shelley leg.; NCSM, NAN0460 • 2 specimens; Montgomery County, Brush Mtn. nr. Blacksburg; 37.2822°N, -80.465°W, ± 5000m; 28 November 1960; R. L. Hoffman leg.; VMNH, NAN0431 • 2 specimens; Montgomery County, RAAP - Radford, 30 m E of RDAISA bldg.; 37.1859°N, -80.5366°W, ± 3000m; 8 May 1998; S. Garriock leg.; VMNH, NAN0432 • 2 specimens; Montgomery County, Blacksburg; 37.221°N, -80.4162°W, ± 500m; 26 September 1957; R. L. Hoffman leg.; VMNH, NAN0434 • 1 specimen; same collection data as for preceding; 28 October 1956; VMNH, NAN0435 • 2 specimens; same collection data as for preceding; 26 October 1957; VMNH, NAN0442 • 4 specimens; same collection data as for preceding; 13 April 1958; R. L. Hoffman, R. Crabill leg.; VMNH, NAN0448 • 1 ♀; Montgomery County, Dry Run, 5 mi. NE of Blacksburg; 37.2792°N, -80.3143°W, ± 2000m; 20 April 1957; R. L. Hoffman leg.; VMNH, NAN0440 • 1 specimen; Montgomery County, 1 mi. NE of Vicker Station; 37.1738°N, -80.4751°W, ± 4000m; 11 April 1964; R. L. Hoffman leg.; VMNH, NAN0444 • 1 specimen; Montgomery County, Trillium Vale, Blacksburg; 37.2286°N, -80.3902°W, ± 1000m; 10 October 1950; R. L. Hoffman leg.; VMNH, NAN0445 • 2 ♂♂ and 1 ♀; Montgomery County, Gateway Trail, Jefferson National Forest on Brush Mtn.; 37.2488°N, -80.4604°W; 18 May 2014; P. E. Marek leg.; VTEC, MPE00032, MPE00038, MPE00039 • 3 ♂♂ and 1 ♀; Montgomery County, Stadium Woods, Virginia Tech Campus; 37.22°N, -80.4156°W; elev. 640 m; 15 June 2014; P. E. Marek leg.; VTEC, MPE00040, MPE00042, MPE00043, MPE00041 • 2 ♂♂; Montgomery County, Gateway Trail, 1/2 mile in from main trail by stream; 37.2506°N, -80.461°W, ± 3m; elev. 642 m; 26 September 2014; J. C. Means, P. E. Marek, E. Francis, K. Lawler, N. Zegler leg.; VTEC, MPE00226, MPE00229 • 1 ♂; Montgomery County, Golden Hills Disc Golf course, in gully; 37.1729°N, -80.4078°W, ± 3m; elev. 628 m; 8 November 2014; J. C. Means, D. A. Hennen, P. E. Marek leg.; VTEC, MPE00276 • 1 ♂; Montgomery County, On Price Mtn., north side, in gully off old road; 37.1916°N, -80.4577°W, ± 3m; elev. 674 m; 28 July 2015; P. E. Marek, P. L. Shorter, J. C. Means, V. Wong leg.; VTEC, MPE00765 • 2 ♂♂; Montgomery County, Pandapas Pond, in bottomland below horse trail parking lot; 37.2824°N, -80.4485°W; 22 September 2015; J. C. Means leg.; VTEC, MPE00835, MPE00837 • 1 ♂; Montgomery County, Blacksburg: Along the edge of the Duck Pond, Virginia Tech Campus; 37.2251°N, -80.4272°W; 15 October 2015; K. Lawler leg.; VTEC, MPE00896 • 1 ♀; Montgomery County, Blacksburg: Virginia Tech campus, Stadium Woods; 37.2208°N, -80.4164°W; 12 October 2015; K. Lawler leg.; VTEC, MPE00897 • 2 ♂♂ and 4 ♀♀; Montgomery County, Jefferson Nat'l Forest, off Craig Creek Rd. (621); 37.3477°N, -80.3251°W, ± 2m; elev. 599 m; 6 October 2016; P. L. Shorter, P. E. Marek, J. C. Means, V. Wong leg.; VTEC, MPE02145, MPE02155, MPE02153, MPE02154, MPE02156, MPE02157 • 5 ♂♂; Montgomery County, Blacksburg: Stadium Woods; 37.2208°N, -80.4167°W; elev. 635 m; 9 November 2017; J. C. Means, D. A. Hennen,

G. G. Schiermeyer leg.; VTEC, MPE03459, MPE03460, MPE03461, MPE03462, MPE03463 • 1 ♀; Montgomery County, Stadium Woods; 37.2208°N, -80.4167°W; 27 October 2017; G. G. Schiermeyer leg.; VTEC, MPE03676 • 1 ♂; Montgomery County, Gateway Trail, near entrance; 37.2488°N, -80.4604°W; elev. 603 m; 25 September 2013; P. E. Marek leg.; VTEC, MPE03716 • 2 ♂♂; Montgomery County, Blacksburg, end of Valley View Drive near quarry; 37.2218°N, -80.3894°W, ± 3m; elev. 680 m; 13 September 2019; F. Vasquez, J. C. Means, P. E. Marek, D. A. Hennen, I. Huerta leg.; VTEC, MPE04999, MPE05000 • 1 specimen; Roanoke County; 37.28°N, -80.05°W; 7 April 1965; VMNH, NAN0437 • 1 specimen; Roanoke County, Along Rt. 624, 4.5 miles SW of Catawba; 37.3512°N, -80.1737°W, ± 1000m; 9 April 1964; R. L. Hoffman leg.; VMNH, NAN0439 • 3 ♂♂ and 1 ♀; Roanoke County, Salem, Carvin's Cove, down a huge gully off the Trough Trail, bank of stream; 37.3599°N, -79.9939°W; elev. 451 m; 20 November 2016; J. C. Means leg.; VTEC, MPE02263, MPE02264, MPE03711, MPE02265. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults *of Nannaria ericacea* can be separated from the geographically close and morphologically similar species *N. liriodendra* sp. nov. and *N. paraptoma* sp. nov. by the following characters. Acropodite arc straight, with abrupt bend at tip, rather than gradually curving as in *N. liriodendra* sp. nov. and *N. paraptoma* sp. nov. Acropodite tip medial flange triangular, not as long as the dorsal triangular projection of *N. paraptoma* sp. nov.

Description. Suppl. material 2. Based on (♂) MPE02263 and (♀) MPE02265.

Measurements: Taken from (♂) specimen MPE02263: BL = 38.48, CW = 4.35, IW = 3.12, ISW = 0.85, B10W = 5.63, B10H = 3.44. **Color.** Tergites with two paranotal orange-red spots, collum outlined in orange-red, and tergites with background black to brown (Fig. 16). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 17A–C). Acropodite anterior bend with gentle twist (Fig. 17C), acropodite medial flange absent. Acropodite tip medial flange a large triangular process, slightly curved (Fig. 17C). Acropodite tip lateral flange triangular (Fig. 17A). Acropodite tip entire, slightly expanded with small lateral and medial lobes (Fig. 17A), acropodite tip directed ventrally. Prefemoral process simple, curving (Fig. 17A), with tip directed cephalically (Fig. 17B). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. Acropodite tip sometimes lacking small distal lobes, size of acropodite medial flange typically large, but sometimes smaller.

Distribution. Restricted to Virginia, *Nannaria ericacea* has been recorded from the following counties: Alleghany, Bath, Botetourt, Craig, Giles, Montgomery, and Roanoke (Fig. 51).

Ecological notes. *Nannaria ericacea* has been collected in a variety of habitats, ranging from pine-oak forests to ericaceous forests of rhododendron and hemlock. Elevation records range from 451 meters to 1097 meters. Hoffman (1949b) provided a thorough description of the habitat at the type locality, describing it as "a deep water-gap in sandstone ridges, with the forest composed chiefly of *Tsuga canadensis*, *Liriodendron tulipifera*, *Quercus alba*, *Q. prinus* [now *Quercus montana* Willd.], *Acer rubrum*, *A. pennsylvanicum*, *Rhododendron maximum*, and *Kalmia latifolia*. Herbaceous plants at the type locality include *Urtica dioica*, *Mitella diphylla*, *Mitchella repens*, and the ferns *Polypodium virginianum* and *Polystichum acrostichoides*."

Etymology. The specific epithet *ericacea* derives from the Greek *ereike*, heather, referring to the flowering plant family Ericaceae, known as the heath or heather family. The name was given based on the abundance of this species in ericaceous habitats (Hoffman 1949b).

***Nannaria filicata* sp. nov.**
http://zoobank.org/0C195C72-A567-472B-99A5-3952628273AC
Vernacular name: The Fern Twisted-Claw Millipede
Figs 18, 19

Material examined. Type material: *Holotype:* United States – **Virginia** • ♂; Alleghany County, McGraw Gap, about 4 km NW of Clifton Forge on RT 606 at fishing area in George Washington National Forest along Smith Creek; 37.8526°N, -79.8512°W, ±9 m; elev. 428 m; 21 June 2016; D. A. Hennen, J. C. Means leg.; dry deciduous litter near stream in forest of oak, rhododendron, maple, mountain laurel, and witch hazel, soil a bit sandy; VTEC, MPE02110. ***Paratypes*:** United States – **Virginia** • 1 ♂ and 1 ♀; same collection data as for holotype; VTEC, MPE01824, MPE01830 • 1 ♂ and 1 ♀; Alleghany County, McGraw Gap, ca 3 mi. [4 km] NW Clifton Forge; 37.8580°N, -79.8661°W, ±4000m; 27 April 1947; R. L. Hoffman leg.; VMNH, NAN0217. **Non type material:** United States – **Virginia** • 2 specimens; Alleghany County, Big Knob, Warm Springs Mtn, ca. 4.5 mi. NE of Covington; 37.8486°N, -79.9272°W, ± 4000m; elev. 1241 m; 15 May 1949; R. L. Hoffman leg.; VMNH, NAN0214 • 4 ♂♂ and 3

Figure 18. *Nannaria filicata* sp. nov., in situ, male (MPE02451) from Allegheny County, Virginia.

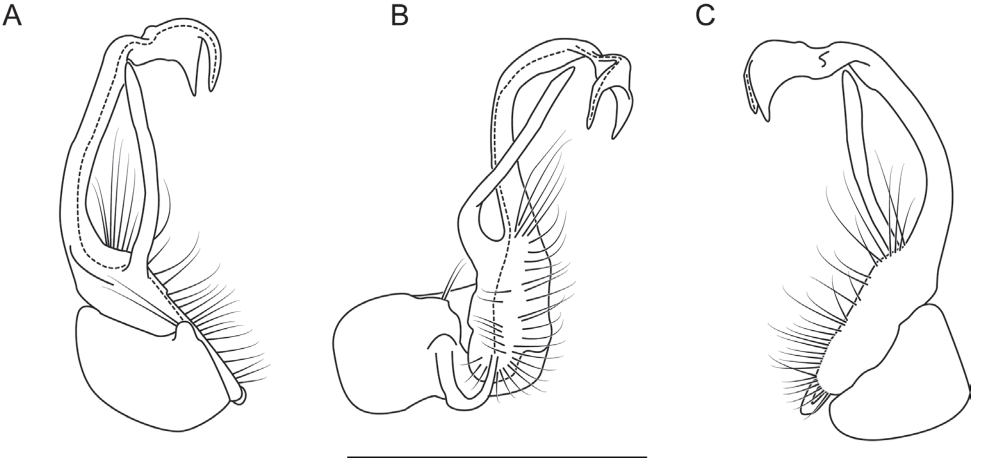

Figure 19. Left gonopod of *Nannaria filicata* sp. nov., male holotype (MPE02110, Allegheny County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

♀♀; Alleghany County, McGraw Gap, about 4 km NW of Clifton Forge on Rt 606 at fishing area in George Washington National Forest along Smith Creek; 37.8526°N, -79.8512°W, ± 9m; elev. 428 m; 21 June 2016; D. A. Hennen, J. C. Means leg.; VTEC, MPE02231, MPE02451, MPE02457, MPE02458, MPE01831, MPE01832, MPE01833. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria filicata* sp. nov. can be separated from the geographically close and morphologically similar species *N. ericacea*, *N. orycta* sp. nov., and *N. vellicata* sp. nov. by the following characters. Acropodite arc gradually curving, not straight with abrupt bend at tip as in *N. ericacea* and *N. vellicata* sp. nov. Acropodite anterior bend only slightly twisted, not acutely bent as in *N. orycta* sp. nov. Acropodite tip medial flange directed caudally, rather than medially as in *N. vellicata* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE02110 and paratype (♀) MPE01830.

Measurements: Taken from holotype (♂) MPE02110: BL = 18.90, CW = 3.25, IW = 2.25, ISW = 0.78, B10W = 3.56, B10H = 2.19. **Color.** Tergites with two paranotal red-orange spots, collum outlined in red-orange, and tergites with background chestnut brown (Fig. 18). **Gonopods.** Male gonopod acropodite arc a gradual curve (Fig. 19A–C). Acropodite with a smooth helical twist at apical bend (Fig. 19C). Acropodite medial flange slightly lobed (Fig. 19C). Acropodite tip medial flange large, laminate and produced into a caudally-directed pointed tip larger than acropodite tip (Fig. 19C). Acropodite tip lateral flange absent. Acropodite tip directed caudally (Fig. 19B). Prefemoral process simple, gradually curving, and crossing acropodite ventrolaterally (Fig. 19B). Prefemoral process tip directed laterally (Fig. 19A). **Cyphopods.** Female cyphopod receptacle enlarged into a triangular hood, covering cyphopod valves.

Variation. No noticeable variation observed.

Distribution. Only known from a small area in Allegheny County, Virginia (Fig. 51).

Ecological notes. Label data indicates this species is found in mesic deciduous forests and rhododendron coves from 428 m to 1241 m in elevation.

Etymology. The specific name is a feminine adjective derived from the Latin *filicatus*, meaning "adorned with ferns." This is in reference to the many ferns observed at its collection localities, with *Polystichum acrostichoides* (Michx.) Schott typically being the dominant fern species.

***Nannaria liriodendra* sp. nov.**

http://zoobank.org/EE80123A-E236-407F-B4C2-177B4C2AF706

Vernacular name: The Tuliptree Twisted-Claw Millipede

Figs 20, 21

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Craig County, Potts Cove, along Cove Branch, next to jeep trail; 37.5833°N, -80.1604°W, ±6m; elev. 772 m; 25 June 2018; D. A. Hennen, J. C. Means, K. Williamson, P. E. Marek leg.; forest of tulip tree, oak, persimmon; VTEC, MPE04200. ***Paratypes*:** United States – **Virginia** • 1 ♂ and 1 ♀; same collection data as for holotype; VTEC,

Figure 20. *Nannaria liriodendra* sp. nov., in situ, male holotype (MPE04200) from Craig County, Virginia.

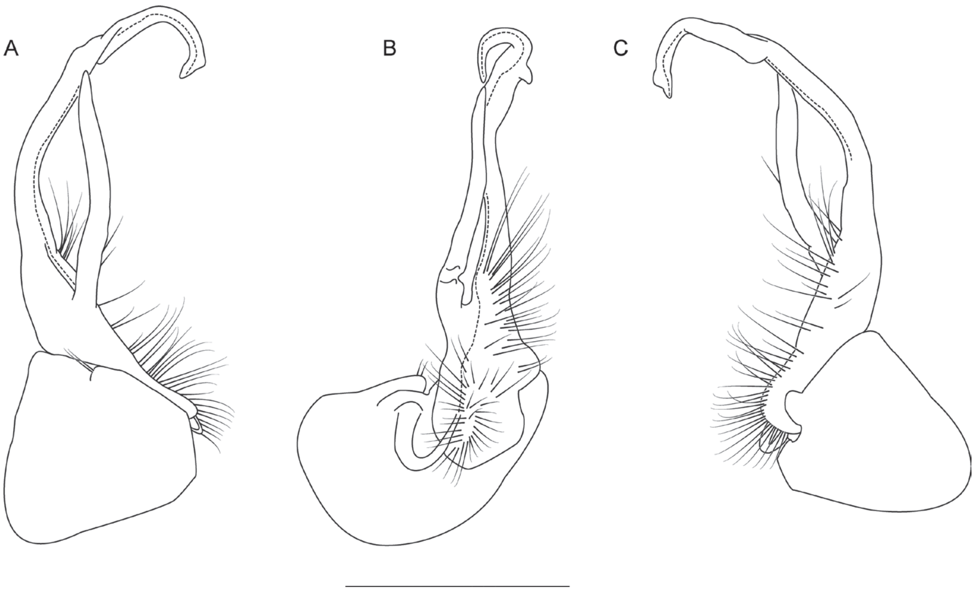

Figure 21. Left gonopod of *Nannaria liriodendra* sp. nov., male holotype (MPE04200, Craig County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm. (Note: the tip of the gonopod acropodite is broken in the holotype specimen, so the tip of a male paratype (NAN0057) was used to illustrate its shape).

MPE04316, MPE04201 • 3 ♂♂ and 1 ♀; Craig County, top of Potts Mtn., E of Paint Bank; 37.6012°N, -80.1533°W, ±5000m; 13 April 1962; R. L. Hoffman leg.; VMNH, NAN0057. **Non type material:** United States – **Virginia** • 14 ♂♂ and 10 ♀♀; Craig County, Potts Cove, Cove Branch, next to jeep trail; 37.5833°N, -80.1604°W, ± 6m; elev. 772 m; 25 June 2018; K. Williamson, D. A. Hennen, J. C. Means, P. E. Marek leg.; VTEC, MPE04310, MPE04317, MPE04318, MPE04319, MPE04320, MPE04321, MPE04322, MPE04323, MPE04324, MPE04325, MPE04326, MPE04327, MPE04328, MPE04329, MPE04202, MPE04203, MPE04204, MPE04205, MPE04330, MPE04331, MPE04332, MPE04333, MPE04334, MPE04335. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria liriodendra* sp. nov. can be separated from the geographically close and morphologically similar species *N. acroteria* sp. nov. and *N. ericacea* by the following characters. Acropodite arc gradually curving, not abruptly bent distally as in *N. ericacea*. Acropodite medial flange lacking a dorsal projection, rather than having a triangular projection as in *N. acroteria* sp. nov. Prefemoral process crimped and with an indentation near base.

Description. Suppl. material 2. Based on holotype (♂) MPE04200 and paratype (♀) MPE4201.

Measurements: Taken from holotype (♂) MPE04200: BL = 35.70, CW = 4.70, IW = 3.32, ISW = 1.12, B10W = 5.75, B10H = 3.13. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 20). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 21A–C). Acropodite anterior bend with gentle twist (Fig. 21A). Acropodite medial flange lobed (Fig. 21C), somewhat triangular in medial view (Fig. 21B). Acropodite tip medial flange absent, acropodite tip lateral flange lobed, rounded (Fig. 21A). Acropodite tip directed caudally (Fig. 21B). Prefemoral process slightly sinuous (Fig. 21A) and crossing acropodite dorsolaterally (Fig. 21A). Prefemoral process with slight indentation near base, appearing crimped and bent (Fig. 21B). Prefemoral process tip directed cephalically (Fig. 21A). **Cyphopods.** Female cyphopod receptacle an enlarged triangular hood, covering cyphopod valves.

Variation. No noticeable variation observed.

Distribution. Only known from the vicinity of Potts Mountain, in Craig County, Virginia (Fig. 51).

Ecological notes. The forest at the type locality is a deciduous oak-tuliptree forest surrounding a stream.

Etymology. The specific name is a feminine adjective derived from the Greek words *leirion* for lily and *dendron* for tree. It is a reference to the tuliptree, *Liriodendron tulipifera* L., known for its flowers that resemble tulips. This beautiful tree is commonly encountered during millipede collecting trips in the eastern U.S.

Nannaria lithographa sp. nov.

Vernacular name: The Stonewriter Twisted-Claw Millipede
Figs 22, 23

Material examined. Type material: *Holotype*: United States – **North Carolina** • ♂; Rutherford County, Chimney Rock State Park, gully on Four Seasons Trail; 35.4315°N, -82.2435°W, ±8m; elev. 457 m; 21 Oct. 2017; D. A. Hennen, J. C. Means leg.; VTEC, MPE03430. ***Paratypes*:** United States – **North Carolina** • 1 ♀; same collection data as for holotype; VTEC, MPE03296 • 1 ♂; Buncombe County, 3 miles [SE] Fairview on US 74, 0.1 mile W Henderson County line; 35.4892°N, -82.3605°W, ±2000m; 28 May 1983; R. M. Shelley, Staton leg.; NCSM, NAN0495. **Non type material:** United States – **North Carolina** • 1 ♂; Rutherford County, along 1306, just E jct. 1314, 3.9 N jct. 64–74, 4 mi. E Chimney Rock; 35.4599°N, -82.187°W; 6 June 1978; R. M. Shelley, W. B. J. leg.; NCSM, NAN0521 • 4 ♀♀; Rutherford County, Chimney Rock State Park, gully on Four Seasons Trail; 35.4315°N, -82.2435°W, ± 8m; elev. 457 m; 21 October 2017; D. A. Hennen, J. C. Means leg.; VTEC, MPE03320, MPE03321, MPE03763, MPE03764; **South Carolina** • 2 ♂♂; Greenville County, Walnut Mountain, 1 mi. N of Chestnut Springs; 35.1897°N, -82.4052°W, ± 2000m; L. Hubricht leg.; VMNH, NAN0317. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria lithographa* sp. nov. can be separated from the geographically close and morphologically similar species *N. austricola* and *N. scutellaria* by

Figure 22. *Nannaria lithographa* sp. nov., in situ, female paratype (MPE03296) from Rutherford County, North Carolina.

the following characters. Acropodite anterior bend slightly twisted rather than acutely twisted or crimped as in *N. austricola* and *N. scutellaria*. Acropodite tip with medial flange laminate and lateral flange produced and hooked, together forming a tapering hood-like structure instead of the parallel-sided acropodite tips of *N. austricola* and *N. scutellaria*. Prefemoral process spear-shaped and attached about halfway up the lateral side of the acropodite, rather than sinuously tapered and attached near base of acropodite as in *N. austricola* and *N. scutellaria*.

Description. Suppl. material 2. Based on holotype (♂) MPE03430 and paratype (♀) MPE03296.

Measurements: Taken from holotype (♂) MPE03430: BL = 26.20, CW = 3.68, IW = 2.76, ISW = 0.90, B10W = 4.88, B10H = 2.81. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 22). **Gonopods.** Male gonopod acropodite arc straight, with bend at midpoint (Fig. 23A–C). Acropodite anterior bend with gently undulating twist (Fig. 23C). Acropodite medial flange absent. Acropodite tip medial flange laminate, smooth (Fig. 23C). Acropodite tip lateral flange hooked and produced into a sharp point and curving dorsally (Fig. 23A, B). Acropodite tip with a hood-like appearance, distally tapering and blunt (Fig. 23A). Prefemoral process spear-shaped, arising from halfway up the lateral side of the acropodite, laminate (Fig. 23A, B). Prefemoral process straight, with slight medial curve distally (Fig. 23B). Prefemoral process tip directed medially (Fig. 23B). Setae present from base of acropodite to three-quarters distally up the full acropodite length (Fig. 23B). **Cyphopods.** Female cyphopod receptacle capsule-shaped; blunt, rounded distally.

Variation. The length of the acropodite tip lateral flange and acropodite tip both vary, and the curve of the acropodite tip varies from medial to ventral.

Distribution. *Nannaria lithographa* sp. nov. is known from Buncombe and Rutherford counties in southwest North Carolina, and adjacent Greenville County, South

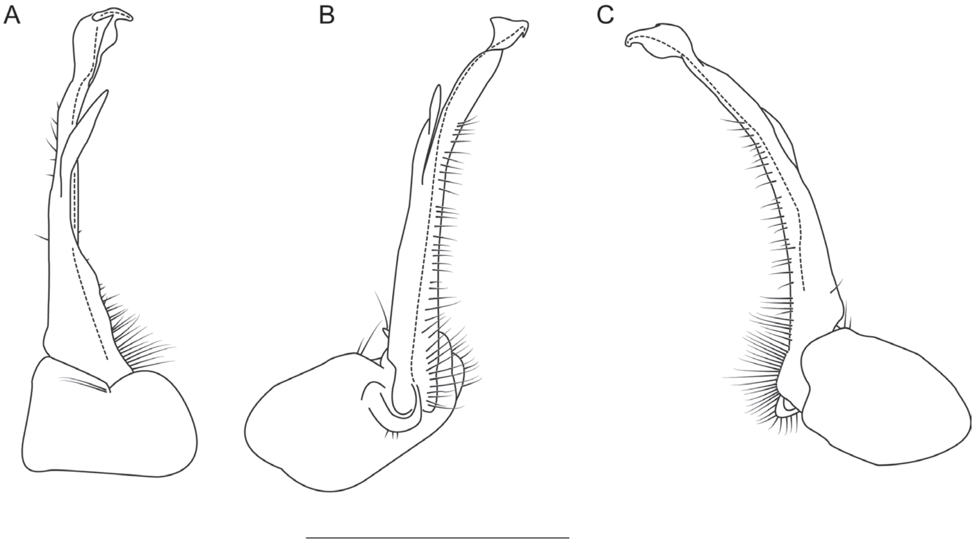

Figure 23. Left gonopod of *Nannaria lithographa* sp. nov., male holotype (MPE03430, Rutherford County, North Carolina) **A** anterior view **B** medial view **C** posterior view Scale bar: 1 mm.

Carolina (Fig. 52). It is bounded at the eastern edge of its distribution by the transition to the Piedmont physiographic region of the Carolinas. On the western edge of its distribution, it may be sympatric with *N. scutellaria*.

Ecological notes. This species has been collected from rhododendron coves in mesic deciduous and ericaceous forests.

Etymology. The specific name is a noun in apposition derived from the Greek *lithos*, meaning stone, and *grapho*, meaning write. The species is named in honor of Chimney Rock State Park, the type locality, where this species was collected at the last moment just as field notes were being recorded before leaving the park.

***Nannaria lutra* sp. nov.**
http://zoobank.org/E7E48D0E-44E4-46ED-B7AA-ED4D5C5C9186
Vernacular name: The Otter Twisted-Claw Millipede
Figs 24, 25

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Rockbridge County, Glasgow: Jefferson National Forest, James River Face Wilderness, Balcony Falls Trailhead, at end of SR 782 off SR 759; 37.6185°N, -79.4709°W, ±9m; elev. 250 m; 18 August 2016; D. A. Hennen, J. C. Means, V. Wong leg.; riparian area near trail in sandy soil, moist oak, maple litter, forest with pawpaw, sourwood; VTEC, MPE02147. ***Paratypes*:** United States – **Virginia** • 1 ♂ and 1 ♀; same collection data as for holotype; VTEC, MPE02232, MPE02233 • 1 ♂; Bedford County, Flat Top Mountain, Peaks of Otter, near mile marker 82.8, Blue Ridge Parkway; 37.4690°N,

Figure 24. *Nannaria lutra* sp. nov., in situ, male holotype (MPE02147) from Rockbridge County, Virginia.

-79.5801°W, ±500m; 27 October 1986; J. C. Mitchell leg.; VMNH, NAN0388. **Non type material:** United States – **Virginia** • 2 specimens; Bedford County, Blue Ridge Parkway, Floyd Field; 37.4937°N, -79.5493°W, ± 1000m; 13 May 1990; J. C. Mitchell leg.; VMNH, NAN0377 • 2 specimens; Bedford County, Peaks of Otter, Blue Ridge Parkway maintenance area; 37.4512°N, -79.5991°W, ± 3000m; 21 June 1990; J. C. Mitchell leg.; VMNH, NAN0381 • 8 specimens; Bedford County, Peaks of Otter, at base of Flat Top; 37.4545°N, -79.5995°W, ± 2000m; 19 May 1967; R. L. Hoffman, et al. leg.; VMNH, NAN0383 • 1 specimen; Bedford County, Peaks of Otter; 37.4512°N, -79.5991°W, ± 3000m; elev. 852 m; 14 to 15 October 1962; R. L. Hoffman leg.; VMNH, NAN0385 • 4 specimens; Bedford County, Peaks of Otter; 37.4512°N, -79.5991°W, ± 3000m; 15 October 1955; R. B., R. L. Hoffman leg.; VMNH, NAN0386 • 2 specimens; Bedford County, Headforemost Mtn Overlook, B. R. P.; 37.4815°N, -79.5633°W, ± 500m; 18 September 1989; C. A. Pague, K. A. Buhlmann leg.; VMNH, NAN0387 • 7 specimens; Bedford County, MP 81, Blue Ridge Pkw.; 37.4929°N, -79.5522°W, ± 500m; elev. 975 m; 20 October 1956; R. L. Hoffman, Highton leg.; VMNH, NAN0391 • 1 specimen; Bedford County, Road to radar station, Apple Orchard Mountain; 37.5176°N, -79.509°W, ± 500m; elev. 1219 m; 15 June 1997; R. L. Hoffman leg.; VMNH, NAN0393 • 6 ♂♂; Bedford County, Blue Ridge Parkway, MM 88, Side of road in gully; 37.4581°N, -79.6295°W, ± 6m; elev. 741 m; J. C. Means leg.; VTEC, MPE00156, MPE00158, MPE00159, MPE00160, MPE00161, MPE00162 • 1 ♂; Bedford County, at base of Sharp Top Mtn. trail behind Nature Center; 37.4407°N, -79.6033°W; 18 June 2016; P. L. Shorter, N. Rodgers leg.; VTEC, MPE01933 • 5 specimens; Botetourt County, "Sugarland" on SW side of Apple Orchard Mtn.; 37.5127°N, -79.5294°W, ± 1000m; 27 May 1962; R.

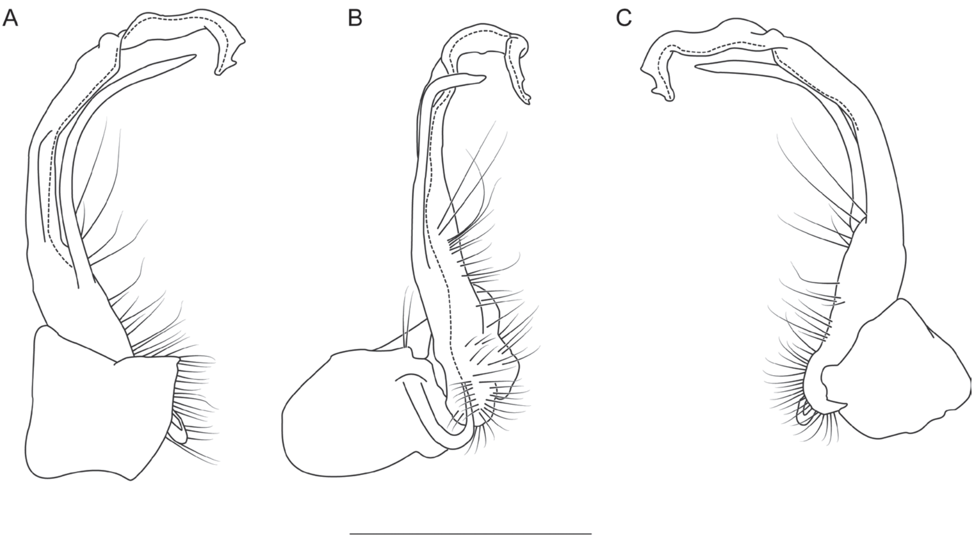

Figure 25. Left gonopod of *Nannaria lutra* sp. nov., male holotype (MPE02147, Rockbridge County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

L. Hoffman leg.; VMNH, NAN0363 • 2 specimens; Botetourt County, MP 92, Blue Ridge Parkway; 37.4768°N, -79.6895°W, ± 1000m; 20 October 1956; M. Highton leg.; VMNH, NAN0374 • 5 specimens; Botetourt County, Jefferson National Forest, Wildcat Mountain; 37.5495°N, -79.5367°W, ± 2000m; 29 October 1989; J. C. Mitchell leg.; VMNH, NAN0375 • 1 specimen; Botetourt County, "Sugarland" on W side of Apple Orchard Mtn.; 37.5127°N, -79.5294°W, ± 1000m; 1 June 1962; R. L. Hoffman leg.; VMNH, NAN0376 • 1 specimen; Botetourt County, west side Apple Orchard Mtn.; 37.5127°N, -79.5294°W, ± 1000m; elev. 1036 m; 11 April 1976; R. L. Hoffman leg.; VMNH, NAN0378 • 2 specimens; Botetourt County, N side of Bearwallow Gap, 3 mi S of Buchanan on Rt. 43; 37.4841°N, -79.6684°W, ± 1000m; 27 May 1962; R. L. Hoffman leg.; VMNH, NAN0379 • 2 specimens; Botetourt County, west side Apple Orchard Mtn near crest, along AT, berleseate; 37.5179°N, -79.5143°W, ± 1000m; 16 May 1998; R. L. Hoffman leg.; VMNH, NAN0380 • 2 specimens; Botetourt County, west slope Apple Orchard Mountain, off USFS 812; 37.5171°N, -79.527°W, ± 1000m; 13 May 1990; J. C. Mitchell leg.; VMNH, NAN0382 • 1 specimen; Botetourt County, North Creek, ca. 1–3 mi. E of Arcadia; 37.5417°N, -79.5847°W, ± 1000m; 13 October 1973; R. L. Hoffman leg.; VMNH, NAN0384 • 7 specimens; Botetourt County, Apple Orchard Mtn.; 37.5324°N, -79.512°W, ± 2000m; elev. 975 m; 14 October 1962; Bio. Club leg.; VMNH, NAN0389 • 1 ♀; Botetourt County, west side of Apple Orchard Mtn., east of Arcadia; 37.5171°N, -79.527°W, ± 2000m; 22 July 1990; J. C. Mitchell leg.; VMNH, NAN0390 • 1 ♀; Botetourt County, Jefferson National Forest, nr Parkers Gap, off FS 812, Apple Orchard Mtn; 37.5351°N, -79.5208°W, ± 1000m; 8 November 1990; J. C. Mitchell leg.; VMNH, NAN0392 • 13 specimens; Botetourt County, Apple Orchard Mtn., ca

6 mi. E of Buchanan; 37.5171°N, -79.527°W, ± 2000m; elev. 914 m; 3 September 1973; R. L. Hoffman leg.; VMNH, NAN0394 • 1 ♂; Rockbridge County, Glasglow: Jefferson National Forest, James River Face Wilderness, Balcony Falls Trailhead, at end of CR 782 off 759; 37.6185°N, -79.4709°W, ± 9m; elev. 250 m; 18 August 2016; J. C. Means, D. A. Hennen, V. Wong leg.; VTEC, MPE03667. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria lutra* sp. nov. can be separated from the geographically close and morphologically similar species *N. cymontana* sp. nov. and *N. ericacea* by the following characters. Acropodite arc gently curving, rather than straight with an abrupt bend at tip and triangular projection as in *N. ericacea*. Acropodite with a median dome-like projection near medial flange, which is absent in *N. cymontana* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE02147 and paratype (♀) MPE02233.

Measurements: Taken from holotype (♂) MPE02147: BL = 25.60, CW = 3.80, IW = 2.76, ISW = 0.87, B10W = 4.75, B10H = 2.69. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 24). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 25A–C). Acropodite undivided, and with an undulating twist at anterior bend (Fig. 25A). Acropodite medial flange slightly lobed, with a median dome-like projection dorsally (Fig. 25C). Acropodite tip medial flange absent. Acropodite tip lateral flange bilobed, the more distal lobe slightly smaller (Fig. 25A). Acropodite tip directed caudally (Fig. 25B). Prefemoral process sinuous; tip directed medially (Fig. 25B). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. Size and shape of the median dome-like projection varies and is sometimes more pointed than rounded. Acropodite tip lateral flange sometimes with lobes smaller and rounder, rather than pointed.

Distribution. *Nannaria lutra* sp. nov. is known from the following Virginia counties: Bedford, Botetourt, and Rockbridge (Fig. 51).

Ecological notes. This species is known from mixed hardwood forests at elevations ranging from 250 m to 1219 m.

Etymology. The specific name is a noun in apposition derived from the Latin word *lutra*, meaning otter. The name is an honorific for the Peaks of Otter, a trio of mountain peaks along the Blue Ridge Parkway in Bedford County and Botetourt County, Virginia.

Nannaria marianae sp. nov.

http://zoobank.org/A929D071-FB10-4D61-A63F-802EE42AC414
Vernacular name: The Maple Flats Twisted-Claw Millipede
Figs 26, 27

Material examined. Type material: *Holotype*: United States – **Virginia** • ♂; Augusta County, Sherando: George Washington National Forest, Maple Flat Ponds area; 37.9776°N, -78.9938°W, ±7 m; elev. 480 m; 12 June 2019; D. A. Hennen, J. C. Means,

Figure 26. *Nannaria marianae* sp. nov., in situ, male holotype (MPE05006) from Augusta County, Virginia.

M. Hellier, P. E. Marek; white oak, hickory, tuliptree forest around sinkhole ponds; VTEC, MPE05006. ***Paratypes*:** United States – **Virginia** • 2 ♂♂ and 1 ♀; same collection data as for holotype; VTEC, MPE05005, VMNH, MPE04982, VTEC, MPE05010. **Non type material:** United States – **Virginia** • 3 ♂♂; Augusta County; VMNH, NAN0158 • 1 ♀; Augusta County, St. Mary's Wilderness Cellar Mountain Trail, near trailhead; 37.9429°N, -79.1382°W, ± 2m; elev. 624 m; 24 June 2017; P. E. Marek, C. Hall leg.; VTEC, MPE02900 • 3 ♀♀; Augusta County, George Washington National Forest, St. Mary's Wilderness, St. Mary's River Trail; 37.9256°N, -79.1309°W, ± 6m; elev. 542 m; 24 May 2018; D. A. Hennen, J. C. Means leg.; VTEC, MPE04013, MPE04014, MPE04017 • 5 ♂♂ and 3 ♀♀; Augusta County, Sherando: George Washington National Forest, Maple Flat Ponds area; 37.9776°N, -78.9938°W, ± 7m; elev. 480 m; 12 June 2019; D. A. Hennen, J. C. Means, P. E. Marek, M. Hellier leg.; VTEC, MPE04983, MPE04986, MPE05007, MPE05008, MPE05009, MPE04984, MPE04985, MPE05010. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria marianae* sp. nov. can be separated from the geographically close and morphologically similar species *N. morrisoni* and *N. orycta* sp. nov. by the following characters. Immediately recognizable by its stout prefemoral process, which projects at a 45° angle from the telopodite, rather than the acicular or slightly curving prefemoral process of *N. morrisoni* and *N. orycta* sp. nov. Additionally, the acropodite tip lateral flange is laminate and very large, with jagged teeth along its edges, unlike any other *Nannaria* species.

Description. Suppl. material 2. Based on holotype (♂) MPE05006 and paratype (♀) MPE05010.

Measurements: Taken from holotype (♂) MPE05006: BL = 29.60, CW = 3.60, IW = 2.57, ISW = 0.82, B10W = 4.35, B10H = 2.67. **Color.** Tergites with two paranotal

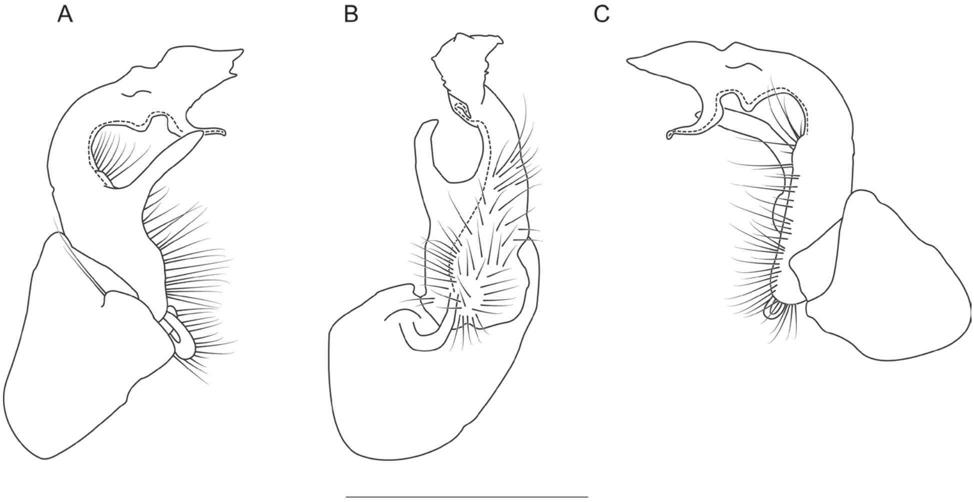

Figure 27. Left gonopod of *Nannaria marianae* sp. nov., male holotype (MPE05006, Augusta County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 26). **Gonopods.** Male gonopod acropodite arc straight, with acute bend at midpoint (Fig. 27A–C). Acropodite anterior bend twist lacking or almost imperceptible (Fig. 27C). Acropodite medial flange lobed (Fig. 27C). Acropodite tip medial flange absent. Acropodite tip lateral flange laminate and greatly enlarged, with various small teeth along its edges and culminating in a broad, triangular tip (Fig. 27A), extremely divergent to any species of *Nannaria*. Acropodite tip sinuous, bifurcate, directed medially (Fig. 27B). Prefemoral process stout, thick; projecting straight at a 45° angle from the acropodite (Fig. 27A), dissimilar to any other *wilsoni* species group prefemoral process. **Cyphopods.** Female cyphopod receptacle enlarged into a triangular hood, covering cyphopod valves.

Variation. The number and shape of the teeth on the laminate acropodite tip lateral flange varies, but are generally quite jagged.

Distribution. *Nannaria marianae* sp. nov. is known from a small area at the base of the Blue Ridge Mountains in southern Augusta County, Virginia (Fig. 51). Males have only been collected at the Maple Flats Sinkhole Ponds complex near Sherando, but genetic analysis places female *Nannaria* specimens collected in the nearby St. Mary's Wilderness area with these males.

Ecological notes. This species has been collected in a mesic white oak, hickory, and tuliptree forest and a mesic oak, hemlock, and mountain laurel forest along a stream. The Maple Flat Ponds area is known to harbor disjunct plant species (Buhlmann et al. 1999). Elevation for these sites ranges from 480 m to 624 m.

Etymology. The specific name is a noun in the genitive case derived as a matronym, named in honor of Marian Winsor Hennen (née Wood), the wife of DAH, in recognition of her patience, love, and support during DAH's doctoral studies. She grew up in Augusta County, Virginia, where all collections of this species have occurred, and has participated in her fair share of millipede collecting trips. The vernacular name for this species references the type locality, where this species was finally found after five years of searching for it at locations throughout Augusta County. Before its discovery at Maple Flats, this species was known only from VMNH specimens that stated the locality simply as "Augusta County."

Nannaria morrisoni **Hoffman, 1948**
Vernacular name: Morrison's Twisted-Claw Millipede
Figs 28, 29

Nannaria morrisoni Hoffman, 1948: 348, figs 3–4. Chamberlin and Hoffman 1958: 41. Hoffman 1999: 367 (351 in pdf version). Means et al. 2021a: S68, fig. 3.

Type material. ***Holotype*****:** United States – **Virginia** • ♂; Albemarle County, Saddle Hollow, about 3 miles [4.8 km] west of Crozet; 38.082°N, -78.731°W, ±1000m; elev. ca. 610 m; 28 March 1948; R. L. Hoffman leg.; "Dominant vegetation *Liriodendron tulipifera*, *Quercus* spp., and *Cercis canadensis*" (Hoffman 1948); USNM Entomology, no. 1834; (non vidi). ***Paratypes*****:** United States – **Virginia** • 2 ♂♂; Page County, along Skyline

Figure 28. *Nannaria morrisoni,* in situ, male (MPE02595) from Greene County, Virginia.

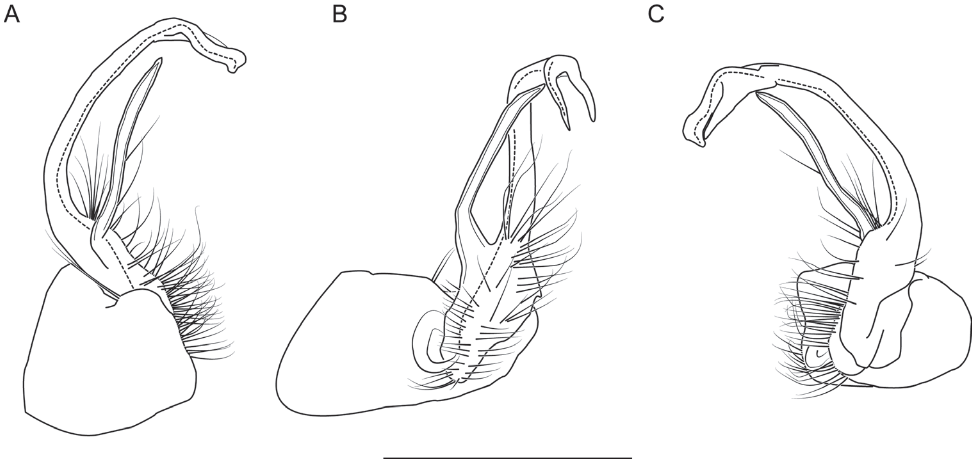

Figure 29. Left gonopod of *Nannaria morrisoni* (MPE02595, Greene County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Drive, 4 miles [6.4 km] north of Thornton Gap; 38.7067°N, -78.3189°W, ±1000m; April 1936; I. Fox, J. P. E. Morrison leg.; USNM Entomology, no. 1836 (non vidi).

Material examined. Non type material: United States – **Virginia** • 2 specimens; Albemarle County, Sugar Hollow; 38.129°N, -78.7234°W, ± 2000m; 21 March 1949; R. L. Hoffman leg.; VMNH, NAN0400 • 1 ♀; Albemarle County, Carters Bridge: Peter Rausse's land, near tasting room before construction, by stream; 37.9456°N, -78.4842°W; 19 July 2014; J. C. Means leg.; VTEC, MPE00114 • 2 ♀♀; Albemarle County, Sugar Hollow, entrance by parking lot; 38.1256°N, -78.7139°W; 28 February 2016; J. C. Means leg.; VTEC, MPE01007, MPE03715 • 1 ♂ and 4 ♀♀; Albemarle County, Sugar Hollow, North of Charlottesville Reservoir; 38.1474°N, -78.7443°W, ± 9m; elev. 487 m; 22 June 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE02107, MPE01885, MPE02015, MPE02016, MPE02149 • 2 ♂♂ and 3 ♀♀; Albemarle County, Shenandoah NP, nr JCT CR-611 & Appalachian Tr., Jarman Gap, near spring; 38.0966°N, -78.7779°W; elev. 709 m; 6 June 2005; P. E. Marek, C. Lin leg.; VTEC, SPC000495, SPC000497, SPC000496, SPC000498, SPC000499 • 13 specimens; Amherst County, South side Tar Jacket Ridge, FS 1167; 37.761°N, -79.1844°W, ± 2000m; 5 June 1998; VMNH survey leg.; VMNH, NAN0395 • 4 specimens; same collection data as for preceding; 15 August to 13 November 1999; VMNH, NAN0397 • 8 specimens; same collection data as for preceding; 6 May 1998; VMNH, NAN0398 • 23 specimens; same collection data as for preceding; 4 August 1998; VMNH, NAN0410 • 8 specimens; Amherst County, DF site on Tar Jacket Ridge, head of Piney River; 37.7707°N, -79.1749°W, ± 2000m; 9 July 1998; Jon Schilling leg.; VMNH, NAN0401 • 1 specimen; Amherst County, Pitfall on Tar Jacket Ridge, off FS 1167; 37.761°N, -79.1844°W, ± 2000m; 7 November to 18 December 1997; VMNH survey leg.; VMNH, NAN0404 • 21 specimens; Amherst County, East slope of Tar Jacket Ridge, ca. 5 mi NE of Oronoco; 37.7712°N, -79.184°W, ± 2000m; 14

May to 23 June 1999; VMNH survey leg.; VMNH, NAN0405 • 1 specimen; Amherst County, DF site on Tar Jacket Ridge, off FS 1167; 37.761°N, -79.1844°W, ± 2000m; 21 October 1997; VMNH survey leg.; VMNH, NAN0406 • 2 ♂♂ and 1 ♀; Amherst County, gully along Mt. Pleasant hiking trail; 37.7547°N, -79.185°W; elev. 1020 m; 31 December 2016; J. C. Means leg.; VTEC, MPE02491, MPE02830, MPE02829 • 1 specimen; Greene County, Hightop Mtn, 2 mi S Swift Run Gap; 38.3376°N, -78.5523°W, ± 2000m; 17 October 1990; C. A. Pague leg.; VMNH, NAN0399 • 1 ♂; Greene County, Shenandoah National Park: Appalachian Trail off South River Falls Trail; 38.385°N, -78.5147°W; elev. 896 m; 29 April 2017; J. C. Means leg.; VTEC, MPE02591 • 3 ♂♂ and 2 ♀♀; Greene County, Shenandoah National Park: tributary above South River Falls; 38.3802°N, -78.5036°W; elev. 679 m; 29 April 2017; J. C. Means leg.; VTEC, MPE02595, MPE02607, MPE02608, MPE02596, MPE02606 • 1 ♂; Greene County, Shenandoah National Park: base of South River Falls; 38.3791°N, -78.4997°W; elev. 607 m; 29 April 2017; J. C. Means leg.; VTEC, MPE02605 • 1 ♀; Greene County, Shenandoah National Park: Fire road intersecting South River Falls Trail; 38.382°N, -78.5097°W; elev. 811 m; 29 April 2017; J. C. Means leg.; VTEC, MPE03669 • 2 ♂♂ and 1♀; Madison County, Luray; 38.6649°N, -78.4593°W; July 1966; C. Ewing leg.; NCSM, NAN0489 • 1 specimen; Madison County, Shenandoah National Park, Little Stony Man Trail; 38.6118°N, -78.3616°W, ± 2000m; 27 May 1990; C. A. Pague leg.; VMNH, NAN0396 • 2 ♀♀; Nelson County, Humpback Mountain; 37.9487°N, -78.8986°W, ± 2000m; 14 October 1948; R. L. Hoffman leg.; VMNH, NAN0409 • 2 ♂♂; Nelson County, Appalachian Trail crossing of 56, up hill over Tye River; 37.8388°N, -79.0213°W; elev. 339 m; 17 September 2016; J. C. Means leg.; VTEC, MPE02115, MPE02116 • 1 ♀; Nelson County, VA-826, 0.8 rd km S of US-56; 37.8425°N, -79.1165°W, ± 2m; elev. 878 m; 24 June 2017; P. E. Marek, C. Hall leg.; VTEC, MPE02872 • 3 specimens; Page County, Panorama, Skyline Drive; 38.6592°N, -78.3213°W, ± 2000m; 21 July 1938; E. M. Loomis, H. F. Loomis leg.; VMNH, NAN0403 • 1 specimen; Rockbridge County, W side of Rocky Mtn. on BRP; 37.7963°N, -79.1988°W, ± 2000m; 24 August 1949; R. L. Hoffman leg.; VMNH, NAN0407. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria morrisoni* can be separated from the geographically close and morphologically similar species *N. shenandoa* and *N. orycta* sp. nov. by the following characters. Acropodite tip medial flange triangular, directed medially rather than laminate with an acuminate tip and directed caudally, as in *N. orycta* sp. nov. Prefemoral process acicular and needle-like, not curving laterally as in *N. shenandoa*.

Description. Suppl. material 2. Based on (♂) (MPE02595) and ♀ (MPE02596).

Measurements: Taken from (♂) specimen MPE02595: BL = 28.88, CW = 3.54, IW = 2.54, ISW = 0.75, B10W = 4.30, B10H = 2.80. **Color.** Tergites with two paranotal pink to orange spots, collum outlined in pink to orange, and tergites with background chestnut brown to black (Fig. 28). **Gonopods.** Male gonopod acropodite arc a gradual curve (Fig. 29A–C). Acropodite medial flange absent, acropodite tip medial flange extended into a large, lobed, triangular projecting process, giving the tip of the acropodite a bifurcate appearance (Fig. 29B). Acropodite tip lateral flange absent. Tips of acropodite directed medially, with a slightly ventral angle (Fig. 29A). Mesal tip of acropodite carrying the seminal groove with slight dorsal expansion. Tip of medial flange ending in a sharp point (Fig. 29C). Prefemoral process acicular, needle-like, with tip directed cephalically (Fig. 29A). **Cyphopods.** Female cyphopod receptacle much enlarged, laminate.

Variation. No appreciable variation was noticed between specimens.

Distribution. Only known from Virginia, *Nannaria morrisoni* occurs in the following counties: Albemarle, Amherst, Bland, Greene, Madison, Nelson, Page, and Rockbridge (Fig. 51). Its distribution in these counties is almost exclusively restricted to the spine of the Blue Ridge Mountains, northeast of the James River.

Ecological notes. Specimen label data indicates *Nannaria morrisoni* is collected in deciduous forests of oak, tuliptree, beech, and maple, rather than in areas with more rhododendron and other ericaceous plants. Many of the sites with habitat data list riparian areas as the habitat for this species. Specimens been collected from elevations as low as 339 m to as high as 1067 m.

Etymology. *Nannaria morrisoni* is named after Dr. Joseph P. E. Morrison, a mollusk curator at the Smithsonian Museum of Natural History in Washington, D.C., who collected millipedes for Richard Hoffman during his own collecting trips for land snails (Hoffman 1948).

Nannaria nessa **sp. nov.**

http://zoobank.org/111DCE2E-629C-418E-B114-E76348830B7B
Vernacular name: The Duck Twisted-Claw Millipede
Figs 30, 31

Nannaria "Puc Puggy": Means et al. 2021a: fig. 3.

Material examined. Type material: *Holotype*: United States – **North Carolina •** ♂; Macon County, 8.2 km WSW of Highlands on NC-106, Nantahala National Forest, near start of Puc Puggy Trail; 35.0288°N, -83.2823°W, ±7m; elev. 1124 m; 7 June 2016; D. A. Hennen, J. C. Means leg.; on hillside along path, moist oak, tuliptree, rhododendron forest, litter of medium depth; VTEC, MPE01465. ***Paratype*:** United States – **North Carolina •** 1 ♀; same collection data as for holotype; VTEC, MPE01500. **Non type material:** United States – **Georgia •** 3 ♂♂; Rabun County, Rabun Bald, about 1 mile south trailhead at Beegum Gap; 34.9694°N, -83.3°W, ± 1500m; 26 October 2019; C. W. Harden leg.; VTEC, MPE05015, MPE05016, MPE05017; **North Carolina •** 1 ♀; Macon County, 8.2 km WSW of Highlands on NC-106, Nantahala National Forest, near start of Puc Puggy Trail; 35.0288°N, -83.2823°W, ± 7m; elev. 1124 m; 7 June 2016; D. A. Hennen, J. C. Means leg.; VTEC, MPE01501. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria nessa* sp. nov. can be separated from the geographically close and morphologically similar species *N. austricola* and *N. spalax* sp.

Figure 30. *Nannaria nessa* sp. nov., in situ, male holotype (MPE01465) from Macon County, North Carolina.

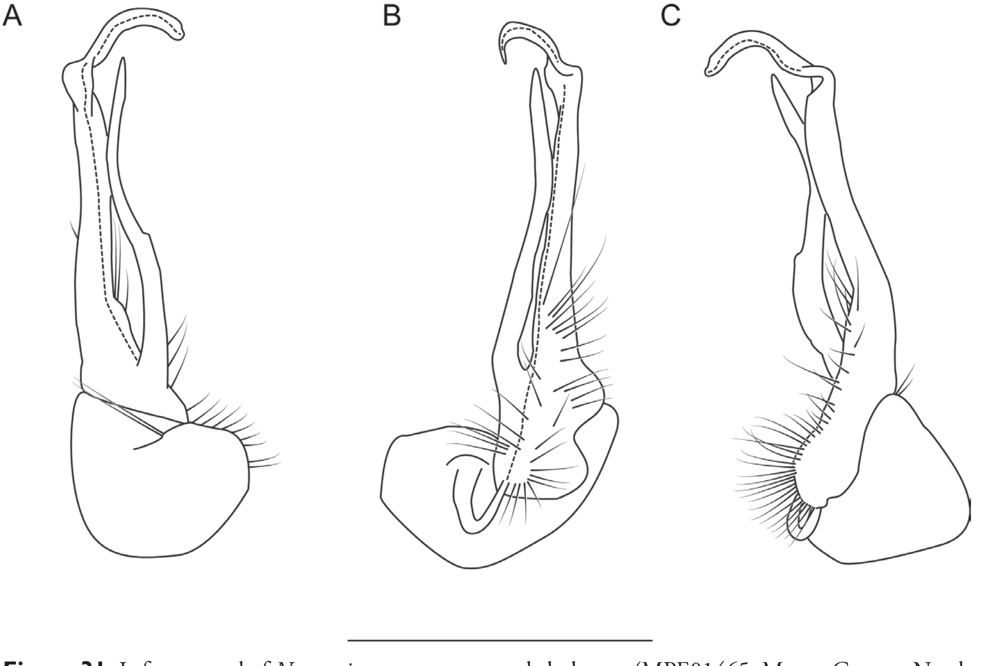

Figure 31. Left gonopod of *Nannaria nessa* sp. nov., male holotype (MPE01465, Macon County, North Carolina) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

nov. by the following characters. Acropodite medial flange lobed, rather than laminate and with a short, triangular tip medial flange as in *N. spalax* sp. nov. Acropodite tip medial flange absent, not lobed as in *N. austricola*. Prefemoral process only slightly curving and with a notch on its medial side near midpoint, not curving laterally as in *N. austricola* or thick and with a jagged medial margin as in *N. spalax* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE01465 and paratype (♀) MPE01500.

Measurements: Taken from holotype (♂) MPE01465: BL = 22.10, CW = 3.28, IW = 2.73, ISW = 0.99, B10W = 3.95, B10H = 2.75. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 30). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend at tip (Fig. 31A–C). Acropodite with acute twist at anterior bend, giving the acropodite a pinched appearance (Fig. 31C). Acropodite medial flange lobed (Fig. 31C). Acropodite tip medial flange and lateral flange both absent. Acropodite tip blunt, directed caudally (Fig. 31B). Prefemoral process sinuously tapered, with basal jutting shelf medially (Fig. 31A, C). Prefemoral process tip directed cephalically (Fig. 31A). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. No noticeable variation observed.

Distribution. *Nannaria nessa* sp. nov. is only known from Macon County, North Carolina and adjacent Rabun County, Georgia (Fig. 52).

Ecological notes. This species is found in deciduous and rhododendron cove habitats, within leaf litter and under rocks.

Etymology. The specific name is a noun in apposition derived from the Greek *nessa*, meaning duck. It is named after Duck Mountain, a mountain near the type locality.

Nannaria orycta sp. nov.

http://zoobank.org/37BBA209-55EE-4453-B995-2CABA512AC75
Vernacular name: The Digging Twisted-Claw Millipede
Figs 32, 33

Material examined. Type material: ***Holotype*****:** United States – **Virginia** • ♂; Rockbridge County, 3.2 air km NW of Collierstown: Lake Robertson Recreation Area, Mountain Trail, hillside near Hawks Creek stream crossing; 37.8065°N, -79.6152°W, ±10m; elev. 457 m; 20 Feb 2018; D. A. Hennen, J. C. Means leg.; tuliptree, maple, sycamore woods, moist, dark soil; VTEC, MPE03810. ***Paratypes*****:** United States – **Virginia** • 1 ♂ and 1 ♀; same collection data as for holotype; VTEC, MPE03819, MPE03823. **Non type material:** United States – **Virginia** • 1 specimen; Amherst County, Staton Creek Gorge, George Washington Natl. For. NE of Buena Vista; 37.7717°N, -79.2437°W, ± 2000m; 1 August 1974; H. Levi, L. Levi, F. Levi leg.; VMNH, NAN0063 • 1 specimen; Augusta County, E of Steele's Tavern, W slope of Blue Ridge 1 mile below summit; 37.9261°N, -79.1151°W, ± 5000m; 24 September 1949; J. P. E. Morrison leg.; VMNH, NAN0061 • 2 specimens; Nelson County, along Appalachian Trail to pitfall site on The Priest, ca. 4 mi SE of Montebello; 37.8254°N, -79.0788°W, ± 3000m; elev. 914 m; 20 September 1992; R. L. Hoffman leg.; VMNH, NAN0058 • 2 specimens; Nelson County, Wintergreen Mountain Resort; 37.9349°N, -78.935°W, ± 2000m; 22 September 1996; R. L. Hoffman leg.; VMNH, NAN0059 • 4 specimens; Nelson County, The Priest, 4 mi. SE Montebello DF site; 37.8202°N, -79.065°W, ± 3000m; elev. 1189 m; 20 September to 18 October 1992; VMNH survey leg.; VMNH, NAN0060 • 2 specimens; same collection data as for

Figure 32. *Nannaria orycta* sp. nov., in situ, male holotype (MPE03810) from Rockbridge County, Virginia.

preceding; 28 August to 21 September 1991; VMNH, NAN0062 • 3 ♂♂; Rockbridge County, 3.2 air km NW of Collierstown: Lake Robertson Recreation Area, Mountain Trail, hillside near Hawks Creek stream crossing; 37.8065°N, -79.6152°W, ± 10m; elev. 457 m; 20 February 2018; D. A. Hennen, J. C. Means leg.; VTEC, MPE03820, MPE03821, MPE03822 • 11 ♂♂ and 9 ♀♀; Rockingham County, Lexington: Washington and Lee University campus, hillside beside community gardens; 37.7956°N, -79.4427°W, ± 6m; elev. 330 m; 14 November 2017; J. C. Means, D. A. Hennen leg.; VTEC, MPE03487, MPE03488, MPE03489, MPE03502, MPE03505, MPE03507, MPE03508, MPE03510, MPE03512, MPE03514, MPE03519, MPE03496, MPE03497, MPE03501, MPE03504, MPE03506, MPE03509, MPE03511, MPE03513, MPE03515. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria orycta* sp. nov. can be separated from the geographically close and morphologically similar species *N. filicata* sp. nov., *N. marianae* sp. nov., and *N. morrisoni* by the following characters. Acropodite anterior bend acutely twisted and folded, not absent as in *N. marianae* sp. nov. and *N. morrisoni* or only slightly twisted as in *N. filicata* sp. nov. Acropodite tip directed caudally, not medially as in *N. marianae* sp. nov. and *N. morrisoni*. Acropodite with basomedial process, rather than absent as in *N. filicata* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE03810 and paratype (♀) MPE03823.

Measurements: Taken from holotype (♂) MPE03810: BL = 28.30, CW = 4.00, IW = 2.88, ISW = 0.90, B10W = 4.90, B10H = 3.00. **Color.** Tergites with two paranotal white spots, collum outlined in white, and tergites with background black (Fig. 32). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 33A–C). Acropodite anterior bend with acute twist, appearing folded over (Fig. 33C). Acropodite medial flange lobed and concave dorsally (Fig. 33C). Acropodite tip medial flange

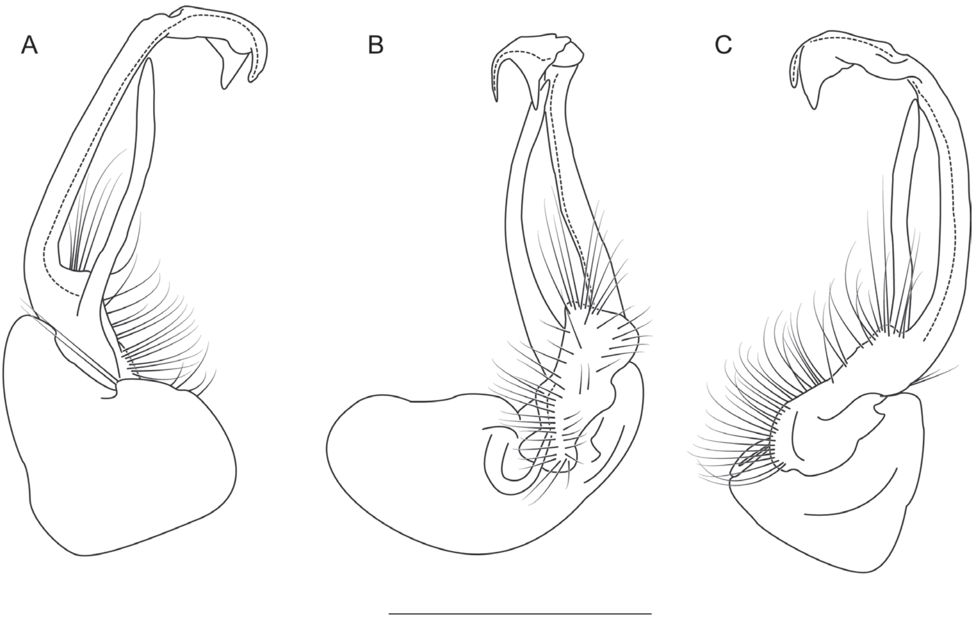

Figure 33. Left gonopod of *Nannaria orycta* sp. nov., male holotype (MPE03810, Rockbridge County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

greatly enlarged and laminate, directed caudally with a pointed tip (Fig. 33C). Acropodite tip lateral flange absent. Acropodite tip directed caudally (Fig. 33B). Acropodite with quadrate basomedial process. Prefemoral process gradually curving, with tip directed laterally (Fig. 33A). **Cyphopods.** Female cyphopod receptacle triangular.

Variation. The color of the paranotal spots in *Nannaria orycta* sp. nov. may be either white or red. The male gonopod twist at the anterior bend ranges from acutely twisted to strongly crimped, with the distal portion of the acropodite almost recurved 270°.

Distribution. This species is known from the following Virginia counties, where it mainly inhabits the Blue Ridge Mountains: Amherst, Augusta, Nelson, Rockbridge, and Rockingham (Fig. 51).

Ecological notes. Label data indicates this species inhabits mesic mixed deciduous woods, at elevations ranging from 330 m to 1189 m.

Etymology. The specific name is a feminine adjective derived from the Greek word *oryktes*, meaning "one who digs," and alludes to the fossorial habits of *Nannaria*.

Nannaria paraptoma sp. nov.

http://zoobank.org/D3166398-0636-4513-B5AA-2144169EED8E
Vernacular name: The Tumbling Twisted-Claw Millipede
Fig. 34

Material examined. ***Holotype*:** United States – **Virginia** • ♂; Bath County, Sunrise, George Washington National Forest, Long Spring Run, above Little Back Creek;

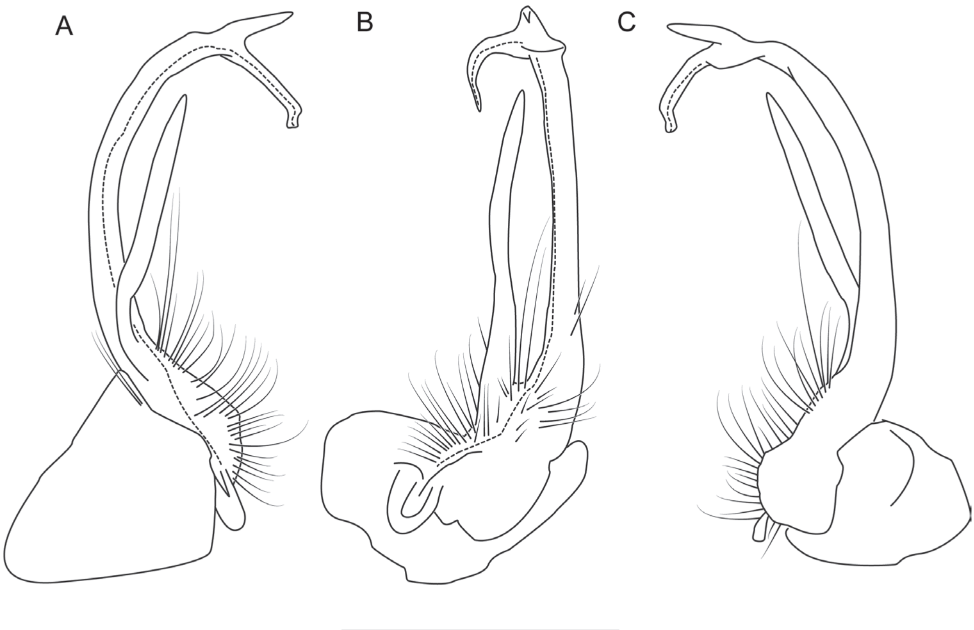

Figure 34. Left gonopod of *Nannaria paraptoma* sp. nov., male holotype (NAN0650, Bath County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

38.2213°N, -79.8387°W, ± 2000m; pitfall trap; 24 July 1992; J. Pagels, D. Kobuszewski leg.; VMNH, NAN0650. ***Paratype*:** United States – **Virginia** • ♂; same collection data as holotype; 11 September 1992; D. Kobuszewski leg.; VMNH, NAN0655.

Non type material: United States – **West Virginia** • 2 ♂♂; Pocahontas County, Watoga State Park, 3 mi. SE of Seebert; 38.1129°N, -80.1217°W, ± 5000m; 17 October 1971; R. L. Hoffman, L. S. Knight leg.; VMNH, NAN0292. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria paraptoma* sp. nov. can be separated from the geographically close and morphologically similar species *N. ericacea*, *N. shenandoa*, and *N. spiralis* sp. nov. by the following characters. Acropodite arc gradually curving, rather than straight with an abrupt bend distally as in *N. ericacea*. Acropodite medial flange with a large dorsal triangular projection, rather than having a small triangular tip medial flange as in *N. ericacea*. Acropodite medial flange lobed, rather than laminate and shield-shaped as in *N. spiralis*. Acropodite undivided distally, not bifurcate as in *N. shenandoa*.

Description. Suppl. material 2. Based on holotype (♂) NAN0650. No females have been collected, thus the female morphology is unknown.

Measurements: Taken from holotype (♂) NAN0650: BL = 27.80, CW = 4.31, IW = 2.95, ISW = 1.02, B10W = 5.06, B10H = 2.69. **Color.** Color in life unknown, but specimen with typical bimaculate pattern, faded in alcohol. **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 34A–C). Acropodite with gently undulating twist at apical bend (Fig. 34C). Acropodite medial flange lobed, small, with a large, dorsal triangular projection (Fig. 34C). Acropodite tip medial and lateral flanges absent. Acropodite tip entire, with a small preapical bump, and directed caudally (Fig. 34A). Prefemoral process acicular, mostly straight but with a slight curve basally (Fig. 34A). Prefemoral process tip directed cephalically (Fig. 34A).

Variation. No noticeable variation observed.

Distribution. *Nannaria paraptoma* sp. nov. is only known from a small area of Pocahontas County, West Virginia and Bath County, Virginia (Fig. 51).

Ecological notes. The label data from the collected specimens do not provide any notes on the habitat, but on a collecting trip to the type locality to search for live individuals by DAH and PEM, the habitat was found to be a mesic oak, hickory, tuliptree, and hemlock forest dissected by streams down in a holler, with an elevation of 840 m.

Etymology. The specific name is a noun in apposition and derives from the Greek word *paraptoma*, meaning false step or slip. This is in reference to the holotype having been collected from a pitfall trap.

Nannaria rhododendra sp. nov.

http://zoobank.org/2415F648-DC81-4793-AECD-384BBD17A3D5
Vernacular name: The Rhododendron Twisted-Claw Millipede
Figs 35, 36

Material examined. Type material: *Holotype*: United States – **Georgia** • ♂; Towns County, Hiawassee: Long Ridge Campground, Harris Cove, off Burch Branch Road; 34.9256°N, -83.7776°W, ±6m; elev. 647 m; 15 October 2018; D. A. Hennen leg.; moist litter and soil in rhododendron, mountain laurel, tuliptree, beech forest near stream; VTEC, MPE04401. ***Paratypes*:** United States – **Georgia** • 1 ♂ and 1 ♀; same collection data as for holotype; VTEC, MPE04796, MPE04399 • 1 ♂; Towns County, Harris Cove, 3 miles SW of Hiawassee; 34.9218°N, -83.7770°W, ±2000m; 1 November 1981; R. L. Hoffman leg.; VMNH, NAN0210. **Non type material:** United States – **Georgia** • 3 ♂♂; Lumpkin County, Chattahoochee NF, Woody Gap Rec Area; 34.675°N, -84.0015°W, ± 9m; elev. 977 m; 14 October 2018; D. A. Hennen leg.; VTEC, MPE04342, MPE04343, MPE04344 • 2 ♂♂; Lumpkin County, Chattahoochee NF, DeSoto Falls Rec Area, Lower Falls Trail; 34.7078°N, -83.915°W, ± 8m; elev. 633 m; 14 October 2018; D. A. Hennen leg.; VTEC, MPE04363, MPE04364 • 2 ♂♂; Towns County, Harris Cove, 2 mi. SW of Hiawassee; 34.9218°N, -83.777°W, ± 2000m; 14 October 1978; R. L. Hoffman leg.; VMNH, NAN0211 • 2 ♀♀; Towns County, Hiawassee: Long Ridge Campground, Harris Cove, off Burch Branch Road; 34.9256°N, -83.7776°W, ± 6m; elev. 647 m; 15 October 2018; D. A. Hennen leg.; VTEC, MPE04400, MPE04799 • 1 ♂ and 1 ♀; Towns County, Hiawassee: Towns County Park; 34.9688°N, -83.7733°W, ± 9m; elev. 610 m; 15 October 2018; D. A. Hennen leg.; VTEC, MPE04336, MPE04337 • 1 ♂ and 5 ♀♀; Towns County, Young Harris: Brasstown Valley Resort, Lodge Connector Trail to Miller Trek; 34.9538°N, -83.8359°W, ± 7m; elev. 670 m; 15 October 2018; D. A. Hennen

Figure 35. *Nannaria rhododendra* sp. nov., in situ, female paratype (MPE04399) from Towns County, Georgia.

leg.; VTEC, MPE04348, MPE04349, MPE04350, MPE04351, MPE04352, MPE04353. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria rhododendra* sp. nov. can be separated from the geographically close and morphologically similar species *N. amicalola* sp. nov. and *N. antarctica* sp. nov. by the following characters. Acropodite tip medial flange produced into a recurved lobe, not laminate and giving the acropodite the appearance of being bifurcate, as in *N. antarctica* sp. nov. Prefemoral process sinuously tapered and curving, rather than erect and laminate as in *N. amicalola* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE04401 and paratype (♀) MPE04399.

Measurements: Taken from holotype (♂) MPE04401: BL = 20.20, CW = 3.10, IW = 2.38, ISW = 0.78, B10W = 3.80, B10H = 2.63. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 35). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 36A–C). Acropodite with a smoothly undulating twist at acropodite bend

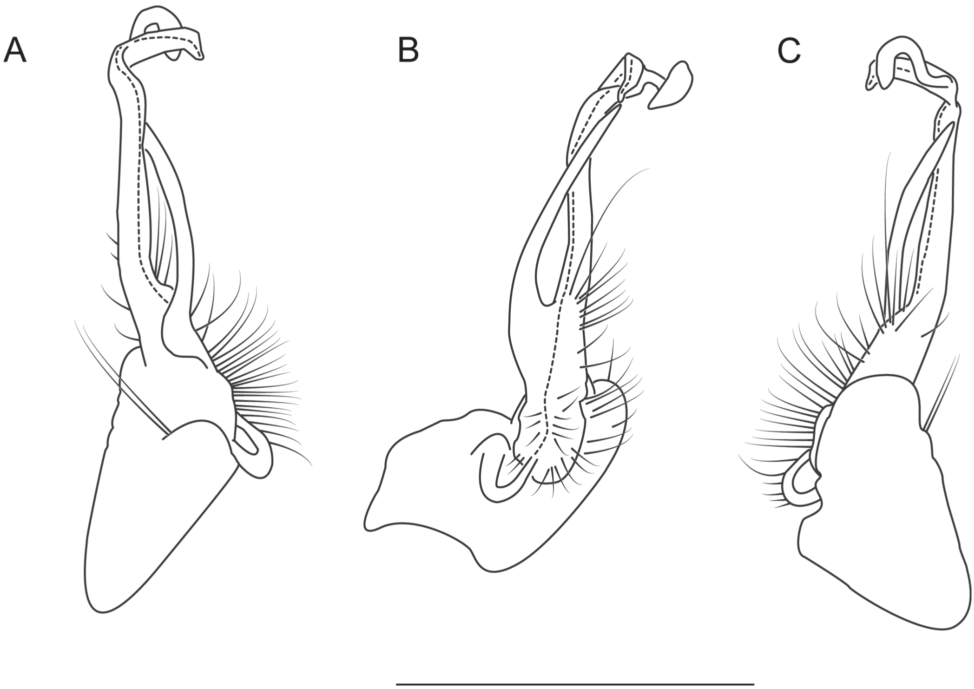

Figure 36. Left gonopod of *Nannaria rhododendra* sp. nov., male holotype (MPE04401, Towns County, Georgia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

(Fig. 36A). Acropodite medial flange slightly lobed (Fig. 36B, C). Acropodite tip medial flange produced into a recurved lobe with a rounded tip and shaped like a rabbit ear (Fig. 36C). Acropodite tip lateral flange slightly lobed before acropodite (Fig. 36A). Acropodite tip blunt, tapering; directed caudally (Fig. 36B). Prefemoral process sinuously tapered, thicker at base (Fig. 36A). Prefemoral process curving laterally (Fig. 36A). Prefemoral process crossing acropodite ventrolaterally; tip directed laterally (Fig. 36B). **Cyphopods.** Female cyphopod receptacle in the shape of a finger-like projection, curving over cyphopod valves and tapering distally.

Variation. No noticeable variation observed.

Distribution. *Nannaria rhododendra* sp. nov. is known from two counties in northern Georgia: Towns and Lumpkin (Fig. 52).

Ecological notes. This species has been collected both in dry and moist situations, ranging from upland oak-hickory forest to riparian cove forests of rhododendron and hemlock. Elevations at collecting localities are between 610 and 977 m.

Etymology. The specific name is a feminine adjective derived from the Greek words *rhodon*, meaning rose, and *dendron*, meaning tree. The species is named for the ericaceous plant genus *Rhododendron* L., which commonly grows in areas where *Nannaria* is found and was abundant at the type locality of *N. rhododendra*.

Nannaria scutellaria **Causey, 1942**
Vernacular name: The Smoky Mountains Twisted-Claw Millipede
Figs 37, 38

Nannaria scutellaria Causey, 1942: 168, figs 6, 7. Causey 1950: 198, figs 1–6. Chamberlin and Hoffman 1958: 41. Wray 1967: 152. Hoffman 1999: 367 (352 in pdf version). Shelley 2000: 197. Means et al. 2021a: S69, fig. 3.

Type material. ***Holotype*:** United States – **Tennessee** • ♂; Sevier County, Great Smoky Mountains National Park, near Chimneys; 35.6369°N, -83.4883°W, ±1000 m; 21 June 1940; N. B. Causey leg.; ANSP; (non vidi). ***Paratype*:** United States – **Tennessee** • 1 ♀; same collection data as for holotype; FSCA; (non vidi). The paratype was retained in Causey's personal collection (Causey 1942), now at the FSCA, where Causey's collection was transferred after her death.

Material examined. Non type material: United States – **North Carolina** • 1 ♀; Clay County, Fires Creek Campground, ca 1.1 mi N Mission Dam Rd on Fires Creek Rd (Fires Creek Wildlife Area), trail due north of parking area; 35.0882°N, -83.866°W; elev. 550 m; 19 April 2003; B. E. Hendrixson leg.; VTEC, MPE03745 • 10 specimens; Haywood County, Great Smoky Mountains National Park: ATBI Plot, Cataloochee; 35.5844°N, -83.0815°W, ± 300m; 15 November 2000; I. C. Stocks leg.; GRSM • 1 specimen; same collection data as for preceding; 30 November 2000; GRSM • 2 specimens; same collection data as for preceding; 10 October 2001; GRSM • 13 specimens; same collection data as for preceding; 26 October 2001; GRSM • 13 specimens; Transylvania County, Pisgah NF, Daniel Ridge Falls aka Jackson Falls Trail; 35.2851°N, -82.8286°W, ± 6m; elev. 818 m; 12 October 2018; D. A. Hennen leg.; VTEC,

Figure 37. *Nannaria scutellaria,* in situ, male (MPE04346) from Transylvania County, North Carolina.

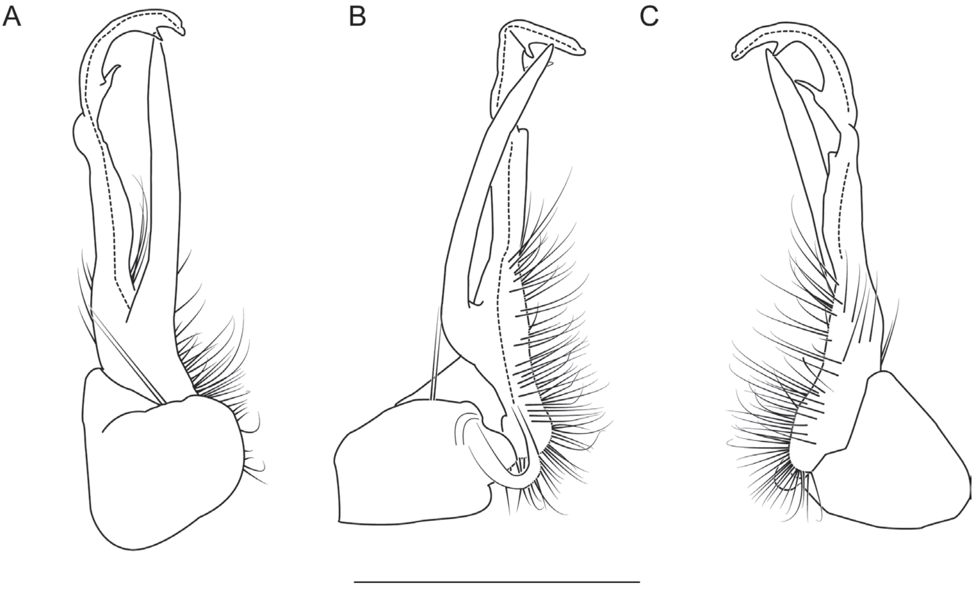

Figure 38. Left gonopod of *Nannaria scutellaria* (MPE01474, Sevier County, Tennessee) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

MPE04346; **Tennessee** • 2 specimens; Cocke County, Great Smoky Mountains National Park: ATBI Plot, Albright Grove; 35.7314°N, -83.2806°W, ± 300m; 14 November 2000; I. C. Stocks leg.; GRSM • 1 specimen; same collection data as for preceding; 9 May 2001; M. McCord leg.; GRSM • 1 specimen; same collection data as for preceding; 6 July 2001; GRSM • 1 specimen; same collection data as for preceding; 22 May 2001; I. C. Stocks, M. Williams leg.; GRSM • 1 ♂;
Cocke County, Cosby Picnic Area and Trail, GSMNP; 35.757°N, -83.2087°W; 18 May 1978; R. M. Shelley, W. B. J. leg.; NCSM, NAN0483 • 1 ♂; Cocke County, Brushy Mtn ATBI plot, pitfall 46; 35.8512°N, -82.9468°W, ± 5000m; 15 to 30 November 2000; Parker, et al. leg.; VMNH, NAN0371 • 1 specimen; Sevier County, Great Smoky Mtns. Natl. Park, Cades Cove; 35.58°N, -83.84°W, ± 3000m; 13 September 1953; D. H. Kistner leg.; FMNH, FMNHINS 0000 002 102 • 2 specimens; Sevier County, Great Smoky Mtns. Natl. Park, Greenbriar Cove; 35.7°N, -83.38°W, ± 2000m; elev. 610 m; 17 September 1946; H. S. Dybas leg.; FMNH, FMNHINS 0000 002 106 • 2 specimens; Sevier County, Great Smoky Mountains National Park: ATBI Plot, Goshen Prong; 35.6088°N, -83.5427°W, ± 300m; 10 November 2000; I. C. Stocks leg.; GRSM • 1 specimen; same collection data as for preceding; 28 November 2000; GRSM • 1 specimen; same collection data as for preceding; 26 February 2001; GRSM • 1 specimen; same collection data as for preceding; 2 July 2001; GRSM • 1 specimen; same collection data as for preceding; 17 September 2001; GRSM • 4 specimens; same collection data as for preceding; 22 October 2001; GRSM • 3 specimens; same collection data as for preceding; 5 November 2001; GRSM • 8 speci-

mens; same collection data as for preceding; 5 December 2001; GRSM • 4 specimens; same collection data as for preceding; 15 October 2002; GRSM • 5 specimens; same collection data as for preceding; 21 November 2002; GRSM • 1 specimen; same collection data as for preceding; 27 April 2001; I. C. Stocks, J. Breeden leg.; GRSM • 1 specimen; same collection data as for preceding; 7 June 2001; I. C. Stocks, M. Butler leg.; GRSM • 2 specimens; same collection data as for preceding; 18 December 2001; C. R. Parker leg.; GRSM • 1 specimen; same collection data as for preceding; 10 February 2002; D. Stair leg.; GRSM • 3 specimens; same collection data as for preceding; 1 April 2002; I. C. Stocks, R. Saczawa, D. Fowler leg.; GRSM • 1 specimen; same collection data as for preceding; 11 April 2002; J. Saczawa, R. Saczawa leg.; GRSM • 1 specimen; same collection data as for preceding; 25 April 2002; GRSM • 1 specimen; same collection data as for preceding; 23 May 2002; GRSM • 1 specimen; same collection data as for preceding; 19 August 2002; GRSM • 1 specimen; same collection data as for preceding; 20 December 2002; I. C. Stocks, G. Graves leg.; GRSM • 1 specimen; Sevier County, Great Smoky Mountains National Park: ATBI Plot, Twin Creeks; 35.6841°N, -83.4994°W, ± 300m; 15 October 2001; I. C. Stocks leg.; GRSM • 2 specimens; same collection data as for preceding; 5 November 2001; GRSM • 1 specimen; same collection data as for preceding; 5 December 2001; GRSM • 1 specimen; same collection data as for preceding; 21 June 2002; B. Merritt leg.; GRSM • 1 specimen; same collection data as for preceding; 16 July 2002; GRSM • 8 specimens; Sevier County, Camping area on Greenbrier Rd.; 35.7119°N, -83.3839°W, ± 5000m; 30 August 1961; VMNH, NAN0195 • 2 ♂♂ and 1 ♀; Sevier County, Chimneys; 35.637°N, -83.4882°W, ± 500m; 28 July 1949; R. L. Hoffman leg.; VMNH, NAN0372 • 1 ♂; Sevier County, Great Smoky Mountains National Park, Chimneys Picnic Area, Cove Hardwood Trail; 35.6360°N, -83.4937°W, ±7m; elev. 877 m; 8 June 2016; D. A. Hennen, J. C. Means leg.; along trail, moist hemlock, oak, maple, tuliptree litter; VTEC, MPE01474. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria scutellaria* can be separated from the geographically close and morphologically similar species *N. antarctica* sp. nov. and *N. austricola* by the following characters. Acropodite with a thin, triangular medial flange, rather than lobed and slightly expanded as in *N. austricola*. Acropodite tip undivided, not bifurcate as in *N. antarctica* sp. nov.

Description. Suppl. material 2. Based on (♂) MPE01474 and (♀) MPE01480.

Measurements: Taken from (♂) specimen MPE01474: BL = 29.70, CW = 3.08, IW = 2.54, ISW = 0.81, B10W = 3.92, B10H = 2.64. **Color.** Tergites with two paranotal pink to red spots, collum outlined in pink, and tergites with background chestnut brown to black (Fig. 37). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 38A–C). Acropodite anterior bend with acute twist, a scooped-out area visible in posterior view (Fig. 38C). Acropodite medial flange a thin, tooth-like, triangular projection (Fig. 38C). Acropodite tip medial flange a medium-sized triangular process (Fig. 38C). Acropodite tip lateral flange absent. Acropodite tip undivided, curving, and directed ventrally. Prefemoral process with a sinuous taper, thicker at base and curving slightly laterally, crossing acropodite ventrolaterally (Fig. 38A). **Cyphopods.** Female cyphopod receptacle in the shape of an enlarged and elongated club.

Variation. *Nannaria scutellaria* has a large amount of gonopodal variation, as documented by Causey (1950b). Her study included males from localities within the Great Smoky Mountains National Park and showed variation in the shape of the acropodite medial flange and number of subterminal teeth (acropodite tip medial flange) near the tip of the acropodite, as well as the shape of the acropodite tip. Additionally, males examined for this study from across the distribution of *N. scutellaria* exhibited a large amount of variation in the processes on the distal portion of the acropodite, and this variation may indicate that *N. scutellaria* is a cryptic species complex. The observed variation included specimens that have a very long acropodite medial flange and lack an acropodite tip medial flange entirely (NAN0077, Transylvania County, North Carolina), specimens with a typical morphology as illustrated in Fig. 38, with an acropodite medial flange and acropodite tip medial flange (NAN0368, Jackson County, North Carolina), and in one case, a specimen with a laminate acropodite tip medial flange, giving the acropodite tip a leaf-like appearance (NAN0369, Swain County, North Carolina). However, without more specimens available for genetic analysis, splitting *N. scutellaria* would be ill-advised, and all of these variable forms are included within this species.

Distribution. The distribution of *Nannaria scutellaria* straddles the border between Tennessee and North Carolina in the southern Appalachian Mountains, and is known from the following counties: (Tennessee) Blount, Cocke, and Sevier; (North Carolina) Jackson, Haywood, Swain, and Transylvania (Fig. 52).

Ecological notes. *Nannaria scutellaria* has been collected mostly from moist mixed oak, maple, tuliptree, hemlock, and rhododendron forests. It has been found at elevations between 610 m and 1918 m.

Etymology. Causey (1942) did not specify the precise meaning of the specific epithet, but it derives from the Latin word *scutella*, meaning a small dish or platter.

Nannaria shenandoa Hoffman, 1949

Vernacular name: The Shenandoah Twisted-Claw Millipede
Figs 39, 40

Nannaria shenandoa Hoffman, 1949a: 82, figs 1–4. Chamberlin and Hoffman 1958: 41. Hoffman 1999: 368 (352 in pdf version). Means et al. 2021a: S69. Means et al. 2021b: 9, fig. 4E.

Type material. ***Holotype***: United States – **Virginia** • ♂; Rockingham County, Shenandoah Mountain, about 15 miles [24.1 km] west of Harrisonburg; 38.57°N, -79.16°W, ± 2000m; elev. ca. 1067 m; 3 July 1948; R. L. Hoffman leg.; Habitat at the type locality was a "rather dry stand of *Quercus* (*Q. alba* and related species) with undergrowth mainly scrub oak and laurel (*Kalmia latifolia*)" on loose sandstone (Hoffman 1949a); USNM Entomology, no. 1848; (non vidi). ***Paratypes***: United

States – **Virginia** • 1 ♂ and 1 ♀; same collection data as for holotype; USNM Entomology, no. 1848 (non vidi). • 2 ♂♂ and 2 ♀♀; same collection data as for holotype; 4 July 1948; VMNH, NAN0067 (vidi). Four paratypes from the same locality were retained in Hoffman's personal collection (Hoffman 1949a), with catalog number RLH no. 160. The VMNH specimen lot NAN0067 is labeled "PARATYPE" and matches this description.

Material examined. Non type material: United States – **Kentucky** • 1 ♂; Powell County, Slade: Natural Bridge State Park, Original Trail; 37.7748°N, -83.6825°W, ± 7m; elev. 325 m; 25 September 2017; D. A. Hennen, J. C. Means leg.; VTEC, MPE03104; **Virginia** • 2 specimens; Augusta County, DF site off FS 85, ca 3 mi. NE of jct. with FS 95, Shenandoah Mt.; 38.4306°N, -79.2743°W, ± 3000m; 17 June 1988; K. A. Buhlmann leg.; VMNH, NAN0064 • 1 ♂; Rockingham County, Shenandoah Mt.; 38.57°N, -79.16°W, ± 5000m; 4 April 1948; MCZ, 87616 • 1 ♂; Rockingham County, Tomahawk Mtn., ca 7 mi NNW Rawley Springs, DF site off FS 72; 38.599°N, -79.1062°W, ± 5335m; elev. 1006 m; 19 November 1988; K. A. Buhlmann leg.; VMNH, NAN0065 • 2 ♂♂; same collection data as for preceding; 17 June 1988; VMNH, NAN0066 • 6 specimens; same collection data as for preceding; 28 May 1988; VMNH, NAN0068 • 2 specimens; Rockingham County, Grottoes; 38.2576°N, -78.7664°W, ± 5000m; 20 April 1950; R. L. Hoffman leg.; VMNH, NAN0408 • 4 ♂♂; Rockingham County, Shenandoah Mountain, DF site off Va. 924, ca. 0.5 mi. E of WVA state line, jct with FS 85; 38.7879°N, -79.0418°W, ± 2000m; 17 June 1988; K. A. Buhlmann leg.; VMNH, NAN0670 • 1 specimen; Shenandoah County, George Washington National Forest near New Market off Rt. 211 on Rd 274 (Massanutten Visitors Center); 38.6531°N, -78.6033°W, ± 2000m; 26 April 1975; T. Eisner leg.; VMNH, NAN0402 • 1 ♂; Shenandoah County, Passage Creek Gorge ~ 2 mi S jct of Rte 678 and VA-55; 38.9407°N, -78.3058°W; 4 May 2018; C. W. Harden leg.; VTEC, MPE03994 **West Virginia** • 8 specimens; Greenbrier County, Droop Mountain Battlefield State Park; 38.1119°N, -80.2716°W, ± 2289m; 23 June 1968; R. L. Hoffman leg.; VMNH, NAN0216 • 1 ♂; Marion County, Palatine: Bunner's Ridge; 39.4369°N, -79.9852°W; 10 October 2014; M. Kasson leg.; VTEC, MPE00231 • 77 specimens; Pocahontas County, Droop Mtn State Park; 38.1137°N, -80.2653°W, ± 3000m; elev. 933 m; 30 April 1972; W. A. Shear leg.; VMNH, NAN0198, NAN0199 • 10 specimens; Pocahontas County, Droop Mountain Battlefield State Park; 38.1119°N, -80.2716°W, ± 2289m; 17 October 1971; R. L. Hoffman, L. S. Knight leg.; VMNH, NAN0215 • 2 specimens; Preston County, Terra Alta; 39.4455°N, -79.5466°W, ± 1876m; 26 June 1971; W. A. Shear leg.; VMNH, NAN0069. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria shenandoa* can be separated from the geographically close and morphologically similar species *N. morrisoni* and *N. spiralis* sp. nov. by the following characters. Acropodite bifurcate, with acropodite tip medial flange lobed and expanded into another branch, rather than acropodite entire as in *N. spiralis* sp. nov. Tips of acropodite directed caudally, rather than medially as in *N. morrisoni*. Prefemoral process curving laterally, rather than acicular as in *N. morrisoni* or sinuously tapering as in *N. spiralis* sp. nov.

Figure 39. *Nannaria shenandoa,* in situ, male (MPE00231) from Marion County, West Virginia.

Description. Suppl. material 2. Based on (♂) MPE03994 and (♀) NAN0067.

Measurements: Taken from (♂) specimen MPE03994: BL = 27.95, CW = 3.46, IW = 2.51, ISW = 0.85, B10W = 4.25, B10H = 2.70. **Color.** Tergites with two paranotal peach-pink spots, collum outlined in peach, and tergites with background olive-brown (Fig. 39). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 40A–C). Acropodite medial flange absent. Acropodite tip medial flange lobed, giving acropodite tip a bifurcate appearance (Fig. 40C). Acropodite tip lateral flange absent. Acropodite lacking an obvious twist at anterior bend. Prefemoral process simple, curving laterally (Fig. 40A). Prefemoral process tip crossing acropodite ventrolaterally; tip directed dorsally. **Cyphopods.** Female cyphopod receptacle enlarged into a triangular hood, covering cyphopod valves.

Variation. No notable variation was observed between specimens.

Distribution. The distribution of *Nannaria shenandoa* extends across eastern West Virginia into northwestern Virginia and includes the following counties: (West Virginia) Marion, Preston, Pocahontas, Greenbrier; (Virginia) Augusta, Rockingham, Shenandoah (Fig. 51). Additionally, one male specimen was collected from Natural Bridge State Park in Powell County, Kentucky, which appears morphologically identical to the specimens from West Virginia and Virginia; genetically, it is located in the same group as the other *N. shenandoa* specimens, and so is included here. Further study may reveal either a larger distribution than is currently known, connecting the Kentucky population with the West Virginia population, or a cryptic species complex within *N. shenandoa*.

Ecological notes. Label information for *Nannaria shenandoa* notes the species has been collected in mixed deciduous forests of oak, maple, and tuliptree, along with hemlock and rhododendron forests. It ranges in elevation from 325 m to 1006 m.

Etymology. This species is named after its type locality, Shenandoah Mountain in Rockingham County, Virginia.

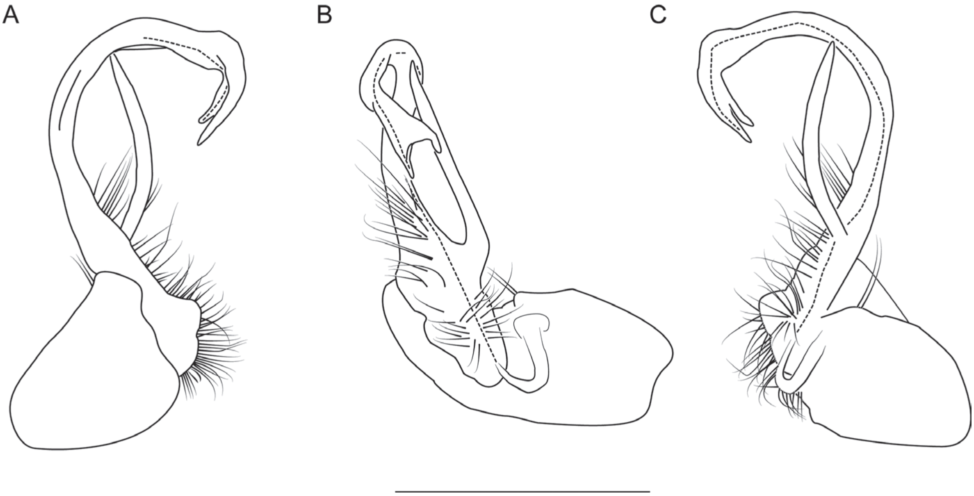

Figure 40. Left gonopod of *Nannaria shenandoa* (MPE03994, Shenandoah County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Nannaria spalax **sp. nov.**
http://zoobank.org/12995EEE-4A07-499C-9D79-1A3BE3302848
Vernacular name: The Mole Twisted-Claw Millipede
Figs 41, 42

Material examined. Type material: *Holotype*: United States – **Georgia** • ♂; Rabun County, Clayton: Chattahoochee National Forest, Warwoman Dell Recreation Area, nature trail near picnic area; 34.8813°N, -83.3539°W, ±8m; elev. 644 m; 13 October 2018; D. A. Hennen leg.; buried in dark sandy soil in patch of beech, tuliptree, rhododendron woods; VTEC, MPE04377. ***Paratypes*:** United States – **Georgia** • 2 ♂♂; same collection data as for holotype; VTEC, MPE04378, MPE04388). Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria spalax* sp. nov. can be separated from the geographically close and morphologically similar species *N. antarctica* sp. nov. and *N. nessa* sp. nov. by the following characters. Acropodite medial flange laminate, rather than lobed as in *N. nessa* sp. nov. Acropodite tip lateral flange a projecting lobe, making the acropodite appear distally bilobed, but not deeply bifurcate as in *N. antarctica* sp. nov. Prefemoral process laminate and curving medially, with medial margin jagged, rather than notched at midpoint as in *N. nessa* sp. nov. or curving laterally as in *N. antarctica* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE04377. Female morphology unknown.

Measurements: Taken from holotype (♂) MPE04377: BL = 26.30, CW = 3.70, IW = 2.88, ISW = 0.92, B10W = 4.50, B10H = 2.40. **Color.** Tergites with two paranotal red spots, collum outlined in red, and tergites with background black (Fig. 41). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally

Figure 41. *Nannaria spalax* sp. nov., in situ, male holotype (MPE04377) from Rabun County, Georgia.

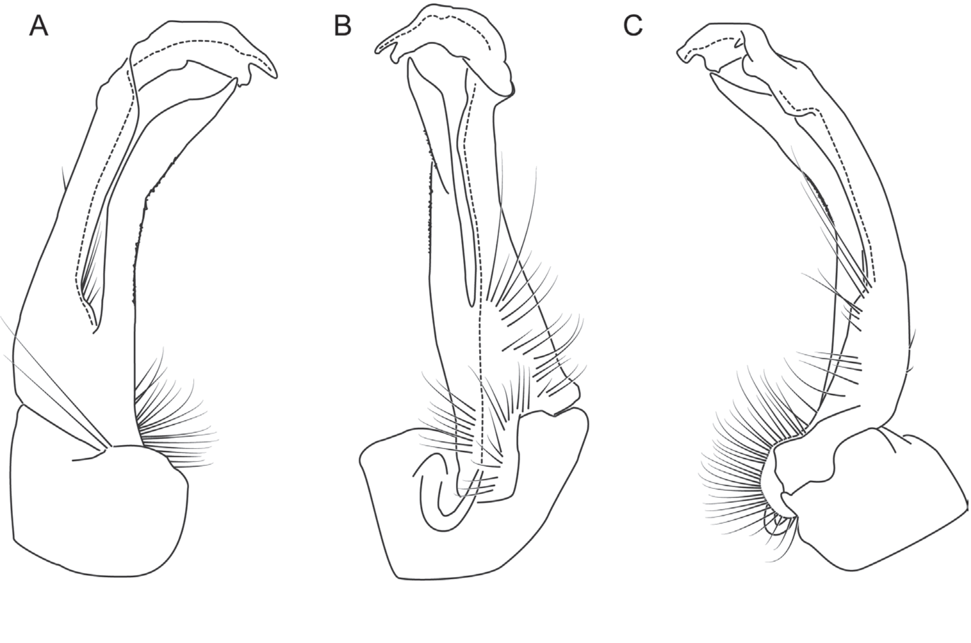

Figure 42. Left gonopod of *Nannaria spalax* sp. nov., male holotype (MPE04377, Rabun County, Georgia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

(Fig. 42A–C). Acropodite with wide, acute twist at anterior bend, giving the acropodite a folded appearance (Fig. 42A). Acropodite medial flange laminate and slightly undulating (Fig. 42C). Acropodite tip medial flange a short, triangular projection (Fig. 42C). Acropodite tip lateral flange a projecting lobe (Fig. 42A). Acropodite tip directed medially and bilobed distally, with a dorsal sharp, tapering, horn-like process and a shorter ventral rounded process (Fig. 42A, B). Prefemoral process laminate, curving medially (Fig. 42A). Prefemoral process with a slight taper distally, tip directed cephalically. Medial margin of prefemoral process somewhat jagged (Fig. 42A).

Variation. Acropodite medial flange size varies from small to large. No other noticeable variation observed.

Distribution. *Nannaria spalax* sp. nov. is only known from the type locality in Rabun County, Georgia (Fig. 52).

Ecological notes. Specimens were found buried 3–5 cm in sandy soil near a stream in a cove forest of beech, tuliptree, and rhododendron.

Etymology. The specific name is a noun in apposition derived from the Greek word *spalax*, meaning mole. The name references the mole-like digging behavior of this species, as only three specimens were collected at the type locality, and all were well-buried in the soil.

Nannaria spiralis sp. nov.

http://zoobank.org/119628C6-23BC-4A6A-BD47-89DE9F3A156F
Vernacular name: The Spiral Twisted-Claw Millipede
Figs 43, 44

Material examined. Type material: *Holotype*: United States – **West Virginia** • ♂; Pendleton County, Brandywine Recreation Area, behind campsite 20, George Washington National Forest; 38.5948°N, -79.1982°W, ±5m; elev. 619 m; 21 June 2016; D. A. Hennen, J. C. Means leg.; moist deciduous litter (oak, maple, hickory) near stream; VTEC, MPE02109. ***Paratypes*:** United States – **West Virginia** • 1 ♂ and 1♀; same collection data as for holotype; VTEC, MPE02111, MPE02112; **Virginia** • 1 ♂; Rockingham County, Tomahawk Mountain, ca. 7 mi NNW Rawley Springs, DF site off FS 72; 38.6234°N, -79.0726°W, ±5000 m; elev. 1006 m; 28 May 1988; K. A. Buhlmann leg.; VMNH, NAN0107. **Non type material:** United States – **Virginia** • 1 ♂; Augusta County, 5 mi W Stokesville, comp. 452-8A, trap 2; 38.3524°N, -79.2416°W, ± 2000m; 23 April 1989; B. Flamm leg.; VMNH, NAN0099 • 5 specimens; Augusta County, GWNF, 5 miles west of Stokesville Comp.: 452-8A Trap 3; 38.3524°N, -79.2416°W, ± 2000m; 12 November 1988; B. Flamm leg.; VMNH, NAN0100 • 7 specimens; Augusta County, 5 mi W Stokesville, comp. 452-6 trap 3; 38.3524°N, -79.2416°W, ± 2000m; 12 November 1988; B. Flamm leg.; VMNH, NAN0101 • 17 specimens; same collection data as for preceding; 24 April 1989; VMNH, NAN0102 • 2 specimens; Augusta County, 5 miles W of Stokesville, GWNF comp. 453-1B trap 3; 38.3524°N, -79.2416°W, ± 2000m; 12 November 1988; B. Flamm leg.; VMNH, NAN0103 •

Figure 43. *Nannaria spiralis* sp. nov., in situ, male holotype (MPE02109) from Pendleton County, West Virginia.

3 specimens; Augusta County, GWNF, ca. 5 miles west of Stokesville Comp. 453-1A, Trap 2; 38.3524°N, -79.2416°W, ± 2000m; 12 November 1988; B. Flamm leg.; VMNH, NAN0104 • 2 specimens; Augusta County, 5 miles W of Stokesville: GWNF comp. 452-6, trap 3; 38.3524°N, -79.2416°W, ± 2000m; 2 September 1989; B. Flamm leg.; VMNH, NAN0105 • 4 specimens; Augusta County, DF site off FS 85, 3 km NE jct. FS 95, Shenandoah Mtn.; 38.4306°N, -79.2743°W, ± 3000m; 28 May 1988; K. A. Buhlmann leg.; VMNH, NAN0106 • 1 specimen; Augusta County, 5 mi W Stokesville, comp. 460-12 trap 3; 38.3524°N, -79.2416°W, ± 2000m; 16 June 1989; B. Flamm leg.; VMNH, NAN0108 • 1 specimen; Augusta County, Shenandoah Mountain, Civil War Hist. site, US 250; 38.3113°N, -79.3842°W, ± 300m; 2 May 1991; C. A. Pague leg.; VMNH, NAN0109 • 1 specimen; Augusta County, 5 mi W Stokesville, comp. 460-5, trap 3; 38.3524°N, -79.2416°W, ± 2000m; 7 August 1989; B. Flamm leg.; VMNH, NAN0110 • 1 specimen; Augusta County, 5 mi W Stokesville, comp. 452-16, trap 2; 38.3524°N, -79.2416°W, ± 2000m; 15 October 1988; B. Flamm leg.; VMNH, NAN0111 • 1 specimen; Augusta County, 5 mi W Stokesville, comp. 452-6, trap 1; 38.3524°N, -79.2416°W, ± 2000m; 24 April 1989; B. Flamm leg.; VMNH, NAN0112 • 2 specimens; Augusta County, GWNF, 5 mi W of Stokesville, comp. 460-5, trap 1; 38.3524°N, -79.2416°W, ± 2000m; 8 July 1989; B. Flamm leg.; VMNH, NAN0113 • 1 specimen; Augusta County, 5 miles W of Stokesville: GWNF comp. 453-18, trap 3; 38.3524°N, -79.2416°W, ± 2000m; 15 October 1988; B. Flamm leg.; VMNH, NAN0114 • 3 specimens; Augusta County, GWNF, ca. 5 mi W of Stokesville, comp. 460-5, trap 1; 38.3524°N, -79.2416°W, ± 2000m; 18 May 1989; B. Flamm leg.; VMNH, NAN0116 • 1 specimen; Augusta County, Ramsey's

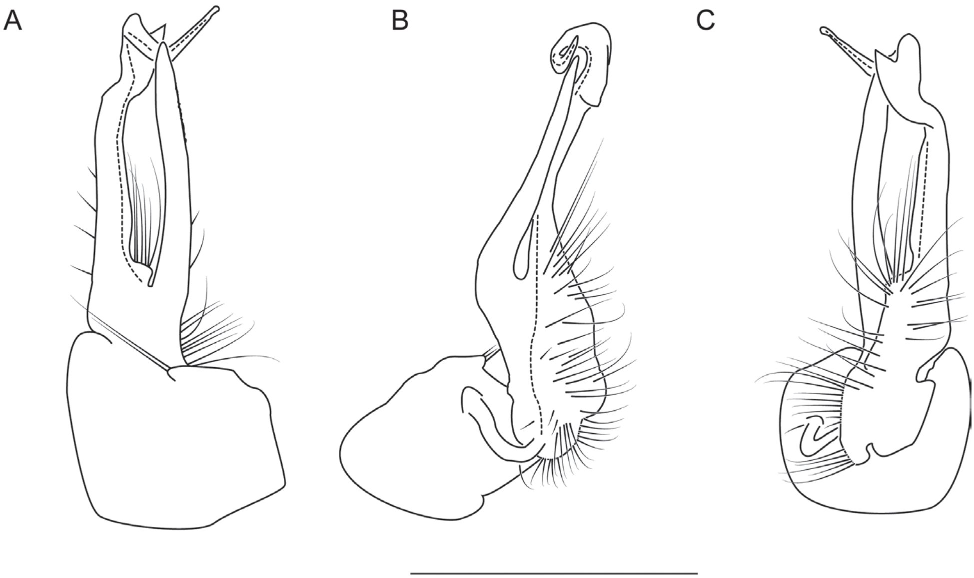

Figure 44. Left gonopod of *Nannaria spiralis* sp. nov. (MPE02111, Pendleton County, West Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Draft, 18 mi N of Staunton; 38.3121°N, -79.356°W, ± 10000m; 19 June 1969; W. A. Shear leg.; VMNH, NAN0118 • 6 specimens; Augusta County, GWNF, 5 mi W of Stokesville Comp. 452-6, Trap 3; 38.3524°N, -79.2416°W, ± 2000m; 17 September 1988; B. Flamm leg.; VMNH, NAN0119 • 1 specimen; Augusta County, GWNF, 5 mi W of Stokesville, comp. 460-12, trap 2; 38.3524°N, -79.2416°W, ± 2000m; 11 November 1988; B. Flamm leg.; VMNH, NAN0530 • 1 specimen; Augusta County, GWNF 460 - 12 T2; 38.3636°N, -79.2602°W, ± 2000m; 14 October 1988; VMNH, NAN0648 • 3 specimens; same collection data as for preceding; 22 December 1988; VMNH, NAN0660 • 1 specimen; Augusta County, GWNF 460 - 3, T1; 38.3658°N, -79.2513°W, ± 2000m; 11 November 1988; VMNH, NAN0649 • 1 specimen; Augusta County, GWNF 453 - 11, T2; 38.3633°N, -79.2382°W, ± 2000m; 12 December 1988; VMNH, NAN0661 • 2 specimens; Augusta County, GWNF 460 - 12 T2; 38.3636°N, -79.2602°W, ± 2000m; 23 April 1989; VMNH, NAN0662 • 5 specimens; Augusta County, GWNF 460 - 12, T3; 38.3636°N, -79.2602°W, ± 2000m; 23 April 1989; VMNH, NAN0652 • 6 specimens; same collection data as for preceding; 11 November 1988; VMNH, NAN0666 • 1 specimen; Highland County, Along US 220, ca. 2 mi. S of Monterey; 38.3882°N, -79.6011°W, ± 3000m; 31 May 1991; K. A. Buhlmann leg.; VMNH, NAN0115 • 1 ♂; Rockingham County, 2.3 km NW of Briery Branch, off Hone Quarry Rd, George Washington National Forest, Hidden Cliff Rocks Trail; 38.452°N, -79.1144°W, ± 5m; elev. 536 m; 24 May 2018; D. A. Hennen, J. C. Means leg.; VTEC, MPE04010; **West Virginia** • 2 ♂♂ and 5 ♀♀; Pendleton County, Brandywine Recreation Area, George Washington National Forest; 38.5948°N, -79.1982°W, ± 5m; elev. 619 m; 21 June 2016; J. C. Means, D. A. Hennen leg.;

VTEC, MPE03666, MPE03704, MPE01840, MPE01861, MPE02113, MPE02114, MPE02146. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria spiralis* sp. nov. can be separated from the geographically close and morphologically similar species *N. shenandoa* and *N. vellicata* sp. nov. by the following characters. Acropodite undivided, rather than bifurcate as in *N. shenandoa*. Acropodite tip medial flange broad, shield-shaped, rather than triangular with a laminate base as in *N. vellicata* sp. nov. Quadrate process present basomedially on acropodite.

Description. Suppl. material 2. Based on holotype (♂) MPE02109 and paratype (♀) MPE02112.

Measurements: Taken from holotype (♂) MPE02109: BL = 27.30, CW = 4.10, IW = 2.85, ISW = 0.96, B10W = 4.85, B10H = 2.70. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 43). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 44A–C). Acropodite with gently undulating twist at anterior bend (Fig. 44C). Acropodite medial flange absent. Acropodite tip medial flange broad and laminate, produced into a shield-shaped process with a sharp point (Fig. 44C). Acropodite tip lateral flange absent. Acropodite tip thin and pointed, acutely recurved (Fig. 44A); tip directed antero-medially. Acropodite with basomedial quadrate process (Fig. 44A). Prefemoral process sinuously tapered (Fig. 44B). Prefemoral process crossing acropodite dorsolaterally; tip directed cephalically (Fig. 44A). **Cyphopods.** Female cyphopod receptacle quadrate, recurved distally.

Variation. No noticeable variation was observed.

Distribution. *Nannaria spiralis* sp. nov. is known from Pendleton County, West Virginia, and the following adjacent Virginia counties: Augusta, Highland, and Rockingham (Fig. 51).

Ecological notes. This species has been found in mesic forests of oak, hickory, and maple, as well as in a rhododendron grove in a rhododendron, hemlock, and oak forest near a stream.

Etymology. This species is named for the spiraling morphology of the acropodite tip, best seen in medial view. The species name is a feminine adjective in the nominative singular, derived from the Latin word *spiralis*, meaning a coil or twist.

Nannaria swiftae sp. nov.

http://zoobank.org/BBF344F8-7FC3-49B2-AAE9-6E5CC30EEAF7
Vernacular name: The Swift Twisted-Claw Millipede
Figs 45, 46

Nannaria sp. nov. 'Cratagae': Means et al. 2021b: 111.

Material examined. Type material: *Holotype*: United States – **Tennessee** • ♂; Van Buren County, Fall Creek Falls State Park, Crane Creek Falls overlook; 35.6628°N,

Figure 45. *Nannaria swiftae* sp. nov., in situ, male holotype (MPE01222) from Van Buren County, Tennessee.

-85.3498°W, ±5m; elev. 483 m; 22 May 2016; J. C. Means, D. A. Hennen leg.; at base of witch hazel tree, in deciduous forest; VTEC, MPE01222. ***Paratypes*:** United States – **Tennessee** • 1 ♀; Van Buren County, Fall Creek Falls State Park, George's Hole area, hillside beside parking lot; 35.6612°N, -85.3464°W, ±7m; elev. 481 m; 22 May 2016; D. A. Hennen, J. C. Means leg.; moist hemlock, maple, tuliptree, oak, and pine litter; VTEC, MPE01226 • 3 ♂♂; Van Buren County, Fall Creek Falls State Park; 35.6561°N, -85.3478°W ±3000m; 13 May 1979; R. M. Shelley leg.; NCSM, NAN0190. **Non type material:** United States – **Tennessee** • 1 ♂ and 3 ♀♀; Cumberland County, Hwy 68, 9 air mi. SE Crossville; 35.8521°N, -84.9182°W; 8 May 1979; R. K. Tardell leg.; NCSM, NAN0457 • 1 ♂; Monroe County, Little Haw Knob; 35.315°N, -84.0361°W, ± 3000m; elev. 1539 m; 27 May 1958; L. Hubricht leg.; VMNH, NAN0189 • 2 ♀♀; Van Buren County, Fall Creek Falls State Park, George's hole area, hillside beside parking lot on both sides of road; 35.6612°N, -85.3464°W, ± 7m; elev. 481 m; 22 May 2016; J. C. Means, D. A. Hennen leg.; VTEC, MPE01268, MPE03713. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria swiftae* sp. nov. can be separated from the geographically close and morphologically similar species *N. austricola* and *N. scutellaria* by the following characters. Acropodite medial flange lobed and with two small bumps, not simply lobed as in *N. austricola* or with a thin, acuminate triangular process as in *N. scutellaria*. Acropodite tip medial flange absent, rather than lobed as in *N. austricola* or triangular as in *N. scutellaria*.

Description. Suppl. material 2. Based on holotype (♂) MPE01222 and paratype (♀) MPE01226.

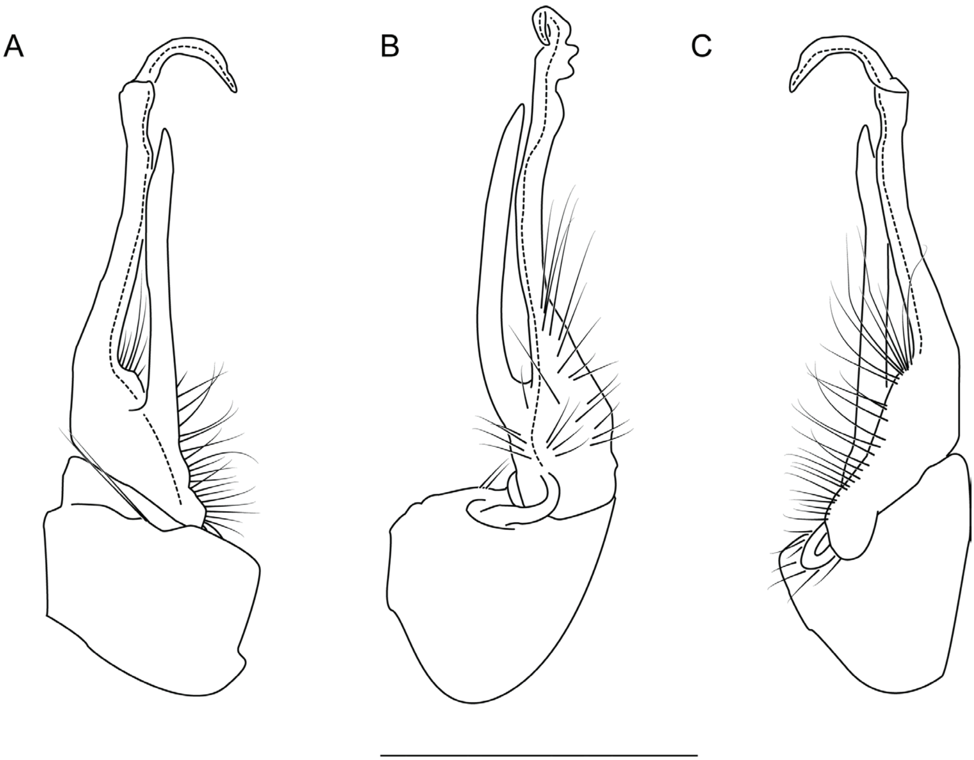

Figure 46. Left gonopod of *Nannaria swiftae* sp. nov., male holotype (MPE01222, Van Buren County, Tennessee) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Measurements: Taken from holotype (♂) MPE01222: BL = 22.40, CW = 3.50, IW = 2.50, ISW = 0.88, B10W = 4.35, B10H = 2.55. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 45). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 46A–C). Acropodite with acute twist at anterior bend, folding distal zone of acropodite (Fig. 46C). Acropodite medial flange lobed, with two small, rounded bumps visible in medial view (Fig. 46B). Acropodite tip medial and lateral flanges absent. Acropodite tip slightly tapering distally and directed medially (Fig. 46A). Acropodite with small basomedial quadrate process. Prefemoral process acicular (Fig. 46A). Prefemoral process tip directed cephalically. **Cyphopods.** Female cyphopod receptacle sinuous, blunt, and rounded distally.

Variation. No noticeable variation observed.

Distribution. *Nannaria swiftae* sp. nov. is only known from Tennessee and has been collected in the following counties: Cumberland, Monroe, and Van Buren (Fig. 52).

Ecological notes. This species has been collected in mesic forests with hemlock, maple, oak, tuliptree, witch hazel, and pine, at elevations ranging from 481 m to 1539 m.

Etymology. The specific name is a noun in the genitive case derived as a matronym, and is named in honor of the artist Taylor Swift, in recognition of her talent as a songwriter and performer and in appreciation of the enjoyment her music has brought DAH.

Nannaria vellicata **sp. nov.**
http://zoobank.org/F764E7D5-A1C2-4DBD-AC12-5818269A75AE
Vernacular name: The Misty Twisted-Claw Millipede
Figs 47, 48

Material examined. Type material: ***Holotype*****:** United States – **Virginia** • ♂; Augusta County, 4.9 km WNW Stokesville, 0.8 km SE Todd Lake Recreation Area, George Washington National Forest, Trimble Mountain Trail off Forest Road 95; 38.3605°N, -79.2048°W, ±9m; elev. 602 m; 24 June 2016; D. A. Hennen, J. C. Means leg.; moist oak, maple forest with scattered pines, on hillside by path; VTEC, MPE02060. ***Paratypes*****:** United States – **Virginia** • 1 ♂; Alleghany County, Griffith; 37.8658°N, -79.7269°W, ±3000m; 8 October 1949; R. L. Hoffman leg.; VMNH, NAN0054 • 1 ♀; Rockbridge County, 12.4 km SW Goshen along VA-780, George Washington National Forest beside Brattons Run; 37.9021°N, -79.5882°W, ±7m; elev. 571 m; 14 November 2017; D. A. Hennen, J. C. Means leg.; base of hillside beside stream in rhododendron and hemlock forest with moist sandy soil, in litter of tuliptree, rhododendron, hemlock, red oak; VTEC, MPE03629. **Non type material:** United States – **Virginia** • 2 ♂♂; Alleghany County, Griffith; 37.8658°N, -79.7269°W, ± 3000m; 5 April 1950; R. L. Hoffman leg.; VMNH, NAN0053 • 3 ♂♂ and 3♀♀; Rockbridge County, 12.4 km SW Goshen along VA-780, George Washington National Forest beside Brattons Run; 37.9021°N, -79.5882°W, ± 7m; elev. 571 m; 14 November 2017; J. C. Means, D. A. Hennen leg.; VTEC, MPE03492, MPE03628, MPE03631, MPE03630, MPE03632, MPE03633. Complete material examined information listed in Suppl. material 1.

Figure 47. *Nannaria vellicata* sp. nov., in situ, male holotype (MPE02060) from Augusta County, Virginia.

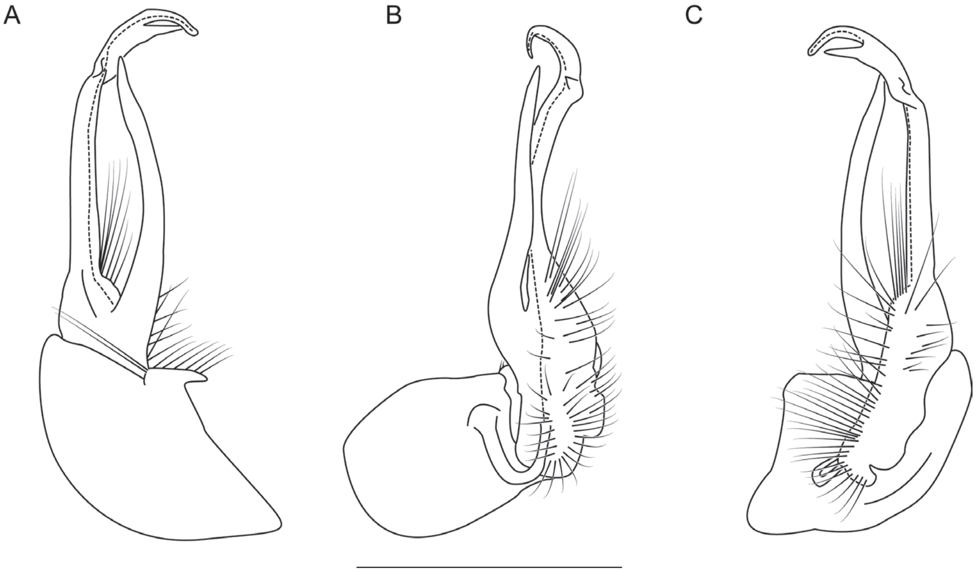

Figure 48. Left gonopod of *Nannaria vellicata* sp. nov., male holotype (MPE02060, Augusta County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

Diagnosis. Adults of *Nannaria vellicata* can be separated from the geographically close and morphologically similar species *N. orycta* sp. nov. and *N. spiralis* sp. nov. by the following characters. Acropodite anterior bend with a gentle twist, rather than acutely twisted as in *N. orycta* sp. nov. Acropodite tip medial flange triangular with a laminate base, rather than broad and shield-shaped as in *N. spiralis* sp. nov. Acropodite undivided distally, rather than bifurcate as in *N. orycta* sp. nov.

Description. Suppl. material 2. Based on holotype (♂) MPE02060 and paratype (♀) MPE03629.

Measurements: Taken from holotype (♂) MPE02060: BL = 23.50, CW = 4.20, IW = 2.82, ISW = 1.02, B10W = 5.00, B10H = 2.75. **Color.** Tergites with two paranotal orange spots, collum outlined in orange, and tergites with background chestnut brown (Fig. 47). **Gonopods.** Male gonopod acropodite arc straight, with abrupt bend distally (Fig. 48A–C). Acropodite anterior bend with gentle twist (Fig. 48A). Acropodite medial flange lobed (Fig. 48C). Acropodite tip medial flange triangular, extended and with a laminate base (Fig. 48C). Acropodite tip entire, directed medially and slightly curved ventrally (Fig. 48A, B). Acropodite tip lateral flange absent. Prefemoral process simple, curving laterally (Fig. 48A). Prefemoral process tip directed laterally. **Cyphopods.** Female cyphopod receptacle triangular.

Variation. No noticeable variation observed.

Distribution. *Nannaria vellicata* sp. nov. is known from three counties in Virginia: Alleghany, Augusta, and Rockbridge (Fig. 51).

Ecological notes. This species has been collected from both rhododendron-hemlock cove habitats and general mesic deciduous forests, at elevations between 571 m and 602 m.

Etymology. This species is named for the shape of the acropodite tip and medial flange, which together resemble a thumb and index finger in a pinching motion. The specific epithet is a feminine adjective derived from the Latin word *vellico*, meaning pinch.

***Nannaria wilsoni* Hoffman, 1949**

Vernacular name: The Wilson Twisted-Claw Millipede
Figs 49, 50

Nannaria wilsoni Hoffman, 1949b: 386, figs 15, 16. Chamberlin and Hoffman 1958: 42. Hoffman 1999: 368 (352 in pdf version). Means et al. 2021a: S70, fig. 3.

Type material. ***Holotype*:** United States – **Virginia** • ♂; Giles County, Mountain Lake Biological Station; 37.3769°N, -80.5227°W, ±1000 m; June and July 1947; Hobbs, Walton, Wilson leg.; USNM Entomology, no. 1808; (non vidi). ***Paratypes*:** United States – **Virginia** • 1 ♂; same collection data as for holotype; USNM Entomology, no. 1808; (non vidi) • 6 ♂♂; Giles County, Mountain Lake Biological Station; 37.3769°N,

Figure 49. *Nannaria wilsoni*, in situ, male (MPE02123) from Giles County, Virginia.

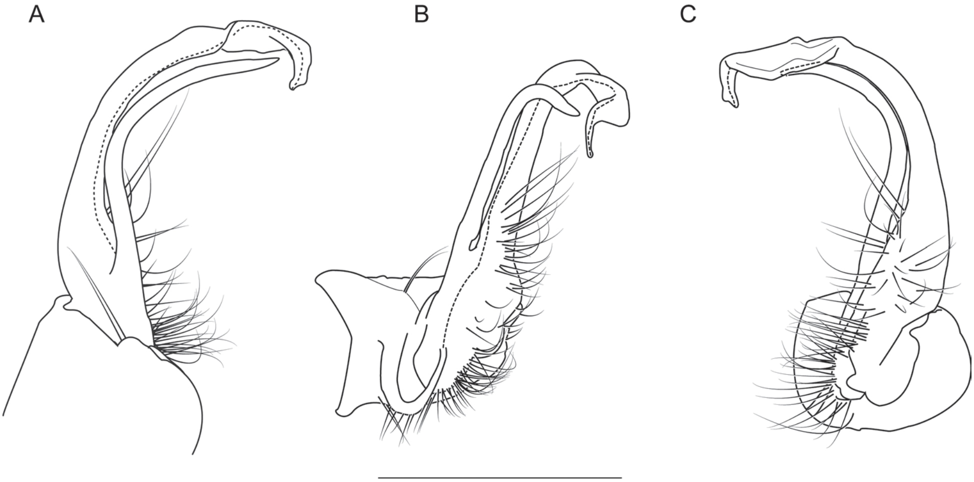

Figure 50. Left gonopod of *Nannaria wilsoni* (MPE02123, Giles County, Virginia) **A** anterior view **B** medial view **C** posterior view. Scale bar: 1 mm.

-80.5227°W, ±1000 m; Wilson, R. L. Hoffman leg.; 28 August 1947; VMNH, NAN0300 (vidi). Habitat at the type locality was a deciduous forest of oak, maple, and yellow poplar (tuliptree), with an undergrowth composed of ericaceous shrubs (Hoffman 1949b). In the original description of this species, Hoffman noted that he retained six "topoparatypes" in his personal collection (Hoffman 1949b). These specimens are VMNH lot NAN0300, a vial that contains six males in a jar labeled "PARATYPE."

Material examined. Non type material: United States – **Virginia** • 1 specimen; Giles County, Mt. Lake; 37.3769°N, -80.5227°W, ± 1000m; 27 August 1947; C. M. Wilson leg.; MCZ, 87614 • 1 specimen; Giles County, Mountain Lake Biological Station; 37.3743°N, -80.524°W, ± 2000m; W. A. Shear leg.; VMNH, NAN0035 • 1 specimen; same collection data as for preceding; 1 July 1936; P. R. Burch leg.; VMNH, NAN0299 • 4 specimens; Giles County, Cascades of Little Stony Creek; 37.3617°N, -80.5866°W, ± 5000m; 17 May 1961; R. L. Hoffman leg.; VMNH, NAN0301 • 1 ♀; Giles County, near Mountain Lake; 37.3743°N, -80.524°W, ± 5000m; 4 August 1963; Kosztarab leg.; VMNH, NAN0302 • 2 ♀♀; Giles County, gully off path in Mountain Lake Biological Station Wilderness, off road to Salt Pond Mountain; 37.3891°N, -80.5052°W; 1 May 2016; J. C. Means leg.; VTEC, MPE01149, MPE01150 • 3 ♂♂ and 3 ♀♀; Giles County, Mountain Lake Wilderness, near Mountain Lake Biological Station, on trail to War Spur Overlook, off Rt. 613; 37.3892°N, -80.5057°W; elev. 1125 m; 3 October 2016; J. C. Means, D. A. Hennen, V. Wong leg.; under moss at base of white oak tree, in deciduous woods of witch hazel, chestnut oak, white oak; VTEC, MPE02123, MPE02132, MPE02133, MPE02131, MPE02134, MPE02135 • 1 ♂; Giles County, Mountain Lake Biological Station Wilderness; 37.3751°N, -80.5218°W, ± 5000m; 2017; J. D. Montemayor leg.; VTEC, MPE02480 • 2 specimens; Montgomery County, Radford; 37.136°N, -80.5665°W, ± 5000m; 1 October 1937; P. R. Burch leg.; VMNH, NAN0297. Complete material examined information listed in Suppl. material 1.

Diagnosis. Adults of *Nannaria wilsoni* can be separated from the geographically close and morphologically similar species *N. acroteria* sp. nov. and *N. cymontana* sp. nov. by the following characters. Acropodite medial flange laminate and wide, rather than small and lobed as in *N. cymontana* sp. nov. Dorsal projection near medial flange of acropodite absent, rather than present as in *N. acroteria* sp. nov. Prefemoral process gradually tapering, rather than spear-shaped distally, as in *N. cymontana* sp. nov. Acropodite lacking the small triangular projection near base of prefemoral process present in *N. acroteria* sp. nov.

Description. Suppl. material 2. Based on ♂ (MPE02123) and ♀ (MPE02131).

Measurements: Taken from ♂ specimen MPE02123: BL = 27.30, CW = 3.88, IW = 2.73, ISW = 0.93, B10W = 5.06, B10H = 3.00. **Color.** Tergites with two paranotal peach spots, collum outlined in peach, and tergites with background chestnut brown (Fig. 49). **Gonopods.** Male gonopod acropodite arc gradually curving (Fig. 50A–-C). Acropodite with a gently undulating twist at anterior bend (Fig. 50A). Acropodite medial flange laminate (Fig. 50C), acropodite tip medial flange absent. Acropodite tip lateral flange lobed, with a small bump just before the tip (Fig. 50A). Acropodite tip blunt, directed ventrally (Fig. 50A, B). Prefemoral process sinuous and curving medially (Fig. 50A). Prefemoral process tip directed medially. **Cyphopods.** Female cyphopod receptacle an enlarged triangular hood.

Variation. No notable variation observed.

Distribution. *Nannaria wilsoni* is limited almost entirely to Giles County, with one dubious record from Montgomery County in southwest Virginia (Fig. 51).

Ecological notes. Habitat information from museum specimens is limited, but *Nannaria wilsoni* has been collected from oak, maple, and rhododendron forests.

Etymology. This species was named in honor of Charles M. Wilson, who collected the species at Mountain Lake Biological Station in Giles County (Hoffman 1949b).

Key to the *wilsoni* species group of *Nannaria* Chamberlin, 1918

1	Gonopod acropodite anterior bend twist absent (Fig. 29)	**2**
–	Gonopod acropodite anterior bend twist present (Figs 13, 50)	**4**
2	Prefemoral process stout, projecting at a 45° angle from telopodite (Fig. 27A); acropodite tip with laminate, jagged lateral flange, much larger than other acropodite branch. Augusta Co., Virginia	***N. marianae* sp. nov. (Figs 26, 27)**
–	Prefemoral process thin, acicular or curving, not projecting at a 45° angle from telopodite (Fig. 29A); acropodite tip lacking lateral flange; bifurcations of acropodite of similar size and shape	**3**
3	Prefemoral process acicular; acropodite tip directed medially (Fig. 29A). Blue Ridge Mountains from Page Co. south to Amherst Co., Virginia	***N. morrisoni* (Figs 28, 29)**
–	Prefemoral process curving; acropodite tip directed caudally (Fig. 40A). Augusta, Rockingham, and Shenandoah cos., Virginia; west to Greenbrier, Marion, Pocahontas, Preston cos., West Virginia; and Powell Co., Kentucky	***N. shenandoa* (Figs 39, 40)**

4 Acropodite anterior bend slightly twisted, in the shape of a smoothly-undulating helix (Fig. 50) **5**
– Acropodite anterior bend acutely bent, appearing crimped or pinched (Fig. 13).. **17**
5 Prefemoral process arising from midway up acropodite (Fig. 23); acropodite arc straight, with bend at midpoint (Fig. 23); acropodite setae present from base of acropodite to three-quarters up the full acropodite length. Buncombe and Rutherford cos., North Carolina and Greenville Co., South Carolina .... ***N. lithographa*** **sp. nov. (Figs 22, 23)**
– Prefemoral process arising from base of acropodite (Fig. 50); acropodite arc either gradually curving (Fig. 34), or straight with abrupt bend at tip (Fig. 17); acropodite setae present from base of acropodite to halfway up the full acropodite length... **6**
6 Acropodite arc straight, with abrupt bend at tip (Fig. 17) **7**
– Acropodite arc gradually curving (Fig. 34) **10**
7 Acropodite medial flange absent (Fig. 17) **8**
– Acropodite medial flange present (Fig. 48)... **9**
8 Acropodite tip medial flange triangular (Fig. 17); acropodite tip lateral flange triangular, fin-shaped; acropodite weakly curving, not tapering towards tip. Ridge and Valley region, from Bath Co. south to Giles and Montgomery cos., Virginia... ***N. ericacea*** **(Figs 16, 17)**
– Acropodite tip medial flange laminate, shield-shaped (Fig. 44); acropodite tip lateral flange absent; acropodite spiraling and tapering towards tip. Augusta, Highland, Rockingham cos., Virginia and Pendleton Co., West Virginia...... .... ***N. spiralis*** **sp. nov. (Figs 43, 44)**
9 Acropodite tip medial flange lobed and recurved (Fig. 36); acropodite tip lateral flange small, lobed; acropodite not tapering distally. Lumpkin and Towns cos., Georgia.................................. ***N. rhododendra*** **sp. nov. (Figs 35, 36)**
– Acropodite tip medial flange triangular (Fig. 48); acropodite tip lateral flange absent; acropodite tapering distally. Alleghany, Augusta, and Rockbridge cos., Virginia .... ***N. vellicata*** **sp. nov. (Figs 47, 48)**
10 Acropodite medial flange lacking a dorsal median projection (Fig. 50)...... **11**
– Acropodite medial flange with a dorsal median projection (Fig. 8)............ **14**
11 Acropodite tip bifurcate (Fig. 19); acropodite tip medial flange laminate, sharp, caudally-directed. Alleghany Co., Virginia....... ***N. filicata*** **sp. nov. (Figs 18, 19)**
– Acropodite tip entire, undivided (Fig. 21); acropodite tip medial flange absent.. **12**
12 Base of prefemoral process crimped and bent on medial side (Fig. 21B); prefemoral process straight, not curving in anterior view (Fig. 21A); prefemoral process tip directed cephalically. Craig Co., Virginia .... ***N. liriodendra*** **sp. nov. (Fig. 20, 21)**
– Base of prefemoral process not crimped, either unmodified (Fig. 15B) or with at most a basal swelling (Fig. 50B); prefemoral process curving medially in anterior view (Fig. 15A); prefemoral process tip directed medially **13**

13 Acropodite medial flange large, laminate (Fig. 50C); acropodite tip lateral flange rounded (Fig. 50C); base of prefemoral process with a slight swelling on medial side; prefemoral process tip without preapical lateral expansion. Giles and Montgomery cos., Virginia...................... ***N. wilsoni* (Figs 49, 50)**

– Acropodite medial flange small, lobed (Fig. 15C); acropodite tip lateral flange sharp (Fig. 15A); base of prefemoral process unmodified; prefemoral process tip spear-shaped, with preapical lateral expansion. Carroll, Floyd, Montgomery, Patrick, and Roanoke cos., Virginia................ ***N. cymontana* sp. nov. (Figs 14, 15)**

14 Prefemoral process acicular to slightly curving (Fig. 8); prefemoral process 3/4 the length of the acropodite or less (Fig. 34)...................................... **15**

– Prefemoral process sinuous, strongly curving (Fig. 6); prefemoral process greater than 3/4 the length of the acropodite (Fig. 25).............................. **16**

15 Acropodite dorsal triangular projection small to medium-sized (Fig. 8A); acropodite tip smoothly curving (Fig. 8A). Southwest Virginia west of the New River.. ***N. aenigma* (Figs 7, 8)**

– Acropodite dorsal triangular projection large (Fig. 34A); acropodite tip straight, with distal kink (Fig. 34A). Pocahontas Co., West Virginia and Bath Co., Virginia.. ***N. paraptoma* sp. nov. (Fig. 34)**

16 Acropodite dorsal projection triangular (Fig. 6A); acropodite tip lateral flange absent (Fig. 6C); base of prefemoral process with a short, thin triangular process (Fig. 6B). Greenbrier and Monroe cos., West Virginia and Giles Co., Virginia.. ***N. acroteria* sp. nov. (Figs 5, 6)**

– Acropodite dorsal projection rounded, dome-shaped (Fig. 25A); acropodite tip lateral flange bilobed (Fig. 25C); base of prefemoral process lacking a triangular process (Fig. 25B). Bedford, Botetourt, Rockbridge cos., Virginia ... . ***N. lutra* sp. nov. (Figs 24, 25)**

17 Acropodite tip bifurcate (Figs 12, 33); acropodite tip medial flange large, laminate, expanded into a separate acropodite branch (Figs 12, 33).......... **18**

– Acropodite tip entire, not split into two branches of similar size (Fig. 10); acropodite tip medial flange absent (Fig. 31), triangular Fig. 38), or lobed (Fig. 13)...... .... **19**

18 Acropodite medial flange pointed, tooth-like (Fig. 12C); acropodite lateral flange lobed (Fig. 12A); acropodite tips directed medially (Fig. 12C); prefemoral process sinuously tapering, with a broad base (Fig. 12A). Macon Co., North Carolina south through Dawson, Towns, and Union cos., Georgia .... ***N. antarctica* sp. nov. (Figs 11, 12)**

– Acropodite medial flange laminate Fig. 33C); acropodite lateral flange absent; acropodite tips directed caudally (Fig. 33A); prefemoral process curving slightly, slightly tapering distally (Fig. 33A). Central Virginia, north of the James River from Rockbridge Co. east through Nelson Co., Virginia........... .... ***N. orycta* sp. nov. (Figs 32, 33)**

19 Acropodite medial flange lobed (Fig. 13) **20**

– Acropodite medial flange laminate (Fig. 42C) or tooth-like (Fig. 10C)......... .... **22**

20 Acropodite tip medial flange present, lobed (Fig. 13A); prefemoral process curving laterally (Fig. 13A). Macon Co., North Carolina and Rabun Co., Georgia .... ***N. austricola*** **(Fig. 13)**

– Acropodite tip medial flange absent (Fig. 31A); prefemoral process erect (Fig. 46A) or with at most only a slight curve (Fig. 31A) **21**

21 Acropodite medial flange singly lobed (Fig. 31C); acropodite tip even-sided (Fig. 31A); prefemoral process notched on medial side at midpoint (Fig. 31A). Macon Co., North Carolina and Rabun Co., Georgia.... ***N. nessa*** **sp. nov. (Figs 30, 31)**

– Acropodite medial flange composed of two rounded bumps (Fig. 46B); acropodite tip tapered distally (Fig. 46A); prefemoral process even-sided, lacking a notch at midpoint (Fig. 46A). Cumberland, Monroe, and Van Buren cos., Tennessee .... ***N. swiftae*** **sp. nov. (Figs 45, 46)**

22 Acropodite medial flange laminate (Fig. 42C); acropodite tip lateral flange lobed, projecting (Fig. 42A); prefemoral process medial margin jagged (Fig. 42A). Rabun Co., Georgia .... ***N. spalax*** **sp. nov. (Figs 41, 42)**

– Acropodite medial flange tooth-like (Figs 10C, 38C); acropodite tip lateral flange absent (Fig. 10A); prefemoral process medial margin smooth (Fig. 10A) **23**

23 Acropodite medial flange hooked, even-sided (Fig. 10C); acropodite tip medial flange always absent (Fig. 10); prefemoral process laminate (Fig. 10). Dawson and Lumpkin cos., Georgia .... ***N. amicalola*** **sp. nov. (Figs 9, 10)**

– Acropodite medial flange straight, tapered (Fig. 38C); acropodite tip medial flange triangular (Fig. 38), small to large or rarely laminate, sometimes absent; prefemoral process sinuously tapered (Fig. 38). Sevier and Cocke cos., Tennessee and Clay, Haywood, Jackson, Swain, and Transylvania cos., North Carolina.. ***N. scutellaria*** **(Figs 37, 38)**

Distributional notes

The distribution of the Central Appalachian species of the *wilsoni* species group extends from southwest Virginia and adjacent Kentucky north to West Virginia and the Maryland border (Fig. 51). Species distributions in this geographic cluster are often limited by rivers and mountain ranges. This is shown in the distribution of *N. aenigma*, for example, which only occurs west of the New River. The courses of the James and Roanoke Rivers also delimit portions of the distribution of multiple species, as do the Blue Ridge Mountains, and to a lesser extent, the mountains in the Ridge and Valley Province of Virginia. One species in this cluster that does not have its distribution greatly affected by physical geography is *N. shenandoa*. This species has the largest distribution of any species in the cluster (and within the *wilsoni* species group), extending from eastern Kentucky to northern Virginia across multiple mountain ranges and rivers. Specimens of *N. shenandoa* from across its range, however, have no discernable differences in gonopod morphology, and genetically appear to form a single species. Concerted collecting in the gap in its distribution in West Virginia and Kentucky may reveal more localities for this species.

The distribution of the Southern Appalachian species cluster extends from western North Carolina and adjacent Tennessee south through northern Georgia and South Carolina (Fig. 52). The distributions of species in this cluster tend to be small, with many species only known from a few collection localities. The only major known river barrier for this cluster is the French Broad River, which separates the distributions of *N. lithographa* sp. nov. and *N. scutellaria*. The French Broad River is also known to act as a biogeographical barrier causing vicariance for other dispersal-limited arthropod taxa, including flightless beetles (Kane et al. 1990; Caterino and Langton-Myers 2019), harvestmen (Thomas and Hedin 2008; Hedin and McCormack 2017), and *Nesticus* Thorell, 1869 spiders (Hedin 1997). The influence of other regional rivers, such as the Little Tennessee and Hiwassee Rivers, as barriers to species dispersal in this group remains to be investigated. *Nannaria scutellaria*, for example, has high morphological variation, and its distribution crosses both the Little Tennessee and Tuckasegee Rivers. Future investigations into the phylogeographical concordance of its distribution and morphological variation may help to resolve questions of cryptic species within *N. scutellaria*. The southern extent of this species cluster is limited by the transition zone from the Blue Ridge physiographic province to the Piedmont in northern Georgia.

Discussion

With the description of 17 new species, the species diversity of the *Nannaria wilsoni* species group has more than tripled to 24 described species and the total richness in the Xystodesmidae has increased to 539 species. The Southern Appalachian Mountains held a plethora of new species: only two of the species in that region had been previously described. It is almost certain that more *Nannaria* species will be found in the region, particularly in the mesic cove habitats of northern Georgia and adjacent South Carolina. Both the Central Appalachian and Southern Appalachian Regions likely harbor new species. In Central Appalachia, large portions of West Virginia have not been sampled for *Nannaria* and other millipedes. Recent revisionary work on the genus *Brachoria* Chamberlin, 1939 revealed ten new species in the Appalachian Mountains, eight of which were described from extreme southwestern Virginia, eastern Kentucky, and southern West Virginia (Marek 2010). Millipedes in the genus *Brachoria* are large-bodied (40–60 mm in length), brightly colored, and comparatively easier to collect in the field than *Nannaria*, so it is likely new *Nannaria* species may have been missed during previous collecting in this area, and that species diversity of the region is significantly underestimated.

The number of described species in the genus *Nannaria* now stands at 78 (Table 1), with its center of species diversity in the Appalachian Mountains of eastern North America. This makes *Nannaria* the largest genus in the Xystodesmidae, a record previously held by the genus *Rhysodesmus* Cook, 1895, which contains 72 species (Means et al. 2021a). Among all North American diplopods, its species richness is only second to the chordeumatidan genus *Cleidogona* Cook, 1895 with 84 species. The great diversity of *Nannaria* in the Appalachian Mountains mirrors that of the genus *Sigmoria*, which exhibits a nonadaptive radiation of 67 mostly parapatric species (Means et al. 2021a). *Nannaria* species have cryptic color patterns, and none of the species can be considered aposematic like apheloriine species, but the genus has still speciated tremendously in the Appalachians, likely due in part to the physiographic history of the region. The Appalachian Mountains are an old mountain range, estimated to have formed around 480 mya during the Ordovician Period, and the region has a markedly rugged terrain. An important factor influencing speciation in *Nannaria* could be vicariance as a result of allopatric fragmentation of populations, as has been suggested for *Brachoria* and other Xystodesmidae (Marek 2010) in the Appalachian Mountains.

The well-delineated clades of the *Nannaria minor* and *Nannaria wilsoni* species groups suggest that the distinction between the two may warrant division at a higher taxonomic level, rather than as species groups, and further study is underway to determine if these groups merit division. The differences between them are supported by genetic, morphological, and biogeographical data. The splits between the *minor* and *wilsoni* species groups, as well as amongst the genus *Nannaria* and *O. pulchella* are all well supported, with bootstrap values greater than 70.

The *minor* and *wilsoni* species groups are also separable morphologically based on the structure of the gonopods (see Genus diagnosis above). The attachment of the prefemoral process at the base of the acropodite in the *wilsoni* species group; lack of an elongation between coxa and telopodite (the basal zone), presence of a twist at the anterior bend, and lack of setae past more than three-quarters the length of the acropodite separate it from the *minor* species group. Species in the *minor* species group have a prefemoral process attached to an acropodite shelf, an elongation between the coxa and telopodite, lack a twist at the anterior bend, and often have setae present at the anterior bend of the acropodite. The valves of the cyphopods appear to vary intraspecifically, but the epigyne, the anterior ventral margin of the third body ring in females (Blower 1985; Zahnle et al. 2020), appears to have utility for female species identification and is perhaps intraspecifically static. Additionally, the receptacle of the female cyphopods differs greatly in size and shape, and may allow identification of females to species in the *wilsoni* group. The *minor* species group is not known to possess such modifications to its cyphopod receptacle, though in *O. pulchella*, the cyphopod receptacle is a large, erect, laminate structure that entirely covers the cyphopod valves. The morphology of the cyphopod receptacles is noted in the morphological matrix and species accounts for each species for which female specimens were available. This will permit future comparison of female specimens and other investigations into the utility of the female genitalia for species identification in the Nannariini. The most common shape of the cyphopod receptacle in the *wilsoni* species group is small and triangular, but many modifications to this configuration are found, particularly in the Southern Appalachian Mountains species cluster.

The utility of female genitalic characters for the identification of genera or species in Polydesmida is not as well-investigated as is the characters of the male genitalia. However, female genitalic characters have been shown to be useful for species identification in some cases, such as with the genera *Euryurus* and *Eurymerodesmus* (Hoffman 1978a; Shelley 1990), and were used to form the defining characters of the subfamily

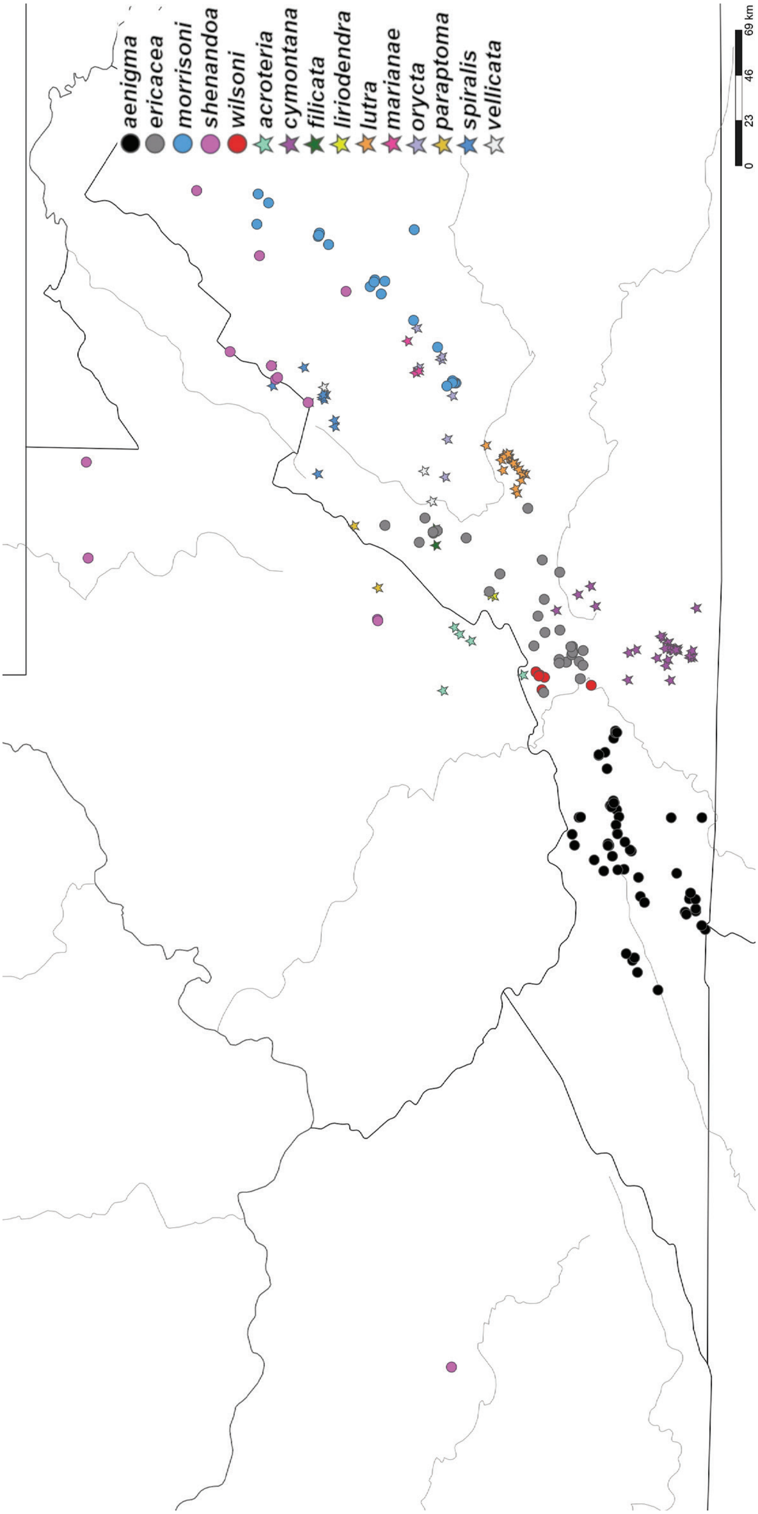

Figure 51. Distribution of the Central Appalachian species of the *Nannaria wilsoni* species group. Dots = described species, stars = new species.

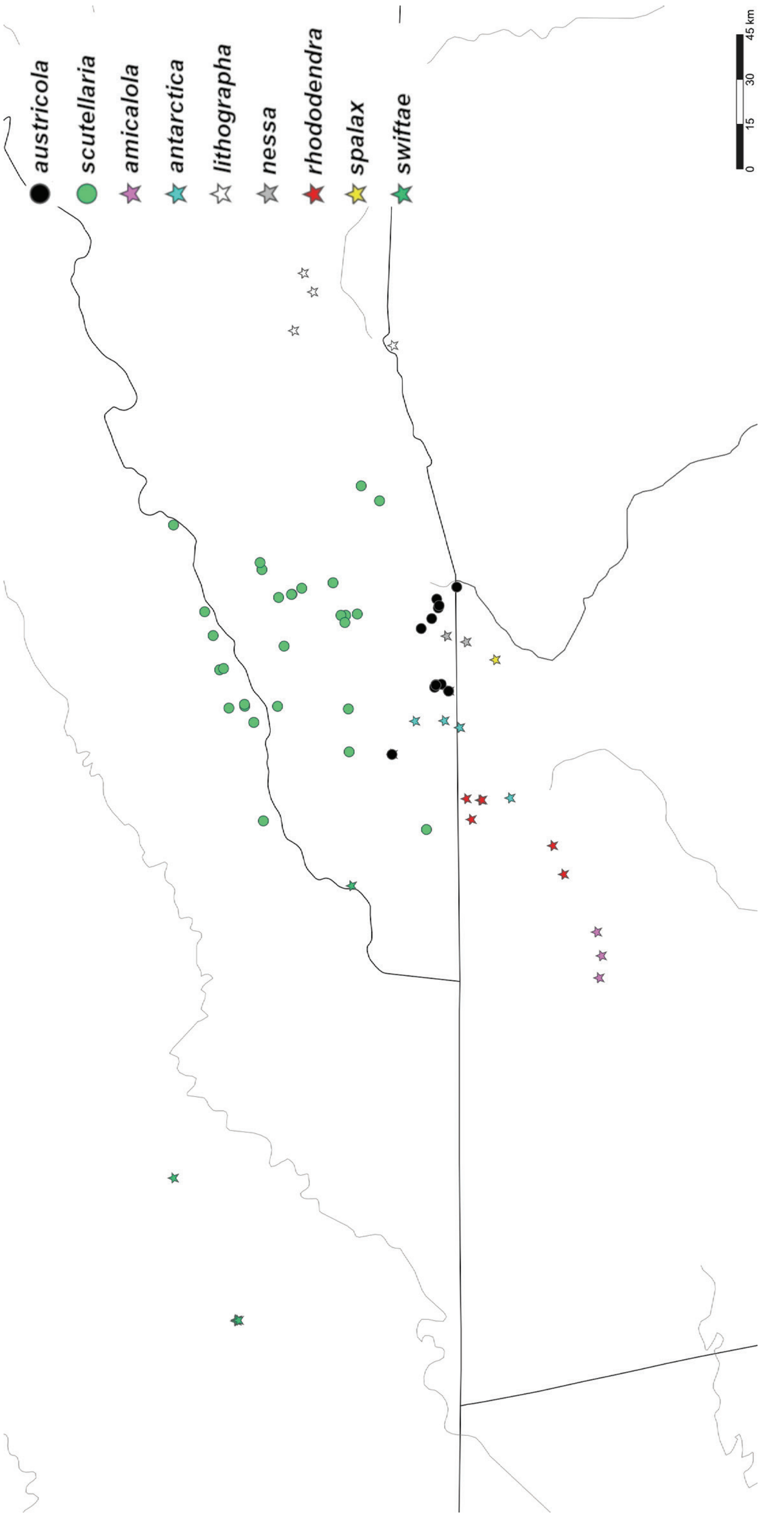

Figure 52. Distribution of the Southern Appalachian species of the *Nannaria wilsoni* species group. Dots = described species, stars = new species.

Parafontariinae Hoffman, 1978 (Hoffman 1978b), now a tribe, Parafontariini (Means et al. 2021a). Other variations within the Xystodesmidae are known, such as in the genus *Cherokia* Chamberlin, 1949, which lacks a receptacle entirely (Hoffman 1960) and the genus *Pachydesmus* Cook, 1895, in which females have modified cyphopodal apertures and receptacles (Hoffman 1958). Other families of Polydesmida are also known to have modified female genitalia, such as the Chelodesmidae, with the species *Plectrogonodesmus gounellei* (Brölemann, 1902) having an enlarged epigyne and recurved receptacles with tubular projections (Brölemann 1902; Bouzan et al. 2019). In the Polydesmidae, *Pseudopolydesmus* Attems, 1898 has recently-identified cyphopod structures that may be useful for species identification (Zahnle et al. 2020).

Biogeographical clusters

Two regional distributions were observed within the *wilsoni* species group: a cluster in the Central Appalachian Mountains, with species known from Kentucky, West Virginia, and Virginia; and another cluster in the Southern Appalachian Mountains, with species known from Georgia, North Carolina, South Carolina, and Tennessee (Fig. 2). These clusters are separated by a gap of approximately 140 km, in which no specimens of the *wilsoni* species group have been collected, despite repeated collecting efforts that revealed multiple species of the *minor* species group occurring in this area. Due to the presence of other *Nannaria* in this area and no lack of collecting, this gap was determined to be a reflection of the biological reality of the *wilsoni* species group, rather than an artifact of a lack of collecting effort. The gap extends from near Abingdon, Virginia south to the vicinity of Asheville, North Carolina, and no obvious biogeographical barriers exist to limit the distribution of each cluster, as evidenced by the presence of species from the *minor* species group. This distributional gap is not directly reflected in the phylogeny (i.e., there are not two distinct clades separating the biogeographical clusters), though generally species are more closely related to other species from their biogeographical cluster. Future collecting in the intervening area may clarify the exact boundaries of this gap. Despite the lack of obvious biogeographical barriers in this gap, there may be unknown abiotic factors that favor the presence of only the *minor* species group, which may be more adaptable to a wider variety of habitats, as exhibited by their presence west of the Appalachian Mountains and in the drier Ozark Mountains and intervening lowlands. Alternatively, although not mutually exclusive of adaptability to a wider variety of habitats, the *minor* species group may be older and therefore have had a longer period to disperse widely. There is also a possibility that species of the *wilsoni* group are rarer in this region and may eventually be found at lower population levels in unsampled habitats in the gap.

Central Appalachian Mountains Biogeographical Cluster. In the Central Appalachian Mountains Biogeographical Cluster, 15 species of the *wilsoni* group are known, and 10 of these species are newly described. In this cluster, species typically have a gradually curving acropodite or a straight acropodite with an abrupt bend distally. In the case of *N. marianae* sp. nov., the acropodite is bent at the midpoint. The acropodite anterior bend twist is generally absent or in the shape of a smoothly-undulating helix, except for

N. orycta sp. nov., which is acutely twisted at the anterior bend of the acropodite. Interestingly, the boundaries of the distributions of four species in this cluster (*N. aenigma*, *N. cymontana* sp. nov., *N. ericacea*, and *N. wilsoni*) provide evidence that the New River acts as a geographical barrier for those taxa and has resulted in the vicariance of these species. Only one species, *N. aenigma*, occurs west of the New River, while the other three species all occur east of the river, and none of these species occur on both sides of the New River (Fig. 51). Similarly, *N. cymontana* sp. nov. appears to have parts of its northern distribution limited by the Roanoke River, and *N. ericacea*, *N. filicata* sp. nov., *N. lutra* sp. nov., *N. morrisoni*, *N. orycta* sp. nov., and *N. vellicata* sp. nov. are limited in portions of their distributions by the James River (Fig. 51).

Southern Appalachian Mountains Biogeographical Cluster. In the Southern Appalachian Mountains Biogeographical Cluster, nine species of the *wilsoni* species group are known, and seven of these species are newly described. In this cluster, all but one species have a straight acropodite with an abrupt bend distally, and only *N. lithographa* sp. nov. differs by having an acropodite bent at its midpoint. The acropodite anterior bend twist is typically acutely contorted and appears almost crimped or pinched, except in *N. rhododendra* sp. nov. and *N. lithographa* sp. nov., in which the twist is in the shape of a smoothly-undulating helix. Acropodite anterior bends with acute, crimped twists are most common in species of the Southern Appalachian Mountains Biogeographical Cluster. Only one species from the Central Appalachian Mountains Biogeographical Cluster, *N. orycta* sp. nov., has an acropodite anterior bend with this condition. In the Southern Appalachian Mountains Biogeographical Cluster, the acropodite tip is typically smooth and entire, although in a few species it is bifurcate. The cyphopod receptacle is typically modified in this cluster, rather than being small and triangular. The most unusual modification of the receptacle is observed in *N. antarctica* sp. nov. and *N. rhododendra* sp. nov., in which the receptacle is modified into a long, finger-like structure that projects outside of the cyphopod aperture and can be observed without dissecting the millipede.

Molecular phylogenetics

The maximum likelihood phylogeny inferred with our analysis (Fig. 3) generally agrees with the morphology-based species concepts, with some exceptions. *Nannaria lithographa* sp. nov. is sister to all other species in the *wilsoni* species group, an unsurprising result considering its divergent gonopod anatomy, with the presence of acropodite setae on up to three-quarters the length of the acropodite, and its spear-shaped prefemoral process attached distally on the acropodite, two morphological characters not present in any other species in the group. The low bootstrap support (average 45) for higher level relationships within the *wilsoni* species group phylogeny precludes discussion about which clades are most closely related, but in general the species in each biogeographical cluster are more closely related to each other than to species from the other geographic cluster. Most species clades from the Central Appalachian Mountains Biogeographical Cluster were highly supported by bootstrap values greater than 70, while few of the species clades from the Southern Appalachian Mountains Biogeographical Cluster had similar high support. Higher-level relationships within the *wilsoni* species group were not well supported, and some species, such as *N. rhododendra* sp. nov., *N. scutellaria,* and *N. vellicata* sp. nov., were recovered in multiple positions in the phylogeny. This may be due to lower quality genetic data, as indicated by longer branches in the phylogeny (e.g., *N. rhododendra* sp. nov. and *N. vellicata* sp. nov.), or possibly cryptic speciation (e.g., *N. scutellaria*).

The two widely separated groups of *N. scutellaria* recovered by the phylogeny make a strong case for cryptic speciation. The three specimens of *N. scutellaria* recovered as monophyletic (spare MPE03745 and MPE04346) were collected from the northern portion of its distribution, and includes a specimen (VTEC, MPE01474) collected at its type locality, Chimneys Picnic Area in Great Smoky Mountains National Park that matches closely with the gonopod morphology of the holotype (Causey 1942). The other specimens of *N. scutellaria* in this type-group vary in the size and position of the acropodite medial flange tooth and in the curve of the acropodite tip. The separate group of *N. scutellaria* does not include the type, and the species warrants further genetic analyses from a wider array of specimens to still determine whether *N. scutellaria* is composed of several species. Nonetheless, due to overall morphological similarity of these specimens they are treated as a single species. Within the *wilsoni* species group, this species is by far the most highly variable in its gonopod morphology. We included many specimens with variable gonopod morphology in *N. scutellaria*. Specimens ascribed to this species typically have a tooth-like acropodite medial flange, a triangular acropodite tip medial flange, and a prefemoral process that is quite wide basally. The gonopod characters may vary in the size of the medial flange, the distance between the tip medial flange and acropodite tip, the size and position of the tip medial flange, the direction the acropodite tip is pointed, and the distal curve of the acropodite. In some specimens, the acropodite tip medial flange is absent. A specimen collected near Nantahala, North Carolina (VMNH, NAN0369) even has the acropodite tip medial flange expanded and laminate, forming a concave leaf- or cup-like shape. The specimens recovered in the non-type *N. scutellaria* group were collected in Transylvania and Clay counties, North Carolina, at the southern edge of the species distribution in the Blue Ridge Mountains, and the collection of fresh material from the southern edge of this distribution could further elucidate the status of this species.

Inclusion of additional specimens of species from the Southern Appalachian Mountains Biogeographical Cluster could resolve some of the low support values recovered for those taxa, which generally had fewer specimens included in the analysis than species from the Central Appalachian Mountains Biogeographical Cluster. Despite being recovered at three separate positions in the phylogeny, no significant gonopod variation was observed in all examined specimens of *N. rhododendra* sp. nov. This situation is likely due to lesser quality genetic data for this species, rather than possible cryptic speciation, as may be the case for *N. scutellaria*.

While the evolutionary relationships between species in the *wilsoni* group remain unclear, this may be rectified in the future with analysis of additional genetic data. Morphology-based species delimitation based on gonopod shape in *Nannaria* has been proven useful in previous work on the genus (Means et al. 2021a, b), and we are confident the species delimited here will be supported by future genetic analysis that solves the previously-identified inconsistencies.

Conservation

Much remains to be learned about the ecology of the *Nannaria wilsoni* species group. Its species are typically limited to mesic deciduous forests or rhododendron coves in the Appalachian Mountains, with few exceptions. The Blue Ridge Mountains are home to many of these species, as are the Alleghany Mountains in the more northern parts of their distribution. More undescribed species in the genus surely await description, particularly in little-collected areas of northern Georgia, eastern Tennessee and Kentucky, and eastern West Virginia. The introduction of the forest pest *Adelges tsugae* Annand, 1924, the hemlock wooly adelgid (Hemiptera: Adelgidae), into the United States from Japan poses a threat to hemlock habitats commonly favored by *Nannaria* species. In some areas, this pest can kill up to 92% of hemlock trees (Rohr et al. 2009), which could greatly impact these millipedes if forests change from the formerly shady, cool hemlock forest microhabitats *Nannaria* prefers to drier habitats less amenable to their preferences. In addition to hemlock habitat loss, rhododendron dieback threatens to affect *Nannaria* populations in the Appalachian Mountains. Like hemlock, the presence of rhododendron provides the cool, shady microhabitats that *Nannaria* prefers, and its importance will increase with the loss of hemlock (Baird et al. 2014). Rhododendron dieback has been reported to affect *Rhododendron maximum* L., which is widespread in the Appalachians, and appears to be caused by environmental stress that weakens the plants and allows opportunistic pests and pathogens to attack them (Baird et al. 2014; Brooks et al. 2019). Additionally, a fungal pathogen specializing on millipedes was recently found to infect the genus (Hodge et al. 2017), but little is known about its effects at a population level.

The small, highly endemic distributions of *Nannaria* are susceptible to habitat loss and fragmentation, a cause for concern as the hemlock wooly adelgid spreads and invades new areas of forest. Habitat loss from human development and invasive species' effects on forests are the primary conservation threats for the *wilsoni* group, particularly due to the small distributions of many of its species. The distributions of some species are limited to small areas in only a few counties, or as in the case of *N. spalax* sp. nov., only one known locality. Due to the secretive habits of *Nannaria*, there is also a risk that microendemic undescribed species exist and may be driven to extinction before they are formally described.

Conclusions

In this study, we accomplished three main objectives, we: (1) confirmed the monophyly of the *wilsoni* species group using molecular phylogenetics, (2) described new species of this species group, and (3) revised the taxonomy of the genus with an investigation of the natural history and ecology of the genus. The genus *Nannaria* has two large clades with species that are morphologically, genetically, and biogeographically separable from each other. We described 17 new species in the *wilsoni* species group, more than tripling the number of known species, from 7 to 24, and increased total species in the family Xystodesmidae to 539. Based on numerous collecting events, natural history data, and data from museum collections, we discovered that *Nannaria* prefers riparian habitats in rhododendron-hemlock cove forests and mesic deciduous forests in North America. Species in the *wilsoni* species group prefer mesic forests of the Appalachian Mountains, and are fossorial in their habits, being found buried in the soil or at the soil-leaf litter interface. The discovery of additional species diversity in the *wilsoni* species group and in the *minor* species group reveals the tribe Nannariini to be one of the most species-rich lineages within the Xystodesmidae, rivaling the species diversity of the Apheloriini. This may be due in part to continuous nonadaptive radiation of *Nannaria* and repeated vicariance of their distributions by the physiographic history of the Appalachian Mountains in eastern North America. Nonadaptive radiation has been previously suggested to occur in the family Xystodesmidae (Marek and Moore 2015, Means et al. 2021a). Additional undescribed species of Nannariini undoubtedly exist in eastern North America, and will be revealed by further fieldwork in undersampled regions of the Central and Southern Appalachian Mountains. Before this study, the true species diversity of the *wilsoni* species group was unknown, particularly in the Southern Appalachian Mountains. The results presented in this study, along with those of Means et al. (2021a, b) have vastly expanded our knowledge of the tribe, and provide a solid taxonomic foundation for further study of this group. The genus *Nannaria* now contains 78 species (Table 1), making it the largest genus in the Xystodesmidae.

Acknowledgements

This research was funded by a National Science Foundation Advancing Revisionary Taxonomy and Systematics grant (DEB# 1655635). We thank the following permitting agencies for granting scientific collection permits: Georgia State Parks, permit #132016, 142018; Kentucky Department of Parks, permit #1708; Kentucky State Nature Preserves Commission, permit #2017-09-05; North Carolina Department of Natural and Cultural Resources, permit #2018_0234; Tennessee Wildlife Resources Agency permit #3914, 1702; Tennessee Department of Environment and Conservation, permit #2017-008; West Virginia Division of Natural Resources, permit #2016.238; Virginia Department of Wildlife Resources, permit #056958; National Parks Service, permit #GRSM-2016-SCI-2369, GRSM-2019-SCI-2369, SHEN-2016-SCI-0018, BLRI-2014-SCI-0033. Thanks go to Bronwyn Williams and Megan McCuller of the North Carolina Museum of Natural Sciences and Kaloyan Ivanov of the Virginia Museum of Natural History for facilitating loans of millipede specimens. We also thank all the collectors who sent us specimens, particularly Curt Harden, Matt Kasson, and Patricia Wooden. We thank Maddie Hellier for assistance in measuring holotype specimens. We thank Nesrine Akkari, Sergei Golovatch, and one anonymous reviewer for their helpful feedback on previous versions of this manuscript. DAH received support from a Virginia Tech Interfaces of Global Change fellowship, a Theodore Roosevelt Memorial Grant from the American Museum of Natural History, and a Graduate Research Development Program award from the Virginia Tech Graduate Student Assembly.

References

Attems CG (1898) System der Polydesmiden I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 67: 221–482.

Attems CG (1938) Polydesmoidea II. Fam. Leptodesmidae, Platyrhachidae, Oxydesmidae, Gomphodesmidae. Das Tierreich 69: 1–487. https://doi.org/10.1515/9783111430645-003

Baird R, Wood-Jones A, Varco J, Watson C, Starrett W, Taylor G, Johnson K (2014) Rhododendron decline in the Great Smoky Mountains and surrounding areas: Intensive site study of biotic and abiotic parameters associated with the decline. Southeastern Naturalist (Steuben, ME) 13(1): 1–25. https://doi.org/10.1656/058.013.0101

Blower JG (1985) Millipedes. Synopses of the British Fauna (New Series) 35, E. J. Brill, London, 242 pp.

Bollman CH (1888) Notes on a collection of Myriapoda from Mossy Creek, Tenn., with a description of a new species. Proceedings of the United States National Museum: 339–342. https://doi.org/10.5479/si.00963801.11-721.339

Bollman CH (1889) Description of a new species of insect, *Fontaria pulchella*, from Strawberry Plains, Jefferson County, Tennessee. Proceedings of the United States National Museum 11(714): e316. https://doi.org/10.5479/si.00963801.11-714.316

Bouzan RS, Iniesta LFM, Souza CARD, Brescovit AD (2019) A new record after a century and description of the female of *Plectrogonodesmus gounellei* (Brölemann 1902) (Polydesmida: Chelodesmidae). Studies on Neotropical Fauna and Environment 54(1): 61–68. https://doi.org/10.1080/01650521.2018.1536018

Brölemann HW (1900) Myriapodes d'Amérique. Mémoires de la Société Zoologique de France 13: 89–131. https://doi.org/10.3406/bsef.1900.22570

Brölemann HW (1902) Myriapodes recueillis par M. E. Gounelle au Brésil. Annales de la Société Entomologique de France 71: 649–694. https://www.biodiversitylibrary.org/page/8252053

Brooks RK, Hansen MA, Bush E, Eisenback J, Day E (2019) Mortality of Great Rhododendron (*Rhododendron maximum*) in Virginia. Virginia Cooperative Extension Publication SPES-151P: 6 pp. https://doi.org/10.21061/SPES-151NP

Buhlmann KA, Mitchell JC, Smith LR (1999) Descriptive ecology of the Shenandoah Valley sinkhole pond system in Virginia. Banisteria 13: 23–51. https://virginianaturalhistorysociety.com/banisteria/pdf-files/ban13/Ban_13_Buhlmann_Mitchell_Smith.pdf

Caterino MS, Langton-Myers SS (2019) Intraspecific diversity and phylogeography in southern Appalachian *Dasycerus carolinensis* (Coleoptera: Staphylinidae: Dasycerinae). Insect Systematics and Diversity 3(6): e8. https://doi.org/10.1093/isd/ixz022

Causey NB (1942) Six new Diplopods of the family Xystodesmidae. Entomological News 53: 165–170. https://www.biodiversitylibrary.org/page/2405645

Causey NB (1950a) A collection of xystodesmid millipeds from Kentucky and Tennessee. Entomological News 61: 5–8. https://www.biodiversitylibrary.org/page/2583543

Causey NB (1950b) Variations in the gonopods of a xystodesmid diplopod. American Midland Naturalist 44(1): 198–202. https://doi.org/10.2307/2421760

Causey NB (1950c) A new genus and species of diplopod (Family Xystodesmidae). Chicago Academy of Sciences Natural History Miscellanea 71: 1–3.

Chamberlin RV (1918) New polydesmoid diplopods from Tennessee and Mississippi. Psyche (Cambridge, Massachusetts) 25(6): 122–127. https://doi.org/10.1155/1918/24852

Chamberlin RV (1921) On some chilopods and diplopods from Knox Co., Tennessee. Canadian Entomologist 53(10): 230–233. https://doi.org/10.4039/Ent53230-10

Chamberlin RV (1928) Some chilopods and diplopods from Missouri. Entomological News 39: 153–155. https://www.biodiversitylibrary.org/page/2630529

Chamberlin RV (1939) On some diplopods of the family Fontariidae. Bulletin of the University of Utah, Biological Series 30: 1–19. https://collections.lib.utah.edu/dl_files/90/6b/906b74cdc183c1c1784aacbd40560fc560b79820.pdf

Chamberlin RV (1940) On some chilopods and diplopods from North Carolina. Canadian Entomologist 72(3): 56–59. https://doi.org/10.4039/Ent7256-3

Chamberlin RV (1943) Some records and descriptions of American diplopods. Proceedings of the Biological Society of Washington 56: 143–152. https://www.biodiversitylibrary.org/page/34564657

Chamberlin RV (1947) Some records and descriptions of diplopods chiefly in the collection of the academy. Proceedings. Academy of Natural Sciences of Philadelphia 99: 21–58. https://www.jstor.org/stable/4064366

Chamberlin RV (1949) A new genus and four new species in the Diplopod family Xystodesmidae. Proceedings of the Biological Society of Washington 62: 3–6. https://www.biodiversitylibrary.org/page/35878747

Chamberlin RV, Hoffman RL (1958) Checklist of the millipeds of North America. Bulletin - United States National Museum 212(212): 1–236. https://doi.org/10.5479/si.03629236.212

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology 65(6): 997–1008. https://doi.org/10.1093/sysbio/syw037

Cook OF (1895) Introductory note on the families of Diplopoda, in Cook & Collins, The Craspedosomatidae of North America. Annals of the New York Academy of Sciences 9: 1–9. https://doi.org/10.1111/j.1749-6632.1896.tb55430.x

de Saussure HF (1859) Note sur la famille des Polydesmides, principalement au point de vue des esp èces américaines. Linnaea Entomologica 13: 318–327.

Ewing B, Hillier L, Wendl MC, Green P (1998) Base-calling of automated sequencer traces using phred. I. Accuracy assessment. Genome Research 8(3): 175–185. https://doi.org/10.1101/gr.8.3.175

Hedin MC (1997) Speciational history in a diverse clade of habitat-specialized spiders (Araneae: Nesticidae: *Nesticus*): inferences from geographic-based sampling. Evolution; International Journal of Organic Evolution 51: 1929–1945. https://doi.org/10.2307/2411014

Hedin M, McCormack M (2017) Biogeographical evidence for common vicariance and rare dispersal in a southern Appalachian harvestman (Sabaconidae, *Sabacon cavicolens*). Journal of Biogeography 44(7): 1665–1678. https://doi.org/10.1111/jbi.12973

Hennen DA, Shelley RM (2015) A contribution on the milliped tribe Nannariini (Polydesmida: Xystodesmidae): revalidation of *Mimuloria* Chamberlin 1928; identities of *Fontaria oblonga* C. L. Koch 1847, and *Nannaria minor* Chamberlin 1918; elucidation of the tribal range; and commentaries on *Nannaria* Chamberlin 1918, and *Oenomaea* Hoffman 1964. Insecta Mundi 0418: 1–21. https://journals.flvc.org/mundi/article/view/0418

Hodge KT, Hajek AE, Gryganskyi A (2017) The first entomophthoralean killing millipedes, *Arthrophaga myriapodina* n. gen. sp. nov., causes climbing before host death. Journal of Invertebrate Pathology 149: 135–140. https://doi.org/10.1016/j.jip.2017.08.011

Hoffman RL (1948) Three new eastern millipeds of the family Xystodesmidae. Journal of the Washington Academy of Sciences 38: 346–350. https://www.jstor.org/stable/24531645

Hoffman RL (1949a) Three new species of Diplopoda from Virginia. Proceedings of the Biological Society of Washington 62: 81–88. https://www.biodiversitylibrary.org/page/35878793

Hoffman RL (1949b) Nine new xystodesmid millipeds from Virginia and West Virginia, with records of established species. Proceedings of the United States National Museum 99(3244): 371–389. https://doi.org/10.5479/si.00963801.99-3244.371

Hoffman RL (1950) Records and descriptions of diplopods from the southern Appalachians. Journal of the Elisha Mitchell Scientific Society 66: 11–33. https://www.jstor.org/stable/24334005

Hoffman RL (1958) Revision of the milliped genus *Pachydesmus* (Polydesmida: Xystodesmidae). Proceedings of the United States National Museum 108(3399): 181–218. https://doi.org/10.5479/si.00963801.108-3399.181

Hoffman RL (1960) Revision of the milliped genus *Cherokia* (Polydesmida: Xystodesmidae). Proceedings of the United States National Museum 112(3436): 227–264. https://doi.org/10.5479/si.00963801.112-3436.227

Hoffman RL (1964) The status of *Fontaria pulchella* Bollman, with the proposal of a new genus and tribe in the diplopod family Xystodesmidae. Proceedings of the Biological Society of Washington 77: 25–34. https://www.biodiversitylibrary.org/page/34605254

Hoffman RL (1965) Revision of the milliped genera *Boraria* and *Gyalostethus* (Polydesmida: Xystodesmidae). Proceedings of the United States National Museum 117(3514): 305–348. https://doi.org/10.5479/si.00963801.117-3514.305

Hoffman RL (1978a) North American millipeds of the genus *Euryurus* (Polydesmida: Platyrhacidae). Transactions of the American Entomological Society 104: 37–68. https://www.jstor.org/stable/25078219

Hoffman RL (1978b) The taxonomic and nomenclatorical status of the milliped generic names *Parafontaria* Verhoeff, *Cyphonaria* Verhoeff, and *Japonaria* Attems (Polydesmida, Xystodesmidae). Spixiana 1: 215–224.

Hoffman RL (1980 "1979") Classification of the Diplopoda. Muséum d'histoire naturelle, Genève, 237 pp. [date of publication 3 June 1980]

Hoffman RL (1999) Checklist of the millipedes of North and Middle America. Virginia Museum of Natural History Special Publication 8: 1–584.

Jeekel CAW (1971) Nomenclator Generum et Familiarum Diplopodorum: A list of the genus and family-group names in the Class Diplopoda from the 10th edn. of Linnaeus, 1758, to the end of 1957. Monografieënvan de Nederlandse Entomologische Vereniging 5: 1–412.

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Kane TC, Barr TC, Stratton GE (1990) Genetic patterns and population structure in Appalachian *Trechus* of the *vandykei* group (Coleoptera: Carabidae). Brimleyana 16: 133–150. https://www.biodiversitylibrary.org/item/228580#page/135/mode/1up

Koch CL (1847) System der Myriapoden mit den Verzeichnissen und Berichtigungen zu Deutschlands Crustaceen, Myriapoden und Arachniden. In: Panzer GWF & Herrich-Schäffer, A.: Kritische Revision der Insectenfaune Deutschlands, III. Bändchen, Regensburg, 1–196. https://doi.org/10.5962/bhl.title.49866

Loomis HF, Hoffman RL (1948) Synonymy of various Diplopods. Proceedings of the Biological Society of Washington 61: 51–54. https://www.biodiversitylibrary.org/page/34498501

Löytynoja A, Goldman N (2005) An algorithm for progressive multiple alignment of sequences with insertions. Proceedings of the National Academy of Sciences of the United States of America 102(30): 10557–10562. https://doi.org/10.1073/pnas.0409137102

Maddison WP, Maddison DR (2010) Mesquite: a molecular system for evolutionary analysis. Version 3.61. http://mesquiteproject.org/

Marek PE (2010) A revision of the Appalachian millipede genus *Brachoria* Chamberlin, 1939 (Polydesmida: Xystodesmidae: Apheloriini). Zoological Journal of the Linnean Society 159(4): 817–889. https://doi.org/10.1111/j.1096-3642.2010.00633.x

Marek PE, Bond JE (2006) Phylogenetic systematics of the colorful, cyanide-producing millipedes of Appalachia (Polydesmida, Xystodesmidae, Apheloriini) using a total evidence Bayesian approach. Molecular Phylogenetics and Evolution 41(3): 704–729. https://doi.org/10.1016/j.ympev.2006.05.043

Marek PE, Bond JE (2009) A Müllerian mimicry ring in Appalachian millipedes. Proceedings of the National Academy of Sciences of the United States of America 106(24): 9755–9760. https://doi.org/10.1073/pnas.0810408106

Marek PE, Moore W (2015) Discovery of a glowing millipede in California and the gradual evolution of bioluminescence in Diplopoda. Proceedings of the National Academy of Sciences of the United States of America 112(20): 6419–6424. https://doi.org/10.1073/pnas.1500014112

Marek PE, Tanabe T, Sierwald P (2014) A species catalog of the millipede family Xystodesmidae. Virginia Museum of Natural History Publications 17: 1–117.

Marek PE, Means JC, Hennen DA (2018) *Apheloria polychroma*, a new species of millipede from the Cumberland Mountains (Polydesmida: Xystodesmidae). Zootaxa 4375(3): 409–425. https://doi.org/10.11646/zootaxa.4375.3.7

McNeill J (1887) Description of twelve new species of Myriopoda chiefly from Indiana. Proceedings of the United States National Museum 10(632): 328–334. https://doi.org/10.5479/si.00963801.10-632.328

Means JC, Marek PE (2017) Is geography an accurate predictor of evolutionary history in the millipede family Xystodesmidae? PeerJ 5: e3854. https://doi.org/10.7717/peerj.3854

Means JC, Francis EA, Lane AA, Marek PE (2015) A general methodology for collecting and preserving xystodesmid and other large millipedes for biodiversity research. Biodiversity Data Journal 3: e5665. https://doi.org/10.3897/BDJ.3.e5665

Means JC, Hennen DA, Tanabe T, Marek PE (2021a) Phylogenetic systematics of the millipede family Xystodesmidae. Insect Systematics and Diversity 5(2): 1–26. https://doi.org/10.1093/isd/ixab003

Means JC, Hennen DA, Marek PE (2021b) A revision of the *minor* species group in the millipede genus *Nannaria* Chamberlin, 1918 (Diplopoda, Polydesmida, Xystodesmidae). ZooKeys 1030: 1–180. https://doi.org/10.3897/zookeys.1030.62544

Mikhaljova EV (2021) Review of the millipede genus *Levizonus* Attems, 1898, with description of a new species from the Far East of Russia (Diplopoda, Polydesmida, Xystodesmidae). European Journal of Taxonomy 751: 159–184. https://doi.org/10.5852/ejt.2021.751.1387

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37(5): 1530–1534. https://doi.org/10.1093/molbev/msaa015

Omernik JM, Griffith GE (2014) Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. Environmental Management 54(6): 1249–1266. https://doi.org/10.1007/s00267-014-0364-1

Rafinesque CS (1820) Annual synopsis of new genera and species of animals and plants discovered in North America. Annals of Nature 1: 1–20.

Rios N (2018) GEOLocate - software for georeferencing natural history data. [Web application software]. http://www.geo-locate.org

Rohr JR, Mahan CG, Kim KC (2009) Response of arthropod biodiversity to foundation species declines: The case of the eastern hemlock. Forest Ecology and Management 258(7): 1503–1510. https://doi.org/10.1016/j.foreco.2009.07.002

Shelley RM (1975) The identity of *Nannaria conservata* Chamberlin, with notes on an abnormal male and descriptions of two new species of *Nannaria* from North Carolina (Diplopoda: Polydesmida: Xystodesmidae). Proceedings of the Biological Society of Washington 88: 179–187. https://www.biodiversitylibrary.org/page/34561171

Shelley RM (1990 “1989”) Revision of the milliped family Eurymerodesmidae (Polydesmida: Chelodesmidea). Memoirs of the American Entomological Society: 1–112. https://www.biodiversitylibrary.org/page/38783956

Shelley RM (2000) Annotated checklist of the millipeds of North Carolina (Arthropoda: Diplopoda), with remarks on the genus *Sigmoria* Chamberlin (Polydesmida: Xystodesmidae). Journal of the Elisha Mitchell Scientific Society 116: 177–205. https://www.jstor.org/stable/24335390

Shelley RM, Sierwald P, Kiser SB, Golovatch SI (2000) Nomenclator generum et familiarum Diplopodorum II. Pensoft, Sofia, Moscow, 1–167 pp.

Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. https://www.simplemappr.net

Thomas SM, Hedin M (2008) Multigenic phylogeographic divergence in the paleoendemic southern Appalachian opilionid *Fumontana deprehendor* Shear (Opiliones, Laniatores, Triaenonychidae). Molecular Phylogenetics and Evolution 46(2): 645–658. https://doi.org/10.1016/j.ympev.2007.10.013

Thorell T (1869) On European spiders. Part I. Review of the European genera of spiders, preceded by some observations on zoological nomenclature. Nova acta Regiae Societatis Scientiarum Upsaliensis 7: 1–108.

Whitehead DR, Shelley RM (1992) Mimicry among aposematic Appalachian xystodesmid millipeds (Polydesmida: Chelodesmidea). Proceedings of the Entomological Society of Washington 94: 177–188. https://www.biodiversitylibrary.org/page/16245230

Williams SR, Hefner RA (1928) The millipedes and centipedes of Ohio. Ohio State University Bulletin 33: 93–146.

Wray DL (1967) Insects of North Carolina, 3rd Supplement. North Carolina Department of Agriculture, Raleigh, 181 pp.

Zahnle XJ, Sierwald P, Ware S, Bond JE (2020) Genital morphology and the mechanics of copulation in the millipede genus *Pseudopolydesmus* (Diplopoda: Polydesmida: Polydesmidae). Arthropod Structure & Development 54: 1–19. https://doi.org/10.1016/j.asd.2020.100913

Supplementary material 1

***Nannaria wilsoni* species group specimens examined**

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Occurrences.

Explanation note: A Darwin Core Standard spreadsheet of the *Nannaria wilsoni* species group specimens examined.

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl1

Supplementary material 2

***Nannaria wilsoni* species group morphology scoring matrix**

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Morphological scoring matrix.

Explanation note: A spreadsheet with the morphological characters scored for each species in the *Nannaria wilsoni* group.

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl2

Supplementary material 3

Key to *Nannaria wilsoni* species group morphological characters

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Key to morphological matrix.

Explanation note: Key listing the qualitative morphological characters used for descriptions and diagnoses.

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl3

Supplementary material 4

Amplification procedures for genes

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Methodology.

Explanation note: Summary of amplification procedures for the newly developed genes used in this project.

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl4

Supplementary material 5

List of taxa and Genbank numbers

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Genetic.

Explanation note: List of taxa used in molecular analyses, organized alphabetically by genus and species. Acc# refer to the NCBI Genbank database. All specimens available from the corresponding author by request and stored in the Virginia Tech Insect Collection, Blacksburg, Virginia, USA.

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl5

Supplementary material 6

Molecular phylogeny of *Nannaria* and outgroups

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Phylogenetic.

Explanation note: Full maximum likelihood phylogeny of *Nannaria* and outgroups used in the analysis. Phylogeny estimated from the gene regions 16S, COI, EF1a, 28S, RPB1, and fbox. Branches colored according to clades: *Oenomaea pulchella* (green), Eurymerodesmini (magenta), Euryurini (red), *Nannaria minor* group (brown), and *Nannaria wilsoni* group (blue). Bootstrap support values > 70 indicated by asterisks (*).

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl6

Supplementary material 7

Individual gene trees

Authors: Derek A. Hennen, Jackson C. Means, Paul E. Marek

Data type: Phylogenetic.

Explanation note: Maximum likelihood phylogenies of *Nannaria* and outgroups used in the analysis. Phylogenies estimated from the gene regions 16S(A), 28s(B), COI(C), EF1a(D), fbox(E), and RPB1(F). Branches colored according to clades: *Oenomaea pulchella* (green), Eurymerodesmini (magenta), Euryurini (red), *Nannaria minor* group (brown), and *Nannaria wilsoni* group (blue). Bootstrap support values > 70 indicated by asterisks (*).

Link: https://doi.org/10.3897/zookeys.1096.73485.suppl7

ZooKeys 1096: 119–160 (2022)
doi: 10.3897/zookeys.1096.79382
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Three new species of Apseudomorpha (Crustacea, Tanaidacea) from Jiaozhou Bay, the Yellow Sea, and the South China Sea off coasts of China

You-Wei Tzeng[1,2,3,4], Lin Ma[1,2,3,4], Xinzheng Li[1,2,3,4]

1 *Department of Marine Organism Taxonomy and Phylogeny, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China* **2** *University of Chinese Academy of Sciences, Beijing 100049, China* **3** *Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao, 266071, China* **4** *Laboratory for Marine Biology and Biotechnology, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, China*

Corresponding authors: Xinzheng Li (lixzh@qdio.ac.cn), Lin Ma (malin@qdio.ac.cn)

Academic editor: Luiz F. Andrade | Received 16 December 2021 | Accepted 10 March 2022 | Published 15 April 2022

http://zoobank.org/2F78255F-081C-429D-B50D-53D252224BB2

Citation: Tzeng Y-W, Ma L, Li X (2022) Three new species of Apseudomorpha (Crustacea, Tanaidacea) from Jiaozhou Bay, the Yellow Sea, and the South China Sea off coasts of China. ZooKeys 1096: 119–160. https://doi.org/10.3897/zookeys.1096.79382

Abstract
Three new species of the crustacean order Tanaidacea are described from the coasts of China. *Apseudes spinidigitus* **sp. nov.** (family Apseudidae), from the South China Sea, can be distinguished from the most similar species, *A. nhatrangensis*, by the features of the maxilliped endite, cheliped dactylus, pereopod 1 carpus and propodus, and pleopods basal article. *Phoxokalliapseudes shandongensis* **sp. nov.** (family Kalliapseudidae), from Jiaozhou Bay and the Yellow Sea, can be differentiated from the most similar species, *P. gibbus*, by the features of the antennule article 1, pereopods 1 and 6 propodi, and uropod basal article. *Swireapseudes planafrontis* **sp. nov.** (family Parapseudidae), from Jiaozhou Bay, can be clearly separated from its congeners by its rostrum, antennule article 1, and pereopod 4 dactylus. A morphological key and comparison table of genus *Apseudes* from the South China Sea, as well as all known species of the genera *Phoxokalliapseudes* and *Swireapseudes* are provided.

Keywords
Apseudes, Apseudidae, Kalliapseudidae, Parapseudidae, *Phoxokalliapseudes*, *Swireapseudes*

Introduction

The suborder Apseudomorpha Sieg, 1980 contains 12 families, including more than 530 extant species recorded to date (WoRMS 2021). All the species of the suborder are small-sized crustaceans mainly below 15 mm that widely inhabit various shallow marine benthic habitats, especially abundant in coral reefs, estuaries, and mangroves from the tropics to temperate waters (Błażewicz-Paszkowycz et al. 2012). Despite their wide distribution in shallow waters, knowledge of species diversity and composition from many areas is still lacking. For example, studies on taxonomy of apseudomorph tanaidaceans from the coasts of China were only intensively focused on the adjacent waters of Hong Kong (Fig. 1; Bamber 1997, 2000, 2008; Bamber and Sheader 2003) and eastern Taiwan (Fig. 1; Tzeng and Hsueh 2014). There is a knowledge gap of more than a decade, and species from the extensive coastline of China remain unknown.

In the present study, three species of Apseudomorpha from coasts of China are recognized. The first species has a well separated eye lobe, one spine-like anterolateral apophysis on pereonites 3–6, denticulate outer margin of mandible, fossorial type of pereopod 1, and one spine-like apophysis on pereopod 1 coxa, belonging to *Apseudes* Leach, 1814, a worldwide genus with over 40 species (Larsen et al. 2011). The second species has ventral spiniform setae on antennule peduncle article 1, numerous long plumose setae on mandible palp, maxilliped palp and cheliped, one distal spiniform seta on mandible palp, four cusps on labrum, very long male pereopod 6 dactylus, and two posterior plumose setae on pleotelson, fitting the diagnosis of *Phoxokalliapseudes* Drumm & Heard, 2011, a genus with species all recorded from western Pacific by far (Drumm and Heard 2011). The third species has fossorial type of pereopod 1 but without spine-like apophysis on coxa, chelate or subchelate dactylus on all pereopods, long and thin pereopod 6 basis, conforming to the features of *Swireapseudes* Bamber, 1997, a small genus with only two species, recorded from the South China Sea and Northwestern Atlantic Ocean (Guţu 2008). Morphological examination confirms that all three species are different from their congeners and are recognised as new to science, and they are described here.

Materials and methods

The specimens of Apseudomorpha were collected from Jiaozhou Bay, the Yellow Sea, and the South China Sea, from 3 to 55 m depth. The first species, belonging to the genus *Apseudes*, were collected from the South China Sea off Guangdong Province during the National Comprehensive Oceanography Survey cruise carried out in 1959–1964. The second species, belonging to the genus *Phoxokalliapseudes*, was collected during the Jiaozhou Bay cruise carried out in 1959–1964, the quarterly Jiaozhou Bay survey cruise during 2003–2021, and the Yellow Sea cruise conducted in 2019. The third species, belongs to the genus *Swireapseudes*, was also collected during the quarterly Jiaozhou Bay survey cruise. The collecting sites of new species from this study, as well as the distribution of previously recorded species from coasts of China, are shown in Fig. 1. All

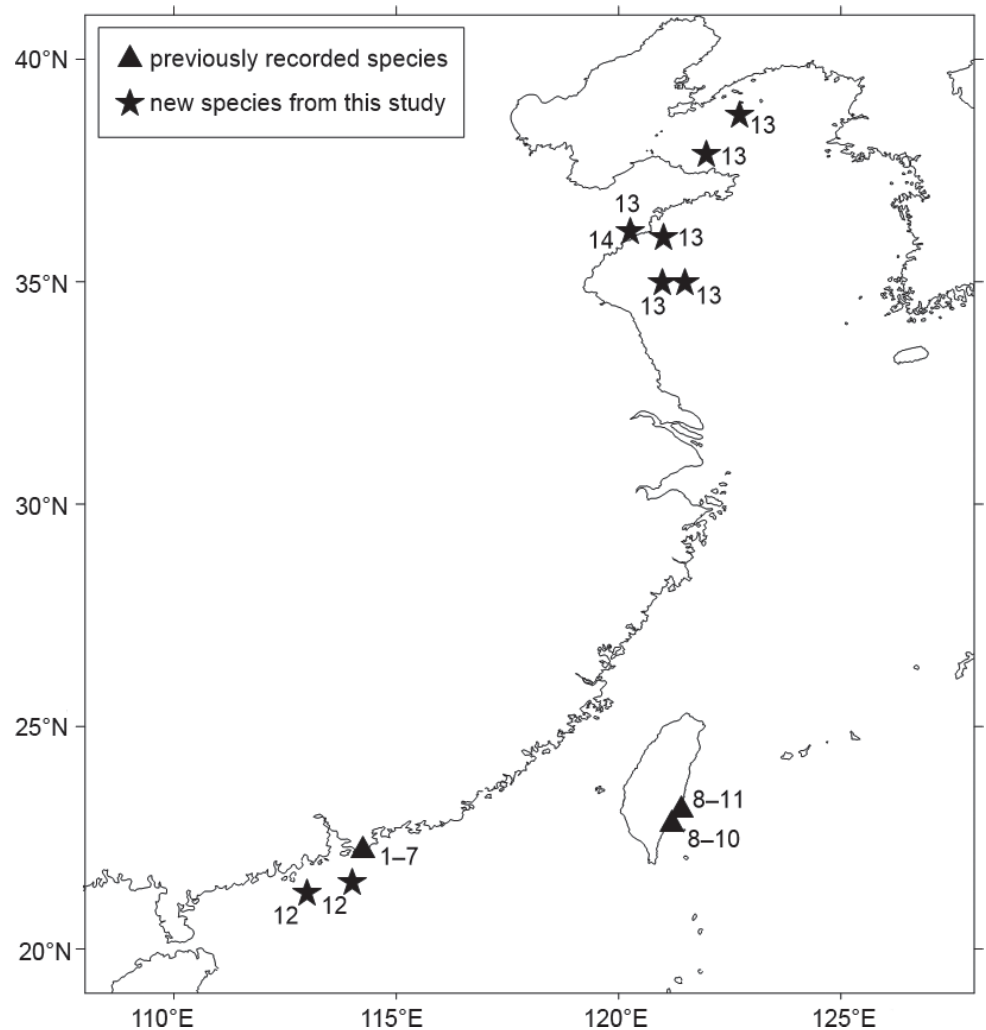

Figure 1. Distribution of Apseudomorpha from coasts of China: **1** *Paradoxapseudes mortoni* (Bamber, 1997) **2** *Discapseudes* (*Discapseudes*) *mackiei* Bamber, 1997 **3** *Swireapseudes toloensis* Bamber, 1997 **4** *Siegius gallardoi* (Shiino, 1963) **5** *Unguispinosus hodgsoni* (Bamber, 2000) **6** *Tanapseudes sinensis* Bamber, 2000 **7** *Apseudes manna* Bamber, 2008 **8** *Paradoxapseudes pangcahi* Tzeng & Hsueh, 2014 **9** *Pseudoapseudomorpha tagopilosus* Tzeng & Hsueh, 2014 **10** *Synapseudes hansmuelleri* Guțu, 2006 **11** *Indoapseudes multituberculata* Tzeng & Hsueh, 2014 **12** *Apseudes spinidigitus* sp. nov. **13** *Phoxokalliapseudes shandongensis* sp. nov. **14** *Swireapseudes planafrontis* sp. nov.

samples were collected using a box corer or a grab, then sieved over a 0.5 mm mesh and specimens were preserved in 75% alcohol or 5% neutral formalin. The specimens were examined and dissected under a stereo microscope (Zeiss Stemi 2000-C). Body parts and appendages of the specimens were examined and photographed using a Nikon Eclipse Ni. Digital images were enhanced with the computer software Helicon Focus 7.0.2.

Drawings were prepared by tracing outlines of examined body parts and appendages from digitised images using CorelDRAW 2020. The descriptions of species are mostly based on paratypes and allotypes. All the measurements and proportions of the morphological structures were based on maximum width, except body length which was measured from rostrum tip to the pleotelson apex. Terminology used in the present study mainly follows Drumm and Heard (2011). All specimens of this study were deposited at the Marine Biological Museum, Chinese Academy of Sciences (**MBM**, or **MBMCAS**), in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China.

Systematics

Order Tanaidacea Dana, 1849
Suborder Apseudomorpha Sieg, 1980
Superfamily Apseudoidea Leach, 1814
Family Apseudidae Leach, 1814
Subfamily Apseudinae Leach, 1814

Genus *Apseudes* Leach, 1814

Type species. *Apseudes talpa* (Montagu, 1808)

***Apseudes spinidigitus* sp. nov.**
http://zoobank.org/025453A4-9F04-4F9F-8FD3-C16CB633FAAF
Figs 2–5, Table 1

Type material. ***Holotype*:** MBM287293, non-ovigerous simultaneous hermaphrodite, 8.3 mm; the South China Sea off Guangdong Province, China, 21 October 1959, from mud-sandy substrate at a depth of 43 m, 21°15'N, 113°00'E. ***Paratypes*:** MBM032095, one non-ovigerous simultaneous hermaphrodite, 8.5 mm, completely dissected and body parts preserved in 75% alcohol; the South China Sea off Guangdong Province, China, 10 January 1960, from muddy substrate at a depth of 55 m, 21°30'N, 114°00'E. MBM032282, four non-ovigerous simultaneous hermaphrodites; same collection data as holotype.

Type locality. Northern South China Sea.

Etymology. The name is derived from the Latin *spinosus* (spinous) and *digitus* (finger), referring to the dactylus and fixed finger of cheliped both equipped with one conspicuous apophysis on the incisive margins.

Diagnosis. ***Non-ovigerous simultaneous hermaphrodite. Rostrum*** cordiform, distally pointed. ***Carapace*** lateral margin with one large spine-like anterior apophysis. ***Pereonites** 3–6* with one curved spine-like anterolateral apophysis. ***Maxilliped*** endite inner margin with two coupling hooks. ***Cheliped*** fixed finger and dactylus incisive

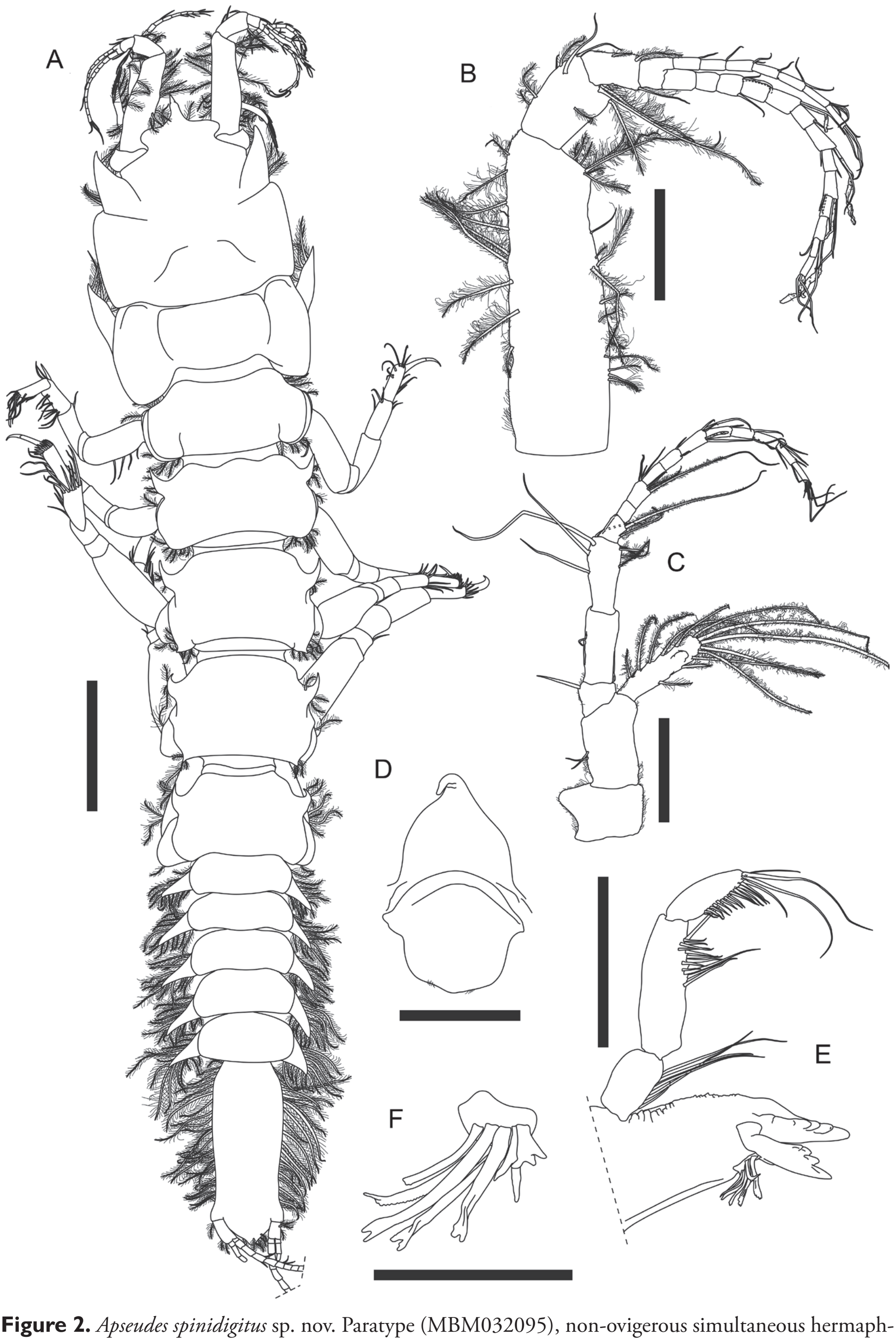

Figure 2. *Apseudes spinidigitus* sp. nov. Paratype (MBM032095), non-ovigerous simultaneous hermaphrodite **A** body dorsal view **B** right antennule **C** right antenna **D** epistome and labrum **E** left mandible **F** right mandible setal row. Scale bars: 1 mm (**A**); 0.2 mm (**B, C, E**); 0.1mm (**D, F**).

margin with one conspicuous apophysis, respectively. ***Pereopod 1*** merus and carpus each with one dorsodistal and one ventrodistal spiniform seta; propodus with one dorsodistal and four ventral spiniform setae. ***Pleopod*** basal article with four inner plumose setae.

Description. ***Simultaneous hermaphrodite*** **(non-ovigerous paratype MBM032095).** ***Body*** (Fig. 2A) dorsoventrally flattened, 8.5 mm long, 5.8× as long as broad, posteriorly narrower. ***Carapace*** subrectangular, ~ 0.2× as long as total body length, 1.1× as long as broad; rostrum cordiform, with proximal half laterally extended, distal half narrow, terminally pointed and slightly down-curved; lateral margin with one large spine-like anterior apophysis adjacent to eye lobe, with three outer and three inner plumose setae on apophysis. ***Eye lobe*** well separated, wide and short, without visual elements. ***Pereon*** ~ 0.5× as long as total body length; pereonite 1 broadest, slightly broader than carapace, 0.5× as long as broad; pereonite 2 0.7× as long as pereonite 1, 0.5× as long as broad, with *ca.* three anterolateral and five posterolateral plumose setae; pereonite 3 slightly longer than pereonite 2, 0.5× as long as broad, anterolateral margin with one curved spine-like apophysis and three plumose setae, posterolateral margin with *ca.* seven plumose setae; pereonite 4 1.2× as long as pereonite 3, 0.7× as long as broad, anterolateral margin with one curved spine-like apophysis and three plumose setae, posterolateral corner pointed, with *ca.* seven plumose setae; pereonite 5 similar to pereonite 4 but with three posterolateral plumose setae; pereonite 6 0.9× as long as pereonite 5, 0.7× as long as broad, anterolateral margin with one curved spine-like apophysis and *ca.* three plumose setae, pereonites 1–5 each with one hyposphenia, pereonite 6 with genital cone. ***Pleon*** as long as carapace, posteriorly narrower, each pleonite with pointed epimera and ~ 12 lateral plumose setae. ***Pleotelson*** 0.9× as long as carapace, 2.5× as long as broad, lateral margin with > 20 plumose setae, terminally subtriangular, with *ca.* six posterior plumose setae.

Antennule (Fig. 2B) peduncle article 1 3.2× as long as broad, outer margin with ~ 17 circumplumose setae, two broom setae and one simple seta, inner margin with nine circumplumose setae; article 2 short, 0.3× as long as article 1, 1.8× as long as broad, with *ca.* seven circumplumose setae and three simple setae; article 3 0.6× as long as article 2, 1.7× as long as broad, with three circumplumose setae; article 4 naked, 0.5× as long as article 3, *ca.* as long as broad; outer flagellum 13-articled, articles 3, 5, 7, 9, 11, and 13 with one distal aesthetasc and 1–4 distal simple setae, other articles with one distal simple seta or naked; inner flagellum 7-articled, articles 1–5 with one or two distal simple setae, articles 6 and 7 with four distal simple setae.

Antenna (Fig. 2C) peduncle article 1 short and covered with setules, 0.9× as long as broad, inner margin with conical apophysis; article 2 1.6× as long as article 1, 1.7× as long as broad, with two inner simple setae; squama slender, slightly longer than article 2, 3.8× as long as broad, with 13 circumplumose setae; article 3 short, 0.4× as long as article 2, 0.9× as long as broad, with one inner distal simple seta; article 4 0.8× as long as article 2, 2.4× as long as broad, with one inner simple seta; article 5 0.8× as long as article 2, 2.2× as long as broad, outer margin with three circumplumose and one broom seta, inner margin with four long simple setae; flagellum 11-articled, article 1 with two long distal circumplumose setae, article 3 with two long distal circumplumose setae and five distal simple setae, article 6 with one distal aesthetasc and four distal simple setae, article 11 with eight distal simple setae, and other articles with 1–4 simple setae or naked.

Epistome (Fig. 2D) with one strong and curved apical apophysis. *Labrum* (Fig. 2D) rounded with some setules.

Left mandible (Fig. 2E) outer margin denticulate; incisor with four or five denticles; lacinia mobilis large and subrectangular, distal margin with four denticles; setal row with four serrate setae and three simple setae; molar not examined; palp 3-articled, article 1 1.7× as long as broad, inner margin with five simple setae, article 2 shorter than articles 1 and 3 combined, 3× as long as broad, inner margin with 12 simple setae and one very long simple seta, article 3 1.2× as long as article 1, 3× as long as broad, inner margin with 15 simple setae and two very long simple setae. *Right mandible* similar to left mandible but without lacinia mobilis, setal row (Fig. 2F) with one trifurcate, four bifurcate, one serrate, and one blunt seta.

Labium (Fig. 3A) antero-outer corner near palp with one small apophysis; palp large and covered with setules, with three distal simple setae.

Maxillule (Fig. 3B) covered with setules; inner endite with five distal plumose setae; outer endite with two subdistal simple setae and ten distal spiniform setae; palp 2-articled, article 2 with seven subdistal plumose setae.

Maxilla (Fig. 3C) outer margin covered with setules; outer lobe of movable endite with two plumose setae and seven serrate setae; inner lobe of movable endite with a row of six blunt setae, a cluster of > 13 simple setae, and two serrate setae; outer lobe of fixed endite with one comb-like seta, two trifurcate setae, one bifurcate seta, two plumose setae, and > 16 simple setae, outer margin covered with setules; inner lobe of fixed endite with two long setae only serrate on distal 1/4, five serrate setae, and ~ 39 simple setae along distal margin.

Maxilliped (Fig. 3D, E) basis covered with setules; endite (Fig. 3E) inner margin with two coupling hooks, inner fold with 11 circumplumose setae, distal margin with two blunt, three bifurcate, and eight simple setae; palp 4-articled, article 1 with two short outer-distal circumplumose setae and two inner circumplumose setae, article 2 outer-distal, distal, and inner margin with > 37 simple and five circumplumose setae; article 3 inner margin with ~ 16 simple setae; article 4 distal margin with nine simple setae.

Epignath (Fig. 3F) typical of genus, partially covered with setules, with one stout plumose seta.

Cheliped (Fig. 4A) exopod 3-articled, article 3 with four plumose setae; basis 2.2× as long as broad, ventral margin with one proximal plumose seta, one strong spiniform seta midway, and three distal plumose setae; merus 0.8× as long as basis, 3× as long as broad, ventral margin with two plumose setae midway, one very large subdistal spine-like apophysis, eight subdistal and one distal plumose seta; carpus elongate, 1.2× as long as basis, 2.8× as long as broad, with one dorsodistal spine-like apophysis, one dorsodistal plumose seta, and six plumose setae along ventral margin; propodus

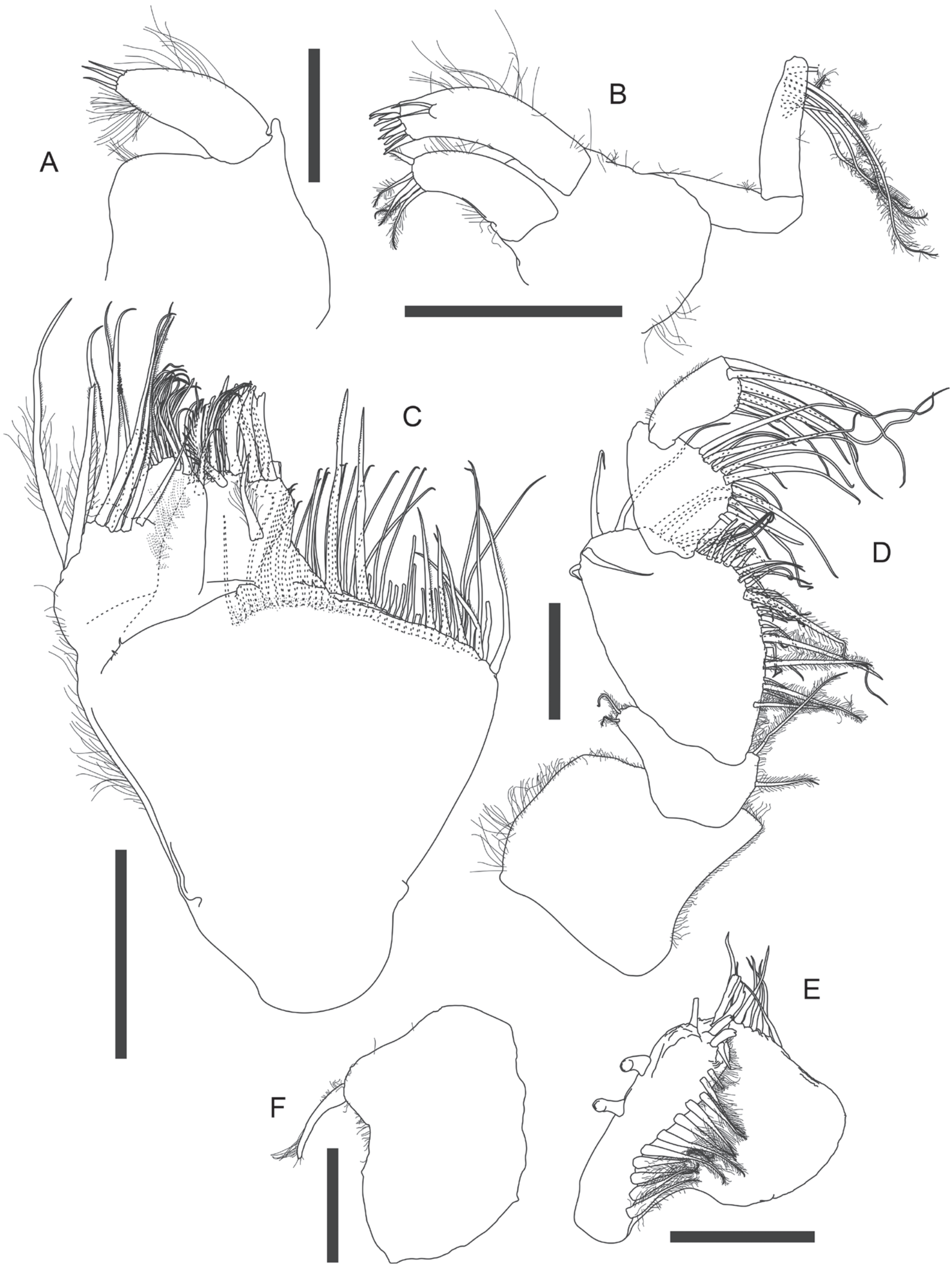

Figure 3. *Apseudes spinidigitus* sp. nov. Paratype (MBM032095), non-ovigerous simultaneous hermaphrodite **A** labium **B** maxillule **C** maxilla **D** maxilliped **E** maxilliped endite **F** epignath. Scale bars: 0.1 mm (**A, D–F**); 0.2 mm (**B, C**).

palm 1.4× as long as broad, with one dorsoproximal plumose seta, two dorsodistal plumose setae, one plumose setae near dactylus articulation, and eight plumose setae along ventral margin of palm and fixed finger; fixed finger (Fig. 4B) nearly as long as

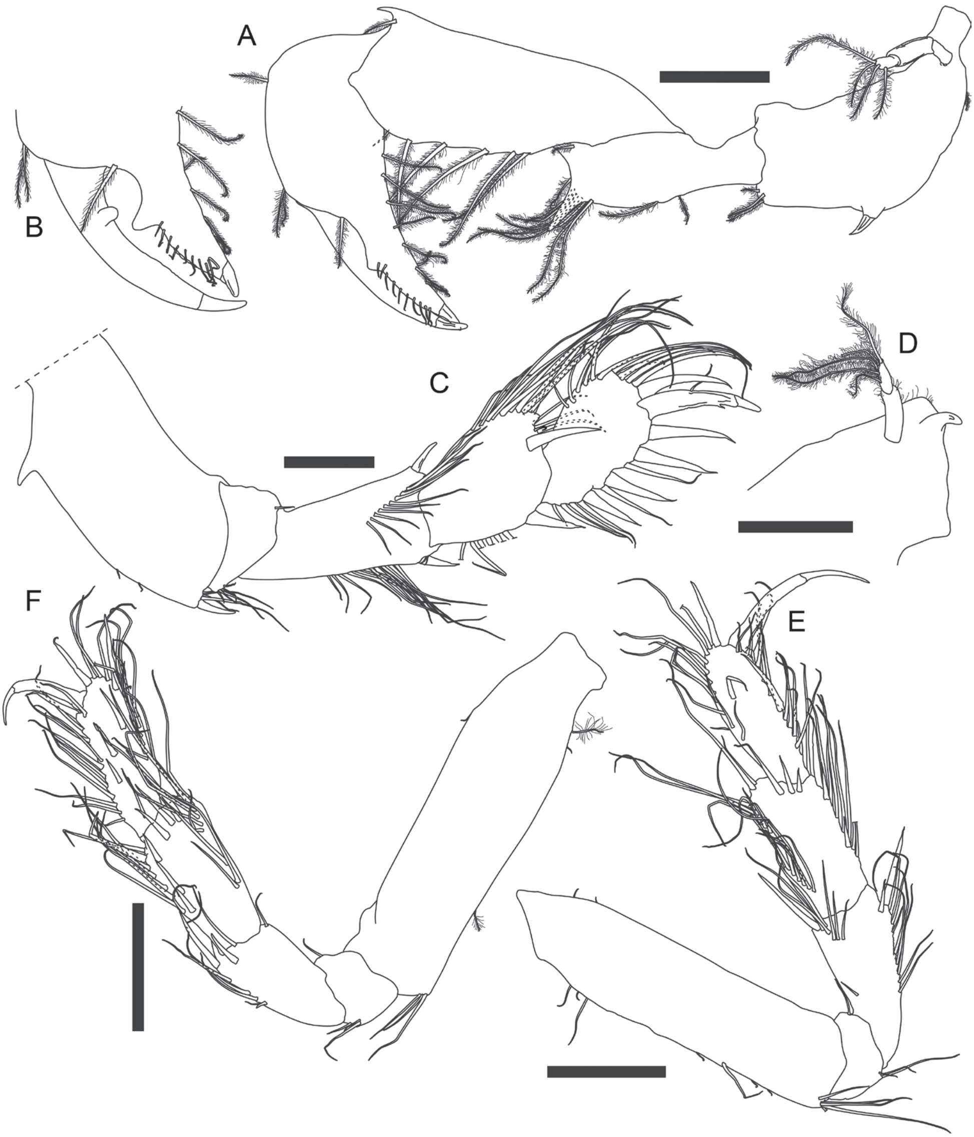

Figure 4. *Apseudes spinidigitus* sp. nov. Paratype (MBM032095), non-ovigerous simultaneous hermaphrodite **A** left cheliped **B** left cheliped fixed finger and dactylus **C** right pereopod 1 **D** proximal end of left pereopod 1 basis **E** right pereopod 2 **F** left pereopod 3. Scale bars: 0.2 mm.

palm, ~ 2.1× as long as broad, incisive margin with one large apophysis and ten simple setae on distal half; dactylus (Fig. 4B) plus unguis 4.3× as long as broad, slightly curved, incisive margin with one conspicuous apophysis.

Pereopod 1 (Fig. 4C, D) coxa (Fig. 2A) with large and pointed spine-like apophysis and five plumose setae; exopod 2-articled, article 2 with five plumose setae; basis ~ 2.4× as long as broad, with one subdorsal proximal apophysis near exopod, ventral margin with one subproximal apophysis, two subdistal simple setae, four distal simple setae and one distal spiniform seta; ischium with one short dorsodistal simple seta and four short ventrodistal simple setae; merus 2.2× as long as broad, with one dorsodistal spiniform seta and a row of ~ 11 lateral simple setae, ventral margin with a row of ~ 11 simple setae on distal half, one distal spiniform seta and two short distal simple setae; carpus short and thick, dorsally extended, 0.7× as long as merus, 1.3× as long as broad, dorsal margin with a row of ~ 12 long simple setae on distal half, one short and three longer distal simple seta, and one large distal spiniform seta, ventral margin with six simple setae midway and one large distal spiniform seta; propodus *ca.* as long as carpus, slightly thinner than carpus, dorsal margin with ~ 11 simple setae on distal half, and one large distal spiniform seta, ventral margin with six simple setae and four large spiniform setae; dactylus plus unguis 0.9× as long as propodus, slightly curved, dorsal margin with one simple seta midway, ventral margin with one subdistal spinule.

Pereopod 2 (Fig. 4E) coxa with one plumose seta; basis 4× as long as broad, dorsal margin with two short simple setae on proximal half, ventral margin with one short and two longer simple setae on proximal half, three short and one longer simple seta on distal half, and a cluster of five distal simple setae; ischium with one dorsodistal and three ventrodistal simple setae; merus ~ 0.5× as long as basis, 2.3× as long as broad, with one subdorsal simple seta on proximal half, a row of six dorsodistal simple setae, one long and slender dorsodistal spiniform seta, ventral margin with eight simple setae along distal half, one long slender subdistal spiniform seta and one shorter subdistal spiniform seta; carpus 0.8× as long as merus, 2× as long as broad, dorsal margin with a row of *ca.* seven simple setae on proximal half, *ca.* six simple setae on distal half, and two distal simple setae, distal margin with a row of three lateral spiniform setae, ventral margin with eight simple setae, one long and slender spiniform seta, and two shorter spiniform setae; propodus slightly longer than carpus, 2.9× as long as broad, with ~ 12 simple setae along distal half of dorsal margin, one long and slender dorsodistal spiniform seta, and one lateral spiniform seta, ventral margin with ~ 11 simple setae, one long and slender spiniform seta midway and one distal spiniform seta; dactylus plus unguis thin and curved, nearly as long as propodus, with one doral seta midway, unguis ~ 0.7× as long as dactylus.

Pereopod 3 (Fig. 4F) basis 3.7× as long as broad, dorsal margin with one short simple seta on proximal half, ventral margin with one broom and one short simple seta on proximal half, one broom seta on distal half, and three simple distal setae; ischium with one dorsodistal and three ventrodistal simple setae; merus 0.4× as long as basis, 2.2× as long as broad, with one dorsodistal simple seta, one distolateral simple seta, and one distolateral spiniform seta, ventral margin with four simple setae on distal half, one small spiniform seta midway, and one long and slender distal spiniform seta; carpus slightly longer than merus, 2.1× as long as broad, with three long simple setae on proximal half, a row of *ca.* seven simple setae on distal half of dorsal margin, and a row of six lateral spiniform setae, distal one longer, ventral margin with six simple setae and one spiniform seta along distal half; propodus slightly longer than carpus, 2.8× as long as broad, with ~ 11 simple setae and two long and slender spiniform setae on distal half of dorsal margin, three longer and one very short lateral spiniform seta, ventral margin with 11 simple setae and one distal spiniform seta; dactylus plus unguis thin and curved, ~ 0.7× as long as propodus, unguis 0.5× as long as dactylus.

Pereopod 4 (Fig. 5A) coxa with one plumose seta; basis 2.9× as long as broad, dorsal margin with two short proximal simple setae and two broom setae midway, ventral margin with two longer and one short distal simple seta; ischium with one dorsodistal simple seta and one ventrodistal simple seta; merus ~ 0.4× as long as basis, 2.3× as long as broad, dorsal margin with one distal simple seta, ventral margin with three simple setae midway, four spiniform setae and two simple setae on distal half; carpus ~ 1.2× as long as merus, 2.7× as long as broad, with ~ 11 spiniform setae and > 17 simple setae along ventral to distal margin; propodus shorter and thinner than carpus, 0.8× as long as carpus, 2.9× as long as broad, with a comb-like row of numerous short and fine dorsodistal serrate setae and a cluster of numerous longer dorsodistal simple setae, ventral margin with ~ 11 longer simple setae and *ca.* seven short simple setae; dactylus plus unguis slender and slightly curved, 0.6× as long as propodus, dorsal margin with one seta midway, unguis 0.5× as long as dactylus.

Pereopod 5 (Fig. 5B) basis dorsal margin with one broom seta on proximal half, ventral margin with one short midway and one longer distal simple seta; ischium with one dorsal and three ventrodistal simple setae; merus 2.4× as long as broad, with one dorsodistal, one subventral, two ventrodistal simple setae, and three ventrodistal spiniform setae; carpus slightly longer and thinner than merus, 2.6× as long as broad, with *ca.* ten spiniform setae and > 19 simple setae along ventral to distal margin; propodus slender, 0.8× as long as carpus, 3.2× as long as broad, dorsal margin with one broom seta midway and five strong distal simple setae, ventral margin with seven simple setae on proximal half, two distal simple setae, one strong spiniform seta midway, one distal spiniform seta, and a comb-like row of ~ 20 short and fine serrate setae between those two spiniform setae; dactylus plus unguis slender and slightly curved, 0.8× as long as propodus, dorsal margin with one simple seta midway, unguis 0.6× as long as dactylus.

Pereopod 6 (Fig. 5C) coxa with three simple setae; basis 4× as long as broad, with one lateral and one subdorsal circumplumose seta on proximal half, dorsal margin with 11 circumplumose setae along distal half, ventral margin with one small spiniform seta midway and 12 circumplumose setae; ischium with three ventrodistal circumplumose setae; merus 0.6× as long as basis, 3.1× as long as broad, dorsal margin with one shorter and two very long circumplumose setae on proximal half, three very long circumplumose setae on distal half, ventral margin with two circumplumose setae on proximal half, one small spiniform seta midway, five circumplumose setae and three small spiniform setae on distal half; carpus slightly shorter than merus, 2.9× as long as broad, dorsal margin with two midway and one distal very long circumplumose seta, ventral to distal margin with ~ 13 circumplumose setae and one distal spiniform seta; propodus 0.8× as long as carpus, 2.9× as long as broad, with two ventroproximal circumplumose setae, a comb-like row of numerous serrate setae along ventral to distal margin, one dorsodistal and two ventrodistal circumplumose setae; dactylus plus unguis slender and slightly curved, 0.9× as long as propodus, dorsal margin with one short simple seta midway, unguis 0.6× as long as dactylus.

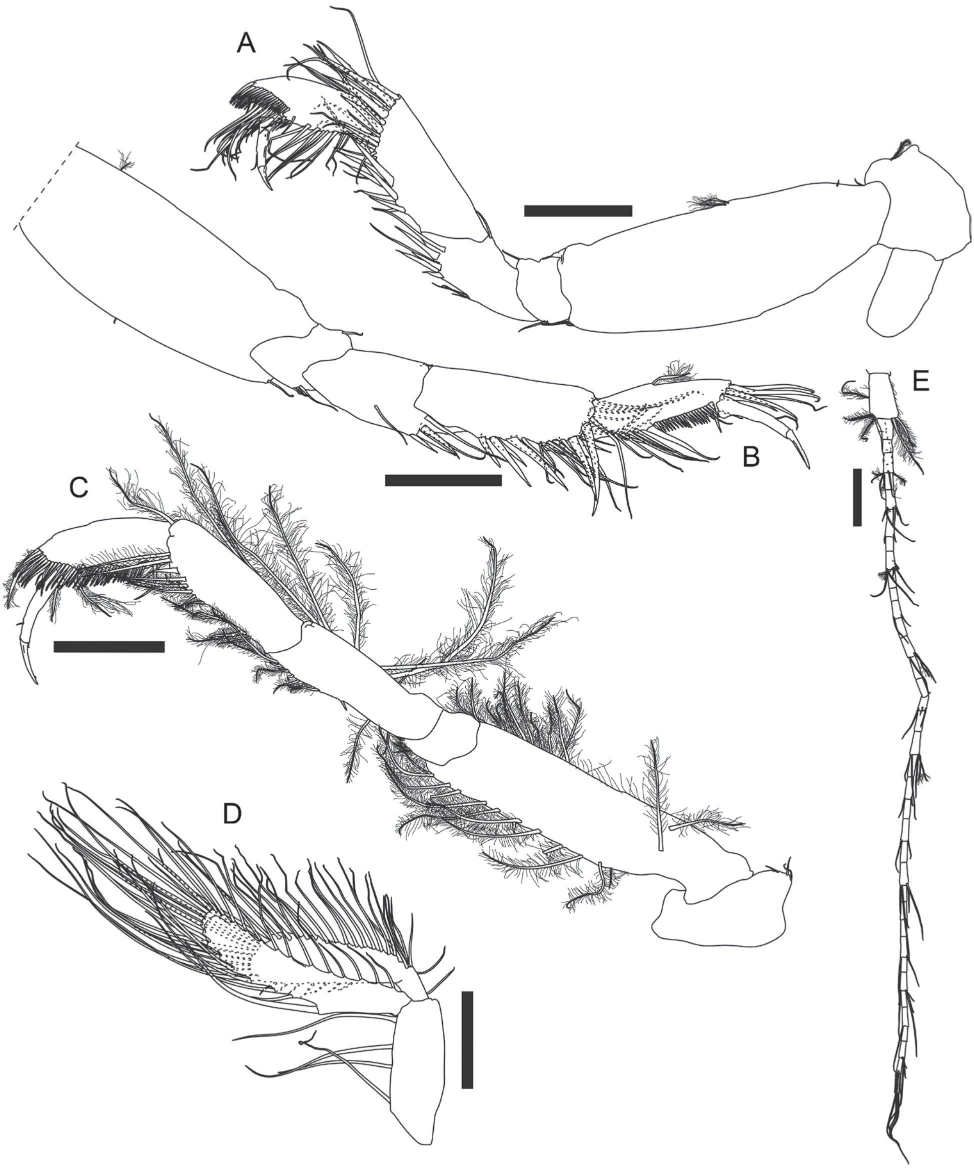

Figure 5. *Apseudes spinidigitus* sp. nov. Paratype (MBM032095), non-ovigerous simultaneous hermaphrodite **A** left pereopod 4 **B** right pereopod 5 **C** left pereopod 6 **D** left pleopod 5 (all setules omitted) **E** left uropod. Scale bars: 0.2 mm.

Pleopods (Fig. 5D, all setae plumose, setules omitted in figure) basal article elongate, 2.7× as long as broad, with four inner plumose setae; exopod slender, 3.6× as long as broad, outer to distal margin with 33 plumose setae, inner margin with seven short simple setae; endopod longer and slender than exopod, 1.2× as long as exopod, 5× as

Table 1. Morphological comparison among species of the genus *Apseudes* from the South China Sea region. N = no apophyses or spiniform setae.

Character / Species name	*A. spinidigitus* sp. nov.	*A. manna*	*A. nagae*	*A. nhatrangensis*
Carapace				
Rostrum	cordiform, pointed	pointed	cordiform, pointed	cordiform, pointed
Lateral apophyses	one spine-like	N	N	one spine-like
Pereonites				
Pereonite 3–6 lateral apophyses	one curved spine-like	N	blunt	one curved spine-like
Pleonites				
Epimera	pointed	blunt	truncated	pointed
Antennule				
Number of outer/inner flagellum articles	13/7	10/5	10–14/5	13/9
Antenna				
Number of flagellum articles	11	8	8	10
Maxilliped				
Number of endite coupling hooks	2	2	3–4	4
Cheliped				
Basis apophyses or spiniform setae	one ventral spiniform seta	one ventral spiniform seta	one ventral spiniform seta	one large ventral apophysis
Merus apophyses or spiniform setae	one ventral subdistal apophysis	N	N	one ventral subdistal apophysis
Carpus apophyses or spiniform setae	one dorsodistal apophysis	N	N	N
Pereopod 1				
Number of basis/merus/carpus/propodus dorsal spiniform setae	0/1/1/1	0/1/1/2	0/1/1/2	0/1/2/2
Number of basis/merus/carpus/propodus ventral spiniform setae	1/1/1/4	3/1/2/5	1/1/2/4	1/0/0/4
Pleopods				
Number of basal article outer/inner setae	0/4	5/4	4/5	8/8
Uropod				
Number of exopod/endopod articles	8/36–38	4–5/multi	13/26	10/40
References	present study	Bamber 2008	Shiino 1963; Bamber 1998	Shiino 1963

long as broad, with 25 plumose setae and one stronger plumose seta on proximal half of inner margin.

Uropod (Fig. 5E) basal article 1.6× as long as broad, outer margin with one midway and three distal circumplumose setae, inner margin with two distal setae; exopod not examined; endopod 36-articled, articles 3, 8, 13, and 18 with 1–3 broom setae and 1–5 simple distal setae, other articles without seta or with at most six simple setae.

Variation. Non-ovigerous simultaneous hermaphrodite holotype (MBM287293, 8.3 mm long) uropod with 8-articled exopod and 38-articled endopod.

Remarks. According to Bamber (1998, 2008), only three species of the genus *Apseudes* have been recorded from South China Sea region previously: *A. manna* Bamber, 2008 (Hong Kong), *A. nagae* Shiino, 1963 (Vietnam, Sabah and Brunei), and *A. nhatrangensis* Shiino, 1963 (Vietnam). Among these three, *A. manna* is the geographically closest to *Apseudes spinidigitus* sp. nov.; the new species, however, is conspicuously distinguished from *A. manna* in morphology, by having the spine-like apophyses on carapace, pereonites, merus, carpus, and fingers of cheliped, and pointed epimera on each pleonite (Fig 2A, 4A, B, Table 1; Bamber 2008: figs 1A, 2A).

Apseudes spinidigitus also closely resembles *A. nhatrangensis* in morphology. Among all known species of *Apseudes*, only *A. nhatrangensis* and the new species have the combination of features of a cordiform and distally pointed rostrum, one large spine-like anterior apophysis on lateral margin of carapace, a pair of wide but short eye lobes without visual elements, one large and curved spine-like anterolateral apophysis on pereonites 3–6, similar numbers of antennule and antenna flagella, uropod exopod and endopod articles, one large spine-like subdistal apophysis on ventral margin of cheliped merus, and one subproximal apophysis on ventral margin of pereopod 1 basis. Nevertheless, there are still several differences between these two species: 1) having two coupling hooks on maxilliped endite in *A. spinidigitus*, vs. four in *A. nhatrangensis*, 2) having a distinct spiniform seta midway on ventral margin of cheliped basis in *A. spinidigitus*, vs. a large apophysis in *A. nhatrangensis*, 3) the presence of one dorsodistal spine-like apophysis on cheliped carpus in *A. spinidigitus*, absence in *A. nhatrangensis*, 4) the presence of one conspicuous apophysis on incisive margin of cheliped dactylus in *A. spinidigitus*, vs. absence in *A. nhatrangensis*, 5) the presence of one ventrodistal spiniform seta on pereopod 1 merus and carpus each in *A. spinidigitus*, vs. absence in *A. nhatrangensis*, 6) having only one dorsodistal spiniform seta on pereopod 1 carpus and propodus each in *A. spinidigitus*, vs. two in *A. nhatrangensis*, 7) having only four plumose setae on inner margin of pleopods basal articles in *A. spinidigitus*, vs. more than four plumose setae on both sides of pleopods basal articles in *A. nhatrangensis* (Figs 2A–C, 3E, 4A–C, 5D, E, Table 1; Shiino 1963: figs 1A, C, D, 2A, H, I, 3A, B, D, E, G, H, 3H).

In addition to the features mentioned above, the presence of circumplumose setae on the antennule, antenna, maxilliped, pereopod 6 and uropod of *A. spinidigitus* is also a rare feature only found in a few species among *Apseudes*, i.e., *A. fecunda* (Guţu, 2006), *A. nagae*, *A. nhatrangensis*, *A. nipponicus* Shiino, 1937, *A. sculptus* Pfeffer, 1888 (Lang 1953), and *A. spectabilis* Studer, 1884 (Shiino 1978).

Key to the species of *Apseudes* from the South China Sea (see also Table 1)

1	All pereonites without apophysis	***A. manna***
–	Pereonites 3–6 with one anterolateral apophysis	**2**
2	Carapace without lateral apophysis	***A. nagae***
–	Carapace with one large spine-like anterolateral apophysis	**3**
3	Cheliped basis with one large apophysis on ventral margin, dactylus incisive margin without apophysis	***A. nhatrangensis***
–	Cheliped basis with one large spiniform seta on ventral margin, dactylus incisive margin with one apophysis	***A. spinidigitus* sp. nov.**

Family Kalliapseudidae Lang, 1956
Subfamily Kalliapseudinae Lang, 1956

Genus *Phoxokalliapseudes* Drumm & Heard, 2011

Type species. *Kalliapseudes gobinae* Bamber, 1998.

Phoxokalliapseudes shandongensis sp. nov.

http://zoobank.org/C248280D-BEC1-4FDC-819B-926AF126929D
Figs 6–10, Table 2

Type material. ***Holotype*:** MBM287298, one non-ovigerous female, 6.8 mm; the Yellow Sea, 19 June 2019, from sand-gravel substrate at depth of 33 m, 35°59'N, 121°00'E. ***Allotype*:** MBM287295, male, 6.1 mm, partially dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 4 February 2018, from muddy substrate with shell fragments at depth of 4 m, 36°06'N, 120°17'E. ***Paratypes*:** MBM287294, one non-ovigerous female, 6.9 mm, completely dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 20 February 2004, from mud-sandy substrate at depth of 5 m, 36°02'N, 120°14'E. MBM287296, one non-ovigerous female, 6.5 mm, partially dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 5 February 2007, from muddy substrate at depth of 3 m, 36°10'N, 120°20'E. MBM287297, one non-ovigerous female and one male; Jiaozhou Bay, Qingdao, Shandong Province, China, 9 August 2004, from muddy substrate at depth of 6 m, 36°02'N, 120°14'E. MBM287299, one non-ovigerous female, 6.5 mm; the Yellow Sea, 26 November 2019, sand-gravel substrate with shell fragments at depth of 36 m, 34°59'N, 120°59'E. MBM287300, four males; the Yellow Sea, 26 November 2019, muddy substrate at depth of 38 m, 34°59'N, 121°30'E.

Other material. MBM147028, one female; Jiaozhou Bay, Qingdao, Shandong Province, China, 2 August 1964, from muddy substrate at depth of 7 m, 36°08'N, 120°15'E. MBM032073, four males; the Yellow Sea, 23 January 1959, from mud-sandy substrate at depth of 41 m, 38°45'N, 122°43'E. MBM147063, one male and one female; Jiaozhou Bay, Qingdao, Shandong Province, China, 4 August 1964, from mud-sandy substrate at depth of 21 m, 36°08'N, 120°15'E. MBM146415, two females; Jiaozhou Bay, Qingdao, Shandong Province, China, 4 August 1964, from muddy substrate at depth of 7 m, 36°08'N, 120°15'E. MBM146430, one female; Jiaozhou Bay, Qingdao, Shandong Province, China, 2 August 1964, from muddy substrate at depth of 9 m, 36°08'N, 120°15'E. MBM146420, one female; Jiaozhou Bay, Qingdao, Shandong Province, China, 4 August 1964, from mud-sandy substrate with gravels at depth of 23 m, 36°08'N, 120°15'E. MBM146419, one female; same collection data as MBM147028. MBM147100, two females; Jiaozhou Bay, Qingdao, Shandong

Province, China, 18 August 1964, from muddy substrate at depth of 5 m, 36°08'N, 120°15'E. MBM030026, one female, Yellow Sea, 20 October 1959, from muddy substrate at depth of 17 m, 37°51'N, 121°58'E.

Type locality. Jiaozhou Bay, Qingdao, Shandong Province, China, and adjacent Yellow Sea area.

Etymology. The name is derived from Shandong, where the species was collected around Shandong Peninsula.

Diagnosis. ***Non-ovigerous female. Antennule*** peduncle article 1 inner margin with row of five spiniform setae on distal half, and two long ventral subdistal spiniform setae. ***Antenna*** peduncle article 1 inner extension with six distal plumose setae. ***Maxilla*** with one small spiniform seta near outer margin. ***Cheliped*** basis with two small ventral spiniform setae. ***Pereopod 1*** propodus with two dorsal and six ventral spiniform setae. ***Pereopod 6*** propodus with five long ventral spiniform setae; dactylus long, 3.8× as long as propodus. *Pleopod* exopod inner margin with one subproximal apophysis. ***Uropod*** basal article with one inner distal spiniform seta. ***Male.*** Similar to female except ***pereonites 2–5*** with one hyposphenia, and one robust spiniform seta on each hyposphenia. ***Each pleonite*** with one hyposphenia. ***Antennule*** peduncle article 1 robust, with one ventral spiniform seta; inner flagellum 5-articled. ***Cheliped*** fixed finger incisive margin with two large triangular apophyses. ***Pereopod 6*** propodus with three or four long ventral spiniform setae; dactylus very long, 4.6× as long as propodus.

Description. Female (non-ovigerous paratype MBM287294). ***Body*** (Fig. 6A) dorsoventrally flattened, 6.9 mm long, 5.8× as long as broad. ***Carapace*** less than 0.2× as long as total body length, as long as broad, rostrum rounded, lateral margin with one simple seta midway. ***Pereon*** half as long as total body length, each pereonite in similar width, slightly broader than carapace, anterolateral margin with one simple seta and several setules; pereonites 1–6 0.5, 0.5, 0.6, 0.8, 0.7, 0.4× as long as broad, respectively. ***Pleon*** 0.2× as long as total body length, each pleonite in similar width, slightly broader than pereonites, with eight or nine plumose setae on blunt lateral margin, one anterolateral simple seta on dorsal surface. ***Pleotelson*** posteriorly tapering and distally bifurcate, *ca.* as long as three pleonites combined, slightly broader than long, with two distal plumose setae.

Antennule (Fig. 7A) peduncle article 1 ~ 0.4× as long as total antennule length, 2.7× as long as broad, with ten simple setae and four broom setae along outer margin, inner margin with six simple setae on proximal half, two simple setae, and a row of five spiniform setae on distal half, and two long ventral subdistal spiniform setae; article 2 0.3× as long as peduncle article 1, 1.7× as long as broad, distal half with three outer, five inner simple setae, and two ventral broom setae; article 3 half as long as article 2, with three distal simple setae; article 4 0.7× as long as article 3, with one distal simple seta; outer flagellum longer than peduncle article 1, 11-articled, each article with at most four distal simple setae, articles 4, 6, and 7 each with one distal aesthetasc; inner flagellum 6-articled, articles 1–4 each with one distal simple seta, article 5 naked, article 6 with three distal setae.

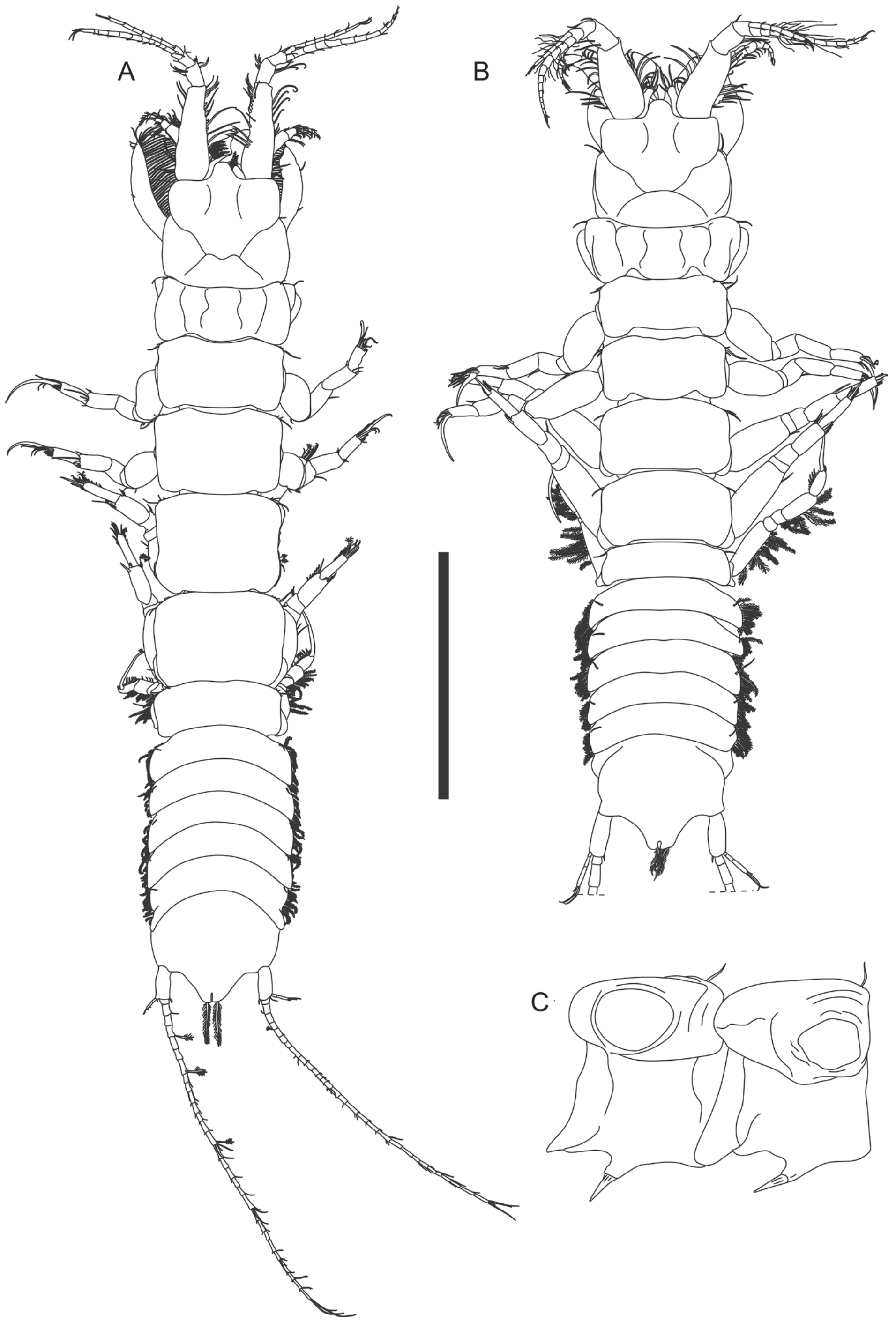

Figure 6. *Phoxokalliapseudes shandongensis* sp. nov. Paratype (MBM287294), non-ovigerous female **A** body dorsal view. Allotype (MBM287295), male **B** body dorsal view **C** pereonites 1–2 lateral view. Scale bar: 2 mm.

Antenna (Fig. 7B) article 1 outer margin with one distal simple seta, inner extension long, covered with setules, with six distal plumose setae; article 2 inner margin covered with setules, squama with six simple setae along outer to distal margin, and spinules along inner margin; article 3 very short, with two inner plumose setae; article 4 nearly half as long as antenna, with one outer broom seta midway, a row of ten plumose setae along inner margin, and a row of 20 ventral plumose setae; article 5 inner and outer margin both with four simple setae, distal margin with five dorsal simple setae and two ventral plumose setae; articles 6 and 7 both with five distal simple setae and two ventral plumose setae; article 8 with one distal simple and two ventral plumose setae; article 9 with two ventral plumose setae; article 10 with five distal simple setae.

Labrum (Fig. 7C, figure and description based on non-ovigerous female paratype, MBM287296, 6.5 mm long) distal margin rounded, covered with numerous setules; clypeus with two robust and two smaller cusps.

Left mandible outer margin with one conspicuous apophysis; both incisor and lacinia mobilis (Fig. 7D, figure based on MBM287296) distal margin denticulate; setal row with five serrate setae; molar distal margin crenulate; palp with 29 long plumose setae along inner margin and one distal spiniform seta. Right mandible (Fig. 7E) similar to left mandible but without lacinia mobilis, incisor (Fig. 7F, figure based on MBM287296) with two large distal denticles.

Labium palp (Fig. 8A) subrectangular, 1.5× as long as broad, covered with setules, with one small spine-like apophysis on inner distal corner.

Maxillule (Fig. 8B) inner endite covered with numerous long setules, with four distal plumose setae; outer endite covered with numerous long setules, with a row of spinules along outer margin, ten spiniform setae on distal margin, two subdistal plumose setae, and one distinct concavity (arrow) on outer distal corner.

Maxilla (Fig. 8C) outer lobe of movable endite with five plumose setae; inner lobe of movable endite with row of 15 distally blunt setae, and two comb-like setae along distal margin; outer lobe of fixed endite with a row of 15 simple setae, four plumose setae, and two robust and one smaller serrate seta; inner lobe of fixed endite with five distally serrate setae and a row of 17 plumose setae; outer margin and sub-outer surface covered with spinules, with one sub-outer spiniform seta (arrowed).

Maxilliped (Fig. 8D) basis with a row of 25 plumose setae along outer margin; endite (Fig. 8E) covered with setules entirely, with ten plumose setae on distal margin, two robust coupling hooks on inner margin, and eight setulose and distally serrate setae on inner fold; palp article 1 with four simple setae on inner margin and one simple seta on outer margin; article 2 with two rows of numerous long plumose setae along inner margin, and four subdistal simple setae on outer margin; articles 3 and 4 both with two rows of numerous long plumose setae along inner margin.

Epignath not examined.

Cheliped (Fig. 9A) exopod 3-articled, article 3 with two distal plumose setae; basis ~ 1.5× as long as broad, ventral margin with one spiniform seta midway, three meddle simple setae, one subdistal spiniform seta, and two subdistal simple setae; merus with one ventral simple seta, anterior corner protruded and rounded, anterior margin crenulate,

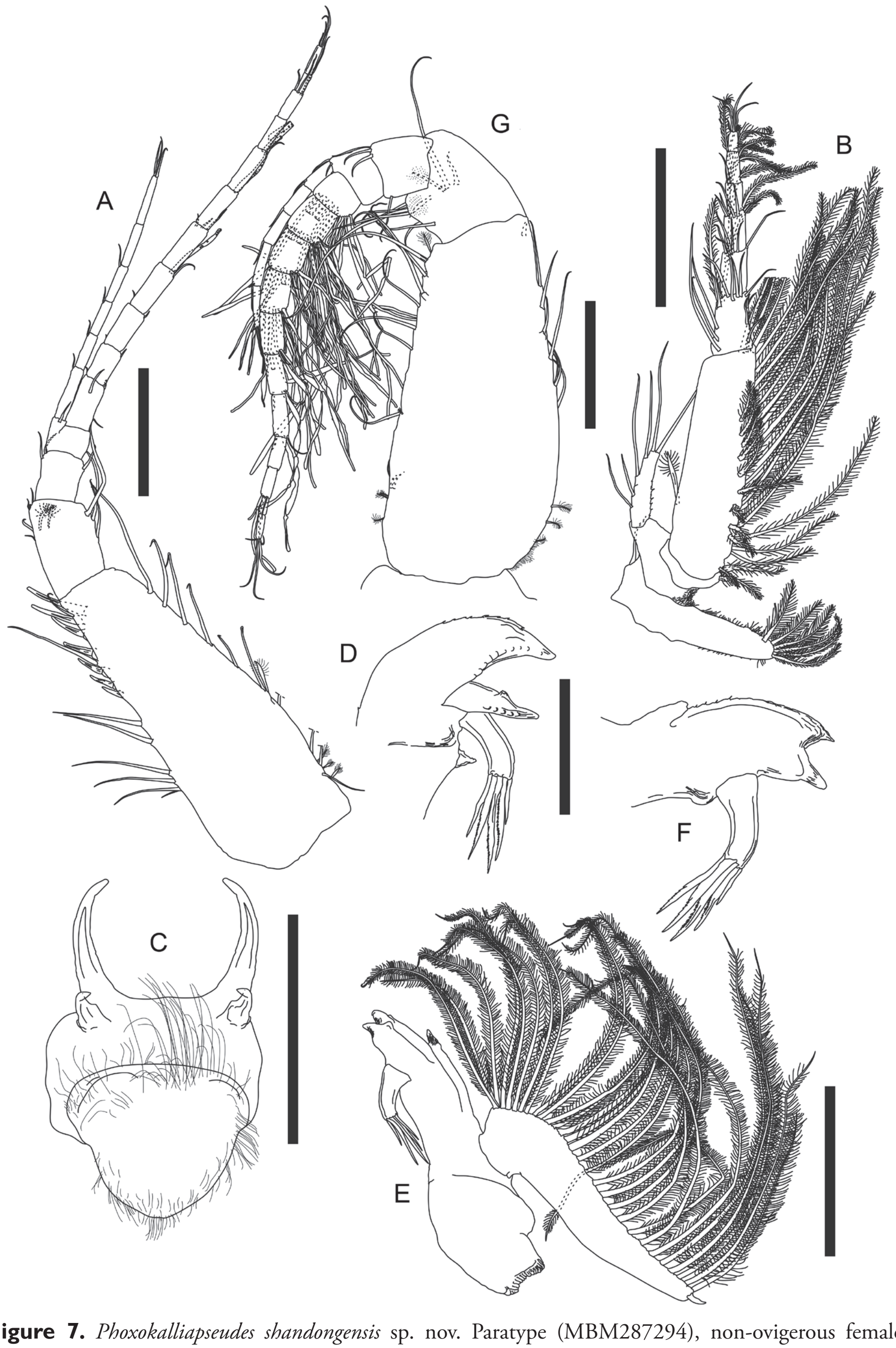

Figure 7. *Phoxokalliapseudes shandongensis* sp. nov. Paratype (MBM287294), non-ovigerous female **A** right antennule **B** left antenna **E** right mandible. Paratype (MBM287296), non-ovigerous female **C** labrum **D** left mandible incisor, lacinia mobilis and setal row **F** right mandible incisor and setal row. Allotype (MBM287295), male **G** left antennule. Scale bars: 0.2 mm (**A–C, E, G**); 0.1 mm (**D, F**).

Figure 8. *Phoxokalliapseudes shandongensis* sp. nov. Paratype (MBM287294), non-ovigerous female **A** labium palp **B** maxillule endites **C** maxilla **D** maxilliped **E** maxilliped endite. Scale bars: 0.1 mm (**A, E**); 0.2 mm (**B–D**).

with three simple setae; carpus ~ 3.5× as long as broad, with two rows of long plumose setae along ventral margin, both rows with ~ 40 setae, dorsal margin with three short and one longer simple setae on distal half, anteroventral corner with four outer simple setae; propodus and fixed finger combined nearly as long as carpus, 2.2× as long as broad, palm 1.6× as long as broad, with a row of 15 inner plumose setae and a cluster of 11 simple setae on anterodorsal corner near insertion of dactylus, fixed finger with 17 simple setae on ventral margin or subventral surface, 17 simple setae and an intensive row of small denticles along incisive margin, a row of 12 outer and four inner simple setae near insertion of dactylus; dactylus plus unguis 4.5× as long as broad, slightly curved, with nine outer and four inner simple setae, and a row of 15 small spiniform setae along incisive margin.

Pereopod 1 (Fig. 9B, figure and description based on MBM287296) exopod 3-articled, article 3 with two distal plumose setae; coxa with one simple seta on blunt apophysis; basis ~ 2.2× as long as broad, dorsal margin with one simple and two broom setae on proximal half, ventral margin with one midway, two subdistal simple setae, and one robust subdistal spiniform setae, and one simple seta on subventral surface; ischium with one ventral simple seta; merus 0.8× as long as basis, 1.9× as long as broad, distal margin with one dorsal simple seta, one dorsal spiniform seta, one outer simple seta, and one ventral spiniform seta, ventral margin with eight simple setae; carpus short, *ca.* half as long as merus, slightly longer than broad, dorsal margin with a cluster of six subdistal simple setae and one robust distal spiniform seta, ventral margin with seven subdistal simple setae and two spiniform setae, outer surface with a cluster of three short simple setae; propodus 0.7× as long as carpus, 1.3× as long as broad, dorsal margin with a row of seven subdistal simple setae and two distal spiniform setae in unequal size, ventral margin with eight simple setae and six spiniform setae, outer surface with four short subproximal simple setae; dactylus 0.7× as long as propodus, covered with intensive long sensory setae.

Pereopod 2 (Fig. 9C) basis 2.5× as long as broad, dorsal margin with two simple setae and one broom seta, ventral margin three simple setae and one broom seta; ischium with three ventrodistal simple setae; merus 0.4× as long as basis, 1.7× as long as broad, dorsal margin with one subdistal simple seta, ventral margin with one subdistal simple seta and one subdistal spiniform seta; carpus slightly shorter than merus, 1.5× as long as broad, dorsal margin with a cluster of two longer and two short distal simple setae, and one outer distal spiniform seta, ventral margin with four simple setae and four spiniform setae on distal half; propodus slightly shorter than carpus, 2.1× as long as broad, with one dorsal broom seta midway, and a row of two distal simple setae and six spiniform setae, ventral margin with three long and three shorter simple setae, and a row of five spiniform setae on distal half; dactylus plus unguis long and slender, 2.2× as long as propodus, without sensory lobe.

Pereopod 3 (Fig. 9D) basis 2.7× as long as broad, dorsal margin with one simple and two broom setae midway, ventral margin with one distal simple seta and one distal spiniform seta; ischium with four ventrodistal simple setae; merus 0.4× as long as basis, 1.6× as long as broad, ventral margin with three simple setae and two spiniform setae on distal half, outer surface with one subdistal simple seta; carpus slightly shorter than merus, 1.4× as long as broad, dorsal margin with one distal spiniform seta and three distal simple setae, ventral margin with three simple setae and four spiniform setae on distal half; propodus and dactylus similar to those of pereopod 2.

Pereopod 4 (Fig. 10A) basis 2.4× as long as broad, dorsal margin with three subproximal broom setae, one midway and two subdistal simple setae, ventral margin with one subproximal broom seta; ischium with four ventrodistal simple setae; merus short, 0.3× as long as basis, 1.3× as long as broad, ventral margin with three subdistal simple setae and two subdistal spiniform setae; carpus 1.4× as long as merus, 1.9× as long as broad, with two dorsodistal simple setae, a row of eight outer spiniform setae, a row of eight inner spiniform setae, and three ventral simple setae, ventral half covered with setules; propodus slightly shorter than carpus, 2.7× as long as broad, with one large dorsoproximal broom seta and a row of five small dorsodistal leaf-like spiniform setae (Fig. 10B), a row of eight outer, eight inner spiniform setae and six simple setae along ventral to distal margin, ventral margin covered with setules; dactylus 0.4× as long as propodus, with nine distal simple setae.

Pereopod 5 (Fig. 10C) basis 2.5× as long as broad, dorsal margin with three broom setae on proximal half and three simple setae on distal half, ventral margin with a cluster of three distal simple setae, and two simple setae on distal half; ischium, merus, propodus and dactylus very similar to those of pereopod 4 but merus with seven inner spiniform setae.

Pereopod 6 (Fig. 10D) basis 3.7× as long as broad, with nine dorsal and three ventral plumose setae, and three ventral subdistal simple setae; ischium with two ventrodistal simple setae; merus short, 0.2× as long as basis, slightly as long as broad, with three dorsal plumose setae and one ventral simple seta; carpus 2.7× as long as merus, 2.4× as long as broad, with six dorsal plumose setae and four ventral simple setae, ventral margin covered with setules; propodus (Fig. 10E) ~ 0.7× as long as carpus, almost twice as long as broad, with five long ventral spiniform setae, a row of 27 short serrate setae along ventral to distal margin, and one dorsodistal spiniform seta; dactylus (Fig. 10E) long and slender, 3.8× as long as propodus.

Pleopods (Fig. 10F) basal article with four inner plumose setae; exopod with 20 plumose setae, inner margin with one subproximal protrusion (arrowed); endopod with 22 plumose setae, innermost seta (Fig. 10G) robust, distally branched and ringed.

Uropod (Fig. 10H, figure and description based on MBM287296) basal article 2.7× as long as broad, with two outer, one inner distal simple seta, and one inner distal spine; exopod 3-articled, article 3 with four distal simple setae; endopod 22-articled, each article naked or with at most five distal simple setae, article 2 with three distal broom setae, articles 4, 6, and 11 each with two distal broom setae.

Male (allotype MBM287295). Similar to female with following variations: ***body*** (Fig. 6B) less slender, 6.1 mm long, 4.8× as long as broad. ***Carapace*** ~ 0.2× as long as total body length, slightly broader than long, lateral margin with one simple seta midway. ***Each pereonite*** with 1–3 anterolateral simple setae, pereonites 1–5 each with one hyposphenia (Fig. 6C), and one robust spiniform seta on each hyposphenia, pereonite 6 with genital cone; pereonite 1 conspicuously broader than subsequent pereonites, 1.2× as broad as pereonite 2, 0.4× as long as broad; pereonites 2–6 in similar width, relatively short, 0.5, 0.5, 0.5, 0.5, 0.3× as long as broad respectively. ***Each pleonite ca.*** as wide as pereonite 1, with one hyposphenia, one dorsolateral simple seta and 6–10 lateral plumose setae.

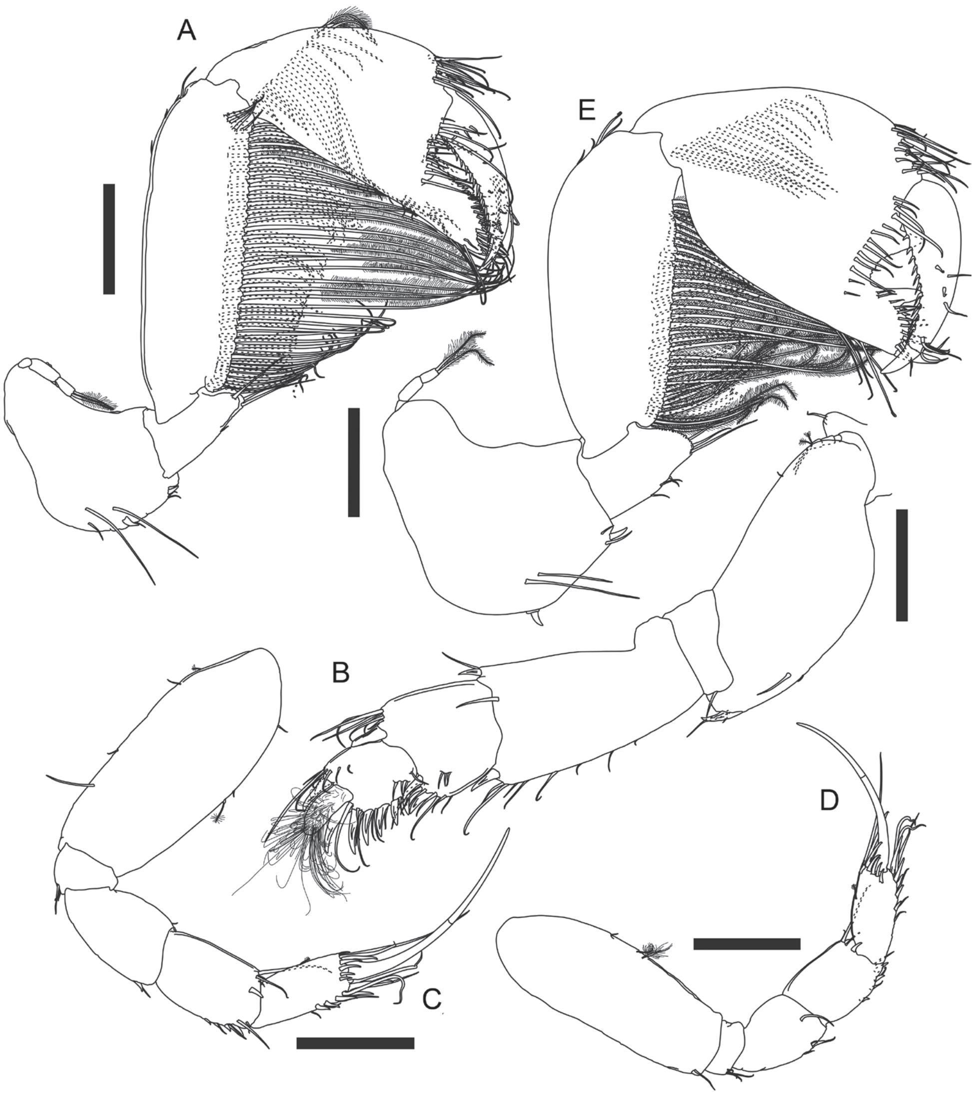

Figure 9. *Phoxokalliapseudes shandongensis* sp. nov. Paratype (MBM287294), female **A** right cheliped **C** right pereopod 2 **D** right pereopod 3. Paratype (MBM287296), non-ovigerous female **B** left pereopod 1. Allotype (MBM287295), male **E** right cheliped. Scale bars: 0.2 mm (**A–E**).

Antennule (Fig. 7G) peduncle article 1 robust, 0.4× as long as total antennule length, 2.2× as long as broad, outer margin with eight simple and five broom setae, inner margin seven simple and three broom setae, and one small ventral spiniform seta near inner distal corner; article 2 0.4× as long as article 1, 1.4× as long as broad, with six inner simple setae, two simple and two broom ventral setae; peduncle article 3 0.5× as long as peduncle article 2, slightly as long as broad, with one outer subdistal and three inner distal simple setae; peduncle article 4 0.7× as long as article 3, distal margin with two inner simple setae; outer flagellum longer than peduncle article 1,

Figure 10. *Phoxokalliapseudes shandongensis* sp. nov. Paratype (MBM287294), non-ovigerous female **A** right pereopod 4 **B** dorsodistal spiniform seta on pereopod 4 propodus **C** right pereopod 5 **D** right pereopod 6 **E** left pereopod 6 propodus and dactylus **F** left pleopod 2 **G** pleopod endopod innermost seta. Paratype (MBM287296), non-ovigerous female **H** right uropod. Allotype (MBM287295), male **I** left pereopod 6. Scale bars: 0.2 mm (**A, C, D, H, I**); 0.1 mm (**E, F, G**).

11-articled, article 1 with 15 distal aesthetascs; article 2 with ~ 15 distal aesthetascs and two distal simple setae, article 3 with 11 distal aesthetascs and two distal simple setae, articles 4 and 5 both with six distal aesthetascs and two distal simple setae, articles 6, 7 and 9 each with one distal aesthetasc and two distal simple setae, articles 8 and 10 naked, article 11 with four distal simple setae; inner flagellum 5-articled, articles 1–3 each with one distal simple seta, article 4 with two distal simple setae, article 5 with four distal simple setae.

Antenna article 1 inner extension with six distal plumose setae.

Cheliped (Fig. 9E) exopod 3-articled, article 3 with two distal plumose setae; basis ~ 1.4× as long as broad, with two long outer setae, ventral margin with one spiniform seta midway, two distal short simple setae and one distal spiniform seta; merus with three ventral simple setae, anterior corner protruced and rounded, anterior margin crenulate, with three simple setae; carpus 2.6× as long as broad, dorsal margin with four subdistal simple setae, ventral margin with two rows of long plumose setae, outer row with 35 plumose setae, inner row with 32 plumose setae; propodus large and robust, combined with fixed finger nearly as long as carpus, 1.8× as long as broad, palm 1.3× as long as broad, with a row of 15 inner plumose setae, a cluster of 17 anterodorsal simple setae and a row of 13 outer simple setae near insertion of dactylus, fixed finger with five ventral simple setae, incisive margin with two strong triangular apophyses, a row of eleven simple setae, and a row of seven small spiniform setae; dactylus plus unguis 3.7× as long as broad, slightly curved, dorsoproximally expanded, with nine outer setae and a row of ten small spiniform setae along incisive margin.

Pereopod 6 (Fig. 10I) basis ~ 4.1× as long as broad, dorsal margin with seven plumose setae, ventral margin with three plumose setae midway and four subdistal simple setae; ischium with three ventral subdistal simple setae; merus short, 0.2× as long as basis, slightly longer than broad, with three dorsal plumose and two ventral simple setae; carpus 2.3× as long as merus, 2.1× as long as broad, with seven dorsal plumose and four ventral simple setae; carpus 0.7× as long as merus, 1.8× as long as broad, with three (on left pereopod 6) or four (on right pereopod 6) long ventral spiniform setae, a row of 24 short serrate setae along ventral to distal margin, and one dorsodistal spiniform seta; dactylus very long and slender, 4.6× as long as propodus.

Some other morphological characters of males given in Table 2.

Remarks. Seven species have been reported for the genus *Phoxokalliapseudes*, all from the western Pacific, i.e., *P. aculeatus* Wi, Kang & Soh, 2017 (southwestern Korea), *P. cinctus* Wi, Kang & Soh, 2017 (southern Korea), *P. gibbus* Wi, Yu & Kang, 2019 (Jeju Island, Korea), *P. gobinae* Bamber, 1998 (Brunei and Sabah; Bamber 2013), *P. multiarticulus* Guţu, 2006 (Darwin, northern Australia), *P. singaporensis* Drumm & Heard, 2011 (Singapore), and *P. tomiokaensis* Shiino, 1966 (Kyushu, Japan). The eighth species, *Phoxokalliapseudes shandongensis* sp. nov. from the present study, is geographically closest to *P. aculeatus* and *P. gibbus*.

Morphologically, *Phoxokalliapseudes shandongensis* also closely resembles *P. gibbus*, by having six distal plumose setae on inner extension of antenna article 1, two ventral spiniform setae on cheliped basis, two large triangular (conical) apophyses on incisive margin of male cheliped fixed finger, similar female and male pereopod 6 dactylus to propodus length ratio, and one subproximal protrusion on inner margin of each pleopod exopod. However, *P. shandongensis* can be distinguished from *P. gibbus* by several significant differences: 1) female antennule peduncle article 1 with two long and conspicuous ventral spiniform setae and five smaller spiniform setae on inner margin, vs. only one ventral spiniform seta in *P. gibbus*; 2) with six ventral spiniform setae on pereopod 1 propodus, vs. nine in *P. gibbus*; 3) with five ventral spiniform setae on pereopod 6 propodus, vs. six in *P. gibbus*; 4) with one inner distal spiniform seta on uropod basal article (Figs 7A, B, 9A, B, E, 10D–I, Table 2; Wi et al. 2019: figs4C, E, 5C–F, H, I, 6F, G, 7E, F, H, I).

Among *Phoxokalliapseudes* species, only *P. shandongensis* and *P. gobinae* have one inner distal spiniform seta on uropod basal article. However, the male of *P. shandongensis* have two large triangular (conical) apophyses on incisive margin of cheliped fixed finger, easily distinguished from the male of *P. gobinae* with one distal square and one triangular (conical) apophysis. In addition, the presence of two ventral spiniform setae on female cheliped basis can also differentiate the new species from *P. gobinae* (Fig. 9A, E, Table 2; Bamber 1998: fig 9A, B; Drumm and Heard 2011: figs 22F, 24D).

Key to the species of *Phoxokalliapseudes* (modified and updated from Wi et al. 2019; see also Table 2)

1	Pereopods 2 and 3 dactylus without proximal sensory lobe; pereopod 6 dactylus without subdistal seta	**2**
–	Pereopods 2 and 3 dactylus with proximal sensory lobe; pereopod 6 dactylus with subdistal seta	**3**
2	Male cheliped fixed finger incisive margin with square-shaped apophysis	***P. gobinae***
–	Male cheliped fixed finger incisive margin with triangular (conical) apophysis	**4**
3	Antennule article 1 with three robust subdistal spiniform setae	***P. multiarticulus***
–	Antennule article 1 with one small subdistal spiniform setae	***P. singaporensis***
4	Male cheliped fixed fingered incisive margin with small triangular (conical) apophysis	***P. cinctus***
–	Male cheliped fixed fingered incisive margin with large triangular (conical) apophysis	**5**
5	Female cheliped basis without ventral spiniform seta	***P. tomiokaensis***
–	Female cheliped basis with two ventral spiniform setae	**6**
6	Female antennule article 1 with two robust and five smaller subdistal spiniform setae	***P. shandongensis*** sp. nov.
–	Female antennule article 1 with two subdistal spiniform setae	7
7	Antennule article 1 with two robust subdistal spiniform setae	***P. aculeatus***
–	Antennule article 1 with one robust and one small subdistal spiniform seta	***P. gibbus***

Table 2. Morphological comparison among all species of *Phoxokalliapseudes*, modified and updated from Wi et al. (2017) and differentiating between female (F) and male (M); T = triangular, S = square, R = rounded, N = no, Y = yes, A = absent, P = present.

Character / Species name	*P. shandongensis* sp. nov.		*P. aculeatus*		*P. cinctus*		*P. gibbus*		*P. gobinae* (Bamber)		*Phoxokalliapseudes cf. gobinae* Drum and Heard		*P. multiarticulus* (Guţu)	*Phoxokalliapseudes cf. multiarticulus* Drum and Heard		*P. singaporensis*	*P. tomiokaensis*	
	F	M	F	M	F	M	F	M	F	M	F	M	F	F	M	M	F	M
Antennule																		
Number of inner flagellum articles	6	5	6	5	4	5	5	5	-	6	4	4	8	6	6	5	6	5
Antenna																		
Number of setae on article 1 inner extension	6	6	7	7	5	5	6	-	-	7	-	6	-	-	8	6	7	6
Number of setae on article 3	2	2	2	2	1	2	2	-	-	0	-	2	-	-	3	1	2	2
Cheliped																		
Number of basis ventral spiniform setae	2	2	2	2	2	2	2	2	0	1	0	2	-	0	2	0	0	2
Propodus long/wide ratio	2.2	1.8	1.6	1.3	3.0	2.5	2.5	1.6	2.7	1.8	3.3	1.5	-	2.1	1.4	1.5	2.1	1.5
Shape of fixed finger apophyses		T		T		T		T		S		S			R	T		T
Pereopod 1																		
Number of propodus ventral/ dorsal spiniform setae	6/2	6/2	7/2	7/2	-	7/2	9/2	-	-	7/2		6/2	4/2	5/2	-	5/2	-	6/2
Pereopod 6																		
Dactylus/propodus length ratio	3.8	4.6	2.6	4.4	3.1	4.3	3.5	4.5	-	4.1	-	4.7	-	2.0	3.9	3.6	-	2.7
Number of propodus long ventral spiniform setae	5	3–4	5	5	4	4	6	-	-	2	-	3	5	5	3	2	-	5
Dactylus distally bifurcated	N	N	N	N	N	N	N	-	-	N	-	N	Y	Y	Y	Y	-	N
Pereopods 2–3																		
Presence of dactylus sensory organ	A	A	A	A	A	A	A	-	A	A	A	A	P	P	P	P	A	A
References	present study		Wi et al. 2017		Wi et al. 2017		Wi et al. 2019		Bamber 1998		Drumm and Heard 2011		Guţu 2006	Drumm and Heard 2011		Drumm and Heard 2011	Shiino 1966	

Family Parapseudidae Guţu, 1981
Subfamily Pakistanapseudinae Guţu, 2008

Genus *Swireapseudes* Bamber, 1997

Type species. *Swireapseudes toloensis* Bamber, 1997

Remarks. This genus has once been synonymised with *Pakistanapseudes* by Bamber and Sheader (2003) but revalidated by Guţu (2006). The main morphological features that distinguish these two genera are: 1) the presence of ventrodistal prolongation on pereopods 2, 3, 5 and 6 in species of *Swireapseudes*, compared to the presence of a ventrodistal prolongation on pereopods 2 and 3 in some species of *Pakistanapseudes* but never on pereopods 5 and 6; 2) the presence of sexual dimorphism of cheliped in species of *Swireapseudes* (Guţu 2008). Two species of *Swireapseudes* have been previously recorded at very distant locations: *Swireapseudes birdi* Guţu & Iliffe, 2008 (Eleuthera Island, Bahamas) and *Swireapseudes toloensis* Bamber, 1997 (Tolo Channel, Hong Kong).

Swireapseudes planafrontis sp. nov.
http://zoobank.org/D8634839-52D1-4117-B015-442224608B68
Figs 11–15, Table 3

Type material. ***Holotype*:** MBM287312, non-ovigerous female, 6.8 mm; Jiaozhou Bay, Qingdao, Shandong Province, China, 20 November 2003, from mud-sandy substrate with shell fragments at depth of 10 m, 36°09'N, 120°19'E. ***Allotype*:** MBM287302, male, 5.0 mm, completely dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 15 March 2021, from muddy substrate with shell fragments at depth of 6 m, 36°06'N, 120°17'E. ***Paratypes*:** MBM287301, one ovigerous female, 6.9 mm, completely dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 12 November 2020, from muddy substrate at depth of 6 m, 36°05'N, 120°10'E. MBM287303, one non-ovigerous female, 6.8 mm, partially dissected and body parts preserved in 75% alcohol; same collection data as allotype. MBM287304, one non-ovigerous female, 6.8 mm, partially dissected, and body parts preserved in 75% alcohol; same collection data as allotype. MBM287305, one non-ovigerous female, 7.1 mm, partially dissected and body parts preserved in 75% alcohol; Jiaozhou Bay, Qingdao, Shandong Province, China, 11 November 2020, from muddy substrate with shell fragments at depth of 4 m, 36°06'N, 120°17'E. MBM287306, one male, 5.2 mm, partially dissected and body parts preserved in 75% alcohol; same collection data as allotype. MBM287307, one male, 4.2 mm, partially dissected and body parts preserved in 75% alcohol; same collection data as allotype. MBM287308, one male, 4.2 mm; same collection data as allotype. MBM287309, one non-ovigerous female, 5.0 mm; Jiaozhou Bay, Qingdao, Shandong Province, China, 3 February 2021, from muddy substrate at depth of 14 m, 36°06'N, 120°15'E. MBM287310, one ovigerous female, 6.0 mm; same collection data as paratype MBM287305. MBM287311, one non-ovigerous female, 7.8 mm; same collection data as allotype.

Other material. MBM147029, two females, Jiaozhou Bay, Qingdao, Shandong Province, China, 2 August 1964, from muddy substrate at depth of 7 m, 36°08'N, 120°15'E.

Type locality. Jiaozhou Bay, Qingdao, Shandong Province, China.

Etymology. The name is derived from the Latin *planula* (flat) and *frontis* (forehead), referring to the wide and flat rostrum.

Diagnosis. *Ovigerous female. Rostrum* rounded, with wide and flat distal margin. ***Antennule*** article 1 inner margin with one strong spiniform seta midway. ***Antenna*** article 2 with one inner distal spiniform seta. ***Labium*** palp without inner distal expansion. ***Cheliped*** slightly dimorphic; left cheliped more setose; right cheliped more slender, exopod article 3 small and naked. ***Pereopod 1*** merus with one short and strong ventrodistal spiniform seta; carpus with two short and strong ventral spiniform setae; dactylus with six pointed ventral denticles and one small ventrodistal spiniform seta, together with unguis subchela-like. ***Pereopods 2, 3, 5, and 6*** with chela-like dactylus. ***Pereopod 4*** dactylus with particularly long ventrodistal prolongation, > 2× as long as unguis. **Male.** Similar to female except: ***Antennule*** outer flagellum proximal articles short and wide, covered with numerous aesthetascs. ***Antenna*** article 2 without inner distal spiniform seta, flagellum inner half covered with numerous aesthetascs, proximal articles very wide and short, distal articles narrower. ***Cheliped*** relatively robust; left and right cheliped dimorphic or not; fixed finger incisive margin with or without one large and blunt apophysis.

Description. Female (ovigerous paratype MBM287301). *Body* (Fig. 11A, figure and description based on non-ovigerous female paratype MBM287303) elongate, dorsoventrally flattened, 6.8 mm long, 6.6× as long as broad, posteriorly narrower. ***Carapace*** subrectangular, ~ 0.1× as long as total body length, 0.9× as long as broad, rostrum wide and rounded, anterior margin flat, with four short simple setae, lateral margin with several simple setae. ***Eye lobe*** well separated, pigmented. ***Pereon*** ~ 0.6× as long as total body length; pereonite 1 broadest, 0.6× as long as broad; pereonite 2 shortest, 0.9× as long as pereonite 1, 0.6× as long as broad; pereonite 3 1.3× as long as pereonite 2, 0.8× as long as broad; pereonite 4 longest, 1.4× as long as pereonite 3, *ca.* as long as broad; pereonite 5 0.8× as long as pereonite 4, *ca.* as long as broad; pereonite 6 0.9× as long as pereonite 5, 0.9× as long as broad, each pereonite with a few anterolateral simple setae. ***Pleon*** ~ 0.25× body length, posteriorly narrower; each pleonite rectangular and similar in length, with several lateral plumose setae. ***Pleotelson*** subrectangular, 1.4× as long as one pleonite, narrower than pleonite 5, 1.2× as long as broad, with four lateral plumose setae, posterior margin rounded, with two pairs of simple setae.

Antennule (Fig. 11B, figure and description based on non-ovigerous female paratype MBM287304, 6.8 mm long) peduncle article 1 2.8× as long as broad, outer margin with three broom and 12 simple setae, inner margin with nine simple setae

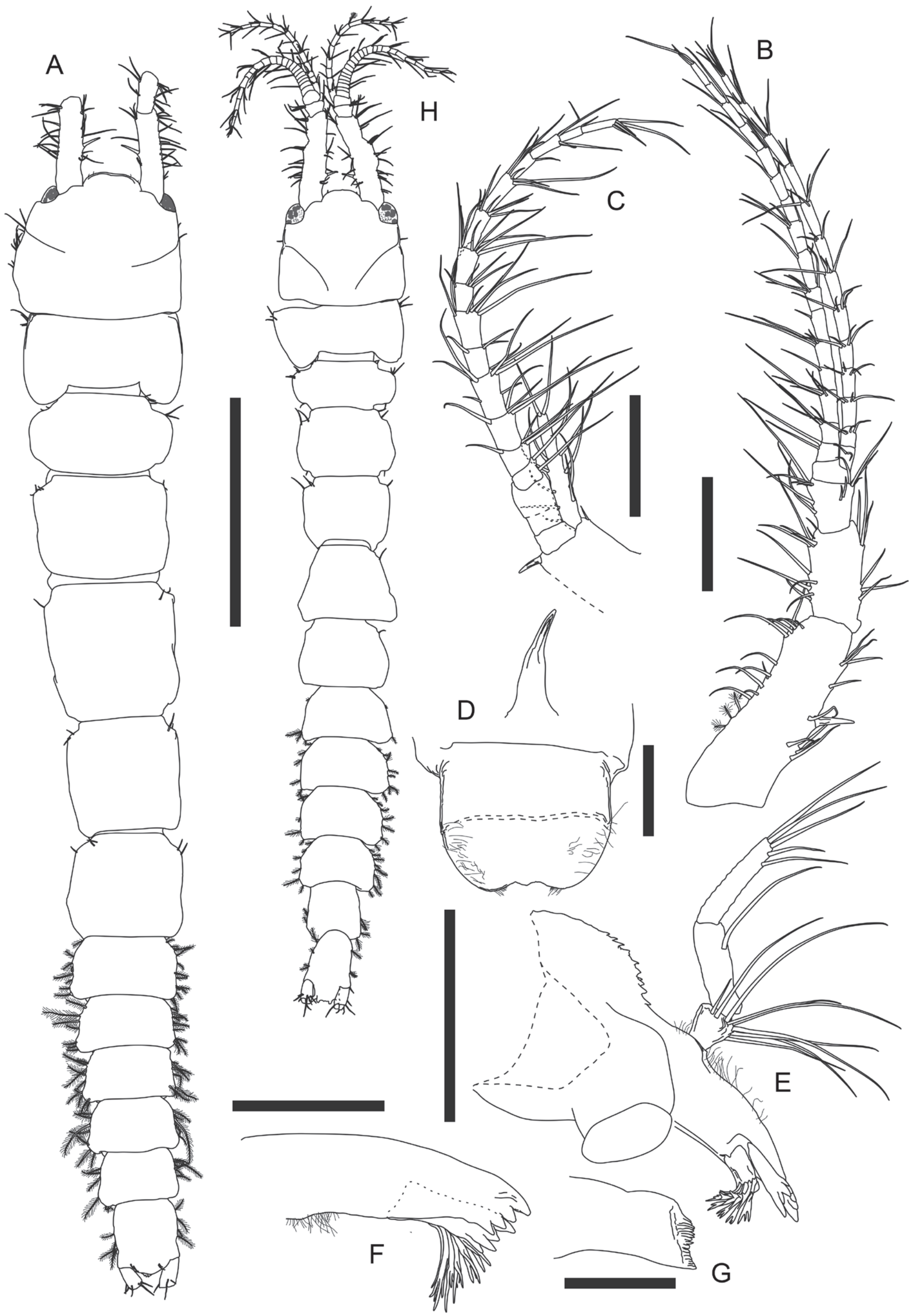

Figure 11. *Swireapseudes planafrontis* sp. nov. Paratype (MBM287303), non-ovigerous female **A** body dorsal view. Paratype (MBM287304), non-ovigerous female **B** left antennule. Paratype (MBM287301), ovigerous female **C** right antenna **D** epistome and labrum **E** left mandible **F** left mandible incisor, lacinia mobilis and setal row **G** left mandible molar. Allotype (MBM287302), male **H** body dorsal view. Scale bars: 2 mm (**A, H**); 0.2 mm (**B, C, E**); 0.1 mm (**D, F, G**).

and one strong spiniform seta midway; article 2 half as long as article 1, twice as long as broad, with 11 outer setae and six inner simple setae; article 3 short, half as long as article 2, 1.2× as long as broad, with seven outer and six inner simple setae; article 4 naked; outer flagellum 16-articled, longer than peduncle, each article naked or with at most five distal simple setae; inner flagellum 13-articled, slightly shorter than outer flagellum, each article with two to five distal simple setae.

Antenna (Fig. 11C) peduncle article 1 not examined; article 2 proximal half not examined, distal margin with one short outer simple seta and one inner spiniform seta, squama elongate, with five outer, five inner, and two distal simple setae; article 3 short and naked; articles 4 and 5 not well separated, naked; flagellum 14-articled, each article with 1–8 setae.

Labrum (Fig. 11D) rounded, distal margin slightly concave, covered with setules; epistomal apophysis present.

Left mandible (Fig. 11E) outer margin denticulate and covered with setules; incisor and lacinia mobilis (Fig. 11F) four-denticled, setal row with one simple and five trifurcate or multifurcate setae; molar (Fig. 11G) crenulate; palp 3-articled, article 1 short, 0.9× as long as broad, with nine simple setae along distal and inner margin, article 2 2.5× as long as article 1, with one simple seta on inner margin, article 3 *ca.* as long as article 2, with five distal simple setae. Right mandible (Fig. 12A) outer margin covered with setules; incisor (Fig. 12B) five-denticled, without lacinia mobilis, setal row similar to that of left mandible; molar not examined; palp similar to that of left mandible but article 2 with two inner simple setae, and article 3 with three distal simple setae.

Labium (Fig. 12C) palp covered with setules, with two distal simple setae.

Maxillule (Fig. 12D) outer endite with ten distal spiniform setae and two subdistal setae, inner and outer margins covered with setules; inner endite with one distal trifurcate seta and four distal plumose setae, inner and outer margin covered with setules; palp 2-articled, article 2 with five distal simple setae.

Maxilla (Fig. 12E) outer lobe of movable endite with eight long distal simple setae; inner lobe of movable endite with ~ 12 distal simple setae; outer lobe of fixed endite distal margin with seven blunt, one leaf-like, four trifurcate, two simple setae, and one seta with several spinules on single side; inner lobe of fixed endite distal margin with a row of ~ 25 “articulate” setae (with distinct demarcation on midway of each seta), a cluster of seven simple setae, and four blunt setae with a row of short setules and serrations on distal one third; inner margin with spinules.

Maxilliped (Fig. 12F) basis outer margin covered with setules covered with setules, distal margin with one seta; endite covered with setules, distal margin with five simple setae and six spiniform setae, inner margin with three coupling hooks, inner fold with six plumose setae; palp article 1 outer margin with one distal simple seta, distal margin with three simple setae, article 2 outer margin with seven long distal simple setae, inner margin with five long simple setae and a row of 45–50 shorter simple setae, article 3 outer margin with one distal simple seta, inner margin with ~ 12 simple setae, article 4 with ~ 12 distal simple setae.

Figure 12. *Swireapseudes planafrontis* sp. nov. Paratype (MBM287301), ovigerous female **A** right mandible **B** right mandible incisor **C** labium **D** maxillule **E** maxilla **F** maxilliped. Scale bars: 0.2 mm (**A, D**); 0.1 mm (**B, C, E, F**).

Chelipeds (Fig. 13A, B) left and right slightly dimorphic, differences in size and setal pattern. Left cheliped (Fig. 13A) exopod 3-articled, article 3 with four plumose setae; basis 3× as long as broad, dorsal margin with two simple setae on distal half, ventral margin with five long simple setae and four shorter simple setae; merus 0.7× as long as basis, 2.3× as long as broad, covered with totally ~ 25 simple setae; carpus long, ~ 1.9× as long as merus, 4.6× as long as broad, covered with totally ~ 44 simple setae; propodus palm 0.5× as long as carpus, 2.4× as long as broad, with three dorsal simple setae, one outer simple seta near insertion of dactylus, and two inner simple setae, fixed finger 0.8× as long as palm, ~ 4× as long as broad, with six ventral and two short distal simple setae; dactylus plus unguis 6.5× as long as broad, slightly curved. Right cheliped (Fig. 13B) slenderer and less setose than left cheliped, ~ 0.7× as long as left cheliped; exopod 3-articled, article 3 small and naked; basis ~ 3× as long as broad, ventral margin with one subdistal simple seta; merus 0.7× as long as basis, ~ 3× as long as broad, with two outer and two ventral setae; carpus long and slender, 1.9× as long as merus, ~ 5× as long as broad, with one outer subdistal simple seta, dorsal margin with one subdistal simple seta, ventral margin with three midway and one subdistal simple seta; propodus palm 0.4× as long as carpus, 2.1× as long as broad, with one outer simple seta near insertion of dactylus, dorsal margin with one subdistal simple seta, fixed finger 0.7× as long as palm, 3× as long as broad, with two ventral and two distal simple setae, incisive margin with one proximal simple seta; dactylus plus unguis 4.9× as long as broad, slightly curved, with seven subdistal simple setae.

Pereopod 1 (Fig. 13C) exopod 3-articled, article 3 with six plumose setae; basis 2.7× as long as broad, dorsal margin with three short, two longer simple setae and a few setules, ventral margin with six simple setae midway and a cluster of eight distal simple setae; ischium with four ventrodistal simple setae; merus 0.6× as long as basis, 1.4× as long as broad, dorsal margin with a cluster of seven distal simple setae and one spiniform seta, ventral margin with a cluster of four simple setae midway, eight simple setae along distal half, three distal simple setae, and one distal short but strong spiniform seta; carpus 0.9× as long as merus, 1.3× as long as broad, distal margin with one long dorsal spiniform seta, a cluster of *ca.* eight dorsal simple setae and two outer setae, ventral margin with nine simple setae and two short but strong spiniform setae; propodus 1.2× as long as carpus, 1.6× as long as broad, dorsal margin with three shorter simple setae on proximal half, six long simple setae and three long spiniform setae on distal half, ventral margin with 11 simple setae and four strong spiniform setae, distal margin with one short subventral simple seta; dactylus (Fig. 13D) plus unguis 0.7× as long as propodus, 5.7× as long as broad, ventral margin with six pointed denticles and one small distal spiniform seta, spiniform seta much shorter than unguis, together subchela-like.

Pereopod 2 (Fig. 13E) basis 3.5× as long as broad, with two short dorsal simple setae, one dorsal broom seta, three subventral distal simple setae, and a cluster of five ventrodistal simple setae; ischium with one dorsal simple seta and a cluster of six ventrodistal simple setae; merus 0.4× as long as basis, 1.7× as long as broad, with one outer subdistal and three outer distal simple setae, ventral margin with seven simple setae

Figure 13. *Swireapseudes planafrontis* sp. nov. Paratype (MBM287301), ovigerous female **A** left cheliped **B** right cheliped **C** right pereopod 1 **D** right pereopod 1 dactylus **E** right pereopod 2 **F** right pereopod 2 dactylus **G** right pereopod 3 **H** right pereopod 3 dactylus. Scale bars: 0.2 mm (**A–C, E, G**).

and one long spiniform seta on distal half; carpus 1.2× as long as merus, 2.2× as long as broad, outer surface with a row of ten simple setae and two long spiniform setae from midway to dorsodistal corner, ventral margin with eight simple setae and two long spiniform setae on distal half, distal margin with three inner simple setae; propodus 0.9× as long as carpus, ~ 3× as long as broad, distal half with a row of five subdorsal simple setae and three spiniform setae, ventral margin with seven simple setae and three spiniform setae; dactylus (Fig. 13F) plus unguis 0.8× as long as propodus, ~ 6× as long as broad, dactylus slightly curved, with one indistinct demarcation midway and one pointed ventrodistal prolongation, unguis curved, slightly longer than prolongation, together chela-like.

Pereopod 3 (Fig. 13G) basis 3.2× as long as broad, with a cluster of six ventrodistal simple setae; ischium with a cluster of seven ventral subdistal simple setae; merus 0.3× as long as basis, 1.8× as long as broad, with eight ventral or subventral simple setae and one ventral spiniform seta on distal half, ventral margin slightly denticulate; carpus 1.4× as long as merus, 2.6× as long as broad, ventral to distal margin and subventral surface covered with ~ 16 simple setae and three spiniform setae, ventral margin slightly denticulate; propodus 0.7× as long as carpus, 2.7× as long as broad, with one dorsoproximal broom seta and a row of six simple setae and three spiniform setae from outer midway surface to dorsodistal corner, ventral margin with four simple setae and three spiniform setae on distal half; dactylus (Fig. 13H) attached to propodus subdistally, similar to that of pereopod 2 but not articled.

Pereopod 4 (Fig. 14A, figure and description based on non-ovigerous female paratype MBM287305, 7.1 mm long) basis 3.2× as long as broad, with a cluster of five ventrodistal simple setae; ischium with a cluster of six ventrodistal simple setae; merus 0.3× as long as basis, 1.6× as long as broad, with one dorsodistal, two outer subdistal, and three ventral simple setae, ventral margin slightly denticulate; carpus 1.8× as long as merus, 2.5× as long as broad, ventral to distal margin covered with ~ 17 simple setae and six spiniform setae, ventral margin slightly denticulate; propodus 0.6× as long as carpus, 3.2× as long as broad, ventral margin with *ca.* eight simple setae and 10 spiniform setae; dactylus (Fig. 13B, figure and description based on MBM287305) attached to propodus subdistally, nearly as long as propodus, > 9× as long as broad, with three ventral spinules and one long ventrodistal prolongation that is 2.3× as long as unguis, together subchela-like.

Pereopod 5 (Fig. 14C) basis 3.2×as long as broad, dorsal margin with two broom setae midway, ventral margin with a cluster of five distal simple setae; ischium dorsal margin with one short subdistal simple seta, ventral margin with a cluster of five distal simple setae, merus 0.3× as long as basis, 1.8× as long as broad, with one dorsodistal simple seta, ventral margin denticulate, six simple setae on distal half; carpus 1.7× as long as merus, ~ 3× as as long as broad, ventral to distal margin covered with ~ 17 simple setae and eight spiniform setae, the distal two spiniform setae very long, ventral margin denticulate; propodus 0.8× as long as carpus, 3.2× as long as broad, ventral margin denticulate, covered with *ca.* ten simple setae and nine spiniform setae; dactylus similar to that of pereopod 3.

Figure 14. *Swireapseudes planafrontis* sp. nov. Paratype (MBM287305), non-ovigerous female **A** right pereopod 4 **B** right pereopod 4 dactylus. Paratype (MBM287301), ovigerous female **C** right pereopod 5 **D** right pereopod 6 **E** right pleopod 1 (all setules omitted). Scale bars: 0.2 mm (**A, C–E**).

Pereopod 6 (Fig. 14D) basis long, 4.8× as long as broad, dorsal margin with one subproximal broom seta, ventral margin with two subdistal simple setae; ischium with two dorsal and three ventral subdistal simple setae; merus 0.3× as long as basis, nearly 2× as long as broad, with one dorsodistal simple seta and one simple seta on inner surface, ventral margin with six simple setae on distal half; carpus 1.7× as long as merus, 3.3× as long as broad, with three dorsodistal simple setae, ventral to distal margin with ~ 17 simple setae and five long spiniform setae, ventral margin slightly denticulate; propodus 0.8× as long as carpus, 3.6× as long as broad, with one dorsodistal, one ventrodistal simple seta, two long and one shorter dorsodistal spiniform setae, ventral margin with one proximal simple seta and a row of ~ 28 serrate setae along ventral margin to distal margin; dactylus similar to that of pereopod 5.

Pleopod 1 (Fig. 14E, all setae plumose, setules omitted in figure) basal article with seven outer and five inner plumose setae; exopod with 30 plumose setae; endopod with 27 plumose setae, most proximal one on inner margin strong.

Uropod basal article with four or five distal and subdistal simple setae; exopod and endopod not examined.

Male (allotype MBM287302). ***Body*** (Fig. 11H) elongate, dorsoventrally flattened, allotype 5.0 mm long, 6.4× as long as broad. ***Carapace*** subrectangular, ~ 0.1× as long as total body length, 0.8× as long as broad; rostrum rounded, anterior margin flat, with two short simple setae; lateral margin with one simple seta. ***Pereon*** half as long as total body length; each pereonite with at most seven anterolateral simple setae and without or with one posterolateral simple seta, pereonite 1 broadest, as wide as carapace, half as long as broad, pereonite 2 shortest, pereonite 4 longest but narrowest. ***Pleon*** 0.3× as long as total body length, posteriorly narrower; each pleonite similar in length, with several lateral plumose setae, pleonites 1–4 trapezoidal, pleonite 5 subrectangular. ***Pleotelson*** subrectangular, 1.3× as long as pleonite 5, 1.5× as long as broad, with three lateral plumose setae, posterior margin with two pairs of blunt apophyses.

Antennule (Fig. 15A, most aesthetascs represented by fine lines) peduncle article 1 ~ 3× as long as broad, outer margin with 11 simple setae, inner margin with seven simple setae and one strong spiniform seta midway; article 2 ~ 0.5× as long as article 1, 1.6× as long as broad, with one ventral simple seta, outer margin with six simple setae, inner margin with one simple seta on proximal half and a cluster of three subdistal simple setae; article 3 short, 0.4× as long as article 2, 0.7× as long as broad, distal margin with three outer and two inner simple setae; article 4 with one inner simple seta; outer flagellum 21-articled, *ca.* as long as peduncle, proximal articles shorter and broader, covered with numerous aesthetascs, distal articles longer and slenderer, each article without or with at most four distal simple setae; inner flagellum 12-articled, slightly longer than outer flagellum, articles 5 and 7 with one distal broom seta, each article without or with at most four distal simple setae.

Antenna (Fig. 15B, most aesthetascs represented by fine lines) peduncle article 1 naked; article 2 with two short outer simple setae, squama elongate, with three outer, three inner, two longer and one short distal simple seta; article 3 very short, naked; article 4 longest, 0.8× as long as broad, with three short outer simple setae; article 5 similar to flagellum articles, covered with aesthetascs, with one outer distal simple seta; flagellum 20-articled, each article very short, proximal articles broader, outer half covered with numerous aesthetascs, each article without or with at most four distal simple setae.

Left cheliped (Fig. 15C, figure and description based on male paratype MBM287307, 4.2 mm long) basis proximal part missing, dorsal margin with one short subdistal simple seta, ventral margin with one short and two longer simple setae; merus 2.2× as long as broad, outer surface with one subdistal simple seta, inner surface with two dorsodistal simple setae, ventral margin with four subdistal simple setae; carpus 2.1× as long as merus, 3.5× as long as broad, with seven ventral simple setae, inner surface with *ca.* ten subdorsal simple setae; propodus palm and fixed finger combined ~ 0.8× as long as carpus, palm 1.8× as long as broad, with one long outer simple seta near insertion of dactylus, dorsal margin with one subproximal and three subdistal simple setae, inner surface with two long subdistal simple setae, fixed finger 2.7× as long as broad, with six ventral, one outer and one inner simple seta, incisive margin with one large and blunt apophysis, and six distal simple setae; dactylus curved, 4.7× as long as broad. *Right cheliped* (Fig. 15D) exopod 3-articled, article 3 with four plumose setae; basis 2.3× as long as broad, ventral margin with one longer and three short but strong simple setae on proximal half, and one longer simple seta on distal half; merus 0.6× as long as basis, 2.4× as long as broad, ventral margin with four simple setae on proximal half, four longer and one short but strong simple setae on distal half, distal margin with two outer and three inner simple setae; carpus 1.7× as long as merus, 3.4× as long as broad, with one inner subventral simple setae, ventral margin with five simple setae and three subdistal simple setae; propodus attached to carpus subdistally, palm half as long as carpus, almost 2× as long as broad, with one outer simple seta near insertion of dactylus, dorsal margin with one proximal simple seta, a cluster of three simple setae on proximal half, one midway and a row of five subdistal simple setae, fixed finger distal part missing, with six ventral and three distal simple setae, incisive margin crenulate; dactylus plus unguis as long as palm, with three outer simple setae, unguis long and slender.

Remarks. The specimens of *Swireapseudes planafrontis* sp. nov. are extremely fragile, with appendages frequently missing. This phenomenon was also found in species of some other parapseudid genera, e.g., *Parapseudes*, *Pakistanapseudes* and *Saltipedis*, and considered to be autotomy (Guţu 1996). As a result, the morphological description of *S. planafrontis* could only be made up by the sum of parts of the several paratypes and allotype. It may be a novel discovery that the chelipeds of the present species not only display sexual dimorphism but also exhibit a little dimorphism between left and right chelipeds of a single female individual. Unfortunately, no male specimens were collected with complete left and right chelipeds, so it is not possible to confirm that the morphological differences between right cheliped of the allotype and left cheliped of the male paratype MBM287307 are the results of dimorphism or simply the result of variation (Figs 13A, B, 15C, D).

Apart from the dimorphism of female left and right cheliped, there are several other unique morphological features that easily distinguish *Swireapseudes planafrontis* sp. nov. from the two previously recorded species, *S. birdi* and *S. toloensis*: 1) rostrum distally wide and flat; 2) the presence of one strong spiniform seta midway on the inner margin of the antennule peduncle article 1; 3) the presence of one inner distal spiniform seta on the female antenna article 2; 4) the presence of one small ventrodistal spiniform seta (rather than

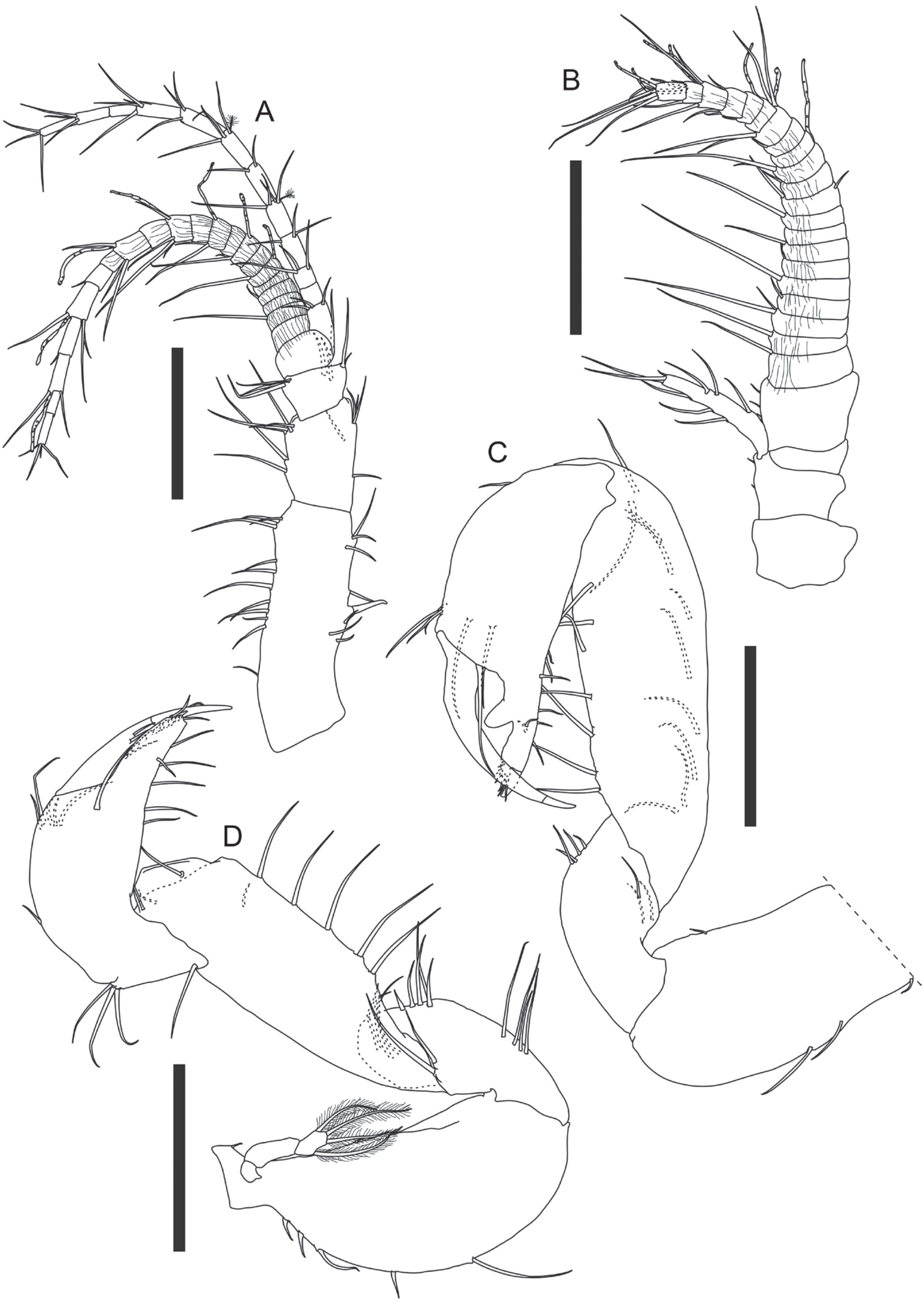

Figure 15. *Swireapseudes planafrontis* sp. nov. Allotype (MBM287302), male **A** left antennule **B** left antenna **D** right cheliped. Paratype (MBM287307), male **C** left cheliped. Scale bars: 0.2 mm.

prolongation) on pereopod 1 dactylus; 5) the long ventrodistal prolongation on pereopod 4 dactylus (Figs 11A–C, H, 13C, D, 14A, B, 15A, Table 3; see also Guţu and Iliffe 2008: figs 1A–D, 2D, 3C, 4A; Bamber 1997: figs 7A, B, 8A, B, 9H).

Key to the species of *Swireapseudes* (see also Table 3)

1 Rostrum distally wide and flat.................................***S. planafrontis* sp. nov.**
– Rostrum distally pointed...**2**
2 Pereopod 1 merus, carpus, and propodus with short and strong ventral spiniform setae ....***S. toloensis***
– Pereopod 1 merus, carpus, and propodus with long and slender ventral spiniform setae ....***S. birdi***

Table 3. Morphological comparison among all species of *Swireapseudes*.

Character / Species name	*S. planafrontis* sp. nov.	*S. birdi*	*S. toloensis*
Carapace			
Shape of rostrum	wide and rounded, distally flat	rounded, distally pointed	rounded, distally pointed
Antennule			
Number of female outer/inner flagellum articles	16/13	14/10	18/12
Antenna			
Number of female flagellum articles	14	8	14
Pereopod 1			
Shape of merus and carpus ventral spiniform setae	short and strong	long and slender	short and strong
Form of dactylus	subchelate	chelate	subchelate
Pereopod 4			
Form of dactylus	ventrodistal prolongation very long	simple, without unguis	subchelate
Pereopods 2, 3, 5, 6			
Form of dactylus	chelate	chelate	subchelate
References	present study	Guţu and Iliffe 2008	Bamber 1997

Acknowledgements

This work was supported by the National Natural Science Foundation of China (nos. 41876178, 42176114), the Senior User Project of RV KEXUE (Grant/Award no. KEXUE2020GZ01), and the Strategic Priority Research Program of the Chinese Academy of Sciences (no. XDA23050304).

References

Bamber RN (1997) Peracarid crustaceans from Cape d'Aguilar and Hong Kong II: Tanaidacea: Apseudomorpha. In: Morton B (Ed.) The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Eighth International Marine Biological workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong, 2–20 April 1995 Hong Kong University Press, Hong Kong, 87–102.

Bamber RN (1998) Tanaidaceans (Crustacea, Peracarida) from the southeast of the South China Sea. Asian Marine Biology 15: 171–199.

Bamber RN (2000) Additions to the apseudomorph tanaidaceans (Crustacea: Peracarida) of Hong Kong. In: Morton B (Ed.) The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Tenth International Marine Biological workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong, 2–26 April 1998 Hong Kong University Press, Hong Kong, 37–52.

Bamber RN (2008) A new species of *Apseudes* (Tanaidacea: Apseudomorpha: Apseudidae) from Hong Kong, with observations on *Gollumudes mortoni* (Bamber, 2001). Journal of Natural History 42(9–12): 877–884. https://doi.org/10.1080/00222930701850505

Bamber RN (2013) Tanaidaceans from Brunei, IV. The Families Kalliapseudidae, Pagurapseudopsidae, Parapseudidae and Apseudidae (Crustacea: Peracarida: Tanaidacea: Apseudomorpha), with descriptions of a new genus and six new species. Zootaxa 3734(4): 401–441. https://doi.org/10.11646/zootaxa.3734.4.1

Bamber RN, Sheader M (2003) A reinterpretation of the taxonomy and zoogeography of Pakistanapseudes and Swireapseudes (Crustacea: Tanaidacea): Hong Kong taxa in the world context. In: Morton B (Ed.) Perspectives on Marine Environment Change in Hong Kong and Southern China, 1977–2001. Proceedings of an International Workshop Reunion Conference. Hong Kong, 21–26 October 2001 Hong Kong University Press, Hong Kong, 167–194.

Błażewicz-Paszkowycz M, Bamber R, Anderson G (2012) Diversity of Tanaidacea (Crustacea: Peracarida) in the World's Oceans – How Far Have We Come? PLoS ONE 7(4): e33068. https://doi.org/10.1371/journal.pone.0033068

Dana JD (1849) Conspectus Crustaceorum quae in Orbis Terrarum Circumnavigatione, Carolo Wilkes e Classe Reipublicae Foederatae Duce, lexit et descripsit. The American Journal of Science and Arts, Series 2 8: 424–428. https://doi.org/10.2307/20021076

Drumm DT, Heard RW (2011) Systematic revision of the family Kalliapseudidae (Crustacea: Tanaidacea). Zootaxa 3142(1): 1–172. https://doi.org/10.11646/zootaxa.3142.1.1

Guţu M (1981) A new contribution to the systematics and phylogeny of the suborder Monokonophora (Crustacea, Tanaidacea). Travaux du Muséum National d'Histoire naturelle. Grigore Antipa 23: 81–108.

Guţu M (1996) Tanaidaceans (Crustacea, Peracarida) from Brazil, with description of new taxa and systematical remarks on some families. Travaux du Muséum National d'Histoire naturelle. Grigore Antipa 36: 23–133.

Guţu M (2006) New Apseudomorph Taxa (Crustacea, Tanaidacea) of the World Ocean. Curtea Veche, Bucharest, Romania, 318 pp.

Guţu M (2008) A revision of the family Parapseudidae, with description of a new tribe and three genera. The diagnoses and the key of the superspecific taxa (Crustacea: Tanaidacea: Apseudomorpha). Travaux du Muséum National d'Histoire naturelle. Grigore Antipa 51: 43–70.

Guţu M, Iliffe TM (2008) A new species and the first description of the male belonging to the genus *Swireapseudes* Bamber, from the submarine caves of the Eleuthera Island (Crustacea: Tanaidacea: Apseudomorpha). Travaux du Muséum National d'Histoire naturelle. Grigore Antipa 51: 7–16.

Lang K (1953) Apseudes hermaphroditicus n.sp. a hermaphroditic Tanaide from the Antarctic. Arkiv för Zoologi, Series 2 4: 341–350.

Lang K (1956) Kalliapseudidae, a new family of Tanaidacea. In: Wingstrand KG (Ed.) Bertil Hanström; Zoological Papers in Honour of his Sixty-fifth Birthday, November 20th, 1956. Zoological Institute, Lund: 205–225.

Larsen K, Bertocci I, Froufe E (2011) *Apseudes talpa* revisited (Crustacea; Tanaidacea). The impact on apseudidaen systematics. Zootaxa 2886(1): 19–30. https://doi.org/10.11646/zootaxa.2886.1.2

Leach WE (1814) Crustaceology. In: Brewster D (Ed.) The Edinburgh Encyclopaedia. Balfour, Edinburgh 7(2): 385–437, 765–766.

Shiino SM (1937) On *Apseudes nipponicus* n. sp. (Crustacea, Tanaidacea). Annotationes Zoologicae Japonenses 16: 53–62.

Shiino SM (1963) Tanaidacea collected by Naga Expedition in the Bay of Nha-Trang, South Viet-Nam. Report of the Faculty of Fisheries. Prefectural University of Mie 4: 437–507.

Shiino SM (1966) On *Kalliapseudes* (*Kalliapseudes*) *tomiokaensis* sp. nov. (Crustacea: Tanaidacea) from Japanese waters. Report of Faculty of Fisheries. Prefectural University of Mie 5: 473–488.

Shiino SM (1978) Tanaidacea collected by French Scientists on board the survey ship "Marion-Dufresne" in the regions around the Kerguelen Islands and other subantarctic islands in 1972, '74, '75, '76. Science Report of Shima Marineland 5: 1–122.

Sieg J (1980) Sind die Dikonophora eine polyphyletische Gruppe? Zoologischer Anzeiger 205(5–6): 401–416.

Studer T (1884) Isopoden, gesammelt während der Reise S.M.S Gazelle um die Erde, 1874–76. Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin 1883: 1–28.

Tzeng YW, Hsueh PW (2014) New species and records of Apseudomorpha (Crustacea: Tanaidacea) from Taiwan. Zootaxa 3869(3): 313–337. https://doi.org/10.11646/zootaxa.3869.3.6

Wi JH, Kang C-K, Soh HY (2017) Two new species in the genus *Phoxokalliapseudes* Drumm & Heard, 2011 (Crustacea: Tanaidacea: Kalliapseudidae) from the southwestern and southern coasts of Korea. Zootaxa 4231(3): 341–363. https://doi.org/10.11646/zootaxa.4231.3.3

Wi JH, Yu OH, Kang C-K (2019) Two new species of Apseudomorpha (Peracarida: Tanaidacea) from the East China Sea, with a key to the species of *Phoxokalliapseudes* Drumm & Heard, 2011. Journal of Crustacean Biology 39(2): 150–161. https://doi.org/10.1093/jcbiol/ruy105

WoRMS (2021) Apseudomorpha. http://www.marinespecies.org/aphia.php?p=taxdetails&id=136150 [accessed on 2021-12-01]

ZooKeys 1096: 161–187 (2022)
doi: 10.3897/zookeys.1096.83011
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Identification key to and checklist of the Swedish Phlaeothripidae (Thysanoptera)

Emma Wahlberg[1], Carl-Axel Gertsson[2]

1 *Department of Zoology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden* **2** *Murarevägen 13, SE-227 30 Lund, Sweden*

Corresponding author: Emma Wahlberg (emma.wahlberg@nrm.se)

Academic editor: Elison Fabricio B. Lima | Received 2 March 2022 | Accepted 7 April 2022 | Published 18 April 2022

http://zoobank.org/1F2F4CF1-5ED6-4ED9-B766-226F03B4C0CE

Citation: Wahlberg E, Gertsson C-A (2022) Identification key to and checklist of the Swedish Phlaeothripidae (Thysanoptera). ZooKeys 1096: 161–187. https://doi.org/10.3897/zookeys.1096.83011

Abstract
The Swedish fauna of thrips (Thysanoptera) in the family Phlaeothripidae consists of 49 species. A key to the species of Phlaeothripidae found in Sweden is provided. One species is recorded as new for the country, and 10 new regional records are presented. A checklist of all Swedish tubuliferan species with regional distributions is also given.

Keywords
Distribution, first record, identification, morphology, taxonomy, Thrips, Tubulifera

Introduction

Thysanoptera Haliday, 1836, more commonly known as thrips, are minute insects which are often not longer than 3 mm; larger species may reach 5 mm in size. Thrips have caught attention not only from researchers but also from the commercial and private sector, due to their impact as pests in agriculture (Paine 1992) and even as invasive species (Held et al. 2005; Boyd and Held 2006). The group least studied in Sweden is the family Phlaeothripidae Uzel, 1895. Some species are found in flowers, e.g., in the genus *Haplothrips* Amyot & Serville, 1843 (Fig. 1), but most of the known species in Sweden are found in soil, leaf litter, and decaying wood.

The research regarding Palaearctic taxa is scarce. Only a few regional checklists have been published in recent years, and the most relevant identification keys focus on the species in Great Britain (Mound et al. 1976, 2018; Kirk 1996). In recent years the fauna of Poland, a region with a previously similarly understudied thrips fauna, has been studied more extensively, which has led to a large gain in both taxonomic and ecological knowledge (Kucharczyk and Zawirska 1994; Kąkol and Kucharczyk 2004; Kucharczyk 2004; Kucharczyk and Kucharczyk 2008; Dubovský et al. 2010; Kucharczyk and Wyrozumski 2015). Most of the knowledge of Swedish taxa is based on older identification literature, e.g., Ahlberg (1926), Mound et al. (1976), and Kirk (1996), often not specific for Scandinavian conditions. A few papers have been published reporting new species at irregular intervals, reporting sporadic observations (Qvick 1977; Vasiliu-Oromulu et al. 2000; Kobro 2011; Sörensson 2012; Gertsson 2015a; Gertsson and Fägerström 2017). Kobro and Rafoss (2006) produced a key to the genus *Hoplothrips* in Norway, and Kobro (2013) produced an identification key to Norwegian thrips in general but only covered the most common and for amateurs easily distinguished species. The overlaps of the distributions the of Swedish and Norwegian species is currently not known, and no identification key to the Swedish fauna exists. Gertsson (2015b) provided a checklist of Nordic thrips. However, this was based only on previously collected specimens in museum collections. Recently new records to the fauna were made from freshly collected material, with a total of 5 new species for Sweden and several new regional records (Gertsson and Fägerström 2017; Gertsson 2021; Gertsson et al. 2022). In this paper we update the Swedish checklist of the family Phlaeothripidae and provide an identification key to the species with photographic illustrations.

Figure 1. *Haplothrips leucanthemi* in flower of *Leucanthemum vulgare*.

Material and methods

For this study we have examined representative specimens from the collections of The Swedish Museum of Natural History, Sweden (**NHRS**), Lund Museum of Zoology (**MZLU**), Sweden, Forschungsinstitut und Naturmuseum Senckenberg (**SMF**), Germany, and the private collections of Sverre Kobro and Manfred R. Ulitzka. In addition, newly collected material has been used, prepared on slides with Euparal according to the method outlined in Kobro (2013). The exception to this method is the preservation prior to maceration and the maceration step, where in this study fresh material has been stored in 80% ethanol prior to DNA extraction. Maceration has thereafter been carried out during DNA extraction before preparation on microscopic slides. This method has successfully been used for one-step DNA extraction and maceration for small insect specimens (Wahlberg and Johanson 2018; Wahlberg 2019). DNA extract is stored at the NHRS for further studies. The material was examined and photographed using manual focus stacking on Nikon Eclipse 80i and Swift 380T microscopes, with Nikon DS-Fi1 and Swift SC1003 cameras. Photos were automatically aligned and stacked using Helicon Focus 8.0.4 and Swift Imaging 3.0, and edited and finalized in Adobe Photoshop CC 23.2.0. The distributional data are provided on county level. The material collected and preserved during this project is deposited at the NHRS.

Swedish faunistic provinces and abbreviations

Sweden is traditionally divided in to faunistic provinces, most based on historical cultural regions overlapping with administrative counties (Fig. 2). They are in the checklist and map abbreviated as below, from south to north.

Sk	Skåne	**Ds**	Dalsland	**Hr**	Härjedalen
Bl	Blekinge	**Nä**	Närke	**Jä**	Jämtland
Ha	Halland	**Sö**	Södermanland	**Ån**	Ångermanland
Sm	Småland	**Up**	Uppland	**Vb**	Västerbotten
Öl	Öland	**Vs**	Västmanland	**Nb**	Norrbotten
Go	Gotland	**Vr**	Värmland	**Ås**	Åsele lappmark
GS	Gotska Sandön	**Dr**	Dalarna	**Ly**	Lycksele lappmark
Ög	Östergötland	**Gä**	Gästrikland	**Pi**	Pite lappmark
Vg	Västergötland	**Hs**	Hälsingland	**Lu**	Lule lappmark
Bo	Bohuslän	**Me**	Medelpad	**To**	Torne lappmark

Characters

The identification key is intended to be used for adult specimens, both females and males in various life stages and both winged and micropterous forms. For this reason, some species that express great intraspecific variation it is possible to find one species at several locations in the key (indicated by "[part]"). In Thysanoptera the most important morphological characters for species identification include antennal shape, presence, shape, and length

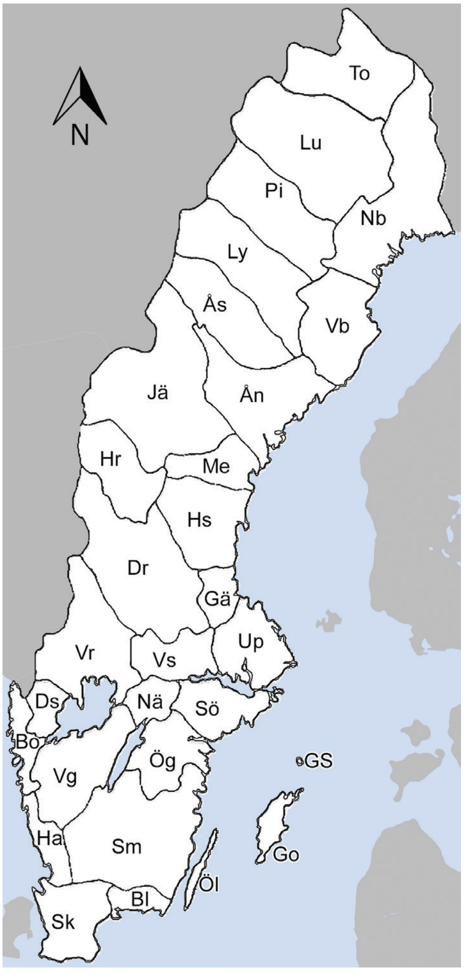

Figure 2. Map of Swedish faunistic provinces.

of setae, structure of mouth parts, and measurements of segments (Fig. 3). This always requires high magnification and specimen preparation. Large setae may be blunt, expanded (Fig. 10G), or acute at apex, and care need to be taken in preparation for avoiding collapse of expanded apices. The antennal segments often carry sensory organs in the shape of large trichomes, sense cones. These are more robust and broader than bristles that they might be confused with (Fig. 6A–C). Maxillary stylets are parts of the feeding apparatus and can be seen in macerated specimens (Fig. 4A, B), and the width and distance of the stylets and presence or absence of the median extension called maxillary bridge are used for separation of subfamilies and species groups. The last abdominal segment, segment X, may be either tapering and longitudinally divided (in most of the Thysanoptera families) or complete and tube-shaped. The latter being one of the defining characters of the family Phlaeothripidae (Fig. 3) and is in the key only referred to as the tube. Comprehensive and detailed descriptions of the anatomy and morphology of Thysanoptera are provided in Schliephake and Klimt (1979) and Moritz (2006).

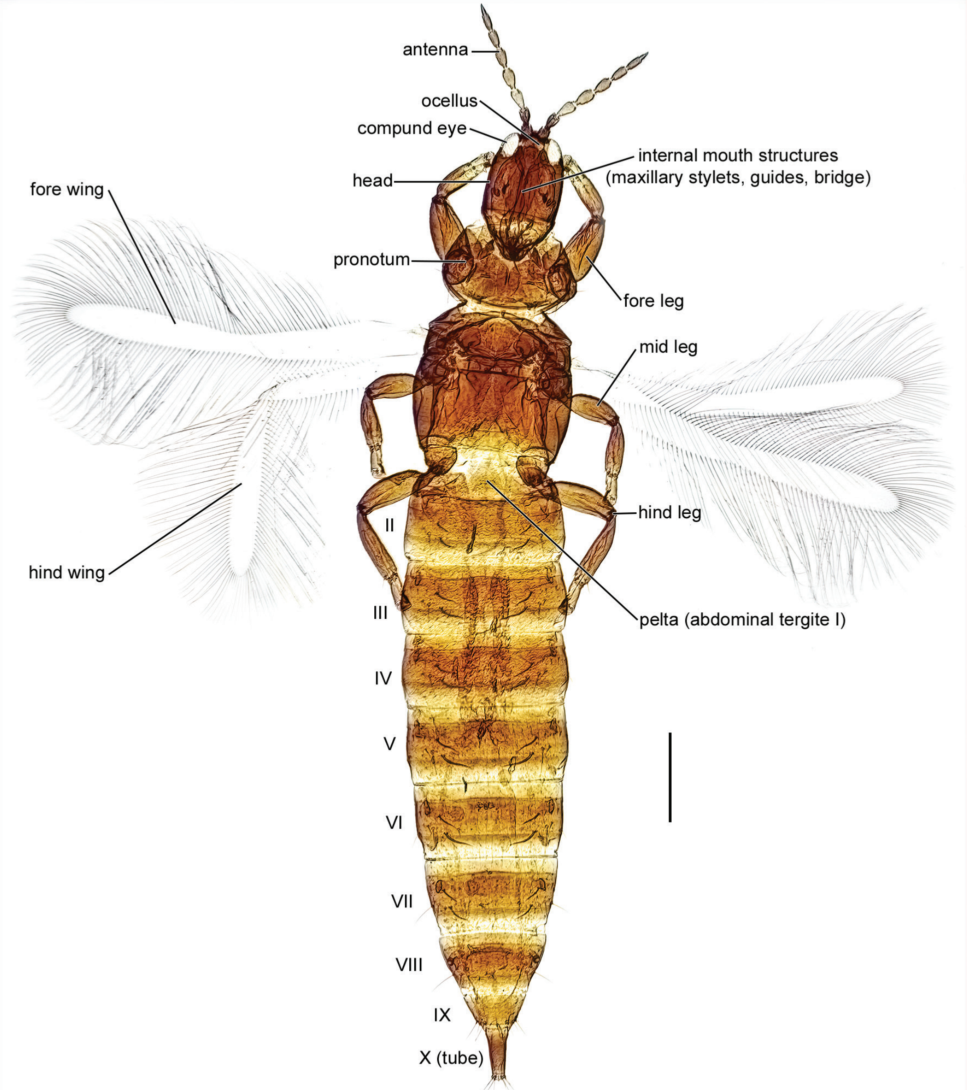

Figure 3. Habitus of *Haplothrips utae*, dorsal view. Roman numbers indicate abdominal segment number. Scale bar: 100 µm.

Taxonomy

Phlaeothripidae Uzel, 1895

Diagnosis. The last abdominal segment, segment X, tubular in both males and females (Figs 3, 5C, 7A, B), without longitudinal division and without saw-like ovipositor. In macropterous forms fore wings without longitudinal veins and surface without microtrichia (Fig. 3). Wing fringes not on sockets but embedded into the wing membrane. Wing retaining setae present in all (European) macropterous species.

Notes. There are about 3,700 known species of Phlaeothripidae in the world (Mound and Tree 2020; ThripsWiki 2022). Most of these species are described from tropical and subtropical areas. In Sweden 49 species are known. The Phlaeothripidae are diverse in their biology; feeding on decaying matter, pollen, fungal spores and hyphae, and prey, and sometimes expressing polymorphism and sociality (Kirk 1996; Mound 2004).

Key to the species of Phlaeothripidae from Sweden

1	Maxillary stylets broad, at least 5 µm wide (twice as wide as base of postocular setae) (Fig. 4A)........ **1 (Idolothripinae)**
–	Maxillary stylets slender, less than 5 µm wide (Fig. 4B)..... **8 (Phlaeothripinae)**
2 (1)	Anterior margin of ocellar triangle with long setae (Fig. 4C); large and dark species with elongated head **3**
–	Setae at anterior margin of ocellar triangle short or absent (Fig. 4D)........ **5**
3 (2)	Lateral wings of pelta (abdominal tergite I) slender (Fig. 5E) .... ***Megalothrips bonanni***
–	Lateral wings of pelta triangular (Fig. 5D) **4**
4 (2)	Tarsi pale and tibiae brown (Fig. 5C) .... ***Bacillothrips nobilis***
–	Tarsi and tibiae yellow (Fig. 5F) .... ***Megathrips lativentris***
5 (2)	Eyes ventrally elongated (Fig. 5A) **6**
–	Eyes ventrally not elongated........ **7**
6 (5)	Body (excluding antennae, legs, and wings) brown with yellow pronotum and yellow transverse band on metanotum .... ***Bolothrips bicolor***
–	Body uniformly brown .... ***Bolothrips dentipes***
7 (5)	Maxillary stylets close together, meeting or almost meeting medially (Fig. 4D)........ ***Cryptothrips nigripes***
–	Maxillary stylets widely separated, at least half of head width apart (Fig. 4A) .... ***Bolothrips icarus***
8 (1)	Maxillary bridge present (Fig. 5B)........ **9**
–	Maxillary bridge absent (Fig. 4B)........ **28**
9 (8)	Antennal segment IV with 2 sense cones (Fig. 6A).... ***Xylaplothrips fuliginosus***
–	Antennal segment IV with 3 or 4 sense cones (Fig. 6B, C)..... **10 (*Haplothrips*)**
10 (9)	Antennal segment III without sense cones (cf. Fig. 9E).... ***Haplothrips minutus***
–	Antennal segment III with at least 1 sense cone **11**
11 (10)	Antennal segment III with 1 sense cone........ **12**
–	Antennal segment III with 2 sense cones........ **14**
12 (11)	Postocular setae expanded or bluntly pointed (Fig. 6D) .... ***Haplothrips subtilissimus***
–	Postocular setae acute (Fig. 6E)........ **13**
13 (12)	Tube more than 2.3 times longer than wide (Fig. 7A) .... ***Haplothrips alpester*** [part]
–	Tube less than 2.3 times longer than wide (Fig. 7B) ..... ***Haplothrips aculeatus***
14 (11)	Postocular setae short, not longer than the width of the eye (Fig. 6F) **15**
–	Postocular setae well developed and long (Fig. 7C) **18**

15 (14) Setae S1 on tergite IX blunt apically (Fig. 7D) **16**
– Setae S1 on tergite IX acute **17**
16 (15) Antennal segment IV yellow at base (Fig. 7E) ....***Haplothrips leucanthemi***
– Antennal segment IV completely brown (Fig. 7F) .... ***Haplothrips propinquus***
17 (15) Both anteromarginal and anteroangular setae stout and at least twice as long as discal setae (Fig. 7G) ....***Haplothrips alpicola***
– Anteromarginal setae minute, anteroangular setae sometimes longer but not as stout ....***Haplothrips angusticornis***
18 (14) Setae S1 on tergite IX blunt apically (cf. Fig. 7D) **19**
– Setae S1 on tergite IX acute **21**
19 (18) Postocular setae acute (Fig. 7H) .... ***Haplothrips tritici*** [part]
– Postocular setae bluntly pointed (Fig. 5B) **20**
20 (19) Maxillary stylets one 1/3–1/4 of head width apart (Fig. 5B); tibia I brown ... . ***Haplothrips senecionis***
– Maxillary stylets about 1/5 of the head width apart (Fig. 7C); tibia I yellow apically ....***Haplothrips statices***
21 (18) Distal cilia of fore wings with barbs (in high magnification), in lower magnification visible as a rough or frizzled surface (Fig. 8A) .... ***Haplothrips setiger***
– Distal cilia of fore wings smooth **22**
22 (21) Postocular setae bluntly pointed (Fig. 8B) **23**
– Postocular setae acute (Fig. 7H) **24**
23 (22) Maxillary stylets about a fourth of head width apart (Fig. 8B); tibia I yellow but brown basally.. ***Haplothrips verbasci***
– Maxillary stylets about half of head width apart (Fig. 8C); tibia I wholly yellow .... ***Haplothrips acanthoscelis***
24 (22) Maxillary stylets close together, almost meeting medially (Fig. 8D).............. .... ***Haplothrips utae***
– Maxillary stylets at least a third of head width apart (Fig. 4E) **25**
25 (24) Maxillary stylets half of head width apart (cf. Fig. 8C) ....***Haplothrips distinguendus***
– Maxillary stylets 0.3–0.4 of head width apart (Fig. 7H) **26**
26 (25) Antennal segments III–IV, sometimes also V–VI, brown with yellow base, segments VII–VIII brown (Fig. 8E) ....***Haplothrips hukkineni***
– Antennal segment III shaded yellow to light brown, IV–VII brown (Fig. 8F) **27**
27 (26) Anteromarginal setae short, about as long as discal setae (Fig. 8G)............... .... ***Haplothrips alpester*** [part]
– Anteromarginal setae long, at least twice as long as discal setae (cf. Fig. 7G) .... ***Haplothrips tritici*** [part]
28 (8) Fore femora with apical teeth (Fig. 9A); 3 sense cones on antennal segment III–IV (Fig. 9B) ....***Acanthothrips nodicornis***
– Fore femora without apical teeth; if teeth are present then antennal segment IV with 4 sense cones.. **29**

29 (28) Eyes ventrally elongated (Fig. 9C) .... ***Cephalothrips monilicornis***

– Eyes not ventrally elongated **30**

30 (29) Mouth cone long and pointed, extending beyond posterior margin of pronotum (Fig. 9D) .... ***Poecilothrips albopictus***

– Mouth cone shorter **31**

31 (30) Antennal segment III without sense cones (Fig. 9E) ..... ***Lispothrips crassipes***

– Antennal segment III with at least 1 sense cone (Fig. 9F) **32**

32 (31) Antennal segment III with 1 sense cone .... **33 (*Liothrips*)**

– Antennal segment III with 2 or 3 sense cones (Fig. 9F) **34**

33 (32) Setae S1 on abdominal tergite IX about as long as tube (Fig. 9G) .... ***Liothrips austriacus***

– Setae S1 on abdominal tergite IX about half as long as tube (Fig. 10A) .... ***Liothrips setinodis***

34 (32) Abdomen clearly bicolored, with at least segment VIII–IX largely yellow (Fig. 10B); tube yellow but often with dark transverse terminal band or shading; micropterous forms usually with head and pronotum yellow **35**

– Abdomen uniformly brown or uniformly yellow, sometimes with pale or red markings **36**

35 (34) Abdominal segment VIII–X yellow (Fig. 10B) ...... ***Hoplothrips pedicularius***

– Abdominal segment VI–X yellow .... ***Hoplothrips caespitis*** [part]

36 (34) Pronotum with 5 pairs of well-developed setae, sometimes short but stout (Fig. 10C) **37**

– Pronotum with 4 pairs of well-developed setae, anteromarginals not distinctly stouter than discal setae **43**

37 (36) Postocular setae present but short, shorter or as long as width of eyes (Fig. 10D); setae S1 on abdominal tergite IX distinctly shorter than half of the length of tube (Fig. 10F) .... **38 (*Phlaeothrips*)**

– Postocular setae well developed and as long as or longer than the length of eyes (Fig. 10E); setae S1 on abdominal tergite IX at least half as long as tube (Fig. 10G) **41**

38 (37) Head with lateral tubercles (Fig. 10H) **39**

– Head without lateral tubercles (Fig. 10D) **40**

39 (38) Antennal segment III about 3 times as long as wide. Tibia I often completely yellow (Fig. 10I) .... ***Phlaeothrips coriaceus***

– Antennal segment III less than 2.6 times as long as wide. Tibia I usually yellow apically (Fig. 10J) .... ***Phlaeothrips denticauda***

40 (38) Fore tibiae largely yellow, mid and hind tibiae distinctly bicolored with yellow apex and base (Fig. 10K) .... ***Phlaeothrips annulipes***

– All tibiae brown .... ***Phlaeothrips bispinosus***

41 (37) Postocular setae (Fig. 10E) and setae S1 on abdominal tergite IX expanded apically (Fig. 10G). Fore wings constricted medially .... ***Hoplandrothrips bidens***

– Postocular setae and setae S1 on abdominal tergite IX acute. Fore wings parallel sided **42**

42 (41) Large pronotal setae expanded apically (Fig. 11A).... ***Holothrips schaubergeri***
– Large pronotal setae acute................................ ***Hoplothrips polysticti*** [part]
43 (36) Antennal segment IV with 2 sense cones (Fig. 9F).................................... **44**
– Antennal segment IV with 3 or 4 sense cones **48**
44 (43) Maxillary stylets about 1/3 of head width apart (Fig. 11B)........................ **45**
– Maxillary stylets close together, meeting or almost meeting medially (Fig. 4B) **46**
45 (44) Large pronotal setae expanded apically (cf. Fig. 11A). Antennal segments VII and VIII broadly attached.. ***Hoplothrips longisetis***
– Pronotal setae acute .... ***Hoplothrips caespitis*** [part]
46 (44) Setae S1 as long as or longer than tube (Fig. 11C)...***Hoplothrips unicolor*** [part]
– Setae S1 shorter than tube **47**
47 (46) Antennal segment I slightly tapering apically, apical width less than 40 microns (Fig. 11D). Macropterous females with clusters of small sense cones on antennal segments IV–V (Fig. 11D) .... ***Hoplothrips semicaecus*** [part]
– Antennal segment I more evenly tubular, apical width more than 40 microns.. ***Hoplothrips carpathicus***
48 (43) Antennal segment IV with 3 sense cones... **49**
– Antennal segment IV with 4 sense cones... **52**
49 (48) Macropterous females with cluster of small sense cones on antennal segments IV–V (Fig. 11D). Males with small eyes, abdominal sternite VIII with irregularly and broadly shaped glandular pore area on sternite VIII .... ***Hoplothrips semicaecus*** [part]
– Antennal segments different. Males without consciously small eyes, if small then with a defined circular glandular pore area on abdominal sternite VIII (Fig. 11E) **50**
50 (49) Setae S1 on abdominal tergite IX blunt apically (Fig. 11F) .... ***Thorybothrips unicolor***
– Setae S1 on tergite abdominal IX acute (Fig. 11G) **51**
51 (50) Setae S1 on abdominal tergite IX as long as or longer than tube (Fig. 11C) .. .. ***Hoplothrips unicolor*** [part]
– Setae S1 on abdominal tergite IX shorter than tube (Fig. 11G).................... .... ***Hoplothrips polysticti*** [part]
52 (48) Major pronotal setae expanded (cf. Fig. 11A) ...***Hoplandrothrips williamsianus***
– Major pronotal setae acute or blunt, not expanded **53**
53 (52) Antennal segment III asymmetric with long and strongly inwards curving sense cone at inner margin (Fig. 11H) .... ***Hoplothrips fungi***
– Sense cones on segment III forwardly pointing and stout.......................... **54**
54 (53) Antennal segments IV–VI brown, IV at most slightly shaded (Fig. 11D) **55**
– Antennal segments IV–VI bicolored with basal half yellow (Fig. 11I) **56**
55 (54) Antennal segment VIII not distinctly constricted at base, VII and VIII confluent (Fig. 11D)... ***Hoplothrips semicaecus*** [part]
– Antennal segment VIII constricted at base, separating VII and VIII (Fig. 11J) .... ***Hoplothrips polysticti*** [part]

56 (54) All tibiae completely yellow (Fig. 11K) .... ***Hoplothrips corticis***
– Only fore tibia yellow, mid and hind tibiae at most yellow basally and apically (Fig. 11L) .... ***Hoplothrips ulmi***

Checklist of the Swedish Phlaeothripidae

Idolothripinae Bagnall, 1908

Diagnosis. The Idolothripinae are distinguished by the broad maxillary stylets. The maxillary stylets are at least 5 µm broad.

Notes. There are seven known species in Sweden in this subfamily. The broad maxillary stylets are hypothesized to be an adaptation to feeding on fungal spores (Mound and Palmer 1983).

Bacillothrips **Buffa, 1908**

Bacillothrips nobilis **(Bagnall, 1909)**
Figs 4C, 5C, D

Distribution. Go.

Remarks. First record for Sweden. In Fennoscandia this species has previously been recorded from Denmark, Norway, and Finland (Kobro 2011; Gertsson 2015b). Feeding on fungal spores (Mound 1974), and found in dry grass, sedges, and on dead branches mainly from *Salix* L. (Mound et al. 1976; Schliephake and Klimt 1979).

Material examined. Sweden • 1♀; Gotland, Gotlands kommun, Vitärtskällan; 57.8512°N, 18.8123°E; 10 Jul. 2011; B. Eklund, leg.; Malaise trap; Loc. 029-06.

Bolothrips **Priesner, 1926**

Bolothrips bicolor **Heeger, 1852**

Distribution. Up.

Bolothrips dentipes **(Reuter, 1880)**
Fig. 5A

Distribution. Sk, Sm, Öl, Ög, Bo, Sö, Up, Lu.

Bolothrips icarus **(Uzel, 1895)**
Fig. 4A

Distribution. Sk, Öl, Go, GS, Sö, Up.

Remark. First record for Sö.

Material examined. Sweden • 1♀; Södermanland, Nyköping kommun, Skeppsvik; dry meadow at roadside with *Crepis*, *Vicia*, and *Plantago*; 58.6399°N, 16.8225°E; 3 Jun. 2021; E. Wahlberg, leg.

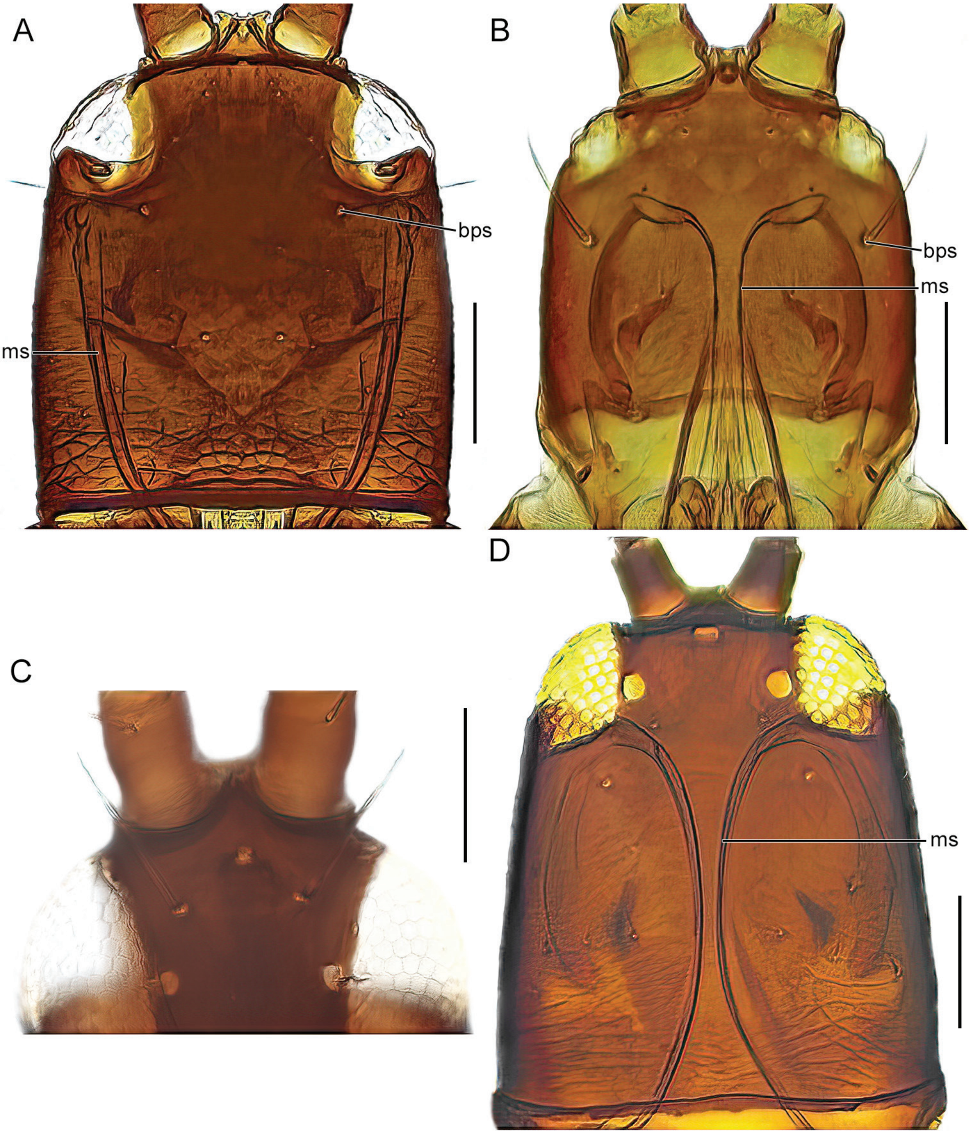

Figure 4. head, dorsal view **A** *Bolothrips icarus* **B** *Hoplothrips carpathicus* **C** *Bacillothrips nobilis* (ocellar triangle) **D** *Cryptothrips nigripes*. Abbreviations: bps: base of postocular seta, ms: maxillary stylets. Scale bars: 100 μm.

Cryptothrips Uzel, 1895

Cryptothrips nigripes (Reuter, 1880)
Fig. 4D

Distribution. Sk, Sm, Öl, Bo, Sö, Up, Vs, Vr, Dr, Lu.

Megathrips Targioni-Tozzetti, 1881

Megathrips lativentris (Heeger, 1852)
Fig. 5F

Distribution. Sk, Bl, Sm, Öl, Go, GS, Ög, Vg, Bo, Ds, Nä, Sö, Up, Vr, Dr, Gä, Hs, Me, Hr, Jä, Ån, Vb, Nb, Ly, Pi, Lu, To.

Megalothrips Uzel, 1895

Megalothrips bonanni Uzel, 1895
Fig. 5E

Distribution. Sk.

Phlaeothripinae Uzel, 1895

Diagnosis. Differentiated from Idolothripinae by the slender maxillary stylets, at most 3 microns wide.

Notes. The majority of phlaeothripids belongs to this subfamily; from Sweden 42 species are known. The life histories are very varying, ranging from species feeding on fungal hyphae to predatory species (Mound and Tree 2020).

Acanthothrips Uzel, 1895

Acanthothrips nodicornis (Reuter, 1880)
Fig. 9A, B

Distribution. Sm, Bo, Sö, Up, Vs, Vr, Dr.

Cephalothrips Uzel, 1895

Cephalothrips monilicornis (Reuter, 1880)
Fig. 9C

Distribution. Sk, Vg, Öl, Sm, Sö, Up, Vr.

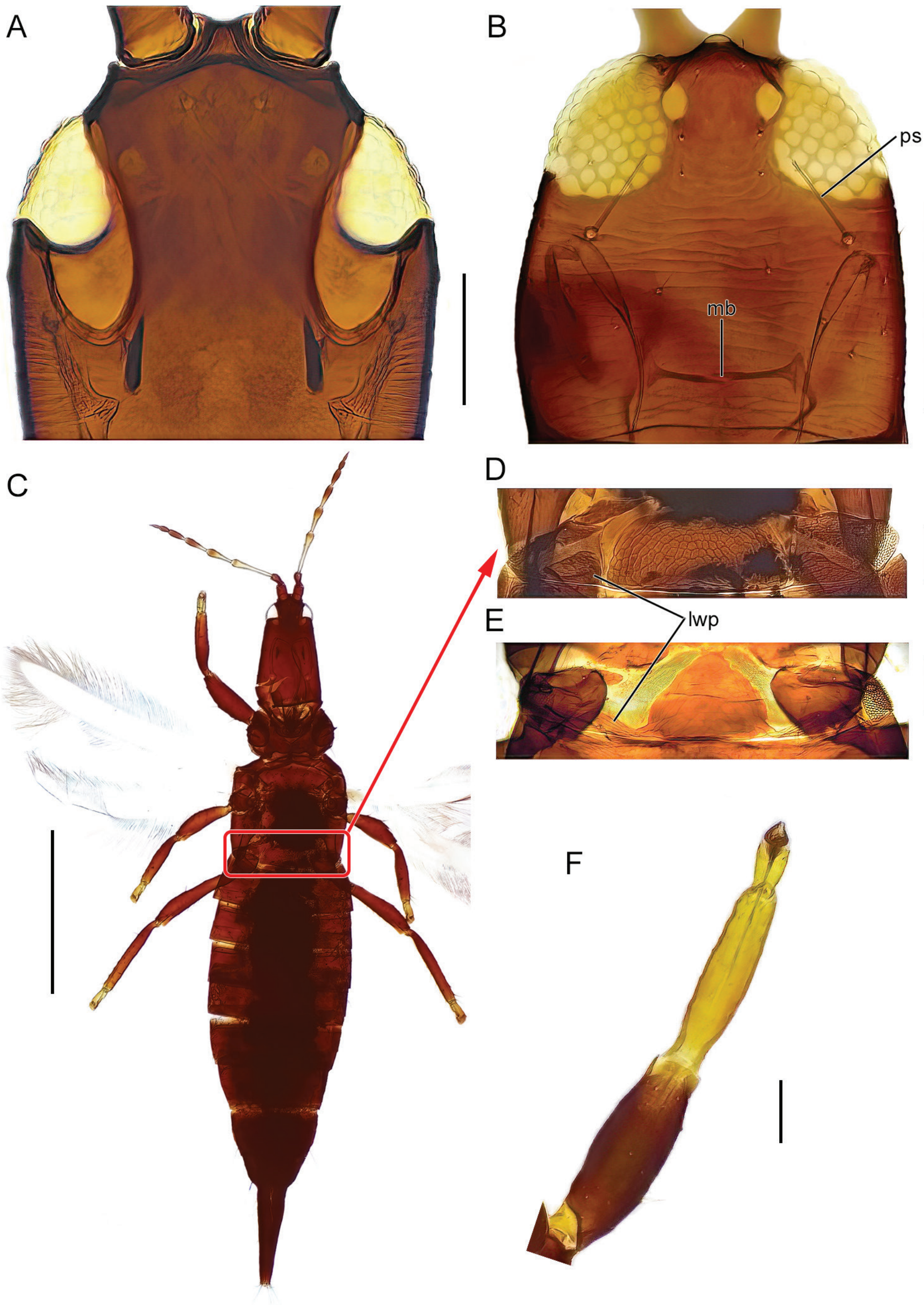

Figure 5. **A, B** head, dorsal view **A** *Bolothrips dentipes* (ventral margins of eyes also visible) **B** *Haplothrips senecionis* **C** habitus, dorsal view, *Bacillothrips nobilis* **D, E** pelta **D** *B. nobilis* **E** *Megalothrips bonanni* **F** fore leg, *Megathrips lativentris*. Abbreviations: mb: maxillary bridge, ps: postocular setae, lwp: lateral wings of pelta. Scale bars: 100 µm (**A, B, D, E**), 1 mm (**C**).

Remark. First record for Vg.

Material examined. Sweden • 2♀♀; Västergötland, Laxå kommun, Finnerödja; sandy slope with *Carex* and *Calluna*; 58.9297°N, 14.3400°E; 5 Jun. 2021; E. Wahlberg, leg.

Haplothrips Amyot & Serville, 1843

Haplothrips acanthoscelis (Karny, 1910)
Fig. 8C

Distribution. Sk, Öl.

Haplothrips aculeatus (Fabricius, 1803)
Fig. 7B

Distribution. Sk, Bl, Ha, Sm, Öl, Go, Ög, Vg, Bo, Sö, Up.

Remarks. First record for Ha.

Material examined. Sweden • 1♀; Halland, Varberg kommun, Tvååker; meadow on old cultivated land with *Quercus*, *Fagus*, and *Fraxinus*; 57.0208°N, 12.4795°E; 19 May 2021; E. Wahlberg, leg.

Haplothrips alpester Priesner, 1914
Figs 6E, 7A, 8G

Distribution. Sk, Öl, Vg, Sö, Vr, Ly.

Remarks. First record for Sö. This species is variable in the number of sense cones on segment III.

Material examined. Sweden • 1♂; Södermanland, Nyköping kommun, Skeppsvik; marsh with *Hierochloë*, *Juncus*, *Carex*, *Luzula* and *Schoenoplectus*; 58.6456°N, 16.8431°E; 3 Jun. 2021; E. Wahlberg, leg.

Haplothrips alpicola Priesner, 1950
Fig. 7G

Distribution. Ly.

Haplothrips angusticornis Priesner, 1921

Distribution. Sk, Ög, Up, Vr.

Haplothrips distinguendus (Uzel, 1895)

Distribution. Sk, Sm, Vg, Up.

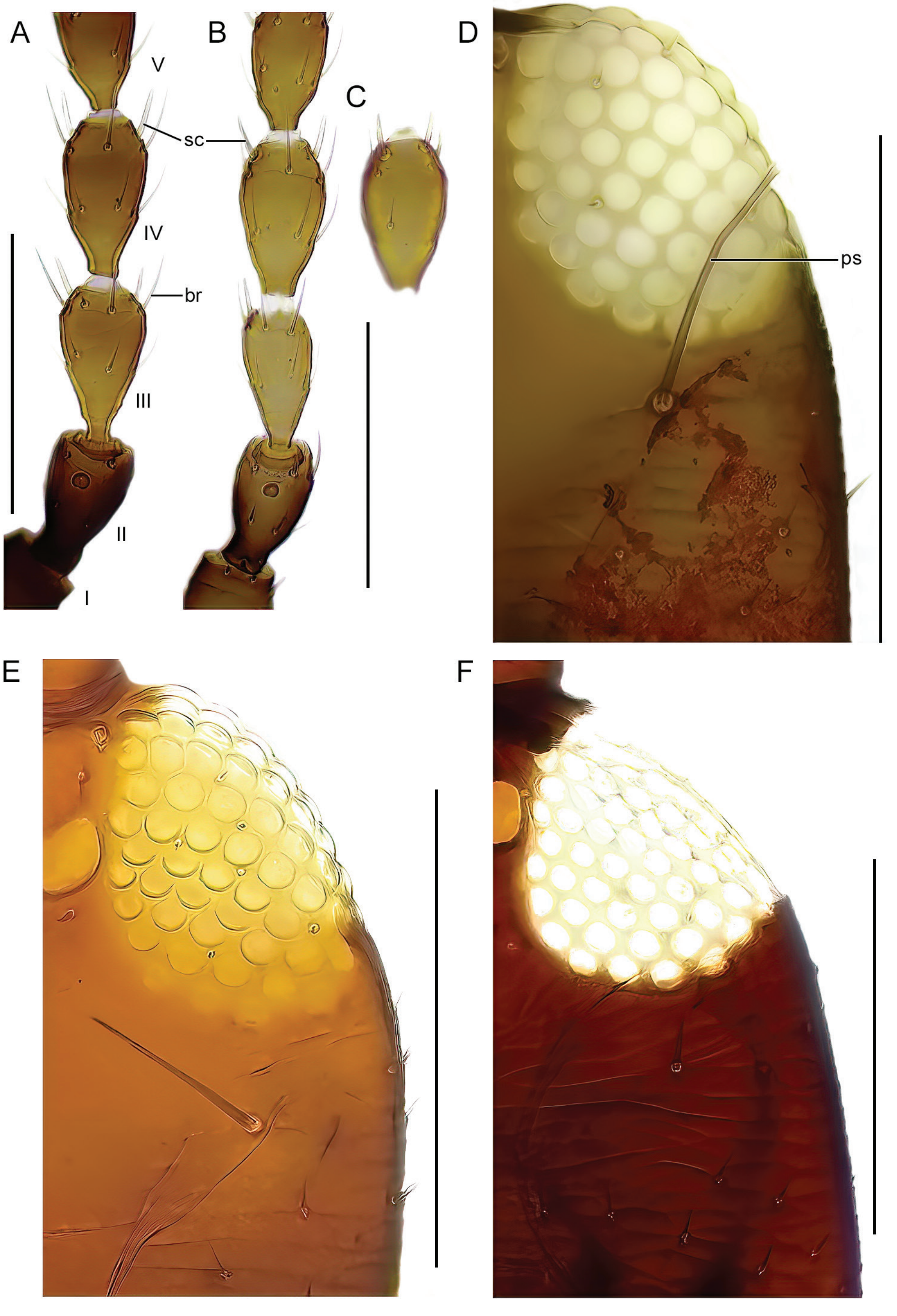

Figure 6. A–C part of antenna, dorsal view, I–VI: segment number **A** *Xylaplothrips fuliginosus* **B** *Haplothrips subtilissimus* **C** segment IV, ventral view, *H. subtilissimus* **D–F** dorsal view of right side of head **D** *H. subtilissimus* **E** *H. alpester* **F** *H. leucanthemi*. Abbreviations: sc: sense cones, br: bristle, ps: postocular setae. Scale bars: 100 µm.

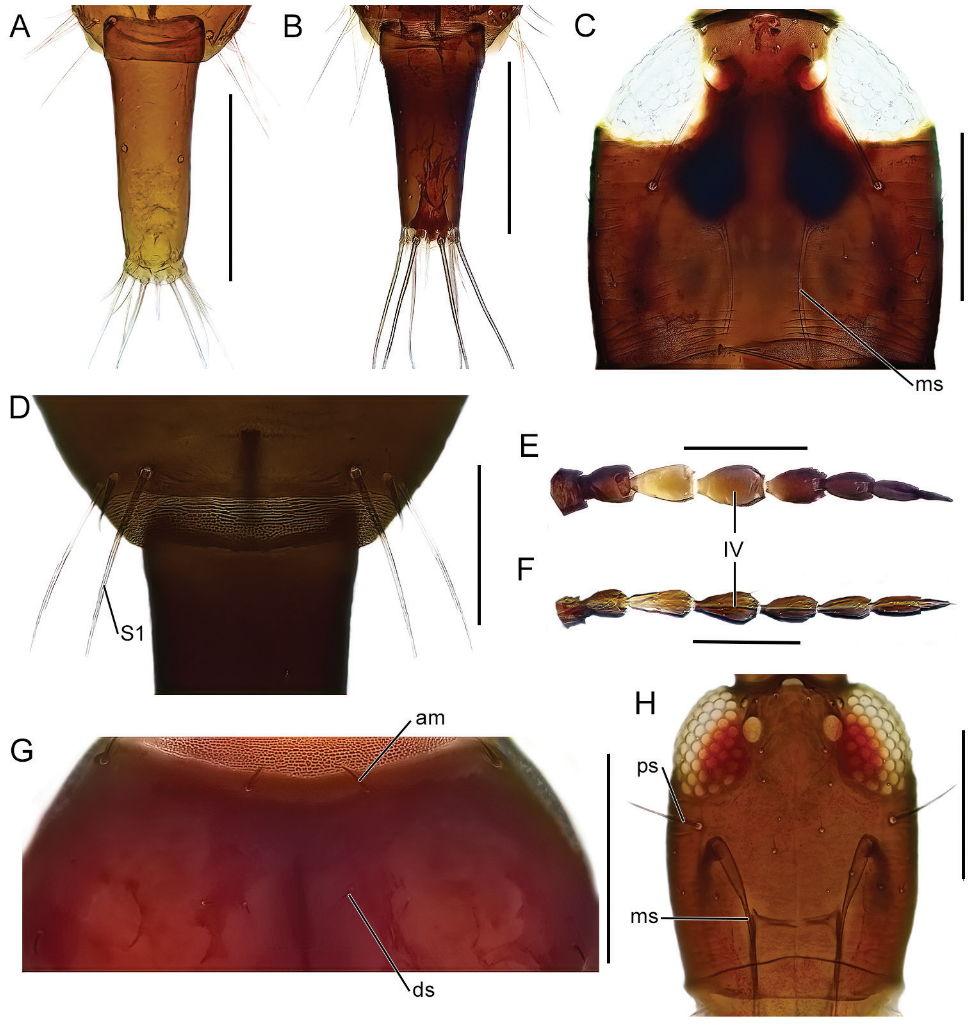

Figure 7. A, B dorsal view of tube **A** *Haplothrips alpester* **B** *H. aculeatus* **C** head, dorsal view, *H. statices* **D** tergite IX, dorsal setae, *H. leucanthemi* **E, F** antennae, dorsal view, antennal segment IV marked **E** *H. leucanthemi* **F** *H. propinquus* **G** part of pronotum, dorsal view, *H. alpicola* **H** head dorsal view, *H. tritici*. Abbreviations: ms: maxillary stylets, S1: setae 1, am: anteromarginal setae, ds: discal setae, ps: postocular setae. Scale bars: 100 microns.

Haplothrips hukkineni Priesner, 1939

Fig. 8E

Distribution. Sk, Sm, Öl, Go Sö, Up, Vr.

Haplothrips leucanthemi (Schrank, 1781)

Figs 1, 6F, 7D–E

Distribution. Sk, Ha, Sm, Öl, Bo, Ds, Nä, Ög, Sö, Up, Vr, Jä, Vb, Lu, To.

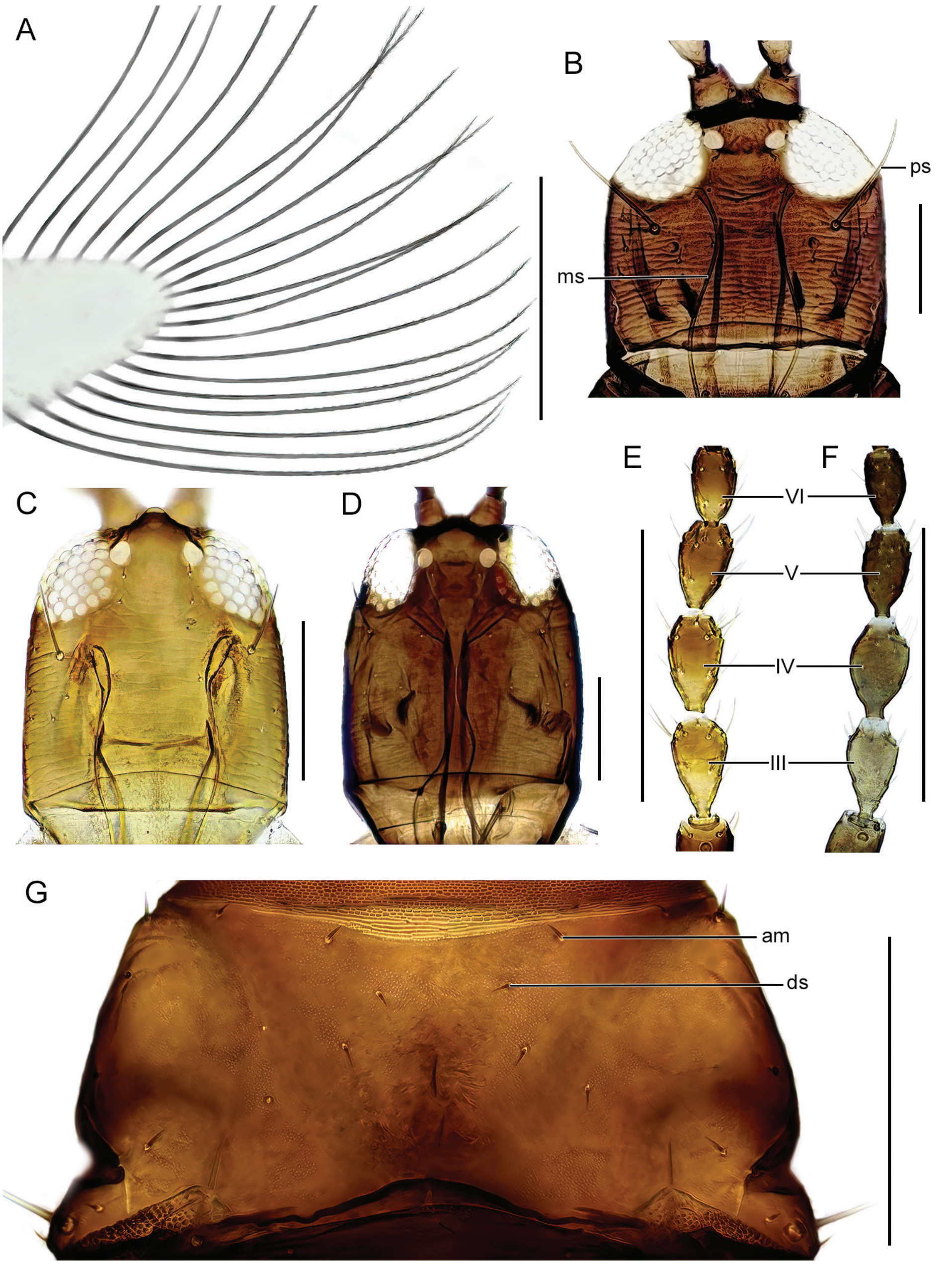

Figure 8. A distal portion of fore wing, *Haplothrips setiger* **B–D** dorsal view of head **B** *H. verbasci* **C** *H. acanthoscelis* **D** *H. utae* **E, F** antennae, III–VI: segment number **E** *H. hukkineni* **F** *H. tritici* **G** pronotum, dorsal view, *H. alpester*. Abbreviations: ps: postocular setae, ms: maxillary stylets, am: anteromarginal setae, ds: discal setae. Scale bars: 100 µm.

Remark. First record for Ha.

Material examined. Sweden • 1♂; Halland, Halmstad kommun, Särdal; on *Armeria maritima*; 56.7367°N, 12.6472°E; 19 May 2021; E. Wahlberg, leg.

***Haplothrips minutus* (Uzel, 1895)**

Distribution. Sk, Sö.

***Haplothrips propinquus* Bagnall, 1933**
Fig. 7F

Distribution. Sk, Sö, Up, Vr, Gä, Hs, Jä, Lu.

***Haplothrips senecionis* Bagnall, 1932**
Fig. 5B

Distribution. Öl.

***Haplothrips setiger* Priesner, 1921**
Fig. 8A

Distribution. Sk.

***Haplothrips statices* (Haliday, 1836)**
Fig. 7C

Distribution. Sk, Bl, Ha, Sm, Öl, Ög, Bo, Sö, Up, Hs, Hr, Jä, Ån, Nb, Lu.

***Haplothrips subtilissimus* (Haliday, 1852)**
Fig. 6B–D

Distribution. Sk, Sm, Sö, Up.

Remark. First record for Sm.

Material examined. Sweden • 1♀; Småland, Kalmar kommun, Bottorp; alley with *Quercus* and *Prunus*; 56.591923°N, 16.212710°E; 11 May 2021; E. Wahlberg, leg.

***Haplothrips tritici* (Kurdjumov, 1912)**
Figs 7H, 8F

Distribution. Sö.

Remark. Setae variable in shape.

***Haplothrips utae* Klimt, 1970**
Figs 3, 8D

Distribution. Sk, Sm.

***Haplothrips verbasci* Osborn, 1896**
Fig. 8B

Distribution. Sk.

***Holothrips* Karny, 1911**

***Holothrips schaubergeri* (Priesner, 1920)**
Fig. 11A

Distribution. Sö.

***Hoplandrothrips* Hood, 1912**

***Hoplandrothrips bidens* (Bagnall, 1910)**
Fig. 10E, G

Distribution. Sk, Öl, Up.

***Hoplandrothrips williamsianus* Priesner, 1923**

Distribution. Vr.

***Hoplothrips* Amyot & Serville, 1843**

***Hoplothrips caespitis* (Uzel, 1895)**

Distribution. Sk.
Remarks. This species is variable in body colour, occurring in both bicolored and completely brown forms.

***Hoplothrips carpathicus* Pelikán, 1961**
Fig. 4B

Distribution. Sk, Ds, Sö, Up, Vr.

***Hoplothrips corticis* (de Geer, 1773)**
Fig. 11K

Distribution. Sk, Bl, Öl, Go, GS, Sm, Ög, Bo, Sö, Up, Vb, Nb.
Remark. First record for Nb.
Material examined. Sweden • 1♀; Norrbotten, Åsele, Björnlandet national park; 63.9702°N, 18.0533°E; 12–26 Jul. 2011; K. Norberg, B.O. Johansson, leg.; Malaise trap; Loc. 034-04.

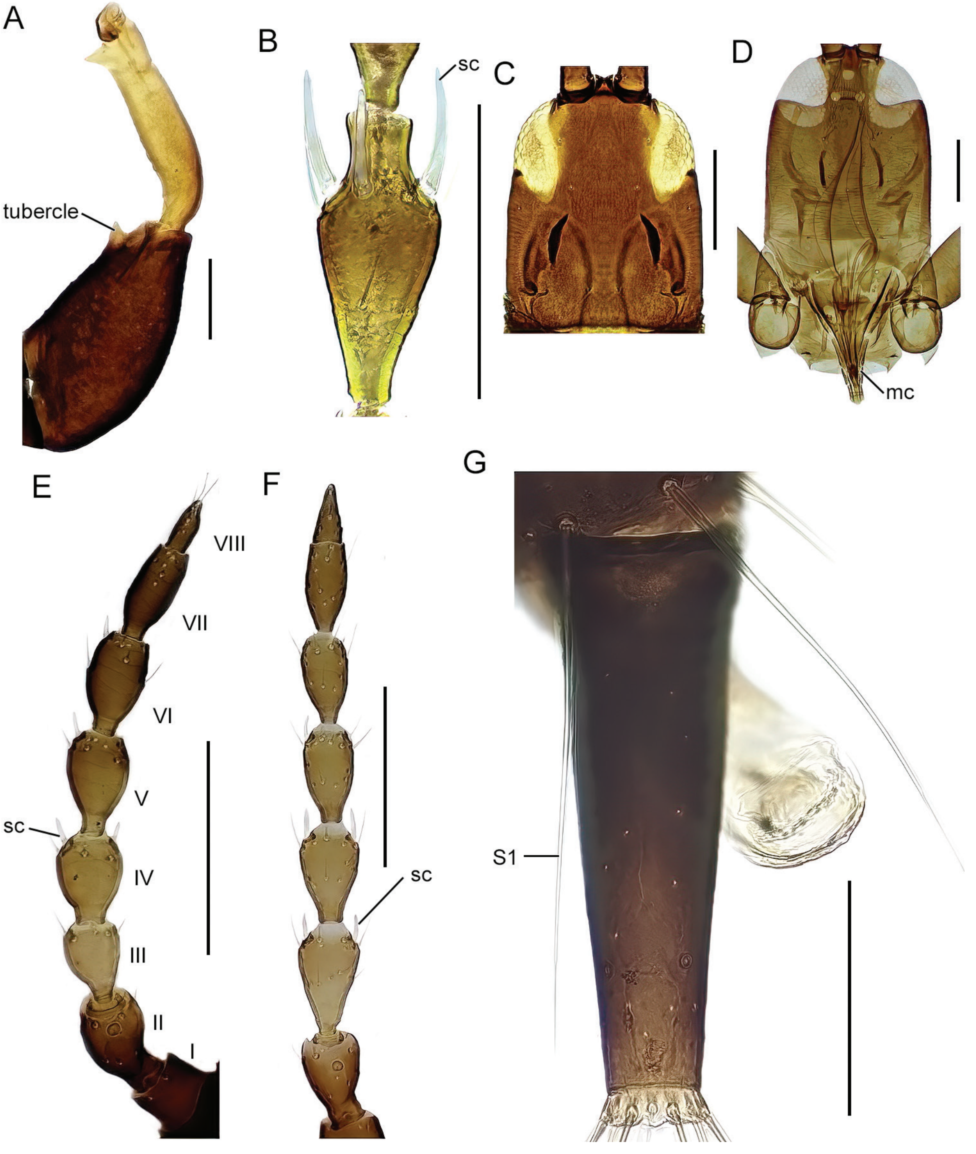

Figure 9. A fore leg, *Acanthothrips nodicornis* **B** antennal segment IV, *A. nodicornis* **C** head, ventral view, *Cephalothrips monilicornis* **D** head and pronotum with mouth cone (mesonotum detached), *Poecilothrips albopictus* **E, F** antennae, I–VIII: segment number **E** *Lispothrips crassipes* **F** *Hoplothrips longisetis* **G** abdominal segments IX–X, parts of the protruding phallus visible right side under the tube, *Liothrips austriacus*. Abbreviations: sc: sense cones, mc: mouth cone, S1: setae 1. Scale bars: 100 µm.

Hoplothrips fungi (Zetterstedt, 1828)

Fig. 11H

Distribution. Bl, Öl, Go, Up, Hs.

Hoplothrips longisetis (Bagnall, 1910)
Figs 9F, 11B

Distribution. Sk, Ds, Vr.

Hoplothrips pedicularius (Haliday, 1836)
Fig. 10B

Distribution. Sk, Sm, Sö, Up, Vr, Dr, Hs.

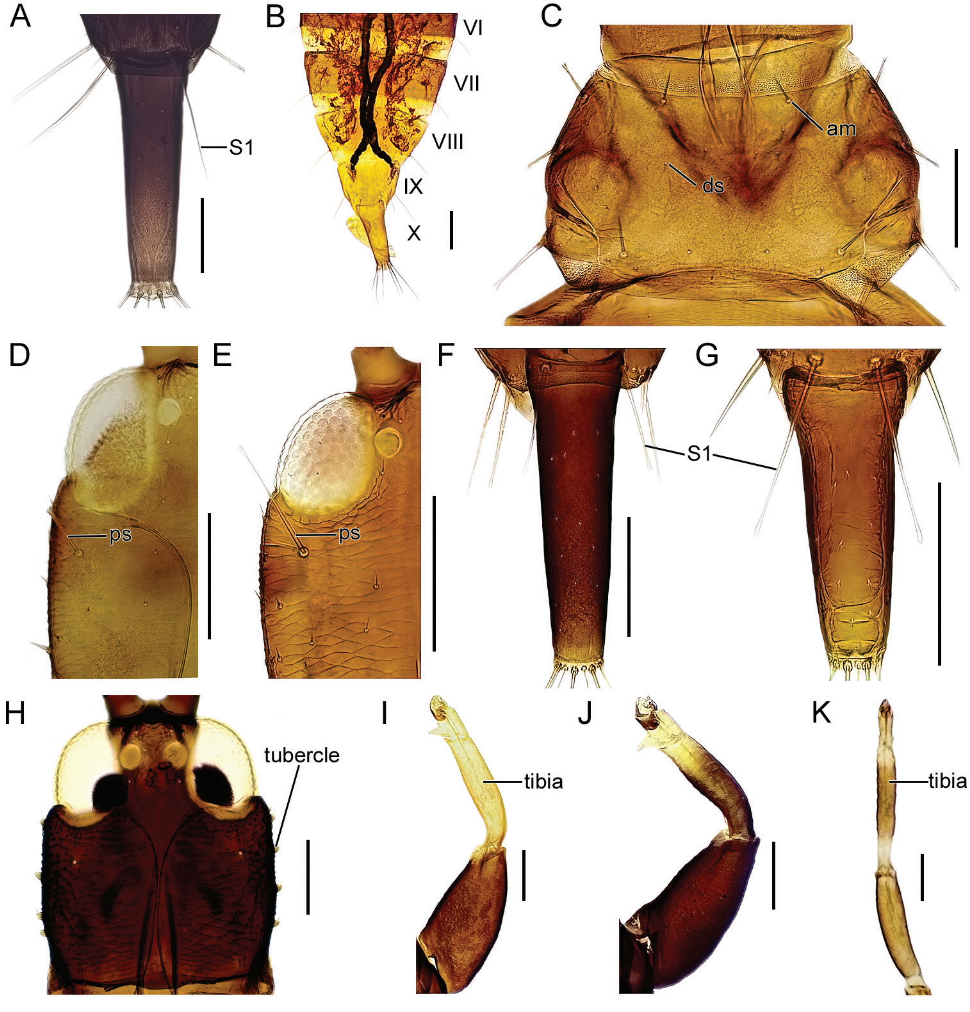

Figure 10. A abdominal segments IX–X, *Liothrips setinodis* **B** abdomen, dorsal view, VI–X: segment number, *Hoplothrips pedicularius* **C** pronotom, dorsal view, *Phlaeothrips annulipes* **D–E** left half of head, dorsal view **D** *P. annulipes* **E** *Hoplandothrips bidens* **F, G** abdominal segments IX (setae) and X **F** *P. annulipes* **G** *H. bidens* **H** head, dorsal view, *Phlaeothrips coriaceus* **I–K** fore legs, dorsal view **I** *P. coriaceus* **J** *P. denticauda* **K** mid leg, *P. annulipes*. Abbreviations: S1: setae 1, am: anteromarginal setae, ds: discal setae, ps: postocular setae. Scale bars: 100 µm.

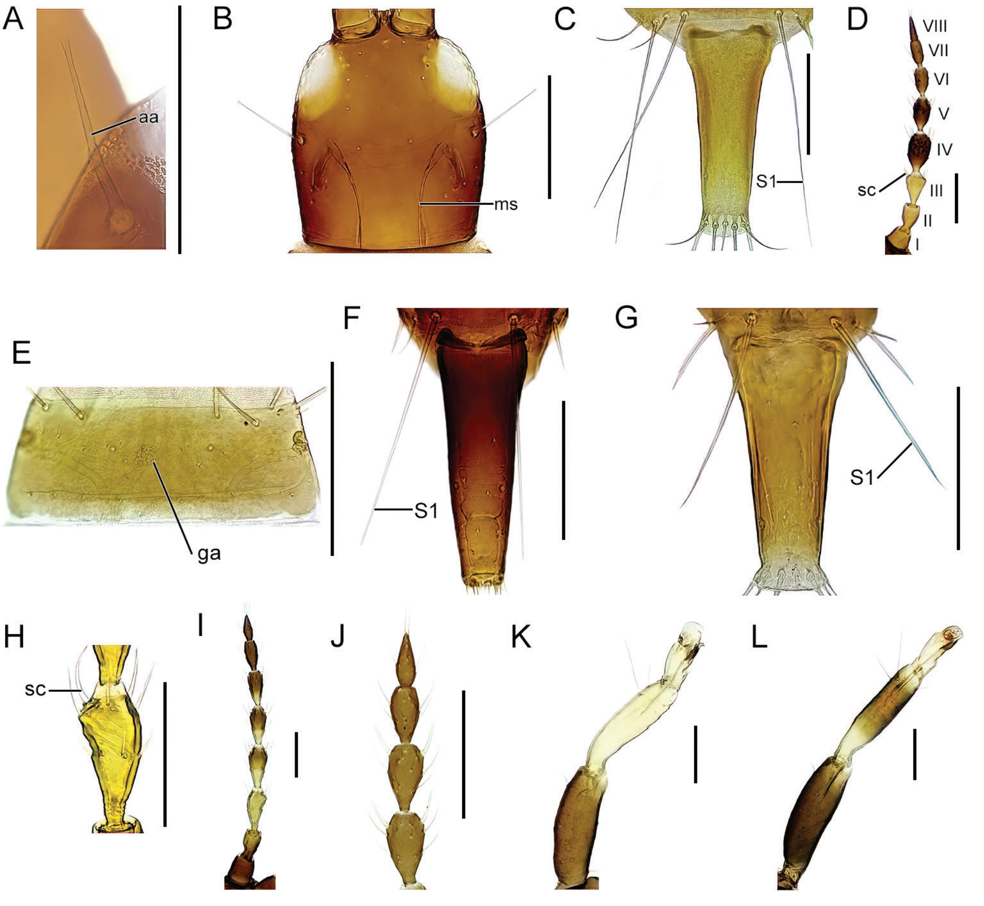

Figure 11. A anterolateral portion of pronotum, dorsal view, *Holothrips schaubergeri* **B** head, dorsal view, *Hoplothrips longisetis* **C** segments IX (setae) and X, *H. unicolor* **D** antennae, I–VIII: segment number, *H. semicaecus* **E** abdominal sternite VIII, *H. unicolor* **F, G** abdominal segments IX–X **F** *Thorybothrips unicolor* **G** *Hoplothrips polysticti* **H** antennal segment III, *H. fungi* **I** antenna, *H. ulmi* **J** antennal segments V–VIII, *H. polysticti* **K, L** mid leg **K** *H. corticis* **L** *H. ulmi*. Abbreviations: aa: anteroangular setae, ms: maxillary stylets, sc: sense cones, ga: glandular pore area. Scale bars: 100 µm.

Hoplothrips polysticti (Morison, 1949)

Fig. 11G, J

Distribution. Sk, Ög, Vr, Dr, Vb.

Remarks. This species is variable in the number of sense cones on both antennal segments III and IV, as well as in number of large pronotal seatae.

Hoplothrips semicaecus (Uzel, 1895)

Fig. 11D

Distribution. Sk, Ha, Up.

Remarks. First record for Ha. Very variable in the number of sense cones on both antennal segments III and IV, as well as many structural differences in macropterous and apterous males and females.

Material examined. Sweden • 3♂♂; Halland, Falkenberg kommun, Vessigebro; deciduous forest (*Fagus*), in *Fomes fomentarius*; 57.0575°N, 12.7888°E; 18 May 2021; E. Wahlberg, leg.

***Hoplothrips ulmi* (Fabricius, 1781)**
Fig. 11I, L

Distribution. Sk, Bl, Ha, Sm, Öl, Go, GS, Ög, Bo, Ds, Sö, Up, Vs, Vr, Dr, Ån, Vb, Lu.

***Hoplothrips unicolor* (Vuillet, 1914)**
Fig. 11C, E

Distribution. Sö.

Remark. This species is variable in the number of sense cones on antennal segment IV.

***Liothrips* Uzel, 1895**

***Liothrips austriacus* (Karny, 1910)**
Fig. 9G

Distribution. Vr.

***Liothrips setinodis* (Reuter, 1880)**
Fig. 10A

Distribution. Ha, Up.

***Lispothrips* Reuter, 1899**

***Lispothrips crassipes* (Jablonowski, 1894)**
Fig. 9E

Distribution. Sm.

***Phlaeothrips annulipes* Reuter, 1880**
Fig. 10C, D, F, K

Distribution. Sk, Sm, Ög, Bo, Sö, Up, Vs, Vr, Dr, Vb.

***Phlaeothrips bispinosus* Priesner, 1919**

Distribution. Vr.

***Phlaeothrips coriaceus* Haliday, 1836**
Fig. 10H, I

Distribution. Sk, Bl, Ha, Sm, Öl, Go, Bo, Sö, Up, Vs, Hs, Vb.

***Phlaeothrips denticauda* Priesner, 1914**
Fig. 10J

Distribution. Sk, Vr.

***Poecilothrips* Uzel, 1895**

***Poecilothrips albopictus* Uzel, 1895**
Fig. 9D

Distribution. Sk, Vr.

***Thorybothrips* Priesner, 1924**

***Thorybothrips unicolor* (Schille, 1911)**
Fig. 11F

Distribution. Öl, Go.

***Xylaplothrips* Priesner, 1928**

***Xylaplothrips fuliginosus* (Schille, 1911)**
Fig. 6A

Distribution. Sm, Ha, Sö, Ds, Vr, Dr, Lu, To.

Remark. First record for Ha and Sö.

Material examined. Sweden • 1♂; Halland, Falkenberg kommun, Vessigebro; on *Larix decidua*, 56.9748°N, 12.7288°E, 19 May 2021; E. Wahlberg, leg. • 2♀♀; Södermanland, Nyköping kommun, Skeppsvik; mixed forest; 58.6458°N, 16.8431°E; 03 Jun. 2021; E. Wahlberg, leg. • 1♀; Södermanland, Gnesta kommun, Fridsta; private garden with mixed vegetation; 59.0673°N, 17.1550°E; 14–21 Jun. 2021; E. Wahlberg, leg., window trap. • 1♂ Södermanland, Gnesta kommun, Önnersta; on dead *Betula*; 59.0470°N, 17.1460°E; 16 Jul. 2021; E. Wahlberg, leg.

Acknowledgements

We thank Andrea Hastenpflug-Vesmanis (Forschungsinstitut und Naturmuseum Senckenberg, Germany), Christoffer Fägerström (Lund Museum of Zoology, Sweden), Manfred R. Ulitzka (Thrips-ID, Offenburg, Germany), and Sverre Kobro (Norwegian Institute of Bioeconomy Research, Norway) for their help in providing material used in this study. Raul Vicente kindly provided proofreading and linguistic help. This study is part of a project funded by the Swedish Taxonomy Initiative (SLU.dha.2020.4.3-228).

References

Ahlberg O (1926) Tripsar. Thysanoptera. Svensk Insektsfauna 6. Sveriges Entomologiska Förening, Stockholm, 62 pp.

Boyd Jr BW, Held DW (2006) *Androthrips ramachandrai* (Thysanoptera: Phlaeothripidae): an introduced thrips in the United States. The Florida Entomologist 89(4): 455–458. https://doi.org/10.1653/0015-4040(2006)89[455:ARTPAI]2.0.CO;2

Dubovský M, Fedor P, Kucharczyk H, Masarovič M, Balkovič J (2010) Zgrupowania wciornastków (Thysanoptera) pni drzew w różnowiekowych lasach dębowych Słowacji. Sylwan 154(10): 659–668.

Gertsson C-A (2015a) Nya intressanta tripsarter från Öland. Lucanus 20: 36–39.

Gertsson C-A (2015b) An annotated checklist of Thysanoptera (thrips) from the Nordic countries. Entomologisk Tidskrift 136: 185–198.

Gertsson C-A (2021) Två för Sverige nya tripsarter: *Haplothrips alpicola* Priesner, 1950 och *Haplothrips utae* Klimt, 1970 (Thysanoptera) samt nya provinsfynd. Entomologisk Tidskrift 142: 21–30.

Gertsson C-A, Fägerström C (2017) Två nya tripsarter (Thysanoptera) för Sverige samt tre nya landskapsfynd från Öland. Entomologisk Tidskrift 138: 131–136.

Gertsson C-A, Fägerström C, Sjödahl M (2022) Två för Skandinavien nya tripsarter (Thysanoptera): *Hoplothrips caespitis* (Uzel, 1895) och *Megalothrips bonannii* Uzel, 1895 samt nya provinsfynd. Entomologisk Tidskrift 143: 17–24.

Held DW, Boyd D, Lockley T, Edwards GB (2005) *Gynaikothrips uzeli* (Thysanoptera: Phlaeothripidae) in the southeastern United States: distribution and review of biology. The Florida Entomologist 88(4): 538–540. https://doi.org/10.1653/0015-4040(2005)88[538:GUTPIT]2.0.CO;2

Kąkol E, Kucharczyk H (2004) Occurrence of thrips on the winter and spring wheat in chosen regions of Poland. Acta Phytopathologica et Entomologica Hungarica 39(1–2): 263–269. https://doi.org/10.1556/APhyt.39.2004.1-3.25

Kirk WDJ (1996) Thrips. Naturalists' Handbooks 25. The Richmond Publishing Co. Ltd, Slough, 70 pp.

Klimt K (1970) Über eine neue, feuchte Standorte bewohnende *Haplothrips*-Art (Thysanoptera) – *Haplothrips utae* spec. nov. Entomologisches Nachrichtenblatt (Vienna, Austria) 13: 121–128.

Kobro S (2011) Checklist of Nordic Thysanoptera. Norwegian Journal of Entomology 58: 20–26.

Kobro S (2013) Norske Insekttabeller 19. Trips (Thysanoptera). Norsk Entomologisk Forening, Oslo, 49 pp.

Kobro S, Rafoss T (2006) Identification of adult males and females of *Hoplothrips* species (Thysanoptera: Tubulifera) known from Norway, and some deductions on their life history. Entomologica Fennica 17(2): 184–192. https://doi.org/10.33338/ef.84327

Kucharczyk H (2004) Thrips (Insecta: Thysanoptera) as an element of ecological monitoring in Białowieża Primeval Forest. Lesne Prace Badawcze 3: 85–94.

Kucharczyk H, Kucharczyk M (2008) The red list of threatened thrips species of middle-eastern Poland. Acta Phytopathologica et Entomologica Hungarica 43: 297–305. https://doi.org/10.1556/APhyt.43.2008.2.13

Kucharczyk H, Wyrozumski Ł (2015) *Hoplothrips carpathicus* Pelikán, 1961 (Thysanoptera: Phlaeothripidae) – a new thrips species in the Polish fauna. Polish Journal of Entomology 84(2): 73–83. https://doi.org/10.1515/pjen-2015-0007

Kucharczyk H, Zawirska I (1994) Study on the thrips fauna (Insecta: Thysanoptera) on xerothermic grassland of South-East Poland. Sonderdruck aus CFS-Courier 178: 3–7.

Moritz G (2006) Thripse – Fransenflügler, Thysanoptera. Pflanzensaftsaugende Insekten Bd. 1. Westarp Wissenschaften, Hohenwarsleben, 384 pp.

Mound LA (1974) The Nesothrips complex of spore-feeding Thysanoptera (Phlaeothripidae: Idolothripinae). Bulletin of the British Museum (Natural History). Entomology 31: 109–188. https://doi.org/10.5962/bhl.part.29485

Mound LA (2004) Thysanoptera – diversity and interactions. Annual Review of Entomology 50(1): 247–269. https://doi.org/10.1146/annurev.ento.49.061802.123318

Mound LA, Palmer JM (1983) The generic and tribal classification of spore-feeding Thysanoptera (Phlaeothripidae: Idolothripinae). Bulletin of the British Museum (Natural History) Entomology 46: 1–174. https://biostor.org/reference/165

Mound LA, Tree DJ (2020) Thysanoptera Australiensis – Thrips of Australia. https://keys.lucidcentral.org/keys/v3/thrips_australia/ [Accessed on 01.iii.2022]

Mound LA, Morison GD, Pitikin BR, Palmer JM (1976) Thysanoptera. Handbooks for the Identification of British Insects, Vol. I. Part 1. Royal Entomological Society, London, 79 pp.

Mound LA, Collins DW, Hastings A (2018) Thysanoptera Britannica et Hibernica – Thrips of the British Isles. https://keys.lucidcentral.org/keys/v3/british_thrips/index.html [Accessed on 01.iii.2022]

Paine TD (1992) Cuban laurel thrips (Thysanoptera: Phlaeothripidae) biology in southern California: seasonal abundance, temperature dependent development, leaf suitability, and predation. Annals of the Entomological Society of America 85(2): 164–172. https://doi.org/10.1093/aesa/85.2.164

Qvick U (1977) New records and notes on the Swedish Thrips fauna (Thysanoptera). Entomologisk Tidskrift 98: 127–131.

Schliephake G, Klimt K (1979) Thysanoptera, Fransenflügler. In: Senglaub K, Hannemann H-J, Schuhmann H (Eds) established by Dahl, F.: Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise 66. VEB Fischer, Jena, 1–477.

Sörensson M (2012) Pilotinventering av den saproxyliska insektsfaunan i Dalby Söderskog 2008. Länsstyrelsen i Skåne, Malmö, 75 pp.

ThripsWiki (2022) ThripsWiki – providing information on the world's thrips. https://thrips.info/ [Accessed on 29.iii.2022]

Vasiliu-Oromulu L, zur Strassen R, Larsson H (2000) New thrips species (Cl. Insecta: Ord. Thysanoptera) for the fauna of Sweden. Revue roumaine de biologie. Série de Biologie Animale 45: 125–135.

Wahlberg E (2019) Revision and morphological analysis of the Ragadidae (Insecta, Diptera). European Journal of Taxonomy 521: 1–19. https://doi.org/10.5852/ejt.2019.521

Wahlberg E, Johanson KA (2018) Molecular phylogenetics reveals novel relationships within Empidoidea (Diptera). Systematic Entomology 43(4): 619–636. https://doi.org/10.1111/syen.12297

ZooKeys 1096: 189–206 (2022)
doi: 10.3897/zookeys.1096.79402
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Molecular phylogeny suggests synonymy of *Sandalia bridgesi* Lorenz, 2009 with *S. triticea* (Lamarck, 1810) (Gastropoda, Ovulidae)

Qiong Wu[1], BingPeng Xing[1,2], Mao Lin[1], GuangCheng Chen[1,2], ChunGuang Wang[1]

1 *Third Institute of Oceanography, Ministry of Natural Resources, PRC. 178#, Daxue Road, Siming District, Xiamen, Fujian, 361005, China* **2** *Observation and Research Station of Coastal Wetland Ecosystem in Beibu Gulf, Ministry of Natural Resources, Beihai, 536015, China*

Corresponding author: ChunGuang Wang (wangchunguang@tio.org.cn)

Academic editor: Nathalie Yonow | Received 15 December 2021 | Accepted 6 April 2022 | Published 18 April 2022

http://zoobank.org/CDCE0D27-58EA-4CEB-ABA6-747C4A2D9C9F

Citation: Wu Q, Xing BP, Lin M, Chen GC, Wang CG (2022) Molecular phylogeny suggests synonymy of *Sandalia bridgesi* Lorenz, 2009 with *S. triticea* (Lamarck, 1810) (Gastropoda, Ovulidae). ZooKeys 1096: 189–206. https://doi.org/10.3897/zookeys.1096.79402

Abstract

The Ovulidae (Gastropoda, Cypraeoidea) is a family of small to medium Mollusca in the order Littorinimorpha, and *Sandalia* is a very small genus containing only three extant species. In the present study, 132 specimens of Ovulidae were collected, belonging to seven genera and nine species, including 54 *Sandalia bridgesi* and three *Sandalia triticea* individuals. The cytochrome c oxidase I gene, 16S rRNA, and ITS1-5.8S-ITS2 sequences were obtained from all specimens and compared with sequences downloaded from GenBank to calculate genetic distances and construct phylogenetic trees. The sequences of *S. bridgesi* and *S. triticea* exhibited a high degree of similarity, and *S. bridgesi* does not form a separate clade, supporting the proposal that *S. bridgesi* should be synonymised with *S. triticea*.

Keywords

16S, COI, DNA sequencing, ITS, molecular phylogeny, taxonomy

Introduction

The family Ovulidae is a group of small and medium sized molluscs distributed in widely tropical and subtropical seas. *Sandalia* Cate, 1973 is a genus belonging to this family, and its known distribution is Korea, Japan (type locality), New Caledonia, and eastern Australia. Shells are mainly characterised by having a pointed adapical terminal beak, peculiarly curving outer lips, and a shoe-like ventral appearance (Cate 1973). According to data from the World Register of Marine Species (WoRMS, https://www.marinespecies.org) and Worldwide Mollusc Species Data Base (WMSDB, https://www.bagniliggia.it/WMSD/WMSDhome.htm), only three extant *Sandalia* species have been described, namely *S. bridgesi* Lorenz, 2009, *S. meyeriana* (Cate, 1973), and *S. triticea* (Lamarck, 1810). All three species are distributed in the West Pacific region: the type localities are Taiwan Strait, Japan, and New Caledonia, respectively.

Recent collections of 132 specimens of ovulid from Chinese coasts prompted an investigation into the identities of the species of *Sandalia* based on 57 fresh specimens.

Sandalia bridgesi differs from its congeners by the obvious and striking transparency of the dorsum in contrast to the calloused labrum and terminals. As described by Lorenz (2009), *S. bridgesi* and *S. triticea* are very similar, with the main differences being as follows: *S. triticea* has lower transparency and usually possesses a red or purple shell and pale-coloured callosities. The middle portion of the dorsal side is normally pale, and the shell is roughly pear-shaped. Under ultraviolet (UV) light, yellow fluorescence can be seen in the terminal collars, callosities, dorsal mid-portion, and sometimes in the entire shell. In contrast, *S. bridgesi* has a relatively uniformly coloured dorsal portion and a wider anterior part and only exhibits fluorescence in a small area at either end of the shell under UV light.

DNA barcoding, which involves using a short DNA sequence for species classification, was used as a tool for species identification and received widespread attention 15 years ago (Meier et al. 2006). This technology breaks through the over-reliance on the personal abilities and experiences of taxonomists in traditional morphological classification and enables the informatisation and standardisation of species identification. In the present study, we sequenced the cytochrome c oxidase subunit I (COI) gene, 16S rRNA, and the ITS1-5.8S-ITS2 (ITS) region for the construction of the phylogenetic trees to elucidate the relationship between *S. bridgesi* and *S. triticea*. We obtained sequence data of the ITS region of Ovulidae for the first time.

Materials and methods

Specimen collection

We collected 132 specimens of Ovulidae from depths of 0–6 m during low spring tides in Hainan, Guangxi, Guangdong, Fujian, and Zhejiang provinces between July 2020 and September 2021. Detailed information of the collected specimens is shown in Fig. 1, Suppl. material 1: Table S1. We have tried but failed to obtain specimens from museums abroad. We also attempted to use the Jiang et al. (2019) method to extract DNA from shells of the Institute of Oceanology (CAS). As the method requires a minimum of 100 mg of sample and our samples were too small, our attempt failed.

All specimens were morphologically identified by WQ, Fan Shihao, and Han Yida in accordance with the identification keys published by Ma (1997), Zhang and Wei (2011), Lorenz and Fehse (2009), Lorenz (2009), and Hardy (2020a), as well as in Worldwide Mollusc Species Data Base (https://www.bagniliggia.it/WMSD/WMSDhome.htm). The specimens were observed and photographed alive (Fig. 2) and from the dorsal, ventral, and lateral sides under a Leica S9D stereomicroscope (Fig. 3, Suppl. material 7: Fig. S1). Specimens were preserved in 95% alcohol.

DNA extraction and sequencing

Amplification was performed on three gene regions for each specimen, namely the mitochondrial markers 16S rRNA and COI, and the nuclear ribosomal internal transcribed spacer (ITS) region.

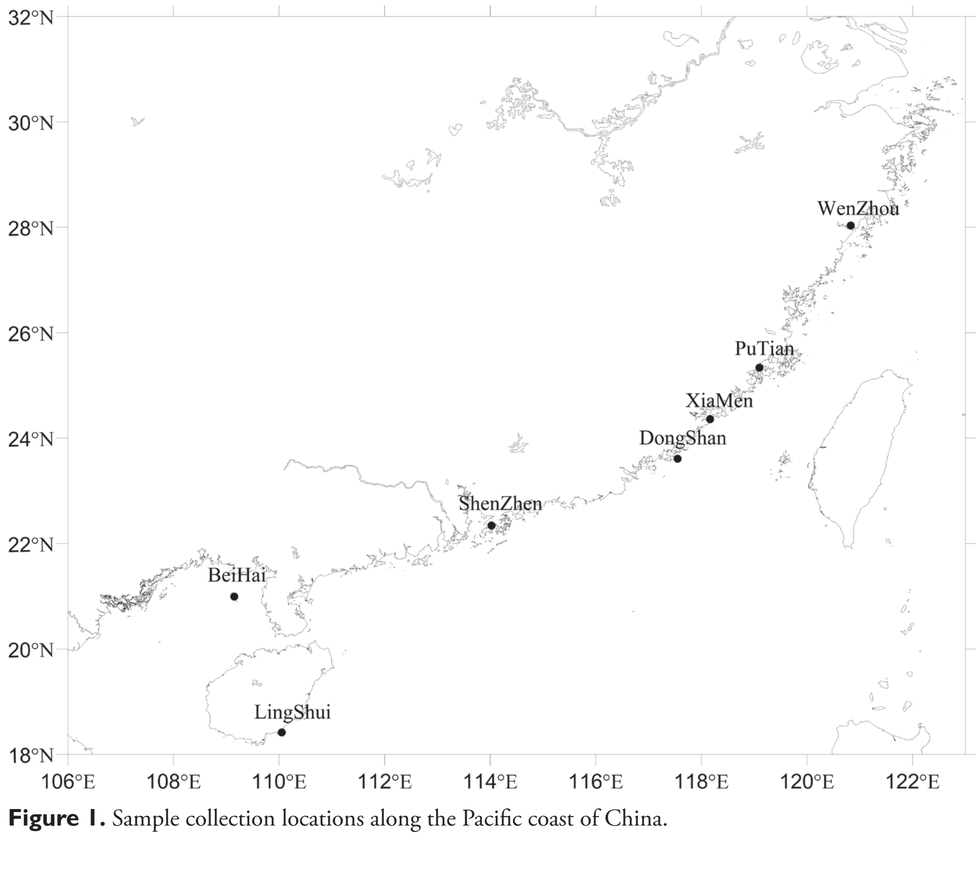

Figure 1. Sample collection locations along the Pacific coast of China.

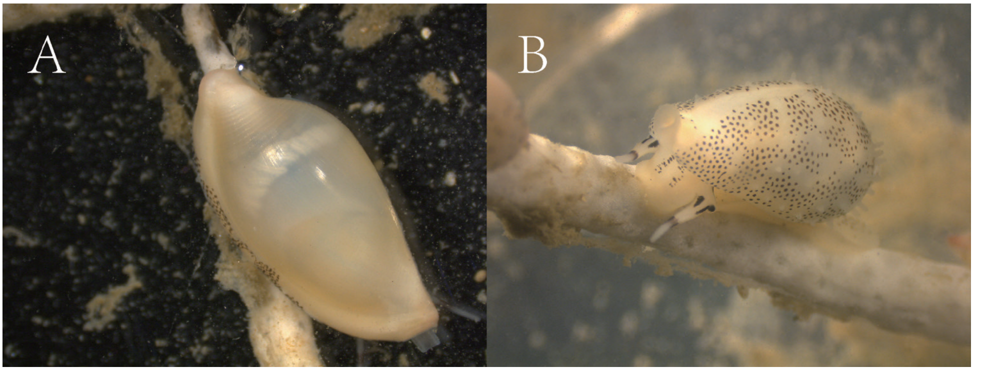

Figure 2. Living animals of *Sandalia bridgesi* Lorenz, 2009 **A** sample 20201117H19 **B** sample 20201117H6.

DNA was extracted from each muscle tissue using the DNeasy Blood & Tissue Kit (QIAGEN, China) following the corresponding protocol for animal tissues. The nucleic acid concentration in the DNA extracts was measured using BioDrop (BioDrop, UK). Due to the presence of inhibitors in the specimen tissues, all DNA extracts were diluted 50–500 fold before PCR amplification (Reijnen and van der Meij 2017, 2019). Our experimental results indicated that the appropriate concentration for the diluted DNA extracts was approximately 0.2 μg/mL.

Each PCR had a reaction volume of 50 μL and contained the following: 25 μL PCR mixture [Taq plus Master Mix II (Dye Plus)], 2 μL of each primer (10 μM), 5 μL (diluted) DNA extract, and 16 μL extra pure water. The details of the PCR performed for the three gene regions are given in Table 1. Not all markers were successfully amplified for all specimens, but the successfully amplified COI and 16S rRNA samples were sent to Sangon Biotech Co., Ltd (Shanghai, China) for PCR cleaning and sequencing.

The quality of the direct sequences obtained for the ITS region was insufficient because of intra-individual variation, secondary structures, and simple sequence repeats (SSRs). Thus, the PCR products were sent to Sangon Biotech Co., Ltd (Shanghai, China) for TA cloning and sequencing. DNA fragments were cloned into *Escherichia coli* cells using the pESI-T Vector System. For each individual, 3–5 clones were sequenced, and the most common sequence of these positive clones was used in the alignment and ITS data treatments. The sequences have been submitted to GenBank (http://www.ncbi.nlm.nih.gov) and the accession data is provided in Suppl. material 1: Table S1.

Table 1. Details of gene regions and associated primer pairs used in the study.

Gene region	Fragment size (bp)	Primers	Annealing temperature	Reference
COI	~680	Lco1490/Hco2198	45 °C, +0.5 °C /cycle,15 cycle, 49 °C, 20 cycle	Vrijenhoek (1994)
16S	~550	16SAR/16SBR	52 °C	Reijnen and van der Meij (2019)
ITS1-5.8S-ITS2	~1200	GastF/GastR	56 °C	Hoy and Rodriguez (2013)

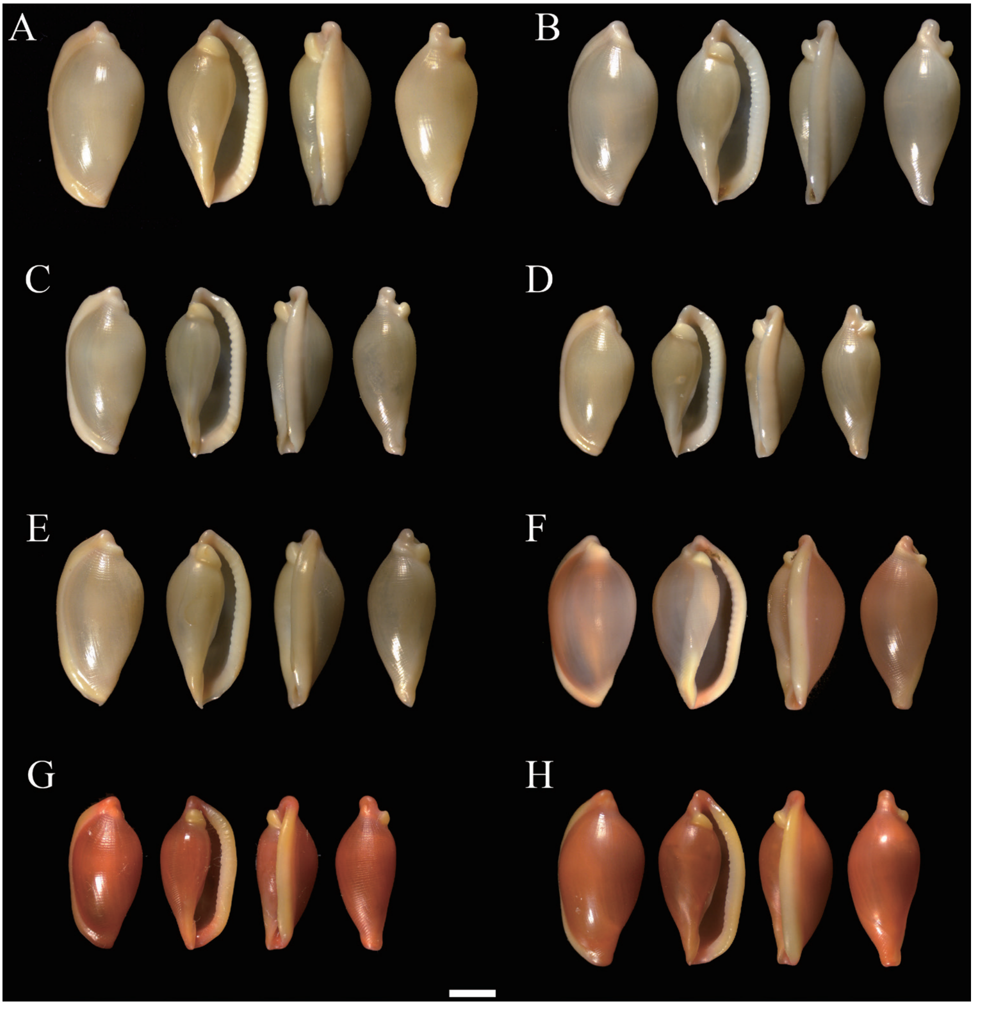

Figure 3. Dorsal, ventral, and lateral views of shells of *Sandalia* **A** *S. bridgesi* Lorenz, 2009 (20200722H1) **B** *S. bridgesi* (20200722H5) **C** *S. bridgesi* (20200722H6) **D** *S. bridgesi* (20200722H9) **E** *S. bridgesi* (20200722H10) **F** *S. triticea* (Lamarck, 1810) (20210626H14) **G** *S. triticea* (20200722T1) **H** *S. triticea* (20200722T2). Scale bar: 2 mm.

DNA data processing and molecular analyses

Joining and alignment of the sequences and trimming of ends with low signal strength were performed using DNAMAN v. 9 (Lynnon Biosoft, Canada) and SeqMan v. 7.1.0 (DNAStar, USA). Multiple sequences were aligned with MAFFT (Katoh and Standley 2013) using 'auto' strategy. One sequence obtained from GenBank was considered as an outgroup (Suppl. material 3: Table S3). The best-fit evolutionary models were selected based on Bayesian Information Criterion (BIC) by using ModelFinder (Kalyaanamoorthy et al. 2017). Bayesian-inference phylogenies were inferred using

MrBayes v. 3.2.6 (Ronquist et al. 2012) (2 parallel runs, 2000000 generations), in which the initial 25% of sampled data were discarded as burn-in. Maximum-likelihood (ML) phylogenies were inferred using IQ-TREE (Nguyen et al. 2015) for 1000 standard bootstraps, as well as the Shimodaira-Hasegawa-like approximate likelihood-ratio test (Guindon et al. 2010). The phylogenetic trees were viewed and edited using iTOL (available at https://itol.embl.de/) following Letunic and Bork (2021).

Evolutionary divergence analyses were conducted in MEGA v. 11(Kumar et al. 2018) and using the Jukes-Cantor model (Jukes and Cantor 1969) (Suppl. materials 4–6: Tables S4–S6). The sequence obtained from GenBank has also been added to the analysis (Suppl. material 3: Table S3).

Results

Morphological data

Based on the photographs and descriptions provided by Lorenz (2009), Lorenz and Fehse (2009), and Hardy (2020a), the 132 specimens were identified as belonging to nine species in seven genera. Fifty-seven of the specimens were *Sandalia* species, among which 54 were identified as *S. bridgesi* and three were identified as *S. triticea* based on differences in shell transparency, external appearance, and colour. Suppl. material 1: Table S1 shows the information and identification outcomes of the collected specimens. Suppl. material 2: Table S2 shows the length/width (L/W) ratio of shells of *S. meyeriana*, *S. bridgesi*, and *S. triticea.*

Molecular data

In total, 122 COI sequences were successfully amplified. After editing, the consensus length of all barcode sequences was 615 bp, and no stop codons, insertions, or deletions were observed in any of the sequences. The sequences were aligned with the 16 COI sequences obtained from GenBank, with detailed information of downloaded sequences provided in Suppl. material 3: Table S3. Phylogenetic trees were constructed using Bayesian and ML methods, and the root location was confirmed by selecting the COI sequence of *Mauritia arabica* as the outgroup (Suppl. material 8: Fig. S2). The best models of the phylogenetic trees are provided in Tables 2, 3. As the results from the two different phylogenetic reconstructions were congruent at the species level, only the ML tree is illustrated in this paper (Suppl. material 8: Fig. S2).

The greatest and smallest genetic distances between *S. bridgesi* and *S. triticea* among our specimens were 0.0215% (*Sandalia bridgesi* (MW410840) and *Sandalia triticea* (MW410844)) and 0% (*Sandalia bridgesi* (MW410824) and *Sandalia rhodia* (= *triticea*; MG450349); *Sandalia bridgesi* (OL674267) and *Sandalia rhodia* (= *triticea*; MG450349), respectively. The smallest and greatest interspecific genetic distances among specimens other than *S. bridgesi* and *S. triticea* were 0.1220% (*Primovula formosa*

(OL674268) and *Crenavolva traillii* (OL471931)), and 0.2663% (*Phenacovolva* sp. (OL471933) and *Crenavolva traillii* (OL471920)), respectively (for more details see Suppl. material 4: Table S4).

One hundred 16S rRNA sequences with lengths of approximately 520 bp were successfully amplified. After trimming, segments with lengths of 460 bp were obtained and aligned with 16 16s rRNA sequence data from GenBank to find the best model. Accession numbers of downloaded sequences are provided in Suppl. material 3: Table S3. The best models of the phylogenetic trees are provided in Tables 2 and 3. The 16S rRNA sequence of *Cypraea gracilis* was selected as the outgroup.

There are some differences between the two trees. As shown in Bayesian tree (Suppl. material 9: Fig. S3), *Calpurnus verrucosus* is the sister group to *Crenavolva traillii*, but the ML tree (Suppl. material 10: Fig. S4) shows that *Naviculavolva deflexa* is the sister group of *Crenavolva traillii*, and then the two groups jointly compose the sister group to *Calpurnus verrucosus* and *Primovula formosa*. Despite these differences, the results of both showed that *S. bridgesi* and *S. triticea* were clustered in the same clade.

The greatest genetic distance between *S. triticea* and *S. bridgesi* was 0.0220% (MW411381 and OL589299). By contrast, the smallest interspecific genetic distance among the other specimens was 0.0860% (*Primovula formosa* (OL589307) and *Crenavolva traillii* (OL614740); *Primovula formosa* (MW411392) and *Crenavolva traillii* (KP033145). For more details, see Suppl. material 5: Table S5.

The amplified ITS sequences had lengths of 1200–1300 bp before trimming and approximately 1200 bp after trimming. Different clones (from the same individual) were highly similar, and the differences were concentrated in the SSR regions. In the high-quality part of the sequencing, the most common sequence of clones was selected. The ITS sequences used to build the tree were assembled by different clones (from the same individual). Results of BIC analysis showed that the best-fit models of ML tree and Bayesian tree are provided in Tables 2 and 3; the two types of phylogenetic trees were fully congruent. Suppl. material 11: Fig. S5 shows the phylogenetic tree

Table 2. The best evolutionary models of ML phylogenomic tree.

Gene region	The best fit models	Reference
COI	HKY+I+G4+F	Hasegawa et al. (1985)
16S	TPM3+G4+F	Kimura (1981)
ITS1-5.8S-ITS2	HKY+F+G4	Hasegawa et al. (1985)

Table 3. The best models of Bayesian phylogenomic tree.

Gene region	The best fit models	Reference
COI	HKY+I+G+F	Hasegawa et al. (1985)
16S	HKY+G+F	Hasegawa et al. (1985)
ITS1-5.8S-ITS2	HKY+F+G4	Hasegawa et al. (1985)

combining support values of both models. The greatest and smallest genetic distances between *S. triticea* and *S. bridgesi* were 0.0077% (*Sandalia triticea* (MW411406) and *Sandalia bridgesi* (MW411417)) and 0% (*Sandalia triticea* (MW411407) and *Sandalia bridgesi* (MW411411), respectively, and the minimum interspecific genetic distance among the ITS sequences obtained in the present study was 0.1375% (*Primovula formosa* (MW411419) and *Sandalia bridgesi* (MW411417)). For more details see Suppl. material 6: Table S6.

Nomenclatural act

Based on morphological and molecular data, *Sandalia bridgesi* Lorenz, 2009 is here synonymised with *S. triticea* (Lamarck, 1810).

Discussion

Morphological data

The colouration of ovulids is variable, and many ovulid names have been introduced on basis of a few specimens; therefore, nominal species of Ovulidae often prove to be synonyms (Rosenberg 1992).

Sandalia bridgesi is the most recently described species in the genus *Sandalia* and was established based on morphological characters by Lorenz (2009). It was said to differ from *S. triticea* mainly in shell transparency and length-to-width ratio. However, in our collected specimens, we observed the presence of a continuous transition in the length-to-width ratios (Suppl. material 2: Table S2) and variations in transparency with observation angle, light intensity, and individual differences. Additionally, there is a co-evolution effect between Ovulidae and Gorgonacea (Reijnen 2016). Shell and mantle colour also show a high degree of variability due to influences by various environmental factors and therefore cannot be used as marker characteristics to distinguish between species (Rosenberg 1992; Schiaparelli et al. 2005). According to Rosenberg (1992), the colour pattern is a more reliable characteristic than colour per se. For instance, *Diminovula culmen* (Cate, 1973), *Serratovolva dondani* (Cate, 1964), and *Crenavolva striatula* (G.B. Sowerby I, 1828) exhibit diverse shell colour changes (Hardy 2020b). In certain species, such as *Crenavolva aureola* (Fehse, 2002), coloured bands on the shell cannot be regarded as stable traits (Hardy 2020c). During our process of species identification, both *S. bridgesi* and *S. triticea* specimens were irradiated with UV light with wavelengths of 395, 365, and 254 nm, but the yellow fluorescence reported by Lorenz (2009) could not be observed. Therefore, fluorescence may not serve as a stable trait in Ovulidae. Given the subjectivity and instability involved in morphological identification, the use of molecular data for taxonomic identification may be the most effective method for resolving these issues.

Molecular data

COI barcoding has been widely applied in identifying species belonging to the class Gastropoda (Stothard and Rollinson 1997; Hou et al. 2013; Quintero-Galvis and Raquel-Castro 2013; Layton et al. 2014). Research evidence has shown that sometimes COI is more capable of reflecting geographical differences than shell characters in certain taxa (Simison and Lindberg 1999). As an apparently rapidly evolving family of gastropod (Lorenz pers. comm. 7 July 2020; pers. obs.), Ovulidae have high phenotypic plasticity (Rosenberg 1992; Sánchez et al. 2016; Reijnen and van der Meij 2017; Lorenz 2020), leading to ambiguity in morphological classification. In recent years, researchers have utilised COI and 16S rRNA to investigate the phylogeny of Ovulidae and found that both are capable of distinguishing specimens at the species level (Schiaparelli et al. 2005; Sánchez et al. 2016; Reijnen and van der Meij 2019), resulting in the discovery of synonymy among ovulid species (Reijnen 2015). Meyer and Paulay (2005) utilised barcoding in the analysis of sequences of more than 2000 individuals in 263 taxa of the family Cypraeidae, the sister group to Ovulidae (Cate 1973; Rosenberg 1992; Meyer 2003, 2004), and found that identification of unknowns was 98% accurate with a neighbour-joining approach against an evolutionary significant unit (ESU) phylogeny. The correspondence between ESU definitions and traditional morphological taxonomy was high, with 255 ESUs (97%) recognised previously at either the specific or subspecific level, indicating that an ESU is a taxonomic unit equivalent to or smaller than a species. Therefore, traditional taxonomy within Cypraeidae at the species or subspecies level is supported by molecular data in addition to independent morphological criteria.

From the phylogenetic tree constructed using COI sequences (Suppl. material 8: Fig. S2), it can be observed that the sequences of *S. bridgesi* and *S. triticea* were clustered in the same clade, indicating the absence of significant genetic differentiation between the COI sequences of these specimens. Other clades were also well supported, which is in agreement with the findings of Meyer and Paulay (2005). The minimum interspecific genetic distance among the COI sequences of specimens other than *S. bridgesi* and *S. triticea* was approximately 5.7 times that of the maximum genetic distance between *S. bridgesi* and *S. triticea*, clearly demonstrating the high degree of similarity between the COI sequences of *S. bridgesi* and *S. triticea*.

The phylogenetic tree constructed from the 16S rRNA sequences showed that different specimens could be clearly distinguished at the species level using 16s rRNA (Suppl. materials 9, 10: Figs S3, S4). A study by Schiaparelli et al. (2005) showed that the minimum and maximum interspecific divergence values (obtained using the Jukes-Cantor model) of the 16S rRNA distance matrix between ovulid species were 0.03 and 22.3%, respectively. In the present study, the smallest genetic distance among species other than *S. triticea* and *S. bridgesi* was 0.0860%, supporting the findings reported by Schiaparelli et al. (2005). The greatest genetic distance between *S. triticea* and *S. bridgesi* was 0.0220%, which was approximately only a quarter of the smallest genetic distance among other specimens. Therefore, the 16S rRNA data further support the synonymy between *S. triticea* and *S. bridgesi*. Suppl. material 5: Table S5 illustrates the details of pairwise distance with the 16S sequences.

Being a non-transcribed spacer region, the ITS region is subject to smaller selective pressures and generally undergoes rapid evolution (Odorico and Miller 1997). It is commonly used for analysis at the population and species levels because of its high degree of sequence variation (Hillis and Dixon 1991; Harris and Crandall 2000). Therefore, ITS1-5.8S-ITS2 provides higher discriminating power at lower taxonomic levels. Among the ITS sequences obtained in the present study, the minimum interspecific genetic distance among specimens was approximately 18 times that of the greatest genetic distance between *S. triticea* and *S. bridgesi*, representing a significantly larger intraspecific-interspecific genetic distance ratio compared with COI and 16S rRNA. This indicates that genetic differentiation did not occur even in the rapidly evolving ITS1-5.8S-ITS2 gene region between *S. triticea* and *S. bridgesi*. In the ITS phylogenetic tree (Suppl. material 11: Fig. S5), *S. triticea* was convincingly clustered with *S. bridgesi* while the other clades were well supported.

Conclusions

In conclusion, the COI, 16S rRNA, and ITS1-5.8S-ITS2 data of the ovulid specimens collected in the present study indicated the absence of genetic differences between *S. bridgesi* and *S. triticea*. Both the phylogenetic trees (Suppl. materials 8–11: Figs S2–S5) and pairwise distances (Suppl. materials 4–6: Tables S4–S6) show a high degree of similarity between *S. bridgesi* and *S. triticea*, suggesting that the morphological differences between the two species may be caused by phenotypic plasticity rather than genetic differences. Most ovulids are cryptic (Rosenberg 1992); the shell and mantle are usually imitating the colour pattern of their octocoral host. Therefore, the difference in colour pattern between the two species may be due to the different colours of the octocoral host.

This study indicated that the colour pattern might not be a reliable identification feature. We also compared the L/W ratio between the *S. meyeriana* holotype, *S. bridgesi*, and *S. triticea*, and there were no significant differences between them. According to Cate (1973), *S. meyeriana* (holotype: 19 mm) is larger than *S. triticea*, and the colour is white to pale violet (Lorenz and Fehse 2009). The front terminal tip of *S. meyeriana* is flat while that of *S. triticea* is sharp (pers. obs.). The taxonomic status of *S. meyeriana* needs further research.

As the high level of phenotypic plasticity in ovulid species results in much ambiguity in morphology-based classification criteria (Rosenberg 1992), the analysis of species through molecular approaches is of great significance to the elucidation of classification and evolutionary history (Schiaparelli et al. 2005). Based on the present knowledge, it is evident that striking phenomena of convergence and homoplasy characterise shell morphology in Ovulidae and that a molecular framework is necessary to recognise phylogenetically related groups.

Acknowledgements

We are very grateful to Han Yida, Fan Shihao, Liu XinMin, and Gao Zhang Bin for their expertise and assistance in specimen collection and identification, and to Li Cui who assist us with data analysis. We greatly appreciate Dr Nathalie Yonow, for without her encouragement, this manuscript may have been delayed for a long time. We also extend sincere thanks to the reviewers for suggestions that improved the manuscript.

This work was supported by The Scientific Research Foundation of Third Institute of Oceanography MNR (22020017), The Marine Biological Sample Museum Upgrade and Expansion, and The National Natural Science Foundation of China (41406216).

References

Cate CN (1973) A systematic revision of the recent cypraeid family Ovulidae. The Veliger (Supplement 15): 1–116.

Guindon S, Dufayard J-F, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

Hardy E (2020a) Hardy's internet guide to marine gastropods (& near classes). http://www.gastropods.com/3/Shell_68033.shtml [accessed 12.2020]

Hardy E (2020b) Hardy's internet guide to marine gastropods (& near classes)–*Crenavolva striatula striatula*. http://www.gastropods.com/5/Shell_8225.shtml [accessed 12.2020]

Hardy E (2020c) Hardy's internet guide to marine gastropods (& near classes)–*Crenavolva aureola*. http://www.gastropods.com/5/Shell_14115.shtml [accessed 12.2020]

Harris DJ, Crandall KA (2000) Intragenomic variation within ITS1 and ITS2 of freshwater crayfishes (Decapoda: Cambaridae): implications for phylogenetic and microsatellite studies. Molecular Biology and Evolution 17(2): 284–291. https://doi.org/10.1093/oxfordjournals.molbev.a026308

Hasegawa M, Kishino H, Yano T-A (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22(2): 160–174. https://doi.org/10.1007/BF02101694

Hillis DM, Dixon MT (1991) Ribosomal DNA: Molecular evolution and phylogenetic inference. The Quarterly Review of Biology 66(4): 411–453. https://doi.org/10.1086/417338

Hou L, Dahms H-U, Dong C, Chen Y, Hou H, Yang W, Zou X (2013) Phylogenetic positions of some genera and species of the family Buccinidae (Gastropoda: Mollusca) from China based on ribosomal RNA and COI sequences. Chinese Science Bulletin 58: 2315–2322. https://doi.org/10.1007/s11434-013-5922-z

Hoy MS, Rodriguez RJ (2013) Intragenomic sequence variation at the ITS1–ITS2 region and at the 18S and 28S nuclear ribosomal DNA genes of the New Zealand mud snail, *Potamopyrgus antipodarum* (Hydrobiidae: Mollusca). The Journal of Molluscan Studies 79(3): 205–217. https://doi.org/10.1093/mollus/eyt016

Jiang Q, Wei L, Gai C, Yu W, He C, Chen M, Zhang Z, Song H, Wang X, Wang X (2019) An improved extraction method reveals varied DNA content in different parts of the shells of Pacific oysters. Aquatic Living Resources 32: e5. https://doi.org/10.1051/alr/2019003

Jukes TH, Cantor CR (1969) Evolution of protein molecules. Mammalian Protein Metabolism 3: 21–132. https://doi.org/10.1016/B978-1-4832-3211-9.50009-7

Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kimura M (1981) Estimation of evolutionary distances between homologous nucleotide sequences. Proceedings of the National Academy of Sciences of the United States of America 78(1): 454–458. https://doi.org/10.1073/pnas.78.1.454

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Layton KK, Martel AL, Hebert PD (2014) Patterns of DNA barcode variation in Canadian marine molluscs. PLoS ONE 9(4): e95003. https://doi.org/10.1371/journal.pone.0095003

Letunic I, Bork P (2021) Interactive Tree Of Life (iTOL) v5: An online tool for phylogenetic tree display and annotation. Nucleic Acids Research 49(W1): W293–W296. https://doi.org/10.1093/nar/gkab301

Lorenz F (2009) Two new species of Ovulidae from the Western Pacific (Gastropoda: Ovulidae). Conchylia 40: 38–44.

Lorenz F (2020) The "Black morph *Cyphoma* " from the Netherlands Antilles (Gastropoda: Ovulidae). Acta Conchyliorum 19: 69–75.

Lorenz F, Fehse D (2009) The Living Ovulidae: a Manual of the Families of Allied Cowries: Ovulidae, Pediculariidae and Eocypraeidae. ConchBooks, Hackenheim, 651 pp.

Ma XT (1997) Fauna Sinica: Class Gastropoda, Order Mesogastropoda, Superfamily Cypraeacea. Science Press, Beijing, 283 pp.

Meier R, Shiyang K, Vaidya G, Ng PK (2006) DNA barcoding and taxonomy in Diptera: A tale of high intraspecific variability and low identification success. Systematic Biology 55(5): 715–728. https://doi.org/10.1080/10635150600969864

Meyer CP (2003) Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. Biological Journal of the Linnean Society. Linnean Society of London 79(3): 401–459. https://doi.org/10.1046/j.1095-8312.2003.00197.x

Meyer CP (2004) Toward comprehensiveness: Increased molecular sampling within Cypraeidae and its phylogenetic implications. Malacologia 46: 127–156.

Meyer CP, Paulay G (2005) DNA barcoding: Error rates based on comprehensive sampling. PLoS Biology 3(12): e422. https://doi.org/10.1371/journal.pbio.0030422

Nguyen L-T, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Odorico D, Miller D (1997) Variation in the ribosomal internal transcribed spacers and 5.8 S rDNA among five species of *Acropora* (Cnidaria; Scleractinia): Patterns of variation consistent with reticulate evolution. Molecular Biology and Evolution 14(5): 465–473. https://doi.org/10.1093/oxfordjournals.molbev.a025783

Quintero-Galvis J, Raquel-Castro L (2013) Molecular phylogeny of the Neritidae (Gastropoda: Neritimorpha) based on the mitochondrial genes cytochrome oxidase I (COI) and 16S rRNA. Acta Biologica Colombiana 18: 307–318.

Reijnen BT (2015) Molecular data for *Crenavolva* species (Gastropoda, Ovulidae) reveals the synonymy of *C. chiapponii*. ZooKeys 501: 15–26. https://doi.org/10.3897/zookeys.501.9144

Reijnen BT (2016) Phylogenetic Ecology of Octocoral-gastropod Associations. Leiden University, Leiden, 192 pp.

Reijnen BT, van der Meij SET (2017) Coat of many colours-DNA reveals polymorphism of mantle patterns and colouration in Caribbean *Cyphoma* Röding, 1798 (Gastropoda, Ovulidae). PeerJ 5: e3018. https://doi.org/10.7717/peerj.3018

Reijnen BT, van der Meij SET (2019) Systematics of the subfamily Aclyvolvinae (Caenogastropoda: Ovulidae) based on molecular and morphometric analyses. The Journal of Molluscan Studies 85(3): 336–347. https://doi.org/10.1093/mollus/eyz020

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Rosenberg G (1992) An introduction to the Ovulidae (Gastropoda: Cypraeacea). American Conchologist 20: 4–7.

Sánchez JA, Fuentes-Pardo AP, Almhain ÍN, Ardila-Espitia NE, Cantera-Kintz J, Forero-Shelton M (2016) The masquerade game: Marine mimicry adaptation between egg-cowries and octocorals. PeerJ 4: e2051. https://doi.org/10.7717/peerj.2051

Schiaparelli S, Barucca M, Olmo E, Boyer M, Canapa A (2005) Phylogenetic relationships within Ovulidae (Gastropoda: Cypraeoidea) based on molecular data from the 16S rRNA gene. Marine Biology 147(2): 411–420. https://doi.org/10.1007/s00227-005-1566-0

Simison WB, Lindberg DR (1999) Morphological and molecular resolution of a putative cryptic species complex: a case study of *Notoacmea fascicularis* (Menke, 1851) (Gastropoda: Patellogastropoda). The Journal of Molluscan Studies 65(1): 99–109. https://doi.org/10.1093/mollus/65.1.99

Stothard J, Rollinson D (1997) Partial DNA sequences from the mitochondrial cytochrome oxidase subunit I (COI) gene can differentiate the intermediate snail hosts *Bulinus globosus* and *B. nasutus* (Gastropoda: Planorbidae). Journal of Natural History 31(5): 727–737. https://doi.org/10.1080/00222939700770361

Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Zhang SP, Wei P (2011) Cowries and Their Relatives of China. China Ocean Press, Beijing, 367 pp.

Supplementary material 1

Table S1

Authors: Qiong Wu

Data type: occurences, Date, GenBank accession numbers

Explanation note: Specimens used in the analyses, including locality, date, and GenBank accession data.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl1

Supplementary material 2

Table S2

Authors: Qiong Wu

Data type: morphological

Explanation note: L/W ratio of the genus *Sandalia* specimens.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl2

Supplementary material 3

Table S3

Authors: Qiong Wu

Data type: GenBank accession numbers

Explanation note: Details of sequences obtained from GenBank.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl3

Supplementary material 4

Table S4

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: Pairwise genetic distance matrix of COI sequences among specimens of Ovulidae. The data of *S. triticea* specimens are marked in red.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl4

Supplementary material 5

Table S5

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: Pairwise genetic distance matrix of 16s sequences among specimens of Ovulidae. The data of *S. triticea* specimens are marked in red.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl5

Supplementary material 6

Table S6

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: Pairwise genetic distance matrix of ITS sequences among specimens of Ovulidae. The data of *S. triticea* specimens are marked in red.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl6

Supplementary material 7

Figure S1

Authors: Qiong Wu

Data type: morphological

Explanation note: Dorsal, ventral, and lateral views of shells. A *Primovula formosa* (G.B. Sowerby II, 1848) (20200722H2) B *Crenavolva traillii* (A. Adams, 1856) (20210616BHH1) C *C. traillii* (20210616BHH9) D *Cuspivolva bellica* (Cate, 1973) (20210718H5) E *Phenacovolva* sp. (20210515DSH2). Scale bar: 2mm

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl7

Supplementary material 8

Figure S2

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: ML phylogenomic tree constructed from COI sequences including *Sandalia bridgesi*, *S. triticea*, *Primovula formosa*, *Naviculavolva deflexa*, and other related species of the family Ovulidae. Bootstrap values are shown above the branch, while the support values based on MrBayes are shown in parentheses. The sequences of *S. triticea* are marked in red. *S. rhodia* is a synonym of *S. triticea* (Sartori 2014).

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl8

Supplementary material 9

Figure S3

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: Bayesian phylogenomic tree constructed from 16S rRNA sequences including *Sandalia bridgesi*, *Sandalia triticea*, *Primovula formosa*, *Naviculavolva deflexa*, and other related species of the family Ovulidae. The sequences of *S. triticea* specimens are marked in red. The coloured bands designate different species.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl9

Supplementary material 10

Figure S4

Authors: Qiong Wu

Data type: phylogenetic

Explanation note: ML phylogenomic tree constructed from 16S rRNA sequences including *Sandalia bridgesi*, *S. triticea*, *Primovula formosa*, *Naviculavolva deflexa*, and other related species of the family Ovulidae. The sequences of *S. triticea* specimens are marked in red. The coloured bands designate different species.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl10

Supplementary material 11

Figure S5
Authors: Qiong Wu
Data type: phylogenetic
Explanation note: ML phylogenomic tree constructed from ITS-region sequences including *S. bridgesi*, *S. triticea*, *Primovula formosa*, and *Cuspivolva bellica*. Bootstrap values are shown above the branch, while the support values based on MrBayes are shown in parentheses. The sequences of *S. triticea* specimens are marked in red.

Link: https://doi.org/10.3897/zookeys.1096.79402.suppl11