RESEARCH ARTICLE



A new orthopteran-parasitizing horsehair worm, Acutogordius taiwanensis sp. n., with a redescription of Chordodes formosanus and novel host records from Taiwan (Nematomorpha, Gordiida)

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Abstract

A description of a new species of horsehair worm, *Acutogordius taiwanensis* **sp. n.**, a redescription of *Chordodes formosanus*, and novel host records for the latter are provided. *Acutogordius taiwanensis* **sp. n.** is morphologically similar to *A. protectus* with moderately flat areoles on its tail tips, but is distinguishable by small mid-body ornamentations. Despite the distinct differences in the post-cloacal crescents between 14 male samples, their conspecific status, along with that of nine female samples, was upheld by a phylogenetic comparison of partial cytochrome oxidase subunit I (COI) sequences. *Chordodes formosanus* is another common horsehair worm species in Taiwan, which was previously believed to specifically parasitize *Hierodula* mantids. However, in this study, five *C. formosanus* were observed emerging from an *Acromantis* mantid, and two long-horned grasshopper hosts (*Leptoteratura* sp. and *Holochlora japonica*). These five worms showed high degrees of similarity in COI sequences and morphology, but one of these individuals bore abnormal crowned areoles, which has never been observed in *C. formosanus*, and may be attributed to the incomplete development of this particular individual.

Keywords

Acutogordius taiwanensis, Chordodes formosanus, immature stage, new species, novel host

Introduction

Horsehair worms (phylum Nematomorpha) are aquatic parasites whose life cycle typically contains a free-living, aquatic phase, including mating and early larval development, and two parasitic stages, including an aquatic paratenic host stage and a terrestrial definitive host stage (Schmidt-Rhaesa 2014, Bolek et al. 2015). Over 350 freshwater species have been described worldwide (Bolek et al. 2015), but only one, *Chordodes formosanus* Chiu, 2011, is known in Taiwan (Chiu et al. 2011). *Acutogordius taiwanensis* sp. n. is another commonly encountered species, which is usually sympatric with *C. formosanus* at low altitudes in Taiwan. In the aquatic paratenic host stage, cysts of *Acutogordius* and *Chordodes* have been found sympatrically in aquatic chironomids (Chiu et al. 2016), whereas the adults generally parasitize various terrestrial hosts.

The definitive hosts of *C. formosanus* are *Hierodula* mantids (Chiu et al. 2011), whereas adults of *Acutogordius taiwanensis* sp. n. in Taiwan generally emerge from orthopteran insects. *Acutogordius* is a small genus that consists of ten described species (de Miralles and de Villalobos 1998, Schmidt-Rhaesa and Geraci 2006, Schmidt-Rhaesa and Schwarz 2016) in the family Gordiidae (Poinar 2008). Only two genera in the Gordiidae, *Acutogordius*, and *Gordius*, are characterized by a post-cloacal crescent located at the base of the two tail lobes, but are distinguishable by the distinctly pointed tips on the *Acutogordius* male's tail lobes (Schmidt-Rhaesa 2002). Classification of *Acutogordius* species is primarily based on the characters of the males' tails. However, interspecific variation has not been well defined, and distinction between the species is still not clear (Schmidt-Rhaesa and Geraci 2006).

In the present study, the conspecific status of 23 Acutogordius samples is established according to minor differences observed in the sequences of their partial mitochondrial DNA cytochrome oxidase subunit I (mtDNA-COI) genes, collected from eleven species of orthopteran hosts, and the morphological differences among these samples is determined as intraspecific variation. Furthermore, the morphology of the immature stages of this species was also described. Five horsehair worm samples that had emerged from Acromantis mantids and two long-horned grasshopper species, i.e., Leptoteratura sp. and Holochlora japonica, were identified as C. formosanus based on morphological and molecular evidence, and thus added these insect species as novel definitive hosts of C. formosanus.

Materials and methods

The morphologies and DNA sequences of 29 adult horsehair worms (24 *Acutogordius* and 5 *Chordodes*) were examined. Two pairs of *Acutogordius* were reared in the laboratory for two weeks to breed and lay eggs, and the morphology of the resulting larvae was examined using a light microscope (Olympus BH-2, PM-10AD, Tokyo, Japan). Specimens (partial bodies with their hosts) were preserved at the Department of En-

tomology, National Taiwan University, Taipei; National Museum of Natural Science, Taichung, Taiwan; and Lake Biwa Museum, Shiga, Japan. Specimen examination followed our previously published methods described in Chiu et al. (2011).

Collection and preservation of horsehair worms

Insect hosts infected with horsehair worms were hand-collected from a riparian environment. To determine if a host was infected with worms, its posterior was examined, and then the worms were collected by immersing the host in water or by host dissection. Except for the two pairs of *Acutogordius* that were kept for breeding, all other horsehair worms were killed with hot water (>80°C), fixed in a 75% alcohol solution with their hosts for few days, and preserved in a 95% alcohol solution. The collection and host data are given in Tables 1 and 2, respectively.

Breeding *Acutogordius* pairs were reared in 800 mL aerated tap water and maintained at room temperature (~28°C). After mating, the males were removed and fixed and preserved in 75% followed by 95% alcohol solutions. After the mated females laid eggs for one month, they were also removed and fixed and preserved in 75% followed by 95% alcohol solutions. Egg strings were detected at approximately three days, and hatched larvae were detected at approximately 2–3 weeks after egg laying. Live larvae were observed under a light microscope.

Snails (*Physa* sp.) infected by horsehair worms were collected with nine other non-infected snails from a small pond in Wufengqi Waterfalls, Jiaushi Township, Yilan County, Taiwan, where free-living adult horsehair worms have been seen. Live snails were maintained together in 2000 mL aerated tap water and were dissected after five days.

Morphological examination

Adult specimens. Fragments (~0.5 cm in length) of the anterior end, mid-body, and posterior end of the preserved adult horsehair worm samples were first examined under a stereomicroscope (Leica S8 APO, Leica, Wetzlar, Germany). The fragments were dehydrated with a series of ethanol and acetone solutions (95% and 100% ethanol (twice) and ethanol/acetone mixtures of 2:1, 1:1, 1:2, 0:1) and critical-point-dried and gold-sputter-coated before being examined under a scanning electronic microscope (SEM) (JEOL JSM-5600, Tokyo, Japan) at a magnification of 100–15,000×.

Immature stages. Eggs and newly hatched larvae were examined and photographed alive on microslides using a light microscope (Olympus BH-2, PM-10AD, Olympus, Tokyo, Japan) at magnifications of 200× and 400×. Larvae, for examination under SEM, were first killed, fixed by 75% alcohol solution, and collected in a paper envelope soaked in 75% alcohol solution. The protocol of dehydration, critical point drying, and gold sputter coating followed that applied in the examination of the adult fragments and they were examined at a magnification of 500–9,000×. To examine the

cysts inside the snail hosts, the snail shells were removed, the soft tissue flattened by two glass slides, and the slides were examined under a light microscope at $200 \times$ magnification.

The measurements of each characteristic were performed using the segmented line function in ImageJ 1.47 (Abràmoff et al. 2004), and calibrated spatially to the scale included in each picture. The terminology for larval stages used in this study primarily followed that of Hanelt and Janovy (2002) and Szmygiel et al. (2014).

Phylogenetic analysis

Genomic DNA from adult horsehair worms was extracted using an ALS Tissue Genomic DNA Extraction Kit (Pharmigene, Kaohsiung, Taiwan). A set of universal primers (LCO1490 and HC02198) (Folmer et al. 1994) were applied to amplify and sequence the partial COI sequence. Fourteen *Acutogordius* samples with COI sequences that could not be well amplified with the universal primers were prepared for use with a newly designed primer set (AcCOiF: TGAGCTGCCTTTTTAG, AcCOiR: TGTATTAATGTTTCGGTC). The PCR for both primer sets was initiated at 95°C for 5 min, and amplification was conducted for 40 cycles of 95°C for 1 min, 50°C for 1 min, with a final extension at 72°C for 10 min.

Pairwise genetic distances and phylogenic tree reconstruction using the neighborjoining (NJ) method, which is based on Kimura's 2-parameter model, were used to verify conspecific status of the horsehair worm samples. COI sequences (450 highquality nucleotide base pairs) were first aligned using CLUSTALX 2.0.10 (Thompson et al. 1997), and the analysis was conducted with MEGA 6.0 (Tamura et al. 2013). COI sequences for *Gordius balticus*, *G. attoni*, and *G. cf. robustus*. (Hanelt et al. 2015, GenBank nos. KM382320, KM382318, KM382277), *C. formosanus* and *C. japonensis* (Chiu et al. 2011, GenBank nos HM044105, HM044124, JF808206), and *Paragordius* sp. (GenBank no. AY428843) were also used in the comparison, and 5,000 bootstrap replicates were used to determine branch supports for the NJ tree.

Taxonomy

Acutogordius taiwanensis sp. n. http://zoobank.org/59379D36-D879-4F8D-BB78-C47C88F818DB

Type locality. Wufengqi Waterfalls (24°49'55.62"N, 121°44'50.10"E), Jiaushi Township, Yilan County, Taiwan (holotype and allotype). Paratypes were collected from Sindian, New Taipei City, and the Fushan Botanical Garden, Yilan County. See Table 1 for detailed information.

Type material. Partial bodies of the holotype and allotype were deposited with their hosts at the National Museum of Natural Science. Paratypes were deposited at

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				Horsehair worm					
Species	Collection date	GenBank no.	Locality	Longitude and latitude	Collector	Depository	Sex	Length (mm)	Host code
A. taiwanensis	16-XI-2014	KX591947	Xindian, New Taipei, Taiwan	24°50'47.70"N 121°32'41.20"E	Shipher Wu	NTU	ц	283	HAc23302
A. taiwanensis	2-VIII-2009	KX591922	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	Μ	334	HAc26201
A. taiwanensis	29-VII-2009	KX591948	Fushan botanical garden, Yilian, Taiwan	ı	Ming-Chung Chiu	NTU	М	278	HAC26401
A. taiwanensis	10-VII-2011	KX591926	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	Μ	312	HAc26206
A. taiwanensis	5-VII-2011	KX591927 ¹	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	Μ	410	HAc26207
A. taiwanensis	5-VII-2011	KX591928	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	Μ	428	HAc26208
A. taiwanensis	18-VIII-2011	KX591929	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	н	360	HAc26209
A. taiwanensis	20-VII-2010	KX591930	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	Μ	387	HAc26210
A. taiwanensis	24-IX-2011	KX591931	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	Μ	262	HAc26211-12
A. taiwanensis	24-IX-2011	KX591932	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	ц	272	HAc26211-12
A. taiwanensis	5-VIII-2012	KX591933 ²	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	ц	288	HAc26214
A. taiwanensis	21-VII-2012	KX591934	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	Μ	133	HAc26215
A. taiwanensis	21-XI-2012	KX591935	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	М	241	HAc26217
A. taiwanensis	31-VIII-2012	KX591937	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	М	222	HAc26219-20
A. taiwanensis	31-VIII-2012	KX591938	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	Μ	216	HAc26219-20
A. taiwanensis	31-VIII-2012	KX591939	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	н	322	HAc26221-21A
A. taiwanensis	31-VIII-2012	NA^3	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	ц	73	HAc26221-21A
A. taiwanensis	31-VIII-2012	KX591940	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NMNS	ц	285	HAc26222
A. taiwanensis	26-VII-2014	KX591941	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	Μ	369	HAc26223
A. taiwanensis	26-VI-2015	KX591942	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	Μ	164	HAc26225-26
A. taiwanensis	26-VI-2015	KX591943	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	NTU	н	166	HAc26225-26
A. taiwanensis	17-VII-2015	KX591944	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	М	280	HAc26228
A. taiwanensis	17-VII-2015	KX591945	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	ц	432	HAc26231
A. taiwanensis	17-VII-2015	KX591946	Jiaushi, Yilian, Taiwan	24°49'55.62"N, 121°44'50.12"E	Ming-Chung Chiu	LBM	ц	237	HAc26232
C. formosanus	11-II-2015	KX591949	Taipei Zoo, Taipei City, Taiwan	24°59'44.70"N, 121°34'49.49"E	Long-Chun Huang	NMNS	Σ	58	HCH11606-8

	Host code	HCH11606-8	HCH11606-8	HCH26207	HAc26216	
	Length (mm)	125	115	43	204	
	Sex	Μ	М	Μ	М	
	Depository	NMNS	NMNS	NTU	NTU	
	Collector	Long-Chun Huang	Long-Chun Huang	Ming-Chung Chiu	Ming-Chung Chiu	
Horsehair worm	Longitude and latitude	24°59'44.70"N, 121°34'49.49"E	24°59'44.70"N, 121°34'49.49"E	24°49'55.62"N, 121°44'50.12"E	24°49'55.62"N, 121°44'50.12"E	
	Locality	Taipei Zoo, Taipei City, Taiwan	Taipei Zoo, Taipei City, Taiwan	Jiaushi, Yilian, Taiwan	Jiaushi, Yilian, Taiwan	
	GenBank no.	KX591950	KX591951	KX591952	KX591953	
	Collection date	11-II-2015	11-II-2015	4-III-2015	10-XI-2015	
	Species	C. formosanus	C. formosanus	C. formosanus	C. formosanus	

LBM: Lake Biwa Museum; NMNS: National Museum of Natural Science; NTU: National Taiwan University

¹ Holotype

² Allotype

³ Female specimen with insufficient DNA for sequencing

Host code (see Table 1)	Host species	Host sex	Host length (mm)
HAc23302	Mecopoda elongata	М	31.5
HAc26201	<i>Eugryllacris</i> sp.	М	27.5
HAC26401	Neanias magnus	F	20.5
HAc26206	Neanias magnus	М	21.9
HAc26207	<i>Eugryllacris</i> sp.	М	27.2
HAc26208	<i>Eugryllacris</i> sp.	М	25.9
HAc26209	Hexacentrus japonicus	F	29.4
HAc26210	Sinochlora longifissa	F	33.5
HAc26211-12	Hexacentrus unicolor	F	28.8
HAc26214	<i>Elimaea</i> sp.	F	27.1
HAc26215	Deflorita apicalis	М	22.3
HAc26217	Pyrgocorypha formosana	F	41.3
HAc26219-20	Phaulula sp.	F	23.1
HAc26221-21A	Hexacentrus unicolor	F	23.9
HAc26222	Hexacentrus unicolor	F	29.1
HAc26223	<i>Elimaea</i> sp.	F	27.2
HAc26225-26	Neanias magnus	М	17.9
HAc26228	Hexacentrus unicolor	М	28.4
HAc26231	<i>Eugryllacris</i> sp.	F	30.6
HAc26232	<i>Isopsera</i> sp.	М	24.1
HCH11606-8	Acromantis japonica	F	29.4
HCH26207	Leptoteratura sp.	F	9.6
HAc26216	Holochlora japonica	F	39.2

Table 2. Mantid and grasshopper horsehair worm host information.

the Department of Entomology, National Taiwan University, Taipei; the National Museum of Natural Science, Taichung, Taiwan; and Lake Biwa Museum, Shiga, Japan. See Table 1 for detailed information.

Type hosts. *Eugryllacris* sp., *Neanias magnus* Matsumura and Shiraki, 1908 (Orthoptera: Gryllacrididae), *Deflorita apicalis* (Shiraki, 1930), *Elimaea* sp., *Hexacentrus japonicus* Karny, 1907, *H. unicolor* Serville, 1831, *Isopsera* sp., *Mecopoda elongata* (Linnaeus, 1758), *Phaulula* sp., *Pyrgocorypha formosana* Matsumura and Shiraki, 1908, *Sinochlora longifissa* (Matsumura and Shiraki, 1908) (Orthoptera: Tettigoniidae). See Table 2 for detailed information.

Etymology. The specific name refers to the type locality, Taiwan.

Diagnosis. Acutogordius taiwanensis sp. n. is morphologically similar to A. protectus Schmidt-Rhaesa and Geraci, 2006 with regards to the (1) distribution pattern of tiny bristles on the ventral posterior end, (2) moderately flat areoles (rounded in elevation) covering the tail tips, and (3) cone-shaped spines scattered on the base of the tail lobes of the male samples. However, it is distinct because of the small ornamentations on the mid-body.

Description (Figs 1–7). *Male adults* (n = 14) (Figs 2, 3). Body length 288.3 ± 90.1 (133–428) mm, width (widest, after dehydration) 623 ± 173 (404–1079) µm.



Figure 1. Anterior end of *Acutogordius taiwanensis* sp. n. **A–C** Images of the anterior end showing the (**A**) white cap and dark-brown collar and **B–C** white spots scattered on the brown collar **D–F** SEM images of the anterior end surface that is **D** smooth **E** smooth but wrinkled on the tip with holes scattered on the dark-brown collar, and **F** wrinkled **A–F** are images from the same individual, respectively. Scale bars 500 μ m (**A–C**), and 200 μ m (**D–F**).

Body light brown, smooth, and slightly mucous covered (liquid on the body surface slightly viscous, light on live worms usually refracted) before fixed in alcohol, alcohol-preserved specimens significantly flat and hard.

Anterior end columnar and slightly narrowed at tip; anterior tip white (white cap) with a dark-brown collar (Fig. 1A); white spots scattered on brown collar (Fig. 1B, C) in some samples (3/14); under SEM, surface of anterior end wrinkled (Fig. 1F) (4/14), smooth (Fig. 1D) (7/14), or smooth but wrinkled on the tip (Fig. 1E) (3/14); short bristles or holes scattered on some samples; no obvious boundary between the white cap and dark-brown collar.

Cuticle in mid-body smooth, slightly wrinkled, or cracked; short or cone-like bristles (Fig. 3D, E) scattered on some samples (6/14).

Posterior end divided into two tail lobes, each 360.25 ± 53.30 (303.70-489.58) µm in length; lobe tips generally tapered, wrinkled, or covered by moderately flat areoles with short spines amongst areoles; inner side of tail lobes smooth; tiny spines scattered around tip; cone-shaped spines or flat areoles scattered on base behind post-cloacal crescent.

Ventral side of posterior end structured with post-cloacal crescent, cloacal opening, and tiny bristles. One post-cloacal crescent not evident as it was covered by larval cuticle, post-cloacal crescent length (extension along longitudinal axis) 275.48 \pm 68.84 (195.78–417.03) µm, width (widest) 44.81 \pm 16.21 (18.73–83.01) µm, located



Figure 2. Posterior end of male *Acutogordius taiwanensis* sp. n. **A–C** Images of the posterior end with the postcloacal crescent extending **A**, **C** over or **B** anterior to the starting point of the tail lobe bifurcation **D–F** SEM images of the posterior end with a **D** angled **E** slightly curved, and **F** semicircular postcloacal crescent **A–F** are images from the same individual, respectively. Scale bars 500 μm (**A–C**), and 200 μm (**D–F**).

near base of tail lobes; post-cloacal crescent slightly curved (Fig. 2B, E) (5/13), nearly at right angle (Fig. 2A, D) (5/13, including two samples reared for laying eggs), or semicircular (which were more slender than the curved or angled ones) (Fig. 2C, F) (3/13). Two ends of post-cloacal crescent extending over (Fig. 2 A, C, D, F) (11/13) or anterior to (Fig. 2B, E) (2/13) starting point of tail lobe bifurcation. Cloacal opening circular or slightly oval-shaped, 26.61 ± 7.86 (14.63–43.23) µm in diameter, 55.50 \pm 19.71 (32.55–89.90) µm away from anterior margin of post-cloacal crescent, surrounding depressed area in four samples, no circumcloacal spine. Cloacal openings of four specimens not visible as they were covered by the larval cuticle or by mold. Tiny bristles scattered over ventral side of posterior end except in two samples covered by larval skin or mold; tiny bristles scattered over ventral posterior end and concentrated on tail lobes (Fig. 3B) (3/13), anterior post-cloacal crescent (Fig. 3A) (1/13), or randomly scattered on the cuticle (Fig. 3D, E) (9/13).

Female adults (n = 10) (Fig. 4). Body length 271.80 ± 99.14 (73–432) mm, width (widest, after dehydration) 896 ± 171 (578–1120) µm, light brown, slightly mucous covered (liquid on the body surface slightly viscous, light on live worms usually refracted) before fixed in alcohol. Alcohol-preserved specimens flat in egg-laying samples. Anterior end (Fig. 4A) columnar and slightly narrowed at tip; white cap and dark-brown collar present. Under SEM, surface of anterior end smooth or wrinkled;



Figure 3. Detailed diagnostic characteristics of male *Acutogordius taiwanensis* sp. n. **A** Tiny bristles scattered anterior to postcloacal crescent **B** Tiny bristles scattered in concentrated groups on tail lobes **C** Lobe tips covered by moderately flat areoles with short spines amongst areoles **D–E** Short bristles scattered on the mid-body cuticle. Scale bars 200 μ m (**A–B**), 100 μ m (**C–D**), and 10 μ m (**E**).

one sample had hole-like structures (Fig. 5J); small spines scattered on surface of three samples; no obvious boundary between the white cap and dark-brown collar. Cuticle in mid-body smooth, wrinkled, or crack-like; most with small spines scattered on cuticle (7/10). Posterior end (Fig. 4B) rounded, smooth, without spines or bristles. Cloacal opening on terminal end circular, 24.70 ± 5.88 (16.80–30.62) µm in diameter, no circum-cloacal spine.

Eggs (Fig. 6G). Egg string (Fig. 6G) length 12.04 ± 3.91 (4.94-19.13) mm, width 0.61 ± 0.11 (0.343-0.708) mm (n = 11), white or light yellow in color, deposited as



Figure 4. Female *Acutogordius taiwanensis* sp. n. **A** Anterior end **B** Posterior end. Clo, cloacal opening. Scale bars 100 μm (**A–B**).

short pieces not adhering to substrate. Eggs (12 days after being laid, nearly hatching) oval-shaped, length 31.93 ± 3.08 (28.79–34.67) µm, width 25.69 ± 1.25 (24.04–27.71) µm (n = 6).

Larvae (Fig. 6A–C, E–F, H). Newly hatched larvae near eggs presented as "wormform" (Fig. 6B, E) or "cyst-form" (Fig. 6A). Both found among crushed egg strings. Under light microscopy, worm form (n = 13) larvae pre-septum length 31.25 ± 2.83 (24.66-34.14) µm, width 13.18 ± 0.44 (12.30-14.13) µm; post-septum length 80.75 ± 3.87 (77.16-89.13) µm, width 11.17 ± 0.70 (9.76-2.60) µm. Proboscis (same as stylet in our previous description in Chiu et al. (2011)) length 11.77 ± 0.87 (10.14-12.46) µm, width 3.29 ± 0.39 (2.79-4.02) µm; pseudo-intestines unequally subdivided, oval with length 48.22 ± 2.86 (44.69-54.32) µm, width 7.99 ± 0.87 (6.57-9.17) µm. Cyst form (n = 15) larvae post-septum folded into an oval shape, length 25.64 ± 1.66 (22.34-27.88) µm, width 17.41 ± 1.40 (14.91-19.38) µm; proboscis the only obvious structure, length 11.19 ± 1.25 (8.22-13.23) µm, width 2.60 ± 0.63 (1.38-3.21) µm.

Under SEM (worm-form larvae), larvae superficially annulated with 13 segments on pre-septum and 35 on post-septum, ectodermal septum not distinguishable (Fig. 6E). Hooks arranged in three rings on anterior pre-septum: outer ring containing seven hooks, including ventral double hooks close to each other; middle and inner rings containing six hooks, and six inner spines, located between each outer hook (Fig. 6F). Proboscis inside the pre-septum covered by sheath, ornamented with two sets of spines: seven larger spines arranged laterally in two lines, except the largest terminal spine; seven smaller spines on dorsal side, no spines on ventral proboscis (Fig. 6H). One single posterior spine located on end of post-septum (Fig. 6E); exterior openings of pseudo-intestine may be present, but not clear (Fig. 6C).

Field-collected cysts (Fig. 6D) Three cysts inside a snail length 23.59–24.35 μ m, width 15.33–16.45 μ m; proboscis length 11.42–11.91 μ m, width 1.67–2.047 μ m. Shape of cysts similar to cyst-form larvae, no cyst wall found, likely ruined during sample preparation.



Figure 5. Morphological variation of the cuticle that may result from mucus. **A** Smooth cuticle **B–C** Wrinkled cuticle **D–E** Cracked surface of cuticle **F** Areole-like structures on the anterior end of the cuticle **G–J** Indentations on the **G–I** mid-body and **J** anterior end of the cuticle surface. Scale bars 100 μ m (**A**), 10 μ m (**B**), 50 μ m (**C–E**), 100 μ m (**F**), 20 μ m (**G**), 100 μ m (**H**), 10 μ m (**I**), and 100 μ m (**J**).

Phylogeny. Except for one female with insufficient DNA for sequencing, the 23 *Acutogordius* COI sequences (GenBank numbers KX591922, KX591926–KX591935, KX591937–KX591948) contained eight haplotypes with 442 invariable sites, six singletons, and two parsimoniously informative sites. The genetic distance among them was 0.0025 with a range of 0.0000–0.0112. The phylogenetic tree had a polytomic topology in which some clades were not highly supported because of low bootstrap values and short genetic distances (Fig. 7). The genetic distance between the COI sequences of these 23 *Acutogordius* individuals and that of *G. balticus* was 0.27948 compared to 0.25455 and 0.27439 for *G. attoni* and *G. cf. robustus*, respectively.



Figure 6. Immature stages of *Acutogordius taiwanensis* sp. n. **A–B** Live **A** cyst-form and **B** worm-form larvae in water **C** Posterior view of a worm-form larva **D** Cysts in an infected snail; **E** Worm-form larva under SEM **F** Anterior view of a larva showing the hook arrangement **G** Egg strings **H** Close-up of the proboscis. DS, dorsal spines; Ho, hooklet; LS, lateral spines; Peo, pseudointestine exterior opening; PostS, postseptum; PreS, preseptum; Pro, proboscis; PS, proboscis sheath; PsI, pseudointestine gland. Scale bars 50 μ m (**A–B**), 2 μ m (**C**), 50 μ m (**D**), 10 μ m (**E**), 5 μ m (**F**), 1 cm (**G**), and 2 μ m (**H**).

Comments. The 23 *Acutogordius* samples from orthopteran hosts were determined to be from a single species based on their low genetic distances, which was similar to the intraspecific pairwise distances found within *G*. cf. *robustus* (0.64–2.63%) (Hanelt et al. 2015) and *C. formosanus* (0–1.92%) (Chiu et al. 2011) and lower than the interspecific pairwise distances among species of the genera *Gordius* (8.0–24.3%) (Hanelt et al. 2015) and *Chordodes* (16.84%) (Chiu et al. 2011).



Figure 7. Neighbor-joining tree of *Acutogordius taiwanensis* sp. n. and *Chordodes formosanus* compared to *C. japonensis, Gordius attoni, G.* cf *robustus, G. balticus,* and *Paragordius* sp. Numbers at the nodes represent the percentage of 5,000 bootstrap replicates.

All three morphological types of post-cloacal crescents identified in *A. protectus* were apparent in the *Acutogordius taiwanensis* sp. n. samples. Nevertheless, post-cloacal crescents significantly extending onto the tail lobes were only described in *Acutogordius taiwanensis* sp. n. and previously in *A. acuminatus* de Miralles and de Villalobos 1998, *A. feae* (Camerano, 1897), *A. obesus* (Camerano, 1895), and *A. sulawensis* Schmidt-Rhaesa and Geraci, 2006. High intraspecific variation in the post-cloacal crescent makes this structure unsuitable as a diagnostic characteristic at the species level, despite that it is the most obvious structure that can be examined by stereomicroscope.

Short bristles on the mid-body were a newly described character, which were first found in A. finni (Schmidt-Rhaesa and Schwarz 2016). This character is not likely to be examined by stereomicroscope, but in Acutogordius taiwanensis sp. n., the short bristles were still not consistently present in all individuals examined under SEM. One of the possible reasons is that the bristles were covered by mucus on the cuticle surface. The surface of Acutogordius has been generally described as totally smooth (de Miralles and de Villalobos 1998, Schmidt-Rhaesa et al. 2006). However, various structures were found on the surface of Acutogordius taiwanensis sp. n., including wrinkled, cracked, or indented structures. A similar structure (fine grooves as described in Schmidt-Rhaesa and Schwarz (2016) have been found in A. finni (Figs. 4D, E in Schmidt-Rhaesa and Schwarz (2016)), and some of the bristles look like "sticks" on the cuticle surface. In addition, the areole-like structure on the anterior end of one female, also suggested the possibility that the moderately flat areoles covering male tail tips were caused by mucus. Thus, although the moderately flat areoles and short bristles were applied as the main diagnostic characters for Acutogordius taiwanensis sp. n. and A. protectus, more information may be necessary to confidently distinguish between the two species.

Chordodes formosanus Chiu, 2011

Material examined. Taipei Zoo (24°59'44.70"N, 121°34'49.49"E), Taipei City, Taiwan (three males from an *Acromantis japonica* individual); Wufengqi Waterfalls (24°49'55.62"N, 121°44'50.10"E), Jiaushi Township, Yilan County, Taiwan (two males from two Tettigoniidae species). For specimen details, see Table 1.

Hosts. *Acromantis japonica* Westwood, 1889 (Mantodea: Mantidae). *Leptoteratura* sp., *Holochlora japonica* Brunner von Wattenwyl, 1878 (Orthoptera: Tettigoniidae). For host details, see Table 2.

Redescription (Fig. 8). *Male adult* (n = 5). Body length 109 ± 64 (43–204) mm, width (widest, after dehydration) 0.56 ± 0.29 (0.32–0.88) mm, dark-brown, rough, and flat with dorsal and ventral grooves in alcohol-preserved specimens.

Except for one sample with the broken posterior end, which was not described, the posterior end of the other 4 samples (Fig. 8A) not lobed, ornamented areoles on margin with short spines between them. Oval cloacal opening subterminal, 61.14 ± 27.61 (44.41–93.00) µm long and 31.23 ± 11.42 (22.00–44.00) µm wide, circum-cloacal spines present. A pair of oval regions free with areoles posterior to cloacal opening with scattered bristles over it. Paired oval bristlefields 171.94 ± 48.32 (127.84-223.59) µm long and 55.94 ± 10.08 (46.34-66.43) µm wide, not found in one sample, located on lateral side of cloacal opening between areas adjacent to flat areoles and normal areoles. Anterior end (Fig. 8B) tapered, with white tip (white cap) under stereomicroscopy. Under SEM, anterior tip smooth or wrinkled, covered with abundant small spines, and scattered, thick bristles; mouth open on terminal end of anterior extremity.



Figure 8. Male adult *Chordodes formosanus* from novel hosts. **A** Posterior end **B** Anterior end **C–D** Variable crowned areole morphologies from different individuals **E** Close view of (**C**) with typical *C. formosanus* crowned areoles; **F** Close view of (**D**) with smaller crowned areoles. Ca, crowned areole. Scale bars 100 μ m (**A**), 10 μ m (**B**), 100 μ m (**C–D**), and 10 μ m (**E–F**).

Mid-body covered with areoles with some ornamentation on surface. Areoles characterized into five types (simple, tubercle, thorn, circumcluster, and crowned areoles). Simple areoles, most abundant, covering entire cuticle of mid-body, 9.70 \pm 1.84 (8.18–12.51) µm in diameter, circular, surface smooth or uneven. Tubercle areoles and thorn areoles scattered among simple areoles, similar in shape, but with a tubercle (ca. 3.96–8.09 µm long) or a solid thorn (ca. 7.35–16.92 µm long), respectively, on the latter or on top of thorn areoles; thorn areoles less abundant than tubercle areoles and not found in one sample. Crowned areoles (Fig. 8C, E) (each 14.90 \pm 3.40 (9.72–21.81) µm in diameter) surrounded by 7–12 circumcluster areoles with a central tubercle in between; each areole with a flat top and medium filaments (13.11 \pm 4.96 (7.41–27.62) µm) originating from the apical center to edges; few long filaments (55.43–179.70 µm) found in one sample. In one small individual from *Acromantis* mantid, crowned areoles (Fig. 8D, F) smaller than usual (10.84 \pm 0.84 (9.60–11.83) µm) and apical filaments (6.56 \pm 1.11 (5.03–8.36) µm), with almost same-sized circumcluster areoles.

Phylogeny. The genetic distances among all horsehair worms from *Acromantis japonica* (GenBank nos: KX591949–KX591951), *Leptoteratura* sp. (GenBank no.: KX591952), *Holochlora japonica* (GenBank no.: KX591953), and *Hierodula* mantid (sequences from Chiu et al. (2011)) COI sequences ranged from 0.000 to 0.010. The phylogenetic tree (Fig. 7) revealed a polytomic topology, whereas the five horsehair worm sequences from the *Acromantis* mantid and Tettigoniidae hosts were randomly inserted into this clade.

Comments. The five male horsehair worms were all determined to be *C. formosanus* because of the low genetic distances between their COI sequences and those of *C. formosanus* individuals as described in Chiu et al. (2011). Their morphology was also similar to that of the species described in Chiu et al. (2011), which consisted of five areole types in male adults with slight differences found in the bristlefield and crowned areoles.

The size of the bristlefields was smaller in individuals in the present study than in those described in Chiu et al. (2011) (70–77 μ m wide and 145–243 μ m long, respectively) and were not found at all in one extremely small individual. Although the difference in the bristlefields in the male *Chordodes* species has not been used to distinguish the species, this character has been used to distinguish *Gordionus kii* from *G. chinensis* (Schmidt-Rhaesa and Sato 2009).

Another abnormal morphological feature was the similar-sized paired crowned areoles and their surrounding circumcluster areoles. These "abnormal crowned areoles" were only found in one extremely small individual, but not in the other horsehair worms, including the two large ones that emerged from the same host individual. Because the molecular data suggested that this individual was conspecific with *C. formosanus*, we believe the abnormal crowned areoles may have been caused by incomplete development during synchronized maturation (see Discussion for details).

Discussion

In this article, a new species, *Acutogordius taiwanensis* sp. n. and its immature stages were described, and 11 species of orthopteran insect hosts of this new species were identified. In addition, three novel hosts of *C. formosanus, Acromantis japonica, Leptoteratura* sp., and *Holochlora japonica*, were identified.

Acutogordius taiwanensis sp. n.

Intraspecific variation. Finding stable diagnostic characters is a crucial step in distinguishing horsehair worm species (Schmidt-Rhaesa and Geraci 2006, Hanelt et al. 2015). This process includes two main challenges: 1) finding a stable diagnostic character and 2) setting the boundary between intra- and interspecific variation. The postcloacal crescent was the main diagnostic character distinguishing the *Acutogordius* and *Gordius* species (Schmidt-Rhaesa 2001). This structure, despite its function being unclear, is easily examined under both an SEM and a stereomicroscope. However, its morphology may be more unstable than previously understood. The potential polymorphism has been documented in *A. protectus*, which has primarily been characterized by tail areoles, instead of the postcloacal crescent (Schmidt-Rhaesa and Geraci 2006). In *Acutogordius taiwanensis* sp. n., distinct intraspecific variation in the postcloacal crescent was further confirmed. Likewise, the small ornamentations on the body cuticle currently described as a diagnostic character in *Acutogordius taiwanensis* sp. n. and *A. finni* (Schmidt-Rhaesa and Schwarz 2016) may also appear in other *Acutogordius* species, especially those that were described without SEM examination before the descriptions of de Miralles and de Villalobos (1998) and Schmidt-Rhaesa et al. (2006).

Using SEM to describe nematormorph species has become standard practice (Schmidt-Rhaesa 2001). However, mucus, which may be present in *Acutogordius* (as well as *Gordius*), is likely to obstruct various morphological features under SEM. This is the first report suggesting that horsehair worms may secrete mucus on its body surface, and the function of this mucus is unknown. As an aquatic animal that parasitizes terrestrial hosts, the horsehair worm is known to avoid emerging on land where it could become dehydrated by manipulating its hosts (Thomas et al. 2002). The mucus secretion could be an additional strategy for retaining moisture caused by the high risk of being out of the water.

Because of high intraspecific variation, the conspecific status of the 28 examined samples of *Acutogordius taiwanensis* sp. n. was primarily based on the comparison of DNA barcodes and secondarily supported by the similarity of hosts and habitat. DNA sequencing, with the application of SEM since 1980 (reviewed in Chandler and Wells 1989), provides a new and standard tool in horsehair worm taxonomy. Although the database of horsehair worm sequences is not yet complete enough to enable determination of a new species, it is useful in judging the conspecific status of a set of samples. The combination of molecular and morphological data has also improved our understanding of intraspecific variation and cryptic species (Chiu et al. 2011, Hanelt et al. 2015). Thus, while here we suggested that *Acutogordius taiwanensis* sp. n. is a newly described species to science, its phylogenetic relationship with nine other *Acutogordius* species (or seven species, see Schmidt-Rhaesa 2002) is still unclear and worth further investigation.

The immature stages of Acutogordius. Studies of the immature stages of horsehair worms have received more attention in recent years. Although morphological identification of the immature stage to the genus level is only now roughly possible (Szmygiel et al. 2014), cysts from a wide range of aquatic hosts have recently been used to estimate geographic distributions (Hanelt et al. 2001, Harkins et al. 2016), species composition (Bolek et al. 2013a), and annual reproductive seasons (Chiu et al. 2016). The morphology of the immature stages of *Acutogordius* in the present study was similar to that of the cysts we found in a field survey (Chiu et al. 2016, Fig. 1, type 2 cyst), which suggests the distribution of *Acutogordius*, despite the fact that no adult worms were found during that survey.

Newly hatched larvae that fold their bodies outside of hosts have rarely been described (Dorier 1930, Bolek et al. 2015). This might not be typical, because larvae of numerous gordiid species have never been observed to encyst in air or water, and species folding their larvae have only occasionally been observed in some individuals (Bolek et al. 2015). In the case of *Acutogordius taiwanensis* sp. n., the folded larvae (cyst form) were found among the crushed egg strings. As there were some dead larvae near the egg strings, it seems the eggs had already hatched for a few days before being examined. It is uncertain if the larvae folded outside of the eggs or inside the eggs and then were pushed out. Nevertheless, because all the larvae inside the eggs were found to be unfolded, we believe they folded themselves at the egg strings after hatching. To date, we do not yet know which factors triggered newly hatched larvae to become worm-shaped or cyst-shaped because both were found under similar living conditions. Larval worms are thought to stay on the river bottom and be passively ingested by paratenic hosts (Hanelt et al. 2005). Folding their bodies may provide a benefit by reducing the water flow or by making them easy to ingest because the postseptum in *Acutogordius*, as well as in *Gordius*, is significantly longer than in other genera (Hanelt and Janovy 2002, Szmygiel et al. 2014).

Acutogordius taiwanensis sp. n. hosts. Prior to this study, the only reported host of Acutogordius was Acanthodis sp. (reviewed in Schmidt-Rhaesa 2013). In the case of Acutogordius taiwanensis sp. n., it was found to emerge from several families of Orthoptera with different foraging behaviors. Most of the hosts are obligate or facultative predators and are frequently found to prey on small insects in the field (e.g., Eugryllacris sp., Neanias magnus, Hexacentrus japonicus, and H. unicolor), but some of them are primarily herbivorous in Taiwan (e.g., Deflorita apicalis, Elimaea sp., Isopsera sp., and Phaulula sp.). Adult horsehair worms have emerged from non-carnivorous hosts, herbivores (Barbitistes serricauda, Leptophyes punctatissima), or detritivores (Cambala annulata) (Schmidt-Rhaesa et al. 2005, 2009). These horsehair worms challenge our current knowledge because these worms typically invade their definitive hosts through paratenic hosts, which require that a carnivorous host ingests a paratenic host carrying the horsehair worm's cyst (Hanelt et al. 2005). A possible pathway for parasitizing these non-carnivorous hosts is via consumption of larvae/cysts in the water or on vegetation (Schmidt-Rhaesa et al. 2005, 2009). Horsehair worm cysts have known to maintain partial infectiousness after the paratenic host dies and after they are dry for 30 days (Bolek et al. 2013b). This makes them capable of being accidentally ingested by herbivorous or detritivorous, if the dead paratenic host is in the water or on the vegetation. In addition, it is also possible that herbivorous hosts facultatively prey on weak or newly emerged paratenic hosts. Regardless of the pathway the horsehair worm cysts follow, the infection rates of non-carnivorous hosts are theoretically lower than that of predators, and this supports our observations in the field in Taiwan.

Chordodes formosanus

Novel hosts. The *Acromantis* mantid and *Leptoteratura* sp. are general predators that can easily ingest the cysts of *C. formosanus* in paratenic hosts, but *C. formosanus* was previously thought to develop specifically inside *Hierodula* mantids (Chiu et al. 2011). The novel hosts suggest flexibility in *C. formosanus* host use. Such a phenomenon may also occur in *C. japonensis*, which primarily parasitizes *Tenodera* mantids (Inoue 1952, 1955; Chiu et al. 2011), but has also been found in long-horn grasshoppers, *Hexacentrus japonicus japonicus* (Inoue 1955).

In the present study, we recorded long-horn grasshoppers and an *Acromantis* mantid as hosts of *C. formosanus*. However, we do not think these novel hosts are the general ones used by *C. formosanus*. Horsehair worm hosts have been recorded for most of horsehair worm genera (Schmidt-Rhaesa 2013), but knowledge of host preference, the extent to which a particular host taxon is used by a parasite (Lymbery 1989), is generally lacking. We believe that *Acromantis* mantids and tettigoniids, compared to *Hierodula* mantids, are rarely parasitized by *C. formosanus* because of the seasonal infection rates of aquatic paratenic hosts in Taiwan. Our previous survey of horsehair worm infections in aquatic paratenic hosts suggested a single infection peak after the adult *C. formosanus* emerge from *Hierodula formosana* individuals. Such an infection peak did not appear, at least not significantly, after the spring when adult worms emerged from *Acromantis* mantids and tettigoniids (Chiu et al. 2016, Fig. 1). Thus, the contribution of *Acromantis* mantids and tettigoniids to the population of *C. formosanus* may be less than that of *Hierodula* mantids. It is not clear if development in novel hosts is ecologically significant or accidental, but flexibility in host use may improve our understanding of the physiological mechanisms triggering cyst metamorphosis.

Abnormal morphology of the smallest individual. Horsehair worm length is strongly correlated to the host's size and to the number of individuals in a single host (Hanelt 2009). However, the relationship between horsehair worm size and its morphology has not been evaluated. The only individual bearing "abnormal crowned areoles" and lacking bristlefields was half the length (58 mm) of the other two (125 and 115 mm) individuals from the same host individual. One hypothesis explaining the abnormal morphology, even though we have no direct evidence, may be related to incomplete development. Thus, the morphological similarity of the abnormal crowned areole and the simple areole might suggest the crowned areole is differentiated from the simple areole were also suggested by the ultrastructure of *Chordodes nobilii* examined by transmission electron microscopy (Schmidt-Rhaesa and Gerke 2006).

The possible reason causing incomplete development may be resource competition and synchronized maturation. Horsehair worms inside a host individual may compete for resources to increase their fecundity, or they may ensure their survival by synchronizing maturation before the host performs the suicide behavior. These actions would subsequently cause the horsehair worm, which may enter the host later than its neighbors, to mature without completing its development. Thus, we suggest that the abnormal crowned areoles may be a result of incomplete development rather than small size. This hypothesis could also be supported by another extremely small *C. formosanus* (43 mm in length) with crowned areoles that were more likely to be normal in this study. This small *C. formosanus* singly developed in a host individual. Without the influence from neighbor horsehair worms, its small size might have been the result of the small host (9.63 mm in length), instead of incomplete development.

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RESEARCH ARTICLE



African Neotermes: redescriptions of imago and soldier castes of N. *aburiensis* and N. *agilis* (Isoptera, Kalotermitidae)

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Abstract

We redescribe the winged imagos and soldiers of two equatorial African species, *Neotermes aburiensis* Sjöstedt and *N. agilis* (Sjöstedt) and describe their unique character attributes. The imago of *N. aburiensis* is adorned with unique spatulate-pointed setae. The soldier of *N. aburiensis* is unique among *Neotermes* in possessing a phragmotic forehead. The imago of *N. agilis* is small and unique among *Neotermes* in having complete coalescence of radial sector and median veins in the forewing while the soldier of *N. agilis* has a broad pronotum.

Keywords

Taxonomy, Ghana, Nigeria, setae, phragmotic, venation

Introduction

Neotermes Holmgren consists of 117 extant species (Krishna et al. 2013) making it the second largest kalotermitid genus after *Glyptotermes* Froggatt. Of these, 48 species are described from the soldier or the imago only and 17 (16 from soldier only) are described from mainland China (Krishna et al. 2013). Among the Kalotermitidae,

Neotermes are usually large species. The imagos are recognized by wing venation in which the media is sclerotized and runs close and parallel to the radial sector to the wing tip. Soldiers possess a long head lacking prominent anterolateral prominences and a faintly depressed frons with a slope of less than 45 degrees (Krishna 1961).

The diversity of *Neotermes* from equatorial central and western Africa is limited to nine species: *N. aburiensis*, *N. agilis*, *N. camerunensis* (Sjöstedt), *N. collarti* Coaton, *N. gestri* Silvestri, *N. lepersonneae* Coaton, *N. nigeriensis* (Sjöstedt), *N. pallidicollis* (Sjöstedt), and *N. sepulvillus* (Emerson). We recently acquired specimens of *N. aburiensis* and *N. agilis* both of which, coincidently, transcend the morphological boundaries of *Neotermes* given above. To contribute to a clearer understanding of African *Neotermes*, we redescribe these two species, including a first description of the *N. agilis* soldier, and highlight their unique morphological characters.

Material and methods

Photographs of imagos and soldiers were taken as multi-layer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Preserved specimens were taken from 85% ethanol and suspended in a pool of Purell Hand Sanitizer to position the specimens on a transparent Petri dish background. Wings (Fig. 3) were mounted on slides using PVA medium (BioQuip, Rancho Dominquez, CA). Montage microphotographs (Fig. 2) were taken from PVA slide mounts of pronotum cuticle (lateral margins) using a Leica CTR 5500 compound microscope.

Taxonomy

Neotermes aburiensis Sjöstedt, 1925

Neotermes aburiensis Sjöstedt 1925: 39 (soldier described; Ghana). Neotermes aburiensis: Grassé 1937: 10-14 (imago and soldier described; Ivory Coast). Neotermes aburiensis: Coaton 1955: 109-113 (soldier described; Congo-Zaire, Ghana, Ivory Coast).

Material examined. NIGERIA, Ijare; 7.36, 5.17; 9 Apr 2016, E. Onagbola, UF no. AFR2965; 15 alates, nymphs, ex: dead cacao tree. Orita Obele, (OSRC Radio Station Yard), Akure; 7.29, 5.16; 29 Apr 2016 AFR2966; 5 soldiers, 13 alates, nymphs, ex: living stump of Quickstic (*Gliricidia sepiun*) tree. Bayduk Road, Akure; 7.301, 5.151, AFR2971; 1 alate, ex: spider web on house fence.

Imago (Figs 1–3, Table 1). Head with vertex and frons dark reddish-brown grading to light orange-brown at genae. Pronotum lighter than dorsum of head; anteclypeus yellowish and labrum concolorous with genae (Fig. 1). Tergites light yellowish-brown, sternites pale yellow to hyaline. Coxa and femora pale yellow, femora and tarsi contras-



Figure 1. Head and thorax of *Neotermes aburiensis* imago. A Dorsal B lateral, and C ventral views.



Figure 2. Neotermes setae on pronotum cuticle. Neotermes aburiensis (**A**, **B**) and N. castaneus (Burmeister) (**C**, **D**).

ting light brown. Chevron pattern from overlapping wing scales and meso and meta notum slightly darker than rest of dorsum. Eyes black; ocelli and antennal articles concolorous with labrum. In dorsal view, lateral margins of head converge to anterior forming distinct trapezoidal outline; cranial sutures absent. Vertex with slight concavity,



Figure 3. *Neotermes aburiensis* forewing (**A**) and hind wing (**B**). *Neotermes agilis* fore wing (**C**) and hind wing (**D**). RS = radial sector, M = median vein.

concavity becoming rugose toward anteclypeus. Eyes of medium size, slightly protruding, and weakly subtriangular. Ocelli large, elliptical, nearly touching eye. Antennae with 17–19 articles, rarely 16. Pronotum in dorsal view collar-shaped. Anterior margin of pronotum very shallowly concave; posterior margin nearly straight; pronotum wider

Measurement	max	min	mean
Head length with labrum	2.00	1.83	1.91
Head length to postclypeus	1.58	0.13	0.85
Head width, maximum at eyes	1.68	1.50	1.59
Head height without postmentum	1.05	0.88	0.96
Labrum width, maximum	0.60	0.50	0.55
Eye diameter with sclerite, maximum	0.50	0.43	0.46
Eye to head base, minimum from sclerite	0.28	0.20	0.24
Ocellus diameter, maximum	0.24	0.14	0.19
Ocellus diameter, minimum	0.16	0.10	0.13
Pronotum, maximum length	1.10	0.75	0.93
Pronotum, maximum width	1.93	1.58	1.75
Total length with wings	15.56	13.17	14.37
Total length without wings	8.73	6.19	7.46
Fore wing length from suture	13.17	11.27	12.22
Fore wing, maximum width	3.75	3.00	3.38
Hind tibia length	1.30	0.88	1.09
No. antennal articles	19	16	18

Table 1. Measurements of Neotermes aburiensis imago (n=16).

than width of head at eyes; widest at posterior 2/5ths. Scattered long (0.25 mm), erect setae on head and pronotum with numerous short and very short setae (Fig. 2A). Tips of long setae rounded at tip; tip weakly spatulate (Fig. 2B). Costal margin, radius, radial sector, and media of forewing brown and sclerotized along their entire lengths (Fig. 3A, B). Cubitus brown just beyond suture line, with about 10 browish branches to middle of wing 3-4 hyaline branched beyond; membrane between media and cubitus with dozens of faint brown reticulations. Arolia present. Mandible dentition typical of genus; left mandible with posterior margin of first plus second marginal tooth equal to anterior margin of third marginal tooth. Right mandible with posterior margin of second marginal tooth subequal to molar plate.

Soldier (Fig. 4, Table 2). Monomorphic. In dorsal view, head capsule dark redish brown at antennae grading to light yellowish orange at occiput. Mandibles black. Three proximal antennal articles reddish brown; distal articles becoming lighter. Eye spots light yellowish brown, elongate, smaller than antennal sockets. Pronotum peripheral margins yellowish orange-brown. Postmentum chestnut; labrum concolorous with vertex. Head capsule in dorsal view, narrowly rectangular; lateral margins slightly concave, narrowing slightly in front. Posterior corners of head evenly rounded; posterior margin rectate. In lateral and oblique view, head capsule almost cylindrical with only slight dorso-ventral compression. In dorsal view, frontal flange squarely angled at 60° forming a deep cleft; in lateral or oblique views antero-lateral corners of flange with knob-like protuberences. Vertex with lateral grooves; lateral margins of vertex with distinct rails. Frons sloping from vertex $\cong 45^{\circ}$; mandibles curved upward $\cong 10^{\circ}$. Setae very short and sparse on frons and vertex. Periantennal carina developed; mandibles stout,



Figure 4. Head and pronotum of *Neotermes aburiensis* soldier. A Dorsal B lateral C ventral, and D oblique views.

Table 2. Measurements	s of Neotermes	aburiensis soldier	(n=5).
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Measurement	max.	min.	mean
Head length to tip of mandibles	5.20	4.30	4.78
Head length to postclypeus	3.90	3.20	3.44
Head width, maximum	2.20	2.10	2.14
Span of frontal processes	1.00	0.88	0.93
Head height, excluding postmentum	1.65	1.50	1.60
Labrum, maximum width	0.53	0.50	0.51
Postclypeus width, maximum	0.60	0.53	0.58
Left mandible length, tip to most distant visible point of ventral condyle	1.70	1.63	1.65
Postmentum, length in middle	2.60	2.30	2.46
Postmentum, maximum width	0.80	0.70	0.77
Postmentum, minimum width	0.38	0.28	0.32
Pronotum, maximum width	2.25	2.08	2.17
Pronotum, maximum length	1.18	1.10	1.13
Hind tibia length	1.30	1.00	1.19
Total length	11.43	10.63	11.02
No. antennal articles	15	15	15

about one-half length of head capsule; dentition well defined; left mandible with three submarginal teeth; two proximal teeth subdivided by slight concavities; right mandible with proximal tooth eclipsed by labrum; apical teeth angled $\cong 70^{\circ}$; basal humps moderate, rugose. Labrum linguiform, medium-sized, with long terminal setae. Antennae

with 15 articles; third antennal article clavate, barely shorter than fourth and fifth combined. Pronotum broader than head, narrow, shield-shaped; anterior margin evenly concave; anterolateral corners acutely angled at 60°, lateral margins converging to posterior; posterior margin forming an evenly shallow convexity. All femora inflated.

Comparisons. The spatulate-tipped setae on the head and pronotum of *N. aburiensis* are unique among *Neotermes* and possibly all Isoptera which have tappering, needle-like setae (Fig. 2C, D). The clefted frontal flange, its lateral protuberences, and sloping rugose frons form a phragmotic forehead unique among *Neotermes* soldiers.

Neotermes agilis (Sjöstedt, 1902)

Calotermes agilis Sjöstedt 1902: 302 (imago). *Calotermes agilis* Sjöstedt 1904: 15–16 (imago described; Cameroon). *Neotermes agilis*, Krishna 1961: 325 (comb. n.).

Material examined. GHANA, Bobiri Butterfly Reserve; 6.690, -1.338, 12 Sept 2006, L.R. Davis, UF no. AFR188; 2 soldiers, 16 alates, nymphs ex: "hard chunk of wood"; 2 alates, 2 nymphs, and soldier photographs sent to K. Krishna 12 Oct 2006.

Imago (Fig. 5, Table 3). Small species. Head with vertex and frons reddish-brown grading to light reddish brown in posterior; lighter near suture of anteclypeus. Pronotum concolorous with dorsum of head except for a lighter area in anterior third; anteclypeus yellowish and labrum concolorous with genae. Tergites yellowish-brown, sternites pale yellow to hyaline. Coxa and femora pale yellow, femora and tarsi light brown. Chevron pattern from overlapping wing scales, meso- and metanotum concolorous with vertex. Eyes greyish black; ocelli and antennal articles concolorous with labrum. In dorsal view, lateral margins of head converge slightely; cranial sutures, thin but distinct. Vertex smooth, slight concavity of frons. Eyes large, slightly protruding, and nearly circular. Ocelli very large, ellipsoid, touching eye. Antennae with 14-16 articles. Pronotum in dorsal view subrectate. Anterior margin of pronotum weakly incised; posterior margin weakly incised in middle; lateral margins evenly rounded. A few scattered erect setae on head; pronotum with numerous long and shorter setae along margins (Fig. 5). Costal margin, radius, radial sector, and media of forewing brown and sclerotized along proximal 1/3 of wing, abrupty becoming hyaline for their remainders (Fig. 3). Median vein with weak posterior bend after suture; coalescing with radial sector at about half length of wing. RS+M hylaline with about 5 anterior branches. Cubitus brown just beyond suture line, with about 4 browish branches to proximal 1/5 of wing 6-7 hyaline branches beyond; membrane pigmented only in basal 1/5; remainder hyaline. Arolia absent. Mandible dentition typical of genus.

Soldier (Fig. 6; Table 4). Monomorphic. Head capsule dark redish brown in a narrow strip anterior to antennae; remainder of head capsule light yellowish orange. Mandibles black beyond humps, humps dark reddish brown. Eye spots faint or absent.



Figure 5. Head and thorax of *Neotermes agilis* imago. A Dorsal and B lateral views.

Pronotum light yellowish orange. Head capsule in dorsal view, subquadrate; lateral margins slightly convex. In lateral view, head capsule ellipsoid. Frons sloping from vertex $\cong 40^{\circ}$; mandibles curved upward $\cong 20^{\circ}$. Scattered medium and short setae on head capsule and pronotum. Periantennal carina weak; mandibles short and stout; left mandible with three submarginal teeth, right mandible with two large subapical teeth, distal tooth forming right angle with apical tooth, apical teeth angled 50°; basal

Measurement	max	min	mean
Head length with labrum	1.68	1.45	1.54
Head length to postclypeus	1.40	1.13	1.28
Head width, maximum at eyes	1.40	1.15	1.33
Head height without postmentum	0.93	0.75	0.84
Labrum width, maximum	0.58	0.43	0.50
Eye diameter with sclerite, maximum	0.53	0.45	0.49
Eye to head base, minimum from sclerite	0.20	0.13	0.16
Ocellus diameter, maximum	0.22	0.14	0.19
Ocellus diameter, minimum	0.18	0.10	0.14
Pronotum, maximum length	0.85	0.63	0.72
Pronotum, maximum width	1.53	1.30	1.41
Total length with wings	12.70	10.16	11.16
Total length without wings	6.98	5.40	5.98
Fore wing length from suture	10.32	8.25	8.90
Fore wing, maximum width	2.75	1.95	2.24
Hind tibia length	1.00	0.90	0.94
No. antennal articles	16	14	15

Table 3. Measurements of *Neotermes agilis* imago (n=10).

Table 4. Measurements of *Neotermes agilis* soldier (n=2).

Measurement	max.	min.	mean
Head length to tip of mandibles	3.30	3.20	3.25
Head length to postclypeus	2.20	2.20	2.20
Head width, maximum	1.55	1.50	1.53
Span of frontal processes	0.95	0.80	0.88
Head height, excluding postmentum	1.25	1.25	1.25
Labrum, maximum width	0.38	0.25	0.31
Postclypeus width, maximum	0.43	0.40	0.41
Left mandible length, tip to most distant visible point of ventral condyle	1.25	1.20	1.23
Postmentum, length in middle	1.35	1.20	1.28
Postmentum, maximum width	0.63	0.48	0.55
Postmentum, minimum width	0.18	0.15	0.16
Pronotum, maximum width	1.50	1.45	1.48
Pronotum, maximum length	0.95	0.85	0.90
Hind tibia length	0.83	0.83	0.83
Total length	7.78	7.62	7.70
No. antennal articles	12	12	12

humps slightly inflated. Labrum linguiform, medium-sized, with long terminal setae. Antennae with 12 articles, third article somewhat enlarged but shorter than fouth and fifth combined. Pronotum as broad as head, wide; anterior margin shallowly incised;



Figure 6. Head and pronotum of *Neotermes agilis* soldier. A Dorsal B lateral, and C ventral views.

anterolateral corners rounded \cong 70°, lateral margins parallel; posterior margin rectate in middle. Front femora inflated.

Comparisons. The fore wing venation of *N. agilis* is unique among *Neotermes* and other kalotermitids in that the major veins are hyaline beyond their bases and the radial sector and median veins coalesce to form a single vein. The venation of *N. agilis* is close to *Rugitermes*, but in *Rugitermes* the distal two thirds of median vein is sclerotized. All other *Neotermes* have fore wings with fully sclerotized major veins and a median vein which remains independent of the radial sector (see Ware et al. 2010). The soldier of *N. agilis* is among the smallest of the genus and has an unusually broad pronotum.

Discussion

As with many older works, Sjöstedt's (1925) description of the soldier of *N. aburiensis* is brief and lacks illustrations. However, he describes the specimen collected "from old wounds in stems of cocoa tree" in Aburi, Ghana, as having its "forehead depressed in back; bordered by a curved keel" (translated from German) and having a head width of 2–2.3 mm. Grassé (1937) described the winged imago of *N. aburiensis* from a cacao trunk in Bingerville, Côte d'Ivoire. He included a detailed drawing of the fore wing (11 mm long) and sketches of the soldier (with curved frons and lateral protuberances), nymph, and soldier antennae. Coaton's 1955 lateral drawing of the *N. aburiensis* soldier head capsule hints of a frontal cleft, and he notes that the "frons is depressed medially, bordered behind by a distinct, concavely curved ridge". Coaton (1955) examined four soldiers from an extreme easterly locality at Lake Albert, Congo.

Sjöstedt's (1904) description, including measurements, of the *N. agilis* imago from Johann Albrechtshöhe station, Cameroon, was compared to our specimens from Ghana. Although lacking illustrations, the body morphology reported by Sjöstedt (1904) matches closely with our material. He notes "wings thin, narrow with constricting rounded tips.....the basal third of the costal and median and the inner branch of the radial sector yellow brown or yellow red..... the remainder is hyaline" (translated from German). The partial pigmentation of the wings is used in Sjöstedt's (1925) key for African *Neotermes*. When RHS first examined the imago of *N. agilis*, the venation did not support inclusion in *Neotermes*. When the imago and soldier specimens were examined by Kumar Krishna in 2006, he placed the specimens in *Neotermes* without comment on morphology. With great respect for Dr. Krishna's knowledge of the group, we keep *N. agilis* in *Neotermes* for now.

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RESEARCH ARTICLE



Rediscovering digitules in Aphidomorpha and the question of homology among Sternorrhyncha (Insecta, Hemiptera)

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Abstract

We explore and expand on the morphological term digitule. The term was originally proposed for toe-like setae on a species of *Phylloxera* Boyer de Fonscolombe, 1834 (Hemiptera, Sternorrhyncha, Aphidomorpha) by Henry Shimer, an American naturalist. While it is standard terminology in scale systematics (Hemiptera, Sternorrhyncha, Coccidomorpha), the term digitule was ignored by aphid specialists despite being the original taxon for which the term was described. Similar setae occur on many arthropod groups, so the homology is poorly understood even within any superfamily of Hemiptera. We provide the etymology of the term, a proposed explanation for why it was used among scale taxonomists and not aphid taxonomists, and discuss briefly options to progress beyond the confusion between terminology for morphology and homology in Sternorrhyncha.

Keywords

Aphididae, Phylloxeridae, Adelgidae, Coccoidea, Coccidae

Introduction

The hemipteran suborder Sternorrhyncha includes the aphids (Aphidomorpha), scale insects (Coccidomorpha), whiteflies (Aleyrodomorpha), and the psyllids or jumping plant lice (Psyllidomorpha) (Carver et al. 1991). Scale insects often have one or more specialized setae on or near the terminus of the leg called digitules. Most scale taxonomists use the term based on setal shape and position on the leg (i.e., it is differentiated from nearby setae in some way, most often enlarged and with an enlarged apex and is near or at the apex of the leg) (Williams 1985, Hodgson 1994, Hardy et al. 2008). If a seta occurs on the claw it is considered to be a digitule regardless of the shape. If the setae on the dorsoapical position of the tarsus are conspicuously larger than the other leg setae they also are treated as digitules. There have been a few inconsistencies in this usage, but they are the exception rather than the rule. Setae with similar shape and position also occur in some species of Aphidomorpha, and differentiated setae occur at or near the apex of the leg in psyllids (pulvillus) (Ossiannilsson 1992) and whiteflies (paronychium) (Gill 1990), but they are not called digitules in these groups. And similar looking setae are found in some mites (Acari) and springtails (Collembola) and are sometimes called digitules (MacGillivray 1923). The lack of congruence among anatomy, morphology, and homology is not uncommon in taxonomy and is often deeply entrenched after years of tradition and unresolved evolutionary relationships among taxa. We had the opportunity to explore this issue with the term digitule after rediscovering the presence of a similar structure in a presumably undescribed species of the genus Phylloxera Boyer de Fonscolombe, 1834 (Insecta, Aphidomorpha, Phylloxeridae).

The genus *Phylloxera* includes 51 valid species; the majority of which were described feeding on *Carya* Nuttall, 1818 in North America (Pergande 1904, Favret 2017). All *Phylloxera* are herbivores with sucking mouthparts and induce the formation of galls on the plant tissues on which they feed. The galls are presumed to be species-specific in their shape, size, color, etc., so species identification relies heavily on host plant and gall morphology. The family Phylloxeridae is part of a monophyletic Aphidomorpha, which includes the superfamilies Phylloxeroidea and Aphidoidea (i.e., aphids), and Aphidomorpha has a sister-group relationship with the Coccidomorpha (scale insects) within the sternorrhynchan suborder of Hemiptera (Gullan and Cook 2007). Scale insects are more diverse and richer in morphology than the other sternorrhynchan groups, taxonomists have relied on these morphological characters to diagnose taxa, and family group relationships among Coccidomorpha are more resolved (Hodgson and Hardy 2013). It's possible that the historical reliance on gall morphology in *Phyl-*

loxera, differing with the use of specimen morphology in scale insects, has contributed to the use and lack thereof of the term digitule in each taxon. We examine that possibility in the purview of the term's etymology and briefly discuss the issue of homology.

History of the term digitule

All of the dictionaries and texts on entomology we checked define digitule with a similar rendition of the same phrase, and are possibly or known to be non-independent repetitions. For example:

The Dictionary of Entomology (Jardine 1913): Digitules. - Appendages usually present on the feet of the Coccidae, either broadly dilated or in the form of knobbed hairs. (From L. digitus)

External Insect-anatomy: A Guide to the Study of Insect Anatomy and an Introduction to Systematic Entomology (MacGillivray 1923, p. 247):

Digitules. - The distal end of the distal tarsal segment and the proximal part of the claws may bear long slender setae that are clavate at the distal end. These setae are known as digitules, also as tenent hairs or empodial hairs. . . . The digitules are of more general occurrence in minute insects like the collembolans and the males of coccids.

The Dictionnaire des Termes D'Entomologie (Séguy 1967):

digitule n. m. Appendice des pattes des Coccides qui peut être une soie dilatée ou terminée par un bouton; soie adhésive; soie empodiale. - Digitule unguéal: chète ou cil placé sur les ongles.

The Torre-Bueno Glossary of Entomology (Nichols1989):

digitule(s), in Coccoidea (Hemiptera: Sternorrhyncha), a pair of normally capitate setae at the inner base of the tarsal claws and at the outer distal margin of the tarsus (T-B, after MacGillivray; Kosztarab and Kozár).

A Dictionary of Entomology (Gordh 2001, 2011):

DIGITULE Noun. (Latin, digitus = finger. Pl., Digitules.) 1. Coccidae: Appendages of the feet that may be broadly dilated or knobbed Setae. 2. Tenent hairs; empodial hairs (MacGillivray).

All the above descriptions associate the term digitule with Coccidae/Coccoidea (=Coccidomorpha), which became part of that taxon's common vernacular by the late 19th to early 20th century based on descriptions of new taxa and other taxonomic works (e.g., Signoret 1872a, 1872b, 1873, 1874; Targioni Tozzetti 1875, Haller 1880, Atkinson 1886, Maskell 1887, Ashmead 1891, Berlese 1893, Cockerell 1893, Hunter 1899a, 1899b, 1900, 1902, Hempel 1900a, 1900b, 1901a, 1901b). A single origin

of the term was unclear until MAM recently uncovered a paper by Henry Shimer (1867a), an American naturalist, wherein he described a new family and genus for a gall-forming hemipteran, *Dactylosphaera globosum* (Shimer, 1867), on *Carya glabra* (Miller), which is currently a valid species in the genus *Phylloxera*. This appears to be the first incidence of the term in the literature (Fig. 1):

Tarsi composed of one joint, terminated by two claws, and from two to six digituli.* *I suggest this name, digituli, from the Latin digitulus, a small finger or toe, for these remarkable organs; it appears to me appropriate, because they are arranged around the foot somewhat like the toes of an animal.

The adoption of digitule to describe toe-like setae at the terminus of the legs in Coccidomorpha instead of Aphidomorpha seems to be historical and serendipitous. The following year, Shimer (1868) used digituli again, referencing his 1867 work therein, when he described a new family, Lepidosaphidae, and genus, *Lepidosaphes*, for the species *Coccus conchiformis* Gmelin, 1790, which was then and is currently classified as a species of scale-insect. Two prominent specialists on Coccidomorpha were Victor Antoine Signoret (1816–1889) of Paris and Adolfo Targioni-Tozzetti (1823–1902) of Florence who recorded in their own articles that they were aware of the other's work. Signoret (1872a) cited Shimer as the source when he first used the term (as digituli), and subsequent works by both authors referred to these structures as digituli or digitules. Their prominence in this field of study presumably led to the community accepting this term for the large part. The term has such wide acceptance that even homology is assumed, as acuminate setae in the same position are still called digitules by some coccidomorph specialists (e.g., Williams and Hodgson 2013).

In contrast, the scientists with the most impact studying Phylloxeridae during that time i.e., Asa Fitch (1809–1879), Charles Valentine Riley (1843–1895), Theodore Pergande (1840-1916), and Benjamin Dann Walsh (1808-1869), were Americans who focused primarily on gall morphology, the biologies of the insects, and the control of pests on commodities. Pergande (1904) used digituli in quotes signifying that the source was from a posthumous or silent coauthors' writings (i.e., Riley was deceased and Dreyfus had to postpone his involvement with Phylloxera indefinitely due to "financial and other troubles."). These authors were less invested in the detailed morphology of the insects themselves throughout their writing. We assume this is a cultural phenomenon rather than a limitation in technology as other investigators of the period were able to visualize these fine structures (e.g., Signoret also published in this family and was a primary investigator of grape *Phylloxera* with Riley (Sorensen et al. 2008)). Of note, Packard (1898) used the term tenent hair instead of digitule, a listed source in MacGillivray's textbook (1923), and Oestlund (1887), perhaps the greatest influence on American aphid classification at the time, described these structures as "two capitate hairs as usually in the genus." This seems to have carried through modern usage in Aphidomorpha (e.g., Foottit and Richards 1993, ventral setae on the apical sclerite (planta) of the pretarsus, Ar = plantar setae).

Methods

AMD collected galls of presumably undescribed species of *Phylloxera* feeding on Carya floridana Sargent, 1913 at two sites in Saint Lucie County, Florida, USA from late February to early March 2012, 2013, and 2015. In the lab we sliced off the top of galls and observed specimens in situ or removed specimens from their galls and secured them to $15 \text{ mm} \times 30 \text{ mm}$ copper plates using ultra smooth, round (12 mm diameter), carbon adhesive tabs (Electron Microscopy Sciences, Inc., Hatfield, PA, USA). We then followed the technique of Fisher et al. (2011) as follows. We froze specimens conductively, in a Styrofoam box, by placing the plates on the surface of a pre-cooled (-196°C) brass bar whose lower half was submerged in liquid nitrogen (LN2). After 20-30 seconds, we transferred the holders containing the frozen samples into a Quorum PP2000 cryo-prep chamber (Quorum Technologies, East Sussex, UK) attached to an S-4700 field emission scanning electron microscope (Hitachi High Technologies America, Inc., Dallas, TX, USA). The specimens were etched inside the cryotransfer system to remove any surface contamination (condensed water vapor) by raising the temperature of the stage to -90°C for 10-15 min. Following etching, we lowered the temperature of the stage inside the cryo-transfer system to -130°C, and coated the specimens with a 10 nm layer of platinum using a magnetron sputter head equipped with a platinum target. Finally, we transferred specimens to a pre-cooled (-130°C) cryostage in the LT-SEM for observation with an accelerating voltage of 5 kV to view the sample and we captured images using a 4 pi Analysis System (Durham, NC, USA).

We also obtained color images and videos of specimens in situ using a Hirox KH-7700 Digital Microscope (Hackensack, NJ) with a MXG-5040RZ lens to assess locomotion. The digital microscope has a motorized stage which allows the capture of several images at 1600×1200 pixels per frame with varying degrees of focus, which were compressed together to develop an image where all fields of view are in focus. We recorded video at 800×600 pixels per frame at 15 frames per second. We collected this imagery before freezing as reference material for observations made with the LT-SEM. MAM reproduced Shimer's (1867a) original illustration of digitules and composed figures with the vector drawing application INKSCAPE and made minor adjustments to the LT-SEM photographs with the photo-editing application GIMP.

Results

Three distinct *Phylloxera* gall morphologies occurred at the sites: one Pergande (1904) group IV type and two Pergande (1904) group II fleshy leaf gall species most similar to *P. rimosalis* Pergande, 1904 and *P. caryaeglobuli* Walsh, 1863. The specimens had egg and adult characteristics most similar to *P. rimosalis*, as originally described by Pergande (1904). AMD sent intact galls from Florida to GLM at the Systematic Entomology Laboratory.

Based on Shimer's (1867a) original figures (Fig. 1) and his description of the structures, we interpret his definition of digitule to be a specialized seta with an expanded tip at the apex of the leg. There are a total of eight setae we would call digitules and two setae that are not digitules on the tarsus of *Phylloxera* we examined. The ventral setae at the apex of the tibia are also digitule-like. The basitarsus (Fig. 3) has a single pair of digitules at the ventroapical margin. The distitarus has a single, acuminate seta in the middle of the dorsum; a single, thick, blunt seta ventromedially at the subapex; two pairs of digitules at the apicoventral margin; and one pair of digitules dorsally at the apex (Figs 3, 5). The foreleg is an exception to the pattern with the anterior seta dorsally at the apex of the distitarsus being acuminate rather than expanded at the tip (Fig. 6). The digitules on the ventral surface all have apices that are spatulate or otherwise expanded in one plane. The dorsal digitules have apices that are expanded radially forming hemispherical knobs that seem membranous such that in some views they are smoothly convex (Fig. 5) while in others they are roughly concave (Figs 3, 4). The digitules are the longest of all the tarsal setae, over twice as long as the acuminate seta on the dorsum of the distitarsus and nearly a third longer than the blunt seta at the subapex of the ventromedial margin of the distitarsus. The digitules of the distitarsus also extend beyond the apices of the tarsal claws.

Digitules seem pliable as they are commonly bent when in contact with the substrate even though in some images the substrate seemed soft enough to take an impression from the digitules and tarsal claws. We did not observe any consistency of position of digitules and claws in relation to specimen activity to make any determinations of their function, and could not indisputably determine that any specimens were in locomotion at the time of freezing. Most specimens with their feet in contact with substrate also had their rostrum embedded in the gall inner wall (Fig. 2), and among these the feet positions varied from leg to leg and specimen to specimen despite the specimens being in an assumed stationary position. In some instances the tarsal claw was plantar flexed so that the dorsal surface of the claw was in contact with the substrate. In others, the ventral surface of the tarsal claw was in contact with the substrate. Again, these positions were likely to occur at the same time on different legs within any one specimen.

Discussion

Through attempts to observe the interaction of *Phylloxera* with their gall substrate, we saw interesting setae on the legs and, after careful mining of the literature, found the originally intended term for these structures. Ironically, the original intent was lost in history, and, unfortunately for Henry Shimer, there is no Principle of Priority for morphological terms! Re-examining these structures with modern equipment, however, did allow us to make some novel observations. At least in the *Phylloxera* we examined, ventral digitules are expanded in only one plane and dorsal digitules are expanded radially. Digitules seem to be pliable, as they often conformed to the gall surface. And while we could not confirm any association of these structures with locomotion, they seem





A. - a side view of the foot of *D*? *vitifoliae* magnified; *a*, the two digituli; *b*, the claws.

B. - a vertical view of the foot of *Dactylosphaera globosum*, from above, magnified; *a*, the six digituli; *b*, the claws, as they may be seen while the insect attempts to walk on the glass plate of a microscope.



Figure 1–6. 1 Reproduction of Shimer's (1867a) original illustration indicating what he considered digitules **2** *Phylloxera* in situ showing leg and feet position **3** Hind leg of *Phylloxera* showing all digitules **4** Close up of dorsal digitule from Figure 3. Note how the ventral surface appears membranous and collapsed **5** Hind leg of *Phylloxera* showing dorsal digitules with expanded ventral surfaces **6** Front left leg of *Phylloxera* showing anterior seta is not a digitule. Scale bar 10 μ m. Scale bars: (**2**, **6**)100 μ m; (**3**) 10 μ m; (**4**) 2 μ m; (**5**) 20 μ m.

unable to support any significant weight, so if they indeed impart some role in association with the substrate perhaps it is sensory or a form of adhesion. Though not called digitules among Aphidomorpha, we did conduct a limited survey of the group. There does not appear to be a correlation between the presence of digitules and the habit of forming a gall, or with any other cryptic behavior. Among Aphidomorpha, digitules occur at least in the genera Anoecia Koch, 1857; Cerataphis Lichtenstein, 1882; Ceratoglyphina van der Goot, 1917; Ceratovacuna Zehntner, 1897; Colopha Monell, 1877; Dinipponaphis Takahashi, 1962; Eriosoma Leach, 1818 (species formerly in Georgiaphis Maxson & Hottes, 1926); Gharesia Stroyan, 1963; Glyphina Koch, 1856; Hamamelistes Shimer, 1867b; Hormaphis Osten-Sacken, 1861; Nipponaphis Pergande, 1906; Phylloxera Boyer de Fonscolombe, 1834; Phylloxerina Börner, 1908; Tamalia Baker, 1920; and Thelaxes Westwood, 1840 at some life stage (Fottit and Richards 1993 and direct observation of specimens). While there are species among these genera that are gall-formers, many make only a pseudogall or do not form galls at all. Likewise, species among the genera Cornaphis Gillette, 1913; Forda von Heyden, 1837; Kaltenbachiella Schouteden, 1906; Melaphis Walsh, 1867; Pachypappa Koch, 1856; Pemphigus Hartig, 1839, Thecabius Koch, 1857; Tetraneura Hartig, 1841; and Tiliphagus Smith, 1965 make either a pseudogall or true gall and have no digitules (Foottit and Richards 1993 and direct observation of specimens). In essence we have come full-circle in terms of digitules in aphids. The structures were first discovered in aphids, we rediscovered them in aphids, but the term digitule is not used in aphids. So the question of digitule homology is not at issue in Aphidomorpha as it is in Coccidomorpha.

The use of the term digitule is prevalent in coccidomorph literature, and is confounded by the lack of distinction between shape and positional homology as we mentioned above. All taxa among Coccidomorpha are considered to have digitules, and all families except Ortheziidae and Stigmacoccidae have species with capitate setae, or setae with expanded apices in some form, in at least one life stage. The following are two examples to illustrate extreme differences in interpretation and not meant to be comprehensive. The recently diagnosed species Arctorthezia helvetica Kozár & Szita, 2015 (Ortheziidae) is described as having claw digitules, as do all the other species treated in that genus by the authors (Szita et al. 2015). These setae are undifferentiated from the setae on the remaining hind leg, but are called digitules because of their position ventrad on the base of the tarsal claw. The most distal setae dorsad on the basal tarsal segment, however, are not described as digitules despite having the same position as digitules from other coccidomorph taxa. These setae are undifferentiated from the remaining setae on that tarsal segment, or from most of the setae on the entire leg. In contrast, the species Steingelia gorodetskia Nasonov, 1908 and Stomacoccus platani Ferris, 1917 (Steingeliidae) have multiple (up to 10) setae with expanded apices located on all surfaces around the base of the tarsal claw. All are called digitules even though they do not share the ventrad position as digitules in other coccidomorph species. We assume these are considered digitules because of their shape rather than their position. Unlike the above authors' treatment in Ortheziidae, however, even fine, hair-like setae dorsad on the apex of the basal tarsal segment are considered digitules in other margarodoid Coccidomorpha (Hodgson and Foldi 2006). Even if these are rare exceptions among scale workers, defining and homologizing these setae uniformly across all of Sternorrhyncha remains a challenge.

So what, if anything, can we recommend to progress towards a stable solution? Testing homology across all of Sternorrhyncha through cladistic analysis is a far-reaching goal and certainly beyond the scope of this work. One possible course of action would be to treat the digitule as morpheme rather than homology (Vogt et al. 2010, Richter and Wirkner 2014). As a morpheme, the term digitule could be applied to those structures similar to what Shimer (1867a) originally observed (viz., setae on the terminus of the legs with expanded apices) to any taxon without assumption of homology. This provides a tool for description of an anatomical element with which others can then use for comparative anatomy and character transformation. This solution, however, would disrupt both the current consensus among scale workers to describe non-differentiated setae as digitules based on position and the complete lack of the term among aphid workers. Currently and ultimately, accurate communication without ambiguity between a taxonomist and the reader is the best course of action. So, we recommend fundamentally that sternorrhynchan taxonomist are clear on their usage or non-usage of the term digitule in light of this work. Because one thing that has become evidently clear is that originally digitules were not just for scales, but for aphids, too.

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RESEARCH ARTICLE



Review of the genera of Conoderinae (Coleoptera, Curculionidae) from North America, Central America, and the Caribbean

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Abstract

The thirty-nine extant genera of Conoderinae known to occur in North America, Central America, and the Caribbean are reviewed based on external morphology. An identification key is provided along with diagnoses, distributions, species counts, and natural history information, when known, for each genus. Morphological character systems of importance for weevil classification are surveyed, potential relationships among the tribes and genera are discussed, and groups most in need of taxonomic and phylogenetic attention are identified. The following genera are transferred to new tribes: *Acoptus* LeConte, 1876 from the Lechriopini to the Othippiini (new placement) and the South American genus *Hedycera* Pascoe, 1870 from the Lechriopini to the Piazurini (new placement). *Philides* Champion, 1906 and *Philinna* Champion, 1906 are transferred from the Lechriopini to Conoderinae *incertae sedis* (new placement) although their placement as conoderines is uncertain. The species *Copturomimus cinereus* Heller, 1895 is designated as the type species of the genus *Copturomimus* Heller, 1895.

Keywords

weevils, Neotropical, taxonomy, Zygopinae

Introduction

Conoderinae Schoenherr, 1833 (*sensu stricto*, Alonso-Zarazaga and Lyal 1999; Conoderitae *sensu* Prena et al. 2014) are a conspicuous representative of the immensely diverse tropical weevil fauna yet have received scant attention from taxonomists in the last century. Despite being one of the most recognizable subfamilies of Curculionidae Latreille, 1802, the classification of tribes and genera remains chaotic and there are currently no phylogenetic hypotheses for the relationships within Conoderinae. The most recent classification suggests that conoderines are part of a larger group composed of Conoderinae, Baridinae Schoenherr, 1836, Ceutorhynchinae Gistel, 1848, and Orobitidinae Thomson, 1859 (Conoderinae *sensu lato*; Prena et al. 2014), but molecular phylogenies, although to date containing very limited sampling of any of these groups, have not been congruent with this classification (e.g. Gunter et al. 2016).

Much of the published literature treating the Conoderinae, including the descriptions of the majority of genera and species, dates from over a century ago and is relatively inaccessible due to its publication in multiple languages and in a quality that does not meet standards of modern taxonomic practice. Several identification keys for the genera north of Mexico exist (see identification key introduction), but for identifying the far more diverse Central and South American fauna the only keys to genera are by Rheinheimer (2011) for French Guiana and Heller (1895) for the New World. Champion (1906b) described 14 genera from Central America, and since many of those are not also known from French Guiana, Guadeloupe and the United States, and were published after Heller's 1895 key, they have not been treated in a published key. Photographs or illustrations of many genera and most species do not exist in the published literature, making confident identifications difficult. Further adding to the difficulty of identifications is the large number of species descriptions based on a single specimen. For example, 83 of Champion's 194 (42.7%) species described in the "Biologia Centrali-Americana" (1906b, 1909, 1910a) that are currently considered to be conoderines are single-specimen descriptions that are reliant on color pattern, often resulting in several similar species equally agreeing with descriptions.

The impetus for this study came from the difficulty in circumscribing taxonomic projects on the Conoderinae due to the large amount of undescribed species that do not fit into generic concepts as currently formed. As such, the intention of this paper is to summarize current knowledge and provide basic phenotypic information for the genera of Conoderinae found in North and Central America and the Caribbean, thus providing a *status quo* of classificatory, systematic and biological knowledge on the Conoderinae, and as a result providing a foundation to facilitate future taxonomic studies and the identification of specimens. While many of the genera are currently suspect in their tribal placements and many of the presently recognized genera are likely to not represent monophyletic groups, only four changes in the placement of genera are proposed here due to the current lack of phylogenetic evidence, limited observances of relevant type material and unexamined potentially related South American taxa. Those four transfers are justified because they have not been hypothesized

to be related to other genera not observed in this study, and furthermore, their new tribal placement strengthens the hypothesis of monophyly both of the tribe they were transferred from and their new tribal placement. Evidence is presented for alternative placements for other genera but further classificatory changes are reserved for an ongoing phylogenetic analysis.

The sequence of this review is as follows: I provide an overview of the diversity, distribution, natural history, and behavior of Conoderinae; a summary of the classificatory history and current morphological circumscription of Conoderinae; a survey of several morphological character systems; an identification key to genera occuring in the focal region; a systematic review section treating each tribe and genus in detail; and suggestions for future studies on the Conoderinae.

Materials and methods

Specimens were observed with a Leica M125 stereomicroscope. Habitus images were taken with a Visionary Digital Passport II system using a Canon EOS 5D Mark II camera, slices were stacked in Zerene Stacker version 1.04 and edited in Adobe Photoshop CS6 version 13.0.1 to produce a uniform background. Images of morphological structures were taken with a BK Lab imaging system with a Canon EOS 7D camera equipped with either a 100 mm macro lens or an Infinity K2 long distance microscope with a 5x objective and stacked in Zerene Stacker, or images were taken with a Leica DFC 450 camera attached to a M205 C stereomicroscope and stacked using the Leica Application Suite (LAS) version 4.1.0. Figure 19 was taken with a JEOL JSM 6300 Scanning Electron Microscope.

Specimens from the following collections were observed in this study:

ASUHIC	Arizona State University Hasbrouck Insect Collection, Tempe, AZ, USA
CMNC	Canadian Museum of Nature Collection, Ottawa, Canada
CWOB	Charles W. O'Brien Collection, Green Valley, AZ, USA
MIUP	Museo de Invertebrados G.B. Fairchild, Universidad de Panamá, Panamá
NMNH	National Museum of Natural History, Washington DC, USA
PCMENT	Programa Centroamericano de Maestria en Entomología, Universidad de
	Panamá, Panamá
SSAC	Salvatore S. Anzaldo Collection, Tempe, AZ, USA
STRI	Smithsonian Tropical Research Institute, Balboa, Ancón, Panamá

Diversity and distribution

At present, Conoderinae is organized into 14 tribes and 209 genera worldwide (following Alonso-Zarazaga and Lyal 1999, Bouchard et al. 2011, and incorporating changes and additions made in Kojima and Lyal 2002, Davis and Engel 2006, and Riedel et al. 2016), and over 2,000 species (Prena et al. 2014), placing it among the largest of the weevil subfamilies. Only five of those tribes and 62 genera are represented in the New World and all five tribes and 40 of the genera occur in the focal region north of South America. An additional 25 genera are placed in the largest three tribes, 22 of which occur exclusively in South America. Little or no material has been observed of many of the South American genera and their treatment is reserved for future study.

Like most groups of weevils, Conoderinae contains numerous undescribed species and genera - Hespenheide (2005b, 2007) reported over 100 undescribed species of the genus Eulechriops Faust, 1896 from a single locality in Costa Rica. The most speciose of the herein treated genera, in numbers of described species from North and Central America only, are Eulechriops (57), Macrocopturus Heller, 1895 (54), Lechriops Schoenherr, 1825 (49), and Cylindrocopturus Heller, 1895 (41), all of which are in need of revision and likely do not represent monophyletic groups as currently constructed. Cratosomus Schoenherr, 1825 (25), Piazurus Schoenherr, 1825 (19), and Zygops Schoenherr, 1825 (18) are also large genera that are much more diverse in South America. Of those largest genera, only *Piazurus* (in Fiedler 1936) and *Cratosomus* (in Emden 1933) have been subject to taxonomic scrutiny since their original description. Including South American diversity, the only New World genera with over 100 described species are Cratosomus and Macrocopturus (Prena et al. 2014). Many of the larger genera can only be identified by negative identification of the likely closely related, less speciose and better circumscribed genera, highlighting the need for a detailed analysis of morphological character systems and a revised classification. Eight genera remain monotypic although undescribed species are known from many of them.

No known genera of conoderines are endemic to the Caribbean region and relatively few species are recorded from there, mainly from Guadeloupe (Hustache 1932a) and Cuba (Zayas 1988). The six Cuban species described by Zayas (1988) have been recorded here in the genera they were originally described in, although from photographs and the descriptions it is evident that some may belong in a different genus. Since the specimens were not examined their generic placement could not be confirmed and thus no changes are made to their placement here.

In addition to the extant genera, five species of the extinct genus *Geratozygops* Davis & Engel, 2006 have been described from Dominican and Mexican ambers (Zimmerman 1971, Davis and Engel 2006, Poinar and Legalov 2013). Only one other species of fossil conoderine has been described, placed in the genus *Eulechriops* (Poinar and Legalov 2013).

Natural history and behavior. Conoderinae are more diverse and abundant in tropical regions, especially at middle-elevation wet forests (Hespenheide 1995). Most conoderines are distinctive from other weevils for their "very active and squirrel-like" behavior (Champion 1906b: 1), being alert and quick to fly when faced with a threat (Lyal 1986). They can be found most commonly in two microhabitats (Hespenheide 1995): on the underside of foliage and on upright or fallen tree trunks, where they often perch motionlessly. A three-year light-trapping study conducted in six localities in Panama (Wolda et al. 1998) yielded 234 different species currently classified as Conoderinae,

of which only 51 (21.7%) could be identified to a described species. Most species are thought to be diurnal (Hespenheide 1995) – only 17 of the 234 species collected by Wolda et al. (1998) were represented by more than 10 specimens.

Conoderines are thought to be mainly wood or stem boring as larvae (Hespenheide 1980: 331, R.S. Anderson 1993: 218, Prena et al. 2014), but host associations for the group are very poorly known. The largest contributions to the knowledge of conoderine host associations are from rearing surveys of specific plant groups – LaPierre (2002) reared 27 species of Conoderinae in 7 genera from stems and petioles of various Urticaceae Juss. and Fassbender (2013) reared 13 species of Conoderinae in 4 genera from dead branches of Lecythidaceae A. Rich. Costa-Lima (1956) summarized known host information for Brazilian species.

Immature stages are known only from a few species of agricultural importance. A contributing factor to this lack of knowledge of larvae and pupae is likely that the majority of specimens are collected with either passive collecting techniques (e.g. malaise traps) or by hand while they perch on tree trunks – neither method results in the recording of a host plant, since the tree perched on is often used by multiple genera (Hespenheide 1995) and is not thought the be the host plant.

A few genera with known host associations are very specialized and are rarely found away from their host plant (e.g. *Lissoderes* Champion, 1906 and *Pseudolechriops* Champion, 1906 on *Cecropia* Loefl. leaves). Many genera remain monotypic (e.g. *Euzurus* Champion, 1906 and *Poecilogaster* Heller, 1895) and are relatively rare in collections – the host plants of these genera remain unknown, and it is possible that they are not actually rare as was the case for *Lissoderes* and *Pseudolechriops*, which were initially described as monotypic from very few specimens and now have multiple described species that are easily collected in a specific microhabitat but rarely found elsewhere in the environment (Hespenheide 1987, LaPierre 2002, Hespenheide and LaPierre 2006).

Review of classificatory history

The first treatment of genera now included in Conoderinae was by Schoenherr (1825, 1826) who included *Cratosomus, Zygops* (including the subgenera *Copturus* Schoenherr, 1825, *Piazurus*, and *Coryssopus* Schoenherr, 1826), *Mecopus* Schoenherr, 1825, *Lechriops*, and *Pinarus* Schoenherr, 1826 under "Divisio 3. Cryptorhynchides" for having a curved rostrum and a more-or-less distinctly deep rostral channel. This classification was refined by Schoenherr (1837, 1838), where the Cryptorhynchides were split into two "*Cohortes*", I (1837: 1; including *Cratosomus* and *Lechriops*) which has the prosternum distinctly canaliculate, continuous on the mesoventrite and distinctly terminated, and II (1837: 360, which included *Zygops, Copturus, Piazurus, Timorus* Schoenherr, 1838, *Pinarus*, and *Mecopus* in 1838) containing those with a less distinctly canaliculate prosternum that is usually not continuous on the mesoventrite and never distinctly terminated. This classification was largely unchanged in the subsequent influential work by Schoenherr (1845), which saw the addition of numerous

species, several of which became type species of subsequently described genera but only two more New World conoderine genera (*Lobops* Schoenherr, 1845 and *Peltophorus* Schoenherr, 1845).

Lacordaire's (1865) classification represents the first grouping of genera into the three largest New World tribes recognized today mainly based on sternal modification to receive the rostrum in repose. He divided the New World representatives of "Tribu *Zygopides*" – those having both a broad metanepisternum that extends between the metacoxae and the elytra, large eyes, a canaliculate prosternum, and an antennal funicle of seven articles (as summarized by Pascoe 1871: 199) – into three groups: the "*Piazurides*", the "*Lechriopides*" and the "*Zygopides vrais*". Pascoe (1871: 198) noted the inadequacy of this system but provided no alternative classification.

Lacordaire's classification was amended only slightly by K.M. Heller (1894) to accommodate the thirty-three mainly Old World genera described by Pascoe since Lacordaire's work as well as the two genera and many species newly described by Heller therein. In Heller's key (1984: 3) the New World Conoderinae are characterized by an antennal funicle composed of seven articles and the presence of a rostral channel at least on the prosternum, but are not further separated morphologically from several Old World genera that share those characters. Heller (1895) further amended this to accommodate seventeen new New World genera, and provided an identification key based largely on eye shape, the modification to the mesoventrite and the relative lengths of the antennal funicular articles.

Champion's (1906b) "Zygopina" section of the Biologia Centrali-Americana represents the most recent major taxonomic treatment of Central American Conoderinae, in which he authored 14 genera and 194 species (also in 1909, 1910a) pertaining to the Conoderinae as currently recognized. Champion noted that his arrangement of the genera would have been presented in the order given by Heller (1895) "...were it not more convenient, to avoid delay in publication, to deal with the genera seriatim, irrespective of their relationships..." (Champion 1906b: 1). Despite this, the order the genera are presented by Champion do seem to have been done so with consideration of potential relationships, and the next catalog of Conoderinae, Hustache's pars 134 of the Coleopterorum Catalogus (1934), presented a classification in nearly the exact order arranged by Champion, with genera treated on Champion's pages 2-21 representing the Piazurini Lacordaire, 1865, 21-87 representing the Zygopini Lacordaire, 1865, and 87-130 the Lechriopini Lacordaire, 1865, with the single exception of *Euzurus* on page 45 placed in the Lechriopini. Many of those genera were grouped in Lacordaire's tribes without bearing the characters originally indicated, and no updated tribal diagnoses have been presented.

This classification scheme remained almost completely unchanged, despite a foreshadowing of its probable inadequacy in reflecting the evolutionary history of numerous lineages of Conoderinae by Böving (1926) and Hustache (1938), until several genera of Zygopini were transferred to the Lechriopini by Lyal et al. (2006). Böving's (1926) comparative study of larvae and pupae (representing the only comparative study of conoderine immatures) of the genera *Peltophorus, Cylindrocopturus*, and *Eulechriops*, all of which at the time were included in the Zygopini, revealed Cylindrocopturus and Eulechriops to share multiple larval and pupal characters, suggesting a closer relationship to each other than either is to *Peltophorus*. Böving later (1927) created the tribe Cylindrocopturini to include both Cylindrocopturus and Eulechriops. The current classification includes Eulechriops in the Lechriopini and Cylindrocopturus and Peltophorus in the Zygopini due to the presence of modification to the mesoventrite in *Eulechriops* in the form of a carinate channel and an unmodified or only slightly modified mesoventrite (not a carinate channel) in Cylindrocopturus and Peltophorus. Cylindrocopturus was included in the Lechriopini by Kissinger (1964) and Hatch (1971) but in the Zygopini in all subsequent works - the genus was not among the lechriopines moved by Lyal et al. (2006) due to both an unmodified mesoventrite and lack of sclerolepidia (modified scales along the metanepisternal suture), while other genera that are possibly related to Cylindrocopturus that have sclerolepidia (e.g. Macrocopturus) were moved. It seems likely that after further examination many of the genera currently in the Zygopini will be shown to be more closely related to lechriopines than to Zygops, Peltophorus, and a few additional South American genera (e.g. Parazygops Desbrochers, 1890, Colpothorax Desbrochers, 1890) that make up the "true zygopines", as Böving's work implied (see treatment of Zygopini below).

Hustache (1938: 58) noted the interesting distribution of "granules" on the metathoracic episterna (i.e. sclerolepidia) and suggested that a further study of these structures may provide an updated classification from that of Lacordaire. The classification used in this paper follows Alonso-Zarazaga and Lyal (1999), accommodating the changes made in Lyal et al. (2006), where twelve genera (eight from the focal region) were moved from Zygopini to Lechriopini due to the presence of sclerolepidia and/or a modified mesoventrite.

Current circumscription of the New World Conoderinae. Presently, most of the species of Conoderinae can be recognized by the following combination of characters, agreeing with Lacordaire (1865) and Heller (1894): large eyes that take up much of the surface of the head, a rostral channel at least on the prosternum to receive the rostrum in repose, and an antennal funicle composed of seven articles (excepting *Philinna* Champion, 1906 and *Philides* Champion, 1906 which have six). See Table 1 for a summary of the classification used in this paper, including all genera currently placed in tribes that have representation in the focal region.

The South American genera *Timorus* and *Hypoplagius* Desbrochers, 1891 each have Mexican records of otherwise South American species. Champion (1906b: 33) and subsequent authors have doubted the validity of the Mexican record for the Brazilian *Timorus suturalis* Rosenschoeld, 1838, and since no material was observed it is also here not considered to be represented in Central America. *Hypoplagius pectoralis* Desbrochers, 1891 is recorded from Brazil, French Guiana, and Veracruz, Mexico (Champion 1906b: 32 mentions three specimens from the Sallé collection). Very little material of *Hypoplagius* has been observed in the course of this study, all of it being from South America. As such, the unusual distribution of *Hypoplagius* is also suspect and the genus is not treated in detail in the present publication, but the issue requires further study. **Table 1.** Summary classification adopted in the present paper, modified from Alonso-Zarazaga and Lyal (1999), Kojima and Lyal 2002, Lyal et al. 2006 and Bouchard et al. 2011. An asterisk (*) next to a generic name indicates it is known only from South America, a circumflex accent (^) indicates an Old World distribution, and a dagger (†) indicates an extinct taxon.

Tribe	Genus
Trichodocerini Champion, 1906a: 713	Trichodocerus Chevrolat, 1879: XCII
1 ·	*Costolatychus Heller, 1906: 35
	Cratosomus Schoenherr, 1825: c.585
	^Guiomatus Faust, 1899: 100
	*Hedycera Pascoe, 1870: 457, new placement from Lechriopini
	*Latychellus Hustache, 1938: 59
Dimensioni I	*Latychus Pascoe, 1872: 486
Plazurini Lacordaire, 1865: 144	Lobops Schoenherr, 1845: 116
	*Piazolechriops Heller, 1906: 44
	Piazurus Schoenherr, 1825: c.586
	*Pinarus Schoenherr, 1826: 307
	Pseudopiazurus Heller, 1906: 32
	Pseudopinarus Heller, 1906: 33
	<i>^Abrimoides</i> Kojima & Lyal, 2002: 168
	Acoptus LeConte, 1876: 264, new placement from Lechriopini
	<i>^Brimoda</i> Pascoe, 1871: 219
Othinni Marimata 1962: 47	<i>^Brimoides</i> Kojima & Lyal, 2002: 163
<i>Sumprum</i> Wommoto, 1902. 4/	<i>^Chelothippia</i> Marshall, 1938: 173
	^Egiona Pascoe, 1874: 51
	<i>^Othippia</i> Pascoe, 1874: 49
	<i>^Rimboda</i> Heller, 1925: 238
	*Balaninurus Heller, 1895: 51
	Copturomimus Heller, 1895: 63
	Copturomorpha Champion, 1906b: 65
	Copturus Schoenherr, 1825: c.586
	Coturpus R.S. Anderson, 1994: 480
	*Crassocopturus Rheinheimer, 2011: 71
	Cylindrocopturinus Sleeper, 1963: 218
	*Damurus Heller, 1895: 55
	Eulechriops Faust, 1896: 91
	<i>Euzurus</i> Champion, 1906b: 45
Lechriopini Lacordaire, 1865: 149	Hoplocopturus Heller, 1895: 50
	Lechriops Schoenherr, 1825: c.586
	*Machaerocnemis Heller, 1895: 60
	Macrocopturus Heller, 1895: 19
	Macrolechriops Champion, 1906b: 126
	Microzurus Heller, 1895: 13
	Microzygops Champion, 1906b: 46
	*Mnemyne Pascoe, 1880: 179
	Mnemynurus Heller, 1895: 54
	Paramnemyne Heller, 1895: 10
	*Paramnemynellus Hustache, 1932b: 207

Tribe	Genus	
<i>Lechriopini</i> Lacordaire, 1865: 149	Poecilogaster Heller, 1895: 16	
	Pseudolechriops Champion, 1906b: 90	
	Psomus Casey, 1892: 458	
	*Rhinolechriops Hustache, 1939: 162	
	* <i>Tachylechriops</i> Heller, 1895: 15	
	Turcopus R.S. Anderson, 1994: 475	
	*Acopturus Heller, 1895: 61	
	Arachnomorpha Champion, 1906b: 47	
	Archocopturus Heller, 1895: 56	
	*Colpothorax Desbrochers, 1890: CXXIX	
	*Copturosomus Heller, 1895: 61	
	Cylindrocopturus Heller, 1895: 56	
	<i>†Geratozygops</i> Davis and Engel, 2006: 255	
	Helleriella Champion, 1906b: 32	
	* <i>Hemicolpus</i> Heller, 1895: 57	
	*Hypoplagius Desbrochers, 1891: 40	
Zugapini Lacordaire 1865, 150	^Isocopturus Hustache, 1931: 23	
Zygopini Lacoldane, 1809. 190	Larides Champion, 1906b: 34	
	Lissoderes Champion, 1906b: 47	
	*Macrotimorus Heller, 1895: 59	
	*Parazygops Desbrochers, 1890: CXXIX	
	Peltophorus Schoenherr, 1845: 451	
	Phileas Champion, 1906b: 34	
	Philenis Champion, 1906b: 43	
	*Timorus Schoenherr, 1838: 680	
	<i>^Xeniella</i> Hustache, 1931: 24	
	Zygops Schoenherr, 1825: c.586	
	Zygopsella Champion, 1906b: 42	
Conoderinge incertae sedis	Philides Champion, 1906b: 129, new placement from Lechriopini	
Conocerniae meriae sears	Philinna Champion, 1906b: 128, new placement from Lechriopini	

In addition to the South American genera, three genera with Old World distributions are currently placed in the largely New World Piazurini and Zygopini: *Guiomatus* Faust, 1899 (Piazurini, from New Guinea), *Isocopturus* Hustache, 1931 (Zygopini, from Cameroon), and *Xeniella* Hustache, 1931 (Zygopini, from Tanzania). No material was observed of those genera so their placement cannot be commented on.

Two groups previously included in the Conoderinae but most recently being treated in another subfamily are the Tachygonina Lacordaire, 1865 (currently in the Curculioninae: Rhamphini Rafinesque, 1815), and the genus *Isotrachelus* Faust, 1896 (currently in the Molytinae Schoenherr, 1823: Cleogonini Gistel, 1856); see the generic treatments for *Philides* and *Psomus* Casey, 1892, respectively, for more information. For the most recent treatments of Old World tribes, see Kojima and Lyal (2002) for Othippiini Morimoto, 1962, Marshall (1959) for Campyloscelini Schoenherr, 1845, and Marshall (1939) for Coryssomerini Thomson, 1859.

Systematic utility of select morphological character systems

Due to the lack of phylogenetic evidence supporting the current classification, it was deemed necessary to evaluate character systems that have both had influence on the present classification of Conoderinae and other character systems that are traditionally used in other groups of weevils, including: the modification to the mesoventrite for receiving the rostrum in repose, the tibial apex, and the structure of the abdomen. These character systems potentially have deeper-level phylogenetic signal and thus can be informative for a revised classification of Conoderinae. Male genitalia also appear promising for providing structure to the mid-level classification. However, they are not comprehensively analyzed here, with the focus of this review being on reliable diagnosis of conoderine genera by external characters as well as with several of the genera remaining undissected due to limited material observed in collections. See the "Systematic Review of Genera" below for a more detailed account of the variation and exceptions of these characters found in each tribe and genus. The following additional character systems that are mostly only useful for diagnosing individual species or subgeneric species groups are also reviewed: eve size and shape, modification to the metaventrite, and mimicry complexes. Morphological terminology for thoracic sclerites was adopted from Oberprieler et al. (2014).

Mesoventrite (Figs 1–18). The character of historical importance for the identification of conoderine tribes and genera is the modification of the mesoventrite for the reception of the rostrum in repose. This remains one of the most influential characters for a genus-level identification; it is thus of paramount importance for future taxonomic work on the Conoderinae to identify the variation in this structure and assess its validity as a character system of significance in the delimitation of tribes and genera.

The tendency of these weevils to fold their legs and tuck the rostrum into the rostral channel with the antenna folded underneath when dying greatly obscures the view of the ventral surface. To expose the mesoventrite, the legs can be gently moved out of the way with an insect pin, and if the rostrum also needs to be moved, the specimen can be relaxed in warm water for several minutes and the head then gently tilted upwards with a pin (while bracing the prothorax) to expose the antennae and rostral channel.

The following types of modification roughly correspond to Lacordaire's original tribal designations, while taking into account the numerous genera described since and potentially improperly placed genera. For further discussion of variation in the mesoventrite see the tribal and individual generic accounts and the Discussion.

The rostral channel is variously referred to in the literature and in the present paper as "closed" or "open". A "closed" rostral channel refers to the posterior margin of the channel, where the apex of the rostrum would fit in repose, being demarcated with a transverse, raised portion (e.g. Fig. 2). An "open" rostral channel refers to a rostral channel with some sort of longitudinal modification, usually in the form of raised, parallel carinae, that are lateral to the rostrum in repose but do not posteriorly demarcate the apex of the rostrum (e.g. Figs 3–4). The rostral channel in weevils can be closed on the prosternum, the meso- or metaventrite or on the abdominal ventrites or open on



Figures 1–9. Variation in the mesoventrite. **I** *Trichodocerus brevilineatus* [ARTSYS0000616] showing a prosternal rostral "sheath" with the sides converging below the procoxae, the transverse ridge anterior to the mesocoxae and the region of the mesoventrite posterior to the ridge with dense yellow scales **2** *Lobops bonvouloiri* [ARTSYS0000527] showing a cup-shaped receptacle for receiving the rostrum **3** *Piazurus trifoveatus* [SSAC0001118] with an "open" channel on the mesoventrite **4** *Pseudopinarus condyliatus* [SSAC0001116] with an "open" channel on the mesoventrite **5** *Acoptus suturalis* [ASUHIC0016914] showing a flat, unmodified mesoventrite **6** *Copturus sanguinicollis* [ASUHIC0086638] showing a closed receptacle on the mesoventrite with lateral flanges **7** *Cylindrocopturinus pictus* [SSAC0001288] showing a rostral channel of the mesoventrite formed by relatively parallel carinae and no posterior termination **8** *Euzurus ornativentris* [ARTSYS000796] **9** *Hoplocopturus javeti* [SSAC0001289] with an inverted U-shaped carina and the region posterior to the carina invaginated.

any of those structures. In the New World Conoderinae, the rostral channel is always present at least on the prosternum in the region anterior to the procoxae and this prosternal part of the rostral channel is open.

Trichodocerine type (Fig. 1). The mesoventrite has a transverse, ventrally produced ridge anterior to the mesocoxae and flattened, yellow scales in the intercoxal process



Figures 10–18. Variation in the mesoventrite. 10 *Lechriops californicus* [ASUHIC0024146] showing relatively parallel carinae marking the lateral margin of the rostral channel and a closure of the channel on the metaventrite 11 *Microzygops nigrofasciatus* [ARTSYS0000797] with tubercles anterior to the mesocoxae and slight, arcuate carinae on the anterior region of the mesoventrite (encircling the central scaled region) 12 *Paramnemyne decemcostata* [ARTSYS0000798] showing tuberculate posterolateral margins of the mesoventrite and a transverse carina near the posterior margin of the metaventrite 13 *Pseudolechriops klopferi* [SSAC0001060] showing a deep ovoid receptacle on the meso- and metaventrite 14 *Turcopus viscivorus* [ARTSYS0000530] showing a receptacle on the mesoventrite with prominently carinate posterior margin 15 *Lissoderes subnudus* [SSAC0001066] showing a completely unmodified mesoventrite covered with multifid setae 16 *Peltophorus adustus* [ASUHIC0031514] showing a ventrally expanded posterior margin of the mesoventrite to receive the rostrum in repose 17 *Philenis fuscofemorata* [ARTSYS0000659] with tubercles at the posterolateral margins of the mesoventrite and a deep depression at the posterior margin in between 18 *Philinna bicristata* [ARTSYS0000799] showing slight lamellate processes at the posterolateral margins of the mesoventrite as well as transversely flattened projections behind the procoxae.

posterior to the ridge. The rostral channel does not extend beyond the prosternum, which in most species can be interpreted as narrowly open. However, since the apex of the channel does not correspond with the apex of the rostrum in repose in any of the species, it is considered to not be truly "closed" on the prosternum even when a distinct termination of the channel is present. This type of modification is only found in the monogeneric tribe Trichodocerini Champion, 1906.

Piazurine type (Figs 2–4, 6, 8, 12). In its typical form, the modification to the mesoventrite in piazurines is open posteriorly ("gutter-like"), allowing the rostrum to extend beyond the mesoventrite to the metaventrite. The posterior margin of the mesoventrite is rounded and flattened, with the lateral portions raised (Figs 3, 4), and often overlapping the anterior border of the metaventrite. Rarely is the channel closed on the mesoventrite, with posterior margin raised to the same level as the lateral margins, forming a "cup-shaped receptacle" similar to the Cryptorhynchinae Schoenherr, 1825 (Fig. 2). The region of the mesoventrite anterior to this is never with modification (i.e. without carina, depression, etc.). This type of mesoventrite is found in all genera treated as Piazurini, the lechriopine genera *Paramnemyne* Heller, 1895 (Fig. 12) *Euzurus* (Fig. 8), *Copturus* (Fig. 6), and *Microzurus* Heller, 1895, which have more similarities with the piazurine type than the lechriopine type although they differ from the typical piazurine form.

Lechriopine type (Figs 7, 9–11, 13–14). The mesoventrite is variously carinate, most typically as a channel with roughly parallel or somewhat arcuate longitudinal carinae delimiting the side of the channel (e.g. Figs 7, 10). The rostral channel can be closed (e.g. Fig. 14) or open (e.g. Fig. 10) on the mesoventrite; if open on the mesoventrite the channel on the metaventrite can similarly be closed (e.g. Fig. 11) or without a distinct termination to receive the apex of the rostum (e.g. Fig. 9). The channel can be very shallow or deep, with the lateral margins slightly carinate or strongly ventrally produced. The lateral carina in some are strongly arcuate and anteriorly fused, forming an inverted U-shaped carina that does not seem to function for rostral reception (Fig. 9) and is depressed or invaginated posterior to the carina. If the posterior margin is tuberculate as in some lechriopines (e.g. Fig. 11), there are always anterior carinae. This type of mesoventrite is found in all genera included here in the Lechriopini, excepting *Paramnemyne, Copturus, Microzurus*, and *Psomus*.

Zygopine type (Figs 5, 15–18). The mesoventrite is unmodified (Figs 5, 15), or if with some modification, the modification is not in the form of a channel to receive the rostrum. This type of mesoventrite is found in Zygopini, in the lechriopine *Psomus*, the othippiine *Acoptus* LeConte, 1876, *Philides* and *Philinna*. Exceptions can be found in most species of *Philenis* Champion, 1906, which have ventrally produced tubercles at the posterolateral margins of the mesoventrite and a posteromedial depression (Fig. 17; but the mesoventrite of the type species is unmodified) and in *Peltophorus*, which has a ventrally produced posterior margin of the mesoventrite (Fig. 16).

Tibial apex (Figs 19–36). The tibial apex of Conoderinae is interpreted for the majority of genera and species, largely following the morphological terminology of Thompson (1992), as bearing a large uncus at the posterior apical angle, a premucro at the anterior apical angle and a variously produced inner flange at the apex between them. The terminology of "anterior" and "posterior" is adopted here instead of the frequently used "inner" and "outer", respectively, to avoid confusion when referencing the "mesal" and "lateral" faces of the femoral apex (which are synonymous with "inner"



Figures 19-36. Variation in the metatibial apex. 19 Mesotibial apex of Lechriops vestitus illustrating parts of the tibial apex: a) posterior apical angle with large, curved uncus; b) middle of the apex with produced, rounded inner flange; c) anterior apical margin with premucro; d) oblique ridge of premucro; e) apical setal tuft 20 Male Trichodocerus brevilineatus [ARTSYS0000609] with a tibial uncus arising at the middle of the apex 21 Cratosomus punctulatus mexicanus [ASUHIC0031510] with thick fascicles of golden setae near the anterior apical margin and a dense setal brush at the posterior apical face 22 Pseudopiazurus centraliamericanus [ASUHIC0086627] with a large, subapical premucro 23 Piazurus laetus [SSAC0001077], showing a typical tibial apex for that genus 24 Acoptus suturalis [ASUHIC0016915]] 25 Cylindrocopturinus pictus [SSAC0001288] with a pointed, premucro-like inner flange 26 Pseudolechriops klopferi [SSAC0001060] showing an elongate, uncus-like inner flange. 27 Arachnomorpha circumlineata [ARTSYS0000535] 28 Archocopturus medeterae [ASUHIC16884] 29 Cylindrocopturus adspersus [ASUHIC0016896] with a rounded, produced inner flange **30** Helleriella longicollis [ASUHIC0065241] with a very short uncus 31 Lissoderes cecropiae [ASUHIC0064707] with an elongate uncus and minute premucro 32 Phileas granulatus [ARTSYS0000528] with the middle of the apex (between uncus and premucro) sunken 33 Peltophorus adustus [ASUHIC0012325] with a short uncus and posterodistal setal comb extending halfway to the base of the tibia 34 Zygops erythropygus [ASUHIC0086640] with short posterodistal setal comb. 35 Philenis flavipes [ASUHIC0065102] 36 Philinna bicristata [ART-SYS0000799] with a small tooth at the anterior apical angle.

and "outer", respectively). The adopted terminology is in reference to the position of the structures of the tibial and femoral apex of the hind leg in its life-like postion (as in the left hind leg of Fig. 101a). The apex usually bears two setal tufts, which can vary from one to a few setae (Fig. 23) to a thick fascicle of setae (Fig. 21), at the anterior apical angle arising from oblique carinae that are part of the premucro. See Figure 19 for a clarification of terminology.

While there can be slight differences between the pro-, meso- and metatibial apices (e.g. the protibial uncus is often larger than the meso- and metatibial uncus), unless otherwise specified the one discussed and figured is the metatibia of the left leg. The shape and size of the uncus is quite variable but most commonly long and slightly curved (e.g. Figs 23, 28, and 34 for typical form) but varies from being more elongate and thin (Fig. 31), hooked (Fig. 29) and very short (Figs 30, 33). The size, position, and orientation of the premucro varies as well, from being large, subapical and oriented at a 45° angle to the longitudinal axis of the tibia (Fig. 22), small, apical, and oriented at 45° angle to the longitudinal axis of the tibia (Figs 32, 35), small, apical, and oriented with the longitudinal axis of the tibia (Figs 28, 29), apical and minute (Figs 27, 31), or absent (Fig. 24). Many genera also have a third apical prominence at the middle of the apex between the uncus and premucro, which here is interpreted as a modification of the inner flange of Thompson (1992). This inner flange varies from being a simple carina, not produced ventrally (Fig. 23), slightly produced ventrally and rounded (Fig. 28), strongly produced ventrally and rounded (Fig. 29), small, pointed and premucro-like (Fig. 25), and elongate, pointed, and uncus-like (Fig. 26). While a few genera can be diagnosed by the structure of the tibial apex alone, many of the modifications, especially those of the inner flange, appear to be homoplasious as they can be found in species of several unrelated genera.

Abdominal sclerites. The structure of the abdominal ventrites and tergites are potentially of significance at the tribal level with the apex of the abdomen being opened in different ways, with either an exposed or concealed pygidium. When exposed, the pygidium can be visible in dorsal view (Figs 99b, 102b) or only in posterior or ventral view (e.g. Fig. 68a), and abdominal ventrites are flat or at most slightly evenly ascending. When concealed, abdominal tergites can be slightly (Fig. 73a) to very strongly (Fig. 76a) ascending with the last three tergites forming a ventral pygidium-like hinge to open the apex of the abdomen. Very few species exhibit sexual dimorphism in the exposure of the pygidium.

Eye size and shape (Figs 37–54). Eye size and shape was used by Heller (1895: 3) as a major character in his key for separating groups of genera, namely the distance between the eyes and the shape of the eyes at the bottom and sides. The eyes of Conoderinae are typically large (taking up much of the surface of the head) and approximate, where they can be subcontiguous and separated by one to a few rows of scales (Figs 37, 41), or contiguous in part (as in Figs 40, 44, 45). Smaller, more widely separated eyes (Figs 38, 39, 51) are less common. Variation in the shape of the eye varies from being circular to ovoid (Figs 38, 52), acuminate at the lower margins (e.g. Fig. 49), sinuous along the lateral margin, with the lower lateral margin being



Figures 37–45. Variation in eye shape. 37 Trichodocerus brevilineatus [ARTSYS0000609] with large, subcontiguous eyes that continue below rostral insertion 38 Cratosomus punctulatus mexicanus [AS-UHIC0031510] with relatively small, widely separated eyes 39 Lobops bonvouloiri [ARTSYS0000658] with widely separated eyes and the frons concave between the upper half of the eye 40 Pseudopiazurus centraliamericanus [ASUHIC0086627] with very large eyes that are contiguous in upper half 41 Pseudopinarus guyanensis [ASUHIC0086636] with large, subcontiguous eyes and an arcuate carina on the vertex of the head 42 Acoptus suturalis [ASUHIC0016914] with subcontiguous eyes separated at the top by a lanceolate space 43 Cylindrocopturinus pictus [SSAC0001288]44 Macrocopturus lynceus [SSAC0001085] with very large, partially contiguous eyes 45 Microzygops nigrofasciatus [ARTSYS0000802] with large eyes contiguous in the bottom 2/3 and widely separated at the top.

inflexed (Fig. 54), with a distinct interocular space (the upper mesal margin being sinuous and inflexed) that can be lanceolate (Figs 42, 48), ovate (Figs 45, 47), or broad (Figs 39, 51). When separated, the interocular space at the top can be evenly convex with the rest of the surface of the head, slightly depressed, or concave (compare Fig. 51 with 97b).



Figures 46–54. Variation in eye shape. 46 Poecilogaster brevis [ARTSYS0000805] with relatively vertical, separated eyes 47 Arachnomorpha circumlineata [ARTSYS0000535] showing subcontiguous eyes separated at the top by a broad interocular space 48 Archocopturus medeterae [ASUHIC0086637] with subcontiguous eyes separated at the top by a thin lanceolate space 49 Cylindrocopturus quercus [ASUHIC0016905] with vertical, separated eyes 50 Helleriella longicollis [ASUHIC0065241] with widely separated eyes and a very thin rostrum 51 Larides cavifrons [ASUHIC0016882], showing a strongly depressed interocular space 52 Male Lissoderes cecropiae [ASUHIC0064708] showing oval, subcontiguous eyes and an apical antennal insertion on the rostrum 53 Philenis fuscofemorata [ARTSYS0000659] showing ovoid eyes and slender antennae 54 Zygopsella ruficauda [ARTSYS0000526] with a sinuous lateral and mesal margin of the eyes which is strongly inflexed at the lower lateral margin.

Metaventrite modification. The modification to the metaventrite for receiving the rostrum is much more variable within a genus than the modification to the mesoventrite and is independent of the presence of modification to the mesoventrite. Modification can be absent (Fig. 15), but when present it is usually limited to the anterior, intermesocoxal portion of the metaventrite in the form of a depression (Fig. 8), an excavated anterior margin to receive the rostrum (Fig. 13), or a deep fovea (Fig. 11). In genera that



Figures 55–66. Miscellaneous morphological structures. **55** *Hoplocopturus sulphureus* [ARTSYS0000801] with an overlay showing an elongate second funicular article that is more than twice the length of the first **56** *Lissoderes subnudus* [SSAC0001064] with an overlay showing a second funicular article that is subequal to the first, and seven distinct funicular articles **57** *Philinna bicristata* [ARTSYS0000799] showing a funiculus composed of six articles **58** *Microzurus* sp. [SSAC0001290] showing a short, slender fifth tarsal article and minute claws **59** *Philides comans* [ARTSYS0000804] with a broad tooth at the base of the tarsal claw **60** Left metafemoral apex of *Piazurus trifoveatus* [SSAC0001118] that is unarmed at the mesal and lateral faces **61** Left metafemoral apex of *Cylindrocopturinus pictus* [SSAC0001288] with a tooth only at the mesal face **62** Left metafemoral apex of *Peltophorus polymitus seminiveus* [SSAC0001117] showing a small tooth at both mesal and lateral faces **63** Left metafemoral apex of *Hoplocopturus sulphureus* [ARTSYS0000801] showing a small tooth at the lateral face and an acuminate process at the mesal face **64** Metaventrite of *Pseudopiazurus centraliamericanus* [SSAC0001291] showing deep, arcuate sulc **65** Lateral view of the metafeorary of *Copturomimus caeruleotinctus* [SSAC0001059] showing denuded, striolate regions.

have longer rostra, there can be a depression in the middle of the metaventrite (Fig. 9), a depression and a transverse carina marking the apex of the rostrum in repose (Fig. 12), or a longitudinal channel or depression along the entire length of the sclerite.

Mimicry complexes. Several putatively mimetic color patterns are hypothesized to have evolved independently in multiple genera of New World Conoderinae, in-

cluding: red-eyed flies (Hespenheide 1973, 1995; Figs 80, 87), dolichopodid flies of the genus *Medetera* Fischer von Waldheim, 1819 (Hespenheide 1995, 2005; Figs 94, 103), ants of the genus *Zacryptocerus* Kempf, 1973 (Hespenheide 1986), other species of ants (Hespenheide 1995; e.g. Figs 86, 93), bees (Hespenheide 1995; Fig. 101), clytrine chrysomelids (Hespenheide 1995, 1996; Fig. 96), and additional convergent color patterns without an identified model, such as the "red-spotted" complex (Hespenheide 1995, Hespenheide 2017). The presence of these mimicry complexes can make genus- and species-level identifications difficult due to strong convergences in body shape and coloration patterns that result in species superficially resembling species in other genera more than closely related species. Characters linked to the mimicry complexes, such as color, are avoided for diagnostic use in the identification key whenever possible.

Systematic review of genera

Format of accounts. Genera are grouped into tribes within subfamily Conoderinae following the classification of Alonso-Zarazaga and Lyal (1999) and Lyal et al. (2006), which largely reflects the status quo for mid-level classification of Conoderinae (see Table 1 for overview). Provided below for each genus is the type species information, synonymic history, gender, differential diagnosis, references to taxonomic treatments, geographic ranges, number of described species from the focal range, number of species known outside the focal range, host associations (if known), and at least a dorsal and lateral habitus image (see "Species Representation" section below). The higher-level entities are also briefly reviewed, providing a classificatory history, variation in the key character systems discussed above and the diversity, distribution and morphological circumscription of genera currently included. Subgenera are indicated by rounded brackets. The gender provided for all generic names follows Alonso-Zarazaga and Lyal (1999).

Diagnosis. Diagnoses provide characters or combinations of characters that distinguish each genus from its putative relatives, some largely following those given by Champion (1906b). Many genera, especially the largest genera, are definable only by a combination of the following three characters: the relative lengths of the first two funicular articles, the modification to the mesoventrite, and the structure of the hind femora (whether it is ventrally toothed and externally carinate). In many cases the combination of these characters is not exclusive to a genus or has exceptions within a genus, but as many of the genera are currently constructed that is the best way to separate the majority of the species. Those three characters are given for most genera regardless of their diagnostic quality for that genus.

Keys. Published keys treating at least some of the currently recognized species in each genus from the focal region are provided, presented in order of relevance (i.e. treating the most number of species or covering a larger geographic range). If the species in that key are treated under a different generic name than their current placement, that name is also provided.

Species numbers and ranges. Species counts and geographic ranges for genera are given from O'Brien and Wibmer (1982) and Alonso-Zarazaga adn Lyal (1999), respectively, with updates where indicated. Species counts provided are the number of species currently recorded for only North and Central America and the Caribbean. A range including "South America" indicates additional species known from South America or the range of at least one Central American species extends into South America. The number of additional species known in South America are also provided, following Wibmer and O'Brien (1986) and including more recent additions.

Species Representation. The species selected for the accompanying habitus images is the type species for the genus if that species is known from the focal region and if specimens were available for study and in acceptable condition; these criteria were met for 21 of the 39 genera. If the type species is not from the focal region or the type species is from the focal region but specimens were not available or in acceptable condition, a species deemed a typical representative of the genus was used instead.

Host associations. All referenced names of botanical species are the accepted name from The Plant List (2013; theplantlist.org) and higher-level entities are the accepted name from Tropicos (2017; tropicos.org) at the time of access

Specimen availability. The species-level identifications of many observed specimens are tentative without comparison to type material, and since many species, especially mimetic ones, are found to consist of complexes of numerous undescribed but closely related sibling species (see Hespenheide 2005), photographed or otherwise referenced specimens in this paper, as often as possible, were given a unique identifier databased in the Symbiota Collections of Arthropod Network (SCAN; Gries et al. 2014). This allows future work on the Conoderinae to build off of this study by making some of the exact specimens used easily located so their identifications and morphological interpretations can be re-evaluated. Images used or specimens referenced belonging to the ASUHIC, SSAC, and STRI collections are accompanied by a unique identifier for their respective repository in SCAN (e.g. ASUHIC0016837, SSAC0001113, STRI_ENT_0123144). Specimens loaned from the other collections listed above were databased in SCAN with a unique identifier in the SCAN-ARTSYS collection, with the home institution entered in the "Owner Code" field (e.g. ARTSYS000530). See Table 2 for a list of all taxa and specimens featured in photographs.

Taxonomic treatment

Conoderinae Schoenherr, 1833: 26

Remarks. The five tribes represented in the New World are unlikely to represent a monophyletic group and as such cannot be satisfactorily diagnosed by morphological characters or separated from the Old World tribes as a whole, even when excluding the aberrant genera.

Tribe	Taxon	Specimen identifier
Trichodocerini		ARTSYS0000616 (Fig. 1)
	Trichodocerus brevilineatus Champion, 1906	ARTSYS0000609 (Figs 20, 37)
	Trichodocerus spinolae Chevrolat, 1879	ARTSYS0000534
	Cratosomus lafontii Guérin, 1844	SSAC0001133
	Cratosomus punctulatus mexicanus Gyllenhal, 1837	ASUHIC0031510
	Lobops bonvouloiri (Hustache, 1932)	ARTSYS0000658 (Fig. 39) ARTSYS0000527 (Figs 2, 69)
	Piazurus caprimulgus (Olivier, 1807)	SSAC0001113
D:	Piazurus laetus Pascoe, 1886	SSAC0001077
Plazurini	Piazurus trifoveatus Champion, 1906	SSAC0001118
	Pseudopiazurus centraliamericanus (Heller, 1906)	SSAC0001291 (Fig. 64) ASUHIC0086627 (Figs 22, 40 71)
	Pseudopinarus condyliatus (Boheman, 1838)	SSAC0001116 (Fig. 4) ASUHIC0086626 (Fig. 72)
	Pseudopinarus guyanensis Hustache, 1938	ASUHIC0086636
Othippiini	Acoptus suturalis LeConte, 1876	ASUHIC0016914 (Figs 5, 73) ASUHIC0016915 (Fig. 24)
	Copturomimus caeruleotinctus Champion, 1906	SSAC0001059
	Copturomimus cinereus Heller, 1895	ASUHIC0086628
	Copturomorpha Champion, 1906 sp.	ASUHIC0086641
	Copturus aurivillianus (Heller, 1895)	ASUHIC0024140
	Copturus sanguinicollis (Champion, 1906)	ASUHIC0086638
	Coturpus arcuatus R.S. Anderson, 1994	ARTSYS0000531
	Cylindrocopturinus pictus (Schaeffer, 1908)	SSAC0001288
	Eulechriops minutus (LeConte, 1824)	ASUHIC0024145
	Euzurus ornativentris Champion, 1906	ARTSYS0000796 (Figs 8, 65) ARTSYS0000800 (Fig. 80)
	Hoplocopturus javeti (Champion, 1906)	SSAC0001289
	Hoplocopturus sulphureus Champion, 1906	ARTSYS0000801
	Hoplocopturus varipes Champion, 1906	SSAC0001086
Lechriopini	Lechriops californicus (LeConte, 1876)	ASUHIC0024146
Lechnophi	Lechriops vestitus (Boheman, 1838)	SSAC0001114 (Fig. 82)
	Macrocopturus lynceus (Champion, 1906)	SSAC0001085
	Macrolechriops spinicoxis Champion, 1906	ARTSYS0000529
	Microzurus championi Hustache, 1934	ASUHIC0031507
	Microzurus Heller, 1895 sp.	SSAC0001290
	Microzygops nigrofasciatus Champion, 1906	ARTSYS0000797 (Fig. 11) ARTSYS0000802 (Fig. 45, 86)
	Mnemynurus poeciloderes Champion, 1906	ARTSYS0000803
	Paramnemyne decemcostata Champion, 1906	ARTSYS0000798 (Fig. 12) ASUHIC0065104 (Fig. 88)
	Poecilogaster brevis (Waterhouse, 1879)	ARTSYS0000805 (Fig. 46) ASUHIC0086631 (Fig. 89)
	Pseudolechriops klopferi Hespenheide & LaPierre, 2006	SSAC0001060
	Pseudolechriops megacephalus Champion, 1906	ASUHIC0086629

Table 2. Taxon and specimen representation used in figures. Each identifier signifies the specimen used for all photos taken for that species unless otherwise specified.

Tribe	Taxon	Specimen identifier
	Psomus armatus (Dietz, 1891)	ARTSYS0000533
Lechriopini	Turcopus viscivorus R.S. Anderson, 1994	ARTSYS0000530
	Arachnomorpha circumlineata Champion, 1906	ARTSYS0000535
	Archocopturus laselvaensis Hespenheide, 2005	ASUHIC0086633
	Archocopturus medeterae Hespenheide, 2005	ASUHIC0016884 (Fig. 28)
	Cylindrocopturus adspersus (LeConte, 1876)	ASUHIC0086657 (Fig. 48)
	Cylindrocopturus quercus (Say, 1831)	ASUHIC0016905 (Fig. 49) ARTSYS0000819 (Fig. 95)
	Helleriella longicollis Champion, 1906	ASUHIC0065241
	Larides cavifrons Champion, 1906	ASUHIC0016882
	Lissoderes cecropiae Hespenheide, 1987	ASUHIC0064707 (Fig. 31)
		ASUHIC0064/08 (Fig. 52)
Zygopini	Lissoderes subnudus Champion, 1906	SSAC0001064 (Fig. 56)
		SSAC0001136 (Fig. 98)
	Peltophorus adustus (Fall, 1906)	ASUHIC0012325
	Peltophorus polymitus seminiveus (LeConte, 1884)	SSAC0001117
	Peltophorus polymitus suffusus (Casey, 1892)	ASUHIC0016837
	Phileas granulatus Champion, 1906	ARTSYS0000528
	Philenis flavipes Champion, 1906	ASUHIC0065102
	Philenis fuscofemorata Champion, 1906	ARTSYS0000659
	Zygops erythropygus Champion, 1906	ASUHIC0086640
	Zygops vitticollis Desbrochers, 1891	ASUHIC0086634
	Zygopsella ruficauda Champion, 1906	ARTSYS0000526
	Philides comans Champion, 1909	ARTSYS0000804
Incertae sedis	Philinna bicristata Champion, 1906	ARTSYS0000799 (Figs 18, 57) ARTSYS0000532 (Fig. 105)

Trichodocerini Champion, 1906: 713

Classificatory history. This monotypic tribe has been enigmatic in its placement in Curculionidae since the description of its sole genus by Chevrolat in 1879. *Trichodocerus* Chevrolat, 1879 was originally considered by Chevrolat to be near *Conotrachelus* Dejean, 1835 and it has since been treated as or had its species described in the Cryptorhynchinae (Champion 1906: 713, Hustache 1936, Papp 1979, O'Brien and Wibmer 1982, Wibmer and O'Brien 1986, Zherikhin and Gratshev 1995), Baridinae (Bondar 1946) and Conoderinae (Wibmer and O'Brien 1989: 15, Wolda et al. 1998, Alonso-Zarazaga and Lyal 1999, Lyal et al. 2006, Bouchard et al. 2011, Prena et al. 2014), where it currently resides.

Trichodocerus Chevrolat, 1879: XCII

Figs 1, 20, 37, 67

⁼ *Mallerus* Bondar, 1946: 86 [Syn.: Bondar 1947: 294]. Type species: *Mallerus antiquus* Bondar, 1946 [by original designation].
Type species. *Trichodocerus spinolae* Chevrolat, 1879 [by subsequent designation: Champion 1906: 713].

Gender. Masculine.

Diagnosis. *Trichodocerus* is easily separated from all other genera treated here by the loose antennal club, the presence of elongate setae on the club and funicular articles, contiguous procoxae, a prosternal rostral channel with the lateral margins strongly converging and meeting below the procoxae, a mesoventrite with a transverse ventrally produced ridge anterior to mesocoxae and the mesoventrite posterior to ridge with dense yellow scales (Fig. 1), and the presence of stridulatory plectra on the male seventh abdominal tergite. Funicular article 1 is short and globose, the hind femora are not carinate and ventrally with one or no teeth, the femoral apices are always unarmed at the lateral and mesal faces, the eyes of most species have a distinct lower constriction lateral to rostral insertion (Fig. 37), the abdominal ventrites are slightly ascending, and the pygidium is concealed (slightly exposed in male *T. spinolae* and male of at least 1 undescribed species).

Notes. The contiguous procoxae efficiently separates *Trichodocerus* from all genera except some species of the very different *Zygops*. The yellow scales of the mesocoxae and mesoventrite have also been observed in *Arachnomorpha* Champion, 1906 (on the pro- and mesocoxae), *Microzygops* Champion, 1906 (on the procoxae), and some species of *Lechriops* and *Macrocopturus* (on the pro- and mesocoxae and ventrally on the mesofemora), but in those genera they are not also present on the mesoventrite between the mesocoxae.

Phylogenetic relationships. The numerous features that easily separate *Tricho-docerus* from the rest of the conoderines are potentially indicative of improper placement in the Conoderinae, however, the same unique characters prevent confident reassignment to another group of Curculionidae. Champion (1906: 713) noted the similarity of the antennal funicle to *Hedycera* Pascoe, 1870, a South American genus here reassigned to the Piazurini.

Host associations. The genus is apparently nocturnal, with most observed specimens being collected at UV light traps – 488 specimens were collected by Wolda et al. (1998), representing three of the 17 species of Conoderinae with more than 10 specimens collected. One undescribed species has been reared from balsa, *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Malvaceae: Bombacoideae Burnett) (Hespenheide, personal communication). An observed specimen of *T. brevilineatus* Champion, 1906 [STRI_ENT_008474] was recorded from dead branches of balsa and an undescribed species [SSAC0001000] was collected on balsa leaves; another observed undescribed species has been collected on dead branches of *Pachira sessilis* Benth. (Bombacoideae) [STRI_ENT_0084793].

Described species. Two species are known from the focal region and one additional described species occurs in South America. I have accumulated and distinguished over 20 species of *Trichodocerus* new to science as part of a revision currently in preparation.

Range. Guatemala, Costa Rica, Panama; South America. Undescribed species are also known from Mexico.



Figures 67–70. Lateral and dorsal habitus images of Trichodocerini and Piazurini. Scale bars = 2 mm unless otherwise specified. **67a–b** *Trichodocerus spinolae* [ARTSYS0000534] **68a–b** *Cratosomus lafontii* [SSAC0001133]; scale bars = 10 mm **69a–b** *Lobops bonvouloiri* [ARTSYS0000527] **70a–b** *Piazurus caprimulgus* [SSAC0001113].

Piazurini Lacordaire, 1865: 144

Classificatory history and current circumscription. This tribe was originally characterized by Lacordaire (1865: 144) for the genera *Cratosomus, Pinarus*, and *Piazurus* in recognition of the strongly canaliculate prosternum, the "gutter-like" modification to the mesoventrite and the clavate, non-carinate hind femora that do not or only slightly exceed the abdominal apex. Heller (1906: 31) produced a key to Piazurini that includes 8 of the 12 currently recognized genera – not included are *Lobops, Latychellus* Hustache, 1938, *Hedycera*, and the Old World *Guiomatus* – based largely on the relative size of abdominal ventrites and the amount that they ascend, relative lengths of funicular articles, and the construction of the mesoventrite.

The monotypic South American genus Hedycera is moved to the Piazurini despite the occurrence of the genus outside the geographic focus of this paper. The exposed pygidium that is not completely visible in dorsal view, the large triangular tooth on the hind femur, the transverse posteromedial depression on the metaventrite (discussed further below), and the unarmed femoral apices place the genus not only in the Piazurini but in a hypothesized clade containing Piazurus, Pseudopiazurus Heller, 1906, Pseudopinarus Heller, 1906 and the South American Piazolechriops Heller, 1906. Hedycera megamera Pascoe, 1870 would key out to couplet 7 of Heller's 1906 key (containing Pseudopinarus and Piazolechriops), for having abdominal segments only slightly ascending, abdominal segment 2 not being longer than 3 and 4 combined, and the presence of "superciliarleisten", referring to the arcuate carina at the vertex of the head found in most members of these genera (though not in a few species of *Pseudopinarus*), a greatly elongate antennal funicular article 2, and a slender rostrum. *Hedycera* can be differentiated from these by the shape of the pronotum in dorsal view, which is widest in the anterior half just before the subapical constriction, and in having elongate setae on the antennal funicular articles. When originally describing the monotypic genus, Pascoe (1870) stated that it was most closely related to Piazurus, which was later agreed with by Champion (1906: 713). Hedycera is the first genus separated in Heller's key (1895) for having similar-sized abdominal ventrites 2, 3, and 4, but is not treated further in that publication. In the catalogs of Hustache (1934: 45) and Blackwelder (1947: 884) Hedycera is listed under the otherwise entirely Old Worlddistributed conoderine tribe Mecopini Lacordaire, 1865 and was moved to Lechriopini in Wibmer and O'Brien (1986: 19), without a justification provided in either placement.

Variation in key character systems. The modification to the mesoventrite in the genera treated here in the Piazurini varies from being a cup-shaped receptacle (as in *Lobops*; Fig. 2) to structured similarly to a cup-shaped receptacle but with the posterior margin flattened and depressed at least slightly below the level of the lateral margins of the channel (Figs 3, 4) allowing the rostrum to pass through to the metaventrite if long enough. The eyes are often smaller and more separated and are not or not as sharply acuminate ventrally or laterally inflexed (Figs 38, 39) as in many Lechriopini and Zygopini, but can be quite large and contiguous or subcontiguous (Figs 40–41), taking up most of the surface of the head as well as be slightly ventrally acuminate to slightly laterally inflexed. The pygidium is exposed but not entirely visible in dorsal view (somewhat

concealed from above by the elytral apex; e.g. Fig. 68), usually only visible completely in posterior or ventral view. Abdominal ventrites are flat to slightly, evenly ascending. The vestiture consists of thick setae to small scales, usually not covering most of the body surface except in *Lobops*, which has large, flat and round scales. The femora are at least slightly clavate, the hind femur is without a lateral carina and lacks teeth at the mesal and lateral apical faces (Fig. 60; in most lechriopines and zygopines, a tooth is usually present at the mesal and/or lateral face of the femoral apex on the middle and/or hind legs as in Figs 61–63), and several genera have a large, laterally compressed, triangular ventral tooth. This large triangular tooth is also found in other conoderine tribes (e.g. Menemachini Lacordaire, 1865; Campyloscelini Schoenherr, 1845) as well as other groups of weevils (e.g. Hylobiini Kirby, 1837). Despite this homoplasious distribution in Curculionidae it likely represents a single origin within the Piazurini, with the genera having it also sharing additional characters; it is also not found in other New World Conoderinae, making it useful for diagnosing the group of Piazurines that bear it.

Additional characters of potential phylogenetic significance. The metaventrite posteromedially has a transverse depression, not with a narrow longitudinal sulcus extending variably anteriorly as in most Lechriopini and Zygopini (but many species of *Cratosomus* have a broad longitudinal depression). The antennal club is typically more spherical to ovoid, with the suture between at least articles 2 and 3 sinuate (but also found in a few lechriopines and zygopines). A mesal process of the procoxae is absent in most piazurines and found in many lechriopines and zygopines (though present, among the Central American species observed, in *Pseudopinarus, Lobops bonvouloiri* (Hustache, 1932), and in the species *Piazurus alternans* Kirsch, 1875). Sclerolepidia are absent in Piazurini (Lyal et al. 2006: 237). Additionally, piazurines are quite different behaviorally from the remainder of the New World Conoderinae, typically being less active in the daytime and no species are known to be part of the several widespread mimicry complexes found in the tribes Lechriopini and Zygopini (Hespenheide 1995).

Diversity and distribution. Fifty-two species are currently known from north of South America in five genera. Six additional genera are known only from South America, and one genus, *Guiomatus*, occurs in Papua New Guinea.

Cratosomus Schoenherr, 1825: c.585

Figs 21, 38, 68

- = Atenismus Chevrolat, 1880: L [Syn.: Emden 1933: 505]. Type species: Atenismus spinipennis Chevrolat, 1880 [by monotypy].
- = Gorgus Schoenherr, 1825: c.585 [Syn.: Gyllenhal 1837: 13]. Type species: Cryptorhynchus lentiginosus Germar, 1824 [by original designation].
- *Gorgus* Schoenherr, 1826: 279 (non Schoenherr, 1825) [Syn.: Gyllenhal 1837: 32]. Type species: *Curculio dubius* Fabricius, 1787 [by original designation] (*=Curculio bombina* Fabricius, 1787).
- (Eucratosomus) Kuschel, 1945: 361. Type species: *Cryptorhynchus sticticus* Germar, 1824 [by original designation].

Type species. *Rhynchaenus herculeanus* Dalman, 1823 [by original designation] (=*Rhynchaenus roddami* Kirby, 1819).

Gender. Masculine.

Diagnosis. *Cratosomus* can be differentiated from the other Piazurines treated here by the setal tufts of the anterior margin of the tibial apex being composed of thick fascicles of golden setae (Fig. 21), the dense setal brush at the posterodistal face of the meso- and metatibia (Fig. 21), the thick rostrum that is apically dorsoven-trally compressed, and generally larger body size. The eyes can be small and widely separated (Fig. 38) or large and approximate; the femora are ventrally with 0-2 teeth, usually with a distinct ventral carina distally; and the elytra and pronotum are often tuberculate or spinose.

Notes. This genus includes some of the largest Neotropical weevils (Champion 1906: 1). Males of some species have lateral tusk-like processes of the rostrum and are presumably under sexual selection and used during male-male competitions.

Keys. Emden 1933 (Central and South America), Champion 1906: 2 (Central America). **Phylogenetic relationships.** Schoenherr's (1838) classification included *Cratoso*tus in a separate *Cahar*: of Cryptorbynchides, thereby distinguished from the rest

mus in a separate *Cohors* of Cryptorhynchides, thereby distinguished from the rest of the then-described Conoderinae. Although somewhat dissimilar in appearance to the Piazurini treated here, it resembles the South American piazurine genera *Latychus* Pascoe, 1872 (and likely also the South American *Costolatychus* Heller, 1906, and *Latychellus* Hustache, 1938, but no specimens were observed of those genera) in the thickened dorsoventrally compressed rostral apex, the smaller and relatively widely separated eyes (as in some *Cratosomus*), and the small ventral femoral tooth.

Host associations. R.S. Anderson (1993: 218) lists Annonaceae Juss., Rutaceae Juss., Lauraceae Juss., Myrtaceae Juss., and Sapotaceae Juss Hosts for several species of Brazilian *Cratosomus* are recorded by Costa-Lima (1956: 213).

Described species. Twenty-five species are known from the focal region (with 14 subspecies or forms) and an additional 126 species (and many subspecies or forms) are known exclusively from South America (Wibmer and O'Brien 1986: 254; Rheinheimer 2011: 66 described one more).

Range. Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama; South America. Distributions of Guadeloupe and the Lesser Antilles are listed with doubt by Emden (1933: 532) and subsequent catalogs.

Lobops Schoenherr, 1845: 116

Figs 2, 39, 69

Type species. Lobops setosus Fåhraeus, 1845 [by original designation].

Gender. Masculine.

Diagnosis. *Lobops* is unique among the Piazurines in having a prominent cupshaped receptacle for receiving the rostrum on the mesoventrite (Fig. 2), a dense covering in flat, round scales, and strongly concave interocular space (Fig. 39). The metafemoral tooth is not especially large, the femora are not strongly clavate, and the second funicular article is relatively short (not longer than the first); these characters are also shared with *Cratosomus* but not other piazurine genera treated here.

Phylogenetic relationships. Of the five piazurine genera covered here, *Lobops* has the least certain placement in the tribe. Schoenherr (1845) originally indicated for the South American type species a relationship with *Conotrachelus*, and the genus was previously placed in the Ithyporini Lacordaire, 1865 (O'Brien and Wibmer 1982: 125, as Cryptorhynchinae; the tribe is currently placed in the Molytinae), overlooking a transfer to the Piazurini by Kuschel (1955: 271). The only known Central American species, *L. bonvouloiri*, was originally described in the genus *Pseudopinarus*. The structure of the mesoventrite is suggestive of placement in the Cryptorhynchinae, but that type of receptacle has been shown to not be exclusive to the subfamily (Riedel et al. 2016: 5). *Lobops* is certainly better placed in the Piazurini than in the other tribes reviewed here – despite differences in a number of characters, the exposed pygidium that is not visible in dorsal view, the unarmed femoral apices, non-carinate femora, and lack of sclerolepidia, in combination, are unique to the Piazurini.

Host associations. Unknown.

Described species. One species is known from the focal region and two additional species are known from South America (Wibmer and O'Brien 1986: 263).

Range. Panama; South America.

Piazurus Schoenherr, 1825: c.586

Figs 3, 23, 60, 70

Type species. *Poecilma stipitosum* Germar, 1824 [by original designation]. Gender. Masculine.

Diagnosis. An elongate second funicular article and broad triangular femoral tooth place *Piazurus* near *Pseudopinarus* and *Pseudopiazurus*, and it can be differentiated from them by the longer second abdominal ventrite (which is as long as the third and fourth ventrites when seen from the side) and the protibial apex that bears a premucro. Being a much more diverse genus than *Pseudopinarus* and *Pseudopiazurus*, it is easiest to arrive at an identification by a negative identification of those two smaller genera: namely, species of *Piazurus* never have a carinate vertex of the head (as in many *Pseudopinarus*), a strongly impressed first abdominal ventrite (as in *Pseudopiazurus*), or a subapical premucro (as in some *Pseudopinarus* and *Pseudopiazurus*) and usually do not have a mesal procoxal process (which is found in most *Pseudopinarus* and a South American *Pseudopiazurus*; it is present at least in *Piazurus alternans*).

Notes. Fiedler (1936) divided *Piazurus* into seven groups based mainly on the shape of the elytra and the presence, location and shape of elytral tubercules.

Keys. Fiedler 1936 (Central and South America), Heller 1906: 33 (*Piazurus s. str.* of Central and South America), Champion 1906: 9 (Central America).

Phylogenetic relationships. Of the genera with a broad ventral metafemoral tooth, *Piazurus* is most similar to *Pseudopiazurus* with a conical prothorax and lack

of a mesal process of the procoxae (though it is present in at least one species of each genus).

Host associations. Some species have been reared from branches of various genera of Lecythidaceae (Fassbender 2013, Fassbender et al. 2014). Maes and O'Brien (1990) report *Piazurus trifoveatus* Champion, 1906 from *Coffea* L. (Rubiaceae Juss.) and Costa-Lima (1956: 218) reports a Brazilian species from fruits of Myrtaceae.

Described species. Nineteen species are known from the focal region and an additional 58 species are exclusive to South America (Wibmer and O'Brien 1986: 260).

Range. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama; South America.

Pseudopiazurus Heller, 1906: 32

Figs 22, 40, 64, 71

Type species. *Piazurus obesus* Boheman, 1838 [by subsequent designation: Rheinheimer 2011: 76].

Gender. Masculine.

Diagnosis. *Pseudopiazurus centraliamericanus* (Heller, 1906), the only recorded Central American species of *Pseudopiazurus*, can be separated from other Central American piazurines by the deep U-shaped depression on the first abdominal ventrite (Fig. 64; also found in a few *Pseudopinarus*, but when present in that genus there is always also present the arcuate carina on the vertex of the head which is never found in *Pseudopiazurus*), the large subapical premucro of the metatibia (Fig. 22; but also at least in *Pseudopinarus guyanensis* Hustache, 1938), the absent premucro at the protibial apex (also in species of *Pseudopinarus*), the very large, ovoid, contiguous eyes (Fig. 40), and the large, deep, ovoid punctures of the elytral striae (but also found in some *Cratosomus* species).

Notes. First described by Heller (1906) along with *Pseudopinarus* as subgenera of *Piazurus*. As documented by Champion (1906: 18), after the subgenus was first introduced in the key the name was erroneously switched with that of *Pseudopinarus* and the key to species of *Pseudopiazurus* is given under the name *Pseudopinarus* (Heller 1906: 34). The catalog of South American species by Wibmer and O'Brien (1986: 262) makes a correction to the two species given for Central America by O'Brien and Wibmer (1982: 160), which overlooked an error by Hustache (1934), leaving *P. centraliamericanus* the only species known from Central America.

Keys. Marshall (1922: 69), Fiedler 1936: 28 and Heller 1906: 34 (under *Pseudopinarus*, in error) also contain keys to species.

Phylogenetic relationships. This genus is most similar in overall appearance to *Piazurus* (see above), but the genus as a whole is incompletely distinguishable from *Pseudopinarus* by obvious characters with the exception of the much larger eyes, usually larger and more ascending mesepipleura, and absent ventral profemoral tooth of *Pseudopiazurus* – the deep arcuate sulci of the first ventrite in *Pseudopiazurus* is appar-



Figures 71–74. Lateral and dorsal habitus images of Piazurini, Othippiini and Lechriopini. Scale bars = 2 mm unless otherwise specified **71a–b** *Pseudopiazurus centraliamericanus* [ASUHIC0086627]; scale bars = 5 mm **72a–b** *Pseudopinarus condyliatus* [ASUHIC0086626]; scale bar for **72a** = 1 mm **73a–b** *Acoptus suturalis* [ASUHIC0016914] **74a–b** *Copturomimus cinereus* [ASUHIC0086628].

ently also found in *Pseudopinarus*, e.g. in *Pseudopinarus quadratus* (Champion, 1906); the mesal process of the procoxae is absent in *Pseudopiazurus centraliamericanus* but present in the South American *Pseudopiazurus spiniventris* Marshall, 1922 as well as in many *Pseudopinarus*, and the subapical premucro of the metatibia is also found in *Pseudopinarus guyanensis*. Despite the overlap in these characters, *Pseudopinarus* is interpreted here as more closely related to the South American *Piazolechriops, Pinarus*, and *Hedycera*.

Host associations. R.S. Anderson (1993: 218) lists Guttiferae Juss. (=Clusiaceae Lindl.). Marshall (1922: 67) records the South American *P. obesus* (=*P. papayanus* (Marshall, 1922)) as a borer of the "leaf-stems" of papaya (Caricaceae Dumort: *Carica papaya* L.).

Described species. One species is known from the focal region and three additional species are known exclusively from South America (Wibmer and O'Brien 1986: 262, including Costa-Lima's (1956: 217) synonymy of *P. papayanus* with *P. obesus*, which was either overlooked or disputed, as they are treated as separate by Wibmer and O'Brien).

Range. Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama; South America.

Pseudopinarus Heller, 1906: 33

Figs 4, 41, 72

= Paralatychus Voss, 1947: 60 [Syn.: Wibmer and O'Brien 1986: 7]. Type species: Paralatychus conotracheloides Voss, 1947 [by original designation] (=Piazurus dentipennis Fiedler, 1936).

Type species. *Piazurus rana* Heller, 1906 [by subsequent designation: Rheinheimer 2011: 76].

Gender. Masculine.

Diagnosis. As a subgenus of *Piazurus, Pseudopinarus* was separated from *Piazurus s. str.*, along with the other subgenus, *Pseudopiazurus*, by Heller (1906) and Fiedler (1936) for having a second abdominal ventrite that is shorter in length than the third and fourth ventrites combined. *Pseudopiazurus* is easily distinguished from *Pseudopiazurus* in body shape, which is much more robust in *Pseudopiazurus*, but as a whole *Pseudopinarus* is the most difficult piazurine genus to characterize. Most species can be further distinguished from *Pseudopiazurus* by the presence of a ventral tooth on the profemora. Some *Pseudopinarus* have an arcuate carina on the vertex of the head (Fig. 41) similar to the South American *Piazolechriops* and *Hedycera*. The eyes are generally smaller and more separate than in *Pseudopiazurus*, but can be large and subcontiguous (as in Fig. 41). The structure of the mesoventrite varies as well, with some species bearing ventrally produced posterolateral tubercles (as in *Pseudopiazurus*) and others with nearly a cup-shaped receptacle. Additionally, the relatively small mesepipleura and the

procoxae with a mesal process differentiates some *Pseudopinarus* from most species of *Piazurus* and the single Central American species of *Pseudopiazurus*.

Keys. Fiedler 1936: 29, Heller 1906: 34.

Phylogenetic relationships. The species of *Pseudopinarus* that have the arcuate carina on the vertex of the head are very similar to the South American genera *Piazolechriops* and *Hedycera* than to other Central American genera. The only character given by Heller (1906) to separate *Pseudopinarus* from *Piazolechriops* is the shorter hind femur of *Pseudopinarus*, which do not, or only very slightly, extend beyond the apex of the abdomen. *Pseudopinarus* differs from *Hedycera* by the short antennal setae and the pronotum in dorsal view, which is not widest just before the apex. Other species of *Pseudopinarus*, e.g. *P. cerastes* (Fabricius, 1801), are more similar to smaller species of *Piazurus* (e.g. *P. alternans*), raising the question of the monophyly of the genus and the validity of the shorter second abdominal ventrite as a character separating monophyletic groups from *Piazurus*.

Host associations. Some species have been reared from branches of various genera of Lecythidaceae (Fassbender et al. 2014). *Pseudopinarus guyanensis* has been reared from seeds of *Gnetum* L. (Gnetaceae Blume) [ASUHIC0086636, STRI_ENT_0082031].

Described species. Seven species are known from the focal region (Wibmer and O'Brien 1986: 263 add *P. guyanensis* to the Central American fauna) and an additional 13 species are known only from South America (Wibmer and O'Brien 1986: 262).

Range. Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama; South America.

Othippiini Morimoto, 1962: 47

Classificatory history and current circumscription. Eleven genera were first grouped into tribe Othippiini by Hustache (1938: 63), which was not treated as a valid name in the catalog of Alonso-Zarazaga and Lyal (1999: 113) for lacking a description. Morimoto (1962: 47) provided some clarification on the distinction of the tribe, and this was further refined in Kojima and Lyal (2002), where seven genera were transferred out of the Othippiini in order to redefine it. Othippiines can be distinguished (*sensu* Kojima and Lyal 2002: 172) by the following combination of characters: the mesepisterna are non-ascending, the scutellum is exposed, the prosternum of most is canaliculate, and the antennal funiculus has 7 articles. However, the monophyly of the tribe has yet to be shown (Kojima and Lyal 2002).

Variation in key character systems. The mesoventrite of othippiines can have a rostral channel or be unmodified (Kojima and Lyal 2002). The number of antennal funicular articles for othippiines given by Kojima and Lyal (2002) serves to separate this tribe from the Mecopini which have been considered to have 6 articles since originally described. However, one of the genera currently treated in the Mecopini (*Emexaure* Pascoe, 1871) has a funiculus with 7 articles (Pascoe 1871: 216), some of the genera are similar in appearance and also in eye shape (Kojima and Lyal 2002: 171) and distinction between the tribes requires further study.

Diversity and distribution. Othippiini now contains eight genera, six of which are currently monotypic. The monotypic genus *Acoptus* is the sole New World representative.

Acoptus LeConte, 1876: 264

Figs 5, 24, 42, 73

Homogaster Provancher, 1877: 530 [Syn.: Blackwelder and Blackwelder 1948: 48].
Type species: *Homogaster quebecensis* Provancher, 1877 [by monotypy].

Type species. Acoptus suturalis LeConte, 1876 [by monotypy].

Gender. Masculine.

Diagnosis. *Acoptus* can be easily recognized from the rest of the conoderines treated here by the following characteristics: the inner margin of eyes towards the top has a large lanceolate space (Fig. 42) and the eyes are nearly touching above and below the lanceolate space, the mandibles are somewhat falcate and are in contact only at the apex (visible in Fig. 5), and the tibial apex distally has the dorsal margin dilated and premucro absent from all tibiae (Fig. 24). The relatively forward facing eyes that do not extend much on lateral portions of head (genae large), the first funicular article that is longer than the second, the unmodified mesoventrite, the ventrally toothed and non-carinate metafemora, the unarmed femoral apices, the small and non-ascending mesopleura, the absent sclerolepidia, and the abdominal ventrites that are not rapidly ascending additionally help diagnose the genus and in combination separate it from all Lechriopini and other New World Conoderinae.

Notes. The species *Homogaster quebecensis* was first placed in synonymy with *Piazurus subfasciatus* LeConte, 1876 (*=Lechriops subfasciatus* (LeConte)) by LeConte (1880: xii), where it remained in catalogs until Blackwelder and Blackwelder (1948: 48) listed it in synonymy with *Acoptus suturalis*. Provancher's description agrees with that of *Acoptus*.

Phylogenetic relationships. In keys to North American genera, *Acoptus* is always separated from the rest of the North American genera along with *Psomus* by the flat abdominal ventrites (e.g. Hespenheide 2002: 755). Casey (1892: 458, 1897: 666) suggested a relationship to *Psomus* on these grounds, but this similarity only suggests they are both aberrant in their placement in the Lechriopini – they are otherwise very different in appearance, as also noted by Casey (1892: 458). LeConte (1876: 264) originally distinguished his genus from *Copturus* (which, with the geographic scope and time of publication of the key included only species currently placed in *Cylindrocopturus* and *Eulechriops*) and *Zygops* by the nearly flat abdominal ventrites and elongate first funicular article. Provancher (1877: 530), apparently independently, separated his genus *Homogaster* from *Zygops* and *Copturus* (as well as the South American *Timorus*) for the same reasons. A phylogeny by Davis (2014) recovered *Acoptus* as closer to the Old World genus *Mecopus* (Conoderinae: Mecopini) than any of the included New World conoderines, a result consistent with the new placement of the genus (the study did not include Othippiini).

Host associations. Mentions in the literature of host plants include *Fagus* L. (Fagaceae Dumort) (Chittenden 1890: 171), *Ulmus americana* L. (Ulmaceae Mirb.) (Hoffman 1942: 12) and *Juglans cinerea* L. (Juglandaceae DC. ex Perleb) (Halik and Bergdahl 2002). Sleeper (1963: 215) additionally reports *Quercus* L. (Fagaceae), *Cercis canadensis* L. (Fabaceae Lindl.), *Carya* Nutt. (Juglandaceae), and *Platanus occidentalis* L. (Platanaceae T. Lestib.). Adults of *A. suturalis* have been implicated as vectors of the chestnut blight fungus, *Cryphonectria parasitica* (Murrill) Barr (Pakaluk and Anagnostakis 1977) and the butternut canker fungus, *Sirococcus clavigignenti-juglandacearum* Nair, Kostichka & Kuntz (Halik and Bergdahl 2002).

Described species. One.

Range. Eastern Canada, Eastern U.S.A., extreme northeastern Mexico (Sleeper 1963: 215). Specimens have not been observed from Mexico or even Texas to confirm Sleeper's range extension; recently the genus was reported for the first time from Arkansas (Skvarla et al. 2015).

Lechriopini Lacordaire, 1865: 149

Classificatory history and current circumscription. This tribe was originally characterized by Lacordaire (1865: 149) for the genus *Lechriops* by the rostral channel, which is closed (horseshoe-shaped) posteriorly to receive the rostrum and the linear, carinate femora that may or may not exceed the apex of the abdomen.

While a subclassification for the Lechriopini is not formally proposed here without also examining the South American genera, the following groups of genera are hypothesized to be related: the "Eulechriops genus complex", including Eulechriops, Macrolechriops Champion, 1906, Copturomorpha Champion, 1906, Cylindrocopturinus Sleeper, 1963, Coturpus R.S. Anderson, 1994, and Turcopus R.S. Anderson, 1994 and the "Macrocopturus genus complex", including Macrocopturus, Copturomimus Heller, 1895, Lechriops, Pseudolechriops, Hoplocopturus Heller, 1895, and Mnemynurus Heller, 1895. The genera Microzygops, Paramnemyne, Poecilogaster, Euzurus, Copturus, Microzurus and Psomus do not fit into either complex as currently conceived. Until the inclusion of the South American lechriopine genera a subtribal classification for the Lechriopini will not be further speculated here.

Variation in key character systems. Among the genera currently placed in the tribe (*sensu* Lyal et al. 2006), the only characters that distinguish them (after the exclusion of *Acoptus, Philinna*, and *Philides*) are a concealed pygidium with rapidly ascending abdominal sclerites, the presence of modification to the mesoventrite and/or the presence of sclerolepidia (just sclerolepidia in *Copturomimus*, most *Macrocopturus* and *Psomus*). The mesepipleura are usually large and somewhat ascending (except in *Paramnemyne* and *Psomus*). Other characters given by Lyal et al. (2006: 229) that separate lechriopines from zygopines are: "larger eyes, extending half-way or more down the side of the head; a longer rostrum, reaching at least the middle coxae; the middle and hind femora with the posterior distal margin extended into an acuminate projection

extending beyond the anterior distal margin", but these appear to be homoplastic – many lechriopines, especially some *Eulechriops* and related genera, have smaller eyes like many zygopines, and many zygopines have a similar femoral apex. The presence of a carina and ventral tooth on the hind femora, and the relative lengths of the first two funicular articles are potentially indicative of infratribal relationships; in the *Eulechriops* genus complex the hind femora are not carinate and unarmed ventrally and the second funicular article is at most subequal to the first, while in the *Macrocopturus* genus complex the hind femora are ventrally toothed and carinate and the second funicular article is longer than the first.

Modification to the meso- and metaventrite to receive the rostrum varies quite a bit in this group, with the typical forms (i.e. deviating the least from Lacordaire's original tribal construction of a closed, horseshoe-shaped channel), being found in most members of the following genera: Lechriops, Poecilogaster, Eulechriops, Macrolechriops, Copturomorpha, Coturpus, Turcopus, Copturus, Microzurus, Euzurus, Microzygops and Pseudolechriops. These genera likely do not represent a monophyletic group, and the mode of closure (whether a simple depression or a strongly carinate apex of the channel) and the location of closure (on the mesoventrite or metaventrite) can vary significantly within genera. Pseudolechriops has arcuate lateral margins of the channel forming an ovoid carina that encircles a deep excavation on the mesoventrite and the anterior margin of the metaventrite (Fig. 13). A few species of the genus Macrocopturus (e.g. M. albidus Champion, 1906) and the genus Microzygops have a similarly constructed mesoventrite (Fig. 11) but the majority of Macrocopturus species and the very similar Copturomimus species have the unmodified "zygopine type" of mesoventrite. The mesoventrites of the genera Hoplocopturus and Mnemynurus are interpreted as of the lechriopine type, with the sides of the channel strongly arcuate and meeting medially, forming an inverted U-shaped carina that no longer appears to serve the function of receiving the rostrum (Fig. 9). Paramnemyne, Euzurus, Copturus, and Microzurus have a mesoventrite that would be classified here as the piazurine type (Heller 1895: 5 also notes the resemblance), with the rostral channel on the mesoventrite open (in Paramnemyne and Euzurus, Figs 8, 12) or closed (in Copturus and Microzurus, Fig. 6) and without anteriorly extending carinae; at least the latter three genera likely belong in the Lechriopini considering other characters. The mesoventrite of Psomus is unmodified.

Diversity and distribution. Two hundred and forty-two species are currently known from north of South America in nineteen genera, comprising nearly half of the genus- and the majority of the species-level diversity of North and Central American Conoderinae. An additional eight genera are known only from South America.

Copturomimus Heller, 1895: 63

Figs 66, 74

Type species. *Copturomimus cinereus* Heller, 1895 [by present designation]. Gender. Masculine.

Diagnosis. *Copturomimus* is similar to the large genus *Macrocopturus* with the elongate second funicular article, unmodified mesoventrite, and carinate and ventrally toothed hind femora, and can only be distinguished externally from that genus by the obliquely striolate area dorsally on the profemora (Fig. 66). The other genus with a striolate patch on the profemora, *Copturomorpha*, tends to have a striolate patch that is less obvious, being more finely striolate and more often concealed by scales; that genus otherwise is more similar to *Eulechriops*.

Notes. The function of the striolate profemora is unknown – the first conoderine species described with it, *Copturomorpha musica* (Kirsch, 1875b), was named, as the specific epithet suggests, for its hypothesized stridulatory function (Kirsch 1875b: 248). The function of the patch was instead suggested to be for antennal grooming purposes (Champion 1906b: 60) due to the lack of an obvious corresponding file structure required for stridulation and the position of the leg relative to the antennal club – observation of *Copturomimus caeruleotinctus* Champion, 1906 [SSAC0001059] revealed the use of the setal comb at the protibial apex (and not the striolate femoral patch) for antennal cleaning purposes.

Keys. Champion 1906b: 60 (for Central America), Muñiz 1965: 5 (for three species on avocado, key modified from Muñiz and Barrera 1958: 2).

Phylogenetic relationships. Heller (1895: 63) originally implied a relationship with his South American genus *Copturosomus* Heller, 1895, which is also difficult to distinguish from *Macrocopturus*. The relationship of both genera with *Macrocopturus* requires much more study to identify natural groupings of species. Whether the striolate femoral patch identifies a natural group is unknown but unlikely (Hespenheide 2009: 337). See also entry on *Macrocopturus* for discussion of the relationships of that hypothesized complex of genera.

Host association. *Copturomimus perseae* (Guenther, 1935) and two other South American species are wood-boring on avocado (Lauraceae: *Persea* Mill.) (Hustache *in* Mariño M. 1947, Kissinger 1957, Muñiz 1965). Associations of other Central American species are unknown.

Described species. Twelve species are known from the focal region (one species described by Hespenheide 2009) and five additional species are known from South America (Wibmer and O'Brien 1986: 271; Muñiz 1965 transferred one species from *Copturus*).

Range. Mexico, Guatemala, Honduras, Costa Rica, Panama; South America.

Copturomorpha Champion, 1906b: 65

Fig. 75

Type species. *Copturomorpha interrupta* Champion, 1906 [by original designation]. **Gender.** Feminine.

Diagnosis. Like *Copturomimus*, *Copturomorpha* can only be distinguished from a much larger genus (*Eulechriops*) by the presence of a striolate patch dorsally on the profemur, and shares the short second funicular article that is not longer than the first, the unarmed and non-carinate metafemora and the excavate mesoventrite.



Figures 75–78. Lateral and dorsal habitus images of Lechriopini. **75a–b** *Copturomorpha* sp. [ASUHIC0086641] **76a–b** *Copturus aurivillianus* [ASUHIC0024140] **77a–b** *Coturpus arcuatus* [ARTSYS0000531] **78a–b** *Cylindrocopturinus pictus* [SSAC0001288]. Scale bars = 2 mm.

Notes. The presence of the striolate patch on the dorsal surface of the profemora is shared only with *Copturomimus*, where the patch is typically larger and more coarsely striolate. *Copturomorpha* will key out to *Eulechriops* if that character is overlooked – it

is often indistinct and obscured by scales. Several South American species described in the genus by Hustache (1938) have a second funicular article that is longer than the first and a carinate and toothed hind femora in addition to the excavated mesoventrite, necessitating further study on the identity of *Copturomorpha* and the species currently placed there.

Keys. Champion 1906b: 65 (for Central America).

Phylogenetic relationships. The combination of characters from the antenna, mesoventrite, and femora place *Copturomorpha* in a hypothesized genus complex including *Eulechriops*; whether the striolate femoral patch identifies a natural group separate from or within *Eulechriops* needs investigation.

Host associations. Hosts of all described species are unknown; Fassbender (2013) and Fassbender et al. (2014) reared specimens from branches of Lecythidaceae that potentially represent a species of this genus.

Described species. Eight species are known from the focal region (one species described by Hespenheide 2011) and an additional 16 species are known from South America (Wibmer and O'Brien 1986: 271).

Range. U.S.A.: Texas, Mexico, Guatemala, Panama; South America.

Copturus Schoenherr, 1825: c.586

Figs 6, 76

- = Zurus Heller, 1895: 5 (non Amyot, 1846). Type species: Zurus aurivillianus Heller, 1895 [by subsequent designation: O'Brien and Wibmer 1982: 8].
- = Neozurus O'Brien & Wibmer, 1982: 168 [replacement name for Zurus] [Syn.: Wibmer & O'Brien 1986: 5].

Type species. *Poecilma papaveratum* Germar, 1824 [by original designation]. Gender. Masculine.

Diagnosis. *Copturus* is very similar to *Microzurus* with a concealed scutellum and a closed receptacle of the mesoventrite that is laterally flanged near the apex (Fig. 6), and can be distinguished from *Microzurus* by the ventrally toothed pro- and mesofemora, larger tarsal claws, and flattened (not costate) elytral intervals. The first two funicular articles vary in length among the species, with the second article being longer than or subequal to the first (Champion 1906b: 87).

Notes. The usage of this generic epithet has a particularly complicated history, as explained by Muñiz-Vélez and Ordóñez-Reséndiz (2010). The first usage of the name *Copturus* was as a subgenus of *Zygops* (Schoenherr 1825: col. 586), where the type species was designated as *Poecilma papaveratum* Germar, 1824. The subgenus was elevated to genus by Dejean (1835), and dozens of additional species were described to the genus (e.g. Schoenherr 1838, 1845, Kirsch 1875a, b). Heller (1895) created several genera out of specimens included in *Copturus* including the genus *Zurus* Heller, 1895 for the species of *Copturus* that have a concealed scutellum, second funicular

article that is barely longer than the first, and a unique, horseshoe-shaped modification to the mesoventrite. Among the species moved from *Copturus* into *Zurus* was *Poecilma papaveratum*, which Heller recognized as the previously designated type species of *Copturus*. *Neozurus* O'Brien & Wibmer, 1982 was created as a replacement name for *Zurus* (O'Brien and Wibmer 1982: 4) which was preoccupied by *Zurus* Amyot, 1846 and was later synonymized with *Copturus* as an unjustified replacement name (Wibmer and O'Brien 1986, Alonso-Zarazaga and Lyal 1999: 111). As a result, all species treated as *Copturus* by Heller became newly recombined as *Macrocopturus*, one of Heller's original subgenera of *Copturus* elevated to genus (Wibmer and O'Brien 1986: 17), and all species treated as *Zurus* by Heller and subsequent authors until Wibmer and O'Brien (1986) became newly recombined as *Copturus*, returning the type species *Poecilma papaveratum* to its original genus.

Keys. Champion 1906: 87 (to Zurus of Central America), Heller 1895: 5 (to Zurus of Central and South America).

Phylogenetic relationships. Hespenheide (1984: 315) suggests a relationship with *Microzurus, Euzurus*, and *Cylindrocopturinus*. Of those three, it is most similar to *Microzurus*, the only differences given by Champion (1906: 87) being the ventrally toothed pro- and mesofemora, the larger body size and comparatively proportionate tarsal claws. *Euzurus* also has a scutellum concealed by a posterior lobe of the pronotum, but the manner of it's concealment differs from *Copturus* and *Microzurus*: where the posterior pronotal lobe of *Copturus* and *Microzurus* subducts the elytra, completely concealing the scutellum, in *Euzurus* the posterior lobe is only extended posteriorly and not below the elytral base, leaving the scutellum visible in posterior view. Despite this difference, Lyal et al. report Type II sclerolepidia to be present in *Copturus*, *Microzurus*, and *Euzurus*, which, among the sclerolepidia-bearing lechriopines, is only also known in the very different *Psomus*. See entry on *Cylindrocopturinus* for the present interpretation of the relationship of that genus. The relationship of *Copturus* and *Microzurus* is found to be the sistergenus is not easily hypothesized by the external characters examined thus far.

Host associations. The widespread Central and South American species *Copturus aurivillianus* (Heller, 1895) is reported by Costa-Lima (1956: 219) to bore stems of *Canavalia* Adans., *Dolichos* L., and *Phaseolus* L. (Fabaceae) as larvae in Brazil.

Described species. Six species are known from the focal region and an additional 27 species are known only in South America.

Range. Mexico, Honduras, Nicaragua, Costa Rica, Panama, Guadeloupe; South America.

Coturpus **R.S. Anderson, 1994: 480** Fig. 77

Type species. *Coturpus arcuatus* R.S. Anderson, 1994. Gender. Masculine. **Diagnosis.** Within the *Eulechriops* complex of genera, *Coturpus* can be identified by lacking a striolate profemoral patch (as in *Copturomimus*), lacking a very prominent receptacle on the mesoventrite (as in *Turcopus*), lacking the premucro-like inner flange at the tibial apex (as in *Cylindrocopturinus*), and can be differentiated from the observed species of *Eulechriops* by bearing elongate setae on the ventral surface of strongly arcuate hind legs at least in the males and by lacking a procoxal mesal tooth (though with the vast numbers of undescribed *Eulechriops* it is difficult to rule out the absence of this character from that genus).

Notes. Females are unknown, and R.S. Anderson (1994: 482) suspects the modified hind legs to be found only in males as similar modification to the hind legs is known only in male *Cylindrocopturinus*.

Phylogenetic relationships. R.S. Anderson (1994: 462) proposed a relationship to *Cylindrocopturinus* based on the presence of elongate setae on the ventral surface of the hind legs in males. This genus is difficult to separate from large and variable *Eulechriops. Coturpus* can be further separated from *Turcopus* and *Cylindrocopturinus* by genitalic characters given by R.S. Anderson (1994).

Host associations. The genus has been collected on mistletoe, *Phoradendron* Nutt. (Santalaceae) on *Quercus* (R.S. Anderson 1994: 484).

Described species. One (R.S. Anderson 1994). **Range.** Mexico.

Cylindrocopturinus Sleeper, 1963: 218

Figs 7, 25, 43, 61, 78

Type species. *Eulechriops pictus* Schaeffer, 1908 [by monotypy].

Gender. Masculine.

Diagnosis. *Cylindrocopturinus* can be differentiated from genera in the *Eulechriops* complex of genera by the tibial apex, which has a modified inner flange that resembles the premucro (Fig. 25), a rostral channel that is laterally carinate on the mesoventrite and not closed posteriorly by carina (Fig. 7), and no striolate profemoral patch (a similar mesoventrite has been seen in *Copturomorpha*, but members of this genus always have a striolate profemoral patch).

Notes. Sleeper's (1963) key to U.S. genera inexplicably contains two couplets that lead to *Cylindrocopturinus*: couplet 6a leads to genus "7. *Cylindricopturinus*, new genus" and couplet 8a leads to genus "7. *Cylindrocopturinus*, new genus". Couplet 6a is where *C. pictus* Schaeffer actually would key out to (in order to reach couplet 8a, couplet 4a would have to be selected, which states that the mesoventrite is not excavated, leading to couplet 8, where *Cylindrocopturinus* is differentiated from *Cylindrocopturus* for *having* such excavation). The use of the epithet in couplet 6a is the first appearance of the name and is spelled differently than the usage in the remainder of the text. Subsequent authors (Kissinger 1964, Hespenheide 1984, Anderson 1994) did not choose among the original spellings as a First Reviser (International Code of Zoological Nomenclature

article 24.2.3) but used the spelling "*Cylindrocopturinus*" in their work. *Cylindrocopturinus* is thus selected here as the correct original spelling, making "*Cylindricopturinus*" an unavailable name as an alternative original spelling.

Keys. R.S. Anderson 1994: 463.

Phylogenetic relationships. See "Phylogenetic relationship" section for *Coturpus.* Hespenheide (1984: 315) suggested a relationship of *Cylindrocopturinus* with *Zurus* (= *Copturus*), *Euzurus, Microzurus, Mnemyne* Pascoe, 1880, and *Paramnemyne*, citing the "...structure of the mesosternum and procoxae, the small size of the tarsal claws, and form of the antennae..." as indicative of a closer relationship to *Microzurus.* The genera *Cylindrocopturinus, Coturpus*, and *Turcopus* were proposed by R.S. Anderson (1994) to be related to *Eulechriops.* As interpreted here, those genera, plus *Macrolechriops* and *Copturomorpha*, compose a group of lechriopines, the majority of which contain a combination of the following characteristics: unarmed and non-carinate hind femora, a rostral channel defined laterally by carina, and a second antennal funicular article that is subequal to or shorter than the first.

Host associations. Species of *Cylindrocopturinus* have been collected on various species of *Phoradendron* on species of *Quercus*, *Acacia* Mill. (Fabaceae), *Juniperus* L. (Cupressaceae Gray), and *Ipomoea* L. (Convolvulaceae Juss.) (R.S. Anderson 1994).

Described species. Four (Hespenheide (1984) described one species, R.S. Anderson (1994) described two).

Range. U.S.A.: AZ, Mexico, Honduras.

Eulechriops Faust, 1896: 91

Fig. 79

= Zygomicrus Casey, 1897: 679 [Syn.: Champion, 1906b: 109 (with doubt); Blatchley and Leng 1916: 423]. Type species: *Eccoptus minutus* LeConte, 1824 [by monotypy].

Type species. *Eulechriops erythroleucus* Faust, 1896 [by subsequent designation: Sleeper 1963: 215].

Gender. Masculine.

Diagnosis. *Eulechriops* is a large and variable genus that can be identified from related genera by the following combination of characters: antennal funicular article 2 is not longer than 1; the mesoventrite has a carinate channel that can terminate on the meso- or metaventrite, but when closed on the mesoventrite it is not pronounced and sharply carinate (as in *Turcopus*); the femora are not carinate and are ventrally unarmed; the profemora lack a striolate patch (as in *Copturomorpha*); the pronotum lacks a strongly convex, arcuate pronotal carina (as in *Macrolechriops*), and the hind legs are not sexually dimorphic (as in *Cylindrocopturinus* and *Coturpus*).

Notes. The genus was erected by Faust (1896: 91, in footnote) to accommodate *Lechriops* that have unarmed, non-carinate femora; Marshall (1922: 70) notes the lack of interdependence of these two characters. The type species was not originally des-



Figures 79–82. Lateral and dorsal habitus images of Lechriopini. **79a–b** *Eulechriops minutus* [ASUHIC0024145] **80a–b** *Euzurus ornativentris* [ARTSYS0000800]. **81a–b** *Hoplocopturus varipes* [SSAC0001086] **82a–b** *Lechriops vestitus* [SSAC0001114]. Scale bars = 2 mm.

ignated by Faust and is given by Sleeper (1963) as the Venezuelan species *E. erythroleucus*, which was the first of three species described by Faust under his new genus – this was apparently overlooked in subsequent catalogs where the type species is listed as undesignated. *Eulechriops* is possibly the most diverse genus of Conoderine when considering the large number of undescribed species (Hespenheide 2007), as well as the most species genus of Conoderinae in the Caribbean region with sixteen species described by Hustache (1932a) from Guadeloupe.

Keys. Champion 1906b: 110 (for Central America), Hustache 1931: 285 (for Guadeloupe), Hespenheide 2003: 95 (for two U.S. species).

Phylogenetic relationships. The genus is likely related to the genera *Copturomorpha*, *Macrolechriops*, *Cylindrocopturinus*, *Turcopus*, and *Coturpus*, most of which have a combination of the following characters: unarmed, non-carinate metafemora, a funicular article 2 that is not longer than article 1, and the rostral channel of the mesoventrite with relatively parallel longitudinal carinae. The species recognized as *Eulechriops* are unlikely to represent a monophyletic group (Hespenheide 2005b) and the species currently recognized in the genus can only be identified to *Eulechriops* by not having the distinguishing characters of the aforementioned related (and smaller) genera.

Host associations. Mostly unknown. Two of the three U.S. species and related Mexican species (of the *E. minutus* species group of Hespenheide 2003) are associated with *Quercus* (Sleeper 1963, Hespenheide 2003). Several undetermined Central American species have been reared from *Cecropia, Coussapoa* Aubl. and *Pourouma* Aubl. (Urticaceae) (Jordal and Kirkendall 1998: 159, LaPierre 2002). Some South American species have been reared from *Rubus* L. (Rosaceae Juss.) (Hespenheide 2005), *Manihot* Mill. (Euphorbiaceae Juss.) (Monte 1938) and *Gossypium* L. (Malvaceae) (Barber 1926).

Described species. Fifty-seven species are known from the focal region (with one described by Hespenheide 2007 and one fossil species described by Poinar and Legalov 2013) and an additional 31 species are known from South America (Wibmer and O'Brien 1986: 264, with one more described by Hespenheide 2005b).

Range. U.S.A., Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Dominican Republic (Poinar and Legalov 2013, fossil), Guadeloupe; South America.

Euzurus Champion, 1906b: 45

Figs 8, 65, 80

Type species. Euzurus ornativentris Champion, 1906 [by original designation].

Gender. Masculine.

Diagnosis. The single species of *Euzurus* can be identified by the posteriorly produced lobe of the pronotum concealing the scutellum from above, the distinctly structured mesoventrite (Fig. 8) which has lamellae extending anteriorly from the posterior modification, and the large tubercle on the metaventrite anterior to the anteroventral border of the metacoxa (Fig. 65). The second antennal funicular article is longer than the first, the eyes are vertical and separated, the metafemur is laterally bicarinate and ventrally toothed, and the tibial uncus is short and curved. **Phylogenetic relationships.** With the genera *Copturus* and *Microzurus*, *Euzurus* shares a concealed scutellum (but see "Phylogenetic relationships" section for *Copturus*), Type II sclerolepidia (Lyal et al. 2006: 229), and modification to the mesoventrite that does not have anteriorly extending carinae. The separated, vertical eyes are similar to some species of *Cylindrocopturus* and *Poecilogaster* (Figs 46, 49). Champion (1906b: 46) mentions a similar appearance to *Macrocopturus* (*Eucopturus*) Heller.

Host associations. Unknown. Described species. One. Range. Costa Rica, Panama.

Hoplocopturus Heller, 1895: 50

Figs 9, 55, 63, 81

Type species. *Copturus armatus* Gyllenhal, 1838 [by original designation]. Gender. Masculine.

Diagnosis. As originally distinguished from the rest of the New World conoderines by Heller (1895) in his key to genera, Hoplocopturus, Mnemynurus, and the South American Balaninurus Heller, 1895 have an arcuate carina on the mesoventrite. This character separates Hoplocopturus and Mnemynurus from the Central American lechriopine genera that have an elongate second funicular article, carinate and ventrally toothed femora and modification to the mesoventrite, especially the often very similar looking species of Lechriops and Macrocopturus. From Mnemynurus caloderes Heller, 1895 (the only species of *Mnemynurus* at the time), Heller (1895) differentiated *Hoplocopturus* by the length of the rostrum and the corresponding rostral channel - in his key, Hoplocopturus species have a rostrum that does not extend beyong the mesocoxae, while Mnemynurus caloderes has a rostrum channel and rostrum that extends to the first abdominal ventrite. Champion (1906b) added several species to each genus, mentioning that "Hoplocopturus is connected to Mnemynurus by intermediate forms, and it can only be separated therefrom by the shorter rostrum" (Champion 1906b: 53). Most species of Mnemynurus described by Champion (except M. longispinis Champion, 1906) have a rostrum that extends at least to the posterior margin of the metaventrite, and species of Hoplocopturus (except H. javeti Champion, 1906 and H. nigripes Champion, 1906) have a shorter rostrum. Those species of Hoplocopturus with a rostrum that reaches near the middle of the metaventrite are additionally difficult to separate from *Mnemynurus* because they have a similar coloration to all described Mnemynurus (the "red-eyed fly" mimicry complex) and the region of the mesoventrite posterior to the arcuate carina is invaginated under the carina (not simply a semicircular depression as in other Hoplocop*turus*). Despite these exceptions, the following characters can be used to separate many of the species of *Hoplocopturus* from *Mnemynurus*: rostrum shorter (never reaching the posterior margin of the metaventrite) and the rostral apex cylindrical (apically flattened and dilated in *Mnemynurus*). The hind femora of both genera can be carinate or not and the femoral apex typically has an elongate spine at the mesal face.

Notes. Some species (e.g. *H. varipes* Champion, 1906) have a mesoventrite densely covered in scales and the distinguishing carina is difficult to see. Most species of *Hoplocopturus* are not clear members of a mimicry complex with the exception of a few species belonging to the "blue-thorax" complex and two described and several undescribed belonging to the "red-headed" fly-mimicking complex (Hespenheide 2005), but all described (and almost all observed undescribed) species of *Mnemynurus* belong to the "red-headed fly" complex. The species that have the "red-headed fly" coloration pattern are the most difficult to separate from *Mnemynurus*.

Keys. Champion 1906: 53 (for Central America).

Phylogenetic relationships. *Hoplocopturus* is very similar to *Mnemynurus* and *Bal-aninurus*, sharing with those genera the arcuate carina on the mesoventrite. Some species are very similar looking to certain *Lechriops* and *Macrocopturus* (e.g. *H. sherrywernerorum* Hespenheide, 2009 and *H. costatipennis* Champion, 1906, respectively), but the structure of the mesoventrite easily separates the species of *Hoplocopturus* from those genera.

Host associations. Some *Hoplocopturus* (e.g. *H. varipes* Champion, 1906) can be found on the upper and lower surface of the large leaves of *Xanthosoma* Schott (Araceae Juss.) [SSAC0001086], a plant family association with Araceae has also been made in *Mnemynurus* (see below). One species has been collected on treefalls of *Sterculia* L. (Malvaceae: Sterculioideae Burnett) [STRI_ENT_0082473, SSAC0001292].

Described species. Eighteen species are known from the focal region (with one more described by Hespenheide 2009) and an additional 12 species are known only in South America (Wibmer and O'Brien 1986: 270).

Range. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama; South America.

Lechriops Schoenherr, 1825: c.586

Figs 10, 19, 82

= Gelus Casey, 1897: 667 [Syn.: Champion, 1906: 91]. Type species: Cryptorhynchus oculatus Say, 1824 [by subsequent designation: Sleeper 1963: 210].

Type species. *Rhynchaenus sciurus* Fabricius, 1801 [by original designation].

Gender. Masculine.

Diagnosis. Most species of *Lechriops* can be distinguished by the following combination of characters: the second antennal funicular article is longer than the first, the mesoventrite has a rostral channel that is bordered laterally by carinae, and the metafemora are carinate and ventrally toothed (Champion 1906b: 91). The anterior margin of the metaventrite is also usually excavated to receive the apex of the rostrum (Fig. 10; Champion 1906b: 91, Hespenheide 2009: 334), and the region of the mesoventrite lateral to the longitudinal carinae is often with dense multifid setae.

Notes. Many species have a white elytral sutural spot (as in Fig. 82b), but this is not exclusive to *Lechriops* (see Hespenheide 2009).

Keys. See Hespenheide 2003: 351 (for the seven U.S. species) and Champion 1906b: 91 (for Central America). Also Sleeper 1963: 210 (for U.S. species), Blatchley and Leng 1916: 418 (for Northeastern U.S. species, as *Gelus*) and LeConte and Horn 1876: 260 (for U.S. species, as *Piazurus*).

Phylogenetic relationships. Some species look superficially very similar to species of *Eulechriops, Macrocopturus*, and *Hoplocopturus*, but the above combination of characters will separate most species. Champion (1906b: 91) considered *Lechriops* to be very close to *Macrocopturus* and in both genera he described species similar to the other genus (*L. copturoides* Champion, 1906 and *Macrocopturus furfuraceus* (Champion, 1906), the latter of which "forms a sort of connecting-link between *Copturus* [*=Macrocopturus*] and *Lechriops*" (Champion 1906b: 69)).

Host associations. Some species in the U.S. and Mexico (the *L. californicus* species group of Hespenheide 2003) are associated with various species of conifers in the genera *Pinus* L. and *Pseudotsuga* Carrière (Pinaceae Spreng. ex Rudolphi). Some Central American species have been reared from petioles and stems of *Cecropia* and *Coussapoa* (Urticaceae) (Jordal and Kirkendall 1998: 159, LaPierre 2002). The Puerto Rican *Lechriops psidii* Marshall, 1922 is known to feed on guava fruits (Myrtaceae: *Psidium guajava* L.) (Marshall 1922: 70), but the placement of that species in *Lechriops* is suspect (though no specimens have been observed) due to the unmodified mesoventrite and lack of a femoral tooth.

Described species. Forty-nine species are known from the focal region [including two more described by Hespenheide 2003] and an additional 42 species are known exclusively from South America (Wibmer and O'Brien 1986: 263, including four more described by Rheinheimer 2011].

Range. Canada, U.S.A., Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Puerto Rico, Guadeloupe; South America. A new species of *Lechriops* was recently described from India (Khairmode and Sathe 2015), though the position of the species in this genus or in the tribe Lechriopini is doubtful.

Macrocopturus Heller, 1895: 19

Figs 44, 83

- (*Macrocopturus*) Heller, 1895: 19 [as subgenus of *Copturus*]. Type species: Not yet designated.
- (Cyphocopturus) Heller, 1895: 19 [as subgenus of Copturus]. Type species: Not yet designated.
- (Eucopturus) Heller, 1895: 20 [as subgenus of Copturus]. Type species: Not yet designated.

(Lamellocopturus) Heller, 1895: 19 [as subgenus of Copturus]. Type species: Not yet designated.

Type species. *Copturus satyrus* Gyllenhal, 1838 [by subsequent designation: Wibmer and O'Brien 1986: 20].



Figures 83–86. Lateral and dorsal habitus images of Lechriopini. **83a–b** Macrocopturus lynceus [SSAC0001085] **84a–b** Macrolechriops spinicoxis [ARTSYS0000529]. **85a–b** Microzurus championi [ASUHIC0031507] **86a–b** Microzygops nigrofasciatus [ARTSYS0000802]. Scale bars = 2 mm.

Gender. Masculine.

Diagnosis. Most of the specimens of this very large and variable genus can be identified by the combination of a second funicular article that is longer than the first, an unmodified

mesoventrite, a carinate and ventrally toothed hind femur, and the absence of a profemoral striolate patch. A few Central American species (and several more in South America – Heller's subgenera *Lamellocopturus* and *Cyphocopturus*) have modification to the mesoventrite similar to *Microzygops* (e.g. *Macrocopturus albidus* (Champion, 1906)) but Champion did not assign them to one of Heller's subgenera. Some smaller species can be difficult to distinguish from *Lechriops* but species of that genus in general tend to have a less spherical head (somewhat obliquely flattened above the rostral base) with comparatively smaller, more strongly acuminate eyes in addition to the modification to the mesoventrite.

Notes. All species included in this genus were treated as *Copturus* until Wibmer and O'Brien (1986: 17), see "Notes" section for *Copturus* above for a clarification of name use. Heller (1895) divided the genus *Copturus* into six subgenera or species groups (including *Macrocopturus*), reiterating Pascoe's (1880: 494) comment on his own struggle with adequately constructing a subgeneric classification for this genus: "*Copturus* illustrates the difficulty of defining a large genus. Every character is liable to exception, not one appearing to have a generic value, although there is a common interresemblance which is not to be mistaken; the group, in fact, is a natural one, but which perhaps might, for the advantage of the systematist, be artificially divided into several genera." Heller noted the probable superficiality of his subgenera.

Macrocopturus is the most widespread genus in the Caribbean, being the only genus of Conoderinae recorded from the Bahamas and Jamaica. Four different putative mimicry complexes are present in *Macrocopturus* as presently defined (Hespenheide 1995). Immature stages are described for *Macrocopturus aguacatae* (Kissinger, 1957) by Muñiz Vélez (1958) and *M. burserophagus* Muñiz-Vélez & Ordóñez-Reséndiz, 2010 by Muñiz-Vélez and Ordóñez-Reséndiz (2010).

Phylogenetic relationships. Some of the described species are very similar in appearance to the following genera: *Cylindrocopturus* (e.g. the Mexican *M. burserophagus* which is placed in *Macrocopturus* because of the presence of a ventral femoral tooth), *Copturomimus* (which have a striolate region on the profemora), *Lechriops, Hoplocopturus*, and the South American genera *Damurus* Heller, 1895 (Champion 1906b: 69, in footnote) and *Copturosomus* (Champion 1906b: 69). Of those genera, *Copturomimus*, *Lechriops*, and *Hoplocopturus* are considered related in this paper, and *Cylindrocopturus*, which is currently in the Zygopini, is also probably a related lechriopine. The few observed specimens of South American *Copturosomus* are very similar to *Macrocopturus* and the genus *Damurus* was not observed in the course of this study, but was considered by Heller (1895: 55) to be related to *Timorus* (also currently in the Zygopini) which Champion (1906: 33) in turn considered related to *Macrocopturus*.

Keys. Champion 1906b: 69 (for Central America) and Heller 1895: 19 (for Central and South America).

Host associations. *Macrocopturus floridanus* (Fall, 1906), known as "the mahogany notcher" (Morton 1987: 191) is wood-boring as a larva and as an adult feeds on foliage of mahogany (Meliaceae Juss.: *Swietenia mahogany* (L.) Jacq.) (Morton 1987). Other species are known from avocado (Lauraceae: *Persea*) (Kissinger 1957: 7, Muniz V. 1965), *Bursera citronella* McVaugh & Rzed. (Burseraceae Kunth) (Muniz-Vélez and Ordóñez-Reséndiz 2010), and *Cecropia*, *Coussapoa*, and *Pourouma* (Urticaceae) (LaPierre 2002).

Described species. Fifty-six species are known from the focal region, including one described by Hespenheide (1984), three by Zayas (1988), one by Muñiz-Vélez and Ordóñez-Reséndiz 2010, and one by Hespenheide (2017), and one species transferred from *Archocopturus* by Hespenheide (2005). An additional 101 species are known from South America (Wibmer and O'Brien 1986: 272, with two additional species described by Rheinheimer (2011)).

Range. USA: FL, Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Bahamas, Cuba (Zayas 1988), Jamaica, Puerto Rico, Guadeloupe (Hespenheide 1984); South America.

Macrolechriops Champion, 1906b: 126

Fig. 84

= Parazurus Hustache, 1937: 108 [Syn.: Rheinheimer 2011: 77]. Type species: Parazurus nodieri Hustache, 1937 [by original designation].

Type species. Macrolechriops spinicoxis Champion, 1906 [by monotypy].

Gender. Masculine.

Diagnosis. *Macrolechriops* belongs in the *Eulechriops* complex of genera with its short second funicular article, non-carinate and unarmed hind femora, and carinate and excavated mesoventrite, but can be distinguished (at least the Central American species) by the hump-like pronotal carina.

Notes. Champion reported the presence of a "...flattened, conical prominence on the intermediate, as well as on the anterior, coxae..." (1906b: 127) as being unique among the conoderines he examined. This character, however, has been observed in other species and genera, including some *Eulechriops*, reducing the diagnostic utility of that character among the putative relatives of *Macrolechriops*.

The specimen in Fig. 84 agrees with Champion's description, which was based on "one worn specimen" (Champion 1906b: 127), but direct comparison of the specimen with the holotype is needed to confirm the identity as no other identified material of that species has been observed in the course of this study.

The South American species of *Macrolechriops* described by Hustache have a pronotum that is strongly convex but without a hump-like carina. This hump-like pronotal carina is known from other genera, such as *Macrocopturus verrucosus* (Champion, 1906), but none described or so far known in the genus *Eulechriops* or genera closely related to it, making it a useful character for separating the only currently known Central American species of *Macrolechriops* from its relatives. A very similar vestiture pattern and pronotal shape has been observed in other genera, most notably in a species of *Copturomimus* which has been seen in several collections incorrectly identified as *Macrolechriops spinicoxis*. **Phylogenetic relationships.** Champion (1906b: 126) notes the similarity with the South American *Machaerocnemis* Heller, 1895 and *Copturosomus*, but the genus is here considered part of the *Eulechriops* genus complex.

Host associations. Unknown.

Described species. One species is known from the focal region and five additional species are known from South America (Wibmer and O'Brien 1986: 266, Rheinheimer 2011).

Range. Mexico, Honduras [ARTSYS0000529]; South America.

Microzurus Heller, 1895: 13

Figs 58, 85

Type species. *Microzurus rhombus* Heller, 1895 [by monotypy].

Gender. Masculine.

Diagnosis. *Microzurus* can be differentiated from *Copturus* by the lack of a ventral tooth on the profemora, a thin fifth tarsomere with minute tarsal claws (Fig. 58), and costate elytral intervals. Champion (1906: 89) described two species that have shallow or absent modification to the mesoventrite – no material was observed of the species without modification (*M. edentatus* Champion, 1906), but the species would still be easily recognized as a *Microzurus* by the concealed scutellum, minute tarsal claws, and absent ventral tooth on the pro- and mesofemora. The second funicular article is not longer than the first and the hind femora are carinate and ventrally toothed. The observed species have a similarly apically laterally flanged receptacle of the mesoventrite as in *Copturus*, though it is usually much less prominent.

Phylogenetic relationships. Hespenheide (1984) suggested a relationship between *Microzurus* and *Cylindrocopturinus*. *Microzurus* is here interpreted as closely related to *Copturus*, but the position of those two genera within the lechriopines is uncertain. See entry on *Copturus*.

Host associations. Hespenheide (1984: 316) reported the possibility of seed-feeding based on label data. Costa-Lima (1956: 219) mentions South American species on fruits of *Campomanesia* Ruiz & Pav. and *Psidium guajava* (Myrtaceae).

Described species. Three species are known from the focal region and an additional four species are known from South America (Wibmer and O'Brien 1986: 266).

Range. Mexico, Belize, El Salvador, Honduras, Panama; South America.

Microzygops Champion, 1906b: 46

Figs 11, 45, 86

Type species. *Microzygops nigrofasciatus* Champion, 1906 [by original designation]. Gender. Masculine.

Diagnosis. *Microzygops* can be distinguished from other lechriopine genera with an elongate second funicular article and modification to the mesoventrite by the fol-

lowing characters: the shape of the eyes, which are very large and contiguous in bottom 2/3 and widely separated in top 1/3 (Fig. 45), the distinct form of the mesoventrite (Fig. 11) which is similar only to the few species of *Macrocopturus* that have modification to the mesoventrite with an elevated posterior margin of the mesoventrite and faint, arcuate longitudinal carinae (as well as a deeply excavated anterior margin of the metaventrite), and the color pattern, which is putatively ant mimetic (Hespenheide 1995) but distinct from the other ant mimics with orange-brown ground color and transverse black fascia of the pronotum and elytra.

The metafemora are very elongate, extending well past the abdominal apex and lacking carina. The pro- and mesofemora are ventrally toothed, but the metafemur is unarmed in *Microzygops nigrofasciatus* though with a small tooth in the South American *M. flavatus* Rheinheimer, 2011 and one undescribed Central American species [SSAC0001210]. Other generic characters given by Champion (1906b: 46) include the "exserted head" and "cylindrical constricted prothorax".

Notes. The species *M. nigrofasciatus* like the species of several other genera originally described as monotypic, is possibly a complex of several species – specimens identified to that species have been observed from Mexico to Peru and at a range of elevations.

Phylogenetic relationships. The exserted head, elongate and slender hind legs, proportionately short and narrow third tarsomere, and linear carina of the vertex of the head, in combination, is only similar to *Pseudolechriops* and, to a lesser extent (excluding the head characters) *Lissoderes*, but the mesoventrite is distinct in each of those genera. *Microzygops* was among the genera moved from the Zygopini to the Lechriopini in Lyal et al. (2006), but the position of the genus within the Lechriopini is at present uncertain.

Host associations. Unknown.

Described species. One species is known from the focal region and one additional species is known from French Guiana (Rheinheimer 2011: 68).

Range. Mexico [ASUHIC0031512], Costa Rica [ASUHIC0086639], Panama; South America.

Mnemynurus Heller, 1895: 54

Fig. 87

Type species. Mnemynurus caloderes Heller, 1895 [by monotypy].

Gender. Masculine.

Diagnosis. All of the described and most of the observed undescribed species of *Mnemynurus* are members of the red-headed fly mimicry complex (Hespenheide 1973, 1995), and are most difficult to distinguish from the similarly patterned species of *Hoplocopturus* and the South American *Balaninurus* which also share the distinctive inverted U-shaped carina on the mesoventrite. See "Diagnosis" for *Hoplocopturus* above for more information on the separation of the genera. The second funicular article is much longer than the first, the apex of rostrum is flattened and dilated, the hind



Figures 87–90. Lateral and dorsal habitus images of Lechriopini. **87a–b** *Mnemynurus poeciloderes* [ARTSYS0000803] **88a–b** *Paramnemyne decemcostata* [ASUHIC0065104] **89a–b** *Poecilogaster brevis* [ASUHIC0086631] **90a–b** *Pseudolechriops megacephalus* [ASUHIC0086629]. Scale bars = 2 mm.

femora are ventrally toothed and sometimes carinate, and the rostrum usually extends past the posterior border of metaventrite (though not in *M. longispinis*) and sometimes beyond the apex of the abdomen.

Notes. *Mnemynurus, Paramnemyne*, and the South American genus *Mnemyne* are the only New World genera having a rostral channel extending at least to the posterior half of the metaventrite. A distinct channel is found only in the larger *Mnemynurus* species and the metaventrites of other species are longitudinally depressed. Zayas (1988) described two species from Cuba, although based on the descriptions their placement in this genus is uncertain.

Keys. Champion 1906b: 49 (for Central America; *M. caloderes* in key = *M. championi* Heller, 1933 (Heller 1933: 150)), Heller 1932a: 5 (only to the three species described by Heller).

Phylogenetic relationships. Most similar to the South American genus *Balaninurus* Heller, but generic limits between these two genera and *Hoplocopturus* need resolving – see *Hoplocopturus* above.

Host associations. Species of *Mnemynurus* have been recorded as gall-inducing on young leaves of *Philodendron* Schott (Araceae) (Hanson et al. 2014: 503).

Described species. Nine species are known from the focal region including two described by Zayas (1988) and two additional species are known from South America (Wibmer and O'Brien 1986: 270).

Range. Mexico, Honduras, Nicaragua, Costa Rica, Panama, Cuba [Zayas 1988]; South America.

Paramnemyne Heller, 1895: 10

Figs 12, 88

Type species. *Paramnemyne arcana* Heller, 1895 [by subsequent designation: Rheinheimer 2011: 78].

Gender. Feminine.

Diagnosis. *Paramnemyne* can be readily distinguished by the transverse carina near the posterior margin of the metaventrite, marking the end of the rostral channel (Fig. 12). The second antennal funicular article is several times longer than the first; the femora are not carinate, are ventrally toothed, and are unarmed at the apices; the mesopleura are small and non-ascending; and the eyes are completely separated with the greatest separation in the middle.

Phylogenetic relationships. The unarmed femoral apices, small and non-ascending mesopleura, and piazurine type of mesoventrite suggest improper placement in the Lechriopini, however transferring the genus without observing the putative relatives of *Paramnemyne*, the South American genera *Mnemyne* (*sec.* Heller 1895: 11) and *Paramnemynellus* Hustache, 1932 (*sec.* Hustache 1932b: 207), would be remiss.

Host associations. Unknown.

Described species. Two species are known from the focal region and three additional species are known only from South America (Wibmer and O'Brien 1986: 270).

Range. Mexico, Guatemala, Costa Rica [O'Brien and Wibmer 1984: 296], Panama; South America.

Poecilogaster Heller, 1895: 16

Figs 46, 89

Type species. *Poecilogaster longior* Heller, 1895 [by subsequent designation: Alonso-Zarazaga and Lyal 1999: 115] (=*Copturus brevis* Waterhouse, 1879).

Gender. Feminine.

Diagnosis. *Poecilogaster* has the general appearance of a large *Lechriops* that lacks a femoral carina. The rostral channel extends to the anteriorly depressed metaventrite and is laterally carinate on the mesoventrite, the second antennal funicular article is slightly longer than the first, the metafemora are not carinate and toothed ventrally, and the mesal face of femoral apex usually bears a long spine. Champion (1906: 44) notes a large tubercle on the prosternum behind the procoxae, which is not unique to *Poecilogaster* and known in other genera (e.g. some *Copturomorpha*).

Phylogenetic relationships. While easily recognized by general appearance it is difficult to place within the Lechriopini. The longer second funicular article, ventrally toothed femora, and long spine at the mesal face of the femoral apices are suggestive of a relationship with *Lechriops* and *Hoplocopturus* while the non-carinate femora and deeply excavated mesoventrite is similar to *Eulechriops*. Heller (1895: 16) suggests a relationship with *Lechriops* and also speculates a potential relationship with the South American genera *Hemigaster* Lacordaire, 1865 (= *Hemicolpus* Heller, 1895) and *Acopturus* Heller, 1895 based on the shape of the second abdominal ventrite. Neither of those latter genera have been observed in the course of this study but both are currently placed in the Zygopini.

Host associations. Unknown.

Described species. Two, including one described by Zayas (1988). **Range.** Costa Rica, Panama, Cuba (Zayas 1988); South America.

Pseudolechriops Champion, 1906b: 90

Figs 13, 26, 90

Type species. *Pseudolechriops megacephalus* Champion, 1906 [by original designation]. Gender. Masculine.

Diagnosis. *Pseudolechriops* is rather distinctive in appearance yet difficult to satisfactorily characterize as a genus, with variation across the species in the following characters: the insertion of the antenna on the rostrum can be in the basal (e.g. in *P. megacephalus* Champion, 1906) or apical half (e.g. *P. klopferi* Hespenheide & LaPierre, 2006), the second funicular article can be longer than (e.g. in *P. megacephalus*) or subequal to the length of the first article (e.g. *P. coleyae* Hespenheide & LaPierre, 2006), the eyes can be vertical and relatively widely separated (e.g. in *P. megacephalus*) or larger and subcontiguous (e.g. in *P. klopferi*), the inner flange of the tibial apex can be flat (with no projection) to bearing an elongate, uncus-like process (Fig. 26), and hind femora that can be completely carinate and ventrally toothed (e.g. *P. megacephalus*), or partially carinate basally and without a tooth (e.g. *P. coleyae*). Despite this variation, the modification to the mesoventrite is unique, with the rostral channel being a deep, ovoid, receptacle (Fig. 13) for receiving the rostrum on the mesoventrite and anterior margin of metaventrite. Additionally, the procoxae lack a mesal process, which is found in many other lechriopines.

Notes. Hespenheide and LaPierre (2006) distinguish two distinct species groups. The species are possibly mimics of ants in the genus *Azteca* Forel, 1878 (Hespenheide and LaPierre 2006: 37).

Phylogenetic relationships. Champion (1906: 90) and Lyal et al. (2006: 229) noted similarities with the South American genus *Tachylechriops* Heller, 1895 and *Lechriops*; Hespenheide and LaPierre (2006: 3) disagree but do not present an alternative hypothesis. The mesoventrite of *Pseudolechriops* is most similar to that of *Lechriops* in shape although the sides of the channel in *Pseudolechriops* are much more ventrally prominent and the median channel deeper. The exserted head, elongate hind femora, and vertex of head with a linear carina are similar to *Microzygops*.

Host associations. Adults can be found on the undersides of leaves of several species of *Cecropia* (Urticaceae), and the larvae develop in living or dead leaf petioles (Jordal and Kirkendall 1998, LaPierre 2002, Hespenheide and LaPierre 2006).

Described species. Ten, including nine described by Hespenheide and LaPierre (2006).

Range. Mexico [Hespenheide and LaPierre 2006], Guatemala, Belize, Honduras [Hespenheide and LaPierre 2006], Nicaragua [Hespenheide and LaPierre 2006], Costa Rica [Hespenheide and LaPierre 2006], Panama; South America [Hespenheide and LaPierre 2006].

Psomus Casey, 1892: 458

Fig. 91

Type species. *Psomus politus* Casey, 1892 [by monotypy] (=*Orchestes armatus* Dietz, 1891). Gender. Masculine.

Diagnosis. The combination of concealed pygidium, appendiculate tarsal claws, and sulcate subapical pronotal constriction readily distinguishes *Psomus* from the other genera treated here. *Philides* is the only other genus without simple tarsal claws and *Peltophorus* and *Zygops* have a sulcate subapical pronotal constriction, but each of those three genera have an exposed pygidium (which *Psomus* does not) and are otherwise distinct in habitus. *Psomus* is unique among the lechriopine genera for having a flattened mesoventrite and Type II sclerolepidia (Type II sclerolepidia also known from *Copturus*, *Microzurus*, and *Euzurus*, though each has a modified mesoventrite) although this combination is also found in *Lissoderes*, which is currently a zygopine (Lyal et al. 2006: 229); neither of those genera seem very well placed in their current tribes.

Some observed species have a ventrally expanded first abdominal ventrite and modifications to the profemora and tibiae that are similar to what is found in some



Figures 91–94. Lateral and dorsal habitus images of Lechriopini and Zygopini. All scale bars = 1 mm unless otherwise specified. **91a–b** *Psomus armatus* [ARTSYS0000533] **92a–b** *Turcopus viscivorus* [ART-SYS000530]; scale bar = 2 mm **93a–b** *Arachnomorpha circumlineata* [ARTSYS0000535] **94a–b** *Archocopturus laselvaensis* [ASUHIC0086633].

Cleogonini (Prena and Whitehead 2012: 57). These differences were not mentioned by Champion when describing three Central American species, but he considered his species as "perfectly congeneric with *P. politus*, Casey [=*P. armatus* (Dietz)]" (Champion 1906b: 128). In addition to the characters given above distinguishing the genus, the species of *Psomus* have a second funicular article that is about equal to the first and a tibial apex with an uncus at the posterior apical angle or the middle of the apex.

Phylogenetic relationships. The appendiculate tarsal claws (shared only with *Philides*) and a deep subapical pronotal constriction (shared only with *Zygops* and *Peltophorus*) are easily observed characters but not particularly suggestive of a relationship. The single U.S. species, *P. armatus* (Dietz, 1891) was originally described in the genus *Orchestes* Illiger, 1798 (Curculioninae: Rhamphini). *Psomus* bears a resemblance to the cleogonine *Isotrachelus* (which was previously placed in the Old World conoderine tribe Lobotrachelini Lacordaire, 1865), but differs from *Isotrachelus* by the insertion of the antenna on the rostrum, which in *Psomus* is in the basal half of the rostrum, and the tarsal claws, which in *Isotrachelus* are simple.

Host associations. *Psomus armatus* can be found on ash trees (Oleaceae Hoffmanns. & Link: *Fraxinus* L.) (Sleeper 1963). Hosts of the Central American species are unknown.

Described species. Four.

Range. Eastern Canada and U.S.A., Guatemala, Panama.

Turcopus R.S. Anderson, 1994: 475

Figs 14, 92

Type species. *Turcopus viscivorus* R.S. Anderson, 1994 [original designation]. Gender. Masculine.

Diagnosis. R.S. Anderson (1994: 463) separates *Turcopus* from *Coturpus*, *Cylin-drocopturinus*, and *Eulechriops minutus* (LeConte, 1824) by the deep, prominently carinate, cup-like receptacle on the mesoventrite (Fig. 14); this has not been seen in the numerous observed specimens of *Eulechriops*, representing mostly undescribed species, but is difficult to generalize the mesoventrite for all species of such a variable genus. *Turcopus* is otherwise difficult to distinguish from *Eulechriops* except by the vestiture pattern (Fig. 92) and host association, which are currently unknown in *Eulechriops*. *Turcopus* can be further separated from *Coturpus* by genitalic characters given by R.S. Anderson (1994: 477).

Phylogenetic relationships. R.S. Anderson (1994: 477) proposed a relationship with the sister taxa of *Coturpus* + *Cylindrocopturinus* (those three taxa are the proposed sister to *Eulechriops*). The difficulty of separation with *Eulechriops* suggests a closer relationship with that genus but much work needs to be done in delimiting generic boundaries in this complex of genera.

Host associations. *Turcopus* has been collected on *Phoradendron* on *Quercus* (R.S. Anderson 1994: 479).

Described species. One (R.S. Anderson 1994). **Range.** Mexico, Guatemala.

Zygopini Lacordaire, 1865: 150

Classificatory history and current circumscription. This tribe was originally characterized by Lacordaire (1865: 150) for the genera *Zygops, Peltophorus, Copturus, Timorus* and *Hemigaster* (=*Hemicolpus*) by a more-or-less canaliculate prosternum, a flat, unmodified mesoventrite, and straight, carinate hind femora that can exceed the apex of the abdomen. Presently, the genera placed in Zygopini lack sclerolepidia (except for *Arachnomorpha, Lissoderes,* and some species of *Philenis*) and lack modification to the mesoventrite (except *Peltophorus* and most species of *Philenis*). Davis and Engel (2006) also suggested the "strongly protuberant compound eyes, deeply depressed pronotal lateral-facing surfaces, and relatively large genae", but these features are also shared with several lechriopine genera.

As indicated previously, of the genera currently placed in the Zygopini from the focal region, *Zygops* and *Peltophorus* are quite distinct from the rest with a large, exposed pygidium that is at least mostly visible in dorsal view and abdominal ventrites that do not ascend rapidly, a fifth abdominal ventrite that is arcuate in lateral profile (deflected apically downwards by the large pygidium). Additionally, most observed specimens of these genera have a quadrate to transversely rectangular scutellum (visible in Fig. 102b). The Dominican and Mexican amber fossil genus *Geratozygops* appears to belong to this group of "true zygopines", and as best could be determined from the images provided by Davis and Engel (2006) and Poinar and Legalov (2013) the species would key out to *Zygops* in the above key. *Latychus*, the South American piazurine proposed by Prena et al. (2014: 300) to be the identity of *Geratozygops*, would run to couplets 7-10, which treats the Piazurini.

The genera besides *Zygops* and *Peltophorus* can be identified by having the following combination of characters: a concealed pygidium, strongly ascending abdominal ventrites, and a second funicular article that is subequal to or shorter than article 1 (except *Philenis* and some *Cylindrocopturus*).

Variation in key character systems. The mesoventrite of most genera and species is unmodified, with exceptions being found in *Peltophorus* (which has the mesoventrite ventrally produced and nearly cup-like, Fig. 16), a few species of *Zygops* (with the posterolateral margins tumescent or with small processes), most species of *Philenis* (with a posteromedial semicircular depression and posterolateral tubercles, Fig. 17), and a few other species with slight posteromedial depressions (e.g. *Archocopturus championi* Hespenheide, 2005). The general form of the tibial apex varies little from the typical conoderine form apart from having a very short and curved uncus (in *Helleriella* Champion, 1906 and *Peltophorus*, Figs 30 and 33, respectively), a minute premucro (in *Lissoderes* and
Arachnomorpha, Figs 27 and 31, respectively), and a premucro oriented at a 45° angle to the longitudinal axis of the tibia (in *Phileas* Champion, 1906 and *Philenis*, Figs 32 and 35, respectively).

Diversity and distribution. Eighty-three species are currently known from the 11 genera occuring north of South America. An additional 8 genera occur exclusively in South America and two more are also recorded from Africa.

Arachnomorpha Champion, 1906b: 47

Figs 27, 47, 93

Type species. *Arachnomorpha circumlineata* Champion, 1906 [by original designation]. **Gender.** Feminine.

Diagnosis. Arachnomorpha can be distinguished from the zygopine genera with a flattened mesoventrite, concealed pygidium and short second funicular article by the broad interocular space between the top of the eyes (Fig. 47), with the eyes closer together below the space than above, the costate elytral intervals, the carinate and ventrally unarmed hind femora and minute premucro (Fig. 27). Additionally, Arachnomorpha circumlineata is part of a "shiny-black" ant-mimicry complex (Hespenheide 1995), with the cuticle in large part glabrous and black with patches or stripes of white or opalescent scales. This mimicry complex, among the New World Conoderinae, is so far known only in Arachnomorpha, Microzurus, Lissoderes and Philides. The observed undescribed Microzurus species [SSAC0001290] also has sharply costate elytral intervals but can be easily distinguished from Arachnomorpha by the concealed scutellum and modified mesoventrite.

Phylogenetic relationships. Champion (1906b: 47) posits a relationship with the South American *Mnemyne* and Hespenheide (1987: 42) notes the similarity with *Lisso-deres*. Of the zygopine genera with a concealed pygidium and a short second funicular article, only *Arachnomorpha* and *Lissoderes* have sclerolepidia, although apparently of a different type (Lyal et al. 2006: 229). *Arachnomorpha* and *Lissoderes* additionally have a minute premucro of the tibial apex, but differently shaped eyes, antennal insertion on different parts of the rostrum (basal third in *Arachnomorpha*), and a different body shape. The genera of Zygopini that have a concealed pygidium and a second funicular article that is not longer than the first (*Arachnomorpha*, *Archocopturus* Heller, 1895, most *Cylindrocopturus*, *Helleriella*, *Larides* Champion, 1906, *Lissoderes*, *Phileas*, and *Zygopsella* Champion, 1906), with the exception of *Cylindrocopturus*, are all small genera (five described species or less) that are very distinct in body shape and/or coloration likely owing to their participation in different mimicry complexes, and are otherwise are also shared with *Archocopturus* and *Zygopsella*.

Host associations. Unknown. Described species. One. Range. Costa Rica, Panama.

Archocopturus Heller, 1895: 56

Figs 48, 94

Type species. Copturus regalis Boheman, 1845 [by monotypy].

Gender. Masculine.

Diagnosis. Archocopturus can be separated from the other zygopines that have a concealed pygidium and a second funicular article that is subequal to the first by the following combination of characters: the eyes are separated at the top by a small lanceolate space (Fig. 48; also in other genera – e.g. many species of *Macrocopturus*), the vertex of head has a triangular, transversely striolate region (visible in Figs 48 and 94b for *Archocopturus* but most noticeable in Fig. 95b for *Cylindrocopturus*; also seen in some species of other genera, e.g. *Zygops, Cylindrocopturus*) the pronotum has deep, close punctures, the profemora are unarmed, and the hind femora are carinate and ventrally toothed and do not extend much beyond the abdominal apex. Additionally, all known species of *Archocopturus* have bluegreen scales on the pronotum, suggesting mimicry of the dolichopodid genus *Medetera* (Hespenheide 2005). While this coloration is found in several other genera of Conoderinae, the only other zygopine with it is *Zygopsella*, which *Archocopturus* can be easily separated from by the lack of a ventral profemoral tooth and the more approximate eyes. The mesoventrite is flat in most species but posteromedially depressed in *A. championi*.

Keys. Hespenheide 2005: 673.

Phylogenetic relationships. Champion (1906b: 42) suggests a relationship with *Zygopsella*. The two genera have in common the deep punctures of the pronotum (also in *Arachnomorpha*) and blue-green scales.

Host associations. The South American *Archocopturus regalis* (Boheman, 1845) has been reared from branches of Lecythidaceae in Peru (Fassbender 2013).

Described species. Four species are known from the focal region, which includes all four species described by Hespenheide (2005). One additional species is known from South America (Wibmer and O'Brien 1986: 270, Hespenheide 2005: 671).

Range. Mexico, Belize, Guatemala, Honduras (Hespenheide 2005), Nicaragua, Costa Rica, Panama; South America.

Cylindrocopturus Heller, 1895: 56

Figs 29, 49, 95

- = Paratimorus Heller, 1895: 58 [Syn.: Champion 1906b: 35]. Type species: Paratimorus ganglbaueri Heller, 1895 [by monotypy].
- = Gyrotus Casey, 1897: 668 [Syn.: Sleeper 1963: 217]. Type species: Gyrotus munitus Casey, 1897 [by monotypy].
- = Copturodes Casey, 1897: 669 [Syn.: Casey 1904: 324]. Type species: Zygops quercus Say, 1831 [by subsequent designation: Sleeper 1963: 217].

Type species. Zygops quercus Say, 1831 [by subsequent designation: Sleeper 1963: 217].

Gender. Masculine.

Diagnosis. Many of the species of Cylindrocopturus can be distinguished by the following combination of characters: the unmodified mesoventrite, the unarmed and non-carinate metafemora, the second antennal funicular article that is not longer than the first, the relatively vertical and separated eyes (Fig. 49), and the body mostly densely covered in round, imbricate scales. Additionally, the body is often somewhat dorsoventrally compressed, the elytra sometimes has prominences or setal tufts, the tibial apex at least of the protibia typically has a large hook-like uncus and a rounded, produced inner flange (Fig. 19), and a group of species (C. mammillatus species group of Fall (1906), Gyrotus Casey of Gluck (1987)) have a pair of tubercles on the second abdominal ventrite. These characters are useful for separation of the species found in the U.S.; of the several observed Mexican, Guatemalan, and Honduran species, including numerous unidentified and likely undescribed, the following exceptions to the above characters have been observed: a depressed posterior border of the mesoventrite, a second funicular article that is longer than the first, and carinate hind femora. These species otherwise appear congeneric with described species, highlighting the need for closer examination and reconstruction of this genus and its relatives.

Notes. *Cylindrocopturus* is in need of comprehensive revision due to the large number of synonymies, uncertain geographic range and lack of good characters separating it from several other genera. An unpublished Ph.D. thesis by W. Gluck (1987) attempted such for the species north of Mexico, but the heavily-relied upon statistical approach employed for generic and specific delimitation necessitates closer examination of many of the classificatory changes proposed.

Immature stages are described for the following species: *C. adspersus* (LeConte, 1876) by Böving (1926), *C. biradiatus* Champion, 1906 by Dampf (1929), *C. crassus* Van Dyke, 1930 by Keifer (1930), *C. furnissi* Buchanan, 1940 by W.H. Anderson (1941), *C. quercus* by Piper (1977). See Gluck (1987: 78) for an index of the seventeen known species of hymenopteran parasites of the species of *Cylindrocopturus*.

Keys. Champion 1906: 36 (to Central American species), Fall 1906: 55 (to *C. mammilatus* species group), LeConte and Horn 1876: 261 (to *Copturus* of the U.S.), Casey 1897: 669 (to *Copturodes* of the U.S.), Blatchley and Leng 1916: 420 (to Northeastern U.S. species), Hatch 1971: 361 (to *Gyrotus* of Northwestern U.S.), Heller 1895: 57, Gluck 1987: 9 (to *Gyrotus* north of Mexico) and Gluck 1987: 30 (to *Cylindrocopturus* north of Mexico).

Phylogenetic relationships. Hespenheide (1980: 330) suggests the genus *Cylindrocopturus* as the closest relative of *Helleriella* due to the shared elongate and compressed habitus and occurrence in arid environments. Champion distinguishes *Cylindrocopturus* from the South American genus *Timorus* by the lack of a ventral femoral tooth, and seems to imply possible relationships between *Timorus*, *Cylindrocopturus*, *Macrocopturus*, *Phileas*, and *Larides* (1906: 33-35). See *Macrocopturus*.

Host associations. Species of *Cylindrocopturus* have been reared from various species of Pinaceae (in the genera *Abies* Mill., *Pinus*, and *Pseudostuga* Carrière), various Asteraceae Bercht. & J. Presl (e.g. *Helianthus* L., *Hemizonia* DC.) and also Cactaceae



Figures 95–98. Lateral and dorsal habitus images of Zygopini. Scale bars = 2 mm unless otherwise specified. **95a–b** *Cylindrocopturus quercus* [ARTSYS0000819]; scale bars = 1 mm **96a–b** *Helleriella longicollis* [ASUHIC0065241] **97a–b** *Larides cavifrons* [ASUHIC0016882] **98a–b** *Lissoderes subnudus* [SSAC0001136]; scale bars = 1 mm.

Juss. (*Opuntia* Mill.); larvae of some species known from roots, stems, branches, galls and spines (Casey 1897, Fall 1906, Blatchley and Leng 1916, Dampf 1929, Van Dyke 1930, Buchanan 1940, Gluck 1987: 77, Martínez et al. 2016). The "sunflower stem weevil", *C. adspersus*, is the most well-studied species of New World conoderine due to its agricultural importance in the Midwestern United States, with studies including insecticide toxicity (e.g. Charlet and Oseto 1983) and overwintering and emergence patterns (Rogers and Serda 1982).

Described species. Forty-one species are known from the focal region and two additional described species are known from South America (Wibmer and O'Brien 1986: 270), though Rheinheimer (2011: 78) suggests *Eulechriops* as a better placement for the French Guianan *C. minutus* Hustache, 1938.

Range. Canada, USA, Mexico, Guatemala, Honduras; South America.

Helleriella Champion, 1906b: 32

Figs 30, 50, 96

Type species. Helleriella longicollis Champion, 1906 [by monotypy].

Gender. Feminine.

Diagnosis. The slender rostrum (Fig. 50), elongate pronotum, linear scales, and a very short tibial uncus (Fig. 30) separates *Helleriella* from the zygopine genera with a concealed pygidium, flattened mesoventrite and second funicular article that is not longer than the first. The eyes are somewhat widely separated, especially near the top, strongly inflexed along outer margin towards bottom where it is sharply acuminate, the femora are non-carinate, with or without a ventral tooth, and are short and thick in some species.

Notes. The species of *Helleriella* have been suggested to belong to different mimicry complexes, including clytrine chrysomelids, *Zacryptocerus* ants, and possibly redeyed flies and other species of ants (Hespenheide 1980).

Phylogenetic relationships. Hespenheide (1980: 330) suggests a relationship with *Cylindrocopturus* due to the "...elongate, compressed habitus... the pronotum distinctly narrower than the elytra, and an investiture of scales that are predominantly linear and only overlap end-to-end in contrast to broad, completely overlapping, encrusting scales of most *Cylindrocopturus*."

Keys. Hespenheide 1980: 329 and 1998: 3.

Host associations. Associated with several species of "swollen thorn *Acacia*" (Fabaceae: Mimosoideae DC.) (Hespenheide 1980). Larvae live and feed in thorns not occupied by ants (Hespenheide 1980).

Described species. Five species are known, including one described by Hespenheide (1998).

Range. Mexico, Guatemala, El Salvador (Hespenheide 1980: 325), Belize, Nicaragua, Costa Rica.

Larides Champion, 1906b: 34

Figs 51, 97

Type species. Larides cavifrons Champion, 1906 [by original designation].

Gender. Masculine.

Diagnosis. *Larides* is distinct from all other zygopine genera treated here with the exception of *Phileas* with the short, stout, arcuate rostrum that does not extend much beyond the procoxae, more strongly developed ocular lobes that partially cover the eye, and eyes widely separated at the top and strongly concave in between (Fig. 51). The antennae are inserted near the middle of the rostrum, the second antennal funicular article is not longer than the first, the mesoventrite is unmodified, and the hind femora are ventrally toothed and faintly carinate in the distal half. The distinction given by Champion (1906b: 35) between *Larides* and *Phileas* in their original descriptions is that *Larides* has the eyes "less acuminate below and more widely separated above, the antennal club shorter and relatively stouter, and the prothorax and elytra subtruncate at the base" seem insufficient for generic distinction, especially when considering the intrageneric variation of those characters in other conoderine genera. Both *Larides* and *Phileas* are monotypic, but *Larides cavifrons* can be easily separated from *Phileas granulatus* Champion by the more strongly depressed interocular space and the metatibial apex that has a premucro oriented along the longitudinal axis of the tibia (at a 45° angle in *Phileas granulatus*).

Notes. Couplet 38 in the below key serves to distinguish the genera *Larides* and *Phileas*, however, few specimens of *Larides* and only one of *Phileas* were observed in this study. Whether the tibial apex character, which easily separates the observed specimens but was not mentioned by Champion in the original descriptions, will hold for generic distinction when additional specimens and species are observed remains to be seen.

Phylogenetic relationships. Very similar to *Phileas*, and as noted by R.S. Anderson (1994: 486) they are possibly congeneric, but insufficient material has been observed to comment further. Both genera share with the South American *Timorus* the short, robust rostrum, ocular lobes that are more developed than in other genera, and similarly shaped eyes.

Host associations. R.S. Anderson (1994: 486) reports specimens collected on the mistletoe *Struthanthus* prob. *quercicola* (Schltdl. & Cham.) D.Don (Loranthaceae).

Described species. One.

Range. Mexico.

Lissoderes Champion, 1906b: 47

Figs 15, 31, 52, 56, 98

Type species. *Lissoderes subnudus* Champion, 1906 [by original designation]. Gender. Masculine.

Diagnosis. *Lissoderes* is easily distinguished by its overall appearance, which is a mostly glabrous, shining body with black or reddish-brown cuticle and small patches

of white scales, elongate, non-carinate, and ventrally unarmed hind femora that extend well past the abdominal apex, and an absent subapical pronotal constriction. The antennal insertion in the middle of the rostrum in females or near apex in males (Fig. 52), the second funicular article is not longer than the first, the unmodified mesoventrite is densely covered in multifid setae (Fig. 15), the premucro of the tibial apex is minute (Fig. 31), and the very narrowly bilobed third tarsal article are additional characters that in combination are unique to *Lissoderes*.

Keys. Hespenheide 1987: 52.

Phylogenetic relationships. Hespenheide (1987) suggests a relationship with *Arachnomorpha*. *Lissoderes*, like mentioned above with *Arachnomorpha*, are both part of a putative ant-mimicry complex (Hespenheide 1995) that includes species in other genera of Conoderine and Curculionidae with a black, glabrous cuticle and patches of white scales. The only other zygopine genera with an antennal insertion in the middle or apical half of the rostrum are *Phileas* and *Larides*, which have it near the middle of the rostrum.

Host associations. *Lissoderes* is one of the few conoderine genera that have been both the subject of a taxonomic revision (Hespenheide 1987) and natural history study (Weng et al. 2007). Adults are easily found on the underside of leaves of several species of *Cecropia* and larvae feed on the parenchyma tissue inside the internodes of the stem (Weng et al. 2007).

Described species. Five species are known from the focal region, including three described by Hespenheide (1987) and one by Hespenheide (2007). An additional two species are known exclusively from South America (Wibmer and O'Brien 1986: 272; one more described by Hespenheide (2007)).

Range. Honduras [Hespenheide 1987], Costa Rica [Hespenheide 1987], Panama; South America.

Peltophorus Schoenherr, 1845: 451

Figs 16, 33, 62, 99

- = Apatorhynchus Desbrochers, 1891: 40 [Syn.: Champion 1906b: 20]. Type species: Zygops leopardinus Desbrochers, 1891 [by monotypy].
- = *Opalocetus* Desbrochers, 1910: 126 [unjustified replacement name for *Peltophorus* (Champion 1910b: 211)].

Type species. Peltophorus polymitus Boheman, 1845 [by original designation].

Gender. Masculine.

Diagnosis. This genus is similar only to *Zygops* with the large exposed pygidium that is visible in dorsal view and the sulcate subapical pronotal constriction, and can be readily distinguished from *Zygops* by the following characters: the shape of the eyes, which in *Peltophorus* are generally not as large and not extending as laterally on the head as in *Zygops*, the distal setal comb of the metatibia that extends more than a third to the base of the tibia (Champion 1906b: 20; Fig. 33) the femora always with one large triangular tooth (with one or several smaller teeth in *Zygops*) and the unique mes-



Figures 99–102. Lateral and dorsal habitus images of Zygopini. Scale bars = 2 mm unless otherwise specified. **99a–b** *Peltophorus polymitus suffusus* [ASUHIC0016837]. **100a–b** *Phileas granulatus* [ART-SYS0000528]. **101a–b** *Philenis flavipes* [ASUHIC0065102]; scale bar for 101a = 1 mm **102a–b** *Zygops vitticollis* [ASUHIC0086634]; scale bar for 102b = 5 mm.

oventrite that is ventrally protruding along the posterior margin (Fig. 16), and differs from the mesoventrite of *Zygops* which is usually unmodified (or with small posterolateral processes in a few species).

Notes. See Böving (1926) for description of larval and pupal morphology and González-Hernández et al. (2015) and Figueroa-Castro et al. (2016) for an overview of the feeding damage of *P. polymitus* Boheman and *P. adustus* (Fall) in Mexico.

Keys. Sleeper 1963: 216 (to U.S. species), Casey 1892: 459 (to U.S. species).

Phylogenetic relationships. Related to *Zygops* and the South American genera *Parazygops* and *Colpothorax* due to the exposed pygidium, large metepimeron, transverse scutellum, and sulcate subapical pronotal constriction.

Host associations. The species of *Peltophorus* are associated with several species of *Agave* L. (Asparagaceae Juss.), including *Agave palmeri* Engelm. (Sleeper 1963: 216, González-Hernández et al. 2015, Figueroa-Castro et al. 2016).

Described species. Three.

Range. Southwestern U.S.A., Mexico, Honduras.

Phileas Champion, 1906b: 34

Figs 32, 100

Type species. Phileas granulatus Champion, 1906 [by original designation].

Gender. Masculine.

Diagnosis. *Phileas* shares with *Larides* the short and thick rostrum, the antenna inserted near the middle of the rostrum, and the ocular lobes that are more produced than in other Central American Conoderinae, and can be distinguished from *Larides* by the less strongly depressed interocular space, the more completely carinate hind femora, and distinct metatibial apex (Fig. 32).

Notes. Lyal et al. (2006: 214) noted the scales along the metanepisternal suture of *Phileas* as being a similar color to the regular scales surrounding the suture and thus considered them unlikely to be true sclerolepidia – a similar situation has been observed in *Larides*.

Phylogenetic relationships. See above entry for Larides.

Host association. One specimen observed, collected "on mistletoe" [ARTSYS0000528]. Described species. One.

Range. Mexico.

Philenis Champion, 1906b: 43 Figs 17, 35, 53, 101

Type species. *Philenis flavipes* Champion, 1906 [by original designation]. Gender. Feminine.

Diagnosis. The short, slender antenna and narrow, acuminate club are given by Champion (1906b: 43) to distinguish the genus from *Copturus* (*=Macrocopturus*), which also separate it from the rest of the genera except for the observed South American specimens of *Hypoplagius*. *Philenis flavipes* has an unmodified mesoventrite but *P. fuscofemorata* Champion, 1906 and three observed undescribed species have a large tubercle at the posterolateral margins of the mesoventrite with the posteromedial margin being strongly depressed (Fig. 17). The two described species are easily distinguished for being the only known members of the putative bee mimicry complex (Hespenheide 1995: 150) with the contrasting yellow and black or brown pattern, but some observed undescribed species are not, with one being a representative of the "red-eyed fly" mimicry complex. The second funicular article is longer than the first, eyes are ovoid and somewhat protruding (Fig. 53), and the femora are non-carinate and ventrally toothed.

Notes. Champion (1906b: 44) notes that the pygidium is slightly exposed in *P. flavipes*, but all observed specimens of that species have the last abdominal ventrites deflected downwards (i.e. not in their natural position during life) so this character has not been confirmed. *Philenis* was not moved to Lechriopini by Lyal et al. (2006) despite having some type of modification to the mesoventrite because of a lack of sclerolepidia. The two described species, *P. flavipes* and *P. fuscofemorata*, lack sclerolepidia, however, observed specimens of three congeneric undescribed species do have sclerolepidia. The genus is not moved to the Lechriopini here due to the lack of a suitably identified sister genus.

Phylogenetic relationships. *Philenis* was regarded by Champion (1906b: 43) to be "closely related to *Copturus* [=*Macrocopturus*] in its restricted sense", but the genus is not very similar in appearance to others in the Lechriopini or Zygopini. Interestingly, both the reported host association and the mesoventrite, which in some species has a deep semicircular depression, are similar to that found in *Hoplocopturus* and *Mnemynurus*.

Host associations. One species has been collected from a "gall on an aroid stem" (Hespenheide 1995: 150).

Described species. Two. Range. Costa Rica, Panama.

Zygops Schoenherr, 1825: c.586

Figs 34, 102

- *Eccoptus* Dejean, 1821: 86 [Syn.: O'Brien and Wibmer 1984: 296]. Type species: *Curculio strix* Olivier, 1790 [by monotypy]. Suppressed for priority (ICZN 1987).
- = Eccyptus [Fischer von Waldheim], 1829: 99. Type species: Curculio strix Olivier, 1790 [by monotypy].

Type species. Poecilma wiedii Germar, 1824.

Gender. Masculine.

Diagnosis. Of the genera occuring north of South America, *Zygops* could be mistaken only with *Peltophorus* with the large, exposed pygidium that is mostly visible in dorsal view and deflecting the fifth abdominal ventrite ventrally at the apex, and the sulcate subapical constriction of the prothorax. *Zygops* can be differentiated from *Peltophorus* by the shorter metatibial setal comb (Fig. 34), the much longer second funicular article (usually at least 2 times longer in *Zygops*, 1.5-2 times longer in *Peltophorus*), the metafemora ventrally with more than one tooth (in many species), the more elongate tibial uncus (Fig. 34), and the less developed mesoventrite, which in *Zygops* is usually flattened, but in some with the posterolateral margin tumescent (e.g. *Z. maculipes* Desbrochers, 1891) or with small projections (e.g. the South American *Z. leucogaster* Desbrochers, 1891). The prosternal channel is sometimes very narrow and scarcely depressed, and the procoxae are sometimes very narrowly separated or even contiguous (e.g. in *Z. maculipes*).

Notes. The genus *Eccoptus* Dejean, 1821 was suppressed despite having priority over *Zygops* Schoenherr, 1825 (petitioned in O'Brien and Wibmer 1986, ruled by ICZN 1987) for the purpose of nomenclatural stability: the name *Eccoptus* had been used much less frequently (though most recently resurrected in O'Brien and Wibmer 1982) and the name *Zygops* formed the base for the subfamilial name in use at the time, *Zygopinae*.

Keys. Champion 1906b: 21.

Phylogenetic relationships. See *Peltophorus*. Most similar to *Peltophorus* of the genera treated here, but the distinction between *Zygops* and the South American genera *Parazygops* and *Colpothorax* is less distinct, based on the shape of the rostrum and the shape of the prothorax, respectively.

Host associations. Some species have been reared from branches of various genera of Lecythidaceae (Fassbender 2013, Fassbender et al. 2014).

Described species. Eighteen species are known from the focal region and an additional 34 species are known only from South America (Wibmer and O'Brien 1986: 267).

Range. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Dominican Republic (Poinar and Legalov 2013, fossil); South America.

Zygopsella Champion, 1906b: 42

Figs 54, 103

Type species. *Zygopsella ruficauda* Champion, 1906 [by original designation]. **Gender.** Feminine.

Diagnosis. Zygopsella is similar in appearance to Archocopturus and some species of Macrocopturus, Hoplocopturus, and Copturomimus with blue-green pronotal scales, but of those genera is similar only to Archocopturus with the subequal first two articles of the funiculus and deep pronotal punctures. From Archocopturus, Zygopsella can be separated by the more widely separated eyes (Fig. 54), the more sharply acuminate lower



Figures 103–105. Lateral and dorsal habitus images of Zygopini and Conoderinae *incertae sedis*. Scale bars = 1 mm unless otherwise specified. **103a–b** *Zygopsella ruficauda* [ARTSYS0000526]; scale bar = 2 mm **104a–b** *Philides comans* [ARTSYS0000804] **105a–b** *Philinna bicristata* [ARTSYS0000532].

margin and more strongly inflexed lower lateral margin of the eyes, the more strongly arcuate lateral margins of the pronotum (Fig. 103b), the ventrally toothed profemora, the ventrally emarginate tibiae to receive the femoral tooth, and the flattened caudal prominences of the elytra (Fig. 103b).

Phylogenetic relationships. Suggested by Champion (1906b: 42) to be closely related to *Archocopturus*. The combination of ascending abdominal ventrites, concealed pygidium, unmodified mesoventrite, carinate and ventrally toothed metafemora and short second funicular article of the antenna is shared only with *Archocopturus*, *Phileas*, and *Larides* (the latter only with a faint carina in the distal half of the femora). Also similar to many *Cylindrocopturus* with the elytral processes and relatively widely separated eyes. *Zygopsella* has a similar eye shape to *Helleriella* that is strongly laterally in-flexed and sharply ventrally acuminate.

Host associations. Unknown.

Described species. Two, including one species transferred from *Archocopturus* by Hespenheide (2005).

Range. Mexico (Hespenheide 2005: 683), Guatemala, Costa Rica (Hespenheide 2005: 682), Panama (Hespenheide 2005: 683), Guadeloupe (Hespenheide 2005: 683).

Conoderinae incertae sedis

Philides Champion, 1906b: 129

Figs 59, 104

Type species. Philides anthonomoides Champion, 1906 [by monotypy].

Gender. Masculine.

Diagnosis. Philides is easily differentiated from all other genera treated here except Philinna by the following characteristics: the body, especially the lateral surfaces, are densely covered in multifid setae; the antennal funiculus has 6 instead of 7 articles (as in Fig. 57 for *Philinna*); the tibial apex does not have an uncus at the posterior apical angle and has either a small process at inner apical angle (as in Fig. 36 for Philinna) or no process at all; the tibial apex is subcircular in cross-section (not laterally compressed as in all other genera) and with distinct fringe of spine-like setae around the apex; the prosternum behind the procoxae has ventrally projecting laterally compressed tubercles (as in Fig. 18 for *Philinna*); the mesoventrite is vertical, unmodified or with posterolateral margins modified into somewhat projecting lamellae (as in Fig. 18); the first elytral interval has elongate, stout setae crossing over the suture in roughly posterior half (Fig. 104b); and the fifth abdominal ventrite is strongly emarginate to accommodate the exposed pygidium. Philides differs from Philinna in the presence of tarsal claws with a broad tooth (Fig. 59; seen in Philides comans Champion, 1909, but not all observed specimens identified to P. anthonomoides had this tooth) and in overall appearance, with the known species of *Philides* belonging to the "shiny black" mimicry complex of Hespenheide (1995: 149). Some observed specimens identified as P. anthonomoides have the mesoventrite unmodified, with slight projections at the posterolateral margins or with the mesoventrite strongly excavated apically to receive the rostrum.

Phylogenetic relationships. The numerous characters that differentiate this genus and *Philinna* from the rest of the conoderines treated here suggest improper placement in Conoderinae, as suggested by Lyal et al. (2006) due to the lack of sclerolepidia and differently constructed mesoventrite. Champion (1906: 130) and Hespenheide (1992: 2, 2002: 756) noted the similarity of these genera with Tachygonini (a group sometimes included in the Conoderinae but since relegated to a subtribe in the Curculioninae: Rhamphini, treated there most recently in Caldara et al. 2014) in having multifid setae covering much of the body. Further similarities of these three genera are the stout,

crossed setae along the elytral suture. Tachygonines, however, have a more conoderinelike tibial apex than either *Philides* and *Philinna*, being laterally compressed and with an uncus at the posterior apical angle. Specimens were not observed for two of the three genera currently placed in the Tachygonina, reserving a reconsideration of the placement of the subtribe for future phylogenetic study. *Philides* also bears a resemblance to the Old World conoderine tribe Lobotrachelini, but the observed species of that tribe also differ from *Philides* and *Philinna* in having a more typical conoderine tibial apex. The only other genus treated here without simple tarsal claws is *Psomus* Casey, which does not have a similar broad, flat tooth as in *Philides*.

Host associations. The larva of at least one species is an inquiline in galls made by a buprestid (Medianero et al. 2007).

Described species. Two. Numerous undescribed species and related genera occur in Central America (H. Barrios, personal communication). One additional described species is known from South America (Rheinheimer 2011).

Range. Mexico, El Salvador, Panama; South America (Rheinheimer 2011).

Philinna Champion, 1906b: 128

Figs 18, 36, 57, 105

Type species. Philinna bicristata Champion, 1906 [by monotypy].

Gender. Feminine.

Diagnosis. *Philinna* can be distinguished from the rest of the genera treated here by characters listed above for *Philides*. It differs from most *Philides* by the following characters: the tarsal claws are simple, the pronotum has a smooth, raised median line, and the elytral humeral angle has dense tufts of elongate setae.

Phylogenetic relationships. Very similar to *Philides* but its relationship to other genera is currently uncertain. See *Philides*.

Host associations. Unknown.

Described species. One species is known from the focal region and one additional species is known in South America (Wibmer and O'Brien 1986: 265).

Range. Mexico (Wibmer and O'Brien 1989: 19), Belize [ARTSYS0000799], Guatemala, Panama [ARTSYS0000806]; South America.

Identification resources

Previous regional keys to genera. The following references provide the publication and page number of a published identification key treating genera from North and/or Central America, the Caribbean, and South America (if they also include genera whose ranges extend to Central America). An asterisk (*) indicates publication in a language other than English.

Blatchley and Leng 1916: 417 (Northeastern U.S.A.), Casey 1897: 667 (U.S.A.), Gluck 1987: 8 (Zygopini north of Mexico), Hatch 1971: 361 (Northwestern U.S.A.), *Heller 1984: 3 (World), *Heller 1895: 3 (New World), *Heller 1906: 31 (New World Piazurini), Hespenheide 2002: 754 (U.S.A.), *Hustache 1932a: 275 (Guadeloupe), Kissinger 1964: 71 (U.S.A.), LeConte and Horn 1876: 259 (U.S.A.), *Muñiz 1965:5 (avocado pests), *Muñiz and Barrera 1958 (avocado pests), *Rheinheimer 2011: 72 (French Guiana), Sleeper 1963: 209 (U.S.A.).

Key to genera from focal region. The genera treated by the below key are listed synoptically in Table 1 along with all genera included in the five tribes that are not from the focal region (as indicated by an asterisk or circumflex accent). This key incorporates elements from previous keys, characters from the original descriptions of genera, as well as many new characters. It will not necessarily work for species outside of the focal range or for undescribed species from the focal range, but as many of those species as possible were worked in. The sequence of the following key is approximately in perceived phylogenetic order with pragmatic deviations to allow for more efficient identification.

1 Antennal club loose and bearing elongate setae (Fig. 67b). Procoxae contiguous. Rostral channel prosternally with the sides converging to a point ventral Antenal club compact and with short setae (Figs 55-57). Procoxae separate (can be very narrowly separated or rarely contiguous – if contiguous, antennal club always compact). Rostral channel on the prosternum not terminating 2 Pygidium broadly exposed (if only narrowly exposed, mesoventrite a cup-Pygidium completely concealed or only very narrowly exposed (if narrowly exposed, mesoventrite not a cup-shaped receptacle for receiving rostrum)...... 11 3 Antennal funicle composed of 6 articles (Fig. 57). Tibial apex without uncus at posterior apical angle (Fig. 36). Lateral and dorsal surfaces of the body in large part covered in multifid setae. First elytral interval with elongate and stout setae that cross over elytral suture in posterior half (Figs 104b, 105b).4 Antennal funicle composed of 7 articles (Fig. 56). Tibial apex with uncus at posterior apical angle (Figs 22-35). If body bearing multifid setae then not covering large portions of the lateral and dorsal surfaces. Elytral interval 1 4 Tarsal claws often with a broad tooth at the base (Fig. 59). Body in large part glabrous, cuticle black and with white setae/scales (Fig. 104) Philides Tarsal claws simple. Cuticle black and reddish brown (Fig. 105). Setal color various.....Philinna Subapical constriction of pronotum sulcate (especially when viewed dorsally 5 as in Fig. 99b). Exposed portion of pygidium mostly to entirely visible in dorsal view (Figs 99b, 102b). Meso- and/or metafemoral apices with teeth at

mesal and/or lateral face (Fig. 62). Scutellum usually distinctly quadrate (Fig. Subapical constriction of pronotum shallow or absent. Exposed portion of pygidium mostly to entirely concealed in dorsal view (Figs 68b-72b) and visible in posterior or ventral view only in most. Femoral apices without teeth (Fig. 60). Scutellum variable but never distinctly quadrate or transversely rectangular7 Longitudinal setal comb of posterior distal face of hind tibia occupying distal 6 half (Fig. 33). Posterior margin of mesoventrite ventrally produced (Fig. 16). Tibial uncus very short (Fig. 33). Femora never armed ventrally with more Longitudinal setal comb of posterior distal face of hind tibia occupying distal third or less (Fig. 34). Posterolateral margin of metaventrite of most flattened but in few slightly tumescent or with small processes. Tibial uncus variable but not as above (Fig. 34). Femora armed ventrally with one to several teeth Zygops 7 Antennal funicular article 2 usually about equal in length to article 1 (as in Fig. 56). Metafemora slightly clavate, ventral tooth present and not especially Antennal funicular article 2 usually at least 2 times longer than article 1 (as in Fig. 55). Metafemora clavate, with large laterally flattened tooth (Fig. 71a) 9 8 Rostral channel closed on the mesoventrite (Fig. 2). Eyes more widely separated dorsally and strongly concave between (Fig. 39). Setal tuft at tibial apex composed of a few golden setae (as in Fig. 23). Setal comb of meso- and metafemora (along posterodistal face) not a dense brush, composed of no more than a few rows of setae. Profemora ventrally with two projections, a pointed tooth near the middle and a smaller, rounded prominence distally...Lobops Rostral channel open on the mesoventrite (as in Figs 3-4). Eyes large and approximate or small and widely separated along entire length (Fig. 38), at most slightly concave between. Setal tuft at tibial apex a thick fascicle of golden setae (Fig. 21). Setal comb of meso- and metafemoral apex a broad, dense setal brush (Fig. 21). Profemora ventrally with one or no teeth (rarely two)..... Cratosomus Abdominal ventrite 2 at the side about as long as 3 and 4 combined (Fig. 9 70a). Pro- and mesotibial apices with premucro. Premucro of metatibial apex never subapical Piazurus Abdominal ventrite 2 at the side shorter than 3 and 4 combined (Figs 71a, 72a). Pro- and mesotibial apices without premucro. Premucro of metatibial apex sometimes subapical......10 10Eyes very large, ovoid and contiguous (Fig. 40). Pronotum conical in dorsal view (Fig. 71b). Mesepipleura large and ascending. Profemora unarmed ventrally. Abdominal ventrite I with two arcuate sulci (Fig. 64). Vertex of head without arcuate carina...... Pseudopiazurus

_	Eyes smaller, more circular, subcontiguous or more separated (Fig. 41). Pro- notum (Fig. 72b) and mesepipleura usually not as above. Profemora ventrally toothed (in most). Vertex of head with arcuate carina (Fig. 41; in many Central American species). Abdominal ventrite I without large U-shaped impression, or if present, then vertex of head always with arcuate carina.
11	Scutellum partially or completely concealed by posteriorly projecting medial lobe of pronotum (Fig. 76b)
12	Scutellum completely exposed
_	<i>Euzurus</i> Rostral channel closed on the mesoventrite (Fig. 6). Eyes not as above. Metaventrite without large tubercle anterior to metacoxa
13	Pro- and mesofemora unarmed ventrally. Tarsal claws very small (Fig. 58). Elytral intervals costate
_	Pro- and mesofemora armed ventrally. Tarsal claws normal. Elytral intervals not costate
14	Mesoventrite with a single arcuate carina in the shape of an inverted "U" (Fig. 9)
_	Mesoventrite with or without carinae, but if present not in the shape of an inverted "U"
15	Metaventrite with complete longitudinal depression or channel (in most). Rostrum very long, extending beyond posterior margin of metaventrite (Fig. 87a; except in <i>M. longispinis</i>). Apex of rostrum flattened and dilated. Posterior margin of mesoventrite invaginated under U-shaped carina (as in Fig. 9)
_	Metaventrite, if modified, with depression or fovea limited mainly to the anterior, intermesocoxal region or the middle of the sclerite and never from the anterior to the posterior border. Rostrum not extending beyond posterior margin of metaventrite (Fig. 81a). Rostral apex not significantly depressed or dilated. Posterior margin of mesoventrite usually depressed (in most) or invaginated (in few; Fig. 9)
16	Rostral channel of mesoventrite with longitudinal or slightly arcuate carinae (e.g. Figs 10, 13). Posterior margin of mesoventrite without ventrally pro- duced tubercles
_	Mesoventrite without carinae, or, if bearing carinae, then the posterolateral margins also tuberculate
17	Hind femora slender and elongate, extending well beyond abdominal apex (Fig. 90a). Rostral channel a deep ovoid receptacle (Fig. 13) <i>Pseudolechriops</i>
_	Hind femora stout, not extending much past abominal apex if at all. Rostral channel not as above
18 —	Femora ventrally toothed. Funicular article 2 longer than article 1 19 Femora ventrally unarmed. Funicular article 2 not longer than article 1 20

19	Metafemora not carinate (as in Fig. 61). Body size > 5 mm <i>Poecilogaster</i>
_	Metafemora carinate (as in Fig. 62). Body size usually < 5 mm Lechriops
20	Profemora dorsally with bare, finely striolate region (as in Fig. 66 or more
	concealed)Copturomorpha
_	Profemora without striolate area21
21	Pronotum with strongly arcuate, hump-like medial longitudinal carina (Fig.
	84a)
_	Pronotum without hump-like carina
22	Hind femora and tibia of males arcuate and bearing erect setae ventrally (Fig.
	77a). Procoxae without mesal conical process
_	Hind femora not elongate and arcuate. Procoxae mesally with small conical
	process
23	Apex of rostral channel without distinct termination (apex is the non-carinate
	anterior margin of the metaventrite) (Fig. 7) Cylindrocopturinus
-	Rostral channel terminating on either mesoventrite or metaventrite, carinate
	or not, but always being a distinctly posteriorly rounded receptacle24
24	Rostral channel ending on mesoventrite in deep carinate cup-like receptacle
	(Fig. 14). On mistletoe (Santalaceae: Phoradendron) Turcopus
_	Rostral channel, if ending on the mesoventrite, not a deep, carinate recepta-
	cle. Hosts various Eulechriops
25	Mesoventrite with some prominent modification at least in posterior half in
	the form of tubercles, carinae or depressions (if unmodified, antenna also very
	short and slender) (Figs 11, 12, 17)
-	Mesoventrite without the abovementioned modification in posterior half
	(Figs 5, 15), with posterolateral corners at most slightly tumescent; antenna
	not short and slender
26	Antenna short and slender (Fig. 53). Posterolateral margin of mesoventrite
	(in most) with tubercles and a deep semicircular depression (Fig. 1/). I ibial
	apex with premucro directed at a roughly 45° angle from the longitudinal axis
	of the tibia (Fig. 35). Eyes ovoid and somewhat protuberant on head (Fig. 52)
	53) Philenis
_	Posterolateral margin of mesoventrite elevated, forming a platform for the
	rostrum to rest on, usually with tubercles at the posterolateral margin and
27	otherwise lacking the above combination of characters $\frac{2}{2}$
27	Posterior margin of metaventrite with short transverse carina marking end of
	cles without carines
	Cles without carinae
_	trite with medial depression delimited by slightly argue longitudinal cari
	the with medial depression deminied by signify arcuate longitudinal car-
28	Hind femore slender and elongate extending well beyond the anex of the
20	abdomen (Fig. 86) Hind femore not carinate and if ventrally toothed tooth
	small and inconspicious
	sinan and inconspicuous

_	Hind femora not extending much beyond the apex of the abdomen, carinate and with distinct ventral tooth
29	Tarsal claws appendiculate. Subapical pronotal constriction sulcate Psomus
30	Abdominal sternites slightly evenly ascending in profile. Tibiae lacking pre- mucro (Fig. 24)
_	Abdominal sternites strongly ascending in profile. Hind tibia at least with
31	Article 2 of antennal funicle not longer than article 1 (as in Fig. 56)
- 32	Article 2 of antennal funicle much longer than article 1 (as in Fig. 55) 39 Antennal insertion clearly in basal half of rostrum (usually basal third) 33 Antennal insertion near middle or in anical half of rostrum
33	Hind femora carinate, never with paired tubercles on the second abdominal ventrite
_	Hind femora not carinate, or if carinate also with paired tubercles on the second abdominal ventrite
34	Hind femora ventrally unarmed. Body of known species with cuticle shining black and vestiture composed of opalescent white scales (Fig. 93)Arachmomorpha
_	Hind femora armed ventrally with 1 tooth. Pronotum of known species with blue-green scales (Figs 94, 103)
35	Profemora armed ventrally with 1 tooth. Elytral apex with flattened processes (Fig. 103b). Vertex of head without triangular, transversely striolate region
_	Profemora ventrally unarmed. Elytral apex without flattened processes. Ver- tex of head with triangular, transversely striolate region (visible in Figs 48, 94b)
36	Vestiture consisting of linear scales (Fig. 96). Tibial apices with very short, curved uncus (Fig. 30). Eyes acuminate ventrally and strongly inflexed laterally towards the bottom (Fig. 50). Elytra and mesoventrite never tuberculate
	Helleriella
_	Vestiture consisting of overlapping, rounded scales at least in part, densely cov- ering most of body surface (in many species). Tibial apex (at least of protibia) usually with hook-like uncus and a produced, rounded inner flange (Fig. 29). Eyes acuminate ventrally and rounded at sides, often vertical and somewhat
	ond abdominal ventrite of some with paired tubercles Cylindrocopturus
37	Ocular lobes absent (Fig. 98a). Hind femora extending well beyond apex of abdo- men (Fig. 98). Subapical pronotal constriction absent (Fig. 98b). Eyes not widely
_	separated at the top and not strongly depressed in between (Fig. 52) <i>Lissoderes</i> Ocular lobes slightly produced (Figs 97a, 100a). Hind femora shorter and more stout (Figs 97a, 100a). Subapical pronotal constriction present. Eyes at the top widely separated and the interocular space strongly depressed (Fig. 51) 38

38	Metafemora completely carinate. Metatibial apex with premucro oriented at
	a ~45° angle to longitudinal axis of tibia (Fig. 32) Phileas
_	Metafemora with faint carina in distal half. Metatibial apex with premucro
	oriented along longitudinal axis of tibia (as in Fig. 28)
39	Profemora dorsally with a denuded, striolate patch (Fig. 66). Femora with a
	single ventral tooth
_	Profemora dorsally without a denuded, striolate patch. Some species with
	more than one ventral femoral tooth

Discussion

The monophyly of the Conoderinae as well that of its tribes and genera have not yet been demonstrated. While the present study is not considered comprehensive enough in both taxon and character system sampling to provide a significantly emended classification of the Conoderinae, it provides a first summary of phenotypic information for many of the treated genera and tribes and an examination of the phylogenetic utility of several morphological character systems that have been traditionally used to define taxa. This has revealed several suspected classificatory changes that will be needed to achieve a phylogenetic classification.

Many genera as they are currently constructed can only be identified by a combination of characters and by negative identification of similar genera, and numerous specimens have been examined that lack part of the character combinations and appear intermediate between genera. Several new genera will likely be created from those that are currently large and unsatisfactorily delimited. Additional character systems, such as the genitalia, are likely to provide more clarity to hypotheses of generic monophyly and relationships as many of the external characters traditionally used have been found to be limited for these purposes. Such characters, like the length of the funicular articles and the presence of a carina or tooth on the hind femora, can be useful at the generic level when used in combination but are certainly not without exception in the larger genera.

Of the characters traditionally influential for conoderine classification, the mesoventrite remains one of the most useful for identification at the level of genus as this structure is relatively invariable within most genera. However, its utility at higher levels, especially that of the tribal level, does not seem to be as originally implicated by Lacordaire (1865). The distribution of the types of modification to the mesoventrite within the current classificatory framework suggests that this is a very homoplasius character system, with certain types appearing independently in multiple lineages (e.g. multiple transitions from unmodified to modified), or that the different types are homologous and the tribes, as currently composed, contain many improperly placed genera. Both, to some degree, are likely to be true, but with limited current knowledge of relationships it is difficult to assign polarity to the different states of modification. The tibial apex of New World Conoderinae conforms to a general structure that varies little, with the exception of the production of the inner flange, which can be quite variable within a genus. Three of the four genera transferred out of the Lechriopini in this paper are genera that deviated most from this general structure, with *Acoptus* having a tibial apex more similar to Old World Conoderinae and *Philinna* and *Philides* having a tibial apex distinct among the observed Conoderinae and likely indicative of a proper placement elsewhere in the Curculionidae. Undoubtedly, much work remains to be done in circumscribing the New World conoderine tribes and genera and elucidating their phylogenetic relationships, but it is hoped that this contribution to conoderine systematics can provide the foundation to facilitate such studies in the future.

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RESEARCH ARTICLE



A new species of Pectinaria (Annelida, Pectinariidae), with a key to pectinariids from the South China Sea

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Abstract

Pectinariidae is a family of polychaetes building unique ice-cream cone shaped sandy tubes. *Pectinaria torquata* **sp. n.** (Pectinariidae) is described from the coastal waters of the northern South China Sea. This new species can be distinguished from all other 25 recognized species in the genus by a combination of characters: 16 chaetigers; 26–32 cirri in the cephalic veil; 11–12 pairs of cephalic spines; uncini with major teeth arranged in two rows, each with 7–8 major teeth; presence of a dorsal posterior lobe on segments 2 and 20; 4–5 pairs of curved scaphal hooks; and an anal flap with a crenulated margin. A key to all recognized pectinariids in the South China Sea is provided.

Keywords

invertebrate, Pectinaria, polychaete, South China Sea, taxonomy

Introduction

Pectinariidae is a family of polychaetes commonly found in the soft bottom of coastal shallow waters. They are easily recognized by their unique ice-cream cone shaped sandy tube, and two bundles of golden thick chaetae called paleae on the first segment which

they use for sediment digging (Fauchald 1977, Wolf 1984). There are 50 recognized species of Pectinariidae in five genera: 15 species of *Amphictene* Savigny, 1818; six species of *Cistenides* Malmgren, 1866; ten species of *Lagis* Malmgren, 1866; 25 species of *Pectinaria* Savigny, 1818; and four species of *Petta* Malmgren, 1866 (Hartman 1941, Hutchings and Peart 2002, Sun and Qiu 2012, García-Garza and de León-González 2014, Nishi et al. 2014, Wong and Hutchings 2015, Zhang et al. 2015). Ten species of *Pectinarii* de have been recorded from the South China Sea, including four species of *Amphictene*, three species of *Lagis*, and three species of *Pectinaria* (Wu and Chen 1985, Yang and Sun 1988, Paxton and Chou 2000, Sun and Qiu 2012, Salazar-Vallejo et al. 2014, Zhang et al. 2015, Glasby et al. 2016).

Pectinaria can be distinguished from other genera of Pectinariidae by a combination of characters: smooth opercular rim; cephalic veil free with numerous cirri; and neurochaetal uncini having major teeth arranged in two or more rows (Wong and Hutchings 2015). Here a new species of *Pectinaria* is described, based on three specimens collected from the coastal waters of the northern South China Sea.

Materials and methods

Specimens were collected while undertaking a benthic ecology monitoring program of the South China Sea Environmental Monitoring Center (SCSEMC), State Oceanic Administration. Benthic samples were collected from the northern South China Sea using a 0.05 m² van Veen grab, and rinsed through a sieve with 0.5 mm mesh size. Samples retained on the sieve were collected, fixed in 5% formalin, and later transferred to 70% ethanol. Type specimens are deposited at the Institute of Oceanology, Chinese Academy of Science (IOCAS), Qingdao. Specimens were examined under a Carl Zeiss Stemi 2000-C dissecting microscope. Morphological features were recorded using a Carl Zeiss AxioCam ICc 1 digital camera attached to the microscopes. A paratype was freeze-dried using a Xiangyi CFD-10D, gold coated using an EDT SC-150, and examined under a TESCAN CEGA 3 scanning electron microscope (SEM). Line drawings were made using a Wacom Intuos Pro Pen and Touch Large Tablet.

The taxonomic terms defined by Hutchings and Peart (2002) were used in the species description.

Results

Pectinariidae de Quatrefages, 1866

Pectinaria Savigny in Lamarck 1818: 348

Type species. Nereis cylindraria belgica Pallas, 1766, designated by Hartman (1959)

Pectinaria torquata sp. n.

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http://zoobank.org/DAFE1881-63F0-454B-922B-8E32B878B7CB
Figs 1–3
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Material examined. All type specimens are deposited in the Marine Biological Museum (MBM), Institute of Oceanology, Chinese Academy of Sciences, Qingdao

Holotype. MBM240082: complete specimen, 22°45.17'N, 114°42.98'E (Daya Bay, Guangdong Province), 9.0 m water depth, muddy sand, August 2015.

Paratypes. MBM240083: complete specimen, 22°35.50'N,114°33.22'E (Daya Bay, Guangdong Province), 11.0 m water depth, muddy sand, June 2015. MBM240084: incomplete specimen with 17 anterior segments, 21°39.42'N, 108°34.46'E (Beibu Gulf, Guangxi Province), 9.7 m water depth, muddy sand, August 2015.

Etymology. The specific epithet *torquata* is a Latin adjective for collar, which refers to the elevated collar-like dorsal posterior lobe on segment 2, a distinctive feature for this species.

Diagnosis. Opercular margin smooth. Cephalic veil free from operculum, with 26–38 cirri along the rim. Segments 2 and 20 with a dorsal posterior lobe respectively. Body with 16 chaetigers. Neurochaetal uncini with major teeth arranged in two rows. Scaphe formed by fusion of five posterior segments. Four or five pairs of scaphal hooks.

Description of holotype. Preserved specimen pale cream in color. Body stout with cephalic region enlarged (Figs 1A, 3A–B). Body length 38.5 mm including scaphe, width 9.0 mm at cephalic region. Tube straight, conical, composed of cemented sand grains and shell fragments (Fig. 3C).

Opercular margin raised with smooth edge (Figs 1A–B, 2A, 3A–B). Cephalic veil free from operculum on dorsal side, with 26 cirri distributed along the rim (Figs 1A–B, 2A–B). Operculum with two bundles of paleae, each bundle with 12 stout, flattened, golden bristles curved dorsally and tapering to pointed tip (Figs 1A–B, 2A–B, 3A–B).

Segment 1 with pair of tentacular cirri arising from antero–ventral edge near outer most paleae. Segment 2 with pair of tentacular cirri arising from both sides; tentacular cirri connected by flattened ridge running across venter (Figs 1B, 2A–C), and dorsal posterior lobe running across both sides and dorsum (Figs 1B, 2A, 3A, 3G). Segments 3 with pair of comb-like lateral branchiae, and a median ventral lobe (Figs 1A–2, 2B, 3B). Segments 4 with pair of comb-like lateral branchiae which are smaller than the branchiae on segment 3, a small medial ventral lobe and two large ventral lateral lobes. Segment 5 with a small medial lobe and two large lateral lobes. Segment 6–9 also with pair of ventral lateral lobes but the size gradually decreased posteriorly. Segment 10 and posterior segments without ventral lateral lobes (Figs 1A, 2A, B). Segment 20 with dorsal posterior lobe.

Chaetigers 1–3 (segments 5–7) uniramous with pair of wedge-shaped notopodia only (Fig. 1A–B). Chaetigers 4–16 (segments 8–20) biramous with pair of wedge-shaped notopodia and pair of ear-shaped neuropodia (Fig. 1A–D). Segment 21 with a dorsal posterior lobe and pair of lateral lobes, but without chaetae (Figs 1C–D, 3H–I).



Figure 1. *Pectinaria torquata* sp. n. Holotype MBM240082. **A** ventral view of the whole worm **B** lateral view of anterior body **C** lateral view of the posterior including the scaphe **D** dorsal view of the posterior including the scaphe **E** an uncinus **F** scaphal hooks **G** anterior view of a notochaeta **H** posterior view of a notochaeta. Abbreviations: al, anal lobe; an, anus; br, branchia; c3 chaetiger 3; (segment 7) c16, chaetiger 16 (segment 20); cv cephalic veil; op opercular palea; pp peristomial palp; s2 dpl, dorsal posterior lobe on segment 2; s21 segment 21 sc, scaphe; sh, scaphal hooks; tc, tentacular cirrus.



Figure 2. *Pectinaria torquata* sp. n. paratype MBM240084. **A** lateral view of anterior body **B** ventral view of anterior body **C** tentacular cirri II **D–F** close-up of notochaetae from chaetiger **3 G**, a notochaeta from chaetiger **5 H–J** close-up of notochaeta from chaetiger 12 **K** uncini from chaetiger 12 Abbreviations: br, branchia; c4, chaetiger 4 (segment 8); cv, cephalic veil; op, opercular palea; pp, peristomial palp; s2 dpl, dorsal posterior lobe on segment 2; s2 vl, ventral lobe on segment 2; tc, tentacular cirrus.

Notopodia with two kinds of capillaries forming bundle: both with finely hirsute surface on anteromedian margin and smooth surface on posterior margin; one kind with serrations along anterior portion of tip; the other kind smooth, tapering to very acute tip (Figs 1G–H, 2D–J). Neuropodia with uncini arranged in row along the ridge, each uncinus with major teeth arranged in two rows, 7–8 teeth per row (Figs 1E, 2K).

Scaphe distinctly separated from segment 21 (Figs 1A, 3A–B), formed by fusion of five posterior segments. Scaphe longer than broad, arched ventrally and flattened dorsally with crenulated lateral margin (Figs 1B–C, 3D, H–I). Anal flap tongue-shaped



Figure 3. *Pectinaria torquata* sp. n., holotype MBM240082. **A** dorsal view of whole specimen **B** ventral view of whole specimen **C** tube **D** dorsal view of posterior end **E** anal flap **F** scaphal hooks **G** lateral view of anterior end **H** ventral view of posterior end. Paratype MBM240083 **I** lateral view of posterior end. Abbreviations: al, anal lobe; br, branchia; c4, chaetiger 4 (segment 8); c16, chaetiger 16 (segment 20); cv, cephalic veil; op, opercular palea; pp, peristomial palp; s2 dpl, dorsal posterior lobe on segment 2; s20 dpl, dorsal posterior lobe on segment 20; s21, segment 21; sc, scaphe; sh, scaphal hooks; tc, tentacular cirrus.

with tip extending beyond posterior scaphal edge; anal flap margin crenulated (Figs 1D, 3D–E). Scaphal hooks short, barely visible, with a curved blunt tip; five on right and four on left; present in the dorsolateral region of scaphe, approximately half way between the junction with segment 21 and the posterior edge (Figs 1F, C–D, 3F, I).

Variation. Comparison among the types shows that the body width in the cephalic region varies from 8 to 10 mm. The number of paleae varies from 11 to 12 pairs. The number of cirri on the cephalic veil margin varies from 26 to 32. The number of scaphal hooks varies from 4 to 5 pairs. Since there are only two complete and one
Pectinaria.
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Table I. Major diagno	stic characters (of Pectinaria.							
	Number	Number of	Doctorodoreal laho	Rows of major	Middosal	Scaphal he	oks	Dietrihu-	
Species	of cirri on cephalic veil	pairs of paleae	in segment 2	teeth per uncinus	anal cirrus of anal flap	Type	Number of pairs	tion	Literatures cited
Pectinaria aegyptia (Savigny, 1818)	60–65	15–17	n.r.	2	present	pointed, strongly curved	4-5,	Red Sea, Japan	Hutchings and Peart 2002, Nishi et al. 2014
<i>P. antipoda</i> Schmarda, 1861	17–29	5-13	absent	2-4	present	blunt, curved or spiral	6-8	Australia	Hutchings and Peart 2002, Hutchings 2015
P. belgica (Pallas, 1766)	17–28	8–15	absent	2-4	present	pointed	6-12	Sweden, Japan	Hutchings and Peart 2002, Nishi et al. 2014
<i>P. brevispinis</i> Grube, 1878	22–30	10-13	absent	2	absent	blunt	8-14	Philippines, Indonesia	Nilsson1928, Hartman 1941
<i>P. californiensis</i> Hart- man, 1941	18–30	13-14	n.r.	2	present	pointed, slight curved	13	Southern California	Hartman 1941
P. c. newportensis Hartman, 1941	19	12–14	n.r.	2	present	pointed, curved	12–13	California	Hartman 1941
P. carnosus Wong & Hutchings, 2015	16	6	absent	2	absent	blunt, slight curved	6	Lizard Island	Wong and Hutchings 2015
P. clava Grube, 1878	10-12	11	absent	3	n.r.	pointed	9	Lapinig Canal, Philippines	Hutchings and Peart 2002, Nilsson 1928
P. chilensis (Nilsson, 1928)	30-60	8-10	n.r.	2	present	slight curved	13-15	Coronel, Chile	Hartman 1941, Moreno et al. 2004
<i>P. torquata</i> sp. n.	26–32	11-12	present	2	absent	blunt, curved	45	South China Sea	This study
<i>P. conchilega</i> Grube, 1878	12	11	absent	3-4	absent	pointed, curved	4	Bohol, Phil- ippines	Nilsson1928
P. dimai Zachs, 1933	n.r.	n.r.	n.r.	3-4	n.r.	n.r.	n.r.	North Japan Sea	Zachs1933, Hutchings and Peart 2002
<i>P. dodeka</i> Hutchings & Peart, 2002	16–28	11-13	absent	2-4	present	pointed, stongly curved	6-10	Queensland, Australia	Hutchings and Peart 2002

	Number	Number of	Doctorrodoreol laka	Rows of major	Middosal	Scaphal ho	oks	Dietrihu	
Species	of cirri on cephalic veil	pairs of paleae	in segment 2	teeth per uncinus	anal cirrus of anal flap	Type	Number of pairs	tion	Literatures cited
gouldii (Verrill, 1874)	12–38	9–15	n.r.	2-4	present	Lanciform, pointed, strait or slight curved	8–22	Long Island Sound	Hartman 1941, Long 1973
' <i>hartmanae</i> Reish, 968	30	8-10	n.r.	2	present	blunt	8-10	California, USA	Reish 1968
? <i>biuchiensis</i> Kitamori, 965	32-35	9-10	absent	2	absent	pointed, slight curved	8-9	Kyushu, Japan	Nishi et al. 2014
? kanabinos Hutchings & Peart, 2002	10-16	12–14	absent	2-4	present	pointed, stongly curved	4–6	Queensland, Australia	Hutchings and Peart 2002
? <i>longisp inis</i> Grube, 1878	17	13	absent	n.r.	n.r.	n.r.	4	Philippines	Grube 1878, Hutchings and Peart 2002
P. meredithi Long, 1973	16–21	8-11	n.r.	2–3	present	pointed, strait or slight curved	6-7	Bahamas and Florida Kevs	Long 1973
P. nana Wesenberg- Jund, 1949	8	11	absent	n.r.	present	n.r.	e,	Gulf of Oman Iran	Wesenberg-Lund 1949
P. okudai (Imajima & Hartman, 1964)	10-15	13–16	absent	3-4	present	pointed, slight curved	12-13	Japan	Nishi et al. 2014
P. panava Willey, 1905	32	10	n.r.	n.r.	n.r.	n.r.	7	Sri Lanka	Hutchings and Peart 2002
P. papillosa Caullery, 1944	24-46	11-13	absent	2	absent	n.r.	3-11	Indonesia	Day 1951
P. parvibranchis Grube, 1878	12-13	10-11	absent	3-4	n.r.	pointed	4	Pangloo, Philippines	Nilsson 1928, Hartman 1941, Hutchings and Peart 2002
<i>P. profunda</i> Caullery, 1944	20	12	n.r.	2	present	n.r.	n.r.	Indonesia	Hutchings and Peart 2002
P. regalis (Verrill, 1901)	21–35	8-14	absent	2–3	present	pointed, strait	0-4	Cony Island, Bermuda	Hartman 1941, Long 1973

n.r. character not recorded.

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incomplete specimens of similar sizes, intraspecific variation amongst these morphological characters may have been underestimated.

Type locality and distribution. Currently only known from Daya Bay (Guangdong Province) and Beibu Gulf (Guangxi Province) in the northern South China Sea.

Remarks. Pectinaria torquata sp. n. can be distinguished from the other 25 described species of *Pectinaria* by several features (Table 1). First, it has a dorsal posterior lobe on segment 2, which is unique among the described species of *Pectinaria* species. This structure is prominent in the type specimens, and does not change by preservation. Second, P. torquata sp. n. has a dorsal posterior lobe on both segment 20 and 21, a feature that has not been reported from any other recognized species in this genus (Hartman 1941, Long 1973, Hutchings and Peart 2002, Nishi et al. 2014, Wong and Hutchings 2015). Third, P. torquata sp. n. has only 4-5 pairs of small blunt scaphal hooks, which is fewer than those in most described species. Fourth, the anal flap lacks a middorsal anal cirrus with a crenulated margin. There are eight species in which the dorsal posterior lobe on segment 2 is not recorded (Table 1). Except for Pectinaria dimai Zachs, 1933 and Pectinaria panava Willey, 1905 for which the middosal anal cirrus is not described, the other five species have a middorsal anal cirrus; *P. torquata* sp. n. lacks a middorsal anal cirrus (Table 1). Furthermore, it differs from *P. dimai* which has 3–4 rows of major teeth on each uncinus, and 6-7 teeth per row; P. torquata sp. n. has 2 rows of major teeth, and 7-8 teeth per row. Pectinaria panava has more scaphal hooks than P. torquata sp. n.

A key to eleven species of Pectinariidae, including *Ptorquata* sp. n., that have been recorded from the South China Sea in the literature is provided below (Wu and Chen 1985, Yang and Sun 1988, Paxton and Chou 2000, Sun and Qiu 2012, Salazar-Vallejo et al. 2014, Zhang et al. 2015, Glasby et al. 2016). The genera *Petta* and *Cistenides* have not been recorded in the South China Sea.

Key to eleven species of Pectinariidae from the South China Sea

1	Opercular rim smooth
_	Opercular rim cirrate
2	Less than 15 pairs of scaphal hooks
_	More than 15 pairs of scaphal hooks
3	5–8 pairs of scaphal hooks; opercular rim with cirri
	Amphictene capensis (Pallas, 1776
_	12 pairs of scaphal hooks; opercular rim with denticles
	Amphictene leioscapha (Caullery, 1944
4	19-24 pairs of scaphal hooks; without pair of dorsolateral lobes on segmen
	3 Amphictene japonica Nilsson, 1928
_	26-37 pairs of scaphal hooks; with pair of dorsolateral lobes on segment 3
5	Cephalic veil laterally attached
_	Cephalic veil free

6	Branchiae absent Lagis crenulatus Sun & Qiu, 2012
_	Branchiae present
7	Margins of anal lobe with long fringes Lagis bocki (Hessle, 1917)
_	Margins of anal lobe without fringes
8	Segment 2 with a posterodorsal lobe Pectinaria torquata sp. n.
_	Segment 2 without a posterodorsal lobe
9	6–8 pairs of scaphal hooks; anal flap with a small cirrus
_	3-4 pairs of scaphal hooks; anal flap without anal cirrus10
10	Cephalic veil with 24–46 cirri; major teeth of uncini in 2 rows
_	Cephalic veil with 12 cirri; major teeth of uncini in 3–4 rows
	Pectinaria conchilega Grube, 1867

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CORRIGENDA



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After our manuscript has been published, we have noticed in our acknowledgment section that the name and the code of our funding program were incorrect. Here, we provide the first sentence of the modified acknowledgment using the correct name and code.

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