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A weighted taxonomic matrix key for species of the rotifer genus *Synchaeta* (Rotifera, Monogononta, Synchaetidae)

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Abstract

A new, weighted matrix identification key for 34 largely undisputed species of *Synchaeta* was created with the aim of providing comparable, detailed and diagnostic character sets for each species that can be applied to live and/or preserved specimens. As part of this process, 14 species of *Synchaeta* were intensively re-investigated with respect to their habitus and trophi morphology using binocular, light, and scanning electron microscopy, which, together with behavioural observations, revealed several new discriminating characters. Whenever possible, missing information for any character was added for the remaining species from the literature, with the two recently described species *Synchaeta arcifera* and *Synchaeta squamadigitata* being considered for the first time in an identification key. Beyond its completeness, our key has two distinct advantages. First, the characters are supported by detailed illustrations of their respective character states whenever possible to both simplify identification and minimize any uncertainty in the descriptions themselves. Second, the new approach of weighting the characters according to their reliability, robustness and/or ease of determination was employed. This latter approach is especially advantageous for soft-bodied rotifers such as species of *Synchaeta*, where, for example, several external characters can be influenced by preservation and are therefore less diagnostic or reliable. Although the key is as comprehensive as possible, information for many species remains missing for many characters, thereby highlighting the need for additional comprehensive and detailed species (re-)investigations within *Synchaeta*.

Keywords

Habitus, morphology, robust characters, species identification, swimming behaviour, trophi

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Introduction

The rotifer genus *Synchaeta* (Monogononta, Synchaetidae) comprises approximately 37 (see Segers 2007) to 39 (see Jersabek et al. 2018) valid and truly planktonic species, of which approximately half occur in brackish and/or marine habitats (Hollowday 2002). Although their importance in aquatic food webs is unquestioned because of their often dominant role in the rotifer (Stemberger and Gilbert 1985) and metazooplankton communities (Arndt et al. 1990), specimens of *Synchaeta* in ecological studies are seldom identified to species level (Obertegger et al. 2006). To a large extent, this situation derives from the identification of and delimitation between species of this genus being regarded as being especially challenging (Pourriot 1965; Ruttner-Kolisko 1972; Koste 1978).

The several comprehensive revisions and keys of *Synchaeta* that exist (e.g., Voigt 1956–1957; Ruttner-Kolisko 1972; Koste 1978; and most recently Hollowday 2002) tend to be restricted in that they limit themselves to describing the most concise set of characters that delimit each species. Although this represents a useful simplifying strategy, the inherently incomplete data set it entails presents two distinct disadvantages. First, because additional, alternative characters are not presented for many species, their identification is impossible when the respective, diagnostic ones are deformed or not clearly visible (e.g., foot morphology when it is retracted). Second, and more importantly, direct comparisons among species are usually not possible because the species are often described using different sets of characters.

To address both sets of issues, we have developed a new identification key for *Synchaeta*, with the dual aims of making it both easy to use and as comprehensive as possible by providing large, comparable data sets for each species. To accomplish this, we thoroughly re-examined live and prepared specimens of 14 species and intensively researched the literature for all members of *Synchaeta*, including the most recently described species *Synchaeta arcifera* Xu, 1998 and *Synchaeta squamadigitata* De Smet, 2006, which are presented for the first time in a comparative identification key. In addition to an in-depth analysis of the habitus, we focussed on the trophi in particular because they are considered to be both species-specific (De Smet 1998; Fontaneto and Melone 2006; Wulfken et al. 2010) and less susceptible to conservation (Kutikova 1970 as cited in Obertegger et al. 2006). Detailed information about the trophi are therefore of great advantage in ecological studies, for example, where the material is necessarily fixed for practical reasons (Obertegger et al. 2006; Labuce and Strake 2017), with the consequence that the species identity of distorted or contracted rotifer specimens might be determinable only via their trophi (De Smet 1998; Segers 2004). By providing comparable data sets for each species, our taxonomic key also functions as a matrix key (also known as free access or multi-access key; see Hagedorn et al. 2010), which is better able to incorporate missing information when identifying species than the more traditional dichotomous key.

In addition, we weighted all characters within our matrix key according to their perceived discriminatory power. This strategy of focussing on more robust and diagnostically conclusive characters potentially facilitates accurate species identification by

giving characters that are more susceptible to variation or artefacts (e.g., body shape, which is strongly affected by the pressure of a cover slip (Koste 1978), fixation/preservation (Ruttner-Kolisko 1972; Segers 2004) or by developing eggs and stomach content in soft-bodied rotifers) less impact than more constant and robust ones (e.g., the number and position of the lateral antennae.) To further simplify the identification process, we supported the characters with detailed illustrations and photographs of the respective character states whenever possible and introduce a consistent and distinctive terminology for homologous structures. Although the latter point seems obvious, the use of synonyms for homologous structures is a widespread problem, even within the same key. For example, Hollowday (2002: 90) variously denotes the apical receptors as "sensory frontal antennae", "sensory antenna", "frontal prominence with tuft of setae" or "sensory setae" in his identification key for species of *Synchaeta*.

Our purpose here is to deliver a comprehensive and robust key for *Synchaeta* by which a reliable identification of live and preserved specimens is feasible through a comprehensive and comparable morphological data set. In so doing, the present study not only confirmed existing discriminatory characters, but also re-described some of them more explicitly (e.g., foot shape and morphology of the apical receptors) as well as established several novel ones for species demarcation (as e.g., behaviour, morphology of the pedal glands, detailed fulcrum and ramus morphology).

Materials and methods

Study site and sampling

Using a 55-µm mesh plankton net, sampling for species of *Synchaeta* took place intermittently between June 2013 and August 2017 in northwest Germany from freshwater habitats in Oldenburg, Lower Saxony and Tecklenburger Land, North Rhine-Westphalia as well as from brackish and marine habitats in Wilhelmshaven, Lower Saxony (Table 1). Species of *Synchaeta* found in the samples (Table 2) were identified using the existing information in Rousselet (1902), Voigt (1956–1957), Ruttner-Kolisko (1972), Koste (1978) and Hollowday (2002).

Binocular and light microscopical (LM) investigations

Undisturbed, living specimens were initially observed in a petri dish using a binocular microscope to examine their (swimming) behaviour. For the LM analyses, single individuals were isolated and carefully sedated with carbonated water before being further immobilized through the slight pressure of a cover glass. For the latter step, extreme care was taken to avoid any deformation of the body, which could lead to morphological artefacts. All observations used differential interference contrast using a LEICA DMLB microscope and digital photographs were taken using a Canon EOS 5D Mark II camera.

Table 1. Sampling locations with their corresponding coordinates and habitat characterizations. Abbreviations: OL = Oldenburg, TL = Tecklenburger Land, WHV = Wilhelmshaven.

Location		Coordinates	Type of Habitat	Salinity in PSU
Schlossteich (ST)	OL	53.1603N; 8.1195E	permanent freshwater pond	0
Löschteich (LT)	OL	53.151957N; 8.166833E	permanent freshwater pond	0
Haarenniederung (HN)	OL	53.147092N; 8.171273E	temporary freshwater winter puddle	0
Haarenstau (HS)	OL	53.155623N; 8.105789E	temporary freshwater winter puddle	0
Heiliges Meer (HM)	TL	52.351944N; 7.633611E	permanent freshwater lake	0
Banter See (BS)	WHV	53.50906N; 8.1143116E	tide-independent, brackish basin	ca. 8
Yachthafen (YH)	WHV	53.5097712N; 8.1216346E	tide-independent, brackish basin	ca. 20
Nassauhafen (NH)	WHV	53.5129901N; 8.1458015E	North Sea coast, marine habitat	ca. 30

Table 2. Sampled species of *Synchaeta*. Abbreviations: BS = Banter See; HM = Heiliges Meer; HN = Haarenniederung; HS = Haarenstau; LT = Löschteich; NH = Nassauhafen; ST = Schlossteich; YH = Yachthafen.

Species	Location	Date	Number of specimens examined
From freshwater habitats			
S. grandis	ST	June 2016	18
S. kitina	HM	April 2017	ca. 25
S. longipes	ST	June and July 2013	15
S. oblonga	ST	March 2016	ca. 70
S. pectinata	ST	April to June 2013 and 2015	ca. 120
S. stylata	ST	June to August 2016 and 2017	ca. 50
S. tremula	ST, LT	March to May 2016	ca. 90
S. tremuloida	HS, HN	November to January 2015/2016	ca. 70
From brackish and marine habitats			
S. triophthalma	NH	April 2016	ca. 25
S. hutchingsi	YH	August 2017	18
S. grimpei	YH, NH	April 2016	13
S. gyrina	BS, NH	January and April 2016	ca. 60
S. baltica	BS, NH	January and April 2016	ca. 35
S. vorax	NH	April 2016	17

Scanning electron microscopical (SEM) investigations

For SEM examinations of the habitus, single specimens were initially sedated with carbonated water before being euthanized with 1% OsO_4 buffered in 0.1 M NaCa cacodylate buffer and fixed with 240 mOsmol picric acid-formaldehyde (Melone and Ricci 1995). To examine the isolated trophi, the surrounding tissue of selected specimens was dissolved according to the protocol of Kleinow et al. (1990) by transferring them into a droplet of dissolving agent (0.1 g dithiothreitol added to a 5-ml stock solution of 5.2 g sodium dodecyl sulphate + 0.24 g NH_4HCO_3 in 100 ml aqua dest; AppliChem, Darmstadt, Germany) for ca. 15 min before being rinsed with distilled water subsequently. Thereafter, samples of either the habitus or the trophi were dehydrated using an ascending, graded ethanol series. Following critical-point drying, each sample was attached onto an SEM stub and coated with gold-palladium before being examined on a Hitachi S-3200N SEM.

Illustrations

All new illustrations of the habitus were made using Adobe Illustrator CS4 based on representative digital photographs. References from drawings that we have obtained and modified from literature are listed below each illustration.

Included species and information from the literature

Overall, 34 species of *Synchaeta* were considered in our key, with six species that are recognized by either Segers (2007) and/or Jersabek et al. (2018) being excluded (see lists below). Information about species that we did not find in our samples derive from their respective initial descriptions and from the literature, with an emphasis on Rousselet (1902), Lauterborn (1905), Lie-Pettersen (1905), Peters (1931), Voigt (1956–1957), Ruttner-Kolisko (1972), Koste (1978) and Hollowday (2002). Information or interpretations that we have made from illustrations or photographs that are derived from other sources than the above-mentioned literature are indicated below each table (Tables 3–8). Species that are in urgent need of re-investigation because of inconsistent, ambiguous or highly incomplete descriptions (see Tables 3–8; "?") and/or species that are known exclusively from preserved material are indicated with an asterisk in the following lists.

List of recognized freshwater species (Fig. 1A–M):

Synchaeta pectinata Ehrenberg, 1832 (Fig. 1A)
Synchaeta grandis Zacharias, 1893 (Fig. 1B)
Synchaeta oblonga Ehrenberg, 1832 (Fig. 1C)
Synchaeta tremula (Müller, 1786) (Fig. 1D)
Synchaeta tremuloida Pourriot, 1965 (Fig. 1E)
Synchaeta prominula Kutikova & Vassiljeva, 1982 (Fig. 1F)*
Synchaeta kitina Rousselet, 1902 (Fig. 1G)
Synchaeta stylata Wierzejski, 1893 (Fig. 1H)
Synchaeta longipes Gosse, 1887 (Fig. 1I)
Synchaeta verrucosa Nipkow, 1961 (Fig. 1J)
Synchaeta lakowitziana Lucks, 1930 (Fig. 1K)*
Synchaeta pachypoida Kutikova & Vassiljeva, 1982 (Fig. 1L)*
Synchaeta pachypoda Jashnov, 1922 (Fig. 1M)*

List of recognized brackish, marine or inland saline species (Fig. 2A–U):

Synchaeta grimpei Remane, 1929 (Fig. 2A)
Synchaeta baltica Ehrenberg, 1834 (Fig. 2B)

Synchaeta johanseni Harring, 1921 (Fig. 2C)*
Synchaeta bicornis Smith, 1904 (Fig. 2D)*
Synchaeta gyrina Hood, 1887 (Fig. 2E)
Synchaeta triophthalma Lauterborn, 1894 (Fig. 2F)
Synchaeta cecilia Rousselet, 1902 (Fig. 2G)
Synchaeta vorax Rousselet, 1902 (Fig. 2H)
Synchaeta fennica Rousselet, 1909 (Fig. 2I)*
Synchaeta cylindrica Althaus, 1957 (Fig. 2J)*
Synchaeta tavina Hood, 1893 (Fig. 2K)*
Synchaeta neapolitana Rousselet, 1902 (Fig. 2L)*
Synchaeta hutchingsi Brownell, 1988 (Fig. 2M)
Synchaeta atlantica Zelinka, 1907 (Fig. 2N)*
Synchaeta rousseleti Zelinka, 1927 (Fig. 2O)*
Synchaeta glacialis Smirnov, 1932 (Fig. 2P)*
Synchaeta hyperborea Smirnov, 1932 (Fig. 2Q)*
Synchaeta arcifera Xu, 1998 (Fig. 2R)*
Synchaeta tamara Smirnov, 1932 (Fig. 2S)*
Synchaeta bacillifera Smirnov, 1933 (Fig. 2T)*
Synchaeta squamadigitata De Smet, 2006 (Fig. 2U)*

Excluded species

In general, we excluded species of *Synchaeta* that are ranked as a species inquirenda (= species of doubtful identity) by Jersabek et al. (2018) or for which we strongly suspect this to be the case based on our own observations.

1. *Synchaeta curvata* Lie-Pettersen, 1905: Insufficient description (Hollowday 2002) and currently ranked as a species inquirenda in Segers (2007).
2. *Synchaeta elsteri* Hauer, 1963: Insufficient description based on preserved specimens (Hollowday 2002). This species was also ranked as a species inquirenda in Segers (2007).
3. *Synchaeta jollyae* Shiel & Koste, 1993: Described based on preserved specimens and synonymy with *S. stylata* suspected (Wilke et al. 2018a).
4. *Synchaeta littoralis* Rousselet, 1902: Synonymy with *S. oblonga* suspected (Koste 1978; Hollowday 2002; Wilke et al. 2018b). This species was also ranked as a species inquirenda in Segers (2007).
5. *Synchaeta monopus* Plate, 1889: Existing descriptions are insufficient, inconsistent and made exclusively on the basis of preserved and presumably deformed specimens (Wilke et al. 2019).
6. *Synchaeta rufina* Kutikova & Vassiljeva, 1982: Synonymy with *S. oblonga* suspected (Wilke et al. 2018b).

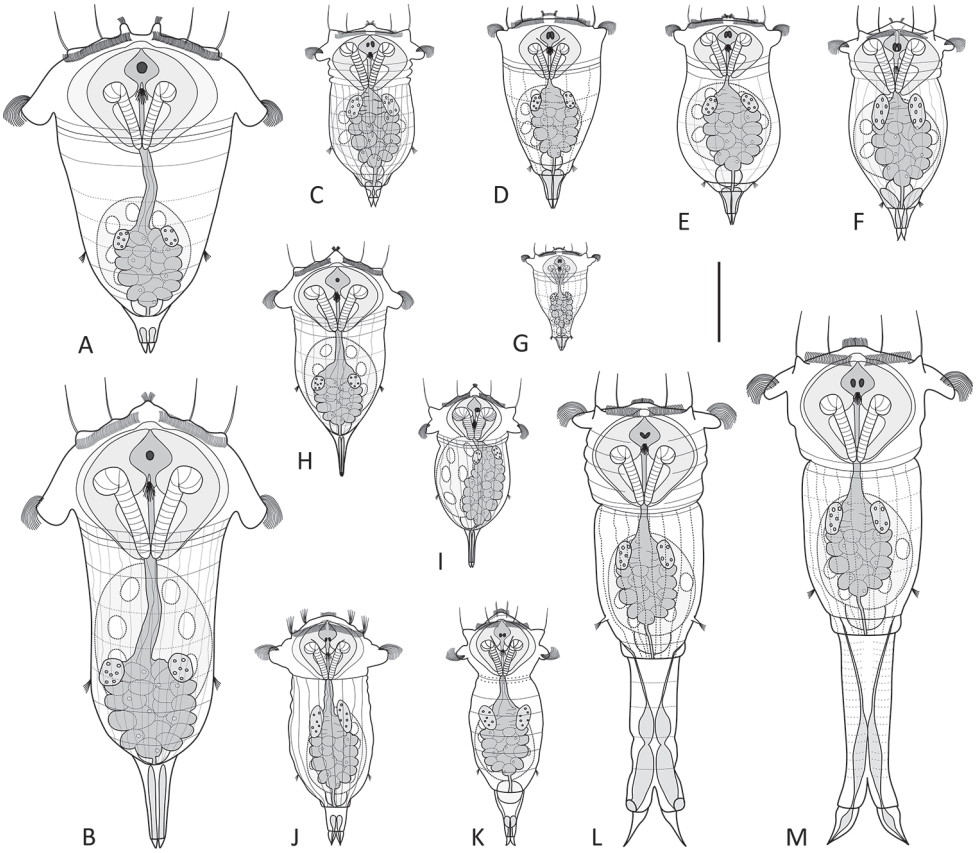

Figure 1. Species of *Synchaeta* from freshwater habitats. **A** *S. pectinata* **B** *S. grandis* **C** *S. oblonga* **D** *S. tremula* **E** *S. tremuloida* **F** *S. prominula* **G** *S. kitina* **H** *S. stylata* **I** *S. longipes* **J** *S. verrucosa* **K** *S. lakowitziana* **L** *S. pachypoida* **M** *S. pachypoda*. Drawings modified from: **F, L, M** Kutikova and Vassiljeva (1982) **J** Jersabek et al. (2003b) **K** Lucks (1930). Scale bar: 100 µm.

Character clarification, character weighting, and species identification

To support the written descriptions, the morphology for each character state is also exemplified both through illustrations as well as the naming of at least one exemplar species that possesses the respective state.

The character states are represented in detailed tables (Tables 3–8) and in a numerical list for each species where the text is formatted according to the perceived reliability and/or discriminatory power of the states:

1. "?": The character state is unknown or ambiguous for the respective species – further examinations are required.
2. brackets: The character state rarely occurs in the species.

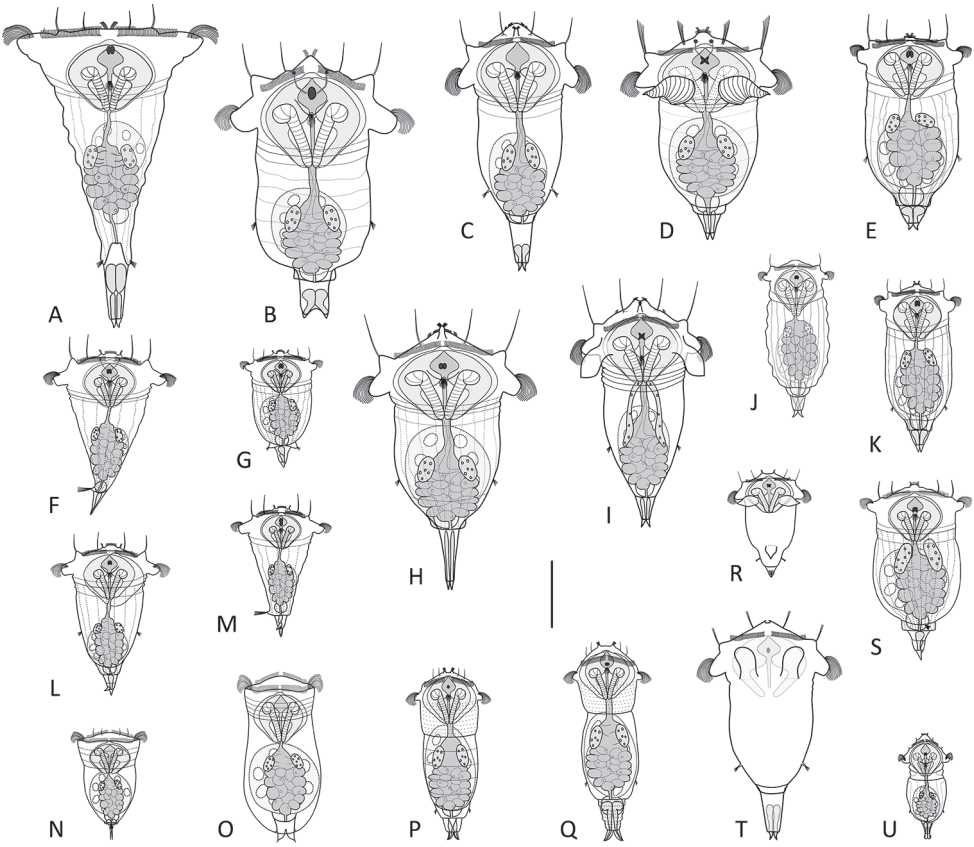

Figure 2. Species of *Synchaeta* from brackish, marine and inland saline habitats. **A** *S. grimpei* **B** *S. baltica* **C** *S. johanseni* **D** *S. bicornis* **E** *S. gyrina* **F** *S. triophthalma* **G** *S. cecilia* **H** *S. vorax* **I** *S. fennica* **J** *S. cylindrica* **K** *S. tavina* **L** *S. neapolitana* **M** *S. hutchingsi* **N** *S. atlantica* **O** *S. rousseleti* **P** *S. glacialis* **Q** *S. hyperborea* **R** *S. arcifera* **S** *S. tamara* **T** *S. bacillifera* **U** *S. squamadigitata*. Drawings modified from: **C** Harring (1921) **D** Koste (1981) **G, K, L** Rousselet (1902) **I** Rousselet (1909) **J** Althaus (1957) **N** Zelinka (1907) **O** Zelinka (1927) **P, Q, S** Smirnov (1932) and Friedrich and De Smet (2000) **R** Rougier and Pourriot (2006) **T** Smirnov (1933) **U** De Smet (2006). Scale bar: 100 µm.

3. *italics*: The character is variably expressed within the species or its interpretation is either subjective or can be easily misunderstood because of potential artefacts that can arise during preparation. These characters should be applied with caution.
4. normal text: The character state is more or less robust, but shared by several, additional species of *Synchaeta*. Many characters of this quality are usually required for species demarcation in the form of a unique character set for each species.
5. blue color: The character state is robust and important insofar as it is unique for the species and/or shared by only a few, additional species of *Synchaeta*. Individual characters in this category typically exclude many other congeneric species to greatly simplify species demarcation.
6. **bold:** The character state is robust and species-specific (autapomorphy).

To simplify the identification process, blank character checklists and tables for recording character states are appended (Suppl. material 1: Tables S1, S2).

Results

The characters are categorized into those for habitat and behaviour (characters 1–6), size (character 7), head and neck region (characters 8–16), trunk (characters 17–23), foot, pedal glands and toes (characters 24–37), sensory system (characters 38–50) and trophi (characters 51–60). The respective character states for each species are presented in Tables 3–8.

Identification characters

Habitat and behaviour (Table 3)

1. Habitat
   a. freshwater (exemplar *S. grandis*)
   b. brackish (exemplar *S. bicornis*)
   c. marine (exemplar *S. atlantica*)
   d. inland saline (exemplar *S. cylindrica*)
2. Swimming duration
   a. exclusively pelagic (exemplar *S. pectinata*) or only adheres to objects transiently when disturbed (exemplar *S. oblonga*)
   b. interrupted by frequent, long-lasting adherences to diverse objects (e.g., plants; exemplar *S. tremula*)
3. Adherence to diverse objects
   a. absent (exemplar *S. pectinata*) or only transiently and only when disturbed (exemplar *S. oblonga*)
   b. long-lasting adherence without any twisting movement about the longitudinal axis (exemplar *S. kitina*)
   c. long-lasting adherence combined with a twisting movement about the longitudinal axis (exemplar *S. tremula*)
4. Swimming motion (always combined with a rotation about the longitudinal axis)
   a. in a straight line (Fig. 3A; exemplar *S. tremula*, *S. kitina*)
   b. slightly coiled (Fig. 3B; exemplar *S. stylata*, *S. tremuloida*)
   c. distinctly coiled (Fig. 3C; exemplar *S. pectinata*, *S. grandis*)
5. Foot position while swimming
   a. partly or fully retracted (Fig. 3D; exemplar *S. baltica*)
   b. not retracted (Fig. 3E; exemplar *S. tremula*)
6. Directional changes while swimming
   a. many sudden directional changes (exemplar *S. stylata, S. oblonga*)
   b. few or no sudden directional changes (exemplar *S. pectinata*)

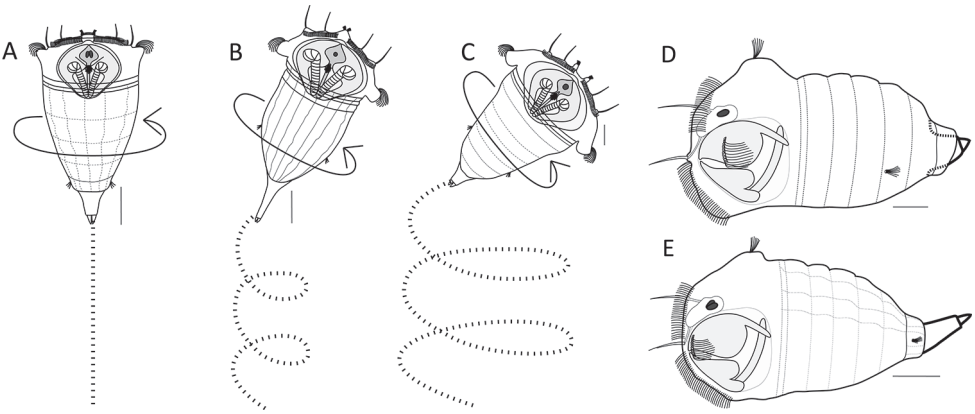

Figure 3. Habitat and behaviour. **A–C** Examples of the swimming behaviour **A** straight (*S. tremula*) **B** slightly coiled (*S. stylata*) **C** distinctly coiled (*S. pectinata*) **D–E** Foot position (thick lines) while swimming **D** foot retracted (*S. baltica*) **E** foot not retracted (*S. tremula*). Scale bar: 50 µm.

Size (Table 3)

7. Overall body length of mature specimens (measured from the apical field to the distal tips of the toes, excluding the cilia)
   a. less than 250 µm
   b. more than 250 µm

Head and neck region (Table 4)

8. Apical field – Width in relation to the trunk width[1]
   a. as wide as the trunk (Fig. 4A; exemplar *S. tremuloida*)
   b. wider than the trunk (Fig. 4B; exemplar *S. longipes*, *S. triophthalma*)
9. Apical field – Elevation with respect to auricles
   a. level (Fig. 4C; exemplar *S. grimpei*) to slightly elevated (Fig. 4D; exemplar *S. tremula*)
   b. intermediate (Fig. 4E; exemplar *S. triophthalma*)
   c. strongly elevated; distinctly convex (Fig. 4F; exemplar *S. grandis*)
10. Dorsolateral styles – Elevation
   a. not raised to very slightly raised (Fig. 4G; exemplar *S. tremula*)
   b. intermediate (Fig. 4H; exemplar *S. gyrina*)
   c. strongly raised (Fig. 4I; exemplar *S. baltica*)
11. Auricles – Size
   a. not clearly distinct from the rotatory organ (Fig. 4J; exemplar *S. grimpei*)

[1] This character strongly depends on the amount of ingested food or presence of developing eggs in some species (e.g., *S. gyrina*; character state "a/b").

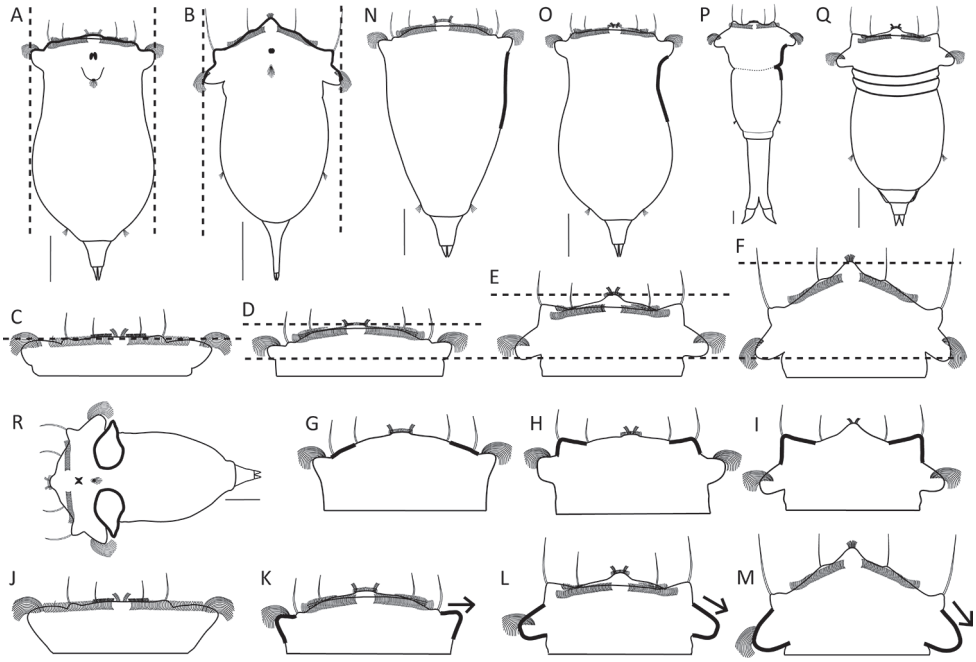

Figure 4. Head and neck region. **A, B** Relative width of the apical field (dashed lines) **A** as wide as the trunk (*S. tremuloida*) **B** wider than the trunk (*S. longipes*) **C–F** Elevation of the apical field (top line) relative to the auricles (bottom line) **C** level (*S. grimpei*) **D** slightly elevated (*S. tremula*) **E** intermediate (*S. oblonga*) **F** strongly elevated (*S. grandis*) **G–I** Elevation of the dorsolateral styles (thick lines) **G** not or very slightly raised (*S. tremula*) **H** intermediate (*S. gyrina*) **I** strongly raised (*S. baltica*) **J–M** Auricle size (thick lines) and orientation (arrows) **J** not clearly demarcated from rotatory organ, directed laterally (*S. grimpei*) **K** small, directed laterally (*S. tremula*) **L** medium, directed semi-caudally (*S. oblonga*) **M** large, directed caudally (*S. grandis*) **N–Q** Separation of the head and trunk region **N** gradual transition, the head is not distinctly offset from the trunk (*S. tremula*) **O** head and trunk are demarcated by the narrower neck (*S. tremuloida*) **P** demarcation by a sharp constriction in the neck region (*S. pachypoda*) **Q** by distinct transversal folds (*S. oblonga*) **R** Presence of saccate appendages (thick lines) caudal to auricles (*S. bicornis*). Drawings modified from: **P** Kutikova and Vassiljeva (1982) **R** Koste (1981). Scale bars: 50 µm.

   b. small (Fig. 4K; exemplar *S. tremula*)
   c. medium (Fig. 4L; exemplar *S. oblonga*)
   d. large (Fig. 4M; exemplar *S. grandis*)

12. Auricles – Orientation
   a. directed laterally (Fig. 4J, K; exemplar *S. tremula*)
   b. directed semi-caudally (Fig. 4L; exemplar *S. oblonga*)
   c. directed caudally (Fig. 4M; exemplar *S. grandis*)

13. Neck region – Demarcation of the head and trunk regions
   a. gradual transition from the head into the trunk region; the neck is neither constricted nor distinctly offset (Fig. 4N; exemplar *S. tremula*)
   b. demarcated; the neck is narrower than the head and trunk (Fig. 4O; exemplar *S. tremuloida*)

c. demarcated by a sharp constriction (Fig. 4P; exemplar *S. pachypoda*) or by distinct transversal folds (Fig. 4Q; exemplar *S. oblonga*)

14. Saccular appendages at the neck region (that compensate for pressure changes in the body fluid through contraction of the body)
    a. absent (Fig. 4A, B; exemplar *S. pectinata*)
    b. present (Fig. 4R; exemplar *S. arcifera*, *S. bacillifera*, *S. bicornis*, *S. fennica*)
15. Saccular appendages – Location
    a. ventral (exemplar *S. bacillifera*)
    b. dorsal (exemplar *S. arcifera*, *S. bicornis*, *S. fennica*)
    c. absent (exemplar *S. pectinata*)
16. Head region – Colour[2]
    a. colourless / transparent (Fig. 5A; exemplar *S. pectinata*)
    b. mastax or parts thereof moderately yellow or orange (Fig. 5B; exemplar *S. longipes*)
    c. parts of rotatory organ or auricles slightly yellow to orange (Fig. 5C; exemplar *S. grandis*)

Trunk (Table 5)

17. Trunk region – Shape[3]
    a. conical: trunk decreases gradually in width caudally (Fig. 6A; exemplar *S. tremula*)
    b. cylindrical: trunk elongate, decreases in width only in its caudal quarter (Fig. 6B; exemplar *S. tavina*)
    c. bell- (Fig. 6C: exemplar *S. tremuloida*) to wineglass-shaped (Fig. 6D; exemplar *S. longipes*), trunk is slightly bulbous and narrows abruptly in its caudal third.
18. Anal pseudosegment
    a. distinct anal pseudosegment present (Fig. 6E; exemplar *S. oblonga*)
    b. anal pseudosegment barely visible or absent (Fig. 6A–D; exemplar *S. longipes*)
19. Posteriodorsal saccate appendage on the integument (that compensates for pressure changes in the body fluid through contraction of the body)
    a. present (Fig. 6F; exemplar *S. arcifera*)
    b. absent (Fig. 6A–E; exemplar *S. longipes*)
20. Longitudinal striae on the dorsal trunk
    a. present (Fig. 6G; exemplar *S. tavina*)
    b. absent (Fig. 6H; exemplar *S. pectinata*)
21. Internal organs – Location
    a. occupy entire trunk region (Fig. 6I; exemplar *S. oblonga*)

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[2] The intensity of the colour is often variable within the species and a less intense colour can appear as colourless

[3] The body shape is strongly influenced by the pressure of the cover glass or fixation/preservation (Koste 1978) as well as from developing eggs and stomach content.

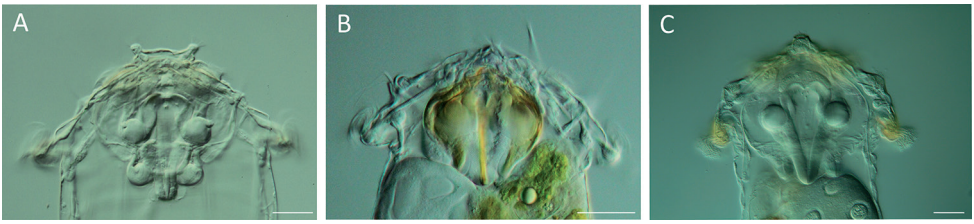

Figure 5. Head and neck region. **A–C** LM images showing different colours in the head region **A** colourless / transparent (*S. pectinata*) **B** mastax moderately yellow or orange (*S. longipes*) **C** parts of rotatory organ or auricles slightly yellow to orange (*S. grandis*). Scale bar: 25 µm.

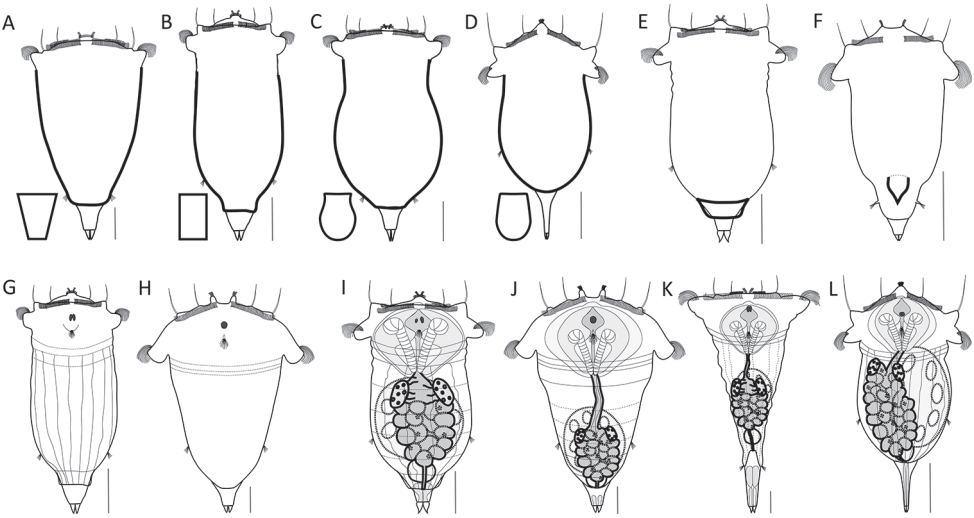

Figure 6. Trunk region. **A–D** Morphology of the trunk region (thick lines) **A** conical (*S. tremula*) **B** cylindrical (*S. tavina*) **C** bell-shaped (*S. tremuloida*) **D** wineglass-shaped (*S. longipes*) **E** Presence of a distinct anal pseudosegment (thick line; *S. oblonga*) **F** Presence of a posteriodorsal saccate appendage (thick line; *S. arcifera*) **G, H** Longitudinal striae on the dorsal trunk **G** present (*S. tavina*) **H** absent (*S. pectinata*) **I–L** Location of the internal organs **I** occupy entire trunk region (*S. oblonga*) **J** occupy middle and caudal trunk regions, oesophagus only structure in the anterior trunk (*S. pectinata*) **K** occupy middle trunk region, cloaca ends anteriorly to the lateral antennae (*S. grimpei*) **L** stomach and ovary each occupy separate sides of the trunk (*S. longipes*). Drawings modified from **B, G** Rousselet (1902) **F** Rougier and Pourriot (2006). Scale bar: 50 µm.

b. occupy middle and caudal trunk regions; the oesophagus is the only structure present in the anterior trunk region (Figs 6J, 7C; exemplar *S. pectinata*)
c. occupy middle trunk region; cloaca ends in posterior quarter of trunk, anteriorly to the lateral antennae (Fig. 6K; exemplar *S. grimpei*)
d. stomach and ovary each occupy separate sides of the trunk (Fig. 6L; exemplar *S. longipes*)

22. Violet globules in the body cavity
    a. present (Fig. 7A, arrow; only known for *S. baltica*, *S. bicornis*, and *S. grimpei*, where the globules can also be absent)
    b. absent (Fig. 7B, C; exemplar *S. pectinata*)
23. Oesophagus – Morphology
    a. short oesophagus that widens in its caudal half to form a proventriculus (Fig. 7B; exemplar *S. tremula*, *S. tremuloida*)
    b. highly tensile oesophagus, narrow or broad and of equal width, with numerous longitudinal striae (Fig. 7C; exemplar *S. pectinata*, *S. baltica*)

Foot, pedal glands and toes (Table 6)

24. Foot – Orientation
    a. directed dorsally (Fig. 8A; exemplar *S. tremula*, *S. baltica*, *S. cecilia*)
    b. coplanar with the longitudinal axis of the body or directed very slightly ventrally (Fig. 8B; exemplar *S. grimpei*)
    c. directed ventrally (Fig. 8C; exemplar *S. longipes*)
25. Foot – Shape
    a. minute, less than one-tenth of the overall body length; as long as or shorter than the toes (Fig. 8D; exemplar *S. atlantica*)
    b. triangular, medium; between one-fourth and one-sixth of the overall body length (Fig. 8E; exemplar *S. triophthalma*)
    c. conical, short to medium; less than one-fourth of the overall body length, but always longer than the toes (Fig. 8F; exemplar *S. tremula*)
    d. slender, medium to long; ca. one-third to one-fifth of the overall body length (Fig. 8G; exemplar *S. longipes*)
    e. broad, long; ca. one-third of the overall body length (Fig. 8H; exemplar *S. johanseni*, *S. baltica*)
    f. cylindrical, massive; approximately one-half of the overall body length (Fig. 8I; exemplar *S. pachypoda*, *S. pachypoida*
26. Pedal glands – Symmetry
    a. asymmetrical; either of different size and shape or only singly present (Fig. 9A–C; exemplar *S. cecilia, S. triophthalma*)
    b. symmetrical (Fig. 9D–I; exemplar *S. tremula*, *S. pectinata*)
27. Pedal gland(s) – Number and arrangement[4]
    a. one single pedal gland (Fig. 9A; exemplar *S. neapolitana*)

[4] Although the present character overlaps with the previous one, it is more specific. It should only be consulted when the state can be determined with certainty because the state "b" can be difficult to determine accurately in the case of a second rudimental gland that can be easily overseen. Otherwise, we recommend character 26 for species identification.

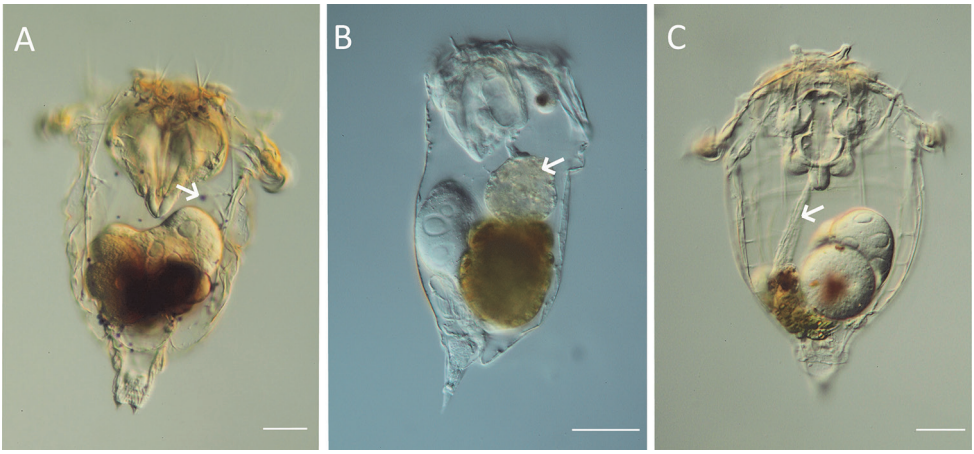

Figure 7. LM images of species of *Synchaeta*. **A** Presence of violet globules in the body cavity (arrow; *S. baltica*) **B, C** LM images of the habitus showing different morphologies of the oesophagus (arrows) **B** oesophagus widens to form a proventriculus (*S. tremuloida*) **C** oesophagus highly tensile with numerous longitudinal striae (*S. pectinata*). Scale bar: 50 µm.

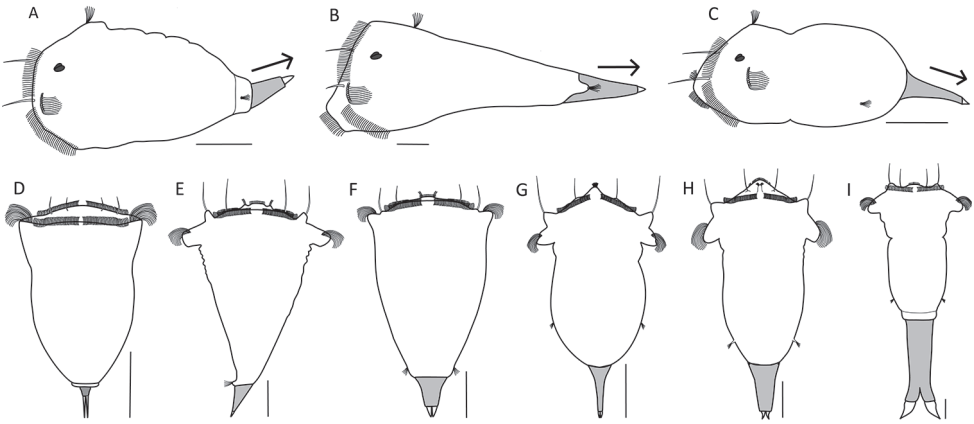

Figure 8. Foot shape. **A–C** Orientation of the foot (grey areas and arrows) **A** directed dorsally (*S. tremula*) **B** coplanar with the longitudinal axis (*S. grimpei*) **C** directed ventrally (*S. longipes*) **D–I** Shape and size of the foot (grey areas) **D** minute, shorter than the toes (*S. atlantica*) **E** triangular, medium (*S. triophthalma*) **F** conical, medium (*S. tremula*) **G** slender, long (*S. longipes*) **H** broad, long (*S. johanseni*) **I** massive, cylindrical (*S. pachypoda*). Drawings modified from: **D** Zelinka (1907) **H** Harring (1921) **I** Kutikova and Vassiljeva (1982). Scale bar: 50 µm.

b. pedal glands are paired but of different size and shape; one is rudimental (Fig. 9B–C; exemplar *S. cecilia*, *S. hutchingsi*, *S. tamara*, *S. triophthalma*)
c. two symmetrical glands are present (Fig. 9D–I; exemplar *S. tremula*, *S. pectinata*)

28. Pedal gland(s) – Length[5]
    a. shorter than the foot (Fig. 9E; exemplar *S. oblonga*)
    b. as long as the foot (Fig. 9A–D; exemplar *S. tremula*)
    c. longer than the foot, extending into the caudal trunk region (Fig. 9F; exemplar *S. atlantica*, *S. prominula*, *S. rousseleti*)
29. Pedal gland(s) – Shape
    a. tubular; of even width along their entire length (Fig. 9G; exemplar *S. longipes*)
    b. club-shaped; voluminous proximally, decreasing gradually caudally (Fig. 9A, D; exemplar *S. tremula*)
    c. voluminous proximally, decreasing abruptly caudally before widening again to form a reservoir in the distal half (Fig. 9E; exemplar *S. oblonga*)
    d. tubular, suspended from the trunk (Fig. 9H; exemplar *S. pachypoda*)
    e. each gland possesses two large and voluminous sections that are demarcated by a narrowing from one another; suspended from the trunk proximally (Fig. 9I; exemplar *S. grimpei*, *S. pachypoida*)
30. Pedal gland(s) – Opening
    a. into the tip(s) of the toe(s) (Fig. 9A, B, D–H; exemplar *S. tremula*, *S. pectinata*)
    b into a toe with the second into a spur (Fig. 9C; exemplar *S. hutchingsi*)
    c. at the base of the toes (Fig. 9I; exemplar *S. pachypoida*)
31. Toes – Symmetry
    a. asymmetrical; only one toe is present (Fig. 9J; exemplar *S. hutchingsi*, *S. neapolitana*, *S. triophthalma*) or two toes are of different size and shape (Fig. 9K; exemplar *S. cecilia*)
    b. symmetrical paired toes (Fig. 9L–Q; exemplar *S. tremula, S. pectinata*)
32. Toe(s) – Number and arrangement
    a. only one toe is present (Fig. 9J; exemplar *S. hutchingsi*, *S. neapolitana*, *S. triophthalma*)
    b. paired toes present that are of different size and shape; one can be rudimental (Fig. 9K; exemplar *S. cecilia*, *S. tamara*)[6]
    c. paired toes of equal size and shape (Fig. 9L–Q; exemplar *S. tremula*, *S. pectinata*)
33. Toe(s) – Size in relation to foot length
    a. minute to small; less than one-tenth of the overall foot length (Fig. 9M; exemplar *S. grandis*)
    b. medium to large; between one-tenth to one-quarter of the foot length (Fig. 9J–L; exemplar *S. tremula*)
    c. very large; at least one-third of the foot length (Fig. 9N; exemplar *S. pachypoda*)

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[5] The length of the pedal glands is related to the foot length. Caution should be exercised with individuals that carry their foot retracted to any degree because in such situations the glands can appear longer than they really are and/or that they extend into the trunk.

[6] The present character overlaps with the previous one but is more specific. It should only be consulted when the state can be determined with certainty because the state "b" can be difficult to determine accurately in the case of a second rudimental toe that can be easily overseen. Otherwise, we recommend character 31 for species identification.

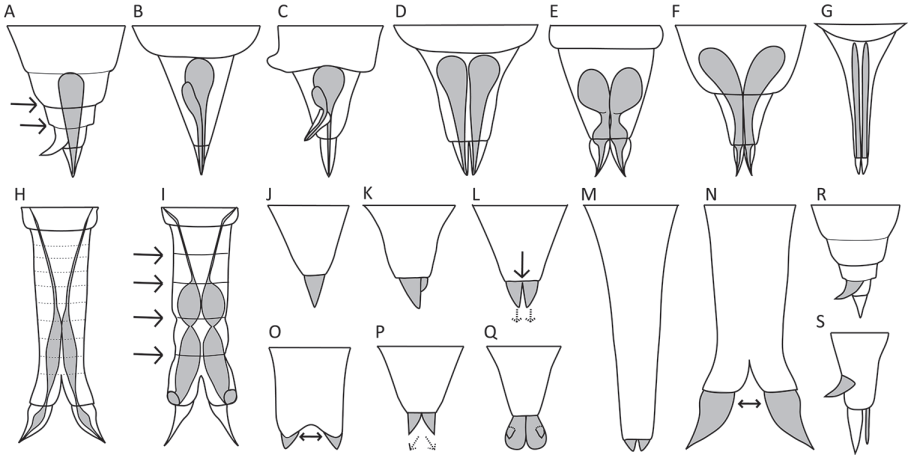

Figure 9. Foot, pedal glands and toes. **A–I** Presence of pseudosegments (arrows) and morphology of pedal glands (grey areas) **A** foot pseudosegmented, pedal gland single and of foot-length (*S. neapolitana*) **B** glands asymmetrical with the larger one being of foot-length, glands terminating in the toes (*S. triophthalma*) **C** glands asymmetrical with one gland terminating in the toe and one in the dorsal spur (*S. hutchingsi*) **D** symmetrical glands of foot-length, voluminous proximally and decreasing gradually in width moving caudally (*S. tremula*) **E** glands shorter than the foot, each spherical proximally and abruptly decreasing caudally before widening again to form a reservoir (*S. oblonga*) **F** glands longer than the foot (*S. prominula*), **G** glands of foot-length and tubular (*S. longipes*) **H** foot with wrinkles, glands tubular, suspended from the trunk (*S. pachypoda*) **I** foot pseudosegmented, each gland with two voluminous sections, suspended from the trunk, glands terminate proximally to the toes (*S. pachypoida*) **J–Q** Symmetry, size and separation of the toes **J** single toe (*S. triophthalma*) **K** asymmetrical, toes of different shape (*S. cecilia*) **L** symmetrical toes of medium size, bases of the toes are in contact (arrow), tips are close to one another or very slightly divergent (dashed arrows; *S. tremula*) **M** toes symmetrical, minute to small (*S. grandis*) **N** toes symmetrical, very large (*S. pachypoda*) **N, O** Bases of the toes widely separated (arrow; *S. pachypoda, S. baltica*) **P** bases of the toes in contact, tips distinctly divergent (dashed arrows; *S. gyrina*) **Q** toes without tips, squamate (*S. squamadigitata*) **R, S** Additional appendages of the foot (grey areas) **R** dorsolateral spur (dorsal view; *S. neapolitana*) **S** ventral spine and dorso-lateral spur (lateral view; *S. hutchingsi*). Drawings modified from: **A, R** Lie-Pettersen (1905) **K** Rousselet (1902) **F, H–I, N** Kutikova and Vassiljeva (1982) **Q** De Smet (2006).

34. Toe(s) – Proximal separation
    a. bases of the toes are widely separated (Fig. 9N, O; exemplar *S. baltica, S. pachypoda*)
    b. bases of the toes are close to or in contact with one another (Fig. 9K–M, P, Q; exemplar *S. tremula*, *S. pectinata*)
    c. only one toe is present (Fig. 9J; exemplar *S. hutchingsi*, *S. neapolitana*, *S. triophthalma*)
35. Toe(s) – Distal separation
    a. tips are close to one another or only very slightly divergent (Fig. 9L; exemplar *S. tremula*)
    b. tips are widely separated, distinctly divergent (Fig. 9P; exemplar *S. gyrina*)
    c. only one toe is present (Fig. 9J; exemplar *S. hutchingsi*, *S. neapolitana*, *S. triophthalma*)

d. toes without tips; squamate, with rounded distal margin (Fig. 9Q; exemplar *S. squamadigitata*)

36. Additional foot appendages
    a. none (Fig. 9J–Q; exemplar *S. tremula, S. pectinata*)
    b. dorsolateral spur present (Fig. 9R; exemplar *S. neapolitana*)
    c. ventral spine and dorsolateral spur present (Fig. 9S; exemplar *S. hutchingsi*)
37. Foot – Number of "pseudosegments"[7]
    a. at least two (Fig. 9A, I; exemplar *S. neapolitana*, *S. pachypoida*, *S. squamadigitata*, *S. tamara*)
    b. only one (Fig. 9B–H; exemplar *S. tremula*)

Sensory system (Table 7)

38. Cerebral eye – Morphology
    a. single (Fig. 10A; exemplar *S. pectinata*)
    b. paired but partially fused or connected by pigment granules (Fig. 10B; exemplar *S. triophthalma*)
    c. paired and distinctly separated from one another (Fig. 10C; exemplar *S. oblonga*, *S. lakowitziana*)
39. Cerebral eye – Size
    a. small to medium, evenly shaped (Fig. 11A, B; exemplar *S. pectinata*)
    b. large, irregularly shaped (Fig. 11C; exemplar *S. baltica*, *S. hutchingsi*)
40. Frontal aggregations of pigment granules[8]
    a. present (Figs 10B, 11A; exemplar *S. triophthalma*)
    b. absent (Figs 10A, C, 11B; exemplar *S. pectinata*)
41. Streams of pigment granules to the anterior margin of the apical field[9]
    a. present (Figs 10B, 11C; exemplar *S. triophthalma*, *S. baltica*)
    b. absent (Figs 10A, C, 11B; exemplar *S. pectinata*)
42. Apical receptors – Separation
    a. Two ciliary tufts, the bases of which are not completely separated from one another (Fig. 10E, H; exemplar *S. grandis*, *S. vorax*)
    b. Two ciliary tufts, the bases of which are slightly separated from one another (Fig.10D; exemplar *S. oblonga*)
    c. Two ciliary tufts that are distinctly separated from one another (Fig. 10F, G; exemplar *S. triophthalma*, *S. pectinata*)

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[7] A general re-examination is recommended here to verify if any apparent pseudosegmentation is actually an artefact caused by wrinkles (e.g., *S. hyperborea*; described as "wrinkled" in Friedrich and De Smet (2000), but "pseudosegmented" in Hollowday (2002)), by the insertion point of the spur (e.g., *S. neapolitana*) or by the preanal-fold overlapping the foot (e.g., *S. oblonga*; Wilke et al. 2018b).

[8] The granules are often regarded as being frontal eyespots, but they are more likely frontal aggregations of pigmented granules of the retrocerebral organ (Wilke et al. in prep.)

[9] The streams of pigment granules appear to be present in the ducts of the retrocerebral organ (Wilke et al. in prep.).

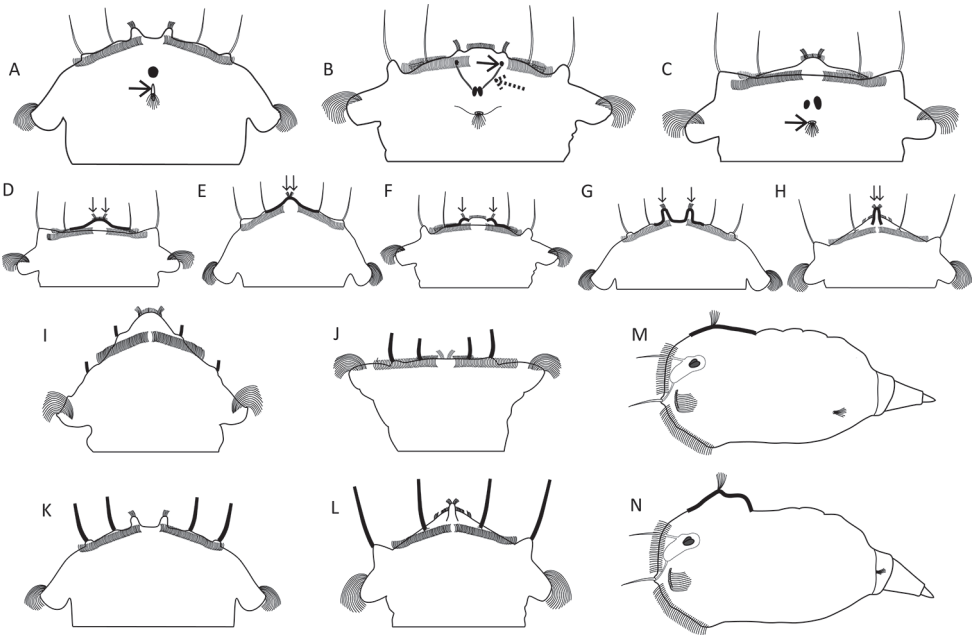

Figure 10. Sensory system. **A–C** Head region showing the cerebral eye, pigment granules and the opening of the dorsal antenna **A** cerebral eye single, dorsal antenna opening slit-shaped (arrow; *S. pectinata*) **B** two partially fused cerebral eyes, frontal aggregations (arrow) and streams (dashed arrow) of pigment granules present (*S. triophthalma*) **C** cerebral eyes distinctly separated, dorsal antenna opening round (arrow; *S. oblonga*) **D–H** Morphology of the apical receptors (thickened lines, arrows) **D** receptors slightly separated, situated on a slight elevation centrally on the apical field (*S. oblonga*) **E** receptors incompletely separated, situated on a strong elevation centrally on the apical field (*S. grandis*) **F** receptors distinctly separated, each situated on a bulge (*S. triophthalma*) **G** receptors distinctly separated, each situated on a strong tentacle-like elevation (*S. pectinata*) **H** receptors incompletely separated, situated on a single tubular elevation (*S. vorax*) **I–L** Lengths of the lateral and dorsolateral styles (thickened lines) **I** minute (*S. squamadigitata*) **J** short (*S. grimpei*) **K** medium (*S. pectinata*) **L** long (*S. vorax*) **M, N** Elevation underlying the dorsal antenna (thickened lines) **M** not elevated to slightly elevated (*S. oblonga*) **N** distinct prominence (*S. tremuloida*). Drawings modified from: **I** De Smet (2006).

Figure 11. Cerebral eye and pigment granules. **A–C** LM images with regard to the cerebral eye (dashed arrows), frontal aggregations and streams of pigment granules (normal arrows) **A** Distinct frontal aggregations of pigment granules present, cerebral eye of normal size (*S. triophthalma*) **B** Frontal aggregations and streams of pigment granules are absent, cerebral eye of normal size (*S. pectinata*) **C** distinct streams of pigment granules are present, large cerebral eye (*S. baltica*). Scale bar: 20 µm.

43. Apical receptors – Elevation
    a. on a flat or slight central elevation of the apical field (Fig. 10D; exemplar *S. oblonga*)
    b. on a strong central elevation of the apical field (Fig. 10E; exemplar *S. grandis*)
    c. on two bulges or pimples (Fig. 10F; exemplar *S. triophthalma*)
    d. on strong, paired elevations (tentacles) (Fig. 10G; exemplar *S. pectinata*)
    e. on a single, tubular elevation (Fig. 10H; exemplar *S. fennica*, *S. johanseni*, *S. vorax*)
44. Lateral and dorsolateral styles – Length[10]
    a. minute (Fig. 10I; exemplar *S. squamadigitata*)
    b. short (Fig. 10J; exemplar *S. grimpei*)
    c. medium (Fig. 10K; exemplar *S. pectinata*)
    d. long (Fig. 10L; exemplar *S. vorax*)
45. Dorsal antenna – Elevation
    a. none to a slight elevation (Fig. 10M; exemplar *S. oblonga*)
    b. distinct prominence to a snout-like projection (Fig. 10N; exemplar *S. tremuloida*)
46. Dorsal antenna – Basal opening
    a. slit-shaped, longer than wide (Figs 10A, 12A; exemplar *S. grandis*, *S. pectinata*)
    b. round (Figs 10B–C, 12B; exemplar *S. tremula*)
47. Lateral antenna(e) – Number
    a. one; left lateral antenna is enlarged, right one is absent (Fig. 13A; exemplar *S. hutchingsi*, *S. triophthalma*)
    b. one; right lateral antenna of normal size, left one is absent (Fig. 13B; exemplar *S. tamara*)
    c. paired symmetrical lateral antennae of normal size (Fig. 13C; exemplar *S. tremula*)

[10] These states are admittedly subjective, especially in the absence of any reference point. However, for those species for which literature data only was available, it was often not possible to be more precise. As such, we have listed all states except the obvious "minute" as subjective in the associated table and highly recommend comparison with our illustrations of the exemplar species for each condition.

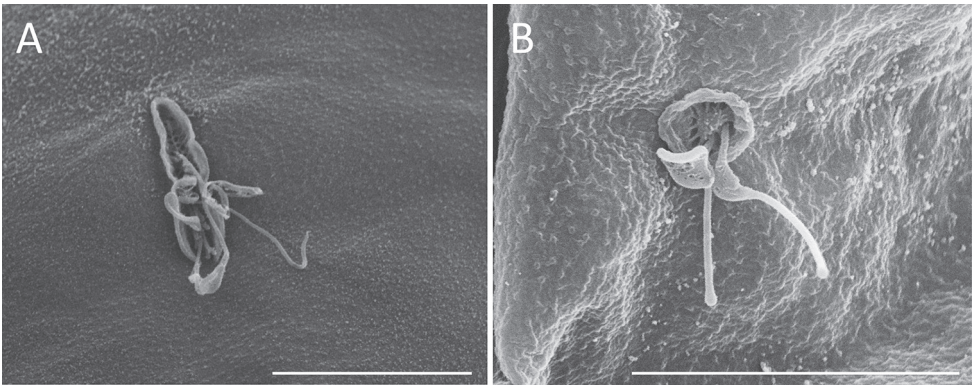

Figure 12. Dorsal antenna. **A, B** REM images of the basal opening of the dorsal antenna **A** slit-shaped (*S. pectinata*) **B** round (*S. tremula*). Scale bar: 10 µm.

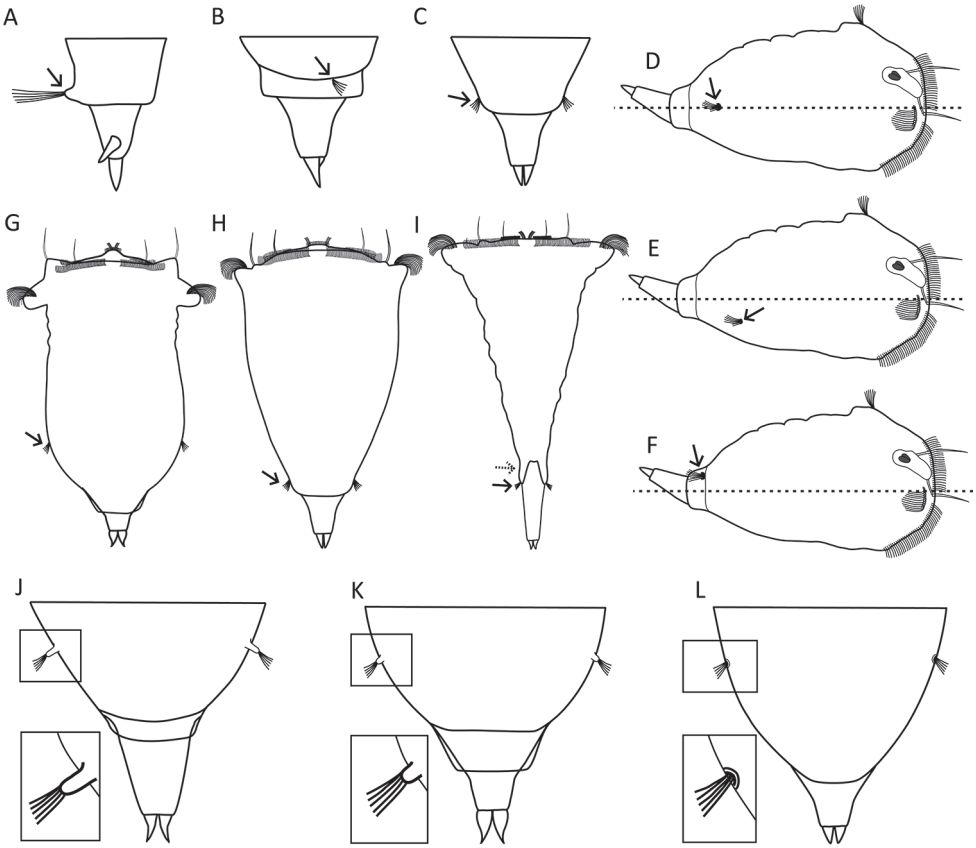

Figure 13. Location and morphology of the lateral antennae. **A–C** Number and size of the lateral antenna(e) (arrow) **A** single, enlarged left lateral antenna (*S. hutchingsi*) **B** single, right lateral antenna (*S. tamara*) **C** lateral antennae paired, symmetrical, and of normal size (*S. tremula*) **D–F** Location of the lateral antenna(e) (arrows) relative to the median transversal axis (dashed line) (lateral habitus is presented as a stylized drawing that is species independent) **D** directly lateral (e.g., *S. tremula*) **E** ventrolateral (e.g., *S. oblonga*) **F** mid-dorsal, single antenna slightly displaced to the right of the body axis (e.g., *S. tamara*) **G–I** Location of the lateral antennae relative to the longitudinal axis (arrows) **G** in the posterior third of the trunk region (*S. oblonga*) **H** in the caudal-most trunk region at or near the base of the foot (*S. tremula*) **I** on lateral lobes (dashed arrow) caudally to the cloaca and in the proximal third of the foot (*S. grimpei*) **J–L** The base of the lateral antennae (detail in inset) **J** surrounded by a tubular epidermal fold (*S. johanseni*) **K** surrounded by a papillary epidermal fold (*S. oblonga*) **L** surrounded by a low epidermal fold (*S. pectinata*). Drawings modified from: **B** Smirnov (1933) and Friedrich and De Smet (2000) **J** Harring (1921).

48. Lateral antenna(e) – Location relative to the median transversal axis of the body
    a. directly lateral on the median transverse axis (Fig. 13D; exemplar *S. tremula*)
    b. ventrolateral to the median transverse axis (Fig. 13E; exemplar *S. pectinata*)
    c. mid-dorsal and slightly displaced to the right of the body axis (Fig. 13F; exemplar *S. tamara*)

49. Lateral antenna(e) – Location relative to the longitudinal plane
    a. in the posterior third of the trunk region (Fig. 13G; exemplar *S. oblonga*)
    b. in the caudal-most trunk region at or near the base of the foot (Fig. 13H; exemplar *S. tremula*)
    c. on lateral lobes caudally to the cloaca (Fig. 13I; exemplar *S. grimpei*)
50. Lateral antenna(e) – Base
    a. surrounded by a tubular (Fig. 13J; exemplar *S. johanseni*) or papillary (Fig. 13K; exemplar *S. oblonga*) epidermal fold
    b. surrounded by a low epidermal fold (Fig. 13L; exemplar *S. pectinata*)

Trophi (Table 8)

51. Ramus[11] ("unci") teeth
    a. Edentulous (Figs 14A, 15A; exemplar *S. pectinata*); plate plain, slightly serrated, fringed or corrugated (Fig. 14B, C; exemplar *S. stylata*)
    b. With several distinct teeth (Figs 14D–G, 15B–F; exemplar *S. gyrina*, *S. triophthalma*)
52. Ramus*[12] ("unci") teeth – Shape
    a. teeth absent (Figs 14A, B, 15A; exemplar *S. pectinata*, *S. stylata*)
    b. one more or less distinct tooth, remainder serrated (Figs 14C, 15B; exemplar *S. vorax*)
    c. one distinctly pointed single tooth, remainder slightly incised and blunt (Fig. 14D; exemplar *S. verrucosa*)
    d. all teeth are distinctly incised (Figs 14E, 15C, D; exemplar *S. gyrina, S. oblonga*)
    e. dorsal teeth are distinctly incised, ventral teeth are comb-like (Figs 14F, 15E; exemplar *S. triophthalma*)
    f. dorsal teeth are comb-like, ventral teeth are distinctly incised (Figs 14G, 15F; exemplar *S. baltica*)
53. Ramus[13] ("unci") teeth – Separation
    a. teeth are separated into two groups, either by a cleft (Fig. 15D, F, arrow; exemplar *S. oblonga*) and/or by their morphological distinctiveness (Figs 14F, G, 15E, F; exemplar *S. triophthalma*, *S. baltica*)
    b. teeth are not separated so that a continuous row of teeth is present (Figs 14E and 15C; exemplar *S. gyrina*)
    c. no distinct teeth present (Figs 14A, B, 15A; exemplar *S. pectinata*)

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[11] The toothed or edentulous plate always considered to be the uncus is actually the ramus (Wilke et al. in prep.).

[12] See statement from character 51. This character overlaps with character 51 but is more specific. Trophi are difficult to examine in their detail, which is why the present character should only be applied when it can be answered with certainty. Otherwise, we recommend character 51 for species identification.

[13] See statement from character 51.

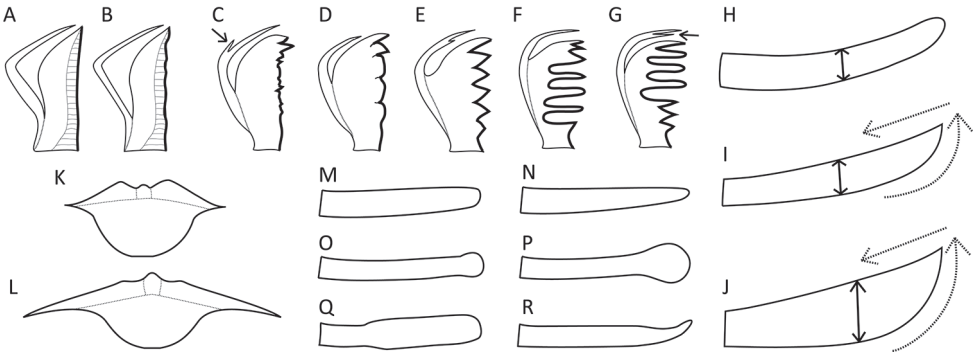

Figure 14. Trophi. **A–G** Morphology of the ramus ("unci") teeth **A** teeth absent (*S. pectinata*) **B** teeth absent, margin slightly corrugated (*S. stylata*) **C** no distinct teeth, only a serrated plate, frontal hook with a spine (arrow; *S. vorax*) **D** one to two teeth are sharply pointed and remainder are blunt (*S. verrucosa*) **E** teeth distinctly incised, frontal hook with a spine (*S. gyrina*) **F** dorsal teeth distinctly incised and ventral comb-like (*S. triophthalma*) **G** dorsal teeth comb-like and ventral distinctly incised, frontal hook with a spine (arrow; *S. baltica*) **H–J** Shape and breadth (double headed-arrow) of the lateral fulcrum **H** blade-like, narrow, distal end not oblique (*S. tremula*) **I** machete-like, narrow, distal end oblique (dashed arrows; *S. oblonga*) **J** axe-shaped to semi-circular, broad to very broad, distal end oblique (dashed arrows; *S. longipes*) **K–L** Shape of the hypopharynx **K** small to medium, robust (*S. tremula*) **L** broad to very broad, laterally pointed / dagger-like (*S. stylata*) **M–R** Shape of the cauda of the manubrium **M** of even width (*S. baltica*) **N** slightly decreasing distally (*S. pectinata*) **O** with a small knob-like thickening distally (*S. hutchingsi*) **P** with a large knob-like thickening distally (*S. grimpei*) **Q** oar blade shaped at the distal half (*S. oblonga*) **R** cauda spatulate or kinked distally (*S. glacialis*). Drawings modified from: **D** Stemberger (1979) (sub. *S. asymmetrica* Koch-Althaus) and Jersabek et al. (2003a) **R** Friedrich and De Smet (2000).

54. Spine of frontal hook[14]
    a. absent (e.g., Fig. 14A, B; exemplar *S. pectinata*)
    b. present (Fig. 14C, G, arrow; exemplar *S. vorax, S. baltica*)
55. Fulcrum – Height
    a. of low to medium height (Figs 14H, I, 15G, H; exemplar *S. tremula*, *S. oblonga*)
    b. high to very high (Figs 14J, 15I, J, 16B; exemplar *S. longipes*, *S. vorax*, *S. grimpei*)
56. Fulcrum – Overall shape
    a. slender, blade-like (Figs 14H, 15G; exemplar *S. tremula*, *S. pectinata*)
    b. machete-like (Figs 14I, 15H; exemplar *S. oblonga*)
    c. robust, axe-shaped to semi-circular (Figs 14J, 15I, J, 16B; exemplar *S. longipes*, *S. vorax*, *S. grimpei*)
57. Fulcrum – Shape of the distal ventral margin
    a. not oblique (Figs 14H, 15G; exemplar *S. tremula*)
    b. oblique (Figs 14I, J, 15H–J, 16B; exemplar *S. S. oblonga*, *S. longipes*, *S. vorax*, *S. grimpei*)

[14] The structure always described as the "frontal hook" actually represents the uncus (Wilke et al. in prep.).

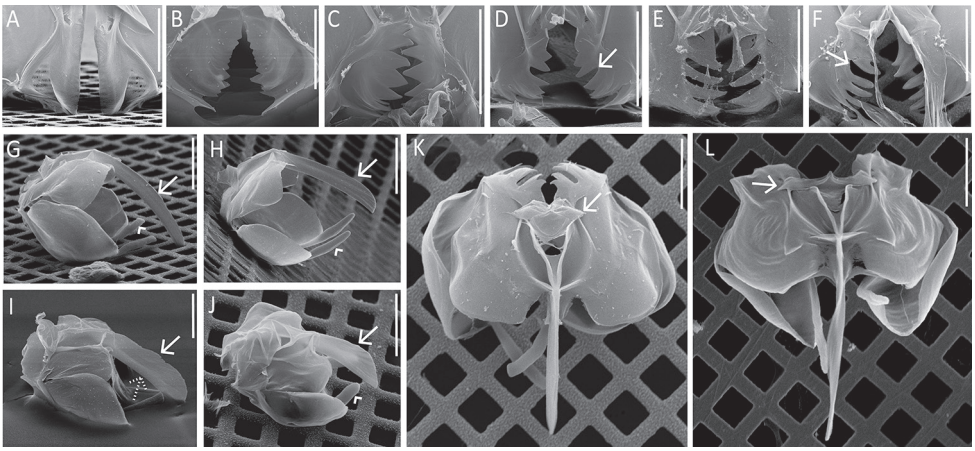

Figure 15. SEM images of the trophi. **A–F** Ramus ("unci") teeth (ventral sides of the trophi directed upwards) **A** teeth absent (*S. pectinata*) **B** no distinct teeth, only a serrated plate (*S. vorax*) **C** teeth distinctly incised (*S. gyrina*) **D** teeth distinctly incised and separated into two groups by a deep sulcus (arrow; *S. oblonga*) **E** dorsal group of teeth distinctly incised and ventral group of teeth comb-like (*S. triophthalma*) **F** dorsal teeth comb-like and ventral teeth distinctly incised, groups of teeth separated by a deep sulcus (arrow; *S. baltica*) **G–J** Shape of the lateral fulcrum (normal and dashed arrows) and thickness of the cauda (arrow-heads) (trophi from lateral view, ventral sides directed upwards) **G** fulcrum blade-like, narrow, distal end not oblique, cauda of medium thickness (*S. tremula*) **H** fulcrum machete-like, distal end oblique, cauda of medium thickness (*S. oblonga*) **I** fulcrum broad, with distinct dorsal thickening (dashed arrow) and ventral lamella (arrow; *S. vorax*) **J** fulcrum axe-shaped, very broad, with oblique distal end, cauda robust (*S. longipes*) **K, L** Shape of the hypopharynx (arrow) **K** small to medium, robust (*S. tremula*) **L** broad to very broad, laterally pointed / dagger-like (*S. stylata*). Scale bar: 20 µm.

58. Fulcrum – Presence of a distinct dorsal thickening (and lamellar ventral side)
    a. present (Figs 15I, 16B; exemplar *S. vorax*, *S. grimpei*)
    b. absent (or very weak) (Figs 15G, H, J; exemplar *S. tremula*, *S. longipes*)
59. Hypopharynx – Width
    a. small to medium, robust (Figs 14K, 15K; exemplar *S. tremula*, *S. oblonga*)
    b. broad to very broad, pointed laterally / dagger-like (Figs 14L, 15L; exemplar *S. stylata*)
60. Manubrium – Shape of cauda
    a. of even width (Figs 14M, 15G; exemplar *S. tremula*) or narrowing slightly distally (Figs 14N, 15H; exemplar *S. pectinata*)
    b. small (Fig. 14O; exemplar *S. hutchingsi*) or large (Figs 14P, 16B; exemplar *S. grimpei*, *S. tremuloida*) knob-like thickening at the distal end
    c. oar blade shaped in the distal half (Fig. 14Q; exemplar *S. oblonga*)
    d. spatulate or kinked at the distal end (Fig. 14R; exemplar *S. glacialis*)
61. Manubrium – Thickness of the cauda
    a. very thin, slender (Fig. 16A; exemplar *S. kitina*, *S. triophthalma*)
    b. medium or robust (Figs 15G, H, J, 16B; exemplar *S. tremula*, *S. longipes*, *S. grimpei*)

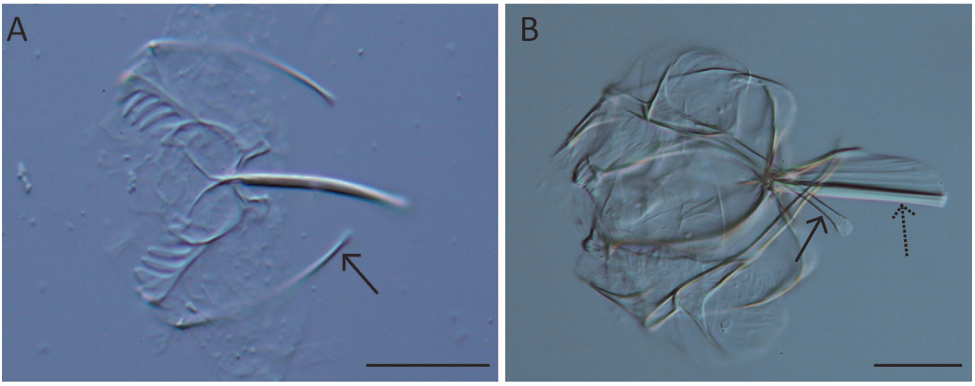

Figure 16. LM images of the trophi. **A, B** Cauda (arrows) and fulcrum (dashed arrow) **A** very thin and slender cauda (*S. kitina*) **B** cauda medium with a large distal knob, fulcrum with dorsal thickening and ventral lamella (*S. grimpei*). Scale bar: 25 µm.

Weighted matrix key for *Synchaeta* – detailed tables

Table 3. Weighted character states for habitat, (swimming) behaviour and size of species of *Synchaeta*.

Category	Habitat			Behaviour			Size
Characters	Limnic, brackish, marine	Swimming duration	Adherence to objects	Swimming motion	Foot position while swimming	Directional changes	Overall size
Character number	**1**	**2**	**3**	**4**	**5**	**6**	**7**
S. arcifera	b/c	a?	?	?	?	?	a
S. atlantica	c	a	?	?	?	?	a
S. bacillifera	c	a	?	?	?	?	b
S. baltica	b/c	a	a	b	a	b	b
S. bicornis	b	a	?	a	a?	a	*a/b*
S. cecilia	b/c	b	b/c	a	b	a	a
S. cylindrica	**d**	?	?	?	?	?	a
S. fennica	b/c	?	?	?	?	?	*a/b*
S. glacialis	c	a	?	?	?	?	a
S. grandis	a	a	a	c	b	b	b
S. grimpei	b/c	a	a	a	b	b	b
S. gyrina	b/c	a†	a†	b/c	b	a	*a/b*
S. hutchingsi	b/c	a	a	a/b	b	a	a
S. hyperborea	c	a	?	?	?	?	*a/b*
S. johanseni	c	a	?	?	?	?	b
S. kitina	a	b	b	a	a	a	a
S. lakowitziana	a	?	?	?	a?	?	b
S. longipes	a	a	a	a	b	a	*a/b*
S. neapolitana	c	?	?	?	?	?	a
S. oblonga	a/(b)	a†	a†	a/b	a	a	a
S. pachypoda	a	?	?	?	b	?	b
S. pachypoida	a	?	?	?	a	?	b
S. pectinata	a	a	a	c	b	b	b
S. prominula	a	?	?	?	?	?	*a/b*
S. rousseleti	c	a	a	?	?	?	a
S. squamadigitata	c	?	?	?	?	?	a
S. stylata	a	a	a	b	b	a	*a/b*
S. tamara	c	a	?	?	?	?	*a/b*
S. tavina	b/c	a/b‡	?	c	?	a	a
S. tremula	a	b	c	a	b	b	*a/b*
S. tremuloida	a	b	c	b	b	a	*a/b*
S. triophthalma	b/c	a	a	a	b	a	*a/b*
S. verrucosa	a	?	?	c	a	?	*a/b*
S. vorax	b/c	a	a	a	b	a	*a/b*

† Adheres to objects only when disturbed and then only for a short time and without any twisting movement.
‡ Adherence to objects observed by Lauterborn (1905) and Remane (1929), but not by Hood (1893).

Table 4. Weighted character states for the morphology of the head and neck region in species of *Synchaeta*.

Category	Apical field		Styles	Auricles		Neck	Appendages		Head
Character	**Width**	**Elevation**	**Elevation**	**Size**	**Orientation**	**Demarcation**	**Presence**	**Location**	**Colour**
Character number	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
S. arcifera	*b*	*b*	*b?*	*?*	*b*	*a*	b	b	*?*
S. atlantica	*b*	*a/b*	*a*	a	a	*a/b*	a	c	*?*
S. bacillifera	*b*	*c*	*b*	*c/d*	*c*	*a*	b	**a**	*?*
S. baltica	*b*	*c*	*c*	d	*c*	*c*	a	c	*c*
S. bicornis	*b*	*c*	*c*	d	*b/c*	*a*	b	b	*a*
S. cecilia	*a*	*b*	*b*	*c*	*a/b*	*a/(c?)*	a	c	*?*
S. cylindrica	*a*	*b*	*a/b*	*b*	*a/b*	*c*	a	c	*?*
S. fennica	*b*	*c*	*b*	*c/d*	*b/c*	*c*	b	b	*?*
S. glacialis	*a/b*	*c*	*a*	*b*	*b*	*c*	a	c	*?*
S. grandis	*b*	*c*	*b*	d	*c*	*a*	a	c	*a/c*
S. grimpei	*b*	*a*	*a*	a	a	*a*	a	c	*a-c*
S. gyrina	*a/b*	*a*	*b*	*b*	*a/(b)*	*b/c*	a	c	*a*
S. hutchingsi	*b*	*b*	*b*	*c*	*a/b*	*c*	a	c	*a/b*
S. hyperborea	*a*	*c*	*a*	*b*	*a/b*	*c*	a	c	*?*
S. johanseni	*b*	*c*	*b*	*c/d*	*b/c*	*c?*	a	c	*a*
S. kitina	*b*	*a/b*	*b*	*c*	a	*a*	a	c	*a/b*
S. lakowitziana †	*a/b*	*b?/c*	*b/c*	*c*	*b*	*a/c*	a	c	*?*
S. longipes	*b*	*c*	*c*	d	*c*	*a*	a	c	b
S. neapolitana	*b*	*b*	*b/c*	d	*a/b*	*c*	a	c	*?*
S. oblonga	*b*	*b*	*b/c*	*c*	*b*	*c*	a	c	*a/b*
S. pachypoda	*a/b*	*a/b*	*b*	*b/c*	*b*	*c*	a	c	*?*
S. pachypoida	*a/b*	*a*	*a*	*b*	a	*c*	a	c	*?*
S. pectinata	*b*	*c*	*a/b*	*c/d*	*c*	*a*	a	c	*a*
S. prominula	*a*	*b*	*b*	*b*	*a/b*	*b*	a	c	*?*
S. rousseleti	*a*	*a*	*?*	a	a	*a*	a	c	*?*
S. squamadigitata	*a/b*	*c*	*a*	*c*	a	*c*	a	c	*?*
S. stylata	*b*	*c*	*b*	d	*b/c*	*a*	a	c	*a*
S. tamara	*a*	*b*	*a*	*b*	a	*b/c*	a	c	*?*
S. tavina	*a/b*	*b*	*b*	*b*	a	*a/b*	a	c	*a*
S. tremula	*b*	*a*	*a*	*b*	a	*a*	a	c	*a/b*
S. tremuloida	*a*	*a*	*a/b*	*c*	a	*b*	a	c	*a/b*
S. triophthalma	*b*	*b*	*b/c*	d	*b*	*a/(c?)*	a	c	*a*
S. verrucosa	*b*	*c*	*a*	d	*a/b*	*c*	a	c	*a*
S. vorax	*b*	*c*	*c*	d	*b/c*	*c*	a	c	*a/c*

† As already noted by Hollowday (2002), this species requires further revision (preferably on living, non-preserved specimens) because of inconsistencies in the published morphological data for it, especially for the neck region and the apical field.

Table 5. Weighted character states for the morphology of the trunk region in species of *Synchaeta*.

Category	External morphology				Internal morphology		
Character	**Shape**	**Anal-pseudosegment**	**Appendages**	**Longitudinal striae**	**Internal organs**	**Violet globules**	**Oesophagus**
Character number	**17**	**18**	**19**	**20**	**21**	**22**	**23**
S. arcifera	*?*	?	**a**	?	a	?	?
S. atlantica	*c*	a	b	?	a	?	?
S. bacillifera	*c*	a	b	?	?	?	?
S. baltica	*c*	a	b	a	*a/b*	a/b	b
S. bicornis	*a/b*	a	b	?	*a/b*	a/b	b
S. cecilia	*c*	b	b	a	a	b	a
S. cylindrica	*b*	a	b	a	a	b	?
S. fennica	*a/b*	?	b	?	*a/b*	b	b
S. glacialis	*b*	?	b	?	a	b	a
S. grandis	*b*	b	b	a	*a/b*	b	b
S. grimpei	*a*	b	b	a	**c**	a/b	?
S. gyrina	*c*	a	b	a	a	b	a
S. hutchingsi	*a*	b	b	a	*a/b*	b	a
S. hyperborea	*b*	b	b	?	a	b	a?
S. johanseni	*c*	?	b	?	b	b	b
S. kitina	*a/c*	b	b	a	a	b	a
S. lakowitziana	*b*	?	b	?	a	b	a?
S. longipes	*c*	b	b	a	**a/d**	b	?
S. neapolitana	*a/c*	a	b	?	*a/b*	b	?
S. oblonga	*c*	a†	b	a	a	b	a

Category	External morphology				Internal morphology		
Character	**Shape**	**Anal-pseudosegment**	**Appendages**	**Longitudinal striae**	**Internal organs**	**Violet globules**	**Oesophagus**
S. pachypoda	*b*	a?	b	a	a	b	a?
S. pachypoida	*b*	b	b	a	a	b	a?
S. pectinata	*a/c*	b	b	**b**	b	b	b
S. prominula	*c*	?	b	a	a	b	a
S. rousseleti	*c*	b	b	?	a	?	?
S. squamadigitata	*c*	b	b	a	b	b	b?
S. stylata	*c*	b	b	a	*a/b*	b	b
S. tamara	*c*	a?	b	?	a	b	?
S. tavina	*b*	b	b	a	a	b	a
S. tremula	*a*	b	b	a	a	b	a
S. tremuloida	*c*	a	b	a	a	b	a
S. triophthalma	*a*	b	b	a	(a)/b	b	a
S. verrucosa	*b/c*	?	b	a	b	b	a
S. vorax	*c*	b	b	a	a	b	b

† In contrast to Hollowday (2002), we found that *S. oblonga* exhibits a foot with only one instead of two pseudosegments. The impression of two pseudosegments being present might derive from the distinct preanal-fold that distinctly overlaps the foot, which itself is predominantly withdrawn (Wilke et al. 2018b).

Table 6. Weighted character states for the morphology of the foot, pedal glands, and toes in species of *Synchaeta*.

Category	Foot		Pedal glands						Toes				Other	
Character	**Orientation**	**Shape and size**	**Symmetry**	**Arrangement**	**Length**	**Shape**	**Opening**	**Symmetry**	**Arrangement**	**Size**	**Separation (prox.)**	**Separation (dist.)**	**Appendages**	**Pseudosegments**
Character number	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**
S. arcifera	?	**a?**	b	c	a	a?	a	b	c	c	b	a	a	b
S. atlantica	c	**a**	b	c	c	c	?	b	c	c	b	*a/b*	a	b
S. bacillifera	?	*c/e*	b	c	a	c	a	b	c	b	b	b	a	b
S. baltica	a	*c/e*	b	c	a	c	a	b	c	a	a	b	a	b
S. bicornis	?	c	b	c	b	c?	a	b	c	b	b	b	a	b
S. cecilia	a	*b/c*	a	b	b	b	?	a	b	b	b	a	a	b
S. cylindrica	b	c	b	c	b	c	?	b	c	b	b	b	a	b
S. fennica	?	c	b	c	b	a	?	b	c	b	b	b	a	b
S. glacialis	b	c	b	c	b	*a/b?*	a	b	c	*b/c*	b	*a/b*	a	b
S. grandis	c	d	b	c	b	a	a	b	c	a	b	a	a	b
S. grimpei	b	e	b	c	a	e	a	b	c	a	b	b	a	b
S. gyrina	*b/c*	c	b	c	a	c	a	b	c	b	b	b	a	b
S. hutchingsi	*b/c*	b	a	b	b	*b/c*	**b**	a†	a†	b	c	c	**c**†	b
S. hyperborea	b	*c/e*	b	c	b	c	a	b	c	b	b	b	a	b
S. johanseni	?	e	b	c	a	*b/c*‡	a	b	c	*a/b*	b	b	a	b
S. kitina	b	*b/c*	b	c	b	b	a	b	c	*b*	b	a	a	b
S. lakowitziana	?	e	b	c	a	c	a	b	c	b	b	b	a	b
S. longipes	c	d	b	c	b	a	a	b	c	b	b	a	a	b
S. neapolitana	?	c	a	**a**§	b	b	a§	a|	a|	b	c	c	**b**§	a
S. oblonga	*b/c*	c	b	c	a¶	c	a	b	c	b	b	*a/b*	a	b
S. pachypoda	?	f	b	c	a	**d**	a	b	c	c	a	b	a	b
S. pachypoida	?	f	b	c	a	e	**c**	b	c	c	?	b	a	a
S. pectinata	c	c	b	c	a	a	a	b	c	*a/b*	b	a	a	b
S. prominula	?	c	b	c	c	b?	?	b	c	b	b	*a/b*	a	b
S. rousseleti	b	?	b	c	c	b	?	b	c	c	b	b	a	b
S. squamadigitata	?	c	b	c	b	*a/b?*	?	b	c	b	b	**d**	a	a
S. stylata	b	d	b	c	b	a	a	b	c	a	b	a	a	b
S. tamara	?	c	a	b	a/b?	b	a	a	b	b	b	?	a	a

Category	Foot		Pedal glands							Toes			Other	
Character	Orientation	Shape and size	Symmetry	Arrangement	Length	Shape	Opening	Symmetry	Arrangement	Size	Separation (prox.)	Separation (dist.)	Appendages	Pseudosegments
S. tavina	*b/c*	c	b	c	b	c#	a	b	c	b	b	a	a	b
S. tremula	a	c	b	c	b	b	a	b	c	b	b	a	a	b
S. tremuloida	c	c	b	c	b	b	a	b	c	b	b	a	a	b
S. triophthalma	b	b	a	b	b	b	a	a	a	b	c	c	a	b
S. verrucosa	b	e	b	c	a	c	a	b	c	*b/c*	b	b	a	b
S. vorax	b	d	b	c	b	*a/b*	a	b	c	b	b	a	a	b

† The dorsolateral spur in *S. hutchingsi* might represent a second toe that is turned upwards because one pedal gland terminates in the spur and eggs are carried attached to it (as is the case for true toes).
‡ "b" according to the drawing by Harring (1921) and "c" according to the LM image of an individual by Jersabek et al. (2003b).
§ It remains to be determined whether the pedal gland of *S. neapolitana* is truly single or is highly asymmetric, with a normal, but vestigial gland that was overseen.
| It remains to be determined if the dorsolateral spur in *S. neapolitana* represents a true toe (as assumed by Rousselet 1902), potentially with a pedal gland terminating in it (contra Lie-Pettersen 1905).
¶ The pedal glands are shorter than the foot (contra Hollowday 2002). The impression of the pedal glands being of foot-length might derive from the foot being partly retracted, something that is typical of *S. oblonga* (Wilke et al. 2018b).
# According to the LM image of an individual by Jersabek et al. (2003b).

Table 7. Weighted character states for the morphology of *the sensory system in* species of *Synchaeta*.

Category	Eyes				Apical receptors		Styles	Dorsal antenna		Lateral antenna(e)			
Character	Morphology	Size	Frontal pigment granules	Streams of pigment granules	Separation	Elevation	Length of the styles	Elevation	Basal opening	Number and size	location (transversal)	location (longitudinal)	Bases of the antenna(e)
Character number	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
S. arcifera	b	a	?	?	c	?	*c*	?	?	c	a?	b	a
S. atlantica	?	?	?	?	?	?	a	?	?	?	?	?	?
S. bacillifera	a	a	?	?	?	?	*b*	?	?	c	?	a	a
S. baltica	*a/b*	b	a	a	a	b	*c*	b	b	c	b	a	a
S. bicornis	b	?	a	a	b	b	*c/d*	a	b	?	?	?	?
S. cecilia	b	a	b	b	c?	c?	*b/c*	b	?	c	a	b	b
S. cylindrica	b	a	?	?	?	?	*b/c*	b	?	?	?	?	?
S. fennica	*a/b*	a	?	?	a	e	d	b	b	c	b	a	b
S. glacialis	*a/b*	a	b	b	c	c	a	a	?	c	a?	a/b	b
S. grandis	a	a	b	b	a	b	*a/b*	a	a	c	b	a	b
S. grimpei	*a/b*	a	*a/b*	*a/b*	b	a	*b*	a	b	c	a	**c**	b
S. gyrina	b	a/(b†)	b	*a/b*	b	a	*c*	a	b	c	b	a	a
S. hutchingsi	a/(b)	b	*a/b*	*a/b*	c	c	*c*	a	?	a	a	b	b
S. hyperborea	*a/b*	a	?	?	c	c	a	a	?	c	a	a/b	b
S. johanseni	?	?	?	?	a	e	*c*	?	b	c	b	a	a
S. kitina	*b/c*	a	*a/b*	*a/b*	c	c	*c*	b	b	c	a	b	b
S. lakowitziana	c	a	b	b	b	*a/b*	*b/c*	b	b	c	?	a	?
S. longipes	*a/b*	a	b	b	a	b	d	a	b	c	b	a	b
S. neapolitana	*a/b*	a	b	b	c?	c?	*c*	b?	b	c	b	a	?
S. oblonga	*a-c*	a	*a/b*	*a/b*	b	a	*c*	a	b	c	b	a	a
S. pachypoda	c	a	?	?	?	?	*b/c*	?	b	c	?	a	b
S. pachypoida	b	a	?	?	?	?	*b/c*	?	b	c	a?	a	a
S. pectinata	a	a	b	b	c	**d**	*c*	a	a	c	b	a	b
S. prominula	b	?	?	a	b	a	*c*	?	b	c	a	b	b
S. rousseleti	?	?	?	?	?	?	?	?	?	?	?	?	?
S. squamadigitata	b	a	?	?	c	?	a	a	?	c	?	a	?
S. stylata	*a/b*	a	b	b	a	b	*c*	a	b	c	b	a	b
S. tamara	b	a	?	?	b?	a	*b/c*	?	?	**b**	**c**	b	?
S. tavina	*b/c*	a	?	?	b	a	*c*	b	b	c	?	a	b
S. tremula	b	a	b	b	b/c	a	*b/c*	b	b	c	a	b	b
S. tremuloida	b	a	b	b	b/c	a	*b*	b	b	c	a	b	b

Category	Eyes				Apical receptors		Styles	Dorsal antenna		Lateral antenna(e)			
Character	Morphology	Size	Frontal pigment granules	Streams of pigment granules	Separation	Elevation	Length of the styles	Elevation	Basal opening	Number and size	location (transversal)	location (longitudinal)	Bases of the antenna(e)
S. triophthalma	b	a	a	a	c	c	*c*	b	b	a	a	b	b
S. verrucosa	c	a	*a/b*	b	?	?	*b*	b	?	c	b	a	?
S. vorax	b	a	*a/b*	*a/b*	a	e	d	b	b	c	b	a	b

† Pale red aggregations of pigment granules located around the darkly pigmented cerebral eyes can make the latter appear large.

Table 8. Weighted character states for the morphology of the trophi in species of *Synchaeta*.

Category	Ramus ("unci")			Unci	Fulcrum				Hyp.	Cauda	
Character	Teeth presence	Shape of the teeth	Separation	Frontal hook with spur	Height	Overall shape	Distal margin	Thickening	Hypopharynx	Shape	Thickness
Character number	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**
S. arcifera	b	e	a	a	a	a	a	b	?	*a/b*	a
S. atlantica	b	*c/d*	b	a	a	b	b	a?	a	b	b
S. bacillifera	b	d	a	b	a	a	?	?	?	?	?
S. baltica	b	f	a	b	a	a	a	b	*a/b*	a	b
S. bicornis	b	d	a	?	a	a	a	?	?	?	?
S. cecilia †	b	e	a	?	a	a	a	b	a	a	a
S. cylindrica	b	d	b	?	b	*b/c*	b	b	?	a	b
S. fennica ‡	a	b	b	b	b	c	b	a	?	?	?
S. glacialis §	b	d	b	b	*a/b*	*b/c*	b	a	a	d	b
S. grandis	a	*a/(b)*	*b/c*	a	a	a	b	b	b	a	b
S. grimpei	*a/b*	c	b	a	b	c	b	a	*a/b*	b	b
S. gyrina	b	d	b	b	a	b	b	b	a	*a/c*	b
S. hutchingsi	b	e	a	a	a	a	a	b	?	*a/b*	a
S. hyperborea §	b	d	b	b	a	b	b	a?	a	*a/b*	b
S. johanseni|	b	f	?	?	?	?	?	?	?	?	?
S. kitina	b	e	a	a	a	a	a	b	?	a	a
S. lakowitziana ¶	b	*c/d*	b	b	a	b	?	?	?	?	?
S. longipes	a	*a/b*	*b/c*	a	b	c	b	a	a	a	b
S. neapolitana#	b	e	a	a	a	a	a	b	?	?	?
S. oblonga	b	d	a	b	a	b	b	b	a	*a/c*	b
S. pachypoda	b	*c*	b	a	?	?	?	?	a	a	b
S. pachypoida	b	*c*	b	a	?	?	?	?	?	a	b
S. pectinata	a	a	c	a	a	a	a	b	*a/b*	a	b
S. prominula	b	d	b	?	?	?	?	?	a	*a/c*	b
S. rousseleti	b	*c/d*	b	a	a	b?	b	a?	a	a	b
S. squamadigitata	b	d	b	b	b	*b/c*	b	a	a	*b/d*	b
S. stylata	a	a	c	a	a	a	b	b	b	*a/d*	b
S. tamara §	*a/b*	*c/d*	b	b	b	*b/c*	b	a	a	a	?
S. tavina	b	d	?	?	b	c	b	?	?	?	?
S. tremula	b	d	a	b	a	a	a	b	a	a	b
S. tremuloida	b	d	a	b	a	a	a	b	a	b	b
S. triophthalma	b	e	a	a	a	a	a	b	a	a	a
S. verrucosa ††	*a/b*	c	b	a	b?	b	b	a	*a/b*	a	?
S. vorax	*a*	b	b	b	b	c	b	a	a	*a/c*	b

† Trophi according to an illustration from Arndt et al. (1990) and a LM image from Rougier et al. (2000)
‡ Trophi according to a LM image from Labuce and Strake (2017)
§ Trophi according to an SEM image from Friedrich and De Smet (2000)
| Ramus according to a LM image of the habitus of an individual by Jersabek et al. (2003b), where the trophi were visible
¶ Trophi according to SEM and LM images from Obertegger et al. (2006)
# Trophi according to LM image from Rougier et al. (2000)
†† Trophi according to Jersabek et al. (2003a)

Weighted matrix key for *Synchaeta* – numerical list

Table 9.

S. arcifera											
1b/c	2a?	?	?	?	?	7a	*8b*	*9b*	*10b?*	?	*12b*
13a	14b	15b	?	?	?	**19a**	?	21a	?	?	?
25a?	26b	27c	28a	29a?	30a	31b	32c	33c	34b	35a	36a
37b	38b	39a	?	?	42c	?	*44c*	?	?	47c	48a?
49b	50a	51b	52e	53a	54a	55a	56a	57a	58b	?	*60a/b*
61a											
S. atlantica											
1c	2a	?	?	?	?	7a	*8b*	*9a/b*	*10a*	11a	12a
13a/b	14a	15c	?	*17c*	18a	19b	?	21a	?	?	24c
25a	26b	27c	28c	29c	?	31b	32c	33c	34b	*35a/b*	36a
37b	?	?	?	?	?	?	44a	?	?	?	?
?	?	51b	*52c/d*	53b	54a	55a	56b	57b	58a?	59a	60b
61b											
S. bacillifera											
1c	2a	?	?	?	?	7b	*8b*	*9c*	*10b*	*11c/d*	*12c*
13a	14b	**15a**	?	*17c*	18a	19b	?	?	?	?	?
25c/e	26b	27c	28a	29c	30a	31b	32c	33b	34b	35b	36a
37b	38a	39a	?	?	?	?	*44b*	?	?	47c	?
49a	50a	51b	52d	53a	54b	55a	56a	?	?	?	?
?											
S. baltica											
1b/c	2a	3a	4b	5a	6b	7b	*8b*	*9c*	*10c*	11d	*12c*
13c	14a	15c	*16c*	*17c*	18a	19b	20a	*21a/b*	22a/b	23b	24a
25c/e	26b	27c	28a	29c	30a	31b	32c	33a	34a	35b	36a
37b	*38a/b*	39b	40a	41a	42a	43b	*44c*	45b	46b	47c	48b
49a	50a	51b	52f	53a	54b	55a	56a	57a	58b	*59a/b*	60a
61b											
S. bicornis											
1b	2a	?	4a	5a?	6a	*7a/b*	*8b*	*9c*	*10c*	11d	*12b/c*
13a	14b	15b	*16a*	*17a/b*	18a	19b	?	*21a/b*	22a/b	23b	?
25c	26b	27c	28b	29c?	30a	31b	32c	33b	34b	35b	36a
37b	38b	?	40a	41a	42b	43b	*44c/d*	45a	46b	?	?
?	?	51b	52d	53a	?	55a	56a	57a	?	?	?
?											
S. cecilia											
1b/c	2b	3b/c	4a	5b	6a	7a	*8a*	*9b*	*10b*	*11c*	*12a/b*
13a(/c)	14a	15c	?	*17c*	18b	19b	20a	21a	22b	23a	24a
25b/c	26a	27b	28b	29b	?	31a	32b	33b	34b	35a	36a
37b	38b	39a	40b	41b	42c?	43c?	*44b/c*	45b	?	47c	48a
49b	50b	51b	52e	53a	?	55a	56a	57a	58b	59a	60a
61a											
S. cylindrica											
1d	?	?	?	?	?	7a	*8a*	*9b*	*10a/b*	*11b*	*12a/b*
13c	14a	15c	?	*17b*	18a	19b	20a	21a	22b	?	24b
25c	26b	27c	28b	29c	?	31b	32c	33b	34b	35b	36a
37b	38b	39a	?	?	?	?	*44b/c*	45b	?	?	?
?	?	51b	52d	53b	?	55b	*56b/c*	57b	58b	?	60a
61b											
S. fennica											
1b/c	2?	?	?	?	?	*7a/b*	*8b*	*9c*	*10b*	*11c/d*	*12b/c*
13c	14b	15b	?	*17a/b*	?	19b	?	*21a/b*	22b	23b	?
25c	26b	27c	28b	29a	?	31b	32c	33b	34b	35b	36a
37b	*38a/b*	39a	?	?	42a	43e	44d	45b	46b	47c	48b
49a	50b	51a	52b	53b	54b	55b	56c	57b	58a	?	?

?

S. glacialis

1c	2a	?	?	?	?	7a	*8a/b*	*9c*	*10a*	*11b*	*12b*
13c	14a	15c	?	*17b*	?	19b	?	21a	22b	23a	24b
25c	26b	27c	28b	*29a/b?*	30a	31b	32c	*33b/c*	34b	*35a/b*	36a
37b	*38a/b*	39a	40b	41b	42c	43c	44a	45a	?	47c	48a?
49a/b	50b	51b	52d	53b	54b	*55a/b*	*56b/c*	57b	58a	59a	60d
61b											

S. grandis

1a	2a	3a	4c	5b	6b	7b	*8b*	*9c*	*10b*	11d	*12c*
13a	14a	15c	*16a/c*	*17b*	18b	19b	20a	*21a/b*	22b	23b	24c
25d	26b	27c	28b	29a	30a	31b	32c	33a	34b	35a	36a
37b	38a	39a	40b	41b	42a	43b	*44a/b*	45a	46a	47c	48b
49a	50b	51a	*52a(/b)*	*53b/c*	54a	55a	56a	57b	58b	59b	60a
61b											

S. grimpei

1b/c	2a	3a	4a	5b	6b	7b	*8b*	*9a*	*10a*	11a	12a
13a	14a	15c	*16a-c*	*17a*	18b	19b	20a	**21c**	22a/b	?	24b
25e	26b	27c	28a	29e	30a	31b	32c	33a	34b	35b	36a
37b	*38a/b*	39a	*40a/b*	*41a/b*	42b	43a	*44b*	45a	46b	47c	48a
49c	50b	*51a/b*	52c	53b	54a	55b	56c	57b	58a	*59a/b*	60b
61b											

S. gyrina

1b/c	2a	3a	4b/c	5b	6a	*7a/b*	*8a/b*	*9a*	*10b*	*11b*	*12a(/b)*
13b/c	14a	15c	*16a*	*17c*	18a	19b	20a	21a	22b	23a	*24b/c*
25c	26b	27c	28a	29c	30a	31b	32c	33b	34b	35b	36a
37b	38b 39a/(b)	40b	*41a/b*	42b	43a	*44c*	45a	46b	47c	48b	
49a	50a	51b	52d	53b	54b	55a	56b	57b	58b	59a	*60a/c*
61b											

S. hutchingsi

1b/c	2a	3a	4a/b	5b	6a	7a	*8b*	*9b*	*10b*	*11c*	*12a/b*
13c	14a	15c	*16a/b*	*17a*	18b	19b	20a	*21a/b*	22b	23a	*24b/c*
25b	26a	27b	28b	*29b/c*	**30b**	31a	32a	33b	34c	35c	**36c**
37b	38a(b)	39b	*40a/b*	*41a/b*	42c	43c	*44c*	45a	?	47a	48a
49b	50b	51b	52e	53a	54a	55a	56a	57a	58b	?	*60a/b*
61a											

S. hyperborea

1c	2a	?	?	?	?	*7a/b*	*8a*	*9c*	*10a*	*11b*	*12a/b*
13c	14a	15c	?	*17b*	18b	19b	?	21a	22b	23a?	24b
25c/e	26b	27c	28b	29c	30a	31b	32c	33b	34b	35b	36a
37b	*38a/b*	39a	?	?	42c	43c	44a	45a	?	47c	48a
49a/b	50b	51b	52d	53b	54b	55a	56b	57b	58a?	59a	*60a/b*
61b											

S. johanseni

1c	2a	?	?	?	?	7b	*8b*	*9c*	*10b*	*11c/d*	*12b/c*
13c?	14a	15c	*16a*	*17c*	?	19b	?	21b	22b	23b	?
25e	26b	27c	28a	*29b/c*	30a	31b	32c	*33a/b*	34b	35b	36a
37b	?	?	?	?	42a	43e	*44c*	?	46b	47c	48b
49a	50a	51b	52f	?	?	?	?	?	?	?	?
?											

S. kitina

1a	2b	3b	4a	5a	6a	7a	*8b*	*9a/b*	*10b*	*11c*	12a
13a	14a	15c	*16a/b*	*17a/c*	18b	19b	20a	21a	22b	23a	24b
25b/c	26b	27c	28b	29b	30a	31b	32c	*33b*	34b	35a	36a
37b	*38b/c*	39a	*40a/b*	*41a/b*	42c	43c	*44c*	45b	46b	47c	48a
49b	50b	51b	52e	53a	54a	55a	56a	57a	58b	?	60a

61a

S. lakowitziana

1a	?	?	?	5a?	?	7b	*8a/b*	*9b?/c*	*10b/c*	*11c*	*12b*
13a/c	14a	15c	?	*17b*	?	19b	?	21a	22b	23a?	?
25e	26b	27c	28a	29c	30a	31b	32c	33b	34b	35b	36a
37b	38c	39a	40b	41b	42b	*43a/b*	*44b/c*	45b	46b	47c	?
49a	?	51b	*52c/d*	53b	54b	55a	56b	?	?	?	?
?											

S. longipes

1a	2a	3a	4a	5b	6a	*7a/b*	*8b*	*9c*	*10c*	11d	*12c*
13a	14a	15c	16b	*17c*	18b	19b	20a	21a/d	22b	?	24c
25d	26b	27c	28b	29a	30a	31b	32c	33b	34b	35a	36a
37b	*38a/b*	39a	40b	41b	42a	43b	44d	45a	46b	47c	48b
49a	50b	51a	*52a/b*	*53b/c*	54a	55b	56c	57b	58a	59a	60a
61b											

S. neapolitana

1c	?	?	?	?	?	7a	*8b*	*9b*	*10b/c*	11d	*12a/b*
13c	14a	15c	?	*17a/c*	18a	19b	?	*21a/b*	22b	?	?
25c	26a	**27a**	28b	29b	30a	31a	32a	33b	34c	35c	**36b**
37a	*38a/b*	39a	40b	41b	42c?	43c?	*44c*	45b?	46b	47c	48b
49a	?	51b	52e	53a	54a	55a	56a	57a	58b	?	?
?											

S. oblonga

1a(/b)	2a	3a	4a/b	5a	6a	7a	*8b*	*9b*	*10b/c*	*11c*	*12b*
13c	14a	15c	*16a/b*	*17c*	18a	19b	20a	21a	22b	23a	*24b/c*
25c	26b	27c	28a	29c	30a	31b	32c	33b	34b	*35a/b*	36a
37b	*38a-c*	39a	*40a/b*	*41a/b*	42b	43a	*44c*	45a	46b	47c	48b
49a	50a	51b	52d	53a	54b	55a	56b	57b	58b	59a	*60a/c*
61b											

S. pachypoda

1a	?	?	?	5b	?	7b	*8a/b*	*9a/b*	*10b*	*11b/c*	*12b*
13c	14a	15c	?	*17b*	18a?	19b	20a	21a	22b	23a?	?
25f	26b	27c	28a	**29d**	30a	31b	32c	33c	34a	35b	36a
37b	38c	39a	?	?	?	?	*44b/c*	?	46b	47c	?
49a	50b	51b	*52c*	53b	54a	?	?	?	?	59a	60a
61b											

S. pachypoida

1a	?	?	?	5a	?	7b	*8a/b*	*9a*	*10a*	*11b*	12a
13c	14a	15c	?	*17b*	18b	19b	20a	21a	22b	23a?	?
25f	26b	27c	28a	29e	**30c**	31b	32c	33c	?	35b	36a
37a	38b	39a	?	?	?	?	*44b/c*	?	46b	47c	48a?
49a	50a	51b	*52c*	53b	54a	?	?	?	?	?	60a
61b											

S. pectinata

1a	2a	3a	4c	5b	6b	7b	*8b*	*9c*	*10a/b*	*11c/d*	*12c*
13a	14a	15c	*16a*	*17a/c*	18b	19b	**20b**	21b	22b	23b	24c
25c	26b	27c	28a	29a	30a	31b	32c	*33a/b*	34b	35a	36a
37b	38a	39a	40b	41b	42c	**43d**	*44c*	45a	46a	47c	48b
49a	50b	51a	52a	53c	54a	55a	56a	57a	58b	*59a/b*	60a
61b											

S. prominula

1a	?	?	?	?	?	*7a/b*	*8a*	*9b*	*10b*	*11b*	*12a/b*
13b	14a	15c	?	*17c*	?	19b	20a	21a	22b	23a	?
25c	26b	27c	28c	29b?	?	31b	32c	33b	34b	*35a/b*	36a
37b	38b	?	?	41a	42b	43a	*44c*	?	46b	47c	48a
49b	50b	51b	52d	53b	?	?	?	?	?	59a	*60a/c*

61b

S. rousseleti

1c	2a	3a	?	?	?	7a	*8a*	*9a*	?	11a	12a
13a	14a	15c	?	*17c*	18b	19b	?	21a	?	?	24b
?	26b	27c	28c	29b	?	31b	32c	33c	34b	35b	36a
37b	?	?	?	?	?	?	?	?	?	?	?
?	?	51b	*52c/d*	53b	54a	55a	56b?	57b	58a?	59a	60a

61b

S. squamadigitata

1c	?	?	?	?	?	7a	*8a/b*	*9c*	*10a*	*11c*	12a
13c	14a	15c	?	*17c*	18b	19b	20a	21b	22b	23b?	?
25c	26b	27c	28b	*29a/b?*	?	31b	32c	33b	34b	**35d**	36a
37a	38b	39a	?	?	42c	?	44a	45a	?	47c	?
49a	?	51b	52d	53b	54b	55b	*56b/c*	57b	58a	59a	*60b/d*

61b

S. stylata

1a	2a	3a	4b	5b	6a	*7a/b*	*8b*	*9c*	*10b*	11d	*12b/c*
13a	14a	15c	*16a*	*17c*	18b	19b	20a	*21a/b*	22b	23b	24b
25d	26b	27c	28b	29a	30a	31b	32c	33a	34b	35a	36a
37b	*38a/b*	39a	40b	41b	42a	43b	*44c*	45a	46b	47c	48b
49a	50b	51a	52a	53c	54a	55a	56a	57b	58b	59b	*60a/d*

61b

S. tamara

1c	2a	?	?	?	?	*7a/b*	*8a*	*9b*	*10a*	*11b*	12a
13b/c	14a	15c	?	*17c*	18a?	19b	?	21a	22b	?	?
25c	26a	27b	28a/b?	29b	30a	31a	32b	33b	34b	?	36a
37a	38b	39a	?	?	42b?	43a	*44b/c*	?	?	**47b**	**48c**
49b	?	*51a/b*	*52c/d*	53b	54b	55b	*56b/c*	57b	58a	59a	60a

?

S. tavina

1b/c	2a/b	?	4c	?	6a	7a	*8a/b*	*9b*	*10b*	*11b*	12a
13a/b	14a	15c	*16a*	*17b*	18b	19b	20a	21a	22b	23a	*24b/c*
25c	26b	27c	28b	29c	30a	31b	32c	33b	34b	35a	36a
37b	*38b/c*	39a	?	?	42b	43a	*44c*	45b	46b	47c	?
49a	50b	51b	52d	?	?	55b	56c	57b	?	?	?

?

S. tremula

1a	2b	3c	4a	5b	6b	*7a/b*	*8b*	*9a*	*10a*	*11b*	12a
13a	14a	15c	*16a/b*	*17a*	18b	19b	20a	21a	22b	23a	24a
25c	26b	27c	28b	29b	30a	31b	32c	33b	34b	35a	36a
37b	38b	39a	40b	41b	42b/c	43a	*44b/c*	45b	46b	47c	48a
49b	50b	51b	52d	53a	54b	55a	56a	57a	58b	59a	60a

61b

S. tremuloida

1a	2b	3c	4b	5b	6a	*7a/b*	*8a*	*9a*	*10a/b*	*11c*	12a
13b	14a	15c	*16a/b*	*17c*	18a	19b	20a	21a	22b	23a	24c
25c	26b	27c	28b	29b	30a	31b	32c	33b	34b	35a	36a
37b	38b	39a	40b	41b	42b/c	43a	*44b*	45b	46b	47c	48a
49b	50b	51b	52d	53a	54b	55a	56a	57a	58b	59a	60b

61b

S. triophthalma

1b/c	2a	3a	4a	5b	6a	*7a/b*	*8b*	*9b*	*10b/c*	11d	*12b*
13a(/c)	14a	15c	*16a*	*17a*	18b	19b	20a	21(a/)b	22b	23a	24b
25b	26a	27b	28b	29b	30a	31a	32a	33b	34c	35c	36a
37b	38b	39a	40a	41a	42c	43c	*44c*	45b	46b	47a	48a
49b	50b	51b	52e	53a	54a	55a	56a	57a	58b	59a	60a

61a											
S. verrucosa											
1a	?	?	4c	5a	?	*7a/b*	*8b*	*9c*	*10a*	11d	*12a/b*
13c	14a	15c	*16a*	*17b/c*	?	19b	20a	21b	22b	23a	24b
25e	26b	27c	28a	29c	30a	31b	32c	*33b/c*	34b	35b	36a
37b	38c	39a	*40a/b*	41b	?	?	*44b*	45b	?	47c	48b
49a	?	*51a/b*	52c	53b	54a	55b?	56b	57b	58a	*59a/b*	60a
?											
S. vorax											
1b/c	2a	3a	4a	5b	6a	*7a/b*	*8b*	*9c*	*10c*	11d	*12b/c*
13c	14a	15c	*16a/c*	*17c*	18b	19b	20a	21a	22b	23b	24b
25d	26b	27c	28b	*29a/b*	30a	31b	32c	33b	34b	35a	36a
37b	38b	39a	*40a/b*	41a/b	42a	43e	44d	45b	46b	47c	48b
49a	50b	*51a*	52b	53b	54b	55b	56c	57b	58a	59a	*60a/c*
61b											

Discussion

Our weighted taxonomic matrix key constitutes the most comprehensive and comparable compilation of morphological and behavioural characters to date for the 34 species of *Synchaeta* that we consider to be valid. Through it, we hope to facilitate the reliable identification of both live as well as of preserved specimens, in part by highlighting those features that are more susceptible to the effects of preservation and, more generally, by indicating the reliability of different characters or individual character states for species identification.

In attempting to make our key as comprehensive as possible, we undertook detailed re-examinations of 14 species of *Synchaeta* (Wilke et al. 2017; Wilke et al. 2018a, Wilke et al. 2018b), supplemented by information from the literature where necessary. Nevertheless, we were restricted exclusively to literature information for 20 species of this genus, resulting in numerous cases of both missing information and uncertainty (indicated with a "?" in the tables 3–8). A pervasive problem in the literature is that many species have not been re-discovered since their initial description (e.g., *S. atlantica* and *S. rousseleti*; see Hollowday 2002) so that little information exists for them at all and that many species descriptions are extremely brief and exclusively restricted to the most obvious, diagnostic characters that discriminate the species from other known species and usually highly similar ones (e.g., *S. tremuloida*; see Pourriot 1965). Thus, it is not uncommon that important, but basic information is missing for many species such as for example the location and number of sensory antennae for *S. atlantica*, *S. rousseleti* and *S. cylindrica* (see Hollowday 2002), information that could also distinguish the species from new ones discovered in future. In addition, information is often missing or conflicting for those characters for which data are hard to obtain. For example, although the trophi are important for species identification in rotifers (De Smet 1998; Segers 2004), special skills and equipment are needed for their investigation (Telesh and Heerkloss 2002) such that they are often disregarded and so incompletely known for several species of *Synchaeta* (e.g., *S. johanseni*; see Hollowday 2002).

A further problem is that many illoricate species like those in *Synchaeta* have been described on the basis of preserved material only and, despite repeated calls not to do so (e.g., Donner 1959), fixation is commonly used in rotifer research (Labuce and Strake 2017), with its practical applications making it a necessary evil. However, in soft bodied rotifers such as *Synchaeta*, preservation is far more evil than it is necessary insofar as it causes deformations and/or distortions (Ruttner-Kolisko 1972; Koste 1978; Shiel and Koste 1993), with the consequence that species potentially include preservation-influenced characters in their respective descriptions. This, in turn, might explain why several species have only ever been found once (e.g., *S. atlantica* and *S. rousseleti*, both of which were described using preserved material). However, even more commonly reported members of *Synchaeta* were described on the basis of preserved material as well (see Hollowday 2002), including *S. lakowitziana*, which is "notoriously disputed" (Hollowday 2002; p. 103) for some aspects of its characteristic morphology (e.g., the sharp neck constriction) that are suspected to be a preparation artefact.

Altogether, these problems highlight the need for standardized and comprehensive species descriptions in *Synchaeta* as well as in rotifers more generally comprising morphological (habitus and trophi), behavioural and molecular data from both live and preserved specimens (e.g., in Wilke et al. 2017; Wilke et al. 2018a, Wilke et al. 2018b). Such an integrative approach ensures the most comprehensive data set for the respective species and facilitates an assessment of which characters are potentially affected by preservation-based deformations and to which degree. Depending on the context (e.g., ecological assessments), it will often be difficult to avoid preservation. However, knowledge of its specific effects and providing sets of characters that are robust to them will facilitate better species identification. As such, we hope that our weighted taxonomic matrix key for *Synchaeta*, both through its comprehensiveness as well as through its use of weighting to indicate character reliability and utility, will not only make species identification in *Synchaeta* easier, but will also serve as a model for future keys within rotifers.

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Supplementary material 1

Blank character checklists and tables

Authors: Tanja Wilke, Wilko H. Ahlrichs, Olaf R.P. Bininda-Emonds

Data type: Microsoft Word file

Explanation note: **Table S1.** Checklist of all characters and their states. **Table S2.** Blank table for recording character states.

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RESEARCH ARTICLE

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A new species of the genus *Dryinus* Latreille (Hymenoptera, Dryinidae) from the USA

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Abstract

A new species of *Dryinus* Latreille, 1804, is described from Georgia (USA). *D. georgianus* **sp. nov**. is morphologically similar to *D. mexicanus* (Perkins, 1907) and *D. splendidus* Guglielmino and Olmi, 2013, but is distinguished by the lateral ocelli not touching the occipital carina (in the other two species, the lateral ocelli touch the occipital carina). The key to the females of the Nearctic species of *Dryinus* group 1 is modified to include the new taxon.

Keywords

Chrysidoidea, Dryininae, Georgia, Sapelo Island, taxonomy, key, Nearctic region, *Dryinus georgianus*, *Dryinus mexicanus*, *Dryinus splendidus*

Introduction

Dryinidae is a small family of Chrysidoidea (Hymenoptera) including 16 subfamilies, 50 genera, and approximately 1900 species worldwide (Olmi and Xu 2015; Tribull 2015; Olmi et al. 2019). The species of this family are parasitoids and often also predators of Hemiptera Auchenorrhyncha (Guglielmino et al. 2013).

Dryinidae of the Nearctic region were studied mainly by Olmi (1984) and Guglielmino and Olmi (2013). In this region, the genus *Dryinus* Latreille, 1804, includes 20 species (Guglielmino and Olmi 2013; Olmi 1984, 1991, 1996, 2010, 2011; Ponomarenko 1981), among which only the following three species are recorded from

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Georgia, USA: *D. alatus* (Cresson, 1872) (Guglielmino and Olmi 2013; Olmi 1984), *D. testaceus* (Olmi, 1984) (unpublished record: Monroe Co., Forsyth, 1.VII.2000, 1 female in RAM), and *D. inconsultus* (Olmi, 1984) (unpublished record: Monroe Co., Forsyth, 18–23.V.1970, 1 female in CNC). All the above three species, including *D. alatus*, are known in Georgia only from one locality: Forsyth, in Monroe Co. In 2017 the authors examined a *Dryinus* specimen collected in Georgia and discovered a new species, described below.

Materials and methods

The description follows the terminology used by Guglielmino et al. (2016a, 2016b, 2018) and Guglielmino and Olmi (2013). The measurements reported are relative, except for the total length (head to abdominal tip, without the antennae), which is expressed in millimetres. In the descriptions the following abbreviations are used:

POL distance between the inner edges of the lateral ocelli;
OL distance between the inner edges of a lateral ocellus and the median ocellus;
OOL distance from the outer edge of a lateral ocellus to the compound eye;
OPL distance from the posterior edge of a lateral ocellus to the occipital carina;
TL distance from the posterior edge of an eye to the occipital carina.

The term "metapectal-propodeal complex" is here used in the sense of Kawada et al. (2015). It corresponds to the term "metathorax + propodeum" sensu Olmi (1984), Olmi and Virla (2014), Olmi and Xu (2015) and Xu et al. (2013). The terms "metapectal-propodeal disc" and "propodeal declivity" sensu Kawada et al. (2015), used here, correspond to the terms "dorsal surface of propodeum" and "posterior surface of propodeum", *sensu* Olmi (1984), Olmi and Virla (2014), Olmi and Xu (2015) and Xu et al. (2013).

The term "ADOs" (= Antennal Dorsal Organs) is here used in the sense of Riolo et al. (2016). It corresponds to the term "rhinaria" *sensu* Olmi (1984, 1994), Olmi and Virla (2014), Olmi and Xu (2015) and Xu et al. (2013). According to Riolo et al. (2016), ADOs are sensory structures, that might mediate the antennal responses to vibratory stimuli. As far as we know, they are present only in antennae of dryinid females attacking Fulgoromorpha (Olmi 1984, 1991, 1994).

The names of cells and veins of the forewing are here used in the sense of Azevedo et al. (2018). In all previous monographs on Dryinidae (Olmi 1984, 1994; Olmi and Virla 2014; Olmi and Xu 2015; Xu et al. 2013) different names were used. The correspondence between old and new names is the following (the first name is the old name): median cell = radial cell (R); submedian cell = first cubital cell (1Cu); stigmal vein = second radial cross & radial sector (2r-rs&Rs). In the text, cells and veins will be named by their respective abbreviations, including costal cell (C). The terminology of tegument sculpture follows Olmi and Virla (2014).

The types of all Nearctic species of *Dryinus* were examined. The holotype of the new species studied in this paper is deposited in the Royal Alberta Museum, Edmonton, Alberta, Canada (**RAM**). Other examined species from Georgia (USA) are deposited in the Canadian National Collection of Insects, Ottawa, Canada (**CNC**).

The description of the new species is based on the study of only a single specimen. The authors are aware that descriptions of new taxa should normally be based on more individuals. However, Dryinidae are so rare that it is uncommon to collect more than one specimen of each species. In addition, on the basis of the experience and knowledge of the authors, the new species is sufficiently delimited by unique characters to justify its description.

Results

Genus *Dryinus* Latreille, 1804

Dryinus Latreille, 1804: 176. Type species: *Dryinus collaris* Linnaeus, 1767, by subsequent monotypy (Latreille 1805).

Diagnosis. Female: Fully winged; occipital carina complete, incomplete, or absent; palpal formula 6/3; mandible with 1–4 teeth; antenna usually with ADOs, rarely without, but always without tufts of long hairs; antennomere 1 longer than 2, variable, and antennomere 3 usually less than five times as long as antennomere 2, occasionally more than five times (in this case, notauli often complete, then mesoscutum completely sculptured by numerous and parallel longitudinal keels); pronotal tubercle reaching or not reaching tegula; forewing with three cells enclosed by pigmented veins (C, R, 1Cu); chela with rudimentary claw; protarsomere 5 less than twice as broad as enlarged claw; enlarged claw as long as, or shorter than protibia; tibial spurs 1/1/2, rarely 1/1/1. Male: Fully winged; occipital carina complete or incomplete; mandible with 1–3 teeth; palpal formula 6/3; epicnemium present and visible, because lateral regions of prothorax not continuous with mesopleura; mesosternum fused with mesopleura and not distinct; forewing with three cells enclosed by pigmented veins (C, R, 1Cu); paramere without dorsal process; tibial spurs 1/1/2.

Dryinus georgianus sp. nov.

http://zoobank.org/74BAFB91-5A11-4D9A-A41F-CAA905AA11C3
Figs 1–2

Diagnosis. Female with body predominantly ferruginous, frontal line complete; OL shorter than POL; OL as long as TL; posterior ocelli not touching occipital carina; head and pronotum granulate; notauli complete; mesoscutum granulate and partly reticulate rugose, enlarged claw spatulate and with one tooth on lateral margin; Protarsomere 5 with approximately 35 lamellae.

Figure 1. *Dryinus georgianus* sp. nov., female holotype: habitus in dorsal (**A**) and lateral (**B**) view; head in dorsal view (**C**). Scale bars: 1.28 mm (**A, B**); 0.46 mm (**C**).

Description. Female (Fig. 1A–C). Fully winged. Length 4.0 mm. Head and antenna ferruginous. Mesosoma ferruginous, except two lateral brown spots on pronotum. Anterior third and lateral regions of mesoscutum darkened. Part of lateral regions of metapectal-propodeal complex and propodeal declivity darkened. Petiole black. Metasoma brown, except first segment almost totally testaceous. Legs ferruginous. Antenna clavate. Antennomeres in following proportions: 9:4:18:9:7:7:6:6:5:8. ADOs present in antennomeres 5–10. Head (Fig. 1C) swollen, dull, granulate, except some irregular longitudinal keels on face. Frontal line complete. Occipital carina complete. Temple distinct. POL = 4; OL = 2; OOL = 7; OPL = 1; TL = 2. Greatest breadth of posterior ocelli about as long as OL. Pronotum dull, granulate, crossed by two transverse impressions, anterior one weak and posterior one strong. Disc of pronotum humped. Posterior collar of pronotum short, reticulate rugose. Pronotal tubercle not reaching tegula. Mesoscutum (Fig. 1A) dull, granulate, reticulate rugose on lateral regions and near posterior margin. Notauli complete, posteriorly separated, hardly visible near posterior margin of mesoscutum. Minimum distance between notauli about as long as POL. Mesoscutellum and metanotum dull, granulate. Metapectal-propodeal complex reticulate rugose, without longitudinal keels on propodeal declivity. Forewing (Fig. 1A, B) with three dark transverse bands. Distal part of 2r-rs&Rs vein much longer than proximal part (11:6). Protarsomere 3 produced into hook. Protarsomeres in following proportions: 17:2:3:11:17. Enlarged claw spatulate (Fig. 2), with one strong subapical tooth and one row of 11 lamellae. Protarsomere 5 (Fig. 2) with two rows of approximately 35 lamellae extending continuously to distal apex. Tibial spurs 1/1/2.

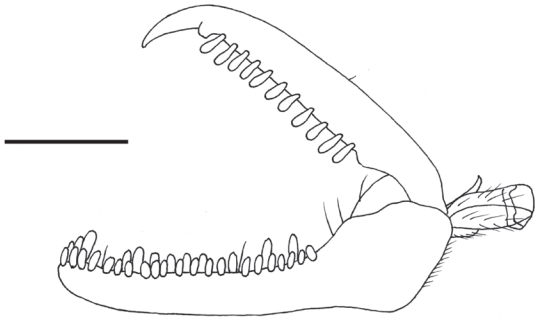

Figure 2. *Dryinus georgianus* sp. nov., female holotype: chela. Scale bar: 0.13 mm.

Male. Unknown.

Material examined. Holotype: female, USA: Georgia, McIntosh Co., Sapelo Island, 19.IX–19.XI.1987, FIT, shrub sand dunes, BRC Hym. Team (RAM).

Hosts. Unknown.

Etymology. The species is named *georgianus*, based on the collecting locality.

Conclusions

The female of the new species has complete notauli (Fig. 1A) and enlarged claw provided with one strong subapical tooth (Fig. 2). Because of these characters, *D. georgianus* belongs to group 1 of *Dryinus*, according to the systematics proposed by Olmi and Virla (2014). In this species, the head is ferruginous (Fig. 1A, C); the mesoscutum is granulate and partly reticulate rugose, notauli complete (Fig. 1A) and the enlarged claw is spatulate (Fig. 2). Because of these characters, *D. georgianus* is similar to *D. mexicanus* (Perkins, 1907) and *D. splendidus* Guglielmino and Olmi, 2013, recorded respectively from Mexico and USA (Guglielmino and Olmi 2013). However, in *D. georgianus* the lateral ocelli do not touch the occipital carina (Fig. 2), whereas in the other two species they do. The key to the females of the Nearctic *Dryinus* group 1 presented by Guglielmino and Olmi (2013), should be modified by replacing couplet 8 as follows:

8 Posterior ocelli not touching occipital carina (Fig. 1C).... ***D. georgianus* sp. nov.**

– Posterior ocelli touching occipital carina ..... **8'**

8' Enlarged claw with lamellae very long (Guglielmino and Olmi 2013: fig. 10); protarsomere 5 with longer rows of lamellae (Guglielmino and Olmi 2013: fig. 10); protarsomere 1 about twice as long as 4; head with TL longer than POL..... ..... ***D. mexicanus* (Perkins)**

– Enlarged claw with shorter lamellae (Guglielmino and Olmi 2013: fig. 12); protarsomere 5 with shorter rows of lamellae (Guglielmino and Olmi 2013: fig. 10); protarsomere 1 less than 1.5 times as long as 4; head with TL shorter than POL ..... ***D. splendidus* Guglielmino & Olmi**

Among the *Dryinus* species recorded from Georgia, *D. alatus* and *D. georgianus* belong to group 1, whereas *D. testaceus* and *D. inconsultus* belong respectively to groups 2 and 3.

Dryinus species are known to parasitize hosts belonging to the following families of Fulgoromorpha (Guglielmino et al. 2013): Acanaloniidae, Cixiidae, Dictyopharidae, Flatidae, Fulgoridae, Issidae, Lophopidae, Ricaniidae, Tropiduchidae. Larvae of *Dryinus* were described by Abril-Ramírez (1992) and Guglielmino et al. (2015).

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RESEARCH ARTICLE

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Two new species of *Molophilus* Curtis from the Mediterranean and Transcaucasia (Diptera, Limoniidae)

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Abstract

Two new species of the genus *Molophilus* Curtis, 1833 are described, *Molophilus* (*Molophilus*) *rohaceki* **sp. nov.** (Italy: Calabria) and *M.* (*M.*) *soldani* **sp. nov.** (Azerbaijan), and their male terminalia are illustrated.

Keywords

Limoniid Crane Flies, West Palaearctic *Molophilus* (*Molophilus*), male terminalia, description

Introduction

The genus *Molophilus* Curtis, 1833 is a cosmopolitan taxon (101 West Palaearctic species, 1018 species worldwide in 11 subgenera, cf. Oosterbroek 2019) and new species are still named even from well-investigated territories. Recently, a paper was published with descriptions, redescriptions, and other nomenclatural changes, dealing principally with the west Palaearctic *Molophilus* (*Molophilus*) species (Starý 2011). As a minor addition to this species-richness, another two west Palaearctic species are described here, *M.* (*M.*) *rohaceki* sp. nov. (Italy: Calabria) and *M.* (*M.*) *soldani* sp. nov. (Azerbaijan). The two species are distantly related to each other, both belonging to the same morphological group distinguished by a comparatively simple shape of the dorsal por-

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tion of the gonocoxite, having no dorsal and/or lateral lobes. Within this group numerous west Palaearctic species are known, such as *M.* (*M.*) *undulatus* Tonnoir, 1920, *M.* (*M.*) *scutellatus* Goetghebuer, 1929, *M.* (*M.*) *brevihamatus* Bangerter, 1947, and many others, sometimes variously modified in the lateral outline of the dorsal portion of the gonocoxite. However, the new species differ from their consubgeners and from each other considerably in various distinctive features. They are somewhat exceptional in having their aedeagal plates smooth, without any microsetae.

Materials and methods

The morphological terminology adopted here follows essentially that of McAlpine (1981). Some special terms of structures of the *Molophilus* male terminalia are referred to in Fig. 1.

All type specimens are preserved dry, glued on cardboard points. Since the specimens of *M.* (*M.*) *soldani* sp. nov. were dried from ethanol, the colour features as indicated in the description may differ somewhat from a normally dried state. The male terminalia were preserved in glycerine in a small plastic tube pinned below the associated specimen.

The following museum and collection acronyms are used in the text:

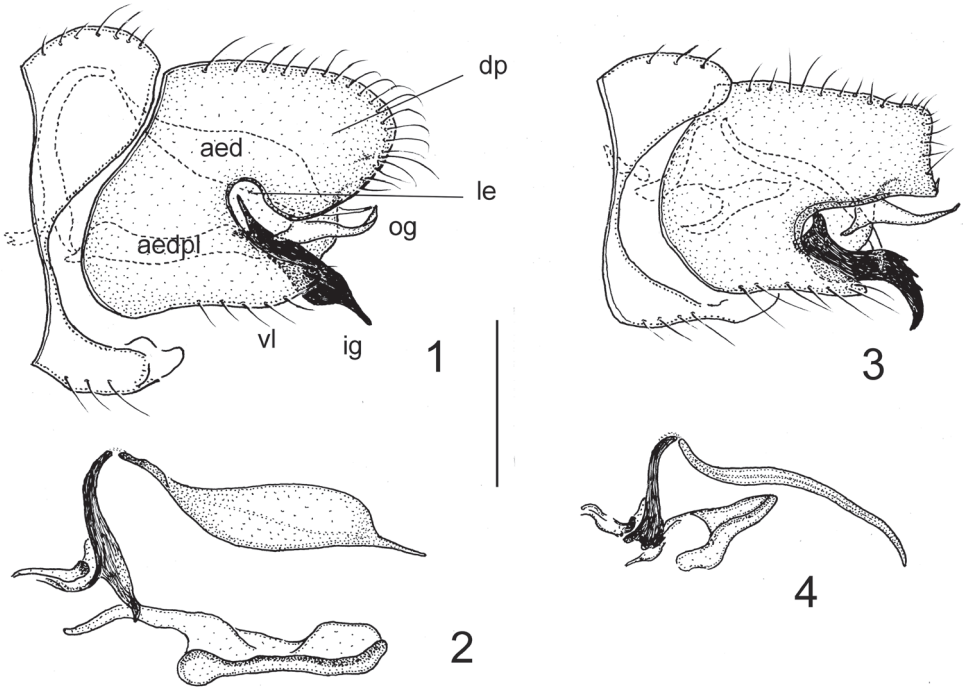
JSO Collection of J. Starý, Olomouc, Czech Republic;
SMOC Slezské zemské museum (Silesian Museum), Opava, Czech Republic.

***Molophilus* (*Molophilus*) *rohaceki* sp. nov.**
http://zoobank.org/611A0D7B-2671-4E51-B2F9-5CA0A328E575
Figs 1, 2

Diagnosis. Medium-sized (wing length 4–5 mm) species within *Molophilus*. Body deep dark brown, almost black, mostly shiny, locally suffused with slight greyish pruinosity, restrictedly patterned with yellow. Male terminalia with outer (dorsal) gonostylus pale, inner (ventral) gonostylus darkly pigmented, latter longer than former. Aedeagus exceedingly swollen for most of its length, except for slender terminal portion. Aedeagal plate long, rectangular in ventral aspect, without microsetae, level with base of terminal portion of aedeagus.

Description. ***Male.*** Head. Antenna slightly lengthened, compared to most other west Palaearctic species, extending beyond wing base, dark brown throughout. Flagellomeres long-ovoid, with longest verticils subequal to length of their respective segments.

Thorax in general deep dark brown to black, mostly shiny. Prescutum and scutum mostly black, shiny, with slight greyish pruinosity and slightly paler laterally, yellowed lateral to prescutal pit and around wing base, pale yellow on paratergite anteriorly. Scutellum and postscutellum shiny black, paler laterally. Pleuron shiny black throughout. Wing length 5.0 mm. Wing membrane slightly infuscate; venation as for genus. Halter yellowish brown. Legs yellowish brown, with tips of femora and tarsi darkened.



Figures 1–4. Male terminalia. **1–2** *M.* (*M.*) *rohaceki* sp. nov. (holotype) **1** general view, lateral **2** aedeagal complex, lateral **3–4** *M.* (*M.*) *soldani* sp. nov. (holotype) **3** general view, lateral **4** aedeagal complex, lateral. Scale bar: 0.25 mm. Abbreviations: aed – aedeagus; aedpl – aedeagal plate; dp – dorsal portion of gonocoxite; ig – inner gonostylus; le – lateral excision; og – outer gonostylus; vl – ventral lobe of gonocoxite.

Abdomen deep dark brown to black. Male terminalia (Figs 1, 2) black. Dorsal portion of gonocoxite rather short and broad, broadly rounded in lateral aspect. Lateral excision deep and moderately wide, compared to similar species. Ventral lobe of gonocoxite broad and rather short, its rounded tip not reaching apex of dorsal portion. Both gonostyli slightly arched medially. Outer gonostylus pale, generally slender, slightly upturned, narrowly obtuse at apex, extending to ca. three fourths length of inner gonostylus. Inner gonostylus darkly pigmented, powerful, reaching beyond ventral lobe by ca. one third its length or more, gradually broadened in lateral aspect, then abruptly tapered into slender, slightly upturned and obliquely truncate apical part. Aedeagus moderate in length, exceedingly swollen for most of its length, abruptly tapered into slender terminal portion, subacute at tip. Aedeagal plate smooth, without microsetae, rectangular in ventral aspect, when preserved under natural configuration of other structures of aedeagal complex, level with base of terminal portion of aedeagus (Fig. 2).

Female. Unknown.

Material examined. ***Holotype*** ♂: Greece, SW Peloponnese, Taygetos Mts, Alagonia 2.4 km NW (1335 m), 37°06'55"N, 22°16'07"E, brook, springs, 9.10.2017 (J. Roháček leg.) (SMOC).

Etymology. The new species is named in honour of its collector, Dr. Jindřich Roháček (Silesian Museum, Opava, Czech Republic), a world-famous specialist of Anthomyzidae and Sphaeroceridae (Diptera). A noun in genitive singular.

Discussion. The new species differs from its similar congeners by details in the structure of the male terminalia, especially its swollen aedeagus and very long aedeagal plate. *Molophilus* (*M.*) *brevihamatus* Bangerter, 1947 has a similarly swollen aedeagus, but is distinctive by various other features, including body colouration (brown in *M.* (*M.*) *brevihamatus*, shiny black in the new species) and shape of gonostyli and aedeagal plate.

***Molophilus* (*Molophilus*) *soldani* sp. nov.**
http://zoobank.org/4CF8ABCD-5B04-4774-8CDD-5426298C15FF
Figs 3, 4

Diagnosis. Medium-sized species within *Molophilus*. Body dark brown, suffused with dense greyish pruinosity, restrictedly patterned with yellow. Male terminalia with outer (dorsal) gonostylus pale, inner (ventral) gonostylus darkly pigmented, latter longer than former, with three distinct teeth on dorsal surface. Aedeagus slender, sinuous, with its tip down-curved. Aedeagal plate short, triangular in ventral aspect, without microsetae, with its tip pointing to ca. one third length of aedeagus.

Description. ***Male.*** Head. Antenna of both holotype and male paratype broken off, but probably much same as that of female paratype, of moderate length, extending to approximately wing base, dark brown throughout. Flagellomeres ovoid, with longest verticils subequal to length of their respective segments.

Thorax in general dark greyish brown. Prescutum and scutum mostly dark brown, suffused with dense greyish pruinosity, slightly paler laterally, yellowed lateral to prescutal pit and around wing base, pale yellow on paratergite anteriorly. Scutellum yellow, dark greyish brown anteriorly, postscutellum dark greyish brown, narrowly yellowed laterally. Pleuron mostly dark greyish brown, restrictedly paler, especially on anepimeron. Wing length 4.2–4.9 mm. Wing membrane slightly infuscate; venation as for genus. Halter pale yellow. Legs yellowish brown, with tips of femora indistinctly darkened and tarsi dark brown.

Abdomen dark greyish brown. Male terminalia (Figs 3–4) dark brown. Dorsal portion of gonocoxite moderately long, quadrangular in lateral aspect, slightly narrowed distally, almost straight at posterior margin, with tiny membranous process at ventral corner. Lateral excision moderately deep and rather wide. Ventral lobe of gonocoxite moderately broad and rather short, its narrowly rounded apex extended shortly beyond base of outer gonostylus. Both gonostyli slightly arched medially. Outer gonostylus pale, gradually tapered distally into slender, obtuse tip, extending to ca. three fourths length of inner gonostylus. The latter darkly pigmented, powerful, sharply sinuous, exceeding ventral lobe by ca. two thirds its length, gradually tapered at ca. mid-length into slender distal part, with three distinct teeth on dorsal surface. Aedeagus moderate

in length, generally slender, slightly sinuous, with its tip down-curved. Aedeagal plate smooth, without any microsetae, generally triangular in ventral aspect, when preserved under natural configuration of other structures of aedeagal complex, pointing with its rounded apex to ca. one third length of aedeagus (Fig. 4).

Female. Female resembling male in general appearance. Female terminalia with cercus very slender, gently upturned, subacute at tip, approximately twice length of tergite 10. Hypogynal valve straight, reaching to ca. three fourths length of cercus.

Material examined. ***Holotype*** ♂: Azerbaijan, Qabala district, S of Durca, nr. tributary of Qaraschay R. (1236 m), 41°02'11.2"N, 47°53'13.6"E (light trap), 30.5.2017 (Ľ. Hrivniak leg.) (SMOC). ***Paratypes*:** 1 ♂, 1 ♀, same data as for holotype (JSO).

Etymology. The new species is named in honour of the late Prof. Dr. Tomáš Soldán, an outstanding Ephemeroptera specialist. A noun in genitive singular.

Discussion. The new species is distinctive by the combination of the quadrangular outline of its dorsal portion of gonocoxite and an unusually shaped inner gonostylus with three distinct teeth on the dorsal surface. The type specimens were dried from ethanol; hence, their body colouration might be darker in a normal dried state.

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An annotated checklist of freshwater Copepoda (Crustacea, Hexanauplia) from continental Ecuador and the Galapagos Archipelago

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Abstract

An annotated checklist of the free-living freshwater Copepoda recorded in different regions in Ecuador (including the Amazon, the Andes, the coastal region, and the Galapagos Islands) is here provided. We revised all published records, critically evaluated the validity of each taxon and provided short taxonomic and biogeographical remarks for each one. A total of 27 taxa have been reported, including species and records at the generic level only. The species and taxa identified only up to the generic level belong to five families and 14 genera. The Cyclopoida is the most diverse group with 16 records belonging to species (or identified to the generic level only) and eight genera, followed by the Harpacticoida with six species, one identification to the generic level only, and four genera, and Calanoida with four species belonging to two genera. A total of 18 taxa are recorded for the Andes. Six have been recorded in the Amazon, two are

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recorded for the coastal region, and six for the Galapagos. One species is shared between the Amazon and the Andes. One species is shared between the coastal region and the Amazon. Seventeen are only reported from the Andes and four are only reported from the Amazon. At the current status of the knowledge, any attempt to analyze and generalize distributional patterns of copepods in Ecuador is premature due to the scarcity of available information, and evidently there is an urgent need for more extensive field collections. A few working hypothesis for future studies are identified.

Keywords
Biodiversity, freshwater Copepoda, geographical distribution, Neotropics, species richness

Introduction

Probably the first published studies on the Copepoda from the Neotropical region are those by Richard (1895, Haiti; 1897, South America), Sars (1901, South America), and Stingelin (1904a, 1904b). The region remained for a long time understudied, with a few taxonomic works realized in the first four decades of the 20th century (e.g., Wierzejski 1892; Daday 1902; Thiébaud 1914; Brehm 1924; Kiefer 1926; Pesta 1927; Wright 1927; Delachaux 1928; Lowndes et al. 1934). From there on, after a gap of almost two decades both faunistic and taxonomic studies became more common (e.g., Noodt 1965; Brandorff 1977; Paggi 1978; Löffler 1981; Collado 1983; Dussart 1984; Reid 1984 and 1985; Santos-Silva et al. 1989, Rocha and Sendacz 1996; Corgosinho and Martínez Arbizu 2005; Perbiche-Neves et al. 2014a). Nowadays, about 561 species of Copepoda are known for the Neotropical region (Boxshall and Defaye 2008). The most diverse families are Cyclopidae (174), Canthocamptidae (109), Diaptomidae (82), and Parastenocarididae (65) (approximate number of species is within parentheses). The calanoid and cyclopoid fauna is relatively well known for the Neotropical region. As for the Harpacticoida, despite recent advances in taxonomy and zoogeography of the Parastenocarididae (e.g., Corgosinho and Martínez Arbizu 2005; Corgosinho et al. 2010), there is still much to explore, especially in the families Canthocamptidae and Parastenocarididae. Moreover, our knowledge on inland water copepod diversity is also quite unevenly distributed geographically, and most data refer to Argentina, Brazil, Colombia, and Venezuela, whereas other countries are inadequately known.

Similarly to the freshwater Cladocera and Rotifera (López et al. 2018a, 2018b), our knowledge of the Copepoda of Ecuador in comparison to other countries in tropical South America is relatively recent and very limited. This is in sharp contrast to the great habitat diversity in the country, ranging from Amazon rainforest, including uphills and the lowlands, to alpine tundra paramo (more than 4000 m a.s.l.) and to the inclusion of Ecuador as a hotspot of biodiversity for plant and vertebrate species (e.g., Myers et al. 2000; Brummitt and Lughada 2003; Rieckmann et al. 2011).

As part of an ongoing project dedicated to collecting and revising the Copepoda, Cladocera and Rotifera from inland water bodies of Ecuadorian mainland and the Galapagos Islands, we assembled a list of the inland water Copepoda known to date for the country and provide a short discussion of relevant nomenclatural issues and

known geographic distribution of the species. Our goal is to identify the major information gaps and pave the way for future studies on the Ecuadorian freshwater copepods, which ultimately might allow better framing of the copepod fauna of Ecuador in the Neotropical region and understanding its origin and affinities.

Methods

The list of the copepods of continental Ecuador and Galapagos Islands compiled herein is based on literature data, including theses and taxonomic and ecological publications. The current valid species names and combinations are mostly based on Dussart and Defaye (2002, 2006) and the WoRMS database (http://www.marinespecies.org). Here we adopt the classifications of Boxshall and Halsey (2004) and Khodami et al. (2017), who have included the Poecilostomatoida families within Cyclopoida.

The geographic distribution of the freshwater taxa within the country is described by dividing continental Ecuador into three subregions (Andean, coastal, and the Amazonian subregions; see Steere 1950) to which the Galapagos Islands are to be added (Fig. 1). References to other regions within South America follow the biogeographical classification proposed by Dussart (1984).

Abbreviations used in the text: **enp1–3** first to third endopodal segment; **exp1–3** first to third exopodal segment; **P1–P5** first to fifth legs.

Results

Twenty-seven records have been reported in literature from the inland water bodies of Ecuador, including the Galapagos Islands. The species and taxa identified only up to the generic level belong to five families and 14 genera. The Cyclopoida is the most diverse group with 16 records belonging to species (or identified to the generic level only) and eight genera, followed by the Harpacticoida with six species, one identification to the generic level only, and four genera, and Calanoida with four species belonging to two genera (Table 1). Eighteen taxa are recorded for the Andes, and six for the Amazon. One cyclopoid species is shared by the Amazon and the Andes. One cyclopoid species is shared between the coastal region and the Amazon. Seventeen are restricted to Andes and 4 confined to Amazon. Two species are recorded for the coastal region, and six to the Galapagos Islands.

Harpacticoida M. Sars, 1903
Canthocamptidae Brady, 1880

***Attheyella* (*Chappuisiella*) *pichilafquensis* Löffler, 1961**

Distribution. Andes (Löffler 1963).

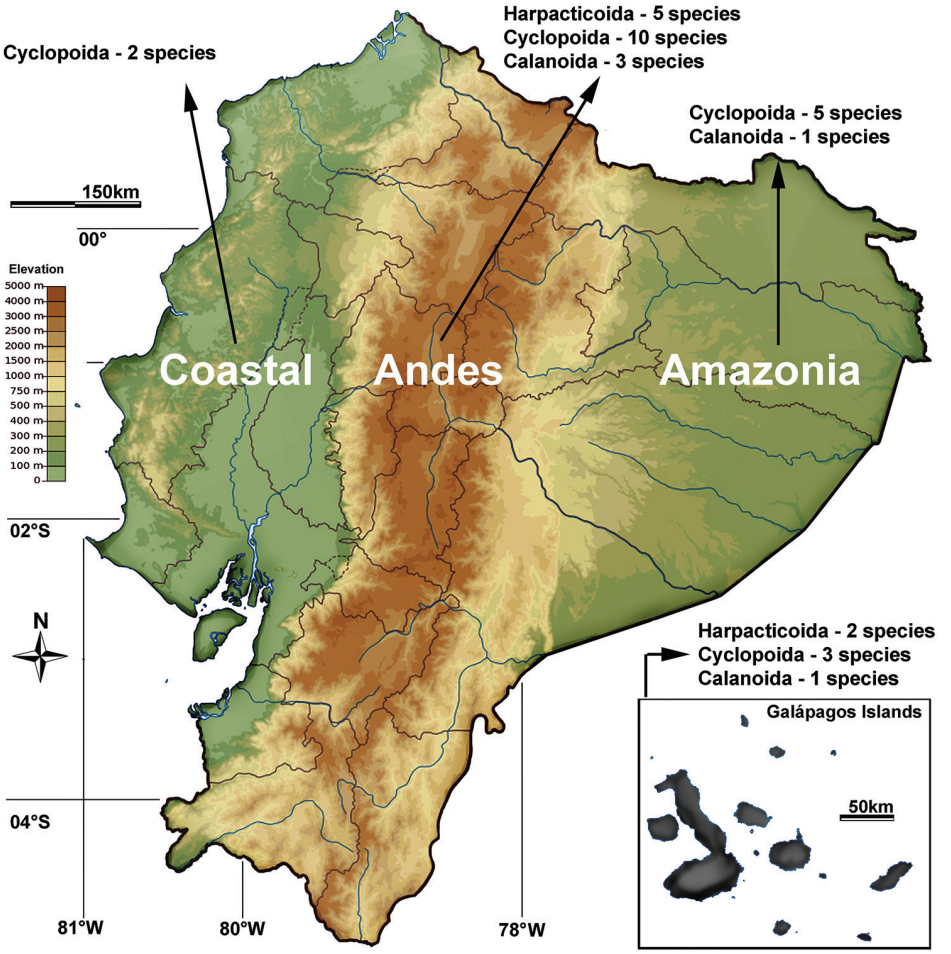

Figure 1. Map of Ecuador showing main geographical regions and number of recorded species for freshwater Cyclopoida, Harpacticoida, and Calanoida.

Remarks. According to Löffler (1963) the type locality lies somewhere between the towns of Villarrica and Llanquihue (straight-line distance between the towns, 227 km), in the southern Chile. The color is distinctly violet and the length of the specimens from the type locality varies between 370–560 µm for males and 400–700 µm for females. In Ecuador, the specimens were larger, the females reaching a length of 900 µm and the males 700 µm. The Ecuadorian males are variable in the armature of the endopodite in P2 and P4.

Attheyella (*Delachauxiella*) *freyi* Löffler, 1963

Distribution. Andes (Löffler 1963).

Table 1. Distribution of the taxa in the four geographical regions of Ecuador. "×" indicates the occurrence of a calanoid "resembling *Notodiaptomus amazonicus*" from Lake El Junco in San Cristobal island.

Taxon	Amazon	Andes	Coastal	Galapagos
Harpacticoida, Canthocamptidae				
Attheyella (*Chappuisiella*) *pichilafquensis*		•		
Attheyella (*Delachauxiella*) *freyi*		•		
Bryocamptus sp.		•		
Cletocamptus axi				•
Cletocamptus ecuadorianus		•		
Cletocamptus schmidti				•
Elaphoidella humboldti		•		
Cyclopoida, Cyclopidae, Cyclopinae				
Acanthocyclops robustus		•		
Acanthocyclops vernalis			•	
Mesocyclops meridianus	•		•	
Metacyclops sp.		•		
Metacyclops leptopus leptopus		•		
Metacyclops mendocinus		•		•
Microcyclops sp.				•
Microcyclops alius	•	•		
Microcyclops anceps	•			
Cyclopoida, Cyclopidae, Eucyclopinae				
Eucyclops agilis		•		•
Eucyclops breviramatus		•		
Eucyclops serrulatus		•		
Macrocyclops albidus	•			
Paracyclops chiltoni		•		
Paracyclops hardingi		•		
Cyclopoida, Ergasilidae				
Ergasilus sp.	•			
Calanoida, Centropagidae				
Boeckella gracilis		•		
Boeckella occidentalis		•		
Calanoida, Diaptomidae				
Notodiaptomus amazonicus occidentalis	•			×
Notodiaptomus cannarensis		•		

Remarks. Originally described from Ecuador. Of the studied males and females, Löffler (1963) found that the P2 enp and the P4 enp can be asymmetric in armature. The dorsal ornamentation of the urosome is also variable in the male, and it can be either dorsally absent or present on the 2nd to 4th urosomites. Males measure are 540–700 µm long, and females are 800–980 µm long. This species was found in a high mountain pond in the southern Colombian Andes (Gaviria and Defaye 2012).

Bryocamptus Chappuis, 1929

Distribution. Torres and Rylander (2006) mentioned *Bryocamptus* from Ecuadorian highland lakes. However, this genus is basically boreal, with a few representatives

known from New Zealand (Reid 1993), and a single species, *Bryocamptus* (*Bryocamptus*) *campaneri* (Reid 1993), from Central Brazil. Records of *Bryocamptus* from a lake in the state of Rio de Janeiro (Reid and Esteves 1984) are a misidentification of *Attheyella* (*Chapuisiella*) *fuhrmanni* (Thiébaud, 1914) (Reid 1993). *Bryocamptus broiensis* Rocha and Matsumura-Tundisi, 1976 described for the state of São Paulo is recognized by Reid (1993) as *Attheyella* (*Delachauxiella*) *broiensis* Reid, 1994. According to Löffler (1972), the North American species of *Bryocamptus* do not occur south of the northern limit of the Eocene-Miocene submergence of Central America.

Cletocamptus axi Mielke, 2000

Distribution. Collected from lagoons of the islands of Santa Cruz and Floreana, Galapagos Archipelago. Mielke (2000) referred to the type locality as "Floreana: lagoon behind the beach".

Cletocamptus ecuadorianus Löffler, 1963

Distribution. Andes (Löffler 1963, as *C. deitersi ecuadorianus*).

Remarks. Originally described from Ecuador. Length of males reaching 620 µm long, females 750 µm long. Asymmetry is observed in the armature of the female P5 basoendopod. Both males and females show variability in the armature of the antennal exopodite. In males, P3 exp3 may be variable in armature. *C. deitersi* (Richard, 1897) has been recorded from Ecuador (Löffler 1963 as *C. deitersi ecuadorianus*), Venezuela (Escaravange and Castel 1989), Peru and Bolivia (Harding 1955), Haiti (Kiefer 1936), and USA (California; Dexter 1995). However, several authors (Dexter 1995; Suárez-Morales et al. 1996; Gee 1999; Mielke 2000, 2001) have suggested that *C. deitersi* consists of a number of morphologically indistinguishable sibling species (Gómez 2005). According to Gómez et al. (2004), *C. deitersi* is a species inquirenda, because Richard's (1897) original description is based on highly conservative features that are not useful for species separation. Future study of specimens from all of these localities is required to show if the records refer to *C. ecuadorianus* or to *C. deitersi.* Both species are in need of redescription, and *C. ecuadorianus* is considered to be a species inquirenda.

Cletocamptus schmidti Mielke, 2000

Distribution. Collected from lagoons of the islands of Santa Cruz, Galapagos. Type locality, Laguna de Puerto Núñez.

Remarks. According to Mielke (2000), *C. axi* and *C. schmidti* slightly differ from each other in their body ornamentation and in the chaetotaxy of the exopodites of P3 and P4. Although Mielke (2000) have provided a very detailed illustration of both

C. axi and *C. schmidti* and a complete description of their anatomical details, Wells (2007) considered *C. axi* a species inquirenda but without giving an explanation. Both species fit well the range of variability of *C. deitersi,* yet co-occurrence of the two morphotypes and the lack of intermediate forms support that *C. axi* and *C. schmidti* are separate species rather than morphological variants of a single species (Mielke 2000).

Elaphoidella humboldti Löffler, 1963

Distribution. Andes (Löffler 1963).

Remarks. Originally described from Ecuador. The male reaches 620 µm and the female is unknown.

According to Gaviria and Defaye (2015: 1026) the "Diversity of *Elaphoidella* Chappuis, 1929 in Colombia (5 species) is lower than in Cuba (10) and Brazil (9), but higher than in Suriname (2) and Argentina (2). However, these data are not the result of extensive research and sampling of all biomes and environments. Thus, we cannot draw any biogeographical pattern from this study. Only one species is known from each of the following Neotropical countries: Mexico, Costa Rica, Venezuela, French Guiana, Ecuador, Peru and Paraguay. The French islands Bonaire and Martinique are also inhabited by one species each." Groundwater, benthic habitats of high Andean lakes, and aquatic habitats within rainforests are potential habitats for harpacticoid copepods and particularly for *Elaphoidella* Chappuis, 1929. Other still poorly investigated biotopes are phytotelmata and semiterrestrial habitats, which would no doubt yield new species of copepods (Gaviria and Defaye 2015).

Cyclopoida Burmeister, 1834
Cyclopidae Rafinesque, 1815
Cyclopinae Rafinesque, 1815

Acanthocyclops robustus (G.O. Sars, 1863)

Distribution. Andes (surroundings of Antisana volcano >3000 m a.s.l.) (Löffler 1963).

Remarks. Löffler (1963) noted that all *Acanthocyclops* Kiefer, 1927 specimens from Ecuador possessed a spine formula of the "*vernalis* type" (2.3.3.3). However, two, three, three, and three spines on the terminal exopodal segments on P1 to P4, respectively, may occur in both *A. robustus* and *A. vernalis* Fischer, 1853, which are currently considered distinct from one another.

Acanthocyclops robustus is supposedly restricted to the northern Holarctic region (Mirabdullayev and Defaye 2002). All records of *A. robustus* from the southern hemisphere need verification, although introduction outside the native range by human activities cannot be excluded. The morphology and taxonomic relationships of *A. robustus* have been revised by Mirabdullayev and Defaye (2002, 2004), but see Miracle et al. (2013) for an alternative opinion on the taxonomy of the *A. robustus* group.

The genus is most diversified in the northern temperate region. So far reported from South America, there are only two species, here not including the southern South American *A. michaelseni* (Mrázek, 1901) and *A. skottsbergi* Lindberg, 1949 for which the generic affinities of which are still under debate. However, a few species ,which are apparently closely related to the *A. vernalis-robustus* group, have been described from Mexico (*A. rebecae* Fiers & Ghenne, 2000, *A. caesariatus* Mercado-Salas & Suárez-Morales, 2009, *A. marceloi* Mercado-Salas & Suárez-Morales, 2009) and Honduras (*A. smithae* Reid & Suárez-Morales, 1998); the geographic distribution is still poorly understood of these species . The occurrence of *Acanthocyclops* in South America may raise intriguing questions of the taxonomic identity and evolutionary origin of these taxa.

Acanthocyclops vernalis (Fischer, 1853)

Distribution. Coastal (Quimi 2014).

Remarks. This species, which was originally described from the neighborhood of St Petersburg, Russia (Fischer 1853), needs redescription. The actual distributional area is likely confined to the Palearctic region (Einsle 1996), and all South American records need verification (see also *A. robustus*).

Mesocyclops meridianus (Kiefer, 1926)

Distribution. Coastal and Amazon (Napo river valley) (Löffler 1963).

Remarks. The species range is likely restricted to South America. *Mesocyclops meridianus* (Kiefer, 1926), which was described from San Bernardino, Paraguay, is morphologically highly similar to *M. pseudomeridianus* Defaye & Dussart, 1988 (type locality: Mana, French Guiana), *M. brasilianus* Kiefer, 1933 (type locality: Manaus, Amazon), *M. varius* Dussart, 1987 (type locality: Taxisco, Guatemala], *M. venezolanus* Dussart, 1987 (type locality: Lake Valencia, Venezuela), and *M. meridionalis* Dussart & Frutos, 1985 (type locality: Corrientes, Argentina) (Hołyńska et al. 2003). Some older records of *M. meridianus*, therefore, might refer to other representatives of the *meridianus*-complex. The native range of the *meridianus*-clade (Hołyńska 2006) is confined to South- and Central America, as far as the Isthmus of Tehuantepec. Hołyńska (2006) hypothesized that *M. pseudomeridianus* and *M. brasilianus* are junior synonyms of *M. meridianus* and that *M. varius* is a junior synonym of *M. venezolanus*. She also emphasized the need to examine the topotypes of taxa (e.g., *M. brasilianus*, *M. meridianus*, and *M. varius*) with old or scarce original material to resolve possible synonymies. The *meridianus-brasilianus-pseudomeridianus* lineage (=? *M. meridianus*) and the *venezolanus-varius* lineage (=? *M. venezolanus*) differ from each other in the shape of the lateral arms of the seminal receptacle (Hołyńska et al. 2003). Gutiérrez-Aguirre and Suárez-Morales (2003) and Gutiérrez-Aguirre et al. (2006) presented another view of the taxonomic relationships of these and considered *M. meridianus* and *M. brasilianus* to be distinct species and put *M. varius* and *M. venezolanus* in synonymy with *M. brasilianus*.

The genus is distributed worldwide and is represented by 13 native species in South America, most of which (10 of 13) are endemic to the continent. This number included *M. aspericornis* (Daday, 1906) but excludes *M. ogunnus* Onabamiro, 1957, which is a supposedly recently introduced species. More extensive sampling will likely reveal more species in Ecuador.

Metacyclops Kiefer, 1927

Distribution. *Metacyclops* are the dominant cyclopoid taxa in glacial lakes in the tropical Andes (Van Colen et al. 2017).

Metacyclops leptopus leptopus (Kiefer, 1927)

Distribution. Glacial lakes, 3800–4000 m a.s.l. in Páramo de Guamaní, Andes (Torres and Rylander 2006).

Remarks. *Metacyclops leptopus leptopus* was originally described from Lake Huarón and Lake Naticocha in Region Pasco in the High Andes of Peru (Kiefer 1926, 1927). Currently four subspecies are distinguished: *M. leptopus leptopus* (high-altitude lakes in Bolivia, Colombia, Ecuador, Peru, and possibly Venezuela; Reid et al. 1990; Dussart and Defaye 2006; Gaviria and Aranguren 2007); *M. leptopus mucubajiensis* Kiefer, 1956 (Laguna de Mucubaji, Venezuelan Andes, 3620–3650 m a.s.l.); *M. leptopus totaensis* Reid, Arevalo & Fukushima, 1990 (Lago de Tota, Colombian Andes, 3015 m a.s.l.); and *M. leptopus venezolanus* Kiefer, 1956 (Mariposa Reservoir, Caracas, Venezuela, ca 985 m a.s.l.). The latter subspecies was considered by Dussart (1984) and Dussart and Defaye (2006) to represent *M. mendocinus* rather than a lineage within *M. leptopus*. For more comments on the taxonomic relationships of *M. leptopus*, see *M. mendocinus*.

Metacyclops mendocinus (Wierzejski, 1892)

Distribution. Löffler (1963) reported this species from numerous sites in the Andes, and Steinitz Kannan (1979) found it in Lake Cuicocha, Chicapan (= San Pablo), and Yaguarcocha. Peck (1994) reported it in the in the Galapagos from temporary pools on Isla Santa Cruz.

Originally described from northern and western Argentina (Jujuy and Mendoza Provinces) (Wierzejski 1892), this species is widely distributed in both South America (Bolivia, Brazil, Chile, Colombia, Paraguay, Peru, Uruguay, and Venezuela), and Middle America (Cuba, Haiti, Nicaragua, and Puerto Rico) (Dussart and Defaye 2006).

Remarks. The remote mid-Atlantic islands of the Azores harbour a subspecies, *M. mendocinus insularis* Defaye & Dussart, 1991, which suggests that this species has

good capacity for dispersal. *Metacyclops mendocinus*, along with *M. leptopus*, belongs to a group of species that are predominantly Neotropical in distribution. They share the 12-segmented state of the antennule and two terminal spines on the terminal endopodal segment of P4 (Herbst 1988). The relationships of *M. mendocinus* to the *M. leptopus*-complex need to be revised. Reid et al. (1990) proposed the use of the relative length of the inner terminal caudal (longest) seta as the main distinguishing character between *M. mendocinus* (seta less than twice as long as caudal ramus) and members of the *M. leptopus*-complex (seta 2.6 or more times longer than caudal ramus). Reid et al. (1990) also mentioned ecological differences between the two species: *M. mendocinus* appears to be eurytopic, while *M. leptopus* apparently inhabits relatively pristine lakes at mostly high altitudes. Accordingly, the records from Andean Ecuador might refer to *M. leptopus* rather than *M. mendocinus* (Reid et al. 1990).

Microcyclops Claus, 1893

Distribution. Peck (1994: 57) mentioned the occurrence of a *Microcyclops* sp. ("probably a native species"), inhabiting temporary freshwater pools in Isla Santa Cruz, tortoise reserve (120 m a.s.l) in the Galapagos Archipelago. Species of *Microcyclops* were the dominant Cyclopoida in glacial lakes in the tropical Andes (Van Colen et al. 2017).

Microcyclops alius (Kiefer, 1935)

Distribution. Andes (Lake San Pablo, Imbabura Province in northern Ecuador; 2700 m a.s.l.) and Amazon (Napo river valley) (Löffler 1963).

Remarks. This species was originally described from Santa Lucia, Southern Uruguay. Rocha (1998) supposed that *M. alius* is a junior synonym of *M. dubitabilis* (Kiefer, 1934) (type locality: Trou Caiman Lake, near Port au Prince, Haiti). In a revision of the American *Microcyclops,* Gutiérrez-Aguirre and Cervantes-Martínez (2016) confirmed the conspecificity of these taxa, and for a redescription of *M. dubitabilis* (Kiefer 1934) (= *M. alius*), see Gutiérrez-Aguirre and Cervantes-Martínez (2016). The geographic range of *M. dubitabilis* stretches from Florida Keys, USA (Reid and Hribar 2006) through Mexico, Central America, and the Caribbean islands to South America, as far as possibly the middle Paraná River, Argentina) (Dussart and Defaye 2006).

The genus, which has approximately 54 species or subspecies, is distributed worldwide, yet most diversified in the tropics, where there are 42 species. South America harbours about 12 species, and we expect more taxa occur in Ecuador.

Microcyclops anceps (Richard, 1897)

Distribution. Amazon (Napo river valley) (Löffler 1963).

Remarks. The type locality is Rio Grande do Sul, Brazil (Richard 1897). Two subspecies are distinguished. The range of the nominotypical subspecies extends from Mexico throughout Central and South America as far as Chubut Province, Argentina (Menu-Marque 2001; Dussart and Defaye 2006). *Microcyclops anceps pauxensis* Herbst, 1962 is known from its type locality at Lago Pauxís in the Brazilian Amazon. Reid (1985) synonymized the form *M. anceps* var. *minor* (Dussart 1984) from the Unaré river valley, northern Venezuela with the Amazonian *M. anceps pauxensis*. Given the current knowledge of the morphology of the American *Microcyclops*, and *M. anceps* s. s. in particular (see Gutiérrez-Aguirre and Cervantes-Martínez 2016), the taxonomic position of *M. anceps pauxensis* and the Venezuelan form need to be revised, as they may represent distinct species rather than subspecies of *M. anceps*.

Eucyclopinae Kiefer, 1927

***Eucyclops agilis* (Koch, 1838)**

Distribution. Galapagos Islands (Isla Santa Cruz), temporary pools, 120 m a.s.l. (Peck 1994); Andes (Lake Cunro, Imbabura Province), as "a cyclopoid resembling *Eucyclops agilis*" (Steinitz Kannan 1979).

Remarks. *Eucyclops agilis* (*Cyclops agilis* in original combination), which has as its type locality Regensburg, Germany, is a nomen dubium, and its use should be avoided (Alekseev et al. 2006). In the past, the name *E. agilis* was often applied to *E. serrulatus*-like copepods, and in the Americas some of these records might refer to *E. pectinifer* (Cragin, 1883) (Dussart and Defaye 2006). The identity of *Eucyclops* Claus, 1893 from the Galapagos and Lake Cunro in the Andes need verification.

***Eucyclops breviramatus* Löffler, 1963**

Distribution. Andes (Löffler 1963).

Remarks. The terra typica of this species is the Lake Papallacta region in the Ecuadorian Andes (3920 m a.s.l.). The general distribution of this species is poorly understood. Records from Mexico are instead another species (Mercado-Salas et al. 2016).

***Eucyclops serrulatus* (Fischer, 1851)**

Distribution. Löffler (1963) reported this species from numerous sites in the Ecuadorian Andes, and Steinitz Kannan (1979) identified a cyclopoid as probably this species from Lake Yambo, Cotopaxi Province. However, these records likely refer to other species; in fact, all records of *E. serrulatus* from the Americas need verification. Alekseev et al. (2006) revised the taxonomy of this species based on classic morphological charac-

ters and integumental pore pattern. In a geographically large-scale overview of the *E. serrulatus*-complex, Alekseev and Defaye (2011) found *E. serrulatus* s. s. to be restricted to the Palearctic region. Mercado-Salas et al. (2016), in revising the Mexican fauna, failed to find *E. serrulatus*, which provides further support that the native range of this species does not include the New World. Mercado-Salas et al. (2016) demonstrated the diagnostic value of several previously overlooked morphological structures (i.e., the surface ornamentation of P4 and antennal coxobasis) in the American *Eucyclops*.

Macrocyclops albidus (Jurine, 1820)

Distribution. Amazon (Napo river valley) (Löffler 1963).

Remarks. *Macrocyclops albidus* s. s. is considered to be cosmopolitan (but see Karanovic and Krajicek 2012) and have been reported from several countries in South America, including Argentina, Chile, Colombia, Ecuador, possibly Paraguay, Uruguay, and Venezuela (Löffler 1981; Reid 1985; Rocha and Botelho 1998; Dussart and Defaye 2006; Gaviria and Aranguren 2007). The other South American subspecies, *M. albidus principalis* Herbst, 1962, differs from the nominal subspecies, among others, in the full development of the inner distal seta on the terminal endopodal segment of P4 (seta reduced to short element in *M. albidus* s. s.). *Macrocyclops albidus principalis* is endemic to the Brazilian Amazon, Venezuela, and Colombia (Herbst 1962; Dussart and Defaye 2006; Gaviria and Aranguren 2007) and might perhaps represent a distinct species rather than subspecies. Löffler (1963) reported *M. albidus* from Ecuador without reference to a subspecific name. He noted that *M. albidus* did not occur in the High Andes.

Paracyclops chiltoni (G.M. Thomson, 1883)

Distribution. Reported by Löffler (1963) as *Paracyclops fimbriatus chiltoni* from the Andes (surroundings of the Antisana volcano).

Remarks. This is one of the few truly cosmopolitan species in the Cyclopidae (Karaytug 1999). *Paracyclops chiltoni* also occurs in remote islands, such as New Zealand (terra typica), the Azores in the Atlantic, Crozet and Amsterdam islands in the southern Indian Ocean, and Tahiti and Easter Island in the Pacific (Lindberg 1958; Karaytug and Boxshall 1998b). This suggests that this species could also occur in the Galapagos Islands.

Paracyclops hardingi Karaytug & Boxshall 1998

Distribution. Löffler (1963) reported this species, as *Paracyclops fimbriatus andinus* Lindberg, 1957, from the Ecuadorian Andes (surroundings of the Antisana volcano).

Remarks. The valid name is *P. hardingi* for the *Paracyclops* originally described by Lindberg (1958) from Peru and also reported by Löffler (1963) from Ecuador. *Paracyclops fimbriatus andinus* Lindberg, 1957 is a junior homonym of *P. andinus* Kiefer,

1957, and *P. hardingi* was proposed as a replacement name (Karaytug and Boxshall 1998a). Outside of Ecuador, *P. hardingi* is known from several localities in the High Andes of Peru: Lake Conococha (Ancash) and Lake Huampucocha (Junín) (the type localities of *Paracyclops fimbriatus andinus*), as well as from various water bodies near Lake Titicaca (Karaytug and Boxshall 1998a).

Ergasilidae von Nordmann, 1832
Ergasilinae von Nordmann, 1832

***Ergasilus* sp.**

Distribution. Amazon (Napo river valley) (Löffler 1963).

Remarks. Ergasilidae are parasitic copepods, parasitizing mainly freshwater sometimes marine coastal fish. The overwhelming majority of the South American ergasilid species (69 of 75) are known from Brazil (Marques et al. 2017).

Calanoida G.O. Sars, 1903
Centropagidae Giesbrecht, 1893

***Boeckella gracilis* (Daday, 1902)**

Distribution. Andes (Löffler 1963; Gaviria 1989). It also occurs in the Patagonian and Paranean zoogeographic zones (Dussart 1984; Bayly 1992; Dussart and Defaye 2002).

Remarks. According to Löffler (1963), in spite of the numerous collections in Peru, this species has so far been found around the Titicaca Lake in the south of the country. Conversely, it is quite common and widespread in Chile and Argentina, especially in southern areas. Gaviria (1989) found this species in the Cordillera Oriental of the Colombian high Andes. The Ecuadorian population is variable in the segmentation and setation of the female P5 endopodite, which has an asymmetrically distally fused segment in some specimens, and both endopodites have one seta less. In some cases, both P5 endopodites are 2-segmented. Additionally, the left and right endopodite of the male is also variable in length, shape, and segmentation. Such pronounced variability is worthy of further study.

***Boeckella occidentalis* Marsh, 1906**

Distribution. Andes (Löffler 1963, Brehm 1924; Delachaux 1928, as *Pseudoboeckella godeti*; Dussart 1984; Bayly 1992; Gaviria 1989; Dussart and Defaye 2002; Van Colen et al. 2017).

Remarks. According to Löffler 1963, the Ecuadorian populations of this species, which is abundant in the Peruvian Andean regions, differ slightly from the type as de-

scribed by Marsh (1906). The enp-3 of the female P5 bears six setae. In the male, the P5 is very similar to the drawings provided by Delachaux (1928), Harding (1955), and Löffler (1955). In both the Peruvian and Ecuadorian populations the distal portion of the right P5 endopodite is recurved, scythe-shaped, and with tuberculi along its outer margin (each tuberculum with a small seta). Gaviria (1989) found this species in the Cordillera Oriental of the Colombian high Andes.

Torres and Rylander (2006) and Araujo et al. (2014) mentioned the subspecies *Boeckella occidentalis intermedia*, yet neither WoRMS (2019) nor Dussart and Defaye (2002) include this taxon. This is probably not a valid name.

Diaptomidae Baird, 1850

Notodiaptomus amazonicus occidentalis Löffler, 1963

Distribution. Amazon (Löffler 1963).

Remarks. Löffler (1963) described the subspecies *N. amazonicus occidentalis* based on a few mature males collected in the Napo river valley of northeastern Ecuador. No mature females were available to Löffler, so that the morphology of the female is currently unknown.

According to Löffler (1963), this taxon is so closely similar to *N. amazonicus* (S. Wright, 1935) and *N. nordestinus* (S. Wright, 1935) that they could be considered as variations of a single polymorphic species. However, this subspecies is currently considered to be a valid taxon (Dussart and Defaye 2002; WoRMS 2019). According to Dussart (1984) the distribution of *N. amazonicus* s.l. includes the Andean, Amazonian, Orinoco-Venezuelan, Guyanean, and the Paranean regions.

The morphological characters discussed by Löffler (1963) seem too vague and incomplete to soundly allow the establishment of a subspecies, and a taxonomic revision of *N. amazonicus* s.l. is desirable. Steinitz-Kannan (1979) reported from Lake El Junco, San Cristobal Island, Galapagos, a calanoid resembling *N. amazonicus*, which was the most abundant zooplanktonic organism in the lake. However, Steinitz-Kannan did not offer drawings or a detailed description that could establish with certainty the identity of this record. Verification of this record is needed.

Notodiaptomus cannarensis Alonso, Santos-Silva & Jaume, 2017

Distribution. Amazon basin, Ecuadorian Andes (Alonso et al. 2017).

Remarks. This species is only known from the type locality, the Mazar reservoir on Paute River, Cañar Province, southern Ecuador. The river is eutrophic, belongs to the Amazon basin, and is 2127 m a.s.l. This species is recorded as the most abundant crustacean in the water column of the reservoir, and, considering its restricted known distribution, it is presumably endemic to the region. *Notodiaptomus cannarensis* has a mean length of 1.4 mm and is a remarkable species among calanoid copepods for its symmetrical aliform projections, which are laterally inserted on the female genital

somite, and the presence of a conspicuous lamella on the exp-2 of the right P5 in males. All information available to the organism comes from its original description in Alonso et al. (2017).

Discussion

The identification of European-like species from other parts of the world was a tendency during the nineteenth century (Boxshall and Defaye 2008), and the same applies to the first half of the twentieth century. In the second half of the twentieth century, revisionary studies based on fine-scale taxonomic resolution have recognized numerous species complexes in place of so-called cosmopolitan species (Boxshall and Defaye 2008). Similar to the Cladocera (López et al. 2018a), some species in this checklist may belong to undescribed species or to groups of species with unresolved taxonomic status in the Neotropics and worldwide. For example, *Acanthocyclops robustus*, *Acanthocyclops vernalis,* and *Eucyclops serrulatus* are considered to be cosmopolitan and obviously distributed in the Americas. Further studies may reveal that these species do not occur in the New World or that they have a much more restricted distribution than what has been reported, as for exemple *Eucyclops serrulatus* according to Mercado-Salas et al. (2016). We cannot, however, exclude the possibility that tropical high-altitude aquatic habitats could harbor relict populations originating from northern latitudes (Van Damme and Eggermont 2011) or that some records might be human-mediated introductions (López et al. 2018a).

Our knowledge on the free-living freshwater copepod fauna from continental Ecuador and Galapagos Archipelago, in comparison to other countries in tropical South America, is relatively recent and rather limited. Countries with ecosystem diversity similar to that occurring in Ecuador have their biodiversity much better documented. For example, a checklist of the free-living copepods of the continental waters of Colombia (Gaviria and Aranguren 2007) reported 69 species and subspecies (14 Calanoida, 41 Cyclopoida, and 14 Harpacticoida). Having examined only 38 crustacean samples, Dussart (1984) increased the number of copepod species known to Venezuela from 28 to 66. From a single Colombian coastal lagoon Fuentes-Reinés and Suárez-Morales (2015) reported 15 copepod species, 10 of which typically live or can occur in freshwater. In a study along La Plata basin, Perbiche-Neves et al. (2014b) found 32 cyclopoid species.

Ecuador is a region with high species richness and high rates of endemism (Myers et al. 2000). Dussart (1984) provided a list of the South American copepod species and showed their distribution among the nine biogeographic zones of the continent. By being situated in both the Andean and the Amazonian biogeographic zones, Ecuador might be home to a significant part of the copepod fauna of both regions. Hence, the current low species richness of the Ecuadorian copepod fauna is most likely the effect of the scarce sampling effort rather than a real biogeographic pattern. We expect that geographically large-scale collections that take the extraordinary diversity of the habitats and strong altitudinal gradients in Ecuador into account will reveal a biodi-

Table 2. Some questions about the biogeography, biodiversity, and evolution of the New World Copepoda that could be answered with extensive taxonomic exploration of the Ecuadorian inland water fauna.

Main topics	Quesions
Dispersal corridor	Might the American Cordillera act as dispersal corridor between North and South America for temperate- or cold-adapted copepods (e.g., see the *Acanthocyclops robustus-vernalis* complex)?
Biogeographical barrier	Are the Andes an insurmountable barrier for the dispersal of lowland/thermophilic copepods (i.e. how does the copepod fauna of the Coastal and Amazonian regions differ from each other)? Comparisons might be made between copepods living in the benthic and in the hyporheic zones of rivers, semiterrestrial and cryptic habitats such as mosses, phytotelmata, forest litter, etc., as well as in temporary collections of water (i.e. ponds, pools and marshes), rather than limnetic copepods, as the coastal region has no natural lakes (Steinitz-Kannan et al. 1983).
Patterns of speciation within islands	Have inland water copepods undergone an evolutionary radiation similar to those found in the terrestrial organisms (Parent et al. 2008) in the Galapagos archipelago, which apparently has a shortage of the fresh surface water bodies (Steinitz-Kannan et al. 1983; López et al. 2018b)? To date, except for the records of the harpacticoids *Cletocamptus axi* and *Cletocamptus schmidti*, the cyclopoids *Eucyclops agilis*, *Microcyclops* sp., and *Metacyclops mendocinus* in Santa Cruz island (Peck 1994), and a calanoid resembling *Notodiaptomus amazonicus* from Lake El Junco in San Cristobal island (Steinitz-Kannan 1979), we have no information on the freshwater copepods of the archipelago.
Dispersal capacity, biodiversity and biogeography	How do the diversity and geographic distributional patterns change in Copepoda with different dispersal ability (Cyclopidae are considered to be good dispersers, while Diaptomidae are poor dispersers; Canthocamptidae are good but most of the Parastenocarididae studied so far seem to be very restricted geographically)?
Diversity and endemism	Are copepods less diverse, but with higher rates of endemism in high altitudinal lakes and rivers?

versity at least a magnitude greater than what is currently known for the Copepoda. The recommendations of López et al. (2018a) for more extensive collections of the Cladocera, including specimens suitable for molecular studies, also hold true for the copepods. From among the four lake provinces [Paramo, Andean (under the Paramo, 2000–3500 m a.s.l.), Amazonia, and coastal plains and Andean foothills; Steinitz-Kannan et al. 1983], the lake-poor coastal region might be the greatest challenge to explore, albeit marsh-lakes and ephemeral swamps can harbor rich fauna of copepods (Reid 1987). Special attention must be directed at various altitudinal and latitudinal zones within the country to transitional or cryptic habitats such as littoral zones, temporary pools, mosses, phytotelmata, hyporheic zones, wetlands, cisterns, and other habitats.

A taxonomic and zoogeographic revision of the inland water copepods of Ecuador, using both morphological and genetic information, might allow us to test of some major questions of copepod biogeography and evolution (Table 2). To date, any attempt to infer local as well as broad biodiversity and biogeographic patterns of copepods within Ecuador would be premature due to the scarcity of data, dubious records and unsolved taxonomic problems. A better understanding of the biogeography, biodiversity and phylogenetic relationships of the Ecuadorian fauna, can only be reached if the taxonomic and faunistic data are interpreted within a broad geographic frame. To achieve this goal, we need a network of collaboration, with limnologists and taxonomists from both Ecuador and outside the country.

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RESEARCH ARTICLE

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Two new species of the genus *Meleonoma* Meyrick from China (Lepidoptera, Gelechioidea, Xyloryctidae)

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Abstract

Two new species of *Meleonoma* Meyrick, 1914a (Gelechioidea, Xyloryctidae) from southeastern China are described: *Meleonoma foliiformis* Yin, **sp. nov.** from Guangxi Province and *M. projecta* Yin, **sp. nov.** from Fujian Province. Adults and male genitalia are described in detail. A list of the *Meleonoma* species occurring in China is given. The taxonomic position of *Meleonoma* has been unstable, and under debate. Nonetheless, it is here tentatively placed in the family Xyloryctidae, following the latest molecular phylogenetic study concerning this genus.

Keywords

Checklist, morphology, moth, taxonomy

Introduction

The genus *Meleonoma* Meyrick was established in 1914 in the family Oecophoridae, for three species, with *Cryptolechia stomota* Meyrick, 1910a as the type species. Prior to this study, 35 valid species had been reported over the world, of which 14 had been discovered in China. The first ever described species of the genus was collected in Heilongjiang Province of China and published by Christoph under the original name of *Euteles flavimaculata* Christoph, 1882. However, it was not transferred into *Meleonoma* until very recently (Lvovsky 2015). After that, 14 species with various distributions were described by Mey-

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rick, successively from 1906 to 1935, of which seven were placed directly in *Meleonoma*, viz. *M. heterota* Meyrick, 1914a and *M. petrota* Meyrick, 1914a, both published along with the generic description; *M. psammota* Meyrick, 1915; *M. implexa* Meyrick, 1918; *M. nephospora* Meyrick, 1930; *M. pardalias* Meyrick, 1931; *M. impulsa* Meyrick, 1934. The other seven were originally published in various genera, and transferred into *Meleonoma* later on, viz. *M. capnodyta* (Meyrick, 1906) in *Borkhausenia* Hübner, [1825] 1816; *M. crocomitra* (Meyrick, 1914b) in *Pseudodoxia* Durrant, 1895; *M. facunda* (Meyrick, 1910b) in *Leptosaces* Meyrick, 1888; *M. stomota* (Meyrick, 1910a), *M. aridula* (Meyrick, 1910c), *M. malacobyrsa* (Meyrick, 1921) and *M. torophanes* (Meyrick, 1935) in *Cryptolechia*, Zeller, 1852. Years later, Viette (1955) reported the new species *M. diehlella* from Madagascar. Li and Wang (2002, 2004) reported five new species from China. Lvovsky (2015) described five new species from Nepal and China and transferred *Cryptolechia peditata* Wang, 2006b into *Meleonoma*. Yin and Wang (2016a, b) reported two new species from Taiwan and four new ones and one new record from Thailand. In the same year, Park and Park (2016) described two new species and one new record from Korea.

Meleonoma are mostly small to medium-sized moths, mainly distributed in the Australian, Afrotropical, Palearctic, and Oriental faunal regions; the genus is especially rich in the Oriental faunal region. *Meleonoma* is characterized by the front of the head usually covered with appressed scales and the vertex with erect and hairlike scales; the labial palpus bearing three segments and recurved upwardly, extending well beyond the vertex, with the third segment shorter than the second one; the scape without pecten; the tibia of all legs clothed with long hairs above; the forewing with ground color usually yellow or black or approaching one of these two colors, forewing patterns diverse, usually with an oblique, wide, yellow or dark brown fascia. The venation of the forewing is as follows: R1 from about middle of cell, R4 and R5 arising from upper angle of cell and stalked at the half of their length, R5 reaching to near apex, M1 and M2 parallel, M2, M3 and CuA1 all arising from near the lower angle of the cell and separated from each other, CuA1 and CuA2 parallel, CuP weakly developed. The venation of hindwings is as follows: Rs, M1 and M2 nearly parallel, M3 and CuA1 stalked at the base or arising from the same point of the cell, CuA2 far from CuA1, arising from about 4/5 of the posterior margin of the cell, and CuP well developed. Tergum II-VII of abdomen with patches of a broad area of directed setae (Figs 3, 4). *Meleonoma* can also be identified by some key characters, such as the male genitalia with a well-developed uncus, a partly sclerotized circular or entirely membranous gnathos, and a well-defined saccus; by the female genitalia with an entirely or partly sclerotized ductus bursae, and one signum, often with spines if present (Wang 2006a; Yin and Wang 2016b; Kim and Lee 2017).

Nothing is known about their host plants.

The taxonomic status of the genus is controversial and the genus has been placed in different families and subfamilies of the Gelechioidea. It was originally described in the family Oecophoridae (Meyrick 1914a). After that, Clarke (1965) placed *Meleonoma* in the Cosmopterigidae (without any comments). Since then, many researchers followed his treatment (e.g., Nye and Fletcher 1991; Li and Wang 2002, 2004). Lvovsky

(2015) transferred the genus into the Lypusidae. The most recent phylogenetic study of Kim et al. (2016) indicated that *Meleonoma* most likely belongs to the Xyloryctidae. Although the taxon sampling in Kim et al. (2016) was limited for this genus, their work is currently the only one based on molecular phylogenetic evidence. Therefore, we tentatively follow this and place *Meleonoma* in the Xyloryctidae.

In this study, two new species are described from China: *M. foliiformis* Yin, sp. nov. from Guangxi Province and *M. projecta* Yin, sp. nov. from Fujian Province. The species number of this genus is thus increased to 37.

Material and methods

The examined specimens were collected from Guangxi and Fujian Provinces in southeastern China in 2018. The descriptive terminology of the anatomical structures generally follows Wang (2006a), however in descriptions of the male genitalia, the more proper term phallus rather than aedeagus is applied here following Kristensen (2003). Photographs of adults were taken using a Canon EOS 6D Mark II camera plus an EF 100 mm f/2.8L MACRO IS USM lens with the help of EOS Utility 3.10.20 software. Images of genitalia were captured using a Leica DM4 B upright microscope and photomontage was performed with Leica Application Suite X imaging software. All type specimens are deposited in the Morphological Laboratory, Guizhou University of traditional Chinese Medicine, Guiyang 550025, Guizhou, China.

Taxonomy

Genus *Meleonoma* Meyrick, 1914a

Meleonoma Meyrick, 1914a: 255. Type species: *Cryptolechia stomota* Meyrick, 1910a, by original designation.

=*Acryptolechia* Lvovsky, 2010: 378. Type species: *Cryptolechia malacobyrsa* Meyrick, 1921. Synonymised by Lvovsky (2015).

Checklist of *Meleonoma* Meyrick in China

1 *Meleonoma apicispinata* Wang, 2016b: 26
Distribution: China (Taiwan Province).

2 *Meleonoma echinata* Li, 2004: 38
Distribution: China (Guizhou Province).

3 *Meleonoma facialis* Li et Wang, 2002: 230
Distribution: China (Henan, Jiangxi, Shaanxi, Sichuan, Yunnan Provinces), Indonesia, Korea, Nepal, Russia, Thailand.

4 *Meleonoma facunda* (Meyrick, 1910b): 155
Distribution: China (Northern and Eastern, Zhejiang Province), India, Japan.
5 *Meleonoma flavimaculata* (Christoph, 1882): 29
Distribution: China (Heilongjiang Province), Russia.
6 *Meleonoma foliata* Li, 2004: 37
Distribution: China (Guangdong Province).
7 *Meleonoma foliiformis* Yin, sp. nov.
Distribution: China (Guangxi Province).
8 *Meleonoma malacobyrsa* (Meyrick, 1921): 394
Distribution: China (Anhui, Fujian, Guizhou, Henan, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Taiwan, Zhejiang Provinces), Japan, Korea.
9 *Meleonoma malacognatha* Li et Wang, 2002: 230
Distribution: China (Shaanxi Province).
10 *Meleonoma margisclerotica* Wang, 2016b: 25
Distribution: China (Taiwan Province).
11 *Meleonoma meyricki* Lvovsky, 2015: 773
Distribution: China (Yunnan Province).
12 *Meleonoma pardalias* Meyrick, 1931: 191
Distribution: China (Sichuan Province).
13 *Meleonoma peditata* (Wang, 2006b): 8
Distribution: China (Hubei Province).
14 *Meleonoma polychaeta* Li, 2004: 35
Distribution: China (Hunan Province).
15 *Meleonoma projecta* Yin, sp. nov.
Distribution: China (Fujian Province).
16 *Meleonoma torophanes* (Meyrick, 1935): 81
Distribution: China (Henan, Hubei, Shaanxi, Shanghai, Zhejiang Provinces), Korea.

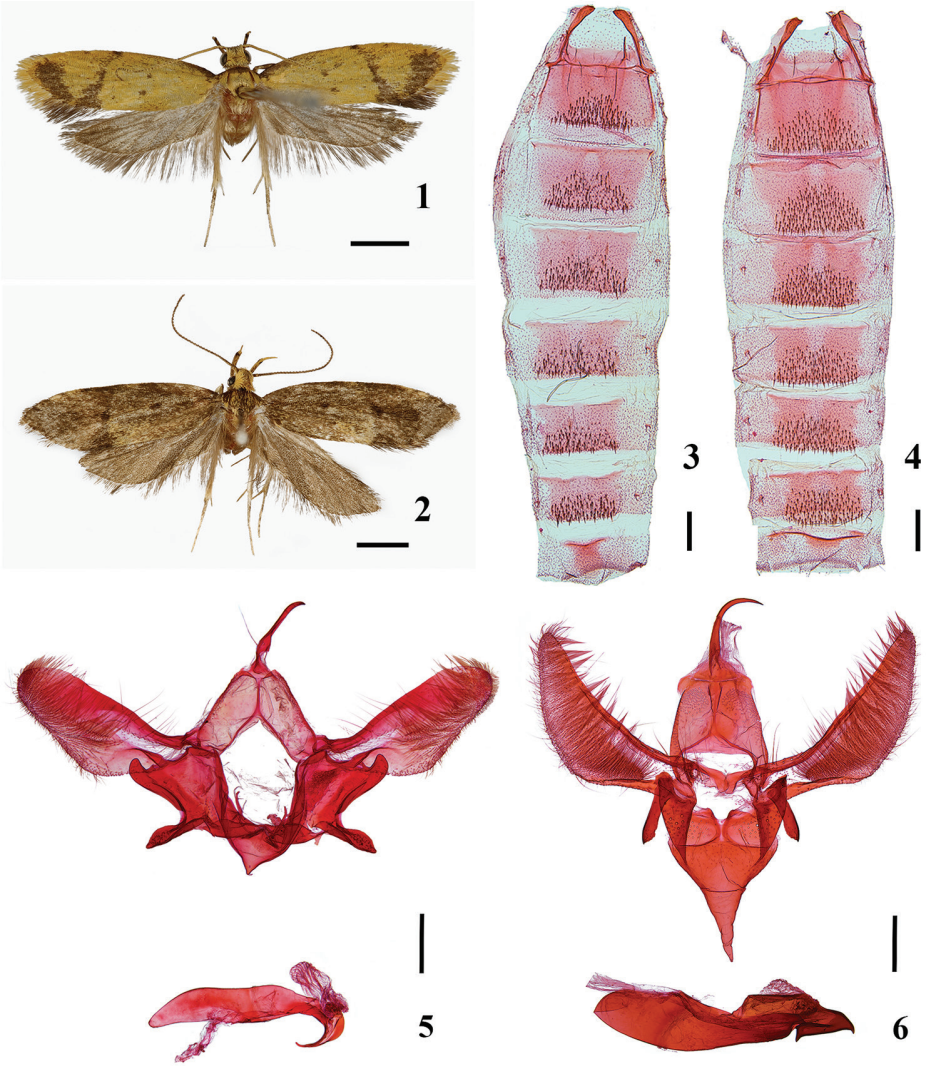
Meleonoma foliiformis **Yin, sp. nov.**

http://zoobank.org/0BC78FAD-DA43-4D1A-BD8D-80A0DE89EA1C
Figs 1, 3, 5

Material examined. Holotype: China • ♂; Guangxi Province, Daming Mountain; alt. 1200 m, 4 Jun. 2018; Yuping Li leg.; YAH18108. **Paratype**: 1 ♂, same collection data as for preceding; YAH19001.

Diagnosis. This new species resembles *M. facunda* (Meyrick, 1910b) in both appearance and genitalia. The differences between *M. foliiformis* and *M. facunda* in the male genitalia are as follows: *M. foliiformis* with the ventral process of the sacculus in a distinct leaf shape and the phallus with the distal 1/4 hooked; *M. facunda* with the ventral process of sacculus tiny, triangular in shape and the phallus straight.

Description. Head: vertex mixed with pale gray scales, front pale yellow; labial palpus long and recurved, extending well beyond vertex, with smooth scales; outer



Figures 1–6. *Meleonoma* species, morphology **1** adult of *Meleonoma foliiformis* Yin, sp. nov., holotype, male (gen. slide no. YAH18108) **2** adult of *M. projecta* Yin, sp. nov., holotype, male (gen. slide no. YAH18125) **3** abdomen of *M. foliiformis* Yin, sp. nov., holotype, male (gen. slide no. YAH18108) **4** abdomen of *M. projecta* Yin, sp. nov., holotype, male (gen. slide no. YAH18125) **5** male genitalia of *M. foliiformis* Yin, sp. nov., paratype, phallus illustrated separately (gen. slide no. YAH19001) **6** male genitalia of *M. projecta* Yin, sp. nov., holotype, phallus illustrated separately (gen. slide no. YAH18125). Scale bar: 2.00 mm (**1, 2**); 0.25 mm (**3–6**).

surface of labial palpus with segment 1 and distal half as well as end of segment 2 densely covered with dark-brown scales, inner surface yellow; segment 3 yellow, about 3/4 length of segment 2; antenna with scape pale yellow; flagellum alternately pale yellow and dark brown on dorsal surface, ventral surface pale yellow; ocelli absent; scales of proboscis pale yellow.

Thorax: Tegula and mesonotum blackish brown anteriorly, yellow posteriorly; legs whitish yellow, tibiae scattered with blackish brown scales and tarsi with blackish brown speckles on outside. Forewing (Fig. 1): Length 6.0–7.0 mm (N = 2), about 3.5 X as long as wide, along costa with blackish brown streak from base to about basal 1/5, distal 1/3 of costa with several blackish brown dots; a dark-brown fascia extending from near middle of costa obliquely to tornus, slightly wider posteriorly; cell with 2 blackish brown dots, one set at middle of cell, the other set at distal 2/5 of fold; apex dark brown, somewhat forming a triangular patch along termen; cilia yellow except dark brown on tornus. Ventral surface yellowish brown. Hindwing (Fig. 1): translucent grayish brown, gradually darkening towards apex; cilia grayish brown.

Abdomen (Figs 3, 5): Male genitalia (Fig. 5): Uncus long and thin, wider basally, sparsely setose at basal 2/5; tegumen inverted V-shaped, lateral arms about same width, posterior margin arched inwards, anterior margin deeply concave, V-shaped; valva gradually widening to middle from a narrow base, distal half long oval in shape, distal half of ventral surface densely covered with long hairs; costa broadly arched forming a shallow notch; transtilla short and weakly sclerotized, with rounded apex; sacculus with basal 1/3 of dorsal margin joined with valva, two sclerotized processes at end of dorsal and ventral margin respectively: dorsal process somewhat semicircular, ventral process leaf-shaped, outer margin heavily sclerotized; saccus inverted triangular in shape, apex narrowly rounded; juxta U-shaped; phallus with basal 1/4 thin, gradually thickened to about 1/4, nearly same width from basal 1/4 to about distal 1/4, distal 1/4 hooked, apex pointed. Female genitalia: unknown.

Biology. The host plant of the larva stage is unknown. The adults were collected using lamp attraction in June.

Distribution. China (Guangxi Province).

Etymology. The specific name, the Latin adjective *foliiformis*, means leaf-like, and refers to the leaf-shaped ventral process of the sacculus.

***Meleonoma projecta* Yin, sp. nov.**
http://zoobank.org/EE0501C4-54A9-4B6D-A7A5-30EB59F0EA0C
Figs 2, 4, 6

Material examined. Holotype: China • ♂, Fujian Province, Wuyi Mountain; alt. 1200 m, 10 May 2018; coll. Yuping Li leg.; YAH18125. **Paratype**: 1 ♂, same collection data as for preceding; YAH19002.

Diagnosis. This new species can be distinguished from its congeners easily by the unique character in the male genitalia. In *M. projecta*, the distal portion of the sacculus with a heavily sclerotized process. It is also slightly similar to *M. malacobyrsa* externally. They can be distinguished by the fascia in the forewings: *M. projecta* with the fascia indistinct, whereas it is clearly outlined in *M. malacobyrsa*. In *M. projecta* the valva has no odontoid process on the ventral margin, sacculus with apex produced and phallus

with tiny teeth near apex; *M. malacobyrsa* has the valva with an odontoid process on the ventral margin, sacculus concave and without a tooth on the phallus.

Description. Head: vertex with grayish brown scales at middle, front yellow; labial palpus long and recurved, extending well beyond vertex, with smooth scales, outer surface of labial palpus with segment 1 and segment 2 dark brown, inner surface yellow, apex of segment 2 with blackish brown dots; segment 3 yellow, scattered with blackish brown dots, about 1/2 of second segment; antenna with scape earthy yellow on ventral surface and blackish brown on dorsal surface, with flagellum ringed, alternately blackish brown and earthy yellow; ocelli absent; scales of proboscis yellow.

Thorax: Tegula and mesonotum blackish brown mixed with yellow; legs light yellow, grayish brown on ventral surface, with grayish brown speckles on outside surface of tibiae and tarsi. Forewing (Fig. 2): Length 7.0–8.0 mm ($N = 2$), about 3.0 X longer than wide, blackish brown mixed with yellow scales; costa with a large diffused yellow blotch at about distal 1/5. Ventral surface dark brown; an oblique dark brown fascia running from basal 2/3 of costa to tornus; cell with 2 blackish brown markings, set at middle and end of cell respectively; cilia dark brown except yellow basally. Hindwing (Fig. 2): grayish brown; cilia grayish brown. Ventral surface of forewing and hindwing dark brown.

Abdomen (Figs 4, 6): Male genitalia (Fig. 6): Uncus with basal 1/4 triangular in shape, distal 3/4 long and hooked, pointed at apex; gnathos weakly sclerotized at base forming two elliptic sclerites, other parts membranous; tegumen inverted V-shaped, lateral arms gradually narrowed to apex, posterior margin straight, anterior margin deeply concave, onion-shaped; valva somewhat knife-shaped, gradually widening to basal 2/5 from a narrow base, distal 3/5 gradually tapered to rounded apex, ventral surface densely covered with long hairs; costa slightly arched inwardly; transtilla greatly protruded forward medially, distal portion curving downward and in contact with each other; sacculus jointed with valva dorsally; distal portion with a long heavily sclerotized process, bladelike, pointed at apex; saccus funnel-shaped, narrowly rounded at apex; phallus with basal 2/3 elongately ovate, distal 1/3 irregularly shaped, bearing three small teeth at distal 1/4 and end. Female genitalia: unknown.

Biology. The host plant of the larva stage is unknown. The adults were collected using lamp attraction in May.

Distribution. China (Fujian Province).

Etymology. The specific name, the Latin adjective *projectus*, refers to the heavily sclerotized process of the sacculus.

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RESEARCH ARTICLE

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Discovery of a specialist Copelatinae fauna on Madagascar: highly ephemeral tropical forest floor depressions as an overlooked habitat for diving beetles (Coleoptera, Dytiscidae)

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Abstract

Diving beetles are generally aquatic and live submerged in water during larval and adult stages. A few groups have colonised hygropetric habitats and fewer species still can possibly be referred to as terrestrial. Here we describe six new Copelatine species that were mainly found in dry shallow forest floor depressions in the eastern and northeastern lowland humid forests of Madagascar. Three new species are described in each of the two genera *Copelatus* and *Madaglymbus*: *Copelatus amphibius* **sp. nov.**, *Copelatus betampona* **sp. nov.,** *Copelatus zanatanensis* **sp. nov.**, *Madaglymbus kelimaso* **sp. nov.**, *Madaglymbus menalamba* **sp. nov.,** and *Madaglymbus semifactus* **sp. nov.** Diagnosis, description, known distribution, ecology, and conservation notes are provided for each species. All species are illustrated with a dorsal habitus image, ventral and lateral views of the male penis, and parameres. Photographs of the unusual terrestrial habitats where the species were found are provided. *Madaglymbus menalamba* **sp. nov.** is also documented with macrophotos and videorecordings of the terrestrial locomotion and behaviour in the field. Although these species should not be classified as terrestrial, or even semi-terrestrial Dytiscidae, they seem to be specialists of very ephemeral aquatic habitats and stay put instead of disperse when the habitat dries up. It is hypothesised that this lifestyle and behaviour on Madagascar is restricted to the high-precipitation humid forest regions mainly in the east. It may also represent a transition step, or stepping-stone, towards becoming fully terrestrial, a step that the few known terrestrial Dytiscid taxa once passed through. It is very likely that this type of habitat is overlooked for aquatic beetles, not only in Madagascar, and the six species herein described may be just the "tip of the iceberg".

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Keywords
Analalava, Betampona, *Copelatus*, humid forest, *Madaglymbus*, Marojejy, Masoala, new species, Nosy Mangabe, overlooked habitat, protected area, rainy season, semi-terrestrial

Introduction

Diving beetles are typically 0.8–48 mm long streamlined aquatic beetles with advanced synchronous hind-leg stroke swimming. They are typical of a variety of water bodies ranging from large rivers to small streams, ponds, marshes, mires, bogs and lakes, forest pools, rock pools, ditches, and canals (Gioria 2014; Jäch and Balke 2008; Balke and Hendrich 2016; Miller and Bergsten 2016). A few groups live in hygropetric, also known as madiculous, habitats. These are seepages, wet rocks along streams or splash zones at the sides of waterfalls forming a millimetre-thin film of water over bedrock (Balke et al. 1997; Gioria 2014; Miller and Bergsten 2016). A number of species have adapted to this environment, and concomitantly locomotion has turned more to crawling, creeping, burrowing or jumping than swimming (Balke and Hendrich 2016).

Even fewer diving beetle species have only been found by sifting litter from terrestrial habitats. Their morphology is notably characterised by the absence, or strong reduction, of natatorial setae on legs and they are therefore tentatively referred to as terrestrial (Brancucci 1979, 1985; Watts 1982; Balke and Hendrich 1996; Brancucci and Hendrich 2010; Toussaint et al. 2016; Miller and Bergsten 2016). The life cycle is not known for any of these, for instance if the adults spend their entire life in terrestrial habitats or if the larval development also takes place out of water. Larvae have never been found for any of the suspected terrestrial species.

While adult dytiscids are typically aquatic, all, as far as known, leave water for pupation and many also leave water for dispersal flights (Miller and Bergsten 2016; Bilton 2014). But diving beetles may also be found in temporarily terrestrial habitats when water has recently dried up. As long as there is still moist or damp habitat it is usually possible to find dytiscids if rock or litter are lifted in recently dried up water pools in for instance riverbeds or pond beds. In our previous experience these have been typical stream, or pond inhabitants, some individuals of which have still to search new water or perhaps take a chance that water will soon return. Such species have always been found in larger quantities in water at other or nearby aquatic sites and have not seemed to be specialists of such habitats or behaviour.

However, in our most recent experience of searching dry forest floor depressions in lowland humid forests of northeastern Madagascar, we came across a handful of Copelatinae species, all undescribed, exclusively or almost exclusively found in such habitats. These seem to be specialist of very ephemeral aquatic habitats as we did not find them in nearby streams or other more permanent water bodies. How often and for how long these depressions fill with water is unknown but there was no water in most of them when visited during the rainy season (February–March 2018). Some where not even depressions but small flat pans along paths that would arguably have just a few millimetres of aquatic habitat and only while raining. In terms of the classification

of water beetles into six categories by Jäch (1998), it is unclear if they would pass the definition of "true water beetles" based on "true water beetles are submerged … for most of their adult stage". The frequency and length of dry and submerged periods of these forest floor depressions and flat pans would need to be followed over the season as well as the natural history and phenology of the beetles. In any case we refrain from labelling these as semi-terrestrial, semi-aquatic, amphibious or amphibiotic following the advice of Jäch and Balke (2008) as these terms are variously defined, overlapping in definition or not. What is most significant is that we seem to have come across a previously largely unknown specialist community of diving beetles in these habitats, at a well-known biodiversity hotspot.

Madagascar is one of the world's most important biodiversity hotspots (Myers et al. 2000) with an extraordinary level of endemism (Goodman and Benstead 2005). The bulk of this unique biodiversity are forest-dwellers and the richest forests are the eastern humid forests. The humid forests climb the north-south running eastern escarpments from sea-level to montane cloud forests where altitude approaches alpine levels above 2000 m. The biodiversity is often altitudinally structured with a different set of species in lowlands, at midaltitude and at high altitude. Deforestation levels on Madagascar have been devastating, with dire consequences also for freshwater fauna as IUCN redlisting status bears witness off (Máiz-Tomé et al. 2018). Although there is still a fair amount of midaltitude humid forests remaining, very little remain of lowland humid forests, and the largest intact lowland forest is that of the Masoala Peninsula in the northeast. Our fieldwork was conducted here as well as in three additional lowland humid forests.

We describe six new species below and note that forest floor depressions and flat pans in tropical humid regions could be an overlooked habitat for specialist diving beetle communities. We provide photos of habitus and of male genitalia, as well as distribution maps for each species. The unusual terrestrial localities are richly illustrated with photos. For one species we also provide *in situ* photos and video recordings from the type locality documenting terrestrial locomotion. The six species belong to the two genera of Copelatinae known from Madagascar, *Copelatus* Erichson, 1832 and *Madaglymbus* Shaverdo & Balke, 2008. *Copelatus* is a megadiverse genus with worldwide distribution while *Madaglymbus* is endemic to Madagascar and the Comoros. The Madagascar fauna of both genera are in different stages of being taxonomically treated (see under Results).

Materials and methods

Fieldwork

New collecting efforts of Dytiscidae were conducted in the four protected areas Masoala NP, Marojejy NP, Betampona RNI and Analalava reserve in 2017 and 2018. In Masoala NP both the south side of the main peninsula with Andranobe as base was

visited, and the separate island in the Antongil bay, Nosy Mangabe reserve. Marojejy National Park is located a bit further north and is unique in harbouring continuous forests from lowland to alpine levels. A rather isolated patch of remaining lowland humid forest is that of Betampona 35 km NW of Toamasina. It constitutes a strict nature reserve only accessible for researchers. Analalava reserve finally is a very small remaining humid littoral forest on the lowland east coast about 30 km NE of Betampona.

We targeted shallow forest floor depressions or flat pans that bore signs of occasionally having water by being more moist or with a more clayish soil than sourrounding forest floor. Several sites were directly on paths in the forest. None, except one site in Marojejy NP and one in Masoala NP had any connection or was in proximity of running water. Specimens were sampled with sieves, white pans and by hand searching through the clay, soil and leaf litter. Material was collected into plastic tubes with 95% ethanol for conservation.

Each locality was given a collecting event code and associated metadata included geographic name(s), forest type, locality type, habitat description, eventual disturbance, collecting date and collectors. Altitude, latitude and longitude were recorded with a handheld GPS (Garmin). Each locality was also documented with photographs using a compact Panasonic digital camera.

Preparations and illustrations

Specimens were examined under dissection microscopes from Leica (M165C and MZ12.5). Genitalia were extracted with a fine forceps or pin from the tip of the abdomen and glued on cards on the same pin as the specimen. Photos of habitus were taken with a Canon EOS 5D Mark II DSLR camera equipped with a MP-E 65 mm 1-5X super macrolens and mounted on a motorised rail (Stackshot) from Cognisys. The system was operated using Canon EOS Utility and Zerene Stacker (Zerene Systems) softwares, the latter also used for stacking the Z-stack of captured images with the PMax or DMap algorithm. Photos of genitalia were taken with a Canon EOS 7D DSLR camera mounted on a BALPRO 1 Universal bellow from Novoflex with a long working distance 10X Plano apochromatic microscope objective from Mitutoyo. The system was mounted on a motorised rail (Stackshot) from Cognisys and operated with the same softwares given above. Photo and video recording of one species in the field was done with a Panasonic Lumix DMC-TZ100 compact camera on a gorillapod.

Label data are given as written and separated by "//" if on separate labels and "|" if on different rows on the same label. All examined specimens (individual mounted specimens, or single alcohol tubes with multiple specimens) have been given unique catalogue numbers and these are listed first, starting with "NHRS" followed by a number made up by four letters and nine digits. A series of specimens with consecutive catalogue numbers are given as a range. Other abbreviations used: GP (Genital Preparation) = male genitalia have been examined, ex. = exemplars (number of individuals), Alc. = in alcohol tube. Coordinates are given for the type localities in decimal degrees format within square brackets, followed by administrative region and district (see Fig. 4D for regions).

Material and depositories

All specimens examined in this study are registered in the Swedish Museum of Natural History, Stockholm, Sweden (NHRS) collection objects database. They are deposited in the following collections and referred to by the abbreviations (paratype series will be shared with other institutions as well):

NHRS	Swedish Museum of Natural History, Stockholm, Sweden.
PBZT/MBC	Parc Botanique et Zoologique de Tsimbazaza/Madagascar Biodiversity Center, Antananarivo, Madagascar.
DEUA	Department of Entomology, Antananarivo University, Antananarivo, Madagascar.

Taxonomy

Copelatus Erichson, 1832

Remark. Twenty-five species of *Copelatus* are currently known from Madagascar. All species except those in the *erichsonii* group were recently revised by Ranarilalatiana et al. (in press). The three species described below all belong to the *erichsonii* species group with ten discal and one submarginal elytral striae. Type materials of all *erichsonii* group species described from Madagascar have been examined in the ongoing second part of the revision.

Copelatus amphibius sp. nov.

http://zoobank.org/440DF910-AAFD-4430-BDF8-EE5E59B1907C
Figs 1A, 2A

Type locality. Masoala National Park [15.6713S; 49.9672E] (Madagascar, Analanjirofo region, Maroantsetra)

Type material. ***Holotype*** ♂ GP (NHRS): // NHRS-JLKB | 000066350 // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-53: depression on forest floor | on path ~1.6 km NE of Andranobe camp |15.6713S, 49.9672E, 220 m, 18.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Holotype | *Copelatus amphibius* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -7♂ GP, 6♀, 45 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000011230–1, 65651–2, 66016, 66347–9, 66351–5, 11232(Alc.) // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-53: depression on forest floor | on path ~1.6 km NE of Andranobe camp |15.6713S, 49.9672E, 220 m, 18.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus amphibius* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

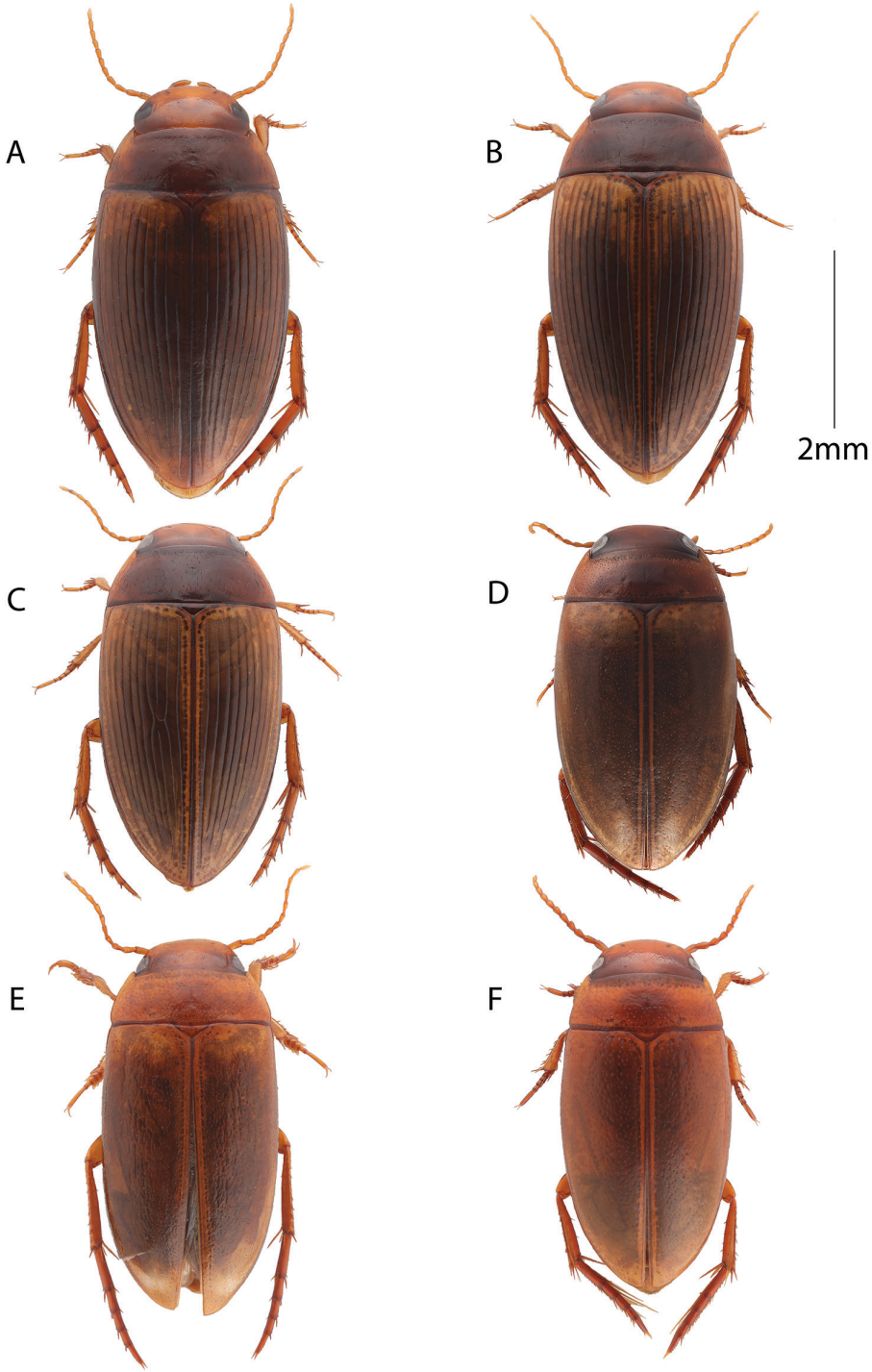

Figure 1. Habitus, dorsal view. **A** *Copelatus amphibius* sp. nov. (female) **B** *Copelatus zanatanensis* sp. nov. (female) **C** *Copelatus betampona* sp. nov. (female) **D** *Madaglymbus semifactus* sp. nov. (female) **E** *Madaglymbus kelimaso* sp. nov. (male) **F** *Madaglymbus menalamba* sp. nov. (female).

-3♂ GP, 5♀, 42 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000011234, 65649–50, 65788, 65790, 65795, 65435–6, 11233(Alc.) // Madagascar: Toamasina: Analanjirofo: | Nosy Mangabe, Masoala NP: MAD18-58 | rainfall-pool with dead leaves nr path | after lighthouse, lowalt. rainforest | 15.5079S, 49.7641E, 195 m, 19.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus amphibius* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂ GP, 2♀ (NHRS): // NHRS-JLKB | 000065642–4 // Madagascar: Antsiranana: Sava: | Marojejy NP: midalt. rainforest: | small stream above camp II on | trail towards Taktajania, MAD18-23 | 14.4375S, 49.7612E, 860 m, 09.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus amphibius* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. A small species with medially infuscated testaceous elytra and oblong-oval body shape. Penis in lateral view with low ventral ”hump”, apical blade with acute apex and somewhat curved non-straight ventral margin, in ventral view apical blade is left-angled (Fig. 2A). Significantly smaller than described species from Madagascar with similar type of genitalia such as *C. owas* Régimbart, 1895 and *C. acamas* Guignot, 1955, and genitalia details also clearly different.

Description. Body length: 4.6–5.4 mm (♀: 4.6–5 mm, ♂: 4.8–5.4 mm).

Body shape oval (Fig. 1A).

Head rufotestaceous with a rather weak v-shaped infuscation between eyes. Pronotum dark brown medially and testaceous laterally. Elytra testaceous brown, variably with darker infuscation medially especially along the striae (Fig. 1A). Basally, laterally and apically lighter testaceous. Appendages testaceous except metatarsus somewhat rufotestaceous.

Elytra with ten discal and one submarginal striae. Ninth striae avbreviated anteriorly. Submarginal striae present posteriorly only, starting at about middle. Posteriorly every second striae abbreviated (2nd, 4th, 6th, 8th, and 10th). Pronotum striolated laterally and basally. Lateral margin of pronotum with a narrow bead, not reaching anterior corner. Head, pronotum and elytra with same type of microreticulation and micropunctures.

Ventral side rufotestaceous except metacoxal plate infuscated brown. Abdominal sternites with vague testaceous spots laterally. Metacoxal plate with coarse strioles, abdominal sternites II–IV with finer strioles. Metacoxal lines anteriorly diverging and ending well before metaventral suture. Prosternal process lanceolate, short, and anterior metaventral process rather broad.

Male protibia modified, angled at base and expanding distally. Pro and mesotarsal segments I–III dilated and ventrally equipped with adhesive discs (constellation I:3 (row 1), 4 (row 2), II:4, III:4). Longer metatibial spur apically slightly more curved than in female.

Male genitalia as in Figure 2A. Penis curved and robust in lateral view with a comparatively low ventral hump and sinuate before the apical blade. Apical blade left-turned in ventral view. Right lateral side with strong rugosity or transverse ridges apically. Parameres as in Figure 2A.

Dorsal structures of females not significantly different from male, but body size on average smaller.

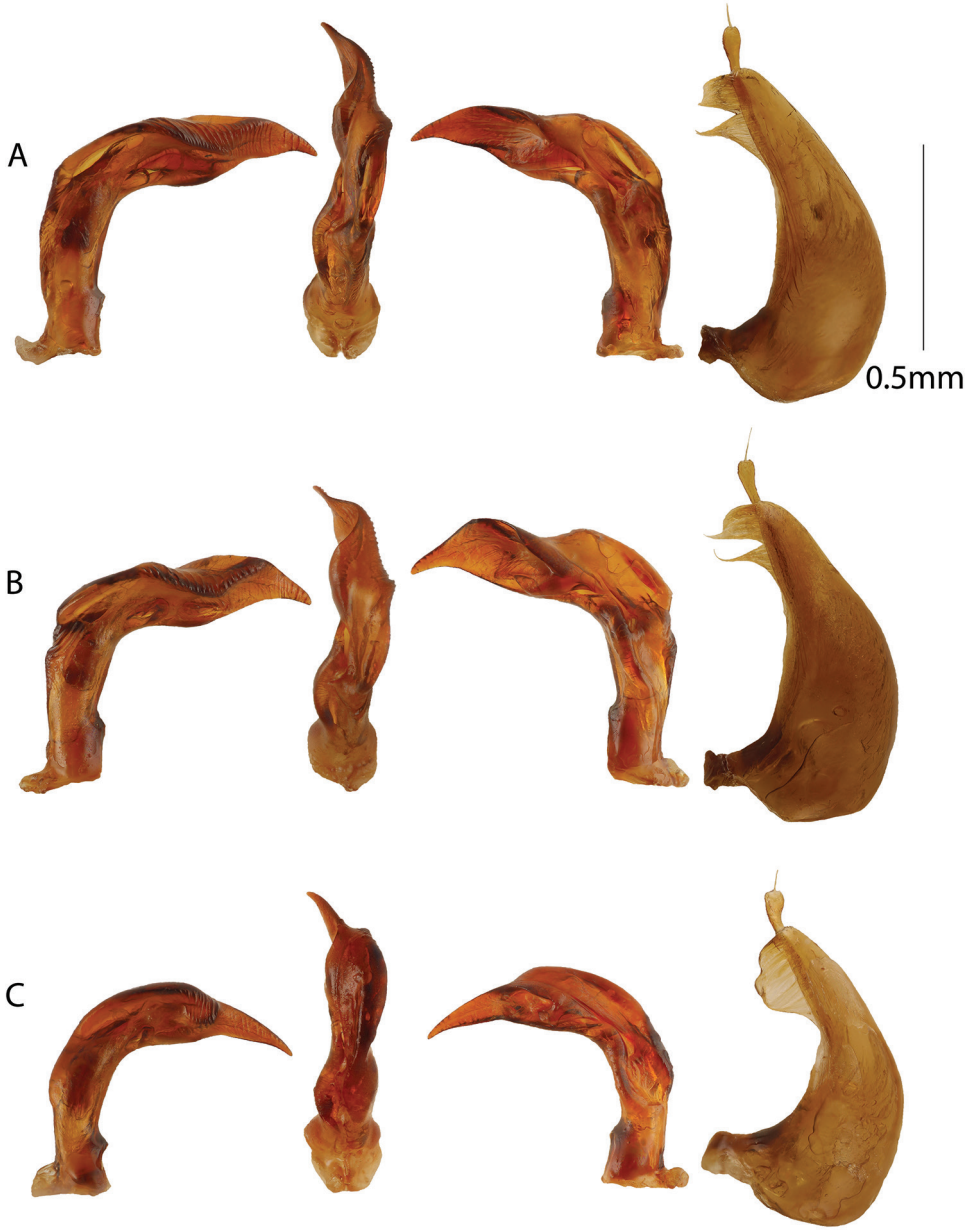

Figure 2. Male genitalia. From left to right aedeagus in right lateral, ventral, left lateral views, and left paramere. **A** *Copelatus amphibius* sp. nov. **B** *Copelatus zanatanensis* sp. nov. **C** *Copelatus betampona* sp. nov.

Distribution. The northeastern humid forest from Marojejy NP to Masoala NP including the island of Nosy Mangabe (Fig. 4A).

Ecology and conservation. *C. amphibius* sp. nov. was found in primary humid forests in dry shallow forest floor depression with dead leaves and soil at Masoala and in

a rainwater-filled pool on Nosy Mangabe (Fig. 8). Both localities were at low altitudes but we also collected the species from Marojejy NP, in residual pools of a small stream at mid-altitude (860 m). Marojejy NP is unique in having continuous humid forest stretching from lowaltitude to the alpine zone and hence it is not surprising that the species can reach into the lower mid-altitude zone here. Both Marojejy and Masoala are since 2007 part of the UNESCO World Heritage Site Rainforests of the Atsinanana. Unfortunately, since 2010 Atsinanana is also on the list of World Heritage in Danger following a surge in illegal logging and hunting threatening its outstanding biodiversity values.

Etymology. The Latin adjective amphibius comes from the ancient Greek word "amphibios" and means capable of living both in water and on land.

***Copelatus zanatanensis* sp. nov.**
http://zoobank.org/4170CE38-15A3-4432-82EA-DF62700D935A
Figs 1B, 2B

Type locality. Masoala National Park [15.6703S; 49.9715E] (Madagascar, Analanjirofo region, Maroantsetra)

Type material. ***Holotype*** ♂ GP (NHRS): NHRS-JLKB | 000011229 // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-45: small muddy depression | on path ~2 km NE. of Andranobe camp | 15.6703S, 49.9715E, 360 m, 16.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Holotype | *Copelatus zanatanensis* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -4♂ GP, 3♀, 17 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000065653, 66019, 66333–7, 11239(Alc.) // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-43: dried out rainwater pool | on path ~3.5 km E. of Andranobe camp| 15.6681S, 49.9835E, 630 m, 16.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus zanatanensis* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-5♂ GP, 5♀, 13 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000011237, 65654, 66017, 66326–32, 11238 (Alc.) // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-44: pristine foreststream | 3 h walk (4 km) E of Andranobe camp | 15.6735S, 49.9886E, 500 m, 16.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus zanatanensis* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-4♂ GP, 6♀, 6 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB |000065655, 65787, 66018, 66302–6, 65437–8, 11228 (Alc.) // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-45: small muddy depression | on path ~2 km NE. of Andranobe camp | 15.6703S, 49.9715E, 360 m, 16.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus zanatanensis* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-6♂ GP, 4♀, 97 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000011235, 65656, 66325, 66362–8, 11236 (Alc.) // Madagascar: Toamasi-

na: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-49: small muddy depression | on path ~2 km NE. of Andranobe camp | 15.6703S, 49.9715E, 360 m, 18.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus zanatanensis* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. Habitus very similar to *C. amphibius* sp. nov. but penis diagnostic with a more distincly offset and higher ventral hump in lateral view and apical blade with a stright to almost concave ventral margin and spine-like acuminate apex (Fig. 2B).

Description. Very similar in all respects to *C. amphibius* sp. nov. and only differences noted below.

Body length: 4.4–5 mm (♀: 4.4–4.8 mm, ♂: 4.7–5 mm).

On average slightly smaller and elytra less infuscated and therefore appearing more unicolorous lighter testaceous, but variation overlap between the species both in infuscation and body size (Fig. 1B).

Ventral side slightly lighter testaceous and therefore infuscation on metacoxal plate more contrasting.

Male genitalia as in Figure 2B. Penis diagnostic in lateral view with a straight to concave ventral margin of apical blade and an acuminate spine-like apex. *Copelatus amphibius* sp. nov. has a weakly convex ventral margin of the apical blade and apex pointed but not spine-like acuminate. Also, the ventral medial hump higher and more distinctly offset in *C. zanatanensis* sp. nov.

Distribution. Only known from Masoala National Park, northeastern Madagascar (Fig. 4B).

Ecology and conservation. *Copelatus zanatanensis* sp. nov. was found in forest floor depressions with leaf litter in pristine humid lowland (360–630 m alt.) forests in Masoala NP (Figs 6, 7). Most specimens were found in dry depressions at two different localities; however, the third place was in proximity of a stream, but still in a terrestrial microhabitat. Masoala National Park covers 230 000 ha of originally primary lowland humid forest, but deforestation rates surged following the political instability of 2009 (Allnutt et al. 2013).

Etymology. Latinisation of the Malagasy word "zana-tany" litterally translated to "child of the land", with the meaning to be native of a country. The new species is endemic and a native of Madagascar.

Copelatus betampona **sp. nov.**

http://zoobank.org/35880EF1-1719-48F5-B8D2-D71BBC4B4D17
Figs 1C, 2C

Type locality. Betampona Réserve Naturelle Intégrale (RNI) [17.9160S, 49.1999E] (Madagascar, Atsinanana region, Toamasina II)

Type material. ***Holotype*** ♂ GP (NHRS): // NHRS-JLKB | 000065440 // Madagascar: Toamasina: Atsinanana | Betampona RNI: lowalt rainforest | Path PPR, ca 100 m in from path PP | Dried out forest floor depression | MAD18-66: 24.II.2018 |

17.9160S, 49.1999E, 520 m | Leg. J. Bergsten & T. Ranarilalatiana // Holotype | *Copelatus betampona* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -6♂ GP, 8♀, 28 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000011227, 65659, 65786, 66015, 66338–46, 65439, 11226 (Alc.) // Madagascar: Toamasina: Atsinanana | Betampona RNI: lowalt rainforest | Path PPR, ca 100 m in from path PP | Dried out forest floor depression | MAD18-66: 24.II.2018 | 17.9160S, 49.1999E, 520 m | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Copelatus betampona* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-3♂ GP, 24 ex. (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000010812, 11222, 65657, 11223 (Alc.) // Madagascar: Toamasina II: Betampona | RNI: MAD17-01: Vohimarangitra: | S-17.91604; E49.19986; 525 m: Dried | up forestpools in preaseape track: | 01/03/2017; Leg. T. Ranarilalatiana // Paratype | *Copelatus betampona* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-3♂ GP, 3♀ (NHRS): // NHRS-JLKB | 000011224–5, 65658, 66294–6 // Madagascar: Toamasina II: Betampona | RNI: MAD17-04: NW of park entrance: | S-17.93059; E49.20261; 321 m: Dried | up pools in Patsitsatra stream: | 03/03/2017; Leg. T. Ranarilalatiana // Paratype | *Copelatus betampona* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. A slightly smaller species than preceding two and in fact the smallest of all known species of the *Copelatus erichsonii* group from Madagascar. Penis diagnostic in lateral view, lacking a sinuation between the ventral hump and the apical blade and with a long extended and narrow apical blade (Fig. 2C). *Copelatus gabonicus* Bilardo & Pederzani, 1978 and *Copelatus evanidus* Bilardo & Rocchi, 1995 (see figures in Bilardo and Rocchi 2015), both described from Gabon, have superficially similar type of genitalia, but differs in habitus and coloration as well as several genitalic details; the hump in lateral view is higher and more robust in *C. evadinus* and *C. gabonicus* have subapical transverse sulcation also in left lateral view.

Description. Body length: 4.2–4.8 mm (♀: 4.2–4.6 mm, ♂: 4.6–4.8 mm).

Very similar in all respects to the two preceding species and only differences noted below.

Slightly smaller than both preceding species and somewhat less elongate (Fig. 1C).

The lightest testaceous species of all three. Elytra with very faint to no infuscation medially and infuscation between eyes on head essentially lacking (faint traces present).

Possibly more extensive striolation on pronotum, but individual variation likely to overlap between the species.

Metacoxal lines projecting anteriorly longer than in preceding two species but does not reach metaventral suture.

Male genitalia as in Figure 2C. Penis in lateral view diagnostic compared to preceding two species, with a ventral hump extending longer towards apex and without a sinuation between end of hump and beginning of apical blade. Apical blade lanceolate in shape with an evenly curved ventral margin. The large anterior portions of the asymetrically right-leaning hump also diagnostic in ventral view.

Distribution. Only known from Betampona RNI, eastern lowland Madagascar (Fig. 4A).

Ecology and conservation. *Copelatus betampona* sp. nov. was found in lowland humid forests (300–550 m alt.) in dry shallow depressions of the forest floor with dead leaves and soil (Fig. 5). Betampona RNI is managed through collaboration between Madagascar National Parks (MNP) and Madagascar Fauna and Flora Group (MFG). Betampona is one of the better-preserved low altitude parcels of rainforest on the eastern coast of Madagascar (Gehring et al. 2010; Rosa et al. 2012). It covers 2228 ha today, was until the late 1950s continuous with nearby forests but has since diminished and it is currently estimated that only around 50% of the area remains as primary forest (Britt 2002). Incursion by slash-and-burn agriculture likely represents the greatest threat to the biodiversity in the reserve. The fact that neither the *Madaglymbus* nor the *Copelatus* species found here were conspecific with those of lowland humid forests further north in Masoala indicates that Betampona, despite its small size, has a high conservation value for endemic eastern lowland fauna.

Etymology. Named after the type locality and protected area where it was found, Betampona Réserve Naturelle Intégrale. The epithet is a noun in apposition.

Madaglymbus Shaverdo & Balke, 2008

Remark. *Madaglymbus* was erected for the Madagascar species of *Aglymbus* Sharp, 1880 by Shaverdo et al. (2008). After Ranarilalatiana et al. (in press) transferred two *Copelatus* species to *Madaglymbus*, and including the three species described below, fifteen species and one subspecies are currently known from Madagascar and Comoros (see checklist below and Nilsson and Hájek 2019). We are constantly finding new species of this genus when collecting across Madagascar and it is premature to present a preliminary checklist including what is known but yet to be described. Revisionary work has been initiated with collegues and type material of all described species consulted directly or indirectly. The three species described below may not form a monophyletic group within the genus. They are described here in advance of a more complete revision of *Madaglymbus* as enigmatic representatives with the terrestrial habitats where they were collected in common.

Checklist

M. alutaceus (Régimbart, 1900) (Madagascar)
M. apicalis (Fairmaire, 1898) (Madagascar)
M. elongatus (H.J. Kolbe, 1883) (Madagascar)
M. fairmairei (Zimmermann, 1919) (Madagascar)
M. formosulus (Guignot, 1956) (Madagascar)
M. johannis (Wewalka, 1982) (Madagascar)
M. kelimaso Ranarilalatiana & Bergsten, 2019 sp. nov. (Madagascar)
M. mathaei (Wewalka, 1982) (Madagascar)

M. menalamba Ranarilalatiana & Bergsten, 2019 sp. nov. (Madagascar)
M. milloti (Guignot, 1959) (Comoros)
M. ruthwildae Shaverdo & Balke, 2008 (Madagascar)
M. semifactus Ranarilalatiana & Bergsten, 2019 sp. nov. (Madagascar)
M. strigulifer (Régimbart, 1903) (Madagascar)
M. strigulifer ssp. *laevis* (Guignot, 1955) (Madagascar)
M. unguicularis (Régimbart, 1903) (Madagascar)
M. xanthogrammus (Régimbart, 1900) (Madagascar)

***Madaglymbus semifactus* sp. nov.**
http://zoobank.org/0AF0971B-F955-4590-87A8-24BDCD7F3088
Figs 1D, 3A

Type locality. Betampona Réserve Naturelle Intégrale (RNI) [17.9160S, 49.1999E] (Madagascar, Atsinanana region, Toamasina II)

Type material. ***Holotype*** ♂ GP (NHRS): // NHRS-JLKB | 000065445 // Madagascar: Toamasina II: Betampona | RNI: MAD17-01: Vohimarangitra: | S-17.91604; E49.19986; 525 m: Dried | up forestpools in preaseape track: | 01/03/2017; Leg. T. Ranarilalatiana // Holotype | *Madaglymbus semifactus* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -4♂ GP, 7♀ (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000066233, 66235–41, 66297–9 // Madagascar: Toamasina: Atsinanana | Betampona RNI: lowalt rainforest | Path PPR, ca 100 m in from path PP | Dried out forest floor depression | MAD18-66: 24.II.2018 | 17.9160S, 49.1999E, 520 m | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus semifactus* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-2♀, 1♂ GP, 4♀ (Alc.) (NHRS): // NHRS-JLKB | 000065446–7, 65456, 65448 (Alc.) // Madagascar: Toamasina II: Betampona | RNI: MAD17-01: Vohimarangitra: | S-17.91604; E49.19986; 525 m: Dried | up forestpools in preaseape track: | 01/03/2017; Leg. T. Ranarilalatiana // Paratype | *Madaglymbus semifactus* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-2♀, 4♀ (Alc.) (NHRS): // NHRS-JLKB | 000065442–3, 65444 (Alc.) // Madagascar: Toamasina II: Betampona | RNI: MAD17-04: NW of park entrance: | S-17.93059; E49.20261; 321 m: Dried | up pools in Patsitsatra stream: | 03/03/2017; Leg. T. Ranarilalatiana // Paratype | *Madaglymbus semifactus* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂ GP (NHRS): // NHRS-JLKB | 000065441 // Madagascar: Toamasina II: Analalava | reserve: MAD17-09: N of nursery | plants: S-17.70532; E49.45702; 75 m: | forest pools: 08/03/2017; Leg. T. | Ranarilalatiana // Paratype | *Madaglymbus semifactus* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. A small *Madaglymbus* species, more oval than the two following species, with continuous outline between pronotum and elytra. Similar to *M. johannis*

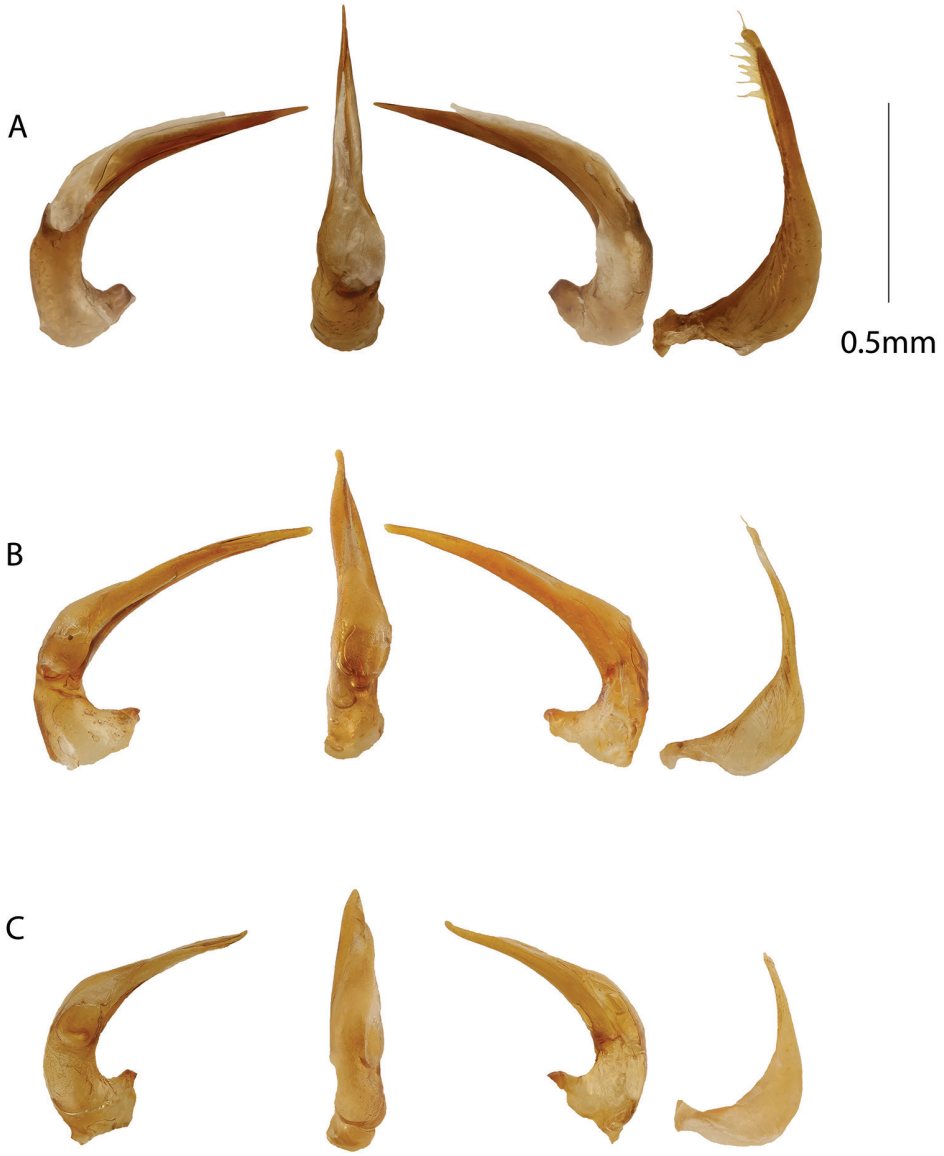

Figure 3. Male genitalia. From left to right aedeagus in right lateral, ventral, left lateral views, and left paramere. **A** *Madaglymbus semifactus* sp. nov. **B** *Madaglymbus kelimaso* sp. nov. **C** *Madaglymbus menalamba* sp. nov.

(Wewalka, 1982) but less elongate and easily distinguishable by the punctured elytra, punctures that are much finer than in *M. menalamba* sp. nov. Penis in ventral view short and straight (Fig. 3A), not right-angled towards apex as in *M. johannis*.

Description. Body length: 3.7–4.2 mm (♀: 3.7–4.2 mm, ♂: 3.9–4.1 mm).

Body shape broadly oval with a continuous outline laterally between pronotum and elytra (Fig. 1D).

Head and pronotum rufous, infuscated inside eyes and vaguely medially on pronotum. Elytra infuscated medially but with testaceous sections basally, laterally and apically. Appendages testaceous except metatarsus rufotestaceous.

Elytra and pronotum covered with fine punctures, much finer than in *M. menalamba* sp. nov, but a distinguishing feature compared with the smooth elytra of *M. johannis*. Punctures on pronotum concentrated laterally with only micropunctures medially. Lateral marginal bead on pronotum thin and present only in posterior half. Head, pronotum and elytra with same type of microreticulation and micropunctures.

Ventral side rufotestaceous, metacoxal plate and abdominal sternites II–IV with few fine strioles laterally. Metacoxal lines absent. Anterior metaventral process broad.

Male pro and mesotarsal segments I–III dilated and ventrally equipped with adhesive discs (constellation I:3, 4, II:4, III:4). Anterodistal angle of protarsal segment IV with a modified stout seta.

Penis bilobed with ventral lobe extending to near, but stops before, apex of dorsal lobe. Penis straight, short and pointed with a thin apex in ventral view, straight and evenly tapering towards apex in lateral view (Fig. 3A). Compared with the longer and thinner penis of *M. johannis*, *M. semifactus* sp. nov. has a shorter and straighter penis, neither right-turned at apex in ventral view nor downturned in lateral view. Parameres with a rather long but broad apical extension (Fig. 3A).

Female similar to male.

Distribution. Known from Betampona RNI and at Analalava reserve, eastern lowland Madagascar (Fig. 4B).

Ecology and conservation. The species was found in Betampona RNI and collected under the same circumstances as *C. betampona* sp. nov. (Fig. 5). One specimen was collected from Analalava reserve in forest pools after a cyclone with heavy rain.

Etymology. "Semifactus" means half-done or half-finished here referring to that this species is possibly less modified to spending time on land compared to next two *Madaglymbus* species.

***Madaglymbus kelimaso* sp. nov.**
http://zoobank.org/9AE65691-3F6E-42F8-8BD3-91FDA4EB9953
Figs 1E, 3B

Type locality. Analalava Reserve [17.70532S, 49.45702E] (Madagascar, Atsinanana region, Toamasina II)

Type material. ***Holotype*** ♂ GP (NHRS): // NHRS-JLKB | 000065449 // Madagascar: Toamasina II: Analalava | reserve: MAD17-06: Taniravo track: | S-17.70548; E49.45934; 52 m: forest | pools: 06/03/2017; Leg. T. | Ranarilalatiana // Holotype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -2♀, 2♀ (Alc.) (NHRS): // NHRS-JLKB | 0000654450–1, 65452 (Alc.) // Madagascar: Toamasina II: Analalava | reserve: MAD17-06: Taniravo track: |

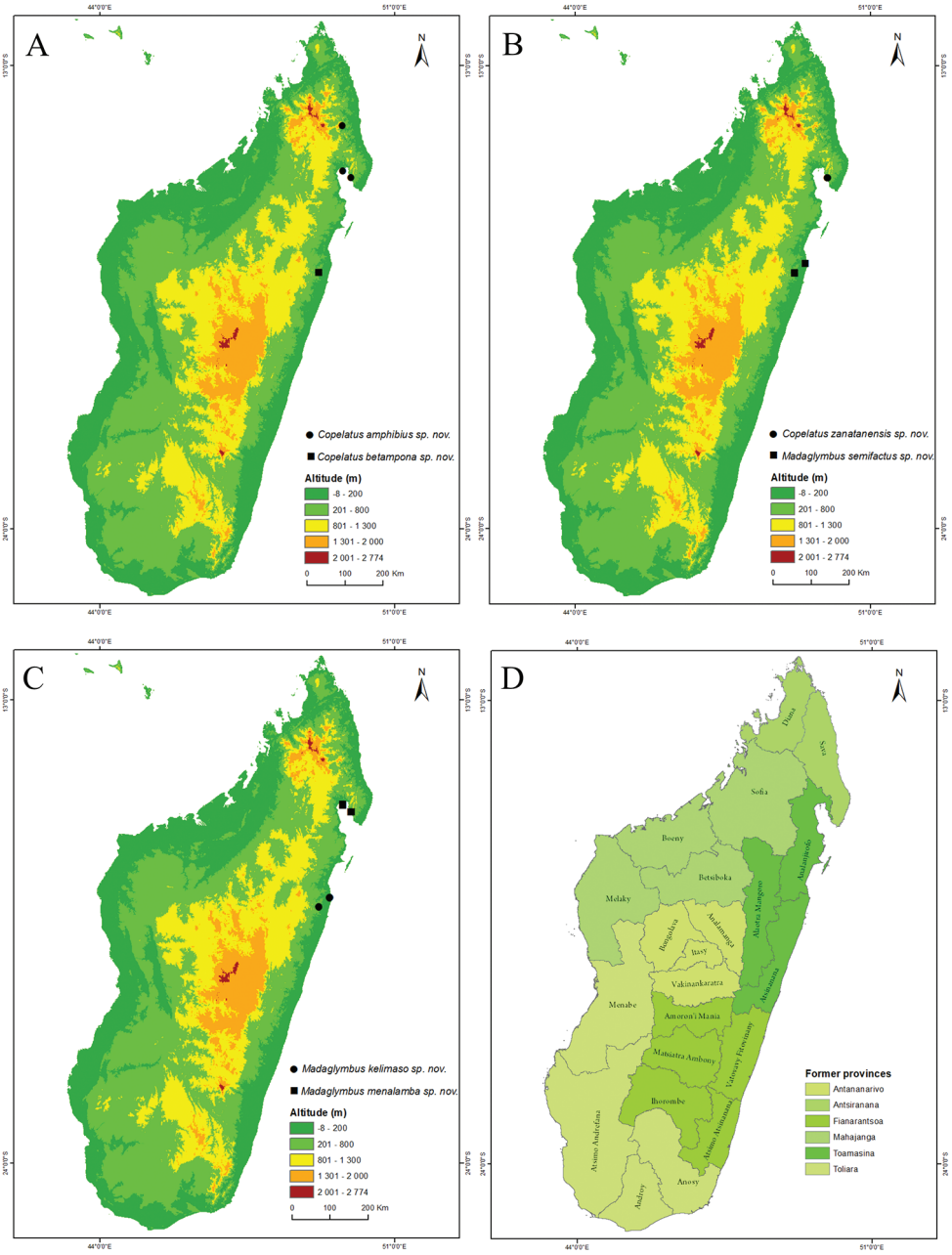

Figure 4. Maps of Madagascar with species distributions and administrative divisions. **A** *Copelatus amphibius* sp. nov. (circle), *Copelatus betampona* sp. nov. (square) **B** *Copelatus zanatanensis* sp. nov. (circle), *Madaglymbus semifactus* sp. nov. (square) **C** *Madaglymbus kelimaso* sp. nov. (circle), *Madaglymbus menalamba* sp. nov. (square) **D** current 22 regions and six former provinces of Madagascar.

Figure 5. Habitat photo of locality MAD18-66, Betampona RNI. The three new species *Madaglymbus kelimaso* sp. nov., *Madaglymbus semifactus* sp. nov., and *Copelatus betampona* sp. nov. were found in this terrestrial habitat.

Figure 6. Habitat photo of locality MAD18-43, Masoala NP where *Copelatus zanatanensis* sp. nov. was found.

Figure 7. Habitat photos of locality MAD18-45, Masoala NP. The two new species *Copelatus zanatanensis* sp. nov. and *Madaglymbus menalamba* sp. nov. were found in this habitat.

S-17.70548; E49.45934; 52 m: forest | pools: 06/03/2017; Leg. T. | Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-3♀, 4♀ (Alc.) (NHRS): // NHRS-JLKB | 000065460–2, 65463 (Alc.) // Madagascar: Toamasina II: Analalava | reserve: MAD17-08: Lemur track: | S-17.70553; E49.45506; 64 m: forest | pools : 07/03/2017; Leg. T. | Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂ GP, 4♀, 1♂ (Alc.), 8♀ (Alc.), (NHRS): // NHRS-JLKB | 000065464–8, 65469 (Alc.) // Madagascar: Toamasina II: Analalava | reserve: MAD17-09: N of nursery | plants: S-17.70532; E49.45702; 75 m: | forest pools: 08/03/2017; Leg. T. | Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♀, 1♀ (Alc.) (NHRS): // NHRS-JLKB | 000065454, 65455 (Alc.) // Madagascar: Toamasina II: Analalava | reserve: MAD17-10: N of nursery | plants: S-17.70812; E49.45171; 84 m: | forest pools beside Lemur track: | 08/03/2017; Leg. T. Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂ GP, 1♀, 1♀ (Alc.) (NHRS): // NHRS-JLKB | 000065457–8, 65459 (Alc.) // Madagascar: Toamasina II: Betampona | RNI: MAD17-01: Vohimarangitra: | S-17.91604; E49.19986; 525 m: Dried | up forestpools in preaseape track: | 01/03/2017; Leg. T. Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂ (Alc.) (NHRS): // NHRS-JLKB | 000065453 // Madagascar: Toamasina II: Betampona | RNI: MAD17-04: NW of park entrance: | S-17.93059; E49.20261; 321 m: Dried | up pools in Patsitsatra stream: | 03/03/2017; Leg. T. Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1 ♂ GP (NHRS): // NHRS-JLKB | 000065789 // Madagascar: Toamasina: Atsinanana | Betampona RNI: lowalt rainforest | Path PPR, ca 100 m in from path PP | Dried out forest floor depression | MAD18-66: 24.II.2018 | 17.9160S, 49.1999E, 520 m | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus kelimaso* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. A small, elongate but rather robust *Madaglymbus* species with reddish coloration on head and pronotum and subrugose elytra with basal and apical testaceous spots (Fig. 1E). Penis evenly narrowing from base to apex in lateral view, non upturned at apex. Penis with bisinuate left side in ventral view and an apical knob is present in both ventral and lateral views (Fig. 3B). Parameres with a long and thin apical extension (Fig. 3B).

Description. Body length: 3.9–4.8 mm (♀: 3.9–4.5 mm, ♂: 4.2–4.8 mm).

Body shape elongate, subparallell and rather convex. Lateral outline non-continuous between pronotum and elytra. Head broad with small eyes creating a wide interocular distance (Fig. 1E).

Pronotum and head rufotestaceous, infuscated inside eyes and slightly medially on pronotum. Elytra infuscated but with basal and apical testaceous spots. All appendages testaceous.

Elytra with longitudinal subugosity formed by shorter and longer strioles, sometimes connected to form longer continuous lines. Pronotum densely covered with large punctures and with a narrow lateral bead not reaching anterior corners. Head covered with finer punctation. Head, pronotum and elytra with same type of microreticulation and micropunctures.

Ventral side entirely testaceous, metacoxal lines absent but suggested ridge present in their place, metacoxal plate and abdominal sternites II–IV with fine strioles. Anterior metaventral process narrow.

Male pro and mesotarsal segments I–III broadly dilated and ventrally equipped with adhesive discs (constellation I:5 (row 1), 4 (row 2), II:4, III:4). Anterodistal angle of protarsal segment IV with a modified stout seta.

Bilobed penis with an apical knob visible in both lateral and ventral views, ventral lobe ending on right side well before apical knob of dorsal lobe. In lateral view apex not upturned (Fig. 3B). In ventral view left side bisinuate (Fig. 3B). Parameres with a long and thin apical extension (Fig. 3B).

Female with similar dorsal subrugosity as in male.

Distribution. Known from Analalava reserve and Betampona RNI, eastern lowland Madagascar (Fig. 4C).

Ecology and conservation. *Madaglymbus kelimaso* sp. nov. was found in lowland humid forests (50–550 m alt.). Most of the type specimens were found in Analalava reserve in forest pools with dead leaves, stagnant pools filled with water immediately after a cyclone with heavy rain (Fig. 11).

Analalava reserve is managed through collaboration between a local people NGO (Velonala) and Missouri Botanical Garden (MBG) since 2004. In 2015, it was designated as a new protected area. It covers 225 ha of typical littoral humid forest and represents one of few remaining forest fragment on the lowland central east coast of Madagascar. One specimen was collected in the same terrestrial habitat as *C. betampona* sp. nov. (Fig. 5).

Etymology. The Malagasy word "kelimaso" means small eyes (keli = small, maso = eye), a characteristic of this species and seemingly an adaptation to spending significant amount of time out of water in the ground litter layer (three of five terrestrial dytiscid species are eyeless).

Madaglymbus menalamba **sp. nov.**

http://zoobank.org/9D7D7816-63C3-476D-B272-9D326FFF95B5
Figs 1F, 3C, 12, Suppl. material 1: Movie 1

Type locality. Nosy Mangabe Special Reserve, part of Masoala National Park [15.4845S, 49.7627E] (Madagascar, Analanjirofo region, Maroantsetra)

Type material. ***Holotype*** ♂ GP (NHRS): // NHRS-JLKB | 000066360 // Mada gascar:Toamasina:Analanjirofo: | Nosy Mangabe, Masoala NP: MAD18-63 | flat dry pansections of path btw camp | and Plage Hollandaise, lowalt. rainforest | 15.4845S,

49.7627E, 50 m, 20.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Holotype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

***Paratypes*:** -4♂ GP, 2♀ (NHRS): // NHRS-JLKB | 000066010, 66307–11 // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-45: small muddy depression | on path ~2 km NE. of Andranobe camp | 15.6703S, 49.9715E, 360 m, 16.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-4♂ GP, 10♀ (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000065792, 65794, 66009, 66314–24 // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-49: small muddy depression | on path ~2 km NE. of Andranobe camp | 15.6703S, 49.9715E, 360 m, 18.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂, 2♀ (NHRS): // NHRS-JLKB | 000066011–3 // Madagascar: Toamasina: Analanjirofo: | Masoala NP: lowalt. rainforest | MAD18-51: depression on forest floor on | path ~1.2 km NE of Andranobe camp, | 15.6735S, 49.9647E, 230 m, 18.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-3♂ GP, 2♀ (NHRS): // NHRS-JLKB | 000010814, 65791, 65793, 66012, 66293 // Madagascar: Toamasina: Analanjirofo: | Nosy Mangabe, Masoala NP: MAD18-57 | flat dry pansections of path after | lighthouse, lowalt. rainforest | 15.5078S, 49.7637E, 210 m, 19.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-1♂, 1♀ (NHRS): // NHRS-JLKB | 000066013, 66292 //Madagascar: Toamasina: Analanjirofo: | Nosy Mangabe, Masoala NP: MAD18-58 | rainfallpool with dead leaves nr path | after lighthouse, lowalt. rainforest | 15.5079S, 49.7641E, 195 m, 19.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

-3♂, 2♀, 14 ex. (6♂, 8♀) (Alc.) (NHRS, DEUA & PBZT/MBC): // NHRS-JLKB | 000066356–9, 66361, 66014(Alc.) // Madagascar: Toamasina: Analanjirofo: | Nosy Mangabe, Masoala NP: MAD18-63 | flat dry pansections of path btw camp | and Plage Hollandaise, lowalt. rainforest | 15.4845S, 49.7627E, 50 m, 20.II.2018 | Leg. J. Bergsten & T. Ranarilalatiana // Paratype | *Madaglymbus menalamba* sp. nov. | Det. Ranarilalatiana | & Bergsten, 2019 //

Diagnosis. A small and robust reddish *Madaglymbus* species similar to *M. kelimaso,* but less elongate and elytra concolorous with pronotum and covered with large punctures instead of subrugosity (Fig. 1F). Penis short and robust in ventral view with upturned apex in lateral view (Fig. 3C).

Description. Body length: 3.7–4.5 mm (♀: 3.7–4.3 mm, ♂: 3.8–4.5 mm).

Body shape subparallell, robust and rather convex anteriorly. A broader body shape compared with *M. kelimaso* sp. nov. Lateral outline non-continuous between pronotum and elytra. Head broad with small eyes creating a wide interocular distance (Fig. 1F).

Figure 8. Habitat photo of locality MAD18-58, Nosy Mangabe, where the new species *Copelatus amphibius* sp. nov. and *Madaglymbus menalamba* sp. nov. were found. Of five different localities recorded for *M. menalamba* sp. nov. this was the only one where the species was found in water.

Figure 9. Habitat photo of locality MAD18-63, Nosy Mangabe, one of several similar localities where *Madaglymbus menalamba* sp. nov. was found.

Figure 10. Habitat photo of locality MAD18-57, Nosy Mangabe, near where *Madaglymbus menalamba* sp. nov. was photographed and video-recorded.

Figure 11. Habitat photo of locality MAD17-08, Analalava reserve, where the new species *Madaglymbus kelimaso* sp. nov. was found. These depressions were water-filled at time of visit 2017, immediately following a cyclone with heavy rain.

Body with a rather uniform reddish coloration, only head partly infuscated between eyes. All appendages testaceous except metatarsus rufotestaceous.

Elytra and pronotum densely covered with large punctures, puncturation reduced posteriorly and towards lateral margins of elytra. Pronotum with a narrow lateral bead not reaching anterior corners. Head covered with finer punctation. Head, pronotum and elytra with same type of microreticulation and micropunctures.

Ventral side entirely testaceous, metacoxal lines absent, suggestion of ridge in their place less distinct compared with *M. kelimaso* sp. nov., metacoxal plate and abdominal sternites II–IV with fine strioles. Anterior metaventral process broader than in *M. kelimaso* sp. nov.

Male pro and mesotarsal segments I–III dilated and ventrally equipped with adhesive discs (constellation I:3, 4, II:4, III:4). Segments less dilated than in *M. kelimaso* and first row with fewer discs. Anterodistal angle of protarsal segment IV with a modified stout seta.

Bilobed penis short and robust with rather blunt apex in ventral view. Ventral lobe twisted around right side of dorsal lobe to a position dorsal of it at apex (Fig. 3C). Apex in lateral view upturned. Parameres with apical extension not as long and thin as in *M. kelimaso* sp. nov. (Fig. 3C).

Female with similar dorsal puncturation as in male.

Figure 12. *Madaglymbus menalamba* sp. nov. photographed in the field on Nosy Mangabe (MAD18-57). Note the very distinctly reddish colour, not known from any previously described *Madaglymbus* species. See also Suppl. material 1: Movie 1 for recordings of the terrestrial locomotion (running) and behaviour of the species.

Distribution. Masoala NP including the island of Nosy Mangabe (Fig. 4C).

Ecology and conservation. The species was found in humid forests at low-altitude between (50–360 m) in dry shallow forest floor depression with dead leaves and soil. In one out of five localities it was collected from a rainwater-filled pit full of dead leaves, the other four places from dry forest floor depressions (Figs 7–10). Although less pristine and with clear signs of former human settlements, an equal number of specimens were found on Nosy Mangabe Island as compared with Masoala NP proper near Andranobe.

Etymology. Menalamba in Malagasy means red clothes and the word is associated with the revolt and anti-colonianism movement in Madagascar's history of independence. Here it refers to the characteristic reddish coloration of the species (Fig. 12, Suppl. material 1: Movie 1).

Notes. At one locality on Nosy Mangabe (MAD18-57) we videorecorded the terrestrial locomotion and behaviour of this species in the field (Suppl. material 1: Movie 1). It was clearly apt at running and its immediate behaviour following exposure from, e.g. lifting up a dead leaf under which it was hiding, was to run and seek shelter again. This was repeated many times making it difficult to get photos of the species. The *Copelatus* species had a greater tendency to jump when exposed among the litter, but *M. menalamba* sp. nov. stayed put initially and then moved by running.

Discussion

Copelatinae constitutes the second largest subfamily of diving beetles, with 759 species distributed in eight genera (Nilsson and Hájek 2019). The subfamily is represented by two genera on Madagascar, *Copelatus* Erichson, 1832 and *Madaglymbus* Shaverdo & Balke, 2008, and they are both diverse and widespread all over the island. The Malagasy Copelatinae was considered restricted to aquatic habitats and have likely never before been actively searched for in dry forest floor depressions. The discovery of a specialised fauna of *Copelatus* and *Madaglymbus* in this habitat was surprising. Although the inhabiting species should not be labelled terrestrial or even semi-terrestrial they have clearly adapted to withstanding periods of living, perhaps with reduced activity, terrestrial life in between heavy rains. Natatorial setae on legs are present and equivalent of those present in congeners collected aquatically why these species cannot be compared with the few terrestrial Hydroporinae taxa known with absent or much reduced natatorial setae on legs (Watts 1982; Brancucci 1979, 1985; Balke and Hendrich 1996). Rather they seem to have been able to occupy the for diving beetles unusual niche of the forest floor in a climatic zone with high rainfall regime. We hypothesise that this behavioural adaptation is restricted to humid forests with high annual precipitation. Andranobe in Masoala NP where *Copelatus amphibius* sp. nov., *C. zanatanensis* sp. nov., and *Madaglymbus menalamba* sp. nov. were found have the highest average (1993–1996) annual precipitation on Madagascar with 5900 mm, at least up to what had been measured up to 1996 (Jury 2003). A station in Sambava district measured an annual average of 3470 mm (2017–2018), which is probably an underestimate for Marojejy NP, although pre-

cipitation may vary with altitude and between slopes facing different directions (Goodman 2000). For Betampona and Analalava the closest station in Toamasina registered a yearly average of 2960 mm (2017–2018). In general, the northeast of Madagascar where all six species were found has the highest precipitation on the island. During the rainy season in the austral summer the northern third of Madagascar receives the greates rainfall, averaging 12 mm/day, which is in the upper 1% of rain intensity in the world (Jury 2003). In the dry season during austral winter, most of the island is dry, except the east coast where orographic uplifts of trade winds ensures year-around precipitation (Jury 2003). The northeast coast of the country therefore optimises both summer and winter precipitation levels. It is likely not a coincidence that this unusual specialist diving beetle fauna were discovered in this region of Madagascar. They are also very likely endemic to this region, or at the very least to humid forests on Madagascar. We collected the species during the rainy season 2017 and 2018. Future fieldwork during the dry-season in these regions would be very interesting to see if they still occupy the same certain-to-be-dry depressions also in this period or if they move to aquatic habitats. Larval development is most likely to take place during the rainy season, but it would also be interesting to know if it takes place in the same forest floor depressions or if more stable aquatic habitats are needed. The larval habitat of the few known truly terrestrial Hydroporinae species is thus far curiously unknown (Balke and Hendrich 2016). This conundrum aside, it is possible that inhabiting similar very ephemeral forest floor depressions was a stepping-stone, or transition step, towards becoming truly terrestrial.

The knowledge of Malagasy Copelatinae is still poor in general. Rocchi (1991) listed twenty-two species of *Copelatus* from Madagascar with twelve species from the *Copelatus erichsonii* group (Nilsson and Hájek 2019). Ranarilalatiana et al (in press) revised the non-*erichsonii* species groups and recognised thirteen species, out of which five were described as new. *Copelatus amphibius* sp. nov., *C. zanatanensis* sp. nov. and *C. betampona* sp. nov. falls in the *erichsonii*-group, based on the number of elytral striae (ten discal and one submarginal). They have in common not only the species group and specialised living but also the small body size, in fact smaller than all twelve previously described Malagasy species from the group. *Madaglymbus* is endemic to Madagascar and the Comoros Islands (Shaverdo et al. 2008; Miller and Bergsten 2016) and is now represented by fifteen described species and one subspecies (see checklist in Results section), although at least two times as many has been collected but are yet to be named and described. *Madaglymbus kelimaso* sp. nov., *M. menalamba* sp. nov. and *M. semifactus* sp. nov. are all three also in the smaller body size category within the genus. While the three *Copelatus* species do not portray any notable morphological attribute that may be an adaptation to terrestrial habits, the *Madaglymbus* species show unusual characteristics for the genus. The densely punctured (*M. menalamba* sp. nov. and *M. semifactus* sp. nov.) to subrugose (*M. kelimaso* sp. nov.) elytral surface is unique in this genus with otherwise typically shiny and smooth or more rarely striolate or aciculate elytra in other representatives. *Madaglymbus menalamba* sp. nov. and *M. kelimaso* sp. nov. additionally have an unusual reddish colour and have a more "caraboid" body shape with a non-continuous outline between pronotum and elytra. Whether any of these unusual characteristics are actual adaptations to terrestrial habits is not known, but the "caraboid"

body shape may represent a higher degree of "terrestrialisation" in the latter two species compared to the other four. In the terrestrial Carabids, with few exceptions pronotum is narrower than elytra at posterior margin and this may enhance movability between pro- and mesothorax, and thereby manoeuvrability in the litter layer. The behaviour of rapid running and hiding when exposed, which was documented for *Madaglymbus menalamba* sp. nov. (Suppl. material 1: Movie 1), was very different to the jumping behaviour seen in the *Copelatus* species. This certainly seems to be a terrestrial adaptation - running requires alternate hind leg movement in contrast to the synchronous hind leg movement when swimming (and jumping). All new species herein described are endemic to Madagascar and could represent the "tip of the iceberg" as this habitat has just started to be explored. Similar forest-flooor specialist communities may also have evolved separately elsewhere in humid forests with high (year-around) precipitation. This is likely not a Madagascar-unique evolutionary trajectory, but to be in the upper one or few % rainfall intensity levels worldwide might be a necessary prerequisite.

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Supplementary material 1

Movie 1 showing terrestrial locomotion of *Madaglymbus menalamba* sp. nov.

Authors: Tolotra Ranarilalatiana, Johannes Bergsten

Data type: video

Explanation note: It was filmed at locality MAD18-57 on Nosy Mangabe Island, part of Masola NP, 18 February 2018.

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RESEARCH ARTICLE

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A new species of the genus *Takydromus* (Squamata, Lacertidae) from southwestern Guangdong, China

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Abstract

A new species, *Takydromus yunkaiensis* J. Wang, Lyu, & Y.Y. Wang, **sp. nov.** is described based on a series of specimens collected from the Yunkaishan Nature Reserve located in the southern Yunkai Mountains, western Guangdong Province, China. The new species is a sister taxon to *T. intermedius* with a genetic divergence of 8.0–8.5% in the mitochondrial cytochrome b gene, and differs from all known congeners by a combination of the following morphological characters: (1) body size moderate, SVL 37.8–56.0 mm in males, 42.6–60.8 mm in females; (2) dorsal ground color brown; ventral surface green to yellow-green, but light blue-green on chin and throat, posteriorly green in adult males; (3) dorsolateral lines paired, strikingly yellowish-white bordered by black above and below, invisible or indistinct in juveniles and adult females; (4) flanks of body blackish brown with light brown marks in adult males; (5) presence of four pairs of chin-shields; (6) four supraoculars on each side; (7) presence of a row of supracilary granules that separate supracilaries from supraoculars; (8) two postnasals; (9) enlarged dorsal scales in six longitudinal rows on trunk of body, with strong keel; (10) enlarged ventral scales in six longitudinal rows, strongly keeled in males, smooth but outermost rows weakly keeled in females; (11) enlarged and keeled lateral scales in a row above ventrals; (12) femoral pores 2–3 on each side; (13) subdigital lamellae 20–23 under the fourth finger, 23–30 under the fourth toe; and (14) the first 2–3 subdigital lamellae under the fourth toe divided. The discovery of *Takydromus yunkaiensis* **sp. nov.** brings the total number of species of this genus to 24, of which nine occur in mainland China.

Keywords

grass lizard, southern China, species diversity, taxonomy, *Takydromus yunkaiensis* sp. nov.

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Introduction

The Asian grass lizard genus *Takydromus* Daudin, 1802 currently contains 23 recognized species, widely distributed in the East Asian islands (Ryukyu Archipelago, Taiwan) and recorded from the Russian far east, extending southward across the Chinese mainland, Indochina, northeastern India, Borneo, the Natuna Islands, Sumatra, Bangka, and Java (Wang et al. 2017; Uetz et al. 2019). Eight species are recorded in mainland China: *T. albomaculosus* Wang, Gong, Liu & Wang, 2017, *T. amurensis* Peters, 1881, *T. intermedius* Stejneger, 1924, *T. kuehnei* van Denburgh, 1909, *T. septentrionalis* Günther, 1864, *T. sexlineatus* Daudin, 1802, *T. sylvaticus* Pope, 1928, and *T. wolteri* Fischer, 1885 (Zhao et al. 1999; Cai et al. 2011; Wang et al. 2017). In addition, *T. formosanus* Boulenger, 1894, *T. hsuehshanensis* Lin & Cheng, 1981, *T. luyeanus* Lue & Lin, 2008, *T. sauteri* Van Dengurgh, 1909, *T. stejnegeri* van Denburgh, 1912, and *T. viridipunctatus* Lue & Lin, 2008 are endemic to Taiwan Island; *T. dorsalis* Stejneger, 1904, *T. smaragdinus* Boulenger, 1887, *T. tachydromoides* Schlegel, 1838, and *T. toyamai* Takeda & Ota, 1996 are known only from Japan. Finally, *T. hani* Chou, Nguyen & Pauwels, 2001 and *T. madaensis* Bobrov, 2013 are only recorded from Vietnam while *T. khasiensis* Boulenger, 1917 and *T. sikkimensis* Günther, 1888 are only recorded from India.

Previous studies have revealed the very high biodiversity level of the genus *Takydromus* in southern China, for which the species diversity is just below that of Taiwan Island (Lue and Lin 2008; Wang et al. 2017). During repeated field surveys in the Yunkai Mountains, located in southwestern Guangdong Province (Fig. 1), a number of lacertid specimens were collected that could be assigned to the genus *Takydromus* by a combination of diagnostic characters defined by Arnold et al. (2007) and Zhao et al. (1999): (1) body slender with an extra-long tail, tail length usually more than two times larger than snout-vent length, (2) dorsal scales enlarged and keeled, ventral scales enlarged, keeled or smooth, (3) scales on flanks small and granular, (4) lateral teeth tricuspid, (5) temporal scales usually keeled, (6) 0–5 femoral pores on each side. Close examination of the external morphology and subsequent molecular analyses revealed that these specimens from Yunkaishan Nature Reserve, Guangdong Province, represented a distinct taxon. They are described below as a new species.

Materials and methods

Sampling

Samples sequenced for molecular analyses were obtained from two specimens of the undescribed *Takydromus* species from Yunkaishan Nature Reserve, Guangdong Province; the paratype specimen (SYS r001292) of *T. albomaculosus*; two specimens of *T. amurensis*; four specimens of *T. intermedius* including a topotypic specimen (SYS

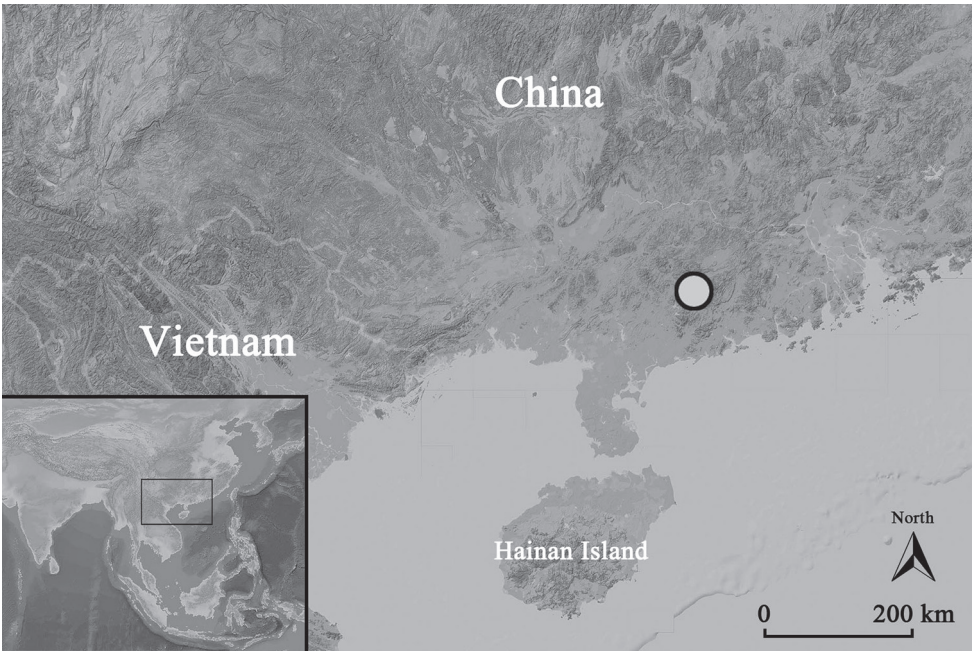

Figure 1. The type locality of *Takydromus yunkaiensis* sp. nov., Yunkaishan Nature Reserve.

r001602) from Mt. Emei, Sichuan; four specimens of *T. kuehnei*; three specimens of *T. septentrionalis*; two specimens of *T. sexlineatus*; one specimen of *T. sylvaticus*; and two specimens of *T. wolteri*, all freshly collected from China. Additional 14 sequences of *T. dorsalis*, *T. formosanus*, *T. hsuehshanensis*, *T. sauteri*, *T. smaragdinus*, *T. stejnegeri*, *T. tachydromoides*, and *T. toyamai* were obtained from GenBank and three sequences of *Eremias persica* Blanford, 1875, *E. strauchi* Kessler, 1878, and *E. velox* (Pallas, 1771) also from GenBank were used as the out-groups. Details of samples sequenced for mitochondrial cytochrome b gene and their associated GenBank accession numbers are listed in Table 1.

All specimens were fixed in 10 % buffered formalin and later transferred to 70% ethanol for preservation, and deposited at the Museum of Biology, Sun Yat-sen University (**SYS**); liver tissue samples were separately preserved in 95% ethanol for molecular studies.

DNA Extraction, PCR and sequencing

DNA was extracted from liver tissue using a standard phenol-chloroform extraction protocol (Sambrook et al. 1989). The fragment of mitochondrial cytochrome b gene was PCR amplified and sequenced using the primers L14919 5'-AACCACCGTT-GTTATTCAACT-3' and H16064 5'-CTTTGGTTTACAAGAACAATGCTTTA-3' (Burbrink et al. 2000). PCR amplifications were performed in a 20 μL reaction volume

Table 1. Localities, voucher information, and GenBank accession numbers (mitochondrial cytochrome b gene) for all specimens/sequences used in this study.

ID	Species	Locality	Voucher	GenBank Number
1	*Takydromus yunkaiensis* sp. nov.	China: Guangdong: Gaozhou: Xianrendong Scenic Area	SYS r001513	MN239954
2	*Takydromus yunkaiensis* sp. nov.	China: Guangdong: Gaozhou: Xianrendong Scenic Area	SYS r001514	MN239955
3	*Takydromus albomaculosus*	China: Guangdong: Ruyuan: Tianjingshan Forestry Station	SYS r001292 (paratype)	MF631870
4	*Takydromus amurensis*	China: Liaoning: Fushun: Nanzamu County: Mt. Langya	SYS r001890	MN239956
5	*Takydromus amurensis*	China: Liaoning: Fushun: Nanzamu County: Mt. Langya	SYS r001891	MN239957
6	*Takydromus dorsalis*	Japan	–	AY248460
7	*Takydromus dorsalis*	Japan	–	AY248461
8	*Takydromus formosanus*	China: Taiwan Island	–	AY248458
9	*Takydromus formosanus*	China: Taiwan Island	–	AY248459
10	*Takydromus hsuehshanensis*	China: Taiwan Island	–	AY248482
11	*Takydromus hsuehshanensis*	China: Taiwan Island	–	AY248483
12	*Takydromus intermedius*	China: Sichuan: Mt. Emei (type locality)	SYS r001602 (topotype)	MN239958
13	*Takydromus intermedius*	China: Guizhou: Libo: Maolan Nature Reserve	SYS r000856	MN239959
14	*Takydromus intermedius*	China: Guangxi: Hechi: Jiuwanshan Nature Reserve	SYS r001553	MN239960
15	*Takydromus intermedius*	China: Guangxi: Hechi: Cenwanglaoshan Nature Reserve	SYS r001741	MN239961
16	*Takydromus kuehnei*	China: Taiwan Island: Xinzhu County	SYS r001797	MN239962
17	*Takydromus kuehnei*	China: Taiwan Island: Taipei	SYS r001798	MN239963
18	*Takydromus kuehnei*	China: Jiangxi: Longnan: Jiulianshan Nature Reserve	SYS r001268	MN239964
19	*Takydromus kuehnei*	China: Zhaoqing: Fengkai: Heishiding Nature Reserve	SYS r001338	MN239965
20	*Takydromus sauteri*	China: Taiwan Island	–	AY248465
21	*Takydromus sauteri*	China: Taiwan Island	–	AY248466
22	*Takydromus septentrionalis*	China: Zhejiang: Lishui: Jingning County: Makeng Village	SYS r000912	MN239966
23	*Takydromus septentrionalis*	China: Zhejiang: Wenzhou: Chashan County	SYSr001886	MN239967
24	*Takydromus septentrionalis*	China: Jiangsu: Xiaotangshan	SYSr001882	MN239968
25	*Takydromus sexlineatus*	China: Zhaoqing: Fengkai: Heishiding Nature Reserve	SYS r001335	MN239969
26	*Takydromus sexlineatus*	China: Zhaoqing: Fengkai: Heishiding Nature Reserve	SYS r001336	MN239970
27	*Takydromus smaragdinus*	Japan: Akashima	–	LC066078
28	*Takydromus stejnegeri*	China: Taiwan Island	–	AY248473
29	*Takydromus stejnegeri*	China: Taiwan Island	–	AY248474
30	*Takydromus sylvaticus*	China: Fujian: Shaowu: Longhu Forestry Station	SYS r001276	MN239971
31	*Takydromus tachydromoides*	Japan: Nagasaki	– (topotype)	LC066067
32	*Takydromus tachydromoides*	Japan: Nagasaki	– (topotype)	LC066068
33	*Takydromus toyamai*	Japan	–	AY248480
34	*Takydromus wolteri*	China: Anhui: Mt. Langya	SYSr001888	MN239972
35	*Takydromus wolteri*	China: Anhui: Mt. Langya	SYSr001889	MN239973
36	*Eremias persica*	Iran	–	FJ416286
37	*Eremias strauchi*	Iran: Yengeje: Neyshabur-Khorasan Razavi	–	KJ468076
38	*Eremias velox*	Iran: Jajarm area-Northern Khorasan	–	KJ468081

with the following cycling conditions: an initial denaturing step at 95 °C for five min.; 35 cycles of denaturing at 95 °C for 40 s, annealing at 53 °C for 40 s, and extending at 72 °C for one min., and a final extending step of 72 °C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using a BigDye Terminator Cycle Sequencing Kit (ThermoFisher Scientific, Waltham, MA) according to the manufacturer's guidelines. The products were sequenced on an ABI Prism 3730 automated DNA sequencer (Shanghai Majorbio Bio-pharm Technology Co., Ltd).

Phylogenetic analyses

Sequence alignments were first conducted using Clustal X 2.0 (Thompson et al. 1997), with default parameters and the alignment being checked and manually revised, if necessary. The data were tested in jmodeltest v2.1.2 with Akaike and Bayesian information criteria, resulting in the best-fitting nucleotide substitution models of GTR + I + G. Phylogenetic relationships were reconstructed using Maximum Likelihood (ML) as implemented in RaxmlGUI 1.3 (Silvestro and Michalak 2012), and Bayesian Inference (BI) using MrBayes 3.12 (Ronquist et al. 2012). For ML analysis, we used the rapid-bootstrapping algorithm (1000 replicates) with the thorough ML search option. Bootstrap values less than 60 were collapsed. For BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for ten million iterations and sampled every 1000th iteration. The first 25 % of samples were discarded as burn-in. Convergence of the Markov Chain Monte Carlo simulations was assessed using Tracer v.1.4 (http://tree.bio.ed.ac.uk/software/tracer/). We also calculated pairwise sequence divergence based on uncorrected p-distance implemented in MEGA 6 (Tamura et al. 2013).

Morphometrics

Measurements of all specimens were taken with a digital caliper to the nearest 0.1 mm. Abbreviations of measurements followed the convention of Lue and Lin (2008):

ALL arm-leg length (from insertion of the forelimb to insertion of hindlimb);
HH head height (measured at the highest point);
HL head length (from tip of snout to anterior margin of ear opening with claw);
HLL hindlimb length (from groin to tip of fourth toe);
HW head width (measured at the broadest point);
LTL length of fourth toe excluding claw;
RUL radius-ulna length;
SAL snout-arm length (from tip of snout to anterior insertion margin of forelimb);
SEL snout-eye length (from tip of snout to anterior margin of eye);
SKL skull length (from tip of snout to posterior margin of occipital);
SVL snout-vent length (from tip of snout to anterior margin of cloaca);
TaL tail length (from cloaca to tip of tail);
TFL tibia-fibula length.

Moreover, 20 external morphological characters were examined from the specimens listed in Appendix 1. Modified abbreviations of these characters followed Arnold (1997), Lue and Lin (2008) and Wang et al. (2017) as follows:

ADSR anterior dorsal scale rows, distinctly enlarged and keeled scales on anterior dorsum, counted transversely at position of forelimbs;

CS chin-shields;
CSR caudal scale rows, counted around the tail in the position of the 11th to 13th subcaudal scales;
ESRF enlarged and keeled lateral scales in longitudinal row(s) above ventrals on lower flanks;
FP femoral pores;
IFL infralabials;
LDSN dorsal scale numbers, counted longitudinally from posterior margin of occipital to posterior margin of hind limbs;
MBSR scales in a transverse row at mid-body, including ventrals;
MDSR transverse dorsal scale rows at mid-body;
PDSR posterior dorsal scale rows, counted transversely at the position of hind limbs;
SDLF-IV subdigital lamellae under fourth finger;
SDLT-IV subdigital lamellae under fourth toe;
SPC supraciliary;
SPL supralabials;
SPO supraocular;
SPT supratemporals;
SSRF small flat and granular scales in a transverse row on flank at mid-body;
TSRF enlarged and keeled scale rows above ventrals on flank;
VN ventral scale numbers, counted longitudinally from the posterior margin of collars to the anterior margin of precloacal scales;
VR ventral scale rows, counted transversely at mid-body.

Comparative morphological data were obtained from the literature for *Takydromus albomaculosus* (Wang et al. 2017), *T. hani* (Chou et al. 2001), *T. viridipunctatus*, and *T. luyeanus* (Lue and Lin 2008), *T. sikkimensis* (Bhupathy et al. 2009), *T. madaensis* (Bobrov 2013), *T. sylvaticus* (Pope 1928, 1929; Yang and Wang 2010), *T. smaragdinus* and *T. toyamai* (Takeda and Ota 1996); *T. kuehnei* (van Denburgh 1909; Arnold1997; Norval et al. 2012; Wang et al. 2017), *T. intermedius* (Stejneger 1924; Wang et al. 2017), *T. amurensis*, *T. dorsalis*, *T. formosanus*, *T. hsuehshanensis*, *T. sauteri*, *T. stejnegeri*, and *T. tachydromoides* (Takeda and Ota 1996; Lue and Lin 2008), *T. sexlineatus*, *T. wolteri*, *T. septentrionalis*, and *T. khasiensis* (Arnold 1997; Zhao et al. 1999). All examined specimens are listed in Appendix I.

Results

BI and ML phylogenetic trees were constructed based on DNA sequences of the mitochondrial cytochrome b gene with a total length of 1074 -bp. The two analyses resulted in essentially identical topologies and are integrated in Figure 2, in which the Bayesian posterior probabilities (BPP) > 0.75 and the bootstrap supports (BS) for ML analysis > 60 were retained. The specimens from Yunkaishan Nature Reserve grouped

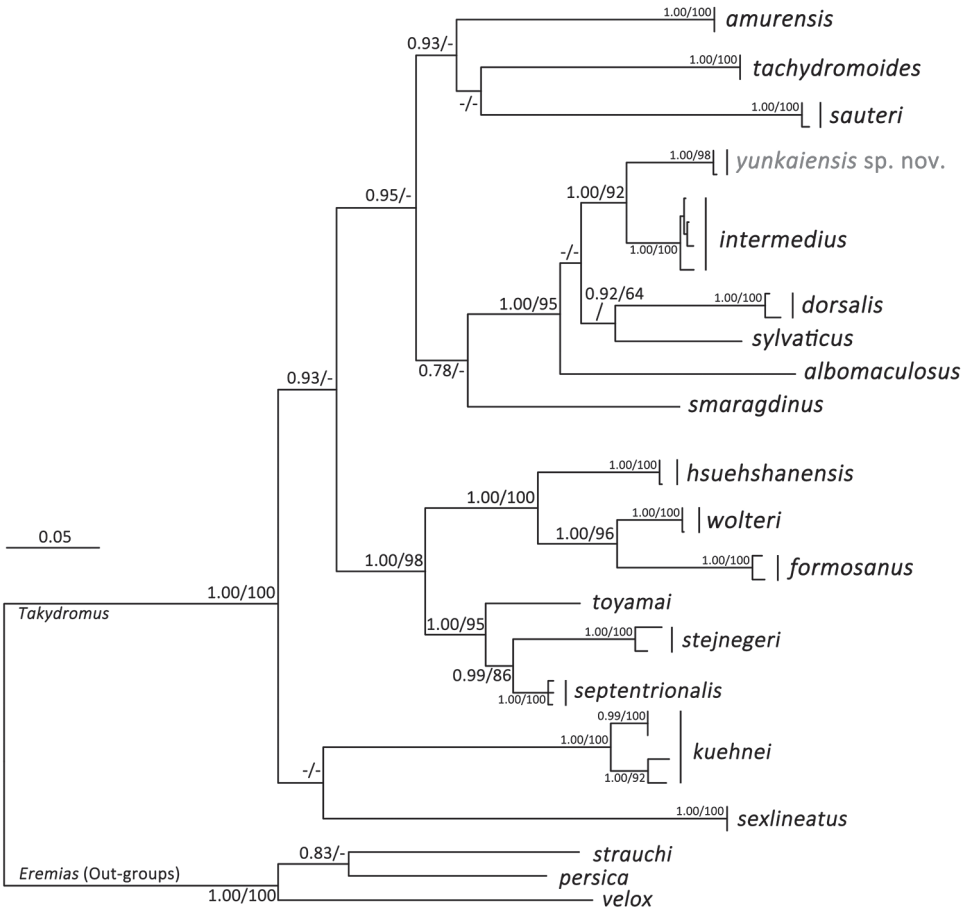

Figure 2. Bayesian Inference and Maximum Likelihood phylogenies. The Bayesian posterior probabilities (BPP) > 0.75 and the bootstrap supports for Maximum Likelihood analysis (BS) > 60 were retained.

in a strongly supported clade (BPP 1.00 and BS 98) with small divergence (*p*-distance 0.2 %), forming the sister taxon to *Takydromus intermedius* with strong support (BPP 1.00 and BS 92) and significant divergences (p-distance 8.0–8.5 %), and then to *T. dorsalis*, *T. sylvaticus*, and *T. albomaculosus* (BPP 1.00 and BS 95), indicating that the population from Yunkaishan Nature Reserve represents a separate evolutionary lineage.

Morphologically, the unnamed specimens can be clearly distinguished from its congeners by the following characters: (1) body size moderate, SVL 37.8–56.0 mm in males, 42.6–60.8 mm in females; (2) dorsal ground color brown; ventral surface green to yellow-green, but light blue-green on chin and throat, posteriorly green in adult males; (3) dorsolateral lines paired, strikingly yellowish-white bordered by black above and below, invisible or indistinct in juveniles and adult females; (4) flanks of body blackish brown with light brown marks in adult males; (5) the presence of four pairs of chin-shields; (6) four supraoculars on each side; (7) presence of a row of supracilary

granules that separate supracilaries from supraoculars; (8) two postnasals; (9) enlarged dorsal scales in six longitudinal rows on trunk of body, with strong keel; (10) enlarged ventral scales in six longitudinal rows, strongly keeled in males, smooth but outermost rows weakly keeled in females; (11) enlarged and keeled lateral scales in a row above ventrals; (12) femoral pores 2–3 on each side; (13) subdigital lamellae 20–23 under the fourth finger, 23–30 under the fourth toe; and (14) the first 2–3 subdigital lamellae under the fourth toe divided.

Based on the comprehensive evidence of molecular and morphological analyses, we hereby describe these specimens from Yunkaishan Nature Reserve as a new species, *Takydromus yunkaiensis* sp. nov. Now, the genus *Takydromus* contains 24 species, nine of which are recorded from mainland China.

***Takydromus yunkaiensis* J. Wang, Lyu & Y.Y. Wang, sp. nov.**
http://zoobank.org/E69D5272-696B-486C-AF44-3AB7C975A699
Fig. 3

Material. Holotype. SYS r001580, adult male, collected by Jian Wang on 16 August 2016 from Dawuling Forestry Station (22°16'32.90"N, 111°11'42.87"E; 1500 m a.s.l.), Yunkaishan National Nature Reserve, Xinyi City, Guangdong Province, China.

Paratypes. Three adult males, collected by Ying-Yong Wang, Jian Wang, Zhi-Tong Lyu and Zhao-Chi Zeng: SYS r001439, 1442 on 15 and 16 April 2016, SYS r001684 on 17 April 2017, all from Dawuling Forestry Station (1200–1500 m a.s.l.). Six adult females: SYS r001513 and SYS r001514 collected by Jian Wang on 9 July 2016 from Xianrendong Scenic Area (22°165'45.99"N, 111°13'16.35"E; 1000 m a.s.l.), Yunkaishan National Nature Reserve, Xinyi City, Guangdong Province; SYS r001434 collected by Jian Wang and Zhi-Tong Lyu on 14 April 2016, SYS r001507 collected by Jian Wang on 28 June 2016, SYS r001581 collected by Jian Wang on 16 August 2016, and SYS r001901 collected by Jian Wang and Hong-Hui Chen on 10 April 2018, all from Dawuling Forestry Station (1200–1500 m a.s.l.).

Etymology. The specific epithet, *yunkaiensis*, is in reference to the type locality of the new species. We propose the standard name "Yunkai grass lizard" and the Chinese name "Yun Kai Cao Xi (云开草蜥)".

Diagnosis. (1) body size moderate, SVL 37.8–56.0 mm in males, 42.6–60.8 mm in females; (2) dorsal ground color brown; ventral surface green to yellow-green, but light blue-green on ventral head and neck, posteriorly green in adult males; (3) dorsolateral lines paired, strikingly yellowish-white bordered by black above and below, invisible or indistinct i n juveniles and adult females; (4) flanks of body blackish brown with light brown marks in adult males; (5) the presence of four pairs of chin-shields; (6) four supraoculars on each side; (7) presence of a row of supracilary granules that separate supracilaries from supraoculars; (8) two postnasals; (9) enlarged dorsal scales with strong keel in six longitudinal rows on trunk of body; (10) enlarged ventral scales in six longitudinal rows, strongly keeled in males, smooth but outermost rows weakly keeled in fe-

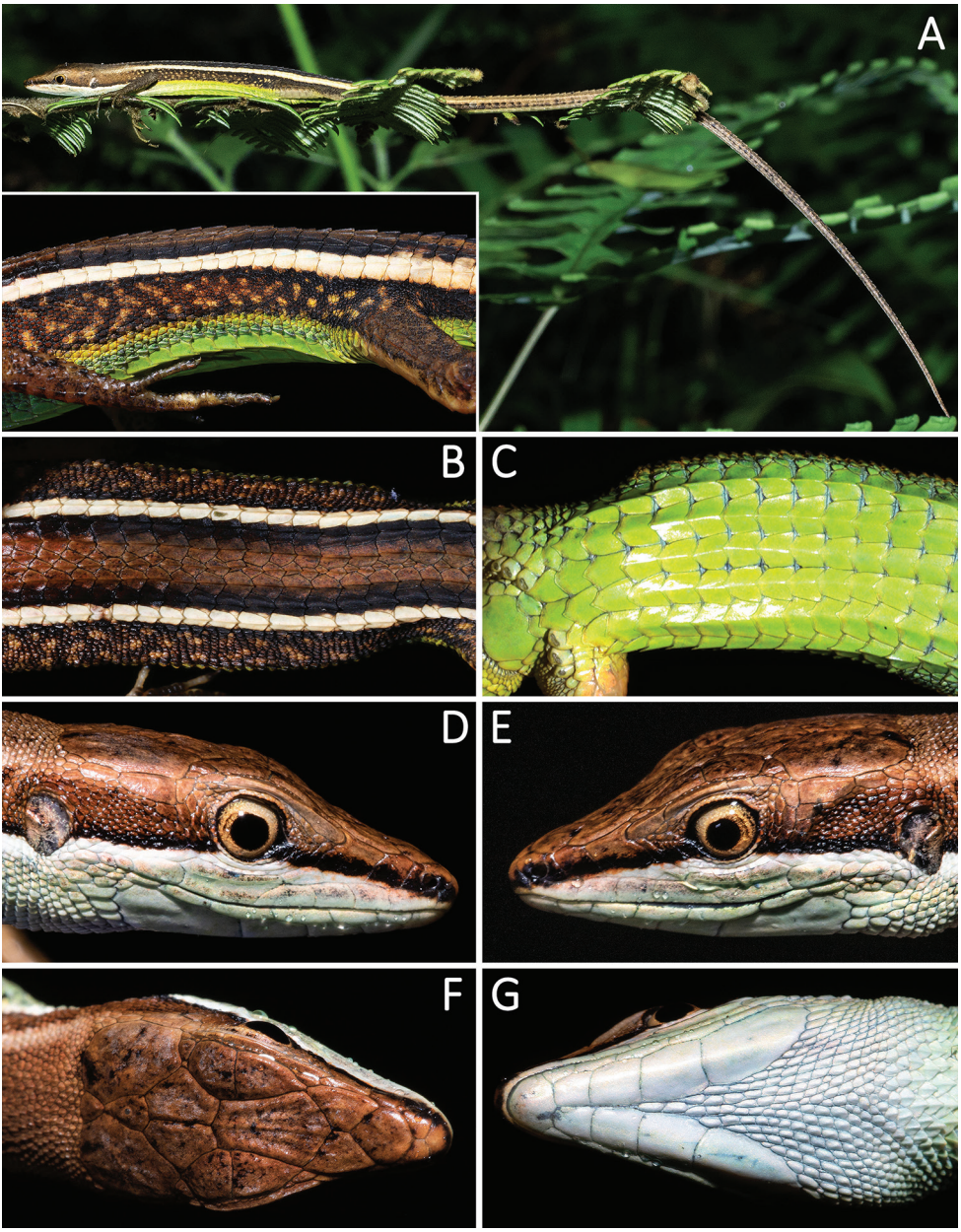

Figure 3. Morphological features of the adult male holotype SYS r001580 of *Takydromus yunkaiensis* sp. nov. in life. **A** Habitus view and close-up of flank **B** close-up of dorsal body **C** close-up of ventral body **D–G** close-up of head scales.

males; (11) enlarged and keeled lateral scales in a row above ventrals; (12) femoral pores 2–3 on each side; (13) subdigital lamellae 20–23 under the fourth finger, 23–30 under the fourth toe; and (14) the first 2–3 subdigital lamellae under the fourth toe divided.

Table 2. Uncorrected *p*-distances among *Takydromus* species based on mitochondrial cytochrome b gene. *Takydromus yunkaiensis* sp. nov. **(1)–(2);** *T. albomaculosus* **(3);** *T. amurensis* **(4)–(5);** *T. dorsalis* **(6)–(7);** *T. formosanus* **(8)–(9);** *T. hsuehshanensis* **(10)–(11);** *T. intermedius* **(12)–(15);** *T. kuehnei* **(16)–(19);** *T. sauteri* **(20)–(21);** *T. septentrionalis* **(22)–(24)**; *T. sexlineatus* **(25)–(26);** *T. smaragdinus* **(27);** *T. stejnegeri* **(28)–(29);** *T. sylvaticus* **(30);** *T. tachydromoides* **(31)–(32);** *T. toyamai* **(33);** *T. wolteri* **(34)–(35)**.

	(1)–(2)	**(3)**	**(4)–(5)**	**(6)–(7)**	**(8)–(9)**	**(10)–(11)**	**(12)–(15)**	**(16)–(19)**	**(20)–(21)**	**(22)–(24)**	**(25)–(26)**	**(27)**	**(28)–(29)**	**(30)**	**(31)–(32)**	**(33)**	**(34)–(35)**
(1)–(2)	0.2																
(3)	16.5–17.0	–															
(4)–(5)	21.9–22.3	24.5	0														
(6)–(7)	13.5–14.4	18.1–18.2	23.2–23.6	1.2													
(8)–(9)	25.9–26.1	25.9–26.1	23.0–23.5	24.5–25.2	1.3												
(10)–(11)	21.9–22.2	23.4–23.6	23.6–23.8	22.6–23.3	15.8–16.2	0.1											
(12)–(15)	**8.0–8.5**	16.3–16.9	20.3–21.3	13.9–15.0	23.1–23.9	20.8–21.6	0.4–1.6										
(16)–(19)	21.5–22.8	24.2–25.2	25.6–25.9	23.0–24.2	22.3–23.6	20.2–22.5	24.2–25.4	0–5.4									
(20)–(21)	23.5	25.5–25.6	22.3–22.5	22.3–22.7	23.2–23.6	23.2–23.6	22.1–23.1	23.9–25.3	0.4								
(22)–(24)	21.1–22.1	24.3–24.7	20.2–22.2	24.2–24.8	17.8–20.0	15.8–17.5	20.2–21.3	21.4–23.4	24.1–24.8	0–0.6							
(25)–(26)	21.0–21.8	25.9	27.6	23.3	25.7–25.9	25.5–25.7	23.4–23.8	24.2–25.0	26.6–26.7	22.1–23.9	0						
(27)	18.9–19.7	21.7	19.8	19.3–19.7	24.2–24.6	21.2–21.4	19.0–19.4	23.4–24.0	21.0–21.2	22.9–23.7	26.3	-					
(28)–(29)	23.6–24.3	24.4–24.6	20.1–20.3	23.6–24.3	17.2–18.2	16.2–16.8	21.7–23.0	20.1–21.8	25.2–25.6	10.3–12.4	24.3–25.2	21.2–21.7	2.2				
(30)	13.3–13.4	18.5	21.5	13.4–13.8	25.6–25.8	20.1–20.3	12.5–12.8	22.2–23.8	22.7–22.9	19.9–20.6	23.7	18.7	20.6–21.2	-			
(31)–(32)	21.8–22.2	23.7	22.5	23.0–23.3	26.6–26.8	23.9–24.1	22.6–23.0	23.7–24.4	21.7	22.4–22.7	29.2	21.6	24.0–24.2	22.2	0		
(33)	21.7–21.9	25.2	19.6	21.5–21.9	19.1–19.9	15.7–15.9	20.9–21.9	22.2–23.2	22.7–23.2	9.5–10.9	21.6	21.9	11.7–12.6	20.5	22.8	/	
(34)–(35)	22.8–23.3	23.9–24.1	21.6	23.1–24.2	10.6–11.1	12.7–12.9	22.8–23.5	23.3–24.1	21.8–22.6	17.2–17.8	25.9–26.0	21.9–22.1	17.4–17.6	21.7–21.8	24.3–24.4	18.1	0.1

Comparisons. In this study we only compare the new species with the other 22 recognized species, excluding *Takydromus haughtonianus*, which is currently an uncertain species and poorly known (Jerdan 1870; Arnold 1997). Measurements, body proportions, and scale counts of the new species are listed in Tables 3 and 4; comparative data of the new species and nine other recognized members of the genus *Takydromus* occurring on the Chinese mainland are listed in Tables 5 and 6.

In our phylogenetic tree, *Takydromus yunkaiensis* sp. nov. is a sister taxon to *T. intermedius*, from which it differs by having two postnasals (only one in *T. intermedius*), having a pair of strikingly yellowish-white dorsolateral lines in adult males (vs. always absent or indistinct in *T. intermedius*), flanks of body blackish brown with light brown spots in adult males (vs. pure brown without spots in *T. intermedius*), ADSR 9–10, PDSR 7 (vs. ADSR 6–8, PDSR 6 in *T. intermedius*).

Morphologically, *Takydromus yunkaiensis* sp. nov. is most similar to *T. kuehnei* (Fig. 4). The new species can be distinguished from *T. kuehnei* by having a pair of strikingly yellowish-white dorsolateral lines in adult males (vs. absent or dorsolateral stripes blurred, pale brown only present in old individuals in *T. kuehnei*); surface of ventrals green (vs. surface of ventrals white or light yellow in *T. kuehnei*), ADSR 9–10, PDSR 7 (vs. ADSR 5–7, PDSR 6 in *T. kuehnei*); TaL/SVL 2.59–2.77 in males (vs. tail relatively longer, TaL/SVL 3.07–3.08 in *T. kuehnei*); relatively shorter trunk (arm-leg length), ALL/SVL 0.46–0.51 in males, 0.48–0.51 in females (vs. relatively larger arm-leg length, ALL/SVL 0.52–0.53 in males and 0.58 in female of *T. kuehnei*).

From the remaining six *Takydromus* species which occur on mainland China (*T. albomaculosus*, *T. amurensis*, *T. wolteri*, *T. septentrionalis*, *T. sexlineatus*, and *T. sylvaticus*), *Takydromus yunkaiensis* sp. nov. can be distinguished by having dense mottles on flanks in males (vs. several particular white round spots on the flanks in *T. albomaculosus*; white ocellus bordered by black edges in males of *T. sexlineatus*); dorsum brown (vs. dorsum green in *T. sylvaticus*); four pairs of chin-shields (vs. three in *T. septentrionalis* and *T. sexlineatus*); two or three pairs of femoral pores (vs. only one in *T. wolteri*, *T. septentrionalis* and *T. sexlineatus*; four in *T. amurensis*); IFL 6–7 (vs. 4–5 in *T. sexlineatus*); SPO 4 (vs. three in *T. sexlineatus*); ADSR 9–10 (vs. six in *T. albomaculosus* and *T. sexlineatus*; 7–8 in *T. amurensis*; 6–8 in *T. septentrionalis*); PDSR 7 (vs. six in *T. albomaculosus*; 4–6 in *T. septentrionalis*; four in *T. sexlineatus*; 9–10 in *T. sylvaticus*); MDSR 7–8 (vs. 5–6 in *T. septentrionalis*; 4 in *T. sexlineatus*; 11–14 in *T. sylvaticus*); LDSN 47–51 (vs. 56 in *T. wolteri*; 67–81 in *T. sylvaticus*); ESRF 1 (vs. three in *T. wolteri*; 2–3 in *T. septentrionalis* and *T. sexlineatus*; none in *T. sylvaticus*).

Takydromus yunkaiensis sp. nov. differs from *T. formosanus*, *T. hsuehshanensis*, *T. luyeanus*, *T. sauteri*, *T. stejnegeri,* and *T. viridipunctatus*, which only occurred in Taiwan Island of China, by having four pairs of chin-shields (vs. three pairs in *T. formosanus*, *T. viridipunctatus*, *T. luyeanus*, *T. hsuehshanensis* and *T. stejnegeri*); FP 2–3 pairs (vs. only one in *T. sauteri* and *T. stejnegeri*); VR 6 (vs. eight in *T. formosanus*, *T. stejnegeri* , *T. viridipunctatus* and *T. luyeanus*); ventrals keeled (vs. ventrals smooth in *T. hsuehshanensis*); mottles on flanks in males (vs. absent in males of *T. formosanus*, *T. sauteri* and *T. stejnegeri*); surface of ventrals green (vs. surface of ventrals white in *T. formosanus*,

Table 3. Measurements and body proportions of type series of *Takydromus yunkaiensis* sp. nov.

Voucher	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r
Number	001439	001442	001580	001684	001434	001507	001513	001514	001581	001901
Sex	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀
SVL	37.8	42.1	43.0	56.0	42.6	60.8	52.5	47.6	49.9	51.9
TaL	100.4	112.0	111.3	155.0	111.5	155.3	143.5	75.7 (broken tail)	148.3	156.7
HL	9.6	10.5	11.1	14.8	10.4	16.3	13.8	13.0	12.0	13.8
HW	6.4	6.6	6.7	8.1	6.5	7.6	6.9	6.3	7.4	7.7
HH	4.6	5.1	5.2	6.0	5.3	6.3	5.3	5.1	5.3	5.5
SKL	10.1	10.9	11.0	14.5	11.0	15.6	12.0	11.3	12.5	13.3
SEL	4.6	4.8	5.0	6.4	4.3	6.8	5.4	5.4	5.6	6.3
ALL	17.7	19.8	19.7	28.3	21.3	30.9	25.0	23.4	25.3	26.6
SAL	14.6	16.6	18.0	21.6	17.7	23.9	20.0	18.5	19.3	20.0
RUL	4.1	5.6	5.6	6.5	4.6	6.9	5.9	5.8	6.5	6.0
HLL	20.0	25.2	25.4	28.3	21.7	29.4	28.1	24.4	28.4	26.9
TFL	4.9	6.3	6.3	7.5	5.3	8.4	7.9	5.9	8.0	7.4
LTL	5.3	7.7	7.9	10.0	7.2	10.2	9.3	8.4	9.2	9.4
TaL/SVL	2.66	2.66	2.59	2.77	2.62	2.55	2.73	1.59	2.97	3.02
HL/SVL	0.25	0.25	0.26	0.26	0.24	0.27	0.26	0.27	0.24	0.27
HL/HW	1.50	1.58	1.66	1.83	1.61	2.14	2.01	2.06	1.63	1.79
SKL/HL	1.05	1.04	0.99	0.98	1.06	0.96	0.87	0.87	1.04	0.96
SEL/HL	0.48	0.46	0.45	0.43	0.41	0.42	0.39	0.41	0.47	0.46
ALL/SVL	0.47	0.47	0.46	0.51	0.50	0.51	0.48	0.49	0.51	0.51
SAL/SVL	0.39	0.39	0.42	0.39	0.42	0.39	0.38	0.39	0.39	0.39
RUL/SVL	0.11	0.13	0.13	0.12	0.11	0.11	0.11	0.12	0.13	0.12
HLL/SVL	0.53	0.60	0.59	0.51	0.51	0.48	0.53	0.51	0.57	0.52
TFL/SVL	0.13	0.15	0.15	0.13	0.12	0.14	0.15	0.12	0.16	0.14
LTL/SVL	0.14	0.18	0.18	0.18	0.17	0.17	0.18	0.18	0.19	0.18
HLL/ALL	1.13	1.27	1.29	1.00	1.02	0.95	0.13	1.04	1.12	1.01

Table 4. Scale counts of type series of *Takydromus yunkaiensis* sp. nov.

Voucher	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r	SYS r
No.	001434	001439	001442	001507	001513	001514	001580	001581	001684	001901
CS	4	4	4	4	4	4	4	4	4	4
FP	3	3	3	3	2	2	3	3	3	3
SPL	7	7	7	7	7	7	6	7/6	7	6
IFL	7	7	7	7	7	6	6	6/7	7	6
SPO	4	4	4	4	4	4	4	4	4	4
SPC	4	4	4	3	4	4	4/2	4	4	4
SPT	3/4	4/3	4/3	4	4/3	4/3	3	3/4	3/4	3
ADSR	9	10	9	9	9	9	9	9	9	9
PDSR	7	7	7	7	7	7	7	7	7	7
MDSR	8	8	8	8	8	8	7	8	7	7
LDSN	47	49	51	47	49	47	47	51	47	47
MBSR	40	44	42	40	46	41	42	41	46	41
SSRF	13/13	17/13	12/16	13/13	16/16	13/14	14/15	14/13	17/16	14/14
VR	6	6	6	6	6	6	6	6	6	6
VN	25	26	25	25	26	25	24	26	25	27
ESRF	1	1	1	1	1	1	1	1	1	1
CSR	13	13	12	10	12	13	12	13	13	12
SDLF-4	20	20	22	23	23	21	21	23	20	21
SDLT-4	27	23	26	28	30	27	26	28	27	25

Table 5. Selected body proportions of *Takydromus yunkaiensis* sp. nov. (data of the female paratype SYS r001514 with a broken tail is not included), and its morphologically most similar species *T. intermedius* and *T. kuehnei*; data obtained from Wang et al. (2017).

T. spp.	*yunkaiensis* sp. nov.		*intermedius*		*kuehnei*	
Sex	**♂ (N = 4)**	**♀ (N = 5)**	**♂ (N = 1)**	**♀ (N = 3)**	**♂ (N = 2)**	**♀ (N = 1)**
TaL/SVL	2.59–2.77	2.55–3.02	2.22	2.54–3.25	3.07–3.08	-
	(2.67±0.07)	(2.78±0.21)		(2.90±0.36)	(3.08)	
HL/SVL	0.25–0.26	0.24–0.27	0.25	0.22–0.25	0.24–0.25	0.22
	(0.26±0.01)	(0.26±0.01)		(0.24±0.02)	(0.25)	
HL/HW	1.50–1.83	1.61–2.14	1.80	1.68–1.72	1.69–1.83	1.84
	(1.64±1.14)	(1.87±0.23)		(1.70±0.02)	(1.76)	
SKL/HL	0.98–1.05	0.87–1.06	1.04	1.02–1.05	1.02–1.03	1.05
	(1.01±0.04)	(0.96±0.08)		(1.04±0.02)	(1.02)	
SEL/HL	0.43–0.48	0.39–0.47	0.46	0.46–0.48	0.45–0.46	0.49
	(0.46±0.02)	(0.43±0.03)		(0.47±0.01)	(0.46)	
ALL/SVL	0.46–0.51	0.48–0.51	0.55	0.53–0.55	0.52–0.53	0.58
	(0.48±0.02)	(0.50±0.01)		(0.54±0.01)	(0.53)	
SAL/SVL	0.39–0.42	0.38–0.42	0.39	0.37–0.42	0.38–0.39	0.36
	(0.40±0.02)	(0.39±0.01)		(0.40±0.03)	(0.38)	
RUL/SVL	0.11–0.13	0.11–0.13	0.16	0.12–0.14	0.13–0.14	0.11
	(0.12±0.01)	(0.12±0.01)		(0.14±0.01)	(0.13)	
HLL/SVL	0.51–0.60	0.48–0.57	0.55	0.48–0.53	0.54–0.57	0.49
	(0.56±0.05)	(0.52±0.03)		(0.51±0.03)	(0.56)	
TFL/SVL	0.13–0.15	0.12–0.16	0.17	0.14–0.16	0.14–0.16	0.13
	(0.14±0.01)	(0.14±0.01)		(0.15±0.01)	(0.15)	
LTL/SVL	0.14–0.18	0.17–0.19	0.19	0.16–0.20	0.20	0.19
	(0.17±0.02)	(0.18±0.01)		(0.19±0.02)		
HLL/ALL	1.00–1.29	0.95–1.13	0.99	0.89–1.01	1.03–1.09	0.85
	(1.17±0.14)	(1.04±0.07)		(0.96±0.06)	(1.06)	

Table 6. Selected scale counts of the nine species of the genus *Takydromus* recorded from the Chinese mainland, modified from Wang et al. (2017); differences are marked in bold.

Takydromus	*yunkaiensis* sp. nov.	*albomaculosus*	*amurensis*	*wolteri*	*septentrionalis*	*sexlineatus*	*intermedius*	*kuehnei*	*sylvaticus*
Species	**(N = 10)**	**(N = 2)**	**(N = 2)**	**(N = 1)**	**(N = 25)**	**(N = 5)**	**(N = 8)**	**(N = 5)**	**(N = 3)**
CS	**4**	4	4	4	**3**	**3**	4–5	4 (rare 3*)	4
FP	**2–3**	3–4	**4**	**1**	**1**	**1**	2–3	3–5	3
SPL	6–7	6–7	5–7	7	5–8	5–6	6–7	6–7	5–7
IFL	**6–7**	6–7	6–7	6–7	5–6	**4–5**	5–7	5–6	5–7
SPO	**4**	3 (rare 4#)	4	4	4 (rare 3■)	**3**	4	4	4
SPC	4 (rarely 2, 3▲)	4–6	4	4	3–5	3	4–5	4	4–5
SPT	3–4	3	2–3	3	1–4	2–3	2–5	3–4	2–4
ADSR	**9–10**	**6**	**7–8**	9	**6–**8	**6**	**6–8**	**5–7**	/
PDSR	**7**	**6**	6–7	7	**4–6**	**4**	**6**	**6**	**9–10**
MDSR	**7–8**	7	7–8	8	**5–6**	**4**	7–8	6–7	**11–14**
LDSN	**47–51**	**52–53**	**46**	**56**	**37–46**	**34–35**	**36–46**	42–47	**67–81**
MBSR	**40–46**	42–43	**33–38**	**36**	34–42	**28–33**	40–44	39–44	45–47
SSRF	**12–17**	13–14	**5–9**	**10**	**7–11**	**6–8**	12–15	13–16	13
VR	**6**	6	**8**	**8**	**8**	**8**	6	6	6
VN	**24–27**	23–26	27	**30**	25–29	26–27	21–24	27–29	26–29
ESRF	**1**	1	1–3	**3**	**2–3**	**2–3**	1	0–1	**0**
CSR	**10–13**	12	**16–18**	**16**	12–14	**14**	12	12–13	12
SDLF-4	**20–23**	23–24	**18–19**	**17**	18–22	**13–16**	20–21	18–20	21–22
SDLT-4	**23–30**	29–30	24–25	22–23	23–28	**19**	26–27	23–24	27–28

▲: Two supraciliaries only present on right side of the holotype SYS r001580 and three present on both sides of SYS r001507, *Takydromus yunkaiensis* sp. nov.; ***:** Three chin-shields only present on left side of SYS r001338, *T. kuehnei*; **#:** Four supraoculars only present on right side of SYS r001292, *T. albomaculosus*; **■:** Three supraoculars only present on one side in three of 25 specimens of *T. septentrionalis*.

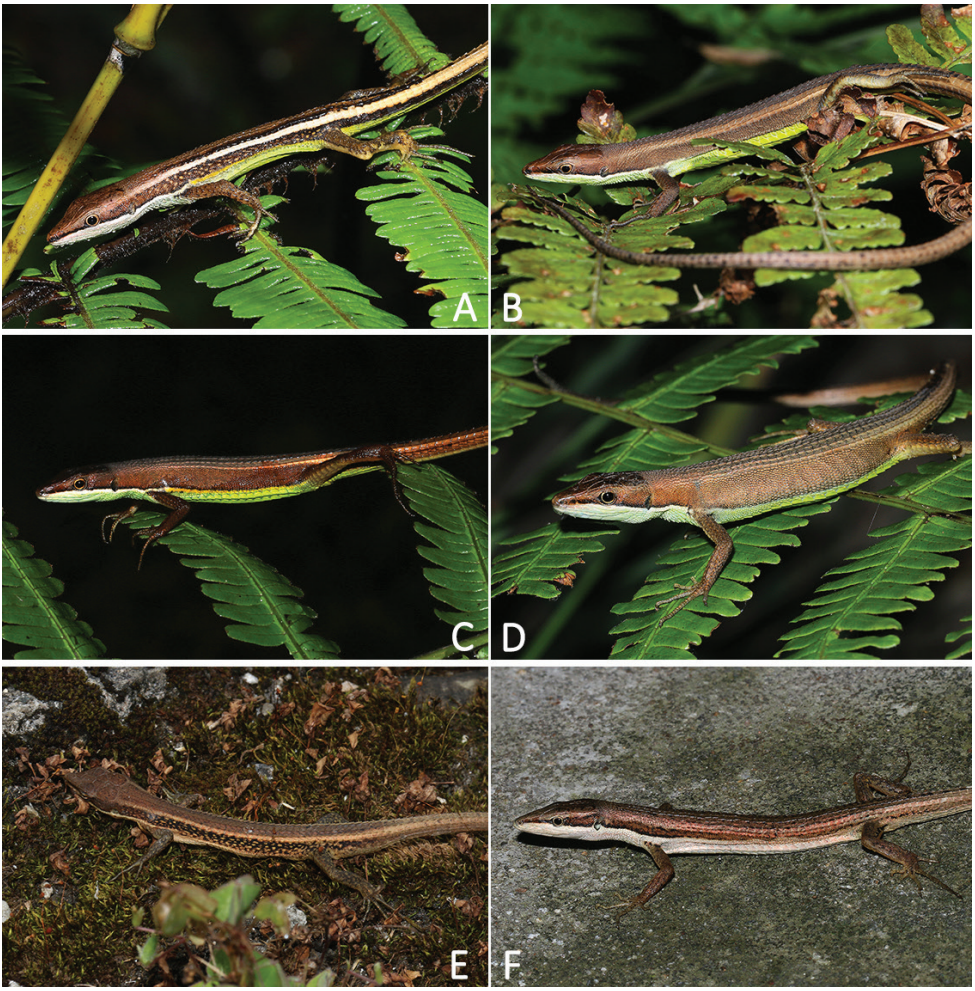

Figure 4. Sexual dimorphism in color patterns. **A** Male paratype of *Takydromus yunkaiensis* sp. nov. (SYS r001439) **B** female paratype of *T. yunkaiensis* sp. nov. (SYS r001901) **C** male topotype of *T. intermedius* (SYS r001601) from Mt. Emei, China **D** female topotype of *T. intermedius* (SYS r001602) from Mt. Emei, China **E** male *T. kuehnei* (SYS r001268) from Jiulianshan Nature Reserve, China **F** female topotype of *T. kuehnei* (SYS r001798) from Taiwan Island, China.

T. hsuehshanensis, and *T. sauteri*); rostral and nostril separated (vs. rostral touching nostril in *T. sauteri*); dorsum brown (vs. dorsum green in *T. sauteri*).

Takydromus yunkaiensis sp. nov. differs from *T. dorsalis*, *T. smaragdinus*, *T. tachydromoides,* and *T. toyamai*, which only occur in Japan, by having a brown dorsum (vs. green dorsum in *T. dorsalis*, *T. smaragdinus,* and *T. toyamai*); dorsal scales large, in longitudinal rows (vs. dorsal scales small, not in obvious longitudinal rows in *T. dorsalis*); FP 2–3 pairs (vs. only one in *T. smaragdinus* and *T. toyamai*); ventrals keeled (vs. smooth in *T. tachydromoides*); VR 6 (vs. 8 in *T. tachydromoides* and *T. toyamai*); CS 4 pairs (vs. 3 in *T. smaragdinus* and *T. toyamai*).

Takydromus yunkaiensis sp. nov. differs from the remaining four members, *T. hani* and *T. madaensis* from Vietnam, *T. khasiensis* and *T. sikkimensis* from India, by having the dorsum brown (vs. dorsum green in *T. hani*); VR 6 (vs. 8 in *T. hani* and *T. khasiensis*; VR 12 in *T. sikkimensis*); CS 4 pairs (vs. 3 in *T. khasiensis* and *T. sikkimensis*); FP 2–3 pairs (vs. FP 6–8 in *T. hani*); loreals 2 (vs. 3 in *T. madaensis*); SPO 4 (vs. 3 in *T. madaensis*); SDLT-4 23–30 (vs. SDLT-4 17 in *T. madaensis*).

Description of holotype. Adult male. Body size slightly small, SVL 43.0 mm; trunk of body short, ALL 19.7 mm, 46 % of SVL; head slightly long, HL 11.1, HW 6.7 mm, HH 5.2 mm, HL 26 % of SVL; skull length larger than head length, SKL 11.9 mm; snout moderately long, SEL in 5.0 mm, SEL 45 % of HL. Rostral large, pentagonal, visible in dorsal view, in contact with the first supralabials posteriorly on both sides, and supranasals dorsolaterally; nostril surrounded by a supranasal, two postnasals and the first supralabial on each side; one supranasal on each side, large, in contact with each other dorso-medially, separating rostral from frontonasal, and in contact with the upper postnasal posteriorly, not in contact with the anterior loreal; postnasals two, both in contact with the anterior loreal posteriorly, the upper one in contact with supranasal dorsolaterally, with frontonasal dorsally, the lower one in contact with the first supralabial ventrally; supralabials six on each side, the fifth one largest, under the eye; two loreals on each side, anterior one smaller than posterior one; posterior loreal in contact with anteriormost supraocular and anteriormost supraciliary scale posteriorly; four supraoculars on each side, the posteriormost one much smaller than others; supraciliaries four on left side, the second one longest; supraciliaries two on right side, the first one longest; supracilary granules arranged in a row, separated supracilaries from supraoculars; frontonasal large, smooth, hexagonal, separated from frontal by a pair of prefrontals; prefrontals two, weakly keeled, in contact with each other medially, with frontal and anterior two supraoculars posteriorly, with loreals laterally, respectively; a single frontal hexagonal, weakly keeled, in contact with second and third supraoculars laterally, with frontoparietals posteriorly; frontoparietals two, pentagonal, in contact with each other medially, with parietal and interparietal posteriorly, respectively; interparietal diamond, surrounded by two frontoparietals, two parietals and the single occipital; parietal pit located in the central of interparietal, distinctly visible; parietals two, large, weakly keeled, slightly in contact with each other medially; a single occipital between two parietals; temporal scales granular, slightly keeled; supratemporals three on each side, keeled, anteriormost one largest, longer than total length of posterior two; mental large, semielliptical; infralabials six on each side; four pairs of chin-shields, anterior two pairs in contact with each other medially, posterior two pairs separated from each other by gular scales; following gular scales gradually increasing in size, keeled, and become imbricated; enlarged, strongly keeled median gular scales extending anteriorly to the line joined posterior edges of ears; collars clear, composed of scales in ten rows pointed backwards, and forming a free serration; enlarged, imbricated dorsal scales on body with strong keel oriented posteriorly that form continuous ridges, extending anteriorly beyond forelimbs on to the nape, in nine rows in position of forelimbs, seven rows in position of hindlimbs; seven rows at mid-body, including

a much smaller and discontinuous central row; longitudinal dorsal scales (LDSN) 47; ventrals in six rows, imbricate, strongly keeled and pointed posteriorly; enlarged and keeled lateral scales in a row above ventrals; longitudinal ventral scales (VN) 24; small flat and granular scales in a transverse row on flank at mid-body (SSRF) 14 on left side and 15 on right side, including a row of scales (enlarged and keeled, shorter than ventrals) adjoining the ventrals; four rows of scales on lower flanks reduced, flattened, keeled; nine rows of small granular scales on upper flanks on left side and ten on right side; a discontinuous row of scales adjoining outermost dorsal scale row reduced, flattened, keeled; a total of 42 scales (MBSR) in a transverse row in mid-body region; a single precloacal entire, enlarged, surrounded by eight continuous moderately sized scales anteriorly and laterally; three femoral pores on each side.

Forelimbs moderately long, RUL 5.6 mm, 13% of SVL; scales on anterior and dorsal surfaces of upper arm enlarged, keeled, rhomboid, imbricate, in seven rows; scales on ventral surface of upper arm granular, homogeneous in size; scales on upper insertion of upper arm granular; scales on dorsal surface of forearm keeled, heterogeneous in size, extending to wrist; dorsal scales on hand slightly keeled; scales on palm granular; dorsal scales on fingers in a row, smooth; subdigital lamellae under fingers I–V respectively (left/right) 9/9 (3 entire + 1 divided + 1 entire), 12/12 (6 entire + 5 divided + 1 entire), 16/16 (10 entire + 5 divided + 1 entire), 22/22 (15 entire + 6 divided + 1 entire), 13/13 (6 entire + 6 decided + 1 entire); relative lengths of adpressed fingers I < V < II < III < IV; hindlimbs slender and long, fourth toe reaching the posterior edge of insertion of upper arm when hindlimb adpressed along the side of the body; HLL 25.4 mm, 59% of SVL, 129% of ALL; TFL 6.3 mm, 15% of SVL; LTL 7.9 mm, 18% of SVL; three rows of large smooth scales running beneath thigh with traces of a fourth row; two rows of enlarged keeled scales and one rows of small keeled scales on dorsal surface of thigh; granular scales homogeneous in size on rear of thigh; internal tibial scale of row one formed by enlarged and smooth tibial scale; dorsal tibial scale flat, keeled, heterogeneous in size, extending to dorsal surface of foot; scales on sole of the foot granular; dorsal scales on toes in a row, smooth; subdigital lamellae under toes I–V respectively (left/right) 9/9 (2 entire + 6 divided + 1 entire), 13/14 (7 entire + 5/6 divided + 1 entire), 18/21 (11 entire + 6 divided + 1 entire), 26/26 (2 divided + 17 entire + 6 divided + 1 entire), 18/18 (2 divided + 7 entire + 7 divided + 1 entire); basal two subdigital lamellae of toe IV and V divided; relative lengths of adpressed toes I < II < V < III < IV.

Tail original, TaL 111.3 mm, TaL/SVL ratio 259%, SVL/TaL ratio 39 %, with strongly keeled scales in 15 rows at base (fifth subcaudal scale), in 13 rows in position of the 13th to 15th subcaudal scales (CSR); paired vertebral series of large scales on tail extending on to hind body.

Coloration of holotype in life. Dorsal surface of head, body, limbs, and tail bright brown, with a pair of strikingly yellowish-white dorsolateral lines bordered by black above and below, each beginning from the posterior margin of the most last supratemporal, running along outermost dorsal scale row, posteriorly extending to the forepart

of the tail; flanks of body blackish brown with light brown marks; a pair of orange ventrolateral lines beginning from axilla, running along lower part of flanks, posteriorly extending to the groin; labial series, mental, chin-shields, granular scales on throat, collars light blue-green, posteriorly yellowish green from chest, venter, until to subcaudal region; ventral surface of limbs brown, tinged with green.

Coloration of holotype in preservative. Dorsal surface of head, body, limbs and tail brown; labial series, mental, chin-shields, granular scales on throat, ventral surface of body and tail pale blue; mottles on flanks blurry, color of mottles on flanks faded; ventral surface of limbs beige; dorsolateral stripes greyish white with black-brown edges at the inner sides; color of ventrolateral stripes faded, greyish white.

Variations and sexual dimorphism. Measurements, body proportions, and scale counts of the type series of *Takydromus yunkaiensis* sp. nov. are listed in Tables 2 and 4.

In the holotype SYS r001580, there are four supraciliaries on left side and two on right side, the first one longest on right side, the second supraciliary longest on left side (vs. four supraciliaries on each side, and the second one longest in the paratypes SYS r001439, 1440, 1442, 1513, 1514, 1581, 1684, 1901; three supraciliaries on each sides, and the second one longest in the paratype SYS r001507); prefrontal in contact with the anterior two supraoculars posteriorly in the holotype (vs. prefrontal only in contact with the first supraocular posteriorly on the right side of the paratype SYS r001439); three pairs of femoral pores in the holotype (vs. only two pairs present in the paratypes SYS r001513, 1514); tail relatively longer in two of the female paratypes, TaL/SVL 2.97 in SYS r001581 and 3.02 in SYS r001901 (vs. TaL/SVL 2.59 in the holotype).

Takydromus yunkaiensis sp. nov. exhibits noticeable sexual dimorphism:

(1) enlarged ventral scales strongly keeled in males (vs. smooth but outermost rows weakly keeled in females);
(2) dorsolateral lines strikingly yellowish-white bordered by black above and below (vs. invisible or indistinct in adult females, also in juveniles);
(3) a pair of orange ventrolateral lines present on lower flanks (vs. invisible in females, also in juveniles);
(4) flanks of body blackish brown with light brown marks in adult males (vs. absent in females).

Distribution and habits. Currently, *Takydromus yunkaiensis* sp. nov. is known only from its type locality of Dawuling Forestry Station, adjacent Xianrendong Scenic Area located in the southern Yunkai Mountains in western Guangdong Province, China (Fig. 1).

The diurnal species was found to be very active in daytime and rapidly escapes when disturbed, and is usually observed resting on fern leaves at night. The surrounding environment was covered by well-preserved montane evergreen broad-leaved forest or mixed forest (Fig. 5) at altitudes of 900–1600 m.

Figure 5. Habitat of *Takydromus yunkaiensis* sp. nov. in Yunkaishan Nature Reserve.

Discussion

The description of *Takydromus yunkaiensis* sp. nov. brings the total number of species of this genus to 24, nine of which occur in mainland China. As noted, six species were recorded from Guangdong Province: *T. albomaculosus*, *T. kuehnei*, *T. septentrionalis*, *T. sexlineatus*, *T. sylvaticus,* and *Takydromus yunkaiensis* sp. nov., which further support the very high biodiversity level of the genus in southern China (Zhao et al. 1999; Lue and Lin 2008; Yang and Wang 2010; Wang et al. 2017).

Most of the early descriptions of *Takydromus* species only listed relatively limited diagnostic characteristics, resulting in considerable challenges in field identification of the species, and causing ambiguities in taxonomy. Moreover, in recent years, a number of new or cryptic species were discovered and described from southern mainland China and Taiwan Island (Lin et al. 2002; Lue and Lin 2008; Wang et al. 2017). These discoveries confirm the substantially underestimated species diversity within the tropical genus *Takydromus*, and more field research is required to increase the knowledge of the diversity.

Located in the western Guangdong Province, the Yunkai Mountains have gradually been recognized for its unique biodiversity. During herpetological surveys during the last several years, we have discovered a number of new species including some cryptic species, as well as providing new regional records of amphibians and reptiles (Yang et al. 2011; Lyu et al. 2018; Wang et al. 2018a; Wang et al. 2018b; Lyu et al. 2019), suggesting that future herpetological exploration will likely continue to yield new discoveries from the region.

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Appendix 1

Examined specimens

Takydromus albomaculosus (*N* = 2): Chia: Guangdong Province: Tianjingshan Forest Station: SYS r001292, 1624.

Takydromus amurensis (*N* = 2): China: Heilongjiang Province: SYS r001635; Suifenhe City: SYS r001647.

Takydromus wolteri (*N* = 1): China: Heilongjiang Province: SYS r001636.

Takydromus septentrionalis (*N* = 25): China: Jiangxi Province: Mt. Sanqing: SYS r000179; Wuyuan County: Mt. Dazhang: SYS r000644, 653–655; Guixi City: Yangjifeng Nature Reserve: SYS r000115, 0133, 0135, 0147; Yanshan County: Wuyishan Nature Reserve: SYS r000642; Guangfeng County: Tongboshan Nature Reserve: SYS r000656, 0471, 0472, 0741, 0742, 0772; Jinggangshan City: Mt. Jinggang: SYS r000282, 1307; Zhejiang Province: Jingning County, Dongkeng: SYS r000912; Fujian Province: Wuyishan City: Sangang Village: SYS r000667, 0676, 0678; Guangdong Province: Ruyuan County: Tianjingshan Forestry Station: SYS r000929, 0930; unknown locality: SYS r000168.

Takydromus sexlineatus (*N* = 5): China: Guangdong Province: Fengkai County: Heishiding Nature Reserve: SYS r001335, 1336, 1337, 1552; Guangxi Zhuang Autonomous Region: Shangsi County: Shiwandashan Forest Park: SYS r000127.

Takydromus intermedius (*N* = 8): China: Sichuan Province: Mt. Emei: SYS r001601, 1602, CIB 3745, 3750; Guizhou Province: Libo County: Maolan Nature Reserve: SYS r000856; Hunan Province: Sangzhi County: Badagongshan Nature Reserve: SYS r001330, 1331; Guangxi Zhuang Autonomous Region: Hechi City: Jiuwanshan Nature Reserve: SYS r001553.

Takydromus sylvaticus (*N* = 3): China: Jiangxi Province: Guixi City: Yangjingfeng Nature Reserve: SYS r000159, 0184; Fujian Province: Shaowu City: Longhu Forestry Station: SYS r001276.

Takydromus kuehnei (*N* = 5): China: Jiangxi Province: Longnan County: Jiulianshan Nature Reserve: SYS r001268; Guangdong Province: Fengkai County: Heishiding Nature Reserve: SYS r000119, 0132, 1338; Renhua County: Huangshakeng Village: SYS r000206.