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Two new species of genus *Oecleopsis* Emeljanov from China, with descriptions of female genitalia of five species (Hemiptera, Fulgoromorpha, Cixiidae)

Yan Zhi[1,2,3], Lin Yang[1,2], Pei Zhang[4], Xiang-Sheng Chen[1,2]

1 *Institute of Entomology, Guizhou University, Guiyang, Guizhou, 550025, P.R. China* **2** *The Provincial Special Key Laboratory for Development and Utilization of Insect Resources of Guizhou, Guizhou University, Guiyang, Guizhou, 550025, P.R. China* **3** *Laboratory Animal Center, Guizhou Medical University, Guiyang, Guizhou, 550025, P.R. China* **4** *Xingyi Normal University for Nationalities, Xingyi, Guizhou, 562400, P.R. China*

Corresponding author: *Xiang-Sheng Chen* (chenxs3218@163.com)

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Abstract

Two new species of genus *Oecleopsis* Emeljanov, 1971, *O. laminatus* Zhi & Chen, **sp. n.** and *O. productus* Zhi & Chen, **sp. n.**, and a new record, *O. yoshikawai* (Ishihara, 1961), are described and illustrated from China. Female genitalia of five species within this genus are compared morphologically: *O. laminatus* Zhi & Chen, **sp. n.**, *O. mori* (Matsumura, 1914), *O. productus* Zhi & Chen, **sp. n.**, *O. sinicus* (Jacobi, 1944) and *O. yoshikawai* (Ishihara, 1961). A key to five Chinese species based on female genitalia, and a key to all known species of *Oecleopsis* based on male genitalia, are provided.

Keywords

Female genitalia, Fulgoroidea, morphology, Pentastirini, planthopper, taxonomy

Introduction

Emeljanov (1971) established the cixiid planthopper genus *Oecleopsis* with *Oliarus artemisiae* Matsumura, 1914 as its type species. This genus belongs to the tribe Pentastirini of subfamily Cixiinae (Hemiptera: Cixiidae). Van Stalle (1991) and Guo et al. (2009) studied this genus, bringing the total of known species to twelve: *Oecleopsis artemisiae* (Matsumura, 1914), *O. articara* Van Stalle, 1991, *O. bifidus* (Tsaur, Hsu & Van Stalle, 1988), *O. chiangi* (Tsaur, Hsu & Van Stalle, 1988), *O. elevatus* (Tsaur, Hsu & Van Stalle, 1988), *O. mori* (Matsumura, 1914), *O. petasatus* (Noualhier, 1896), *O. sinicus* (Jacobi, 1944), *O. spinosus* Guo, Wang & Feng, 2009, *O. tiantaiensis* Guo, Wang & Feng, 2009, *O. wuyiensis* Guo, Wang & Feng, 2009 and *O. yoshikawai* (Ishihara, 1961).

Herein, two new species: *Oecleopsis laminatus* Zhi & Chen, sp. n. and *O. productus* Zhi & Chen, sp. n. are described and illustrated from China (Yunnan province), and *O. yoshikawai* (Ishihara, 1961) is recorded from China for the first time. The genus now contains fourteen species, and all species from China.

Female genitalia of *Oecleopsis* are known relatively little: genitalia in ventral view and anal segment in dorsal view of *O. articara*, *O. sinicus*, *O. spinosus* and *O. tiantaiensis* and the anal segment of *O. mori* were illustrated; *O. bifidus*, O. el*evatus*, *O. petasatus* and *O. wuyiensis* were described briefly (Fennah 1956; Tsaur et al. 1988; Van Stalle 1991; Guo et al. 2009). These characters of external genitalia are not effective to distinguish among species of *Oecleopsis*. Zhi et al. (2017) discussed external and internal structures of female genitalia in cixiid planthoppers and found that the characteristics of posterior vaginal walls can be considered as key diagnostic features for female identification in genus *Neocarpia*. Using the characters of posterior vagina in species identification is also practicable in genus *Oecleopsis* by comparing female genital morphological features of five species (other species are not included, as we do not have the female specimens): *Oecleopsis laminatus*, *O. mori*, *O. productus*, *O. sinicus* and *O. yoshikawai*. A key to five Chinese species based on female genitalia, and a key to all known species of *Oecleopsis* based on male genitalia, are provided.

Materials and methods

The morphological terminology and measurements follow Tsaur et al. (1988), Bourgoin et al. (2015) and Van Stalle (1991). The morphological terminology of female genitalia follows Bourgoin (1993). Body length was measured from apex of vertex to tip of forewing; vertex length was measured the median length of vertex (from apical transverse carina to tip of basal emargination). External morphology and drawings were done with the aid of a Leica MZ 12.5 stereomicroscope. Photographs of female genitalia were taken with Nikon SMZ25 and other photographs with KEY-

ENCE VHX-1000 system. Illustrations were scanned with CanoScan LiDE 200 and imported into Adobe Photoshop CS7 for labeling and plate composition. The dissected male genitalia are preserved in glycerine in small plastic tubes pinned together with the specimens.

The type specimens examined are deposited in the Institute of Entomology, Guizhou University, Guiyang, Guizhou Province, China (**GUGC**).

Taxonomy

Oecleopsis Emeljanov, 1971

Oecleopsis Emeljanov, 1971: 621; Anufriev and Emeljanov 1988: 460; Van Stalle 1991: 20; Guo et al. 2009: 46.

Type species. *Oliarus artemisiae* Matsumura, 1914, original designation.

For the relationship and diagnosis of *Oecleopsis* see Van Stalle (1991: 20) and Guo et al. (2009: 46).

Distributions. China, Japan, Korea, Russia, Thailand, Malaya, Cambodia, Borneo.

Checklist and distributions of species of *Oecleopsis*

O. artemisiae (Matsumura, 1914); China (Sichuan), Japan, Korea, Russia (Kunashir Island).
O. articara Van Stalle, 1991; China (Hainan, Henan, Sichuan), Malaya, Borneo.
O. bifidus (Tsaur, Hsu & Van Stalle, 1988); China (Fujian, Taiwan).
O. chiangi (Tsaur, Hsu & Van Stalle, 1988); China (Taiwan).
O. elevatus (Tsaur, Hsu & Van Stalle, 1988); China (Guizhou, Taiwan), Japan (Honshu).
O. laminatus Zhi & Chen, sp. n.; China (Yunnan).
O. mori (Matsumura, 1914); China (Guangxi, Taiwan, Yunnan).
O. productus Zhi & Chen, sp. n.; China (Yunnan).
O. petasatus (Noualhier, 1896); China (Hainan, Sichuan, Yunnan), Cambodia.
O. sinicus (Jacobi, 1944); China (Anhui, Fujian, Guangxi, Guizhou, Henan, Hunan, Shanxi, Sichuan), Japan.
O. spinosus Guo, Wang & Feng, 2009; China (Shaanxi).
O. tiantaiensis Guo, Wang & Feng, 2009; China (Shaanxi).
O. wuyiensis Guo, Wang & Feng, 2009; China (Fujian, Henan, Hunan, Shaanxi).
O. yoshikawai (Ishihara, 1961); China (Guizhou), Thailand (Chiengmai).

Key to five Chinese species (females) of *Oecleopsis*

1 Basal sclerite on right side of posterior vagina with a process ventrally **2**
– Basal sclerite on right side of posterior vagina without process ventrally (Figs 63–64) .... ***O. sinicus***
2 Right side of posterior vagina with a triangular sclerite ventrally (Figs 51–52) .... ***O. laminatus* sp. n.**
– Right side of posterior vagina without triangular sclerite ventrally **3**
3 Terminal area on right side of posterior vagina with a long and narrow sclerite, curved, towards the right ventrally (Figs 55–56) .... ***O. mori***
Without the same sclerite ventrally **4**
4 Right side of posterior vagina with one sclerite, which constricted medially in ventral view (Figs 59–60) .... ***O. productus* sp. n.**
– Right side of posterior vagina with two sclerites, terminal irregular sclerite forming three projecting oblong structures in ventral view (Figs 67–68) .... ***O. yoshikawai***

Key to species (males) of the genus *Oecleopsis* (revised from Van Stalle (1991) and Guo et al. (2009))

1 Spinose process on right side near apex of periandrium long, longer than 1/2 length of periandrium **2**
– Spinose process on right side near apex of periandrium short, not longer than 1/4 length of periandrium **9**
2 Apex of flagellum circular **3**
– Apex of flagellum not circular **4**
3 Left side near apex of periandrium with a short spinose process; dorsal margin of flagellum with a long spinose process and left side with a short process (Figs 31–34) .... ***O. productus* sp. n.**
– Left side of periandrium without spinose process; dorsal margin of flagellum without process and left side with a long process (Van Stalle 1991: fig. 79) .... ***O. articara***
4 Apical process of flagellum not bifurcated (Figs 45–48) .... ***O. yoshikawai***
– Apical process of flagellum bifurcated **5**
5 Flagellum with a large laminal process (Figs 17–20) .... ***O. laminatus* sp. n.**
– Flagellum without laminal process **6**
6 Left side near base of flagellum with a spinose process (Van Stalle 1991: fig. 72) .... ***O. petasatus***
– Left side of flagellum without process **7**
7 Flagellum with one subapical process (Tsaur et al. 1988: fig. 9 (C–D)) ... ***O. bifidus***
– Flagellum with two subapical processes **8**

8 Two subapical processes of flagellum short, much shorter than apical process (Anufriev and Emeljanov 1988: fig. 358; Van Stalle 1991: fig. 101) .... ***O. artemisiae***

– Two subapical processes of flagellum long, nearly equal to apical process in length (Tsaur et al. 1988: fig. 10 (F–G)) .... ***O. elevatus***

9 Apical process of flagellum not bifurcated **10**

– Apical process of flagellum bifurcated **11**

10 Spinose process on right side of periandrium rather short, directed ventrally; vertex 2.6 times longer than wide (Guo et al. 2009: fig. 10–11)..... ***O. spinosus***

– Spinose process on right side of periandrium longer, directed dorsocephalically; vertex 1.5 times longer than wide (Tsaur et al. 1988: fig. 8 (C–D))...... .... ***O. chiangi***

11 Rami of bifurcation symmetrical, almost equal in length (Van Stalle 1991: fig. 92) .... ***O. sinicus***

– Rami of bifurcation asymmetrical, unequal in length **12**

12 Left ramus of bifurcation rudimentary, only a small protuberance (Guo et al. 2009: figs 20–21) .... ***O. tiantaiensis***

– Left ramus of bifurcation well developed **13**

13 Length of right ramus of apical process about 1.8 times as long as that of left ramus, ventral margin near base of periandrium with a spinose process (Guo et al. 2009: figs 31–32) .... ***O. wuyiensis***

– Length of right ramus of apical process about 3.0 times as long as that of left ramus, ventral margin near base of periandrium without process (Van Stalle 1991: fig. 85) .... ***O. mori***

Oecleopsis laminatus **Zhi & Chen, sp. n.**

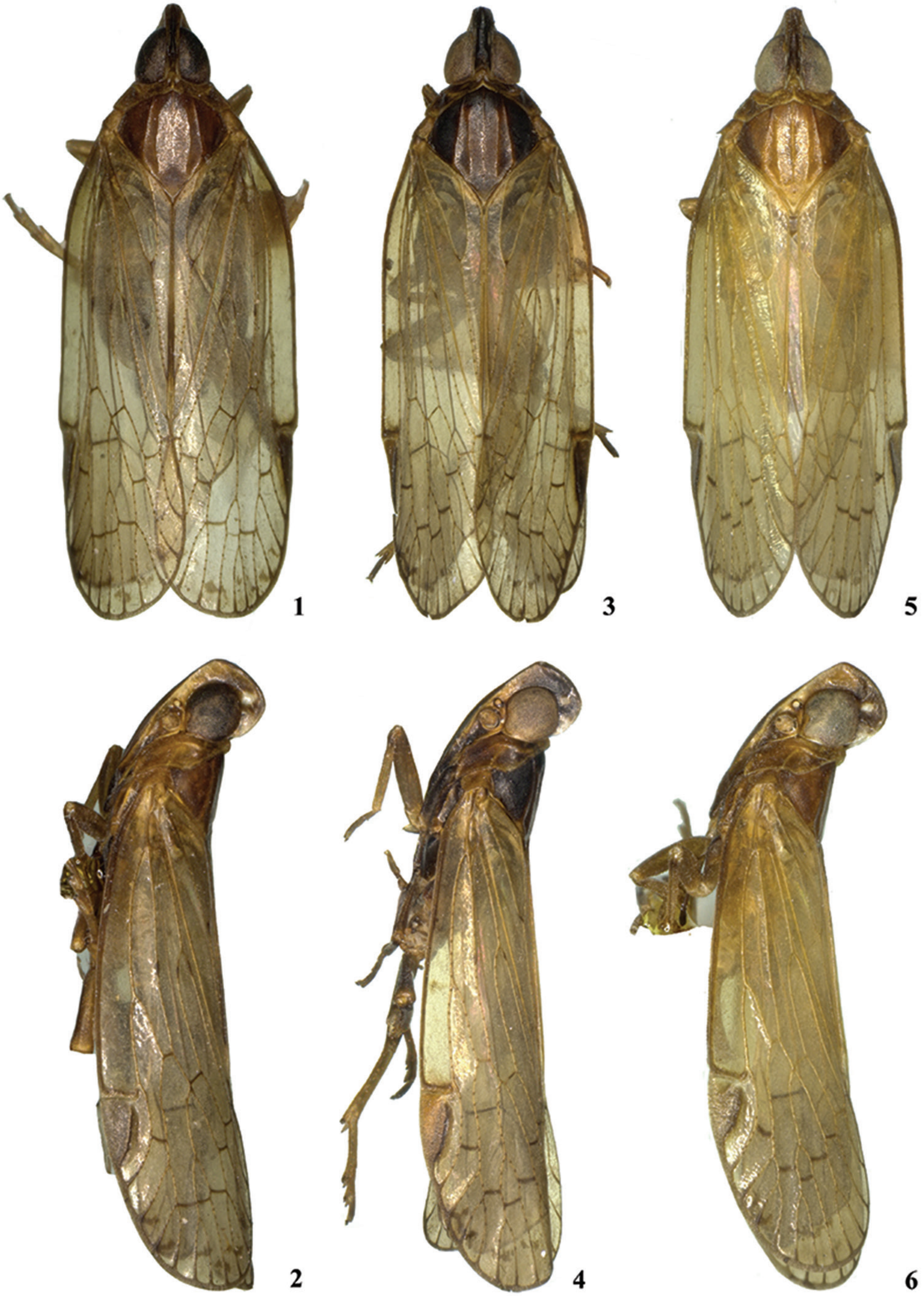
http://zoobank.org/D59DDB8B-7041-46DD-A5A5-E197C5B049FA

Figs 1–2, 7–20, 49–52

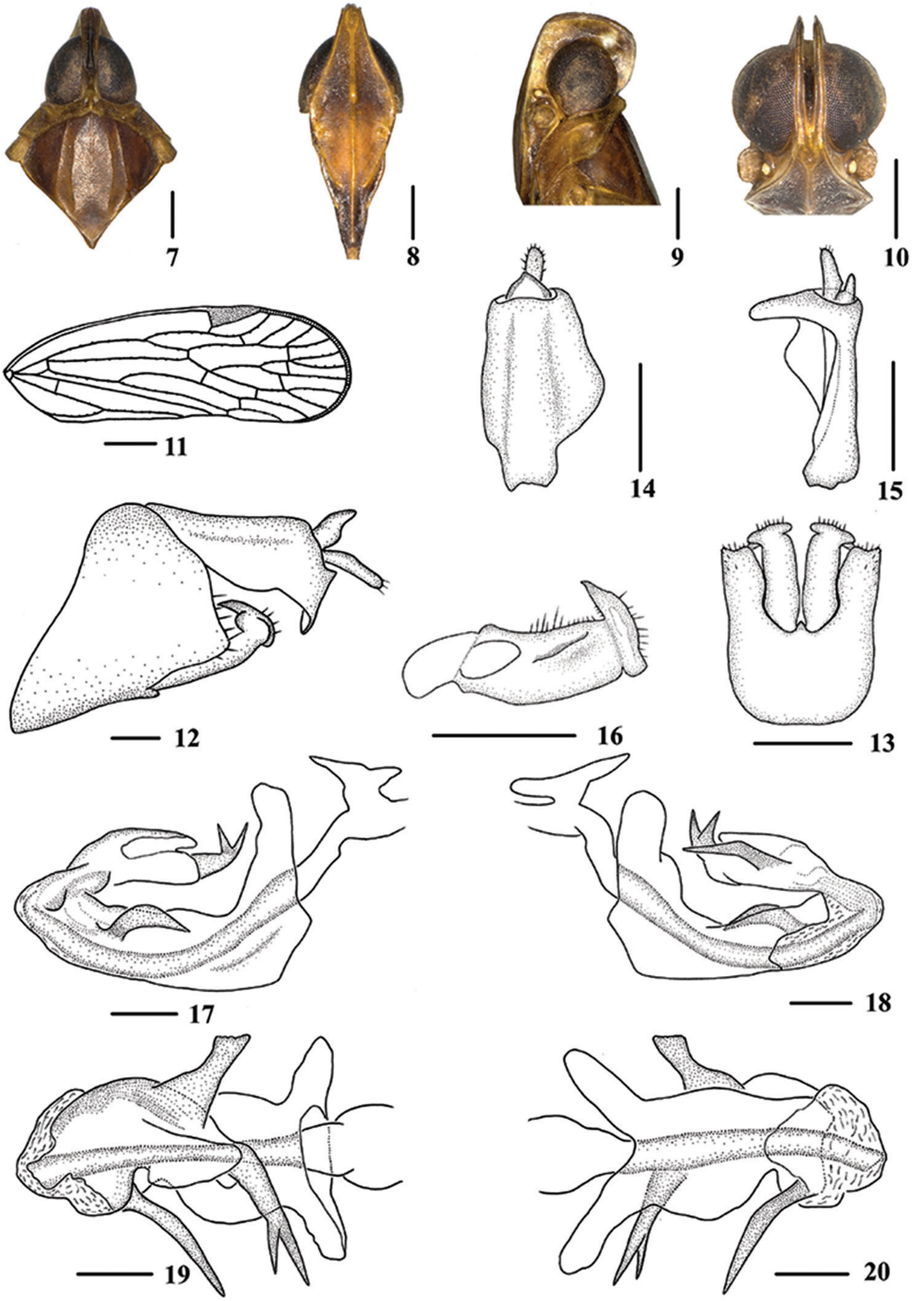
Type material. Holotype: ♂, **China:** Yunnan Province, Jingdong County, Taizhong Town (24°30'N, 100°56'E), 18 August 2009, Bin Zhang; paratypes: 1♂, 2♀♀, same data as holotype; 1♀, Yunnan Province, Jingdong County, Dajie Town, 22 August 2009, Bin Zhang; 3♂♂, 2♀♀, Yunnan Province, Lanping County, Lajin Town, 4 August 2012, Yong-Gang Xiao.

Description. Body length: male 6.7–7.7mm (*N* = 5), female 7.0–9.0mm (*N* = 5).

Coloration. General color mid brown (Figs 1–2, 7–10). Eyes mid brown, ocelli yellowish brown. Vertex blackish brown. Face yellowish to blackish brown, carinae lighter; rostrum blackish brown. Pronotum mid to blackish brown with carinae yellowish or light brown; mesonotum mid to blackish brown, sometimes area between lateral carinae lighter. Forewing semi-translucent, light brown, stigma yellowish or mid brown. Hind tibiae and abdominal sternites mid brown.



Figures 1–6. *Oecleopsis* species (male). **1–2** *O. laminatus* sp. n. **1** dorsal view **2** lateral view **3–4** *O. productus* sp. n. **3** dorsal view **4** lateral view **5–6** *O. yoshikawai* **5** dorsal view **6** lateral view.



Figures 7–20. *Oecleopsis laminatus* sp. n., male **7** Head and thorax, dorsal view **8** Face, ventral view **9–10** Head **11** Forewing **12** Genitalia, lateral view **13** Pygofer and genital styles, ventral view **14–15** Anal segment **14** dorsal view **15** right lateral view **16** Genital styles, inner lateral view **17** Aedeagus, right side **18** Aedeagus, left side **19** Aedeagus, dorsal view **20** Aedeagus, ventral view. Scale bars: 0.5 mm (**7–10, 12–20**); 1.0 mm (**11**).

Head and thorax. Vertex (Fig. 7) narrow, 4.3 times longer than wide; Frons (Fig. 8) 1.3 times as long as wide. Forewing (Fig. 11) 3.0 times longer than wide, with 11 apical and 6 subapical cells; fork Sc+RP distal to fork CuA1+CuA2; RP 3 branches, MA 3 branches, MP 2 branches. Hind tibia with 3–4 lateral spines; chaetotaxy of hind tarsi: 7/5.

Male genitalia. Pygofer (Figs 12–13) dorsal margin concave and U-shaped ventrally, widened towards apex; in lateral view, lateral lobes triangularly extended caudally. Medioventral process triangular ventrally. Anal segment (Figs 12, 14–15) tubular, asymmetrical, widened towards apex in left side view; in right side view, left ventral margin convex and right ventral margin excavated near apex; 1.9 times longer than wide in dorsal view; anal style fingerlike, beyond anal segment. Genital styles illustrated in Fig. 16. Aedeagus (Figs 17–20) in total with four processes. Spinose process on right side near apex of periandrium long, directed right side, more than 1/2 length of periandrium. Flagellum terminating into a bifurcate process, asymmetrical; left side near apex of flagellum with a large laminal process, apex transversal and directed left side.

Female genitalia. Genitalia as shown in Fig. 49 ventrally. Anal tube (Fig. 50) 1.8 times longer than wide in dorsal view. Posterior vagina (Figs 51–52) elongate, with a long longitudinal sclerite dorsally, large. In ventral view, left side with a long longitudinal sclerite; right side with a rhombic sclerite basally, which with a process, the process directed left-ventrally and longer than shown in the figure, terminal area with a triangular sclerite.

Distribution. China (Yunnan).

Etymology. The specific name is derived from the Latin word "*laminatus*", referring to the left side of flagellum with a large laminal process.

Remarks. Male genitalia of *O. laminatus* sp. n. is similar to *O. bifidus*, but differs in: (1) left side near apex of flagellum with a laminal process, apex transversal and directed left side (in *O. bifidus*, with a spinose process, apex pointed, curved right-dorsally); (2) process on right side of periandrium directed right side (directed left side slightly in *O. bifidus*); (3) left ramus of bifurcate process longer than right one (in *O. bifidus*, left ramus of bifurcate process shorter than right one); (4) vertex rather narrow, about 4.3 times longer than wide (in *O. bifidus*, about 1.6 times).

Female genitalia of *O. laminatus* sp. n. is similar to *O. mori*, but differs in: (1) terminal area on right side of posterior vagina with a triangular sclerite in *O. laminatus* (the sclerite long and narrow, curved, towards the right in *O. mori*); (2) left side of posterior vagina with a straight sclerite ventrally in *O. laminatus* (the sclerite in the same position much longer and curved, towards the right in *O. mori*).

Oecleopsis mori **(Matsumura, 1914)**

Figs 53–56

Oliarus mori Matsumura, 1914: 426; Tsaur et al. 1988: 48, fig. 7 (A–G).
Oecleopsis mori (Matsumura, 1914): Van Stalle 1991: 23, figs 85–91; Guo et al. 2009: 50.

Material examined. China: 7♂♂, 11♀♀, Guangxi Province, Jinxiu County, Lianhua Mountain, 30 April 2011, Xiao-Fei Yu, Rong Huang; 3♂♂, 2♀♀, Guangxi Province, Wuming County, Daming Mountain, 14 May 2011, Rong Huang; 6♂♂, 12♀♀, Guangxi Province, Wuming County, Daming Mountain, 14–15 May 2012, Rong Huang, Hu Li, Wei-Cheng Yang, Zhi-Hua Fan.

Supplementary description. *Female genitalia*. Genitalia as shown in Fig. 53 ventrally. Anal tube (Fig. 54) 1.8 times longer than wide in dorsal view. Posterior vagina (Figs 55–56) elongate, with a long longitudinal sclerite dorsally, large. In ventral view, left side with a long longitudinal sclerite, curved, towards the right; right side with a longitudinal sclerite basally, which with a torsional oblong sclerite and a process, the process directed left-ventrally and longer than shown in the figure; terminal area with a long and narrow sclerite, curved, towards the right.

Distributions. China (Guangxi, Taiwan, Yunnan).

Note. The female genitalia of this species is described and illustrated in detail for the first time.

Oecleopsis productus **Zhi & Chen, sp. n.**

http://zoobank.org/AD015429-772E-4B7F-809D-5CD8CBE35EF9

Figs 3–4, 21–34, 57–60

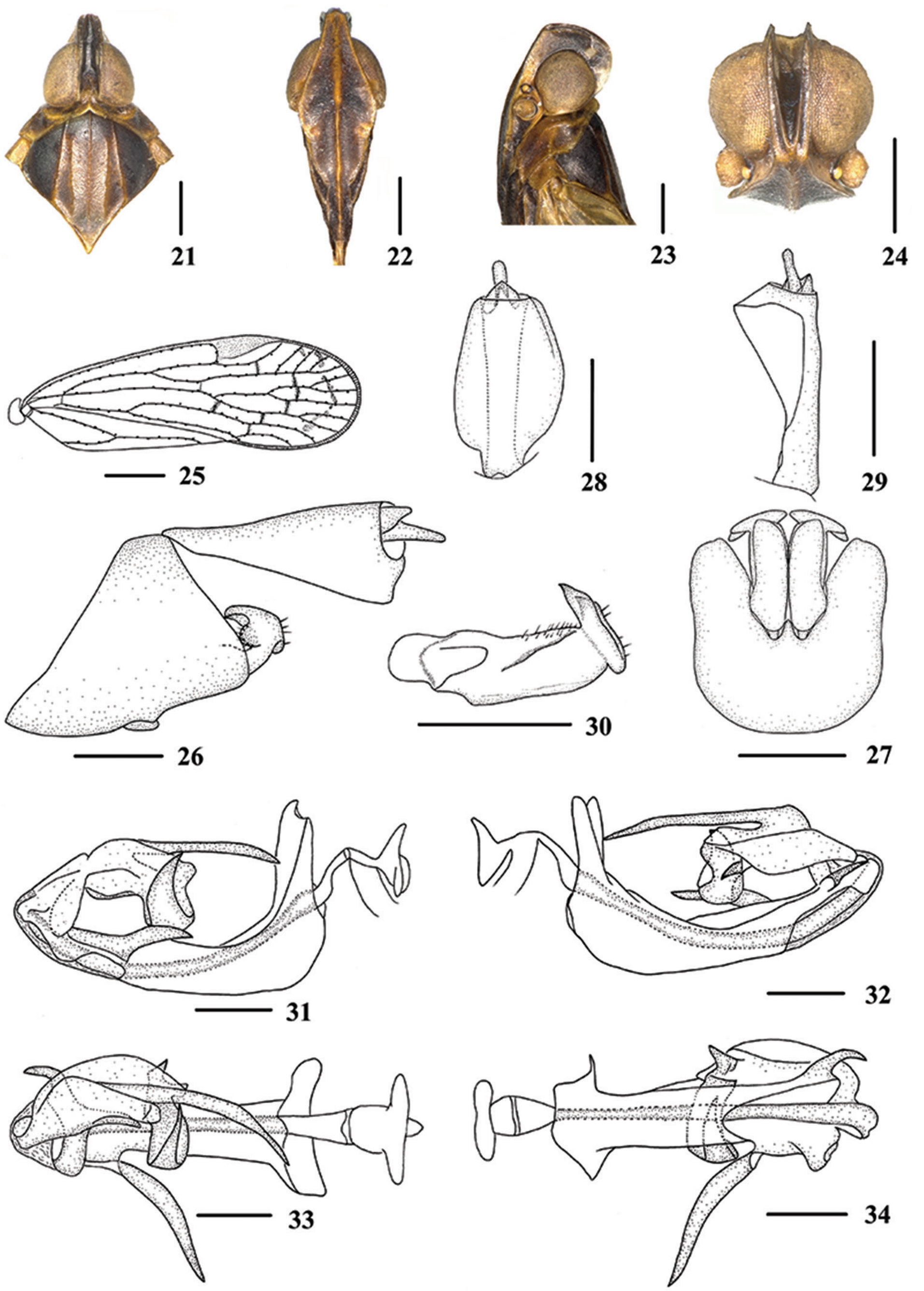
Type material. Holotype: ♂, **China:** Yunnan Province, Baoshan, Baihua ridge (25°17'N, 98°48'E), 15 June 2011, Jian-Kun Long; paratypes: 1♂, 14♀♀, same data as holotype, 13–15 June 2011; 3♂♂, 1♀, collection area same as holotype, 6 May 2010, Bin Zhang, Yan-Li Zheng; 2♂♂, 1♀, Fugong County, Yunnan Province, 17 May 2011, Bin Zhang, Yan-Li Zheng, Bin Yan.

Description. Body length: male 6.7–6.9mm ($N = 7$), female 6.7–7.8mm ($N = 16$).

Coloration. General color blackish brown (Figs 3–4, 21–24). Eyes mid brown, ocelli light yellow. Vertex blackish brown. Face mid to blackish brown, carinae lighter; rostrum mid to blackish brown. Pronotum mid to blackish brown with carinae lighter; mesonotum mid to blackish brown, area between lateral carinae lighter. Forewing semi-translucent, light brown, stigma mid brown. Hind tibiae and abdominal sternites blackish brown.

Head and thorax. Vertex (Fig. 21) narrow, 3.5 times longer than wide; frons (Fig. 22) 1.7 times as long as wide. Forewing (Fig. 25) 3.0 times longer than wide, with 12 apical and 6 subapical cells; fork Sc+RP distal to fork CuA1+CuA2; RP 4 branches, MA 3 branches, MP 2 branches. Hind tibia with 4 lateral spines; chaetotaxy of hind tarsi: 7/5.

Male genitalia. Pygofer (Figs 26–27), dorsal margin concave and U-shaped ventrally, widened towards apex; in lateral view, lateral lobes triangularly extended caudally. Medioventral process narrowly triangular ventrally. Anal segment (Figs 26, 28–29) tubular, asymmetrical, widened towards apex in left side view; in right side view, left ventral margin convex and right ventral margin excavated near apex; 1.8 times longer than wide in dorsal view; anal style fingerlike, beyond anal segment. Genital styles il-



Figures 21–34. *Oecleopsis productus* sp. n., male **21** Head and thorax, dorsal view **22** Face, ventral view **23–24** Head **25** Forewing **26** Genitalia, lateral view **27** Pygofer and genital styles, ventral view **28–29** Anal segment **28** dorsal view **29** right lateral view **30** Genital styles, inner lateral view **31** Aedeagus, right side **32** Aedeagus, left side **33** Aedeagus, dorsal view **34** Aedeagus, ventral view. Scale bars: 0.5 mm (**21–24, 26–34**); 1.0 mm (**25**).

lustrated in Fig. 30. Aedeagus (Figs 31–34) in total with five processes. Spinose process on right side near apex of periandrium long, directed right-dorsocephalically, more than 1/2 of periandrium in length; left side near apex of periandrium with a short reversed spinose process, curving slightly, directed dorsocaudally. Flagellum tapering, apex curved in a semi-circle; a long spinose process arising from dorsal margin, reaching to basal margin of periandrium, curving right side, directed ventrocephalically; left side with a short triangular process, directed ventrocephalically.

Female genitalia. Genitalia as shown in Fig. 57 ventrally. Anal tube (Fig. 58) 1.9 times longer than wide in dorsal view. Posterior vagina (Figs 59–60) elongate, with a long longitudinal sclerite dorsally, large. In ventral view, left side with a long longitudinal sclerite, semi-sclerotized, right side with a large median constricted sclerite, which with a process, the process directed left-ventrally and longer than shown in the figure.

Distribution. China (Yunnan).

Etymology. The specific name is derived from the Latin *productus*, referring to the dorsal margin of flagellum with a long process.

Remarks. Male genitalia of *O. productus* sp. n. is similar to *O. articara*, but differs in: (1) left side near apex of periandrium with a short process (in *O. articara*, left side without process); (2) a very long spinose process arising from dorsal margin of flagellum (dorsal margin of flagellum without process in *O. articara*); (3) left side near apex of flagellum with a very short process (in *O. articara*, left side near middle of flagellum with a much longer process); 4) forewing with RP 4 branches (in *O. articara*, 3 branches).

Female genitalia of *O. productus* sp. n. is similar to *O. yoshikawai*, but differs in: (1) right side of posterior vagina with one sclerite, which constricted medially in ventral view in *O. productus* (with two sclerites, terminal irregular sclerite forming three projecting oblong structures in ventral view in *O. yoshikawai*); (2) in ventral view, distal part of the sclerite on left side of posterior vagina not extended and curved to right in *O. productus* (extended and curved to right in *O. yoshikawai*).

Oecleopsis sinicus **(Jacobi, 1944)**

Figs 61–64, 69

Mnemosyne sinica Jacobi, 1944: 12.

Oliarus sinicus (Jacobi, 1944): Van Stalle 1988: 46.

Oliarus cucullatus Noualhier, 1896: 255; Fennah 1956: 453, fig. 3(G–H) (misidentification); Chou et al. 1985: 23, fig. 20 (misidentification).

Oecleopsis sinicus (Jacobi, 1944), Van Stalle 1991: 23, figs 92–100; Guo et al. 2009, 51, figs 1–6.

Material examined. China: 3♂♂, 2♀♀, Shanxi Province, Lishan National Nature Reserve (1300–2200m), 12–15 July 2012, Xiao-Hui Hou; 2♂♂, Anhui province, Huangshan city, Tangkou town (500m), 20 May 2008, Zheng-Guang Zhang; 9♂♂, 4♀♀, Fujian province, Shanghang county, Natural Reserve of Meihua Mountain, Gutian town, 17 August 2009, Pei Zhang, Jun-Qiang Ni; 3♂♂, 5♀♀, Henan province, Jiyuan City, Wangwu Mountain, 22 August 2009, Yu-Jian Li; 2♂♂, Sichuan province, Yaan city, Zhougong Mountain, 15–18 July 2010, Pei Zhang; 1♂, Sichuan Province, Tianquan County, Labahe, 25 July 2012, Zhi Hua Fan; 21♂♂, 15♀♀, Sichuan Province, Mianyang City, Anzhou District, Chaping, 19–22 July 2010, Pei Zhang, Yan-Li Zheng, Ke-Bin Li, Zhi-Min Chang; 5♂♂, 2♀♀, Sichuan Province, Mianyang City, Wanglang National Nature Reserve, Changbaigou (2587m), 25 July 2016, Meng-Shu Dong; 17♂♂, 6♀♀, Guizhou province, Wangmo county, Fuxing Town, 9 August 2012, Wei-Chen Yang; 7♂♂, 13♀♀, Guizhou province, Wangmo county, Dayi Town, 15–16 July 2016, Liang-Jing Yang, Yong-Shun Ding; 14♂♂, 3♀♀, Guizhou province, Wangmo county, Dayi Town, 25–26 June 2013, Jian-Kun Long, Ji-Chun Xing, Hai-Yan Sun; 11♂♂, 4♀♀, Guizhou province, Maolan county, Banzhai Town, 5–6 July 2010, Xiao-Hui Hou, Pei Zhang; 4♂♂, 1♀, Guizhou province, Bijie City, Bazhai Town, Jinyin mountain, 7 July 1977, collector unknown; 11♂♂, 14♀♀, Guizhou Province, Weining County, Caohai National Natural Reserve, 1–6 August 2017, Ying-Jian Wang, Liang-Jing Yang, Nian Gong, Guan-Fu Ma; 1♂, Guizhou province, Rongjiang county, Pingyang Town, Xiaodanjiang, 9 July 2011, Jian-Kun Long; 1♂, 1♀, Guizhou province, Luodian county, Moyang Town, 10 May 2013, Zhi-Hua Fan.

Supplementary description. *Female genitalia.* Genitalia as shown in Fig. 61 ventrally. Anal tube (Fig. 62) 2.1 times longer than wide in dorsal view. Posterior vagina (Figs 63–64) elongate, with a longitudinal sclerite respectively dorsally and medially. In ventral view, right side with a more or less triangular sclerite basally, terminal area with a transverse long sclerite.

Host plant. *Artemisia* sp. (Compositae); *Zea mays* Linnaeus (Panicoideae).

Distributions. China (Anhui, Fujian, Guangxi, Guizhou, Henan, Hunan, Shanxi, Sichuan), Japan.

Remarks. Female genitalia of *Oecleopsis sinicus* can be distinguished from other species of the genus by the following characters: basal sclerite on right side of posterior vagina without process ventrally; terminal area with a transverse long sclerite ventrally.

Note. The female genitalia of this species is described and illustrated in detail for the first time.

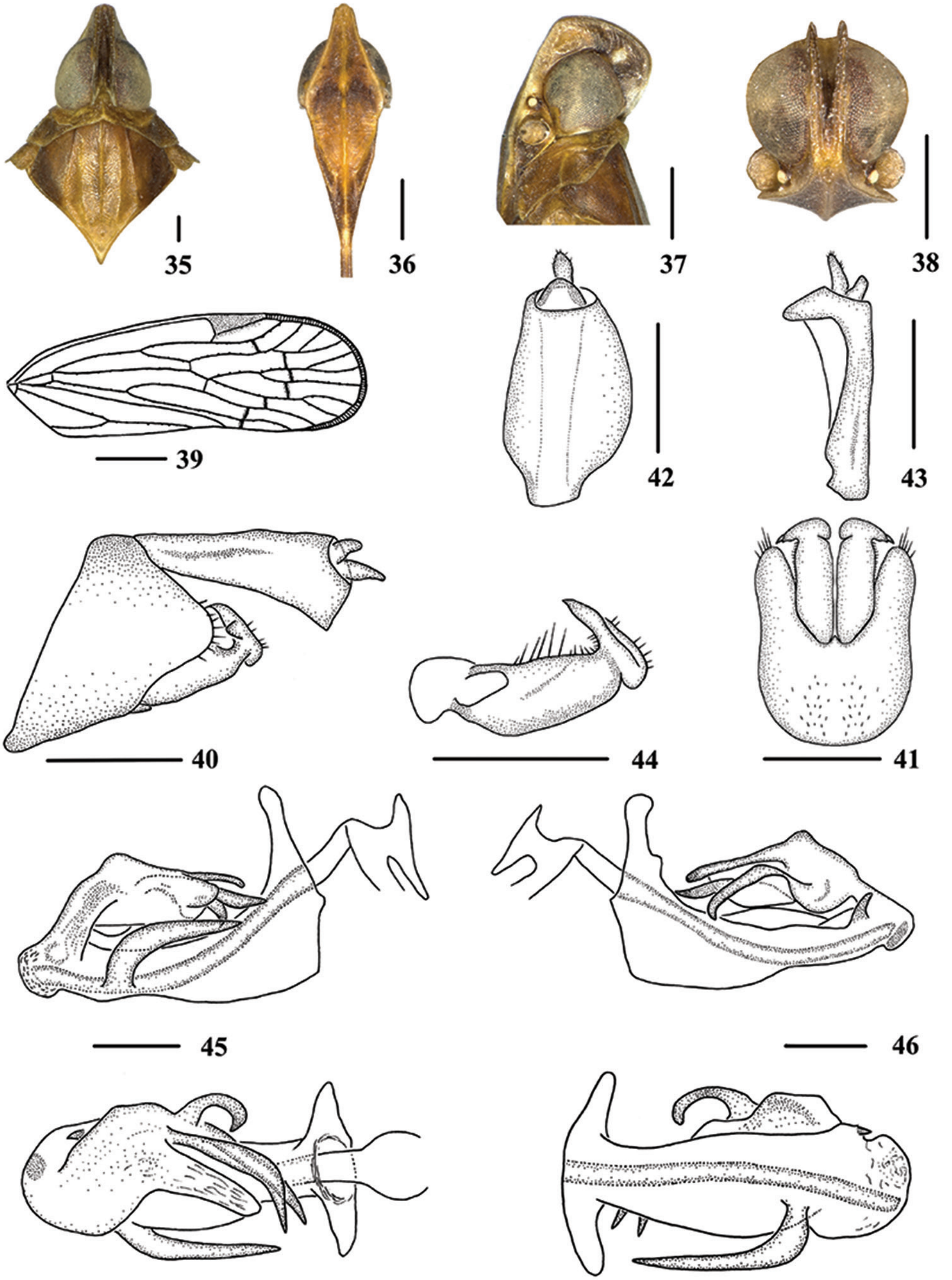
Oecleopsis yoshikawai **(Ishihara, 1961)**

Figs 5–6, 35–48, 65–68

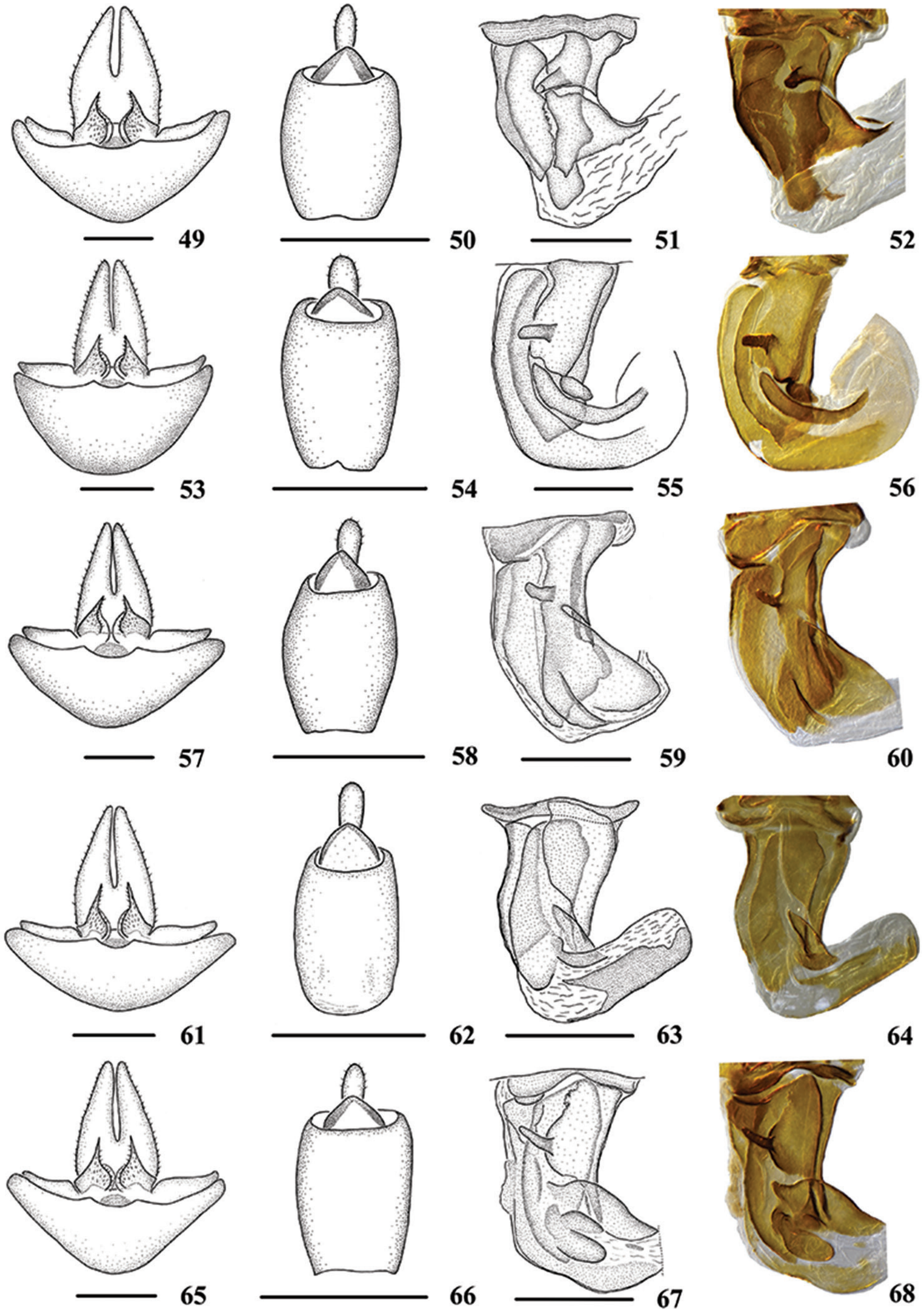
Oliarus yoshikawai Ishihara, 1961: 228, figs 6–7.

Oecleopsis yoshikawai (Ishihara, 1961): Van Stalle 1991: 22, figs 65–71; Guo et al. 2009, 58.

Material examined. China: 2♂♂, 2♀♀, Guizhou province, Wangmo county, Xintun Town, Bakang Village, 19 August 2012, Jian-Kun Long, Shi-Yan Xu, Wei-Bin Zheng; 2♂♂, 2♀♀, Guizhou province, Wangmo county, Xintun Town, Bakang Village, 2013-



Figures 35–48. *Oecleopsis yoshikawai* (Ishihara, 1961), male **35** Head and thorax, dorsal view **36** Face, ventral view **37–38** Head **39** Forewing **40** Genitalia, lateral view **41** Pygofer and genital styles, ventral view **42–43** Anal segment **42** dorsal view **43** right lateral view **44** Genital styles, inner lateral view **45** Aedeagus, right side **46** Aedeagus, left side **47** Aedeagus, dorsal view **48** Aedeagus, ventral view. Scale bars: 0.5 mm (**35–38, 40–48**); 1.0 mm (**39**).



Figures 49–68. Female genitalia of *Oecleopsis* species. **49–52** *O. laminatus* sp. n. **53–56** *O. mori* **57–60** *O. productus* sp. n. **61–64** *O. sinicus* **65–68** *O. yoshikawai* **49, 53, 57, 61, 65** Genitalia, ventral view **50, 54, 58, 62, 66** Anal segment, dorsal view **51–52, 55–56, 59–60, 63–64, 67–68** Posterior vagina, ventral view. Scale bars: 0.5 mm.

Figure 69. Adult of *Oecleopsis sinicus* (Jacobi, 1944), lateral view, female (Caohai National Natural Reserve, Weining County, Guizhou Province, 1 August 2017, photograph by X-S Chen).

VI-28, Jian-Kun Long, Hai-Yan Sun, Yang-Yang Liu; 1♂, Guizhou province, Anlong county, Xianheping Nature Reserve, 22 July 2016, Liang-Jing Yang; 1♀, Guizhou province, Wangmo county, Zhexiang Town, 19 July 2016, Liang-Jing Yang; 1♂, Guizhou province, Guanling county, Bangui Town, 20 August 2009, Ji-Chun Xing.

Redescription. Body length: male 6.0–6.5mm (*N* = 6), female 6.8–7.5mm (*N* = 5).

Coloration. General color mid brown (Figs 5–6, 35–38). Eyes mid to blackish brown, ocelli light yellow. Vertex blackish brown. Face yellowish to blackish brown, carinae yellowish to mid brown; rostrum yellowish to blackish brown. Pronotum mid to blackish brown; mesonotum yellowish to mid brown. Forewing semitranslucent, light brown, stigma mid brown. Hind tibiae and abdominal sternites mid brown.

Head and thorax. Vertex (Fig. 35) narrow, 3.6 times longer than wide; frons (Fig. 36) 1.2 times as long as wide. Forewing (Fig. 39) 3.2 times longer than wide, with 11 apical and 6 subapical cells; fork Sc+RP slightly distal to fork CuA1+CuA2; RP 3 branches, MA 3 branches, MP 2 branches. Hind tibia with 3 lateral spines; chaetotaxy of hind tarsi: 7/5.

Male genitalia. Pygofer (Figs 40–41), dorsal margin concave and U-shaped ventrally, widened towards apex; in lateral view, lateral lobes triangularly extended caudally, apex round. Medioventral process triangular ventrally, short. Anal segment (Figs 40, 42–43) tubular, asymmetrical, widened towards apex in left side view; in right side view, left ventral margin convex and right ventral margin excavated near apex; 2.0 times longer than wide in dorsal view; anal style fingerlike, beyond anal segment. Genital styles illustrated in Fig. 44. Aedeagus (Figs 45–48) in total with five processes. Spinose process on right side near apex of periandrium long, basal part curving upward and distal part parallel to periandrium, directed towards cephalum, more than 1/2 of periandrium in length; left side near apex of periandrium with a short spinose process, curved and directed dorsocaudally. Flagellum bearing three spinose processes: the upper one originating the middle of flagellum, apex curved strongly and directed right side; the apical one curved right-ventrocephalically; the one on left side shortest, curved strongly and directed ventrally.

Female genitalia. Genitalia as shown in Fig. 65 ventrally. Anal tube (Fig. 66) 1.8 times longer than wide in dorsal view. Posterior vagina (Figs 67–68) elongate, with a long longitudinal sclerite dorsally. In ventral view, left side with a long longitudinal sclerite, curved, towards the right; right side with a longitudinal sclerite basally, which with a process, the process directed left-ventrally and longer than shown in the figure; terminal area with an irregular sclerite, which forming three projecting oblong structures.

Host plant. Bamboo (Bambusoideae).

Distributions. China (Guizhou), Thailand.

Note. This species is recorded from China for the first time and the female genitalia of this species is described and illustrated for the first time.

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The authors are grateful to the specimen collectors for their hard work in the field collections. We wish to express our sincere thanks to Dr. B. Löcker (Department of Primary Industries, Orange Agricultural Institute, Australia) for providing literature. This work was supported by the National Natural Science Foundation of China (No. 31472033), the Program of Excellent Innovation Talents, Guizhou Province (No. 20154021), the Program of Science and Technology Innovation Talents Team, Guizhou Province (No. 20144001), the International Cooperation Base for Insect Evolutionary Biology and Pest Control (No. 20165802), Joint Foundation of Collaboration Project between Scientific and Technological Bureau of Guizhou Province and Colleges/Universities of Guizhou Province (No. LH[2015]7353) and the Science and Technology Project of Guiyang (No. [2017]5-25).

References

Anufriev GA, Emeljanov AF (1988) Suborder Cicadinea (Auchenorrhyncha). In: Lehr PA (Ed.) Keys to the Insects of the Far East of the USSR. Volume 2. Homoptera and Heteroptera. Nauka Publishing House, Leningrad, 496 pp.

Bourgoin T (1993) Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetic data. Annales de la Société Entomologique France 29(3): 225–244.

Bourgoin T, Wang RR, Asche M, Hoch H, Soulier-Perkins A, Stroiński A, Yap S, Szwedo J (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). Zoomorphology 134: 63–77. https://doi.org/10.1007/s00435-014-0243-6

Chou I, Lu JS, Huang J, Wang SZ (1985) Economic Insect Fauna of China. Fasc. 36. Homoptera: Fulgoroidea. Science Press, Beijing, China, 137 pp.

Emeljanov AF (1971) New genera of leafhoppers of the families Cixiidae and Issidae (Homoptera, Auchenorrhyncha) from the fauna of the USSR. Entomologicheskoe Obozrenie 50(3): 619–627.

Fennah RG (1956) Fulgoroidea from Southern China. Proceedings of the California Academy of Science 28: 441–527.

Guo HW, Wang YL, Feng JN (2009) Taxonomic study of the genus *Oecleopsis* Emeljanov, 1971 (Hemiptera: Fulgoromorpha: Cixiidae: Pentastirini), with descriptions of three new species from China. Zootaxa 2172: 45–58.

Ishihara T (1961) Homoptera of Southeast Asia collected by the Osaka City University Biological Expedition to Southeast Asia 1957–58. Nature and Life in Southeast Asia 1: 255–257.

Jacobi A (1944) Die Zikadenfauna der Provinz Fukien in Südchina und ihre tiergeographischen Beziehungen. Mitteilungen der Münchner Entomologischen Gesellschaft 34: 5–66.

Matsumura S (1914) Die Cixiinen Japans. Annotationes Zoologicae Japonenses 8: 393–434.

Noualhier JM (1896) Note sur les Hémiptères récoltés en Indo-Chine et offerts au Muséum par M. Pavie. Bulletin du Muséum d'Histoire Naturelle de Paris 10: 251–259.

Tsaur SC, Hsu TC, Van Stalle J (1988) Cixiidae of Taiwan, Part I. Pentastirini. Journal of Taiwan Museum 41(1): 35–74.

Van Stalle J (1988) A revision of the Oriental species of *Mnemosyne* Stål (Homoptera, Cixiidae). Annnales Entomologici Fennici 54: 33–47.

Van Stalle J (1991) Taxonomy of Indo-Malayan Pentastirini (Homoptera, Cixiidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 61: 5–101.

Zhi Y, Yang L, Zhang P, Chen XS (2017) Taxonomic study of the genus *Neocarpia* Tsaur & Hsu, with descriptions of two new species from China (Hemiptera, Fulgoromorpha, Cixiidae). ZooKeys 695: 19–35. https://doi.org/10.3897/zookeys.695.12809

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RESEARCH ARTICLE

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North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae)

Demian F. Gomez[1], Robert J. Rabaglia[2], Katherine E. O. Fairbanks[3], Jiri Hulcr[1,4]

1 *School of Forest Resources and Conservation, University of Florida, 136 Newins-Ziegler Hall, Gainesville, FL 32611, USA* **2** *USDA-Forest Service, Forest Health Protection, 201 14 St, SW, Washington DC 20250, USA* **3** *Florida Department of Agriculture and Consumer Services, Division of Plant Industry, 1911 SW 34th Street, Gainesville, FL 32608, USA* **4** *Entomology and Nematology Department, University of Florida, 1881 Natural Area Drive, Gainesville, FL 32611, USA*

Corresponding author: *Demian F. Gomez* (demiangomez@ufl.edu)

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Abstract

Bark and ambrosia beetles (Scolytinae) are the most successful group of invasive wood borers worldwide, and the most invasive among them are species in the tribe Xyleborini. This haplodiploid, highly inbred, fungus-farming group is represented by 30 non-native species in North America, of which at least five are serious pests. The few identification resources for Xyleborini that exist are becoming outdated due to new species arrivals and nomenclatural changes. Here we present a new comprehensive key to Xyleborini currently known from the continental United States. Compared to the previous key, the following species have been added to the North American fauna: *Ambrosiodmus minor* (Stebbing), *Ambrosiophilus nodulosus* (Eggers), *Anisandrus maiche* Kurentsov, *Coptoborus pseudotenuis* (Schedl), *Cyclorhipidion fukiense* (Eggers), *Dryocoetoides reticulatus* Atkinson, *Dryoxylon onoharaense* (Murayama), *Euwallacea interjectus* (Blandford), *Xyleborinus andrewesi* (Blandford), *Xyleborinus artestriatus* (Eichhoff), *Xyleborinus octiesdentatus* (Murayama), *Xyleborus bispinatus* Eichhoff, *Xyleborus seriatus* Blandford, *Xyleborus spinulosus* Blandford, and *Xylosandrus amputatus* (Blandford).

Keywords

ambrosia beetles, exotic species, invasive species, wood-boring insects

Introduction

Bark and ambrosia beetles (Curculionidae: Scolytinae) are considered one of the most injurious groups of insects in native and planted forests (Raffa et al. 2015). The vast majority breeds in dead or dying tissues and do not have economic impact. However, some species attack living trees, seedlings, or seeds of commercial importance causing severe damage (Raffa et al. 2015). Scolytines are among the most commonly intercepted taxa at United States ports of entry. True bark beetles (phloeophagous species) are intercepted more often than ambrosia-feeding species; however, ambrosia beetles of the tribe Xyleborini represent half of the 60 non-native scolytines established in the United States (Haack and Rabaglia 2013).

The Xyleborini, with 1177 recognized species, is the most species-rich tribe within Scolytinae (Smith and Hulcr 2015). This tribe of ambrosia beetles also includes some of the most abundant and widely distributed species (Rabaglia et al. 2006). The combination of fungus-farming, wide host range, and arrhenotokous inbreeding (haplodiploidy) makes the Xyleborini one of the most successful groups of colonizers in the world (Atkinson et al. 1990, Smith and Hulcr 2015).

In the last decade, several exotic species of Xyleborini have successfully established in North America. The detection and control of both native and exotic species relies on a solid understanding of the systematics and identity of species. Since the last review of North American Xyleborini (Rabaglia et al. 2006), 15 additional non-native species have been recorded in North America and several nomenclatural changes have been made. The aim of this article is to review the species of Xyleborini occurring in continental North America, diagnose the new species for the region, and provide illustrated keys to genera and species.

Materials and methods

Specimens examined were from the cryo-preserved collection University of Florida Forest Entomology lab managed by JH (University of Florida, Gainesville, Florida, USA), the Florida State Collection of Arthropods (Gainesville, Florida, USA), and/or collected by the authors during various state, regional, and national surveys. Distribution records are as reported in Wood and Bright (1992), Atkinson (2017), recent publications, and unpublished data from the authors. Diagnostic characters used in the keys and notes are for the identification of genera and species occurring in North America and may not be useful for taxa occurring in other regions. Antennal club types are described as Hulcr et al. (2007). Interstria 1 is defined as the sutural interstria. Table 1 includes the complete list of species of Xyleborini occurring in continental North America.

Synonyms listed for each genus and species are cited from Alonso-Zarazaga and Lyal (2009), Alonso-Zarazaga et al. (2017), Beaver 2011, Bright (2014), and Wood and Bright (1992). References to original descriptions and synonymies are cited from Bright and Rabaglia (1999), Hulcr and Cognato (2009), Wood and Bright

Table 1. List of species of Xyleborini occurring in continental North America north of Mexico.

Ambrosiodmus devexulus (Wood, 1978)
Ambrosiodmus lecontei Hopkins, 1915
Ambrosiodmus lewisi (Blandford, 1894)
Ambrosiodmus minor (Stebbing, 1909)
Ambrosiodmus obliquus (LeConte, 1878)
Ambrosiodmus opimus (Wood, 1974)
Ambrosiodmus rubricollis (Eichhoff, 1875)
Ambrosiodmus tachygraphus (Zimmermann, 1868)
Ambrosiophilus atratus (Eichhoff, 1875)
Ambrosiophilus nodulosus (Eggers, 1941)
Anisandrus dispar (Fabricius, 1792)
Anisandrus maiche Kurentsov, 1941
Anisandrus obesus (LeConte, 1868)
Anisandrus sayi Hopkins, 1915
Cnestus mutilatus (Blandford, 1894)
Coptoborus pseudotenuis (Schedl, 1936)
Cyclorhipidion bodoanum (Reitter, 1913)
Cyclorhipidion fukiense (Eggers, 1941)
Cyclorhipidion pelliculosum (Eichhoff, 1878)
Dryocoetoides reticulatus Atkinson, 2009
Dryoxylon onoharaense (Murayama, 1934)
Euwallacea fornicatus (Eichhoff, 1868)
Euwallacea interjectus (Blandford, 1894)
Euwallacea similis (Ferrari, 1867)
Euwallacea validus (Eichhoff, 1875)
Theoborus ricini (Eggers, 1932)
Xyleborinus andrewesi (Blandford, 1896)
Xyleborinus artestriatus (Eichhoff, 1878)
Xyleborinus attenuatus (Blandford, 1894)
Xyleborinus gracilis (Eichhoff, 1868)
Xyleborinus octiesdentatus (Murayama, 1931)
Xyleborinus saxesenii (Ratzeburg, 1837)
Xyleborus affinis Eichhoff, 1868
Xyleborus bispinatus Eichhoff, 1868
Xyleborus celsus Eichhoff, 1868
Xyleborus ferrugineus (Fabricius, 1801)
Xyleborus glabratus Eichhoff, 1877
Xyleborus horridus Eichhoff, 1869
Xyleborus impressus Eichhoff, 1868
Xyleborus intrusus Blandford, 1898
Xyleborus pfeilii (Ratzeburg, 1837)
Xyleborus planicollis Zimmermann, 1868
Xyleborus pubescens Zimmermann, 1868
Xyleborus seriatus Blandford, 1894
Xyleborus spinulosus Blandford, 1898
Xyleborus viduus Eichhoff, 1878
Xyleborus volvulus (Fabricius, 1775)
Xyleborus xylographus (Say, 1826)
Xylosandrus amputatus (Blandford, 1894)
Xylosandrus compactus (Eichhoff, 1875)
Xylosandrus crassiusculus (Motschulsky, 1866)
Xylosandrus curtulus (Eichhoff, 1869)
Xylosandrus germanus (Blandford, 1894)

(1987, 1992), and Wood (1986). The type material collection information and repository correspond to Wood and Bright (1992). Abbreviations for location of type material are:

BMNH	British Museum of Natural History, London;
CNCI	Canadian National Collection of Insects, Ottawa;
FRI	Forest Research Institute, Dehradun;
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels;
IZM	Institute of Zoology at Moscow, Moscow;
MCZ	Museum of Comparative Zoology, Cambridge, MA;
NHMB	Natural History Museum Budapest, Budapest;
NHMW	Naturhistorisches Museum Wien, Wien;
NMNH	National Museum of Natural History, Washington, DC;
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg;
UZMC	Universitets Zoologisk Museum, Copenhagen;
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg;
ZMFK	Zoological Research Museum Alexander Koenig, Bonn; and
ZMUH	Zoologisches Institut und Zoologisches Museum, Hamburg.

Photographs were taken by JH and DG using an Olympus SZX16 stereomicroscope. Each image is a composite of up to 50 separate images taken with a Canon EOS Rebel T3i camera, and later stacked using the Helicon Focus software (v 6.0, Helicon Soft).

Systematics

Key to genera of female American Xyleborini north of Mexico

1 Body conspicuously long, 3.5 times as long as wide; protibiae narrow with five large teeth on outer margin; elytral declivity deeply concave and densely pubescent, declivital surface and lateral margins not armed..........***Dryoxylon***

– Body stout to slender, never 3.5 times as long as wide; protibiae broad and with more than 5 small denticles on the outer margin; elytral declivity usually not concave; if impressed, lateral margins armed with denticles **2**

2 Scutellum minute, conical; base of elytra at suture notched, with abundant setae..........***Xyleborinus***

– Scutellum flat, shiny, its surface flush with adjacent elytra, or scutellum rounded, surrounded by a moderately deep impressed area at the base of elytra **3**

3 Procoxae moderately to widely separated; intercoxal piece continuous, not longitudinally emarginate **4**

– Procoxae contiguous; intercoxal piece longitudinally emarginate..........**5**

4 Elytra wider than long, shorter than pronotum, truncate; pronotum with lateral carina ....***Cnestus***

– Elytra never wider than long nor shorter than pronotum, usually not truncate; pronotum with lateral margins rounded..........***Xylosandrus***

5 Pronotal asperities extending from apex to base ....***Ambrosiodmus***

– Pronotal asperities confined to apical half, basal half flat, shiny, or dull **6**

6 Posterior face of antennal club with segments 2 and 3 at least partially visible (type 3) (Fig. 1) 7

– Posterior face of antennal club with no sutures visible at or near apex (type 1 or 2) (Fig. 1) **12**

7 Elytral punctures confused; elytral vestiture abundant and confused ....***Cyclorhipidion***

– Strial and interstrial punctures in rows; elytral vestiture confined to strial and interstrial rows **8**

8 Elytra narrowly rounded at apex, sutural apex strongly emarginate (Fig. 7), body slender .... ***Coptoborus***

– Elytral apex broadly rounded, sutural apex entire, body stout **9**

9 Posterolateral margin of declivity costate and broad; pronotum subquadrate or rounded.......... ***Euwallacea***

– Posterolateral margin of declivity rounded, costa blunt; pronotum rounded, never quadrate **10**

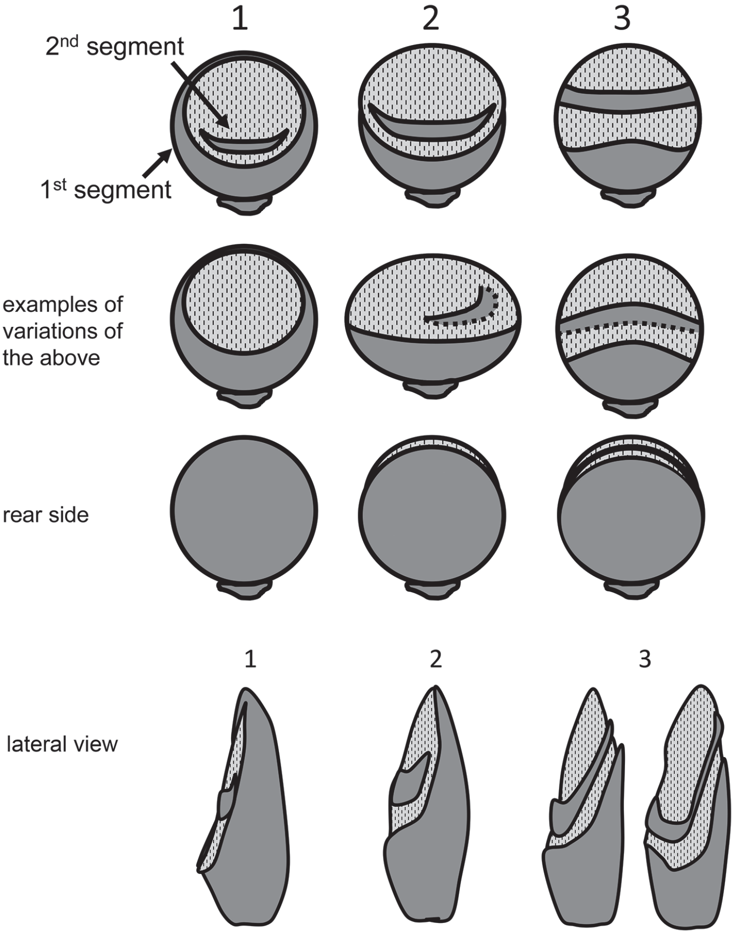

Figure 1. Antennal club types in Xyleborini. First row, types of antennae; second row, examples of variation; third row, rear face; fourth row, lateral view. Modified from Hulcr et al. (2007).

10 Protibia stick-like, posterior face rugose .... ***Dryocoetoides***

– Protibia flattened, posterior face smooth **11**

11 Color black; segment 2 of antennal club non-corneous or corneous only on anterior face .... ***Ambrosiophilus***

– Color light-brown; segment 2 of antennal club corneous on both sides .... ***Theoborus***

12 Anterior margin of pronotum distinctly armed by several coarse serrations (flat teeth); body stout, < 2.2 times as long as wide .... ***Anisandrus***

– Anterior margin of pronotum not armed by large serrations; if serrations present, they are not larger than asperities on anterior slope of pronotum; body more slender, > 2.3 times as long as wide .... ***Xyleborus***

Ambrosiodmus Hopkins, 1915

Phloeotrogus Motschulsky, 1863. Synonymy Wood 1966.
Brownia Nunberg, 1963. Synonymy Wood 1980.

Type species. *Xyleborus tachygraphus* Zimmermann.

Species of *Ambrosiodmus* differ from other members of the tribe by the asperities covering the entire surface of the pronotum.

Key to species of female *Ambrosiodmus*

1 Declivital interstriae 2 either unarmed or granules smaller than those on 1 or 3 .... **2**
– Declivital interstriae 2 with tubercles as large as or larger than those on 1 or 3 .... **3**
2 Declivital interstriae 1 feebly elevated, usually as high as 3, 2 feebly sulcate, its granules as large as those on 1; discal interstriae 3 to 4 times as wide as striae; color reddish brown to black; slightly larger, length 2.0–2.4 mm .... ***obliquus* (LeConte)**
– Declivital interstriae 1 not elevated, declivital granules absent; elytral punctures larger, deeper; discal interstriae twice as wide as striae; color very dark brown to black; smaller, length 1.8–2.1 mm .... ***devexulus* (Wood)**
3 Interstrial punctures on elytral disc strongly confused to irregularly biseriate, smooth to weakly granulate **4**
– Interstrial punctures on elytral disc weakly confused to uniseriate, finely granulate **5**
4 Declivital interstriae all equally tuberculate, tubercles somewhat irregular in size, but those on 2 not distinctly larger than those on other interstriae; length 3.5 mm .... ***minor* (Stebbing)**
– Declivital interstriae 1 unarmed or bearing small granules, 2 strongly tuberculate; length 3.6–4.0 mm .... ***lewisi* (Blandford)**
5 Declivital interstriae all equally granulate, granules somewhat irregular in size, but those on 2 not distinctly larger than those on other interstriae; 2.4–2.6 mm .... ***rubricollis* (Eichhoff)**
– Declivital interstriae 1 unarmed or bearing very small granules, 2 strongly granulate or tuberculate **6**
6 Sutural area of declivity feebly impressed, interstriae 1 armed by several fine granules; rare; 2.4 mm .... ***opimus* (Wood)**
– Sutural area of declivity moderately to strongly impressed, interstriae 1 unarmed; longer than 2.4 mm **7**
7 Strial punctures on disc coarse, deep; interstriae less than 1.5 times as wide as striae; reddish, slightly bicolored; smaller, 2.5–3.0 mm .... ***lecontei* Hopkins**
– Strial punctures on disc rather small, very shallow; interstriae more than 2 times as wide as striae; black; larger, 3.7–3.9 mm .... ***tachygraphus* (Zimmermann)**

Ambrosiodmus devexulus (Wood, 1978)

Fig. 2

Xyleborus devexus Wood, 1977. Preoccupied Schedl 1977.
Xyleborus devexulus Wood, 1978. Replacement name for *X. devexus* Wood.
Xyleborus woodi Schedl, 1979. Unnecessary replacement name.

Type material. Holotype female; Homestead, FL; NMNH.

Distribution. North America: Antilles, United States: Florida.

Notes. This species is very similar to *A. obliquus*, but it is distinguished by its smaller size, lack of declivital granules, and interstriae 1 not elevated. It is only known from southern Florida, Puerto Rico, and the Dominican Republic.

Ambrosiodmus lecontei Hopkins, 1915

Fig. 2

Xyleborus gundlachi Eggers, 1931. Synonymy Wood 1972.

Type material. Holotype female; Keene, FL; USNM.

Distribution. North America: Antilles, United States: Alabama, Florida, Louisiana, South Carolina, Texas; South America: Brazil.

Notes. In North America, this species is distinguished by the smaller size and the much deeper, coarser strial punctures compared to *A. tachygraphus*.

Ambrosiodmus lewisi (Blandford, 1894)

Fig. 2

Xyleborus lewisi Blandford, 1894.
Ozopemon tuberculatus Strohmeyer, 1912. Synonymy Beaver and Liu 2010.
Xyleborus tegalensis Eggers, 1923. Synonymy Schedl 1950.
Xyleborus lewekianus Eggers, 1923. Synonymy Wood 1989.

Type material. Syntypes female; Japan; BMNH.

Distribution. Asia; North America (introduced): United States: Alabama, Georgia, Pennsylvania.

Notes. *Ambrosiodmus lewisi* was first reported in North America from southeastern Pennsylvania (Hoebeke 1991). This non-native species is the largest *Ambrosiodmus* in North America, and can be distinguished from *A. minor* by the tubercles on declivital interstriae 2, which are distinctly larger than those on other interstriae.

Figure 2. Lateral and dorsal views of *Ambrosiodmus* species. From top left, *Ambrosiodmus devexulus*, *A. lecontei*, *A. lewisi*, and *A. minor*. Scale bar: 1.0 mm.

Ambrosiodmus minor (Stebbing, 1909)

Fig. 2

Phloeosinus minor Stebbing, 1909.
Xyleborus crassus Hagedorn, 1910. Synonymy Schedl 1962.

Type material. Syntypes female; Assam: labeled Kochujan, printed as Goalpara Sal Forests; FRI.

Distribution. Asia; North America (introduced): United States: Alabama, Florida, Georgia, Mississippi.

Notes. The first collection in North America of *A. minor* was in Florida in 2011 (Rabaglia and Okins 2011). Similar to *A. lewisi* but with tubercles on declivital interstriae 2 not distinctly larger than those on other interstriae.

Ambrosiodmus obliquus (LeConte, 1878)

Fig. 3

Pityophthorus obliquus LeConte, 1878.
Xyleborus gilvipes Blandford, 1898. Synonymy Wood 1975.
Ambrosiodmus linderae Hopkins, 1915. Synonymy Bright 1968.
Xyleborus brasiliensis Eggers, 1928. Synonymy Wood 1975.
Xyleborus mexicanus Eggers, 1931. Synonymy Wood 1972.
Xyleborus pseudobrasiliensis Eggers, 1941. Synonymy Bright 1985.
Xyleborus illepidus Schedl, 1941. Synonymy Wood 1975.
Xyleborus melanarius Schedl, 1978. Synonymy Wood 1989.

Type material. Holotype female; Enterprise, FL; MCZ.

Distribution. Africa; Central America: Costa Rica, Guatemala, Honduras, Panama; North America: Antilles Islands, Mexico, United States: Alabama, Delaware, District of Columbia, Florida, Georgia, Louisiana, Maryland, Mississippi, North Carolina, South Carolina, Tennessee, Texas, Virginia; South America: Brazil, Colombia, Ecuador, Peru.

Notes. Similar to *A. devexulus* but with less prominent punctures.

Ambrosiodmus opimus (Wood, 1974)

Fig. 3

Xyleborus opimus Wood, 1974.

Type material. Holotype female; Sebring, FL; NMNH.

Distribution. North America: United States: Florida; South America: Brazil.

Notes. Similar to *A. lecontei* in North America, but interstriae 1 armed by several fine granules in *A. opimus*.

Ambrosiodmus rubricollis (Eichhoff, 1875)

Fig. 3

Xyleborus rubricollis Eichhoff, 1875.
Xyleborus taboensis Schedl, 1952. Synonymy Wood 1989.
Xyleborus strohmeyeri Schedl, 1975. Synonymy Wood 1989.

Figure 3. Lateral and dorsal views of *Ambrosiodmus* species. From top left, *Ambrosiodmus obliquus*, *A. opimus*, *A. rubricollis*, and *A. tachygraphus*. Scale bar: 1.0 mm.

Type material. Holotype Female; Japan; IRSNB.

Distribution. Asia; Australia (introduced); Europe (introduced): Italy; North America (introduced): Mexico, United States: Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Indiana, Louisiana, Maryland, Michigan, Mississippi, Missouri, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia.

Notes. This non-native species, first found in Maryland (Bright 1968), is now well-established and commonly found in the mid-Atlantic and southeastern states. This species is distinguished from other *Ambrosiodmus* by the combination of the red color, the small size, and the equally granulate declivital interstriae.

Ambrosiodmus tachygraphus (Zimmermann, 1868)

Fig. 3

Xyleborus tachygraphus Zimmermann, 1868.

Type material. Holotype female; North Carolina; MCZ.

Distribution. North America: United States: Alabama, Arkansas, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Kentucky, Louisiana, Maryland, Mississippi, New Jersey, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia.

Notes. Widely distributed in the eastern United States. It is among the largest species of Xyleborini in North America.

Ambrosiophilus Hulcr & Cognato, 2009

Type species. *Ambrosiodmus restrictus* (Schedl).

Species of *Ambrosiophilus* differ from other members of the tribe by the black and robust body combined with the absence of asperities on a flat pronotal disc, and the rounded edge of elytral declivity.

Key to species of female *Ambrosiophilus*

1 Body larger (length 3.0–3.2 mm); declivital striae 1 and interstriae 2 weakly impressed and finely granulate .... ***atratus*** **(Eichhoff)**

– Body smaller (length 2.4–2.7 mm); declivital striae 1 impressed and interstriae 2 convex, with evenly spaced tubercles from base to apex.................... .... ***nodulosus*** **(Eggers)**

Ambrosiophilus atratus (Eichhoff, 1875)

Fig. 4

Xyleborus atratus Eichhoff, 1875.

Type material. Holotype female; Japan. ZMUH, lost.

Distribution. Asia; North America (introduced): United States: Alabama, Delaware, Florida, Georgia, Kansas, Kentucky, Louisiana, Maine, Maryland, Michigan, Mississippi, Missouri, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, West Virginia; Oceania.

Notes. *Ambrosiophilus atratus* was first reported in eastern North America from Georgia, Maryland, Tennessee, Virginia and West Virginia (Atkinson et al. 1990). Differs from *A. nodulosus* by the absence of tubercles on the declivity.

Figure 4. Lateral and dorsal views of *Ambrosiophilus* species. From top left, *Ambrosiophilus atratus* and *A. nodulosus*. Scale bar: 1.0 mm.

Ambrosiophilus nodulosus (Eggers, 1941)

Fig. 4

Xyleborus nodulosus Eggers, 1941.
Xyleborus pernodulus Schedl, 1957. Synonymy Browne 1961.
Ambrosiophilus peregrinus Smith & Cognato, 2015. Synonymy Smith et al. 2017.

Type material. Holotype female; Fukien [Fujian Province, China]; ZMFK.

Distribution. Asia; North America (introduced): United States: Georgia.

Notes. A recent introduction in the U.S. (Smith and Cognato 2015, Smith et al. 2017), *A. nodulosus* is likely to expand its distribution. Differs from *A. atratus* by its smaller size and by the presence of evenly spaced tubercles on the declivity.

Anisandrus Ferrari, 1867

Type species. *Anisandrus dispar* (Fabricius).

Species of *Anisandrus* differ from other members of the tribe by the combination of serrations on the frontal edge of pronotum, a tuft of setae at the base of the pronotum, the contiguous procoxae, and an obliquely truncate antennal club with the first segment of club covering the entire posterior side.

Key to species of female *Anisandrus*

1 Posterolateral costa on declivity armed by 3–5 distinct tubercles .... ***obesus*** **(LeConte)**

– Posterolateral costa on declivity, may appear undulating, but without distinct tubercles **2**

2 Anterior margin of pronotum armed by 2–6 serrations, median pair conspicuously larger than the others; declivity evenly convex, granules few and small; body length 2.5–2.7 mm .... ***sayi*** **Hopkins**

– Anterior margin of pronotum armed by 6–8 subequal serrations; declivital interstriae 1 slightly to conspicuously raised, granules numerous; body length smaller than 2.5 mm or larger than 3.2 mm **3**

3 Larger, body length 3.2–3.7 mm; declivital interstriae 1 slightly raised, 2 and 3 even; interstrial punctures on elytral disc confused to irregularly biseriate .... ***dispar*** **(Fabricius)**

– Smaller, body length 1.8–2.3 mm; declivital interstriae 1 raised, 2 impressed, 3 raised with numerous distinct granules; interstrial punctures on elytral disc uniseriate .... ***maiche*** **Kurentsov**

Anisandrus dispar (Fabricius, 1792)

Fig. 5

Apate dispar Fabricius, 1792.
Bostrichus brevis Panzer, 1793. Synonymy Eichhoff 1878.
Bostrichus thoracicus Panzer, 1793. Synonymy Hagedorn 1910.
Scolytus pyri Peck, 1817. Synonymy Hubbard 1897.
Bostrichus tachygraphus Sahlberg, 1834. Synonymy Eichhoff 1878.
Bostrichus ratzeburgi Kolenati, 1846. Synonymy Ferrari 1867.
Anisandrus aequalis Reitter, 1913. Synonymy Mandelshtam 2001.
Anisandrus swainei Drake, 1921. Synonymy Wood 1957.
Xyleborus dispar rugulosus Eggers 1922.
Xyleborus cerasi Eggers, 1937. Synonymy Schedl 1964.
Xyleborus khinganensis Murayama, 1943. Synonymy Knížek 2011.

Type material. Syntypes female; Germaniae; UZMC.

Distribution. Asia; Europe; North America (introduced): Canada: British Columbia, New Brunswick, Nova Scotia, Ontario; United States: California, District of Columbia, Idaho, Illinois, Indiana, Maine, Maryland, Massachusetts, Michigan, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Utah, Virginia, Washington, West Virginia.

Notes. Representing the first non-native scolytine reported in North America (Rabaglia et al. 2006), *Anisandrus dispar* was likely unintentionally introduced before 1817 (Wood 1977). Found across North America from southern Canada through northern United States. Similar to *A. maiche* but larger.

Anisandrus maiche Kurentsov, 1941

Fig. 5

Xyleborus maiche Kurentsov, 1941.

Type material. Syntypes female; Ussuri, USSR [Russia]; IZL [ZIN], Leningrad [St. Petersburg].

Distribution. Asia; North America (introduced): United States: Ohio, Pennsylvania, West Virginia, and Wisconsin.

Notes. *Anisandrus maiche* was first reported in the US from Pennsylvania, Ohio, and West Virginia (Rabaglia et al. 2009). Similar to *A. dispar* but smaller. This non-native species was originally reported from western Pennsylvania and eastern Ohio, but is becoming increasingly common in northeastern states.

Anisandrus obesus (LeConte, 1868)

Fig. 5

Xyleborus obesus LeConte, 1868.
Xyleborus serratus Swaine, 1910. Synonymy Hopkins 1915.
Anisandrus populi Swaine, 1917. Synonymy Schedl 1964.

Type material. Lectotype female; Virginia; MCZ.

Distribution. North America: Canada: New Brunswick, Ontario, Quebec; United States: Connecticut, Illinois, Kentucky, Massachusetts, Michigan, Minnesota, New Jersey, New York, Ohio, Virginia, West Virginia, Wisconsin.

Notes. Distinguished from other *Anisandrus* by the presence of a series of tubercles on the posterolateral margin of the declivity.

Anisandrus sayi Hopkins, 1915

Fig. 5

Xyleborus obesus var. *minor* Swaine, 1910. Synonymy Wood 1957.
Xyleborus neardus Schedl, 1950. Synonymy Wood 1957.

Type material. Holotype female; Morgantown, WV; NMNH.

Figure 5. Lateral and dorsal views of *Anisandrus* species. From top left, *Anisandrus dispar*, *A. maiche*, *A. obesus*, and *A. sayi*. Scale bar: 1.0 mm.

Distribution. North America: Canada: New Brunswick, Ontario, Quebec; United States: Alabama, Connecticut, Delaware, District of Columbia, Georgia, Illinois, Indiana, Iowa, Kentucky, Maine, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia.

Notes. This is the most common species of *Anisandrus* in the northeastern U.S. Distinguished from other *Anisandrus* by the absence of significant sculpture on the elytral declivity. Wood (1957) synonymized *A. sayi* with *X. obesus* var. *minor*, but Swaine's name is available and should have priority.

Cnestus Sampson, 1911

Tosaxyleborus Murayama, 1950. Synonymy Browne 1955.

Type species. *Cnestus magnus* Sampson

Species of *Cnestus* differ from other members of the tribe by the truncate elytra, which are shorter than the pronotum.

Cnestus mutilatus (Blandford, 1894)

Fig. 6

Xyleborus mutilatus Blandford, 1894.
Xyleborus sampsoni Eggers, 1930. Synonymy Wood 1989.
Xyleborus banjoewangi Schedl, 1939. Synonymy Kalshoven 1960.
Xyleborus taitonus Eggers, 1939. Synonymy Wood and Bright 1987.

Type material. Holotype female; Japan; BMNH.

Distribution. Asia; North America (introduced): United States: Florida, Georgia, Kentucky, Louisiana, Mississippi, Pennsylvania, South Carolina, Tennessee, Texas; Oceania.

Notes. *Cnestus mutilatus* was first collected in North America from Mississippi in 1999 (Schiefer and Bright 2004). This species is easily distinguished from other Xyleborini by the truncate and short elytra, with a circular declivity delimited by a distinct carina posteriorly and laterally.

Coptoborus Hopkins, 1915

Type species. *Coptoborus emarginatus* Hopkins

Species of *Coptoborus* differ from other members of the tribe by the type 3 antennal club, the light brown or yellowish color, and the narrowed or acuminate elytral apex.

Coptoborus pseudotenuis (Schedl, 1936)

Fig. 7

Xyleborus pseudotenuis Schedl, 1936.
Xyleborus tenuis Schedl, 1948. Synonymy Wood 1976.

Figure 6. Lateral and dorsal view of *Cnestus mutilatus*. Scale bar" 1.0 mm.

Type material. Holotype female; Brasilien; Schedl Collection in NHMW.

Distribution. Central America: Costa Rica, Panama; North America: Mexico, United States: Florida; South America: Bolivia, Brazil, Ecuador, French Guiana, Peru, Venezuela.

Notes. *Coptoborus pseudotenuis* was first documented in the US based on a reared specimen from southern Florida in 2004 (Atkinson et al. 2010). Common in South America, either introduced or naturally spread to Florida. Distinguished from other *Coptoborus* by the slightly impressed interstria 2, 1 and 3 with 3–5 small denticles, and by the elevated apical margin of interstriae 1 and 2.

Cyclorhipidion Hagedorn, 1912

Terminalinus Hopkins, 1915. Synonymy Wood and Bright 1992.
Kelantanius Nunberg, 1961. Synonymy Wood 1986.

Type species. *Cyclorhipidion pelliculosum* Hagedorn

Figure 7. Lateral and dorsal view of *Coptoborus pseudotenuis*. Scale bar: 1.0 mm.

Species of *Cyclorhipidion* differ from other members of the tribe by being overall pubescent and covered with minute, dense, confused punctures.

Key to species of female *Cyclorhipidion*

1 Body length 1.82–2.16 mm; elytra pale yellowish brown; elytral declivity dull, almost flat, not impressed between interstriae 1 and 3; pronotum longer than wide; declivital strial punctures large, shallow, distinct, with interior surfaces reticulate, separated by less than their diameter; denticles on declivital interstriae 1 and 3 small and more or less uniform in size........................ ....***bodoanum* (Reitter)**

– Body length more than 2.40 mm; elytra chestnut brown to blackish brown; elytral declivity shining, impressed between interstriae 1 and 3; pronotum only slightly longer than wide or nearly quadrate; declivital strial punctures smaller and reticulate, generally separated at least by their diameter or slightly more; denticles on declivital interstriae 1 and 3 larger than others **2**

2 Body length 2.45–2.76 mm; declivital interstriae 2 slightly impressed; elytra chestnut-brown; strial punctures and interstrial punctures on elytral declivity of equal size, confused..***fukiense* (Eggers)**

– Body length 3.07–3.36 mm; declivital interstriae 2 noticeably impressed; elytra blackish brown; strial punctures on elytral declivity clearly distinct and larger than interstrial punctures, distinctly seriate ....***pelliculosum* (Eichhoff)**

Cyclorhipidion bodoanum (Reitter, 1913)

Fig. 8

Xyleborus bodoanus Reitter, 1913.
Xyleborus punctulatus Kurentsov, 1948. Synonymy Mandelshtam 2001.
Xyleborus californicus Wood, 1975. Synonymy Knížek 2011.

Type material. Syntypes female; Ostsibirien: Sotka-gora; NHMB.

Distribution. Asia; North America (introduced): United States: Alabama, Arkansas, California, Delaware, Florida, Georgia, Kansas, Louisiana, Maryland, Michigan, Mississippi, Missouri, North Carolina, Ohio, Oklahoma, Oregon, South Carolina, Tennessee, Texas, Washington.

Notes. *Cyclorhipidion bodoanum* was first reported in the eastern US (Maryland, Delaware, South Carolina, and Arkansas) in 2000 (Vandenberg et al. 2000) but was originally known by its synonym *Xyleborus californicus* Wood. Distinguished from other *Cyclorhipidion* in North America by the size and the yellowish brown color.

Cyclorhipidion fukiense (Eggers, 1941)

Fig. 8

Xyleborus fukiensis Eggers, 1941.
Xyleborus ganshoensis Murayama, 1952. Synonymy Beaver 2011.
Xyleborus tenuigraphus Schedl, 1953. Synonymy Beaver and Liu 2010.

Type material. Holotype female; Fukien [Fujian Province, China]; ZMFK.

Distribution. Asia; North America (introduced): United States: Florida, Georgia.

Notes. This recently detected non-native species is very similar in general appearance to both *C. bodoanum* and *C. pelliculosum* except for body length, with an intermediate size (Hoebeke et al. 2018).

Cyclorhipidion pelliculosum (Eichhoff, 1878)

Fig. 8

Xyleborus pelliculosus Eichhoff, 1878.
Xyleborus seiryorensis Murayama, 1930. Synonymy Knížek 2011.
Xyleborus quercus Kurenzov, 1948. Synonymy Knížek 2011.
Xyleborus starki Nunberg, 1956. Synonymy Knížek 2011.

Type material. Syntypes female; Japan; ZMUH, lost.

Figure 8. Lateral and dorsal views of *Cyclorhipidion* species. From top left, *Cyclorhipidion bodoanum*, *C. fukiense*, and *C. pelliculosum*. Scale bar: 1.0 mm.

Distribution. Asia; North America (introduced): United States: Delaware, Illinois, Kentucky, Maine, Maryland, Massachusetts, Missouri, New Jersey, North Carolina, Ohio, Pennsylvania, Rhode Island, Tennessee, Virginia.

Notes. *Cyclorhipidion pelliculosum* was first documented in the US from Pennsylvania in 1987 and from Maryland in 1989 (Atkinson et al. 1990). Distinguished from other *Cyclorhipidion* in North America by the larger size and the blackish brown color.

Dryocoetoides Hopkins, 1915

Type species. *Dryocoetoides guatemalensis* Hopkins.

Species of *Dryocoetoides* differ from other members of the tribe by the stick-like protibia, the posterior face of which is rugose.

Dryocoetoides reticulatus Atkinson, 2009

Fig. 9

Type material. Holotype female; United States; NMNH.

Distribution. North America: United States: Florida.

Figure 9. Lateral and dorsal view of *Dryocoetoides reticulatus*. Scale bar: 1.0 mm.

Notes. Distinguished from other *Dryocoetoides* by the clearly indicated punctures in the declivital striae, the uniseriate tubercles in the interstriae, and the dull declivity. Only known from south Florida (Atkinson 2009).

Dryoxylon Bright & Rabaglia, 1999

Type species. *Xyleborus onoharaensis* Murayama.

Species of *Dryoxylon* differ from other members of the tribe by the long body, the not impressed submentum, the narrow protibia with a few large teeth on outer margin, and by the deeply concave elytral declivity.

Dryoxylon onoharaense (Murayama, 1934)

Fig. 10

Xyleborus onoharaensis Murayama, 1934.

Dryoxylon onoharaensum Bright & Rabaglia, 1999 (incorrect subsequent spelling).

Dryoxylon onoharaense: Alonso-Zarazaga & Lyal, 2009. Correction for *Dryoxylon onoharaensum* Bright & Rabaglia.

Type material. Lectotype female; Japan; NMNH.

Distribution. Asia; North America (introduced): United States: Alabama, Arkansas, Delaware, Florida, Georgia, Louisiana, Maryland, Mississippi, North Carolina, Ohio, South Carolina, Tennessee, Texas, Virginia.

Figure 10. Lateral and dorsal view of *Dryoxylon onoharaense*. Scale bar: 1.0 mm.

Notes. This is the only species of the genus. Bright and Rabaglia (1999) placed it in the Dryocoetini based on tibial characters, but molecular analyses place it within the Xyleborini (Jordal et al. 2000, Jordal 2002). Distinguished by the obliquely truncate antennal club, the narrow protibiae with a few large teeth on outer margin, and by the distinctly concave, densely pubescent, and unarmed elytral declivity.

Euwallacea Hopkins, 1915

Type species. *Xyleborus wallacei* Blandford.

Species of *Euwallacea* differ from other members of the tribe by the costate and broad posterolateral edge of declivity. In most species the pronotum is subquadrate.

Key to species of female *Euwallacea*

1 Body slender, length 1.8–2.5 mm; light reddish brown color; pronotum subquadrate from above; elytral declivity with striae 1 strongly diverging from suture on lower half, interstriae 1 with one to three small tubercles near base, and one large tubercle slightly below middle........................***similis* (Ferrari)**

– Body stout; dark brown to black; pronotum subquadrate to subcircular; elytral declivity with striae parallel throughout, declivity without distinctive tubercles........................**2**

2 Body length 1.9–2.3 mm; elytra 1.2 times as long as wide; pronotum subcircular anteriorly (not subquadrate), anterior margin procurved, coarsely serrate........................***fornicatus* (Eichhoff)**

– Body length 3.4–3.8 mm; elytra at least 1.5 times as long as wide; pronotum more nearly subquadrate........................**3**

3 Body narrower, 3.7–3.9 mm; elytra 2 times as long as wide; elytral declivity steeply sloped from summit to apex, surface dull, punctures in striae deep, interstriae 2 with tubercles mostly absent from the apical half..... ***validus* (Eichhoff)**

– Body stout, 3.4–3.6 mm; elytra 1.5 times as long as wide; elytra gradually sloped from the base to the apex, surface shiny, punctures in striae shallow, interstria 2 with tubercles present from the base to the apex..***interjectus* (Blandford)**

Euwallacea fornicatus (Eichhoff, 1868)

Fig. 11

Xyleborus fornicatus Eichhoff, 1868.
Xyleborus fornicatior Eggers, 1923. Synonymy Beeson 1930 (as variety).
Xyleborus whitfordiodendrus Schedl, 1942. Synonymy Wood 1989.
Xyleborus perbrevis Schedl, 1951. Synonymy Wood,1989.
Xyleborus schultzei Schedl, 1951. Synonymy Beaver 1991.
Xyleborus tapatapaoensis Schedl, 1951. Synonymy Wood 1989.

Type material. Syntypes: Ceylon; ZMUH, lost.

Distribution. Africa; Asia; Central America (introduced): Costa Rica, Panama; North America (introduced): Mexico, United States: California, Florida, Hawaii; Oceania (introduced); South America (introduced): Brazil.

Notes. This species is a complex of several distinct genotypes, the most common of which are known as the Tea shot hole borer, Polyphagous shot hole borer, and the Kuroshio shot hole borer (Stouthamer et al. 2017). The different lineages are supported by rapidly evolving mitochondrial genes and more conserved nuclear gene regions. Although these potential different species display morphological differences, reliable morphological diagnosis has not been established (Chen et al. 2016).

Euwallacea interjectus (Blandford, 1894)

Fig. 11

Xyleborus interjectus Blandford, 1894.
Xyleborus pseudovalidus Eggers, 1925. Synonymy Schedl 1958.

Type material. Holotype female; Japan, China [presumably syntypes]; BMNH.

Distribution. Asia; North America (introduced): United States: Florida, Georgia, Hawaii, Kentucky, Louisiana, South Carolina, Texas, Virginia.

Notes. The first American occurrence of this species was in Louisiana in 1984, originally confused with *E. validus* (Cognato et al. 2015). Specimens from Asia can be larger in size, up to 3.8 mm long, overlapping with *E. validus* body size.

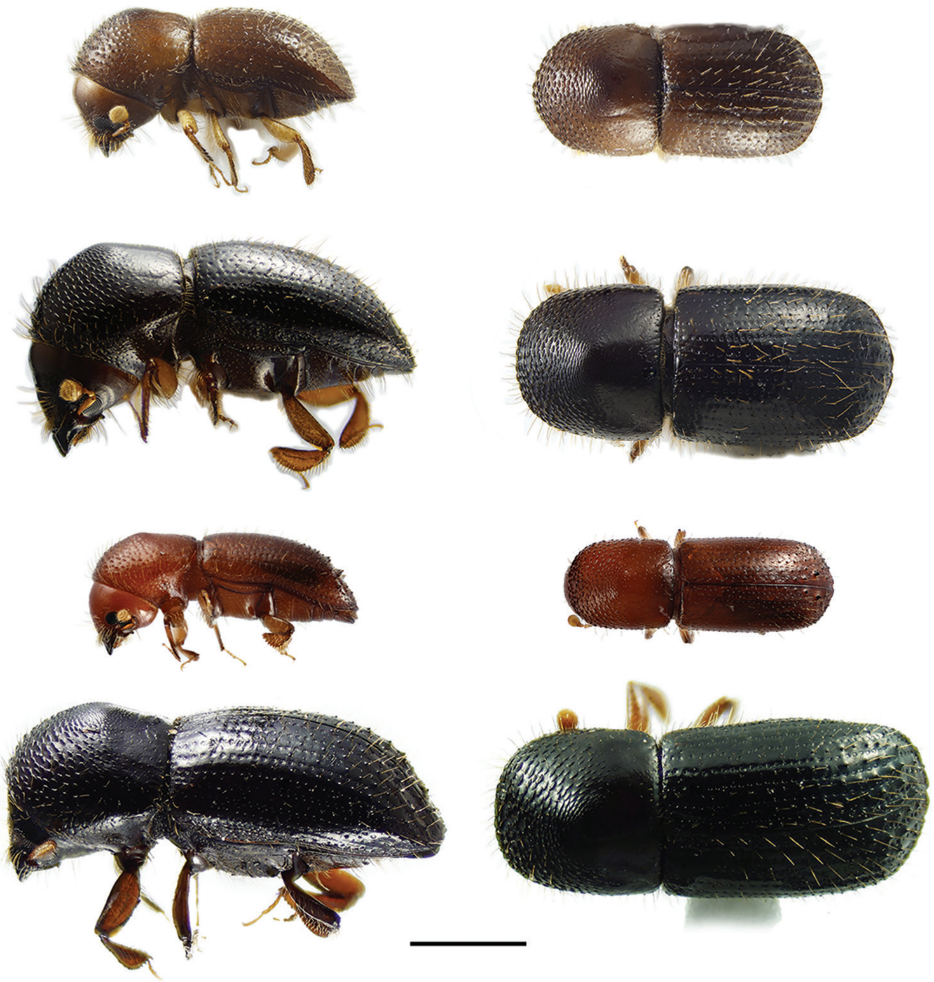

Figure 11. Lateral and dorsal views of *Euwallacea* species. From top left, *Euwallacea fornicatus*, *E. interjectus*, *E. similis* and *E. validus*. Scale bar: 1.0 mm.

Euwallacea similis (Ferrari, 1867)

Fig. 11

Bostrichus ferrugineus Boheman, 1858. Synonymy Schedl 1960.
Xyleborus similis Ferrari, 1867.
Xyleborus parvulus Eichhoff, 1868. Synonymy Schedl 1959.
Xyleborus dilatus Eichhoff, 1876. Synonymy Schedl 1959.
Xyleborus submarginatus Blandford, 1896. Synonymy Eggers 1929.
Xyleborus bucco Schaufuss, 1897. Synonymy Schedl 1959.
Xyleborus capito Schaufuss, 1897. Synonymy Schedl 1959.

Xyleborus novaguineanus Schedl, 1936. Synonymy Wood 1989.
Xyleborus dilatatulus Schedl, 1953. Synonymy Wood 1989.

Type material. Holotype female; "Insula Keeling". NHMW.

Distribution. Africa; Asia; North America (introduced): United States: Texas; Oceania; South America (introduced): Brazil.

Notes. The designation of *Anodius denticulus* Motschulsky, 1863 as a synonym of this species (Mandelshtam and Nikitskij 2010) is not considered valid (Alonso-Zarazaga pers. comm.). Wood designated a specimen of *Xyleborus perforans* as the lectotype of *Anodius denticulus*, not a specimen of *X. similis* (although they occurred on the same pin).

Euwallacea validus (Eichhoff, 1875)

Fig. 11

Xyleborus validus Eichhoff, 1875.

Type material. Syntypes female; Japan; IRSNB.

Distribution. Asia; North America (introduced): Canada: Ontario; United States: Alabama, Delaware, Georgia, Kentucky, Maryland, Michigan, Mississippi, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia.

Notes. *Euwallacea validus* was first collected in the US from Nassau County, New York in 1975 (Wood 1977) and later from Pennsylvania in 1980 (Wood 1982) and Louisiana in 1984 (Chapin and Oliver 1986). This species is distinguished from *E. interjectus* in North America by the larger size, the absence of tubercles from the apical half of the interstriae 2, and by uneven and tuberculate declivital costae.

Theoborus Hopkins, 1915

Type species. *Theoborus theobromae* Hopkins.

Species of *Theoborus* differ from other members of the tribe by the light-brown color, the type 3 antennal club, the pointed elytral declivity apex in dorsal view, and the smooth posterior face of protibia.

Theoborus ricini (Eggers, 1932)

Fig. 12

Xyleborus ricini Eggers, 1932.
Xyleborus solitariceps Schedl, 1954. Synonymy Wood 1989.

Figure 12. Lateral and dorsal view of *Theoborus ricini*. Scale bar: 1.0 mm.

Type material. Holotype female; "Congostaat"; NMNH.

Distribution. Africa (introduced); Central America: Costa Rica; North America: Antilles, Mexico, United States: Florida; South America: Brazil, Colombia, Venezuela.

Notes. It is unclear if this species was introduced from South America or is native to North America. Distinguished by the light-brown color, the short and steep elytral declivity with stout and short interstrial setae, and the smooth posterior face of protibia.

Xyleborinus Reitter, 1913

Type species. *Bostrichus saxesenii* Ratzeburg.

Species of *Xyleborinus* differ from other members of the tribe by the conical scutellum surrounded by setae.

Key to species of female *Xyleborinus*

1 Elytral apex strongly convergent .... ***andrewesi* (Blandford)**

– Elytral apex broadly rounded **2**

2 Declivital interstriae 1 with small denticles; 1 and 3 equally, weakly elevated **3**

– Declivital interstriae 1 without denticles and not elevated **4**

3 Denticles on declivital interstriae 1 and 3 larger, those on 3 pointed, spine-like, slightly incurved; denticles on ventrolateral area of the elytra large,

sharply pointed, spine-like, curved slightly downwards and to the suture; declivital interstriae 2 flattened; 2.5–2.8 mm............. ***attenuatus* (Blandford)**

– Denticles on declivital interstriae 1 and 3 smaller, obtusely pointed; denticles on ventrolateral areas of the elytra small, less pointed; declivital interstriae 2 slightly impressed; 2.0–2.4 mm. .... ***saxesenii* (Ratzeburg)**

4 Declivity flattened, declivital interstriae 3 slightly elevated with 3 pairs of small tubercles, the pair near the posterior margin largest and often blunt; 1.6–1.9 mm..***gracilis* (Eichhoff)**

– Declivity sulcate, interstriae 2 impressed, tubercles on interstriae 3 of equal size; longer than 2.0 mm..**5**

5 Declivital interstriae 3 slightly elevated with 2–3 pairs of tubercles, with bases wider than their length; 2.0–2.5 mm. ....***artestriatus* (Eichhoff)**

– Declivital interstriae 3 strongly elevated with 4 pairs of long, narrow, pointed spines increasing in size approaching posterior margin, 2.1–2.4 mm............ ....***octiesdentatus* (Murayama)**

Xyleborinus andrewesi (Blandford, 1896)

Fig. 13

Xyleborus andrewesi Blandford, 1896.
Xyleborus persphenos Schedl, 1970. Synonymy Beaver and Brownie 1978.
Xyleborus insolitus Bright, 1972. Synonymy Bright 1985.
Cryptoxyleborus gracilior Browne, 1984. Synonymy Beaver 1995.

Type material. Holotype female; India; BMHN.

Distribution. Africa; Asia; North America (introduced): Antilles, United States: Florida, Hawaii; Oceania.

Notes. *Xyleborinus andrewesi* was first reported in the US from Lee County, Florida (Okins and Thomas 2010). Distinguished by the narrow, strongly convergent (as opposed to rounded) posterior margin of elytra.

Xyleborinus artestriatus (Eichhoff, 1878)

Fig. 13

Xyleborus artestriatus Eichhoff, 1878.
Xyleborus laticollis Blandford, 1896. Synonymy Schedl 1958.
Xyleborus rugipennis Schedl, 1953. Synonymy Wood 1989.
Xyleborinus beaveri Browne, 1978. Synonymy Bright 2014.

Type material. Holotype female; ZMUH, lost.

Distribution. Asia; North America (introduced): United States: Georgia, Texas; Oceania.

Figure 13. Lateral and dorsal views of *Xyleborinus* species. From top left, *Xyleborinus andrewesi*, *X. artestriatus*, *X. attenuatus* and *X. gracilis*. Scale bar: 1.0 mm.

Notes. *Xyleborinus artestriatus* was reported for the first time in North America based on specimens from Georgia and Texas (Cognato et al. 2013). Distinguished by the wide denticles of interstriae 3 and the sulcate declivity.

Xyleborinus attenuatus (Blandford, 1894)

Fig. 13

Xyleborus attenuatus Blandford, 1894.
Xyleborinus alni Niisima, 1909. Synonymy Knížek 2011.

Type material. Holotype female; Nikko, Japan; BMNH.

Distribution. Asia; Europe (introduced); North America (introduced): Canada: British Columbia, Nova Scotia, Ontario, Quebec; United States: Maine, Maryland, Michigan, New York, Oregon, Pennsylvania, Washington.

Notes. Similar to *X. saxesenii*, but can be distinguished by the larger size and the pointed and hooked tubercles on the declivity (Holzschuh 1994, Hoebeke and Rabaglia 2007).

Xyleborinus gracilis **(Eichhoff, 1868)**

Fig. 13

Xyleborus gracilis Eichhoff, 1868.
Xyleborus aspericauda Eggers, 1941. Synonymy Bright 1985.
Xyleborus neogracilis Schedl, 1954. Synonymy Bright 1985.
Xyleborus schoenherri Schedl, 1981. Synonymy Bright 2014.

Type material. Lectotype; Brasilia; NMNH.

Distribution. Africa; Central America: Costa Rica, Honduras, Panama; North America: Mexico, United States: Florida, Louisiana, Missouri, North Carolina, South Carolina, Texas; South America: Argentina, Brazil, Colombia, Ecuador, Venezuela.

Notes. Distinguished from other *Xyleborinus* by the blunt tubercles of declivital interstriae 3.

Xyleborinus octiesdentatus **(Murayama, 1931)**

Fig. 14

Xyleborus octiesdentatus Murayama, 1931.

Type material. Holotype; Kannanri, Korea; NMNH.

Distribution. Asia; North America (introduced): Alabama, Louisiana, Mississippi, South Carolina.

Notes. *Xyleborinus octiesdentatus* was reported for the first time from North America based on specimens from Alabama and Louisiana (Rabaglia et al. 2010). Distinguished from other *Xyleborinus* by the 4 pairs of long, pointed spines increasing in size towards apex, on interstriae 3.

Xyleborinus saxesenii **(Ratzeburg, 1837)**

Fig. 14

Bostrichus saxesenii Ratzeburg, 1837.
Tomicus dohrnii Wollaston, 1854. Synonymy Eichhoff 1878.
Tomicus decolor Boieldieu, 1859. Synonymy Ferrari 1867.
Xyleborus aesculi Ferrari, 1867. Synonymy Eichhoff 1878.
Xyleborus sobrinus Eichhoff, 1875. Synonymy Schedl 1964.
Xyleborus subdepressus Rey, 1883. Synonymy Bedel 1888.
Xyleborus frigidus Blackburn, 1885. Synonymy Samuelson 1981.

Xyleborus floridensis Hopkins, 1915. Synonymy Wood 1962.
Xyleborus pecanis Hopkins, 1915. Synonymy Wood 1962.
Xyleborus quercus Hopkins, 1915. Synonymy Wood 1962.
Xyleborus arbuti Hopkins, 1915. Synonymy Wood 1957.
Xyleborus subspinosus Eggers, 1930. Synonymy Wood 1989.
Xyleborinus tsugae Swaine, 1934. Synonymy Wood 1957.
Xyleborinus librocedri Swaine, 1934. Synonymy Wood 1957.
Xyleborus pseudogracilis Schedl, 1937. Synonymy Wood 1989.
Xyleborus retrusus Schedl, 1940. Synonymy Wood 1989.
Xyleborus peregrinus Eggers, 1944. Synonymy Schedl 1980.
Xyleborinus pseudoangustatus Schedl, 1948. Synonymy Schedl 1964.
Xyleborus paraguayensis Schedl, 1948. Synonymy Wood 1989.
Xyleborus opimulus Schedl, 1976. Synonymy Wood 2007.
Xyleborus cinctipennis Schedl, 1980. Synonymy Wood 1989.

Type material. Syntypes female; "Südlichen Deutschland"; type location is indicated as presumably at SDEI by Wood and Bright (2007), unconfirmed.

Distribution. Africa (introduced); Asia, Europe (introduced), North America (introduced): Mexico, Canada: British Columbia, New Brunswick, Ontario, United States: Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, Florida, Georgia, Hawaii, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, South Carolina, Tennessee, Texas, Utah, Virginia, Washington, West Virginia; Oceania (introduced); South America (introduced): Argentina, Brazil, Chile, Ecuador, Paraguay, Uruguay.

Notes. This species is widely distributed. Wood and Bright (1992) and most authors list this species as *X. saxeseni*, but Holzschuh (1994) points out that Ratzeburg's original description was *saxesenii*, with the *ii* ending. The synonymy stated by Wood (1989) between *X. cinctipennis* Schedl, 1980 with *X. saxesenii*, supported by Brockerhoff et al. (2003), Knížek (2011) and Alonso-Zarazaga et al. (2017), may be in error (Beaver pers. comm.).

Xyleborus Eichhoff, 1864

Anaeretus Dugès, 1887. Synonymy Hagedorn 1910.
Progenius Blandford, 1896. Synonymy Hagedorn 1910.
Mesoscolytus Broun, 1904. Synonymy Bain 1976.
Heteroborips Reitter, 1913. Synonymy Schedl 1934.
Boroxylon Hopkins, 1915. Synonymy Schedl 1952.
Notoxyleborus Schedl, 1934. Synonymy Wood 1986.

Figure 14. Lateral and dorsal views of *Xyleborinus* species. From top left, *Xyleborinus octiesdentatus* and *X. saxesenii*. Scale bar: 1.0 mm.

Type species. *Bostrichus monographus* Fabricius.

Species of *Xyleborus* differ from most (but not all) members of the tribe by the truncate antennal club, the first segment of which is corneous. Species of *Xyleborus* s. str. (Hulcr and Cognato 2013) have an inflated prosternal posterocoxal process. Some species currently placed in *Xyleborus* do not have this feature, but the proper genus placement of many such species is unclear.

Key to species of female *Xyleborus*

1 Area adjacent to scutellum impressed; pronotum nearly as broad as long, posterolateral areas distinctly, strongly asperate; 1.9–2.5 mm. ......***seriatus* Blandford**

– Area adjacent to scutellum not impressed, flush with elytral base; pronotum stout or elongate, posterolateral areas not asperate **2**

2 Declivital striae completely obscured by abundant, confused punctures and setae; body slightly more stout, 2.3–2.6 times as long as wide; 3.8–4.2 mm .... ***horridus* Eichhoff**

– Declivital striae obviously indicated or not, never obscured as above; body slender, more than 2.6 times as long as wide **3**

3 Tubercles on declivital interstriae 1 distinctly larger than tubercles on other interstriae.. **4**

– Tubercles on declivital interstriae 1 either similar in size to tubercles on other interstriae or absent (except at base or apex)... **5**

4 Elytral disc and declivity setose; all declivital interstriae armed by strong tubercles at base; declivital interstriae 1 armed by two very large pointed tubercles, declivital interstriae 3 armed by several smaller tubercles; declivity weakly sulcate; larger species, 3.6–4.5 mm............................ ***celsus* Eichhoff**

– Elytral disc and declivity glabrous; all declivital interstriae armed by small granules, gradually decreasing in size toward apex; interstriae 1 near apex armed by one or two small tubercles; declivity flattened, convex at suture toward apex; smaller species, 2.0 mm. ***glabratus*** **Eichhoff**

5 Tubercles on declivital interstriae 3 distinctly larger than tubercles on other interstriae; tubercles absent on interstriae 1 (one or two small denticles may be present at base or apex, but not on declivital face); declivity shallowly to strongly sulcate ... **6**

– Tubercles on declivital interstriae 3 not distinctly larger than those on other interstriae; tubercles present on interstriae 1; declivity flat to convex ... **10**

6 Anterior portion of pronotum flattened, weakly sulcate; 2.0–2.5 mm. ***viduus*** **Eichhoff**

– Anterior portion of pronotum convex, normal ... **7**

7 Apex of declivity at interstriae 3 armed by two prominent, elongate tubercles; declivital setae spatulate; 1.8–2.6 mm. ***spinulosus*** **Blandford**

– Apex of declivity at interstriae 3 unarmed; declivital setae hairlike ... **8**

8 Declivital interstriae 1 unarmed, interstriae 3 with usually three prominent tubercles; declivity distinctly sulcate, interstriae 2 impressed, strial punctures less distinct; 2.0–2.5 mm ... ***impressus*** **Eichhoff**

– Declivital interstriae 1 armed by one or two small denticles at base, interstriae 3 with one prominent tubercle near middle of declivity (minor denticles may also be present); declivity flat to subsulcate, interstriae 2 not impressed, strial punctures distinct ... **9**

9 Discal interstrial setae regularly spaced, numerous; larger, more robust species; color dark reddish brown; 2.8–3.2 mm. ... ***bispinatus*** **Eichhoff**

– Discal interstrial setae sparse or absent; smaller, more slender species; color light orange to reddish brown; 2.4–2.9 mm. ***ferrugineus*** **(Fabricius)**

10 Surface of declivity opaque ... **11**

– Surface of declivity shining ... **13**

11 Anterior portion of pronotum flattened, weakly sulcate; 2.3–2.4 mm. ***planicollis*** **Zimmermann**

– Anterior portion of pronotum convex, normal ... **12**

12 Declivity broadly sloping, occupying posterior 30-40% of elytra, shagreened; declivital denticles on interstriae 1 and 3 small but conspicuous; 2.0–2.7 mm. ***affinis*** **Eichhoff**

– Declivity steep, occupying posterior 15% of elytra; denticles on declivital interstriae 1 and 3 very small; 2.3–2.7 mm. ... ***xylographus*** **(Say)**

13 Declivity steep, posterolateral margin rounded ... **14**

– Declivity broadly sloping, posterolateral margin subacute ... **15**

14 Discal interstriae twice the width of striae; some declivital tubercles with height and basal width greater than the diameter of strial punctures; declivital strial punctures small, deep; 2.2–2.7 mm. ... ***intrusus*** **Blandford**

– Discal interstriae less than 1.5 times width of striae; some declivital tubercles with height and basal width less than the diameter of strial punctures; declivital strial punctures large, shallow; 2.3–2.7 mm. .... ***pubescens* Zimmermann**

15 Color reddish brown; declivity flattened to slightly convex, interstriae 2 moderately impressed, interstriae 1 near apex less elevated; punctures of declivital striae 1 and 2 small, anterolateral margin of punctures not raised; smaller, 2.1–2.8 mm.. ***volvulus* (Fabricius)**

– Color usually black; declivity flattened, interstriae 2 impressed, especially from middle of declivity, interstriae 1 near apex distinctly elevated; punctures of declivital striae 1 and 2 large, shallow, anterolateral margin of punctures produced into a short ridge; larger, 3.0–3.6 mm ....***pfeilii* (Ratzeburg)**

Xyleborus affinis Eichhoff, 1868

Fig. 15

Xyleborus affinis parvus Eichhoff, 1878. Synonymy Schedl 1959.
Xyleborus affinis mascarensis Eichhoff, 1878. Synonymy Wood 1960.
Xyleborus affinis fuscobrunneus Eichhoff, 1878. Synonymy Schedl 1959.
Xyleborus sacchari Hopkins, 1915. Synonymy Schedl 1959.
Xyleborus subaffinis Eggers, 1933. Synonymy Schedl 1959.
Xyleborus societatis Beeson, 1935. Synonymy Beaver 1991.
Xyleborus proximus Eggers, 1943. Synonymy Schedl 1962.

Type material. Syntypes female; “America bor.”, Cuba; ZMUH, lost; 1 in NMNH.

Distribution. Africa (introduced); Asia (introduced); Central America: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; Europe (introduced), North America: Antilles, Canada: Quebec, Mexico, United States: Alabama, Arkansas, California, Delaware, District of Columbia, Florida, Georgia, Hawaii, Illinois, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia; Oceania (introduced); South America: Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Fr. Guiana, Guyana, Paraguay, Peru, Suriname, Trinidad, Uruguay, Venezuela.

Notes. This widely distributed species can cause economic damage in moist lowland areas of the Neotropics. This species is distinguished by the broadly sloping shagreened declivity and the small denticles in interstriae 1 and 3.

Xyleborus bispinatus Eichhoff, 1868

Fig. 15

Type material. Syntypes female; Brazil; IRSNB.

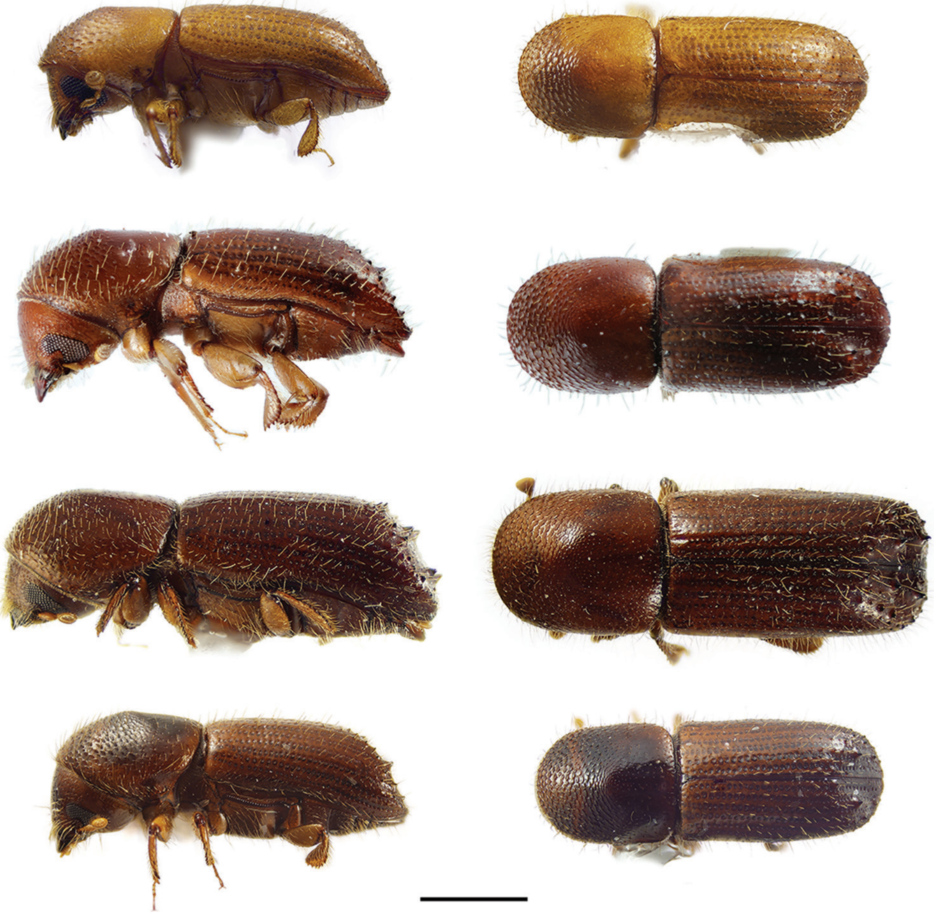

Figure 15. Lateral and dorsal views of *Xyleborus* species. From top left, *Xyleborus affinis*, *X. bispinatus*, *X. celsus* and *X. ferrugineus*. Scale bar: 1.0 mm.

Distribution. Central America: Belize, Costa Rica, Guatemala, Honduras, Panama; North America: Mexico, United States: Florida, Georgia, Louisiana, North Carolina, Texas; Oceania; South America: Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela.

Notes. This species was removed from synonymy with *X. ferrugineus* by Kirkendall and Jordal (2006) and its taxonomic status is unclear.

Xyleborus celsus Eichhoff, 1868

Fig. 15

Xyleborus biographus LeConte, 1868. Synonymy Eichhoff 1878.

Type material. Syntypes female; “America boreali”. ZMUH, lost.

Distribution. North America: Canada: Ontario, United States: Alabama, Arkansas, Connecticut, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Michigan, Minnesota, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Texas, Vermont, Virginia, West Virginia.

Notes. This species is distinguished by its large size and its two pairs of large pointed tubercles on declivital interstriae 1.

Xyleborus ferrugineus **(Fabricius, 1801)**

Fig. 15

Bostrichus ferrugineus Fabricius, 1801.
Tomicus trypanaeoides Wollaston, 1867. Synonymy Schedl 1960.
Xyleborus fuscatus Eichhoff, 1868. Synonymy Schedl 1960.
Xyleborus confusus Eichhoff, 1868. Synonymy Schedl 1957.
Xyleborus retusicollis Zimmermann, 1868. Synonymy Bright 1968.
Xyleborus amplicollis Eichhoff, 1869. Synonymy Schedl 1960.
Xyleborus insularis Sharp, 1885. Synonymy Schedl 1960.
Xyleborus tanganus Hagedorn, 1910. Synonymy Schedl 1960.
Xyleborus soltaui Hopkins, 1915. Synonymy Bright 1968.
Xyleborus nyssae Hopkins, 1915. Synonymy Schedl 1960.
Xyleborus hopkinsi Beeson, 1929. Synonymy Schedl 1960.
Xyleborus argentinensis Schedl, 1931. Synonymy Schedl 1960.
Xyleborus rufopiceus Eggers, 1932. Synonymy Wood 1989.
Xyleborus schedli Eggers, 1934. Synonymy Schedl 1960.
Xyleborus nesianus Beeson, 1940. Synonymy Beaver 1991.
Xyleborus notatus Eggers, 1941. Synonymy Schedl 1960.
Xyleborus subitus Schedl, 1948. Synonymy Schedl 1960.

Type material. Lectotype female; “America meridionali”; UZMC.

Distribution. Africa (introduced); Asia; Central America: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; North America: Antilles, Canada: Ontario, Mexico, United States: Alabama, Arizona, Arkansas, California, Delaware, District of Columbia, Florida, Georgia, Hawaii, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia; Oceania (introduced); South America: Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Fr. Guiana, Guyana, Paraguay, Peru, Suriname, Trinidad, Uruguay, Venezuela.

Notes. This species was removed from synonymy with *X. bispinatus* by Kirkendall and Jordal (2006). It is distinguished from *X. bispinatus* by the smaller size, discal interstrial setae sparse or absent, and by its light orange to reddish brown color (Atkinson et al. 2013).

Xyleborus glabratus Eichhoff, 1877

Fig. 16

Type material. Syntype female; Japan. IRSNB.

Distribution. Asia; North America (introduced): United States: Alabama, Florida, Georgia, Mississippi, South Carolina.

Notes. In the US, *X. glabratus* was first detected in a survey trap near Port Wentworth, Georgia in 2002 (Rabaglia et al. 2006). The ambrosia fungus vectored by this species is responsible for the death of 300 million bay trees (*Persea* spp.) and other Lauraceae in the southeastern United States (Hughes et al. 2017). This species is distinguished by the dark color and the glabrous elytral disc and declivity with small granules in all interstriae decreasing in size toward apex.

Xyleborus horridus Eichhoff, 1869

Fig. 16

Xyleborus flohri Schedl, 1972. Synonymy Wood 1977.

Type material. Lectotype female; Mexico. IRSNB.

Distribution. Central America: Belize, El Salvador, Guatemala, Honduras, Panama; North America: Mexico, United States: Texas.

Notes. This species is distinguished by the presence of abundant, confused punctures and setae, which completely obscure declivital striae.

Xyleborus impressus Eichhoff, 1868

Fig. 16

Type material. Lectotype female; “Amer. Bor.”; NMNH.

Distribution. North America: United States: Alabama, Arkansas, Florida, Georgia, Illinois, Indiana, Louisiana, Massachusetts, Mississippi, Missouri, New Jersey, North Carolina, Ohio, Oklahoma, South Carolina, Tennessee, Texas, Virginia.

Notes. This species was removed from synonymy with *X. ferrugineus* by Rabaglia (2005). It is distinguished by the presence of three prominent tubercles on declivital interstriae 3, while interstriae 1 are unarmed.

Xyleborus intrusus Blandford, 1898

Fig. 16

Xyleborus howardi Hopkins, 1915. Synonymy Wood 1972.
Xyleborus fitchi Hopkins, 1915. Synonymy Bright 1968.

Figure 16. Lateral and dorsal views of *Xyleborus* species. From top left, *Xyleborus glabratus*, *X. horridus*, *X. impressus* and *X. intrusus*. Scale bar: 1.0 mm.

Xyleborus scopulorum Hopkins, 1915. Synonymy Wood 1972.

Type material. Lectotype female; Guatemala; BMNH.

Distribution. Central America: El Salvador, Guatemala, Honduras; North America: Antilles, Canada: British Columbia, Mexico, United States: Arizona, California, Colorado, District of Columbia, Georgia, Idaho, Maine, Maryland, Mississippi, Montana, New Jersey, New Mexico, North Carolina, Oregon, Pennsylvania, South Carolina, South Dakota, Utah, Virginia, West Virginia.

Notes. One of the few species of the genus restricted to conifers. Distinguished from other *Xyleborus* by the steep declivity which occupies the apical ¼ of the elytra, and broadly rounded posterolateral margin of the declivity. It is distinguished from *X. pubescens* by the larger declivital denticles and smaller, deeply impressed declivital strial punctures.

Xyleborus pfeilii (Ratzeburg, 1837)

Fig. 17

Bostrichus pfeilii Ratzeburg, 1837.
Bostrichus alni Mulsant & Rey, 1856. Synonymy Hagedorn 1910.
Xyleborus vicarius Eichhoff, 1875. Synonymy Schedl 1963.
Xyleborus adumbratus Blandford, 1894.Synonymy Schedl 1963.

Type material. Syntypes female; "im Lüneburgschen und in Bayern"; not located, if extant, probably in SDEI.

Distribution. Africa; Asia; Europe; North America (introduced): Canada: British Columbia; United States: Maryland, Oregon, Pennsylvania, Washington; South America: Brazil.

Notes. *Xyleborus pfeilii* was first detected in North America in Maryland in 1992 (Vandenberg et al. 2000) and in Oregon in 1997–98 (Mudge et al. 2001). Distinguished from *X. volvulus* by its larger size. Wood and Bright (1992) suggest that this species may be a synonym of *X. volvulus*.

Xyleborus planicollis Zimmermann, 1868

Fig. 17

Type material. Holotype female; Pennsylvania; MCZ.

Distribution. North America: United States: Arkansas, Illinois, Indiana, Maryland, Michigan, Mississippi, Missouri, North Carolina, Pennsylvania, Texas, West Virginia.

Notes. Distinguished by the flattened anterior portion of pronotum.

Xyleborus pubescens Zimmermann, 1868

Fig. 17

Xyleborus pini Eichhoff, 1868. Erroneous identification.
Xyleborus propinquus Eichhoff, 1869. Synonymy Wood 1973.

Type material. Lectotype female; "southern states", USA; MCZ.

Distribution. Central America: El Salvador; North America: Antilles, Canada: Ontario; United States: Alabama, Arkansas, Delaware, District of Columbia, Florida, Georgia, Kentucky, Louisiana, Maryland, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia, West Virginia.

Notes. This species and *X. intrusus* are common in pines. It can be distinguished from *X. intrusus* by the larger, shallow strial punctures and the smaller declivital denticles.

Figure 17. Lateral and dorsal views of *Xyleborus* species. From top left, *Xyleborus pfeili*, *X. planicollis*, *X. pubescens* and *X. seriatus*. Scale bar: 1.0 mm.

Xyleborus seriatus Blandford, 1894

Fig. 17

Xyleborus orientalis Eggers, 1933. Synonymy Mandelshtam 2007.
Xyleborus orientalis kalopanacis Kurenzov, 1941. Synonymy Wood and Bright 1992.
Xyleborus orientalis aceris Kurenzov, 1941. Synonymy Wood and Bright 1992.
Xyleborus perorientalis Schedl, 1957. Synonymy Browne 1962.

Type material. Syntypes; Higo, Japan; BMNH.

Distribution. Asia; North America (introduced): United States: Massachusetts.

Notes. First found in Massachusetts in 2005 and 2006 (Hoebeke and Rabaglia 2008), *X. seriatus* is distinguished from other *Xyleborus* by the distinctly impressed area adjacent to the scutellum and the alternating series of longer and shorter setae on the elytra (Hoebeke and Rabaglia 2008). Both *X. orientalis kalopanacis* Kurenzov and *X. orientalis aceris* Kurenzov were listed as synonyms of *X. orientalis* by Wood and Bright (1992). Mandelshtam (2007) synonymised *X. orientalis* with *X. seriatus*, without mentioning Kurenzov's subspecies.

Xyleborus spinulosus Blandford, 1898

Fig. 18

Xyleborus fusciseriatus Eggers, 1934. Synonymy Wood 1979.
Xyleborus spinosulus Schedl, 1934. Synonymy Wood 1966.
Xyleborus artespinulosus Schedl, 1935. Synonymy Wood 1979.

Type material. Lectotype female; San Geronimo, Guatemala; BMNH.

Distribution. Central America: Costa Rica, Guatemala, Honduras; North America (introduced): Antilles Mexico, United States: Hawaii, Texas; South America: Argentina, Brazil, Colombia, Ecuador, Guyana, Peru, Venezuela.

Notes. *Xyleborus spinulosus,* native to Central America and lowland Mexico, was first found in the US in Texas in 1994 (Atkinson and Riley 2013). It is distinguished by its unique declivity, which is armed by spine-like tubercles.

Xyleborus viduus Eichhoff, 1878

Fig. 18

Type material. Syntypes female; uncertain: Brasilia or America septentrionali (USA). ZMUH, lost.

Distribution. North America: United States: Alabama, Arkansas, Florida, Illinois, Indiana, Kansas, Maryland, Mississippi, Missouri, Oklahoma, Tennessee, Texas, West Virginia.

Notes. Distinguished by the impressed anterior portion of pronotum. Distinguished from *X. planicollis* by the impressed, shining, and tuberculate declivity.

Xyleborus volvulus (Fabricius, 1775)

Fig. 18

Bostrichus volvulus Fabricius, 1775.
Xyleborus torquatus Eichhoff, 1868. Synonymy Wood 1960.
Xyleborus alternans Eichhoff, 1869. Synonymy Eggers 1929.
Xyleborus badius Eichhoff, 1869. Synonymy Wood 1960.

Figure 18. Lateral and dorsal views of *Xyleborus* species. From top left, *Xyleborus spinulosus*, *X. viduus*, *X. volvulus* and *X. xylographus*. Scale bar: 1.0 mm.

Xyleborus interstitialis Eichhoff, 1878. Synonymy Wood 1982.
Xyleborus guanajuatensis Dugès, 1887. Synonymy Wood 1983.
Xyleborus hubbardi Hopkins, 1915. Synonymy Schedl 1952.
Xyleborus schwarzi Hopkins, 1915. Synonymy Bright 1968.
Xyleborus rileyi Hopkins, 1915. Synonymy Bright 1968.
Xyleborus grenadensis Hopkins, 1915. Synonymy Wood 1972.
Xyleborus continentalis Eggers, 1920. Synonymy Beaver 2011.
Xyleborus silvestris Beeson, 1929. Synonymy Wood 1989.
Xyleborus vagabundus Schedl, 1948. Synonymy Wood 1972.

Xyleborus granularis Schedl, 1950. Synonymy Wood 1989.

Type material. Lectotype female; “America ligno Dom v. Rohr (presumably Cuba)”; UZMC.

Distribution. Africa; Asia; Central America: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; North America: Antilles, Mexico, United States: Florida, Hawaii; Oceania; South America: Argentina, Bolivia, Brazil, Colombia, Ecuador, Fr. Guiana, Guyana, Paraguay, Peru, Suriname, Trinidad, Uruguay, Venezuela.

Notes. Distinguished by the slightly convex to flattened declivity bearing prominent tubercles of varying sizes.

Xyleborus xylographus (Say, 1826)

Fig. 18

Bostrichus xylographus Say, 1826.
Xyleborus inermis Eichhoff, 1868. Synonymy Eichhoff 1878.
Xyleborus canadensis Swaine, 1917. Synonymy Wood 1957.

Type material. Neotype female; North Carolina; CNCI.

Distribution. Asia (introduced); North America: Antilles, Canada: British Columbia, Ontario, Quebec; United States: Arkansas, California, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, South Carolina, Utah, Virginia, West Virginia, Wisconsin.

Notes. Distinguished by the lusterless and steep declivity, occupying no more than posterior 15% of elytra.

Xylosandrus Reitter, 1913

Apoxyleborus Wood, 1980. Synonymy Wood 1984.

Type species. *Xyleborus morigerus* Blandford.

Species of *Xylosandrus* differ from other members of the tribe by widely separated procoxae.

Key to species of female *Xylosandrus*

1 Elytral declivity sharply truncate, margin of declivity with posterolateral carina extending to suture, forming a complete cirumdeclivital ring; body length 2.7–2.9 mm .... ***amputatus* (Blandford)**

– Elytral declivity rounded or only obliquely truncate, margin of declivity with carina not extending beyond 7th interstriae..**2**

2 Declivity without punctures or carina, surface with dense and confused granules, dull; body length 3.0 mm.; reddish brown ....***crassiusculus* (Motschulsky)**

– Declivital striae with punctures clearly impressed, in rows; declivital surface shining, granules in sparse rows when present; body length less than 2.7 mm; black or dark brown..**3**

3 Body length 2.0–2.3 mm; strial setae on declivity absent (only interstrial setae present); declivital striae at least weakly impressed, interstriae very slightly elevated; typically black..***germanus* (Blandford)**

– Body length 1.7 mm or less; strial setae on declivity present, at least one-third as long as those on interstriae; declivital striae not impressed, interstriae flat........ **4**

4 Elytra almost evenly arched from middle of disc to apex; setae on pronotal disc more evenly distributed, slightly more abundant on a transverse row in median area at the base; posterior portion of pronotum shining; body black, length 1.6–1.7 mm. .... ***compactus* (Eichhoff)**

– Elytra more abruptly arched from base of declivity to middle of declivity; pronotal disc glabrous except for a dense, median tuft of setae extending from base about half distance to summit; posterior portion of pronotum mostly reticulate; body dark brown, length 1.6–1.8 mm. ....***curtulus* (Eichhoff)**

Xylosandrus amputatus (Blandford, 1894)

Fig. 19

Xyleborus amputatus Blandford, 1894.
Xyleborus melli Eggers, 1926. Synonymy Beaver 2010.

Type material. Holotype female; Japan: Higo; BMNH.

Distribution. Asia; North America (introduced): Florida, Georgia.

Notes. *Xylosandrus amputatus* was first discovered in the US from Florida in 2010 (Cognato et al. 2011). Distinguished by the truncate elytral declivity with a carina forming a complete cirumdeclivital ring.

Xylosandrus compactus (Eichhoff, 1875)

Fig. 19

Xyleborus compactus Eichhoff, 1875.
Xyleborus morstatti Hagedorn, 1912. Synonymy Murayama and Kalshoven 1962.

Type material. Syntypes female; Japan; ZMUH, lost. 1 syntype Schedl Collection NHMW.

Distribution. Africa; Asia; North America (introduced): Antilles, United States: Alabama, Florida, Georgia, Hawaii, Illinois, Louisiana, Mississippi, North Carolina, Pennsylvania, Texas; Oceania (introduced); South America: Brazil, Fr. Guiana, Peru, Trinidad.

Notes. Commonly known as the black twig borer, *X. compactus* was first collected in the US at Ft. Lauderdale, Florida in 1941 (Wood 1982). It attacks healthy twigs of living trees and shrubs in the southeastern United States. Distinguished by the small size, the black color, and the shining declivity.

Xylosandrus crassiusculus (Motschulsky, 1866)

Fig. 19

Phloeotrogus crassiusculus Motschulsky, 1866.
Xyleborus semiopacus Eichhoff, 1878. Synonymy Wood 1969.
Xyleborus semigranosus Blandford, 1896. Synonymy Schedl 1959.
Xyleborus ebriosus Niisima, 1909. Synonymy Choo 1983.
Dryocoetes bengalensis Stebbing, 1908. Synonymy Beeson 1915.
Xyleborus mascarenus Hagedorn, 1908. Synonymy Eggers 1923.
Xyleborus okoumeensis Schedl, 1935. Synonymy Schedl 1959.
Xyleborus declivigranulatus Schedl, 1936. Synonymy Schedl 1959.

Type material. Syntypes female; Ceylon; IZM.

Distribution. Africa; Asia; Central America (introduced): Costa Rica, Guatemala, Panama;, North America (introduced): Antilles, Canada: Ontario; United States: Alabama, Delaware, Florida, Georgia, Hawaii, Indiana, Kentucky, Louisiana, Maryland, Michigan, Mississippi, Missouri, North Carolina, Ohio, Oklahoma, Oregon, South Carolina, Tennessee, Texas, Virginia; Oceania (introduced); South America (introduced): Argentina, Brazil, Fr. Guiana, Uruguay.

Notes. A widely introduced species around the globe, *X. crassiusculus* has spread in the US along the lower Piedmont region and coastal plain to North Carolina, Louisiana, Florida, and beyond (Atkinson et al. 2012). The first US record is based on a specimen collected in South Carolina in 1974 (Anderson 1974, as *Xyleborus semiopacus*). Distinguished by the confused declivital granules giving the declivity a dull appearance. Causes economic damage in nurseries and stored hardwood lumber (Smith and Hulcr 2015).

Xylosandrus curtulus (Eichhoff, 1869)

Fig. 19

Xyleborus curtulus Eichhoff, 1869.
Anisandrus zimmermanni Hopkins, 1915. Synonymy Bright 2014.
Xyleborus curtuloides Eggers, 1941. Synonymy Wood 1982.
Xyleborus biseriatus Schedl, 1963. Synonymy Wood 1973.
Xyleborus strumosus Schedl, 1972. Synonymy Wood 1992.

Type material. Holotype female: Brazil; IRSNB.

Figure 19. Lateral and dorsal views of *Xylosandrus* species. From top left, *Xylosandrus amputatus*, *X. compactus*, *X. crassiusculus*, *X. curtulus* and *X. germanus*. Scale bar: 1.0 mm.

Distribution. Central America: Costa Rica, Guatemala, Honduras, Nicaragua, Panama; North America: Antilles, Mexico, United States: Florida; South America: Argentina, Bolivia, Brazil, Colombia, Venezuela.

Notes. This species is currently only known from central and southern Florida in the United States. Distinguished by the dark brown body, the small size, and the hairy and shagreened declivity.

***Xylosandrus germanus* (Blandford, 1894)**
Fig. 19

Xyleborus germanus Blandford, 1894.
Xyleborus orbatus Blandford, 1894. Synonymy Choo 1983.

Type material. Syntypes; Japan; BMNH.

Distribution. Asia; Europe (introduced); North America (introduced): Canada: British Columbia, Ontario, Quebec; United States: Alabama, Connecticut, Delaware, Florida, Georgia, Hawaii, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, West Virginia.

Notes. Originating from Asia, *X. germanus* has now spread across much of North America, including the Northeast, South and Southeast, and the Pacific Northwest (Weber and McPherson 1982; LaBonte et al. 2005); it was first thought to have been introduced into the US in a Long Island area greenhouse in 1932 (Felt 1932). Distinguished by the black color and the lack of strial setae on declivity.

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References

Alonso-Zarazaga MA, Lyal CHC (2009) A catalogue of family and genus group names in Scolytinae and Platypodinae with nomenclatural remarks (Coleoptera: Curculionidae). Zootaxa 2258: 112–127.

Alonso-Zarazaga MA, Barrios H, Borovec R, Bouchard P, Caldara R, Colonnelli E, Gültekin L, Hlaváč P, Korotyaev B, Lyal CHC, Machado A, Meregalli M, Pierotti H, Ren L, Sánchez-Ruiz M, Sforzi A, Silfverberg H, Skuhrovec J, Trýzna M, Velázquez de Castro AJ, Yunakov NN (2017) Cooperative Catalogue of Palaearctic Coleoptera Curculionoidea. Monografías electrónicas S.E.A. 8: 1–729.

Anderson DM (1974) First record of *Xyleborus semiopacus* in the continental United States (Coleoptera, Scolytidae). United States Department of Agriculture Cooperative Economic Insect Report 24: 863–864.

Atkinson TH (2009) A new species of *Dryocoetoides* Hopkins from southern Florida (Coleoptera: Curculionidae: Scolytinae). Zootaxa 2311: 66–68.

Atkinson TH (2017) Bark and Ambrosia Beetles www.barkbeetles.info

Atkinson TH, Riley EG (2013) Atlas and checklist of the bark and ambrosia beetles of Texas and Oklahoma (Curculionidae: Scolytinae and Platypodinae). Insecta Mundi 292: 1–46.

Atkinson TH, Carrillo D, Duncan RE, Peña JE (2013) Occurrence of *Xyleborus bispinatus* (Coleoptera: Curculionidae: Scolytinae) Eichhoff in southern Florida. Zootaxa 3669: 96–100. https://doi.org/10.11646/zootaxa.3669.1.10

Atkinson TH, Foltz JL, Wilkinson RC, Mizell RF (2012) Featured Creatures: *Xylosandrus crassiusculus* (Motschulsky) (Insecta: Coleoptera: Curculionidae: Scolytinae). DPI Circular 310.

Atkinson TH, Rabaglia RJ, Bright DE (1990) Newly detected exotic species of *Xyleborus* (Coleoptera: Scolytidae) with a revised key to species in eastern North America. The Canadian Entomologist 122: 92–104. https://doi.org/10.4039/Ent12293-1

Atkinson TH, Rabaglia RJ, Cognato AI (2010) Two newly detected bark and ambrosia beetles from southern Florida (Coleoptera: Curculionidae, Scolytinae). Zootaxa 2338: 63–68.

Beaver RA (2011) New synonymy and taxonomic changes in bark and ambrosia beetles. Koleopterologische Rundschau 81: 277–289.

Bright DE (1968) Review of the tribe Xyleborini in North America, save Mexico (Coleoptera: Scolytidae). The Canadian Entomologist 100: 1288–1323. https://doi.org/10.4039/Ent1001288-12

Bright DE (2014) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 3 (2000–2010), with notes on subfamily and tribal reclassifications. Insecta Mundi 0356: 1–336.

Bright DE, Rabaglia RJ (1999) *Dryoxylon*, a new genus for *Xyleborus onoharaensis* Murayama, recently established in the southeastern United States (Coleoptera: Scolytidae). The Coleopterists Bulletin 53: 333–337.

Brockerhoff E, Knížek M, Bain J (2003) Checklist of indigenous and adventive bark and ambrosia beetles (Curculionidae: Scolytinae and Platypodinae) of New Zealand and interceptions of exotic species (1952-2000). New Zealand Entomologist 44: 29–44.

Browne FG (1961) The generic characters, habits and taxonomic status of *Premnobius* Eichhoff (Coleoptera, Scolytidae). Fourth WATBRU Report 1961: 45–51.

Chapin JB, Oliver AD (1986) New records for *Xylosandrus* and *Xyleborus* species (Coleoptera: Scolytidae). Proceedings of the Entomological Society of Washington 88: 68– 683.

Chen Y, Dallara PL, Nelson LJ, Coleman TW, Hishinuma SM, Carrillo D, Seybold SJ (2016) Comparative morphometric and chemical analyses of phenotypes of two invasive ambrosia beetles (*Euwallacea* spp.) in the United States of America. Insect Science 24: 647–662. https://doi.org/10.1111/1744-7917.12329

Cognato AI, Olson RO, Rabaglia RJ (2011) An Asian ambrosia beetle, *Xylosandrus amputatus* (Blandford) (Curculionidae: Scolytinae: Xyleborini), discovered in Florida, U.S.A. The Coleopterists Bulletin 65: 43–45. https://doi.org/10.1649/0010-065X-65.1.43

Cognato AI, Rabaglia RJ, Vandenberg NJ (2013) Another Asian ambrosia beetle, *Xyleborinus artestriatus* (Eichhoff 1878) (Coleoptera: Curculionidae: Scolytinae: Xyleborini), newly detected in North America. The Pan-Pacific Entomologist 89: 27–31. https://doi.org/10.3956/2012-53.1

Cognato AI, Hoebeke ER, Kajimura H, Smith SM (2015) History of the Exotic Ambrosia Beetles *Euwallacea interjectus* and *Euwallacea validus* (Coleoptera: Curculionidae: Xyleborini) in the United States. Journal of Economic Entomology 108: 1129–1135. https://doi.org/10.1093/jee/tov073

Felt EP (1932) A new pest in greenhouse grown grape stems. Journal of Economic Entomology 25: 418.

Haack RA, Rabaglia RJ (2013) Exotic bark and ambrosia beetles in the USA: Potential and current invader. In: Peña JE (Ed.) Potential Invasive Pests of Agricultural Crops. CAB International, Boston, MA, 48–74.

Hoebeke ER (1991) An Asian ambrosia beetle, *Ambrosiodmus lewisi*, new to North America (Coleoptera: Scolytidae). Proceedings of the Entomological Society of Washington 93: 420–424.

Hoebeke ER, Rabaglia RJ (2007) First reported occurrence of *Xyleborinus alni* (Coleoptera: Curculionidae: Scolytinae) in the eastern United States, with notes on its recognition and tree hosts. Proceedings of the Entomological Society of Washington 109: 240–248.

Hoebeke ER, Rabaglia RJ (2008) *Xyleborus seriatus* Blandford (Coleoptera: Curculionidae: Scolytinae), an Asian ambrosia beetle new to North America. Zootaxa 110: 470–476.

Hoebeke ER, Rabaglia RJ, Knížek M, Weaver JS (2018) First records of Cyclorhipidion fukiense (Eggers) (Coleoptera: Curculionidae: Scolytinae: Xyleborini), an ambrosia beetle native to Asia, in North America. Zootaxa 4394: 243–250.

Holzschuh C (1994) Zur unterscheidung von *Xyleborinus saxesenii* (Ratzeburg) und *X. alni* (Niisima) (Coleoptera, Scolytidae). Entomologica Basiliensia 17: 311–318.

Hughes MA, Riggins JJ, Koch FH, Cognato AI, Anderson C, Formby JP, Dreaden TJ, Ploetz RC, Smith JA (2017) No rest for the laurels: symbiotic invaders cause unprecedented damage to southern USA forests. Biological Invasions 19: 2143–2157. https://doi.org/10.1007/s10530-017-1427-z

Hulcr J, Cognato AI (2009) Three new genera of oriental Xyleborina (Coleoptera: Curculionidae: Scolytinae). Zootaxa 2204: 19–36.

Hulcr J, Cognato AI (2013) Xyleborini of New Guinea, a Taxonomic Monograph (Coleoptera: Curculionidae: Scolytinae). Thomas Say Publications in Entomology: Monographs, Entomological Society of America, Annapolis, 176 pp.

Hulcr JS, Dole SA, Beaver RA, Cognato AI (2007) Cladistic review of generic taxonomic characters in Xyleborina (Coleoptera: Curculionidae: Scolytinae). Systematic Entomology 32: 568–584. https://doi.org/10.1111/j.1365-3113.2007.00386.x

Jordal BH, Normark BB, Farrell BD (2000) Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae, Scolytinae). Biological Journal of the Linnean Society 71: 483–499. https://doi.org/10.1111/j.1095-8312.2000.tb01270.x

Jordal BH (2002) Elongation Factor 1 α resolves the monophyly of the haplodiploid ambrosia beetles Xyleborini (Coleoptera: Curculionidae). Insect Molecular Biology 11: 453–465. https://doi.org/10.1046/j.1365-2583.2002.00354.x

Kirkendall LR, Jordal BH (2006) The bark and ambrosia beetles (Curculionidae, Scolytinae) of Cocos Island, Costa Rica and the role of mating systems in island zoogeography. Biological Journal of the Linnean Society 89: 729–743. https://doi.org/10.1111/j.1095-8312.2006.00698.x

LaBonte JR, Mudge AD, Johnson KJR (2005) Nonindigenous woodboring Coleoptera (Cerambycidae, Curculionidae: Scolytinae) new to Oregon and Washington, 1999–2002: consequences of the intercontinental movement of raw wood products and solid wood packing materials. Proceedings of the Entomological Society of Washington 107: 554–564.

Mandelshtam MY, Nikitsky NB (2010) Review of Scolytidae (Coleoptera) type specimens from V. Mot. Biulleten' Moskovskogo Obschestva Ispytatelei Prirody. Otdel Biologicheskii 115: 13–21.

Mudge AD, LaBonte JR, Johnson KJR, LaGasa EH (2001) Exotic woodboring Coleoptera (Micromalthidae, Scolytidae) and Hymenoptera (Xiphydriidae) new to Oregon and Washington. Proceedings of the Entomological Society of Washington 103: 1011–1019.

Okins KE, Thomas MC (2010) New North American record for *Xyleborinus andrewesi* (Coleoptera: Curculionidae: Scolytinae). Florida Entomologist 93: 133–134. https://doi.org/10.1653/024.093.0122

Rabaglia RJ (2005) The validity of *Xyleborus impressus* Eichhoff as distinct from *Xyleborus ferrugineus* (F.). The Coleopterists Bulletin 59: 261–266. https://doi.org/10.1649/768

Rabaglia RJ, Okins KE (2011) Entomology section. Tri-ology 50(3): 6–9.

Rabaglia RJ, Vandenberg NJ, Acciavatti RE (2009) First records of *Anisandrus maiche* Stark (Coleoptera: Curculionidae: Scolytinae) from North America. Zootaxa 2137: 23–28.

Rabaglia RJ, Dole SA, Cognato AI (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an Illustrated Key. Annals of Entomological Society of America 99: 1034–1056. https://doi.org/10.1603/0013-8746(2006)99[1034:ROAXCC]2.0.CO;2

Rabaglia RJ, Knížek M, Johnson W (2010) First records of *Xyleborinus octiesdentatus* (Murayama) (Coleoptera, Curculioidae, Scolytinae) from North America. ZooKeys 56: 219–226. https://doi.org/10.3897/zookeys.56.528

Raffa KF, Gregoire JC, Lindgren BS (2015) Natural History and Ecology of Bark Beetles. In: Vega FE, Hofstetter RW (Eds) Bark Beetles: Biology and Ecology of Native and Invasive Species. Elsevier Inc., San Diego, 1–28. https://doi.org/10.1016/B978-0-12-417156-5.00001-0

Schiefer TL, Bright DE (2004) *Xylosandrus mutilatus* (Blandford), an exotic ambrosia beetle (Coleoptera: Curculionidae: Scolytinae: Xyleborini) new to North America. The Coleopterists Bulletin 58: 431–438. https://doi.org/10.1649/760

Smith SM, Cognato AI (2015) *Ambrosiophilus peregrinus* Smith and Cognato, new species (Coleoptera: Curculionidae: Scolytinae), an exotic ambrosia beetle discovered in Georgia, USA. The Coleopterists Bulletin 69: 213–220. https://doi.org/10.1649/0010-065X-69.2.213

Smith SM, Hulcr J (2015) *Scolytus* and other economically important bark and ambrosia beetles. In: Vega FE, Hofstetter RW (Eds) Bark Beetles: Biology and Ecology of Native and Invasive Species. Elsevier Inc., San Diego, 495–532. https://doi.org/10.1016/B978-0-12-417156-5.00012-5

Smith SM, Beaver RA, Cognato AI (2017) The ambrosia beetle *Ambrosiophilus peregrinus* Smith and Cognato, introduced to the USA, is *Ambrosiophilus nodulosus* (Eggers), new combination (Coleoptera: Curculionidae: Scolytinae). The Coleopterists Bulletin 71: 552–553. https://doi.org/10.1649/0010-065X-71.3.552

Stouthamer R, Rugman-Jones P, Thu PQ, Eskalen A, Thibault T, Hulcr J, Wang LJ, Jordal BH, Chen CY, Cooperband M, Lin CS, Kamata N, Lu S, Masuya H, Mendel Z, Rabaglia R, Sanguansub S, Shih H, Sittichaya W, Zong S (2017) Tracing the origin of a cryptic invader: phylogeography of the *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) species complex. Agricultural and Forest Entomology 19: 366–375. https://doi.org/10.1111/afe.12215

Vandenberg NJ, Rabaglia RJ, Bright DE (2000) New records of two *Xyleborus* (Coleoptera: Scolytidae) in North America. Proceedings of the Entomological Society of Washington 102: 62–68.

Wood SL (1977) Introduced and exported American Scolytidae (Coleoptera). The Great Basin Naturalist 37: 67–74.

Weber BC, McPherson JE (1982) The distribution of *Xylosandrus germanus* in America north of Mexico (Coleoptera: Scolytidae). Great Lakes Entomologist 15: 171–174.

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs 6: 1–1359.

Wood SL (1986) A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Naturalist Memoirs 10: 1–126.

Wood SL (1989) Nomenclatural changes and new species of Scolytidae (Coleoptera), part IV. Great Basin Naturalist Memoirs 49: 167–185. https://doi.org/10.5962/bhl.part.22642

Wood SL (2007) Bark and ambrosia beetles of South America (Coleoptera, Scolytidae). Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, 900 pp.

Wood SL, Bright DE (1987) A Catalog of Scolytidae and Platypodidae (Coleoptera), Part 1: Bibliography. Great Basin Naturalist Memoirs 11: 1–833.

Wood SL, Bright DE (1992) A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic index, volumes A and B. Great Basin Naturalist Memoirs 13: 1–1553.

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RESEARCH ARTICLE

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Evidence of hidden diversity and taxonomic conflicts in five stream fishes from the Eastern Zimbabwe Highlands freshwater ecoregion

Albert Chakona[1,2], Wilbert T. Kadye[2], Taurai Bere[3],
Daniel N. Mazungula[1,2], Emmanuel Vreven[4,5]

1 *South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown, South Africa, 6140* **2** *Department of Ichthyology and Fisheries Science, Rhodes University, P.O. Box 94, Grahamstown, South Africa, 6140* **3** *School of Wildlife, Ecology and Conservation, Chinhoyi University of Technology, P. Bag 7724, Chinhoyi, Zimbabwe* **4** *Royal Museum for Central Africa, Section of Vertebrates, Ichthyology, Leuvensesteenweg 13, 3080, Tervuren, Belgium* **5** *KU Leuven, Department of Biology, Laboratory of Biodiversity and Evolutionary Genomics, Deberiotstraat 32, 3000 Leuven, Belgium*

Corresponding author: *Albert Chakona* (a.chakona@saiab.ac.za)

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Abstract

Stream fishes of the Eastern Afromontane region are among the least studied vertebrates in this region, despite the potential for harbouring cryptic diversity. The present study examined mitochondrial cytochrome oxidase subunit I (COI) sequence divergence in 153 specimens of stream fishes belonging to four genera and three families, [(*Amphilius* and *Zaireichthys* (Amphiliidae); *Chiloglanis* (Mochokidae); and *Hippopotamyrus* (Mormyridae)], in the Eastern Zimbabwe Highlands (EZH) freshwater ecoregion to explore the extent to which the current taxonomy conceals the ichthyofaunal diversity in the region. The General Mixed Yule Coalescent (GMYC) species delineation method identified 14 clusters within five currently recognised 'species' from the EZH ecoregion. Only one of these clusters represents a named species, while 13 of them represent candidate or undescribed species. Our results revealed that effective conservation of this region's unique biota is limited by the incomplete knowledge of taxonomic diversity and inaccurate mapping of species distribution ranges.

Keywords

Amphilius, candidate species, *Chiloglanis,* cryptic diversity, DNA barcoding, fish, freshwater, GMYC, *Hippopotamyrus*, *Zaireichthys*

Introduction

The Eastern Zimbabwe Highlands (EZH) freshwater ecoregion (Thieme et al. 2005; Abell et al. 2008), also referred to as the Manica Highlands (Clark et al. 2017), is renowned as a centre of floral diversity and endemism, harbouring approximately 150 endemic plant species (Clark et al. 2017; Van Wyk and Smith 2001). However, to date, the EHZ's ichthyofaunal diversity is considered comparatively low. Marshall (2011) listed 25 freshwater fishes for the EZH freshwater ecoregion, of which one species, *Labeobarbus pungweensis* (Jubb, 1959), is endemic to this ecoregion. The continued recognition of many of the stream fishes from the EZH freshwater ecoregion as having wide geographic ranges (see Skelton 2001; Marshall 2011) demonstrates the poor taxonomic attention and lack of systematic knowledge in this region and the broader southern African subregion. Growing evidence from previous and ongoing DNA-based studies shows that many species of freshwater fishes that were previously considered to have wide geographic ranges are instead complexes comprising several genetically divergent lineages (e.g., Chakona et al. 2013; Goodier et al. 2011; Kramer et al. 2004; Kramer and Wink 2013; Linder et al. 2010; Swartz et al. 2007, 2009). These studies have stimulated renewed interest in the systematics of freshwater fishes in the region as evidenced by the recent revalidation of some junior synonyms as well as the identification and description of several new species (e.g., Chakona and Swartz 2013; Chakona et al. 2014; Chakona and Skelton 2017; Kramer et al. 2003, 2007, 2012, 2013, 2014; Kramer and Swartz 2010; Kramer and van der Bank 2011; Maake et al. 2014). There is thus need for expanding the application of molecular approaches as these may lead to the identification of presently unrecognised diversity and provide insights on the patterns of endemism of stream fishes from other understudied regions in southern Africa such as the EZH freshwater ecoregion.

To examine the hypothesis that the perceived broad geographical ranges for many stream fishes in the EZH freshwater ecoregion may be due to overlooked diversity, the present study used genetic data to explore the possible existence of species level differentiation in fishes from tributaries of four river systems, the Lower Zambezi, Pungwe, Save and Buzi, in this ecoregion (Figure 1). The present study used the mitochondrial cytochrome oxidase subunit I (COI) gene to examine the patterns of intraspecific divergence within five morphologically defined fish species, *Chiloglanis neumanni* Boulenger, 1911, *Amphilius natalensis* Boulenger, 1917, *A. uranoscopus* (Pfeffer, 1889), *Zaireichthys monomotapa* Eccles et al., 2011 and *Hippopotamyrus ansorgii* (Boulenger, 1905), from sub-catchments of the lower Zambezi River system (the Nyangombe and Kairezi rivers and their tributaries), the Pungwe River system and its tributaries (the Rwera, Pungwe mainstream, Honde and Nyamukwarara rivers), tributaries of the Buzi River system (the Haruni and Rusitu rivers) and the Save River system and its tributaries (the Odzi and Nyanyadzi rivers) (Figure 1). These taxa were selected due to uncertainties about their taxonomic status (Marshall 2011), their perceived broad geographic distribution ranges that are surprising considering recent evidence from studies of other freshwater fishes that were previously thought to be wide ranging species (e.g.,

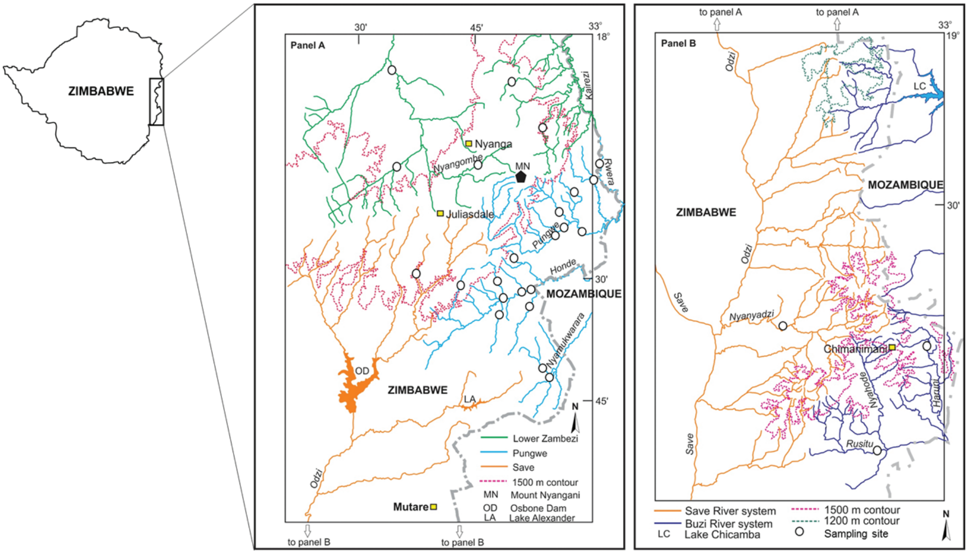

Figure 1. Map of the Eastern Zimbabwe Highlands (EZH) freshwater ecoregion showing the river systems (Lower Zambezi, Pungwe, Buzi and Save) that drain this region and the sampling localities for the present study.

Chakona and Skelton 2017; Decru et al. 2012, 2013, 2015; Zengeya et al. 2011), as well as their peculiar disjunct distribution patterns (i.e., discontinuous and separated by wide geographic distance) in the case of *A. natalensis* and *H. ansorgii* (Marshall 2011; Skelton 2001).

The taxonomic uncertainty of the suckermouth catlet of the EZH freshwater ecoregion has persisted for decades. The first published detailed checklist of freshwater fishes of Zimbabwe by Jubb (1961) contained one species of suckermouth catlet, identified as *Chiloglanis neumanni*, despite the enormous geographic distance between the EZH ecoregion and the type locality of *C. neumanni* which is in the Upper Bubu River (Rufiji River system) in Tanzania (Boulenger 1911; Eschmeyer et al. 2018). Bell-Cross and Minshull (1988) listed two species of *Chiloglanis* from the EZH ecoregion that were identified as *C. emarginatus* Jubb & Le Roux, 1969 and *C. neumanni*. Distribution maps in Skelton's (2001) guide to the freshwater fishes of southern Africa suggested that there are three species of suckermouth catlets in the EZH ecoregion, *C. emarginatus*, *C. neumanni* and *C. pretoriae* van der Horst, 1931. *Chiloglanis emarginatus* was described from the Lekkerloop River in the Inkomati River system in South Africa (Jubb and Le Roux 1969). The distribution of this species was previously divided into northern (Pungwe and Lower Zambezi Rivers) and southern (Inkomati and Phongolo Rivers) populations (Skelton 2001). Engelbrecht et al. (2007) subsequently considered records of the northern population to have been incorrectly identified, and indicated that *C. emarginatus* was restricted to the Inkomati and Phongolo River systems. *Chiloglanis pretoriae* was described from the Crocodile River, a tributary of the Limpopo River system in South Africa. More recently, Marshall (2011) summarised the existing knowledge of the fishes of Zimbabwe and indicated that *C. pretoriae* does not occur in the EZH ecoregion as the Limpopo River system is the northern-most distribution limit for this species. Marshall (2011) also commented that *C. neumanni* is unlikely to occur in Zimbabwe, and highlighted the need for detailed evaluations to determine the diversity and taxonomic integrity of suckermouth catlets in the country.

Similar to *Chiloglanis*, the species of *Amphilius* in the EZH freshwater ecoregion also continue to be surrounded by taxonomic uncertainty. Jubb (1961) listed a single species of *Amphilius* for this ecoregion, and identified it as *A. grandis* Boulenger, 1905, originally described from the Tana River system in Kenya. In their review of the Amphiliidae of southern Africa, Bell-Cross and Jubb (1973) recognised three species of *Amphilius* from the EZH ecoregion: *A. platychir* (Günther, 1864), originally described from Sierra Leone, west Africa; *A. lampei* Pietschmann, 1913, originally described from the Ethiopian Highlands near Harar, east Africa, and *A. natalensis* Boulenger, 1917, originally described from the Kranzkloof River, which is part of the Umgeni River system in South Africa. In a comprehensive revision of *Amphilius* species from west, east and southern Africa, Skelton (1984) considered *A. grandis* to be a junior synonym of *A. uranoscopus* (Pfeffer, 1889), a species which was originally described from the Wami River system in Tanzania. In this revision, Skelton (1984) presented unequivocal evidence that supported Günther's (1902) assertion that *A. platychir* was restricted to west Africa, and transferred the southern African specimens that were previously identified as *A. platychir* to *A. uranoscopus*. Skelton (1984) further considered that Bell-Cross and Jubb's (1973) identification of mountain catfish specimens from the Nyazengu River in the Eastern Highlands as *A. lampei* was erroneous, and transferred these specimens to *A. natalensis*. These taxonomic changes were followed by subsequent authors (Bell-Cross and Minshull 1988; Marshall 2011; Skelton and Teugels 1986; Skelton 2001). Skelton (1984) also described a new species, *A. laticaudatus* from the Lower Buzi in Mozambique. This species is currently only known from its type locality. Thus, *A. uranoscopus* and *A. natalensis* are the only two mountain catfish species that are currently recognised from the EZH freshwater ecoregion (Marshall 2011; Skelton 1984, 2001). However, a recent taxonomic revision of *A. uranoscopus* complex in Kenya and Tanzania by Thomson and Page (2010) resulted in the resurrection of two species, *A. grandis* and *A. krefftii*, which were both previously considered to be junior synonyms of *A. uranoscopus*, as well as the description of a new species, *A. athiensis* Thomson & Page (2010). Occurrence of three distinct species in such a small geographic area, which represents only a very small portion of the *A. uranoscopus* sensu lato distribution, raises the possibility that this complex may contain many undescribed species across its current wide geographic range. It is also likely that *A. uranoscopus* sensu stricto may not even occur in southern Africa. If this is ascertained, investigations will need to be made to determine the taxonomic status of the three synonyms of *A. uranoscopus* from southern Africa, *A. hargeri* Boulenger, 1907, *A. brevidorsalis* Pellegrin, 1919 and *A. cubangoensis* Pellegrin, 1936 and identify possible new species.

The genus *Zaireichthys* contains the smallest catfishes in Africa, with a total of 18 species (Eschmeyer et al. 2018). The EZH freshwater ecoregion is currently thought to harbour a single valid species of sand catlets, *Z. monomotapa*, originally described from the Save River system (Eccles et al. 2011), the largest river basin in Zimbabwe. The species is currently considered to be widely distributed in tributaries of the middle and lower Zambezi, Pungwe, Buzi and Save River systems in Zimbabwe (Marshall 2011). However, the discovery of substantial levels of intraspecific genetic differentiation within almost all wide-ranging stream fishes studied thus far in southern Africa raises the possibility that *Z. monomotapa* may also contain hidden diversity.

There are uncertainties about the origin of the specimens that were used for the original description of *Hippopotamyrus ansorgii* as the type locality is vaguely described as 'between Benguella and Bie' (Boulenger 1909). This region encompasses the Angolan highlands which are drained by at least five river systems, with the Kwanza, Upper Zambezi, Okavango and Kunene being the four major systems. Kramer and Swartz (2010) postulated that the Kunene could probably be the type river for *H. ansorgii*. For a long time, *H. ansorgii* was the only recognised species of the genus *Hippopotamyrus* in southern Africa, with a disjunct distribution broadly divided into western (Kwanza, Kunene, Okavango and Upper Zambezi) and eastern (lower Zambezi, Pungwe and Buzi) populations (Skelton 2001). Recently, integrated systematic studies uncovered the existence of deeply divergent lineages within *H. ansorgii*, which led to the description of two new species, *H. szaboi* from the Upper Zambezi (Kramer et al. 2004) and *H. longilateralis* from the Kunene River system (Kramer and Swartz 2010). These findings, coupled with the wide geographic gap between the western (i.e., the type region) and eastern populations of *H. ansorgii*, raise the possibility that the populations of the EZH freshwater ecoregion may be genetically distinct, and potentially represent previously unrecognised species.

In the present study, extensive sampling of *C. neumanni*, *A. natalensis*, *A. uranoscopus*, *Z. monomotapa* and *H. ansorgii* was done from 27 localities in the EZH freshwater ecoregion (Figure 1), and mitochondrial COI sequences were generated to determine the degree of genetic distinctiveness of these populations and identify unique lineages. The study included additional sequences downloaded from BOLD and, where available, topotypes (conspecific specimens collected from or in the vicinity of the type locality) were included in the analyses for comparisons. This study represents the first comprehensive and fine scale geographical and molecular assessment of stream fishes of the EZH freshwater ecoregion to assess levels of intraspecific genetic differentiation and explore if potential conflicts with their current taxonomic status can be identified.

Materials and methods

Ethics statement

This research was carried out following the evaluation and approval of the sampling protocols by the South African Institute for Aquatic Biodiversity (SAIAB) ethics committee (Ref: 2014/03). Permits to carry out this research were obtained from the Parks and Wildlife Authority of Zimbabwe.

Study systems

The EZH freshwater ecoregion receives a mean annual precipitation of 900 to 3000 mm/a (Mazvimavi 2010) which sustain perennial flow in the rivers and streams of this region. There are four major river systems that drain this ecoregion: the Lower Zambezi, Pungwe, Save and Buzi systems (Figure 1). Two tributaries of the Lower Zambezi (the Nyangombe and Kairezi rivers) drain the western and northern parts of this ecoregion. Three localities were sampled in the Nyangombe subcatchment and two localities were sampled in the Kairezi subcatchment (Figure 1; Suppl. material 1). The Pungwe River flows eastwards from the EZH, and the river has a length of about 400 km from its source to its discharge point into the Indian Ocean near Beira in Mozambique. A total of 17 localities covering four major subcatchments of the Pungwe River system (i.e., the Rwera, Pungwe mainstream, Honde and Nyamukwarara) were sampled (Figure 1; Suppl. material 1). Riparian zones of the Rwera and mainstream Pungwe subcatchments are covered with remnants of the Afromontane rainforests, whereas miombo woodlands are the dominant vegetation types in the riparian zones of the Honde and Nyamukwarara subcatchments. The Buzi River system has three eastward draining subcatchments (the Buzi, Rusitu and Revue). Two localities were sampled in the Rusitu subcatchment (Haruni and Upper Rusitu) which drains the Chimanimani Mountains. The Odzi River, a major subcatchment of the Save River system, drains southwards from the EZH (Figure 1). Two localities were sampled in the Odzi subcatchment (the Nyamazi and Nyanyadzi rivers). A single locality in the Upper Save was also sampled to collect specimens and tissue samples from the type system of *Zaireichthys monomotapa* (Suppl. material 1).

Fish sampling

Fishes were collected in December 2013 and 2014 using a Samus-725M electrofisher. Captured fishes were anaesthetised with clove oil, digitally photographed and a small piece of muscle tissue was dissected from the right side of each specimen and preserved in 95% ethanol in the field for genetic analysis. Tissue samples were stored at -80°C at the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown. Voucher specimens were fixed in 10% formalin in the field. They were then transferred through 10% and 50% to 70% ethanol for long-term storage. All voucher specimens were deposited into the fish collection facility at SAIAB as reference material. Species were identified using regional identification keys and their known geographic distributions according to Skelton (2001) and Marshall (2011).

DNA Extraction, PCR and sequencing

DNA was extracted from preserved tissue using the salting out method (Sunnucks et al. 1996). DNA concentration was quantified using a Nanodrop ND-1000 (Nanodrop

Technologies, Inc). A fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified by polymerase chain reaction (PCR) using universal fish DNA barcoding primer sets: VF2-T1 and VR1-T1 (Ivanova et al. 2007), FishF1 and FishR1 or FishF2 and FishR2 (Ward et al. 2005). PCRs were performed with a Veriti 96 well thermal cycler (Applied Biosystems) and each reaction mixture (25 μL) contained 100–200 ng template DNA, 14.4 μL of water, 2.5 μL deoxynucleotide triphosphate (dNTP) (10 mM), 2.5 mM $MgCl_2$, 2.5 μL PCR buffer (10X), 0.5 μL of each primer (20 pmol) and 0.1 μL *Taq* DNA polymerase (Southern Cross Biotechnology, Cape Town). The PCR amplification profile was 94 °C for 3 min, followed by 38 cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 50 s, and then final extension at 72 °C for 7 min. PCR products were purified with Exosap (Applied Biosystems), cycle-sequenced using BigDye Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and sequenced at SAIAB using an ABI 3730xl DNA Analyzer (Applied Biosystems). Sequences generated from this study were submitted to GenBank (accession numbers: *Amphilius* (MH431952 - MH432017); *Chiloglanis* (MH432018 - MH432062); *Hippopotamyrus* (MH432063 - MH432086); *Zaireichthys* (MH432087 - MH432119); Suppl. material 1). BOLD sequences that were included in this study are also listed in Suppl. material 1.

Data analyses

Sequences were cleaned, aligned and trimmed to equal lengths using the program SeqMan7.2.1 (DNASTAR, Madison, WI, USA). The appropriate models of sequence evolution for each genus were selected using the Akaike's Information Criteria (AIC) (Burnham and Anderson 2002) as implemented in jModeltest 2 (Darriba et al. 2012). Phylogenetic relationships among unique haplotypes within each genus were inferred using MrBayes 3.1.2 (Ronquist et al. 2012). The analysis for each genus had two replicate searches of 10 million generations with four Markov chains. Trees were sampled every 1000 generations to obtain 10000 sampled trees. TRACER 1.5 (Rambaut and Drummond 2007) was used to assess if the chains had converged and determine the burn-in. We discarded 10% of the sampled trees as burn-in and the remainder were used to calculate the consensus tree and Bayesian posterior probabilities. Model corrected genetic distances between unique lineages identified for each genus were calculated using PAUP (Swofford 2003). To explore the possible taxonomic distinctiveness of the genetic lineages that will be uncovered from the Eastern Highlands, sequences of topotypes (i.e., samples collected from or within the vicinity of the type localities of currently described species), whenever available, were also included in the analyses.

The General Mixed Yule Coalescent (GMYC) method (Pons et al. 2006) was used to delineate candidate species or operational taxonomic units (OTUs). The GMYC is a robust method that models branching thresholds for intraspecific (coalescent) and interspecific (speciation/diversification) patterns (Fujisawa and Barraclough 2013). This approach has been widely applied in a number of studies to identify cryptic diversity within morphologically defined species (e.g., Crivellaro et al. 2017; Grabowski et al. 2017; Kordbacheh et al.

2017). The ultrametric trees for GMYC analyses were estimated in BEAST (Drummond and Rambaut 2007) using two priors (Yule model and Coalescent model with constant population size) and two rates of molecular evolution (constant and relaxed clock). For each of the four genera considered in the present study, we compared three trees which were built based on the following combinations of priors and rates of molecular evolution: (i) yule model and a constant clock, (ii) yule model and a relaxed clock, and (iii) coalescent model with constant population size and a constant clock. The GMYC analyses were conducted with the package 'splits' (Species Limits by Threshold Statistics (http://r-forge.r-project.org/projects/splits) using R v.3.4.1 (R Development Core Team 2011).

Results

A total of 153 COI sequences were generated from individuals representing five currently recognised species considered in the present study from the Eastern Zimbabwe Highlands freshwater ecoregion: *Chiloglanis neumanni* (43 sequences), *Amphilius natalensis* (37 sequences), *A. uranoscopus* (26 sequences), *Zaireichthys monomotapa* (32 sequences) and *Hippopotamyrus ansorgii* (16 sequences). An additional 107 sequences were downloaded from BOLD for comparison (Suppl. material 1). Read lengths of all sequences used in this study were over 530 bp long. No stop codons were observed when examining amino acid translations, indicating that the amplified domains were functional mitochondrial copies.

Genetic structure in *Chiloglanis neumanni*

The COI dataset for *Chiloglanis* consisted of 73 sequences (included 30 BOLD sequences; Suppl. material 1) and an edited alignment of 534 bp with 175 polymorphic sites which resulted in 48 unique haplotypes. Bayesian analysis divided haplotypes of *C. neumanni* from the EZH ecoregion into two well-supported clades (Figure 2a). Estimates of the number of candidate species using GMYC ranged from eight to 16, excluding outgroups (Figure 2a). The coalescent model with constant population size and a constant clock (CONC) gave the most conservative estimate of the number of candidate species, and these were largely consistent with the clades inferred using the Bayesian analysis, with the exception of one sample in the *C.* sp. 'rough skin' clade and two samples in the *C.* sp. 'dwarf' clade which were assigned to separate clusters from these two major clades (Figure 2a). Both the Yule model and a constant clock (YULE), and the Yule model and a relaxed clock (RELA) clearly overestimated the number of candidate species due to over splitting of samples in the *C.* sp. 'rough skin' and *C.* sp. 'dwarf' clades (Figure 2a). A conservative approach was therefore considered in the present study, and six candidate species or molecular operation taxonomic units (MOTUs) were delimited within *C. neumanni* from the EZH ecoregion and the adjacent Shire and Ruo rivers in Malawi (Figure 2a). The first major clade in Figure 2a

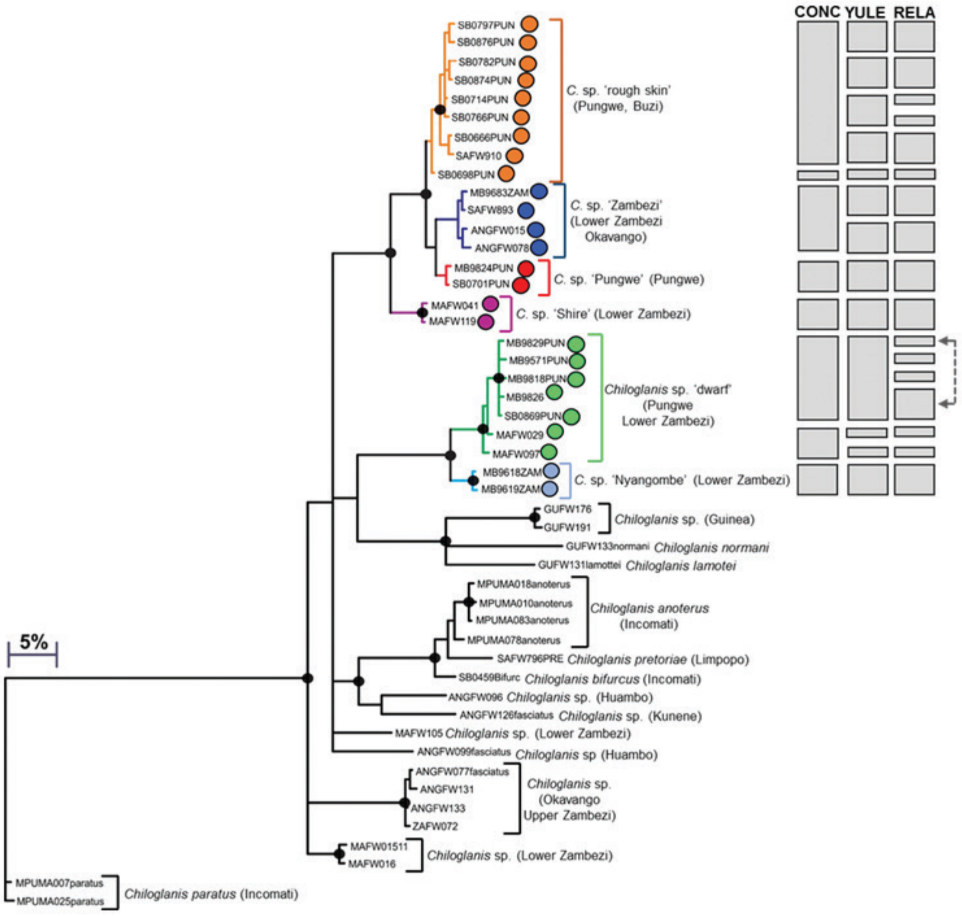

Figure 2a. Bayesian phylogenetic tree based on mtDNA cytochrome oxidase sub unit I (COI) sequences showing the candidate species or molecular operational taxonomic units (MOTUs) identified within *Chiloglanis neumanni* from the Eastern Zimbabwe Highlands freshwater ecoregion. Well supported nodes are shown by a solid circle. The indicated candidate species or MOTUs were identified using the GMYC method based on trees that were built using three different combinations of priors and rates of molecular evolution: (i) coalescent model with constant population size and a constant clock (CONC), (ii) yule model and a constant clock (YULE) and (iii) yule model and a relaxed clock (RELA).

contained four candidate species, *C.* sp. 'rough skin', *C.* sp. 'Zambezi', *C.* sp. 'Pungwe', and *C.* sp. 'Shire', with model corrected genetic divergences between these candidate species ranging from 1.35–7.60% (Table 1). The second major clade contained two candidate species, *C.* sp. 'dwarf' and *C.* sp. 'Nyangombe' which were separated by 4.01–5.27% sequence divergence.

Chiloglanis sp. 'rough skin' comprised haplotypes from the Pungwe and Buzi river systems (Figure 2b). *Chiloglanis* sp. 'Zambezi' contained haplotypes from the Nyangombe River in the EZH ecoregion, as well from a tributary that flows into Lake Cahora Bassa and from the Cubango River which is part of the Okavango River system

Table 1. Mitochondrial COI genetic distances (%) between *Chiloglanis* lineages from the Eastern Highlands of Zimbabwe and selected species from southern Africa.

	***C.* sp. 'rough skin'**	***C.* 'Zambezi'**	***C.* sp. 'Pungwe'**	***C.* sp. 'Shire'**	***C.* sp. 'dwarf'**	***C.* sp. 'Nyangombe'**	***C. pretoriae***	***C. anoterus***
C. sp. 'rough skin'	0.00–1.38							
C. sp. 'Zambezi'	2.36–4.24	0.00–0.76						
C. sp. 'Pungwe'	1.35–2.67	2.19–3.12	0.18					
C. sp. 'Shire'	5.01–7.14	6.33–7.60	6.47–7.04	0.19				
C. sp. 'dwarf'	16.88–19.86	17.13–19.08	18.30–20.10	18.48–20.14	0.00–1.33			
C. sp. 'Nyangombe'	13.95–16.04	13.25–14.54	15.37–16.15	16.86–17.64	4.01–5.27	0.18		
C. pretoriae	19.24–20.89	18.94–20.18	19.24–19.76	18.38–18.81	16.59–17.26	17.45–17.83		
C. anoterus	15.77–19.70	16.44–19.03	16.62–19.63	17.04–20.04	18.60–22.03	17.55–19.88	4.29–5.12	0.00–1.98
C. bifurcus	17.40–18.90	16.59–17.34	18.34–18.83	15.79–16.18	16.16–17.01	17.20–17.57	5.14	2.85–3.59

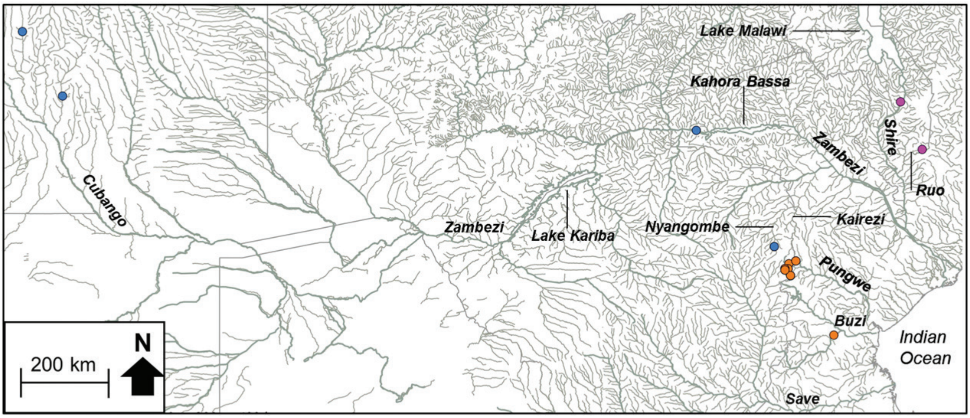

Figure 2b. The distribution of *Chiloglanis* sp. 'rough skin' (orange circle), *Chiloglanis* sp. 'Zambezi' (blue circle) and *Chloglanis* sp. 'Shire' (purple circle) in the Eastern Zimbabwe Highlands freshwater ecoregion and adjacent areas.

(Figure 2b). *Chiloglanis* sp. 'Pungwe' contained haplotypes that were confined to the Pungwe River system (Figure 2c). *Chiloglanis* sp. 'Shire' was confined to the Shire and Ruo rivers (Figure 2b). *Chiloglanis* sp. 'dwarf' was distributed in the Pungwe and Ruo rivers, while *C.* sp. 'Nyangombe' was only recorded from the Nyangombe subcatchment during the present study (Figure 2c). The genetic divergences between almost all the candidate species identified from the present study are consistent with interspecific genetic divergences between morphologically distinguishable *Chiloglanis* species, for example *C. anoterus* and *C. bifurcus* from the Inkomati River system which are separated by 2.85–3.59% COI sequence divergence (Table 1). It is also important to note

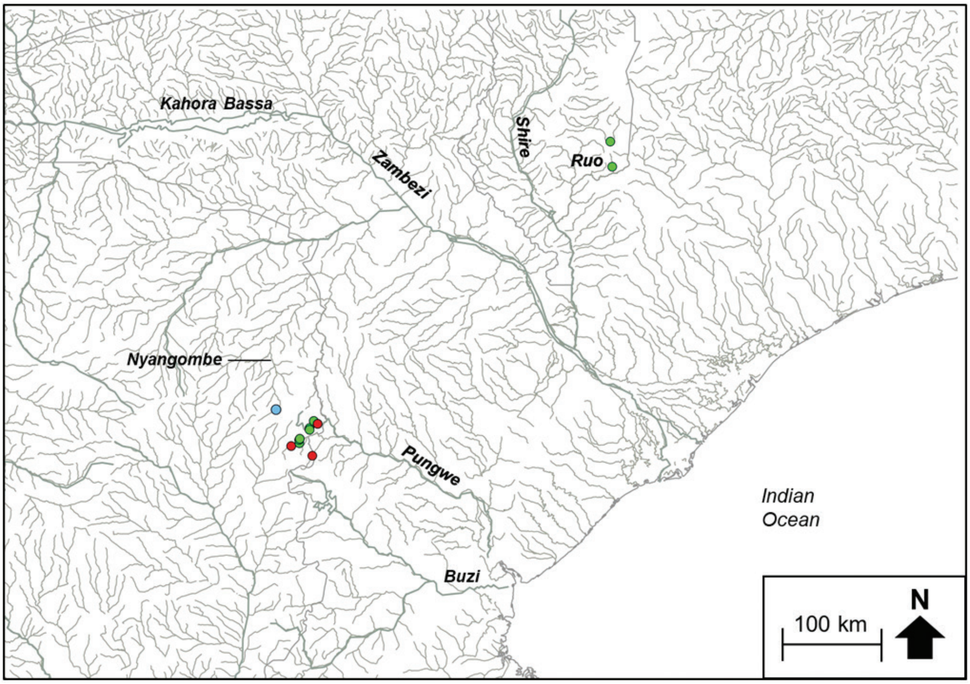

Figure 2c. The distribution of *Chiloglanis* sp. 'dwarf' (green circle), *Chiloglanis* sp. 'Nyangombe' (blue circle) and *Chloglanis* sp. 'Pungwe' (red circle) in the Eastern Zimbabwe Highlands freshwater ecoregion and adjacent areas.

that all the candidate species identified from the EZH freshwater ecoregion are deeply divergent from *C. pretoriae* (16.59–20.89% sequence divergence; Table 1; Figure 2a), a name that was previously assigned to the EZH ecoregion suckermouth catlets. Unfortunately, sequences of both *C. neumanni* sensu stricto and *C. emarginatus*, two other species names that were previously used for the EZH freshwater ecoregion suckermouth catlets, were not available for comparison in the present study.

Genetic structure in *Amphilius*

The COI dataset for *Amphilius* consisted of 79 sequences (included 16 BOLD sequences; Suppl. material 1) and an edited alignment of 572 bp with 166 polymorphic sites which resulted in 34 unique haplotypes. Bayesian analysis divided samples of *A. natalensis* and *A. uranoscopus* into two separate and well-supported clades (Figure 3a). Estimates of the number of candidate species within *A. natalensis* using GMYC ranged from one to six (Figure 3a). Yule model and a relaxed clock (RELA) clearly underestimated the number of candidate species in *A. natalensis* sensu lato due to the geographic isolation and disjunct distribution of the populations within this 'species'. Five candidate species were therefore delineated based on trees generated using the Yule model and a constant clock (YULE), which gave the next most

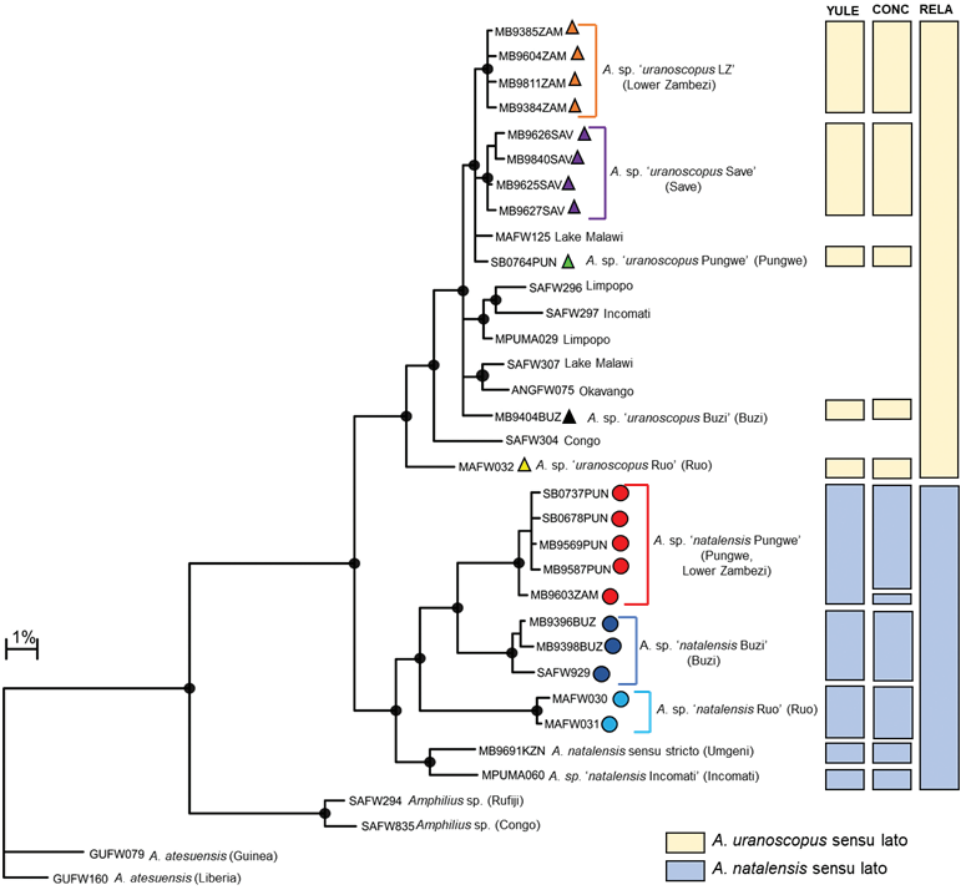

Figure 3a. Bayesian phylogenetic tree based on mtDNA cytochrome oxidase sub unit I (COI) sequences showing the candidate species or molecular operational taxonomic units (MOTUs) identified within *Amphilius uranoscopus* and *A. natalensis* from the Eastern Highlands of Zimbabwe. Well supported nodes are shown by a solid circle. The indicated candidate species or OTUs were identified using the GMYC method based on trees that were built using three different combinations of priors and rates of molecular evolution: (i) yule model and a constant clock (YULE), (ii) coalescent model with constant population size and a constant clock (CONC) and (iii) yule model and a relaxed clock (RELA).

conservative estimate on the number of species (Figure 3a). Two of these candidate species, *A.* sp. '*natalensis* Pungwe' and *A.* sp. '*natalensis* Buzi' are confined to the Pungwe and Buzi river systems, respectively (Figure 3b). These two candidate species are allopatrically distributed and are separated by substantial genetic divergence (Figure 3a; 6.86–8.58% genetic divergence; Table 2). Divergences within candidate species ranged from 0.00–0.72% in *A.* sp. 'Pungwe' and from 0.00–1.30% in *A.* sp. 'Buzi'. *Amphilius* sp. 'Pungwe' was collected from multiple localities in the Pungwe River system and a single locality in the Kairezi River, a tributary of the Lower Zambezi, while *A.* sp. 'Buzi' was collected from the Haruni, Rusitu, and the mainstream

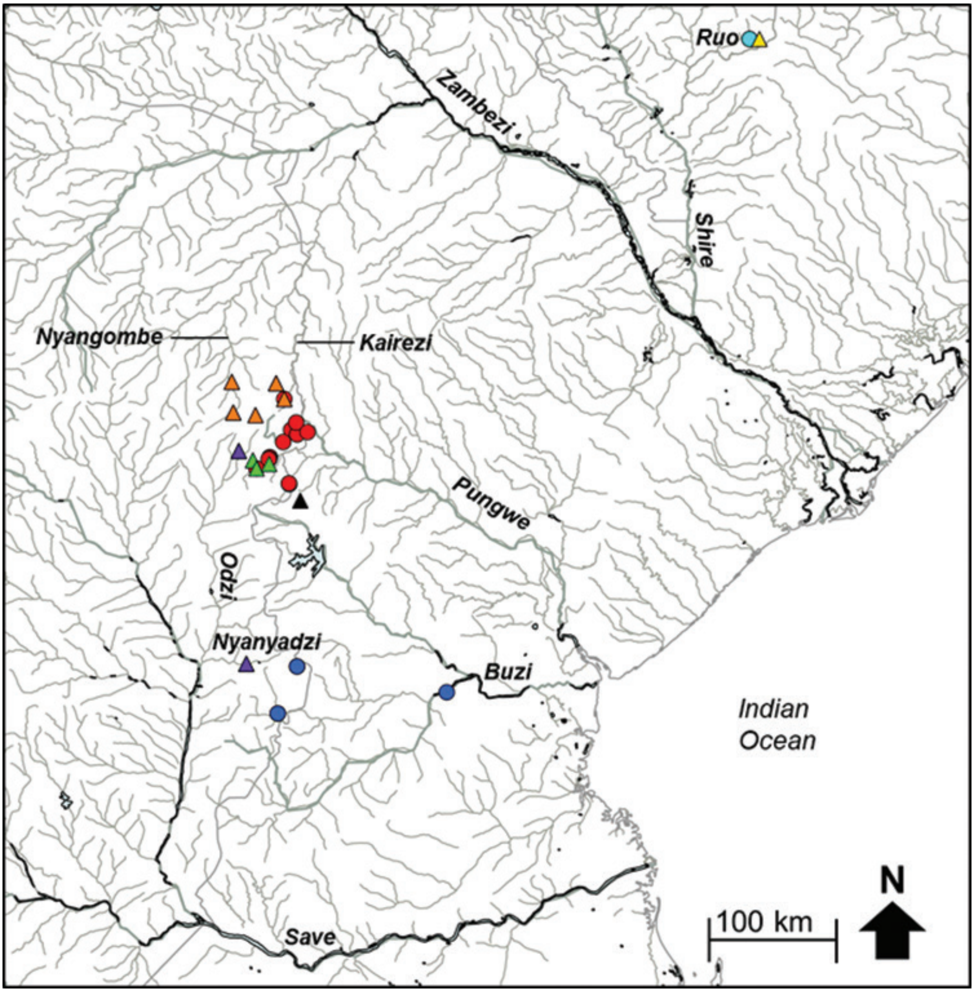

Figure 3b. The distribution of *Amphilius* sp. 'natalensis Buzi' (dark blue circle), *Amphilius* sp. 'natalensis Pungwe' (red circle) and *Amphilius* sp. 'natalensis Ruo' (light blue circle), *Amphilius* sp. 'uranoscopus Save' (purple triangle), *Amphilius* sp. 'uranoscopus Buzi' (black triangle), *Amphilius* sp. 'uranoscopus Pungwe' (green triangle), *Amphilius* sp. 'uranoscopus Zambezi' (orange triangle) and *Amphilius* sp. 'uranoscopus Ruo' (yellow triangle) in the Eastern Zimbabwe Highlands freshwater ecoregion and adjacent areas.

Buzi River (Figure 3b). The present study revealed that *A.* sp. 'Pungwe' and *A.* sp. 'Buzi' are genetically distinct (10.44–12.71% sequence divergence, Table 2; Figure 3a) from *A. natalensis* sensu stricto based on a specimen collected from the Umgeni River (the type system for *A. natalensis*) in South Africa.

Bayesian analysis revealed a well-supported shallow clade corresponding to the species currently recognised as *A. uranoscopus* in southern Africa (Figure 3a). Estimates of the number of candidate species within *A. uranoscopus* using GMYC gave consistent results for the EZH ecoregion (four candidate species) based on both the Yule model and a constant clock (YULE) and the coalescent model with constant population size and a con-

Table 2. Mitochondrial COI genetic distances (%) between lineages of *Amphilius natalensis* sensu lato identified from the Eastern Highlands of Zimbabwe and other lineages within this 'species' from selected populations in southern Africa.

	***A.* sp. 'Pungwe'**	***A.* sp. 'Buzi'**	***A.* sp. 'Ruo'**	***A. natalensis* s.s**
A. sp. 'Pungwe'	0.00–0.72			
A. sp. 'Buzi'	6.86–8.58	0.00–1.30		
A. sp. 'Ruo'	15.20–15.63	14.32–16.77	0.35	
A. natalensis s.s	11.16–12.71	10.44–11.06	13.05–13.91	-
A. sp. 'Inkomati'	13.16–14.05	11.65–12.32	14.42–15.33	4.44

Table 3. Mitochondrial COI genetic distances (%) between populations of *Amphilius uranoscopus* from the Eastern Highlands of Zimbabwe and selected localities in southern Africa.

	***A.* sp. 'Zambezi'**	***A.* sp. 'Pungwe'**	***A.* sp. 'Buzi'**	***A.* sp. 'Save'**	***A.* sp. 'Ruo'**
A. sp. 'Zambezi'	0.00–0.36				
A. sp. 'Pungwe'	0.72–0.92	-			
A. sp. 'Buzi'	1.88–2.13	2.06	-		
A. sp. 'Save'	0.54–1.34	0.73–1.13	2.07–2.56	0.00–0.54	
A. sp. 'Ruo'	5.21–5.86	6.07	6.21	6.12–6.81	-
A. sp. 'Cubango'	2.42–2.89	2.64	2.71	2.67–3.17	7.23

stant clock (CONC) models (Figure 3a). All the candidate species within *A. uranoscopus* from the EZH ecoregion are allopatrically distributed. Haplotypes within *Amphilius* sp. '*uranoscopus* Save' were collected from the Nyamazi River, a tributary of the Odzi River, and from the mainstream Nyanyadzi River (Figure 3b). Both *A.* sp. '*uranoscopus* Buzi' and *A.* sp. '*uranoscopus* Pungwe' were confined to the Buzi and Pungwe river systems, respectively (Figure 3b). Haplotypes within *A.* sp. '*uranoscopus* LZ' occurred in the Nyangombe and Kairezi rivers, which are both tributaries of the Lower Zambezi (Figure 3b). The candidate species within *A. uranoscopus* sensu lato had shallow divergences among them (0.54–2.56% sequence divergence; Table 3) compared to the deep divergences found among lineages within *A. natalensis* sensu lato (Table 2). Notable exceptions were samples of *A. uranoscopus* collected from the Ruo River (BOLD sequence MAFW032) which is the type river for *A. hargeri* and from the Cubango River (BOLD sequence ANGFW075) which is the type river for *A. cubangoensis* which were respectively deeply and moderately divergent from all the other lineages within the *A. uranoscopus* sensu lato clade (Table 3). The analysis also showed that the Ruo and Cubango samples of *A. uranoscopus* were genetically distinct, being separated by 7.23% (Table 3).

Genetic structure in *Zaireichthys monomotapa*

The edited alignment of 47 *Zaireichthys* sequences (included 15 BOLD sequences, Suppl. material 1) was 534 base pairs in length with 151 polymorphic sites which

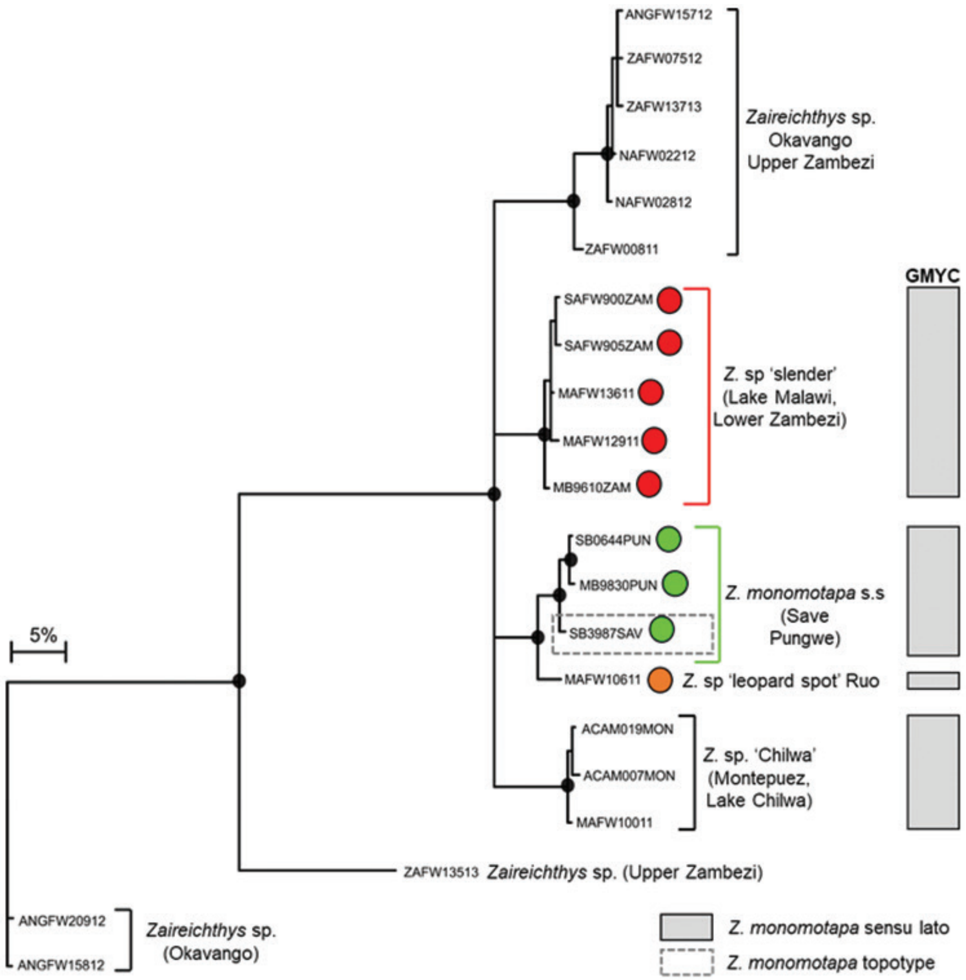

Figure 4a. Bayesian phylogenetic tree based on mtDNA cytochrome oxidase sub unit I (COI) sequences showing the candidate species or molecular operational taxonomic units (MOTUs) identified within *Zaireichthys monomotapa* from the Eastern Zimbabwe Highlands freshwater ecoregion. Well supported nodes are shown by a solid circle. The indicated candidate species or MOTUs were identified using the GMYC method based on trees that were built using three different combinations of priors and rates of molecular evolution: (i) yule model and a constant clock, (ii) yule model and a relaxed clock, and (iii) coalescent model with constant population size and a constant clock.

resulted in 21 unique haplotypes. GMYC analyses delimited *Z. monomotapa* sensu stricto which is distributed in the Save and Pungwe river systems, and identified one candidate species from the EZH ecoregion, *Z.* sp. 'slender', which occurred in the mainstream Nyangombe River and its tributary, the Chidiya River (Figure 4a, b). BOLD sequences (SAFW899, SAFW900, SAFW905, SAFW907, SAFW908) for individuals collected from three streams which flow into Lake Cahora Bassa, as well

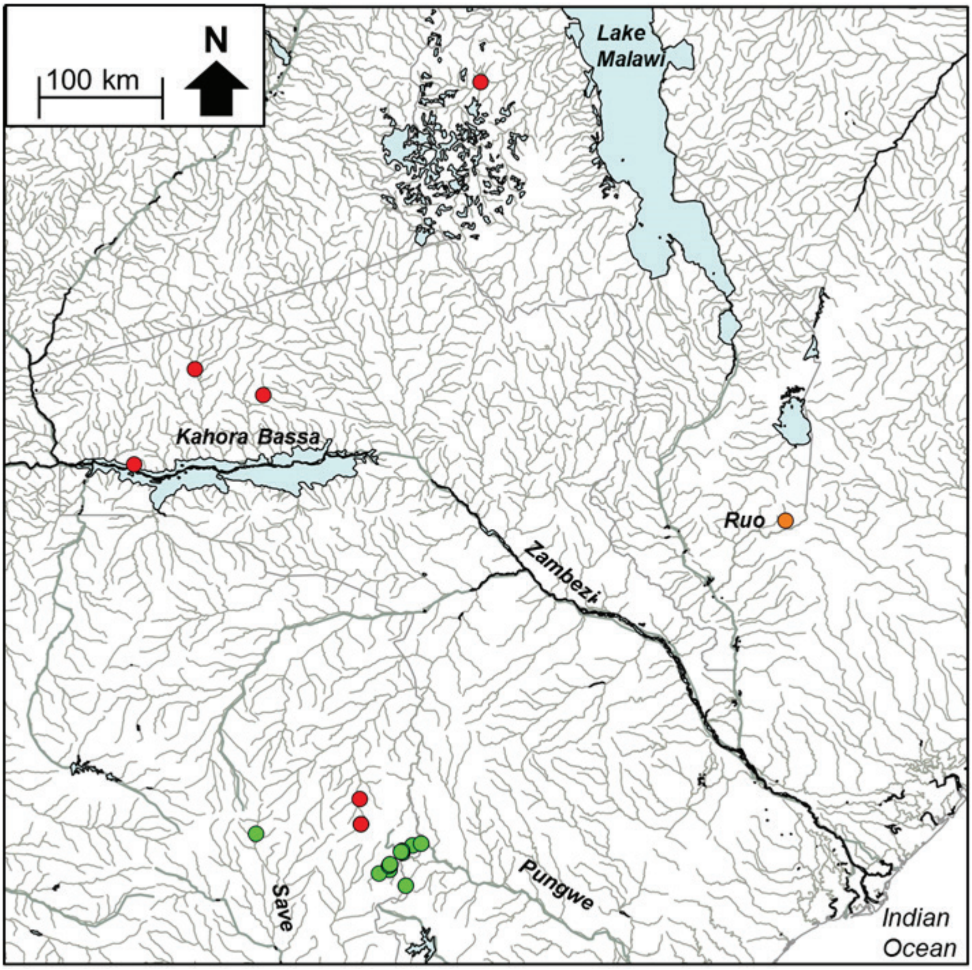

Figure 4b. The distribution of *Zaireichthys monomotapa* sensu stricto (green circle), *Zaireichthys* sp. 'slender' (red circle) and *Zaireichthys* sp. 'leopard spot' (orange circle) in the Eastern Zimbabwe Highlands freshwater ecoregion and adjacent areas.

as sequences MAFW12911 and MAFW13611 for individuals collected from two tributaries which flow into Lake Malawi also belonged to this clade (Figure 4b; Suppl. material 1), indicating that this taxon may be widespread in the Lower Zambezi and Lake Malawi catchments (Figure 4b). *Zaireichthys monomotapa* sensu stricto and *Z.* sp. 'slender' were separated by 9.26–11.00% sequence divergence, while divergences within these taxa ranged from 0.0–0.96%. *Zaireichthys* sp. 'leopard spot', a candidate species from the Ruo River, was basal to *Z. monomotapa* sensu stricto (Figure 4a), with a divergence of 3.22–3.80% between these two sister taxa. A second candidate species, *Z.* sp. 'Chilwa', within the *Z. monomotapa* complex occurred in the Montepuez River system in northern Mozambique and the Lake Chilwa system in Malawi is also shown in Figure 4a.

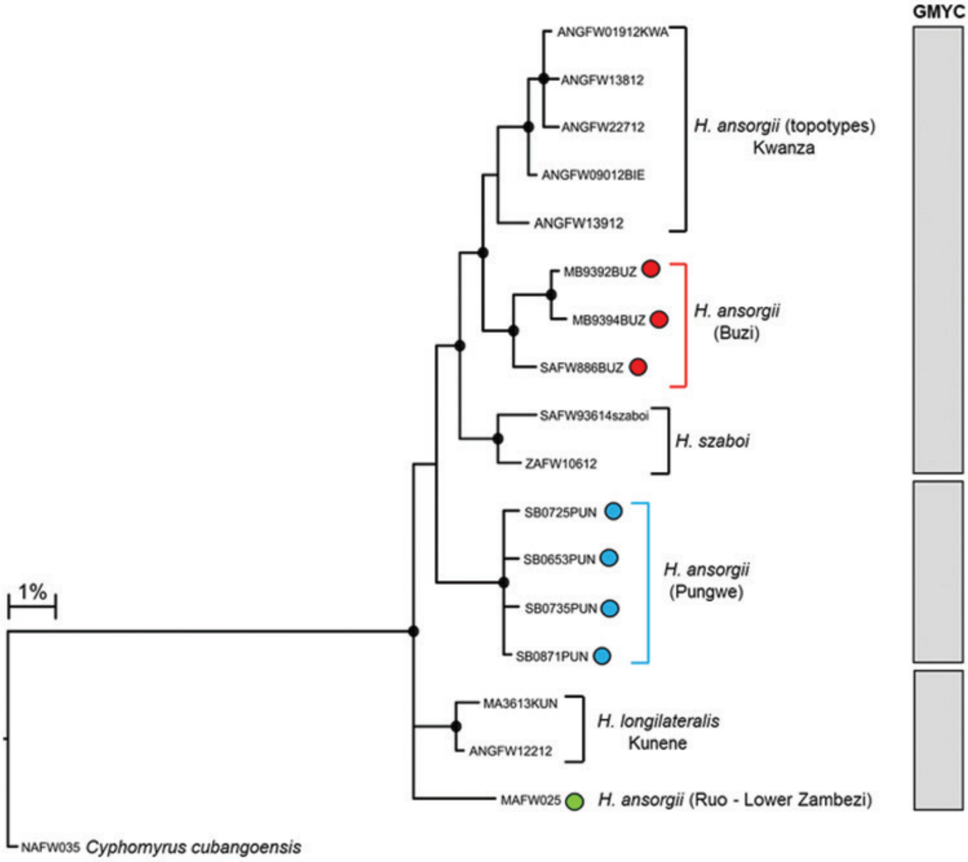

Figure 5a. Bayesian phylogenetic tree based on mtDNA cytochrome oxidase sub unit I (COI) sequences showing the candidate species or molecular operational taxonomic units (MOTUs) identified within *Hippopotamyrus ansorgii* from the Eastern Zimbabwe Highlands freshwater ecoregion. Well supported nodes are shown by a solid circle. The indicated candidate species or MOTUs were identified using the GMYC method based on trees that were built using three different combinations of priors and rates of molecular evolution: (i) yule model and a constant clock, (ii) yule model and a relaxed clock, and (iii) coalescent model with constant population size and a constant clock.

Genetic structure in *Hippopotamyrus ansorgii*

The edited alignment of 27 *Hippopotamyrus* sequences (included 11 BOLD sequences, Suppl. material 1), including a single *Cyphomyrus cubangoensis* sequence, was 580 base pairs and had 88 polymorphic sites which defined 17 haplotypes. Phylogenetic inference assigned the Pungwe and Buzi populations of *H. ansorgii* to two distinct clades that were separated by 2.85–3.27% divergence (Figure 5a; Table 4). Divergences within lineages were 0.0–0.35% for *H.* sp. 'Pungwe' and 0.00–1.25% for *H.* sp. 'Buzi'. GMYC analysis identified three clusters (or candidate species): (i) samples from the Kwanza, Upper Zambezi and the Buzi River system, (ii) samples from the Kunene

Table 4. Mitochondrial COI genetic distances (%) between lineages and species of in the *Hippopotamyrus ansorgii* complex from southern Africa.

	H. sp. 'Pungwe'	*H.* sp. 'Buzi'	*H.* sp. 'Ruo'	*H.* sp. 'Kwanza'	*H. szaboi*
H. sp. 'Pungwe'	0.00–0.35				
H. sp. 'Buzi'	2.85–3.27	0.00–1.25			
H. sp. 'Ruo'	3.50–3.71	4.17–4.40	-		
H. sp. 'Kwanza'	3.50–3.96	1.64–2.63	3.50–3.96	0.17–1.73	
H. szaboi	3.03–3.25	2.42–2.63	3.92	2.61–3.03	-
H. longilateralis	2.64–3.47	3.06–3.74	2.85–3.27	2.44–3.74	3.23–3.68

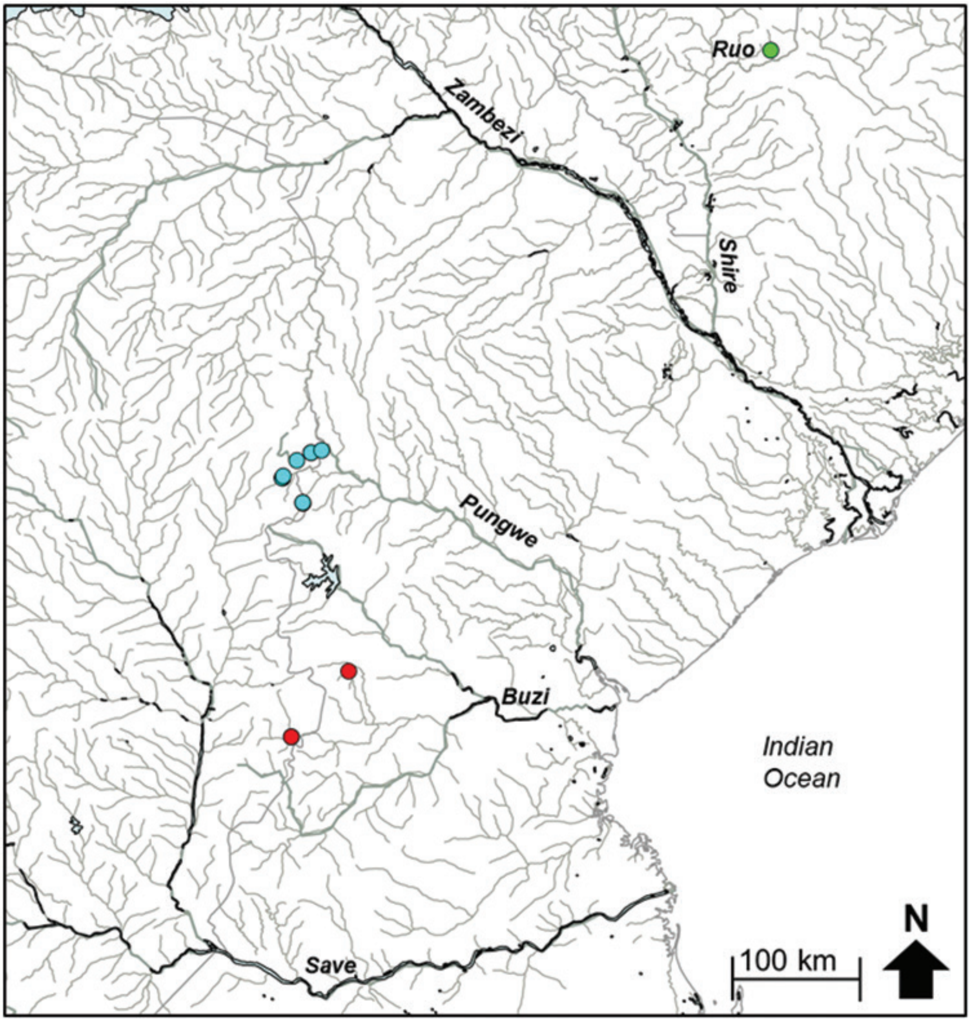

Figure 5b. The distribution of *Hippopotamyrus* sp. 'Buzi', (red circle), Hippopotamyrus sp. 'Pungwe' (blue circle) and *Hippopotamyrus* sp. 'Ruo' (green circle) in the Eastern Zimbabwe Highlands freshwater ecoregion and adjacent areas.

River system and the Ruo River, and (iii) samples from the Pungwe River system represented a candidate species, *H.* sp. 'Pungwe' (Figure 5a, b). The genetic divergences between lineages within these clusters are presented in Table 4.

Discussion

Hidden diversity in stream fishes of the Eastern Zimbabwe Highlands freshwater ecoregion

This study represents the first fine scale geographical survey and genetic exploration to determine the extent of hidden diversity in stream fishes of the Eastern Zimbabwe Highlands (EZH) freshwater ecoregion. Species delimitation assessment using the GMYC method revealed existence of 16 molecular operational taxonomic units (MOTUs) or putative species in five currently recognised nominal species (i.e., six MOTUs in *Chiloglanis neumanni*, two MOTUs in *Amphilius natalensis*, four MOTUs in *A. uranoscopus*, two MOTUs in *Z. monomotapa* and two MOTUs in *H. ansorgii*) collected from the EZH freshwater ecoregion. Given that all these five 'species' (with the exception of *Z. monomotapa* sensu stricto) were described from systems outside the EZH freshwater ecoregion, 15 of the 16 identified MOTUs within these 'species' are likely to represent new species that were previously unrecognised by science. Although the GMYC is a robust method for species delimitation (Fujisawa and Barraclough 2013), the entities identified in the present study were not designated as 'distinct species', but rather considered to represent 'candidate or potential species' pending critical evaluation using integrative approaches that combine molecular, morphological and ecological data to determine their taxonomic integrity. Ongoing assessments by the authors have revealed consistent morphological differences between *Chiloglanis* sp. 'rough skin' and *C.* sp. 'dwarf', and formal descriptions of these newly identified species are underway.

While the present study's main focus was on the EZH freshwater ecoregion, it is important to indicate that the diversity of stream fishes in the broader Eastern Afromontane Region may be much higher than currently documented as highlighted by the presence of other candidate species outside the EZH freshwater ecoregion. These include *Amphilius* sp. 'Ruo', *Zaireichthys* sp. 'Chilwa' and *Hippopotamyrus* sp. 'Ruo', as well as lineages within the *A. uranoscopus* complex. Additional fine-scale geographic surveys are therefore required to fill missing sampling gaps to more accurately map the distribution ranges of these lineages and potentially identify additional hidden diversity. Results of the present study also showed that samples collected from the type localities of the three synonyms of *A. uranoscopus* from southern Africa, *A. hargeri* (BOLD sequence MAFW032), *A. brevidorsalis* (sequence MB9404BUZ) and *A. cubangoensis* (BOLD sequence ANGFW075) were genetically differentiated from other populations of *A. uranoscopus* sensu lato (see Figure 4a). This warrants further taxonomic investigations to determine whether these synonyms represent valid species that may need to be resurrected.

The existence of such high taxonomic diversity within a small portion of the Eastern Afromontane Region is consistent with findings from a number of previous studies that have uncovered substantial hidden diversity and narrow range endemic species (or lineages) within several stream fishes that were previously thought to have wide geographic ranges in southern Africa (e.g., Chakona et al. 2013; Goodier et al. 2011; Maake et al. 2014; Morris et al. 2015; Swartz et al. 2007, 2009; Wishart et al. 2006). Results of the present study thus add to the growing board of evidence that shows that a large proportion of freshwater fishes in southern Africa remain scientifically undocumented, because many river systems remain poorly explored as much of the previous research effort and application of molecular approaches has predominantly focussed on fishes of the Cape Fold Ecoregion (Ellender et al. 2017). Despite being one of the geographically and taxonomically well explored regions in southern Africa, new species and deeply divergent genetic lineages continue to be discovered within almost all fish taxonomic groups of the Cape Fold Ecoregion (Chakona and Swartz, 2013; Chakona and Skelton, 2017; Chakona et al. 2013, 2014; Wishart et al. 2006), and estimates indicate that there are about 43 undescribed species within the 21 currently recognised fish species of this region (Linder et al. 2010). The discovery of hidden diversity in the EZH freshwater ecoregion adds to the growing evidence for the existence of high species-level diversity within a number of fish species from high altitude streams in southern, east and west Africa (e.g., Friel and Vigliotta 2011; Morris et al. 2016; Schmidt and Pezold 2011; Schmidt et al. 2014, 2015, 2016; Thomson 2013; Thomson and Page 2010). Given that many regions in southern Africa, in particular the subtropical and tropical river systems, have not been adequately explored, and the use of modern approaches for rapid species discovery remains very limited, additional diversity is likely to remain hidden within other wide-ranging ‘species’ in the region.

Conservation implications

Findings from the present study have considerable implications for aquatic biodiversity conservation in the EZH freshwater ecoregion, and the broader Eastern Afromontane region. Existence of such high cryptic diversity within five ‘species’ from a few mountain tributaries which represent a very small portion of the Eastern Afromontane region indicates that the overall conservation value of this globally important biodiversity hotspot has been severely underestimated. This is because the current biodiversity estimates and level of endemism in this region does not include cryptic diversity within stream fishes. Because many of the stream fishes from the EZH freshwater ecoregion are thought to have wide geographic ranges, they are considered to be of least conservation concern (Tweddle et al. 2009). This has resulted in stream fishes being neglected from ongoing conservation efforts in the EZH freshwater ecoregion, and the broader Eastern Afromontane region. This can be seen in the calls for research funding, where the primary focus is on other vertebrate groups such as birds, amphibians, reptiles and small mammals (e.g., see http://www.cepf.net/grants/project_database/Pages/default.

aspx#). The present study uncovers a classic example where underestimation of taxonomic diversity and poor understanding of the spatial distribution of species has misdirected conservation efforts, to the extent that the EZH freshwater ecoregion is currently not listed among the priority freshwater Key Biodiversity Areas within the Eastern Afromontane Biodiversity Hotspot (see CEPF 2012). This is however unfortunate because the highly sensitive Afromontane streams and rivers in this region have been severely transformed and are experiencing ongoing human impacts, including illegal mining activities, deforestation, increased sedimentation, uncontrolled burning and introduction of non-native invasive piscivorous species (Kadye and Magadza 2008; Kadye et al. 2013). For example, the rocky streams which drain the Chimanimani Mountains used to have intact indigenous riparian vegetation, had clear water and perennial flow, but surveys in 2013 revealed that human encroachment, increased agricultural activities and the associated loss of riparian vegetation has transformed these streams into sluggish flowing, and highly turbid and heavily silted habitats. This increases the risk of losing sensitive fish species and other aquatic taxa from the EZH freshwater ecoregion whose value as an endemic hotspot has been previously underestimated.

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References

Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny MLJ, Skelton P, Allen GR, Unmack P, Naseka A, Ng R, Sindorf N, Robertson J, Armijo E, Higgins JV, Heibel TJ, Wikramanayake E, Olson D, López HL, Reis RE, Lundberg JG, Pérez MHS, Petry P (2008) Freshwater ecoregions of the world: A new map of biogeographic units of freshwater biodiversity conservation. Bioscience 58: 403–414. https://doi.org/10.1641/B580507

Bell-Cross G, Minshull JL (1988) The fishes of Zimbabwe. National Museums and Monuments of Zimbabwe, Harare, Zimbabwe, 294 pp.

Bell-Cross G, Jubb RA (1973) The Amphiliidae of southern Africa and record of *Amphilius lampei* Pietchmann, 1913, from the Inyanga Mountains, Rhodesia. Arnoldia, Rhodesia 6: 1–9.

Boulenger GA (1909) Catalogue of the Fresh-Water Fishes of Africa in the British Museum (Natural History), Vol. 1. British Museum (NH), London.

Burnham KP, Anderson DR (2002) Model Selection and Multi-Model Inferences: A Practical Information-Theoretic Approach (2nd edn). Springer, New York, 488 pp.

Chakona A, Skelton PH (2017) A review of the *Pseudobarbus afer* (Peters, 1864) species complex (Teleostei, Cyprinidae) in the eastern Cape Fold Ecoregion of South Africa. ZooKeys 657: 109–140. https://doi.org/10.3897/zookeys.657.11076

Chakona A, Swartz ER, Gouws G (2013) Evolutionary drivers of diversification and distribution of a southern temperate stream fish assemblage: testing the role of historical isolation and spatial range expansion. PlosOne 8: e70953. https://doi.org/10.1371/journal.pone.0070953

Chakona A, Swartz ER (2013) A new redfin species, *Pseudobarbus skeltoni* (Cyprinidae, Teleostei) from the Cape Floristic Region, South Africa. Zootaxa 3686: 565–577. https://doi.org/10.11646/zootaxa.3686.5.5

Chakona A, Swartz ER, Skelton PH (2014) A new species of redfin (Teleostei, Cyprinidae, *Pseudobarbus*) from the Verlorenvlei River system, South Africa. ZooKeys 453: 121–137. https://doi.org/10.3897/zookeys.453.8072

Clark VR, Timberlake JR, Hyde MA, Mapaura A, Palgrave MC, Wursten BT, Ballings P, Burrows JE, Linder HP, McGregor GK, Chapano C, Plowes DCH, Childes SL, Dondeyne S, Müller T, Barker NP (2017) A first comprehensive account of floristic diversity and endemism on the Nyanga Massif, Manica Highlands (Zimbabwe-Mozambique). Kirkia 19: 1–53.

Crivellaro MS, Zimmermann BL, Bartholomei-Santos ML, Crandall KA, Pèrez-Losada M, Bond-Buckup G, Santos S (2017) Looks can be deceiving: species delimitation reveals hidden diversity in the freshwater crab *Aegla longirostri* (Decapoda: Anomura). Zoological Journal of the Linnean Society 182: 24–37. https://doi.org/10.1093/zoolinnean/zlx030

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Decru E, Snoeks J, Vreven E (2015) Taxonomic evaluation of the *Hepsetus* from the Congo basin with the revalidation of *H. microlepis* (Teleostei: Hepsetidae). Ichthyological Exploration of Freshwaters 26: 273–287.

Decru E, Vreven E, Snoeks J (2012) A revision of the west African *Hepsetus* (Characiformes: Hepsetidae) with a description of *Hepsetus akawo* sp. nov. and a redescription of *Hepsetus odoe* (Bloch, 1794). Journal of Natural History 46: 1–23. https://doi.org/10.1080/00222933.2011.622055

Decru E, Vreven E, Snoeks J (2013) A revision of the Lower Guinean *Hepsetus* species (Characiformes; Hepsetidae) with the description of *Hepsetus kingsleyae* sp. nov. Journal of Fish Biology 82: 1351–1375. https://doi.org/10.1111/jfb.12079

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214. https://doi.org/10.1186/1471-2148-7-214

Eccles DH, Tweddle D, Skelton PH (2011) Eight new species in the dwarf catfish genus *Zaireichthys* (Siluriformes: Amphiliidae). Smithiana Publications in Aquatic Biodiversity 13: 3–28.

Ellender BR, Wasserman RJ, Chakona A, Skelton PH, Weyl OLF (2017) A review of the biology and status of Cape Fold Ecoregion freshwater fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 27: 867–879. https://doi.org/10.1002/aqc.2730

Engelbrecht J, Bills R, Cambray J (2007) *Chiloglanis emarginatus*. The IUCN Red List of Threatened Species 2007: e.T63366A12663280. http://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T63366A12663280.en [Downloaded on 17 April 2018]

Eschmeyer WN, Fricke R, van der Laan R [Eds] (2018) Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp [Electronic version accessed 10 /04/ 2018]

Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent (GMYC) approach: a revised method and evaluation on simulated data sets. Systematic Biology 62: 707–724. https://doi.org/10.1093/sysbio/syt033

Friel FP, Vigliotta TR (2011) Three new species of African suckermouth catfishes, genus *Chiloglanis* (Siluriformes: Mochokidae), from the lower Malagarasi and Luiche rivers of western Tanzania. Zootaxa 3063: 1–21.

Goodier SAM, Cotterill FPD, O'Ryan C, Skelton PH, de Wit MJ (2011) Cryptic diversity of African tigerfish (Genus *Hydrocynus*) reveals palaeogeographic signatures of linked Neogene geotectonic events. PlosOne 6: e28775. https://doi.org/10.1371/journal.pone.0028775

Grabowski M, Mamos T, Bącela-Spychalska, Rewicz T, Wattier RA (2017) Neogene paleogeography provides context for understanding the origin and spatial distribution of cryptic diversity in a widespread Balkan freshwater amphipod. PeerJ 5: e3016. https://doi.org/10.7717/peerj.3016

Ivanova N, Zemlak TS, Hanner RH, Hebert PDN (2007) Universal primer cocktails for fish DNA barcoding. Molecular Ecology Notes 6: 998–1002. https://doi.org/10.1111/j.1471-8286.2006.01428.x

Jubb RA (1959) A new species of *Varicorhinus* Rueppell, 1836, from the Pungwe River, Inyanga district, Southern Rhodesia. Occasional Papers of the National Museums of Southern Rhodesia. B, Natural Sciences 3: 306–308.

Jubb RA (1961) An illustrated guide to the freshwater fishes of the Zambezi River, Lake Kariba, Pungwe, Sabi, Lundi and Limpopo rivers. Stuart Manning, Bulawayo, Zimbabwe.

Jubb RA, Le Roux P (1969) Revision of the *Chiloglanis* (Pisces: Mochokidae) of southern Africa and descriptions of two new species. Annals of the Cape Provincial Museums (Natural History) 8: 13–23.

Kadye WT, Chakona A, Marufu LT, Samukange T (2013) The impact of non-native rainbow trout within Afro-montane streams in Eastern Zimbabwe. Hydrobiologia 720: 75–88. https://doi.org/10.1007/s10750-013-1624-4

Kadye WT, Magadza CHD (2008) Trout induces a shift from preferred habitat types for indigenous species: the example of the indigenous catfish, *Amphilius uranoscopus* (Pfeffer, 1889), on an African montane plateau. Hydrobiologia 614: 329–337. https://doi.org/10.1007/s10750-008-9517-7

Kordbacheh A, Garbalena G, Walsh EJ (2017) Population structure and cryptic species in the cosmopolitan rotifer *Euchlanis dilatata*. Zoological Journal of the Linnean Society. https://doi.org/10.1093/zoolinnean/zlx027

Kramer B, Bills IR, Skelton PH, Wink M (2012) A critical revision of the churchill snoutfish, genus *Petrocephalus* Marcusen, 1854 (Actinopterygii: Teleostei: Mormyridae), from southern and eastern Africa, with the recognition of *Petrocephalus tanensis*, and the description of five new species. Journal of Natural History 46: 2179–2258. https://doi.org/10.1080/00222933.2012.708452

Kramer B, Skelton PH, van der Bank FH, Wink M (2007) Allopatric differentiation in the *Marcusenius macrolepidotus* species complex in southern and eastern Africa: the resurrection of *M. pongolensis* and *M. angolensis*, and the description of two new species (Mormyridae, Teleostei). Journal of Natural History 41: 647–708. https://doi.org/10.1080/00222930701250987

Kramer B, Swartz ER (2010) A new species of slender stonebasher within the *Hippopotamyrus ansorgii* complex from the Cunene River in southern Africa (Teleostei: Mormyriformes). Journal of Natural History 44: 2213–2242. https://doi.org/10.1080/00222931003764089

Kramer B, van der Bank FH, Wink M (2004) The *Hippopotamyrus ansorgii* species complex in the Upper Zambezi River System with a description of a new species, *H. szaboi* (Mormyridae). Zoologica Scripta 33: 1–18. https://doi.org/10.1111/j.1463-6409.2004.00132.x

Kramer B, Van der Bank FH (2000) The southern Churchill, *Petrocephalus wesselsi*, a new species of mormyrid from South Africa defined by electric organ discharges, genetics, and morphology. Environmental Biology of Fishes 59: 393–413. https://doi.org/10.1023/A:1026562827022

Kramer B, van der Bank FH (2011) The Victoria Falls, a species boundary for the Zambezi Parrotfish, *Cyphomyrus discorhynchus* (Peters, 1852), and the resurrection of *Cyphomyrus cubangoensis* (Pellegrin, 1936) (Mormyridae: Teleostei). Journal of Natural History 45: 2669–2699. https://doi.org/10.1080/00222933.2011.597945

Kramer B, Van der Bank H, Flint N, Sauer-Gürth H, Wink M (2003) Evidence for parapatric speciation in the mormyrid fish, *Pollimyrus castelnaui* (Boulenger, 1911), from the Okavango – Upper Zambezi river systems: *P. marianne* sp. nov., defined by electricorgan discharges, morphology and genetics. Environmental Biology of Fishes 77: 47–70. https://doi.org/10.1023/A:1024448918070

Kramer B, Van der Bank H, Wink M (2014) Marked differentiation in a new species of dwarf stonebasher, *Pollimyrus cuandoensis* sp. nov. (Mormyridae: Teleostei), from a contact zone with two sibling species of the Okavango and Zambezi rivers. Journal of Natural History 48: 429–463. https://doi.org/10.1080/00222933.2013.807950

Kramer B, Wink M (2013) East-west differentiation in the *Marcusenius macrolepidotus* species complex in Southern Africa: the description of a new species for the Cunene River, Namibia (Mormyridae, Teleostei). Journal of Natural History 47: 2327–2362. https://doi.org/10.1080/00222933.2013.798699

Linder HP, Johnson SD, Kuhlmann M, Matthee CA, Nyffeler R, Swartz ER (2010) Biotic diversity in the Southern African winter-rainfall region. Current Opinion in Environmental Sustainability 2: 109–116. https://doi.org/10.1016/j.cosust.2010.02.001

Maake PA, Gon O, Swartz E (2014) Descriptions of three new species of *Marcusenius* Gill, 1862 (Teleostei: Mormyridae) from South Africa and Mozambique. Zootaxa 3780: 455–480. https://doi.org/10.11646/zootaxa.3780.3.2

Marshall B (2011) The fishes of Zimbabwe and their biology. Smithiana Monograph, Volume 3. Royal Museum for Central Africa. 291 pp.

Mazvimavi D (2010) Investigating changes over time of annual rainfall in Zimbabwe. Hydrology and Earth System Sciences 14: 2671–2679. https://doi.org/10.5194/hess-14-2671-2010

Morris J, Ford AGP, Ali JR, Peart CR, Bills R, Day JJ (2015) High levels of genetic structure and striking phenotypic variability in a sexually dimorphic suckermouth catfish from the African Highveld. Biological Journal of the Linnean Society 117: 528–546. https://doi.org/10.1111/bij.12650

R Development Core Team (2011) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Rambaut A, Drummond AJ (2007) Tracer v.1.4. http://beast.bio.ed.ac.uk/Tracer

Riddin MA, Bills IR, Villet MH (2016) Phylogeographic, morphometric and taxonomic reevaluation of the river sardine, *Mesobola brevianalis* (Boulenger, 1908) (Teleostei, Cyprinidae, Chedrini). ZooKeys 641: 121–150. https://doi.org/10.3897/zookeys.641.10434

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rubinoff D, Cameron S, Will K (2006) A genomic perspective on the shortcomings of mitochondrial DNA for 'Barcoding' identification. Journal of Heredity 97: 581–594. https://doi.org/10.1093/jhered/esl036

Schmidt RC, Bart Jr HL, Nyingi DW, Gichuki NN (2014) Phylogeny of suckermouth catfishes (Mochokidae: Chiloglanis) from Kenya: the utility of Growth Hormone introns in species level phylogenies. Molecular Phylogenetics and Evolution: 79: 415–421. https://doi.org/10.1016/j.ympev.2014.07.011

Schmidt RC, Bart Jr HL, Nyingi DW (2015) Two new species of African suckermouth catfishes, genus Chiloglanis (Siluriformes: Mochokidae), from Kenya with remarks on other taxa from the area. Zootaxa 4044: 45–64. https://doi.org/10.11646/zootaxa.4044.1.2

Schmidt RC, Bart Jr, Pezold F (2016) High levels of endemism in suckermouth catfishes (Mochokidae: Chiloglanis) from the Upper Guinean forests of West Africa. Molecular Phylogenetics and Evolution 100: 199–205. https://doi.org/10.1016/j.ympev.2016.04.018

Schmidt RC, Pezold F (2011) Morphometric and molecular variation in mountain catfishes (Amphiliidae: *Amphilius*) in Guinea, west Africa. Journal of Natural History 45: 521–552. https://doi.org/10.1080/00222933.2010.534560

Skelton PH (1984) A systematic revision of species of the catfish genus *Amphilius* (Siluroidei, Amphiliidae) from east and southern Africa. Annals of the Cape Provincial Museums (Natural History) 16: 41–71.

Skelton PH, Teugels GG (1986) Amphiliidae. In: Daget J, Gosse J-P (Eds) Thys van den Audenaerde DFE (Eds) Check-list of the freshwater fishes of Africa. CLOFFA. ISNB Bruxelles, MRAC Tervuren, ORSTOM Paris 2, 54–65.

Skelton PH (2001) A Complete Guide to the Freshwater Fishes of Southern Africa. Struik Publishers, Cape Town, 395 pp.

Sunnucks P, England PR, Taylor AC, Hales DF (1996) Microsatellite and chromosome evolution of parthenogenetic Sitobion aphids in Australia. Genetics 144: 747–756.

Swartz ER, Skelton PH, Bloomer P (2007) Sea-level changes, river capture and the evolution of populations of the Eastern Cape and fiery redfins (*Pseudobarbus afer* and *Pseudobarbus phlegethon*, Cyprinidae) across multiple river systems in South Africa. Journal of Biogeography 34: 2086–2099. https://doi.org/10.1111/j.1365-2699.2007.01768.x

Swartz ER, Skelton PH, Bloomer P (2009) Phylogeny and biogeography of the genus Pseudobarbus (Cyprinidae): Shedding light on the drainage history of rivers associated with the Cape Floristic Region. Molecular Phylogenetics and Evolution 51: 75–84. https://doi.org/10.1016/j.ympev.2008.10.017

Swofford DL (2003) PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4.0 beta version. Sinauer Associates, Sunderland.

Thieme ML, Abell R, Stiassny MLJ, Skelton, P, Lehner P, Teugels GG, Dinerstein E, Toham AK, Burgess N, Olson D (2005) Freshwater ecoregions of Africa and Madagascar: a conservation assessment. Bibliovault OAI Repository, the University of Chicago Press, 431 pp.

Thomson AW, Page LM (2010) Taxonomic revision of the *Amphilius uranoscopus* group (Teleostei: Siluriformes) in Kenya, with the description of a new species from the Athi River. Florida Museum Bulletin 49: 45–66.

Thomson WA (2013) Systematics of the African catfish family Amphiliidae (Teleostei: Siluriformes). PhD Thesis, University of Florida.

Tweddle D, Bills R, Swartz E, Coetzer W, Da Costa L, Engelbrecht J, Cambray J, Marshall B, Impson D, Skelton PH (2009) The status and distribution of freshwater fishes. In: Darwall WRT, Smith KG, Tweddle D, Skelton PH (Eds) The Status and Distribution of Freshwater Biodiversity in Southern Africa. Gland, South African Institute for Aquatic Biodiversity, IUCN, Grahamstown, 21–37.

Van Wyk AE, Smith GF (2001) Regions of Floristic Endemism in Southern Africa. Umdaus Press, Hatfield, 160 pp.

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN (2005) DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society B-Biological Sciences 360: 1847–1857. https://doi.org/10.1098/rstb.2005.1716

Wishart M, Hughes J, Stewart B, Impson D (2006) Extreme levels of intra-specific divergence among Cape Peninsula populations of the Cape Galaxias, *Galaxias zebratus* Castelnau 1861, reveal a possible species complex. African Journal of Aquatic Science 31: 99–106. https://doi.org/10.2989/16085910609503876

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, aberrations in global climate 65 Ma to present. Science 292: 686–693. https://doi.org/10.1126/science.1059412

Zengeya T, Decru E, Vreven E (2011) Revalidation of *Hepsetus cuvieri* (Castelnau, 1861) (Characiformes: Hepsetidae) from the Quanza, Zambezi and Southern part of the Congo ichthyofaunal provinces. Journal of Natural History 45: 1723–1744. https://doi.org/10.1080/00222933.2011.560724

Supplementary material 1

Evidence of hidden diversity and taxonomic conflicts in five stream fishes from the Eastern Zimbabwe Highlands freshwater ecoregion

Authors: Albert Chakona, Wilbert T. Kadye, Taurai Bere, Daniel N. Mazungula, Emmanuel Vreven

Data type: (Mitochondrial COI sequences, sample size, occurrence)

Explanation note: Locality information, sample size, BOLD and GenBank accession numbers for mitochondrial COI sequences, and the candidate species identified in *Amphilius natalensis*, *A. uranoscopus*, *Chiloglanis neumanni*, *Hippopotamyrus ansorgii* and *Zaireichthys monomotapa* from the Eastern Zimbabwe Highlands freshwater ecoregion.

Link: https://doi.org/10.3897/zookeys.768.21944.suppl1

ZooKeys 768: 97–104 (2018)
doi: 10.3897/zookeys.768.24460
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RESEARCH ARTICLE

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Macrocheles kekensis sp. n., a new macrochelid mite associated with a centoniin beetle from Hungary (Acari, Mesostigmata)

Jenő Kontschán[1]

[1] *Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, H-1525 Budapest, P.O. Box 102, Hungary*

Corresponding author: *Jenő Kontschán* (kontschan.jeno@agrar.mta.hu)

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Abstract

A new species, *Macrocheles kekensis* **sp. n.**, is described based from three specimens associated with a cetoniin beetle (*Hoplia hungarica* Burmeister, 1844). The new species differs from the other known European macrochelid species in having 29 pairs of dorsal setae, j1 and z1 short and robust, other dorsal setae long and pilose, and the absence of apodemes between the genital and ventrianal shields. This is the 34th Hungarian macrochelid species.

Keywords

Acari, Coleoptera, phoresy

Introduction

Members of the mite family Macrochelidae (Parasitiformes: Mesostigmata) are large, fast-moving predators inhabiting soil substrates, litter and decomposing organic matter. The macrochelids feed on nematodes, eggs and larvae of insects or weakly sclerotized mites, and very often live in association with certain insect groups (e.g. flies and beetles) (Mašán 2003). Macrochelidae is relatively well known in some Central European countries like Germany (Karg 1993), Austria (Johnston 1970) and Slovakia (Mašán 2003). However, information about their occurrence in Hungary is insufficient, although numerous records were presented over the past 20 years (e.g. Ács and Kontschán 2014, Kontschán 2005, 2006, 2015, Kontschán et al. 2014, 2015a, 2015b, 2016, Salmane and Kontschán 2005, 2006). Only a few beetle-associated macrochelids have been mentioned (Kontschán 2006) from Hungary, while macrochelid mites associated with centoniin beetles are rarely collected. The association of macrochelid mites with flower beetles seems to be a rare phenomenon. Mašán (2003) in his monograph about the macrochelid mites of Slovakia mentioned only four species associated with a centoniin species (*Potosia cuprea* Fabricius, 1775).

The subfamily Cetoninae is a very species-rich group in Hungary (Enyedi 2006), majority of the species can be observed on the flowers of the plants in summertime. So far only one species [*Macrocheles glaber* (J. Müller, 1860)] has been reported from *Cetonia aurata* from Hungary (Ács and Kontschán 2014). Recently, some macrochelids were collected on a *Hoplia hungarica* Burmeister, 1844 beetle (Scarabaeidae: Cetoniinae), which are described as a new species here.

Materials and methods

The three mite specimens were collected as phoretic individuals on a *Hoplia hungarica* Burmeister, 1844 beetle in the eastern part of Hungary. The host beetle was attracted to a lamp of the house and was found on the ground close to the house wall. The specimens assigned here to the new species (n = 3, females) were collected from the body of the host beetle using a brush observed under a BTC binocular microscope. Later they were cleared in lactic acid and were placed on a slide with deep cavity for examination. Drawings were made with the aid of a drawing tube on a Leica 1000 microscope. All specimens are stored in 75% ethanol and the holotype and one paratype are deposited in the Natural History Museum, Budapest, plus one paratype in the Natural History Museum in Geneva. Measurements are presented in minimum and maximum size. Measurements and the scales in the figures are given in micrometers (μm). The new species was also tested using the keys provided by Bregetova (1977), Karg (1993) and Mašán 2003.

Taxonomy

Macrochelidae Vitzthum, 1930
Macrocheles Latreille, 1829

Macrocheles kekensis sp. n.

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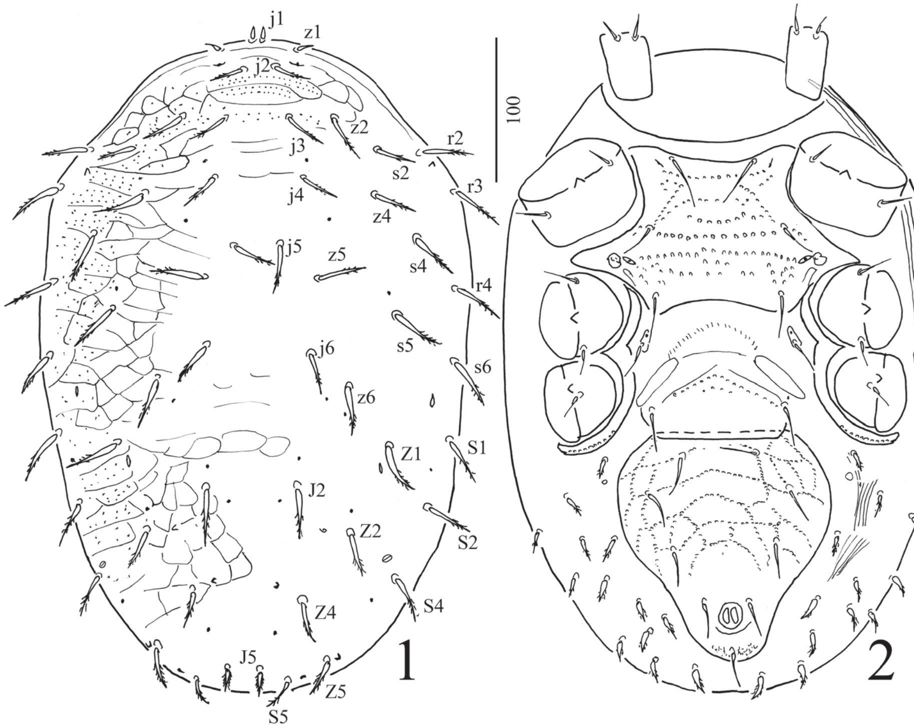
Figures 1–15

Diagnosis. All dorsal setae pilose, except setae j1 and z1 which short and spine-like. Anterior and lateral parts of dorsal shield dotted, majority of dorsal surface with reticulate sculptural pattern.

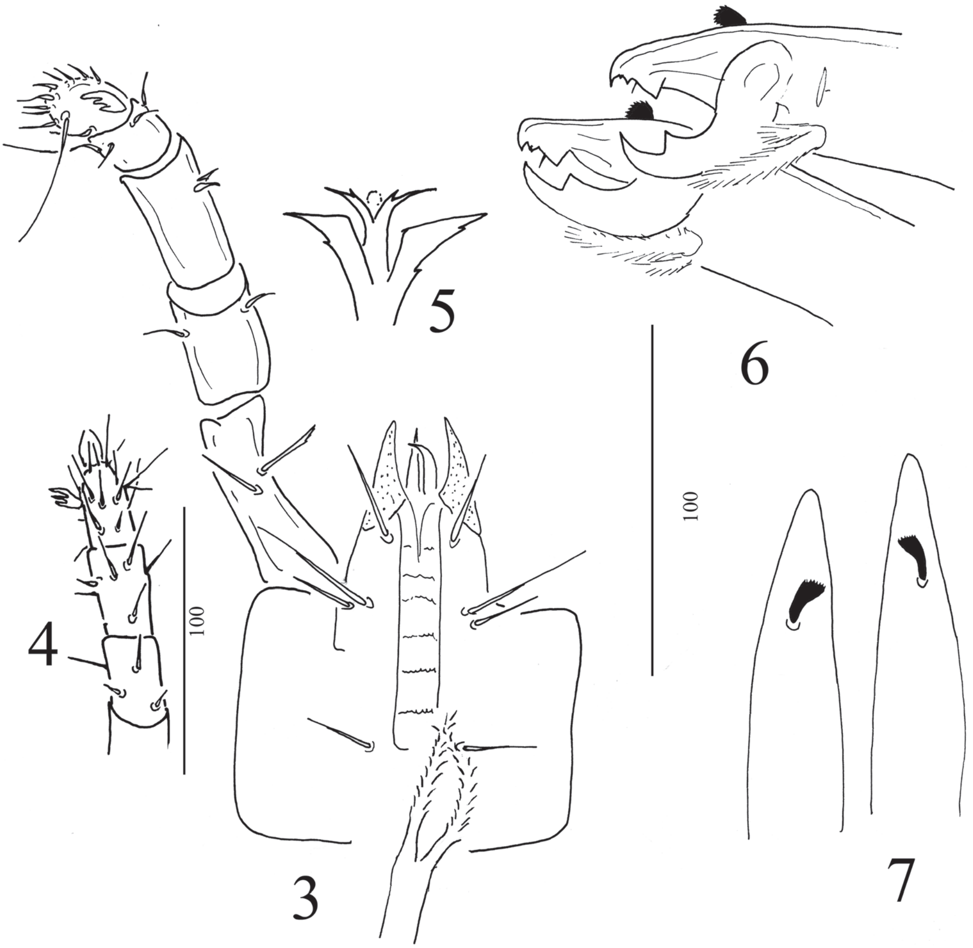


Figures 1–2. *Macrocheles kekensis* sp. n., female. **1** Dorsal view of body **2** Ventral view of body (without legs and gnathosoma, only the coxae illustrated).

Material examined. Holotype. Female. Collected from *Hoplia hungarica* Burmeister, 1844 Hungary, Kék village, 48°06'38"N, 21°52'51"E, 10 m a.s.l., 05 May 2017. Kontschán, J. coll. *Paratypes.* Two females, locality, date and host same as for holotype. The holotype and one paratype were deposited in the Soil Zoology Collections of the Hungarian Natural History Museum, Budapest, the other paratype in the Arachnida collection of the Natural History Museum, Geneva, Switzerland.

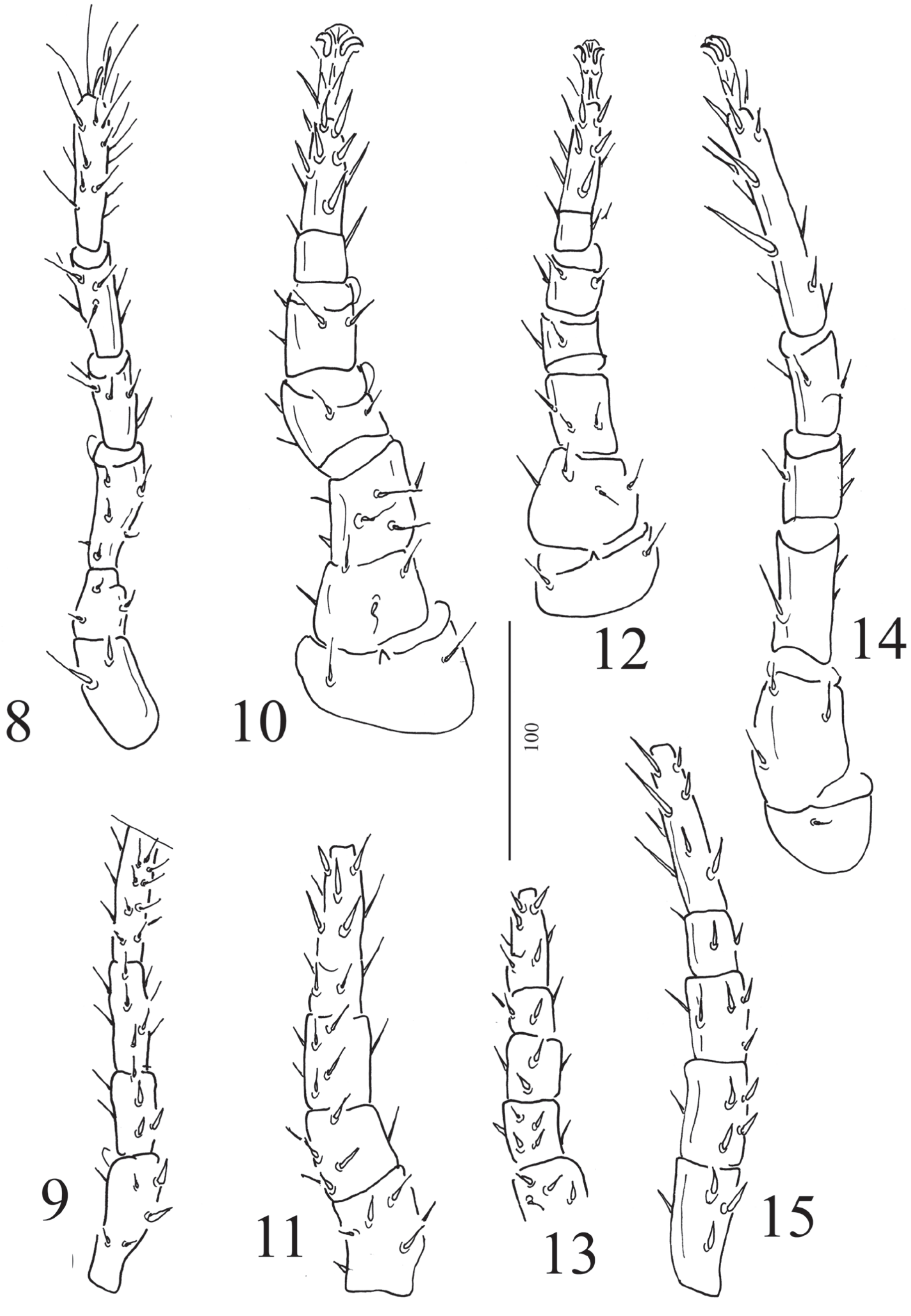
Description. Female. *Dorsum* (Figure 1). Shape of dorsal shield oblong, with length 440–460 and width 280–310 at level of the coxae II (n=3), micropunctation on anterior and lateral surface with reticulate sculptural pattern. Majority of setae on dorsal shield long and pilose in distal half, except setae j1 and z1 which are short, smooth and spine-like, and J5 with pilose margins for entire length. Length of dorsal setae: j1 and z1= 8–9, j2 = 22–24, j2, s2, Z2, Z5 and S5 = 24–26, j3, j4, j6, z2, z4, z5, z6, s4, s6, J2, Z1, Z4, S1, S2, S4 = 30–32, j5, s5, s6, r3, r3, r4 = 34–35, J5 = 16. Dorsal shield with four pairs of lyrifissures (close to z1, s6, S5 and between Z2 and S4), ten pairs of gland pores (close to j3, j4, s5, j6, z6, Z1, Z2, S4, Z4 and two close to J2), and four pairs of microspicules (close to r2, Z2, Z4 and Z5). Peritreme reaches the bases of setae z1.

Venter (Figure 2). Sternal shield 87–95 long and 100–110 wide at level of coxae II, bearing 3 pairs of needle-like setae and two pairs of lyrifissures. Posterior margin



Figures 3–7. *Macrocheles kekensis* sp. n., female. **3** Ventral view of gnathosoma and palp **4** Palp in dorsal view **5** Tectum **6** Dorsal view of chelicerae **7** Lateral view of chelicerae.

of sternal shield concave. Surface with linearly arranged punctures. Measurements of setae: St1 = 34–36, St2 = 30–32 and St3 = 26–28. Cuticle with a thin punctuation. Metasternal seta on metasternal platelet with length 20–23. Posterior margin of genital shield straight. Genital shield with length 75–78 and width 89–93. The length of seta on genital shield 23–26. Apodemes between ventrianal and genital shields absent. Ventrianal shield pentagonal with length 158–162 and width at level of Jv2 145–148, surface reticulated with linearly arranged punctures. Three pairs of ventrianal setae 22–25 long, needle-like, adanal setae needle-like and 22 long. Post-anal seta similar in shape and length to adanal setae. Opisthogaster bearing more than twelve pairs of slightly pilose setae (12–19 long). Sperm access system not visible.



Figures 8–15. *Macrocheles kekensis* sp. n., female **8** Leg I in ventral view **9** Leg I in dorsal view **10** Leg II in ventral view **11** Leg II in dorsal view **12** Leg III in ventral view **13** Leg III in dorsal view **14** Leg IV in ventral view **15** Leg IV in dorsal view.

Gnathosoma (Figures 3–7). Gnathosoma well developed. Deutosternal groove (Figure 3) with six rows of denticles, 3 pairs of hypostomal setae and one pair of palpcoxal setae present, all setae needle-like. Internal posterior hypostomal seta (h2) longer than others. Measurements of hypostomal setae: h1 = 27–30, h2 = 38–42, h3 = 18–25 and capitulate seta = 20–27. Tectum (Figure 5) with a pair of lateral processes and a bifurcated medial stem, margins of lateral processes and medial stem weakly serrate. Cheliceral fixed digit with apically serrate dorsal seta, four teeth (two smaller and two larger), pilus dentilis and terminal hook (Figures 6–7). On moveable digit large tooth and terminal hook present. Arthrodial brush with a short and a long branch and densely pilose. Length of fixed digit 52–55, moveable digit 41–44. Palp 164–170 long, palp trochanter with one smooth and one apically serrate ventral setae, other setae on palp smooth, palp apotele three-tined (Figures 3–4).

Legs (Figures 8–15). Tarsi II–IV with well-developed ambulacra and claws, claws and ambulacrum is missing from the tip of leg I. All setae simple on legs. Leg chaetotaxy typical for the genus. Length of legs: I 325–370, II 250–320, III 240–260, IV 380–420. Coxal glands not visible.

Etymology. The name of the new species refers to the village (Kék, East-Hungary) where the species was collected.

Remarks

The short, robust, and small setae j1 and z1 are present in numerous macrochelid mites distributed in Europe, but the majority or all dorsal setae are smooth in these known species, contrary with new one, where only the latter mentioned two pairs of setae are smooth and the others are marginally pilose. *Macrocheles subbadius* (Berlese, 1904) and *Macrocheles insignitus* Berlese, 1918 have similar ornamentations on sternal and ventral shields and have short and robust j1 setae, but these two species have smooth setae on dorsal shield, which are pilose in the new one.

Discussion

The systematic position of the new species is questionable. The serrate dorsal seta on chelicerae are a distinctive character of the genus *Nothrholaspis*, but members of the genus *Nothrholaspis* has three pairs of small apodemes between genital and ventrianal shields and tectums are forked to lateral and central branches (Emberson 2010, Babaeian et al. 2014, Özbek and Bal 2013). The dorsal seta of the chelicera of the new species is apically serrate, which matches the diagnosis of the genus *Nothrholaspis*. However, the apodemes are missing in the new species and the shape of tectum is also different. Due to the shape of tectum and the absence of apodemes between the genital and ventrianal shield, I cannot place the new species into the genus *Nothrholaspis*, therefore it is temporarily placed in the genus *Macrocheles* sensu lato.

The host species (*Hoplia hungarica*) is a rare beetle found in Hungary. Usually only one or two localities are mentioned in faunistic studies (Ádám 1997, Enyedi 2006, Rozner 2001). Therefore the finding of the macrochelid mite on this infrequently collected beetle was absolutely unexpected.

Acknowledgements

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References

Ács A, Kontschán J (2014) Contribution to the Macrochelidae Vitzthum, 1930 fauna of the Carpathian Basin and the Balkan Peninsula (Acari: Mesostigmata). Opuscula Zoologica Budapest 45(2): 109–118.

Ádám L (1997) The species of Scarabaeoidea (Coleoptera) from Őrség. Savaria 24 (2): 63–72.

Babaeian E, Joharchi O, Jamshidian MK (2014) A new species of the genus *Nothrholaspis* Berlese (Acari: Macrochelidae) from Iran. Zootaxa 3784 (5): 585–590. https://doi.org/10.11646/zootaxa.3784.5.

Berlese A (1904) Acari nuovi. Manipulus IIus. Redia 1: 258–280.

Berlese A (1918) Centuria quarta di Acari nuovi. Redia 13: 113–190.

Bregetova NG (1977) Family Macrochelidae Vitzthum, 1930. In: Ghilyarov MS, Bregetova NG (Eds) Key to the Soil–Inhabiting Mites. Mesostigmata. Nauka, Leningrad, 346–411.

Burmeister HCC (1844) Besondere Entomologie. Fortsetzung. Coleoptera Lamellicornia Xylophila et Pectinicornia. Handbuch der Entomologie. Fünfter Band. TCF Enslin, Berlin viii, 584 pp.

Emberson RM (2010) A reappraisal of some basal lineages of the family Macrochelidae, with the description of a new genus (Acarina: Mesostigmata). Zootaxa 2501: 37–53.

Enyedi R (2006) Contributions to the Scarabaeoidea fauna of Hungary (Coleoptera: Scarabaeoidea). Folia Historico Naturalia Musei Matraensis 30: 215–225.

Fabricius JC (1775) Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Officina Libraria Kortii, Flensburgi et Lipsiae [Flensburg and Leipzig, Germany], pp. xxxii + 832.

Johnston D (1970) Notes on a collection of Austrian Macrochelidae with the description of *Macrocheles beieri*, sp. n. Annalen des Naturhistorischen Museums in Wien 74: 145–150.

Karg W (1993) Acari (Acarina), Milben Parasitiformes (Anactinochaeta) Cohors Gamasina Leach. Raubmilben. Jena, Stuttgart, New York Gustav Fischer Verlag, 96–114.

Kontschán J (2005) Contribution of the Macrochelidae fauna of Hungary (Acari: Mesostigmata). Folia Historico Naturalia Musei Matraensis 29: 77–80.

Kontschán J (2006) Check list of the Hungarian Mesostigmatid mites. I–II. Zerconidae and Macrochelidae. Folia Historico Naturalia Musei Matraensis 30: 129–136.

Kontschán J (2015) Atkák mikroskálán: Akarológiai vizsgálat egy kis kertben. (Mites on microscales: acarological studies in a small garden.) Integrált termesztés a kertészeti és szántóföldi kultúrákban 32: 63–69.

Kontschán J, Ács A, Neményi A (2014) Adatok a magyarországi bambuszok atkáihoz. (Data to the mites of the Hungarian bamboo brushes). Növényvédelem 50(7): 339–343.

Kontschán J, Ács A, Wang GQ, Neményi A (2015a) New data to the mite fauna of Hungarian bamboo plantations. Acta Phytopathologica et Entomologica Hungarica 50(1): 77–83. https://doi.org/10.1556/038.50.2015.1.7

Kontschán J, Ács A, Suták A, Kiss B (2015b) A hazai autópályák pihenőinek atkái. Akarologiai tanulmányok 4. (Mites of the rest stops of the Hungarian motorways. Acarological studies 4.). StormingBrain Kiadó, Budapest, 124 pp.

Kontschán J, Ács A, Suták A (2016) Contribution to the soil-dwelling mite fauna of the Hungarian agroecosystems (Acari). Acta Phytopathologica et Entomologica Hungarica 51(1): 133–143. https://doi.org/10.1556/038.51.2016.1.12

Mašán P (2003) Macrochelid Mites of Slovakia (Acari, Mesostigmata, Macrochelidae). Bratislava, Institute of Zoology, Slovak Academy of Sciences, 149 pp.

Müller J (1860) Die Insektenepizoen mährischen Fauna. Jahresbericht der mährisch-schlesische Gesellschaft, Brünn, 1859, 157–184.

Özbek HH, Bal DA (2013) Three new species of the genus *Nothrholaspis* (Acari: Macrochelidae) from the Kelkit Valley, Turkey. Zootaxa 3635 (1): 40–50. https://doi.org/10.11646/zootaxa.3635.1.4

Rozner I (2001) Somogy megye dögbogár, sutabogár és lemezescsápú bogár faunája (Coleoptera: Silphidae, Histeridae, Lamellicornia). (Carrion, steel and lamellicorn beetle fauna of Somogy county (Coleoptera: Silphidae, Histeridae, Lamellicornia.) Natura Somogyiensis 1: 161–167.

Salmane I, Kontschán J (2005) Soil Gamasina Mites (Acari, Parasitiformes, Mesostigmata) from Hungary. I. Latvijas Entomologs 42: 39–44.

Salmane I, Kontschán J (2006) Soil Mesostigmata Mites (Acari: Parasitiformes) from Hungary II. Latvijas Entomologs 43: 14–17.

Vitzthum HG (1930) Acarologische Beobachtungen. 14. Reihe. Zoologischer Jahrbücher, Abteilung für Systematik 59: 282–348.

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RESEARCH ARTICLE

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Barsine podbolotskayae sp. n. from Flores Island, Lesser Sunda Archipelago, Indonesia (Lepidoptera, Erebidae, Arctiinae)

Vitaly M. Spitsyn[1,2], Ivan N. Bolotov[1,2]

1 *Northern Arctic Federal University, Severnoy Dviny Emb. 17, 163002, Arkhangelsk, Russia* **2** *Federal Center for Integrated Arctic Research of the Russian Academy of Sciences, Northern Dvina Emb. 23, 163000, Arkhangelsk, Russia*

Corresponding author: *Vitaly M. Spitsyn* (vitalik91993@yandex.ru)

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Abstract

Herein *Barsine podbolotskayae* **sp. n.** (Lepidoptera: Erebidae: Arctiinae) is described from Flores Island, Lesser Sunda Archipelago, Indonesia. This local endemic species externally resembles *Barsine exclusa* Butler, 1877 from Sundaland and the Andaman Islands but differs by marking patterns and male genitalia structure.

Keywords

East Nusa Tenggara, island biogeography, lichen moths, Wallacea

Introduction

The Lesser Sunda Archipelago is a vast island group, which includes several large islands such as Timor, Sumbawa, Sumba, and Flores. This archipelago together with Sulawesi and the Moluccas is a part of the Wallacea. This region consists of two mostly distinct transition zones between the Oriental and Australasian biotas, i.e., a humid forest northerly zone from the Philippines to Sulawesi and the Moluccas, and a seasonal forest and savannah southerly zone along the Lesser Sunda chain from Java to Timor (Holloway and Jardine 1968). Contacts between the two zones has mostly been through Sulawesi, whose fauna is mainly Oriental, whereas the Moluccas are predominantly Australasian (Holloway 2003). The major discontinuity between the Oriental and Australasian Lepidoptera is Weber's Line of Faunal Balance that runs between Sulawesi and the Moluccas and then south to east of Timor (Holloway and Jardine 1968). There is a continuum of species turnover from Oriental to Australasian affinity from Java to Timor, but there is also some endemism within the Lesser Sunda Islands (Holloway 2003; Lohman et al. 2011; Bolotov et al. 2017, 2018; Spitsyn et al. 2018).

The lichen moth genus *Barsine* Walker, 1854 (Lepidoptera: Erebidae: Arctiinae) (type species: *Barsine defecta* Walker, 1854) is widespread across the Oriental tropics from the mainland to the Lesser Sunda Islands and Moluccas, but it is replaced by *Cyme* Felder, 1861, another morphologically similar and possibly related genus, in New Guinea and Australia (Holloway 2001). To the best of our knowledge, published occurrences of any species of *Barsine* from Flores are lacking. As for the entire Lesser Sunda Islands, *B. dohertyi* (Rothschild, 1913) is the only known member of this group that has been described from Sumbawa (Rothschild 1913; Holloway 1982, 2001). Additionally, *B. sanguitincta* (Hampson, 1900) is the only known species of the genus from the Moluccas (Hampson 1900; Holloway 1982, 2001).

The present short correspondence describes *Barsine podbolotskayae*, a species new to science that occurs in Flores.

Materials and methods

This study is based on the materials from the collection of the Russian Museum of Biodiversity Hotspots (RMBH thereafter) of the Federal Center for Integrated Arctic Research of the Russian Academy of Sciences, Arkhangelsk, Russia. The genitalia were dissected and mounted on a glass slide with Histofluid® (Paul Marienfeld GmbH & Co., Germany). The images of specimens were taken with a Canon EOS 650D camera (Canon, Tokyo, Japan). The photos of the genitalia were obtained using two research stereomicroscopes (SteREO Discovery.V8 and AXIO Zoom.V16, Carl Zeiss, Germany).

Results

Barsine podbolotskayae sp. n.

http://zoobank.org/43B36AA3-CA81-4AA8-A163-FD55288A6743
Figs 1–3

Type material. Holotype: ♂, INDONESIA, Lesser Sundas, East Nusa Tenggara, Flores Island: Sano Ngoang Lake, camp site, secondary mountain forest with old nutmeg trees on a hill slope, 8°42'33.50"S, 119°59'51"E, 21–22 January 2015, Bolotov leg., in RMBH (voucher no. Sph0682). Paratypes: 3♂♂, 2♀♀, same data as holotype, all in RMBH (vouchers nos. Sph0683, Sph0731, Sph0732, Sph0733 and Sph0734).

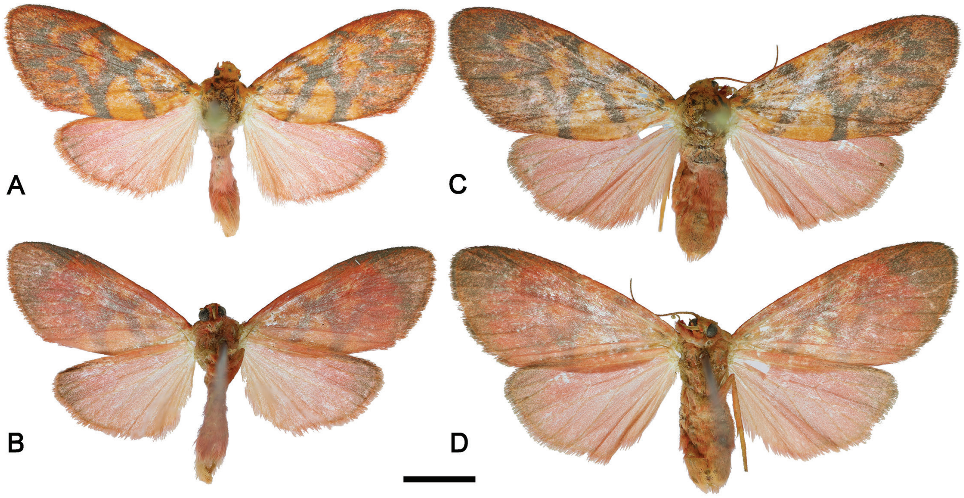

Figure 1. Type specimens of *Barsine podbolotskayae* sp. n., Flores Island, Indonesia. **A** Holotype male (upperside) **B** Holotype male (underside) **C** Paratype female (upperside) **D** Paratype female (underside). Scale bar 5 mm (photographs Vitaly M. Spitsyn).

Diagnosis. The new species externally resembles *Barsine exclusa* Butler, 1877, similarly patterned on forewing, both showing the outer boundary of the discal patch of ground color lined by W-shaped postmedial line. However, the new species differs by the lack of a discal spot within that patch (vs presence of a gray discal spot), its bright crimson-colored hindwing (vs pinkish-yellow or pinkish-white), and stronger developed gray markings on forewing, with broad dark shading beyond the postmedial line (vs weaker developed gray markings and lack of broad dark terminal shading). The male of *B. podbolotskayae* sp. n. can be distinguished from those of all other known species of *Barsine*, including *B. exclusa*, by a dorsally directed, robust, spine-like central costal process of the valve and a bundle of dorsally directed, long setae proximal to it (vs lack of such features). It differs from *B. exclusa* also by the narrower neck of cucullus, this rounded and apically setose (vs wider neck of acutely pointed cucullus).

Description. Male. Wingspan 22–24 mm, forewing length 11–12 mm (N = 4). Eye black; antenna red dorsally and gray ventrally; frons red-orange, vertex orange with black spot in the middle; labial palpus stout, straight and short (equal to eye diameter), brick red. Thorax dorsally orange-red; patagium and tegula brick-red with black spot in the middle; underside and legs crimson. Forewing upperside brick red, with a few indistinct gray dots in basal area, angled antemedial and medial wide gray lines joined at middle in shape of 'X' mark (Fig. 1A). Outer boundary of discal patch of ground color W-shaped due to inwardly projected jags from postmedial line, this gray too; distal field with extended dark gray suffusion and some indistinct gray dots. Hindwing upperside uniformly bright crimson. Underside of both wings crimson-red, with brownish shading near apex (Fig. 1B). Abdomen light crimson.

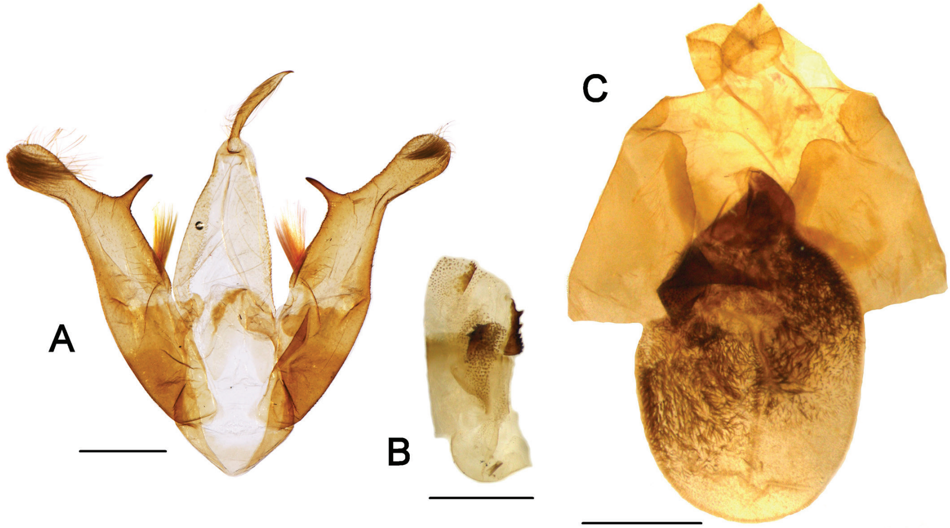

Figure 2. Male and female genitalia of *Barsine podbolotskayae* sp. n., Flores Island, Indonesia. **A** Male genitalia (holotype) **B** Aedeagus (holotype) **C** Female genitalia (paratype). Scale bar 1 mm (photographs Vitaly M. Spitsyn).

Female. Wingspan 27–28 mm, forewing length 13–14 mm (N = 2). Patterned as in male (Fig. 1C–D).

Male genitalia. Tegumen comparatively long and broad; saccus broad, short, V-shaped (Fig. 2A). Valva narrow, elongated; costa with single robust, straight spine-like central process, approximately perpendicular, and subbasal bundle of stiff, dorsally directed long setae; neck of cucullus narrower than cucullus, this membranous, rounded and distally setose; sacculus weakly developed, consisting of a fold on the inner surface of the valva. Uncus long and thin, laterally compressed, broadened subapically and slightly curved, with spine-like apex. Scaphium narrow. Juxta broad, U-shaped, weakly sclerotized. Aedeagus short and broad; vesica broad, with two sclerotised plates bearing numerous teeth, and two granulose fields (Fig. 2B).

Female genitalia. Ostium bursae broad, funnel-shaped, sclerotized, fused with the seventh sternite; antrum not traced; ductus bursae very short, sclerotized (Fig. 2C). Bursa copulatrix elliptical, thickly covered with long spinules in medial and posterior sections, with strongly sclerotized cervix. Apophyses anteriores and posteriores of similar length, long and thin. Papillae anales (ovipositor lobes) broad, with rounded edges, covered densely with long fine setae.

Etymology. This new species is named in memory of Dr. Marina V. Podbolotskaya (1956–2014), a well-known Russian entomologist.

Distribution. Flores Island, Lesser Sunda Archipelago; only known from the type locality (Fig. 3).

Conservation status. The new species appears to be Critically Endangered (CR B1a) because it is known to exist at only a single location.

Figure 3. Type locality of *Barsine podbolotskayae* sp. n.: Flores Island, shore of Lake Sano Nggoang, secondary mountain forest with old nutmeg trees on a hill slope (photographs M. Albarran Valle).

Remarks. Here we placed *B. podbolotskayae* sp. n. within the genus *Barsine* but its placement is in need of further investigation. Features of the costal margin of valva have so far not been found in any other known members of the genus (cf. Černý and Pinratana 2009; Holloway 2001; Bucsek 2012; Volynkin and Černý 2017a, b, c, 2018), so that solely on these grounds *B. podbolotskayae* sp. n. might represent another genus. Nonetheless, we hesitate to erect a new genus for this species pending upon a thorough review of *Barsine*, *Cyme* and other closely related genera, whose systematic relationships are still largely unclear and need to be phylogenetically assessed (Holloway 2001; Volynkin and Černý 2017c).

Discussion

The fauna of the Lesser Sunda Islands comprises two species of *Barsine*: *B. podbolotskayae* sp. n. (Flores) and *B. dohertyi* (Sumbawa). Holloway (2001) noted that that the *Barsine* is a genus with clear affinities to the mainland Southeast Asia and Sundaland, the species richness of which decreases abruptly east of the Wallace Line. Mainland Southeast Asia is considered the most probable evolutionary hotspot of this group (Holloway 2001; Černý and Pinratana 2009; Bucsek 2012). Possible sister relationships between

Barsine and *Cyme* (Holloway 2001) are in need of future research using a molecular approach as this may uncover putative ancient connections between the Oriental and Australasian faunas (Holloway 2003).

Acknowledgements

We thank the Associate Editor Dr. Alberto Zilli, Dr. Jeremy Holloway, and an anonymous reviewer for their helpful and insightful comments on the manuscript. This study was supported by the Russian Ministry of Education and Science (project no. 6.2343.2017/4.6), Federal Agency for Scientific Organizations (project no. 0409-2015-0143), and Northern Arctic Federal University. We are grateful to Mr. Mikel Albarran Valle (Labuan Bajo, Indonesia) for his great help during this study.

References

Bolotov IN, Kondakov AV, Spitsyn VM, Gofarov MY, Kolosova YS (2017) *Leptocneria vinarskii* sp. nov. (Lepidoptera: Erebidae: Lymantriinae), an overlooked Wallacean lineage of the Australian genus. Scientific Reports 7: 12430. https://doi.org/10.1038/s41598-017-12797-3

Bolotov IN, Kondakov AV, Spitsyn VM (2018) A review of tiger moths (Lepidoptera: Erebidae: Arctiinae: Arctiini) from Flores Island, Lesser Sunda Archipelago, with description of a new species and new subspecies. Ecologica Montenegrina 16: 1–15.

Bucsek K (2012) Erebidae, Arctiinae (Lithosiini, Arctiini) of Malay Peninsula – Malaysia. Slovakia: Bratislava, 170 pp.

Černý K, Pinratana A (2009) Arctiidae. Moths of Thailand 6: 1–283.

Hampson GF (1900) Catalogue of the Arctiadae (Nolinae, Lithosinae) in the collection of the British Museum. Catalogue of the Lepidoptera Phalaenae in the British Museum 2: 1–589.

Holloway JD (1982) Taxonomic Appendix. In: Barlow, H.S. An Introduction to the Moths of South East Asia. The author, Kuala Lumpur, 174–271.

Holloway JD (2001) The Moths of Borneo: family Arctiidae, subfamily Lithosiinae. Malaysian Nature Journal 55: 279–458.

Holloway JD, Jardine N (1968) Two approaches to zoogeography: a study based on the distributions of butterflies, birds and bats in the Indo-Australian area. Proceedings of the Linnean Society of London 179: 153–188. https://doi.org/10.1111/j.1095-8312.1968.tb00975.x

Holloway JD (2003) Biological images of geological history: through a glass darkly or brightly face to face? Journal of Biogeography 30: 165–179. https://doi.org/10.1046/j.1365-2699.2003.00826.x

Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PK, Shih HT, Carvalho GR, von Rintelen T (2011) Biogeography of the Indo-Australian archipelago. Annual Review of Ecology, Evolution, and Systematics 42: 205–226. https://doi.org/10.1146/annurev-ecolsys-102710-145001

Rothschild W (1913) New Lithosianae. Novitates Zoologicae 20 (1): 192–226.

Spitsyn VM, Kondakov AV, Bolotov NI, Thi Pham N, Gofarov MY, Bolotov IN (2018) DNA barcoding unravels contrasting evolutionary history of two widespread Asian tiger moth species during the Late Pleistocene. PLoS ONE 13: e0194200. https://doi.org/10.1371/journal.pone.0194200

Volynkin AV, Černý K (2017a) A review of the *Barsine obsoleta* species-group with description of a new species from Vietnam (Lepidoptera, Erebidae, Arctiinae). Zootaxa 4254: 188–200. https://doi.org/10.11646/zootaxa.4254.2.2

Volynkin AV, Černý K (2017b). Revision of the *Barsine cardinalis-anomala* 'species-complex' (Lepidoptera, Erebidae, Arctiinae). Zootaxa 4358: 441–461. https://doi.org/10.11646/zootaxa.4358.3.3

Volynkin AV, Černý K (2017c) On the taxonomy of the genus *Barsine* Walker, 1854 (Lepidoptera: Erebidae: Arctiinae). Far Eastern Entomologist 346: 17–32. https://doi.org/10.25221/fee.346.3

Volynkin AV, Černý K (2018) Revision of the *Barsine zebrina* species-complex, with description of three new species (Lepidoptera, Erebidae, Arctiinae, Lithosiini). Zootaxa 4402: 339–352. https://doi.org/10.11646/zootaxa.4402.2.6

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Three new genera of acidocerine water scavenger beetles from tropical South America (Coleoptera, Hydrophilidae, Acidocerinae)

Jennifer C. Girón[1], Andrew Edward Z. Short[1]

[1] *Department of Ecology & Evolutionary Biology, and Division of Entomology, Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA*

Corresponding author: *Jennifer C. Girón* (jcgiron@ku.edu; aezshort@ku.edu)

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Abstract

Recent collecting efforts in the Neotropics have led to the discovery of numerous new species and lineages of aquatic beetles. Here, three new genera are described to accommodate fifteen new species of water scavenger beetles of the subfamily Acidocerinae from northern South America: *Crucisternum* **gen. n.** for *C. escalera* **sp. n.** (Venezuela), *C. ouboteri* **sp. n.** (Guyana, French Guiana, Suriname, Venezuela), *C. queneyi* **sp. n.** (French Guiana), *C. sinuatus* **sp. n.** (Brazil), *C. toboganensis* **sp. n.** (Venezuela), *C. vanessae* **sp. n.** (Suriname), and *C. xingu* **sp. n.** (Brazil); *Katasophistes* **gen. n**. for *K. charynae* **sp. n.** (Peru), *K. cuzco* **sp. n.** (Peru), *K. merida* **sp. n.** (Venezuela) and *K. superficialis* **sp. n.** (Ecuador); and *Nanosaphes* **gen. n.** for *N. castaneus* **sp. n.** (Brazil), *N. hesperus* **sp. n.** (Suriname), *N. punctatus* **sp. n.** (Guyana), and *N. tricolor* **sp. n.** (Guyana, Suriname). It was also found that the monotypic Neotropical endemic genus *Dieroxenus* Spangler, 1979, **syn. n.** is congeneric with *Chasmogenus* Sharp, 1882 resulting in the single new combination *Chasmogenus cremnobates* (Spangler, 1979), **comb. n.**. *Katasophistes merida* **sp. n.** is known exclusively from seepage habitats, while the remaining taxa described herein are primarily associated with the margins of densely forested streams. Diagnoses, illustrations, distribution maps, and habitat summaries are provided for all new genera and species. A key to the genera of Acidocerinae of the New World is provided.

Resumen

Recientes esfuerzos de colecta en el neotrópico han llevado al descubrimiento de numerosas especies y linajes nuevos de escarabajos acuáticos. Aquí se describen tres géneros nuevos, para acomodar quince especies nuevas de escarabajos acuáticos de la subfamilia Acidocerinae, del norte de Suramérica: *Crucisternum* **gen. n.** para *C. escalera* **sp. n.** (Venezuela), *C. ouboteri* **sp. n.** (Guyana, Guyana Francesa, Surinam, Venezuela), *C. queneyi* **sp. n.** (Guyana Francesa), *C. sinuatus* **sp. n.** (Brasil), *C. toboganensis* **sp. n.** (Venezuela), *C. vanessae* **sp. n.** (Surinam), y *C. xingu* **sp. n.** (Brasil); *Katasophistes* **gen. n**. para *K. charynae* **sp. n.** (Perú), *K. cuzco* **sp. n.** (Perú), *K. merida* **sp. n.** (Venezuela) y *K. superficialis* **sp. n.** (Ecuador); y *Nanosaphes* **gen. n.** para *N. castaneus* **sp. n.** (Brazil), *N. hesperus* **sp. n.** (Surinam), *N. punctatus* **sp. n.** (Guyana), y *N. tricolor* **sp. n.** (Guyana, Surinam). También se encontró que el género *Dieroxenus* Spangler, 1979, **syn. n.**, el cual es monotípico, neotropical y endémico, es congenérico con *Chasmogenus* Sharp, 1882, lo que resulta en la nueva combinación *Chasmogenus cremnobates* (Spangler, 1979), **comb. n.**. *Katasophistes merida* **sp. n.** se conoce exclusivamente de hábitats higropétricos, mientras que los taxa restantes que se describen aquí, están primordialmente asociados con los márgenes de corrientes densamente forestadas. Diagnosis, ilustraciones, mapas de distribución y un resumen de los hábitats, son provistos para todos los géneros y especies nuevas. Se provee además una clave para la identificación de géneros de Acidocerinae del nuevo mundo.

Keywords

aquatic beetles; new species; taxonomy; seepage habitat

Introduction

Recent fieldwork in northern South America has significantly expanded our knowledge of water beetle diversity, not only in terms of the number of species, but also in illuminating the extraordinary diversity of habitats that they occupy (Short 2018). In particular, many new apparent forms of the water scavenger beetle subfamily Acidocerinae have been identified from a range of habitats from seepages to forest streams to savanna ponds. The Acidocerinae presently contains 14 genera and about 300 species (Short and Fikáček 2011, 2013). Although they are distributed worldwide, most acidocerine species occur in tropical regions. Four new Neotropical genera have already been described in the last twenty years: *Quadriops* Hansen, 1999, *Globulosis* García, 2001, *Tobochares* Short & García, 2007, and *Radicitus* Short & García, 2014. An ongoing review of the phylogeny and generic concepts within the subfamily has led to the discovery of yet more taxa that cannot be accommodated within existing genera. Here we describe three of these new genera to accommodate fifteen new species from tropical South America. In the course of this work we also discovered a new generic junior synonym, which we formally designate as well.

Materials and methods

Depositories of examined material:

CBDG	Center for Biological Diversity, University of Guyana, Georgetown
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (N. Hamada)

MALUZ	Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela (J. Camacho, M. García)
MIZA	Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (L. Joly)
MNHN	Muséum National d'Histoire Naturelle, Paris, France (A. Mantilleri)
NHMUK	The Natural History Museum, London, United Kingdom (formerly British Museum (Natural History BMNH; M. Barclay, C. Taylor)
NZCS	National Zoological Collection of Suriname, Paramaribo (P. Ouboter, V. Kadosoe)
PQPC	Personal collection of Pierre Queney, Paris, France.
PUCE	Pontificia Universidad Católica del Ecuador, Quito, Ecuador (C. Kiel)
SEMC	Snow Entomological Collection, University of Kansas, Lawrence, KS (A. Short)
USNM	U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC (C. Micheli).

Over 650 specimens were examined. Specimen preparation and examination methods are identical to those given in Girón and Short (2017). Dissected male genitalias were packed in microvials with glycerin and pinned under the specimens, except for the species of *Nanosaphes*, for which each minute genitalia was glued onto the specimen point using alcohol soluble translucent glue.

Descriptive sequence and morphological terminology largely follows Hansen (1991) except for the use of meso- and metaventrite instead of meso- and metasternum, and abdominal ventrites instead of abdominal sternites (see Lawrence and Ślipiński 2013). Terms for the ventral surface of head follows Komarek (2004). Terminology for the metafurca follows Velázquez de Castro (1998).

Descriptions of genera and species are organized in alphabetical order, whereas in the habitus figures species are grouped by similarity for ease of comparison.

All specimen data which can be searched by species and/or collecting event are available online through the Collection Resources for Aquatic Coleoptera (CReAC) portal at http://creac.kubiodiversityinstitute.org/collections/.

Results

List of species and their provenance

Crucisternum **gen. n.**

1. *Crucisternum escalera* **sp. n.**	Venezuela (Bolívar)
2. *Crucisternum ouboteri* **sp. n.**	French Guiana, Guyana, Suriname, Venezuela (Amazonas)
3. *Crucisternum queneyi* **sp. n.**	French Guiana
4. *Crucisternum sinuatus* **sp. n.**	Brazil (Minas Gerais, Pará)
5. *Crucisternum toboganensis* **sp. n.**	Venezuela (Amazonas)
6. *Crucisternum vanessae* **sp. n.**	Suriname
7. *Crucisternum xingu* **sp. n.**	Brazil (Pará)

Katasophistes **gen. n.**

8. *Katasophistes charynae* **sp. n.**	Peru (Madre de Dios)
9. *Katasophistes cuzco* **sp. n.**	Peru (Cuzco)
10. *Katasophistes merida* **sp. n.**	Venezuela (Mérida)
11. *Katasophistes superficialis* **sp. n.**	Ecuador (Pastaza)

Nanosaphes **gen. n.**

12. *Nanosaphes castaneus* **sp. n.**	Brazil (Pará)
13. *Nanosaphes hesperus* **sp. n.**	Guyana, Suriname
14. *Nanosaphes punctatus* **sp. n.**	Guyana, Suriname
15. *Nanosaphes tricolor* **sp. n.**	Guyana, Suriname

Taxonomy

Crucisternum gen. n.

http://zoobank.org/9235AE60-8431-4ECB-9C93-F13D4C663F9F

Figs 1–8

Type species. *Crucisternum ouboteri.*

Differential diagnosis. Small beetles, total body length 2.0–2.5 mm, width 1.1–1.4 mm. Color orange brown to dark brown. Body shape elongated oval in dorsal view; moderately convex in lateral view (see Figs 1–3). Antennae with nine antennomeres (e.g., Fig. 2C). Maxillary palps curved inward, moderately long (e.g., Fig. 2D). Elytra without sutural striae; serial punctures, ground punctures and systematic punctures similar in size and degree of impression, either shallow or rather sharply marked; all punctures seemingly arranged in rows; outer margins of elytra slightly flared. Prosternum with a well-developed median longitudinal carina (e.g., Fig. 3B). Posterior elevation of mesoventrite with a strongly produced, anteriorly pointed transverse ridge, longitudinally carinate (Figs 4A, 5A). Posterior femora glabrous at most along apical fifth. Fifth abdominal ventrite apically rounded, truncate or slightly emarginate, without stout setae (e.g., Figs 1G, 4C, 5B).

Although *Crucisternum* is generally unremarkable dorsally from other small-bodied acidocerines, several sternal features easily separate the genus from all others. Within the Acidocerinae, the strongly-developed prosternal carina found in the genus is extremely rare, occurring only in the Afrotropical genus *Acidocerus*. Additionally, the strongly produced postero-medial projection of the mesoventrite, formed by the fusion of both transverse and longitudinal ridges (Figs 4A, 5A), is unique in the subfamily. It is most likely to be confused in samples as a small *Chasmogenus*, but can also easily be distinguished from that genus by the lack of a sutural stria.

Description. Body elongate oval, moderately convex, orange brown to dark brown in color, sometimes slightly paler on ventral surface and appendages. **Head.** Frons and clypeus (e.g., Fig. 2D) with moderately marked ground punctures, irregularly and rather densely distributed over the surface, accompanied by scattered seta-bearing systematic punctures, particularly noticeable on anterior area of frons; surface between punctures smooth and shiny; anterior corners of clypeus roundly angulated; anterior margin of clypeus widely roundly emarginate. Eyes subquadrate in dorsal view. Labrum wide, fully exposed, nearly half as long, and collinear to perpendicular to clypeus (e.g., Fig. 2H); dorsal surface slightly convex, with scattered fine punctures; anterior margin roundly bent inwards, mesally emarginate and with tiny denticles along emargination; lateral and anterior margins fringed by rather long setae. Temporae densely covered by very short and fine setae (hydrofuge pubescence). Mentum parallel sided, with lateral oblique longitudinal ridges; anterior margin with wide, deep, concave median impression marked by a u- or bell-shaped transverse carina. Submentum sunken and pubescent at base, glabrous, shiny and ascending at apex; ocular ridge well-developed (e.g., Fig. 1G). Maxilla (see Fig. 2C) with ventral surface of cardo and stipes smooth and shiny, with scattered and shallow punctures; outer dorsal margin of palpifer with a row of stiff, decumbent, curved, spiniform setae; limit between cardo and stipes oblique; maxillary palps brown to orange, longer than antennae, with palpomere I usually darker at base, gradually paler towards apex; apex of palpomere 3 bearing sensilla. Mandibles with apex bifid (examined in *C. ouboteri* and *C. sinuatus*). Labial palps yellowish to brown, usually shorter than mentum, at most nearly as long, dorsoventrally flattened; palpomere 2 with outer margin convex apicad of midpoint, sometimes with one (preapical) or two (one median, one preapical) setae on outer surface; palpomere 3 digitiform, with a long subapical seta on outer corner. Antennae (see Fig. 2C) with 9 antennomeres, either similar or paler than general coloration of head; antennomere 1 anteriorly projected near base, at most reaching midpoint of ventral surface of eye (not reaching cardo-stipes joint), nearly 1.7–2.5-times longer than antennomere 2; antennomere 2 nearly as long as antennomeres 3–5 combined; antennomere 6 forming a well differentiated, symmetric cupule; antennomeres 7–9 slightly flattened, forming a loosely articulated, pubescent club (antennomere 8 shortest, 9 longest); apex of antennomere 9 with longer setae than general pubescence of club. **Thorax.** Pronotum widest at base, narrowed anteriorly, surface evenly convex; ground punctation moderate, uniformly dense, with surface between punctures smooth and shiny; seta bearing systematic punctures forming paired anterolateral semicircles. Scutellar shield of moderate size, triangular, nearly as long as wide, with punctation as in pronotum. Prosternum (e.g., Fig. 2C) nearly as long as 2/3 the length of a procoxa, with a strong median longitudinal carina; anterior margin of prosternum mesally projected as a wide triangle; surface of prosternum usually convex and with scarce crenulations, with scattered, rather long, fine setae; intercoxal process projected from posterior margin of procoxal cavities, triangularly shaped in outline, mesally longitudinally carinate. Mesoventrite (Figs 4A, 5A) not fused to mesepisterna, with anterior margin nearly 0.3-times as wide as anterior margin of mesepisternum; anterior rib of mesoventrite bearing a medial teardrop-shaped, pearlescent macula; posterior elevation of mesoventrite with a strongly produced, anteriorly pointed transverse ridge, longitudinally carinate, bearing scarce, rather long setae; surface of mesoventrite reticulated for the most part, with an anteromedial depression, and posterolateral smooth and glabrous areas; mesepisternum obliquely widely concave, with reticulated surface; mesepimeron trapezoid, with reticulate and pubescent surface. Mesofurca (examined in *C. ouboteri*) with short arms, 0.8-times length of mesocoxae; apical half of arms free, irregularly explanate at apex. Metaventrite mesally elevated, with elevation smooth and glabrous (Fig. 5A), rather narrow anteriorly, wide and flat posteriorly; surface of metaventrite densely pubescent, except for median and postero-lateral glabrous areas. Metepisterna approximately 3-times longer than wide, narrowing only at posterior end. Metepimeron triangular and acute posteriorly. Metafurca (examined in *C. ouboteri*, Fig. 4B) 1.45-times wider than long, with furcal arms (fa) slightly longer than stalk (s); stalk triangular (wider near the crux (c), gradually narrowing ventrally), with paired longitudinal keels extending along basal third of posterior face, fusing together towards crux, with a well-developed median keel on anterior face extending to anterior margin of dorsal sheets (ds); outer margins of stalk diverging from basal third towards distal third of furcal arms; furcal arms somewhat trapezoid, with apex (hemiductus (h)) only slightly explanate, with apex pointing obliquely; anterior tendons (at) inserted at mid length of dorsal edge of furcal arms; dorsal sheaths well-developed, wider than widest point of lateral sheaths (ls). **Elytra.** Surface even (without elevations or depressions), without sutural striae; serial punctures, ground punctures and systematic punctures similar in size and degree of impression, either shallow or rather sharply marked; all punctures seemingly arranged in rows; serial punctures not impressed into striae; seta bearing systematic punctures rather scarce; elytral margins slightly flared. Epipleura well-developed, surface slightly oblique, with sparse setae and irregular sculpture, anteriorly wide, gradually narrowing posteriorly, extending up to line of posterior margin of first abdominal ventrite; inner margin of epipleura with small indentation articulating anterior outer corner of metepisternum; pseudepipleura well-developed, perpendicularly positioned, nearly half as wide as anterior portion of epipleura, extending along entire outer margin of elytra. Hind wings well-developed. **Legs.** All femora with dense pubescence, except on at most apical fifth, in which surface is glabrous, shiny and slightly reticulated; all femora antero-posteriorly flattened; metafemora with rather weak tibial grooves. Tibiae slender, rather cylindrical; well-developed spines along pro- and mesotibiae, smaller and sparser in metatibiae; protibiae with a median longitudinal row of spathulate setae along anterior surface. All tarsi with five tarsomeres, bearing long apical hair-like setae on dorsal face, and two lateral rows of spines and/or hair-like spines on ventral face of tarsomeres 2–4; tarsomeres 1–4 similar in size and shape; tarsomere 5 approximately as long as tarsomeres 3–4 combined, without spines on ventral face; claws rather large, curved; empodium well-developed, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, medially convex; all ventrites with uniform, dense, fine pubescence; posterior margin of fifth ventrite uniformly rounded, truncate or slightly emarginate, without thick, flat spine-like setae (Figs 4C, 5B). Aedeagus (Fig. 6) with basal piece between 0.2 and 0.25-times the length of parameres; apical half of median lobe wider to narrower than a paramere; median lobe with well-developed lateral basal apodemes, and acute to narrowly rounded apex; parameres nearly as long as median lobe, with outer margins usually sinuate, usually with setae at apex; gonopore situated distad of mid length of median lobe.

Larvae. The immature stages are unknown.

Etymology. Named from the Latin *crucis*, meaning cross, combined with the word sternum, in reference to the conspicuous cruciform elevation of the mesoventrite in species of the genus. To be treated as masculine.

Distribution. Brazil, Guyana, French Guiana, Suriname, Venezuela. See Fig. 7.

Biology. Without exception, all species of the genus are associated with forested streams, usually along margins that contain ample detritus. A single specimen of *C. ouboteri* was collected at a black light trap.

Characters of taxonomic importance for *Crucisternum*. The external morphology of *Crucisternum* is highly homogeneous across species, with characters of the aedeagus being the most reliable for species identification, in particular for those with sharply marked elytral punctures. Unassociated female specimens may not be able to be authoritatively identified in some cases.

Punctation. Two groups of species can be recognized by the degree of impression of the elytral ground punctures: *Crucisternum toboganensis*, *C. ouboteri*, *C. queneyi*, and *C. vanessae* exhibit rather sharply marked punctures, whereas the ground punctures of *C. escalera*, *C. sinuatus*, and *C. xingu* are more shallowly impressed (compare Fig. 1A to Fig. 1E).

Coloration. The dorsal coloration of the body can be either uniform as in *C. escalera* (Fig. 1A), and *C. xingu*, or the elytra can be darker than the head and pronotum, as in *C. ouboteri* (Fig. 2A), *C. queneyi*, and *C. vanessae*. Specimens of *C. sinuatus* collected in 1986 in northern Brazil were preserved in 70% alcohol until the time of this revision, and are darker in coloration, whereas the freshly collected specimens from Minas Gerais, are paler (orange brown). It is possible that the alcohol affected the coloration of the specimens over time causing them to darken. General coloration (e.g., light vs. dark brown) should not be used exclusively as diagnostic.

Aedeagus. The basal piece is strongly reduced in *Crucisternum* (see Fig. 6). Characters of the median lobe and the parameres are diagnostic at the species level.

Key to the species of *Crucisternum*

1	Elytra with ground punctures rather sharply marked	**2**
–	Elytra with ground punctures shallowly marked	**5**
2	Aedeagus fusiform; gonopore on apical region of median lobe; aedeagus widest near midlength (Fig. 6A–C)	**3**
–	Aedeagus pear-shaped; gonopore located near midlength of median lobe; aedeagus widest near basal third (e.g., Fig. 6D–J)	**4**
3	Apical third of parameres nearly parallel-sided; outer margins of parameres slightly sinuate along apical half	***C. ouboteri***
–	Apical third of parameres gradually narrowing towards apex; outer margins of parameres nearly straight along apical half	***C. toboganensis***

4 Apical third of median lobe parallel-sided, nearly as wide as a paramere at the base of its apical third; apex of parameres pointing inwards (Fig. 6D) ...... ***C. vanessae***

– Apical third of median lobe with converging margins, narrower than a paramere at the base of its apical third; apex of parameres pointing outwards (Fig. 6J) .... ***C. queneyi***

5 Outer margins of parameres widely curved, at most slightly sinuated; median lobe constricted at midlength, continuing as a narrow and roundly pointed bar (Fig. 6I) .... ***C. escalera***

– Outer margins of parameres abruptly constricted at apical third, or nearly straight to sinuated only if median lobe gradually narrowing towards apex (Fig. 6E–H) ... **6**

6 Median lobe constricted at apical third, continuing as a narrow and roundly pointed bar; outer margins of parameres abruptly constricted at apical third, continuing nearly parallel towards apex; concavity of inner margins of parameres extending only along apical sixth (Fig. 6G, H) .... ***C. sinuatus***

– Median lobe gradually narrowing towards apex; apex of median lobe rounded; outer margins of parameres sinuate to nearly straight; concavity of inner margins of parameres extending along apical third (Fig. 6E, F) .... ***C. xingu***

Crucisternum escalera sp. n.

http://zoobank.org/8C7098E9-13C8-4EEE-88FA-C548CEB1BA23

Figs 1A–D; 6I; 7; 8E, F

Type material examined. Holotype (male): "**VENEZUELA**: Bolívar State/ 6°2'10.5"N, 61°23'57.8"W, 630 m/ Along La Escalera; 31.vii.2008/ leg. A. Short, M. García, L. Joly/ AS-08-058; rocky stream" // "Barcode/ SM00828756/ KUNHM-ENT" (MIZA). **Paratypes (2):** Same data as holotype (SEMC, 2).

Differential diagnosis. *Crucisternum escalera* is very similar to *C. sinuatus* and *C. xingu* in the shallowness of the punctation and the uniform coloration along the body. It shares with *C. sinuatus* the shape of the median lobe (constricted at midlength, continuing as a narrow and roundly pointed bar, see Fig. 6 G–I), but can be distinguished from it by the outer margins of the parameres, which are widely curved, to at most slightly sinuate (see Fig. 6I; as opposed to strongly constricted near midlength, Fig. 6G, H).

Description. Body length 2.1–2.2 mm, width 1.1–1.2 mm. General coloration uniformly orange brown (Fig. 1 A–D). Elytra with punctures shallowly marked. Aedeagus (Fig. 6I) with outer margins of parameres widely curved, at most slightly sinuated; median lobe strongly constricted near midlength, continuing as a narrow and roundly pointed bar; gonopore located at midlength of narrow apical half of median lobe.

Etymology. Noun in apposition. Named after the type locality of "La Escalera", which is the road that ascends from lowlands to the high-elevation plateau known as the "Gran Sabana".

Distribution. Venezuela (Bolívar). Collected at 630 m in elevation. See Fig. 7.

Biology. The only known series of this species was collected along the margin of a densely forested rocky stream. See Fig. 8E, F.

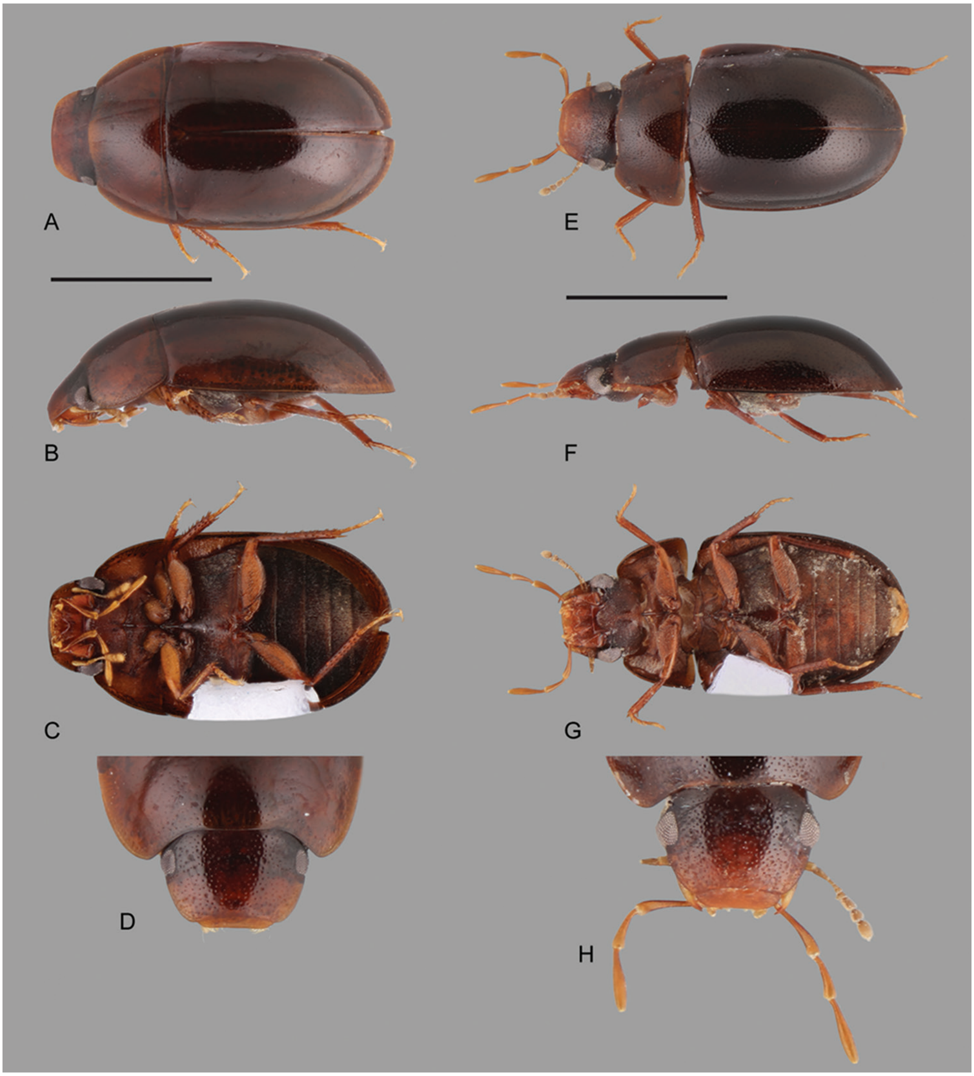

Figure 1. Habitus of *Crucisternum* spp.: **A–D** *Crucisternum escalera*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Crucisternum queneyi*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 1 mm.

Crucisternum ouboteri sp. n.

http://zoobank.org/AD02C73E-2E54-4352-96C4-584A5D6B6982

Figs 2A–D; 4; 5A, B; 6A, B; 7; 8A–C

Type material examined. Holotype (male): "**SURINAME:** Sipaliwini district/ 04°56.871'N, 55°10.911'W, 462 m/ Brownsberg Nature Park, forested/ stream with lots of detritus; leg./ Short, Maier, McIntosh; 4.viii.2012/ SR12-0804-01A" // "Barcode/ SEMC1113824/ KUNHM-ENT" (NZCS). **Paratypes (155): GUYANA: Region IX:**

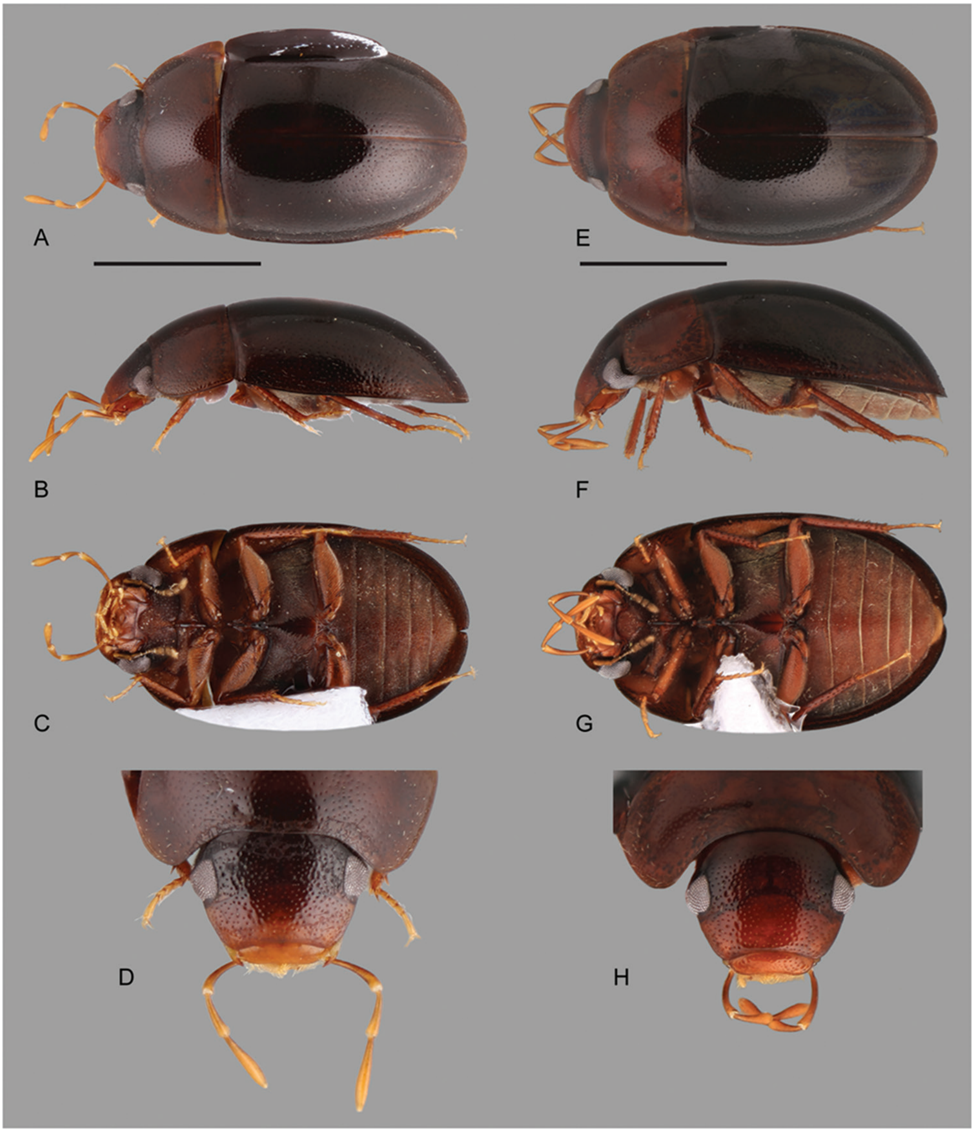

Figure 2. Habitus of *Crucisternum* spp.: **A–D** *Crucisternum ouboteri*: **A** dorsal view, **B** lateral view **C** ventral view, **D** head **E–H** *Crucisternum vanessae*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 1 mm.

"2°06.492'N, 59°13.653'W, 274 m/ Parabara, N. side of river/ small flowing forested creek/ detritus margins & leaf packs/ leg. Short, Isaacs, Salisbury/ 3.xi.2013; GY13-1103-02A" (5, SEMC). **FRENCH GUIANA: Roura:** "[Patawa: crique/ Diamant]/ 16.xi.2007/ P. Queney réc." (1, PQPC). **SURINAME: Sipaliwini district:** "2°21.776'N, 56°41.861'W, 237 m/ Camp 3, Wehepai; leg. Short &/ Kadosoe; sandy forest creek/ 4–6.ix.2010; SR10-0904-01A/ 2010 CI-RAP Survey" (2, SEMC); "N 2.97731°, W

55.38500°, 200 m/ Camp 4 (low), Kasikasima; sandy stream on trail to METS camp/ 20.iii.2012; SR12-0320-02A/ leg. A. Short; 2012 CI-RAP Survey" (27, SEMC, including DNA voucher SLE 472); same, except "sandy creek, trail to Kasikasima/ 22.iii.2012; SR12-0322-02A" (12, SEMC); "04°42.480'N, 56°13.159'W, 24 m/ Raleighfallen Nature Reserve, trail/ to Raleighfallen; creek margins/ leg. Short, McIntosh, & Kadosoe/ 27.vii.2012; SR012-0727-03A" (1, SEMC); same data as holotype (89, NZCS, SEMC, MALUZ). **VENEZUELA: Amazonas:** "Cerro de la Neblina, basecamp 140m./ 0°50'N, 66°10'W/ 18 February 1985// Berlese of leaf packs/ among rocks in small/ stream in rainforest/ P.J. & P.M. Spangler, R. Faitoute, W. Steiner" (16, USNM, MIZA); same, except "rainforest at black light/ 21.ii.1985; leg. Spangler et al." (1, USNM).

Differential diagnosis. *Crucisternum ouboteri* is very similar to *C. vanessae* and *C. queneyi* in the sharpness of the punctation (compare Fig. 2A–D to 2E–H and Fig. 1E–H). It is nearly indistinguishable from *C. toboganensis* based on external characters beyond coloration (uniform along the body in *C. toboganensis*, paler pronotum in *C. ouboteri*). *Crucisternum ouboteri* can be recognized by the fusiform aedeagus, with the apical third of the parameres parallel-sided with sinuate outer margins (Fig. 6A, B).

Description. Body length 2.0–2.4 mm, width 1.2–1.4 mm. General coloration dark brown on elytra, slightly paler on pronotum and head (Fig. 2A). Elytra with punctures rather sharply marked. Aedeagus fusiform, widest near mid length; median lobe gradually narrowing from basal fifth towards apical region; gonopore usually presented longitudinally on apical region of median lobe; apical third of parameres parallel-sided, with sinuate outer margins (Fig. 6A, B).

Etymology. Named in honor of Dr. Paul Ouboter, director of the National Zoological Collection of Suriname and leading authority on the biodiversity of Suriname. Dr. Ouboter's assistance has been invaluable in our efforts to document the water beetle fauna of the country.

Distribution. French Guiana, Guyana, Suriname, and Venezuela (Amazonas). See Fig. 7. Collected at 24 – 462 m elevation.

Biology. This species is known from densely forested streams throughout much of the Guiana Shield region of South America (e.g., Fig. 8A–C). One specimen was collected at a UV light in southern Venezuela.

Crucisternum queneyi sp. n.

http://zoobank.org/00079818-D26E-4DBE-862B-C78C7D6F6D99

Figs 1E–H; 6J; 7

Type material examined. Holotype (male): FRENCH GUIANA: Sinnamary: "[Pripris de Yiyi]/ 25.xi.2007/ P. Queney réc." (MNHN). **Paratypes (2): FRENCH GUIANA: Roura:** "[Patawa: ru]/ 19.xi.2007/ P. Queney réc." (1, SEMC); "[N2, PK 73,5: petite crique accidentée, 250m]/ 23.xi.2007/ P. Queney réc." (1, PQPC).

Differential diagnosis. *Crucisternum queneyi* is very similar to *C. ouboteri* and *C. vanessae* in the sharpness of the punctation and the general coloration of the body (compare Fig. 1E–H to Fig. 2). It can be readily recognized by the pear-shaped aedeagus (as opposed to fusiform), with simple (as opposed to broadened) margins of the apical region of the median lobe, as well as outwardly pointing apices of the parameres (see Fig. 6J).

Description. Body length 1.9–2.3 mm, width 1.0–1.1 mm. General coloration dark brown on elytra, slightly paler on pronotum and head (Fig. 1E). Elytra with punctures rather sharply marked. Aedeagus pear-shaped, widest along basal third; apex of parameres pointing outwards; apical third of median lobe narrower than a paramere at the base of its apical third, with simple converging margins; gonopore located near midlength of median lobe (Fig. 6J).

Etymology. Named after French coleopterist Pierre Queney, who collected and beautifully prepared the known specimens of this species.

Distribution. French Guiana (Roura). See Fig. 7. Collected at 250 m elevation.

Biology. This species is known from streams.

Crucisternum sinuatus **sp. n.**

http://zoobank.org/BD20616D-2360-4509-84FE-210B65E9D54E
Figs 3A–D; 6G, H; 7

Type material examined. Holotype (male): BRAZIL: Minas Gerais: Lassance, -17.83384, -44.50515, 568 m, Cachoeira da Palmeira, flotation of root mats and moss from side of waterfall and seepage, 2.iii.2018, leg. Benetti & team; BR18-0302-04A (INPA). **Paratypes (10): BRAZIL: Pará:** Rio Xingu Camp 52°22'W, 3°39'S, Altamira, ca 60km S., 3.x.1986, leg. P. Spangler & O. Flint, Colln. #6, 1st jungle stream on trail 1 (1, USNM); same, except 14.x.1986, Colln. #23, stream on left branch of trail 1 (3; SEMC, USNM); **Minas Gerais:** same data as holotype (2 INPA, 4 SEMC).

Differential diagnosis. *Crucisternum sinuatus* is very similar to *C. escalera* and *C. xingu* in the shallowness of the punctation. In addition, it can be distinguished from *C. xingu* by the aedeagus with median lobe constricted at midlength, continuing as a narrow and roundly pointed bar (see Fig. 6G, H; as opposed to gradually narrowing towards the apex, see Fig. 6E, F), and the outer margins of the parameres, which are strongly constricted at apical third, continuing nearly parallel (as opposed to nearly straight to sinuate).

Description. Body length 2.0–2.4 mm, width 1.1–1.4 mm. General coloration variable, either orange brown or uniformly dark brown (Fig. 3A–D). Elytra with punctures shallowly marked. Aedeagus with outer margins of parameres strongly constricted at apical third, continuing nearly parallel towards apex; inner margins of parameres slightly concave only along apical sixth; median lobe constricted at midlength, continuing as a narrow and roundly pointed bar (Fig. 6G, H).

Etymology. Named in reference to the abrupt constriction of the outer margins of the parameres at their apical third, with the Latin word *sinuatus* meaning bent, curved.

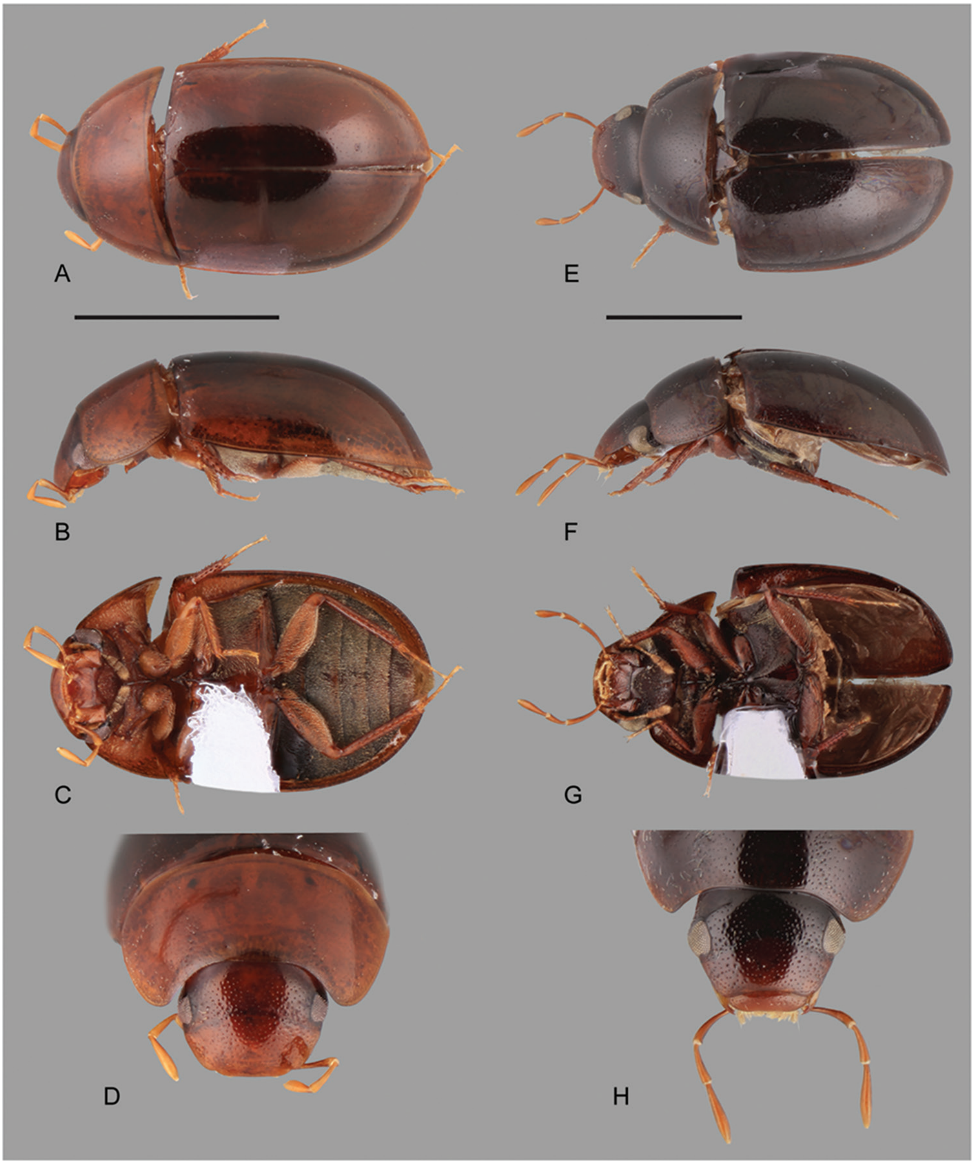

Figure 3. Habitus of *Crucisternum* spp.: **A–D** *Crucisternum sinuatus*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Crucisternum xingu*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 1 mm.

Distribution. Brazil (Minas Gerais, Pará). See Fig. 7.

Biology. The series from Lassance was collected by floating root mats and detritus that were on rock at the margin of a river and waterfall. The specimens from Altamira were collected in streams.

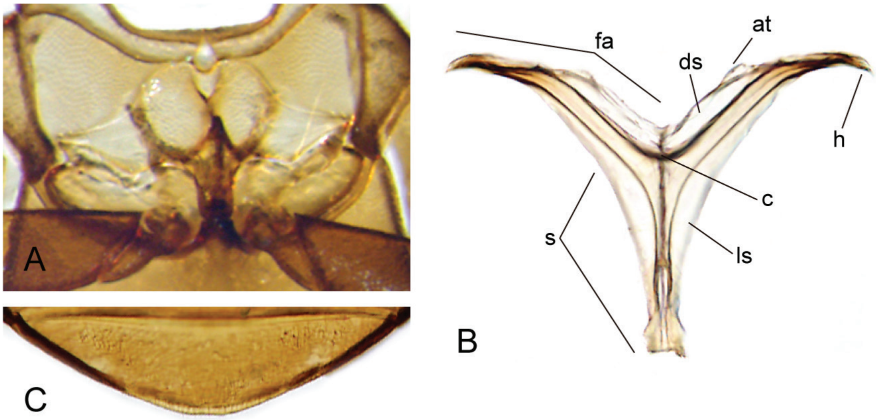

Figure 4. Thorax and abdomen of *Crucisternum ouboteri*: **A** ventral view of mesoventrite (white arrow pointing longitudinal carina and transverse ridge); **B** posterior view of metafurca: (at) anterior tendon, (c) crux, (ds) dorsal sheath, (fa) furcal arm, (h) hemiductus, (ls) lateral sheath, (s) stalk; **C** fifth abdominal ventrite.

Crucisternum toboganensis **sp. n.**

http://zoobank.org/D6CCF6F9-9452-4074-A71C-B8891F894008

Figs 6C; 7

Type material examined. Holotype (male): VENEZUELA: Amazonas: "Puerto Ayacucho (40 km S)/ El Tobogán, Caño Coromoto/ 26 January 1989/ CL2388, John T. Polhemus/ side stream/ head of lower falls" (USNM) **Paratypes (2):** Same data as holotype (1, USNM); same locality but leg. M. Balke (1, SEMC; DNA voucher SLE 734).

Differential diagnosis. *Crucisternum toboganensis* is nearly indistinguishable from *C. ouboteri* based on external characters beyond coloration (uniform along the body in *C. toboganensis*, paler pronotum in *C. ouboteri*). They can be recognized by characters of the aedeagus: the apical third of the parameres gradually narrow towards the apex, with straight outer margins in *C. toboganensis* (Fig. 6C), whereas in *C. ouboteri* the apical third of the parameres is parallel-sided and has sinuate outer margins (Fig. 6A, B).

Description. Body length 2.1–2.4 mm, width 1.2–1.3 mm. General coloration uniformly brown along body regions. Elytra with punctures rather sharply marked. Aedeagus (Fig. 6C) fusiform, widest slightly beyond mid length; median lobe gradually narrowing from basal fifth towards apical region; gonopore on apical region of median lobe; apical third of parameres gradually narrowing towards apex, with straight outer margins.

Etymology. Named after the type locality: El Tobogán de la Selva in Venezuela.

Distribution. Venezuela (Amazonas). See Fig. 7.

Biology. Nothing is known about the biology of this species except that it was collected from the margin of the Rio Coromoto, the infamous locality for many water beetle species including the family Meruidae (see Spangler and Steiner 2005).

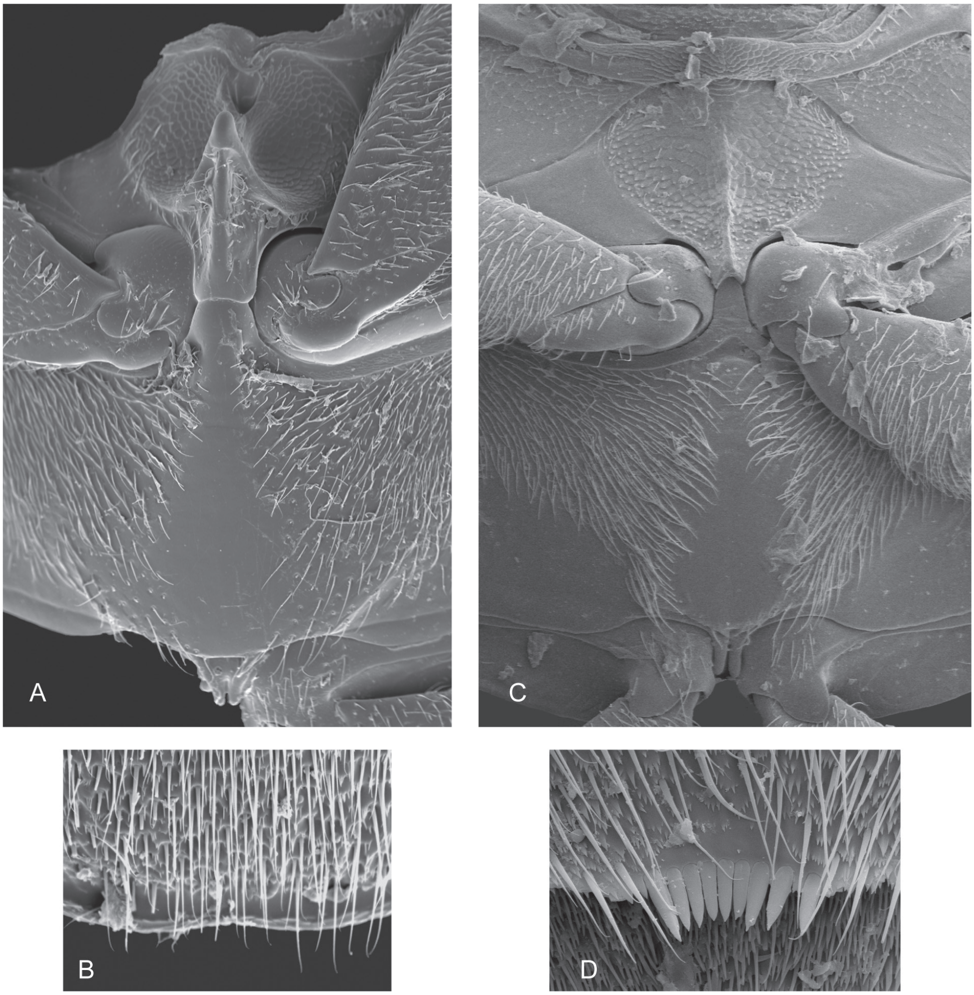

Figure 5. SEM images of thorax and abdomen: **A–B** *Crucisternum ouboteri*: **A** meso- and metaventrite **B** apex of fifth abdominal ventrite; **C–D** *Nanosaphes tricolor* **C** meso- and metaventrite **D** apex of fifth abdominal ventrite.

Crucisternum vanessae sp. n.

http://zoobank.org/1AF57F85-A0E3-4F1E-B524-089391139907

Figs 2E–H; 6D; 7; 8D

Type material examined. Holotype (male): "**SURINAME:** Sipaliwini district/ N3°53.942' W56°10.849', 733 m/ CSNR: Tafelberg Summit, near/ Caiman Creek Camp, margins & leaf packs in Caiman Creek/ leg. Short & Bloom; 19.viii.2013/ SR13-0819-05D" (NZCS). **Paratypes (188): SURINAME: Sipaliwini district:** "N3°55.600', W56°11.300', 600 m/ CSNR: Tafelberg Summit/ Augustus Creek, seepage on/ wall; leg. Short & Bloom/ 14.viii.2013; SR13-0814-01B" (3, SEMC);

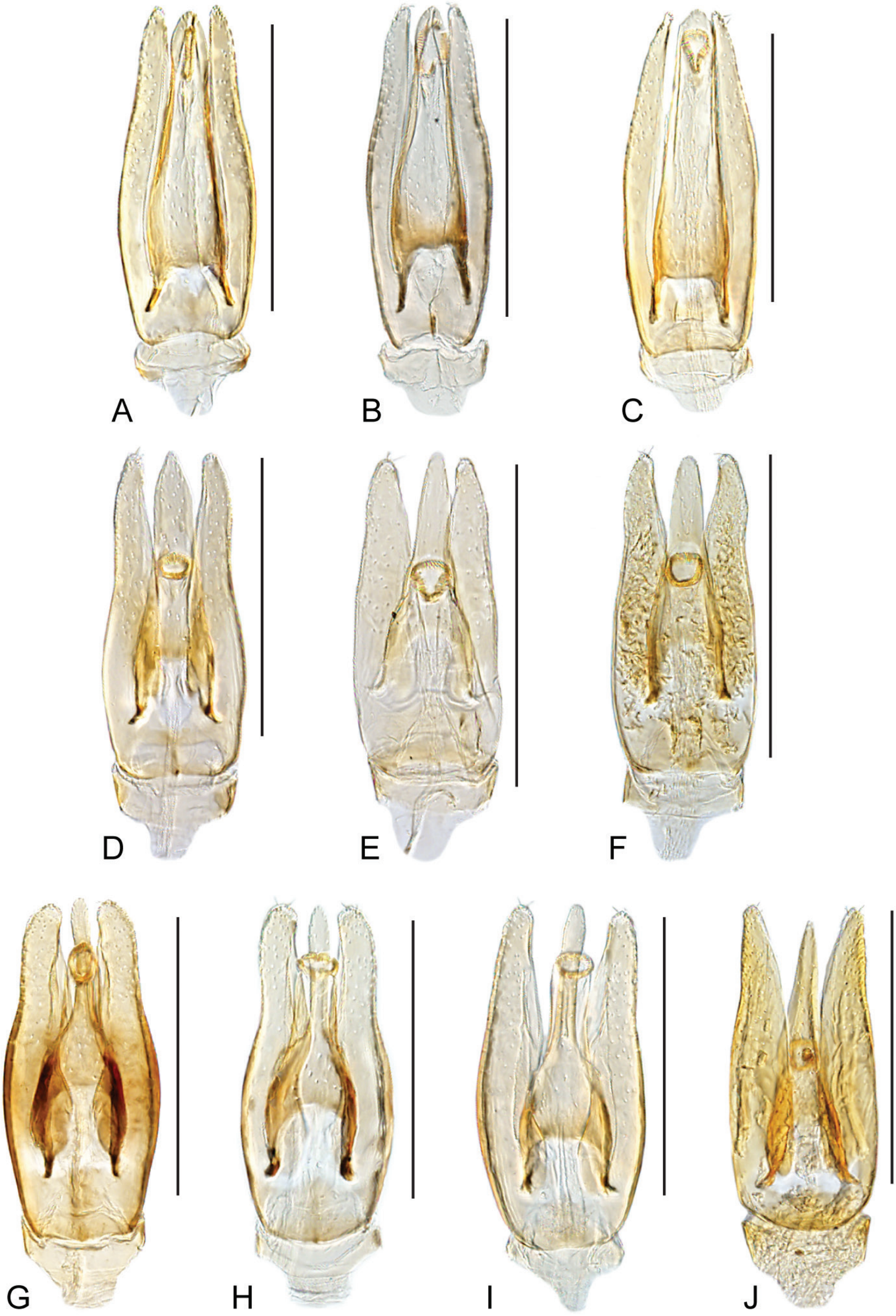

Figure 6. Aedeagus of *Crucisternum* spp.: **A–B** *Crucisternum ouboteri*: **A** Guyana **B** Brownsberg **C** *Crucisternum toboganensis* **D** *Crucisternum vanessae* **E–F** *Crucisternum xingu*: **E** colln#6 **F** colln#23 **G–H** *Cuscisternum sinuatus*: **G** colln#23 **H** BR18-0302-04A **I** *Crucisternum escalera* **J** *Crucisternum queneyi*. Scale bars: 0.25 mm.

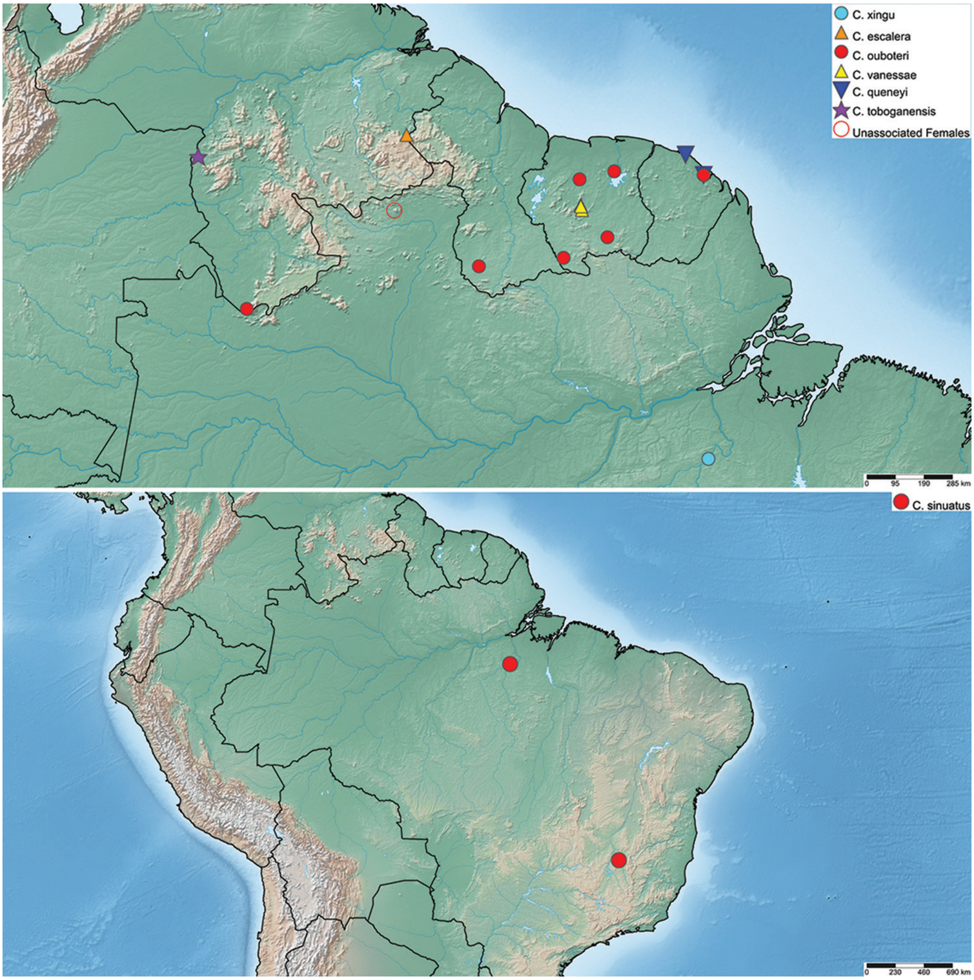

Figure 7. Distribution of *Crucisternum* species.

“N3°56.351’, W56°10.954’, 614 m/ CSNR: Tafelberg Summit/ Geijskes Creek, margin of creek/ w/ detritus; leg. Short & Bloom/ 15.viii.2013; SR13-0815-02A” (24, NZCS, SEMC); same, except “seep on wall/ 16.viii.2013; SR13-0816-01A” (1, SEMC); same, except “leaf packs & wood jams/ SR13-0816-01B” (4, SEMC); same, except “leaf packs & rock scrubbing; leg. D. Bloom/ SR13-0816-01D” (13, SEMC); “N3°55.600’, W56°11.300’, 600 m/ CSNR: Tafelberg Summit, nr/ Augustus Creek Camp pools &/ creeks on trail into Arrowhead/ basin; leg. Short & Bloom/ 17.viii.2013; SR13-0817-01A” (3, SEMC); “N3°55.600’, W56°11.300’, 600 m/ CSNR: Tafelberg Summit/ nr Augustus Creek Camp/ 17.viii.2013; SR13-0817-03A” (26, NZCS, SEMC); “N3°53.942’, W56°10.849’, 733 m/ CSNR: Tafelberg Summit, near/ Caiman Creek Camp, stream/ margins; leg. Short & Bloom/ 18.viii.2013; SR13-0818-01A” (11, SEMC); same, except “forest detrital pools; SR13-0818-02A”

Figure 8. Habitat of *Crucisternum* spp. **A–B** Habitat for *C. ouboteri* Suriname, Raleighvallen, collecting event SR12-0727-03A **C** Type locality and habitat for *C. ouboteri*, Suriname, Brownsberg Nature Park, collecting event SR12-0804-01A **D** Type locality and habitat for *C. vanessae*, Suriname, Tafelberg Summit, Caiman Creek, collecting event SR13-0819-05D **E–F** Type locality and habitat for *C. escalera*, Venezuela, Bolivar State, along La Escalera, collecting event AS-08-058.

(1, SEMC); same, except "pools in forest/ 19.viii.2013; SR13-0819-05B" (8, SEMC); same, except "margins & leaf packs in Caiman Creek/ SR13-0819-05D" (79, MIZA, MALUZ, SEMC); "N3°55.600', W56°11.300', 600 m/ CSNR: Tafelberg Summit, near/ Augustus Creek Camp, detrital/ creek; leg. Short & Bloom/ 22.viii.2013; SR13-0822-01A" (14, SEMC); same, except "leaf packs/ SR13-0822-03A" (1, SEMC).

Differential diagnosis. *Crucisternum vanessae* is very similar to *C. ouboteri* and *C. queneyi* in the sharpness of the punctation and the general coloration of the body (compare Fig. 2E–H to 2A–D and Fig. 1E–H, respectively). It can be readily recognized by the pear-shaped aedeagus (as opposed to fusiform), with the apical third of the median lobe parallel-sided, as well as inwardly pointing apices of the parameres (Fig. 6D).

Description. Body length 2.0–2.5 mm, width 1.2–1.4 mm. General coloration dark brown on elytra, slightly paler on pronotum and head (Fig. 2E). Elytra with punctures rather sharply marked. Aedeagus (Fig. 6D) pear-shaped, widest at basal third; apex of parameres slightly pointing inwards; apical third of median lobe parallel-sided, nearly as wide as a paramere at the base of its apical third; gonopore located at apical third of median lobe.

Etymology. Named after Surinamese entomologist Vanessa Kadosoe who has assisted us on numerous expeditions in Suriname, including the expedition to Tafelberg on which this species was discovered.

Distribution. Currently known only from several streams on the summit of Tafelberg Tepui in central Suriname. Collected at elevations from 600 to 733 m. See Fig. 7.

Biology. This species was collected in several forested streams that drain the summit of a low-elevation tepui. Specimens were abundant in several spots, usually where lots of fallen leaves and detritus had accumulated along the stream margins. Specimens were collected by submerging the leaf packs and catching the specimens that floated to the water surface. See Fig. 8D.

***Crucisternum xingu* sp. n.**

http://zoobank.org/7EF9B5FF-DD04-423E-80F8-CDF21AE0DD1A
Figs 3E–H; 6E, F; 7

Type material examined. Holotype (male): "**BRAZIL:** Pará/ Rio Xingu Camp 52°22'W, 3°39'S/ Altamira, ca 60km S.; 14.x.1986/ leg. P. Spangler & O. Flint// Colln. #23, stream on/ left branch of trail 1" (USNM). **Paratype (1): BRAZIL: Pará:** same, except "3.x.1986; Colln. #6;/ 1st jungle stream on trail 1" (1, USNM).

Differential diagnosis. *Crucisternum xingu* is very similar to *C. sinuatus* and *C. escalera* in the shallowness of the punctation and the uniform coloration along the body. It can be readily recognized by its dark brown coloration (as opposed to orange brown; compare Fig. 3E–H to Fig. 1), which is shared with *C. sinuatus*, from which it can be distinguished by the median lobe gradually narrowing towards the apex (see Fig. 6E, F; as opposed to constricted at midlength, continuing as a narrow and roundly pointed bar, see Fig. 6G, H), and the nearly straight to sinuate outer margins of the parameres (as opposed to strongly constricted at apical third, continuing nearly parallel).

Description. Body length 2.2–2.4 mm, width 1.3–1.4 mm. General coloration uniformly dark brown (Fig. 3E). Elytra with punctures shallowly marked. Aedeagus with outer margins of parameres sinuate to nearly straight; inner margins of parameres concave along apical third; median lobe gradually narrowing towards apex; apex of median lobe rounded (Fig. 6E–F).

Etymology. Noun in apposition. Named after the Xingu River where the known specimens were collected.

Distribution. Brazil (Pará). See Fig. 7.

Biology. This species is known from forest streams.

Crucisternum sp.

Material examined (8). BRAZIL: Pará: "Rio Xingu Camp 52°22'W, 3°39'S/ ca 60km S. of Altamira; 3.x.1986/ leg. P. Spangler & O. Flint; Colln. #6;/ 1st jungle stream on trail 1" (6; USNM; unassociated females; likely either *C. sinuatus* or *C. xingu*); **Roraima:** Amajari: Serra do Tepequém, Igarape Preto Negro, Quebrada do Canara, 3°46.715'N, 61°45.405'W, 637 m, 14.i.2018, forested stream, Short, Benetti & Santana, BR18-0114-05A (1, SEMC). **FRENCH GUIANA: Roura:** "[Patawa: crique/ Diamant]/ 16.xi.2007/ P. Queney réc." (1, SEMC; unassociated female; likely either *C. ouboteri* or *C. queneyi*); "[Patawa: ru]/ 19.xi.2007/ P. Queney réc."; "[N2, PK 73,5: petite crique accidentée, 250m]/ 23.xi.2007/ P. Queney réc." (1, SEMC; unassociated female; likely either *C. ouboteri* or *C. queneyi*). **SURINAME: Sipaliwini district:** "N3°47.479', W56°08.968', 320 m/ CSNR: near Kappel airstrip/ at Tafelberg trail, in creek/ leg. Short & Bloom; 13.viii.2013; SR13-0813-06B" (1, SEMC; unassociated female; likely either *C. ouboteri* or *C. vanessae*).

Remarks. Given our current inability to identify some species based only on external characters, these unassociated females could not be identified with confidence, especially in the localities where more than one species are known to occur.

Katasophistes gen. n.

http://zoobank.org/3EB28C66-5B17-4540-8E86-DB99504C7227
Figs 9–14

Type species. *Katasophistes merida*

Differential diagnosis. Medium to small beetles, total body length 2.7–4.5 mm, width 1.7–2.4 mm. Color orange brown to dark brown, rather uniform along body regions. Body shape oval to elongated in dorsal view; moderately convex in lateral view (see Figs 9–10). Antennae with nine antennomeres (e.g., Fig. 10C). Maxillary palps curved inward, moderately long to long (e.g., Fig. 10D, H). Each elytron with five rows of deep/large systematic punctures (Fig. 10A; not as evident in *K. charynae*, *K. cuzco* and *K. superficialis*); elytra without sutural striae, with outer margins slightly flared; serial punctures not evident. Posterior elevation of mesoventrite, with a well-defined, curved transverse ridge (Fig. 11A). Posterior femora glabrous at most along apical third. Fifth abdominal ventrite apically truncate to slightly emarginate, with stout setae (see Fig. 11C–E).

At first glance the genus may appear similar to some species of *Chasmogenus*, however the lack of sutural striae easily separates the two. The enlargement of the rows of elytral systematic punctures is also rare within the Acidocerinae (found in some *Chasmogenus* and *Agraphydrus*) and will separate it from other New World *Helochares*, with which it may also be confused.

Description. Body oval to elongate, weakly to moderately convex (e.g., Figs 9F, 10F), coloration rather uniform along body regions, orange brown to dark brown, often with maxillary palps slightly paler. **Head.** Frons and clypeus (e.g., Fig. 9D) with moderately marked ground punctures, irregularly and rather densely distributed over the surface, accompanied by seta-bearing systematic punctures, particularly noticeable on frons behind frontoclypeal suture and around inner margins of eyes, and on lateral areas of clypeus; surface between punctures smooth and shiny; anterior corners of clypeus roundly angulated; anterior margin of clypeus widely roundly emarginate. Eyes subquadrate in dorsal view (e.g., Fig. 10H). Labrum wide, fully exposed, nearly half as long, and collinear to clypeus (e.g., Fig. 9D); dorsal surface slightly convex, with scattered fine punctures; anterior margin mesally slightly emarginate and barely bent inwards; lateral and anterior margins fringed by rather long setae. Temporae densely covered by very short and fine setae (hydrofuge pubescence). Mentum parallel sided, with lateral oblique longitudinal ridges; anterior margin with wide, deep, concave median impression, not demarcated by a transverse carina. Submentum rather flat and pubescent at base, glabrous, shiny and ascending at apex, with sparse rather long setae near limit of pubescent/glabrous line; ocular ridge well-developed (e.g., Fig. 9C). Maxilla (e.g., Fig. 9C) with ventral surface of cardo and stipes smooth and shiny, with scattered and shallow punctures (basal outer margin of cardo with a fringe of fine and rather long setae in *K. merida*); outer dorsal margin of palpifer with a row of stiff decumbent spiniform setae; limit between cardo and stipes oblique; maxillary palps brown to orange, slender, longer than antennae (slightly so and stout in *K. merida*); apex of palpomere 3 bearing sensilla. Mandibles with apex bifid (observed in *K. merida* and *K. charynae*). Labial palps yellowish, nearly as long as mentum, dorsoventrally flattened; palpomere 2 with inner and outer margin convex apicad of midpoint; palpomere 3 digitiform, with a long subapical seta on outer corner. Antennae (e.g., Fig. 10C) with nine antennomeres, either similar or paler than general coloration of head; antennomere 1 anteriorly projected near base, almost reaching midpoint of ventral surface of eye (not reaching cardo-stipes joint), nearly 1.4–1.8-times longer than antennomere 2; antennomere 2 nearly as long as antennomeres 3–4 combined; antennomere 6 forming a well differentiated, only slightly asymmetric cupule; antennomeres 7–9 similar in size (8 shortest, 9 longest) and shape, slightly flattened (less so in *K. merida*), forming a loosely articulated, pubescent club; apex of antennomeres 7–9 with few scattered setae longer than general pubescence of club. **Thorax.** Pronotum widest at base, narrowed anteriorly, with anterior and posterior margins only slightly sinuate; surface evenly convex, ground punctation moderate, uniformly dense, with surface between punctures smooth and shiny; seta bearing systematic punctures forming paired anterolateral semicircles. Scutellar shield of moderate size, triangular, nearly as long as wide, with punctation as in pronotum. Prosternum (e.g., Fig. 9C) nearly as long as 2/3 of length of a coxa, weakly convex to only slightly ascending longitudinally on central area; anterior margin of prosternum mesally projected as a wide, roundly pointed triangle, usually with a low carina along midline of projection; surface of prosternum covered by rather long, fine, scattered setae; intercoxal process projected from posterior margin of procoxal cavities, rectangular shaped in outline, with pyramidal surface. Mesoventrite not fused to mesepisterna, with anterior margin 0.2-times as wide as anterior margin of mesepisternum; anterior rib of mesoventrite bearing a medial semitriangular, pearlescent macula; posterior elevation of mesoventrite with a well-defined, curved transverse ridge, sometimes swollen at midpoint (as in *K. cuzco*); surface of mesoventrite reticulated for the most part; mesepisternum obliquely widely concave, with reticulated surface; mesepimeron trapezoid, with reticulate and pubescent surface. Mesofurca (examined in *K. merida*) with short arms, 0.6-times length of mesocoxae; apical half of arms free irregularly explanate, with outer corners sharply pointed. Metaventrite posteromesally elevated, with elevation rather flat; surface of metaventrite reticulate and pubescent, except for postero median and glabrous patch. Metepisterna 3–4-times longer than wide, only slightly narrowing posteriorly. Metepimeron triangular and acute. Metafurca (examined in *K. merida*, Fig. 11B) 1.6-times wider than long, with furcal arms (fa) slightly longer than stalk (s); stalk triangular (wider near the crux (c), gradually narrowing ventrally), with paired longitudinal keels extending along basal third of posterior face, and a well-developed median keel on anterior face extending to anterior margin of dorsal sheets (ds); outer margins of stalk diverging from base towards proximal third of furcal arms; furcal arms somewhat trapezoid, with apex (hemiductus (h)) only slightly explanate, obliquely positioned; anterior tendons (at) inserted at basal third of dorsal edge of furcal arms; dorsal sheaths well-developed, slightly wider than widest point of lateral sheaths (ls). **Elytra.** Surface even (without elevations or depressions), serial punctures not clearly defined (e.g., Fig. 9E), not impressed into striae; seta bearing systematic punctures rather enlarged and deep (less strikingly so in *K. charynae*, *K. cuzco* and *K. superficialis*), forming five longitudinal rows, fifth row very close to outer margin of elytron; elytral margins slightly flared. Epipleura well-developed, slightly oblique, with sparse setae, anteriorly wide, gradually narrowing posteriorly, extending up to line of posterior margin of first abdominal ventrite; pseudepipleura well-developed, perpendicularly positioned, nearly half as wide as anterior portion of epipleura, extending along entire outer margin of elytra. Hind wings well-developed. **Legs.** All femora with dense pubescence, at least along basal two thirds, remainder of surface glabrous, shiny and slightly reticulated; all femora antero-posteriorly flattened; metafemora with rather weak tibial grooves. Tibiae slender, weakly flattened, with well-developed spines; protibiae with a median longitudinal row of long spathulate setae along anterior surface. All tarsi with five tarsomeres, bearing long apical hair-like setae on dorsal face, and two lateral rows of spines and/or hair-like spines on ventral face of tarsomeres 2–4; protarsomeres 1–4 similar in size and shape; meso- and meta tarsomeres with tarsomere 2 nearly as long as tarsomere 5; tarsomere 5 approximately as long as tarsomeres 3–4 combined, without spines on ventral face; claws rather large, curved; empodium well-developed, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, medially weakly convex; all ventrites reticulated, with uniform, dense, fine pubescence; posterior margin of fifth ventrite truncate to mesally weakly emarginated, set with a row of thick, flat spine-like setae (see Fig. 11C–E). Aedeagus (Fig. 12) nearly parallel sided, with basal piece between 0.5 and 1.1-times the length of parameres; median lobe wider than each paramere, gradually narrowing apically, with a conspicuous median longitudinal sclerotization, and well-developed lateral basal apodemes; apex of median lobe acute; parameres nearly as long as median lobe, with apical setae; gonopore preapically situated.

Larvae. The immature stages are unknown.

Etymology. Named from the Greek word *katasophistes*, meaning trickster, in reference to the disparity of the general appearance of some of the known species. Name to be treated as masculine.

Distribution. Venezuela (Mérida), Ecuador (Pastaza), Peru (Cuzco, Madre de Dios). See Fig. 13.

Biology. Species in this genus exhibit a combination of ecologies: *K. merida* is restricted to seepage habitats, while the type series of *K. superficialis* was collected from forested stream pools with abundant detritus. See Fig. 14.

Characters of taxonomic importance for *Katasophistes*. With the exception of the enlarged elytral systematic punctures, there is nothing particularly remarkable about the external morphology of *Katasophistes*. Careful examination of the elytral systematic punctures is needed in order to recognize *K. charynae*, *K. cuzco,* and *K. superficialis*.

Punctation. The most prominent feature of *Katasophistes* is the enlargement of the elytral systematic punctures, which is evident in *K. merida* (Fig. 10A, B), but much less so in *K. charynae*, *K. cuzco* and *K. superficialis*. One way to recognize the enlarged elytral systematic punctures would be by spotting the long setae that systematic punctures bear.

Posterior elevation of mesoventrite. It is usually well-defined and shaped as a curved transverse ridge. Only in *K. cuzco* is this transverse ridge additionally medially swollen, as to form a low bump.

Aedeagus. In *Katasophistes* the aedeagus exhibits the same general shape of the median lobe, combined with a wide variety of shapes of the parameres (see Fig. 12).

Key to the species of *Katasophistes*

1 Elytra with strikingly large and deeply impressed systematic punctures (Fig. 10A, B); maxillary palps relatively short and stout (Fig. 10D) .... ***K. merida***

– Elytra with slightly enlarged systematic punctures which are shallowly impressed; maxillary palps relatively long and slender (e.g., Fig. 10H) **2**

2 Body length around 4.5 mm; basal piece of aedeagus nearly as long as parameres (Fig. 12E) .... ***K. superficialis***

– Body length less than 4 mm; basal piece of aedeagus nearly half as long as parameres (Fig. 12A–C) **3**

3 Transverse ridge on posterior elevation of mesoventrite uniformly wide; parameres with widest basal point clearly wider than pre-apical width (Fig. 12A, B) .... ***K. charynae***

– Transverse ridge on posterior elevation of mesoventrite swollen at midpoint; parameres with widest basal point nearly as wide as pre-apical width (Fig. 12C) .... ***K. cuzco***

Katasophistes charynae sp. n.

http://zoobank.org/CF86E4B5-FA2D-4CA8-B17B-AB5F0114F7DF
Figs 9A–D; 11D; 12A, B; 13

Type material examined. Holotype (male): "**PERU: Madre de Dios:** Parque Manu, Pakitza/ 12°07'S 70°58'W/ R.A. Faitoute, colln 32/ 250 m, stream/ Trocha Dos, c72/ 10 Sept 1989" (USNM). **Paratypes (39): PERU: Madre de Dios:** Same data as holotype (14, SEMC, USNM); same, except "colln 32a, berlesed leaf litter" (12, SEMC, USNM); same, except "11–15 Sept 1989, colln 35a, Trocha uno, c 11, flight intercept trap in dry narrow stream bed" (2, USNM); same, except "16 Sept 1989, colln 42a, Trocha Dos, c.53, berlesed leaf litter" (2, USNM), same, except "18 Sept 1989, colln 46, Trocha Dos, c 14, spring seepage" (4, USNM, SEMC); same, except "19 Sept 1989, colln 47, Trocha Uno, c 14, stream" (2, USNM); same, except "colln 47a, berlesed leaf litter" (2, USNM); same, except "22 Sept 1989, coll 55a, TC 22, berlesed leaf litter & root mats" (1, USNM).

Differential diagnosis. *Katasophistes charynae* is very similar to *K. cuzco*, from which it can be distinguished by its smaller size, generally darker coloration, simple curved transverse ridge on the posterior elevation of mesoventrite and characters of the aedeagal parameres.

Description. Body length 2.6 to 3.5 mm, width 1.5 to 1.9 mm. Body elongate oval, weakly convex (Fig. 9B). General coloration uniformly dark brown, with slightly paler margins of pronotum. Each elytron with five rows of shallow enlarged systematic punctures. Posterior elevation of mesoventrite with well-defined, curved, uniformly wide transverse ridge. Apex of fifth abdominal ventrite weakly emarginate (Fig. 11D). Aedeagus (Fig. 12A, B) with basal piece 0.4 to 0.5-times the length of parameres; greatest width of parameres near base, clearly wider than pre-apical width, with inner margin sinuate, at widest point, parameres nearly 0.7-times greatest width of median lobe; apex of parameres rounded, slightly widened at apex; apex of median lobe forming an acute angle.

Etymology. Named after Charyn Micheli (USNM), Coleopterist and museum specialist in charge of the aquatic beetle collection (among others) at the Smithsonian Institution who has assisted the authors on numerous occasions and diligently oversees the largest water beetle collection in the world.

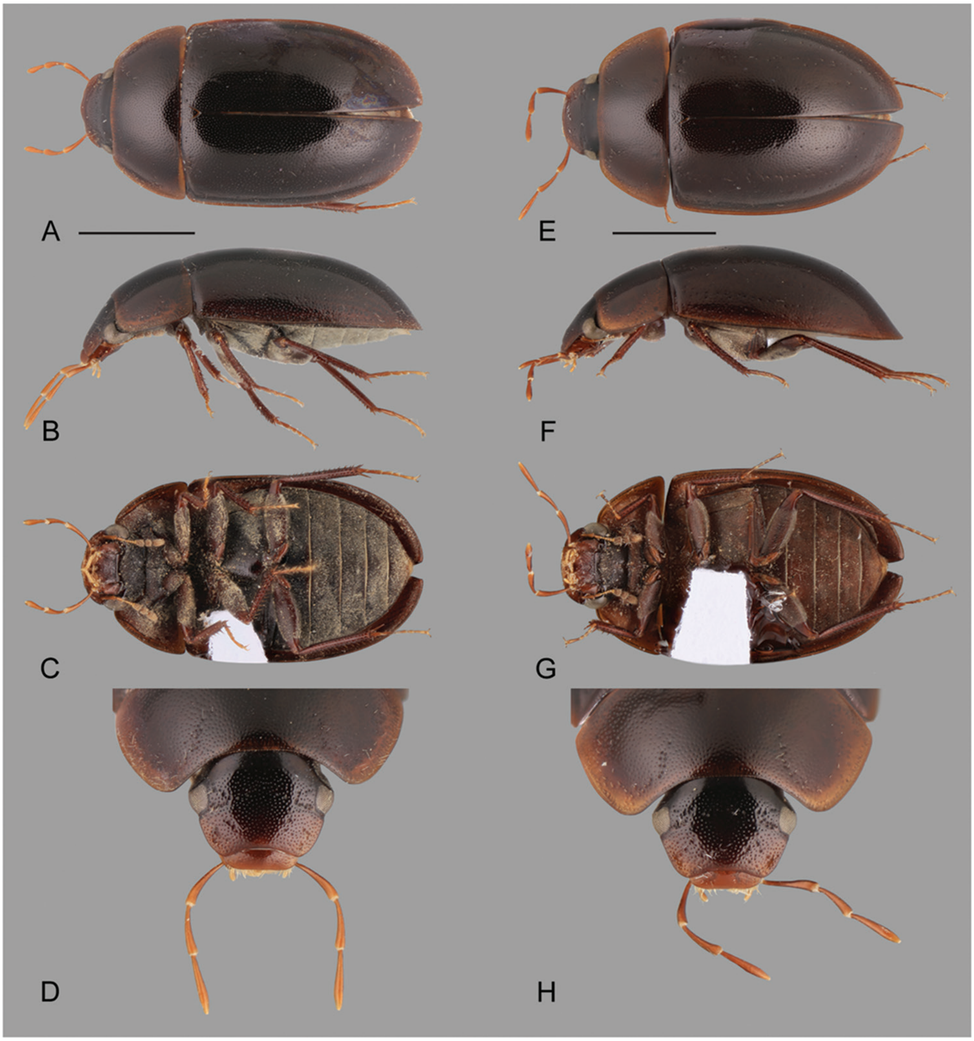

Figure 9. Habitus of *Katasophistes* spp.: **A–E** *Katasophistes charynae*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Katasophistes cuzco*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 1 mm.

Distribution. Peru (Madre de Dios). See Fig. 13.

Biology. Most specimens were collected in streams.

Remarks. There is variation in the relative proportions of the aedeagus and the shape of the parameres, with some specimens having a wider and shorter aedeagus (Fig. 12A), and some with a more slender aedeagus bearing slender parameres (Fig. 12B). As there are no external features to distinguish them, and both forms of aedeagi were found at the same localities, we refrain from calling them different species until more material and/or possibly molecular data are available.

Katasophistes cuzco sp. n.

http://zoobank.org/3CF1C324-BCAB-4CB2-9475-53865C2039B3
Figs 9E–H; 11E; 12C; 13

Type material examined. Holotype (male): "**PERU: Cuzco:** Quita Calzón, at/ km 164, 1030 m/ 13°09'S 71°22'W// 2 Sept 1989/ colln 17/ R.A. Faitoute" (USNM). **Paratypes (3): PERU: Cuzco:** Same data as holotype (2, SEMC, USNM); at Km 152 & 1 Km E. of San Pedro, 1430 m/ 13°09'S 7126'W/31 Aug 1989/ colln 10/ R.A. Faitoute" (1 male, USNM).

Differential diagnosis. *Katasophistes cuzco* is very similar to *K. charynae*, from which it can be distinguished by its larger size, generally paler coloration, the medially swollen curved transverse ridge on the posterior elevation of mesoventrite, as well as characters of the aedeagal parameres.

Description. Body length 3.6 to 3.7 mm, width 2.0 to 2.2 mm. Body elongate oval, moderately convex (Fig. 9F). General coloration uniformly brown, with slightly paler margins of pronotum. Each elytron with five rows of shallow enlarged systematic punctures. Posterior elevation of mesoventrite with a well-defined, curved transverse ridge, swollen at midpoint. Apex of fifth abdominal ventrite moderately emarginate (Fig. 11E). Aedeagus (Fig. 12C) with basal piece nearly 0.6-times the length of parameres; greatest width of parameres near base, nearly as wide as pre-apical width, with inner margin sinuate; at widest point, parameres nearly 0.6-times greatest width of median lobe; apex of parameres rounded, slightly widened at apex; apex of median lobe forming an acute angle.

Etymology. Noun in apposition. Named after Cuzco, the Peruvian province where specimens were collected.

Distribution. Peru (Cuzco). See Fig. 13.

Biology. Although no biological information is listed in the label, we were able to cross reference the original field notes for these collecting events and confirm that the holotype event ("colln 17") was made in a stream, probably from leaf packs. The paratype from "colln 10" has a combination notation of "roadside ditch" and "seep".

Katasophistes merida sp. n.

http://zoobank.org/56F9F802-091F-4404-8BAF-0B8FEB7E43F1
Figs 10A–D; 11A–C; 12D; 13; 14A–D

Type material examined. Holotype (male): "**VENEZUELA**: Mérida State/ 8°51.933'N, 70°37.131'W, 1682 m/ ca. 12 km SE of Santo Domingo/ leg. Short, Arias & Gustafson, wall seeps along river; 22.i.2012; VZ12-0122-03C" (MIZA). **Paratypes: (33): VENEZUELA: Mérida State:** "12Km SE/ Sta. Domingo/II-24-1969/ P. & P. Spangler" (3, USNM); "12 Km. SE Sto. Dom./ 24 Feb. 76/ C.M. & O. S. Flint" (1, USNM); same data as holotype (14, SEMC); same data as holotype except "leg. Short, Arias, & Gustafson; log

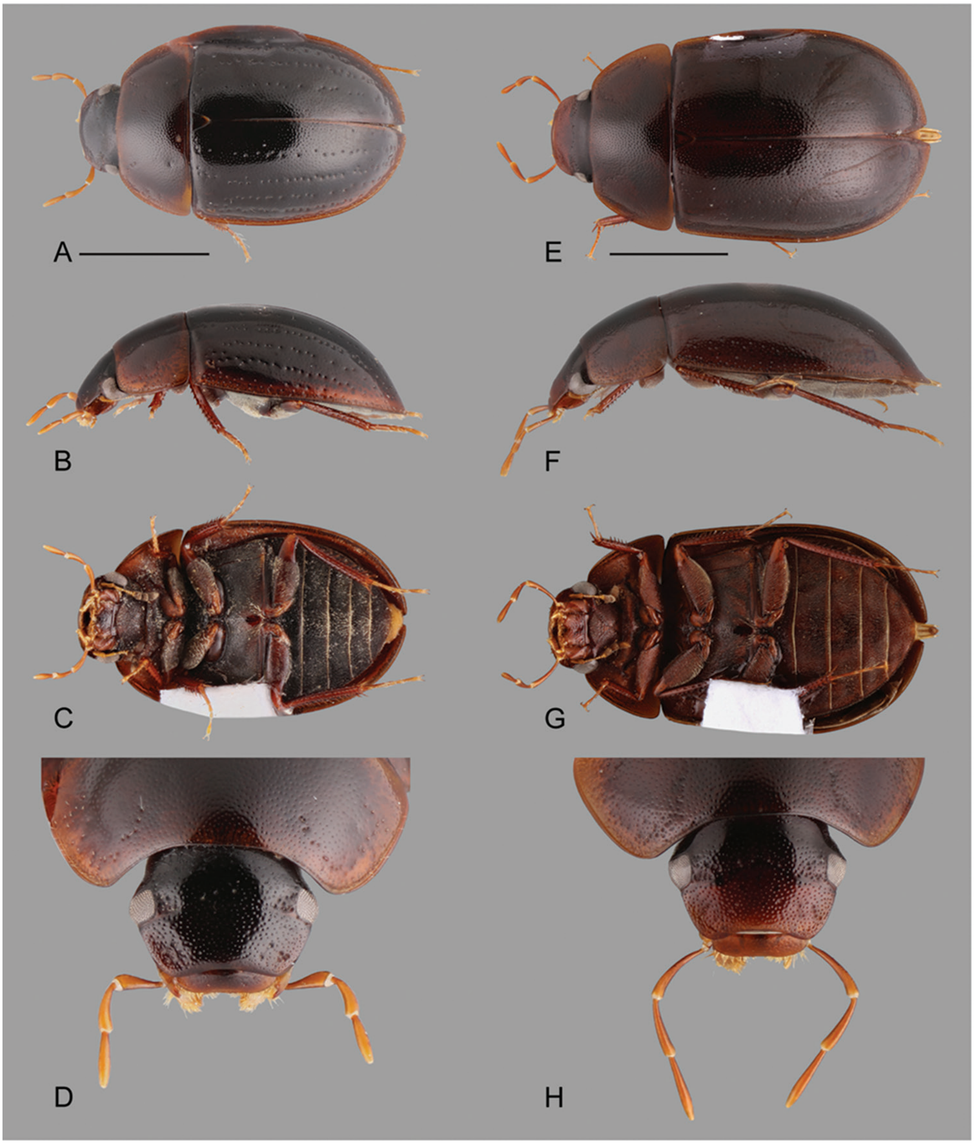

Figure 10. Habitus of *Katasophistes* spp.: **A–E** *Katasophistes merida*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Katasophistes superficialis*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bar: 1 mm.

and stick jams in river; VZ12-0122-03B" (3, SEMC); same, except "Short & Arias; wall seeps; VZ12-0122-03A" (6, MIZA, MALUZ, SEMC); same, except "VZ12-0122-03C2" (1, SEMC, DNA voucher SLE 426); "8°52.423' N, 70°37.611'W, 1616 m/ Cascada Velo de la Novia; 24.i.2012/ leg. Short, Arias, & Gustafson / seeps by waterfall/; VZ12-0124-01A" (4, SEMC); same, except "logs & Kicknetting; VZ12-0124-01B" (1, SEMC).

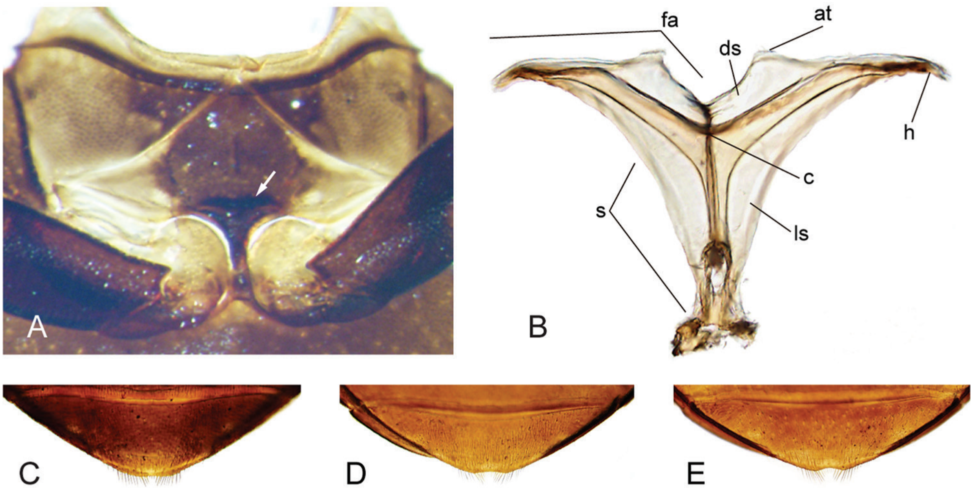

Figure 11. Thorax and abdomen of *Katasophistes* spp.: **A–C** *Katasophistes merida*: **A** ventral view of mesoventrite (white arrow pointing transverse ridge) **B** posterior view of metafurca: (at) anterior tendon, (c) crux, (ds) dorsal sheath, (fa) furcal arm, (h) hemiductus, (ls) lateral sheath, (s) stalk **C** fifth abdominal ventrite **D** *Katasophistes charynae*, fifth abdominal ventrite; **E** *Katasophistes cuzco*, fifth abdominal ventrite.

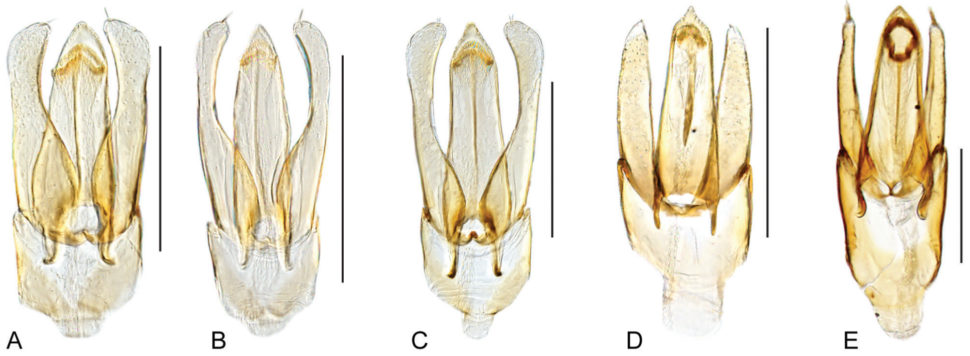

Figure 12. Aedeagus of *Katasophistes* spp.: **A–B** *Katasophistes charynae*: **A** "colln 32" **B** "colln 42a" **C** *Katasophistes cuzco*; **D** *Katasophistes merida* **E** *Katasophistes superficialis*. Scale bars: 0.3 mm.

Differential diagnosis. *Katasophistes merida* is easily recognized because of the striking rows of large and deep systematic punctures along the elytra and its relatively short and stout maxillary palps.

Description. Body length 2.7–3.4 mm, width 1.7–2.4 mm. Body broadly oval, moderately convex (Fig. 10A, B). General coloration dark brown, slightly paler along margins of pronotum and elytra (Fig. 10 A, B). Each elytron with five rows of large and deep systematic punctures. Apex of fifth abdominal ventrite truncate (Fig. 11C). Aedeagus (Fig. 12D) with basal piece nearly 0.8-times the length of parameres; parameres at widest point, nearly 0.6-times greatest width of median lobe; apex of parameres narrowly round; apex of median lobe with median pointed projection.

Figure 13. Distribution of *Katasophistes* species.

Etymology. Noun in apposition. Named after the Venezuelan State of Mérida, where the beetles have been collected.

Distribution. Venezuela (Mérida). Elevation range 1616–1682 m. See Fig. 13.

Biology. This species is associated with seepage and waterfall habitats in the Andes, where it has been collected at several sites in wet rock. See Fig. 14 A–D.

Katasophistes superficialis sp. n.

http://zoobank.org/D0584735-1F2E-440E-9C76-3ADC14CFDFD6

Figs 10E–H; 12E; 13; 14E, F

Type material examined. Holotype (male): "**ECUADOR**: **Pastaza Province**: "AGIP platform Villano B/ along transect 1 & 2/ 24.v.2008; leg. A.E.Z. Short/ small forest stream AS-08-08b" (PUCE). **Paratypes (1): ECUADOR:** Same data as holotype (1, SEMC, DNA voucher SLE 1189).

Figure 14. Habitat of *Katasophistes* spp. **A–B** Type locality and habitat of *K. merida*: Venezuela: Merida State, Collecting Event VZ12-0122-03A **C–D** Habitat of *K. merida*: Venezuela: Merida State, Collecting Event VZ12-0124-01A **E–F** Type locality and habitat of *K. superficialis*: Ecuador: Pastaza Province, Collecting Event AS-08-08b.

Differential diagnosis. *Katasophistes superficialis* can be easily differentiated by its size (~4.5 mm), elongate oval shape, the shallow rows of enlarged systematic punctures along the elytra and its relatively long and slender maxillary palps.

Description. Body length 4.5 mm, width 2.4 mm. Body elongate oval, weakly convex (Fig. 10 E, F). General coloration uniformly brown. Each elytron with five rows of shallow enlarged systematic punctures. Apex of fifth abdominal ventrite weakly emarginated. Aedeagus (Fig. 12E) with basal piece nearly 1.1-times the length of parameres; parameres at widest point, nearly 0.4-times greatest width of median lobe; apex of parameres rounded; apex of median lobe forming an acute angle.

Etymology. Named in reference to the shallowness of the enlarged systematic punctures along the elytra, with the Latin word *superficialis* meaning shallow.

Distribution. Ecuador (Pastaza). See Fig. 13.

Biology. This species was collected in forested stream pools with abundant detritus in lowland rainforest. See Fig. 14E, F.

Nanosaphes gen. n.

http://zoobank.org/92C19CA3-E66E-4339-8B36-D9D4BC0A196B
Figs 5C, D; 15–20

Type species. *Nanosaphes tricolor*

Differential diagnosis. Very small beetles, total body length 1.15–1.45 mm, width 0.7–0.9 mm. Coloration uniformly brown, to variable along the body (see Figs 15–16). Body shape oval in dorsal view; uniformly, slightly to moderately convex in lateral view (e.g., Figs 15F, 16F). Antennae with eight antennomeres (e.g., Fig. 16G). Maxillary palps curved inward, moderately long (e.g., Fig. 16H). Each elytron with ground punctures usually only shallowly marked, seemingly forming longitudinal rows (e.g., Fig. 16E), with irregularly distributed systematic punctures bearing rather long setae, denser along lateral and posterior regions; elytra without sutural striae. Posterior elevation of mesoventrite, usually only projected as a low and short longitudinal carina between mesocoxae (Figs 5C, 17A; sharply carinated and posteriorly pointed in *N. hesperus*). Metaventrite with posterolateral and mesal glabrous patches (Fig. 5C). Posterior femora for the most part densely covered by setae. Fifth abdominal ventrite apically emarginated, with stout setae (Figs 5D, 17C–D).

The minute size of *Nanosaphes* make them smaller than any other Acidocerinae in the New World, and about equal in size as the smallest *Agraphydrus* species in the Old World. They are among the smallest water scavenger beetles worldwide. The lack of elytral serial or sutural striae and the antennae with eight antennomeres also separate *Nanosaphes* from all other Neotropical Acidocerinae genera except the co-occurring *Globulosis*. The genus can be easily separated from *Globulosis* by its smaller size and narrower, more parallel sided body form (broader and almost rotund in *Globulosis*, see Short et al. (2017)).

Description. Body oval, uniformly and usually weakly convex (moderately convex in *N. punctatus*, see Fig. 15F), coloration uniformly brown, or variable along the body (e.g., paler pronotum in *N. hesperus* and *N. tricolor*, see Fig. 16). **Head.** Frons and clypeus (e.g., Fig. 16H) with shallow ground punctures irregularly distributed over the surface, accompanied by scattered seta-bearing systematic punctures; setae particularly noticeable on frons behind frontoclypeal suture; surface between punctures smooth, at most only finely reticulated along anterior and lateral margins of clypeus; anterior corners of clypeus roundly angulated; anterior margin of clypeus widely roundly emarginate. Eyes oval (e.g., Fig. 16D). Labrum rather short and wide, fully exposed and positioned nearly perpendicular to clypeus (e.g., Fig. 16B); dorsal surface convex, basally smooth, apically and laterally finely reticulated, with scattered shallow punctures; anterior margin mesally emarginate and bent inwards; anterolateral margins bearing a row of long setae. Temporae densely covered by setae (hydrofuge pubescence), with few longer setae along outer posteroventral margin of eye. Mentum nearly 1.5–1.7-times wider than long, parallel sided, basilaterally flat, with lateral oblique longitudinal ridges; anterior margin with wide, deep, concave median impression. Submentum rather flat, with sparse rather long setae; ocular ridge well-developed (e.g., Fig. 16G). Maxilla (e.g., Fig. 15G) with ventral surface of cardo and stipes smooth and shiny, with a row of stiff decumbent spiniform setae along outer dorsal margin of palpifer; limit between cardo and stipes oblique; maxillary palps yellowish, longer than antennae; palpomere 1 extending beyond base of cardo, with inner margin straight, only slightly concave at base, and outer margin distally convex; palpomere 2 similar in shape to palpomere 1, 0.7-times as long; palpomere 3 fusiform, slightly longer and wider than palpomere 1, apically widely rounded; apex of palpomere 3 bearing sensilla. Mandibles with apex bifid (examined in *N. hesperus*). Labial palps yellowish, nearly as long as mentum, dorsoventrally flattened; palpomere 2 with inner and outer margin convex apicad of midpoint; palpomere 3 digitiform, markedly shorter and narrower than palpomere 2, with a long subapical seta on outer corner. Antennae (e.g., Fig. 16G) with eight antennomeres, paler than general coloration of head; antennomere 1 anteriorly swollen near anterior margin of eye, reaching midpoint of ventral surface of eye (reaching cardo-stipes joint), nearly 1.4-times longer than antennomere 2; antennomere 2 slightly longer than antennomeres 3–4 combined; antennomere 5 forming a rather small, but well differentiated cupule; antennomeres 6–8 similar in size (7 shortest, 8 longest), slightly flattened, forming a loosely articulated, pubescent club; setae at apex of antennomere 8 longer than general pubescence of club. **Thorax.** Pronotum widest at base, narrowed anteriorly, surface evenly convex; ground punctation shallow, uniformly sparse, with surface between punctures smooth and shiny; seta bearing systematic punctures particularly noticeable as transverse anterolateral and mediolateral bands. Scutellar shield of moderate size, triangular, nearly as long as wide, with scarce shallow punctures. Prosternum (e.g., Fig. 16G) very short, flat, at most only weakly convex, not carinate; anterior margin of prosternum mesally projected, with a preapical fringe of setae; intercoxal process truncate, aligned with posterior margin of procoxal cavities. Mesoventrite not fused to mesepisterna, with anterior margin nearly as wide as anterior margin of mesepisternum; posterior elevation of mesoventrite either flat (as in *N. punctatus*), or longitudinally carinate (weakly as in *N. tricolor* (Figs 5C, 17A) and *N. castaneus* or sharply as in *N. hesperus*); mesepisternum obliquely widely concave; surface of mesoventrite and mesepisternum reticulated; mesepimeron narrow and trapezoid, with pubescent surface. Mesofurca (examined in *N. hesperus*) with short arms, 1.3-times longer than length of mesocoxae; each arm expanding ventrally as a lamina, reaching mesoventrite; apex of arms free (not forming part of lamina), oval and explanate. Metaventrite (Fig

5C) posteromesally elevated, with elevation rather flat and metathoracic discrimen well defined; anterior and lateromedian surfaces of metaventrite pubescent, with median and posterolateral glabrous patches. Metepisterna 3–4-times longer than wide, slightly narrowing posteriorly. Metepimeron triangular and acute. Metafurca (Fig. 17B, examined in *N. hesperus*) 1.25-times wider than long, with furcal arms (fa) nearly as long as stalk (s); stalk triangular (wider near the crux (c), gradually narrowing ventrally), with paired longitudinal keels extending along basal two thirds of posterior face, and a well-developed median keel on the anterior face extending to anterior margin of dorsal sheets (ds); outer margins of stalk diverging from ventral third towards midpoint of furcal arms; furcal arms somewhat rectangular, with apex (hemiductus (h)) slightly explanate, perpendicularly positioned; anterior tendons (at) inserted along half third of dorsal edge of furcal arms; dorsal sheaths well-developed, slightly wider than widest point of lateral sheaths (ls). **Elytra.** Surface even (without elevations or depressions), with serial punctures seemingly longitudinally aligned, usually shallowly marked (e.g., Fig. 16E) (except in *N. punctatus* which has rather coarsely punctate elytra, see Fig. 15 E, F), not impressed into striae; seta bearing systematic punctures scattered along interstriae; setae of systematic punctures rather long; elytral margins simple (as opposed to explanate). Epipleura well-developed, nearly glabrous, at most with scarce setae, oblique, anteriorly wide, gradually narrowing posteriorly, extending up to line of first abdominal ventrite; pseudepipleura reduced, limited to margin of elytra. Hind wings well-developed. **Legs.** All femora with dense pubescence, along basal three fourths, remainder of surface glabrous and shiny; all femora antero-posteriorly flattened; metafemora with rather sharp tibial grooves along apical half. Tibiae moderately slender, rather weakly flattened, with moderately fine and sparse spines. All tarsi with five tarsomeres, bearing few long apical hair-like setae on dorsal face, and two lateral rows of spines on ventral face of tarsomeres 2–4; tarsomeres 1–4 similar in size and shape; tarsomere 5 approximately as long as tarsomeres 3–4 combined, without spines on ventral face; claws rather large, curved; empodium well-developed, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, medially longitudinally weakly convex, all ventrites with uniform, fine pubescence, either dense (as in *N. tricolor*, see Fig. 16C) or scanty (as in *N. castaneus*, *N. hesperus* and *N. punctatus*; e.g., Fig. 16G); posterior margin of fifth ventrite mesally weakly emarginated, set with a row of thick, flat spine-like setae (Figs 5D, 17C, D). Aedeagus (Fig. 18) nearly parallel sided, with basal piece between 0.3 and 0.6-times the length of parameres; median lobe with well-developed lateral basal apodemes, wider at base than base of each paramere, usually narrower at apex than preapical width of parameres; apex of median lobe rounded; parameres from slightly shorter to longer than median lobe, and only narrowing at apex; gonopore situated beyond midpoint of median lobe.

Larvae. The immature stages are unknown.

Etymology. Noun in apposition. Named after the small size of the beetles (the smallest known acidocerines), with the Greek word *nanos* meaning little and the Greek word *saphes* meaning distinct, in reference to the relative ease of recognizing the species of the genus. Genus is to be treated as neutral.

Distribution. Brazil (Pará), Guyana, Suriname. See Fig. 19.

Biology. Species are associated with stream margins, particularly where there are banks for margins of sand and roots.

Characters of taxonomic importance for *Nanosaphes*. In contrast to some to of the other acidocerines treated here, the known species of *Nanosaphes* are diagnosable by external characters alone.

Punctation. The well-marked ground and serial elytral punctures differentiate *N. punctatus* from the remaining species, in which the punctation is only shallowly marked.

Coloration. The most common and widespread species of *Nanosaphes* (*N. tricolor* and *N. hesperus*) have a distinctive yellow coloration on the pronotum, and can be distinguished from each other by the coloration of the head. The entire body of *N. castaneus* is uniform in coloration.

Posterior elevation of mesoventrite. In *Nanosaphes* the overall shape and sharpness of the carina formed in the posterior elevation of the mesoventrite aids species identification, where only *N. hesperus* has a sharp carina.

Density of abdominal pubescence. It is uncommon in the Acidocerinae that this character varies. Only *Nanosaphes tricolor* has densely pubescent abdominal ventrites, whereas the remainder species of the genus the pubescence is sparser.

Key to the species of *Nanosaphes*

1 Elytra with well-marked punctures (Fig. 15E, F); posterior elevation of mesoventrite flat .... ***N. punctatus***
– Elytra with shallowly marked punctures (e.g., Fig. 15A, B); posterior elevation of mesoventrite weakly to sharply carinate **2**
2 Coloration of the body rather uniformly brown (Fig. 15A–D)... ***N. castaneus***
– Coloration of pronotum yellow (see Fig. 16)........ **3**
3 Coloration of the head and clypeus uniformly dark brown (Fig. 16D); posterior elevation of mesoventrite weakly carinate; ventral surface densely pubescent (Fig. 16C) .... ***N. tricolor***
– Coloration of the head brown, with orange clypeus (Fig. 16H); posterior elevation of mesoventrite sharply carinate; ventral surface scantily pubescent (Fig. 16G)........ ***N. hesperus***

Nanosaphes castaneus sp. n.

http://zoobank.org/7B7969CA-49EB-495B-AEF2-4BF1BC8A74C9
Figs 15A–D; 18D; 19

Type material examined. Holotype (male): "**BRAZIL: Pará:** Rio Xingu/ Camp (52°22'W, 3°39'S)/ Altamira (ca 60km S.)/ 12 Oct 1986/ P. Spangler & O. Flint// Colln. #21, pond at 2nd/ palm grove on trail 1" (USNM). **Paratypes (3): BRAZIL:**

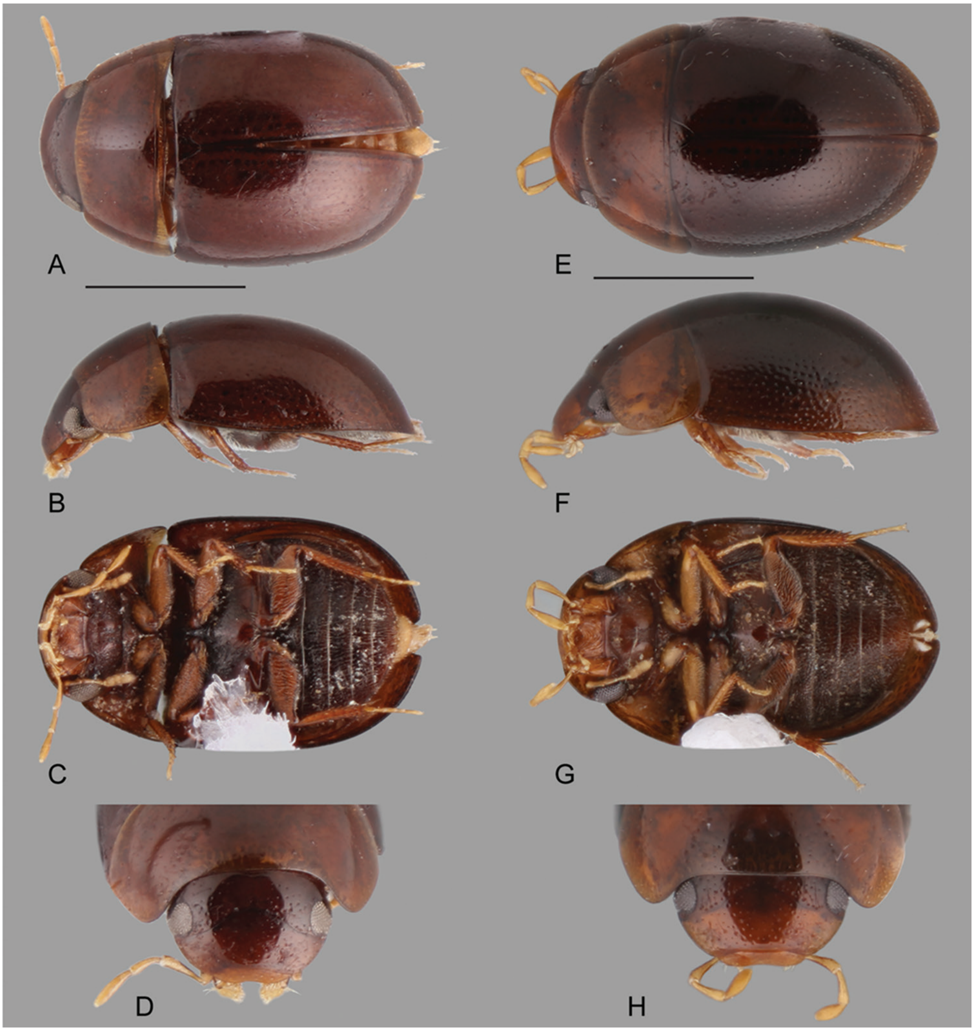

Figure 15. Habitus of *Nanosaphes* spp.: **A–D** *Nanosaphes castaneus*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Nanosaphes punctatus*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 0.5 mm.

Pará: Rio Xingu, Camp (52°22'W, 3°39'S)/ Altamira (ca 60km S.)/ 12 Oct 1986/ P. Spangler & O. Flint (1, USNM); same data as holotype (2, USNM, SEMC).

Differential diagnosis. *Nanosaphes castaneus* can be easily recognized by its smooth elytra (as opposed to rather coarsely punctate as in *N. punctatus*, compare Fig. 15A, B to Fig. 15E, F), and the uniform brown coloration along the body (as opposed to having yellow pronotum and brown elytra (as in *N. hesperus* and *N. tricolor*, compare Fig. 15A–D to Fig.16).

Description. Body length 1.3–1.4 mm, width 0.8–0.9 mm. Body elongate oval, weakly convex, uniformly brown throughout (Fig. 15A, B). Dorsal surface shallowly punctate. Posterior elevation of mesoventrite weakly carinate. Pubescence of ventral surface scanty. Aedeagus (Fig. 18C) with basal piece 0.4-times the length of parameres; parameres longer than median lobe, with rounded apex; gonopore situated near apical third of median lobe.

Etymology. Named in reference to the uniform brown coloration along the body, with the Latin word *castaneus* meaning brown, of the color of chestnuts.

Distribution. Brazil (Pará). Only known from one locality. See Fig. 19.

Biology. In referencing Spangler's original field notes, these specimens were collected in forested pond.

Nanosaphes hesperus **sp. n.**

http://zoobank.org/30B9FA31-A93F-4004-A94B-187EB6AD1070
Figs 16E–H; 17A–C; 18B; 19; 20A, C, D

Type material examined. Holotype (male): "**SURINAME**: Sipaliwini District/ 2°10.521'N, 56°47.244'W, 228 m/ Camp 1, on Kutari River; leg. Short/ & Kadosoe; forest stream/ 20.viii.2010; SR10-0820-01A/ 2010 CI-RAP Survey" (NZCS). **Paratypes (38): GUYANA: Region IX:** "2°06.492'N, 59°13.653'W, 274 m/ Parabara, N. side of river/ small flowing forested creek/ detritus margins & leaf packs/ leg. Short, Isaacs, Salisbury/ 3.xi.2013; GY13-1103-02A" (1, SEMC); **Region VI:** "4°09.143'N, 58°11.207'W, 105 m/ Upper Berbice, c. 1 km W/ Basecamp 1; washing sand/ banks; leg. A. Short; 22.iv.2014/ GY14-0921-03E" (1, SEMC); "margins of creek/ leg. Short, Salisbury, La Cruz/ 22.iv.2014/ GY14-0921-03H" (1, SEMC). **SURINAME: Sipaliwini District**: "2°21.776'N, 56°41.861'W, 237 m/ Camp 3, Wehepai; leg. Short &/ Kadosoe; sandy forest creek/ 4–6.ix.2010; SR10-0904-01A/ 2010 CI-RAP Survey" (19, SEMC); same, except "small stream/ 5.ix.2010; SR10-0905-01A" (1, SEMC); same, except "2°10.521'N, 56°47.244'W, 228 m/ Camp 1, on Kutari River/ Short & Kadosoe; forest stream/ 19.viii.2010; SR10-0819-02A" (1, SEMC); same, except "20.viii.2010; SR10-0820-01A" (8, SEMC); same, except "N 2.97731°, W 55.38500°, 200 m/ Camp 4 (low), Kasikasima; sandy/ stream on trail to METS camp/ 20.iii.2012; SR12-0320-02A/ leg. A. Short; 2012 CI-RAP Survey" (3, SEMC, including DNA voucher SLE485); "04°40.966'N, 56°11.262'W, 96 m/ Raleighfallen Nature Reserve/ plateau below Voltzberg; rock pool/ leg. A. Short, Maier & McIntosh/ 28.vii.2012; SR12-0728-01F" (1, SEMC); "04°40.910'N, 56°11.138'W, 78 m/ Raleighfallen Nature Reserve/ Voltzberg trail; margin of stream/ leg. C. Maier & V. Kadosoe/ 30.vii.2012; SR12-0730-01A" (1, SEMC); Raleighfallen Nature Reserve, 17.iii.2016, leg. Girón, SR16-0317-04A (1, SEMC, DNA voucher SLE1070).

Differential diagnosis. *Nanosaphes hesperus* (Fig. 16E–H) can be easily recognized by its smooth elytra (as opposed to rather coarsely punctate as in *N. punctatus*, see Fig. 15E, F), and the coloration pattern along the body, with brown elytra, yellow pronotum and brown head with orange clypeus (as opposed to uniform brown coloration along the body as in *N. castaneus*, or uniformly dark brown head (including the

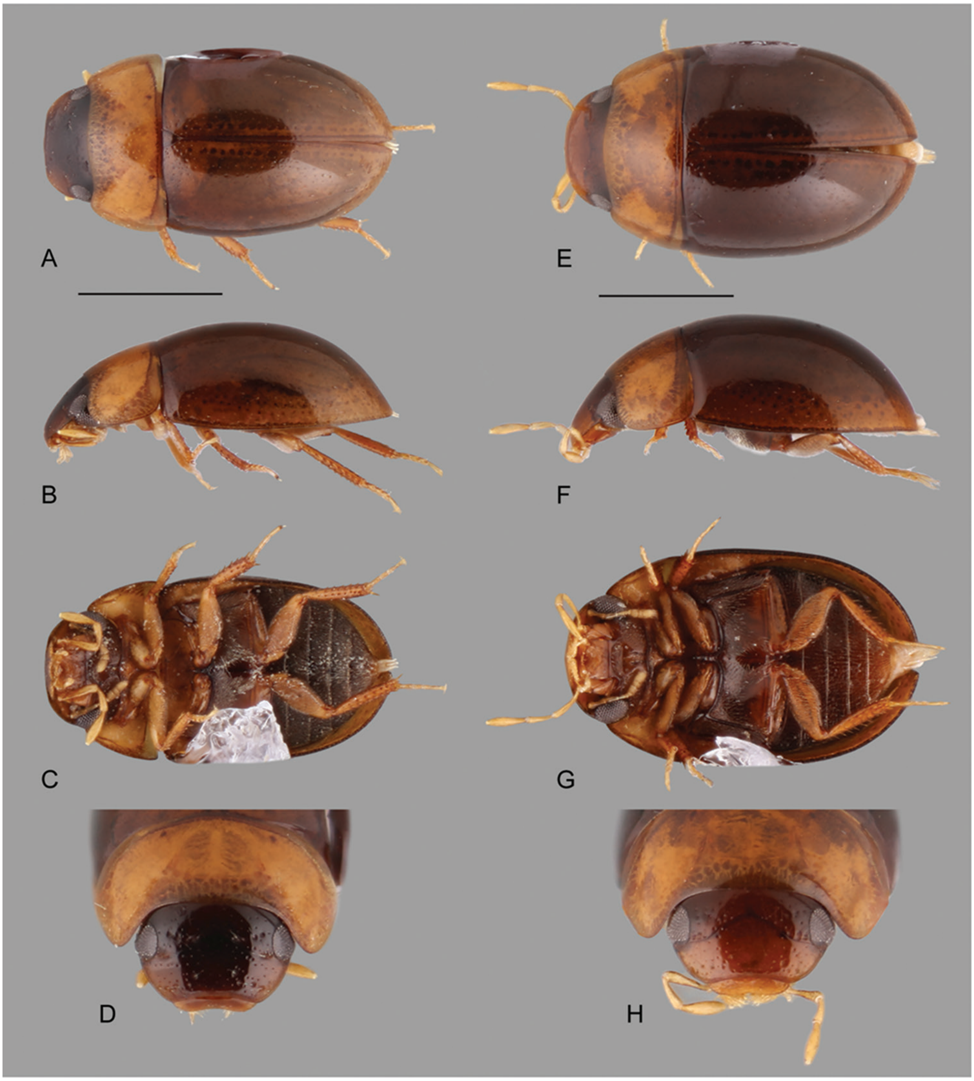

Figure 16. Habitus of *Nanosaphes* spp.: **A–D** *Nanosaphes tricolor*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E–H** *Nanosaphes hesperus*: **E** dorsal view **F** lateral view **G** ventral view **H** head. Scale bars: 0.5 mm.

clypeus) as in *N. tricolor*, see Fig. 16D). Furthermore, it differs from the remaining known species by the sharp, strongly elevated, and pointed carina on the mesoventrite (as opposed to weakly elevated).

Description. Body length 1.3–1.5 mm, width 0.7–0.9 mm. Body elongate oval, weakly convex, with brown head, orange clypeus, yellow pronotum and brown elytra (Fig. 16E–H). Dorsal surface shallowly punctate. Posterior elevation of mesoventrite sharply carinate. Pubescence of ventral surface scanty. Aedeagus (Fig. 18B) with basal

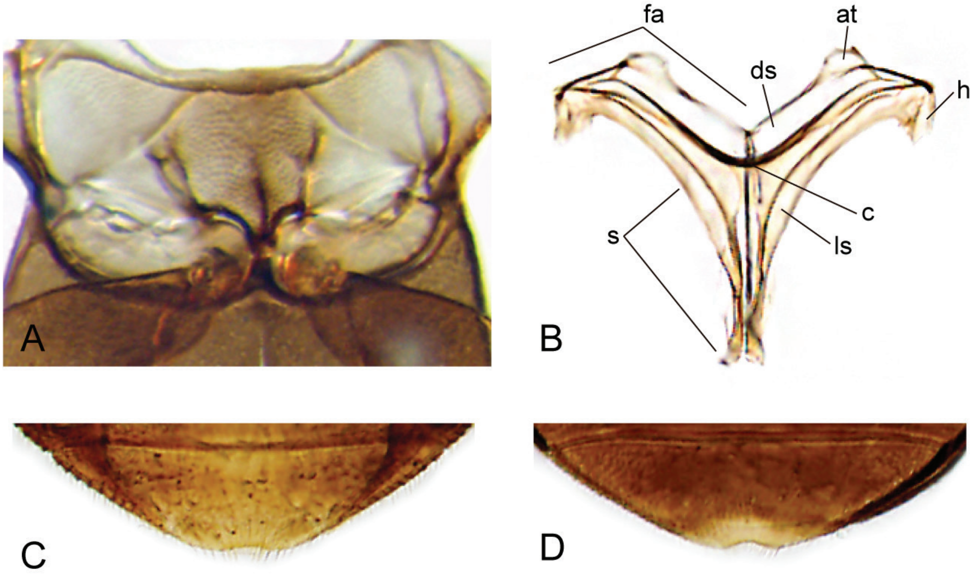

Figure 17. Thorax and abdomen of *Nanosaphes* spp.: **A–C** *Nanosaphes hesperus*: **A** ventral view of mesoventrite (white arrow pointing longitudinal carina) **B** posterior view of metafurca: (at) anterior tendon, (c) crux, (ds) dorsal sheath, (fa) furcal arm, (h) hemiductus, (ls) lateral sheath, (s) stalk **C** fifth abdominal ventrite **D** *Nanosaphes punctatus*, fifth abdominal ventrite.

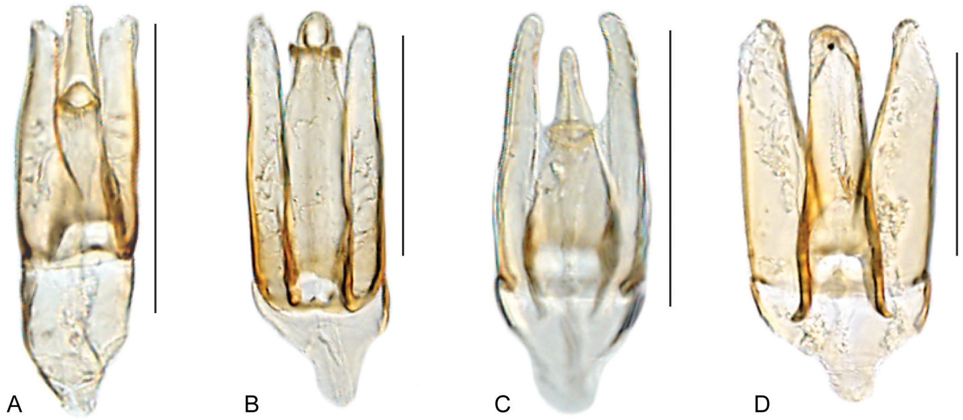

Figure 18. Aedeagus of *Nanosaphes* spp.: **A** *Nanosaphes tricolor* **B** *Nanosaphes hesperus* **C** *Nanosaphes castaneus* **D** *Nanosaphes punctatus*. Scale bars: 0.1 mm.

piece 0.35-times the length of parameres; parameres as long as median lobe, with narrowly round apex; gonopore situated near apex of median lobe.

Etymology. Named in reference to the gradation of orange to brown colorations along the body of the beetles, which resembles the colors of the sunset, with the Latin word *hesperus* meaning evening.

Distribution. Guyana, Suriname. Elevation range 105–228 m. See Fig. 19.

Biology. This species has been collected along the margins of forested streams (see Fig. 20A, C, D.

Nanosaphes punctatus sp. n.

http://zoobank.org/59E30D06-ADB4-4C39-8AE4-4ED03ED8F58F

Figs 15E–H; 17D; 18D; 19; 20B

Type material examined. Holotype (male): "**SURINAME**: Sipaliwini District/ 04°56.871'N, 55°10.911'W, 462 m/ Brownsberg Nature Park, forested/ stream with lots of detritus; leg./ Short, Maier, McIntosh; 4.viii.2012/ SR12-0804-01A" (NZCS). **Paratypes: (40): GUYANA: Region XII:** "5°0.730'N, 59°38.965'W, 585 m/ Upper Potaro Camp I (c. 7 km/ NW Chenapau), Ridge Trail/ leg. Short, Baca, Salisbury/ 11.iii.2014/ GY14-0311-02A" (32, SEMC, CBDG); "5°10.514'N, 59°28.970'W, 440 m/ Kaieteur National Park, trail by guest-/ house; forest pools; leg. Short/ Salisbury, La Cruz; 21.iii.2014/ GY14-0321-01B" (1, SEMC). **SURINAME: Sipaliwini District**: same data as holotype (6, SEMC, including DNA vouchers SLE 507 and 508); "3°55'36.0012", -56°11'17.9952", 600 m/ Central Suriname Nature Reserve: Tafelberg Summit, nr. Augustus Creek Camp; 17.viii.2013; leg. Short & Bloom; SR13-0817-01A" (1, SEMC, DNA voucher SLE 1069).

Differential diagnosis. *Nanosaphes punctatus* is readily recognized among its congeners by its coarse elytral ground punctation (as opposed to shallowly punctate) (see Fig. 15E, F). In addition, the dorsal outline in lateral view is more convex in comparison.

Description. Body length 1.2–1.4 mm, width 0.7–0.9 mm. Body elongate oval, moderately convex, uniformly brown throughout (see Fig. 15E–H). Dorsal surface coarsely punctate. Posterior elevation of mesoventrite flat. Pubescence of ventral surface scanty. Aedeagus (Fig. 18D) with basal piece 0.4-times the length of parameres; parameres nearly as long as median lobe, with round apex; gonopore situated near apex of median lobe.

Etymology. Named in reference to the relative coarseness of the dorsal punctation of the species, with the Latin word *puncta* meaning puncture.

Distribution. Guyana, Suriname. Elevation range 440–585 m. See Fig. 19.

Biology. This species was collected in small forested streams and pools with abundant detritus (Fig. 20B).

Nanosaphes tricolor sp. n.

http://zoobank.org/8A659E25-1129-4A7E-A696-3FD01BC7E3B6

Figs 5C, D; 16A–D; 18A; 19; 20D–F

Type material examined. Holotype (male): "**SURINAME**: Sipaliwini District/ N 2.97731°, W 55.38500°, 200 m/ Camp 4 (low), Kasikasima; sandy/ creek, trail to Kasikasima; leg. A. Short/ 22.iii.2012; SR12-0322-02A/ flotation; 2012 CI-RAP Survey" (NZCS).

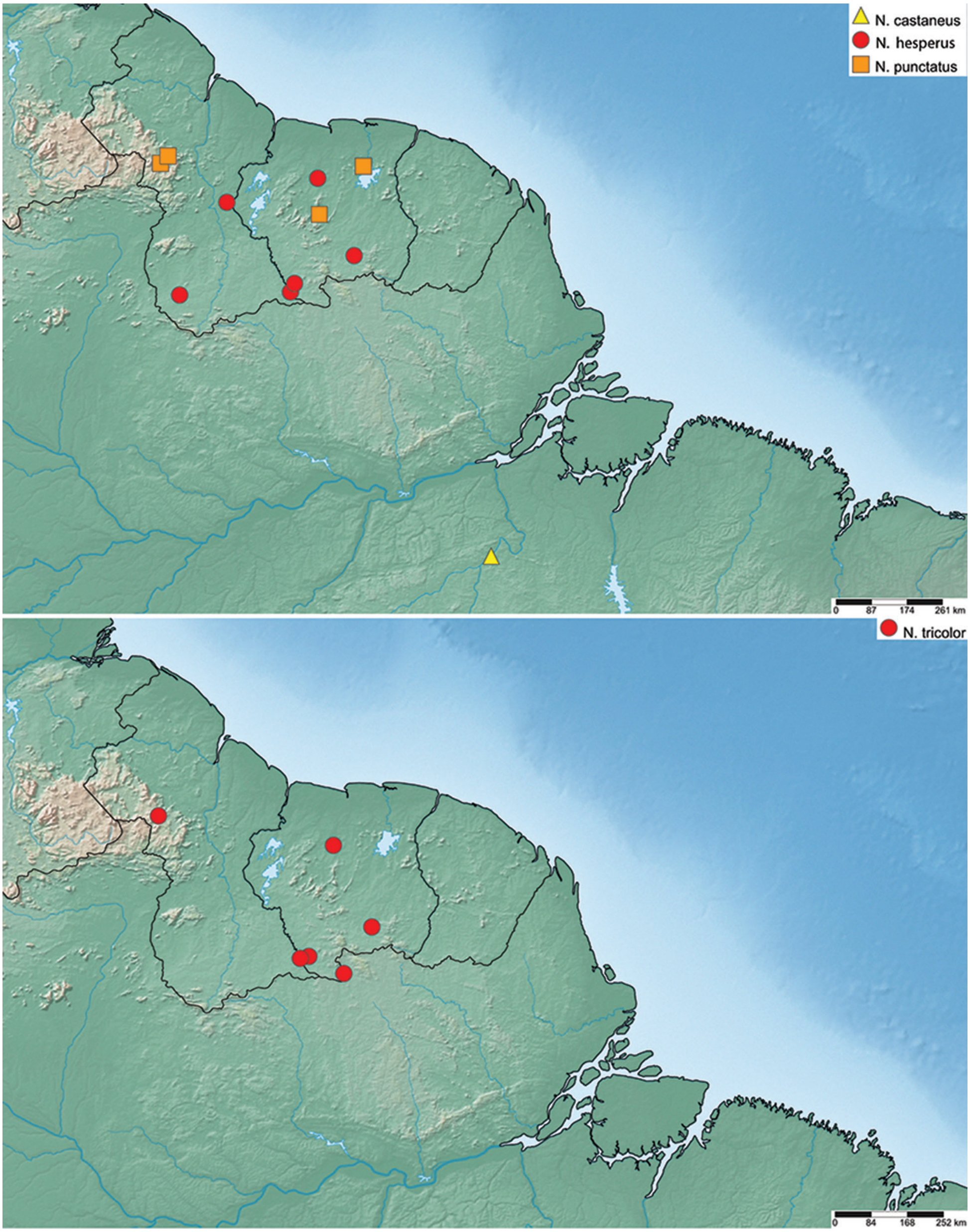

Figure 19. Distribution of *Nanosaphes* species.

Paratypes (136): GUYANA: Region XII: "5°17.823'N, 59°50.000'W, 684 m/ Ayanganna Airstrip, trail from/ Blackwater Creek Camp to Potaro/ River; sand/gravel washing in/ gravel bar; leg. A. Short / 18.iii.2014; GY14-0318-03C" (1, SEMC; DNA voucher SLE1067). **SURINAME: Sipaliwini District**: "2°21.776'N, 56°41.861'W, 237 m/ Camp 3, Wehepai; leg. Short &/ Kadosoe; sandy forest creek/ 4–6.ix.2010; SR10-0904-01A/ 2010 CI-

Figure 20. Habitat of *Nanosaphes* spp. **A** Habitat for *N. hesperus*, Guyana: near Parabara; collecting event GY13-1103-02A **B** Habitat of *N. punctatus*, Guyana, upper Potaro near Chenapau, collecting event GY14-0311-02A **C** Type locality and habitat for *N. hesperus*, Suriname, along Kutari River, collecting event SR10-0820-01A **D** Habitat for *N. hesperus* and *N. tricolor*, Suriname, near Kasikasima, collecting event SR12-0320-02A **E** Habitat for *N. tricolor*, Suriname, near Voltzberg, collecting event SR12-0729-02C **F** Habitat for *N. tricolor*, Suriname, Sipaliwini Savanna, collecting event SR17-0331-01B.

RAP Survey" (47, SEMC, including DNA voucher SLE130); same, except "small stream/ 5.ix.2010; SR10-0905-01A" (1, SEMC); same, except "2°19.280'N, 56°52.595'W, 224 m/ Rapids on Kutari River/ leg. A.E.Z. Short; forest stream/ 18.viii.2010; SR10-0818-01A" (1, SEMC); same, except "N 2.97731°, W 55.38500°, 200 m/ Camp 4 (low), Kasikasima; sandy/ stream on trail to METS camp/ 20.iii.2012; SR12-0320-02A" (4, SEMC); same data as holotype (9, SEMC); same, except "04°42.480'N 56°13.159'W, 24 m/ Raleighfallen Nature Reserve, trail/ to Raleighfallen; creek margins/ leg. Short, McIntosh, & Kadosoe/ 27.vii.2012; SR12-0727-03A" (3, SEMC); same, except "04°40.910'N, 56°11.138'W, 78 m/ Raleighfallen Nature Reserve / Voltzberg Station; sand bar in/ stream; leg. C. McIntosh / 29.vii.2012; SR12-0729-02C" (8, SEMC); same, except "Votlzberg trail; margin of stream; leg. C. Maier, V. Kadosoe; 30.vii.2012; SR12-0730-01A" (1, SEMC); "2°00.342'N, 55°58.149'W, 337 m/ Sipaliwini Savanna Nature Res./ 4-Brothers Mts.; clearwater stream/ sandy w/detritus; 31.iii.2017/ leg. Short & Baca; SR17-0331-01B" (32, SEMC); same, except "sandy w/ emergent veg; SR17-0331-01C" (19, SEMC); same, except "at night; leg. Short; SR17-0331-01F" (10, SEMC).

Differential diagnosis. *Nanosaphes tricolor* can be easily recognized by its smooth elytra (as opposed to rather coarsely punctate as in *N. punctatus*, see Fig. 15E, F), and the coloration pattern along the body, with uniformly dark brown head (including the clypeus, see Fig. 16D), yellow pronotum and brown elytra (see Fig. 16A, B; as opposed to uniform brown coloration along the body as in *N. castaneus*, Fig. 15E, H). It is similar to *N. hesperus* in the paler coloration of the pronotum, but differs from it by the uniform and darker coloration of the head (orange in *N. hesperus*) and the weak development of the longitudinal elevation of the mesoventrite (as opposed to strongly elevated as to form a sharp and pointed carina in *N. hesperus*).

Description. Body length 1.1–1.4 mm, width 0.7–0.75 mm. Body elongate oval, weakly convex, with uniformly dark brown head (including clypeus, Fig. 16D), yellow pronotum and brown elytra (Fig. 16A, B). Dorsal surface shallowly punctate. Posterior elevation of mesoventrite weakly carinate. Pubescence of ventral surface very dense. Aedeagus (Fig. 18A) with basal piece nearly 0.6-times the length of parameres; parameres slightly shorter than median lobe, with obliquely round apex; gonopore situated near apical third of median lobe.

Etymology. Noun in apposition. Named after the three colors present along the body of the beetles (uniformly dark head, yellow pronotum and brown elytra), with the Latin prefix *tri* meaning three and the Latin word *color*.

Distribution. Guyana, Suriname. Elevation range 24–684 m. See Fig. 19.

Biology. This species has been collected along the margins of forested streams (see Fig. 20D, F).

Chasmogenus Sharp, 1882

Chasmogenus Sharp, 1882: 72.
Dieroxenus Spangler, 1979: 753. **Syn. n.**

Discussion. In comparing the new taxa described here to existing genera, we observed striking similarities between the monotypic Andean genus *Dieroxenus* Spangler and the widespread genus *Chasmogenus* Sharp. *Dieroxenus* shares most diagnostic characters of New World *Chasmogenus*, including general body size, the presence of sutural striae (extremely rare in Acidocerinae), antennae with eight antennomeres, a longitudinal carina on the mesoventrite, and a "simple" tri-lobed aedeagus (Hebauer 1992). It does differ from *Chasmogenus* in a few respects: *Dieroxenus* has a slightly more robust body form, slightly shorter maxillary palps, and its elytral systematic punctures are enlarged and easily distinguished from the ground punctation. However, most if not all of these features could be attributed to the unusual seep-inhabiting nature of this species, while other *Chasmogenus* are known from streams and marshes. Additionally and perhaps most convincing morphologically, is that the aedeagal form of *Dieroxenus* (Fig. 21E) matches that of some Neotropical *Chasmogenus* (e.g., see Figs 1–4 in Short 2005).

When *Dieroxenus* was described nearly 40 years ago, the systematics and classification of the Hydrophilidae was radically different. *Chasmogenus* was then considered part of *Helochares*, and most genera that are now in the Acidocerinae were assigned to different tribes than they are today. Consequently, Spangler (1979) did not consider what we now call *Chasmogenus* when making his comparisons, and instead focused on its similarities and differences from *Enochrus*, which we now know is not very closely related (Short and Fikáček 2013).

Chasmogenus cremnobates **(Spangler, 1979), comb. n.**

Fig. 21

Dieroxenus cremnobates Spangler, 1979: 754

Type material examined. Holotype: "ECUADOR: Napo, Baeza (72 km E), 16 May 1975, Spangler, Langley, and Cohen" (USNM). **Paratypes: ECUADOR: Napo**: same data as holotype (44 males; 42 females); **Tungurahua:** "Baños (35 km E), 29 May 1975, Langley, Cohen, and Monnig (8 males; 6 females); "Baños (18 km E), 25 Jan 1976, Spangler, et al. (15 males; 18 females); "Baños (20 km E), 28 Jan 1976, Spangler, et al. (7 males; 6 females); "Baños (39 km E), 28 Jan 1976, Spangler, et al. (2 females).

Additional material. ECUADOR: Napo: "San Francisco de / Borja 17 Jan 1978/ 1610 m PJ Spangler/ & J. Anderson // seep on stream bank" (6 males, 6 females; USNM).

Key to the genera of New World Acidocerinae

1 Eyes absent. Known only from a cave in Ecuador .... ***Troglochares***
– Eyes present **2**
2 Eyes completely divided into dorsal and ventral sections by a lateral projection of frons. Size small (<3 mm) .... ***Quadriops***
– Eyes not divided into dorsal and ventral sections by frons. Size variable **3**

3 Labrum concealed by clypeus, elytral margins broadly explanate. Body extremely dorsoventrally compressed..***Helobata***

– Labrum not concealed by clypeus elytral margins not or at most weakly explanate. Body form variable but rarely dorsoventrally compressed...............**4**

4 Elytra with distinctly impressed sutural striae. Only Neotropical region...***Chasmogenus***

– Elytra without sutural striae. Both Neotropical and Nearctic **5**

5 Prosternum with strongly elevated median carina ....***Crucisternum***

– Prosternum without median carina; at most tectiform medially..................**6**

6 Metafemora entire glabrous. Size small (<3 mm) .... ***Tobochares***

– Metafemora pubescent at least on basal half or anterior third. Size variable...7

7 Fifth ventrite entire, without apical emargination or truncation. Antennae with nine antennomeres. Maxillary palps shorter than the width of the head...***Radicitus***

– Fifth ventrite with apical emargination or truncation. Antennae with eight or nine antennomeres. Maxillary palps variable in length **8**

8 Elytral systematic punctures very distinct, distinctly larger than surrounding ground punctation. Antennae with nine antennomeres...........***Katasophistes***

– Elytral systematic punctures indistinct, usually blending with surrounding ground punctation. Antennae with eight or nine antennomeres..................**9**

9 Antennae with nine antennomeres. Size variable, but rarely less than 4 mm. Extremely common and widespread throughout the New World....***Helochares***

– Antennae with eight antennomeres. Rare and only known from the Guiana Shield region of South America. Size very small (< 3 mm) **10**

10 Body form circular, rounded. Size very small (1.9-2.3 mm) .... ***Globulosis***

– Body form ovoid, parallel sided. Size exceedingly small (1.1–1.5 mm)...***Nanosaphes***

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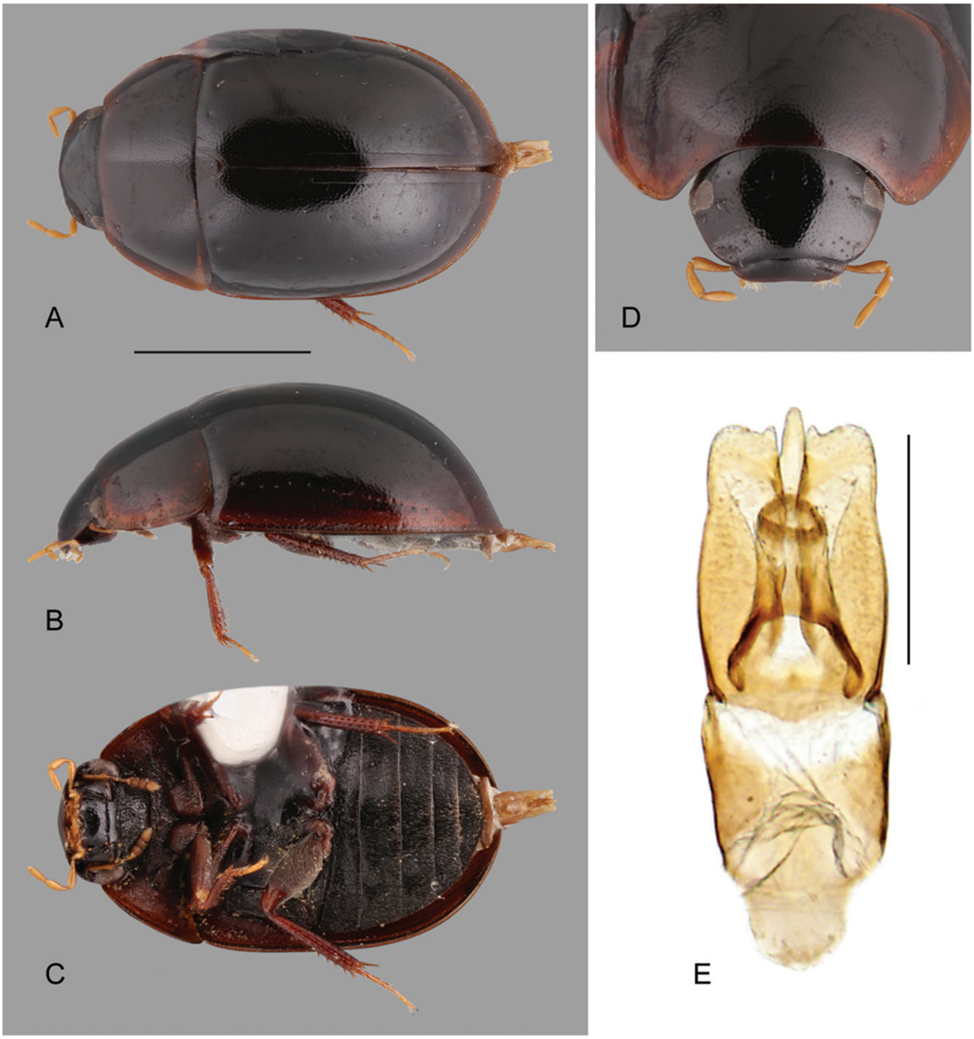

Figure 21. Habitus of *Chasmogenus cremnobates*: **A** dorsal view **B** lateral view **C** ventral view **D** head **E** aedeagus. Scale bar 1 mm.

References

García M (2001) Nueva subtribu, género y especie de Hydrophilini (Coleoptera: Hydrophilidae) del extremo suroriental de Venezuela. Boletín del Centro de Investigaciones Biológicas Universidad del Zulia 35: 151–160. http://produccioncientificaluz.org/index.php/boletin/article/view/3978

Girón JC, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 705: 115–141. https://doi.org/10.3897/zookeys.705.19815

Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophilidae). Biologiske Skrifter 40: 1–367.

Hansen M (1999) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. Insect Systematics & Evolution 30(2): 121–172. https://doi.org/10.1163/187631200X00228

Hebauer F (1992) The species of the genus *Chasmogenus* Sharp, 1882 (Coleoptera, Hydrophilidae). Acta Coleopterologica 8(2): 61–92. https://web.archive.org/web/20160304194744/http://www.hydrophiloidea.org/pdfs/Hebauer1992_Chasmogenus.pdf

Komarek A (2004) Taxonomic revision of *Anacaena* Thomson, 1859. I. Afrotropical species (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 74: 303–350.

Lawrence J, Ślipiński A (2013) Australian Beetles: morphology, classification and keys. CSIRO Publishing, Melbourne, Australia, 576 pp.

Short AEZ (2005) A review of the subtribe Acidocerina of Central America with special reference to Costa Rica (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 75: 191–226. http://www.zobodat.at/pdf/KOR_75_2005_0191-0226.pdf

Short AE, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51(1): 83–122. http://www.cercyon.eu/Publications_PDF/ShortFikacek_CatalogueUpdateII.pdf

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38(4): 723–752. https://onlinelibrary.wiley.com/doi/abs/10.1111/syen.12024

Short AEZ, García M (2014) A new genus of egg case-carrying water scavenger beetle from the Guiana Shield (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 3835(2): 251–262. https://biotaxa.org/Zootaxa/article/view/zootaxa.3835.2.5

Short AEZ (2018) Systematics of aquatic beetles (Coleoptera): current state and future directions. Systematic Entomology 43(1): 1–18. https://doi.org/10.1111/syen.12270

Short AEZ, García M, Girón JC (2017) Revision of the Neotropical water scavenger beetle genus *Globulosis* García, 2001 (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4232 (2): 271–281. https://biotaxa.org/Zootaxa/article/view/zootaxa.4232.2.10

Spangler PJ (1979) A new genus of madicolous beetles from Ecuador (Coleoptera: Hydrophilidae: Hydrobiinae). Proceedings of the Biological Society of Washington 92(4): 753–761. https://www.biodiversitylibrary.org/item/110033#page/787/mode/1up

Spangler PJ, Steiner WE (2005) A new aquatic beetle family, Meruidae, from Venezuela (Coleoptera: Adephaga). Systematic Entomology 30(3): 339–357. https://doi.org/10.1111/j.1365-3113.2005.00288.x

Velázquez de Castro AJ (1998) Morphology and taxonomy of the genus *Sitona* Germar 1817, (I): The metendosternite (Col., Curc.). In: Colonnelli E, Louw S, Osella G (Eds) 2. Taxonomy, ecology and distribution of Curculionoidea (Coleoptera: Polyphaga). XX International Congress of Entomology, Florence (Italy), August 1996. Atti del Museo Regionale di Scienze Naturali, Torino, 109–123.