RESEARCH ARTICLE



Two new species of genus *Limnias* from Thailand, with keys to congeners (Rotifera, Gnesiotrocha)

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Abstract

Two new species and two morphological variant taxa of sessile rotifers found during a survey of Thai rotifers are reported upon. Living specimens were collected and identified from twelve sampling sites. The specimens were photographed, and prepared for SEMs of dorsal plates and trophi. Two new species of genus *Limnias* are recognized. *Limnias lenis* **sp. n.** possesses a corona with a relatively shallow ventral sinus, and a dorsal plate without any projection, whereas *Limnias novemceras* **sp. n.** carries a corona with a deep and wide ventral sinus, and a dorsal plate with nine projections. Two morphological variants of *Limnias melicerta* are discussed, which are designated as *L. melicerta* SH and *L. melicerta* LH on the basis of the length of the horns on their dorsal plates. Moreover, both a dichotomous key and a formula key are provide including all *Limnias* species known to date.

Keywords

corona, dorsal plate, horny process, SEM, sessile rotifers

Introduction

Limnias Schrank, 1803 is a cosmopolitan genus of sessile rotifers (Segers 2007). This taxon is recognized by a combination of four characteristics: (1) a corona with two lobed and a wide dorsal gap, (2) a pair of distinct ventral antenna, (3) presence of a

stiff dorsal plate, and (4) a firm tube that the adults inhabit (see figure 1 of Wallace et al. 2018). At present, six valid names of congeners are known: L. ceratophylli Schrank, 1803, L. melicerta Weisse, 1848, L. myriophylli (Tatem, 1868), L. shiawasseensis Kellicott, 1888, L. cornuella Rousselet, 1889 and L. nymphaea Stenroos, 1898 (Jersabek et al. 2015; Wallace et al. 2018). In Thailand, two species of Limnias had to date been identified, L. melicerta and L. ceratophylli by Koste (1975) and Meksuwan et al. (2011). One easily recognized characteristic that separates species in the genus is the architecture of tube. For example, in L. melicerta the tube is composed of a series of rings stacked vertically forming a tube (Wright, 1954). The tube of *L. ceratophylli* lacks rings. Moreover, besides the ringed tube, L. melicerta possesses a deep ventral sinus corona and dorsal plate with seven projections, while *L. ceratophylli* has a corona with a shallow ventral sinus and a dorsal plate without projection. Based on our survey of diversity of sessile rotifers in Thailand started in 2011, we recognized two taxa belonging to Limnias which have distinct characters that do not fit any of the known members. They are here described as new species. We also update the dichotomous and formula keys to all species of genus *Limnias* by Wallace et al. (2018).

Materials and methods

Collecting sessile rotifers

Specimens of *Limnias* species were collected from different localities in Thailand (Supplementary material 1). Collecting method for sessile rotifers was described by Edmondson (1944), Wallace (1977), and Meksuwan et al. (2011). Briefly, it includes moving live, aquatic plants into a container filled with water from the sampling site to a container without adding any anesthetics or other chemicals for preservation. In laboratory, plants were dissected into convenient sizes for manipulation and examination for presence of sessile rotifers. These were identified alive. We suggest filtering some source water through a 60-µm, mesh plankton net and adding this to the containers to provide phytoplankton and organic particles as food source for the rotifers. By using this mesh size, larger zooplankton that may hinder examination are removed. Samples may be held for several days by providing suitable conditions. For examination plasticine was used to form small supports at the four corners of a coverslip to prevent compression of specimens.

Scanning electron microscopy (SEM)

Dorsal plate. Each fixed, contracted specimen in 95% ethyl alcohol is extracted from its tube, and placed into a small drop of distilled water on a piece of cover glass. The specimen is oriented dorsally and left until the water is completely evaporated. Dried specimens on cover glasses are coated with gold, followed by examination under SEM.

Trophi. A sorted specimen is placed into a drop of commercial bleach (7% NaO-Cl). The remaining trophi is picked up and rinsed several times in drops of distilled water on a piece of cover glass. Then, the trophi is air dried, coated with gold and examined under SEM. SEM photographs were processed by a FEI Quanta 400 SEM.

Results

Descriptions of new species

Classification of genus *Limnias* follows Segers (2002). We adhere to this view as it is supported by a number of molecular analysis that support Eurotatoria, as taxon consisting of subclass Bdelloidea and subclass Monogononta (e.g., Melone et al. 1998, Mark Welch 2000). Subclass Monogononta comprises superorder Pseudotrocha and superorder Gnesiotrocha. Genus *Limnias* is located in the Gnesiotrocha where the members lack a toe.

Phylum Rotifera Cuvier, 1817 Class Eurotatoria De Ridder, 1957 Subclass Monogononta Plate, 1889 Superorder Gnesiotrocha Kutikova, 1970 Order Flosculariaceae Harring, 1913 Family Flosculariidae Ehrenberg, 1838 Genus *Limnias* Schrank, 1803

Limnias lenis sp. n. http://zoobank.org/8D2467C6-7CF9-4F0D-8ABA-52AC36E4E176

Material examined. *Holotype.* A contracted female in a mounted slide deposited in Princess Maha Chakri Sirindhorn Natural History Museum (PSUNHM), Prince of Songkla University, Songkhla, Thailand: PSUZC-PK5PM4–1. *Paratypes.* Two females in PSUNHM: PSUZC-PK5PM4-2–3; two females in Zoology Laboratory, Science Program, Faculty of Science and Technology, Phuket Rajabhat University, Phuket, Thailand: PKRU-RF2-1–2. In total, seven specimens were examined.

Type locality. Jik peat swamp, Phuket Province, Thailand: 8°8.683'N, 98°17.983'E. Size of the peat swamp is about 230×140 meters. Individuals of *L. lenis* sp. n. were found attached to roots of Water hyacinth (*Eichhornia crassipes* (C.Mart.) Solms). November 15th, 2015.

Etymology. The species name is an adjective, derived from the Latin "lenis", meaning "soft, smooth, gentle" and refers to the smooth surface of its dorsal plate.

Diagnosis. The species is unique by its corona having a relatively shallow ventral sinus compared to other taxa, and by its smooth dorsal plate, without any projection (Figs 1A–C, 3A–C, 7A).



Figure I. Line drawings of habitus and dorsal plate. **A–C** *Limnias lenis* sp. n. **D–F** *Limnias novemceras* sp. n. Scale bars: 50 µm (**A**, **D**); 25 µm (**B**, **C**, **E**, **F**).

Description. Tube ringed, proximal part smooth, usually transparent. Trunk slender, tapers into slender foot with short stalk (Figs 1A, 3A). Corona two-lobed, twice as wide as trunk, lobes nearly circular, ventral sinus shallow, dorsal gap large, as wide as trunk or nearly so (Figs 1A, 3B). Two short ventral antennae not extending beyond the corona. Dorsal plate smooth, without any projection. Dorsal antenna aperture situated one-fifth of dorsal plate length from the anterior margin (Figure 7A). Trophi malleoramate, symmetrical. Left and right proximal unci teeth: 3/3, distal teeth: 17/17 (Figure 8A). Rami apophyses equal. Manubria crescent-shaped with three chambers. Corona width: 98–110, corona height: 49–58, depth of ventral sinus: 7–12, width of dorsal gap: 33–38, length of lateral antennae: 9–14 (in µm).

Distribution. The species is known only from its type locality.



Figure 2. Line drawings of habitus and dorsal plate. **A–C** *Limnias melicerta* SH **D–F** *Limnias melicerta* LH. Scale bars: 50 µm (**A**, **D**); 25 µm (**B**, **C**, **E**, **F**).

Limnias novemceras sp. n.

http://zoobank.org/A54A2E46-DE6B-4F0C-A401-B9A69F248CE8

Material examined. Holotype. A contracted female in a mounted slide was deposited in Princess Maha Chakri Sirindhorn Natural History Museum (PSUNHM), Prince of Songkla University, Songkhla, Thailand: PSUZC-PK5PM3-1. **Paratypes.** Two females in PSUNHM: PSUZC-PK5PM3-2–3; four females in Zoology Laboratory, Science Program, Faculty of Science and Technology, Phuket Rajabhat University, Phuket, Thailand: PKRU-RF1-1–4. In total, nine specimens were examined.

Type locality. A stream in Krabi Province, Thailand: 8°12.687'N, 98°46.899'E. Individuals of *L. novemceras*, sp. n. were found on leaves of *Hydrilla verticillata* (L.f.) Royle growing in littoral area of the stream. June 2^{nd} , 2011.



Figure 3. LM photographs of *Limnias lenis* sp. n. **A** habitus **B** corona **C** dorsal plate. Scale bars: 50 μ m (**A**); 25 μ m (**B**, **C**).



Figure 4. LM photographs of *Limnias novemceras* sp. n. **A** habitus **B** corona **C** dorsal plate. Scale bars: 50 μm (**A**); 25 μm (**B**, **C**).

Etymology. The species name is a substantive, and refers to the number of projections (nine, from the Latin *novem*, and horn, from the Greek *ceras*) on the dorsal plate.

Diagnosis. *Limnias novemceras* sp. n. is easily recognized by its dorsal corona gap being much wider than the tube diameter, by its long ventral antennae that reach beyond the fully extended corona, and by its dorsal plate carrying nine projections. In addition, this species never raises its corona far beyond the tube opening (Figs 1D–F, 4A–C, 7B).

Description. Tube ringed, transparent, proximal part smooth, transparent. Trunk slender, tapers into slender foot with short stalk (Figs 1D, 4A). Corona two-lobed,



Figure 5. LM photographs of *Limnias melicerta* SH. **A** habitus **B** corona **C** dorsal plate. Scale bars: 50 μ m (**A**); 25 μ m (**B**, **C**).



Figure 6. LM photographs of *Limnias melicerta* LH. **A** habitus **B** corona **C** dorsal plate. Scale bars: 50 μm (**A**); 25 μm (**B**, **C**).

more than twice as wide as trunk, ventral sinus depth between one third and one half of corona height, dorsal gap nearly 1.5 times as wide as trunk width (Figs 1D, 4B). Two long ventral antennae extending beyond the extended corona. Dorsal plate stiff, with nine projections, upper row a pair of short and broad projections, middle row with a central, distally bifid projection, two lateral rounded projections and, slightly



Figure 7. SEM photographs of dorsal plate (dorsal view). **A** *Limnias lenis* sp. n. **B** *Limnias novemceras* sp. n. **C** *Limnias melicerta* SH **D** *Limnias melicerta* LH. Scale bars: 10 μm.

more distally, two low and broad, ridges, lower row a pair of oblique, rounded, low projections, these rounded triangular with straight inner margin in SEM preparation. Dorsal antenna aperture situated at one fifth of the dorsal plate length from the anterior margin (Figure 7B). Trophi malleoramate, symmetrical. Left and right proximal unci teeth: 3/3, distal teeth: 16–17/16–17 (Figure 8B). Rami apophyses equal. Manubria crescent-shaped with three chambers. Corona width: 114–126, corona height:



Figure 8. SEM photographs of trophi (frontal view). **A** *Limnias lenis* sp. n. **B** *Limnias novemceras* sp. n. **C** *Limnias melicerta* SH **D** *Limnias melicerta* LH. Scale bars: 5 μm.

41–47, depth of ventral sinus: 11–16, width of dorsal gap: 74–80, length of lateral antennae: 43–44 (in μ m).

Distribution. The species is known only from its type locality.

Keys to species of genus Limnias

We constructed dichotomous and formula keys of all known *Limnias* species based on investigation of four species, including the two new species, observed in Thailand. In addition to the four species, we reevaluate the identity of *L. cornuella, L. myriophylli, L. nymphaea* and *L. shiawasseensis*, based on original publications, the most recent revision of the group by Wallace et al. (2018), and illustrations available in the Rotifer World Catalog (Jersabek and Leitner 2013). We recognize that number of dorsal plate projections, length of ventral antennae, and tube structure are useful characters for species identification in genus *Limnias*.

Dichotomous key

1	Tube without ringed structure, usually covered with debris2
_	Tube with ringed structure, clear or slightly colored (yellow or brownish) and
	sometimes covered with debris
2	Dorsal plate with seven projections L. shiawasseensis
_	Dorsal plate without projection
3	Ventral antennae short, not reaching beyond fully extended corona
	L. ceratopbylli
_	Ventral antennae longer than fully extended corona
4	Dorsal plate without projection
_	Dorsal plate with projections
5	Ventral antennae short
_	Ventral antennae long7
6	Seven projections on dorsal plate
_	Fourteen projections on dorsal plate
7	Four projections on dorsal plate, tube curved or twisted L. cornuella
_	Nine projections on dorsal plate, corona lobes separated by a very wide dorsal
	gap (nearly twice of truck width) L. novemceras sp. n.

Formula key to species

- 1 Ring tube: (a) absent; (b) present (Figs 1A, 3A)
- 2 Dorsal plate projections: (a) absent (Figs 3C, 7A); (b) four; (c) seven (Figs 5C, 7C);
 (d) nine (Figs 1F, 7B); (e) fourteen
- 3 Ventral antennae length relative to fully extended corona: (a) shorter; (b) longer

Species included in the formula key:

- L. ceratophylli: 1a, 2a, 3a
- L. myriophylli: 1a, 2a, 3b
- L. shiawasseensis: 1a, 2c, 3b
- L. cornuella: 1b, 2b, 3b
- L. melicerta: 1b, 2c, 3a
- L. nymphaea: 1b, 2e, 3a
- L. lenis sp. n.: 1b, 2a, 3a
- L. novemceras sp. n.: 1b, 2d, 3b

Discussion

The most distinctive features of genus *Limnias* are the bilobed corona, and apparently, the presence of a rigid dorsal plate. While feeding this plate is located in the neck region on dorsal side of the body. When the rotifers are disturbed, however, they retract the corona into the tube and the dorsal plate is moved into an antero-dorsal position such that the horn-like projections are exposed towards the opening of the tube (Figs 4C, 6A). The dorsal plate would seem to act as a lid to the tube, and, hence, a possible defensive mechanism against predators, and may therefore be of adaptive value.

Our keys to species of *Limnias*, as well as those by Wallace et al. (2018), start off with tube having either ringed (annulated) or smooth appearance, albeit that it may be covered by debris. However, R.L. Wallace (personal communication) informed that there is uncertainty on tube structure of *L. shiawasseensis*. The photomicrograph of a mounted specimen deposited in the Academy of Natural Sciences of Drexel University identified as *L. shiawasseensis* (ANSP No.486) appears to show what looks like rings (Jersabek and Leitner 2013). To the contrary, the original description of the species by Kellicott, 1888 reads as follows: "The tube is normal in form, clear below and covered above by dark floccose; the surface is not smooth nor yet annulate, but beset with transverse, parallel rows of minute raised points which serve to hold the floccose which the animal packs against the tube by its dorsal processes". We concur with Wallace that the original description should be privileged over the identification of the ANSP specimen. Therefore, we included *L. shiawasseensis* in our keys as a species lacking a ringed tube, until prove to the contrary.

At present, four species of *Limnias* rotifers have been recorded from Thailand: *L. ceratophylli, L. melicerta, L. lenis* sp. n. and *L. novemceras* sp. n. However, we found two additional, clearly distinguishable morphological variants of *L. melicerta* that both fit the original description of this species. Because no type specimens are known to exist for *L. melicerta* (see Jersabek et al. 2015), and as the original description of the species lacks the necessary detail, we are unable to determine whether, or which of the two Thai variants corresponds with the species. The two forms differ in the length and shape of the upper pair of projections (horns) on their dorsal plate; we refer to them as *L. melicerta* SH (Figs 2A–C, 5) and *L. melicerta* LH (Figs 2D–F, 6). SH has shorter horns (6.45 ± 0.98 SD; n = 8) and was found in sampling sites S4, S5, S6 and S10, while the LH has longer horns (13.94 ± 1.37 SD; n = 3), and was found in S5, S6, S10, S11 and S12 (Supplementary material 1). We were unable to find any additional characteristic on which we could base a separation; thus, molecular data will need to be analyzed to confirm whether the two taxa are separate species.

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Supplementary material I

Sampling sites (S1-S12) in Thailand with GPS coordinates.

Authors: Phuripong Meksuwan, Rapeepan Jaturapruek, Supiyanit Maiphae Data type: occurence

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RESEARCH ARTICLE



First records of Gnathia Leach, 1814 and Tachaea Schioedte & Meinert, 1879 from South Korea, with descriptions of two new species (Isopoda, Cymothoida, Cymothooidea)

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Abstract

Two new species of cymothoid isopods, *Gnathia koreana* **sp. n.** and *Tachaea koreaensis* **sp. n.**, are described from South Korea. The genera *Gnathia* Leach, 1814 and *Tachaea* Schioedte & Meinert, 1879 are recorded for the first time in South Korea. *Gnathia koreana* **sp. n.** is distinguished from its congeners by having the smooth dorsal surface of the pereon, the strongly ridged unornamented paraocular ornamentation, the strong bifid mediofrontal process, and the serrated superior frontolateral process. *Tachaea koreaensis* **sp. n.** is distinguished from its congeners by having the expanded propodus with serrated inferior margins in pereopods 1–3, the propodus with serrated inferiori margins in pereopods 4–7, one seta on the apical lobe of the maxilla, and ten robust setae on the posterior margin of the pleotelson.

Keywords

Corallanidae, Gnathia, Gnathiidae, Isopoda, South Korea, Tachaea

Introduction

The isopod crustacean family Gnathiidae Leach, 1814 is one of the nine families belonging to the superfamily Cymothooidea Leach, 1814. This family is unusual among isopods as its members exhibit peculiar morphological differences between juveniles (praniza stage) and adults (Cohen and Poore 1994, Ota 2012, Tanaka 2004, Tanaka and Nishi 2011). In addition, they have biphasic life cycles with ectoparasitic larva (praniza stage) and free-living adults (Hadfield et al. 2009, Ota et al. 2012, Smit et al. 2003). Pranizas are regarded to be parasites of fishes, whereas adults are non-feeding and have a degenerated intestine (Golovan 2006; Tanaka and Nishi 2011). The genus *Gnathia* Leach, 1814 is the largest group in this family and is currently composed of 126 species distributed worldwide (Boyko et al. 2008; Cohen and Poore 1994).

The family Corallanidae Hansen, 1890 also belongs to the superfamily Cymothooidea. The genus *Tachaea* Schioedte & Meinert, 1879 is the smallest group in this family and is currently composed of seven species (Boyko et al. 2008). The type species, *Tachaea crassipes* Schioedte & Meinert, 1879 is the only marine species found in the coral reefs of Singapore, whereas other species are found in freshwater habitats as ectoparasites of fish and various shrimp species (Delaney 1989).

Herein, we report two new species collected from South Korea, *Gnathia koreana* sp. n. and *Tachaea koreaensis* sp. n. The genera *Gnathia* and *Tachaea* were first found in the United Kingdom and Singapore, respectively, but the present study represents the first record of these genera in South Korea.

Materials and methods

Sampling

Specimens of *G. koreana* sp. n. were collected using light traps from Geomun-do Island (approximately 10 m depth) in South Korea. The sediment at the sampling site was characterized as organic-rich muddy sand. Specimens of *T. koreaensis* sp. n. were collected as ectoparasites on the freshwater shrimps *Macrobrachium nipponense* (De Haan, 1849) and *Palaemon paucidens* De Haan, 1844 collected from reservoirs in South Korea. All specimens were preserved immediately after collection in 95% ethyl alcohol. The type specimens of the two new species have been deposited in the National Institute of Biological Resources (**NIBR**), Incheon, South Korea.

Morphological analysis

The specimens were transferred to glycerine for dissection, and then examined and dissected under a dissection microscope (Olympus, model SZX-7). Figures of dissected appendages were drawn under a light microscope with an attached drawing tube (Leica, model DM 2500). Figures of the whole body were drawn using a draw-

ing tube attached to a stereomicroscope (Olympus, model SZX-12). The lengths of

all appendages and the whole body were measured with a stage micrometre (Leica, model no. 11513106) and an ocular micrometre. The photograph of the whole body of *G. koreana* sp. n. was taken using a digital camera (eXcope, model K6) mounted on a stereomicroscope, and those of the cephalon was taken using a scanning electron microscope (Hitachi, model S-4200). Pre-treatments were performed based on the methods described by Song and Min (2016).

Morphological terminology and the orientation of each appendage largely follows Bruce (2009); some morphological terms were taken from Cohen and Poore (1994) to retain descriptive consistency for the cephalic appendages of *G. koreana* sp. n. Setal terminology largely follows Watling (1989). Unless otherwise specified, the setae are simple.

Taxonomy

Suborder Cymothoida Wägele, 1989 Superfamily Cymothooidea Leach, 1814 Family Gnathiidae Leach, 1814

Genus Gnathia Leach, 1814

Type species. Gnathia maxillaris (Montagu, 1804) by original designation.

Key to the species of Gnathia from Japan, Korea, and Russian Far East

This key is based on males.

1	Dorsal surface of pereon without tubercles2
_	Dorsal surface of pereon with tubercles, especially anteriorly
2	Paraocular ornamentation absent; mandible without incisor
_	Paraocular ornamentation present; mandible with incisor
3	Dorsal surface of cephalon with tubercles; pylopod with three articles
	<i>G. limicola</i> Ota & Tanaka, 2007
_	Dorsal surface of cephalon without tubercles; pylopod with two articles4
4	Body very setose; inferior margins of pereopods without tubercles
	<i>G. capillata</i> Nunomura & Honma, 2004
-	Body smooth or sparsely setose; inferior margins of pereopods with tubercles5
5	Mediofrontal process bifid6
_	Mediofrontal process a single projection7
6	Mediofrontal process broad, not elongated; superior frontolateral process tri-
	angular; mandible mediocre G. bungoensis Nunomura, 1982
_	Mediofrontal process narrow anteriorly, elongated; superior frontolateral pro-
	cess rounded; mandible stout

7	Mediofrontal process acute; mandibular setae absent
	<i>G. nasuta</i> Nunomura, 1992
_	Mediofrontal process rounded; mandibular setae present
	G. sanrikuensis Nunomura, 1998
8	Mediofrontal process absent G. maculosa Ota & Hirose, 2009
_	Mediofrontal process present9
9	Mediofrontal process dividing into two apices; internal lobe of mandible
	Mediofrontal process not divided a single projection internal lobe of mandi
_	ble present
10	Lateral marging of personites 2 and 3 with corrections, mediofrontal process
10	Lateral margins of perconness 2 and 5 with senations, methodological process
	Lateral marging of personites 2 and 3 without corrections, mediofrontal pro
_	Lateral margins of perconness 2 and 5 without serrations; mediofrontal pro-
11	Cess narrow, with bind apex
11	raraocular ornamentation forming a fidge; superior frontolateral process
	rounded, serrated
-	Paraocular ornamentation not forming a ridge, with three indistinct tubercles;
1.2	superior frontolateral process acute, not serrated G. excavata Ota, 2012
12	Cephalon without tubercles; paraocular ornamentation forming a ridge; me-
	diofrontal process conical, longer than superior frontolateral process
	G. camuripenis Tanaka, 2004
-	Cephalon with tubercles; paraocular ornamentation not forming a ridge,
	with several tubercles; mediofrontal process rounded, shorter than superior
	frontolateral process <i>G. kumejimensis</i> Ota, 2012
13	Mandible as long as or shorter than half-length of cephalon, with smooth
	blade14
-	Mandible longer than half-length of cephalon, with dentate blade16
14	Cephalon with distinct serrations on lateral margins; mandible as long as
	half-length of cephalon G. tuberculata Richardson, 1909
_	Cephalon serrated, but without distinct serrations on lateral margins; mandi-
	ble shorter than half-length of cephalon15
15	Epimera linguiform, visible dorsally on pleonites 1-5, directed to the side-
	ward G. derzhavini Gurjanova, 1933
_	Epimera acute, visible dorsally on pleonites 4 and 5, directed downward
	<i>G. schmidti</i> Gurjanova, 1933
16	Body sparsely setose; pylopod with two articles G. teruyukiae Ota, 2011
_	Body very setose, covered with long setae; pylopod with three articles17
17	Mediofrontal process broad, not elongated; epimera not visible dorsally on all
	pleonites
_	Mediofrontal process narrow anteriorly, elongated; epimera visible dorsally
	on pleonites 3–5
18	Mediofrontal process dividing into two apices; supraocular lobe with
	blunt apex
	-

-	Mediofrontal process not divided, rounded; supraocular lobe with dentate
	apex19
19	Dorsal surface of pereonite 4 without tubercles; superior frontolateral process
	with four setae G. albipalpebrata Ota, 2014
_	Dorsal surface of pereonite 4 with tubercles; superior frontolateral process
	with several setae and tubercles G. parvirostrata Ota, 2014
20	Dorsolateral surface of pereonites 5 and 6 with tubercles; pleotelson with
	acute apex G. nubila Ota & Hirose, 2009
_	Dorsolateral surface of pereonites 5 and 6 without tubercles; pleotelson with
	rounded apex G. dejimagi Ota, 2014

Gnathia koreana sp. n.

http://zoobank.org/BF1A7F54-5E72-41B3-9573-54D967EF55BE Figures 1–4

Material examined. Holotype: adult male (4.6 mm, NIBRIV0000554213); Yeogaekseon terminal, Geomundo Island, Yeosu-si, Jeollanam-do, South Korea; 34°01'37"N, 127°18'27"E; 31 May 2014; approximately 10 m; coll. J.-H. Song. Paratype: adult male (4.3 mm, NIBRIV0000554214), same sample as holotype.

Etymology. The specific name '*koreana*' is derived from the name of the nation from which the specimens were collected.

Diagnosis. Pereon dorsal surface smooth, sparsely setose, without tubercles. Cephalon dorsal surface sparsely setose with several granules medially. Paraocular ornamentation strongly developed, forming a ridge, without tubercles. Mediofrontal process strong and bifid. Superior frontolateral process shorter than mediofrontal process, rounded, and serrated. Mandible without pseudoblade and internal lobe.

Description (adult male, holotype). Body (Figures 1A, B, 2A) 3.2 times as long as greatest width; dorsal surfaces smooth, sparsely setose. Cephalon (Figure 1C) rectangular, 0.7 times as long as wide, lateral margins slightly convex and smooth; dorsal surface sparsely setose with several granules medially; dorsal sulcus wide, deep; paraocular ornamentation (Figure 1E, F) strongly developed, forming ridge, without tubercles; posteromedian tubercle present. Eyes (Figure 2A) 0.3 times as long as cephalon. Supraocular lobe (Figure 2A) weak, with blunt apex; accessory supraocular lobe not pronounced. Mediofrontal process (Figure 2B) elongated, bifid. Superior frontolateral process (Figure 2B) shorter than mediofrontal process, serrated. Inferior frontolateral process absent. Pereonites 1-7 (Figure 2A) without tubercles on dorsal surface, lateral margins smooth; pereonite 1 not fused dorsally with cephalon, dorsolateral margins fully obscured by cephalon; pereonite 2 wider than pereonite 1; pereonite 4 with anterior constriction; areae laterales present on pereonite 5; pereonite 6 with lobi laterales; pereonite 7 narrow, overlapping pleon; lobuii weak, globular. Pleonites 1-5 (Figure 2A), epimera not visible dorsally. *Pleotelson* (Figure 4F) 0.9 times as long as anterior width, lateral margins smooth, anterolateral margins not concave, posterolateral margins



Figure I. *Gnathia koreana* sp. n., male holotype **A** body, dorsal view **B** body, dorsal view **C** cephalon **D** mandible **E** paraocular ornamentation, dorsal view **F** paraocular ornamentation, lateral view. Scale bars: 1 mm (**A**, **B**), 0.5 mm (**C**, **F**), 0.4 mm (**D**), 0.1 mm (**E**).

weakly concave; mid-dorsal surface with two sub-median setae, posterolateral margins with two submarginal setae, apex with two setae.

Antennula (Figure 2C) peduncle article 2 0.6 times as long as article 1; article 3 1.7 times as long as article 2; flagellum with five articles. *Antenna* (Figure 2D) peduncle article 4 3.0 times as long as wide, 1.2 times as long as article 3, with two penicillate setae; flagellum with seven articles.



Figure 2. *Gnathia koreana* sp. n., male holotype **A** body, dorsal view **B** mediofrontal process and superior frontolateral process **C** antennula **D** antenna **E** mandible **F** maxilliped **G** pylopod. Scale bars: 1 mm (**A**), 0.5 mm (**B**), 0.1 mm (**C–E**), 0.2 mm (**F, G**).



Figure 3. *Gnathia koreana* sp. n., male holotype. **A** pereopod 2 **B** pereopod 3 **C** pereopod 4 **D** pereopod 5 **E** pereopod 6. Scale bars: 0.2 mm (**A–E**).

Mandible (Figures 1C, D, 2E) 0.5 times as long as width of cephalon, curved upward; mandibular seta present; carina present, unornamented; incisor elevated, distally rounded; dentate blade with five weak processes; pseudoblade absent; internal lobe absent; dorsal lobe absent; basal neck short; erisma absent; lamina dentate absent. *Maxilliped* (Figure 2F) article 1 lateral margin with continuous marginal setae; article 2 lateral margin with three plumose setae; article 3 lateral margin with seven plumose setae; article 4 lateral margin with four plumose setae; article 5 with seven plumose setae; endite extending to distal margin of article 2; without coupling setae. *Pylopod* (Figure 2G) with three articles; article 1 1.4 times as long as wide, without distolateral lobe, with three areolae; posterior and lateral margins forming rounded curve; lateral margin with 30 plumose setae; mesial margin with continuous setae, distal margin with 5–6 setae; article 2 1.3 times as long as wide; article 3 minute.

Pereopods 2–6 (Figure 3A–E) without long plumose setae; basis superior margin with 2–3 penicillate setae; dactylus superodistal margin with one penicillate seta. Pereopod 2 basis 2.4 times as long as greatest width, superior margin with two setae, inferior margin with three setae; ischium 0.7 times as long as basis, 2.4 times as long as wide, superior margin with three setae; inferior margin with four setae and four tubercles; merus 0.6 times as long as ischium, 1.8 times as long as wide, superodistal margin with one seta, inferior margin with one seta and four tubercles; carpus as long as merus, 2.1 times as long as wide, superodistal margin with one seta, inferior margin with three setae and three tubercles; propodus 0.8 times as long as ischium, 3.5 times as long as wide, superior margin with three setae, inferior margin with two robust setae; dactylus 0.3 times as long as propodus. Pereopods 3–6 similar, but basis superior margin with 3–6 tubercles.

Pleopods 1–5 (Figure 4A–E) similar. Pleopod 2 exopod 2.3 times as long as wide, with 8 plumose setae; endopod 2.5 times as long as wide, with seven plumose setae; appendix masculina with parallel margins, 0.6 times as long as endopod, distally rounded. Uropod (Figure 4F) rami extending beyond pleotelson, apices rounded; peduncle with two setae; endopod 2.6 times as long as greatest width, lateral margin with three setae, mesial margin with eight plumose setae, dorsally with one penicillate seta; exopod not extending to end of endopod, 4.0 times as long as greatest width, lateral margin with three setae; mesiodistal margin with three plumose setae.

Habitat. This species was collected at approximately 10 m depth corresponding to a sedimentary bottom of muddy sand.

Remarks. *Gnathia koreana* sp. n. is distinguished from other known species of *Gnathia* by the following characters: 1) the dorsal surface of the pereon without tubercles, 2) the paraocular ornamentation is strongly developed, forming a ridge, without tubercles, 3) the mediofrontal process is strong and bifid, 4) the superior frontolateral process is shorter than the mediofrontal process, rounded, and serrated, and 5) the mandible without internal lobe.

Gnathia koreana sp. n. is most similar to *G. excavata* from Japan in terms of the following characters: the body is smooth, the mediofrontal process is bifid, and the mandible without internal lobe. However, the new species is distinguished from *G. excavata*



Figure 4. *Gnathia koreana* sp. n., male holotype **A** pleopod 1 **B** pleopod 2 **C** pleopod 3 **D** pleopod 4 **E** pleopod 5 **F** pleotelson and uropod. Scale bars: 0.2 mm (**A**–**E**), 0.1 mm (**F**).

by the shape of the paraocular ornamentation and superior frontolateral process. In *G. excavata*, the paraocular ornamentation with three indistinct tubercles and the superior frontolateral process is acute and not serrated. In comparison, in the new species, the paraocular ornamentation with distinct unornamented ridge and the superior frontolateral process is rounded and serrated.

Distribution. Only known from the type locality.

Family Corallanidae Hansen, 1890

Genus Tachaea Schioedte & Meinert, 1879

Type species. Tachaea crassipes Schioedte & Meinert, 1879

Distribution. Six species are distributed in Asia: *Tachaea chinensis* Thielemann, 1910 (China, Japan, Thailand, and Malaysia); *T. crassipes* Schioedte & Meinert, 1879 (Singapore); *T. koreaensis* sp. n. (South Korea); *T. lacustris* Weber, 1892 (Indonesia); *T. spongillicola* Stebbing, 1907 (India); and *T. tonlesapensis* Nunomura, 2006 (Cambodia). Two species are distributed in Australia: *T. caridophaga* (Riek, 1953) (Queensland); *T. picta* (Riek, 1967) (Queensland and New South Wales) (Delaney 1989; Nunomura 2006).

Key to the species of Tachaea

This key is based on females. Therefore, we excluded *T. crassipes* that is designated the holotype based on the male specimen.

1	Propodus of pereopod 1 expanded on inferior margin2
_	Propodus of pereopod 1 not expanded on inferior margin4
2	Maxillipedal palp with three articles; endopod of uropod surpassing pleo-
	telson
_	Maxillipedal palp with four articles; endopod of uropod not surpassing
	pleotelson
3	Pereonite 1 as long as pereonite 2; incisor of mandible with two cusps; apical
	lobe of maxilla without seta; pleotelson with eight robust setae on posterior
	margin
_	Pereonite 1 1.7 times longer than pereonite 2; incisor of mandible with one
	cusp; apical lobe of maxilla with one seta; pleotelson with ten robust setae on
	posterior margin T. koreaensis sp. n.
4	Incisor of mandible with three cusps; maxillipedal palp with five articles
	T. tonlesapensis
_	Incisor of mandible with one or two cusps; maxillipedal palp with three or
	four articles

5	Pereonite 1 longer than other pereonites, 2.0 times longer than pereonite 5;
	apex of pleotelson with truncated margin T. lacustris
_	Pereonite 1 marginally longer or shorter than pereonite 5; apex of pleotelson
	with rounded margin
6	Pereonite 1 longer than pereonite 5; maxillipedal palp with three articles
	T. caridophaga
_	Pereonite 1 shorter than pereonite 5; maxillipedal palp with four articles
	T. picta

Tachaea koreaensis sp. n.

http://zoobank.org/4FB4AD83-2912-448A-8734-19C4CAD443D6 Figures 5–7

Material examined. Holotype: non-ovigerous female (4.8 mm, NIBRIV0000554215); Buheungji reservoir, Yeongcheon-si, Gyeongsangbuk-do, South Korea; 35°55'19"N, 128°59'14"E; 18 April 2013; approximately 2 m; coll. K.-S. Sim; ectoparasites of *Macrobrachium nipponense*. Paratype: non-ovigerous female (4.3 mm, NIBRIV0000754063); Wolga reservoir, Wolga-ri, Gunnae-myeon, Jindo-gun, Jeollanam-do, South Korea; 34°29'36"N, 126°17'35"E; 23 September 2016; 1.4 m; using a landing net; coll. D.-H. Ahn, C. W. Lee, H.-M. Yang and J.-H. Song; ectoparasites of *Palaemon paucidens*.

Etymology. The specific name '*koreaensis*' is derived from the name of the nation from which the specimens were collected.

Diagnosis. Pereopods 1–3 propodus expanded with serrations on inferior margins. Pereopods 4–7 propodus with serrations on inferodistal margins. Mandible incisor with one cusp. Maxilla apical lobe with one seta. Maxillipedal palp with four articles. Pleotelson with ten robust setae on posterior margin.

Description (non-ovigerous female, holotype). *Body* (Figure 5A) 2.2 times as long as greatest width. Colour yellowish; chromatophores on all somites, including both antennae and uropods. *Cephalon* (Figure 5A) 2.6 times wider than medial length. *Eyes* (Figure 5A) with 26–28 ommatidia. *Pereonite 1* (Figure 5A) longest, 1.7 times as long as pereonite 2 and 4, 1.4 times as long as pereonite 3, 1.8 times as long as pereonite 5, 2.1 times as long as pereonite 6, 2.8 times as long as pereonite 7.

Frontal lamina (Figure 5B) elongate, narrow; clypeus short and broad.

Antennula (Figure 5C) peduncle article 1 triangular, 1.1 times as long as wide, with four setae and two penicillate setae; article 2 0.7 times as long as article 1, with two setae and one penicillate seta; article 3 minute, 0.2 times as long as article 2, with three setae distally; flagellum with seven articles, articles 3–6 with 2 aesthetascs, articles 6 and 7 minute. *Antenna* (Figure 5D) peduncle article 1 0.8 times as long as article 2, with two setae; article 2 shortest, with two setae; article 3 2.0 times as long as article 2, with two setae; article 4 with two setae; article 5 with six setae and two penicillate setae; articles 4 and 5 similar length; flagellum with 12 articles, each articles with six setae.



Figure 5. *Tachaea koreaensis* sp. n., female holotype. **A** body, dorsal view **B** ventral view of bases of antennula, frontal lamina, and clypeus **C** antennula **D** antenna **E** mandible **F** maxilliped **G** maxillula **H** maxilla. Scale bars: 1 mm (**A**), 0.5 mm (**B**), 0.2 mm (**C**, **D**), 0.1 mm (**E**–**H**).



Figure 6. *Tachaea koreaensis* sp. n., female holotype. **A** percopod 1 **B** percopod 2 **C** percopod 3 **D** percopod 4 **E** percopod 5 **F** percopod 6 **G** percopod 7. Scale bars: 0.2 mm (**A–G**).



Figure 7. *Tachaea koreaensis* sp. n., female holotype. **A** pleopod 1 **B** pleopod 2 **C** pleopod 3 **D** pleopod 4 **E** pleopod 5 **F** uropod **G** uropod endopod **H** uropod exopod **I** pleotelson. Scale bars: 0.2 mm (**A**–**H**), 0.4 mm (**I**).

Mandible (Figure 5E) palp article 2 with four serrate setae and two setae; article 3 with seven short serrate setae, three serrate setae. Lacinia mobilis and molar process absent; incisor monocuspid. *Maxillula* (Figure 5G) lateral lobe forming single large curved spine. *Maxilla* (Figure 5H) short, apical lobe with one seta. *Maxilliped* (Figure 5F) without endite; palp with four articles, narrow, 4.4 times as long as wide.

Pereopods 1–3 (Figure 6A–C) similar, propodus inferior margins expanded with serrations. Pereopod 1 basis 2.7 times as long as greatest width, superior margin with three setae, inferodistal margin with one seta; ischium 0.6 times as long as basis, 1.8 times as long as wide, superior margin with two setae, inferior margin with two setae; merus 0.6 times as long as ischium, 0.8 times as long as wide, superodistal margin with two setae and one robust setae, inferodistal margin with three robust setae, inferior margin with one seta; carpus shortest, 0.4 times as long as merus, 0.3 times as long as wide, superodistal margin without setae, inferodistal margin with five robust setae; propodus 1.2 times as long as ischium, 1.7 times as long as wide, superior margin with one seta and one penicillate seta, inferior margin with three robust setae, one comb seta and one seta; dactylus 0.5 times as long as propodus. Pereopods 4–7 (Figure 6D–G) similar, propodus inferodistal margins with serrations. Pereopods 4 and 5 carpi with three comb setae; pereopod 6 carpus with four comb setae, propodus with three comb setae.

Pleopods 1–5 (Figure 7A–E) similar; exopod broader, longer than endopod, with plumose setae; endopod naked. Pleopods 1–4 peduncle wider than long, with 5–6 coupling spines and 1–2 plumose setae. Pleopod 5 peduncle without coupling spines. Uropod (Figure 7F) rami reaching pleotelson; peduncle distal margin with three setae, proximal margin with two setae, lateral margin with one seta; endopod (Figures 5A, 7G) not surpassing pleotelson, 2.1 times as long as greatest width, lateral margin with one robust setae and plumose setae, mesial margin truncate, with seven robust setae and plumose setae; exopod (Figures 5A, 7H) not extending to end of endopod, 3.1 times as long as greatest width, lateral margin with four robust setae and plumose setae; mesiodistal margin with three robust setae and plumose setae. Pleotelson (Figure 7I) 0.8 times as long as anterior width; posterior margin rounded, with ten robust setae and numerous plumose setae.

Remarks. *Tachaea koreaensis* sp. n. is distinguished from other known species of *Tachaea* by the following combination of characters: 1) the inferior margins of the propodus of pereopods 1–3 is expanded with serrations, 2) the inferodistal margins of the propodus of pereopods 4–7 with serrations, 3) the apical lobe of the maxilla with one seta, and 4) the posterior margin of the pleotelson with ten robust setae.

Tachaea koreaensis sp. n. is most similar to *T. spongillicola* from India, but it can be distinguished from the latter by the following characters: the ratio of pereonite 1 to pereonite 2, the number of cusps on the mandible, the presence or absence of setae on the apical lobe of the maxilla, and the number of robust setae on the posterior margin of the pleotelson. In *T. spongillicola*, the pereonite 1 is as long as the pereonite 2, the incisor of the mandible with two cusps, the apical lobe of the maxilla without seta, and the posterior margin of the pleotelson with eight robust setae. In comparison, in the new species, the pereonite 1 is 1.7 times as long as the pereonite 2, the incisor of the

mandible with one cusp, the apical lobe of the maxilla with one seta, and the posterior margin of the pleotelson with ten robust setae.

Distribution. Jeollanam-do and Gyeongsangbuk-do (South Korea).

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RESEARCH ARTICLE



A revision of the genus Eurhoptus LeConte, 1876 (Curculionidae, Cryptorhynchinae) of America north of Mexico

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Abstract

The genus *Eurhoptus* LeConte, 1876 is revised for America north of Mexico. Eight species are recognized including *E. pyriformis* LeConte, 1876, *E. sordidus* (LeConte, 1876), *E. curtus* (Hamilton, 1893), resurrected name, and five new species as follows: *E. rileyi* new species (type locality, Texas, Hidalgo County, Bentsen Rio Grande State Park), *E. imbricatus* new species (type locality, Texas, Bandera County, Lost Maples State Natural Area), *E. cariniventris* new species (type locality, Texas, Bandera County, Lost Maples State Natural Area), *E. occidentalis* new species (type locality, Texas, Brewster County, Big Bend National Park), and *E. aenigmaticus* new species (type locality, Alabama, Winston County, Bankhead National Forest). Descriptions or redescriptions, and images of taxonomically important structures are presented for all species. A key to the eight species is included.

Keywords

Biodiversity, new species, phylogeny, species discovery, taxonomy, weevils

Introduction

The genus *Eurhoptus* was established by LeConte in 1876 for the species *E. pyriformis* LeConte, 1876. The genus was differentiated from the closely related *Acalles* Schoenherr, 1825 by the pear-shaped body and a stouter antennal club. Blatchley and Leng (1916) noted the presence of a deep triangular polished impression on the first ventrite in *E. pyriformis* but did not notice the similar impression in *A. sordidus* LeConte, 1876, likely because specimens are often encrusted in dirt, and left this latter species in *Acalles*. It was not until Kissinger (1964) recognized this similarity in abdominal ventrite sculpture and moved *Acalles sordidus* LeConte into the genus *Eurhoptus* that the definition of the genus came to rely primarily on the presence of this variously impressed first abdominal ventrite. Until the present publication, the genus contained, in addition to these two described species from the U.S.A., nine described Mexican and Central American species (O'Brien and Wibmer 1982). Here, we add five new species and resurrect the name *A. curtus* Hamilton, 1893 as a valid species and not a synonym of *A. sordidus* LeConte, 1876. The genus is tremendously diverse from Mexico south to Panama with likely a few hundred undescribed species (Anderson and O'Brien 1996; Anderson and Ashe 2000).

At least three new species have been known to occur in the U.S. for some time (Anderson 2002), but their exact limits and relationships to the described species have remained unclear. A phylogeographic study (Caterino and Langton-Myers in press) on *E. pyriformis* revealed deep divisions within this species in the southeastern U.S., suggesting a more complex taxonomic situation than expected, and prompting the current attempt to more completely revise the taxonomy of the known and unknown U.S. species.

The natural history of *Eurhoptus* is essentially unknown. The adults are frequently sifted from various types of leaf litter, where they may feed on fungus-infested plant debris, as some related taxa are thought to do (Luna-Cozar et al. 2014). The adults are flightless, and flightless relatives in Europe have been alleged to be important indicators of well-preserved ancient woodlands (Buse 2012). This does not necessarily appear so for the North American species, which have been found in a variety of secondary forest habitats. No larvae of the genus have been found or described.

Materials and methods

Standard taxonomic procedures for the examination of pinned specimens have been used. Maps were prepared with Simplemappr (http://www.simplemappr.net). Species identifications of outlying individuals were confirmed. GenBank numbers, label data, and voucher numbers for all sequences analyzed here are provided in Suppl. material 1: Table S1. Coordinates given for specimens examined are in decimal degrees. This study was based on 1250 specimens, obtained from (or deposited in) the following collections (listed by these acronyms in 'Specimens examined' sections):

ASUIC Arizona State University Insect Collection, Tempe, Arizona, U.S.A. (includes specimens from the Charles W. O'Brien collection)

BMNH	The Natural History Museum, London, England
CMNC	Canadian Museum of Nature, Ottawa, Canada
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.
CNCI	Canadian National Collection of Insects, Ottawa, Canada
CUAC	Clemson University Arthropod Collection, Clemson, South Carolina, U.S.A.
CWOB	Charles W. O'Brien Insect Collection, Green Valley, Arizona, U.S.A.
EGRC	Edward G. Riley Insect Collection, College Station, Texas, U.S.A.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.
INHS	Illinois Natural History Survey, Champaign, Illinois, U.S.A.
KSC	Kyle Schnepp Collection, Gainesville, Florida, U.S.A.
LSAM	Louisiana State Arthropod Museum, Baton Rouge, Louisiana, U.S.A.
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MEM	Mississippi State Entomology Museum, Mississippi, Mississippi, U.S.A.
TAMU	Texas A & M University Insect Collection, College Station, Texas, U.S.A.
ТММС	University of Texas Insect Collection, Austin, Texas, U.S.A.
UAAM	University of Arkansas Arthropod Museum, Fayetteville, Arkansas, U.S.A.
UCFC	University of Central Florida Collection of Arthropods, Orlando, Florida,
	U.S.A.
USNM	United States National Museum, Washington D.C., U.S.A.
UTCI	University of Tennessee Chattanooga Collection of Insects, Chattanooga,
	Tennessee, U.S.A.

Phylogeny

In part to test the distinctiveness of the species we have recognized among Nearctic Eu*rhoptus*, we undertook a molecular phylogenetic analysis including multiple representatives where possible, of as many species as possible. Our main questions regarded the distinctiveness of a few morphological variants related to both *E. pyriformis* and *E. sordidus*. Our data set largely relies on data generated for a population level analysis of E. pyriformis in the southern Appalachians (Caterino and Langton-Myers in press). However, we have generated a number of additional sequences for the current study, and have pruned out many redundant or highly similar sequences (mainly within E. pyriformis) for the present analysis. In total, the present analysis includes data from 87 Eurhoptus individuals, and nine outgroup Cryptorhynchinae (representatives of Acalles, Peracalles, Trichacalles, Ouroporopterus, and Trigonopterus, the last three from sequences previously published by Riedel et al. (2016). Thus, analyses were based on 96 taxa overall. These include representatives of four of the eight species we now recognize in Eurhoptus, including E. curtus, E. sordidus, E. aenigmaticus, and E. pyriformis. Extractions of pointed specimens of other species were attempted, but none succeeded. See Suppl. material 1: Table S1 for full data and GenBank accession numbers for all individuals and genes sequenced.

We dissected each specimen and used the GeneJet Genomic DNA Purification Kit (ThermoFisher Scientific, Waltham, MA) to extract DNA from the dissected head and prothorax. Following tissue digestion, we removed the remaining exoskeleton and mounted the body parts as vouchers. Most vouchers are deposited in the Clemson University Arthropod Collection. We sequenced portions of four genes for this analysis. We sequenced 826 bp of the mitochondrial cytochrome oxidase I (COI) gene, which is represented in 78 individuals. The portion sequenced is from the 5' half of the gene, mainly using the primers C1-J-2183 ('Jerry') and TL2-N-3014 ('Pat'; both from Simon et al. 1994). We developed one additional forward primer to amplify some difficult lineages, C1-J-2406 (TTYACTTCAGCWACWATAATYATTGC). Three nuclear genes were targeted, mainly selecting one or two individuals for each distinct mitochondrial haplotype. These included partial sequences of the internal transcribed spacer 2 (ITS2) for 56 individuals, using the primers TW81 and HITR (from Richards et al. 1997), aligned length 1611 bp; 921 bp of the protein coding rudimentary (CAD) gene from 78 individuals, using the primers CD821F and CD1098R2 (from Wild and Maddison 2008); and 344 bp of an intron in the krotzkopf verkehrt (kkv) gene from 67 individuals using the primers KKV2768F and KKV3023R (from Polihronakis-Richmond and Caterino 2012). Amplifications via PCR started with a 3-minute initial denaturation at 95°, a 30 second denaturation at 94°, 35-40 cycles with annealing temperatures of 50-62° (see Suppl. material 1: Table S1 for details), a 1-minute extension at 72°, and a 5-minute final extension at 72°. Successful PCR products were sent to Macrogen USA (Rockville, MD) for Sanger sequencing in both directions. Sequence chromatograms were compiled, inspected, and preliminarily aligned in Geneious (Auckland, NZ).

Sequences of COI were length invariant, and alignment was trivial. Sequences of all other markers included length variation. These were aligned using MAFFT online (Katoh et al. 2017), using the 'Auto' setting, which selected an internal algorithm depending on number, length, and complexity of sequences. Combined sequences were analyzed under parsimony in PAUP* (Swofford 2002), with all sequences weighted equally, gaps treated as missing data, 100 random sequence addition replicates, saving no more than 1000 trees at each step; and under Bayesian criteria using Mr-Bayes (v.3.2.6 [Ronquist and Huelsenbeck 2003]) on the CIPRES Science Gateway, partitioning the four-gene data set, and implementing a GTR+I+ Γ model; nruns=2, ngen=10,000,000, nchains=4, burninfrac=0.25.

Results and discussion

Phylogeny

There is a high degree of molecular diversity and divergence among species and populations of Nearctic *Eurhoptus*. Uncorrected pairwise divergences in COI exceeded 10% between all of the species we recognize below (for which we had data). Some still contain intraspecific divergences approaching this. However, the higher divergences in these cases are spanned by intervening populations, and are united by morphology, and we do not yet see clear grounds for further separation.

Both parsimony and Bayesian analyses (see Figure 1) supported a deep primary division between *E. pyriformis* and three species very similar to and including *E. sordidus*,



Figure 1. One of a number of equally parsimonious trees (numerous rearrangments within species were equally parsimonious). Numbers on branches represent Bayesian posterior probabilities >75% for major clades. Terminal units are named by DNA extraction code/voucher number, followed by state of collection (two letter abbreviation) and COI haplotype, as reported in Caterino and Langton-Myers (in press), or newly here. Dotted lines represent hypothetical placements of two other species, yet unsampled for DNA.

which exhibit a narrowed pronotal base. Preliminary morphological work suggested that '*E. pyriformis*', as previously circumscribed (all those populations with a broad pronotal base), contained up to three species. One of these, referred to below as *E. cariniventris* n. sp., was not represented by molecular data, but appears justifiably distinct based on male genitalia. Another morphotype, referred to in Caterino and Langton-Myers (in press) as 'patterned *E. pyriformis*' turns out to be neither genetically nor morphologically supportable. Individuals showing these distinctively patterned elytra (Figures 2A, B) are now known from across the range (specifically individuals from NC, GA, and AR), and these are resolved as paraphyletic with respect to a 'plain' morphotype. Genitalia are somewhat variable in both, particularly with regard to the shape of the aedeagal tip.

Morphological and molecular data agree in distinguishing multiple species within what has been referred to as *E. sordidus*. *Eurhoptus sordidus* itself is restricted to eastern Texas, western Arkansas, and eastern Oklahoma. Sequenced individuals from Arkansas and Texas are strongly supported as monophyletic, and minimally divergent among themselves. A largely more eastern lineage is strongly supported as the sister to *E. sordidus*, and for this we resurrect Hamilton's (1893) name *E. curtus*. There is some potentially interesting subdivision among *E. curtus*, particularly with regard to some southeastern-most representatives (South Carolina specimens from Greenville and McCormick Counties). However, molecular sampling across this widespread species' broad range is not yet adequate to assess variation patterns. A third species in the *sordidus* lineage is that which we describe below as *E. aenigmaticus*. This is restricted to a rather small area of southern Alabama, Mississippi, and Lousiana. The genitalia of this species is quite distinct. We've only been able to sequence DNA from Alabama specimens, and their monophyly is not well supported (probably because COI has only been sequenced for two of the four individuals). However, it appears to represent a sister to *E. sordidus* + *E. curtus*.

With regard to species not represented by molecular data, we would predict that *E. cariniventris* would be resolved as the sister to *E. pyriformis. Eurhoptus occidentalis* from west Texas appears morphologically close to *E. sordidus*, and would likely fall out somewhere in that clade. *Eurhoptus imbricatus* and *E. rileyi* would appear further from these other Nearctic species, and may represent one or more independent lineages with closer relationships to groups known from Mexico and southward. Much broader representation from this largely undescribed Neotropical fauna will be necessary before anything can be said about their relationships.

Taxonomy

Eurhoptus LeConte, 1876

Eurhoptus LeConte, 1876: 245; Blatchley and Leng 1916: 496; Kissinger 1964: 64; Papp 1979: 163; O'Brien and Wibmer 1982: 136; Downie and Arnett 1996: 1581; Alonso-Zarazaga and Lyal 1999: 131; Salsbury 2000: 347; Anderson 2002: 765; Ciegler 2010: 166.

Europtus; Fiedler 1940: 300 (error, in key).

Eurrhoptus Rye 1878: 93 (unjustified emendation).

Type species. Eurhoptus pyriformis LeConte, 1876: 245 (by monotypy). Gender masculine.



Figure 2. *Eurhoptus pyriformis.* **A** Dorsal view of scaled form **B** Lateral view of scaled form **C** Dorsal view of 'plain' form **D** Lateral view of 'plain' form **E** Ventral view showing impressions on ventrites **F** Lateral view of aedeagus **G**, **H** Dorsal views showing range of variation of aedeagus.

Redescription (U.S.A. species only). Small, convex, rounded, dull black or darkbrown. Body length (exclusive of head and rostrum) 1.8–3.2 mm, cuticle either largely bare, variously covered with short, fine to coarse, recurved seta-like scales, lacking other scales or variously clothed with dense approximate to imbricate flat scales in addition to recurved seta-like scales. Rostrum short, stout, flattened dorsally, about as long as pronotum or slightly less, scaly towards base, glabrous, finely punctured towards apex in female, more coarsely so in male; medially carinate or not. Eyes small, flat, oval, largely covered by slight post-ocular lobes when rostrum in repose. Head with frons scaly, not impressed. Antennae red-brown, funicle of 7 desmomeres, club small, oval. Pronotum about as wide as long, lateral margins rounded or straight; if straight, then margins tapered more or less evenly from base to apex with greatest width at base; if rounded, then apical portion constricted, tubulate with greatest width before base. Basal margin nearly straight, disc variously punctured, medially carinate, sulcate or evenly punctured; post-ocular lobes slight. Elytra robust, strongly rounded dorsally and laterally, striae distinct, of small to very large punctures; all elytral intervals evenly elevated, slightly rounded, each with single row of recurved seta-like scales. Scutellar shield not visible. Mesoventral cup distinct, metaventrite short, medially impressed behind cup or carinate. Abdomen with ventrite 1 variously modified with large median or paired rather deep pits, pit either glabrous, shining or filled with erect scales; areas around pit often with dense, fine golden setae encircling depression; ventrite 5 broadly triangular, about as long as ventrites 2-4 combined. Legs with femora not toothed, narrow to stout (greatly so in some species where width accentuated by dense, erect scales along dorsal and lateral margins); tibiae narrow to stout (greatly so in some species where width accentuated by dense, erect scales along dorsal and lateral margins); tarsi fine, narrow, article 3 widest, bilobed; tarsal claws minute. Male with aedeagus short, one-half or less length of aedeagal apodemes, in lateral view very slightly curved ventrally to almost straight, in dorsal view with lateral margins subparallel, slightly to abruptly convergent towards apex at about apical one-third to one-fifth. Internal sac with apical sclerite complex of modified cruciform arrangement. Female with bursa copulatrix and vagina lacking any internal sclerotization, spermatheca L-shaped; distal gonocoxite elongate-triangular, with distinct long, slender apical stylus, sternite 8 with apical lamellae short, basally widely divergent, basal apodeme rather robust, elongate, expanded slightly at apex, tergite 8 tapered towards truncate or acuminate finely irregularly serrate apex.

Diversity. For many years two species have been recorded as occurring in the eastern U.S.A., *E. pyriformis* and *E. sordidus*; however, specimens from central Texas of *E. sordidus* differed in the structure of ventrite 1 with two separate impressions and not a single larger impression thus suggesting a third species was present. This species and two additional undescribed species were noted by Anderson (2002).

Natural history. Almost all records of specimens of *Eurhoptus* are from sifting leaf litter in various forested habitats. Otherwise, nothing is known of life history and immature stages.

Eurboptus pyriformis LeConte, 1876

Figures 2-3

Eurhoptus pyriformis LeConte, 1876: 245; Salsbury 2000: 347; Ciegler 2010: 167. *Eurhoptus pyriformis* (part); Blatchley and Leng 1916: 497; Kissinger 1964: 64; Papp

1979: 164; O'Brien and Wibmer 1982: 136; Downie and Arnett 1996: 1581; Alonso-Zarazaga and Lyal 1999: 131; Anderson 2002: 765.



Figure 3. Records of Eurhoptus pyriformis.

Notes about types. This species was described from a single specimen labelled "Ill[inois]". It has a red square label with "Type 5316" and a handwritten label "Eurhoptus pyriformis Lec.". It is not dissected but appears to be a male based on the more coarsely punctate rostral apex. The type was not examined although high resolution images posted on the MCZC Online Type Database (http://140.247.96.247/mcz/Species_record. php?id=5050) were examined. There is little doubt as to the identity of this species.

Redescription. Body length (exclusive of head and rostrum) 2.1–2.9 mm, cuticle largely bare, variously covered with short, fine recurved seta-like scales, most specimens lacking other scales but some with head and base of rostrum scaly and with a few broad, flat pale imbricate scales variously arranged in irregular oblique band across elytra in apical one-half on intervals 2–7 and at bases of intervals 3–4 and 7. Pronotum with lateral margins straight, margins tapered more or less evenly from base to apex with greatest width at base, not medially carinate but may be medially impunctate in

some specimens. Elytra strongly rounded dorsally and laterally, striae distinct, of large punctures, especially in posthumeral region; all elytral intervals evenly elevated, slightly rounded, each with single row of fine recurved seta-like scales. Metaventrite medially deeply impressed behind mesoventral cup. Abdomen with ventrite 1 with large median deep glabrous shining pit, area around pit with dense, fine golden inwardly directed scales encircling depression. Legs with femora and tibiae at most fringed with a few erect scales especially along outer margin of tibiae, hind tibiae subequal in width throughout most of length. Aedeagus about as long as one-half length of aedeagal apodemes, in lateral view slightly ventrally curved, in dorsal view with margins subparallel but abruptly strongly tapered towards apex at about apical one-quarter to one-fifth, apex produced medially as narrow extension, broadly rounded at tip, extension slightly narrower or more acuminate in some (scaly) specimens. Internal sac with large distinct cruciform apical sclerite complex, anterior bars longer than posterior bars, bars well defined, subparallel.

Distribution (Figure 3). This species is widely distributed in the eastern U.S.A. from Illinois, Pennsylvania and Michigan in the north, to the Gulf Coast of Mississippi and Louisiana in the south, and from Arkansas in the west, east to the Carolinas. Any literature records of this species from Texas are of *E. cariniventris*. Salsbury (2000) records a single specimen of this species from Kansas without further details; Ciegler (2010) records it from South Carolina. Blatchley and Leng (1916), followed by O'Brien and Wibmer (1982) include Colorado in the distribution but this seems in error.

Notes about variation. Some specimens examined have a few broad, flat pale imbricate scales variously arranged in an irregular oblique band across the elytra in the apical one-half on intervals 2–7 and at bases of intervals 3–4 and 7 (Figures 2A–B). These specimens also possess a slightly narrowed apex of the aedeagus but otherwise do not seem to be different from unscaled specimens and the two forms appear to be broadly sympatric. Sequences available to date are predominantly from southern Appalachia, the majority of which represent the unscaled form (Figures 2C–D). However, the scaled form is in fact more widespread, ranging from Arkansas in the west to South Carolina, and north to Michigan, and the molecular data suggest that this form is paraphyletic with respect to those unscaled populations in Appalachia. Similar scaling and the structure of abdominal ventrite 1 in *E. cariniventris* lead us to suggest its relationship as sister to *E. pyriformis*.

Specimens examined (293). **ALABAMA:** Escambia Co.: Brewton, Jct. Hwy 41 & Escambia R. Trib (31.07, -87.06), C.W. O'Brien & P.W. Kovarik, 31 Dec 1997, leaf litter from beech-magnolia forest (1, ASUIC); Monroe Co.: 1.6 km. S Claiborne Dam (31.5917, -87.5392), C.E. Carlton, 31 May 1995, beech/magnolia riparian berlese (1, ASUIC); Sumter Co.: Highway 17 at Noxubee River (32.918, -88.298), J.A. McGown, 27 May 2004, under dead *Quercus nigra*, floodplain (1, MEM). **ARKANSAS:** Logan Co.: Mount Magazine, 0.64 km. S. Green Field Park (35.167, -93.645), C. Carlton, 21 May 1987, (4, CMNC); Logan Co.: Mount Magazine, Green Bench, Gutter Rock Ck. (35.21, -93.66), D. Bowles, 5 May 1988, leaf litter (1, UAAM); Logan Co.: Mount Magazine, Signal Hill Trail (35.17, -93.64), E.G. Riley, 13 May 1995 (6, EGRC);

Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 19 Dec 1991, deciduous litter (1, UAAM); Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 24 Mar 1992, deciduous litter (1, UAAM); Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 4 May 1992, deciduous litter (1, UAAM); Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 16 May 1992, deciduous litter (1, UAAM); Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 16 Nov 1991, deciduous litter (1, UAAM); Montgomery Co.: Collier Spring (34.4839, -93.5929), C.E. Carlton & J.S. Park, 17 Oct 2012, berlese (2, CUAC), DNA extract SSM431; Montgomery Co.: Crystal Recreation Area, E. of campground (34.5, -93.6), C.E. Carlton & H.W. Robison, 21 Jan 1992, deciduous litter (1, UAAM); Montgomery Co.: Little Missouri Falls Recreation Area, slopes SW of river (34.4, -93.9), C.E. Carlton & H.W. Robison, 17 Aug 1991, deciduous litter (1, UAAM); Montgomery Co.: Little Missouri Falls Recreation Area, slopes SW of river (34.4, -93.9), C.E. Carlton & H.W. Robison, 26 Jul 1991, deciduous litter (1, UAAM); Newton Co.: Buffalo National River (36.0369, -93.3411), M.J. Skvarla, 12 Jun 2013, litter next to log (1, UAAM); Newton Co.: Buffalo National River (36.0369, -93.3411), M.J. Skvarla, 25 Sep 2013, litter next to log (1, UAAM); Newton Co.: Buffalo National River (36.0372, -93.3408), M.J. Skvarla, 25 Sep 2013, leaf litter in pile (1, UAAM); Newton Co.: Buffalo National River (36.0372, -93.3411), M.J. Skvarla, 25 Sep 2013, thin litter next to log (1, UAAM); Newton Co.: Buffalo National River (36.03777, -93.34), M.J. Skvarla, 29 May 2013, pitfall in wooded area (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.3403), M.J. Skvarla, 28 Aug 2013, pitfall (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.3411), M.J. Skvarla, 28 Jun 2013, red pan/intercept (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.34), M.J. Skvarla, 29 May 2013, pitfall in wooded area (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.3408), M.J. Skvarla, 17 Jul 2013, litter under low bush (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.34), M.J. Skvarla, 29 May 2013, pitfall in wooded area (1, UAAM); Newton Co.: Natural Bridge at Deer (35.827, -93.21), R.T. Allen, 1 Jun 1987, (1, CMNC); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 18 Dec 1991, maple beech litter (1, UAAM); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 6 Jul 1991, maple beech litter (1, UAAM); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 7 Mar 1992, maple beech litter (1, UAAM); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 24 Mar 1992, maple beech litter (1, UAAM); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 15 Nov 1991, maple beech litter (1, UAAM); Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 28 Sep 1991, maple beech litter (1, UAAM); Polk Co.: Rich Mt., Acorn

Overlook (34.6, -94.2), C.E. Carlton & H.W. Robison, 5 Jun 1992, deciduous litter (1, UAAM); Polk Co.: Rich Mt., Eagleton Overlook (34.6, -94.3), C.E. Carlton & H.W. Robison, 9 Jan 1992, deciduous litter (1, UAAM); Polk Co.: Rich Mt., intersec 272-88 (34.68, -94.36), C.E. Carlton & H.W. Robison, 25 Jul 1991, deciduous litter (1, UAAM); Polk Co.: Rocky, Talimena Drive (34,619, -94,276), D. Beyers; M. Jenks, 14 Apr 1984, hardwood berlese (5, CMNC); Scott Co.: Dry Creek Wilderness Area (35, -93.7), C.E. Carlton & H.W. Robison, 15 May 1992, deciduous litter (1, UAAM); Scott Co.: Hogan Mt. Turkey Area (35, -93.8), C.E. Carlton & H.W. Robison, 25 Aug 1991, deciduous litter (1, UAAM); Searcy Co.: 6 mi N Co line on Hwy 27 (35.8, -92.78), C.E. Carlton & H.W. Robison, 30 Aug 1977, deciduous litter (1, UAAM); Yell Co.: 6.44 km. S. Blue Mt. Lake (35, -93.7), C.E. Carlton & H.W. Robison, 18 Jun 1992, deciduous litter (1, UAAM). GEORGIA: Dade Co.: Cloudland Canyon State Park, (34.83, -85.48), W. Suter, 21 Apr 1983, rhododendron litter (1, ASUIC); Dade Co.: Cloudland Canyon State Park, (34.83, -85.48), S. & J. Peck, 16 May 1972, litter (3, CNCI); Rabun Co.: Rabun Bald (34.97, -83.3), Q. Wheeler, 2 Aug 1981, leaf litter (1, ASUIC); Rabun Co.: Rabun Bald (34.97, -83.3), Q. Wheeler, 11 Aug 1981, leaf litter (1, ASUIC); Rabun Co.: Summit (34.97, -83.3), Q. Wheeler, 5 Jun 1981, leaf litter (1, ASUIC); Union Co.: 9.66 km. E. Blairsville, Brasstown Bald (34.87, -83.81), W. Suter, 15 Jun 1973, Rhododendron litter (1, CWOB); Walker Co.: Lula Lake (34.9312, -85.3733), S. Chatzimanolis, 18 May 2015, sifted litter (1, UTCI); Walker Co.: Lula Lake (34.9315, -85.3729), S. Chatzimanolis, 1 Dec 2012, sifted litter (1, UTCI); Walker Co.: Lula Lake (34.9338, -85.3716), S. Chatzimanolis, 26 May 2015, sifted litter (1, UTCI), DNA extract MSC2520. ILLINOIS: McHenry Co.: Algonquin (42.2, -88.3), W. Nason, (1, INHS). INDIANA: Huntington Co.: 3.22 km. E. Mount Etna (40.74, -85.51), R. Wilkey, 5 May 1977 (2, CWOB); Marion Co.: Southport (39.7, -86.1), R.F. Wilkey, 28 Apr 1978, (1, ASUIC); Marion Co.: 8.05 km. S. Indianapolis (39.67, -86.15), 10 Jul 1977, maple/Celtis litter (2, CWOB); Owen Co.: 8.05 km. N.W. Clav City (39.34, -87.03), R. Wilkey, 17 Aug 1973, berlese duff (2, CWOB); Tippecanoe Co.: 22 May 1971, N. Downie (1, CWOB); Montgomery Co.: Shades State Park, Pine Hills (39.93, -87.07), J. Wagner, 23 Aug 1960, beech tree hole (1, CWOB); Wells Co.: Bluffton 4H Park (40.897, -83.893), R. Wilkey, 25 Apr 1973, berlese Fagus duff (1, CMNC; 5, CWOB); Wells Co.: 8.05 km. S. Bluffton (40.68, -85.16), R. Wilkey, 24 Sep 1974 (3, CWOB). KENTUCKY: Edmonson Co.: Mammoth Cave National Park, Cave Entrance Trail (37.185, -86.099), R.S. Anderson, 24 Jun 1988, berlese hardwood litter (1, CMNC); Edmonson Co.: Mammoth Cave National Park, Cabin Woods (37.20, -86.10), W. Suter, 29 Mar 1974, litter (1, CWOB); Laurel Co.: Bald Rock Picnic Area (37.03, -84.22), C.E. Carlton, 4 Apr 1991, hardwood berlese (1, ASUIC); Whitley Co.: 1.6 km. E. Cumberland Falls. Road 195 (36.838, -84.344), S. O'Keefe, 22 Aug 1990, (1, CMNC). LOUISIANA: West Feliciana Par.: Tunica Hills Wildlife Management Area, Magnolia Glen Trail (30.94, -91.51), D. Pashley, 15 Jul 1995 (2, LSAM). West Feliciana Par.: nr. St. Francisville, Tunica Hills Wildlife Management Area (30.94, -91.51), S. Dash, 23 Sep 1999, lower ravine berlese (1, CWOB). West Feliciana Par.: nr. St. Francisville, Tunica Hills Wildlife Management Area (30.94, -91.51), J. & T. Fassbender, 23 Sep 1999, lower ravine berlese (1, CWOB); West Feliciana Par.: Feliciana Preserve (30.78, -91.25), J. Fassbender, 14 Jul 1998, mixed pine/hardwood litter (2, LSAM);. West Feliciana Par.: D.P. Cabin (30.795, -91.256), J.L. Johnson, 21 Dec 1995, berlese (2, CWOB); MICHIGAN: Berrien Co.: Warren Woods State Park (41.83, -86.62), D.S. Chandler, 19 Aug 1990, beech log litter (1, ASUIC). MISSISSIPPI: Hinds Co.: Lefleur's Bluff State Park (32.24, -90.15), J.A. MacGown, 20 Jul 2011, berlese bottomland hardwood forest (1, MEM); Harrison Co.: 3 mi NW Ridgeway (30.5, -89.1), D.S. Chandler, 27 Oct 1978, litter (1, ASUIC). NORTH CAROLINA: Alleghany Co.: Roaring Gap, 2000', Stone Mountain State Park (36.382, -81.022), S.B. Peck, 16 Aug 1981, log - leaf litter (1, CMNC); Avery Co.: Linville Falls, 3500', Blue Ridge Parkway km. 317 (35.959, -81.942), S.B. Peck, 16 Aug 1981, Rhodendron litter at log (2, CMNC); Burke Co.: Linville Gorge Wilderness (35.922, -81.9175), S.S. Myers & L. Vasquez-Velez, 18 Mar 2016, sifted litter (1, CUAC), DNA extract SSM567b; Burke Co.: Linville Gorge Wilderness (35.9241, -81.9131), S.S. Myers & L.Vasquez-Velez, 18 Mar 2016, sifted litter (1, CUAC), DNA extract SSM556b; Burke Co.: Linville Gorge Wilderness (35.9294, -81.9109), S.S. Myers & L. Vasquez-Velez, 18 Mar 2016, sifted litter (1, CUAC), DNA extract SSM365; Burke Co.: Linville Gorge Wilderness, Bynum Bluff Trail (35.9331, -81.9282), M.S. Caterino & P.R. Caterino, 19 Aug 2017, sifted litter (4, CUAC), DNA extract SSM555; Burke Co.: Linville Gorge Wilderness, Pine Gap Trail (35.9403, -81.9297), M.S. Caterino & P.R. Caterino, 19 Aug 2017, sifted litter (5, CUAC), DNA extract SSM551; Cherokee Co.: Nantahala National Forest, Hickory Branch Trail (35.2118, -83.6987), S.S. Myers, 26 Jul 2015, sifted hardwood litter (1, CUAC), DNA extract SSM335; Cherokee Co.: Nantahala National Forest, Hickory Branch Trail (35.2165, -83.7047), S.S. Myers, 26 Jul 2015, sifted hardwood litter (2, CUAC), DNA extracts SSM240-SSM241; Cherokee Co.: Nantahala National Forest, Hickory Branch Trail (35.2176, -83.7055), S.S. Myers, 26 Jul 2015, sifted hardwood litter (6, CUAC), DNA extracts SSM043-SSM046, SSM327-SSM328; Cherokee Co.: Nantahala National Forest, London Bald Trail (35.2179, -83.7062), S.S. Myers, 26 Jul 2015, sifted hardwood litter (4, CUAC), DNA extracts SSM047-SSM050; Cherokee Co.: Nantahala National Forest, London Bald Trail (35.2231, -83.7011), S.S. Myers, 26 Jul 2015, sifted hardwood litter (6, CUAC), DNA extracts SSM331-SSM332, SSM389-SSM392; Graham Co.: Joyce Kilmer Memorial Forest (35.3426, -83.966), M.S. Caterino & S.S. Myers, 24 Jun 2015, sifted litter (2, CUAC), DNA extracts SSM028, SSM305; Graham Co.: Joyce Kilmer Memorial Forest (35.3433, -83.9621), S.S. Myers, 20 Jul 2015, sifted litter (2, CUAC), DNA extracts SSM017, SSM030; Graham Co.: Joyce Kilmer Memorial Forest (35.3433, -83.966), M.S. Caterino & S.S. Myers, 24 Jun 2015, sifted litter (2, CUAC), DNA extracts SSM026, SSM304; Graham Co.: Joyce Kilmer Memorial Forest (35.3435, -83.977), S.S. Myers, 20 Jul 2015, sifted litter (1, CUAC), DNA extract SSM020; Graham Co.: Joyce Kilmer Memorial Forest (35.3441, -83.966), M.S. Caterino & S.S. Myers, 24 Jun 2015, sifted litter (2, CUAC), DNA extracts SSM027, SSM303; Graham Co.: Joyce Kilmer Memorial Forest (35.3448, -83.9649), M.S. Caterino & S.S. Myers, 24 Jun 2015, sifted litter (2, CUAC), DNA extracts SSM029, SSM306; Graham Co.: Joyce Kilmer Memorial Forest (35.345, -83.967), M.S. Caterino & S.S. Myers, 24 Jun 2015, sifted litter (2, CUAC), DNA extracts SSM017, SSM025; Graham Co.: Joyce Kilmer Memorial Forest (35.3467, -83.9688), S.S. Myers, 20 Jul 2015, sifted litter (1, CUAC), DNA extract SSM019; Graham Co.: (35.32, -83.9918), S. Chatzimanolis, 12 Sep 2014, sifted litter (1, UTCI); Haywood Co.: Great Smoky Mountains National Park (35.816, -83.121), J.A. MacGown; J.G. Hill, 11 Jun 2009, rock pine/hardwood forest (1, MEM); Haywood Co.: Great Smoky Mountains National Park, Balsam Mountain Trail, 1500 m (35.637, -83.183), A. Tishechkin, 20 Oct 2001, hardwood berlese (1, CMNC); Jackson Co.: Balsam Mountain Preserve (35.3772, -83.0921), S.S. Myers, 17 Jun 2015, sifted litter (3, CUAC), DNA extracts SSM542-SSM544; Jackson Co.: Balsam Mountain Preserve (35.398, -83.1088), S.S. Myers, 17 Jun 2015, sifted rich cove litter (2, CUAC), DNA extracts SSM224, SSM227; Jackson Co.: Nantahala National Forest, Bad Creek Trail (35.002, -83.1071), S.S. Myers, 29 Jun 2015, sifted litter (5, CUAC), DNA extracts SSM450-SSM454; Macon Co.: Highlands (35.05, -83.19), Q. Wheeler, 4 Jun 1981, leaf litter (3, ASUIC); Macon Co.: Highlands, California Gap (35.1, -83.29), Q. Wheeler, 12 Aug 1981, leaf litter (1, ASUIC); Macon Co.: Highlands, Cows Bald (35.05, -83.19), Q. Wheeler, 9 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Highlands, Franklin (35.2, -83.4), Q. Wheeler, 8 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Highlands, Franklin (35.2, -83.4), Q. Wheeler, 10 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Nantahala National Forest, Ellicott Rock Trail (35.0075, -83.1348), S.S. Myers, 18 Jul 2015, sifted litter (2, CUAC), DNA extracts SSM253-SSM254; Macon Co.: Nantahala National Forest, Ellicott Rock Trail (35.0096, -83.1245), S.S. Myers, 18 Jul 2015, sifted litter (6, CUAC), DNA extract SSM255-SSM260; Macon Co.: Nantahala National Forest, Hickory Gap (35.0697, -83.2825), S.S. Myers, 16 Jul 2015, sifted litter (2, CUAC), DNA extracts SSM456-SSM457; Macon Co.: Nantahala National Forest, Hickory Gap (35.0746, -83.2855), S.S. Myers, 16 Jul 2015, sifted litter (3, CUAC), DNA extracts SSM342-SSM343, SSM455; Macon Co.: Nantahala National Forest, Highlands (35.05, -83.19), Q. Wheeler, 4 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Nantahala National Forest, Highlands (35.05, -83.19), Q. Wheeler, 6 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Nantahala National Forest, Highlands (35.05, -83.19), Q. Wheeler, 7 Jun 1981, leaf litter (1, ASUIC); Macon Co.: Nantahala National Forest, Highlands (35.05, -83.19), Q. Wheeler, 8 Jun 1981, leaf litter (1, ASU-IC); Macon Co.: Nantahala National Forest, Jones Gap (35.0752, -83.2883), S.S. Myers, 16 Jul 2015, sifted litter (2, CUAC), DNA extracts SSM340-SSM341; Macon Co.: Nantahala National Forest, Jones Gap (35.0785, -83.2923), S.S. Myers, 22 Jul 2015, sifted litter (2, CUAC), DNA extracts SSM176-SSM177; Macon Co.: Nantahala National Forest, Jones Gap (35.0801, -83.2947), S.S. Myers, 22 Jul 2015, sifted litter (3, CUAC), DNA extracts SSM169-SSM172; Macon Co.: Nantahala National Forest, Jones Gap (35.0841, -83.2976), S.S. Myers, 28 Jul 2015, sifted litter (8, CUAC), DNA extracts SSM159-SSM162, SSM393-SSM396; Macon Co.: Standing Indian Campground (35.0761, -85.5284), S. Chatzimanolis, 18 Oct 2014, sifted litter (1, UTCI); McDowell Co.: Blue Ridge Parkway, mile 320 (35.94, -81.96), Q. Wheeler, 4 Aug 1981, leaf litter (1, ASUIC); McDowell Co.: Mackey Mountain Trail (35.7224, -82.1725), S.S. Myers & S. Langton, 25 Jul 2015, sifted litter (4, CUAC), DNA extract SSM274; McDowell Co.: Mackey Mountain Trail (35.7246, -82.1838), S.S. Myers & S. Langton, 25 Jul 2015, sifted litter (1, CUAC), DNA extract SSM273; McDowell Co.: Pisgah National Forest, Courthouse Falls Trail (35.2716, -82.8964), S.S. Myers, 23 Jul 2015, sifted litter (1, CUAC), DNA Extract SSM271; McDowell Co.: Pisgah National Forest, Courthouse Falls Trail (35.2727, -82.8932), S.S. Myers, 23 Jul 2015, sifted litter (1, CUAC), DNA Extracts SSM267-SSM270; McDowell Co.: Pisgah National Forest, Courthouse Falls Trail (35.2747, -82.8902), S.S. Myers, 23 Jul 2015, sifted litter (1, CUAC), DNA Extracts SSM272, SSM266; McDowell Co.: Snooks Nose (35.6905, -82.2055), S.S. Myers, 17 Mar 2016, sifted litter (3, CUAC), DNA extracts SSM320; McDowell Co.: Snooks Nose (35.6928, -82.207), S.S. Myers, 17 Mar 2016, sifted litter (4, CUAC), DNA extracts SSM357; McDowell Co.: Snooks Nose (35.693, -82.2061), S.S. Myers & L. Vasquez-Velez, 17 Mar 2016, sifted litter (1, CUAC), DNA extract SSM361; Mitchell Co.: Blue Ridge Parkway, mile 329 (35.86, -82.04), Q. Wheeler, 4 Aug 1981, leaf litter (1, ASUIC); Sevier Co.: Great Smoky Mountains National Park, Chimneys Picnic Area Nature Trail, 891 m (35.635, -83.496), A. Tishechkin; V. Moseley, 28 Jun 2001, leaf litter berlese (1, CMNC); Swain Co.: Great Smoky Mountains National Park, Flat Creek Trail, 1500 m (35,55, -83.172), A. Tishechkin, 31 Jul 2001, leaf litter berlese (1, CMNC); Swain Co.: off Coopers Creek Rd. (35.4825, -83.3797), M. Caterino, 15 Mar 2015, sifted litter (1, CUAC), DNA extract SSM470; Swain Co.: off Coopers Creek Rd. (35.4825, -83.378), M. Caterino, 15 Mar 2015, sifted riparian litter (2, CUAC), DNA extracts SSM468-SSM469; Transylvania Co.: Pisgah National Forest, off Blue Ridge Parkway (35.2871, -82.908), S.S. Myers, 29 May 2015, sifted litter (2, CUAC), DNA Extracts SSM458-SSM459; Transylvania Co.: Pisgah National Forest, off Blue Ridge Parkway (35.2915, -82.9136), S.S. Myers, 29 May 2015, sifted litter (2, CUAC), DNA Extracts SSM459-SSM460; Yancey Co.: Mount Mitchell Viewpoint, 1451 m (35.723, -82.219), I. Agnarson, 31 May 2013, (4, CMNC); OHIO: Franklin Co.: Sharon Woods Metro Park (40.12, -82.95), A.J. Penniman, 1973, pitfall (1, ASUIC); Franklin Co.: Columbus (39.97, -83.05), L. Watrous, 13 Sep 1975, berlese (2, CWOB); Licking Co.: Blackhand Gorge (40.056, -82.252), P.W. Kovarik, 3-4 May 1989, berlese leaf litter (1, CMNC); Columbus, Antrim Park (40.078, -83.038), 27 Apr 1989, (1, CMNC). PENNSYLVANIA: Allegheny Co.: nr. Sutersville (40.24, -79.80), W. Suter, 16 Jul 1977, litter (2, CWOB). SOUTH CAROLINA: Darlington Co.: Great Pee-Dee Heritage Preserve (34.3892, -79.7098), M.S. Caterino, 10 Jan 2017, sifted litter (1, CUAC), DNA extract MSC2484; Greenville Co.: Chestnut Ridge Heritage Preserve (35.1406, -82.279), S.S. Myers, 5 Jun 2015, hardwood litter (3, CUAC), DNA extract SSM096; Greenville Co.: Chestnut Ridge Heritage Preserve (35.1501, -82.282), S.S. Myers, 5 Jun 2015, hardwood litter (2, CUAC), DNA extract SSM092; Greenville Co.: Chestnut Ridge Heritage Preserve (35.1523, -82.2814), S.S. Myers, 5 Jun 2015, hardwood litter (1, CUAC), DNA extract SSM089; Oconee Co.: Coon Branch Natural Area (35.0269, -83.0057), M. & K. Caterino, 28 Feb 2016, sifted hardwood litter (1, CUAC), DNA Extracts SSM465-SSM466; Oconee Co.: Coon Branch Natural Area (35.0272, -83.0069), M. & K. Caterino, 28 Feb 2016, sifted hardwood litter (1, CUAC), DNA Extract SSM467; Oconee Co.: Sumter National Forest, East Fork Trail (34.9838, -83.0979), M.S. Caterino & S.S. Myers, 4 May 2015, sifted litter (1, CUAC), DNA extracts SSM462, SSM463, SSM464; Oconee Co.: Sumter National Forest, East Fork Trail (34.9843, -83.0981), M.S. Caterino & S.S. Myers, 4 May 2015, sifted litter (1, CUAC); Oconee Co.: Sumter National Forest, East Fork Trail (34.9962, -83.1022), S.S. Myers, 29 Jun 2015, sifted litter (1, CUAC), DNA extract SSM317; Oconee Co.: Sumter National Forest, Indian Camp Creek (34.9886, -83.0729), M.S. Caterino & S.S. Myers, 4 May 2015, sifted litter (1, CUAC), DNA extract SSM315; Oconee Co.: Sumter National Forest, Indian Camp Creek (34.9899, -83.0724), M.S. Caterino & S.S. Myers, 4 May 2015, sifted litter (1, CUAC), DNA extract SSM316; Oconee Co.: Sumter National Forest, Indian Camp Creek (34.9903, -83.0723), M.S. Caterino & S.S. Myers, 4 May 2015, sifted litter (2, CUAC), DNA extracts SSM261, SSM262; Oconee Co.: Sumter National Forest, Riley Moore Falls (34.7403, -83.1804), M. Caterino, 3 Mar 2018, sifted litter (1, CUAC), DNA extract MSC2522; Pickens Co.: Eastatoe Heritage Preserve (35.1577, -82.491), S. Myers, 28 Feb 2016, sifted hardwood litter (3, CUAC), DNA Extracts SSM398-SSM400; Pickens Co.: Sassafras Mountain (35.0634, -82.776), S.S. Myers, 10 Jun 2015, sifted hardwood litter (5, CUAC), DNA Extracts SSM080-SSM084; Pickens Co.: Sassafras Mountain (35.0645, -82.7774), S.S. Myers, 10 Jun 2015, sifted hardwood litter (5, CUAC), DNA Extracts SSM075-SSM079. TENNESSEE: Blount Co.: Great Smoky Mountains National Park, Sinks Trail (35.67, -83.66), R.T. Allen & R. Chenowith, 13 Oct 1976, leaf litter (1, UAAM); Cocke Co.: Great Smoky Mountains National Park, lower Crosby House (35.7781, -83.2139), P.E. Skelley, 20 Jul 2003, litter at rock wall by stream (1, ASUIC); Marion Co.: Tennessee River Gorge, Pot Point Tr. (35.0864, -85.3922), S. Chatzimanolis, 24 May 2015, sifted litter (2, UTCI); Sevier Co.: Cove Forests S&E Gatlinburg (35.7, -83.5), Hlavac & Lawrence, 10–23 May 1972, litter (1, ASUIC); Sevier Co.: Cove Forests, S.E. Gatlinburg (35.706, -83.5), T. Hlavac; J. Lawrence, 10-23 May 1972, litter (1, CMNC); Sevier Co.: Great Smoky Mountains National Park, Greenbrier Cove (35.71, -83.38), W.B. Suter, 14 Apr 1973, litter at log under rhododendron (1, ASUIC); Sevier Co.: Great Smoky Mountains National Park, Maddron Bald Trail (35.75, -83.27), R.T. Allen & R. Chenowith, 15 Oct 1976, leaf litter (1, UAAM); Sevier Co.: Cove Forests, S & E Gatlinburg (35.64, -83.48), T. Hlavac & J. Lawrence, 10-23 May 1972, litter (6, CWOB); Unicoi Co.: Unaka Mountain (36.148, -82.302), 5 Jul 1953, (1, CMNC); Wilson Co.: Cedars of Lebanon State Park (36.08, -86.315), J.G. Hill, 26 Jul 2010, cedar hardwood litter (2, MEM); Wilson Co.: Cedars of Lebanon State Park (36.08, -86.315), J.M. Campbell, 10 Jun 1997, cedar hardwood litter (1, MEM). WEST VIRGINIA: Mercer Co.: Camp Creek State Forest, Mashfork Falls (37.5, -81.14), S. Bird, 24 Feb 1970 (3, CNCI); Putnam Co.: Winfield (38.5, -81.9), L. Torres-Miller, 1 Oct 1996, (2, ASUIC). WISCONSIN: Kenosha Co.: Woodworth, Benedicts Prairie (42.55, -88.00), W. Suter, 16 Jun 1976 (1, CWOB); Kenosha Co.: 4.83 km. W. Somers, County Line Forest (42.64, -87.94), W. Suter, 18 Sep 1965, Rhododendron litter (1, CWOB); Racine Co.: 6.44 km. E. Wind Lake (42.83, -88.12), W. Suter, 23 Apr 1966, grassy swamp floor (1, CWOB).

Eurhoptus sordidus LeConte, 1876

Figures 4-5

Acalles sordidus LeConte, 1876: 243; Blatchley and Leng 1916: 501. Eurhoptus sordidus (part); Blatchley and Leng 1916: 501; Kissinger 1964: 64; O'Brien and Wibmer 1982: 136.

Notes about types. This species was described from a single specimen labelled "Tex". It has a rectangular label "776" and a red square label with "Type 5268" and a handwritten label "A. sordidus Lec.". It is not dissected but appears to be a male based on the more coarsely punctate rostral apex. The type was not examined although high resolution images posted on the MCZC Online Type Database (http://140.247.96.247/mcz/ Species_record.php?id=5002) were examined. The name E. sordidus has been consistently applied to specimens of Eurhoptus that were not E. pyriformis from Texas east into eastern North America; however, specimens from Texas are distinct from those further east and at least two species under this name have been suggested (Anderson 2002). LeConte's type came from Gustaf Wilhelm Belfrage who collected insects mainly in Bosque County, Texas, where he lived from 1870–1879 (Geiser 1933). We here apply the name E. sordidus to specimens from throughout Texas north into bordering Oklahoma and Arkansas, and east through Louisiana to Mississippi. The herein described new species and the resurrected species closely related to *E. sordidus* occur further to the east and not into Texas although the three are narrowly sympatric in Louisiana and Arkansas. Kissinger (1964) was the first to recognize this species as Eurhoptus.

Redescription. Body length (exclusive of head and rostrum) 2.1–2.7 mm, cuticle largely bare, variously covered with short, fine recurved seta-like scales only, although often encrusted and coated with a fine film. Pronotum with lateral margins rounded, margins strongly constricted at about apical one-third such that apical one-third is distinctly tubulate, greatest width at about basal one-third, medially carinate or not. Elytra strongly rounded dorsally and laterally, striae distinct, punctures moderate in size and depth; all elytral intervals evenly elevated, slightly rounded, each with single row of fine recurved seta-like scales. Metaventrite medially impressed behind mesoventral cup. Abdomen with ventrite 1 with pair of obliquely arranged transversely elongate pits which are shallowly continuous medially (but because of encrustation appearing as separate in most specimens), area around pits with dense inwardly directed scales. Legs with femora and tibiae at most fringed with a few erect scales especially along outer margin of tibiae, hind tibiae subequal in width throughout most of length. Aedeagus about as long as one-half length of aedeagal apodemes, in lateral view slightly ventrally curved, in dorsal view with margins subparallel but gradually tapered towards apex at about apical one-third where more strongly tapered, apex not produced medially as narrow extension, broadly rounded at tip. Internal sac with large distinct cruciform apical sclerite complex, with well-defined transverse bar, anterior and posterior bars not well defined.

Distribution (Figure 5). This species is distributed from Texas and Oklahoma east into Arkansas and Louisiana with a single outlying specimen from southern Missis-



Figure 4. *Eurhoptus sordidus*. A Dorsal view B Lateral view C Ventral view showing impressions on ventrites D Dorsal view of aedeagus E Lateral view of aedeagus.

sippi. Any literature records of this species from the eastern U.S.A. are of *E. curtus* or *E. aenigmaticus*. We have been able to sequence individuals from Arkansas and Texas, and they are very similar and closely related.

Specimens examined (208). ARKANSAS: Montgomery Co.: 2.42 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, 19 Jun 1992, (1, UAAM); Montgomery Co.: Crystal Recreation Area, S. of campground (34.5, -93.6), C.E. Carlton & H.W. Robison, 27 Sep 1991, deciduous litter (1, UAAM); Montgomery Co.: Little Missouri Falls Recreation Area, SW of river (34.4, -93.9), C.E. Carlton & H.W. Robison, 25 Apr 1992, maple beech litter (1, UAAM); Montgomery Co.: (34.29035, -93.35577), C.E. Carlton, (1, CUAC), DNA extract SSM512; Polk Co.: Caney Creek Wilderness Area, 5.63 km. N. Bard Springs (34.4, -94.1), C.E. Carlton & H.W. Robison, 25 Jun 1991, maple beech litter (1, UAAM); Polk Co.: Ouachita National Forest (34.3808, -94.0273), C.E. Carlton & J.S. Park, 16 Oct 2012, leaf litter (2, CUAC; 2, LSAM), DNA extracts SSM491, SSM476, SSM477, SSM492. LOUISI-ANA: Calcasieu Par.: Sam Houston Jones State Park (30.3, -93.267), A. Cline; A. Tishechkin, 11 Feb 2002, leaf litter (2, CMNC); Natchitoches Par.: Kisatchie National Forest, Kisatchie Bayou (31.44, -93.09), A.R. Cline & S. Dash, 20 Sep 2003, sifting (1, CWOB); Natchitoches Par.: Kisatchie National Forest, Kisatchie Bayou (31.44, -93.09), A.R. Cline, 20 Jul 2003, litter/tree holes (3, CWOB); Natchitoches Par.: Kisatchie Na-



Figure 5. Records of Eurhoptus sordidus, E. occidentalis, and E. rileyi.

tional Forest. Red Bluff Campground (31.5, -93.14), E.G. Riley; L. Prochaska, 1 Apr 1989, beech-Magnolia-pine litter (1, CMNC). MISSISSIPPI: Jackson Co.: Ocean Springs (30.41, -88.828), R.L. Brown, 10 May 1981 (1, MEM). OKLAHOMA: Latimer Co.: 11.26 km. S. Wilberton (34.81, -95.31), P.W. Kovarik, 15 Oct 1989, sawdust (1, CMNC); Latimer Co.: (34.9, -95.1), K. Stephan, Mar 1983, (1, ASUIC); Latimer Co.: (34.9, -95.1), K. Stephan, Dec 1981, (1, TAMU); Latimer Co.: (34.9, -95.1), K. Stephan, Feb 1983, (1, TAMU); Latimer Co.: (34.9, -95.1), K. Stephan, Mar 1983, (5, TAMU); Latimer Co.: (34.9, -95.1), K. Stephan, Apr 1983, (5, TAMU); Latimer Co.: (34.9, -95.1), K. Stephan, Nov 1982, (1, ASUIC); Latimer Co.: (34.9, -95.1), K. Stephan, 8 Aug 1990, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Dec 1987, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Dec 1991, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Jul 1992, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Jun 1991, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, May 1990, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, May 1991, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, May 1992, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Nov 1990, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Nov 1991, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Sep 1991, (1, FSCA); Latimer Co.: (34.9, -95.1), K. Stephan, Dec 1985, (2, ASUIC); Latimer Co.: (34.9, -95.1), K. Stephan, Dec 1986, (2, ASUIC); Latimer Co.: (34.9, -95.1), K. Stephan, Mar 1986, (2, ASUIC); Latimer Co.: (34.9, -95.1), K. Stephan, 4 Apr 1990, (2, FSCA); Latimer Co.: Buffalo Mountains (34.9, -95.1), K. Stephan, Jun 1991, (2, TAMU); Latimer Co.: Red Oak (34.95, -95.08), K. Stephan, 14 May 1978 (3, CWOB). LeFlore Co.: Rich Mt. (34.7, -94.5), K. Stephan, 24 Feb 1992, (1, FSCA). LeFlore Co.: Ouachita National Forest (34.78, -94.99), K. Stephan, Jul 1994, (2, TAMU). McCurtain Co.: Beaver Bend State Park (34.13, -94.70), W. Suter, 31 Jul 1968, litter (1, CWOB); McCurtain Co.: Beaver Bend State Park (34.13, -94.70), W. Suter, 27 Jul 1968, litter (1, CWOB); McCurtain Co.: Beaver Bend State Park (34.13, -94.70), W. Suter, 27 Jul 1968, litter (1, LSAM). TEX-AS: Bandera Co.: Hill Country Natural Reserve (29.6, -99.2), C.W. O'Brien & E. Gage, 11 Mar 2001, mixed oak litter (1, ASUIC); Bandera Co.: Lost Maples State Natural Area (29.81958, -99.57066), R.S. Anderson, 28-30 Apr 1988, berlese leaf litter (1, CMNC); Bandera Co.: Lost Maples State Natural Area (29.81958, -99.57066), R.S. Anderson, 28 Apr-2 May 1987, berlese leaf litter (4, CMNC); Bandera Co.: Lost Maples State Natural Area, Maple Trail (29.82, -99.57), C.W. O'Brien & Gages, 10 Mar 2001, litter (1, ASUIC); Bandera Co.: Lost Maples State Natural Area, (29.82, -99.57), C.W. O'Brien, 9 Mar 2001, litter (2, CWOB); Bastrop Co.: Buescher State Park (30.041, -97.162), R.S. Anderson, 3 May 1988, leaf litter berlese (2, CMNC); Bell Co.: Camp Kachina, 6.44 km. W. Temple (31.16, -97.49), E.G. Riley, 5 Mar 1995, leaf litter berlese (1, EGRC); Bexar Co.: San Antonio, Ebony Hill Research Station (29.488, -98.700), E.G. Riley, 9 Feb 1996, berlese forest litter (2, TAMU); Blanco Co.: Pedernales Falls State Park, Nature Trail (30.306, -98.256), R.S. Anderson, 3 May 1988, oak-elm-juniper litter (2, CMNC); Blanco Co.: Pedernales Falls State Park, Twin Falls (30.334, -98.252), R.S. Anderson, 3 May 1988, Caryal Celtis leaf litter berlese (2, CMNC); Brazos Co.: Ball's Ferry, 9.66 km. S.W. College Station (30.49, -96.34), E.G. Riley, 26 Nov 2004, cottonwood leaf litter berlese (1, EGRC); Burnett Co.: Inks Lake State Park, Pecan Flat Campground (30.733, -98.364), R.S. Anderson, 21 May 1989, pecan-juniper leaf litter berlese (5, CMNC); Colorado Co.: 1 km. S. Altair on #71 (29.54, -96.45), R.S. Anderson, 1 Feb 1989, live oak/Ilex woodland litter berlese (1, CMNC); Colorado Co.: Columbus (29.70665, -96.53534), R.S. Anderson, 4 Nov 1988, riparian ravine hardwood litter (1, CUAC), DNA extract MSC2474; Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 4 Nov 1988, riparian ravine litter (12, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 21 Feb 1989, riparian ravine litter (15, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 22 Mar 1988, riparian ravine litter (2, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 6 Apr 1988, riparian ravine litter (3, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 1 Feb 1988, riparian ravine litter (5, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 17 May 1987, riparian ravine litter (9, CMNC); Gonzales Co.: Palmetto State Park, near East entry (29.59339, -97.58558), R. Anderson, 17-18 Apr 1989, leaf litter berlese (16, CMNC); Grimes Co.: limestone outcrop, 6.44 km. E. Navasota (30.453, -96.026), E.G. Riley, 17 Feb 1996, berlese soil surface litter (5, TAMU); Houston Co.: Big Slough Wilderness Area, FR517 and Four C's Hiking Trail (31.496, -95.118), R.S. Anderson, 9 May 1988, bottomland hardwood litter (2, CMNC); Houston Co.: Big Slough Wildlife Area, 0.8 km. N. junction FR517 and FR511-3 (31.496, -95.118), R.S. Anderson, 9 May 1988, pine-hardwood litter berlese (1, CMNC); Sabine Co.: 14.5 km. E. Hemphill, Beech Bottom (31.386, -93.706), R. Anderson; E. Riley; E. Morris, 24 Apr 1989, leaf litter berlese (5, CMNC); Sabine Co.:

14.5 km. E. Hemphill, Beech Bottom (31.386, -93.706), E.G. Riley, 16 Mar 1997, litter Berlese beech-Magnolia forest (2, EGRC); Sabine Co.: Hemphill Sabine National Forest, 0.8 km. N. of P. Gomer Rd (31.36489, -93.70636), beech bottom litter (2, CUAC; 2, LSAM), DNA extracts SSM480, SSM481, SSM482, SSM497; San Patricio Co.: Welder Wildlife Refuge (28.118, -97.407), H. & A. Howden; C. Scholtz, 17-25 May 1985, (2, CMNC); San Patricio Co.: Welder Wildlife Refuge (28.118, -97.407), R.S. Anderson, 18–19 Apr 1989, (4, CMNC); San Patricio Co.: Welder Wildlife Refuge, Hackberry Motte (28.118, -97.407), R.S. Anderson, 12–13 Oct 1988, (3, CMNC); San Patricio Co.: Welder Wildlife Refuge, Hackberry Motte (28.118, -97.407), R.S. Anderson, 13-15 Jun 1988, Celtis leaf-branch litter (9, CMNC); San Patricio Co.: Welder Wildlife Refuge, 11.26 km. N. Sinton (28.118, -97.406), R.S. Anderson, 18-19 Apr 1989, (1, CUAC), DNA extract MSC2473; San Patricio Co.: Welder Wildlife Refuge, near Hackberry Motte (28.118, -97.407), R.S. Anderson, 1-2 Nov 1988, berlese (1, CMNC); San Patricio Co.: Welder Wildlife Refuge, Big Lake (28.120, -97.372), E.G. Riley, 8 Dec 2007 (2, EGRC); San Patricio Co.: Welder Wildlife Refuge (28.118, -97.407), J.M. Mora, 20 Jul 1989, pitfall trap, live oak woodland (3, TAMU); Travis Co.: Austin, Brackenridge Field Lab (30.284, -97.778), E.G. Riley, 10 Feb 1996, berlese rotten pecan log (1, EGRC); Travis Co.: vic. Long Hollow Creek (30.458, -97.875), 7 May 1994, E.G. Riley, berlese forest litter (2, TAMU); Travis Co.: Shelberg Tract, near Cypress Creek arm of Lake Travis (30.44, -97.87), E.G. Riley, 7 May 1994, berlese forest litter and dung pellets (2, TAMU); Tyler Co.: 4.5 km. W. 3 km. N. Spurger, Big Thicket Natural Preserve, Beech Woods Trail (30.719, -94.227), R.S. Anderson, 8 Mar 1989, beech-Magnolia leaf litter berlese (1, CMNC); Uvalde Co.: Garner State Park (29.6, -99.7), C.W. O'Brien, 10 Mar 2001, oak litter (1, ASUIC); Uvalde Co.: Concan, Neal's Lodge Area (29.494, -99.714), E.G. Riley, 9 Apr 1995, berlese forest litter (6, EGRC); Walker Co.: Sam Houston National Forest, Stubblefield Lake Campground (30.56, -95.64), E.G. Riley, 15 Oct 1995, berlese forest litter (1, EGRC).

Eurhoptus curtus (Hamilton, 1893), resurrected name

Figures 6-7

- Acalles curtus Hamilton, 1893: 308; Blatchley and Leng 1916: 501 (as synonym of A. sordidus).
- Eurhoptus curtus; O'Brien and Wibmer 1982: 136 (as synonym of E. sordidus).

Eurhoptus sordidus; Ciegler 2010: 167.

Eurhoptus sordidus (part); O'Brien and Wibmer 1982: 136; Downie and Arnett 1996: 1581.

Notes about types. This species was described from Pennsylvania from a series of 4 specimens (CMNH) of which we have selected one as lectotype. It is labelled with a handwritten label "Type", a second rectangular pink blank label, a third rectangular label "Carn. Mus. / Acc. 349", a fourth red square blank label and our lectotype des-



Figure 6. *Eurhoptus curtus.* **A** Dorsal view **B** Lateral view **C** Ventral view showing impressions on ventrites **D** Dorsal view of aedeagus **E** Lateral view of aedeagus.

ignation label. It is not dissected but appears to be a male based on sculpture of the rostral apex. This name has long been considered a junior synonym of *E. sordidus* but with the recognition of the latter species as distinct from specimens occurring further east and north, the oldest available name for these eastern forms becomes *E. curtus*.

Redescription. Body length (exclusive of head and rostrum) 1.8–2.8 mm, cuticle largely bare, variously covered with short, fine recurved seta-like scales only, although often encrusted and coated with a fine film. Pronotum with lateral margins rounded, margins constricted at about apical one-third such that apical one-third is tubulate, greatest width at about basal one-third, medially carinate or not. Elytra strongly rounded dorsally and laterally, striae distinct, punctures moderate in size and depth; all elytral intervals evenly elevated, slightly rounded, each with single row of fine recurved seta-like scales. Metaventrite medially impressed behind mesoventral cup. Abdomen with ventrite 1 with pair of obliquely arranged transversely elongate pits which are continuous medially, area around pits with inwardly directed scales. Legs with femora and tibiae at most fringed with a few erect scales especially along outer margin of tibiae, hind tibiae subequal in width throughout most of length. Aedeagus about as long as one-half length of aedeagal apodemes or slightly shorter, in lateral view slightly ventrally curved, in dorsal view with margins very gradually tapered towards apex at about apical one-quarter to one-fifth where abruptly constricted, apex produced medially as



Figure 7. Records of Eurhoptus curtus.

broad lobe-like extension, broadly rounded at tip. Internal sac with large distinct cruciform apical sclerite complex, with well-defined posterior bars, anterior and transverse bars not well defined.

Distribution (Figure 7). This species is widely distributed in the eastern U.S.A. from Illinois and Pennsylvania in the north, south nearly to the Gulf Coasts of Louisiana and Mississippi. Across this range it exhibits a high degree of intraspecific genetic variation, with some surprisingly well supported subclades, especially in a group of populations from central South Carolina (Greenville and McCormick Counties). However, most of the range of the species is sparsely represented in the sequence data set, and no further subdivision appears warranted.

Specimens examined (219). **ALABAMA:** Monroe Co.: 1.6 km. S. Claiborne Dam (31.5917, -87.5392), C.E. Carlton, May 31 1995, beech/magnolia riparian berlese (1,

ASUIC); Monroe Co.: Big Flat Creek (31.6083, -87.4147), C.E. Carlton, May 27 1995, riparian litter (1, ASUIC); Monroe Co.: Haines Island Park (35.7231, -87.4694), K. Schnepp, Jun 12 2016, leaf litter (1, KSC), DNA extract MSC2515; Monroe Co.: Haines Island Park (35.7231, -87.4694), C.E. Carlton, May 31 1995, beech/magnolia berlese (1, ASUIC). ARKANSAS: Cleburne Co.: Greers Ferry Dam, Mossy Bluff Trail (35.52, -91.99), R. Chenowith, 30 Jun 1976, litter (1, CWOB); Conway Co.: Petit Jean State Park (35.118, -92.942), J.A. MacGown; J.G. Hill, Aug 5 2008, litter hardwood forest (6, MEM); Cross Co.: Village Creek State Park (35.168, -90.721), R.S. Anderson, Aug 14 1988, hardwood berlese (1, CMNC); Garland Co.: 4.83 km. W. Crystal Springs (34.521, -93.389), J. Pakaluk, Jun 1 1984, hardwood berlese (1, CMNC); Greene Co.: Crowleys Ridge State Park (36.04, -90.67), R. Chenowith, 8 Jun 1976, litter (1, CWOB); Izard Co.: 20.9 km. S. Melbourne (35.97, -92.05), R. Chenowith, 30 Aug 1977, hardwood litter (2, CWOB); Logan Co.: Cove Lake Recreation Area (35.228, -93.627), C.E. Carlton, 16 Jun 1990, berlese (2, CMNC; 2 LSAM); Logan Co.: Mount Magazine Road, 1.6 km. N. Greenfield intersection (35.167, -93.645), C. Carlton, May 21 1987, hardwood berlese (3, CMNC); Logan Co.: Mount Magazine State Park (35.1686, -93.6428), A.P.G. Dowling, Jun 11 2013, oak/hickory litter (1, UAAM); Logan Co.: Mount Magazine State Park (35.1686, -93.6428), J.R. Fisher & M.J. Skvarla, May 25 2013, oak/hickory litter (1, UAAM); Logan Co.: Mount Magazine State Park (35.1919, -93.6447), A.P.G. Dowling, Sep 22 2014, paw-paw/ sassafras litter (1, UAAM), DNA extract MSC2527; Logan Co.: Mount Magazine, Signal Hill Trail (35.17, -93.64), E.G. Riley, 13 May 1995 (1, EGRC); Marion Co.: 7 mi E County line on Hwy 14 (36.36, -92.8), R. Chenowith, Sep 27 1977, mixed hardwood litter (1, ASUIC); Montgomery Co.: 2.41 km. E. Crystal Recreation Area, slopes at FS 177K (34.5, -93.6), C.E. Carlton & H.W. Robison, Aug 17 1991, deciduous litter (1, UAAM); Newton Co.: Buffalo National River (36.0369, -93.34), M.J. Skvarla, Aug 16 2013, litter (1, UAAM); Newton Co.: Buffalo National River (36.0369, -93.34), M.J. Skvarla, Jul 31 2013, litter along log (1, CUAC), DNA extract MSC2526; Newton Co.: Buffalo National River (36.0369, -93.34), M.J. Skvarla, May 29 2013, oak/ hickory litter (1, UAAM); Newton Co.: Buffalo National River (36.0372, -93.3417), M.J. Skvarla, Sep 25 2013, litter next to large branch (1, UAAM); Newton Co.: Buffalo National River (36.0375, -93.34), M.J. Skvarla, May 29 2013, pitfall (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.3411), M.J. Skvarla, Apr 13 2013, pitfall in grassy area (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.34), M.J. Skvarla, Aug 28 2013, pitfall (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.34), M.J. Skvarla, May 15 2013, pitfall (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.3411), M.J. Skvarla, May 29 2013, oak/hickory litter (1, UAAM); Newton Co.: Buffalo National River (36.0386, -93.3417), M.J. Skvarla, Sep 25 2013, litter in short shrubs (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.3401), M.J. Skvarla, Apr 30 2013, litter in blueberry (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.3408), M.J. Skvarla, Aug 16 2013, litter (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.34), M.J. Skvarla, Aug 28 2013, pitfall (1, UAAM); Newton Co.: Buffalo National River (36.0389,

-93.3408), M.J. Skvarla, Jul 17 2013, litter under low bush (1, UAAM); Newton Co.: Buffalo National River (36.0389, -93.3403), M.J. Skvarla, Sep 25 2013, thick litter in flats (1, UAAM); Newton Co.: Buffalo National River (36.0392, -93.3411), M.J. Skvarla, Jul 17 2013, litter in low bushes (1, UAAM); Newton Co.: Buffalo National River (36.0394, -93.3401), M.J. Skvarla, Aug 16 2013, litter (1, UAAM); Perry Co.: Cedar Creek Gorge, ca. 19.3 km. W. Oppelo (35.12, -92.94), E.G. Riley, 14-16.Oct 1999, berlese forest litter (5, EGRC); Polk Co.: Bard Springs Recreation Area (34.4, -94), C.E. Carlton & H.W. Robison, Apr 24 1992, deciduous litter (1, UAAM); Polk Co.: Bard Springs Recreation Area (34.4, -94), C.E. Carlton & H.W. Robison, Jun 6 1992, deciduous litter (1, UAAM); Polk Co.: Rich Mt., Eagleton Overlook (34.6, -94.3), C.E. Carlton & H.W. Robison, Nov 29 1991, deciduous litter (1, UAAM); Polk Co.: Rich Mt., intersec 272-88 (34.68, -94.36), C.E. Carlton & H.W. Robison, Apr 3 1992, deciduous litter (1, UAAM); Polk Co.: Rich Mt., intersec 272-88 (34.68, -94.36), C.E. Carlton & H.W. Robison, Nov 16 1991, deciduous litter (1, UAAM); Polk Co.: Rich Mt., intersec 272-88 (34.68, -94.36), C.E. Carlton & H.W. Robison, Oct 18 1991, deciduous litter (1, UAAM); Polk Co.: Rich Mt., Ouachita Trail (34.7, -94.4), C.E. Carlton & H.W. Robison, May 3 1992, deciduous litter (1, UAAM); Polk Co.: Rocky, Talimena Drive (34.619, -94.276), D. Beyers; M. Jenks, Apr 14 1984, hardwood berlese (2, CMNC); Pope Co.: Mt. Nebo State Park, entrance area (35.2, -93.3), C.E. Carlton & R.A.B. Leschen, Apr 16 1989, hardwood berlese (1, UAAM); Scott Co.: Dry Creek Wilderness Area (35, -93.7), C.E. Carlton & H.W. Robison, Jan 19 1992, deciduous litter (1, UAAM); Searcy Co.: Hwy 853.9 mi E County line (36.06, -92.87), R. Chenowith, Mar 25 2977, (1, ASUIC); Yell Co.: 6.44 km. S. Blue Mt. Lake (35, -93.7), R. Chenowith, Aug 16 1991, hardwood berlese (1, ASUIC); Yell Co.: Dry Creek Wilderness Area (35, -93.7), C.E. Carlton & H.W. Robison, Mar 6 1992, deciduous litter (1, UAAM). GEORGIA: White Co.: (34.7, -83.7), R. Morris II, Jun 19 1984, (1, FSCA). ILLINOIS: Alexander Co.: Shawnee National Forest, nr. McClure (37.2894, -89.3427), M.L. Ferro, May 17 2016, sifted forest litter (2, CUAC), DNA extract SSM504; Pope Co.: Shawnee National Forest. Dixon Springs Agricultural Centre (37.434, -88.667), I. Askevold, Jun 4 1983, (1, CMNC); Union Co.: Cobden (37.52, -89.26), H.S. Dybas, 23 Aug 1960, litter (1, CWOB); Union Co.: Dongola (37.36, -89.17), D. Dillo, 15 Aug 1968, litter (1, CWOB); Union Co.: Pine Hills Field Station (37.55, -89.43), J.M. Campbell, 15-22 May 1967 (10, CNCI). INDIANA: Crawford Co.: Hemlock Cliffs Trail (38.2785, -86.5393), R.S. Anderson, Sep 30 2017, mixed hardwood litter (1, CUAC), DNA extract MSC2479-2480, 2487-2488; Floyd Co.: rest stop nr. Georgetown (38.2775, -85.9626), M.L. Ferro, May 13 2016, sifted forest litter (2, CUAC), DNA extract SSM511; Orange Co.: Pioneer Mothers Memorial Forest (38.5356, -86.4568), R.S. Anderson, Sep 30 2017, mixed hardwood litter (1, CUAC), DNA extract MSC2477-2478, 2485-2486; Tippecanoe Co.: (40.4, -86.9), K. Schnepp, Mar 22 2009, leaf litter (1, KSC), MSC2514. KENTUCKY: Bull Co.: Bernheim Forest, Clermont (37.9, -85.6), R.M. Reeves, Dec 7 1988, box elder leaf litter (1, ASUIC); Christian Co.: 8.05 km. W. Hopkinsville (36.86. -87.41), J.M. Campbell, 22 Sep 1967 (5, CNCI); Edmonson Co.: Mammoth Cave National Park, Cabin Woods

(37.20, -86.10), W. Suter, 24 Mar 1973, litter (1, CWOB); Laurel Co.: 24.14 km. W. London (37.161, -84.35), S. Marshall, Jun 4-30 1984, (2, CMNC); Lee Co.: Hwy. 11 2 km S. Zoe (37.6607, -83.6966), M.L. Ferro, May 11 2016, sifted forest litter (1, CUAC), DNA extract SSM508; Whitley Co.: I-75 Welcome Center (36.6144, -84.1047), M.L. Ferro, May 11 2016, forest litter (1, CUAC), DNA extract SSM509. LOUISIANA: West Feliciana Parish: St. Francisville (30.76, -91.39), S. McGlynn, Feb 9 1999, beech/magnolia litter near lake (1, ASUIC). MISSISSIPPI: Warren Co.: Vicksburg (32.3, -90.8), C.W. O'Brien & P.W. Kovarik, Apr 24 1996, beech/magnolia berlese (1, ASUIC); Winston Co.: Legion State Park (33.155, -89.045), J.A. MacGown; J.G. Hill, Aug 4 2006, berlese litter (2, MEM). NORTH CAROLINA: Buncombe Co.: Big Butt Trail (35.80174, -82.3401), S.S. Myers, Jul 26 2015, sifted litter (1, CUAC), DNA extract SSM326; Graham Co.: Joyce Kilmer Memorial Forest (35.3441, -83.966), M.S. Caterino & S.S. Myers, Jun 24 2015, sifted litter (1, CUAC), DNA extract SSM018; Jackson Co.: Balsam Mountain Preserve (35.3653, -83.1062), S.S. Myers, Jun 17 2015, sifted litter (1, CUAC), DNA extract SSM222; Jackson Co.: Balsam Mountain Preserve (35.3681, -83.1036), S.S. Myers, Jun 17 2015, sifted litter (1, CUAC), DNA extract SSM388; Jackson Co.: Balsam Mountain Preserve (35.3691, 83.1191), S.S. Myers, Jun 15 2015, sifted litter (1, CUAC), DNA extract SSM547; Jackson Co.: Balsam Mountain Preserve (35.3699, -83.1212), S.S. Myers, Jun 15 2015, sifted litter (1, CUAC), DNA extract SSM546; Jackson Co.: Balsam Mountain Preserve (35.37, -83.1216), S.S. Myers, Jun 15 2015, sifted litter (1, CUAC), DNA extract SSM545; Jackson Co.: Balsam Mountain Preserve (35.372, -83.0998), S.S. Myers, Jun 17 2015, sifted litter (3, CUAC), DNA extract SSM387; Jackson Co.: Balsam Mountain Preserve (35.3916, -83.1091), S.S. Myers, Jun 17 2015, sifted litter (1, CUAC), DNA extract SSM355; Jackson Co.: Balsam Mountain Preserve (35.398, -83.1088), S.S. Myers, Jun 17 2015, sifted litter (2, CUAC), DNA extract SSM225; Jackson Co.: Balsam Mountain Preserve (35.4025, -83.1049), S.S. Myers, Jun 17 2015, sifted litter (2, CUAC), DNA extract SSM228; Macon Co.: Coweeta Hydrological Station, Shope Fork Rd. (35.1, -83.5), D.S. Chandler, May 30 1983, oak and ash litter (1, ASUIC); Macon Co.: Jones Gap (35.0785, -83.2923), S.S. Myers, Jul 22 2015, sifted litter (1, CUAC), DNA extract SSM178; McDowell Co.: Blue Ridge Parkway, mile 320 (35.94, -81.96), Q. Wheeler, Aug 4 1981, leaf litter (1, ASUIC); Swain Co.: Miller cove, Appalachian Trail (35.3367, -83.6021), S.S. Myers, Jul 20 2015, sifted litter (2, CUAC), DNA extract SSM351; Transylvania Co.: 1.6 km. S. Rosman (35.14, -82.82), J. Cornell, 26 Apr 1988, litter (1, CWOB); Co.: Great Smoky Mountains National Park, Chestnut Branch Trail (35.76, -83.123), A. Tishechkin, Aug 1 2001, forest leaf litter (3, CMNC). OHIO: Adams Co.: 1 mi W Lynch (38.8, -83.4), L.E. Watrous, Sep 3 1978, litter rotten log (3, ASUIC); Hocking Co.: 11.26 km. S. Lancaster (39.67, -82.60), L.E. Watrous, 4 Jun 1977, litter around swamp (1, CWOB); Lawrence Co.: Wayne National Forest, Sharps Creek, Bluegrass Trail (38.62, -82.56), Jun 1 1995, pitfall (1, AS-UIC; 1, CWOB); Preble Co.: Hueston Woods State Park (35.814, -88.209), P. Kovarik, May 19 1990, (1, CMNC); Ross Co.: Scioto State Park (39.23, -82.95), L.E. Watrous, Sep 4 1978, leaf litter (1, ASUIC); Ross Co.: Scioto Trail State Park (39.23, -82.956), P.

Kovarik, Apr 17 1989, (1, CMNC); Scioto Co.: Shawnee State Forest, 12.87 km. W. Portsmouth (38.71, -83.15), P. Kovarik, Apr 22 1989, (9, CMNC); Vinton Co.: 8.05 km. N. Ratcliffburg (39.28, -82.68), L.E. Watrous, 15 May 1977, litter along stream (2, CWOB); Warren Co.: Caesar Creek State Park (39.519, -84.025), P. Kovarik, May 19 1990, (4, CMNC). PENNSYLVANIA: Huntingdon Co.: Rothrock State Forest, Seeger Natural Area (40.69, -77.76), D.S. Chandler, May 30 1985, mixed leaf litter (1, ASU-IC); Somerset Co.: 1.6 km. S. Kantner (40.09, -78.94), L.E. Watrous, 10 Jun 1976, litter (1, CWOB); Westmoreland Co.: Chestnut Ridge (40.2, -79.4), W. Suter, Sep 29 1978, litter at log (1, ASUIC); Westmoreland Co.: Forbes State Forest, Laurel summit (40.12, -79.18), D.S. Chandler, Jul 10 1984, oak litter (1, ASUIC); Westmoreland Co.: Linn Run State Park, Adams Falls (40.17, -79.23), D.S. Chandler, Jul 11 1984, leaf litter at stream edge (1, ASUIC); Westmoreland Co.: Linn Run State Park, Linn Run (40.17, -79.23), D.S. Chandler, Jul 12 1984, leaf litter (1, ASUIC); Allegheny (40.45, -80.01), J. Hamilton, Apr, under stones near beech trees (3, CMNH). SOUTH CAR-OLINA: Chester Co.: nr. Great Falls on US 21 at Rockey Creek Bridge (34.60, -80.89), J. & S. Cornell, 28 Mar 2009, old stream debris (2, CWOB); Greenville Co.: Chestnut Ridge Heritage Preserve (35.1406, -82.279), S.S. Myers, Jun 5 2015, hardwood litter (4, CUAC), DNA extract SSM540; Greenville Co.: Chestnut Ridge Heritage Preserve (35.1518, -82.2839), S.S. Myers, Jun 5 2015, hardwood litter (3, CUAC), DNA extract SSM87; Greenville Co.: Chestnut Ridge Heritage Preserve (35.1523, -82.2814), S.S. Myers, Jun 5 2015, hardwood litter (5, CUAC), DNA extract SSM90; McCormick Co.: Stevens Creek Heritage Preserve (33.6893, -82.1603), M.S. Caterino, S.S. Myers & L.Vasquez-Velez, Feb 14 2016, sifted litter (4, CUAC), DNA extract SSM549; Oconee Co.: Sumter National Forest, Riley Moore Falls (34.7403, -83.1804), M.S. Caterino & S.S. Myers, Mar 3 2018, sifted litter (1, CUAC), DNA extract MSC2523; Pickens Co.: Eastatoe Heritage Preserve (35.1577, -82.491), S.S. Myers, Jun 30 2015, sifted litter (1, CUAC), DNA extract SSM397. TENNESSEE: Cocke Co.: 6 mi SE Cosby (35.8, -83.2), D.S. Chandler, May 31 1983, forest litter (1, ASUIC); Cocke Co.: Snowbird Mt. (35.79, -83.05), K. Schnepp, Oct 12 2014, sifted litter (2, KSC), DNA extracts MSC2512, MSC2513; Franklin Co.: Tims Ford State Park (35.222, -86.253), J.A. MacGown, Jun 17 2010, soil/litter hardwood forest (1, MEM); Hamilton Co.: Chattanooga Nature Centre (35.0052, -85.3648), S. Chatzimanolis et al., 30 Apr-1 May 2010, leaf litter (2, CMNC); Hamilton Co.: Chattanooga Nature Centre (35.0052, -85.3648), S. Chatzimanolis et al., May 21 2011, Magnolia leaf litter (1, CMNC); Hamilton Co.: Tennessee River Gorge (35.08643, -85.39215), S. Chatzimanolis, Oct 20 2012, leaf litter (1, CMNC); Henderson Co.: I40, 3.2 km. E. Natchez Trace State Park (35.814, -88.209), R.S. Anderson, Jun 24 1988, hardwood litter (1, CMNC); Madison Co.: Route 152, 1.6 km. W. I40 (35.71, -88.659), P. Kovarik, Mar 6 1988, (2, CMNC); Marion Co.: near Nicklejack Lake (35.029, -85.549), S. Chatzimanolis et al. , Nov 25 2009, leaf litter (2, CMNC); Marion Co.: Tennessee River Gorge (35.1046, -85.4122), S. Chatzimanolis, Jun 15 2015, sifted litter (2, CUAC); Marion Co.: Tennessee River Gorge, Pot Point Tr. (35.0864, -85.3922), S. Chatzimanolis, May 24 2015, sifted litter (3, CUAC), DNA extract MSC2521; Scott Co.: 1.6 km. S. New River

(36.37, -84.57), H.S. Dybas, 20 Dec 1969, litter (1, CWOB); Sevier Co.: Great Smoky Mountains National Park (35.679, -83.6), J.A. MacGown; J.G. Hill, Jun 9 2009, litter old growth hardwood forest (1, MEM); Wilson Co.: Cedars of Lebanon State Park (36.08, -86.315), J.G. Hill, Jun 4 2010, cedar hardwood litter (3, MEM). VIRGINIA: Boutetourt Co.: Cave Mountain Lake Campground, 404 m (37.566, -79.54), I. Agnarson, May 28 2013, (2, CMNC). WEST VIRGINIA: Greenbrier Co.: Greenbrier State Park (37.7, -80.4), W. Suter, Jul 8 1982, litter at birch log (1, ASUIC); Morgan Co.: Cacapon State Park (39.5, -78.3), D.S. Chandler, May 31 1983, litter near stream (1, ASUIC); Pendleton Co.: George Washington National Forest, High Knob Trail (37.57, -79.17), K. Schnepp, May 9 2017, under rock (2, KSC), DNA extracts MSC2510, MSC2511; Pendleton Co.: George Washington National Forest, High Knob Trail (37.57, -79.17), K. Schnepp, May 9 2017, fermenting sugar pitfall (1, KSC); Pendleton Co.: George Washington National Forest, High Knob Trail (37.57, -79.17), K. Schnepp, May 10 2017, leaf litter (1, KSC); Pocahontas Co.: Watogas State Park, 3.2 km. NE Seebert (38.1, -80.1), W. Suter, Jul 8 1982, under rhododendron (2, ASUIC); Pochahontas Co.: Highway 150, Cranberry Glades Overlook (38.23, -80.234), P. Kovarik, Jun 8 1990, (2, CMNC); Pochahontas Co.: Watogas State Park, 3.2 km. N.E. Seebert (38.121, -80.138), W. Suter, Jul 8 1982, (1, CMNC); Pochahontas Co.: Hills Creek Falls (38.17, -80.34), W. Shear, 19 Jun 1971 (1, CNCI); Randolph Co.: Monongahela National Forest, Laurel Fork Campground, 855 m (38.74, -79.693), I. Agnarson, May 27 2013, (1, CMNC); Summers Co.: 19.3 km. N. Athens (37.59, -80.97), W.A. Shear, 16 Jun 1971 (1, CNCI); Wythe Co.: Stoney Fork Campground, 713 m (37.009, -81.182), I. Agnarson, May 29 2013, (1, CMNC).

Eurhoptus imbricatus Anderson & Caterino, sp. n. http://zoobank.org/3AFF4D3A-E68D-4DFF-97F2-732E2E0BFAF9

Figures 8–9

Description. Body length (exclusive of head and rostrum) 2.3–3.0 mm, cuticle almost fully covered with broad, flat scales and scattered short, fine recurved (pronotum) to appressed (elytra) seta-like scales. Pronotum with lateral margins rounded, margins constricted at about apical one-third such that apical one-third is tubulate, greatest width at about basal one-third, not medially carinate; pale scales almost entirely covering pronotum to limited to midline and pair of lateral lines (giving some specimens a trivittate appearance). Elytra strongly rounded dorsally and laterally, striae distinct, of small punctures; all elytral intervals flat, each with single row of fine almost appressed seta-like scales; broad flat scales largely dark brown, approximate, scales pale and imbricate in an irregular oblique band across elytra in apical one-half, at bases of interval 3, at humeri and at elytral apex. Metaventrite medially impressed behind mesoventral cup. Abdomen with ventrite 1 with large median deep shining pit, base of pit with numerous erect, broad pale scales, scales somewhat condensed along midline in anterior portion of pit (giving a divided appearance); area around pit with dense, fine golden



Figure 8. *Eurhoptus imbricatus.* **A** Dorsal view **B** Lateral view **C** Ventral view showing impressions on ventrites **D** Dorsal view of aedeagus **E** Lateral view of aedeagus.

inwardly directed scales encircling depression. Legs with femora and tibiae fringed with dense erect scales along outer and inner margins, hind tibiae distinctly wider at about basal one-third. Aedeagus about as long as slightly less than one-half length of aedeagal apodemes, in lateral view slightly ventrally curved, in dorsal view with margins subparallel but gradually rounded towards apex at about apical one-quarter, apex produced medially as slight extension, broadly rounded at tip. Internal sac with apical sclerite complex with well-defined pair of hook-like sclerites.

Distribution (Figure 9). This species is distributed in the Edwards Plateau region of central Texas, east into Louisiana and southern Arkansas.

Etymology. We name this species "imbricatus" (L., an adjective or participle in the nominative singular, tiled, having adjacent edges overlapping) after the overlapping or imbricate scales of the oblique band on the elytra.

Variation. There is some variation in the extent of the distribution of pale scales on the pronotum.

Specimens examined. Holotype male (CMNC), labelled "USA: TX: Bandera Co. / 29.81958°N, 99.57066°W / Lost Maples St. Nat. Area / IV.28–30.1988, leaflit. / Berlese, R.S. Anderson", dissected. Extracted MSC2469 (unsuccessful). Paratypes (125): **TEXAS:** Bandera Co.: Lost Maples State Natural Area (29.81958, -99.57066), R.S. Anderson, 28–30 Apr 1988, berlese leaf litter (11, CMNC; 2, CNCI; 1, CWOB; 4, TMMC); Bandera Co.: Lost Maples State Natural Area (29.81958, -99.57066), R.S. Anderson, 28 Apr-2

May 1987, leaf / log litter (4, BMNH; 13, CMNC; 1, CWOB; 4 USNM); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), P.W. Kovarik, 21 Apr 1986, leaf litter (1, FSCA; 2, TAMU); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), P.W. Kovarik, 26 Apr 1986, leaf litter (2, TAMU); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), R.S. Anderson, 28-30 Apr 1988, leaf litter (1, CUAC); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), E.G. Riley, 27 Mar 1999, forest litter (1, EGRC); Bandera Co.: Lost Maples State Natural Area, Maple Trail (29.82, -99.57), C.W. O'Brien, 9 Mar 2001, leaf litter (5, CWOB); Bandera Co.: Lost Maples State Natural Area, Maple Trail (29.82, -99.57), C.W. O'Brien, 10 Mar 2001, leaf litter (8, CWOB); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), C.E. Carlton, 19 May 2005, forest litter (2, LSAM); Hays Co.: 9.66 km. N.W. Dripping Springs (30.226, -98.184), E.G. Riley, 24 Feb-30 Mar 2006, pitfall, Juniperus, unmanaged plot (2, EGRC); Hays Co.: 9.66 km. N.W. Dripping Springs (30.226, -98.184), E.G. Riley, 28 Apr-2 Jun 2006, FIT Juniperus, unmanaged plot (1, EGRC); Hays Co.: 9.66 km. N.W. Dripping Springs (30.226, -98.184), E.G. Riley, 31 arr-26 Apr 2006, FIT Juniperus, unmanaged plot (1, EGRC); Kerr Co.: 10.46 km. S.W. Hunt (29.99, -99.387), E.G. Riley, 28 Apr-2 Jun 2006, pitfall, upland deciduous forest (1, EGRC); Sabine Co.: 14.48 km. E. Hemphill 'Beech Bottom' (31.38, -93.71), R.S. Anderson, 11 May 1988, beech/ magnolia berlese (1, CUAC); Sabine Co.: 14.48 km. E. Hemphill 'Beech Bottom' (31.38, -93.71), R.S. Anderson & E. Morris, 8 Mar 1989, beech/magnolia berlese (1, CUAC); Sabine Co.: 14.48 km. E. Hemphill 'Beech Bottom' (31.38, -93.71), E. Riley & E. Morris, 24 Apr 1989, beech/magnolia berlese (1, CUAC); Sabine Co.: 14.48 km. E. Hemphill, Beech Bottom (31.386, -93.706), R.S. Anderson, 11 May 1988, litter, beech-magnolia forest (10, CMNC; 1, CWOB); Sabine Co.: 14.48 km. E. Hemphill, Beech Bottom (31.386, -93.706), R. Anderson; E. Morris, 8 Mar 1989, litter, beech-magnolia forest (9, CMNC; 1, CWOB); Sabine Co.: 14.48 km. E. Hemphill, Beech Bottom (31.386, -93.706), R. Anderson; E. Riley; E. Morris, 24 Apr 1989, litter, beech-magnolia forest (6, CMNC); Sabine Co.: 14.48 km. E. Hemphill, Beech Bottom (31.386, -93.706), E. Morris; R. Anderson, 18–26 Apr 1989, FIT, beech-magnolia forest (1, CMNC); Sabine Co.: 14.48 km. E. Hemphill, Beech Bottom (31.386, -93.706), E. Morris; R. Anderson, 9–16 Apr 1989, FIT, beech-magnolia forest (3, CMNC); Tyler Co.: 4.5 km. W., 3.05 km. N. Spurger, Big Thicket Natural Preserve, Beech Woods Trail (30.72, -94.227), R.S. Anderson, 12 May 1988, beech/magnolia leaf litter (6, CMNC); Travis Co.: vic. Long Hollow Creek (30.458, -97.875), 17 Mar 1994, E.G. Riley, berlese forest litter (2, TAMU); Travis Co.: vic. Long Hollow Creek (30.458, -97.875), 7 May 1994, E.G. Riley, berlese forest litter (3, TAMU); Tyler Co.: 4.5 km. W., 3.05 km. N. Spurger, Big Thicket Natural Preserve, Beech Woods Trail (30.72, -94.227), R.S. Anderson, 24 Apr 1988, beech/magnolia leaf litter (3, CMNC); Tyler Co.: Big Thicket National Preserve, 4.5 km. W, 3.05 km. N. Spurger, Beech Woods Trail (30.72, -94.23), R.S. Anderson, 24 Apr 1988, beech/ magnolia berlese (1, CUAC); Tyler Co.: Highway 190 at FM 256 (30.76, -94.50), R.H. Turnbow Jr., 8 Feb 2003, berlese leaf litter (1, CWOB). ARKANSAS: Pike Co.: Crater of Diamonds State Park (34.04, -93.67), R.S. Anderson, 13 Aug 1988, hardwood berlese (1, CMNC). LOUISIANA: Calcasieu Par.: Sam Houston Jones State Park (30.3, -93.27), A.



Figure 9. Records of Eurhoptus imbricatus and E. cariniventris.

Cline; A. Tishechkin, 11 Feb 2002, leaf litter (2, CMNC); Evangeline Par.: Chicot State Park (30.8, -92.28), A. Tishechkin, 19 Feb 2004, berlese (1, CMNC); Evangeline Par.: Chicot State Park (30.794, -92.278), A.K. Tishechkin, 19 Feb 2004, berlese (1, CUAC); Madison Par.: Tallulah, Tensas National Wildlife Refuge (32.34, -91.34), S.T. Dash, 24 Mar 2004, leaf litter (1, CMNC); Natchitoches Par.: Kisatchie National Forest, Red Bluff Camp (31.5, -93.14), E. Riley; L. Prochaska, 1 Apr 1989, berlese beech/magnolia/pine litter (1, CMNC); Pointe Coupee Par.: Sam Houston Jones State Park (30.297, -93.259), 19 Feb 2003, A.R. Cline (1, CWOB).

Eurhoptus rileyi Anderson & Caterino, sp. n.

http://zoobank.org/DB5D4864-1058-444F-B71E-58F0871998C7 Figures 5, 10

Description. Body length (exclusive of head and rostrum) 3.2 mm, cuticle almost fully covered with broad, flat scales and scattered short, broad recurved, seta-like scales. Pronotum with lateral margins rounded, margins strongly constricted at about apical one-third such that apical one-third is distinctly tubulate, greatest width at about basal one-third, medially sulcate, median line glabrous, impunctate. Elytra strongly rounded dorsally and laterally, striae distinct, of small punctures; all elytral intervals evenly elevated, slightly rounded, each with single row of broad recurved seta-like scales. Metaventrite medially slightly impressed behind mesoventral cup. Abdomen with ventrite 1 with large median deep glabrous shining pit, area around pit with



Figure 10. Eurhoptus rileyi. A Dorsal view B Lateral view C Ventral view showing impressions on ventrites.

dense, fine golden inwardly directed scales encircling depression and entering pit along anteriorly along midline such that pit appears somewhat divided. Legs with femora and tibiae fringed with dense erect scales along outer and inner margins, hind tibiae distinctly wider at about midlength. Single specimen likely female, not dissected.

Distribution (Figure 5). This species is known only from a single specimen collected in southern Texas. No records of the species from Mexico are known.

Etymology. We name this species after Edward G. Riley (retired), former collections manager at the Texas A & M University Insect Collection, College Station, Texas. An invariable word in genitive.

Specimens examined. Holotype female (TAMU), labelled "USA: TEX: Hidalgo Co. / Bentsen R.G.V.S.P. (site 1) / 26.17830°N, 98.38577°W / IX.6–19.2008, FIT-ground / J. King & E. Riley – 0104 / cedar elm forest", not dissected.

Eurhoptus occidentalis Anderson & Caterino, sp. n. http://zoobank.org/B207EA8E-A7D6-4D1E-9383-EB12A142D8E4 Figures 5, 11

Description. Body length (exclusive of head and rostrum) 1.8–2.7 mm, cuticle largely bare, variously covered with dense, short, fine recurved seta-like scales only. Pronotum



Figure 11. *Eurhoptus occidentalis*. A Dorsal view B Lateral view C Ventral view showing impressions on ventrites D Dorsal view of aedeagus E Lateral view of aedeagus.

with lateral margins rounded, margins constricted at about apical one-third such that apical one-third is tubulate, greatest width at about basal one-third, not medially carinate. Elytra strongly rounded dorsally and laterally, striae distinct, punctures moderate in size and depth; all elytral intervals evenly elevated, slightly rounded, each with single row of dense, fine recurved seta-like scales. Metaventrite medially slightly impressed behind mesoventral cup. Abdomen with ventrite 1 with pair of obliquely arranged transversely elongate pits which are separate medially, and with second pair of small rounded pits along posterior margin of ventrite; ventrite 5 with small pair of central, rounded impressions. Legs with femora and tibiae at most fringed with a few erect scales especially along outer margin of tibiae, hind tibiae subequal in width throughout most of length. Aedeagus about as long as one-half length of aedeagal apodemes, in lateral view slightly ventrally curved, in dorsal view with margins gradually convergent from base to apex, apex not produced, broadly rounded. Internal sac with large distinct apical sclerite complex, with median pyriform sclerite, bordered laterally by pair of apically convergent longitudinal bars these each bordered posteriorly by well-defined transverse pyriform sclerite, longitudinal bars not well-defined.

Distribution (Map 2). This species is distributed in west Texas in the Guadalupe and Chisos Mountains. Despite extensive sampling, no specimens are known from New Mexico or Arizona. **Etymology.** We name this species "occidentalis" (L., an adjective or participle in the nominative singular, westerly, connected or coming from the west) after its western Texas distribution.

Specimens examined. Holotype male (CMNC), labelled "USA: TEX: Brewster Co. / 29.2611°N, 103.2539°W / BigBend NP, Pine Cyn / 1615 m, ix.6.1988, hardwd / Berlese, R.S. Anderson", dissected. Paratypes (261): TEXAS: Brewster Co.: Big Bend National Park, Pine Canyon, 1615 m (29.2611, -103.2539), R.S. Anderson, 6 Sep 1988, hardwood litter berlese (26, CMNC; 3, CNCI); Brewster Co.: Big Bend National Park, Oak Canyon (29.28, -103.34), R.S. Anderson, 8 Sep 1988, hardwood berlese (1, CUAC); Brewster Co.: Big Bend National Park, Pine Canyon (29.27, -103.24), R.S. Anderson, 6 Sep 1988, hardwood berlese (1, CUAC); Brewster Co.: Big Bend National Park, Window Trail (29.27, -103.32), W. Suter, 29 May 1983, moldy log (1, CUAC); Brewster Co.: Big Bend National Park, Boot Canyon & Emory Peak Trail, 2070 m (29.245, -103.304), R.S. Anderson, 7 Sep 1988, berlese hardwood litter (1, CMNC); Brewster Co.: Big Bend National Park, Boot Spring, 6300' (29.24, -103.298), S.B. Peck, 7 Aug 1975, oak-maple litter (1, CMNC); Brewster Co.: Big Bend National Park, Cattail Falls, 1310 m (29.273, -103.336), R.S. Anderson, 6 Sep 1988, berlese hardwood litter (14, CMNC; 4, TAMU); Brewster Co.: Big Bend National Park, Cattail Falls (29.273, -103.3356), R.S. Anderson, hardwood berlese (1, CUAC); Brewster Co.: Big Bend National Park, Cattail Falls, (29.273, -103.336), C.E. Carlton, 4 Aug 2000, berlese (10, LSAM); Brewster Co.: Big Bend National Park, below Cattail Falls, (29.275, -103.317), W. Suter, 30 Mar 1983, oak treehole (16, CWOB); Brewster Co.: Big Bend National Park, Cattail Falls, 4300' (29.273, -103.336), S.B. Peck, 5 Aug 1975, forest litter (10, CMNC; 7, CWOB); Brewster Co.: Big Bend National Park, Green Gulch, 1700m (29.278, -103.284), W. Suter, 1 Jun 1983, litter oak-juniper (1, CMNC); Brewster Co.: Big Bend National Park, Green Gulch, nr. Panther Pass, 1700 m (29.278, -103.284), W. Suter, 1 Jun 1983, litter oak-juniper (1, CWOB); Brewster Co.: Big Bend National Park, 7.4 km. up from Basin (29.27, -103.30), C.E. Carlton, 31 Jul 2000, berlese (6, LSAM); Brewster Co.: Big Bend National Park, Lost Mine Trail, (29.27, -103.28), W. Suter, 6 Jun 1983, litter (1, CWOB); Brewster Co.: Big Bend National Park, Oak Canyon, 1463 m (29.281, -103.336), R.S. Anderson, 8 Sep 1988, berlese hardwood litter (11, CMNC); Brewster Co.: Big Bend National Park, Oak Spring, (29.28, -103.33), W. Suter, 8 Jun 1983, litter under oaks (3, CWOB); Brewster Co.: Big Bend National Park, Pine Canyon, 1615 m (29.2611, -103.2539), R.S. Anderson, 6 Sep 1988, hardwood litter berlese (6, BMNH; 18, CMNC; 6, USNM); Brewster Co.: Big Bend National Park, Pine Canyon, 1830 m (29.267, -103.253), S.B. Peck, 9 Aug 1975, oak maple litter (4, CMNC); Brewster Co.: Big Bend National Park, The Window, 4500' (29.275, -103.319), S.B. Peck, 2 Aug 1975, (9, CMNC); Brewster Co.: Big Bend National Park, Window Outlet, Rd to Cattail Falls, 1200 m (29.273, -103.34), R.S. Anderson, 6 Sep 1988, berlese hardwood litter (5, CMNC); Brewster Co.: Big Bend National Park, Window Trail, 1370 m (29.275, -103.317), S.B. Peck, 2 Aug 1975, madroneoak litter (6, ASUIC; 10, CMNC; 11, CWOB; 6, TMMC); Brewster Co.: Big Bend

National Park, Window Trail, 1370 m (29.275, -103.317), W. Suter, 29 May 1983 (4, CMNC; 6, CWOB); Brewster Co.: Big Bend National Park, Window Trail, 1370 m (29.275, -103.317), W. Suter, 27 August 1983 (14, CWOB); Brewster Co.: Big Bend National Park, Basin Area, (29.27, -103.30), E.G. Riley, 20–21 July 2002, berlese oak ravine litter (10, EGRC; 23, TAMU);); Brewster Co.: Big Bend National Park, Emory Peak Trail (29.26, -103.30), C.E. Carlton, 4 Aug 2000, berlese (2, LSAM); Culberson Co.: Guadalupe Mountains National Park, McKittrick Canyon (31.98, -104.78), P.W. Kovarik, 4 Sep 1986, leaf litter (2, CMNC).

Eurhoptus aenigmaticus Anderson & Caterino, sp. n.

http://zoobank.org/53E13EA1-3692-4194-A23B-2BF35ADE5DCF Figures 12–13

Eurhoptus sordidus (part); O'Brien and Wibmer 1982: 136; Downie and Arnett 1996: 1581.

Description. Body length (exclusive of head and rostrum) 2.2–2.5 mm, cuticle largely bare, variously covered with short, fine recurved seta-like scales only, although often encrusted and coated with a fine film. Pronotum with lateral margins rounded, margins constricted at about apical one-third such that apical one-third is tubulate, greatest width at about basal one-third, medially carinate (most) or not (few). Elytra strongly rounded dorsally and laterally, striae distinct, punctures large in size, deep; all elytral intervals evenly elevated, slightly rounded, each with single row of fine recurved setalike scales. Metaventrite medially deeply impressed behind mesoventral cup. Abdomen with ventrite 1 with pair of rounded pits which are continuous medially, area around pits with inwardly directed scales. Legs with femora and tibiae at most fringed with a few erect scales especially along outer margin of tibiae, hind tibiae subequal in width throughout most of length. Aedeagus slightly longer than one-half length of aedeagal apodemes, in lateral view very slightly ventrally curved, in dorsal view with margins gradually tapered towards very blunt, truncate apex, apex not produced medially. Internal sac with large distinct apical sclerite complex, with median pyriform sclerite, bordered laterally by pair of inwardly arcuate longitudinal bars these each bordered posteriorly by an elongate oblique sclerite.

Distribution (Figure 13). This species is distributed in the southern coastal plain of the U.S.A. from Alabama and Florida west to Louisiana. We have been able to sequence KKV, CAD, and COI from some individuals from Alabama. In COI these are rather divergent, though the other two genes show minimal difference from *Eurhoptus curtus*. Further effort to obtain sequences from these and other populations of *E. aenigmaticus* will help support its placement relative to *E. sordidus* and *E. curtus*.

Etymology. We name this species 'aenigmaticus' (L., an adjective or participle in the nominative singular, enigma, puzzle or riddle) after encountering difficulty in separating it from closely related species of the genus.



Figure 12. *Eurhoptus aenigmaticus*. A Dorsal view **B** Lateral view **C** Ventral view showing impressions on ventrites **D** Dorsal view of aedeagus **E** Lateral view of aedeagus.

Specimens examined. Holotype male (CMNC), labelled "AL: Winston Co.: Bankhead NF / Brushy Ck Lake CG, N34.297° / W87.2697°cols. CEC, MLF, JSP, AT / 3.Wink216h3/4", dissected. Extracted SSM-478. Paratypes (163): ALABAMA: Blount Co.: Blount Springs (33.9, -86.8), T. King, 31 Oct 1982, oak tree hole (1, UAAM); Blount Co.: Highland Lake (33.88, -86.42), T. King, 6 May 2009, litter (2, CWOB); Blount Co.: Highland Lake (33.88, -86.42), T. King, 20 Mar 2010, litter (1, CWOB); Cleburne Co.: Cheaha State Park (32.493, -85.809), R. Brown; J.A. McGown, 16 May 1998, berlese magnolia leaf litter (2, MEM); Jackson Co.: 3.2 km. N. Scottsboro (34.75, -86.04), 16 May 1972, S. & J. Peck (1, CNCI); Jackson Co.: Woodville (34.627, -86.274), S. Peck, 12 Jul 1965, leaf litter (2, CWOB); Lauderdale Co.: Joe Wheeler State Park (34.80, -87.33), J.A. McGown, 27 May 2004, soil humus at base Fagus grandofilia (1, MEM); Joe Wheeler State Park (34.80, -87.33), J.A. McGown, 27 May 2004, litter under rotten log (1, MEM); Joe Wheeler State Park (34.786, -87.388), J.A. McGown, 26 May 2004, mixed litter (1, MEM); Marshall Co.: 1.6 km. N. Guntersville Dam (34.43, -86.39), S. Peck, 11 Jun 1967, litter (1, CWOB); Monroe Co.: Haines Island Reserve (31.724, -87.470), V. Behan, 17 Mar 1994, mixed litter (1, MEM); Monroe Co.: Haines Island Park (31.723, -87.469), C.E. Carlton, 31 May 1995, beech/magnolia litter (3, LSAM); Monroe Co.: Haines Island Park (31.723, -87.469), C.E. Carlton, 26 May 1995, beech/magnolia litter (2, CMNC; 4, LSAM); Monroe Co.: 1.6 km.km. S. Claiborne Dam (31.54, -87.52), A.


Figure 13. Records of Eurhoptus aenigmaticus.

Tishechkin, 16 Sep 2005, litter (1, CWOB); Monroe Co.: 1.6 km. S. Claiborne Dam (31.54, -87.52), C.E. Carlton, 31 May 1995, litter (2, LSAM); Monroe Co.: Big Flat Creek (31.54, -87.52), A. Tishechkin, 16 Sep 2005, litter (1, CWOB); Morgan Co.: 5.63 km. S.E. Favette (31.608, -87.414), C.E. Carlton, 27 May 1995, litter (1, LSAM); Morgan Co.: 5.63 km. S.E. Fayette (31.608, -87.414), S.B. Peck, 21 May 1972, litter (2, CMNC); Morgan Co.: Newsom Sinks, Turtle Cave area (34.43, -86.58), A. Cline & J. Skeens, 26 Nov 2004, litter (2, LSAM); Sumter Co.: Highway 17 at Noxubee River (32.918, -88.298), J.A. McGown, 27 May 2004, under dead Quercus nigra, floodplain (3, MEM). LOUISIANA: East Baton Rouge Par.: Place Du Plantier Apartments (30.4, -91.1546), E.G. Riley, 30 Dec 1993, berlese leaf litter (4, ASUIC; 2, BMNH; 16, CMNC; 2, CNCI; 4, LSAM; 22, TAMU; 2, USNM); East Baton Rouge Par.: Place Du Plantier Apartments (30.4, -91.1546), E.G. Riley, 27 Nov 1993, berlese leaf litter (20, EGRC; 11, TAMU); Evangeline Par.: Chicot State Park (30.795, -92.279), A. Tishechkin, 19 Feb 2004, berlese (4, CMNC); West Feliciana Par.: Feliciana Preserve (30.78, -91.25), J.L. Fassbender, 21 Apr 1999, sifting litter mixed pine hardwood forest (2, CMNC; 1, LSAM); West Feliciana Par.: D.P. Cabin (30.795, -91.256), J.L. Johnson, 21 Dec 1995, berlese (3, CWOB); West Feliciana Par.: Tunica Hills WMA, Magnolia Glen Trail (30.79. -91.38), D. Pashley, 15 Jul 1995 (1, LSAM); West Feliciana Par.: Tunica Hills WMA (30.79. -91.38), D. Pashley, 24 May 1995 (1, LSAM); West Feliciana Par.: Tunica Hills WMA, nr. St. Francisville (30.79. -91.38), J. & T. Fassbender, 23 Sep 1999, lower ravine berlese (10, CWOB). **MISSISSIP-PI:** Chickasaw Co.: Natchez Trace Parkway mile 241.1 (34.01, -88.90), J.A. McGown; J.G. Hill, 21 Jul 2003, mixed litter (1, MEM); Claiborne Co.: Natchez Trace Parkway (31.97, -90.956), J.A. McGown; J.G. Hill, 8 Jul 2005, mixed litter (4, MEM); Warren Co.: Vicksburg, Waterways Experiment Station (32.355, -90.878), P.W. Kovarik, 23. Mar 1998, beech magnolia litter (2, CMNC; 14, CWOB); Wilkinson Co.: Clark Creek Natural Area (31.058, -91.521), A. Tishechkin, 2 Dec 2005, forest litter (5, CWOB).

Excluded from type series: **ARKANSAS:** Marion Co.: 7 mi E County line on Hwy 14 (36.36, -92.8), R. Chenowith, 27 Sep 1977, mixed hardwood litter (1, ASUIC).

Eurhoptus cariniventris Anderson & Caterino, sp. n.

http://zoobank.org/59AF7223-87AA-4BAF-B4F2-0C9DBB65CC53 Figures 9, 14

Eurhoptus pyriformis (part); Blatchley and Leng 1916: 497; Kissinger 1964: 64; Papp 1979: 164; O'Brien and Wibmer 1982: 136; Downie and Arnett 1996: 1581; Alonso-Zarazaga and Lyal 1999: 131; Anderson 2002: 765.

Description. Body length (exclusive of head and rostrum) 1.8–2.4 mm, cuticle largely bare, variously covered with short, fine recurved seta-like scales, most specimens lacking other scales but some with head and base of rostrum scaly and with a few broad, flat pale scales variously arranged on elytra in apical one-half and at bases of intervals 2–4. Pronotum with lateral margins straight, margins tapered more or less evenly from base to apex with greatest width at base, medially carinate or not. Elytra strongly rounded dorsally and laterally, almost globular, striae distinct, of very large punctures, especially in posthumeral region; all elytral intervals evenly elevated, slightly rounded, each with single row of fine recurved seta-like scales. Metaventrite medially distinctly carinate behind mesoventral cup. Abdomen with ventrite 1 with large median deep glabrous shining pit, area around pit with dense, fine golden inwardly directed scales encircling depression. Legs with femora and tibiae fringed with erect scales along outer margin of tibiae, hind tibiae subequal in width throughout most of length to slightly wider at basal one-third. Aedeagus about as long as one third length of aedeagal apodemes, in lateral view almost straight, in dorsal view with margins subparallel but strongly tapered towards apex at about midlength, apex produced medially as fine acuminate point. Internal sac with distinct apical sclerite complex of pair of longitudinal parallel bars.

Distribution (Figure 9). This species is distributed throughout central Texas and appears to be disjunct to the panhandle of Florida and adjacent Alabama and Georgia. All published Texas records of *E. pyriformis* are this species.

Etymology. We name this species "cariniventris" (L., an adjective or participle in the nominative singular, carina, keeled, and ventris, belly) after the distinctly carinate metaventrite posterior to the mesoventral cup.



Figure 14. *Eurhoptus cariniventris.* **A** Dorsal view **B** Lateral view **C** Ventral view showing impressions on ventrites and metaventral carina (arrow, mc) **D** Dorsal view of aedeagus **E** Lateral view of aedeagus.

Variation. This species appears to have two disjunct portions of its range; central Texas and Florida panhandle and adjacent Alabama into eastern Georgia. We know of no specimens from the intervening areas. Specimens from Florida/Alabama have larger, deeper elytral punctures (especially in the posthumeral area) but have similar male genitalia and do not differ in other structural characters. At present, we consider these eastern specimens to be conspecific with the Texas specimens but have excluded them from the type series.

Specimens examined. Holotype male (CMNC), labelled "TEX: Bandera Co. / Lost Maples St. Nat. Area / 28.IV.-2.V.87 R. Anderson / Berlese leaf/log litter", dissected. Paratypes (312): **TEXAS:** Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), R.S. Anderson, 28 Apr-2 May 1987, leaf/log litter (42, CMNC; 5, CNCI; 1, CUAC; 5, CWOB; 1, UCFC); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), R.S. Anderson, 28–30 Apr 1988, leaf litter (42, CMNC; 1, CUAC; 5, CWOB); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), R.S. Anderson, 28–30 Apr 1988, leaf litter (42, CMNC; 1, CUAC; 5, CWOB); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), C.E. Carlton, 19 May 2005, forest litter (2, LSAM); Bandera Co.: Lost Maples State Natural Area, East Trail to pond (29.82, -99.58), C.W. O'Brien, 9 Mar 2001, sifted mixed hardwood litter (2, ASUIC); Bandera Co.: Lost Maples State Natural Area, Maple Trail (29.82, -99.57), C.W. O'Brien & Gages, 10 Mar 2001, sifted mixed hardwood litter (1, ASUIC); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), E.G. Riley, 24 Apr 2005, berlese maple forest litter (1, EGRC); Bandera Co.: Lost

Maples State Natural Area (29.82, -99.57), E.G. Riley, 11 May 1997, forest litter (2, EGRC); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), E.G. Riley, 27 Mar 1999, forest litter (1, EGRC); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), P.W. Kovarik, 21 Apr 1986, leaf litter (1, TAMU); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), P.W. Kovarik, 26 Apr 1986, leaf litter (12, TAMU); Bandera Co.: Lost Maples State Natural Area (29.82, -99.57), P.W. Kovarik, 10 May 1986, leaf litter (3, TAMU); Bastrop Co.: Buescher State Park (30.041, -97.162), R.S. Anderson, 3 May 1988, leaf litter berlese (15, CMNC); Bastrop Co.: Buescher State Park (30.041, -97.162), R.S. Anderson, 3 May 1988, leaf litter (1, CUAC); Blanco Co.: Pedernales Falls State Park, Nature Trail (30.306, -98.256), R.S. Anderson, 3 May 1988, oak/elm/juniper litter (10, CMNC); Colorado Co.: 2 mi S Columbus (29.6, -96.5), C.W. O'Brien & G.J. Wibmer, 12 Dec 1984, sifted hardwood litter (1, ASUIC); Colorado Co.: Columbus (29.7065, -96.5353), R.S. Anderson, 17 May 1987, riparian ravine hardwood litter (1, CUAC); Colorado Co.: Columbus (29.7065, -96.5353), R.S. Anderson, 1 Feb 1989, riparian ravine hardwood litter (1, CUAC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 1 Feb 1988, riparian ravine litter (25, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 22 Mar 1988, riparian ravine litter (8, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 4 Nov 1988, riparian ravine litter (33, CMNC); Colorado Co.: Columbus (29.7072, -96.5344), R.S. Anderson, 21 Feb 1989, riparian ravine litter (10 BMNH; 31, CMNC; 1, CUAC; 10 CWOB; 10, TAMU; 5, TMMC; 10 USNM); Colorado Co.: Columbus (29.7065, -96.5353), C.V. Riley, 24 Aug 1929 (1, CWOB); Fort Bend Co.: Brazos Bend State Park (29.37, -95.63), B. Raber & E.G. Riley, 15 Jun 2000, FIT (1, EGRC); Travis Co.: Austin, Mayfield Park (30.3126, -97.771), R. Jones, 15 Apr 1989, leaf litter (10, CMNC); Travis Co.: Austin, Brackenridge Field Lab (30.284, -97.778), E.G. Riley, 10 Feb 1996, berlese rotten pecan log (1, EGRC).

Excluded from type series: ALABAMA: Dale Co.: Fort Rucker Military Reserve (31.29, -85.72), R. Turnbow, 31 Mar 1993, leaf litter (1, CMNC); Dale Co.: Fort Rucker Military Reserve (31.29, -85.72), R. Turnbow, 27 Sep 1991, leaf litter (1, CMNC); Dale Co.: Fort Rucker (31.349, -85.711), R.H. Turnbow, Jr., 27 Oct 2001 (1, CWOB). FLORIDA: Gadsden Co.: 4 mi SE Havana, junction Co. Rd. 153 & Ochlokonee River (30.58, -84.36), C.W. O'Brien & G.B. Marshall, 23 Mar 2001, sifted hardwood litter (1, ASUIC; 3, CWOB); Gilchrist Co.: Hart Springs (29.675, -82.951), L.R. Davis Jr., 23 Apr 1993 (1, CWOB); Jackson Co.: Florida Caverns State Park (30.812, -85.225), P.E. Skelley, 8 Apr 1994, leaf litter around rock outcroppings, cave area (4, CMNC; 2, CWOB; 3 FSCA); Liberty Co.: TNC Apalachicola Bluffs & Ravines Preserve, Travelers Tract (30.46, -84.98), P.E. Skelley, 23 Mar 1996, leaf litter (3, ASUIC); Liberty Co.: Okaloosa Co.: Milligan (30.752, -86.64), G.B. Marshall, 21 Apr 1977 (2, CWOB); Torreya State Park (30.56, -84.96), R. Turnbow, 25 Jun-8 Jul 1989, pitfall (2, FSCA); Liberty Co.: Torreya State Park (30.56, -84.96), C.W. O'Brien & G.B. Marshall, 23 Mar 2001, berlese beech litter (2, CWOB). GEORGIA: Tatnall Co.: Big Hammock Natural Area, 19.3 km. S.W. Glennville (31.863, -82.058), C.W. O'Brien & P. Kovarik, 20 Mar 1999, live oak, mixed hardwood litter (1, CWOB).

Key to species of Eurhoptus LeConte in America north of Mexico

1 Body surface almost fully densely covered with broad flat scales, elytra with an irregular oblique band of lighter scales across elytra in apical one-half (Figures 8, 10). Legs with femora and tibiae fringed with dense erect scales on both inner and outer margins, hind tibiae with width distinctly greatest at basal one-third of length or at midlength2 Body surface lacking broad flat scales, or with a few broad, flat scales arranged in an irregular oblique band across elytra in apical one-half and at bases of intervals 3-5. Legs with tibiae at most fringed with a few erect scales especially along outer margin, hind tibiae subequal in width throughout most of length (except some E. cariniventris which have tibiae fringed along outer margin 2 Pronotum with broad, glabrous median line extended from apical one-quarter to base (Figure 10A), line recessed in a broad furrow between dorsal swellings on disc. Elytra with broad flat scales dense, imbricate, matte; intervals each with single row of rather broad, fully arched seta-like scales. Abdomen with large median pit on ventrite 1 lacking erect scales within pit (Figure 10C). (Hidalgo County, Texas) *E. rileyi* Pronotum lacking median line or with narrow median glabrous carina of various length (Figure 8A), pronotal disc uniformly rounded, lacking any dorsal swellings. Elytra with scales dense, imbricate, shining (may be matted); intervals each with single row of incompletely arched to appressed, narrow seta-like scales. Abdomen with large median pit on ventrite 1 with numerous erect scales within pit (Figure 8C)...... E. imbricatus 3 Pronotum with lateral margins more or less uniformly convergent from base to apex (e.g. Figure 2A), greatest width at base. Abdomen with ventrite 1 with single large cavernous, shining median pit (Figure 2E)......4 Pronotum with lateral margins rounded from apex to base (e.g. Figure 4A), greatest width in front of base. Abdomen with ventrite 1 with paired separate small round shallow pits (Figures 4C or 11C) to larger transversely elongate-4 Metaventral midline raised and carinate (Figure 14C). Elytra with scales of intervals fine, narrow. Many specimens with elytral punctures large and pitlike in area behind humeri (Figure 14B). Aedeagus as in Figures 14D–EE. cariniventris Metaventral midline impressed, not raised. Elytra with scales of intervals slightly broader but narrow. Most specimens with elytral punctures slightly larger in area behind humeri but not large and pit-like (Figure 2B). Aedeagus Abdomen with ventrite 1 with four distinct impressions (2 anteriorly, 2 pos-5 Abdomen with ventrite 1 with two distinct impressions (not, or variously confluent medially)......6

6	Impressions of abdominal ventrite 1 separate (Figure 4C). Pronotum with
	anterior constriction strong, lateral margins strongly sinuate; Aedeagus as in
	Figures 4D–E E. sordidus
_	Impressions of abdominal ventrite 1 variously confluent. Pronotum with an-
	terior constriction weak, lateral margins slightly sinuate7
7	Aedeagus as in Figures 12D-E. Pronotum usually with distinct median ca-
	rina. Abdomen with pits of ventrite 1 smaller, rounder (Figure 12C)
	E. aenigmaticus
_	Aedeagus as in Figures 6D–E. Pronotum usually lacking distinct median carina.
	Abdomen with pits of ventrite 1 larger, more obliquely oval (Figure 6C)
	E. curtus

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Supplementary material I

Table S1. Full data and GenBank accession numbers for all individuals and genes sequenced

Authors: Robert S. Anderson, Michael S. Caterino

Data type: molecular data

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Link: https://doi.org/10.3897/zookeys.787.26948.suppl1

RESEARCH ARTICLE



Two new species of genus Magadhaideus Long & Chen, 2017 from China (Hemiptera: Fulgoromorpha: Achilidae)

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Abstract

Two new species of the planthopper genus *Magadhaideus* Long & Chen, 2017 from China, *Magadhaideus luchunensis* **sp. n.** and *Magadhaideus pingbianensis* **sp. n.**, are described and illustrated. Photographs of the new species are provided and a key to species of *Magadhaideus* is also given.

Keywords

Achilid, distribution, new species, planthopper, taxonomy

Introduction

The planthopper tribe Plectoderini (Hemiptera: Achilidae) established by Fennah (Fennah, 1950), containing about 99 genera 346 species, is the largest tribe of Achilidae (Hemiptera: Fulgoromorpha). It is also the most widely disperssed in the world. Plectoderini consists of 13 genera and 26 species (Chen et al. 1989) in China. After that, some new species and genera were described by Wang et al. (2008), Xu and Liang (2012), He et al. (2010), and Long et al. (2015). The planthopper genus *Magadhaideus* (Achilidae: Plectoderini) was established by Long and Chen (2017) with *Magadhaideus xiphos* Long & Chen, 2017 from China as the type species. *Magadhaideus* is similar to *Magadha* in mesonotum bearing a transverse callus on anterior third of disc (readily distinguished from other known genera in the tribe Plectoderini), but differs from *Magadha* in the characteristics of pygofer, medioventral process and phallobase (Long et al. 2017).

The genus, so far, includes only two species, *M. cervina* and *M. xiphos*, which are only found in China (Fennah 1956; Long et al. 2017). In this paper, the specimens of *Magadhaideus*, depositing in the Institute of Entomology, Guizhou University, Guiyang, China, were re-examined, and yielded a further two new species from Yunnan, China. These are described and illustrated, bringing the total number of species of *Magadhaideus* to four species.

Material and methods

The morphological terminology and measurements used in this study follow Chen et al. (1989) and Yang and Chang (2000). The standard terminology for hind and forewing venation follow Bourgoin et al. (2015). The methods follow Long et al. (2017). Body length was measured from apex of vertex to tip of forewing; vertex length was measured the median length of vertex (from apical transverse carina to tip of basal emargination). The genital segments of the examined specimens were macerated in 10% KOH and drawn from preparations in glycerine jelly using a Leica M125 ster-eomicroscope. The type material is deposited in the Institute of Entomology, Guizhou University, Guiyang, China (**GUGC**).

Taxonomy

Magadhaideus Long & Chen, 2017 in Long et al. 2017

Magadhaideus Long et al., 2017: 22.

Type species. Magadhaideus xiphos Long & Chen, 2017 (original designation).

Diagnosis. Genus diagnostic characters mainly follow Long et al. (2017). Mesonotum with a transverse callus on anterior third of disc (Figs 5, 26; Long et al. 2017: fig. 5); pygofer in lateral view with dorsal margin distinctly shorter than ventral margin (Figs 11, 32; Long et al. 2017: fig. 11); each side of male anal segment with a strong spinous process, directed ventrally (Figs 10, 31; Long et al. 2017: fig. 10); medioventral process of male broad and short, with a small sharp process lateroapically (Figs 12, 33; Long et al. 2017: Fig. 12); phallobase with apical half branched into many more and longer processes.

Female genitalia. Anal segment (Figs 17, 38; Long et al. 2017: fig. 17) in dorsal view suborbicular, basal margin M-shaped approximatively. First valvula with five spines

(Figs 19, 40; Long et al. 2017: fig. 19). Second valvula with two lateral lobes incompletely symmetrical (Figs 20, 41; Long et al. 2017: fig. 20). Third valvula with outer surface shagreened (Figs 16, 37; Long et al. 2017: figs. 16, 18), in lateral view apical margin sinuate, with an angulate process ventrally (Figs 18, 39; Long et al. 2017: fig. 18).

Distribution. Oriental region (South China).

Key to the species of the genus Magadhaideus based on males

1	Medioventral process of pygofer with apical margin truncate, two lateroapical
	processes small or slender
_	Medioventral process of pygofer with apical margin not truncate, two later-
	oapical processes large
2	Medioventral process of pygofer with apical margin in the middle distinctly
	convex; phallobase of aedeagus with outermost left lateral processes with api-
	cal 1/2 distinctly bent, directed inwards (Fennah, 1956: fig. 15: D)
	M. cervina
_	Medioventral process of pygofer with apical margin in the middle concave;
	phallobase of aedeagus with outermost left lateral processes with apical 1/2
	hardly bent, directed apically (Figs 35-36)
3	Medioventral process of pygofer with two slender long lateroapical processes
	(Long et al., 2017: fig.12); phallobase of aedeagus in ventral
_	Medioventral process of pygofer with two much smaller and shorter later-
	oapical processes, not directed outward (Figure 12); aedeagus with phallobase
	in ventral view with six processes (Figure 15)
	M. luchunensis sp. n.

Magadhaideus luchunensis sp. n.

http://zoobank.org/3A4A9E53-0871-4563-B5A5-9E9661F001E7 Figs 1–21

Type material. Holotype: 3° , CHINA, **Yunnan**: Lüchun County, Huanglianshan, sweeping, 14 Aug 2014, Zheng-Xiang Zhou. Paratypes: **Yunnan**: $23^{\circ}3^{\circ}9^{\circ}9^{\circ}$, same data as holotype; $13^{\circ}2^{\circ}9^{\circ}$, Lüchun County, Lüboshuiku, sweeping, 13 Aug 2014, Mei-Na Guo; $13^{\circ}3^{\circ}9^{\circ}$, Lüchun County, Lüboshuiku, sweeping, 8 Aug 2017, Yang-Yang Liu.

Diagnosis. The salient features of the new species include the following: medioventral process of pygofer with two much smaller lateroapical processes (Fig. 12); and phallobase of aedeagus with right basal long lobe single, left apical short lobe directed laterally (Figs 14 - 15).

Description. Measurements. Body length (from apex of vertex to tip of forewing): male 4.9-5.1 mm (n = 2), female 5.0-5.5 mm (n = 7); forewing length: male 4.6-4.8 mm (n = 2), female 4.7-5.2 mm (n = 7).



Figures 1–15. *Magadhaideus luchunensis* sp. n. 1–2 Male habitus (dorsal and lateral views) 3–4 Female habitus (dorsal and lateral views) 5 Head and thorax, dorsal view 6 Face 7 Head, lateral view 8 Forewing 9 Hindwing 10 Anal segment of male, dorsal view 11 Male genitalia, lateral view 12 Male genitalia, ventral view 13 Left genital style, dorsal view 14 Aedeagus, dorsal view 15 Aedeagus, ventral view. Scale bars: 0.2 mm (8–13); 0.5 mm (5–7, 14–15).



Figures 16–21. *Magadhaideus luchunensis* sp. n. 16 Female genitalia, ventral view 17 Anal segment of female, dorsal view 18 Female genitalia, lateral view 19 First valvula, from inside 20 Second valvula, ventral view 21 Sclerite on entrance of bursa copulatrix, ventral view. Scale bars: 0.2 mm (16–18, 20–21); 0.5 mm (19.)

Colouration. Head yellowish brown. Vertex (Figs 1, 3, 5) along each lateral margin with one dark brown marking at base and another one brown marking at level of anterior margin of eyes, two short longitudinal dark brown markings along median carina apically. Frons (Figure 6) with seven dark brown markings along lateral margin, in middle scattered yellowish-white dots between eyes. Postclypeus pale yellowish, with a transverse brown band near apex. Frontoclypeus (Figure 6) dark brown, with the base and apex pale yellowish. Rostrum yellowish brown, with apex brown. Genae dark brown, as in Figure 7, area along anterior and dorsal margins combined pale yellowish brown, and four transverse short dark brown stripes along anterior margin, a broad transverse yellowish white band under the suture and another narrower one at level of junction of post- and frontclypeus. Eyes (Figs 1–7) generally reddish brown; ocellus (Figs 1, 3, 5) brown, lateral lobe with four to five dark brown areas along posterior margin, three carinae pale yellowish brown. Mesonotum (Figs 1, 3, 5) brown, transverse callus pale, posterior two-thirds between lateral carinae with few scattered ivorywhite dots, two dark markings at level of lateral carinae and posterior margin joined with peripheries pale yellowish brown, each lateral angle with a large ivory-white marking along posterior margin. Tegula (Figs 1–5) yellowish brown, along posterior margin paler. Forewing (Figs 1–4, 8) greyish brown, veins pale yellowish brown with small variably sized dark markings scattered, clavus with a broad irregular longitudinal dark brown band from base to apex. Hindwing pale brown, veins brown. Legs with colour pattern as in Figs 2 and 4, abdomen dark brown.

Head and thorax. Ratio width of vertex at posterior margin to its length in midline 1.8 (Figure 5), anterior third produced before eyes. Ratio length of frons in midline to its maximum width 1.1, ratio maximum of width to width at apex 1.7. Ratio length of postclypeus in midline to length of frons 0.5 (Figure 6). Rostrum with ratio apical to subapical segment 1.4. Lateral lobes of pronotum with three short longitudinal carinae behind eye, ratio length in midline to length of vertex 0.8 (Figure 5). Mesonotum (Figure 5) in midline 5.3 times longer than pronotum, 2.5 times longer than pronotum and vertex combined. Forewing (Figure 8) with ratio of length to maximum width 3.0, vein R with subapical cell. Hindwing (Figure 9) with length to maximum width ratio of 2.0. Post-tibiae with a lateral spine in basal one-fifths, spinal formula 7–6–6.

Male genitalia. Anal segment in dorsal view (Figure 10) with ratio length to maximum width 1.2, basal margin slightly concave, apical margin angularly convex in middle, in lateral view (Figure 11) with basal 2/3 broad, apical 1/3 slender as finger, roundly bent ventrally, lateral margin near middle with a strong spinous process, directed ventrally. Anal style (Figure 10) not exceeding apical margin of anal segment in lateral view. Pygofer in lateral view (Figure 11) with posterior margin with a large short process in the middle. Medioventral process (Figure 12) with width distinctly wider than length, apical not margin truncate, lateroapical margins with two small sharp processes. Genital style (Figure 13) with apical margin roundly convex, widest part at apical 2/5, a tortuous process rising from basal 1/3 of dorsal margin, branched into three lobes. Aedeagus (Figs 14–15) asymmetrical, phallobase in ventral view (Figure 15) with three long lateral processes rising from base, three short processes rising from base. Phallic appendages straight with apical margin roundly convex, not exceeding apical margin of phallobase.

Female genitalia. Seventh abdominal sternum in ventral view (Figure 16), posterior margin truncate or slightly concave. Anal segment (Figs 17–18) in dorsal view with ratio of length to its maximum width 1.4, anal stylet not exceeding apical margin of anal segment. Second valvula in ventral view (Figure 20), with ratio of width to its maximum length 1.1. Sclerite on entrance of bursa copulatrix in ventral view (Figure 21) prominent Y-shaped.

Etymology. This specific name refers to the type locality, Lüchun, Yunnan Province, China.

Host plant. Unknown. Distribution. China (Yunnan). **Remarks.** This species is similar to *M. xiphos* Long & Chen, 2017, but differs from the latter in: medioventral process of pygofer with two small teeth-like lateroapical processes (*M. xiphos* with two finger-like lateroapical processes); phallobase of aedeagus in ventral view with six processes (*M. xiphos* with seven processes).

Magadhaideus pingbianensis sp. n.

http://zoobank.org/84A1ED6C-97C0-480A-9EC0-2C17C9E2CF33 Figs 22–42

Type material. Holotype: \Im , CHINA: **Yunnan**, Pingbian County, Daweishan, 7 Aug 2014, Zheng-Xiang Zhou; Paratypes: $1\Im$, as paratypes Qiang Luo, 20 Aug 2017; $4\Im$, 8 Aug 2017, Hai-Yan Sun.

Diagnosis. The salient features of the new species include the following: medioventral process of pygofer with two larger lateroapical processes, directed inward (Figure 33); and phallobase of aedeagus with right basal long lobe branched into two processes, apexes bent, directed inwards, left apical short lobe directed apically (Figs 35–36).

Description. Measurements. Body length (from apex of vertex to tip of forewing): male 4.9-5.1 mm (n = 2), female 5.0-5.3 mm (n = 4); forewing length: male 3.5-3.9 mm (n = 2), female 4.6-4.8 mm (n = 4).

Colouration. Body with colour pattern (Figs 22–28) except the form of a broad irregular longitudinal dark brown band from base to apex of clavus (Figure 29), as same as *M. luchunensis* sp. n.

Head and thorax. Ratio width of vertex at posterior margin to its length in midline 2.0 (Figure 26), anterior third produced before eyes. Ratio length of frons in midline to its maximum width 1.2, ratio maximum of width to width at apex 1.8 Ratio length of postclypeus in midline to length of frons 0.5 (Figure 27). Rostrum with ratio apical to subapical segment 1.5. Lateral lobes of pronotum with three short longitudinal carinae behind eye, ratio length in midline to length of vertex 0.8 (Figure 26). Mesonotum (Figure 26) in midline 5.5 times longer than pronotum, 2.5 times longer than pronotum and vertex combined. Forewing (Figure 29) with ratio of length to maximum width 3.0, vein R with subapical cell. Hindwing (Figure 30) with length to maximum width ratio of 2.0. Post-tibiae with a lateral spine in basal 1/5, spinal formula 7–6–6.

Male genitalia. Anal segment in dorsal view (Figure 31) with ratio length to maximum width 1.2, basal margin roundly concave in middle, apical margin angularly convex in middle, anal style not exceeding apical margin of anal segment; in lateral view (Figure 32) with basal 2/3 broad, apical 1/3 slender as finger, roundly bent ventrally, lateral margin near middle with a strong spinous process, directed ventrally. Pygofer in lateral view (Figure 32) with posterior margin slightly sinuate. Medioventral process (Figure 33) short and broad, with two large lateroapical processes, apical margin truncate. Genital style (Figure 34) with apical margin roundly convex, widest part at apical 2/5, a twisted process rising from nearly basal 1/2 of dorsal margin, branched into three lobes. Aedeagus (Figs 35–36) asymmetrical, phallobase in ventral



Figures 22–36. *Magadhaideus pingbianensis* sp. n. 22–23 Male habitus (dorsal and lateral views) 24–25 Female habitus (dorsal and lateral views) 26 Head and thorax, dorsal view 27 Face 28 Head, lateral view 29 Forewing 30 Hindwing 31 Anal segment of male, dorsal view 32 Male genitalia, lateral view 33 Male genitalia, ventral view 34 Left genital style, dorsal view 35 Aedeagus dorsal view, 36 Aedeagus ventral view. Scale bars: 0.2 mm (29–34); 0.5 mm (26–28, 35–36).



Figures 37–42. *Magadhaideus pingbianensis* sp. n. **37** Female genitalia, ventral view **38** Anal segment of female, dorsal view **39** Female genitalia, lateral view **40** First valvula, from inside **41** Second valvula, ventral view **42** Sclerite on entrance of bursa copulatrix, ventral view. Scale bars: 0.2 mm (**37–39, 41–42**); 0.5 mm (**40**).

view (Figure 36) with three long lateral processes rising from apex, five long processes rising from base, with another single long irregular flaky bifurcation ventral processes rising from base. Phallic appendages straight with apical margin roundly convex, distinctly exceeding apical margin of phallobase.

Female genitalia. Seventh abdominal sternum in ventral view (Figure 37) with posterior margin distinctly concave. Anal segment (Figs 38–39) in dorsal view with ratio of width to its maximum length 1.0, anal stylet distinctly exceeding apical margin of anal segment. Second valvula in ventral view (Figure 41), with ratio of width to its maximum length 1.2. Sclerite on entrance of bursa copulatrix in ventral view (Figure 42) prominent, T– shaped.

Etymology. This specific name refers to the type locality, Pingbian, Yunnan Province, China.

Distribution. China (Yunnan).

Remarks. This species is similar to *M. cervina* (Fennah, 1956), but differs from the latter in: Medioventral process of pygofer with apical margin in the middle concave (*M. cervina* with apical margin in the middle distinctly convex); phallobase of aedeagus with outermost left lateral processes with apical 1/2 hardly bent, directed apically (*M. cervina* with outermost left lateral processes with apical 1/2 distinctly bent, directed inwards).

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RESEARCH ARTICLE



Roisinitermes ebogoensis gen. & sp. n., an outstanding drywood termite with snapping soldiers from Cameroon (Isoptera, Kalotermitidae)

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Abstract

Termites have developed a wide array of defensive mechanisms. One of them is the mandibulate soldier caste that crushes or pierces their enemies. However, in several lineages of Termitinae, soldiers have long and slender mandibles that cannot bite but, instead, snap and deliver powerful strikes to their opponents. Here, we use morphological and molecular evidence to describe *Roisinitermes ebogoensis* Scheffrahn, **gen. & sp. n.** from near Mbalmayo, Cameroon. Soldiers of *R. ebogoensis* are unique among all other kalotermitid soldiers in that they possess snapping mandibles. The imago of *R. ebogoensis* is also easily distinguished from all other Kalotermitidae by the lack of ocelli. Our study reveals a new case of parallel evolution of snapping mandibles in termites, a complex apparatus responsible of one of the fastest biological acceleration rates measured to date.

Keywords

Ethiopian Region, mandibles, ocellus, taxonomy

Introduction

Termites are extremely abundant (Martius 1994, Eggleton et al. 1996) and colonies may contain millions of individuals attracting a wide variety of predators (Deligne et al. 1981). Additionally, termites experience strong intra- and inter-specific competition (Levings and Adams 1984, Thorne and Haverty 1991). To combat against the plethora of agonistic opponents, termites have developed a rich array of defensive strategies. The most important defenses are expressed in the soldier caste that is ancestral to all extent termites (Roisin 2000).

Soldiers are specialized sterile colony defenders possessing exaggerated morphology of the head and mandibles (Prestwich 1984). One of their most intriguing defenses is exemplified by long and slender snapping mandibles (Deligne et al. 1981). The snapping mandibles are paired with muscles to store potential energy which, when released, delivers a powerful strike producing one of the fastest accelerations known among animals (Seid et al. 2008). All termite species with snapping soldiers described so far belong to the Termitinae (Bourguignon et al. 2017), suggesting that snapping soldiers evolved several times independently within this subfamily. Alternatively, soldiers with snapping mandibles might have evolved once, and independently reverted to a biting strategy in several lineages.

The monophyletic family Kalotermitidae (Inward et al. 2007) constitutes almost half of all "lower termite" genera and species (Krishna et al. 2013) and has fossil records to the mid-Cretaceous (Engel et al. 2009). Kalotermitids live entirely in wood as "one-piece" nesters (Abe 1987) which facilitates transoceanic dispersal (Scheffrahn and Postle 2013). Kalotermitids occur in all ecozones and numerous genera have vast distributions (e.g. *Calcaritermes, Cryptotermes, Glyptotermes, Kalotermes, Marginitermes, Neotermes*, and *Procryptotermes*). A few species of *Cryptotermes* (Scheffrahn et al. 2009) and *Incisitermes* (James et al. 2013, Yasuda et al. 2003) have also been dispersed by human activity. A few species are major pests of dry wood (Su and Scheffrahn 2000) or minor pests of tree crops (Constantino 2002).

The monumental revision of the Kalotermitidae by Krishna (1961) provided the morphological diagnoses for all extant genera with the exception of the recently described *Longicaputermes* (Ghesini et al. 2014). Aside from *Longicaputermes*, all new kalotermitid species described after Krishna's 1961 revision, ca. 115, have been assigned to one of the 21 genera he recognized. The soldier caste of several genera has unmistakable characters: e.g., the scooped out frons of *Eucryptotermes*, the massive third antennal article of *Marginitermes*, the large ovoid head of *Pterotermes*, or the spur on the fore tibia of *Calcaritermes*. We herein describe a new genus and species of Kalotermitidae, *Roisinitermes ebogoensis*, which possesses equally unmistakable soldiers. The soldier of *R. ebogoensis* is the first outside the Termitinae to have snapping mandibles.

Material and methods

Illustrations and measurements

Images of individuals were taken as multi-layer montages using a Leica M205C stereomicroscope with a Leica DFC 425 module run with Leica Application Suite software version 3. Preserved specimens, stored in 85% ethanol, were positioned in a transparent petri dish filled with Purell hand sanitizer (70% EtOH). Measurements (Tables 1–2) were obtained using an Olympus SZH stereomicroscope fitted with an ocular micrometer. A field photograph of live specimens placed in a small paper-lined Petri dish was taken with a Canon EOS 5DS R combined with a Canon EF 100mm f/2.8L Macro IS USM lens. Morphological terminology follows that of Krishna (1961).

Phylogenetic analyses

DNA was extracted from five individuals of *R. ebogoensis*, after removal of the digestive tract. The full mitochondrial genome was amplified with TaKaRa LA Taq in two long PCR reactions using primers specifically designed for termites (Bourguignon et al. 2016). Long PCR fragments were pooled in equimolar concentration, and 75bp paired-end reads were obtained using Illumina MiSeq. We subsampled a total of 10,000 reads and assembled the full mitochondrial genome with SPAdes, under default parameters (Bankevich et al. 2012). The total coverage of the assembly was 82-fold.

We used the mitochondrial genomes of ten species of Kalotermitidae, including one sample of *Roisinitermes ebogoensis* sequenced in this study. We used four non-Kalotermitidae termite species as outgroups to root the tree: *Zootermopsis angusticollis*, *Hodotermopsis sjostedti*, *Coptotermes sjostedti*, and *Termitogeton planus*. All mitochondrial genomes, except that of *R. ebogoensis*, have been published recently (Suppl. material 1: Table S1). Each gene of the mitochondrial genome was aligned separately using MAFFT v7.300b with the option "--maxiterate 1000 --globalpair" for higher accuracy. For protein-coding genes, we first aligned genes as protein, then converted protein sequence alignments into the corresponding codon alignments using PAL2NAL (Suyama et al. 2006). The 22 tRNAs and the two ribosomal RNAs were aligned as DNA. The resulting alignments were concatenated with FASTconCAT v1 (Kück and Meusemann 2010). Alignments were separated in five partitions: one for each codon position of the protein-coding genes, one for the combined ribosomal RNA genes, and one for the combined tRNA genes.

We reconstructed phylogenetic trees using Maximum Likelihood and Bayesian approaches. We ran the analyses twice, once with the third codon position included, and once without third codon position. The Bayesian phylogenies were implemented in MrBayes 3.2 (Ronquist et al. 2012) with unlinked partitions, each of four chains (three hot and one cold). The chain length was of two million generations with sampling every 2000 generations. 800,000 generations were discarded as burnin, to ensure that the chain reached convergence, as determined by Tracer 1.5 (Rambaut and Drummond 2007). We ran two replicates of each analysis to ensure consistency of the results. For each partition of the data, we assigned an independent Generalized Time Reversible model with gamma-distributed rate variation across sites and a proportion of invariable sites (GTR + G +I). The reconstruction of Maximum Likelihood phylogenies was carried out with RAxML (Stamatakis et al. 2008). We used the GTR-GAMMA model of rate heterogeneity across sites. Node support was estimated using 1000 bootstrap replicates.

Results

Phylogenetic analysis

Our phylogenetic analyses supported the monophyly of Kalotermitidae (Figure 1). The four analyses yielded identical tree topologies, with one exception: in the Bayesian analysis without third codon position *Rugitermes* was the sister group of *Neotermes* + *Cryptotermes* + *Incisitermes* + *Roisinitermes*, while in the other three analyses *Rugitermes* + *Neotermes* sp. A formed the sister group of *Neotermes insularis* + *Cryptotermes* + *Incisitermes*. *Roisinitermes* was consistently placed next to *N. insularis*.

Systematics

Roisinitermes Scheffrahn, gen. n.

http://zoobank.org/9AE40F98-CA9E-45AC-849E-A034F19E8DAE

Type-species. Roisinitermes ebogoensis Scheffrahn sp. n.

Winged Imago. Ocelli not visible either by pigmentation or cuticular protrusion (Figure 2A–C). Fore wing with unsclerotized media and cubitus arising from a common vein distal from scale suture; radial sector with 5–6 anterior branches; subcosta very close and difficult to discern from costal margin (Figure 2D). Hind wing with radial sector and cubitus arising from a common vein distal to suture. Tibial spurs 3:3:3; tarsi without arolia. The left imago/nymph mandible with anterior margin of their marginal tooth ca. 1.5 times longer than length of the posterior margin of second marginal tooth; right mandible with posterior margin of second marginal tooth 1.4 times as long as molar plate (Figure 3).

Diagnosis. The lack of visible ocelli is unique among all other Kalotermitidae. In Krishna's 1961 generic key, *Roisinitermes* would lead to couplet 2 (*Epicalotermes*).



Figure 1. Phylogenetic tree of Kalotermitidae based on full mitochondrial genomes. The tree depicted was reconstructed with RAxML using the data matrix without third codon position. Node labels are the Maximum Likelihood bootstrap supports and the Bayesian posterior probabilities in the following order, from left to right: posterior probability of the analysis with third codon position included, posterior probability of the analysis with third codon position included, posterior probability of the analysis without third codon position, bootstrap support of the analysis with third codon position, *indicates 100% bootstrap support and 1.0 posterior probability for all four analyses.

Soldier. Monomorphic (Figs 4, 5). Eye spots prominent; large, dark brown. Frons bilobed in dorsal view, crested with rugose longitudinal wrinkles, rugosity below frons oriented longitudinally. Small horn-like projection at terminus of ventral genae. Mandibles sticklike; downward arching in lateral view. Dentition very weak; basal humps project sharply.

Diagnosis. Stick-like mandibles unique among all other kalotermitid soldiers. In Krishna's 1961 key, *Roisinitermes* leads to couplet 17 (*Allotermes*). In dorsal view, the mandibular blades of *Allotermes*, especially *A. denticulatus* Krishna 1962, somewhat resemble those of *Roisinitermes* as those of the former are long, rather narrow and with rudimentary dentition. In lateral view, however, the *Roisinitiermes* mandibles differ from all other kalotermitids with projecting mandibles in that the *Roisinitermes* mandibles arch downward. Although the *Roisinitermes* imago venation and dentition is very similar to those of *Epicalotermes*, the soldier of *Roisinitermes* shares no major characters with the *Epicalotermes* soldier.

Etymology. The genus is named in honor of Dr. Yves Roisin for his many contributions to the study of termites.



Figure 2. Imago of *Roisinitermes ebogoensis* gen. & sp. n. **A** Dorsal view of head and thorax **B** Oblique view of head **C** Lateral view of head and thorax **D** Right forewing (arrow on subcosta) and right hind wing.

Roisinitermes ebogoensis Scheffrahn, sp. n.

http://zoobank.org/129573FB-E5DE-4673-9E1B-EF062D413FEB

Material examined. *Holotype*. Soldier from colony UF no. AFR3327. CAMEROON: Ebogo II, (+3.37723N, +11.46135E), 647 m elev., 18FEB18, col. Raphael Onana, AFR3327 ca. 500 alates, 50 soldiers, and many pseudergates, nymphs, larvae, and eggs. *Paratypes*. CAMEROON, Ebogo II (+3.38273N, +11.46190E), 664 m elev., 10DEC2016, col. Jan Šobotník and collaborators, AFR2982 4 soldiers (1 damaged), one female dealate, and 46 brachypterous nymphs.

Diagnosis. See generic diagnosis above.

Description. *Winged Imago* (Figure 2, Table 1) Head and pronotum light brownish orange; eye ovoid, anterior margin truncate abdominal tergites lighter, concolorous with legs and labrum; postclypeus nearly hyaline. Compound eyes black, of medium size and protrusion; ellipsoid but truncated near antennal socket, composed of approximately 85 facets. Ocelli not visible either by pigmentation or cuticular protrusion. Antennae with more than nine articles; formula 1>2=3=4<5. Pronotum width twice that of median length; several long and shorter setae project from lateral margins. Fore wing scale with basal origins of all major veins; wing membrane covered with papillae. Tibial spurs 3:3:3; tarsi without arolia.

Soldier (Figs 4–6; Table 2) Monomorphic. In dorsal view, head capsule yellowish orange in posterior grading to orange in middle and reddish brown from frons to ante-



Figure 3. Brachypterous nymph of *Roisinitermes ebogoensis* gen. & sp. n. Top: Dorsal view of mandibles. Bottom: lateral view of head and thorax.

clypeus. Three proximal antennal articles sepia brown; distal articles light brown. Post clypeus and labrum yellowish with brown highlights. Eye spots prominent; large, dark brown, elliptical; formed from a mass of discrete ommatidia. Pronotum concolorous with posterior head capsule. Head capsule in dorsal view, subrectangular; lateral margins nearly parallel, length 1.5 times width. Posterior corners of head evenly rounded;

	Males (n=6)				Females (n=6)			
Measurement	max	min	mean	max	min	mean		
Head max. width	1.05	0.95	1.00	1.05	1.00	1.03		
Pronotum max. width	1.00	0.89	0.96	1.05	0.93	1.01		
No. antennal articles	15	14	14.67	17.00	14.00	15.17		
Max diam. eye	0.40	0.32	0.36	0.39	0.35	0.37		
Body length with wings	9.63	8.63	9.10	9.88	9.50	9.65		
Fore wing length (suture to tip)	7.50	6.80	7.20	7.80	7.20	7.43		

Table 1. Measurements (mm) of Roisinitermes ebogoensis alates from a single colony.

Table 2. Measurements of *Roisinitermes ebogoensis* soldier (n=17 from two colonies).

Measurement	Max	Min	Mean
Head length to lateral mandible base	1.92	1.60	1.79
Head width, maximum	1.28	1.18	1.22
Head height with gula, max.	1.08	0.92	1.00
Pronotum length	0.70	0.56	0.65
Pronotum width	1.18	1.05	1.13
No. antennal articles	14	10	12.70
Left mandible width @ basal humps	0.35	0.21	0.26
Left mandible width @ middle	0.18	0.16	0.17
Max. diam. eye	0.26	0.18	0.21
Length left mandible from condyle (ventral)	1.78	1.46	1.66

posterior margin rectate. In lateral and oblique view, head capsule almost cylindrical with only slight dorso-ventral compression; frons bilobed in dorsal view, crested with rugose longitudinal stripes, rugosity lateral below frons to mandibles. In lateral view, frons sloping from vertex ~45°; mandibles bow upward to form a 15° arch. Setae short and sparse on pronotum and head capsule. Periantennal carina rugose, in dorsal view partially eclipsing the first antennal article. Small horn-like projection at terminus of ventral genae. Mandibles stick-like; long, blade narrower in middle than distal third, dentition very weak; left mandible with faint equilateral tooth approx. three fifths from base, serrations along blade from tooth to tip. Right mandible with single tooth approx. one third distance from base; blade narrowest before tooth; after tooth blade widens slightly and then gradually narrows at tip. In dorsal view, basal humps project sharply as rugose hemispheres. In lateral view, humps are columnar and equal in height to that of the mandibles. Anteclypeus shallowly incised in middle; labrum linguiform with gradual point; 4-5 long terminal setae. Antennae with 12-13 articles, third antennal article subclavate, barely shorter than fourth and fifth combined. Pronotum collar-shaped; much wider than long. Anterior margin weakly concave; lateral margins weakly convex, posterior margin forming 25° angle with incised middle. Femora moderately inflated, tibial spurs 3:3:3. Habitus as in Figure 6.

Brachypterous nymph (Fig. 3, Table 3) Body hyaline. Head, thorax, and abdomen similar in shape and pilosity of imago. Compound eyes with approx. 85 dark



Figure 4. Soldier (holotype) of *Roisinitermes ebogoensis* gen. & sp. n. Dorsal (**A**), lateral (**B**), and ventral (**C**) views of head and pronotum.



Figure 5. Dorsal view of frons and mandibles of *Roisinitermes ebogoensis* gen. n. sp. n. Inset: oblique ventral view of columnar hump (arrow).

Measurement	Max	Min	Mean
Head max. width	1.10	1.00	1.07
Pronotum max. width	1.16	1.08	1.11
No. antennal articles	15	15	15
Maximum diam. eye	0.20	0.20	0.20

Table 3. Measurements (mm) of *Roisinitermes ebogoensis* brachypterous nymph (n=10).

facets; both eyes and facets smaller than imago. Antennae with 15 articles; formula 1>2>3=4=5. Left mandible with anterior margin of marginal tooth 1.5 times longer than length of the posterior margin of the first plus second marginal tooth. Right mandible with posterior margin of second marginal tooth 1.4 times as long as molar plate.

Biology and distribution. The type colony of *R. ebogoensis* was collected in the forest on an island in the Nyong River near the Ebogo II village. The colony lived in a



Figure 6. Live habitus of soldier and brachypterous nymphs of Roisinitermes ebogoensis gen.et sp. n.

relatively thin (3 cm) and long (over 3 m) broad-leaf tree branch suspended from the canopy approximately 2 m above the ground. The colony contained roughly 2,000 members. A second colony of *R. ebogoensis* was collected in a nearly pristine rain forest near the village of Ebogo II. The colony was taken from a dead liana branch (ca. 15 mm diam.) hanging from the canopy at a height of approx. 1 m above the ground. Liana stems have been generally overlooked as a colonization site for Kalotermitidae (Scheffrahn et al. 2018). In light of Emerson's 1925 description of *Cryptotermes cubioceps* from a single soldier collected from a dead liana, this host should be probed routinely as a colonization site for kalotermitids.

Etymology. The species is named for the village of Ebogo II, the type locality for this termite.

Discussion

Kalotermitids inhabit a single woody item and are largely unable to move to a new food source once the original is exhausted. The lone exception is *Paraneotermes simplicicornis* that builds underground galleries connecting several wood pieces (Light 1937). The ability to feed on sound wood represents a defensive adaptation in itself as the hard food source acts as an efficient physical barrier against intruders. Kalotermitids thus show low soldier-to-worker ratios (see Haverty 1977) and soldiers reach a high level of polymorphism, reflected especially in the development of the headcap-

sule and mandibles. Some genera such as Bicornitermes, Cryptotermes, Eucryptotermes, Calcaritermes, or Glyptotermes, possess very short mandibles and a plug-like headcapsule to prevent intruder entry into a nest gallery (phragmosis). In C. cryptognathus from Jamaica, the mandibles are reduced to small stubs that do not project beyond the frontogenal boundaries of the head capsule, and therefore cannot be used to bite opponents (Scheffrahn et al. 1998). Some other genera (e.g., Bifiditermes, Epicalotermes, Incisitermes, Kalotermes, Neotermes) possess long mandibles with robust dentition (crushing mandibles *sensu* Prestwich 1984) used to injure an opponent mechanically. This is often combined with release of defensive secretions originating in the labial glands (Šobotník et al. 2010, Sillam-Dussès et al. 2012). Epicalotermes pakistanicus has particularly long and serrated mandibles (Akhtar 1974). The defensive strategy of Roisinitermes soldiers does not match any of these; instead, Roisinitermes employs a unique strategy of snapping, achieved by long and slender mandibles pressed against each other in a defensive encounter. When this potential energy is released, the left mandible springs over the right and the resultant snap is forced onto the opponent if it is in the path of the strike. This singular mandibular modification was previously known in several lineages of Termitinae (Deligne et al. 1981, Prestwich 1984, Seid et al. 2008), and was portrayed as a defensive strategy unique to this group. Roisinitermes represents the first undisputable evidence of parallel evolution of snapping soldiers.

Our phylogenetic analyses consistently placed *Roisinitermes* on a long branch, next to *N. insularis. Neotermes insularis* is a large termite species from Northern Australia with soldiers endowed with biting mandibles of crushing type. The smaller *Roisinitermes* shares no obvious similarity with *N. insularis*, supporting its generic status. Currently, the number of mitochondrial genomes available for Kalotermitidae is limited to a handful of genera, and there is a possibility that future phylogenetic analyses will support affinities between *Roisinitermes* and yet-to-be sampled taxa. In any case, the highly unusual morphology of *Roisinitermes* suggests that it shares no close relatives among modern Kalotermitidae. Future studies should focus on whether the mechanisms used by soldiers of *Roisinitermes* to snap are like those of the distantly related Termitinae.

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Supplementary material I

Table S1

Authors: Rudolf H. Scheffrahn, Thomas Bourguignon, Pierre Dieudonné Akama, David Sillam-Dussès, Jan Šobotník

Data type: molecular data

- Explanation note: Sources and GenBank accession numbers of mitochondrial sequences used for Fig. 1.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: https://doi.org/10.3897/zookeys.787.28195.suppl1

RESEARCH ARTICLE



Ecological diversity of a snake assemblage from the Atlantic Forest at the south coast of Paraíba, northeast Brazil

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Abstract

Despite an increase in studies focusing on snake ecology and composition in the northeastern Atlantic Forest, several poorly studied sites and environments remain. The aim of this study was to assess species richness and natural history attributes of the snakes of an assemblage in the Restinga, Tabuleiro and Forest environments of the Atlantic Forest of the south coast of Paraíba, northeastern Brazil. A total of 151 individuals of 27 species, 23 genera, and six families of snakes were found. The most effective sampling methods were time-constrained searches and incidental encounters. Species sampled most frequently were the blindsnake *Epictia borapeliotes*, the Boa Constrictor *Boa constrictor*, the Brown Vinesnake *Oxybelis aeneus*, and the Brazilian False Coral Snake *Oxyrhopus trigeminus*. The snake fauna is characterized mainly

by terrestrial species found in open-area environments of Restinga and Tabuleiro, and with most species feeding on amphibians and small mammals. The rarefaction curve did not reach the asymptote and new species should be recorded for south coast of Paraíba in future studies. Despite the richness and composition of snakes of the south coast being similar to other areas in the state, there is a lack of some species typically linked to forests, and this is probably because of the high level of deforestation that the south area of the state has suffered.

Keywords

inventory, natural history, open formations, restinga, Serpentes, species richness

Introduction

Biological surveys are the foundation for our knowledge on biodiversity. They also provide the groundwork for ecological studies and provide an outline for implementing conservation strategies (Greene 1994, Sutherland 1997). Since 1990, there has been an increase in surveys of Brazilian snakes, with information about richness and natural history published for different biomes, such as Amazonia (Martins and Oliveira 1998, Bernarde and Abe 2006), Southeast Atlantic Forest (Margues and Sazima 2004, Pontes et al. 2009), Northeast Atlantic Forest (França et al. 2012, Dias and Rocha 2014, Marques et al. 2016, Roberto et al. 2017), Caatinga (Vitt and Vangilder 1983, Mesquita et al. 2013), Cerrado (França et al. 2008, França and Braz 2013), Pantanal (Strussmann and Sazima 1993, Strüssmann et al. 2011), and Pampas grasslands (Winck et al. 2007). However, some sites and environments are still poorly known, such as coastal restingas and mangroves. Although some studies have been carried out in the restingas areas of the southeast of Brazil and in the State of Bahia in the northeast of Brazil (e.g. Rocha 2000, Hamdan and Lira-da-Silva 2012, Santos et al. 2012, Dias and Rocha 2014, Marques et al. 2016), no study was conducted in these environments in the most septentrional portion of the Atlantic Forest of the Northeast.

The Atlantic Forest is the most threatened biome in Brazil, and it has been suffering from intense deforestation and fragmentation since the time of European colonization. Even though less than six percent of the original vegetation remains, the Atlantic Forest still harbors high levels of biodiversity with more than 8,000 endemic species of vascular plants, amphibians, reptiles, birds and mammals (Myers et al. 2000). This degradation is even more evident in the portion of the Atlantic Forest located north of the São Francisco River, where an important endemism center in South America, the Pernambuco Endemism Center (hereafter PEC), is situated (Prance 1982, Tabarelli et al. 2005). In this region, sugarcane is the main agricultural crop, and other anthropogenic actions, such as animal and vegetal extraction, have reduced biodiversity in this region (Coimbra-Filho and Câmara 1996, Dean 1996). Today, the remaining 2% of the original forest cover of the PEC is represented by small fragments (mostly less than 10 ha) inserted in urban and agricultural matrices (Brown and Brown 1992, Ranta et al. 1998, Silva and Tabarelli 2000). The high richness and extensive threat of Northeast Atlantic Forest's loss underscore the urgency to
increase our knowledge of this region's biodiversity to develop effective conservation plans for the biome (Tabarelli et al. 2005).

In the Atlantic Forest of the four states (Rio Grande do Norte, Paraíba, Pernambuco and Alagoas) that comprise the PEC, the four main vegetation physiognomies in the region are: (a) Mangroves, saline-adapted tropical vegetation on the coast; (b) Coastal Restingas, low forest that grows on coastal sand dunes; (c) Semi-deciduous Forests, also known as Lowland Tabuleiro Forests, that are evergreen forests with natural savanna enclaves (called tabuleiros) that occur over faster-draining sand soils, and (d) Highland Stationary Forests, that are humid forest remnants scattered throughout Caatinga Highlands, known as Brejos de Altitude (Oliveira-Filho and Carvalho 1993, Thomas and Barbosa 2008).

The snake fauna of the Atlantic Forest of Paraíba State, in Northeast Brazil, has been studied previously, in the central and north portions, but the south of the State remains unknown (Pereira-Filho et al. 2017). Herein, we describe the snake composition at the south coast of Paraíba, providing information on richness and natural history attributes of the species, and comparing it with other snake assemblages of the region.

Materials and methods

The study was conducted in Barra de Gramame, located in the south of the municipality of João Pessoa at the South Coast of Paraíba State, Northeast Brazil (Figure 1) (07°14'00.5"S, 34°48'21.6"W; SAD69). In addition, we include specimens previously collected and housed in CHUFPB (Herpetological Collection of Universidade Federal da Paraíba) from adjacent municipalities of south coast of Paraíba State. These specimens were added for better characterization of snake fauna of the region. The municipalities that compose the south coast are Alhandra, Caaporã, Conde, Pedras de Fogo, Pitimbu, and the south of João Pessoa (Figure 1). The south coast extends for 33 km in Paraíba State.

The Barra de Gramame area covers approximately 843 ha (Figure 1), with mean annual precipitation of 1,800 mm and a rainy season between May and August, according to the data provided by Instituto Nacional de Meteorologia (INMET, http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep) (Figure 2). Surveys were conducted from 1 January 2012 through 31 December 2013 in all three physiognomies present in the area: Evergreen Forests and Savanna enclaves – both from Lowland Tabuleiro Forests – and in Coastal Restingas (Figure 3).

For the fieldwork conducted in Barra de Gramame, we employed the following snake survey methods: time-constrained search, incidental encounters, and specimens donated by local people. Snake specimens were obtained from January 2012 to December 2013 predominantly through 2520 man-hours of time-constrained search (see Martins and Oliveira 1998) in both diurnal (1620 men/h) and nocturnal (900 men/h) surveys. Regarding the donated specimens, we did not encourage local people to kill snakes, but they usually kill all encountered snakes, so we asked them to preserve the dead snakes for further identification. The collection methods for specimens of other municipalities (not Barra de Gramame in João Pessoa) were not available in the Herpetological Collection.



Figure 1. Schematic map showing the south coast of Paraíba state. Detail box: Barra de Gramame, located in the municipality of João Pessoa. The numbers represent the following municipalities: **1** João Pessoa **2** Conde **3** Alhandra **4** Pitimbu **5** Caaporã and **6** Pedras de Fogo.



Figure 2. Variation of temperature, maximum (line with square) and minimum (line with triangle), precipitation as bars. Data from January 2012 and December 2013 (Source: INMET, http://www.inmet. gov.br/portal/index.php?r=bdmep/bdmep).



Figure 3. Phytophisiognomies of Atlantic Forest in south coast of Paraíba. **A** Forest **B** Restinga **C** Savanna enclave (Tabuleiro). Photograph credits: Ivan L. Sampaio (**A**, **B**), Frederico G. França (**C**).

For each specimen found in Barra de Gramame, we recorded information on location (with GPS), time, habitat use and microhabitat, and morphology. Snakes were collected under ICMBio collecting permit (SISBIO license 37318-1), preserved in 10% formalin and deposited in Coleção Herpetológica da Universidade Federal da Paraíba (Appendix). Some individuals of the most common species were released after we marked them by clipping ventral scales to identify them as previously captured. No recapture was obtained in this study. We categorized the snake size considering the mean body size of each species based on published data (França and Araújo 2006, Pereira-Filho et al. 2017) as small (<500mm), moderate (501–1000mm) and large (>1001mm).

We constructed the species accumulation curves for the snakes of the South Coast using the individual-based rarefaction method (with the nonparametric Mao Tau estimator) to evaluate the relationship between collection effort and species saturation in the assemblage (Gotelli and Colwell 2001). The function of richness (Mao Tau) was calculated as the accumulation function of species throughout the number of individuals collected. The species rarefaction curve was made without replacement using 1000 randomizations. In addition, we used species richness estimators (with nonparametric incidence-based estimators: Bootstrap, Chao 2, ICE, Jacknife 1 and 2, and abundance-based data: ACE and Chao 1) to determine the expected richness of snakes in each area (Colwell and Coddington 1994). The species rarefaction and richness estimators were performed with EstimateS 9.1.0 software (Colwell 2013).

Results

We recorded 151 individuals of 27 species, 23 genera, and six families (Boidae, Colubridae, Elapidae, Leptotyphlopidae, Typhlopidae, and Viperidae) (Table 1, Figures 4, 5). The most common snake species were the blindsnake *Epictia borapeliotes*, the Boa Constrictor *Boa constrictor*, the Brown Vinesnake *Oxybelis aeneus*, the Brazilian False Coral Snake *Oxyrhopus trigeminus*, and the Patagonia Green Racer *Philodryas patagoniensis* representing more than 50% of all records (Table 1). The rarest species were the Garden Tree Boa *Corallus hortulanus*, Boettger's Sipo *Chironius flavolineatus*, the Rio Tropical Racer *Mastigodryas bifossatus*, the Caninana *Spilotes pullatus*, the watersnake *Erythrolamprus taeniogaster*, the Forest Flame Snake *Oxyrhopus petolarius*, the Argentine Pampas Snake *Phimophis guerini*, Wagler's Snake *Xenodon merremii*, the Caatinga Coral Snake *Micrurus ibiboboca*, and Brongersma's Worm Snake *Amerotyphlops brongersmianus*, with only one record each. All sample methods contributed to the snake sampling. Of the 118 individuals found in Barra de Gramame, 52 were captured during time-constrained searches, local collectors donated 13 individuals, and 48 were found by incidental encounters.

The individual-based rarefaction curves didn't reach stability (Figure 6) and the species richness estimators produced estimates greater than the observed richness, indicating a higher number of species for the locality. Estimates varied between 31.09 ± 0.35 and 51.83 ± 32.04 (Table 2).



Figure 4. Species from the Atlantic Forest in south coast of Paraíba. A Boa constrictor B Epicrates assisi C Corallus hortulanus D Chironius flavolineatus E Oxybelis aeneus F Mastigodryas bifossatus G Spilotes pullatus H Tantilla melanocephala I Erythrolamprus taeniogaster J Helicops angulatus K Hydrodynastes gigas L Oxyrhopus petolarius M Oxyrhopus trigeminus N Philodryas nattereri O Philodryas olfersii. Photograph credits: Ivan L. Sampaio (A, B, C, E, K, L, M, N, O), Frederico G. França (D, H, I, J), Mayara Morais (F), Willianilson Pessoa (G).



Figure 5. Species from the Atlantic Forest in south coast of Paraíba: A Philodryas patagoniensis B Phimophis guerini C Sibon nebulatus D Sibynomorphus mikanii E Taeniophallus occipitalis F Xenodon merremii
G Micrurus ibiboboca H Micrurus potyguara I Epictia borapeliotes J Amerotyphlops brongersmianus K Bothrops leucurus L Crotalus durissus. Photograph credits: Ivan L. Sampaio (A, B, D, E, H, I), Frederico G. França (F, G, J, L), Pedro T. S. Moura (C) Rafaela C. França (K).

The snakes showed a diversity of habits and food preferences (Table 1). Three species are fossorial (11%), three are primarily cryptozoic (11%), three show aquatic habits (11%), ten are strictly terrestrial (37%), five utilize both terrestrial and (semi-) arboreal habits (18%), and three are strictly arboreal snakes (11%). Of the 27 snake species, 22 were found exclusively in one habitat of the south coast: 13 in Tabuleiro, four in Restinga, and five in Forest. In addition, two were found in Tabuleiro and Restinga, two in Tabuleiro and Forest, and only *Boa constrictor* was found in all habitats (Table 1).



Figure 6. Individual-based rarefaction curve with standard deviation of snake species of south coast of Paraíba.

Natural history of species

Below we present information on morphology, habitat use, and activity of all snake species found on the south coast of Paraíba. We include data on diet, habitat, and habits from published literature.

BOIDAE: *Boa constrictor* – A large terrestrial species (average SVL = 904.25 mm; range from 400 to 2000 mm; N = 16). Second most common species in the study area. Six individuals were found active during the day between 10:40 and 17:30, despite literature records indicating nocturnal activity for the species (Henderson and Powell 2007). Four snakes showed aggressive behavior during the approach, striking and opening their mouth. Other three individuals were found dead by local people. This species eats mammals and birds (Marques et al. 2001); *Corallus hortulanus* – A large arboreal snake (SVL = 945 mm; N = 1). The species was found resting in the roof of a house at 15:30 and was striking constantly during the capture. This species eats mammals and birds (Marques et al. 2001); *Epicrates assisi* – A large terrestrial species (average SVL = 788 mm; range from 560 to 1240 mm; N = 5). All individuals were collected alive and active at night (from 18:00 to 19:25) both in Tabuleiro and Forest. This species eats mammals, birds and lizards (Vitt and Vangilder 1983).

COLUBRIDAE: COLUBRINAE: *Chironius flavolineatus* – A moderate-sized semiarboreal species (SVL = 598 mm; N = 1). No data of habitat use for the south coast is available. This species eats primarily amphibians (Pereira-Filho et al. 2017). *Oxybelis aeneus* – An arboreal, moderate-sized species (average SVL = 721 mm; range 550 to 985 mm; N = 14). All individuals were found active during the day (from 7:40 to 16:00) and most (11) were in trees and shrubs, while three were found active on the ground. Some **Table 1.** Summary of the Information of Natural History of the Snakes in Barra de Gramame. Abbreviations of Municipalities are: AL = Alhandra; CA = Caaporá; CO = Conde; JP = João Pessoa (Barra de Gramame), PF = Pedras de Fogo, PI = Pitimbu. Habits are: AB = arboreal, AQ = aquatic, CR = cryptozoic, FO = fossorial, TE = terrestrial, SAB = semi-arboreal. Habitats are: T = tabuleiro, F = forest, R = restinga, * = Data from Herpetological Collection. Diet are: am = amphibians, an = anfisbaenas, ar = arthropods, bi = birds, fi = fishes, li = lizards, ma = mammals, sl = snails, sn = snakes. Capture Methods are: TCS = time-constrained search, DO = donated, IE = incidental encounters; – No data available (see methods).

Family / Species (number of species)	Ν	Municipality	Habits	Habitats	Diet	Capture method
Boidae (3)						
Boa constrictor Linnaeus, 1758	16	JP	SAB	T, F, R	ma, bi	TCS, DO, IE
Corallus hortulanus (Linnaeus, 1758)	1	JP	AB	Т	ma, bi	DO
Epicrates assisi Machado, 1945	10	AL, CO, JP, PI	TE, SAB	T, F	ma, bi, li	TCS, DO
Colubridae; Colubrinae (5)						
Chironius flavolineatus Jan, 1863	1	AL	SAB	F*	am	_
Oxybelis aeneus (Wagler, 1824)	14	JP	AB	Т	li	TCS, DO, IE
Mastigodryas bifossatus (Raddi, 1820)	1	СО	TE	T*	ma	_
Spilotes pullatus (Linnaeus, 1758)	1	PF	SAB	F*	ma, bi	_
<i>Tantilla melanocephala</i> (Linnaeus, 1758)	5	AL, JP	FO	T, R	ar	TCS, IE
Colubridae; Dipsadinae (13)						
Erythrolamprus taeniogaster (Jan, 1863)	1	JP	TE, AQ	R	fi, am	IE
Helicops angulatus (Linnaeus, 1758)	3	CA, JP	AQ	R	fi, am	TCS
<i>Hydrodynastes gigas</i> (Duméril, Bibron & Duméril, 1854)	5	JP	AQ	R	fi, am, sn, ma	TCS, IE
Oxyrhopus petolarius Reuss, 1834	1	JP	TE	Т	ma, li	TCS
Oxyrhopus trigeminus Duméril, Bibron & Duméril, 1854	16	CA, CO, JP	TE	T, F	ma, li	TCS, DO, IE
Philodryas nattereri Steindachner, 1870	8	AL, JP	TE	Т	ma, bi, li, an	TCS, DO, IE
Philodryas olfersii (Lichtenstein, 1823)	10	JP, PI	TE, SAB	Т	ma, bi, li, an	TCS, DO, IE
Philodryas patagoniensis (Girard, 1858)	11	JP	TE	T, R	ma, bi, li, an	TCS, DO, IE
<i>Phimophis guerini</i> (Duméril, Bibron & Duméril, 1854)	3	CO, JP	CR, TE	Т	li	IE
Sibon nebulatus (Linnaeus, 1758)	1	PF	AB	F	sl	-
Sibynomorphus mikanii (Schlegel, 1837)	10	AL, CA, JP	TE	Т	sl	DO
Taeniophallus occipitalis (Jan, 1863)	7	AL, CA, JP	TE	Т	am	TCS, DO, IE
Xenodon merremii (Wagler, 1824)	1	СО	TE	F*	am	_
Elapidae (2)						-
Micrurus ibiboboca (Merrem, 1820)	1	AL	CR, TE	T*	an, sn	-
Micrurus potyguara Pires, Silva, Feitosa, Prudente, Pereira Filho & Zaher 2014	3	JP	CR, TE	Т	an, sn	TCS, DO
Leptotyphlopidae (1)						
Epictia horapeliotes (Vanzolini, 1996)	16	IÞ	FO	Т	ar	TCS DO IF
Typhlopidae (1)	10	JI	10	1	ui	100, 20, 12
Ameratyphlaps brangersmianus						
(Vanzolini, 1976)	1	CA	FO	T*	ar	-
Viperidae (2)		1	1	L		1
Bothrops leucurus Wagler, 1824	2	AL, CA	TE	F*	ma, li, an	_
Crotalus durissus Linnaeus, 1758	2	СО	TE	R*	ma	_

individuals presented open-mouth threats and striked during the approach, while others remained immobile, swaying their body like a branch. In addition, many individuals displayed cloacal discharge during handling. This species eats primarily lizards (França and Araújo 2007); *Mastigodryas bifossatus* – A large terrestrial species (SVL = 325 mm; N = 1). No data of habitat use for the south coast is available. This species eats amphibians and small mammals (Marques and Muriel 2007). *Spilotes pullatus* – A large, semi-arboreal species (SVL = 580 mm; N = 1). No data of habitat use for the south coast is available. This species eats araphibians and small mammals (Marques and Muriel 2007). *Spilotes pullatus* – A large, semi-arboreal species (SVL = 580 mm; N = 1). No data of habitat use for the south coast is available. This species eats primarily mammals and birds (Pereira-Filho et al. 2017). *Tantilla melanocephala* – A small-sized terrestrial species (average SVL = 193 mm; range 150 to 210 mm; N = 4). One individual captured in tabuleiro and one found dead on unpaved road. Two individuals were active during the afternoon (16:00–16:30), although the species is known to forage at night for active prey, mainly centipedes (Marques and Puorto 1998).

COLUBRIDAE: DIPSADINAE: Erythrolamprus taeniogaster - A moderate-sized semi-aquatic species (SVL = 385 mm; N = 1). One individual was found resting in the water at 9:00. This species eats anurans (França et al. 2012). Helicops angulatus – A moderate-sized aquatic species (SVL = 635 mm; N = 1). One individual was found in mangroves in the river. This species eats fishes and anurans (Ford and Ford 2002); Hydrodynastes gigas – A large aquatic species (average SVL = 884 mm; range 714 to 1048 mm; N = 5). Despite this species being considered rare in Northeast Brazil (Pereira-Filho et al. 2017), we recorded an intermediate abundance (N = 5). Local fisherman killed two individuals in the morning (approximately 8:00 and 8:30) when they were moving between sand beaches and salty water. Another two were found dead on a paved road near a river. One active individual was captured in restinga at 10:00 and displayed several defensive behaviors such as striking and biting, tail whip, and cloacal discharge. This species eats fishes, anurans, snakes and mammals (López and Giraudo 2004); Oxyrhopus petolarius - A moderate-sized terrestrial species (SVL = 245 mm; N = 1). The individual found was active in tabuleiro habitat at 18:20. This species eats lizards, small mammals and birds (Cunha and Nascimento 1978). Oxyrhopus trigeminus – A moderate-sized terrestrial species (average SVL = 420 mm; range 174 to 900 mm; N = 12). Seven individuals were active at night (18:00-20:30), and two in the afternoon (15:50 and 17:00). Five were found moving on the ground of tabuleiro and two were immobile on leaf litter. Some individuals displayed cloacal discharge during handling. This species eats lizards and small mammals (França et al. 2008); Philodryas nattereri – A large-sized terrestrial (or semi-arboreal) species (average SVL = 813 mm; range from 500 to 981 mm; N = 6). All individuals were found active during the day (from 10:40 to 13:30) moving on sandy soil or near residences. Three individuals displayed aggressive behaviors of striking and biting. This species has a generalized diet, which includes mammals, birds, lizards and amphibians (Vitt and Vangilder 1983); Philodryas olfersii – A moderate-sized semi-arboreal species (average SVL = 557 mm; range from 410 to 750 mm; N = 9). Seven individuals were found active during the day (from 10:00 to 15:20). Four snakes displayed aggressive behaviors of striking, biting and cloacal discharge. This species eats anurans, small mammals, lizards and

Richness Estimators	Mean ± Std Deviation
Observed Richness	27
ACE	40.59 ± 1.16
CHAO 1	51.83 ± 24.08
CHAO 2	51.83 ± 32.04
ICE	40.21 ± 1.13
JACKNIFE 1	36.93 ± 3.05
JACKNIFE 2	44.84 ± 0.91
BOOTSTRAP	31.09 ± 0.35

Table 2. Richness estimators of snake assemblages for the south coast of Paraíba.

birds (Hartmann and Marques 2005, Leite et al. 2009); Philodryas patagoniensis - A moderate-sized terrestrial species (average SVL = 576 mm; range from 250 to 885 mm; N = 11). Six individuals were found active during the day (from 10:00 to 13:00), and all displayed defensive behaviors of striking, biting and cloacal discharge. This species has a generalized diet, which includes mammals, birds, lizards and amphibians (Hartmann and Marques 2005); Phimophis guerini - A moderate-sized terrestrial species (SVL = 687 mm; N = 1). Only one individual was found active in the twilight (17:50) moving on a paved road. It eats lizards (Sawaya et al. 2008). Sibon nebulatus – A small to moderate size arboreal species (SVL = 400mm; N=1). One individual was found active at 13:00 in a forest edge. This species eats snails (Pereira-Filho et al. 2017); Sibynomorphus mikanii – A small to moderate size terrestrial snake (average SVL = 287 mm; range from 155 to 420 mm; N = 2). One individual was found inactive on the floor of a house and one was active at night near a small pond. This species eats snails (Laporta-Ferreira et al. 1986). Taeniophallus occipitalis – A small to moderate size terrestrial species (average SVL = 295 mm; range from 150 to 450 mm; N = 5). Four individuals were found active during the day (from 15:00 to 17:30) in tabuleiro habitat. This species eats amphibians (Marques et al. 2001). Xenodon merremii - A large size terrestrial species (SVL = 388 mm; N = 1). No data of habitat use for the south coast is available. This species eats frogs (Pereira-Filho et al. 2017).

ELAPIDAE: *Micrurus ibiboboca* – A moderate-sized cryptozoic species (SVL = 525 mm; N = 1). No data of habitat use for the south coast is available. This species eats amphisbaenians and snakes (Roze 1996). *Micrurus potyguara* – A moderate-sized cryptozoic species (average SVL = 634 mm; range 320 to 925 mm; N = 3). Three individuals found active at night (from 19:00 to 21:00) and near residences. Two snakes displayed defensive behaviors of tail raising and head hiding. This species eats amphisbaenians and snakes (Pereira-Filho et al. 2017).

LEPTOTYPHLOPIDAE: *Epictia borapeliotes* – A small-sized fossorial species (average SVL = 110 mm; range from 70 to 136 mm; N = 16). This was the most common species in Gramame and it was very adapted to anthropic areas. All individuals were found active moving on sand, on grass and on unpaved and paved roads, during the day and twilight (from 8:45 to 17:30). Many individuals stung with tail points when handled. The representatives of this family eat ants and larvae, but there is no information on the diet of this species.

TYPHLOPIDAE: *Amerotyphlops brongersmianus* – A small-sized fossorial species (SVL = 212 mm; N = 1). No data of habitat use for the south coast is available. This species eats ant larvae (Ávila et al. 2006).

VIPERIDAE: *Bothrops leucurus* – A large terrestrial species (SVL = 587 mm; N = 1). This species frequently is found in the urban area and in preserved forest patches. No data of habitat use for the south coast is available. This species eats frogs (juveniles) and small mammals (adults) (Campbell and Lamar 2004). *Crotalus durissus* – A large terrestrial species (SVL = 1070 mm; N = 2). No data of habitat use for the south coast is available. This species eats small mammals (Campbell and Lamar 2004).

Discussion

The snake fauna of Barra de Gramame presents similar richness and composition compared with other snake assemblages from central and north coast of Paraíba State (Pereira-Filho et al. 2017). The snake fauna of the south coast comprises species found in other areas of Atlantic Forest of Paraíba State in the north coast (Pereira-Filho et al. 2017). However, some common species were absent and should appear in future surveys, such as the Pernambuco Worm Snake *Typhlops paucisquamus* and the Yellow-bellied Swamp Snake *Erythrolamprus poecilogyrus*. Nevertheless, some snakes that are rare at the north coast, such as the False Water Cobra *Hydrodynastes gigas*, and the Garden Tree Boa *Corallus hortulanus*, were found in the area and represent new distribution records for the State (Pereira-Filho et al. 2017).

Despite the savanna enclaves extending along all the Northeast Atlantic Forest, this physiognomy is poorly known and highly threatened because of agriculture and pastures (Endres et al. 2007, Thomas and Barbosa 2008). Nevertheless, these open environments can harbor high diversity and a rich snake fauna, with species found in other open biomes, such as Cerrado and Caatinga, but not in forest portions of Atlantic Forest (Rodrigues et al. 2015. Fossorial species (such as scolecophidians) are commonly found in these environments, mainly because of the sandy soil (Rodrigues et al. 2015).

Although the reptiles of costal Restingas have been commonly studied in the Southeast and Central Atlantic Forest (Rocha 2000, Santos et al. 2012, Marques et al. 2016), little information is available for northern portions of the biome, and here we present the first records of snakes from coastal Restingas of Paraíba State. We found some similarities of composition in this habitat with both *Boa constrictor* and *Tantilla melanocephala* that also commonly are found in southeastern Restingas (Dias and Rocha 2014, Martins et al. 2012), and aquatic snakes found both in fresh and salty water. The Cascabel Rattlesnake *Crotalus durissus* is also found in other Restingas (Marques et al., 2016). This species is associated with open areas, commonly found in Cerrado and Caatinga (França et al. 2008; Vanzolini et al. 1980) and it supposedly reaches Brazilian coast regions dispersing through deforested areas of Atlantic Forest (Bastos et al. 2005).

Two species are typical of forest environments (*Sibon nebulatus* and *Bothrops leucurus*), and six are habitat generalist, occurring also in open areas. This richness of forest snake species for the south coast is low if compared with assemblages studied for the north and central coasts (Pereira-Filho et al. 2017). While we found only 20% of snakes inhabiting forests of the south coast, the snake fauna of north and central coast of the state are represented by more than 50% of forests snake species (Pereira-Filho et al. 2017).

Despite the presence of open area of Restinga and Tabuleiros, there is a lack of large forest patches in the south coast that are present in other areas of Paraíba State (Rodrigues et al. 2015). Most of the forest in the south coast has been lost or reduced to small fragments since the occupation of the area for agriculture and urbanization (Furrier and Silva Barbosa 2016). Therefore, the snake fauna seems to be depleted, lacking some species typically linked to forests, such as *Imantodes cenchoa, Thamnodynastes hypoconia, Pseustes sulphureus,* and *Lachesis muta.* The open areas of restinga and tabuleiro still are preserved more than forests, reflecting in more species found in these locations. However, the region of Gramame, in the south of João Pessoa municipality, and other south coast beaches, such as Coqueirinho and Tambaba, in Conde municipality, and Praia Bela, in Pitimbu municipality are parts of a tourist occupation program of the south coast of Paraíba, which should increase the damage both on vegetation and on the Gramame river basin (Silva et al. 2002).

It is important to emphasize that there are large gaps in the conservation status of snake species in the PEC region; of the 27 species of snakes reported in this study, only two species (*Corallus hortulanus* and *Crotalus durissus*) were evaluated by the IUCN. In addition, some species are still being discovered in the PEC region, and have little information available, such as *Micrurus potyguara* (described in 2014) (Pires et al. 2014) and *Amerothyplops arenensis* (described in 2015).

Finally, comparing with other snake assemblages in Paraíba, the fauna of south coast shows some peculiarities. The most common species was a blindsnake, the same as the North Coast (Rodrigues et al. 2015). However, the species differ in the areas (*Epictia borapeliotes* in Gramame vs *Typhlops paucisquamus* in Guaribas Biological Reserve). The scolecophidian snakes are small and fossorial species, and the sandy soil of restinga and tabuleiro forests may favor the presence of these species. Also, we recorded the presence of two rare species for Paraíba state, the False Water Cobra *Hydrodynastes gigas* and the Garden Tree Boa *Corallus hortulanus*. These species have only been found in few areas in Paraíba (Pereira-Filho et al. 2017), and the former seems to be threat-ened in the State, mostly because of the high levels of water pollution in rivers where the species is present (Pereira-Filho et al. 2017). Additional species are expected to appear in future surveys in Gramame and in the south coast of Paraíba. The information acquired from snake species composition, ecology and distribution should be used for the planning of urbanization and conservation of the south coast of Paraíba.

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Appendix I

Snake species collected at the Paraíba state's south coast, northeast Brazil, and housed at the Coleção Herpetológica da Universidade Federal da Paraíba

João Pessoa - Barra de Gramame: Boa constrictor (CHUPB 12252/RT 419, RT 603, RT 661, RT 790), Corallus hortulanus (BG 40), Epicrates assisi (RT 792), Epictia borapeliotes (RT 531, RT 645, RT 646, RT 705, RT 825, RT 864, RT 887, RT 890), Erythrolamprus taeniogaster (RF 106), Helicops angulatus (RT 847), Hydrodynastes gigas (BG 26), Micrurus potyguara (RT 860), Oxybelis aeneus (RT 606, RT 700, RT 747, RT 861, RT 862, RT 889), Oxyrhopus petola (RT 701), Oxyrhopus trigeminus (RT 703, RT 765, RT 793, RT 859, RT 891, RT 892), Philodryas nattereri (CHUFPB 7669/RT 166, RT 763), Philodryas olfersii (RT 072, RT 702, RT 748, RT 888), Philodryas patagoniensis (RT 223, RT 604, RT 605, RT 706, RT 750, RT 791), Taeniophallus occipitalis (RT 704, RT 749), Tantilla melanocephala (RT 766, RT 893); Alhandra: Bothrops leucurus (UFPB 12963); Chironius flavolineatus (UFPB 9374); Epicrates assisi (UFPB 13163), Micrurus ibiboboca (UFPB 13636); Philodryas nattereri (UFPB 13642); Sibynomorphus neuwiedi (UFPB 12643); Taeniophallus occipitalis (UFPB 9390); Tantilla melanocephala (UFPB 9389); Caaporã: Amerotyphlops brongersmianus (CHUFPB 15704); Bothrops leucurus (UFPB 12961); Helicops angulatus (CHUFPB 15670, 15715); Oxyrhopus trigeminus (CHUFPB 15806); Sibynomorphus mikanii (UFPB 12948-53); Taeniophallus occipitalis (CHUFPB 15837); Conde: Crotalus durissus (UFPB 5053, 5803); Epicrates assisi (UFPB 13163), Mastigodryas bifossatus (UFPB 4825); Oxyrhopus trigeminus (UFPB 13157-8); Phimophis guerini (UFPB 13976-7); Xenodon merremii (UFPB 13974); Pitimbu: Epicrates assisi (UFPB 13164, 13179, 13199), Philodryas olfersii (UFPB 13650); Pedras de Fogo: Spilotes pullatus (UFPB 13981).

RESEARCH ARTICLE



New records of Niceforo's big-eared bat, Trinycteris nicefori (Sanborn, 1949) (Chiroptera, Phyllostomidae), from the state of Maranhão, Brazil

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Abstract

Niceforo's big-eared bat, *Trinycteris nicefori* (Sanborn, 1949), is a monotypic species which has been recorded in a number of Brazilian states, but has a disjunct distribution in this country. This study presents the first record of *T. nicefori* in the Brazilian state of Maranhão. The specimens were collected in the municipalities of Godofredo Viana and Cândido Mendes, in fragments of the Amazon forest. One male (forearm: 38.00 mm, weight: 6 g) and one female (39.68 mm, 8 g) specimens were collected. The specimens presented chestnut-colored fur, and a chin with a pair of dermal pads arranged in a V-shape, without a central papilla. The COI gene sequences were plotted in the BOLD Systems platform, which confirmed the morphological identification of the species, with a 99.1% similarity in the male, and 99.4% in the female to existing sequences. This record extends the known distribution of *T. nicefori* in Brazil by approximately 310 km to the most eastern part of the Amazon Biome.

Keywords

Bats, COI gene, Maranhão, mitochondrial, range extension

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Introduction

The genus *Trinycteris* Sanborn, 1949 was originally described as a subgenus of *Micronycteris* Gray, 1866, and subsequently recognized as a monotypic genus by Simmons (1996) and Simmons and Voss (1998). Wetterer et al. (2000) confirmed the validity of the genus through a combined analysis of morphological and molecular features. Nogueira et al. (2014) and Reis et al. (2017) re-allocated *Trinycteris nice-fori* to the subfamily Glyphonycterinae (rather than Phyllostominae), following the proposal of Baker et al. (2003). Given the problems of the classification of this genus, further analyses are required to conclusively determine its taxonomic placement (Reis et al. 2017).

Niceforo's big-eared bat, *Trinycteris nicefori*, is an insectivore (Reis et al. 2013, 2017). The diagnostic characteristics of the species include: its small size, with an adult head-body length of 51–58 mm; forearm of 35–41 mm; faintly tricolored dorsal hairs, with a darker base and tip; ventral fur dark; ventral margin of the nasal leaf horseshoe merging gradually with the upper lip, chin with a pair of dermal pads arranged in a V shape, without a central papilla; face and anterior orbital region of the cranium not inflated (Reis et al. 2013, 2017).

The known geographic distribution of *T. nicefori* ranges from southern Mexico to Central America, Trinidad, Colombia, Venezuela, Guiana, Suriname, Peru, Ecuador, Bolivia, and Brazil (Peracchi et al. 2011, Rocha et al. 2013). In Brazil, the species has been recorded in the states of Acre, Amazonas, Amapá, Bahia, Espirito Santo, Mato Grosso, Pará, Roraima, Santa Catarina, Rondônia and Tocantins (Tavares et al. 2008, Peracchi et al. 2011), Rocha et al. 2013). Although there are records of *T. nicefori* in transitional areas between the Amazon forest and the Cerrado savanna of central Brazil (Nunes et al. 2005, Peracchi et al. 2011), there are considerable areas not yet surveyed from the Amazon and Atlantic forests (Rocha et al. 2013).

More than 100 bat species are known to occur in the Amazon region. In the Amazonian domain of the Brazilian state of Maranhão, 47 species have been recorded representing 29 genera (Oliveira et al. 2011, Lópes-Baucells et al. 2016). Despite considerable sampling effort in Maranhão, in comparison with other states, its bat species list is still considered incomplete (Oliveira et al. 2011). Maranhão has a diversity of landscapes, and is considered to be an ecotone between three major biomes, the Amazon, Cerrado, and Caatinga (Batistella et al. 2014, Spinelli-Araujo et al. 2016). The taxonomy and geographic distribution of the state's small mammals, in particular its bats, are still relatively poorly known (Oliveira et al. 2011, Olímpio et al. 2015). An increase in the sampling of these areas will provide a better understanding of the current distribution of bat species, including *T. nicefori* (Rocha et al. 2013). The present study reports the species *T. nicefori* for the first time in the state of Maranhão, extending its distribution to the eastern end of the Amazon biome through morphological and molecular identification.

Material and methods

The specimens of *T. nicefori* were collected from fragments of forest in the Amazonian domain of Maranhão in April 2017, in the municipalities of Godofredo Viana and Cândido Mendes. The bats were captured in mist-nets, 3 m high, and 9–12 m in length, with a 25 mm mesh, which were fixed to the ground with poles and cords. The age of the specimens was estimated based on the ossification of the phalangeal epiphyses, and the reproductive condition was determined by palpation of the teats and abdomen in the female and the position of the testicles in the male (Brunet and Austad 2004). The specimens were photographed, euthanized, labelled, weighed, and measured. Specimens were kept cold until their arrival at the Laboratory of Genetics and Molecular Biology (GENBIMOL) at CESC/UEMA in Caxias, Maranhão, where samples of muscle tissue were extracted and stored in 70% ethanol for subsequent molecular analyses. The cranial structure was also analyzed after preparation.

The morphological and craniometric measurements were obtained using a manual caliper, following Vizzoto and Taddei (1973), and Simmons and Voss (1998) (Table 2): right and left forearm, ear, tragus, foot, tail, skull length, basal skull length, width of the mastoid and zygomatic processes, braincase breadth, palate length, length of the upper and lower tooth-row series, and the length of the mandible. The specimens were fixed in 10% formalin and conserved in 90% ethanol. The species was identified using the classification keys of Uieda et al. (2006), Peracchi et al. (2011), and Reis et al. (2013). The collection of samples was authorized by IBAMA/SISBIO license 42670-3. The specimens will be deposited in the Mastozoology collection of the Federal University of Paraíba, in João Pessoa, Brazil.

For the molecular analyses, total DNA was extracted from the samples of muscle tissue using the Wizard Genomic DNA Purification kit (Promega), according to the manufacturer's instructions. The mitochondrial Cytochrome Oxidase Subunit I (COI) gene was amplified by Polymerase Chain Reaction (PCR) using the primers LCO-1490 and HCO-2198 described by Folmer et al. (1994). The samples were sequenced using Sanger et al.'s (1977) dideoxyterminal method, run in an ABI Prism 3500 automatic DNA sequencer (Applied Biosystems, USA) with the Big Dye kit. The sequences were edited and aligned in BIOEDIT 7.0 (Hall 1999), and plotted in the BOLD Systems v4 platform (http://www.boldsystems.org) to evaluate their similarity with existing sequences.

Results

Two specimens of *T. nicefori* were captured at the study sites in the Amazonian domain of Maranhão (Table 1, Figure 1). The female specimen (field number: RRM 07, fore-arm: 39.68 mm, body mass: 8 g) was larger than the male specimen (field number: RRM 126, 38.00 mm, 6 g). The two specimens were sexually mature adults, although

the female was not lactating; the testicles of the male were scrotal, an indicator that it was sexually active (Kunz et al 1983). The pelage color was chestnut, with a more lightlycolored venter and faintly tricolored dorsal hairs. The specimens were also identified based on a set of diagnostic cranial characters: two pairs of upper incisors and three lower premolars; the incisors were not chisel-shaped, were protruding and were not aligned with the canines, being much shorter and narrower, rostrum shorter than the braincase, rostrum and anterior orbital region of the cranium not inflated (Table 2, Figure 2).

The analysis of the COI molecular marker on the Bold System platform confirmed the morphological identification of the specimens collected in the present

Table 1. Geographical location of specimens of *Trinycteris nicefori* collected in the state of Maranhão, with voucher and GenBank accession numbers.

Species	Biome	Collecting locality	Geographic coordinates	Field number/ Voucher	GenBank accession number
T i f i	Amazonian domain	Godofredo Viana	1°24.891'S, 45°46.446'W	RRM 07	MH807256
1. nicejon of Mai	of Maranhão, Brazil	Cândido Mendes	1°26.971'S, 45°44.201'W	RRM 126	MH807257



Figure 1. Geographic distribution of *Trinycteris nicefori* in Brazil. The area in which the specimens analyzed in the present study were collected in Brazil is indicated by open circles (\circ). The Brazilian biomes are shaded dark gray (Atlantic Forest), light gray (Cerrado), and medium gray (Amazon).

Constal footune	Preser	it study	Sanborn (1949)	Simmons an	d Voss (1998)
Cramai leature	Male	Female	Holotype	Male (n = 3)	Female $(n = 2)$
Greatest length of skull	20.0	21.0	20.5	19.54-20.39	19.71-20.49
Condylobasal length	18.0	18.5	18.5	18.06-18.72	17.99-19.07
Mastoid breadth	8.6	9.0	8.9	8.74-9.05	8.43-8.62
Zygomatic breadth	8.5	9.0	9.6	8.84-9.51	9.05-9.14
Breadth of braincase	7.0	7.5	8.2	7.92-8.22	7.97-8.26
Postorbital constriction	4	4	4.3	3.92-4.11	4.21
Palatal length	8	8	8.2	_	_
Length of upper tooth row	7	7	7.3	7.14-7.45	6.99-7.56
Length of lower tooth row	7	7	7.6	7.14-7.45	6.99-7.56
Length of mandible	13	13	-	_	_

Table 2. Craniometric measurements, in mm, of *Trinycteris nicefori* obtained in the present study, compared with the holotype (Sanborn 1949), and the specimens analyzed by Simmons and Voss (1998), showing the range of values (minimum-maximum) for the males and females.



Figure 2. Cranium of *Trinycteris nicefori*: (**A**) lateral view showing protruding upper incisors not aligned with the canines (**B**) protruding upper incisors (**C**) frontal view of the cranium showing rostrum shorter than the braincase and anterior orbital region. Scale bar: 10 mm.

work. These specimens present 99% of similarity with the sequences of *T. nicefori* of Costa Rica and a divergence of 1-3% in comparison with sequences of *T. nicefori* from Guiana.

Discussion

Given the similarities with species of the genus *Carollia* Gray, 1838, the coloration of the pelage is not a diagnostic feature of the genus *Trinycteris*, although the two genera can be distinguished primarily by the absence of the central protuberances of the papilla in *Trinycteris* (Charles-Dominique et al. 2001, Rocha et al. 2013). *Trinycteris* can also be distinguished from the other Phyllostominae genera by the lack of papilla-like protuberances on the lips and chin, the tail enclosed by the interfemoral membrane, which does not extend to its posterior margin, and the lack of a layer of bare skin on the top of the head that joins the ears, in addition to craniometric measurements (Williams and Genoways 2008, Rocha et al. 2013, Reis et al. 2017). All these characteristics were observed in both specimens examined in the present study. The data on the COI gene revealed a high degree of similarity with the *T. nicefori* specimens from Guiana, which is consistent with the 3% DNA barcode threshold defined by Hebert et al. (2003). The genetic data also confirm the morphological identification and provided conclusive evidence of the occurrence of *T. nicefori* in Maranhão.

The body mass and craniometric parameters recorded in the present study were consistent with those reported by Sanborn (1949) and Simmons and Voss (1998), since the female presented body mass and craniometric measurements larger than in the male. In addition, morphological characters such as coat coloring and forearm measurements are consistent with descriptions provided by Sanborn (1949), Simmons and Voss (1998), Peracchi et al. (2011) and Reis et al. (2013, 2017).

The available data on *T. nicefori* show an important gap in the Amazon biome to the east of Brazil, indicating a disjunctive distribution between the Amazon and Cerrado biomes. The species is also absent from the Caatinga and Cerrado (*sensu stricto*) biomes, which indicates that it probably prefers mesic environments and is relatively intolerant to arid conditions (Rocha et al. 2013). In the present study, the distribution of *T. nicefori* was extended to the eastern extreme of the Amazon biome.

Conclusion

The present study registered the occurrence of *T. nicefori* in the Brazilian state of Maranhão, based on the analysis of morphological and molecular data. This is the first record of the species for the state, where it was found in the Amazonian domain. This record extends the known distribution of *T. nicefori* 303 km to Godofredo Viana and 310 km to Cândido Mendes.

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CHECKLIST



A checklist of marine bryozoan taxa in Scottish sea regions

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Abstract

Contemporary and historical bryozoan records were compiled to provide a comprehensive checklist of species in Scottish waters. The checklist comprises 218 species in 58 families, with representatives from each of the extant bryozoan orders. The fauna was relatively sparse compared to other regions for which bryozoan checklists were available e.g. New Zealand and Australia. Six non-indigenous bryozoan species from the Scottish seas region were included in the checklist. Baseline information on species distributions, such as that presented in this checklist, can be used to monitor and manage the impact of human activities on the marine environment, and ultimately preserve marine biodiversity.

Keywords

Bryozoa, distribution, non-indigenous species, Scotland

Introduction

The phylum Bryozoa comprises approximately 6000 known/described extant species of filter feeding invertebrates that predominantly occur in the marine environment (Gordon and Costello 2016). There are three classes and four orders of extant bryozo-

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ans (class Gymnolaemata, orders Cheilostomatida and Ctenostomatida; class Phylactolaemata (freshwater), order Phylactolaemata *incertae sedis*; class Stenolaemata, order Cyclostomatida). The order Cheilostomatida is the most diverse.

All bryozoans are clonal and the colonies can take many different forms including encrusting, erect and arborescent forms (McKinney and Jackson 1991). The majority of bryozoan species have a calcium carbonate skeleton, but there are also a number of chitinous and gelatinous species. Colony growth proceeds via the asexual budding of individual units, called zooids, with sexual reproduction producing free-swimming larvae (McKinney and Jackson 1991). Bryozoan species occur in all major marine habitats, from the Polar regions to the tropics, ranging from the intertidal zone to the deep sea. The vast majority of species live attached to a substrate, which may be rocks, biogenic structures (e.g. coral, shells), algae or man-made debris (Hayward and Ryland 1998).

Bryozoans contribute to ecosystem functioning and services through the provision of three-dimensional structure and habitat for other species, and by serving as a food source for other marine species (Bitschofsky et al. 2011; Lidgard 2008). Bryozoans are also recognized for their potential economic importance due to the pharmaceutical and active compounds that are associated with a number of species. (Narkowicz et al. 2002). Several bryozoan species are recognized as invasive and are potentially harmful to native marine species (O'Brien et al. 2013; Yorke and Metaxas 2011). Despite these ecological and economic roles, knowledge on local bryozoan species and faunistic inventories are often lacking or incomplete (Rouse et al. 2014). Such baseline information on species distributions is required to monitor and manage the impact of human activities on the marine environment, and ultimately preserve marine biodiversity (Powney and Isaac 2015).

Scotland lays claim to one of the largest marine resources in Europe with over 9910 km of mainland coastline, 8092 km of island coastline, and an estimated 88,600 km² of territorial seas (Baxter et al. 2011). The west coast of Scotland has numerous exposed islands, high sea cliffs, and fjordic inlets, while the east coast is less variable and dominated by low-lying sedimentary shores. Marine spatial planning has been identified as priority by the Scottish Government (Baxter et al. 2011), and there is a drive towards providing reliable information on species occurrences and distribution. Scotland has historically been the focus of much marine biological research and as such a vast back catalogue of bryozoan records exist (e.g. Norman 1869, Hiscock 1996). These records, however, are often disparate, unreliable and/or difficult to locate. Rouse et al. (2014) analysed records of marine bryozoan from Scotland between 1792 and 2010 to assess spatial and temporal trends in bryozoan diversity. Records were compiled from museum collections, professional/academic surveys, consultancy reports and a citizen science scheme consisting of trained amateurs. Records for which the location was uncertain or not provided, and/or the species seemed likely to be wrong based on its generally accepted distribution (e.g. tropical or Antarctic) were discarded. Other records that had only been documented in Scotland by one source, with an unknown or non-expert identified, were also excluded from the analysis. Approximately 8% of these records were museum collections with associated specimens, 60% from a tenyear expert survey of the British coastline and 16% from the citizen science scheme, with the latter two relying on identification via optical microscopes. The remaining records were compiled from published manuscripts that used a combination of optical and scanning electron microscopy for identification.

Using these records, Rouse et al. (2014) found bryozoan diversity to be higher on the west coast of Scotland than other regions, but this was largely attributed to a sampling bias towards the west coast. The study also highlighted the lack of a bryozoan species list for Scottish waters. The aim of the present study, therefore, is to combine the data collated by Rouse et al. (2014) with recent bryozoan studies in Scotland to provide to a comprehensive species checklist of marine bryozoan species in the region.

Methods

Study area

The Scottish sea region was defined according to the 'Clean Sea Assessment' in the Scottish Government's Marine Atlas (Baxter et al. 2011). The region constitutes 15 sub-regions covering coastal and offshore areas (Figure 1). Previous sub-divisions of the Scottish seas (e.g., the MNCR regions used by Rouse et al. (2014)) are restricted to coastal areas, and as such have not been selected for use in this checklist. There is no a priori reason to expect that the Scottish sea region would have a distinct fauna, however the region does support a greater range of habitat types than the adjoining English Sea area (Baxter et al. 2011). The north of Scotland also represents a transitional area between arctic and boreal species (Boulton et al. 1991).

Data sources

Historical and contemporary records of bryozoans were obtained from sources including museum collections, literature, and online databases according to the methods of Rouse et al. (2014). These records were supplemented with records from occasional field surveys carried around Scottish harbours and marinas as part of an on-going invasive species survey programme (Collin et al. 2015; Loxton 2014; Nall et al. 2015; Porter et al. 2015; Wasson and De Blauwe 2014). The checklist represents the species known from Scotland up until 2015.

Organization of the checklist

The checklist is arranged phylogenetically for the higher-level taxa, with the families, genera, and species listed alphabetically. Taxonomy was checked against the World Register of Marine Species (Horton et al. 2016), and names that were currently listed as 'ac-



Figure 1. Scottish sea regions. The abbreviations given are used in the checklist. BLY (Bailey), CLD (Clyde), ESH (East Shetland), EST (East Scotland), FDN (Fladen), FRT (Forties), FSC (Faroe-Shetland Channel), FTH (Forth), HBD (Hebrides), MMS (Minches and Malin Sea), MRF (Moray Firth), NSC (North Scotland), RK (Rockall), SFN (Solway Firth and North Channel), WSH (West Shetland).

cepted' are presented. The number in parentheses immediately to the right of the family name indicates the number of associated taxa, and the abbreviations next to each species specify the sub-region from which records originated (see Figure 1 for definitions of abbreviations). Bryozoan non-indigenous species (NIS) are denoted with an asterisk (*) in the checklist. Individual bryozoan records are provided in the Suppl. material 1.

Results

Table 1 shows the checklist of marine Bryozoa from the Scottish sea regions. A total of 218 species are included in the list, belonging to 128 different genera from 58 families. The Scottish records represent approximately 3.7% of the total number of bryozoan species known worldwide (n = 5869) (Bock and Gordon 2013). There are representatives from each of the extant marine bryozoan orders (Cyclostomatida, Ctenostomatida, and Cheilostomatida). The most species bryozoan families in Scotland were the Calloporidae (13 species) and the Romancheinidae (13 species), which both contain mainly encrusting species.

Six NIS were identified as part of the Scottish fauna. These were *Bugulina fulva* (Ryland, 1960), *Bugulina simplex* (Hincks, 1886), *Bugula neritina* (Linnaeus, 1758), *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, *Fenestrulina delicia* Winston, Hayward & Craig, 2000, *Schizoporella japonica* Ortmann, 1890. The Clyde subregion contained the greatest number of NIS (all except *B. fulva*).

STENOLAEMATA (30)			
Order Cyclostomatida (30)	Sub-region		
Family Annectocymidae (2)			
Annectocyma major (Johnston, 1847)	ESH, MMS, RK, WSH		
Entalophoroecia deflexa (Couch, 1842)	CLD, HBD, MMS, RK		
Family Crisiidae (8)			
Bicrisia abyssicola Kluge,1962	HBD, NCS		
Crisia aculeata Hassall,1841	CLD, EST, FTH, HBD, MMS, NCS, WSH		
Crisia denticulata (Lamarck, 1816)	CLD, EST, FTH, HBD, MMS, NCS, SFN, WSH		
Crisia eburnea (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, NCS, SFN, WSH		
Crisia ramosa Harmer, 1891	HBD, MMS		
Crisidia cornuta (Linnaeus, 1758)	CLD, EST, HBD, MMS, NCS, SFN, WSH		
Crisiella producta (Smitt, 1865)	CLD, WSH		
Filicrisia geniculata (Milne Edwards, 1838)	CLD, HBD, MMS,		
Family Horneridae (1)			
Hornera lichenoides (Linnaeus, 1758)	ESH, FSC, RK, WSH		
Family Lichenoporidae (3)			
Coronopora truncata (Fleming, 1828)	MMS, NCS, RK, WSH		

Table 1. Checklist of marine bryozoan fauna occurring in the Scottish sea region. Species denoted with an asterisk (*) indicate those considered to be non-indigenous within Scotland.

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Alcyonidium polyoum (Hassall, 1841) HBD Family Arachnidiidae (2) Arachnidium clavatum Hincks, 1877 CLD, MMS, WSH Arachnidium fibrosum Hincks, 1880 CLD Family Buskiidae (1) Buskia nitens Alder, 1857
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Arachnidium fibrosum Hincks, 1880 CLD Family Buskiidae (1)
Family Buskiidae (1) Buskia nitens Alder, 1857
Buskia nitens Alder, 1857 WSH
Family Farrellidae (1)
<i>Farrella repens</i> (Farre, 1837) SFN
Family Flustrellidridae (1)
<i>Flustrellidra hispida</i> (O. Fabricius, 1780) CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
<i>Hustrellidra hispida</i> (O. Fabricius, 1780) CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH Family Hypophorellidae (1) Family Hypophorellidae (1)
Flustrellidra hispida (O. Fabricius, 1780) CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH Family Hypophorellidae (1)

Nolella dilatata (Hincks, 1860)	CLD, FTH, MMS, NCS, WSH
Nolella pusilla (Hincks, 1880)	CLD
Nolella stipata Gosse, 1855	MMS
Family Spathiporidae (1)	
Spathipora sertum Fischer, 1866	WSH
Family Triticellidae (2)	
<i>Triticella flava</i> Dalyell, 1848	CLD, SFN
<i>Triticella pedicellata</i> (Alder, 1857)	CLD
Family Vesiculariidae (6)	
Amathia gracilis (Leidy, 1855)	CLD, FTH, MMS
Amathia gracillima (Hincks, 1877)	MMS
Amathia imbricata (Adams, 1798)	CLD, EST, FTH, HBD, MMS, NCS, SFN
Amathia lendigera (Linnaeus, 1758)	SFN
Amathia pustulosa (Ellis & Solander, 1786)	CLD, MMS, SFN
Vesicularia spinosa (Linnaeus, 1758)	CLD, FTH, MMS, SFN
Family Walkeriidae (1)	
Walkeria uva (Linnaeus, 1758)	CLD, ESH, MMS, NCS
Order Cheilostomatida (160)	
Family Aeteidae (3)	
Aetea anguina (Linnaeus, 1758)	EST, FTH, HBD, MMS, NCS, WSH
Aetea sica (Couch, 1844)	CLD, MMS, NCS
Aetea truncata (Landsborough, 1852)	CLD, MMS, NCS
Family Antroporidae (1)	·
Rosseliana rosselii (Audouin, 1826)	ESH, WSH
Family Beaniidae (1)	
Beania mirabilis Johnston, 1840	EST, MMS, NCS
Family Bitectiporidae (7)	
Hippoporina pertusa (Esper, 1796)	CLD, MMS, NCS, SFN, WSH
Pentapora fascialis (Pallas, 1766)	HBD, MMS, SFN
Schizomavella auriculata (Hassall, 1842)	MMS, NCS, SFN, WSH
Schizomavella cornuta (Heller, 1867)	WSH
Schizomavella discoidea (Busk, 1859)	NCS, WSH
Schizomavella hastata (Hincks, 1862)	WSH
Schizomavella linearis (Hassall, 1841)	CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Family Bryocryptellidae (8)	
Marguetta lorea (Alder, 1864)	ESH, WSH
Palmiskenea skenei (Ellis & Solander, 1786)	CLD, EST,MMS, MRF, RK, WSH
Porella alba Nordgaard, 1906	EST, MRF, NCS
Porella compressa (J. Sowerby, 1805)	CLD, HBD, MMS, MRF, NCS, RK, WSH
Porella concinna (Busk, 1854)	CLD, ESH, EST, MMS, MRF, WSH
Porella laevis (Fleming, 1828)	WSH
Porella minuta (Norman, 1868)	MRF, WSH
Porella struma (Norman, 1868)	ESH, WSH
Family Bugulidae (12)	
Bicellariella ciliata (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, NCS, WSH
Bicellarina alderi (Busk, 1859)	MMS, NCS, WSH
Bugulina avicularia (Linnaeus, 1758)	CLD, HBD, MMS, NCS, SFN, WSH
Bugulina calathus (Norman, 1868)	MMS
<i>Bugulina flabellata</i> (Thompson in Gray, 1848)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH

* <i>Bugulina fulva</i> (Ryland, 1960)	MMS, NCS
Bugulina turbinata (Alder, 1857)	CLD, FTH, HBD, MMS, NCS, WSH
*Bugulina simplex (Hincks, 1886)	CLD, ESH, MMS, NCS
*Bugula neritina (Linnaeus, 1758)	CLD
Crisularia plumosa (Pallas, 1766)	CLD, EST, FTH, HBD, MMS, NCS, SFN
Crisularia purpurotincta (Norman, 1868)	ESH, EST, FTH, HBD, MMS, NCS, WSH
<i>Dendrobeania murrayana</i> (Bean in Johnston, 1847)	ESH, MMS, NCS, WSH
Family Calloporidae (13)	
Alderina imbellis (Hincks, 1860)	MMS, NCS, WSH
Amphiblestrum auritum (Hincks, 1877)	EST, MMS, NCS, WSH
Amphiblestrum flemingii (Busk, 1854)	CLD, EST, FTH, MMS, MRF, NCS, RK, WSH
Amphiblestrum solidum (Packard, 1863)	ESH, MMS, MRF, WSH
Callopora craticula (Alder, 1856)	CLD, MMS, WSH
Callopora dumerilii (Audouin, 1826)	MMS, MRF, NCS, SFN, WSH
Callopora lineata (Linnaeus, 1767)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Callopora rylandi Bobin & Prenant, 1965	EST, FTH, HBD, MMS, NCS
Cauloramphus spiniferum (Johnston, 1832)	EST, MMS, NCS, WSH
Crassimarginatella solidula (Hincks, 1860)	EST. WSH
Megapora ringens (Busk 1856)	FST FSC WSH
Ramphonotus minar (Busk, 1850)	FSH RK WSH
Tegella unicornis (Eleming, 1828)	EST, ME, WSH
Femily Condidee (9)	
Cabarag allicii (Eleming, 1814)	NCS WSH
Caberea eussi (Fielding, 1814)	CID ECH ECT ETH HED MMC NCC CEN WCH
Cradoscrupoceuaria reptans (Linnaeus, 1738)	CLD, ESH, ESH, FIH, HDD, MMS, NCS, SFN, WSH
Notoplites harmeri Kyland, 1965	WSH
Notoplites jeffreysu (Norman, 1863)	ESH, MMS, WSH
O'Donoghue, 1926)	FTH, MMS, WSH
Scrupocellaria scruposa (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, NCS, SFN, WSH
* <u>Tricellaria inopinata</u> d'Hondt & Occhipinti <u>Ambrogi, 1985</u>	CLD, EST, MMS, MRF, NCS
<i>Tricellaria peachii</i> (Busk, 1851)	ESH, EST, MRF, NCS, WSH
Tricellaria ternata (Ellis & Solander, 1786)	ESH, EST, FTH, FRT, HBD, NCS, WSH
Family Cellariidae (4)	
Cellaria fistulosa (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Cellaria salicornioides Lamouroux, 1816	CLD, MMS, WSH
Cellaria sinuosa (Hassall, 1840)	CLD, EST, HBD, MMS, SFN, WSH
Euginoma vermiformis Jullien, 1883	RK
Family Celleporidae (11)	
Buskea dichotoma (Hincks, 1862)	CLD, EST, MMS, MRF, WSH
Buskea nitida Heller, 1867	CLD, MMS
Cellepora pumicosa (Pallas, 1766)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, RK, WSH
Celleporina caliciformis (Lamouroux, 1816)	CLD, ESH, FTH, HBD, MRF, MMS, NCS, WSH
Celleporina decipiens Hayward, 1976	HBD
Celleporina pygmaea (Norman, 1868)	FSC, MRF, WSH
Lagenipora lepralioides (Norman, 1868)	ESH, WSH
Omalosecosa ramulosa (Linnaeus, 1767)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, WSH
Palmicellaria elegans Alder, 1864	WSH
Turbicellepora avicularis (Hincks, 1860)	CLD, EST, FRT, HBD, MMS, MRF
1	

<i>Turbicellepora boreale</i> Hayward & Hansen, 1999	RK
Family Chaperiidae (1)	·
Larnacicus corniger (Busk, 1859)	FSC, RK, WSH
Family Chorizoporidae (1)	·
Chorizopora brongniartii (Audouin, 1826)	EST, MMS, NCS, SFN, WSH
Family Cribrilinidae (7)	·
Collarina balzaci (Audouin, 1826)	CLD, MMS, WSH
Cribrilina annulata (O. Fabricius, 1780)	CLD, EST, FTH, MMS, NCS, WSH
Cribrilina cryptooecium Norman, 1903	EST, MMS, MRF, NCS, WSH
Cribrilina punctata (Hassall, 1841)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Membraniporella nitida (Johnston, 1838)	CLD, EST, FTH, HBD, MMS, NCS, WSH
Puellina innominata (Couch, 1844)	CLD
Puellina venusta (Canu & Bassler, 1925)	CLD, WSH
Family Cryptosulidae (1)	
Cryptosula pallasiana (Moll, 1803)	CLD, MMS, MRF, NCS, WSH
Family Doryporellidae (1)	
Doryporellina reticulata (Ryland, 1963)	RK
Family Electridae (7)	
Aspidelectra melolontha (Landsborough, 1852)	NCS
Conopeum reticulum (Linnaeus, 1767)	CLD, EST, FTH, FRT, MMS, NCS, MRF
Conopeum seurati (Canu, 1928)	NCS
Einhornia crustulenta (Pallas, 1766)	NCS
Electra monostachys (Busk, 1854)	MMS, NCS, SFN
Electra pilosa (Linnaeus, 1767)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Pyripora catenularia (Fleming, 1828)	CLD, FRT, MMS, NCS, SFN, WSH
Family Escharinidae (5)	
Escharina alderi (Busk, 1856)	FSC, MMS, RK, WSH
<i>Escharina dutertrei haywardi</i> Zabala, Maluquer & Harmelin, 1993	FSC, WSH
Escharina johnstoni (Quelch, 1884)	CLD, MMS
Herentia hyndmanni (Johnston, 1847)	NCS, WSH
Phaeostachys spinifera (Johnston, 1847)	FTH, MMS, NCS, WSH
Family Eucrateidae (1)	
Eucratea loricata (Linnaeus, 1758)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, SFN, WSH
Family Exechonellidae (1)	
Anarthropora monodon (Busk, 1860)	FSC, WSH
Family Exochellidae (2)	
Escharoides coccinea (Abildgaard, 1806)	CLD, EST, FTH, HBD, MMS, MRF, NCS, WSH
Escharoides mamillata (Wood, 1844)	EST, MMS, NCS, WSH
Family Flustridae (7)	
Carbasea carbasea (Ellis & Solander, 1786)	EST, FTH, HBD, WSH
Chartella barleei (Busk, 1860)	ESH, NCS, WSH
Chartella papyracea (Ellis & Solander, 1786)	CLD, HBD, MMS
Flustra foliacea (Linnaeus, 1758)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, SFN, WSH
Hincksina flustroides (Hincks, 1877)	HBD
Sarsiflustra abyssicola (Sars G.O., 1872)	WSH
Securiflustra securifrons (Pallas, 1766)	CLD, ESH, EST, FTH, FRT, HBD, MMS, MRF, NCS, SFN, WSH
Family Haplopomidae (4)	

Haplopoma graniferum (Johnston, 1847)	CLD, FTH, NCS, WSH
Haplopoma impressum (Audouin, 1826)	CLD, MMS, NCS, WSH
Haplopoma planum Ryland, 1963	ESH, WSH
Haplopoma sciaphilum Silén & Harmelin, 1976	HBD
Family Hippoporidridae (2)	
Hippoporella hippopus (Smitt, 1867)	MRF
Hippoporidra lusitania Taylor & Cook, 1981	WSH
Family Hippothoidae (4)	·
Celleporella hyalina (Linnaeus, 1767)	CLD, EST, FTH, HBD, MMS, MRF, NCS, WSH
Haplota clavata (Hincks, 1857)	CLD
Hippothoa divaricata Lamouroux, 1821	CLD, EST, NCS
Hippothoa flagellum Manzoni, 1870	CLD, MMS, NCS
Family Lacernidae (1)	
Cylindroporella tubulosa (Norman, 1868)	HBD, MRF, NCS, WSH
Family Membraniporidae (1)	·
<i>Membranipora membranacea</i> (Linnaeus, 1767)	ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Family Microporellidae (3)	
<i>Fenestrulina delicia</i> Winston, Hayward & Craig, 2000	CLD, WSH
Fenestrulina malusii (Audouin, 1826)	CLD, EST, HBD, MMS, MRF, NCS, SFN, WSH
Microporella ciliata (Pallas, 1766)	CLD, EST, FTH, MMS, NCS, SFN, WSH
Family Microporidae (3)	
Micropora coriacea (Johnston, 1847)	CLD
Micropora normani Levinsen, 1909	WSH
Mollia multijuncta (Waters, 1879)	WSH
Family Phidoloporidae (5)	
Reteporella beaniana (King, 1846)	MMS, NCS, RK, WSH
<i>Reteporella incognita</i> Hayward & Ryland, 1996	RK, WSH
Reteporella watersi (Nordgaard, 1907)	WSH
Rhynchozoon bispinosum (Johnston, 1847)	WSH
Schizotheca fissa (Busk, 1856)	MMS
Family Romancheinidae (13)	
Arctonula arctica (M. Sars, 1851)	EST, WSH
Escharella abyssicola (Norman, 1869)	FSC, WSH
Escharella immersa (Fleming, 1828)	CLD, EST, MMS, MRF, NCS, WSH
Escharella labiosa (Busk, 1856)	HBD, MMS
Escharella laqueata (Norman, 1864)	MMS, WSH
Escharella octodentata (Hincks, 1880)	FSC, RK, WSH
Escharella variolosa (Johnston, 1838)	CLD, EST, MMS, MRF, WSH
Escharella ventricosa (Hassall, 1842)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Hemicyclopora polita (Norman, 1864)	ESH, MMS, WSH
Neolagenipora collaris (Norman, 1867)	MMS, MRF, NCS, WSH
Neolagenipora eximia (Hincks, 1860)	WSH
Ragionula rosacea (Busk, 1856)	CLD, NCS, WSH
Temachia microstoma (Norman, 1864)	ESH, WSH
Family Schizoporellidae (6)	
Schizoporella cornualis Hayward & Ryland,	MMS
1995	
Schizoporella dunkeri (Reuss, 1848)	MMS, NCS, WSH
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*Schizoporella japonica Ortmann, 1890	CLD, ESH, EST, MMS, MRF, NCS, WSH
<i>Schizoporella patula</i> Hayward & Ryland, 1995	ESH, FSC, NCS, WSH
<i>Schizoporella umbonata</i> O'Donoghue & O'Donoghue, 1926	WSH
<i>Schizoporella unicornis</i> (Johnston in Wood, 1844)	CLD, HBD, MMS, MRF, NCS, WSH
Family Scrupariidae (2)	
Scruparia ambigua (d'Orbigny, 1841)	EST, HBD
Scruparia chelata (Linnaeus, 1758)	CLD, EST, FTH, HBD, MMS, NCS, WSH
Family Setosellidae (1)	
Setosella vulnerata (Busk, 1860)	ESH, WSH
Family Smittinidae (8)	
Parasmittina trispinosa (Johnston, 1838)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS, RK, SFN, WSH
Phylactella labrosa (Busk, 1854)	MRF, NCS, WSH
Pseudoflustra virgula Hayward, 1994	FSC
Smittina bella (Busk, 1860)	CLD, EST, WSH
Smittina crystallina (Norman, 1867)	MMS, MRF, NCS, WSH
Smittoidea amplissima Hayward, 1979	WSH
Smittoidea marmorea (Hincks, 1877)	EST, FTH, MMS, NCS, WSH
Smittoidea reticulata (MacGillivray, 1842)	CLD, EST, FTH, MMS, MRF, NCS, WSH
Family Stomachetosellidae (3)	
Stomachetosella normani Hayward, 1994	WSH
Stomacrustula cruenta (Busk, 1854)	CLD, ESH, WSH
Stomacrustula sinuosa (Busk, 1860)	CLD, MMS, WSH
Family Tessaradomidae (1)	
Tessaradoma boreale (Busk, 1860)	HBD, RK, WSH
Family Umbonulidae (1)	
Oshurkovia littoralis (Hastings, 1944)	CLD, ESH, EST, FTH, HBD, MMS, MRF, NCS SFN, WSH

Discussion

The Scottish sea regions contain 218 bryozoan species with representatives from each of the extant bryozoan orders. Based on the checklist, it can be concluded that Scotland has fewer bryozoan species than New Zealand (n = 953), Australia (n = 886), and the Mediterranean (n = 556) (Gordon 1999; Gordon et al. 2010; Rosso and Di Martino 2016). Given Scotland's location within a single biogeographical region, this relative lack of species is as expected (Baxter et al. 2011). When coastline length is accounted for, Scotland has approximately half the number of species per km (0.01) as Australia (0.02 species/km) and approximately six times fewer than New Zealand (0.06 species/km). The proportion of ctenostomes in Scotland (12% of total species) is greater than the global average (~5%) (Bock and Gordon 2013), and greater than the proportion of ctenostomes reported from New Zealand (5%), Australia (4%), Argentina (4%) and the Mediterranean (10%) (Gappa 2000; Gordon 1999; Rosso and Di Martino 2016). Only the bryozoan fauna of Brazil has a greater percentage (26.2%) of ctenostomes. Previously, higher incidences of ctenostomes (and/or cyclostomes) have been attributed to the results

of focused taxonomic efforts in certain regions (Gappa 2000; Rosso 2003). Rosso and Di Martino (2016), however, suggested that the abundance of ctenostomes in the Mediterranean could also reflect the availability of high-energy algal and seagrass dominated habitats, for which the flexible uncalcified ctenostome colony forms are well adapted to exploit. Scotland, and the Scottish west coast in particular, has a high abundance and diversity of algae and algal dominated habitats (Smale et al. 2013), which may explain the high number of ctenostomes found in the study region.

As with other benthic marine invertebrates in Scotland, the bryozoan fauna includes NIS (Nall et al. 2015). The presence of all but one NIS within the Clyde Sea region most likely represents the fact that the area is both a well-studied region and the location of a significant number of ports. As global shipping and aquaculture increase, along with climate change, it is expected that the number of invasive or non-indigenous bryozoans in the Scottish sea regions will increase in the future (Stretaris et al. 2005).

The estimate of bryozoan species number in Scotland, presented here, is likely to be conservative, since much of the offshore shelf areas and seamounts have not been fully explored. Estimates of the global number of bryozoan species yet to be discovered range from 2800–5200 (Appeltans et al. 2012). Given that the Scottish bryozoan fauna currently constitutes 3.7% of global bryozoan species richness, and assuming that this proportion will remain constant, it could be expected that there are approximately 104–192 bryozoan species in Scotland yet to be discovered.

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Supplementary material I

Scottish bryozoan records

Authors: Sally Rouse, Jennifer Loxton, Mary E. Spencer Jones, Joanne S. Porter Data type: occurence

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