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Synonymy of *Mangabea* and *Stenorhamphus*, with the description of two new species (Hemiptera: Reduviidae: Emesinae: Collartidini)

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Abstract. Rarely collected, Collartidini (4 genera, 14 species) are a tribe of Emesinae (Hemiptera: Heteroptera: Reduviidae), the thread legged assassin bugs, that have retained a number of plesiomorphic features within Emesinae. The group has long been believed to be restricted to equatorial Africa, Madagascar, and Sri Lanka, with more recent additions from the Canary Islands, Sudan, Israel, and Taiwan, and a fossil species from Baltic amber. The discovery of two undescribed species from Thailand and Malaysia (Borneo) has created the need for a reassessment of genera within Collartidini. We analysed a morphological matrix of 25 characters and 11 ingroup species that represents the four collartidine genera, finding that while *Collartida* Villiers, 1949 is recovered as monophyletic, *Collarhamphus* Putshkov & Popov, 1995 and *Stenorhamphus* Elkins, 1962 render *Mangabea* Villiers, 1970 paraphyletic. We here synonymise the fossil genus *Collarhamphus* and extant genera *Mangabea* and *Stenorhamphus*, provide a revised diagnosis and description of *Stenorhamphus*, and describe *Stenorhamphus segerak*, new species and *S. phuphan*, new species, from Malaysia (Sarawak) and Thailand, respectively. Lateral and dorsal habitus images as well as images of diagnostic characters are provided. A map showing the known distribution of *Stenorhamphus* spp. is provided, in addition to images highlighting diagnostic genus and species level characters.

Key words. Reduviidae, Emesinae, taxonomy, biodiversity, new species, new synonymy

INTRODUCTION

Emesinae, the thread legged assassin bugs, are a species rich subfamily within Reduviidae, including over 950 species in 95 genera (Maldonado, 1990). Emesinae are widely distributed, and one of the few subfamilies of Reduviidae with numerous endemic island species (Wygodzinsky, 1966). Spider-associated behaviors occur in various groups of Emesinae (Soley et al., 2011; Wignall & Taylor, 2011; Mercado & Santiago-Blay, 2015) and may have contributed to their diversification. Collartidini, with only four described genera, two of which are monotypic, is the smallest of the six tribes within Emesinae (Putshkov & Popov, 1995; Villiers, 1970; Wygodzinsky, 1966). Wygodzinsky (1966) hypothesised Collartidini to form the sister group to the rest of Emesinae in his scheme of relationships of Emesinae and closely related subfamilies Saicinae and Visayanocorinae, based on characters such as the relatively unmodified (compared to other Reduviidae) wing venation, simple foreclaws, and setae on the labium. Recent phylogenetic analyses (Smith et al., in prep.) support the notion that Collartidini are a relatively early diverging lineage of Emesinae and place them as sister taxon to Leistarchini within a paraphyletic Emesinae. This effectively supports the original classification by Villiers (1949), who treated *Collartida* as part of the Leistarchini.

The three extant genera included within Collartidini are *Collartida* Villiers, 1949, *Stenorhamphus* Elkins, 1962 and *Mangabea* Villiers, 1970. *Collartida* was originally described based on one species from the Democratic Republic of Congo, with eight additional species documented from Chad, Sudan, Israel, and Spain (Canary Islands) (Maldonado, 1990), and one more recently from Taiwan (Rédei & Tsai, 2010), resulting in a substantial range extension. *Stenorhamphus* was erected by Elkins (1962) to accommodate a species originally described by Distant (1906) in the genus *Guithera* Distant, 1906, subfamily Leistarchini, from Sri Lanka. When Villiers (1970) discovered collartidine specimens from Madagascar that distinctly differed from the mostly African *Collartida*, he placed this species in his new genus *Mangabea*. The two subsequently described collartidine species from Madagascar were also placed in this genus (Chłond et al., 2018; Weirauch, 2008). The fourth genus of Collartidini is *Collarhamphus* Putshkov & Popov, 1995 that comprises one species from Baltic amber, suggesting that Collartidini are relatively old and have conserved a fairly uniform and distinctive habitus for more than 36 million years (Wolfe et al., 2009). Diagnostic features appear to clearly separate *Collartida* from the three other genera. In contrast, the distinction between *Stenorhamphus* and *Mangabea*, and to a lesser extent *Collarhamphus,* is less clear cut, and is further blurred by the combination of diagnostic features observed in two undescribed species discovered by us from Malaysia

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(Borneo: Sarawak) and Thailand. While documenting and describing these two species, we realised that a reassessment of generic boundaries across Collartidini based on a cladistic analysis has been overdue.

We here document and describe the two newly discovered species of Collartidini that were collected in a yellow pan trap trail in Sarawak and a Malaise trap in Thailand. To determine their placement in either *Stenorhamphus* or *Mangabea*, we include the two species in a matrix of morphological characters, with representatives of all extant and fossil collartidine genera, and outgroup taxa.

MATERIAL AND METHODS

Material. The male specimen from Sarawak was collected by two of us in a yellow pan trap, while surveying Heteroptera at the Nanga Segerak Ranger Station in Lanjak Entimau Wildlife Sanctuary. The male specimen from Thailand was collected in a Malaise trap as part of the TIGER (Thailand Inventory Group for Entomologists) initiative. The *Stenorhamphus nubiferus* (deposited at the British Museum of Natural History) and *Mangabea barbiger* (deposited at the California Academy of Sciences) holotypes were examined and imaged by the authors. Images of the *Mangabea orientalis* (deposited at the Muséum National d'Histoire Naturelle, Paris, France) holotype were studied by the authors. *Collarhamphus mixtus* and *Mangabea troglodytes* were documented with such detail that it was not necessary to examine the type specimen.

Imaging, dissections, and measurements. Specimens were imaged using a Leica DFC 450 C110 Microsystems system (Leica, Wetzlar, Germany) with a Planapo 1.0× and 2.0× objective. Leica113 Application Suite V4.3 software was used to stack images, with an average of 30 images per stack. Dissections of male genitalia followed standard protocols for the dissection of Reduviidae (e.g., Forero & Weirauch, 2012). Measurements were made in Photoshop V19.1.5; head and pronotum lengths were measured dorsally along the midline.

Map. The map was built using the online version of SimpleMappr (Shorthouse, 2010), using localities from holotype collection sites when available, for fossil species locality from center of collection site was used.

Abbreviations. The abbreviations used in figures and text are as follows: bp, basal plate of aedeagus; bpext, basal plate extension of aedeagus; cly, clypeus; cp, capitate process; dps, dorsal phallothecal sclerite; ell, endosomal lateral lobe; escl, endosoma sclerites; est, endosomal struts of aedeagus; evl, endosomal ventral lobe; fsc, fascicle; lr, labrum; ph, phallosoma; prs, posterior pronotal spine; mns, metanotal spine; rm, cross vein between media and radius; st, setae.

Phylogenetic analysis. Building on characters that have previously been used to diagnose collartidine genera (e.g., Wygodzinsky, 1966; Putshkov & Popov, 1995; Weirauch, 2008), we coded a morphology matrix of 25 characters and 11 species of Collartidini and five outgroup taxa representing leistarchine Emesinae (*Bagauda similis* Wygodzinsky, 1966; *Ploiaria stysi* Ishikawa & Okajima, 2008 *in* Ishikawa, Susila & Okajima, 2008), Visayanocorinae (*Carayonia camerunensis* Villiers, 1951), and Saicinae (*Kiskeyana palassaina* Weirauch & Forero, 2007; *Oncerotrachelus amazonensis* Gil-Santana, 2013). Eleven taxa of Collartidini were included, comprising four species of *Collartida,* all three species of *Mangabea*, the single described species of *Stenorhamphus* and *Collarhamphus*, and the two undescribed collartidine species. The five outgroup taxa consisted of two species of leistarchine Emesinae, two Saicinae, and one Visayanocorinae. Characters were coded using published species descriptions (Villiers, 1949, 1961, 1969, 1979; Elkins 1962; Wygodzinsky, 1966; Linnavuori, 1974; Putshkov & Popov, 1995; Weirauch & Forero, 2007; Ishikawa et al., 2008; Weirauch, 2008; Rédei & Tsai, 2010; Gil-Santana, 2013; Chłond et al., 2018); type images (*Stenorhamphus nubiferus* [Distant, 1906]), as well as specimens examined and/or documented in this paper (*Mangabea orientalis* Villiers, 1970: Muséum National d'Histoire Naturelle, Paris, France; *Mangabea barbiger* Weirauch, 2008: California Academy of Sciences; *Stenorhamphus phuphan,* new species: Queen Sirikit Botanic Garden, Chang Mai (Thailand); *Stenorhamphus segerak,* new species: National University of Singapore, Zoological Reference Collection). A parsimony analysis in TNT V1.5 (Goloboff & Catalano, 2016) using New Technology search with ratchet, sectorial search, drift and tree fusing resulted in three most parsimonious trees. The strict consensus tree was generated in WinClada V1.00.08 (Nixon, 1999–2002).

Morphological characters used in analysis, coded from specimens and the following literature.

1. Total size: less than 5.5 mm (0), greater than 5.5 mm (1). Total size was measured from the apex of the head to the posterior tip of the abdomen, in dorsal view. If membrane surpassed tip of abdomen, measured from apex of head to posterior tip of membrane. When size was not given in a species description we estimated it from figures if a scale bar was provided.

Head (Figs. 3B, G, 4B, H; Rédei & Tsai, 2010, Fig. 3; Weirauch, 2008, Fig. 1E; Weirauch & Forero, 2007, Fig. 1B; Putshkov & Popov, 1995, Fig. 2; Elkins, 1962, Fig. 19).

2. Head to total length ratio: ratio less than 0.1 (0), ratio between 0.1 and 0.2 (1), ratio greater than 0.2 (2). This ratio was determined using species descriptions and images (approximations). The distance from the apex of the head to the anterior portion of the neck was divided by the total body length.
3. Head, dorsal view: distance from posterior head margin to anterior margin of eye more than 1/3 length of head (0), about 1/3 of head (1), less than 1/3 (2).
4. Eye shape: drop-shaped (Figs. 3G, 4H) (0), subhemispheric (Weirauch, 2008, Fig. 1E) (1). Putshkov & Popov (1995) used eye shape to distinguish between *Mangabea*, *Stenorhamphus*, *Collartida* and *Collarhamphus.* The

shape of the eye in dorsal view is coded as drop-shaped when the anterior and posterior eye margins are straight (or almost so) while the lateral margin (in dorsal view) is curved; all margins are curved in the subhemispheric eye shape.

5. Pair of ventral setae in position 1 (anterior): absent (0), present (Fig. 3B) (1). Collartidini may have up to five pairs of setae ventrally on the head (in addition to the fascicle or setae anteriorly on the gena), in the area where the gula merges into the gena in (see Figs. 3B, 4B). They appear to be species specific and have been used as diagnostic features for several species. The pair of setae we refer to as position 1 is the anteriormost pair.
6. Pair of ventral setae in position 2 (anterior): absent (0), present (Fig. 3B) (1). This is the second pair of setae; it is located anterior to the eye.
7. Pair of ventral setae in position 3 (posterior): absent (0), present (Fig. 3B) (1). This is the first pair of setae located posterior to the eye.
8. Pair of ventral setae in position 4 (posterior): absent (Fig. 3B) (0), present (Fig. 4B) (1). This is the second pair of setae posterior to the eye.
9. Pair of ventral setae in position 5 (lateral to eye): absent (Fig. 3B) (0), present (Fig. 4B) (1). This is the only pair of setae on the lateral surface of the head, directly posterior to the eye.
10. Ventrolateral vestiture anteriorly on gena: absent (Weirauch & Forero, 2007, Fig. 1B) (0), one pair of setae (Rédei & Tsai, 2010, Fig. 3) (1), two pairs of setae (Putshkov & Popov, 1995, Fig. 2) (2), fascicle of multiple setae (Fig. 4B) (3). At the anterior-most end of the head, ventrally on the gena, species of Collartidini show a range of types of vestiture, or the vestiture is absent.
11. Second labial (first visible) segment longest: absent (Fig. 4B) (0), present (Rédei & Tsai, 2010, Fig. 2) (1). In the original diagnosis of *Collartida* the second labial segment is longer than segments three and four, and it reaches the anterior margin of the eye; the proportion of anterior head region and labial segments is different in other taxa. The second labial segment in Visayanocorinae (*Carayonia camerunensis*) is relative to both the anterior region of the head and other labial segments, longer than that seen in *Collartida*.
12. Third labial (second visible) segment longest: absent (0), present (Fig. 3B) (1). The length of the third (second visible) labial segment appears to be more variable, it is not consistently longer when the second labial segment is not the longest. The second and third labial segments can be of equal length, or the fourth labial segment can be the longest.
13. Ventral surface of second labial segment: without setae (Elkins, 1962, Fig. 19) (0), with one or two pairs of setae (Rédei & Tsai, 2010, Fig. 3) (1), at least apical half with dense vestiture (Fig. 4B) (2). Vestiture is common on the labium of Collartidini, Saicinae and Visayanocorinae, but the distribution and shape of setae vary.
14. Ventral surface of third labial segment: without setae (Elkins, 1962, Fig. 19) (0), with one or two setae (Rédei & Tsai, 2010, Fig. 3) (1), with row of stiff setae (Fig. 3B) (2). The third labial segment does not show the high degree of setal variation found on the second labial segment.

Thorax (Figs. 3G, 4F, H; Weirauch & Forero, 2007, Fig. 1E).

15. Length of posterior lobe of pronotum (dorsal view): shorter than anterior lobe (0), approximately equal to anterior lobe (Fig. 3G) (1), distinctly longer than anterior lobe (Fig. 4H) (2).
16. Spine on mesonotum: absent (0), present (Weirauch & Forero, 2007, Fig. 1E) (1).
17. Spine on pronotum: absent (0), present (Fig. 4F) (1).

Foreleg (Figs. 3A, C, 4A, F; Rédei & Tsai, 2010, Fig. 4; Ishikawa et al., 2008, Fig. 21; Weirauch & Forero, 2007, 1E).

18. Acetabula: forward opening (Fig. 3A) (0), not forward opening (Weirauch & Forero, 2007, 1E) (1). Forward opening acetabula in the forelegs have historically been used to diagnose Emesinae and separate them from Saicinae and Visayanocorinae.
19. Number of ventral spine-like setae on forecoxa: none (Ishikawa et al., 2008, Fig. 21) (0), one (1), two (Rédei & Tsai, 2010, Fig. 4) (2), three (3), four (Fig. 4F) (4).
20. Large spine-like setae of forefemur: not extending to apex (Rédei & Tsai, 2010, Fig. 4) (0), extending to apex (Fig. 4A) (1), absent (2).
21. Foretarsal length: first tarsal segment shortest (Fig. 3c) (0), first tarsal segment not shortest (Ishikawa et al., 2008, Fig. 21) (1).

Forewing (Figs. 5A, B; Ishikawa et al., 2008, Fig. 23; Weirauch, 2008, Fig. 4B; Rédei & Tsai, 2010, Fig. 5).

22. Shape of basal cell of forewing: roughly rhomboid (Fig. 5A, B) (0), roughly pentagonal (Weirauch, 2008, Fig. 4B) (1), roughly triangular (Rédei & Tsai, 2010, Fig. 5) (2), basal cell absent (Ishikawa et al., 2008, Fig. 23) (3). The basal cell is located proximad of the discal cell (as seen in Fig. 5). The cell is here coded to be rhomboid when at least two opposing veins are not roughly parallel, pentagonal when there are four veins or cross veins with opposite sides roughly parallel, and roughly triangular when there appear to be only three bordering veins and cross veins.
23. Length of discal cell of forewing: short, less than 3/4 of the length between rm and the tip of wing (Rédei & Tsai, 2010, Fig. 5) (0), long, more than 3/4 of length between rm and tip of wing (Figs. 5A, B) (1). The length of the discal cell varies mostly between short (in *Collartida*) and long (in all other ingroup taxa).
24. Cross vein proximal to rm vein: absent (Figs. 5A, B) (0), present (Weirauch, 2008, Fig. 4B) (1). This cross vein was first noticed in *Mangabea orientalis* and is also present in *M. barbiger*. The cross vein creates an extra cell in the wing.
25. Distal tip of corium reaching to: about 3/5 between rm cross vein and apex of wing (Fig. 5A) (0), 4/5 between rm cross vein and apex of wing (Fig. 5B) (1), apex or

nearly apex of wing (Ishikawa et al., 2008, Fig. 23) (2), less than 3/5 (3). The distal tip of corium varies in its extension towards the apex of the wing. The coded ratios were obtained by dividing the distance between the rm cross vein and the apex of the distal tip of the corium and the apex of the wing.

PHYLOGENETIC ANALYSIS

The analysis resulted in three most parsimonious trees (see Fig. 1). The three trees differ in the relationships between species of *Collartida*; since investigating relationships within this genus are not the focus of this study, we do not discuss these differences. As relationships between *Stenorhamphus* species did not differ between fundamental trees, the first was arbitrarily chosen as an example (Fig. 1). Collartidini is supported as a monophyletic group (unambiguous optimisations only) by the distal tip of the corium reaching about 4/5 between rm cross vein and apex of wing (25:1). The small size (total size less than 5.5 mm; char 1:0) is a synapomorphy of *Collartida*, as are the pair of setae anteriorly on the gena (10:1) and the two ventral spine-like setae on the forecoxa (19:2). The clade comprising *Collarhamphus* + *Stenorhamphus* + *Mangabea* is supported by two synapomorphies, the dense vestiture apically on the ventral surface of the second labial segment (13:2) and a row of stiff setae on the ventral surface of the third labial segment (14:2). *Stenorhamphus nubiferus* and *Collarhamphus mixtus* Putshkov & Popov, 1995, render *Mangabea* paraphyletic; *Stenorhamphus segerak*, new species was recovered as sister to *Stenorhamphus phuphan*, new species + *Stenorhamphus. nubiferus.* Though uncommon, several fossils from Baltic amber have been placed within extant genera, e.g., within Coleoptera (Alekseev, 2013). As *Collarhamphus* is nested within the *Mangabea* + *Stenorhamphus* clade and is not the first Baltic fossil placed within an extant genus we feel confident in including it within *Stenorhamphus*. Clearly, for the past 30 or so million years *Stenorhamphus* has maintained a uniform and distinctive morphology. Based on the outcomes of this analysis, we are synonymising *Collarhamphus, Mangabea* and *Stenorhamphus.*

TAXONOMY

Stenorhamphus Elkins, 1962

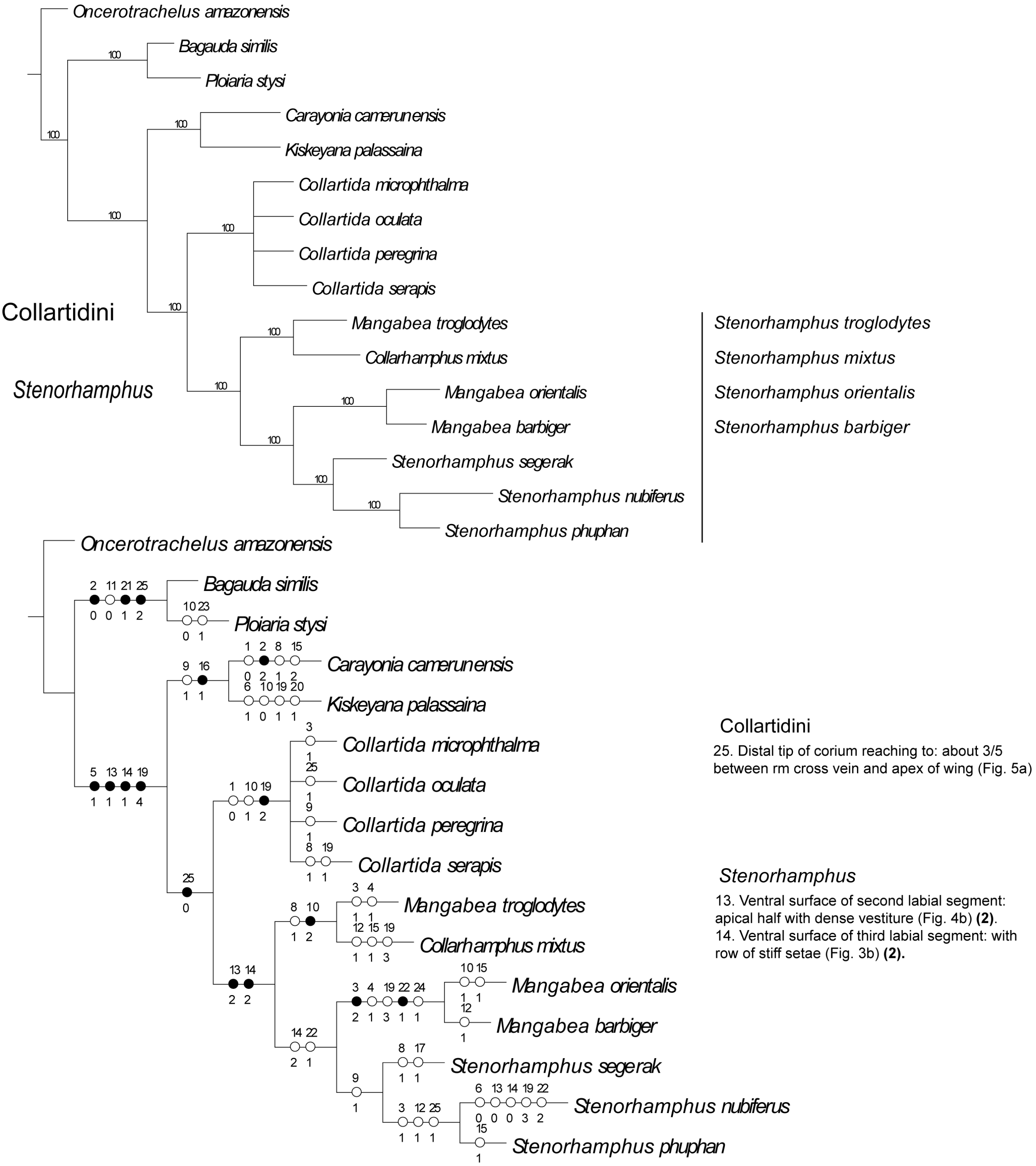
(Tables 1, 2, Figs. 1–8)

Stenoramphus Elkins, 1962: 422. Type species: *Stenorhamphus nubiferus* (Distant, 1906).
Stenorhamphus Wygodzinsky, 1966: 86.
Mangabea Villiers, 1970: 809, **new synonym**. Type species: *Mangabea orientalis* Villiers, 1970.

Type species. *Guithera nubifera* Distant, 1906, by original designation.

Diagnosis. Recognised within Collartidini by long discal cell on the forewing, second labial segment not reaching anterior margin of the eye with either a row of stiff setae along the entire segment or apically, and third labial segment with row of stiff setae.

Redescription. Total length 5.7–11.8 mm. COLOURATION: fairly uniform brown or yellow, coxa and abdomen ventrally often lighter. VESTITURE: Body and appendages covered with evenly spaced, short setae (Figs. 3A, B, G, 4F); Head: ventral surface of head with three to five pairs of long, stout setae located posterior to antennifer, at anterior and posterior margins of eye (Figs. 3B, 4B), with either fascicle or two pairs of stout setae on gena ventrad of apex of maxillary plate (Figs. 3B, 4B); second labial segment (first visible) with fascicle of medium-length stout setae on ventral surface in apical half of segment or with row of stiff setae along entire segment (Figs. 3B, 4B), third labial segment (second visible) with short setae on entire ventral surface (Figs. 3B, 4B); scapus of antenna with short setae (Figs. 3B, 4B) Legs: forecoxa, in addition to short vestiture, with posterodorsal series and three or four stout, long setae (Figs. 3A, 4A), foretibia and foretarsus with relatively dense vestiture (Figs. 3C, 4C). STRUCTURE: Head: (Figs. 2A, B, C, D, 3B, G, 4B, H) elongate, anteocular portion long (Figs. 3B, 4B), postocular large and sometimes semiglobular (Figs. 3B, 4B), apex of stout antennifer approximately equidistant from apex of clypeus and anterior margin of eyes (Figs. 3B, 4B), head anterior to antennifer narrow in dorsal view (Figs. 3B, 4B), maxillary plate very small, triangular (Fig. 3B, 4B), mandibular plate very small (Figs. 3B, 4B); gena with pronounced, elongate anterior portion (Figs. 3B, 4B), clypeus slender, not produced, labrum small, elongate (Figs. 3B, 4B). Eyes: either globulose and subsemispheric in dorsal perspective or drop–shaped (Figs. 3G, 4H); consisting of relatively few, large ommatidia (Figs. 3B, 4B). Antenna: extremely long, slender (Figs. 2A, B, C, D). Labium (Figs. 3B, 4B): second (first visible) labial segment slender, elongate, not reaching anterior margin of eye, third (second visible) labial segment slender and elongate, fourth (third visible) segment slender, tapering towards apex, second, third or fourth labial segment longest. Thorax (Figs. 3B, G, 4F, H): pronotum longer than wide, anterior and posterior lobes separated by distinct furrow (Fig. 3B, 4F); posterior lobe slightly wider than long, distinctly wider than anterior lobe, except in *Stenorhamphus troglodytes*, new combination, where anterior lobe is wider than posterior lobe, slightly depressed medially, posterior margin concave, with *Stenorhamphus segerak*, new species (Fig. 4F) or without spine laterally on posterior lobe; scutellum subrectangular (Fig. 4G). Legs (Figs. 2A, C, 3A, C, D, E, 4A, C, D, F): slender, foreleg distinctly stouter and shorter than mid and hind leg, hind leg longer than middle leg (Figs. 2A, C), tarsi with three, slender tarsomeres, first tarsomere very short, second and third tarsomeres of equal length (Figs. 3C, 4C); foreleg with coxa very long and slender (Figs. 3A, 4A), trochanter spined, femur straight, relatively slender (Figs. 3E, 4A), tibia straight, slightly wider toward the apex (Fig. 4A); mid and hind legs with coxae ovoid, femora and tibiae very long and slender. Forewing (Figs. 5A, B): if macropterous, forewing elongate, R vein with setae along basal portion, basal area between R, M+Cu, Pcu, and posterior margin of wing slightly more sclerotised than actual membrane, M and Cu fused, basal cell rhomboid or



Collartidini

25. Distal tip of corium reaching to: about 3/5 between rm cross vein and apex of wing (Fig. 5a)

Stenorhamphus

13. Ventral surface of second labial segment: apical half with dense vestiture (Fig. 4b) **(2)**.
14. Ventral surface of third labial segment: with row of stiff setae (Fig. 3b) **(2).**

Fig. 1. Phylogenetic hypothesis of Collartidini, based on morphological characters. Upper phylogeny: Fundamental parsimony tree, built using 25-character morphology matrix. Percentages above branches are jackknife support values (100 replications). As each fundamental tree differs only in relationships among *Collartida,* the first tree was arbitrarily chosen for jackknife analysis. Lower phylogeny: Strict consensus tree out of three equally parsimonious trees, with 11 Collartidini and 5 outgroup species. Numbers above branches refer to characters from morphology matrix, numbers below branches refer to character states. Synapomorphies for Collartidini and *Stenorhamphus* are listed.

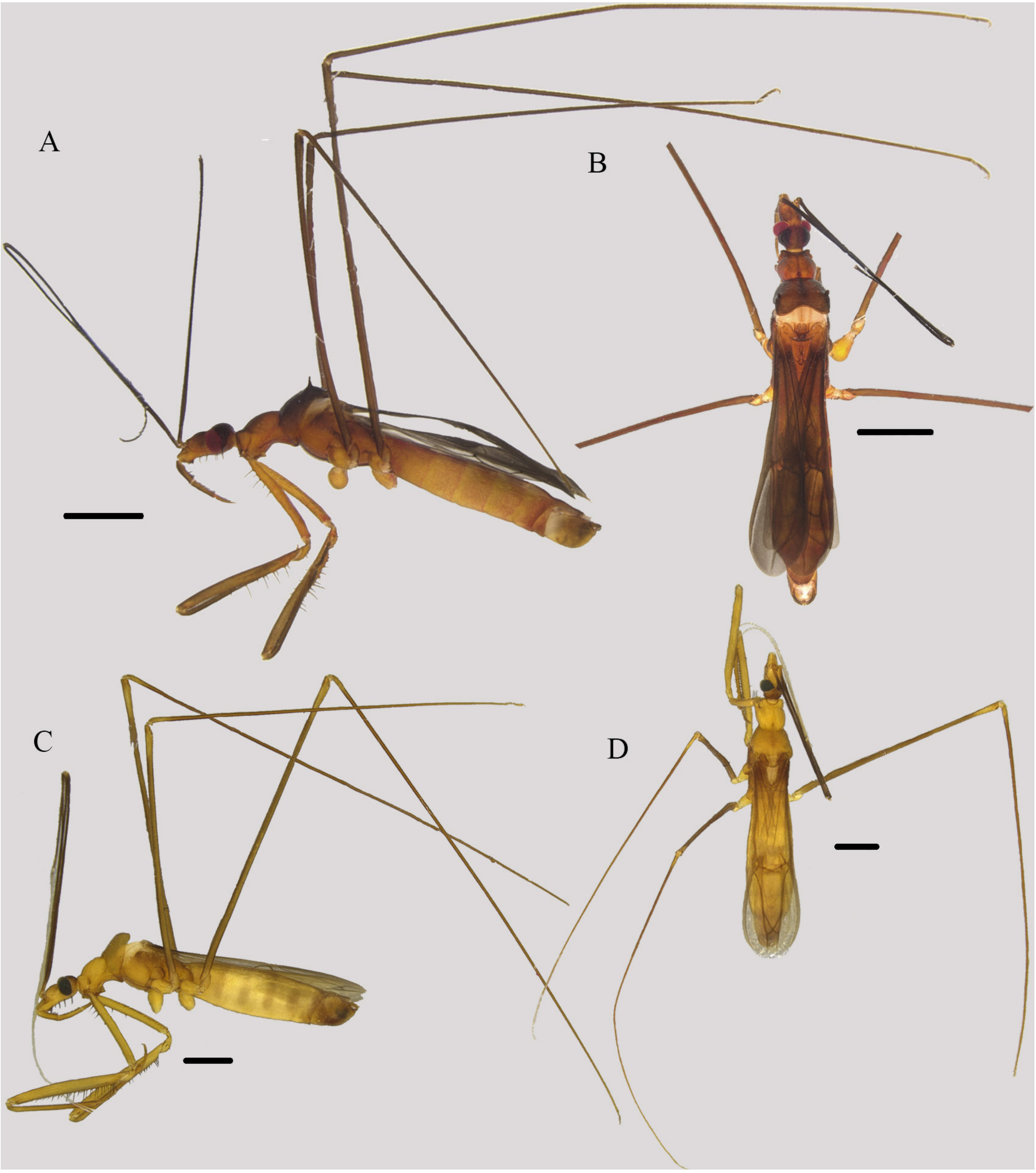


Fig. 2. Dorsal and lateral habitus of the holotypes of *Stenorhamphus segerak,* new species and *S. phuphan,* new species. A, *S. segerak*, male, lateral (note four spines on head, spines along labium, spine on posterior lobe of pronotum, long coxa and antenna); B, *S. segerak*, male, dorsal (note spines on posterior lobe of pronotum, length of hemelytra, size of postocular region, length of posterior lobe of pronotum); C, *S. phuphan*, male, lateral (note ventral spines on head, length of mid and hind legs, general colouration); D, *S. phuphan*, male, dorsal (note long legs, postocular segment present).

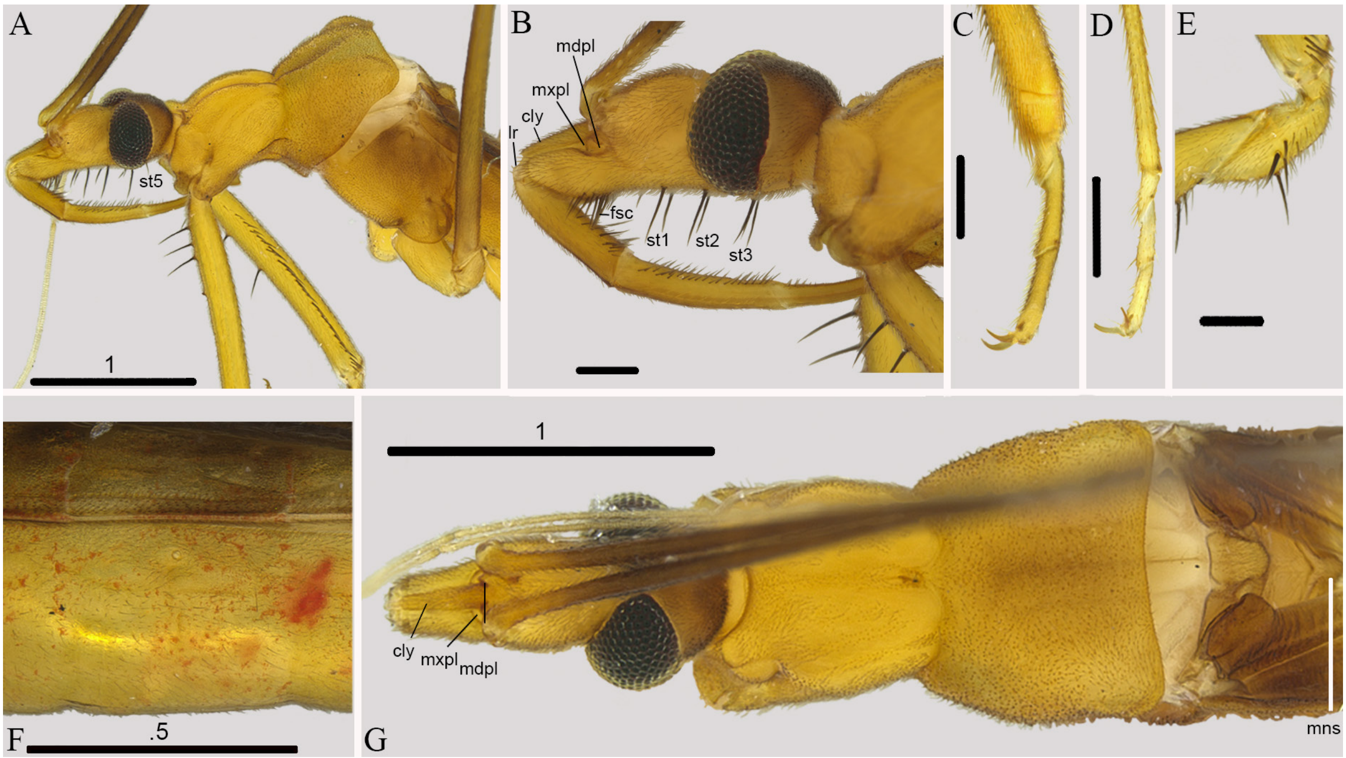


Fig. 3. *Stenorhamphus phuphan* details of head, legs and metanotum. Scale set to 0.2 mm unless otherwise specified. A, Head and thorax, lateral view (two pairs of ventral setae anterior to eye, one pair of ventral setae posterior to eye, one pair of lateral setae posterior to eye); B, Head, lateral view (fascicle, setae 1, 2, 3, labrum (lr), clypeus (cly), maxillary plate (mxpl), mandibular plate (mdpl)); C, Foretarsus (simple); D, Midtarsus (simple); E, Foretrochanter (four spines); F, Spiracle on 7th abdominal segment; G, Head, dorsal view, pronotum, metanotum (clypeus, eyes drop-shaped, metanotal spine).

pentagonal, discal cell very long and slender, rmcu cross vein absent or present (Figs. 5A, B). Abdomen (Figs. 2A, B, C, D, 3F, 4E): elongate ovoid, lateral margin smooth, second to seventh spiracle small, circular, on mediosternites (Fig. 3F, 4E), eighth spiracle on dorsolateral surface of segment 8. Genitalia (Figs. 6, 7): segment 8 well developed, membranous on dorsal surface; pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Fig. 6); parameres slender, curved, apex rounded (Fig. 6); aedeagus (Fig. 7) with basal plates stout and strongly curved and capitulate process relatively large, ponticulus basilaris slender or nonexistent, basal plate extension relatively short (Figs. 7A, D), basal plate struts short (Figs. 7G, I), dorsal phallothecal sclerite curved, more heavily sclerotised anteriorly and posteriorly (Fig. 7A), endosoma with sclerotised ventral and lateral lobes with small spicules (Fig. 7E).

Discussion. Prior to the discovery of the two new Collartidini species from the Oriental Region described below, though morphological differences were small, geographic boundaries kept *Stenorhamphus* (Sri Lanka) and *Mangabea* (Madagascar) separate. However, with the additions of *Stenorhamphus segerak*, new species and *Stenorhamphus phuphan*, new species, it became clear that the characters defining *Collarhamphus, Stenorhamphus* and *Mangabea* overlap, making the assignment of the two new species to genus difficult. The discovery of the species from Borneo also considerably extends the known species range distributions of Collartidini further south in the Oriental Region. As Collartidini are extremely rarely collected, most species descriptions are based solely on the holotype. This makes it impossible to evaluate the variability of morphological features within species, and negatively impacts our ability to identify species-diagnostic characters. Previous authors have also sometimes relied on geographic distribution to assign species to existing or new genera (e.g., Villiers [1970] in describing *Mangabea*). Our phylogenetic analysis is an effort to better understand character distributions across genera, and to identify genus-diagnostic characters that show low homoplasy. We refrain from a full revision of *Stenorhamphus*, and key to species, for two reasons: the recently described taxa from Madagascar (Weirauch, 2008; Chłond et al., 2018) are well documented and revised diagnoses and descriptions are unnecessary. In contrast, the redescription of *Stenorhamphus nubiferus* by Elkins (1962) does not comprehensively document this species, but since both the holotype and paratype appear to be in poor shape, we believe that fresh material from Sri Lanka will be critical to better document this species. Since the non-Madagascan species of *Stenorhamphus* are currently clearly separated by their geographic distribution, and the three Madagascan species are morphologically very distinct (see Weirauch, 2008; Chłond et al., 2018), we are not providing a key to species.

Elkins (1962) original spelling of *Stenorhamphus nubiferus* was *Stenoramphus nubifera.* Wygodzinsky (1966) used the spelling *Stenorhamphus nubiferus,* which has subsequently been used by all later authors (Maldonado, 1990; Putshkov & Popov, 1995; Rédei, 2004; Rédei & Tsai, 2010) except

Fig. 4. *Stenorhamphus segerak* details of head, legs and metanotum. Scale set to 0.5 mm unless otherwise specified. A, Head and thorax, lateral view (4 spines on forecoxa, spines along femur, trochanter spined); B, Head, lateral view (Four pairs of spines dorsally on head, two pairs laterally postocular, fascicle on apical portion of head, spines along labium, clypeus [cly], maxillary plate [mxpl], mandibular plate [mdpl], gena [ge], labrum [lr]); C, Foretarsus (simple); D, Midtarsus (simple); E, Spiracle on 6th abdominal segment; F, Head and pronotum, lateral view (Spine on posterior lobe of pronotum, evenly spaced hairs along antenna); G, Mesoscutellum (lateral edge rounded ridge, anterior portion sub-rectangular); H, Head, pronotum and metanotum dorsal view (pronotal spine [prs], clypeus, drop-shaped eyes).

Weirauch (2008) who included a "[sic]". *Stenorhamphus nubiferus* is therefore in prevailing usage, "that usage of the name which is adopted by at least a substantial majority of the most recent authors concerned with the relevant taxon, irrespective of how long ago their work was published." (International Code of Zoological Nomenclature, fourth edition) and we are adopting the spelling used by Wygodzinsky (1966).

This revision not only greatly enlarges the range of *Stenorhamphus,* but also places the age of the genus at approximately 36 to 54 million years old (Wolfe et al., 2009) greatly increasing our understanding of the evolution of the group. It is now clear that *Stenorhamphus* species*,* despite being rarely collected, are widespread, and have maintained relatively similar morphological characters for around 30 million years.

***Stenorhamphus barbiger* (Weirauch, 2008), new combination**

Mangabea barbiger Weirauch, 2008: 394.

Distribution. Currently only known from the holotype collected at Parc National Ranomafana in Fianarantsoa, Madagascar, via Malaise trap at a forest edge at fairly high elevation (1,130 m, 21.2261°S, 47.3698°E), and from one male specimen collected from Province Fianarantsoa, Manombo Special Reserve camp site 32 km SSE of Farafangana via Malaise trap in lowland rainforest (36 m, 23.0218°S, 47.720°E). Deposited at the California Academy of Sciences, UCR_ENT 00005202 and UCR_ENT 00127634.

Discussion. In our analysis, *Stenorhamphus orientalis* and *S. barbiger*, new combination, are identified as sister taxa by

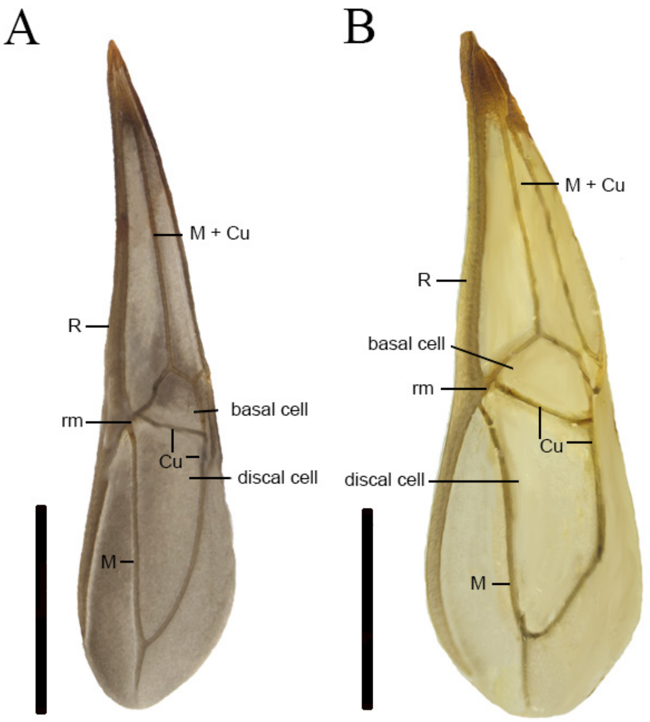


Fig. 5. *Stenorhamphus segerak* and *S. phuphan* forewing. Anterior wing margin on the left. A, *S. segerak* forewing, Pcu vein present but not visible in image; B, *S. phuphan* forewing.

several synapomorphies, including wing venation and head shape. *Stenorhamphus barbiger* differs from *S. orientalis* by the fascicle of stout setae on the anterior area of the gena (two pairs of setae in *S. orientalis*) and the posterior pronotal lobe being slightly longer than the anterior. *Stenorhamphus orientalis* is found in NE Madagascar (Villiers, 1970), while *S. barbiger* is found in SE Madagascar (Weirauch, 2008). Though *S. troglodytes* is also found in Madagascar, it was collected along the eastern side of the country in a cave and appears to have diverged significantly from *S. barbiger* and *S. orientalis.*

Stenorhamphus mixtus (Putshkov & Popov, 1995), new combination

Collarhamphus mixtus Putshkov & Popov, 1995.

Holotype. Male, from Baltic amber, Coll. Geological-Paleontological Institute and Museum, University of Hamburg; Typ.Kat.Nr.3602. Locality used in Fig. 8 based on approximation of Baltic amber collection sites.

Discussion. *Stenorhamphus mixtus* was described as a fossil in the genus *Collarhamphus* due to apparently sharing similarities with all three extant Collartidini genera. As the three genera of Collartidini share many similarities, distinguishing between them can be extremely difficult. However, our morphological analyses placed *Collarhamphus* within the *Mangabea* + *Stenorhamphus* clade. Though not within Emesinae, previously described coleopteran Baltic amber fossils have been placed within extant genera (Alekseev, 2013). We feel confident in synonymising *Collarhamphus* with *Stenorhamphus*. This further emphasises the age of this group to be between 36 to 54 million years old (Wolfe et al., 2009) and that little morphological change appears to have occurred during this period.

Stenorhamphus nubiferus (Distant, 1906)

Guithera nubifera Distant, 1906: 365.
Stenoramphus nubifera: Elkins, 1962: 423.
Stenorhamphus nubiferus: Wygodzinsky, 1966: 86.

Distribution. This species is only known from Peradeniya in Sri Lanka, (approximately 7.26°N, 80.59°E). Both the holotype and the paratype are deposited at British Museum of Natural History. No data is given on how it was collected.

Discussion. *Guithera nubifera* was described by Distant (1906), based on the holotype and one paratype. Elkins (1962) recognised that it did not belong in *Guithera* and erected the new genus *Stenorhamphus* based on examination of the female paratype. We have examined the holotype that is in poor condition.

Stenorhamphus orientalis (Villiers, 1970), new combination

Mangabea orientalis Villiers, 1970: 811.

Distribution. Currently known from Maroantsetra district, Fampanambo in Madagascar (–15.3735° S, 49.6216° E). Holotype and allotype deposited at the Muséum National d'Histoire Naturelle, Paris, France, paratype deposited at the Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

Discussion. See discussion of *S. orientalis*.

Stenorhamphus phuphan, new species

(Figs. 1–3, 5B, 6E–H, 7C, D, H, I, 8)

Diagnosis. Recognised within *Stenorhamphus* by the total length approximately 6.9 mm, one pair of setae posterior to each eye, setae along apex of second labial segment, along entire third segment, and basally along the fourth segment, four spines on the trochanter, fascicle of stout setae on the anterior area of the gena, postocular region long, not globulose, posterior lobe of pronotum approximately equal to anterior lobe, legs long, mid and hind coxae longer than length of abdomen, without spines on posterior lobe of pronotum.

Description. *Male*: small (total length, holotype: 6.89 mm) COLOURATION: general colouration yellow, with base of wings and posterior portion of head brown (Figs. 2C, D). Head: postocular region brown, anterior anteocular region lighter (Fig. 3B). Antenna: brown, flagellomeres light brown. Labium: light brown to yellow. Thorax: anterior pronotum yellow, posterior dark yellow to brown. Legs: coxae light brown to yellow, trochanters, femora, tibiae, and tarsi pale brown. Wings: basally brown, rest hyaline. Abdomen: tergites yellow; mediosternites pale brown, laterosternites somewhat darker; pygophore brown. VESTITURE: as in

Table 1. *Stenorhamphus phuphan,* new species and *S. segerak,* new species measurements.

In mm	**Length**						
	Total	Head	Anteocular	Ant. pron. lobe	Post. pron. lobe	Visible scutellum	Wing
Stenorhamphus segerak	5.70	0.81	0.20	0.59	0.66	0.12	3.32
Stenorhamphus phuphan	6.89	1.06	0.15	0.65	0.70	0.17	4.43
	Labium			**Width**			
	Lab. 2	Lab. 3	Lab. 4	Head	Ant. pron. lobe	Post. pron. lobe	Abdomen
Stenorhamphus segerak	0.31	0.32	0.34	0.52	0.52	0.73	0.86
Stenorhamphus phuphan	0.38	0.50	0.48	0.60	0.63	0.90	1.03

Table 2. Collartidini morphology matrix. Includes 25 characters based on diagnostic characters used in previous analyses. Outgroup taxa listed first, then *Collartida* spp., then *Stenorhamphus* spp.

Taxon										**1**										**2**					
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Bagauda similis	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	2	1	3	0	0	2
Ploiaria stysi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1	0	2
Carayonia camerunensis	0	2	0	0	1	0	1	1	1	3	1	0	1	1	2	1	0	1	4	0	0	2	0	0	3
Kiskeyana palassaina	1	1	0	0	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	1	0	?	?	?	?
Oncerotrachelus amazonensis	1	1	0	0	0	0	0	0	0	3	1	0	0	0	2	0	1	1	0	2	0	0	0	1	3
Collartida microphthalma	0	1	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	?
Collartida oculata	0	?	0	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	1
Collartida peregrina	0	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	0	0	2	0	0	2	0	0	0
Collartida serapis	0	1	0	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	1	?	0	2	0	0	0
Collarhamphus mixtus	1	1	0	0	1	0	1	1	0	2	0	1	2	2	1	0	0	0	3	0	0	0	0	0	0
Mangabea orientalis	1	?	2	1	1	1	1	0	0	1	0	0	3	2	1	0	0	0	3	0	0	1	1	1	0
Mangabea barbiger	1	1	2	1	1	1	1	0	0	3	0	1	2	2	2	0	0	0	3	1	0	1	1	1	0
Mangabea troglodytes	1	1	1	1	1	1	1	1	0	2	1	0	3	2	0	0	0	0	4	0	0	?	?	?	?
Stenorhamphus nubiferus	1	1	1	0	1	0	1	0	1	3	0	1	0	0	2	0	0	0	3	1	0	2	1	0	1
Stenorhamphus phuphan	1	1	1	0	1	1	1	0	1	3	0	1	3	2	1	0	0	0	4	1	0	0	1	0	1
Stenorhamphusa segerak	1	1	0	0	1	1	1	1	1	3	0	0	2	2	2	0	1	0	4	1	0	0	1	0	0

genus description with the following additions: Head: ventral surface with three to four pairs of long, stout setae located posterior to antennifer, at anterior and posterior margins of eye, lateral surface of head with one long, stout setae posterior to eye (four ventral and one lateral setae visible on right side, three setae on left) (Figs. 3A, B) fascicle of eight stout setae on gena ventrad of apex of maxillary plate (Figs. 3A, B); second labial segment (first visible) with medium-length stout setae on ventral surface in apical half of segment (Figs. 3A, B). Legs: forecoxa, in addition to short vestiture, with posterodorsal series and four stout, long setae anteroventral (Figs. 3A), foretrochanter with four stout setae on anterior surface (Fig. 3E), ventral surface of forefemur with about 16 medium stout setae in basal 2/3, interspersed with short setae (Fig. 2C). STRUCTURE: Head (Figs. 2C, D, 3A, B, G): postocular region long and slender, anteocular region less globulose than in *S. segerak*, new species. Thorax (Figs. 2C, D, 3A, G): posterior lobe wider than long, distinctly wider than anterior lobe, slightly depressed medially and with distinct, raised, lateral areas in posterior half of lobe, posterior margin slightly concave (Figs. 2C, D, 3A, G). Raised portion of mesoscutellum tongue shaped (Fig. 3G).

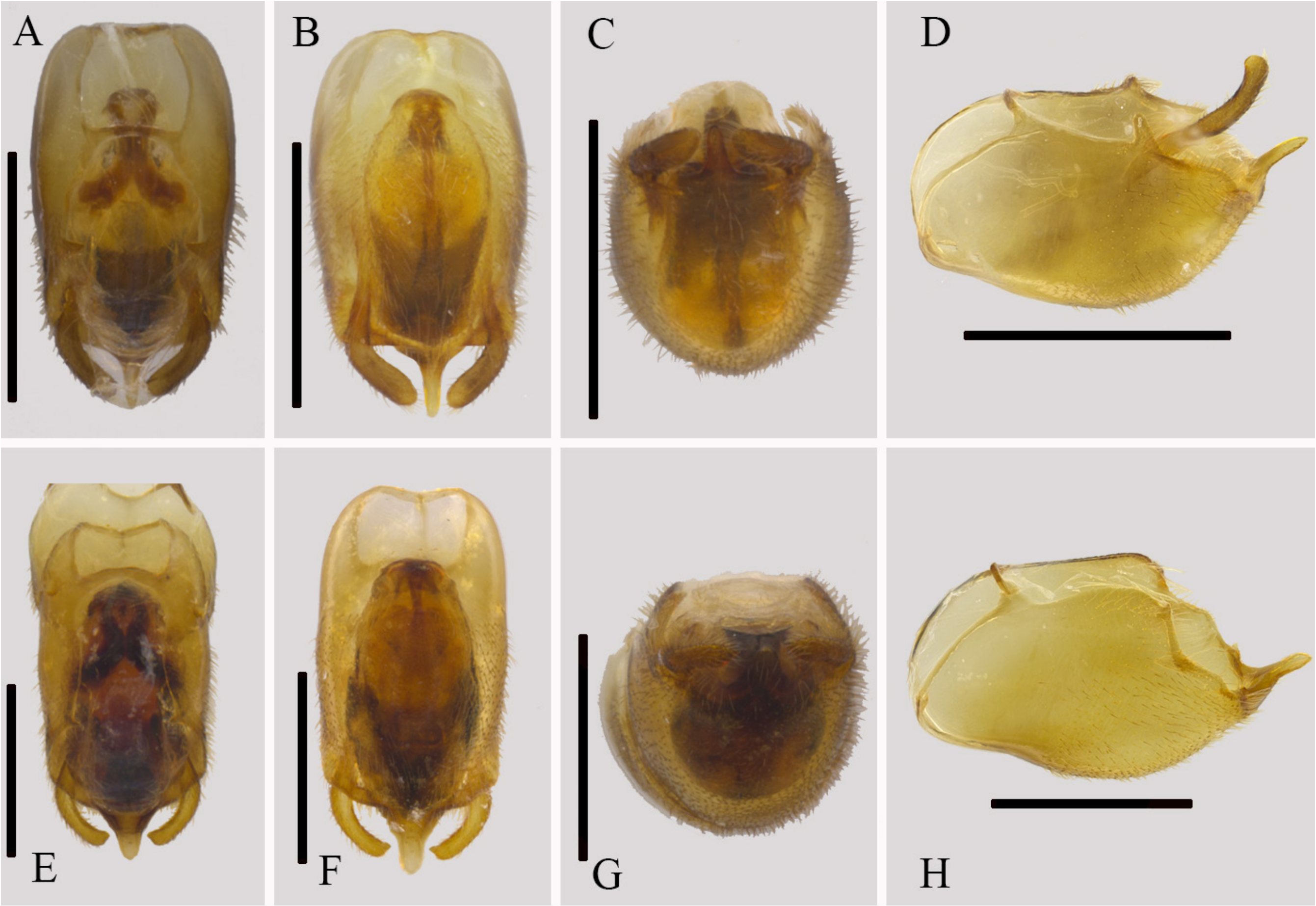


Fig. 6. Pygophores of *Stenorhamphus segerak* and *S. phuphan* in dorsal, ventral, posterior and lateral views. Scale set to 0.5 mm. A–D, *S. segerak* pygophore, dorsal, ventral, posterior, and lateral view respectively; E–H, *S. phuphan* pygophore, dorsal, ventral, posterior, and lateral view respectively.

Legs (Figs. 2C, D, 3A, C, D, E). Wings (Figs. 2D, 5B): elongate, surpassing apex of abdomen, rmcu cross vein not present (Fig. 5B). Abdomen (Figs. 2C, D, 3F). Genitalia (Figs. 6E, F, G, H, 7C, D, H, I): segment 8 well developed; pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Figs. 6E, F, G, H); parameres slender, curved, apex pointed (Figs. 6E, F, 7C); aedeagus (Figs. 7D, H, I) with basal plates stout and strongly curved, ponticulus basilaris very slender to nonexistent, basal plate extension relatively short, stout (Fig. 7D), dorsal phallothecal sclerite heavily sclerotised posteriorly (Fig. 7A), endosoma with ventral and lateral, heavily sclerotised lobes, lateral lobes as tall as wide (Figs. 7D, H, I).

Measurements. See Table 1.

Female. Unknown.

Etymology. Named after the locality of the holotype, Phu Phan National Park in Thailand; a noun in apposition.

Distribution. Only known from the type locality in Thailand.

Biology. Collected in lowland dry dipterocarp forest with deciduous trees and high canopy cover.

Type material. Holotype: male, THAILAND: Sakon Nakhon: Phu Phan National Park, behind forest protection unit at Huay Wien Prai, 17.1143°N, 104.0054°E, 387m, 25 Feb – 3 March 2007 Malaise trap, Sailom Tongboonchai (RCW4869), type deposited in the Queen Sirikit Botanic Garden, Chang Mai (Thailand) (QSBG).

Discussion. Most similar to *S. nubiferus* due to the following shared characters: the distance from the posterior margin of the head to the anterior margin of the eye is approximately 1/3 the total length of the head (3:1), the third labial segment is the longest (12:1), and the pterostigma reaches 4/5 between rm cross vein and apex of wing (25:1). However, it is separated from *S. nubiferus* by the length of the posterior lobe of the pronotum in dorsal view being approximately equal to the anterior lobe (15:1), the pair of ventral setae in position 2 present (6:1), and four ventral spine-like setae on forecoxa (19:4).

***Stenorhamphus segerak*, new species**
(Figs. 1, 2, 4, 5A, 6A–D, 7A, B, E–G)

Diagnosis. Recognised within *Stenorhamphus* by the relatively small total length (5.7 mm), two pairs of stout setae posterior to the eye, spines on the trochanter, fascicle of stout setae on the anterior area of the gena postocular region developed, posterior lobe of pronotum longer than

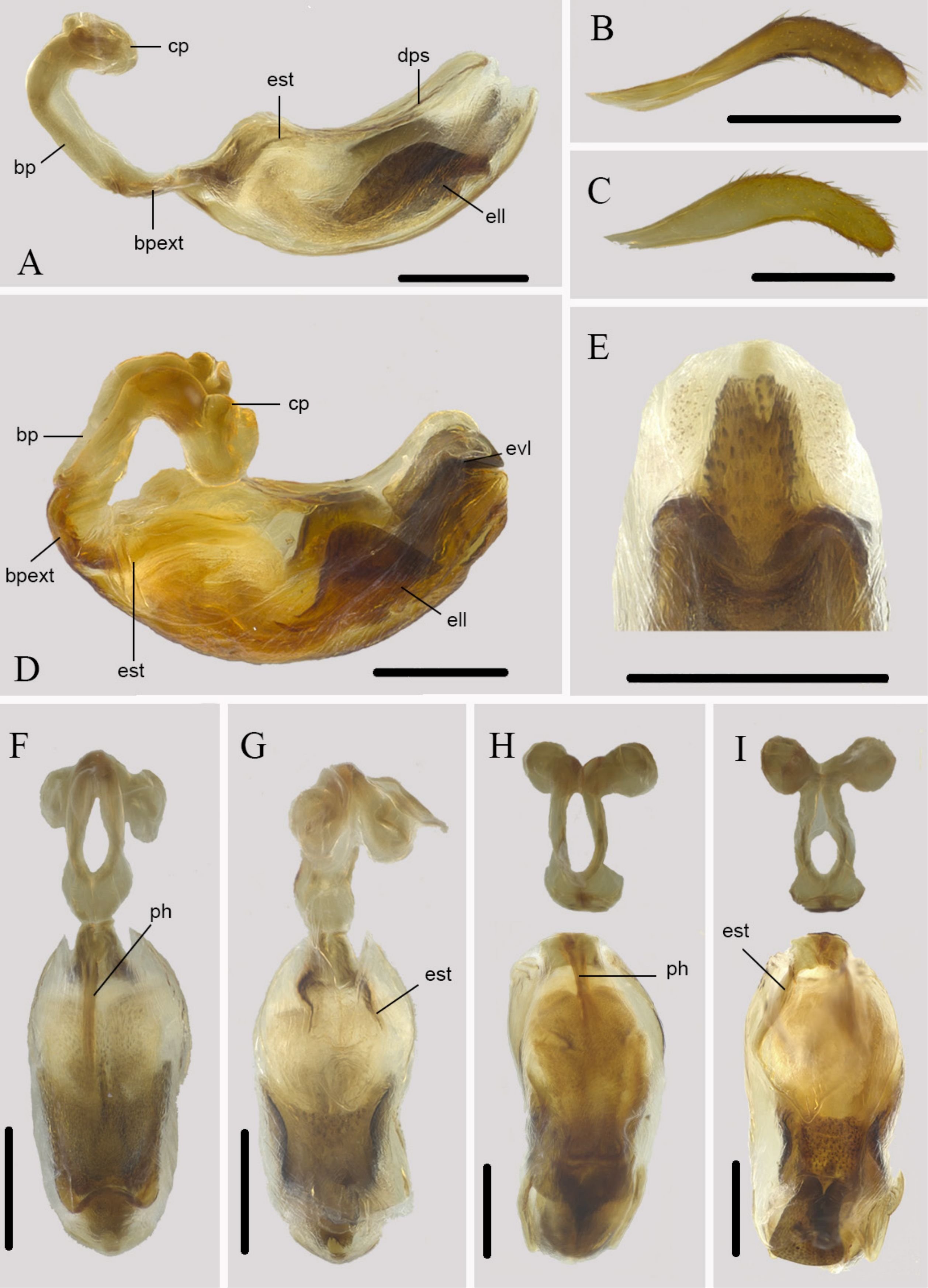


Fig. 7. Paramere and phallus of *Stenorhamphus segerak* and *S. phuphan* in dorsal, ventral, posterior and lateral views. Scale set to 0.2 mm unless otherwise stated; A, *S. segerak,* phallus; capitate process (cp), basal plate (bp), basal plate extension (bpext), endosomal struts of aedeagus (est), endosomal lateral lobe (ell), dorsal phallothecal sclerite (dps); B, *S. segerak* paramere; C, *S. phuphan* paramere. D: *S. phuphan* phallus; basal plate (bp), basal plate extension (bpext), capitate process (cp), endosomla lateral lobe (ell), (est), endosomal ventral lobe (evl); E, *S. segerak* ventral phallotheca, spined; F, G, *S. segerak* dorsal, ventral phallus respectively; H, I, *S. phuphan* dorsal, ventral pygophore respectively.

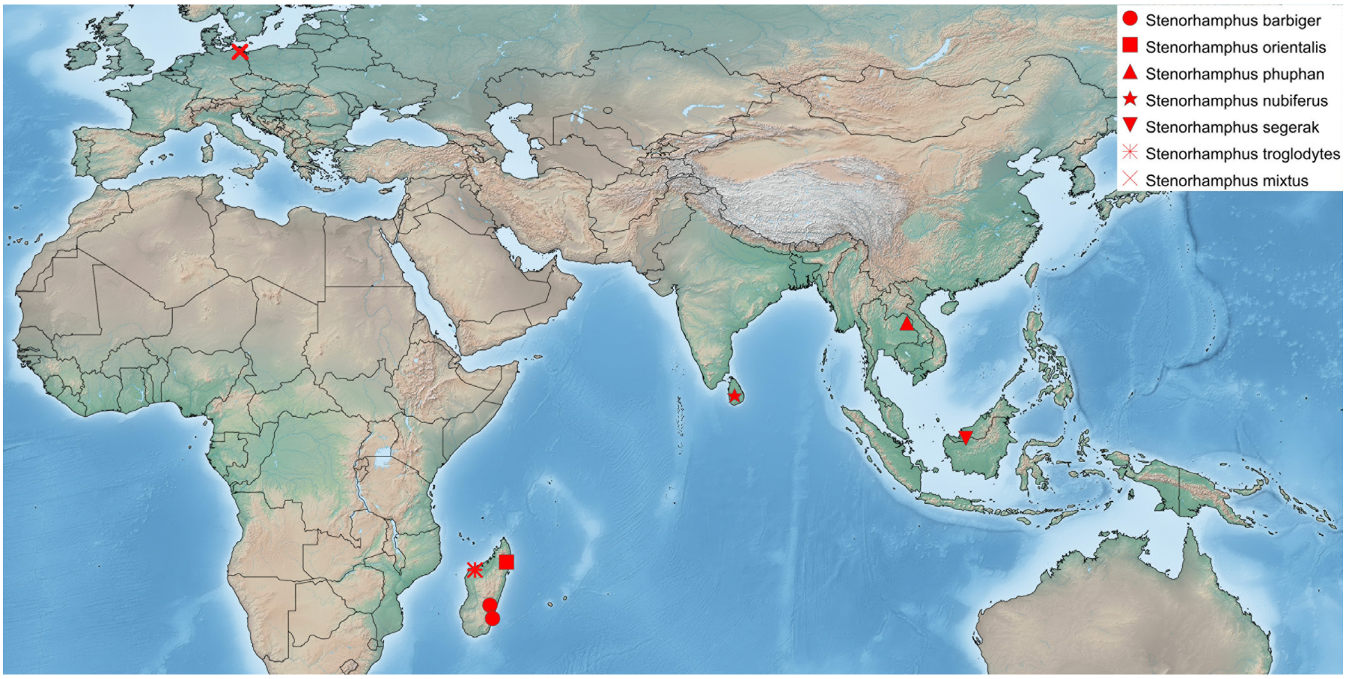


Fig. 8. Map showing expanded range of *Stenorhamphus* Localities based on holotype collection. *S. mixtus* locality based on approximation of Baltic amber collection sites.

anterior, almost covering metanotum, legs long, mid and hind coxae longer than length of abdomen, forecoxa extending past pronotum, two spines on posterior lobe of pronotum.

Description. *Male:* small (total length, holotype: 5.7 mm) COLOURATION: general colouration brown, with posterior pronotal lobe, pygophore, postocular region and wings darker brown, abdomen, forecoxa and anterior region of head yellowish (Figs. 2A, B). Head: postocular region dark brown with spots, anterior anteocular region yellow (Figs. 4A, B). Antenna: brown, flagellomeres light brown. Labium: light brown. Thorax: brown, posterior pronotum darker. Legs: Coxae light brown to yellow, trochanters, femora, tibiae, and tarsi pale brown. Wings: uniformly dark brown. Abdomen: tergites pale brown; mediosternites pale brown, laterosternites somewhat darker; pygophore dark brown. VESTITURE: as in genus description with the following differences: Head: ventral surface with four pairs of long, stout setae located posterior to antennifer, at anterior and posterior margins of eye (Figs. 4A, B), fascicle of more than twelve stout setae on gena ventrad of apex of maxillary plate (Fig. 4B), two pairs of stout setae dorsolaterally posterior to eye (Fig. 4B); second labial segment (first visible) with fascicle of medium-length stout setae on ventral surface in apical half of segment (Fig. 4B); Legs: posterodorsal series and four stout, long setae anteroventral, one stout, long seta posteroventral (Figs. 4A, F), foretrochanter with five stout setae on anterior surface (Fig. 4A), ventral surface of forefemur with about 13 medium and long, stout setae in basal 3/4, interspersed with short setae (Fig. 4A). STRUCTURE: as in genus description with the following differences: Head: (Figs. 4A, B, H): Eyes: globulose and subhemispheric in dorsal perspective (Fig. 4A, H), oval in lateral view, reaching dorsal surface of head, almost reaching ventral surface of head (Figs. 4A, B). Antenna: extremely long, slender; scapus (directed posteriad) surpassing hind coxa (Figs. 2A, B). Labium (Figs. 4A, B). Thorax (Figs. 4F, G, H): collar of pronotum pronounced, posterior lobe of pronotum slightly wider than long, distinctly wider than anterior lobe, slightly depressed medially and with raised, spined, lateral areas in posterior half of lobe, posterior margin concave (Figs. F, H). Mesoscutellum subrectangular, lateral edge a rounded ridge (Fig. 4G). Legs (Figs. 4A, C, D). Wings (Figs. 5A): basal cell trapezoidal, rmcu cross vein absent (Fig. 5A). Abdomen (Figs. 2A, B, 4E): Genitalia (Figs. 6A, B, C, D, 7A, B, E, F, G): pygophore elongate ovoid, with spine-like medial process, transverse bridge present (Figs 6A, B, C, D); parameres slender, curved, apex rounded (Figs. 6A, B, C, D, 7B); aedeagus (Figs. 7A, F, G) with basal plates stout and strongly curved, a relatively large capitulate process, ponticulus basilaris slender or nonexistent, basal plate extension relatively short (Figs. 7A, F, G), basal plate struts short (Figs. 7A, G), phallothecal sclerite curved, more heavily sclerotised anteriorly and posteriorly (Fig. 7A), endosoma with sclerotised ventral and lateral lobes with small spicules (Fig. 7A), lateral lobes long, phallosoma laterally with heavily sclerotised lobe, with short, stout spicules (Fig. 7E).

Measurements. See Table 1.

Female. Unknown.

Etymology. Named after the collecting locality of the holotype at Nanga Segerak in Sarawak; a noun in apposition.

Distribution. Only known from the type locality.

Biology. Found in lowland dipterocarp forests at mid elevation.

Type material. Holotype: male, Malaysia, Sarawak, Lubok Antu District, Lanjak Entimau Wildlife Sanctuary, Nanga Segerak, 1.4200°N, 112.0044°E, 506 m, yellow pan trap, Hwang et al., 16–17 Oct 2017 [SW17 L46] (RCW5465), type currently deposited in National University of Singapore, Lee Kong Chian Natural History Museum, Zoological Reference Collection (ZRC).

Discussion. Most closely related to *Stenorhamphus nubiferus* and *S. phuphan,* with which this species shares the presence of a pair of ventral setae in position 5, lateral to the eye (9:1). Distinguished from these two species by the presence of a pair of ventral setae in position 4 (8:1) and a pair of spines on the posterior pronotal lobe (17:1).

Stenorhamphus troglodytes (Chłond, Guilbert, Baňař & Davranoglou, 2018), new combination

Mangabea troglodytes Chłond, Guilbert, Baňař & Davranoglou, 2018: 2.

Distribution. Only known from the type locality at Namoroka Canyon, Tsingy de Namoroka National Park, Grotte Canyon (16.4693°S, 45.3380°E), where it was collected in the deepest part of the cave. Deposited in the Muséum National d'Histoire Naturelle, Paris, France.

Discussion. It is likely that many of the unique characters, such as small eyes and brachyptery, of *Stenorhamphus troglodytes*, new combination, are adaptations for dwelling in caves. Because of these autapomorphies that may obscure morphological synapomorphies with other species, the placement of *Stenorhamphus troglodytes* in our phylogenetic analysis as sister to a clade containing the two remaining Madagascan species and the species from Sri Lanka and Thailand should be considered as tentative.

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Many thanks to Michael Sharkey (the University of Kentucky, Lexington) and Brian Brown (Natural History Museum of Los Angeles County) for providing us with Reduviidae specimens from the TIGER project. We'd also like to thank Doug Yanega for his input, as well as the Willi Hennig Society (TNT). The specimen from Sarawak was collected under the RIMBA Sarawak initiative by Sarawak Forestry Corporation (SFC), permit no. NPW.907.4.4.(jld.14)-11, park permit no. 006/2017. We are very thankful for the administrative and logistical support provided by the staff of SFC, especially Nickson Joseph Robi and his team for on-site field assistance.

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