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In Focus

The cover picture shows habitus of male *Dioncomena* versicolor Hemp, sp. nov.

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Change of Editor-in-Chief

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Founded in 1957, the DEZ is one of the oldest active entomological journals in the world. A total of 30 editors have steered the journal throughout this period and the end of this issue ushers in a new holder of the post of Editor-in-Chief. Nine years have passed since the transition of the DEZ to the publisher Pensoft, a timespan in which the journal has opened up to scientists from all over the world employing the wide range of tools offered by the Pensoft platform. The generous waivers granted by the Museum für Naturkunde Berlin allowed many authors to publish their research in Platinum Open Access - free of charge for both authors and readers. The journal has maintained and expanded its internationality through these years: 133 articles were published with corresponding authors from all continents. Their contributions to taxonomy and systematics are of fundamental importance. Specifically, ninety-seven taxa new to science have been published since 2014, including one subtribe, fourteen genera and subgenera and eighty-two new species and subspecies. While the focus on comprehensive taxonomic and systematic contributions has been maintained, articles on the anatomy and biology of species have also been among the publications. As a result of all these changes, the journal's impact factor more than doubled since 2014 and now stands at 1.174, making the DEZ a very attractive bulletin for amateur, and even more so for academic entomologists.

With the handover of the Editor-in-Chief position, the journal embraces a fresh look and a renewed focus, which will hopefully contribute to its visibility and attractiveness to authors. While the head of the journal changes, its backbone, an excellent team of subject editors and editorial staff from Pensoft, will remain to guarantee a dependable continuity. Together we hope to maintain the positive trends while further growing and diversifying the journal.

Matthias Seidel and Dominique Zimmermann

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Bush-crickets with very special ears and songs – review of the East African Phaneropterinae genus *Dioncomena* Brunner von Wattenwyl, 1878, with notes on its biogeography and the description of new species

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Abstract

This study focuses on the genus *Dioncomena* and its acoustics, particularly the unique songs produced by male *Dioncomena* that consist of several distinct elements in a fixed sequence, culminating in a coda that typically elicits a response from a receptive female. We also examine the inflated pronotal lobes, which we term prebullae, that are prominently developed in some *Dioncomena* species but not in others. We discuss the role of prebullae in the context of acoustic communication in *Dioncomena* and other related Phaneropterini genera that have similar lateral pronotal lobes. We found that prebullae size is correlated with habitat distribution, with larger prebullae occurring in isolated species while aggregation-prone species have smaller or less pronounced prebullae. Using micro-computer tomography we show sexual dimorphism in the 3D geometry of the acoustic tracheae, being larger in the male. Interestingly, the tracheae are coupled by a septum, like in field crickets, which suggests potential cross talk.

We define three groups of *Dioncomena* based on altitude preferences, ecology, color patterns, and songs: the *jagoi-, tanneri-*, and *ornata*-groups. We describe the songs of several species, including newly identified species such as *D. flavoviridis* **sp. nov.**, *D. magombera* **sp. nov.**, *D. ngurumontana* **sp. nov.**, *D. sanje* **sp. nov.**, *D. tanneri*, *D. versicolor* **sp. nov.**, and *D. zernyi*. We also provide information on the nymphs, development time, and mating behavior of various species reared in the laboratory, shedding light on their phenology and adaptations to their habitats.

Key Words

bioacoustics, biogeography, biology, Eastern Arc Mountains, morphology, phenology, Tanzania

Introduction

Acoustic signals play a vital role in the mating system of almost all bush-crickets (or katydids; Tettigonioidea). The males produce loud calling songs, which are answered by females through either a phonotactic approach or self-produced sounds, depending on the species. In the subfamily Phaneropterinae, females typically respond acoustically, resulting in sophisticated male-female duets (e.g., Heller and Hemp 2020). Unlike the system with stationary singing males waiting for silently approaching females, in this group, both sexes have to hear, localize, and evaluate sounds. Consequently, the largest ears among Tettigonioidea are found in this group, with auditory bullae "running to the top of the prothorax" (Bailey 1990). Although the exact function of these conspicuous structures is not well understood (for hypotheses, see Mohsin and Schul 2011; Celiker et al. 2022), they undoubtedly enhance hearing capabilities. However, even these inflated auditory tracheae, which nearly completely fill the prothorax, are not the end point in ear evolution. In the genus *Dioncomena*, reviewed here (and in some other

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genera; see below), the lateral lobes of the pronotum are inflated, creating an additional space presumably used to improve hearing. Brunner von Wattenwyl (1878) named the genus after these inflated lateral lobes (διογκώνομαι in Greek, latinized to Dioncomena, for "inflated"), without having any idea about the function of this structure. Until Ragge's review of African Phaneropterinae in 1980, only Letana inflata (Brunner von Wattenwyl, 1878) was known, in addition to D. ornata, to have a similarly shaped pronotum. Some more genera resembling Dioncomena in this character were described by Rehn (1914) for Atlasacris, Ragge (1980) for some species of Ivensia, and later by Massa (2015) and Hemp and Heller (2019), but no hypotheses were made about their function. In the meantime, the understanding of the auditory system of bush-crickets has considerably improved, and it is now well-known that the prothoracic tracheal opening is the main entrance for sound reaching the auditory sensory cells situated in the tibia of the front legs (Bailey 1990; Rössler et al. 2006). For his reviews about the morphology of the ears in tettigoniids, Bailey (1990, 1993) has obviously overlooked the inflations and assumed that all modification of the paranota he found functioned as protection of the tracheal entrance. We will describe the structures in more detail and argue that the modifications, which are often sex-specific in size, have an important auditory function, probably improving the sensitivity of the ears.

Dioncomena is also special concerning sound production. Ragge (1980) discovered that the type species and all six new species he described differed in the structure of their stridulatory files, presenting quite complicated patterns of tooth intervals. The songs themselves remained unknown until the study of Hemp (2021), who provided oscillograms of sections of the very complicated songs of four species. She also presented photographs of living animals and coined the English name "Jewels" for the genus based on the colorful appearance of the species.

The genus Dioncomena was established by Brunner von Wattenwyl in 1878, based on the observation of D. ornata from Zanzibar, which is a widespread species in Tanzania and Kenya. This genus is characterized by the shape of the tegmina, the open tympana of the fore legs, the dorsally unarmed tibiae of the fore and mid legs, and the inflated lateral lobes of the pronotum. In his review of the African Phaneropterinae with open tympana, Ragge (1980) re-described the genus and added conspicuously hooked spurs of the male mid tibiae as a generic character distinguishing Dioncomena from the genera Meruterrana Sjöstedt, 1912, and Pronomapyga Rehn, 1914, which also have a contrasting variegated colour pattern. Ragge (1980) described six species from eastern Africa, and subsequently, Hemp (2017) described another species, D. scutellata, on museum material from coastal Tanzania, and Massa (2021) added D. takanoi from Zambia. Hemp and Heller (2019) established the genus Kefalia, which is morphologically similar to Dioncomena. Like Dioncomena, Kefalia

Kefalia species may be confused with *Dioncomena* due to their variegated color pattern and similar body shape. However, female *Kefalia* have strongly reduced scale-like wings, while *Dioncomena* females resemble the males, being fully winged.

species have hooked spurs of the mid tibiae. Males of

In this study, we present data on the bioacoustics of *Dioncomena*, describing their complex structured songs, and highlighting their morphological peculiarities in connection with their acoustics. We also provide data on the biology and phenology of several of these beautifully colored insects, which are found in the last remaining forests in East Africa. Furthermore, we describe six new species and the female of *D. zernyi*.

Methods and materials

Depositories

BMNH	British Museum (Natural History), London;
ССН	Collection of Claudia Hemp, Bayreuth;
NHMW	Naturhistorisches Museum, Vienna.

Sound files of all species studied acoustically are given in the Suppl. materials and will be deposited in OSF (Cigliano et al. 2023).

Rearing and keeping of animals

The specimens were housed either in plastic containers or gauze cages and were provided with a daily diet of *Taraxacum officinale* or *Fragaria* sp. leaves, as well as leaves from other shrubs and trees which were regularly replaced.

Bioacoustics

Specimens studied

For this study sounds from 9 species and 50 specimens $(37 \Diamond \Diamond, 13 \heartsuit \heartsuit)$ were analyzed (about 39 GB sound data corresponding to 84 h recording at 2×64 kHz sampling rate), all collected in Tanzania by Claudia Hemp.

- *D. flavoviridis* sp. nov.: Nguru Mountains, 2∂∂ + offspring, 4∂∂, 4♀♀, (CH8855-8862), December 2020; 1 ∂, March 2021.
- D. jagoi Ragge, 1980: East Usambara Mountains, Amani/Zigi, 1 (CH8619), November 2018; 1 (, February 2021.
- D. magombera sp. nov.: Udzungwa Mountains, 1♂, near Mangula Gate (paratype), 2016; 1♂ 2021.
- *D. sanje* sp. nov.: Udzungwa Mountains, 1♂ + offspring 3♂♂, 2♀♀ (CH8167-70), December 2015; 1♂, 2♀♀ (CH8863-65), December 2020.

- D. ornata B. v. Wattenwyl, 1878: 1♂, West Usambara Mountains, Lutindi, January 2015; 1♂, East Usambara Mountains, Nilo Forest Reserve, April 2016; 2♂♂, 1♀, East Usambara Mountains, Amani/Zigi, (CH8093-5), November 2015; 1♂, January 2021; 3♂♂, 2♀♀ (CH8951-5), December 2021; 3♂♂, 1♀, Nguru Mountains, February 2021 (CH8150-2); 1♂, Coastal forest: near Kisarawe, Kazimzumbwi Forest Reserve, July 2015; 3♂♂, Zanzibar, near Jozani Nationalpark, June 2017 (CH8450), October 2018 (CH8620), and February 2022.
- D. ngurumontana sp. nov.: 3♂♂, 1♀, Nguru Mountains above Dibago (CH8986-9), November 2021.
- D. tanneri Ragge, 1980: 1♂, West Usambara Mountains, Mazumbai Forest Reserve, March 2021.
- D. versicolor sp. nov.: 1♂, Uluguru Mountains, February 2016.
- D. zernyi Ragge, 1980: 2 ට ට, Udzungwa Mountains (CH8034), July 2015, and February 2016.

We could not obtain acoustic data on the following species: *D. bulla* Ragge, 1980, *D. nitens* Ragge, 1980, *D. scutellata* Hemp, 2017, *D. takanoi* Massa, 2021, and *D. ugandana* sp. nov. From *D. grandis* Ragge, 1980 the tick song (see below) is figured by Naskrecki and Guta (2019).

Recording

The male calling songs were recorded in the laboratory using a digital bat detector (Pettersson D1000X) mostly with a sampling rate of 100 kHz (rarely 192 or 300 kHz), often from field-collected animals, but in some species also from animals reared in the laboratory. The singers were caged in plastic tubes or gauze cages with microphone fixed or handheld at distances between 5 and 60 cm. The female response behavior was studied in the laboratory using virgin females, reared from field-collected nymphs (rarely) or from eggs. Duets were recorded in stereo using a Sony ECM-121 microphone (frequency response relatively flat up to 30 kHz according to own tests) and an Uher M645 audio microphone connected to a personal computer through an external soundcard (Transit USB, "M-Audio"; 64 kHz sampling rate). Here, male and female were placed separately into two plastic tubes (Drosophila tube 28.5 × 95 mm, Biosigma, Cona, Italy) mostly standing side by side, with one microphone placed inside or on top of each vial. Both microphones typically picked up male and female sounds, but with different amplitudes. Most recordings were made at temperatures between 20 and 25 °C, only rarely also between 15 and 28 °C.

The stridulatory movements in *D. sanje* sp. nov. were registered using an opto-electronic device (Helversen and Elsner 1977, modified as in Heller 1988) as well as the equipment described in Montealegre-Z and Mason (2005; output used for Fig. 27). In summary, the equipment used the optical system proposed by Hedwig (2000), and a sampling rate of 100 k-samples/s for both sound and motion traces.

Sound signals were recorded using a wide-bandwidth response 1/8-inch microphone (Brüel and Kjaer, 4138-A-015, with pre-amplifier model 2670, Brüel and Kjaer, Nærum, Denmark), and the Polytec software (PSV 9.2, Waldbronn, Germany) for multi-channel data acquisition.

For the recording of wing vibrations the method of micro-scanning Doppler vibrometry was used, described in previous studies (e.g. Chivers et al. 2017). Specimens were immobilized by exposure to a triethylamine-based mix (FlyNap, Carolina Biological Supply Company, Burlington, NC, USA) for 3–5 min. The specimens were placed on a block of BluTack (Bostik, La Défense, Paris, France) and their legs were gently clamped to the block with small staple clamps. The wings were extended and maintained in position by putting a small drop of a mix of beeswax (Fisher Scientific Loughborough, UK) and Colophonium (Sigma-Aldrich, Dorset. UK) (50:50). The BluTack block was affixed to a brass plate which itself was attached to an articulated aluminium rod allowing the specimen to be maneuvered into the required position.

Vibration-compliant areas of forewings, and associated frequency characteristics, were measured using a micro-scanning laser Doppler vibrometer (Polytec PSV-500; Waldbronn, Germany) fitted with a close-up attachment. The mounted specimens were positioned so that the extended wings were perpendicular to the lens of the laser unit. A loudspeaker was positioned above the laser unit and facing the animal to broadcast the sound stimulus. The acoustic stimulus used was periodic chirps, generated by the Polytec software (PSV 9.2), passed to an amplifier (A-400, Pioneer, Kawasaki, Japan), and sent to the loudspeaker (Ultrasonic Dynamic Speaker Vifa, Avisoft Bioacoustics, Glienicke, Germany). The periodic chirps spanned frequencies between 2 and 100 kHz, and the stimulus was flattened so all frequencies were represented at 60 ± 1.5 dB (SPL re. 20 μ Pa) at the position of the wings. A Brüel and Kjaer 1/8-inch condenser microphone was placed at the position of the wings to monitor and record the acoustic stimulus at the position of the wings as a reference. The laser system was used in scan mode.

Analysis

Song measurements were obtained using Amadeus II and Amadeus Pro (Martin Hairer; http://www.hairersoft. com). Oscillograms of the songs were prepared using Turbolab (Bressner Technology, Germany). Data are presented as mean \pm standard deviation. For spectral analysis, short song parts (echemes or syllables) were analyzed using the mean of 512 points wide Hanning windows, overlapping by 100 points.

Morphology

The stridulatory files were photographed using a Canon EOS 550 D fixed on a Leica MZ 125 stereomicroscope or a Sony Cyber-shot DSC-P120 on an Olympus SZ Binocular Stereo Zoom Microscope. Programs used for processing the photos were EOS Utility, Helicon Focus, and Adobe Photoshop.

To get an impression of the three-dimensional geometry, the auditory tracheae of *D. sanje* sp. nov. were scanned using a SkyScan 1172 X-ray μ -CT scanner (Bruker Corporation, Billerica, MA, USA) with a resolution of 12.9 μ m (50 kV source voltage, 200 μ A source current, 200 ms exposure and 0.2° rotation steps). For obtaining a series of orthogonal slices, the μ -CT projection images were reconstructed with NRecon (v. 1.6.9.18, Bruker Corporation, Billerica, MA, USA). The three-dimensional segmentation of the auditory tracheae were performed with the software Amira-Aviso 6.7 (Thermo Fisher Scientific, Waltham, MA, USA) (Celiker et al. 2022).

Acoustical terminology

Tettigonioids produce their songs by opening and closing movements of their tegmina. The sound resulting during one cycle of movements is called a syllable, often separable in opening and closing hemisyllable (Ragge and Reynolds 1998). Syllable duration: time period measured from the beginning of the first impulse to the last; syllable period: time period measured from the beginning of a syllable to the beginning of the next (reciprocal value: syllable repetition rate, SRR). In many species and also in Dioncomena, these syllables can be grouped into echemes: first-order assemblage of syllables (duration, period and rate as for syllable). However, the male songs are typically long and complex, contain different elements and cannot be described by syllable and echeme only. The uninterrupted sequence of sounds lasting typically many seconds and which is answered by the female is called main song. Its final part - where typically the female responds - is called coda (a term from music, Italian, meaning tail). Isolated syllables (or short echemes) which are produced in intervals of a few to many seconds are onomatopoeically called ticks (correspondingly ticking song). Each syllable consists of impulses: a simple, undivided, transient train of sound waves (here: the damped sound impulse arising as the effect of one tooth of the stridulatory file).

Results

Aspects of habitat and the ecology

The *Dioncomena* species under investigation can be classified into three groups based on their color pattern, habitat, and ecology. The first group is the *jagoi*-group, characterized by a green and black color pattern with turquoise colors in males (*D. jagoi*, *D. magombera* sp. nov., *D. flavoviridis* sp. nov., *D. sanje* sp. nov., and probably *D. ugandana* sp. nov., Figs 1, 10, 11). Initially, individuals resembling *D. jagoi* were collected from forest areas in Tanzania, but further examination of their morphology

and songs revealed that D. jagoi is only found in the East Usambara Mountains and Kimboza Forest Reserve. Similar species collected from the Nguru and Udzungwa Mountains and also Kimboza Forest Reserve were identified as distinct species based on differences in their songs and morphology, particularly in their stridulatory files and color patterns. Therefore, we describe three new species in the D. jagoi-group: D. sanje sp. nov., D. magombera sp. nov., and D. flavoviridis sp. nov. These species are common in the Udzungwa Mountains and along the Eastern Arc chain, with D. flavoviridis sp. nov. found in lowland wet and submontane forests of the Nguru Mountains. These species are found in low densities scattered in closed forest in Uganda and lowland to submontane forests along the Eastern Arc chain in Tanzania (see map Fig. 36).

The *ornata*-group comprises three species: *D. ornata* found in southern Kenya and northern to central Tanzania, *D. zernyi* inhabiting lowland to submontane forested areas in southern Tanzania, and *D. grandis* distributed in the border region of Mozambique with Zambia. None of the three species were found to occur together (refer to map Fig. 36). Male *D. scutellata's* color pattern indicates its possible relation to *D. zernyi*, though its live color pattern is unknown as one of the two known specimens has lost its color due to preservation in alcohol (stored in Copenhagen), and the other is preserved in the collection of London. All four species have a three-parted stridulatory file.

D. ornata populations on the mainland exhibit distinct coloration, with black wings and turquoise areas on the head, face, and dorsal abdomen in males. In contrast, the Zanzibar population lacks turquoise coloration, but males have a vivid yellow, yellow-red to red pronotum, similar to females (see Hemp 2021 for images of live specimens). Females of mainland populations of D. ornata are less brightly colored, lacking the conspicuous turquoise color typical of males, and their tegmina are often more brown or light black, but not as deep black as males. The body of D. ornata is uniformly colored green or yellow-green, without lateral fasciae, as is typical for the *jagoi*-group. A dorsal black or light black fascia is usually present. D. zernyi males and females are less conspicuously colored, with brown tegmina and a green body with white and/or yellow fasciae, and both sexes show no differences in coloration (Fig. 16). D. grandis has a color pattern very similar to mainland D. ornata. Like D. ornata, this species produces tick-songs (depicted in Naskrecki and Guta 2019), but its full song is not known. Naskrecki and Guta (2019) state that D. grandis is relatively abundant on low herbaceous vegetation along forest edges and thus is classified in the ornata-group, occupying a similar habitat. Species of the ornata-group are found in forest edges and clearings, often aggregated with several males and females sitting on bushes and tall herb vegetation together (this behavior is known for D. ornata and D. zernyi only).

Species of the *tanneri*-group, consisting of *D. tanneri*, *D. versicolor* sp. nov., and *D. ngurumontana* sp. nov., are

found in forests of the montane zones along the Eastern Arc Mountains. All three species are highly colorful, with patterns of turquoise, yellow, red to red-brown, and black, especially in males (Figs 12, 15). Like members of the *ornata*-group, individuals of all three species are found along forest edges or on forest clearings, and are often aggregated.

Taxonomy

Dioncomena flavoviridis Hemp, sp. nov.

https://zoobank.org/C174DC5F-2B7F-4C74-B68F-5344AAD1BF0B Figs 1D, E, 2B, 3E, F, 4C, D, 5, 6B, 8A, 19, 20A, B, 21, 22A–C, 23–25, 29, 30, 35A, 36

Type material. *Holotype* male. Tanzania, Nguru Mountains, area between 6°03'40"S, 37°33'13"E 800 m and 6°02'39"S, 37°33'35"E 1500 m, lowland to submontane forest, November 2020. *Paratypes:* 433, 1799, same data as holotype and February 2017, March 2017, March 2019, March 2020, and November 2022. Depository: CCH.

Description. Male: General habitus and color pattern. Typical for the genus, with a contrasting pattern of green, bluish and black colours. Head & antennae. The fastigium of the vertex is compressed and narrower than the scapus, sulcate above. Thorax & legs. The pronotum has a broad pitch black stripe along the disc, widening at the metazona and completely covering this part (Fig. 1E). The fore coxa is black with a small yellow spine. The fore and mid femora have few very small spinules along ventral ridges, while the hind femur has a double row of widely spaced, irregularly positioned spinules. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have few spines in a double row ventrally, with tiny and only slightly hooked spurs. The hind tibia has four rows of spines irregularly set along its length. Tegmina & wings. The tegmina and wings have a typical shape and coloration for Dioncomena. The stridulatory file on the underside of the left tegmen is continuous, about 1.7 mm long, and with around 40 evenly and widely spaced teeth (Fig. 2B). Abdomen. The tenth abdominal tergite is slightly incurved at the posterior margin, with a membranous structure medially (Fig. 3E). The subgenital plate is longer than wide, v-shaped and incurved medially (Fig. 3F).

Female. With a similar habitus, size, and color pattern to males (Fig. 1F), but lack the hooked spines on the mid tibiae. The ovipositor is relatively small and strongly upcurved (Fig. 4C), and the subgenital plate has a broad base with a triangular posterior margin (Fig. 4D).

Nymphs. Nymphs of this species are only a few millimeters long when freshly hatched, with antennae that are 4–5 times longer than the body length. A conical hump is present on the head, a feature typical of all observed L1 stages of *Dioncomena* species (Fig. 5A, B). As they grow, the nymphs become progressively larger and may

stay predominantly green (L2, Fig. 5D) or become more brownish (L3, Fig. 5C), with brown bands appearing along the hind legs from about stage 3.

Measurements, (mm) males (n = 2). Body length 15.2–15.5. Length of pronotum 3.3-3.9. Length of tegmina 24.5–26.5. Length of hind femur 18.0–19.3.

Measurements, (mm) females (n = 6). Body length 15.5-17.0. Length of pronotum 4.2-4.5. Length of tegmina 27.0-27.5. Length of hind femur 19.5-20.1. Ovipositor 4.2-4.5.

Biology. The eggs are black, oval-shaped, and approximately 3–4 mm long and 2 mm wide. They are typically deposited into the midribs of leaves or small twigs (Fig. 6B). In November 2020, females collected from the Nguru Mountains laid numerous eggs that hatched three and a half months later, at the end of February 2021. The first adult emerged at the end of May 2021, three months later. Similar to other species studied, such as *D. sanje* sp. nov. and *D. ornata*, males transfer only small spermatophores to females during mating (Fig. 8A).

Song. See Bioacoustics.

Habitat and distribution. Lowland to submontane forest. Individuals occur single in more or less closed forest. Tanzania, Nguru Mountains.

Etymology. The species is named after the distinctive bright yellowish-green colored lobes of the pronotum which contrast with the black stripe on the dorsal side of the pronotum and the remaining pattern of black, yellowish-green, and bluish-green on the body and tegmina. The name *"flavo-viridi"* is derived from Latin, meaning "yellowish-green".

Dioncomena magombera Hemp, sp. nov.

https://zoobank.org/ADA3E824-194A-488C-BF9E-69AF874BA223 Figs 1G–I, 2C, 3G, H, 4E, F, 7, 19, 21, 22F, G, 26B–D, 30, 36

Type material. *Holotype* male. Tanzania, Udzungwa Mountains, Mangula Gate, lowland wet forest, 7°50'38"S, 36°53'08"E, 340 m, January 2016. Depository: CCH.

Paratypes: all Tanzania; 3♀♀, same data as holotype and March 2016. 1♂, 3♀♀, Magombera Forest Reserve, lowland forest, 7°49'10"S, 36°58'42"E, 280 m, January 2019. 2♀♀, Kihansi Forest Reserve, area between 8°36'35"S, 35°51'08"E, 370 m and 8°35'48"S, 35°50'59"E, 800 m, lowland to submontane forest, January 2016. 1♀, Kanga Hill, Nguru Mountains, 5°59'04"S, 37°45'36"E, 420 m, riverine vegetation, March 2022; 1♂, 4♀♀, Kimboza Forest Reserve, Morogoro Region, 200– 300 m a.s.l., 7.03°S, 37.78°E, disturbed lowland forest, March 2022. 1♀, Miombo woodlands, Msaze near Gulwe, Mpwapwa District, 6°31'21"S, 36°22'15"E, 1000 m, May 2022. Depository: CCH.

Description. Male. Typical *Dioncomena* in habitus and size, with contrasting green, bluish, and black colors (Fig. 1G, H). Head. Fastigium of vertex compressed, sulcate above. Thorax & legs. Pronotum with slightly



Figure 1. *Dioncomena* species of the *D. jagoi*-group: A–C. Male (A, B) and female (C) of *D. jagoi*, East Usambara Mountains; D, E. Male (D, E) and female (F) of *D. flavoviridis* sp. nov.; G–I. Male (G, H) and female (I) of *D. magombera* sp. nov.; J–L. Male (J, K) and female (L) of *D. sanje* sp. nov.

inflated posterior part of lateral lobes. Broad black stripe with fine median green line on pronotal disc, widening at metazona. Fore coxa brownish or black with broad-based short yellow spine. Fore and mid femora with double row of small ventral spinules, hind femur with widely spaced irregular positioned spines. Fore tibia with ventral double row of irregular set small spinules and a pair of short ventral spurs; dorsal inner side with short spine below tympanum and 1–3 short black spines along length. Mid tibiae with ventral double row of hooked black spinules and spurs, dorsal on mid tibiae at apical part with few hooked black spines. Tegmina & wings. Typical shape and coloration for *Dioncomena*, with continuous stridulatory file on left tegmen (Fig. 2C). Abdomen. Tenth abdominal tergite incurved at posterior margin with shallow membranous structure medially. Cerci green and stout, with black inwardly hooked tips (Fig. 3G). Subgenital plate longer than wide, v-shaped incurved medially (Fig. 3H).

Female. Similar habitus, size, and coloration as male (Fig. 1I). Ovipositor long and slightly upcurved (Fig. 4E). Subgenital plate narrow and triangular with evenly curved posterior margin (Fig. 4F), without hooked spines on mid tibiae.

Nymphs. Similar to the adults. Fig. 7 shows the last instar of a female *D. magombera* sp. nov.

Measurements, (mm) males (n = 3). Body length 16.8-25.0. Length of pronotum 3.6-4.0. Length of tegmina 22.5-25.1. Length of hind femur 18.2-19.3



Figure 2. Stridulatory files of *Dioncomena* species, tegmen articulation to the right. A–E. *D. jagoi*-group: A. *D. jagoi*; B. *D. flavoviridis* sp. nov.; C. *D. magombera* sp. nov.; D. *D. sanje* sp. nov.; E. *D. grandis* (from Naskrecki and Guta 2019); F. *D. ornata* (Nguru Mts.); G. *D. zernyi*; H. *D. tanneri*; I. *D. versicolor* sp. nov.; J. *D. ngurumontana* sp. nov.

Measurements, (mm) females (n = 6). Body length 14.5– 17.8. Length of pronotum 5.4–6.9. Length of tegmina 22.4– 27.5. Length of hind femur 18.7–21.7. Ovipositor 5.4–6.9.

Habitat and distribution. Lowland to submontane forest. Mostly found singularly in understory vegetation of closed forest. Distributed in Tanzania's Udzungwa, Uluguru, and Nguru Mountains, as well as Miombo woodlands in the Mpwapwa District.

Etymology. Named after the Magombera Forest Reserve at the Udzungwa Mountains' foothills near Mangula, where the first specimens were collected. Noun in apposition.

Remarks. Ragge (1980) reported two female *Dioncomena jagoi* individuals from Kimboza Forest Reserve at the Uluguru Mountains' foothills. Our team's specimens collected in March 2022 from the same location belong to the new species *D. magombera*. A female specimen captured at the Nguru Mountains' foothills and another in Miombo woodlands in the Mpwapwa District near Gulwe also belong to this species, indicating *D. magombera* sp. nov. is widespread in lowland forests along the southern branch of the Eastern Arc Ranges. Two female specimens listed by Ragge (1980) from Kimboza Forest Reserve were studied in the Natural History Museum London and found to belong to *D. jagoi*, labelled as paratypes by David Ragge. Further collecting is necessary to determine whether two *Dioncomena* species of the *jagoi*-group exist in Kimboza Forest Reserve, and studies on their song must be undertaken.



Figure 3. Male apices of the *Dioncomena jagoi*-group. **A**, **B**. Dorsal (**A**) and ventral (**B**) view of *D*. *jagoi*; **C**, **D**. Dorsal (**C**) and ventral (**D**) view of *D*. *sanje* sp. nov.; **E**, **F**. Dorsal (**E**) and ventral (**F**) view of *D*. *flavoviridis* sp. nov.; **G**, **H**. Dorsal (**G**) and ventral (**H**) view of *D*. *magombera* sp. nov.

Dioncomena sanje Hemp, sp. nov.

https://zoobank.org/491B0F5E-501E-4F8B-89AE-184A3CA2CB3E Figs 1J–L, 2D, 3C, D, 4G, H, 6A, 8B, 9, 19, 21, 22H, I, 23–25, 27, 30–34, 35B, 36

Type material. *Holotype* male. Tanzania, Mangula, 7°50'38"S, 36°53'08"E, 340 m, lowland wet forest, December 2015. *Paratypes*: 233, 1199, same data as holotype and March 2015, July 2015, September 2015, January 2016, March 2016, November 2017. Further paratypes: All Tanzania, all Udzungwa Mountains. 733, 2099, Sanje Trail, lowland wet to submontane forest, August 2019, April 2020, July 2020, October 2020, January and April 2021, May and September 2022. 333, 19, Magombera Forest Reserve, 7°49'12"S, 36°58'42"E, 300 m, lowland forest, January 2019. Depository: CCH.

Description. Male. General Habitus and Color Pattern. The typical *Dioncomena* species can be identified by its contrasting pattern of yellow, white, greenish, and black colors on its general habitus and size (Fig. 1J, K). Head and Antennae. The fastigium of the vertex in the head is compressed and narrower than scapus, sulcate above, and is typical for the genus. Thorax & legs. The pronotum has a posterior part of lateral lobes that are not or only slightly inflated. A black stripe on the pronotum is narrow and widens in metazona, parting between a yellowish triangular field (Fig. 1J, K). The fore coxa is black with a broad-based short yellow spine. The fore spinules at the apical part, while the hind femur has a double row of few irregularly positioned spines at the apical part. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. On the dorsal inner side, a short and slender spine is present just below the tympanum, and 1-3 short black spines are along the length. The mid tibiae have a ventral double row of black spinules and three longer black, slender, and clearly hooked spines at the inner ventral apex. Tegmina & wings. Typical shape and coloration for Dioncomena. They are black with a yellowish or green field at the base (Fig. 1J, K). The stridulatory file is present on the underside of the left tegmen and is between 1.4–1.6 mm long with around 50 teeth. The teeth are broad and densely set on the inner side, getting continuously narrower towards the apical part of the file, and ending with 8-10 shorter and more widely spaced teeth (Fig. 2D). Abdomen. The tenth abdominal tergite is slightly incurved at the posterior margin with a membranous structure medially (Fig. 3C). The cerci have an apical third that is laterally flattened. The subgenital plate is longer than wide and v-shaped incurved medially (Fig. 3D).

and mid femora have a double row of few small ventral

Female. Habitus, size and color pattern are similar to the male (Fig. 1L) but lack hooked spines on the mid tibiae. Ovipositor is short and strongly upcurved (Fig. 4G). Subgenital plate has a broadly-based triangular posterior margin (Fig. 4H).

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Figure 4. Female *Dioncomena* species. A, B. Ovipositor and subgenital plate of *D. jagoi*; C, D. Ovipositor and subgenital plate of *D. fla-voviridis* sp. nov.; E, F. Ovipositor and subgenital plate of *D. magombera* sp. nov.; G, H. Ovipositor and subgenital plate of *D. sanje* sp. nov.



Figure 5. Nymphal stages of *Dioncomena flavoviridis* sp. nov. A, B. Freshly hatched nymph; C. L3 stage; D. L2 stage, about 3 weeks old.



Figure 6. Eggs deposited into the stems of leaves and small branches. A. D. sanje sp. nov.; B. D. flavoviridis sp. nov.



Figure 7. Last instar of female *Dioncomena magombera* sp. nov., distinguished by its long ovipositor from *D. sanje* sp. nov. which occurs syntopically.

Nymphs. Freshly hatched nymphs are greenish-yellow with speckles and brown markings along the hind femora (Fig. 9A, B). Nymphs grow in size until stage three without changing their habitus (Fig. 9C, about two weeks old, probably stage 2). From stage 3, wings become visible and grow larger with each stage. Depending on the environment, nymphs may become more greenish or gain more brown colors (Fig. 9D, F). From stage 5 onwards, wings are clearly visible and are slightly inflated a day or so before molting to an adult (Fig. 9E).

Measurements, (mm) males (n = 3). Body length 12.8–14.8. Length of pronotum 3.2-3.8. Length of tegmina 23.0–25.6. Length of hind femur 17.11–17.3.

Measurements, (mm) females (n = 6). Body length 14.0–16.5. Length of pronotum 3.1-3.3. Length of tegmina 25.0–27.5. Length of hind femur 18.0–20.2. Ovipositor 4.2–4.6.

Biology. The eggs are oval and black and are deposited in the midribs or stems of leaves (Fig. 6A). Eggs laid by a female in October 2020 hatched at the end of February

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2021, 4 months later, and developed into adults at the beginning of June 2021. A female collected in April 2021 laid numerous eggs in stems on April 24, which hatched on July 7, 2021. Most individuals were captured in the Udzungwa Mountains during the warm months, from December to March, but single adults were also obtained from July to September, indicating that the species is present year-round. Like the other species studied (*D. flavoviridis* sp. nov. and *D. ornata*), males transfer only very small spermatophores to females during mating (Fig. 8B).

Song. See Bioacoustics.

Habitat and distribution. The species inhabits lowland wet to submontane forests. Individuals were mostly collected as single specimens in the understory vegetation of closed forests. Its distribution is restricted to Tanzania's Udzungwa Mountains.

Etymology. The species is named after the Sanje Trail in the Udzungwa Mountains National Park and is a noun in apposition.

Diagnosis. The four species of Dioncomena (D. jagoi from the East Usambara Mountains, D. flavoviridis sp. nov. from the Nguru Mountains, D. sanje sp. nov. from the Udzungwa Mountains, and the widespread D. magombera sp. nov.) are morphologically similar, sharing a similar color pattern (Fig. 1). However, there are several distinguishing features. The pronotal lobes in D. magombera sp. nov., D. flavoviridis sp. nov., and D. jagoi are uniformly bright yellow or yellow-green, while both sexes of D. sanje sp. nov. have a large central diffuse formed black patch on the pronotal lobes. The 10th abdominal tergite of males is very similar in the four species of the D. jagoi-group, being incurved and with a more or less conspicuous membrane between the edges (although it is very shallow in D. magombera sp. nov.). The male cerci are mostly green with black incurved tips, but in D. sanje sp. nov., the last third or so of the male cerci is laterally flattened, and in D. magombera sp. nov., the black tips of the male cerci are hooked inwardly. The pronotal lobes are laterally considerably inflated in D. flavoviridis sp. nov. and D. jagoi, but less so in *D. sanje* sp. nov. and *D. magombera* sp. nov. In D. flavoviridis sp. nov., the hind femur has a ventral



Figure 8. Dioncomena females with spermatophores immediately after mating. A. D. flavoviridis sp. nov.; B. D. sanje sp. nov.; C. D. ornata.

black stripe reaching to about the middle or covering more than half of the outer side of the femoral area (Fig. 1D). The outer side of the hind femur is black in D. jagoi distally, then turns yellow or green and gets black again basally at the joint with the coxa (Fig. 1A, B), similar to the femoral pattern of D. magombera sp. nov. The yellow or green area on the outer side of the hind femur is often more diffuse and smaller in D. sanje sp. nov. (Fig. 1J, K). Additionally, D. ugandana sp. nov. could belong to the jagoi-group because of its general color pattern and the outer genitalic morphology of the male apex. The pronotum is largely deep black with a yellow stripe at the anterior margins of the lateral pronotal lobes (Fig. 10A). In D. flavoviridis sp. nov., the black median fascia on the pronotum is solid and broad, a bit narrower along the pro- and mesozona of the pronotum, then extending to cover the whole disc of the metazona (Fig. 1D, E). The central black fascia of D. jagoi is much narrower (Fig. 1B). In D. sanje sp. nov., the black fascia is also broad and solid but fuses with the black patches of the pronotal lobes on both sides (Fig. 1J, K). In D. sanje sp. nov. as well as in D. magombera sp. nov., the black fascia parts at the anterior base of the metazona into two stripes leaving a green or yellow-green triangular patch on the disc of the metazona (Fig. 1H, J). While in D. sanje sp. nov. the black median stripe of the pronotum is solid, in D. magombera sp. nov. a fine central green or yellowish line is present throughout the whole course of the black fascia (Fig. 1H). Characters distinguishing the other species and groups of Dioncomena are provided in the key. For song description see Bioacoustics section.

Dioncomena ugandana Hemp, sp. nov.

https://zoobank.org/57973B18-DC63-4C13-8317-3D1EA0B54ED3 Figs 10, 11, 36

Type material. *Holotype* male, Uganda, Bwamba Valley, VII 1921, G.D.H. Carpenter, Pres. By Imp. Bur. Ent. Brit. Mus. 1927-77. Depository: BMNH.

Paratypes: 1 \bigcirc , same data as holotype. 1 \bigcirc , Bugoma Forest, 21. VI 1933, H. B. Johnston. 1 \bigcirc , Toro¹, 4000–4500 ft., 25–29. Dec 1911, S.A. Neave, BM 1912-192; 1 \bigcirc , Mabira forest, 28.6.1913, CC Gowdey, BM 1927-77; 1 \bigcirc , Mabira forest, Chagwe, 17.-20.7. 1911. Depository: BMNH.

Description. Male. General Habitus and Color Pattern: Typical Dioncomena species in terms of its general habitus and size, with a contrasting pattern of yellow and black colors (Fig. 10A, B). The black fascia of the pronotum is solid and very broad, covering the entire disc of the pronotum and parts of the lateral lobes, leaving only a yellow stripe along the anterior lateral lobes and a small yellow patch at the posterior margin of the pronotum. Around the fastigium verticis, a triangular area is yellow while the remaining head is black, except for a thin line posterior to the fastigium, running to the anterior margin of the pronotum (Fig. 10B), and two broader yellow fasciae parallel on the face. Head & antennae. The fastigium of the vertex is typical for the genus, compressed, narrower than scapus, and sulcate above. Thorax & legs. The pronotum has an inflated posterior part of lateral lobes. The fore coxa is black with a very short, stout black spine. The fore and mid femora are unarmed, while the hind femur has very few small spines at the apical part. The fore tibia has a ventral double row of few irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have a double row of spines near the distal end of the tibia, with four hooked spines on the outer dorsal side. The hind tibiae have a dorsal double row of spines, ventral rows with only a few spines set irregularly at the apical part, and three short spurs on each side. Tegmina & wings. The tegmina and wings have a typical shape and coloration for Dioncomena, black with a yellowish or green field at the base. The left tegmen is missing in the holotype, and the stridulatory area is destroyed in the male paratype. Abdomen. The tenth abdominal tergite is incurved at the posterior margin with a membranous structure medially (Fig. 10C). The cerci are yellow, round with strongly inwardly curved black-tipped apices. At the apical third

¹ The label reads Daro or Durro Forest and Toro. Toro is a region in the west of Uganda and could refer to the Toro Semliki Wildlife reserve.



Figure 9. Nymphal stages of *Dioncomena sanje* sp. nov. A, B. Freshly hatched nymph; C. Nymph about 2 weeks old; D, F. L4 stage with wings visible, two different colour forms; E. L5 stage, female, shortly before molting to adult.

cerci, on the inner side, there is a small groove (Fig. 10C). The subgenital plate is longer than wide and v-shaped, incurved medially (Fig. 10D).

Female. Habitus, size, and color pattern similar to male with larger yellow spot on the posterior part of the pronotum (Fig. 11A, C). Yellow area at the anterior mar-



Figure 10. Male holotype of *Dioncomena ugandana* sp. nov. A. Habitus; B. Head and pronotum; C. Dorsal view on apex; D. Subgenital plate.

gins of the pronotal lobes is not neatly confined and the margins are uneven and undulating between the yellow and black areas in females (Fig. 11B). Leg spination similar to male but without hooked dorsal spurs on mid tibiae. Ovipositor short and strongly upcurved, basal part black, remaining part yellow (Fig. 11D). Subgenital plate broadbased with triangular posterior margin, median v-shaped incision, and small lateral styli (Fig. 11E).

Measurements, (mm) males (n = 2). Body length 15.0– 16.0. Length of pronotum 3.2–3.9. Length of tegmina 25.3–26.2. Length of hind femur 17.

Measurements, (mm) females (n = 4). Body length 15.5–17.5. Length of pronotum 3.2-3.4. Length of tegmina 26.0–26.5. Length of hind femur 16.8–18.0. Ovipositor 4.8–5.2.

Habitat and distribution. The holotype was found in the Bwamba valley, an area located between Lake Albert in the north and Lake Edward in the south, with the Semuliki National Park in the northwest. This region has an elevation ranging from about 700 to 800 m a.s.l. and is characterized by lowland wet forest.

Song. Unknown.

Etymology. Named after the country Uganda.

Dioncomena ngurumontana Hemp, sp. nov.

https://zoobank.org/64E8E74D-BE3F-47D0-82B3-EC17943103DF Figs 2J, 12, 13E, F, 14, 19, 21, 22P, 23–25, 28E, F, 30, 36

Type material. *Holotype* male. Tanzania, Nguru Mountains, montane forest above Dibago/Maskati, 6°03'05"S, 37°29'09"E, 1950 m, November 2021. Depository: CCH.

Paratypes. $2\Im\Im$, $3\Im$, $3\Im$, same locality as holotype. $2\Im\Im$, same locality as holotype but February 2022. Depository: CCH.

Description. Male. General habitus and color pattern. *Dioncomena* species with a very colourful pattern of black tegmina with a blue or greenish field at the basal part, a black and white patterned head, and a pronotum with a central turquoise blue or green line, bordered by irregular black lines and interrupted medially by a black line as well (Fig. 12A, B). Part of the disc and lateral lobes of the pronotum partly yellow, at the lower margin again green or turquoise with an irregular longish black patch. Legs are black except for the hind femora that are of light brown colour at their inflated basal parts. The abdomen is striped green or blue and black. Head and antennae. Fastigium of vertex typical



Figure 11. Female *Dioncomena ugandana* sp. nov. A. Habitus; B. Lateral view on head and pronotum; C. Dorsal view on pronotum; D. Ovipositor; E. Subgenital plate.



Figure 12. *Dioncomena ngurumontana* sp. nov. A, B. Male; C, D. Female; E, F. Morphological details of female *D. ngurumontana* sp. nov., ovipositor (E) and subgenital plate (F).

for the genus, compressed, narrower than scapus, sulcate above. Thorax & legs. Pronotum with posterior part of lateral lobes not markedly inflated. Fore coxa without a spine. Fore, and mid femora unarmed, hind femur only at apical slender part ventrally with few very small spines. Fore tibiae ventrally with double row of very few and irregularly set small spinules and a pair of short ventral spurs. Mid tibiae with ventral double row of very few spinules, spinules at apical part only very slightly hooked; few spinules also apically on dorsal side of mid tibiae. Hind tibiae with dorsal double row of spines getting denser apically and double row of irregular set spines also on dorsal side in apical third of the tibiae. Tegmina & wings. Typical for *Dioncomena*, narrow, tegmina black with an elongated blue or green field at base (Fig. 12A, B). Stridulatory file on the un-



Figure 13. Morphological details of male *Dioncomena* species A–C. *D. versicolor* sp. nov., semilateral view on apex (A, B) and subgenital plate (C) Dorsal view on apex of *D. tanneri* (D), apex (E) and subgenital plate (F) of *D. ngurumontana* sp. nov.



Figure 14. Last instar nymph of D. ngurumontana sp. nov.

derside of left tegmen about 1.1 mm long with about 45 teeth (n = 1); teeth densely set along length, apically teeth getting smaller and are more widely set (Fig. 2J). Abdomen. Tenth abdominal tergite black, incurved at posterior margin (Fig. 13E, F). Cerci laterally flattened, especially at apex, green with a black tip (Fig. 13E, F). Subgenital plate longer than wide, with v-shaped incision in the middle, beside the incision short slender styli-like processes (Fig. 13F).

Female. With a similar habitus as the male, but with a different color pattern consisting mainly of greenish hues on the head, body, and hind femora (Fig. 12C, D). The pronotal lobes are bordered in bluish to turquoise,

but less prominent than in the male. The pronotal disc and lobes are yellowish to hazel brown, similar to the male. Unlike the male, the tegmina are of greenish to brown color, without the black base and turquoise or green stripe. The ovipositor is green and strongly upcurved (Fig. 12E), while the subgenital plate forms a flap with an evenly rounded posterior margin (Fig. 12F).

Nymphs. The nymphs resemble the adults, but with an inconspicuous greenish coloration with some dark spots on the legs and white dots on the abdomen (Fig. 14).

Measurements, (mm) males (n = 3). Body length 12.0–14.7. Length of pronotum 3.2–2.4. Length of tegmina 20.0–21.5. Length of hind femur (one individual with hind femora) 16.

Measurements, (mm) females (n = 3). Body length 9.8–15.5. Length of pronotum 2.9–3.3. Length of tegmina 18.5–20.8. Length of hind femur 15.8–16.6. Ovipositor 4.7-5.0.

Phenology. Nymphs were observed in November 2021 on sunny patches along a forest path. Most nymphs were in stages L4 and L5, with only a few smaller nymphs seen. L5 nymphs collected from the forest molted to adults in captivity about one week later. Similar to *D. tanneri*, it is likely that the hatching of *D. ngurumontana* sp. nov. is triggered by rising temperatures from September onwards. This species probably forms only one generation per year as an adaptation to the montane zone.

Song. See Bioacoustics.



Figure 15. Habitus of male (A) and female (B) *D. versicolor* sp. nov. and male (C) and female (D) *D. tanneri*. Morphological details of female *D. versicolor* sp. nov., subgenital plate (E) and ovipositor (F). Scale bars: 1 mm.

Habitat and distribution. *D. ngurumontana* sp. nov. was found on forest paths and clearings in the montane zone (1850–2000 m). The collected individuals were found clustered together, with adult individuals and nymphs collected sitting nearby on single bushes or herb vegetation. This species is found in the Nguru Mountains of Tanzania.

Etymology. This species is named after the Nguru Mountains and the montane zone in which it occurs.

Dioncomena versicolor Hemp, sp. nov.

https://zoobank.org/9A696474-1FB6-4318-8412-94A41C74F076 Figs 2I, 13A–C, 15A, B, D, E, 19, 21, 22O, 26I, J, 30, 36

Type material. *Holotype* male. Tanzania, Uluguru Mountains, montane forest above Morningside, 6°53'46"S, 37°40'14"E, 1600 m, February 2016. *Paratypes.* 233, 2, 2, same locality as holotype and February 2017 and March 2020. Depository: CCH.

Description. Male. General habitus and color pattern. Small for Dioncomena but with a typical habitus for the genus and a striking color pattern. Head and pronotum blue with black lines or stipes. The pronotum has a green median part bordered by red-brown fasciae, with a longitudinal black stripe in the midline of the pronotal lobes, and the remaining part of the lateral lobes is blue. The abdomen has a yellow broad fascia on the lateral sides, bordered by black fascia, and a median black fascia on the tergites, with a blue venter. The legs are predominantly black, with the hind femora's basal parts in red-brown (Fig. 15A). Head & antennae. The fastigium of the vertex is compressed, narrower than the scapus, and sulcate above, typical for the genus. Thorax & legs. The posterior part of the lateral lobes is not markedly inflated. The fore coxa lacks a spine, only a blunt knob is present. The fore, mid, and hind femora have only a few very tiny spinules ventrally in the apical area. The fore tibia has a ventral double row of irregularly set small spinules and a pair of short ventral spurs. The mid tibiae have a ventral double row of black spinules, with the apical part's spinules only slightly hooked. Tegmina & wings. The tegmina and wings are black with an elongated blue field at the base (Fig. 15A). The stridulatory file on the underside of the left tegmen is about 1 mm or less long, with around 54-55 teeth. The teeth are densely set along the length, with the apically teeth getting smaller and more widely set. The file is slightly downcurved in its apical part (Fig. 2I). Abdomen. The tenth abdominal tergite is black and incurved at the posterior margin (Fig. 13A, B). The cerci are laterally flattened, especially at the apex, green with a black tip (Fig. 13A-C). The subgenital plate is longer than wide, u-shaped incurved medially (Fig. 13C).

Female. The female has a similar habitus to the male but lacks the male's colorful pattern, with mostly brownred and green colors. The head, pronotum, tegmina, and body lack the blue parts present in males, and the tegmina are brown rather than black (Fig. 15B). The ovipositor is small and upcurved (Fig. 15F), and the subgenital plate is small, triangular, with an evenly curved posterior margin (Fig. 15E).

Measurements, (mm) males (n = 3). Body length 10.4–11.5. Length of pronotum 3.1–3.3. Length of tegmina 18.5–19. Length of hind femur 15.5–16.0.

Measurements, (mm) females (n = 2). Body length 11.5–13.5. Length of pronotum 2.8–3.0. Length of tegmina 17.7–18.0. Length of hind femur 16.1–16.2. Ovipositor 4.5–4.6.

Phenology. Similar to *D. ngurumontana* sp. nov. and *D. tanneri*, this species likely has only one generation per year, which is an adaptation to the cooler temperatures found in montane elevations. Adult specimens were only collected twice, in February 2016 and March 2020. During all other months when the forest was visited (March, April, June, August, November 2016, February, November 2017, April 2019, October 2020), no adult specimens were observed.

Habitat and distribution. This species can be found in montane forests (1800–2100 m) along open paths and clearings in the Uluguru Mountains of Tanzania. Song. See Bioacoustics.

Etymology. Named for its distinct and colorful pattern, as reflected in its Latin name, *versicolor*, which means variegated or colorful.

Diagnosis. D. versicolor sp. nov. and D. ngurumontana sp. nov. are similar in morphology, but can be differentiated by the number of teeth on the male stridulatory files (over 50 in *D. versicolor* sp. nov. and 32 in *D. ngurumontana* sp. nov.) and overall color pattern, which is a stable character in Dioncomena. Both species are the sister group to D. tanneri, endemic to the Usambara Mountains (Fig. 15C, D). D. tanneri has a compact stridulatory file with about 35 teeth, similar to D. ngurumontana sp. nov. All three lack a median dark stripe on the pronotum, but have a blue (males of D. versicolor sp. nov. and both sexes of D. ngurumontana sp. nov.) or green (females of D. versicolor sp. nov. and both sexes of D. tanneri) colored medial area bordered by brownish fasciae mottled or bordered with white or black areas, while the rest of the pronotum is green, blue, yellow, or hazel (see Figs 12, 15). The tenth abdominal tergite and male cerci are similar in all three species (Fig. 13). See key for differentiation from other species. For song descriptions see Bioacoustics section.

D. zernyi Ragge, 1980

Figs 2G, 16, 19, 21, 22M, 26E, F, 30, 36

Note. Ragge (1980) only described the male of *D. zernyi* from a single specimen collected at Lake Malawi (Lake Nyasa, Randberge) and did not describe the female, as the only individual that could have been conspecific with the new species was collected at another locality (near Songea) and differed considerably in size and general color pattern (stored in NHMW). We collected a large series of both males and females of *D. zernyi* in the Udzungwa Mountains, where it is a common species, and describe the female here. Further information on this species is also given in Hemp (2021).

Both male and female *D. zernyi* are colorful, with a pattern of black tegmina, a green body, and legs with some white, yellowish, and blue parts (Fig. 16A–D). Males especially have bluish parts on the pleura, face, and cerci (Fig. 16A). A dark stripe is present dorsally on the pronotum, ending at the margin to the metazona of the pronotum, and not reaching the posterior margin of the pronotum (Fig. 16D). The hind tibiae are uniformly light brown in both sexes.

The male of *D. zernyi* is characterized mainly by its ninth abdominal tergite, which is produced posteriorly, covering most of the tenth abdominal tergite (Fig. 17A). Additionally, the last few tergites are profusely hairy above. The 10th abdominal tergite is raised at its posterior margin and has a deep, circular gap in the middle. The male cerci are rather thick and densely covered with hairs. The stridulatory file is slightly undulating with large and widely set teeth on its inner side, about 10 very densely set teeth in the middle, and smaller and again more widely set teeth at its apical part (Fig. 2G). The file has about 42–45 teeth.



Figure 16. Male (A, C, D) and female (B) Dioncomena zernyi.



Figure 17. Morphological details of D. zernyi. A. Lateral view on male apex; B. Ovipositor; C. Female subgenital plate.

Material examined. All Tanzania: $13\Im$, $10\Im$,

Description of the female. In habitus, size and color pattern similar to the male (Fig. 16B). The ovipositor is typical for the genus, rather small and upcurved, serrated at the valves (Fig. 17B). The subgenital plate is triangular with a v-shaped indentation at its posterior margin (Fig. 17C).

Measurements, (mm) males (n = 6). Body length 14.4– 15.5. Length of pronotum 3.1–3.2. Length of tegmina 22–24. Length of hind femur 18.5–19.1.

Measurements, (mm) females (n = 6). Body length 17.2–18. Length of pronotum 2.7–3.2. Length of tegmina 22.5–25. Length of hind femur 19.7–21.0. Ovipositor 4.1-4.4.

Biology. *D. zernyi* individuals were frequently observed in groups on forest paths and clearings. Males, similar to *D. ornata*, often perched openly on branch tips while females were spotted in lower vegetation nearby.

Habitat and distribution. *D. zernyi* inhabits lowland wet to submontane forests and is found in the Udzungwa Mountains of southern Tanzania, which is also the type locality according to Ragge (1980).

Song. See Bioacoustics.

Diagnosis. Male *D. zernyi* can be easily distinguished by the produced 9th abdominal tergite and the dense cover



Figure 18. Nymphal stages of *Dioncomena ornata*. A, B. Freshly hatched L1, Magoroto Forest Estate, East Usambara Mountains; C. L3 stage; D. L5 nymph.

of hairs on the last few tergites. Females exhibit a coloration pattern similar to males and have a V-shaped subgenital plate that is indented at its posterior margin (Fig. 17C). Syntopic species belonging to the *D. jagoi*group, such as *D. magombera* sp. nov. and *D. sanje* sp. nov., have entirely different coloration patterns.

Dioncomena ornata Brunner von Wattenwyl, 1878

Figs 2F, 18, 19, 21, 22J–L, 23, 24, 25, 28A–C, 30, 35C, D, 36

Dioncomena superba Karsch, 1889. Syn.

Biology. Female *Dioncomena ornata*, as well as *D. flavoviridis* sp. nov., *D. tanneri*, and *D. sanje* sp. nov., deposit their eggs into the ribs of leaves or stems of small branches. A female collected from Kazimzumbwi Forest Reserve near the coast of Dar es Salaam deposited eggs in December 2015, with the first nymphs hatching in February 2016 and molting into adults in April 2016.

dez.pensoft.net

Another female collected from Magoroto Forest Estate in the East Usambara Mountains laid eight eggs into the midrib of a leaf on August 31, 2019. The first L1 nymph hatched on November 3, 2019, while the last nymph emerged on December 30, 2019, almost two months later. It takes about two to four months for nymphs to develop into adults (Fig. 18).

In the field, individuals of *D. ornata* were often observed in clusters on certain bushes, with males perched at the tops of branches and females gathering further down. In contrast to *D. flavoviridis* sp. nov. and *D. sanje* sp. nov., males of *D. ornata* transfer only small spermatophores to females during mating. However, in the three observed copulations, the process lasted 60 minutes or longer, unlike the other two species.

Phenology. *D. ornata* adults were collected yearround in lowland and coastal forests, while at higher elevations in the submontane zone, such as Amani in the East Usambara Mountains or Lutindi forest in the West Usambara Mountains, only one generation per year was present, with adult individuals rarely collected between April and October. In the Uluguru Mountains, where D. ornata was screened from 2016, the species was only encountered once in March 2020 at elevations between 1700 and 2100 m, indicating that its development is likely triggered by temperature and that only one generation is produced in the montane zone. In Zanzibar, D. ornata probably develops only one main generation per year, with adults found from December to April, with highest abundance in February, while only a few individuals were found in October 2018, and the species was not observed during other checks in October (2016, 2017). Eggs from D. ornata laid in the laboratory in February 2022 hatched at the end of May 2022, with the first adults molting at the beginning of August 2022. However, laboratory conditions make it difficult to exclude the possibility that high temperatures and constant moisture may have triggered earlier hatching.

Habitat and distribution. *D. ornata* is a species of clearings and forest paths, distributed from coastal to montane forests in Kenya and Tanzania.

Notes on *D. ornata* from Zanzibar and mainland Africa. In 1878, Brunner v. Wattenwyl established the genus *Dioncomena* based on specimens of *D. ornata* collected on Zanzibar. Later, Karsch (1889) described *D. superba* from the East Usambara Mountains, noting that the new species differed from Zanzibar specimens only in its color pattern. Ragge (1980) compared a large series of specimens from mainland Africa and Zanzibar and concluded that the differences between the two populations were only in color pattern, while other features such as stridulatory files, the 10th abdominal tergites in males, and general measurements were similar. Therefore, he synonymized *D. superba* with *D. ornata*.

However, since Ragge only examined dried specimens and did not see alive specimens from Zanzibar and various mainland areas, he may not have been aware of the significant differences in color pattern. Zanzibar populations are distinctly red and black, while mainland specimens never show any red in their color pattern but often have vivid turquoise stripes (see Fig. 35C, D). Generally, the color pattern in *Dioncomena* species, including the widespread *D. ornata* from various mountain ranges and along the coast, is highly stable, suggesting that subspecies status should be considered for mainland populations of *D. ornata*. Further studies on genetics and chromosomes are needed to clarify the status of the Zanzibar and mainland populations.

Dioncomena tanneri Ragge, 1980

Figs 2H, 13D, 15C, D, 19, 21, 22N, 26G, H, 28D, 30, 36

Notes on biogeography and phenology. Dioncomena tanneri is exclusively found in the Usambara Mountains. Despite extensive screening of various forests in the West Usambara Mountains (such as Magamba, Shagayu, Ambangulu, and Lutindi forest remains), D. tanneri individuals were only found in Mazumbai Forest Reserve, where they were observed in forest clearings and in tall herb vegetation and low bushes along a sunny road through the forest. The reserve was screened for almost all months of the year, but D. tanneri individuals were only captured during the warm period between December and April. A single female that was either conspecific or closely related to D. tanneri was discovered in the montane elevations of the Nilo Forest Reserve in the East Usambara Mountains. Further investigation is required to determine whether D. tanneri is present at montane elevations in the East Usambara Mountains, or if a closely related species has evolved in these forests.

Biology. Females caught in March 2021 along a road passing through Mazumbai Forest Reserve laid numerous eggs onto thin branches in early April 2021. The first nymphs hatched in mid-September 2021 and became adult at the beginning of December 2021. Development took roughly two and a half months from L1 to the adult. When placed together in captivity, *D. tanneri* fed on each other once individuals became weak or died. This indicates that *Dioncomena* species are partly carnivorous, despite the fact that nymphs were solely reared on herb vegetation such as *Taraxacum officinale*. In the field, individuals were frequently found clustered, with several males and females located in close proximity to one another. However, no individuals were observed in other suitable locations along paths or on clearings.

Habitat and distribution. *Dioncomena tanneri* is typically found along open forest paths and clearings in the montane zone. It is restricted to the Usambara Mountains.

Key to the species of *Dioncomena* (males) (adapted from Ragge (1980) and Hemp (2021))

1	10th abdominal tergite flap-like elongated and downcurved. Lowland and coastal forests Tanzania D. scutellata Hemp, 2017
_	10 th abdominal tergite not flap-like elongated and downcurved
2	Without a variegated color pattern, predominantly dark on head, pronotum and body. Also, pronotum predominantly of
	uniform dark color, without fasciae, except for margins of pronotal lobes bordered by light thin fasciae. Zambia
_	With a variegated conspicuous color pattern of bright colours on head, pronotum and body contrasting with the black or
	dark tegmina. Pronotum with a median dark or light stripe and mostly differently colored than the pronotal lobes3
3	Fore wings with a shiny surface. Most of the costal, radial and medial areas translucent with a regular, ladder-like ar-
	rangement of crossveins. ZambiaD. nitens Ragge, 1980
_	Fore wings opaque with a matt surface and largely irregular crossveins 4
4	10 th abdominal tergite with a median dorsal protuberance. Malawi
_	10 th abdominal tergite without a median dorsal protuberance

 9th abdominal tergite not or produced posteriorly but not hairy above	5	9 th abdominal tergite markedly produced posteriorly and profusely hairy above. Lowland forests Southern Tanzania D. zernvi Ragge, 1980
 9th abdominal tergite produced somewhat posteriorly, covering most of the 10th abdominal tergite. Stridulatory file clearly divided into three parts of similar length, one with coarse, one with fine and one with semi-fine teeth (see Fig. 2F). Widespread in lowland forests of the Eastern Arc Mountains, on Zanzibar and coastal forests of Kenya and Tanzania	_	9 th abdominal tergite not or produced posteriorly but not hairy above
 9th abdominal tergite unmodified, not covering most of the 10th abdominal tergite. Stridulatory file not clearly divided into three parts of similar length	6	9 th abdominal tergite produced somewhat posteriorly, covering most of the 10 th abdominal tergite. Stridulatory file clear- ly divided into three parts of similar length, one with coarse, one with fine and one with semi-fine teeth (see Fig. 2F). Widespread in lowland forests of the Eastern Arc Mountains, on Zanzibar and coastal forests of Kenya and Tanzania
 Pronotum without a dark median stripe	-	9 th abdominal tergite unmodified, not covering most of the 10 th abdominal tergite. Stridulatory file not clearly divided into three parts of similar length.
 Pronotum with a dark median stripe	7	Pronotum without a dark median stripe
 8 Stridulatory file with fewer than 40 teeth	_	Pronotum with a dark median stripe
 Stridulatory file with more than 40 teeth. Endemic to the Uluguru Mountains	8	Stridulatory file with fewer than 40 teeth
 9 Pronotum with an uninterrupted green central stripe bordered lateral black (male) or white to yellowish (females). Endemic to the montane zone of the West Usambara Mountains	-	Stridulatory file with more than 40 teeth. Endemic to the Uluguru Mountains
 Endemic to the montane zone of the West Usambara Mountains	9	Pronotum with an uninterrupted green central stripe bordered lateral black (male) or white to yellowish (females).
 Central pronotal stripe interrupted by black transverse line (males) or diffuse brownish area (females) at around the middle. Endemic to the montane zone of the Nguru Mountains		Endemic to the montane zone of the West Usambara Mountains D. tanneri Ragge, 1980
 middle. Endemic to the montane zone of the Nguru Mountains	-	Central pronotal stripe interrupted by black transverse line (males) or diffuse brownish area (females) at around the
 Dark median stripe on the pronotum not extending to the hind margin. Stridulatory file with more than 70 teeth, arranged much more densely towards the centre. Zambia and MozambiqueD. grandis Ragge, 1980 Dark median stripe on the pronotum extending to the hind margin (near which it becomes wider)		middle. Endemic to the montane zone of the Nguru Mountains
 Park median stripe on the pronotum extending to the hind margin (near which it becomes wider)	10	Dark median stripe on the pronotum not extending to the hind margin. Stridulatory file with more than 70 teeth, ar-
 Dark median stripe on the pronotum extending to the finite margin (hear which it becomes wher)		ranged much more densely towards the centre. Zambia and Mozambique
 Dark median stripe on the pronotum solid, covering the whole of the metanotal disc	- 11	Dark median stripe on the pronotum extending to the finite finite finite median stripe on the proportion solid, covering the whole of the metanotal disc.
 and median stripe of the profistant separating into two stripes at metazona, forming green of yenow triangular patent on metazona of pronotum		Dark median stripe on the pronotum senarating into two stripes at metazonal forming green or vellow triangular natch
 Pronotal median stripe pitch black; thick along length and thus only slightly expanded at posterior part to fully cover the metanotal disc. Stridulatory file with around 40 widely spaced teeth (Fig. 2B). Colline to submontane forests Nguru Mountains		on metazona of pronotum
 the metanotal disc. Stridulatory file with around 40 widely spaced teeth (Fig. 2B). Colline to submontane forests Nguru Mountains	12	Pronotal median stripe pitch black; thick along length and thus only slightly expanded at posterior part to fully cover
 Mountains		the metanotal disc. Stridulatory file with around 40 widely spaced teeth (Fig. 2B). Colline to submontane forests Nguru
 Pronotal median stripe narrow on pro- and mesozona, then broadly expanded to cover metanotal disc of pro- notum. Stridulatory file between 50 and 55 evenly spaced teeth (Fig. 2A). Lowland forests East Usambara and Uluguru Mountains		Mountains
 notum. Stridulatory file between 50 and 55 evenly spaced teeth (Fig. 2A). Lowland forests East Usambara and Uluguru Mountains. D. jagoi Ragge, 1980 Pronotal lobes with median dark patch. Lowland forests Udzungwa MountainsD. sanje sp. nov. Pronotal lobes without dark patch 	-	Pronotal median stripe narrow on pro- and mesozona, then broadly expanded to cover metanotal disc of pro-
Uluguru Mountains		notum. Stridulatory file between 50 and 55 evenly spaced teeth (Fig. 2A). Lowland forests East Usambara and
 Pronotal lobes with median dark patch. Lowland forests Udzungwa MountainsD. sanje sp. nov. Pronotal lobes without dark patch 14 		Uluguru Mountains
– Pronotal lobes without dark patch 14	13	Pronotal lobes with median dark patch. Lowland forests Udzungwa MountainsD. sanje sp. nov.
	_	Pronotal lobes without dark patch
14 Medial dark fascia solid (in some specimens a very thin light line is present medially), very broad covering the whole	14	Medial dark fascia solid (in some specimens a very thin light line is present medially), very broad covering the whole
pronotal disc and parts of the lateral lobes with only a yellow area along the anterior margin of the pronotal lobes being		pronotal disc and parts of the lateral lobes with only a yellow area along the anterior margin of the pronotal lobes being
 Medial dark fascia parrow divided into two parallel fasciae with a vellow or green thin line medially restricted to dorsal 	_	Medial dark fascia narrow divided into two narallel fasciae with a vellow or green thin line medially restricted to dorsal
part of the pronotal disc with lateral lobes being uniformly green or vellow-green. I owland to submontane forests along		part of the pronotal disc with lateral lobes being uniformly green or vellow-green. I owland to submontane forests along
the Eastern Arc Mountains of Tanzania		the Eastern Arc Mountains of Tanzania

Bioacoustics

Pattern of male calling songs and female responses

All studied species of *Dioncomena* produced long lasting calling songs, often with durations between one to several minutes (see Fig. 19). These songs differ from the well-known continuous and long lasting tettigoniid songs because they consist of several different elements following each other in a more or less fixed sequence and they end in a coda during or after which a female ready to mate typically responds.

Here at first the songs of the species of the *D. jagoi*group are described (in alphabetical order: *flavoviridis* sp. nov., *jagoi*, *magombera* sp. nov., *sanje* sp. nov.), then those of *ornata*-group (*ornata*, *zernyi*) and finally those of the *tanneri*-group (*tanneri*, *versicolor* sp. nov., and *ngurumontana* sp. nov.).

D. flavoviridis sp. nov.

The main part of the calling song (Fig. 19; Suppl. material 1) starts with a 25-30 s long series of relatively uniform syllables. At the beginning, the duration of these bi-parted syllables is around 40 ms (SRR 12 Hz), but increases towards the end to 55 ms with a simultaneous reduction of the syllable intervals (SRR 17 Hz). Now the amplitude modulation changes and single long (140 m) syllables are introduced in a rhythm of about 1 Hz (Fig. 20A). Shortly afterwards short (200-400 ms) silent intervals appear, always before every second long syllable. At the beginning the long syllables are sometimes produced at a lower rate and before each gap (Fig. 21). The (3-5) syllables before the gap have a much higher amplitude (typically > 6 dB) than the song before (Fig. 25). This pattern is produced for another 30 s nearly until the end of the main part. Here often a few soft syllable groups are observed.



Figure 19. Oscillograms of male calling songs of *Dioncomena* species. Overview (150-s-sections).

As long as the male does not hear a female response it produces this main part at intervals of many minutes. In the mean time long sequences of other song parts can be heard, called here ,ticking song' and ,slow song'. Some time after the end of a main part, typically very short, isolated sound elements can be heard, following each other at intervals of a few seconds - the ticking song (Fig. 22A). These elements consist mainly of an isolated impulse, sometimes accompanied by a second softer and a series of very much softer impulses. After some time they are combined with longer syllables, resulting in the ,slow song'. Its basic units are echemes repeated at a rate of about 0.5 Hz (Fig. 20B). Each echeme is made up of 10-15 short syllables, the last being an isolated impulse, and is separated from the next by 0.3-0.5 s. The short syllables (25-30 ms; ca. 20 impulses) follow each other with 5 Hz. This ,slow song' can change to the next main part. During long lasting tick sequences also isolated impulses combined with an impulse series are observed (Fig. 22B). Two males singing together can alternate (Fig. 22C).

A female ready to mate responds one to many times during the gaps which follow the high-amplitude syllables of the main part of the male song (Figs 23, 24; Suppl. material 2). Its response consists of one to several impulses, often one louder than the others. The delay of the response is about 200 ms, measured from the end of the last male syllable (Fig. 25).

D. jagoi²

The song of *D. jagoi* has some similarities to that of *D. flavoviridis* sp. nov. The main part of the calling song (Fig. 19; Suppl. material 3) starts with a ca. 60 s long series of relatively uniform syllables which show, however, some variability in amplitude modulation and rhythm resulting in an irregular echeme-like pattern. The duration of these bi-parted syllables varies between 50 and 60 ms (SRR 12–17 Hz; Figs 20C, 26A), but does not change with time, while the amplitude increases slowly and continuously. The series ends abruptly (or with a transition phase of some seconds) and 0.5 s long echemes appear, separated by intervals of about 1 s. They consist of 10–12 syllables (SRR ca. 25 Hz) with increasing amplitude (Fig. 26A). At the beginning of this final part (duration 30–60 s) some short echemes are interspersed (or they form the transition part exclusively).

Directly before the main part often a ,slow song' is observed (see *D. flavoviridis* sp. nov.). Its basic units are echemes repeated at a rate of about 0.5 Hz (Fig. 20). Each echeme is made up of 10–15 short syllables, the last being an isolated impulse, and is separated from the next by 0.5–0.8 s. The short syllables (40–50 ms) follow each other with 8 Hz. *D. jagoi* produces also ,ticking songs' (Fig. 22D) as *D. flavoviridis* sp. nov. However, the ticks are not isolated impulses but nearly always short echemes (duration < 100 ms).

D. magombera sp. nov.

The song of D. magombera sp. nov. is even more complicated than that of D. flavoviridis sp. nov. and D. jagoi. Typically, it consists of a sequence of three large parts (Fig. 19; Suppl. material 14) from which the last two may correspond to the main part in D. flavoviridis sp. nov. In the following, they are described using this name. Female sound recordings are not available. This so-called main part starts with a long (30 s), homogeneous series of short echemes (ca. 100 ms; ERR 4 Hz) containing 4-5 syllables each (SRR 30 Hz) (Fig. 26B). Each syllable is made of one large impulse and a series of softer ones its number increasing during the echeme. At the beginning of the second half of the main part these short echemes are interspersed by longer (1.5 s) and more complex combination of syllables (Fig. 26C). Each combination starts with syllables similar to that in the short echemes but then the number of soft impulses becomes larger, the single loud impulse disappears and the rhythm of the now bi-parted syllables becomes faster (50 Hz). With time, this core syllable combination becomes shorter but at the beginning and end other syllables are added (Fig. 26D) until the main part ends with a few short echemes. The first part of the song - before the so-called main part -

² Only the sound file Dioncomena jagoi_C.wav on the DVD (Hemp 2021) belongs to this species.



Figure 20. Oscillograms of male calling song of *Dioncomena flavoviridis* sp. nov. (A, B) and *D. jagoi* (C). A. Change of amplitude pattern in first half of the main part; B. Transition from ticking song to ,slow' song; C. ,Slow' song.

contains long syllable combinations quite similar to that immediately after the homogenous echeme series. Sometimes – in contact with other males? – some three-part sequences follow immediately one after another. Occasionally the males produce, ticking songs' with ticks similar (Fig. 22G) or slightly different (Fig. 22F) as in *D. jagoi*.

D. sanje sp. nov.3

The males of D. sanje sp. nov. produce very long uninterrupted sequences. During two hours of recording, for example, an isolated male made two sequences each lasting more than 20 min. These long songs consisted of two parts (section in Fig. 19; Suppl. material 8) each taking several minutes and each consisting of syllable groups followed by one or several impulses. At the beginning one type of combination (ca. 16 syllables with a duration of 30 ms each, SRR 15 Hz) is repeated in a rhythm of 0.7 Hz, but at the end it becomes shorter (1 Hz) while the syllable duration (38 ms) and SRR (19 Hz) slightly increase. Each syllable is separated from the next by a distinct gap of more than 10 ms (and a soft hemisyllable; Fig. 27A). Therefore these sound combinations are called ,gappy'. Each series is followed by a loud, short, tick-like syllable. After a somewhat irregular transition period of ca 10 s another syllable combination is heard, produced a little bit faster (1.25 Hz) (Fig. 21). Here both hemisyllables are similar in amplitude leaving no large gaps in the syllable group (Fig. 27B). This combination is called ,dense'. It is followed by a single syllable of a different type which varies in amplitude between softer and louder than the preceding group (compare Fig. 21 and Fig. 27B) and which ends with a few loud isolated impulses. The syllable is called high frequency (HF) syllable, because the carrier



Figure 21. Oscillograms of male calling songs of *Dioncomena* species. Central portion of main part of song; 20-s-sections.

frequencies of the first part are much higher than in all other song parts (Fig. 29; only very weak in Fig. 25 due to the restricted frequency range of this recording; Suppl. material 9). Outside the long uninterrupted sequences the males produce long (1–3 min) series of regularly spaced elements of a ticking song (Fig. 22H). Occasionally also short sequences of gappy sound combinations are observed (Fig. 22I).

³ Sound files Dioncomena jagoi_A, B (in text Dioncomena sp. nr jagoi A, B) on the DVD (Hemp 2021) belong to this species.



Figure 22. Oscillograms of male tick songs of *Dioncom*ena species. A–C. *D. flavoviridis*; A, B. ticks; C. alternating males; D. *D. jagoi*; E. *D. grandis* (from Naskrecki and Guta 2019); F, G. *D. magombera* sp. nov.; H, I. *D. sanje* sp. nov.; J–L. *D. ornata*; M. *D. zernyi*; N. *D. tanneri*; O. *D. versicolor* sp. nov.; P. *D. ngurumontana* sp. nov.

The females respond preferentially and regularly to the dense sound combinations (Figs 23, 24; Suppl. material 10). Their sounds follow about 50–70 ms after the end of the male impulse group (Fig. 25). If the male switches ,back' to the gappy pattern, the females stop responding. However, they react acoustically sometimes also to the gappy combinations.

D. ornata

The main part of the song of D. ornata contains two long parts (Fig. 19; Suppl. material 6). It begins with a long homogeneous series of hemisyllables (SRR 14-25 Hz (-30 Hz at 26 °C), duration 15–150 s; Fig. 28A). Only one male was found to produce bi-parted syllables (Fig. 28B). The directly following part consists of a characteristic short combination of a few sound elements (Fig. 28C) which is repeated for many seconds (repetition rate 2.3–2.6 Hz; durations up to 110 s observed). How these sound elements are produced is unclear and not all elements are found in every recording. Possibly each group results from one stridulatory movement cycle (syllable) using all parts of the complicated file (Fig. 2). Sometimes a series of syllables resembling that from the first half of the main part are found isolated without the second half of the main part. Between the main parts often single ticks or occasionally even long series of ticks can be heard, rarely



Figure 23. Oscillograms of male-female-duets in *Dioncomena* species. Overview (150-s-sections).



Figure 24. Oscillograms of male-female-duets in *Dioncomena* species. Detail (20-s-sections).

immediately before a main part. These short sounds often consist of pairs of syllables (Fig. 22K), but more complicated combinations are also observed (Fig. 22J, L).

The females respond only during the second half of the main song (Figs 23, 24; Suppl. material 7). Typically, the responses are registered 50–150 ms after the end of the longest part of the short combination (Fig. 25).

D. zernyi

From *D. zernyi* only few recordings are available. According to the data, the main part of the song (uninterrupted part) is relatively short (Figs 19, 21; Suppl. material 13). It starts with a series of hemisyllables with an irregular but slowly increasing SRR (e.g., 2 Hz to 15 Hz in 10 s). During the next few seconds the syllables be-



Figure 25. Oscillograms of male-female-duets in *Diocomena* species. Detail (3-s-sections).

come bi-parted until the pattern changes into a sequence of short isolated syllables (or echemes?) (SRR 5 Hz; Fig. 26E). This part lasts about 5 s. Then the singing continues with a kind of ticking song with elements separated by intervals of about 3-6 s (Fig. 22). This ticking song is sometimes heard for hours without the main part. Before the main part often the male produces short echeme sequences (Fig. 26F).

D. tanneri

Also from D. tanneri only few recordings are available. In structure, the song has some similarities to that of D. versicolor sp. nov. In the longest recording of the main part, the song starts with several combinations consisting of two different types of syllables (Figs 19, 21; Suppl. material 11). A series of about 30 syllables (SRR 14 Hz) each with ca. 12 impulses is followed by a single short syllable (1-2 impulses). After a few of these combinations one distinctly longer one of the same type is heard. Then a long series of syllables (18 s) is observed, which is relatively homogeneously in rhythm but shows changes in amplitude (Fig. 28F). After its end a short (2 s) series of bi-parted syllables (SRR 25 Hz) is produced followed by some short isolated syllables (or echemes?) (SRR 6 Hz) (Fig. 26G). These combination of two different types of echemes is repeated several times with varying durations. At the end the isolated syllables become longer (Fig. 26H) and are followed at first by one or two impulses which finally disappear.

D. ngurumontana sp. nov.

An isolated male of *D. ngurumontana* sp. nov. produced the main part of its song typically at intervals of many minutes. It often lasted about one minute and consisted of two parts (Fig. 19; Suppl. material 4). The song started with a long (ca. 50 s), homogeneous series of syllables (SRR 7 Hz) which was – after some irregular echemes – followed by a much shorter final part (Fig. 21). This



Figure 26. Oscillograms of male calling songs of *Dioncomena* species. Detail (3-s-sections). A. *D. jagoi*; B–D. *D. magombera* sp. nov.; E, F. *D. zernyi*; G, H. *D. tanneri*; I, J. *D. versicolor* sp. nov.



Figure 27. Oscillograms of stridulatory movement and song [synchronous registration of left tegmen movement (red; upward deflection represents opening, downward closing) and sound (black)] in *D. sanje* sp. nov. A. Gappy sound combination; **B.** Dense sound combination with HF-syllable (*).

,coda' began with a series of bi-parted syllables (SRR 28 Hz) and closed with a short (≤ 1 s) sequence of hemisyllables slightly decreasing in amplitude and SRR (25 to 10 Hz; Fig. 28E). In between the main parts single tick elements were observed. If a male is or has been in acoustical contact with a female it often produced much longer (up to 5.5 min documented) songs. While the coda remained similar in structure, the first part became much longer and the SRR changed often. Fast series with 15–20 Hz alternated with 6 Hz parts (Fig. 28F), both lasting several to many seconds (5–60 s). A female ready to mate responds with a series of impulse-like syllables after the male coda (Fig. 23; Suppl. material 5). Sometimes the responses overlap with the latest syllables of the male but there was no short-time relation to any male song parts as in the other *Dioncomena* species (Figs 24, 25). The response series sometimes lasted nearly one second.

D. versicolor sp. nov.

Also from *D. versicolor* sp. nov. only few recordings are available. According to the data, the main part of the song (uninterrupted part) is relatively short (Figs 19, 21; Suppl. material 12). Before this part, the song consists of 1–2 s long series of bi-parted syllables (SRR 20–28 Hz) crescendoing slightly in amplitude (Fig. 26J). These echemes are produced continuously and with silent intervals (ERR ca. 0.4 Hz) for about a minute. Then the male starts to fill the intervals with a series of isolated syllables (at first syllables (or echemes?) become longer, louder and more widely spaced (SRR 7 Hz; (Fig. 26I) 1), until after a very long (ca. 4 s) echeme the song ends. Outside this main part the male produces also a ,ticking song'. It can be heard for quite a long time and consists often of two syllables (Fig. 22O).

B Stridulatory organs

The areas containing the stridulatory organs differ clearly in structure between the left and the right tegmen. The part of the left tegmen which carries the stridulatory file at its lower side is non-translucent and shows the typical species-specific coloration like the other parts of the tegmen. In the corresponding part of the right tegmen in all species one large translucent mirror cell is found



Figure 28. Oscillograms of male calling songs of *Dioncomena* species. Detail (1-s-sections). A–C. *D. ornata*: A. Section of first part; B. Section of first part in atypical male; C. Section of second part; D. *D. tanneri*; E, F. *D. ngurumontana* sp. nov.: E. Change from fast to slow rhythm; F. ,coda⁴.

(Fig. 29A). Its frontal edge (right edge in resting animal) is distinctly elevated above the mirror plane.

The stridulatory files in *Dioncomena* species differ widely in tooth number, length and structure (Fig. 2, Table 1). The lowest tooth numbers are found in *D. ngurumontana* sp. nov. and *D. nitens*, followed by a broad range with many species similar in number and two species (*D. ornata* and *D. grandis*) with high numbers. Five species (*flavoviridis* sp. nov., *jagoi*, *sanje* sp. nov., *grandis*, *scutellata*) have longer files than the others. The variation in complexity does not seem to be correlated with any other file characteristic. Several species (*grandis*, *scutellata*, *ornata*, *zernyi*; see Fig. 2) have very unusual tri-parted files with three regions differing in file density, but even in these four species length and tooth number of the different parts vary distinctly.

The stridulatory organs of females are typical for Phaneropteridae (see e.g. Heller et al. 1997); several to many short rows of teeth on cross veins in the upper side of the right tegmen are present, while the scraper is formed by the amplified inner edge of the left tegmen.

C Spectral characteristics of the male songs

As to be expected for songs consisting of damped impulses (non-resonant song), in most species studied the spectra are relatively broad-banded with the carrier frequencies showing the highest amplitudes situated between 20 and 30 kHz (Fig. 30). Checking sonograms for spectral differences, often in some components (hemisyllables etc.) the higher frequencies (partly harmonics) are stronger than in others parts of the song (for examples see Fig. 28; details see legend). Only in D. sanje sp. nov. one special type of hemisyllable was registered with the main part having its maximum at 60 kHz (Fig. 30; green), called HF-syllable (high frequency). The syllables before and the following impulses are much lower in frequency (Fig. 31). When studied by laser Doppler vibrometry, the single mirror cell shows a narrow peak around 40 kHz (Fig. 32; n = 2 specimens: 33 kHz, 46 kHz), demonstrating a distinct mismatch of natural frequency of the mirror and the peak frequencies of the either of the call types. The left wing is completely damped and probably not involved in sound radiation.

D Stridulatory movements

After the observation that in *D. sanje* sp. nov. one syllable type has a different spectral composition from the others, we began to analyze the stridulatory movements in this species (Fig. 27). Interestingly, in the gappy as well as in the dense sound combination the most intense song parts are produced during opening movements of the tegmina. In the gappy combination the opening hemisyllables are much louder than the closing ones, and also the tick-like syllable of this combination is produced during an opening movement (Fig. 27A). In the dense combination the differences in amplitude between opening and closing



Figure 29. *Dioncomena flavoviridis* sp. nov. A. Base of male left tegmen; B. Base of male right tegmen; C. Base of female left tegmen; D. Base of female right tegmen. Scale bar: 5 mm.

hemisyllable are much smaller. The HF-syllable is also produced during an opening movement. Here the amplitude of the movement is larger than in the other syllables of the combination and the speed of the movement slower, but always the same part of the file seems to be used. Even the few loud isolated impulses are produced during the opening movement of the tegmina but with the teeth situated farer away from the articulation than that used for the other parts of the combination.

E Auditory organs

The tympanic membranes near to the auditory sensillae in the fore tibia are exposed, naked, and show no obvious modifications. However, the major input to the hearing organs is via the auditory spiracles in the prothorax, es-

 Table 1. Data on stridulatory file and size (as hind femur length)

 in *Dioncomena* species.

Species	Hind femur	File	Teeth	Remarks	Source
	(length; mm)	(length; mm)	n	on file	
flavoviridis	19.8	1.6-1.68	39-42		
jagoi	17.3	1.5	45-50-53		Ragge 1980
magombera	18.75	1.3	50		
sanje	17.2	1.4-1.5	49-53		
grandis	19,7	1.6 (1.5–1.7)	81 (75–90)	3-parted	Ragge 1980
scutellata	20.4	ca. 1.5	41	3-parted	Hemp 2017
ornata	16.7	1.2 (1.1–1.3)	92 (80-100)	3-parted	Ragge 1980
zernyi	19.5	1.05	43	3-parted	Ragge 1980
tanneri	16.4	0.98	37		Ragge 1980
versicolor	15.75	1.0	54-55		
ngurumontana	16	1	32		
takanoi	18.5	1.2	60		Massa 2021
bulla	18.6	1.2 (1.05–1.3)	49 (45–55)		Ragge 1980
nitens	15.8	ca. 1	33		Ragge 1980

pecially for higher sound frequencies (reviewed e.g. by Strauß 2019; Römer 2020). The large acoustic spiracles are permanently open, and continue into the prothoracic auditory bullae, the first parts of the auditory (acoustic) trachea (Bailey 1990). The outer parts of auditory trachea run without obvious change in diameter from the bullae to the sensory organs in the tibiae (Fig. 33). In Dioncomena, these bullae are very large - as in many phaneropterids -, but even the space before the openings is enormously enlarged due to the inflated paranota (Figs 34, 35) in many species. This structure is called prebulla. These prebullae show an impressive size variation in Dioncomena, also depending on the sex (Fig. 35, Table 2). While this variation is easily recognizable with the naked eye, it is much more difficult to quantify. Calculating relative pronotal width (overall width / overall length) gives only a first clue (Table 2), the scatter probably resulting from differently shaped pronota. Combining visual impression and measurements, prebullae are most distinct in the males of the D. jagoi-group, D. grandis and D. nitens. In females, only D. flavoviridis sp. nov. approaches or even surpasses the size of the male prebulla (Fig. 35A). The males of the other species have smaller prebullae, while they are completely missing in the females of some species.

However, not only the interspecific, but also the intraspecific variability may be quite large as can be seen in the data of *D. ornata* (Table 2, Fig. 35C, D), the only species with a relatively large number of populations studied.

Surprisingly, prebullae were discovered in a series of other East Africa phaneropterids, but always in males only. They are very pronounced in all species of the genus *Kefalia* which is morphologically similar to *Dioncomena* (Table 2, Fig. 35E). However, prebullae were found also in genera with uncertain relationship [*Merumontana*] 50

Fig. 25, for D. ngurumontana sp. nov. in Fig. 23.

Intensity

-30

Ó



kHz 90 kHz 90 Ó kHz 90 Frequency Figure 30. Power spectra of the male calling songs of the Dioncomena species studied. Asteriks in the respective color mark the positions of the analysed sounds, for D. flavoviridis sp. nov. in Fig. 23, for D jagoi in Fig. 20, for D. magombera sp. nov. in Fig. 25, for D. sanje sp. nov. see Figs 26, 29 (dense combination: blue and violett, high frequency syllable: green, gappy combination: red), for D. ornata in Fig. 27, for D. zernyi in Fig. 25E (song), Fig. 21M (ticks), for D tanneri in Fig. 25, for D. versicolor sp. nov. in

50

0



Figure 31. Sonogram of second half of the dense sound combination of Dioncomena sanje sp. nov. with HF-syllable.

Sjöstedt, 1912 (Table 2, Fig. 35E) and in some species of Ivensia Bolivar, 1890] or even placed in other tribes [Atlasacris Rehn, 1914 (Table 2, Fig. 35G)]. Some other species were also checked and no prebullae were found [from OSF: Arostratum oblitum Massa, 2015 \Diamond , \bigcirc , Pronomapyga grandis Rehn, 1914 ∂, ♀, Pro. graueri Rehn, 1914 ♂, ♀, Gabonella cothurnata (Bolívar, 1906) $\mathcal{F}, \mathcal{Q}, \mathsf{Poecilogramma annulifemur Karsch, 1887} \mathcal{F}, \mathcal{Q}, \mathsf{Poecilogramma annulifemur Karsch, 1887}$ Poe. cloetensi (Griffini, 1908) \mathcal{J}, \mathcal{Q}), Poe. striatifemur

Karsch, 1887 ♂, ♀, Pardalota asymmetrica Karsch, 1896 \mathcal{O} , \mathcal{Q} , *P. haasi* Griffini, 1908 \mathcal{O} , \mathcal{Q} , *P. karschiana* Enderlein, 1907 \Diamond , \bigcirc , *P. reimeri* La Baume, 1911 \Diamond , \bigcirc , P. superba Sjöstedt, 1913 ♂, ♀, P. versicolor Brunner von Wattenwyl, 1878 \mathcal{J}, \mathcal{Q} ; from specimens in Collectio Hemp: Odonturoides hanangensis Hemp, 2009 ♂, ♀, O. insolitus Ragge, 1980 ∂, ♀, Monticolaria meruensis Sjöstedt, 1910 $\mathcal{F}, \mathcal{Q}, M$. manyara Sjöstedt, 1910 $\mathcal{F}, \mathcal{Q}, M$. kilimandjarica Sjöstedt, 1910 ♂, ♀].

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Figure 32. Forewing vibrational response in *Dioncomena sanje* sp. nov. A. Displacement of forewings in response to acoustic stimulus. The left wing is completely damped and probably not involved in sound radiation B. Deflection through phases of one oscillation C. Top panel: velocity gain of the mirror of the right wing as recorded through laser Doppler vibrometry. Middle panel: relative intensity of a section of the ,normal call. Bottom panel: relative intensity of the HF-syllable. Note the mismatch of natural frequency of the mirror and the peak frequencies of the either of the call types.

The two bullae of the *Dioncomena* are also coupled via a membrane or 'septum' in males but not in females (Fig. 33A–F). The surface area of this connection in one micro-CT scanned male of *D. sanje* sp. nov. is ~ 0.56 mm² (Fig. 33G, H).

Discussion

Little was known at present on the biogeography, phenology, biology and the bioacoustics of species of the genus *Di*oncomena, a genus with mostly colorful species first depicted alive in Naskrecki and Guta (2019) and Hemp (2021).

A species recently described by Massa (2021) occurs in riverine and thus wet forest in Zambia while another species described from Zambia, *D. nitens*, was also collected from riverine forests in northern Zambia on the border with Tanzania and thus are probably

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restricted to riverine forests along rivers. *D. bulla* is recorded from southern Malawi, specimens in the British Museum coming from near the towns of Blantyre and Thyolo and the Mt Mulanje area (Ragge 1980). While the areas around Blantyre and Thyolo are almost completely deforested, today this species very likely is restricted to the forest reserve of Mt Mulanje in the north-west of Malawi (Fig. 36). Nothing is known about their bioacoustics and whether they are found aggregated or not, so an assignment of these species to any of the above-mentioned groups or to new groups is not possible.

The remaining known species of *Dioncomena* occur in Tanzania, Kenya and Uganda (except for *D. grandis*) and as outlined above can be divided into three groups on the basis of their habitat, their distribution, their behavior, their morphology, and their color pattern: the *ornata*-, *jagoi*-, and *tanneri*-group.


Figure 33. Outer parts of the auditory tracheae in *D. sanje* sp. nov. A–C. Female auditory tracheae in lateral (A), dorsal (B), and anterior (C) axes; D–F. Male auditory tracheae in lateral (D), dorsal (E), and anterior (F) axes; G. Male head and thorax (sagi-tal-section) showing membrane which connects the two bullae; H. Male thorax (cross-section) at the point of the membrane in G.



Figure 34. Auditory tracheae in pronotum of male *Dioncomena* sanje sp. nov. from behind, abdomen removed.

The ornata-group is comprised of D. ornata, a species widely distributed throughout forested areas in Tanzania with records also from forests in southern Kenya (Ragge 1980), D. zernvi with a distribution in southern Tanzania (Ragge 1980; Hemp 2021) and D. grandis with records in the border area between Mozambique and Zambia. D. ornata and D. zernyi have a posteriorly produced 9th abdominal tergite covering parts of the 10th abdominal tergite, in D. grandis the 9th tergite is only very slightly produced (images in Naskrecki and Guta 2019). In contrast to D. ornata and D. grandis the last tergites are hairy in D. zernyi and the color pattern differs between D. ornata and D. grandis on the one side and D. zernyi on the other. Both, D. ornata and D. zernyi are dwellers of forest clearings and show aggregation behavior - several individuals often found closely together on single bushes or the herb vegetation while on other suitable patches nearby no individuals were seen. These two species were not found syntopically up to now. Naskrecki and Guta (2019) state for D. grandis that it is relatively abundant along forest edges, thus this species occurs in analogue habitats. D. scutellata has a conspicuously flap-like 10th abdominal tergite which is unique for Dioncomena being very different from the 10th abdominal tergite of D. ornata and D. zernyi. Thus, and also since D. ornata and D. scutellata occur sym-

Species Male				Female	Aggregation behaviour	Source		
-		Pron	_ 00 0					
Pronotal lobes inflated	praebullae	rel. width	n	praebullae	Rel. width	n		
D. flavoviridis sp. nov.	yes	1.15-1.33 (mean: 1.28)	3	yes	1.09-1.16 (mean: 1.13)	6	-	
D. jagoi	yes	1.03-1.15	2	yes	1.11-1.13	2	-	
D. magombera sp. nov.	small	0.97-1.02 (mean: 1.0)	3	no		6	-	
D. sanje sp. nov.	yes	1.03-1.17 (mean: 1.08)	6	small	0.98-1.16 (mean: 1.09)	6	-	
D. ornata East Usambara	yes	0.92-1.1 (mean: 1.01)	6	small			+	
D. ornata West Usambara	yes	0.98-1.15 (mean: 1.18)	6	small				
D. ornata Uluguru (Kimboza)	yes	1.08-1.12 (mean: 1.1)	6	small			+	
D. ornata Nguru	yes	1.02-1.17 (mean: 1.08)	3	small				
D. ornata coast	yes	1.0-1.15 (mean: 1.05)	6	small			+	
D. ornata Zanzibar	yes	1.05-1.17 (mean: 1.1)	6	small				
D. zernyi	small	0.89-1.1 (mean: 1.01)	6	small			+	
D. ngurumontana sp. nov.	small	0.93-1.07 (mean: 1.0)	3	no		6	+	
D. tanneri	no	0.9-1.07 (mean: 0.96)	6	no		6	+	
D. versicolor sp. nov.	small	0.88-0.96 (mean: 0.94)	3	no			+	
D. bulla	yes	1.15						
D. grandis	yes	1.1 (n = 2)						
D. nitens	yes	1.26						
D. scutellata	yes	1.14					?	
D. takanoi	yes	0.96					?	
D. ugandana	yes	1.09-1.15		small	1.05-1.17 (mean: 1.13)	4		
Kefalia grafika Hemp, 2019	yes	1.17		no				
Kefalia laeta Hemp, 2019	yes	1.59		no				
Kefalia omorfa Hemp, 2019	yes	1.39		no				
Atlasacris peculiaris Rehn, 1914	yes	1.25		very slightly	?			OSF
Atlasacris brevipennis Massa, 2015	yes	1.11		?	?			Massa 2015
Ivensia breviala Ragge, 1980	yes	1.37		?	?			OSF
Ivensia longispina Ragge, 1980	slightly/no	1.18		?	?			OSF
Ivensia parva Ragge, 1980	yes	1.5		?	?			OSF
Ivensia scaura Ragge, 1980	slightly/no	1.16		?	?			OSF
Meruterrana elegans Sjöstedt, 1912	yes	1.52		no	0.94			
Arostratum oblitum Massa, 2015	(very) slightly			?				Massa 2015

Table 2. Expansion pronotal lobes (prebullae) in males and females of *Dioncomena* species and similar genera. Relative width (of pronotum) = pronotal width / pronotal length.

patrically, the relationship of *D. scutellata* to any of the here mentioned groups is unclear. Only if more individuals were found, the songs studied and the color pattern of living individuals compared more about the relationship of this species to other groups may be encountered. A common character between *D. ornata*, *D. grandis*, *D. zernyi*, and *D. scutellata* is a three-parted stridulatory file. Both, *D. ornata* and *D. scutellata*, are distributed throughout coastal and lowland habitats while *D. ornata* is also found at submontane to montane elevations (e.g. in the West Usambara and the Uluguru Mountains). The only two known males of *D. scutellata* were found in the East Usambara Mountains (Kwamgumi Forest Reserve) and the Pugu Hills near Dar es Salaam thus suggesting a coastal/lowland forest distribution.

The other specimens known from Tanzania are restricted to mountain ranges of the Eastern Arc Chain and form the other two groups – lowland/submontane and montane species – with each group characterized by a color pattern typical for the species of each group. The *jagoi*group (*D. jagoi*, *D. flavoviridis* sp. nov., *D. magombera* sp. nov., *D. sanje* sp. nov., and probably *D. ugandana* sp. nov. from Uganda) consists of species restricted to lowland and submontane elevations along the Eastern Arc chain with a contrasting color pattern of black and green or yellow with males sometimes having a turquoise tinge (Fig. 1). Also, as far as it can be judged from dried specimens, *D. ugandana* sp. nov., belongs to this group. In all species medially on the pronotum a black stripe is present solid black or divided into parallel lines with greenish or yellowish color between them but always running to the posterior margin of the pronotum. All studied species of the *jagoi*-group occur in closed forest and were never found to reach high abundancies at a certain locality, as observed e.g. in *D. ornata*.

The montane tanneri-group on the other hand does not show conspicuously inflated pronotal lobes, only slightly inflated in the males of some of the species and not at all in females. Individuals of these species are often found clustered and maybe due to montane elevations they also depend on open situations within forests to be able to bask and thus gain enough warmth for development. Therefore the radius addressing a female partner with the song must not be as large as in species occurring in closed forest with a low density sitting far apart as in the jagoigroup with partly strongly inflated pronotal lobes. The montane group is comprised of D. tanneri endemic to the West Usambaras, D. ngurumontana sp. nov., endemic to the Ngurus, and D. versicolor sp. nov., endemic to the Uluguru Mountains. In terms of their color pattern, only slightly inflated pronotal lobes, and occurring on clearings and open forest paths as well as exhibiting aggregation behavior they could be related to the ornata-group, however with an adaptation to montane elevations. As in the tanneri-group, males of the ornata-group also can have slightly, but also distinctly inflated pronotal lobes with differences between the single populations from small prebullae to considerably inflated ones (Table 2).



Figure 35. Dorsal view of pronotum in *Dioncomena* and related genera, indicating different degrees of widening. A. D. flavoviridis sp. nov.; B. D. sanje sp. nov.; C. D. ornata, Amani; D. D. ornata, Jozani, Zanzibar; E. Kefalia laeta Hemp, 2017; F. Meruterrana elegans Sjöstedt, 1912; G. Atlasacris brevipennis Massa, 2015 (photo OSF); 1 male, 2 female.

D. tanneri is a rare species in the West Usambara Mountains as is *D. versicolor* sp. nov. in the Uluguru Mountains. As in *D. ornata* populations found in submontane elevations, *D. tanneri* and *D. versicolor* sp. nov. only have one generation per year. In contrast to *D. ornata* where hatching of the eggs is very likely triggered by temperature and precipitation, *D. tanneri* seems to be fully adapted to a montane climate. Although eggs of *D. tanneri* laid in March 2021 were kept moist and were exposed to summer temperatures in the laboratory, nymphs did not hatch before September 2021 while *D. ornata* and *D. sanje* sp. nov. eggs hatched more or less 2 months later during the same time period and under the same climatic conditions.

Acoustics

Among bush-crickets, phaneropterines are well-known for their complicated songs. Their sounds may contain up to five syllable types and more than 1000 syllables per song unit (see Heller et al. 2015). However, species with these extremely complicated songs are not common. Species with more than 200 syllables per song unit, for example, are known only from six genera worldwide. Most Dioncomena species are above this value. They all have complex songs, strongly differing between the species (Fig. 18). Most of them have clearly structured songs with a starting, a middle and an end sequence, only D. sanje produces a continuous song lasting sometimes many minutes with two parts alternating. All species are diurnal, i.e. their songs are heard only during daytime (and sometimes at dusk). However, regular tick sounds - often for hours - were recorded in some species also at night (e.g. D. jagoi, D. zernyi, D. ornata).

Females respond very precisely at certain points of the male song (Figs 23–25) – an indication that these duets are very important for mate localization. However, what happens really before the sexes meet? Unfortunately, data from the behavior in the field do not exist. In the lab and without female contact males were observed to sit at one place for the whole day and sing. One could assume that the females approach a singing male silently – by day and night? – and start to respond (during daytime) when his song is loud enough and sufficient for her standards. In such a scenario the male ticking song could be used for a rough mate localization by the female. The last steps before the contact would have to be done by the male (strategy 3 in Spooner 1995).

During the production of the complicated songs the sounds produced during opening movements of the tegmina are louder than those during the closing movements. This was demonstrated by the recording of the stridulatory movement in *D. sanje* sp. nov., where the closing movement can sometimes even be completely mute. In the other species the sound production is not known in detail, but the structure of the file teeth suggest the same mechanism: the teeth are often curved with the tip towards the articulation (e.g., Fig. 2H) and/or the steep side of the teeth faces this direction (e.g., Fig. 2B). Sound production by opening wing movements (called ,reverse stridulation' by Mon-



Figure 36. Distribution of *Dioncomena* species in East Africa. Locality data this paper, Ragge 1980; Hemp 2017; Massa 2021; Naskrecki and Guta 2019. Source: Google maps.

tealegre-Z 2012) is rare among Tettigonioidea and among phaneropterines documented only for Phaneroptera spp. Serville, 1831 and Monticolaria kilimandjarica (see Heller et al. 2015). The stridulatory files in Dioncomena are quite diverse. However, in no species lumps (or wing stoppers) as in Ischnomela Stål, 1873 (Montealegre-Z 2012) or a bend in the file like in *Phaneroptera* (Heller et al. 2021) are found, which were interpreted as a protection against "complete separation of the wings and subsequent erroneous wing overlapping during the ongoing cycle" (Montealegre-Z 2012). However, another character of reverse stridulation, tooth spacing gradually increasing towards the anal margin of the wing (Montealegre-Z 2012), can be observed in several species, although it is not necessary for a pure-tone sound not found in Dioncomena. Within the genus, the number of stridulatory teeth varies between 30 and 100. More surprising, not only the number of teeth differs by a factor of three, but also their arrangement shows huge differences. In Dioncomena flavoviridis sp. nov. the file bears ca. 50 uniformly spaced teeth (Fig. 2B), in D. jagoi and D. magombera sp. nov. the basal end of the file differs distinctly from the rest (Fig. 2A, C), and in the three species D. ornata, D. grandis and D zernyi the file is divided into three parts of very different tooth density (Fig. 2E-G). Phaneropterines are well known for complicated files and in some cases the function of the file modification is understood (e.g., genus *Acrometopa* Fieber, 1853; Hemp et al. 2018). In *Dioncomena*, however, the situation is more complicated. From the amplitude pattern alone the use of different file parts cannot be safely predicted. The stridulatory movement is known only in *D. sanje* sp. nov., a species with a relatively simple file. Nevertheless, using this file the males are able to produce syllable types with a widely different spectral composition (see Fig. 30).

Except D. sanje sp. nov., most sounds produced by investigated Dioncomena males were relatively similar in the spectral composition (Fig. 30). The broad main peak was nearly always situated around 20 kHz. Some song parts had ultrasonic components in addition, only in D. zernyi and D. ngurumontana sp. nov. very broad-banded sounds were observed with peaks around 45 kHz. D. sanje sp. nov. males, however, produced a special type of syllables at certain points of their song. These HF-syllables have a peak at 60 kHz and only weak components with lower frequencies (Fig. 30, green curve; Fig. 31). They are placed after the dense sound combination and before the loud, short ticking sound which may trigger the female response. Possibly the HF-syllable helps the female to estimate the distance to the singing male as hypothesized for the HF-syllables in Phaneroptera (Heller et al. 2021). Surprisingly, the HF-syllables seem to be produced with exactly the same part of the file as the dense sound combination (Fig. 27B) which is much lower in frequency. In the phaneropterine Gonatoxia helleri Hemp, 2016 the males sing with different frequencies very likely by using differently structured parts of the file (Heller and Hemp 2017). The different frequencies are also not easily explained by the tegmen morphology, since as in D. flavoviridis sp. nov. (Fig. 29) and all Dioncomena species studied so far, the right tegmen bears only one large mirror cell. The mismatch of the natural frequency of the mirror and the peak frequencies of the either of the call types (in D. sanje sp. nov.) suggests that the apparent sharp tuning of the mirror is not being exploited during stridulation (i.e. matched to the tooth strike rate): a case of non-resonant stridulation. The observed tuning peak in the mirror may be the natural response of a membrane which acts to radiate all and any input frequencies or a vestigial trait of a resonantly calling ancestor.

Sounds at 20–30 kHz are certainly easily perceived by the animals since they are in the typical frequency range of tettigoniid signals. At higher frequencies the ears often become less sensitive. However, there are exceptions where the hearing threshold falls continuously until at least 40 kHz (see *Poecilimon elegans* Brunner von Wattenwyl, 1878 in Strauß et al. 2014). These special adaptions cannot be recognized from morphology and have to be studied neurophysiologically.

In some *Dioncomena* species (and some other species; see Table 2) the ears show unusual modifications, but they are probably not related to improved frequency sensitivity. The inflation of the pronotal lobes, the prebullae, have most likely evolved to increase the general auditory sensitivity and/or the directionality of the ears. The physiological function of these ears having huge auditory tracheae with left and right one touching each other are not well understood. A first detailed study was done by Ce-

liker et al. (2022), but they could not model the cross-talk between left and right ear. That this connectivity exists – similar to the situation in field crickets (Michelsen and Löhe 1995) – was already described in 2011 by Mohsin and Schul in a conference presentation. Improving sensitivity and/or the directionality would easily explain why mostly the males possess prebullae: to detect the short, rare and probably faint female signals.

But why are these structures not found in all Dioncomena species? Their presence in the closely related Kefalia (Grzywacz et al. in prep.) indicates that they evolved in the common ancestor of both, if not earlier. At least in Dioncomena the size of the lateral lobes is strongly correlated with the behavior and ecology of the species, i. e. the population density. The largest inflations of the pronotal lobes are found in species living scattered within closed forest while species living on clearings and along forests edges often found in clusters have less or not inflated pronotal lobes, especially in the females. Obviously the costs of such ears are not negligible (see Stumpner and Heller 1992; Lehmann 2012; Strauß et al. 2014) and the hearing sensitivity evolves towards an optimum but not a maximum. Unfortunately, hard data for this point are nearly completely missing (see Helversen et al. 2012) but from the variability seen in and between populations of D. ornata one could assume that here costs and benefits are nearly balanced.

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Supplementary material 1

Dioncomena flavoviridis, male calling song at 22 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 2

Dioncomena flavoviridis, male female duet at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 3

Dioncomena jagoi, male calling song at 22 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

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Supplementary material 4

Dioncomena ngurumontana, male calling song at 21 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 5

Dioncomena ngurumontana, male female duet at 21 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 6

Dioncomena ornata, male calling song at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

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Supplementary material 7

Dioncomena ornata, male female duet at 22 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 8

Dioncomena sanje, male calling song at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: https://doi.org/10.3897/dez.70.100804.supp18

Supplementary material 9

Dioncomena sanje, male calling song at 24 °C, sampling rate 192 kHz

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Link: https://doi.org/10.3897/dez.70.100804.suppl9

Supplementary material 10

Dioncomena sanje, male female duet at 21 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 11

Dioncomena tanneri, male calling song at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 12

Dioncomena versicolor, male calling song at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 13

Dioncomena zernyi, male calling song at 28 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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Supplementary material 14

Dioncomena magombera, male calling song at 23 °C

Authors: Claudia Hemp, Fernando Montealegre-Z, Charlie Woodrow, Klaus-Gerhard Heller

Data type: video file

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- Link: https://doi.org/10.3897/dez.70.100804.suppl14

<u>PENSOFT</u>.



An "American" silkmoth endemic to Himalayas, part I: life history and natural distribution of *Antheraea compta* Rothschild, 1899 (Lepidoptera, Saturniidae)

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Abstract

Females of the uncommon *Antheraea compta* Rothschild, 1899 were collected at the natural habitat in the Tibetan Sub-Himalayas, descendants of which were reared on *Quercus yunnanensis* (Fagaceae) successfully, with all the preimaginal instars recorded morphologically. Correlated characters revealed a close relationship between this taxon and New World *Antheraea* spp., suggesting more attention and protection towards this key species is necessary in the future.

Key Words

chaetotaxy, ecoregion, evolution, Kachin, Meghalaya, morphology, protection, Quercus, SEM, silkworm, Telea, Tibet

Introduction

Species of Antheraea Hübner, 1819 have long been known in the history of sericulture as excellent sources for non-mulberry silk (Peigler 1993). Research surrounding the genus has always been a focus in Lepidoptera, occupying most of the scientific works on the family Saturniidae around the world because of their spectacular appearances and considerable economic benefits. After a systematic review, Nässig (1991) proposed to classify these silkmoths into three subgenera, i.e., Antheraea, Antheraeopsis Wood-Mason, 1886 and Telea Hübner, 1819. Textiles called Chinese tussah (from Antheraea pernvi (Guérin-Méneville, 1855)), Japanese tensan (from Antheraea yamamai (Guérin-Méneville, 1861)) and Indian tasar (from Antheraea paphia (Linnaeus, 1758)) make the subgenus Antheraea the center of attention, while the golden muga silk (from Antheraea assamensis (Helfer, 1837)) produced in Sub-Himalayas renders Antheraeopsis famous (Peigler 2020). The venerable polyphemus moth (Antheraea polyphemus (Cramer, 1775)) within Telea is a cultural icon in American entomology. From southern Siberia to the Indonesian islands, from central Europe to the Japanese archipelago, the subgenus *Antheraea* occupies almost all the humid broad-leaved forests from temperate to tropical Eurasia. *Antheraeopsis* flies in Asia only south of the level of Qinling Mountains, but in any case, populations within these two subgenera are all entirely limited to the Palearctic-Indo-Malayan regions. The main habitats of *Telea* are in the Nearctic-Neotropical realms, but one putative member, namely *Antheraea compta* Rothschild, 1899 (Fig. 1), is endemic to the northeastern part of the Indian subcontinent (Peigler 1999), this disjunct distribution considered one of the core mysteries in saturniid evolution.

The original type series of *A. compta* was stated to be from "Khasia Hills, Assam, 8 $\Diamond \Diamond$, no \heartsuit [*sic*]", regarded from the beginning to be an adelphotaxon allied to *A. assamensis* within *Antheraeopsis* (Rothschild and Jordan 1899). Such judgment may have been based largely on the superficial features, especially the similar eyespots and the shared natural habitat. Subsequently, Rothschild and Jordan (1901) provided a color photo of a male *A. compta* and supplemented "The \heartsuit is similar to the \Diamond , but has a shorter and broader forewing [*sic*]". Watson (1912: pl. 2) first

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Figure 1. Living adults of *Antheraea compta*, dorsal views. **A.** \mathcal{J} , calm condition; **B.** \mathcal{J} , frightened condition; **C.** \mathcal{Q} , calm condition; **D.** \mathcal{Q} , frightened condition. Scale bar: 4 cm.

illustrated the female, captured at the type-locality. Packard (1914: 197) cited this taxon without additional comments, while Conte (1919: 14-15) and Seitz (1926-1928: 511) continued to associate A. compta with A. assamensis. The first entomologist who recognized the problem was Bouvier (1936: 167) who definitively stated that there is a fairly high morphological similarity between the male genitalia of Himalayan A. compta and Central American Antheraea godmani (Druce, 1892), especially their threelobed valvae, although he did not transfer the former into his checklist for Telea. After a comparison with A. polyphemus, Lemaire (1978: 207) further acknowledged the strong homology with A. compta about male genital structures, a taxonomic opinion recognized in more recent works (Nässig 1991; Nässig et al. 1996; d'Abrera 2012: 126-127; Naumann and Löffler 2015), but Meister (2011: 144) still regarded A. compta as a member of the gerontogeous subgenus Antheraea, while Paukstadt et al. (2000, 2003) suggested that the issue requires further clarification. Arora and Gupta (1979: 30) drew the venations of Indian Antheraea spp. and noticed the forewing R1 [radial vein 1] of A. compta ("Maghalaya, Cherra Punji, 1220-1524 m., 1 d, 24.vii.1931 [sic]") is relatively longer than that of A. assamensis, with a more medial arising point on the anterior margin of the discal cell, but those two authors did not discuss the New World taxa.

Except for Khasi Hills, specimens of *A. compta* have also been collected from "Assam, Jaintia Hills... 12 Juill. 1922 [*sic*]" and recorded by Bouvier and Riel (1931: 53), subtropical forests of the two areas were formerly in Assam, but belong to Meghalaya today (Gupta 2000); furthermore, a male moth from the adjacent Hahim of Assam was reported by Peigler (1999). Bryk (1944) published a more distant record of specimens mentioned as *A. compta* discovered at "Kambaiti, 2000 m, 9.VI–17.VI [*sic*]" [Kanpaikti Sub-Township, Kachin State] in northeastern Burma by the entomological expedition of René Malaise in 1934 (specimens viewed by

Richard S. Peigler in Stockholm in 2005, personal communication to Liu from Peigler on 31 Aug. 2022). The third core population of the species inhabits southeastern Tibet (Fig. 2), first noted as "Motuo [Metok] County... 2120 m, VII.2013 [*sic*]" by Naumann and Löffler (2015) (a separate species? see below), and in 2019, living material from the same ecoregion was unsuccessfully reared on *Quercus* sp. (Fagaceae), died in L₃ without detailed description (Naumann and Nogueira 2021), but suggested the caterpillars "fit very well with typical habitus of *Telea* larvae [*sic*]".

The above mentioned moths were collected at upland mid-altitudes (ca. 1000–2500 m) in the height of summer, basically June-July (Bouvier and Riel 1931: 53: "11 Déc. 1903 [*sic*]" possibly invalid), so the species is considered to be a strictly univoltine Himalayan flyer. It must be admitted that specimens of *A. compta* are rare in collections worldwide, so obviously knowledge of its complete preimaginal stages is of great significance for our understanding of the evolutionary history of the genus *Antheraea* or even the family Saturniidae.

Material and method

INSIZE 1108-150C 0-150 mm / 0.01 mm (\pm 0.02 mm) was used to measure general lengths. XINGYUN FA1204E 120 g / 0.0001 g (\pm 0.0002 g) for recording weights. BENETECH GM1365 (\pm 2 RH%; \pm 0.3 °C) for recording air humidity and temperatures. BENETECH GM1020 (\leq 10000 Lux \pm 3%; \geq 10000 Lux \pm 4%) for recording illuminances. PHILIPS TL 6W (UV-A, peak: 365 nm), was used for fluorescence photographs. All color figures were photographed by a NIKON D5500 with SIGMA 10–20 mm f/4–5.6 lens or LAOWA 60 mm f/2.8–22 lens. ZEISS GeminiSEM 360 was used for the SEM observations and photographs, based on sputter-coated samples of 2 ova, 6 L₁, 1 L₅, 1 L₆ and 1 cocoon of *A. compta*. The



Figure 2. The natural habitat of *Antheraea compta* in southeastern Himalayas. Mêdog County, Tibet Autonomous Region, China, 2122 m. 28 Jun. 2021.

Terms involving continuity in time or space, the corresponding numbers use the subscript format, including: $L_{1-6} = 1^{st}-6^{th}$ larval instars; $T_{1-3} = 1^{st}-3^{rd}$ thoracic segments; $A_{1-10} = 1^{st}-10^{th}$ abdominal segments.

Structures not having the above relationship between each other are cited: S = stemma [ocellus]; BaS = sensillum basiconicum; ChS = sensillum chaeticum; TrS = sensillum trichodeum; PIS = sensillum placodeum; CaS = sensillum campaniformium; DiS = sensillum digitiformium; StS = sensillum styloconicum. If necessary, ending with Arabic numerals (non-subscript) for coding (e.g., "S1", "ChS1"). Classification of the sensilla mostly consults some lepidopterous works, i.e., Dethier (1937, 1941), Schoonhoven and Dethier (1966), Grimes and Neunzig (1986a; 1986b) and Faucheux (1999: 247-280). Ryan (2002: 113-114) expressed that the term "chaetic" is applicable to thicker-walled bristles or spines, the word "trichoid" means slender and hair-like, and both can be used for chemo- or mechanosensilla (Zacharuk and Shields 1991; Keil 1999; Shields 2008), so they are sometimes hardly distinguishable externally. Schneider (1964) thought such definitions are strictly morphological, the former "distinguished by a specialized and flexible circular membrane at the base [sic]", and the latter "without any specialized basal cuticular ring serving as articulating membrane [sic]". In addition, the word "sensillum (sensilla)" is used in figures only for some specified structures which are borne on antennae, maxillary palpi, maxillary mesal lobes and labial palpi. Here are labelled other primary setae and pores on labrum, mandibles and maxilla-hypopharynx-labial complex into only "lateral (L)", "medial (M)", "dorsal (D)" and "ventral (V)" in figures, but does not rule out that they may have special sensory functions.

Larval chaetotaxy, described below as far as possible, follows the universal terminology named in earlier Lepidoptera publications, primarily based on Heinrich (1916), Gerasimov (1935) and Hinton (1946), with also the reviews by Chu (1956), Stehr (1987), Piao and Lee (1998) and Hasenfuss and Kristensen (2003). Additional works treating the standard setal coding of the family Saturniidae were consulted, of which Pease (1960), Heppner and Wang (1987) and Rougerie and Estradel (2008) are examples. The abbreviations of general areas are as follows: O = ocellar [stemmatal]; SO = subocellar [substemmatal]; F = frontal; AF = adfrontal; C = clypeal; G = genal [microgenal/midgenal]; A = anterior; V = ventral; SV = subventral; L = lateral; M = medial; XD = tactile dorsal (on the anterior margin of prothoracic shield and near the dorsal midline); D = dorsal; SD = subdorsal; MD = microdorsal [vertical]; P = parietal [posterodorsal]. Combined with these directional terms, Arabic numerals (non-subscript) and lowercase letters respectively code related primary setae and pores of the head (e.g., seta "SO1", pore "MDa"). The term "pore" for text below may appear to be depressed (pierce the cuticle, or not) or elevated. Further, the term "palpifer" is only used for the maxillae in this work, whereas "palpiger" is considered as a part of the labium, although some entomologists used the latter term within the maxillae (e.g., Peterson 1948: 119; Schoonhoven and Dethier 1966).

Nässig (1989) and Deml and Dettner (2002) classified saturniid scoli focusing on their basal morphology and functionality (secretions), but this article only divides related primary setae into the following four conditions expressed by Roman numerals on the setal map of T_1-A_{10} (Fig. 3); each of them is considered as a "term" for modifying singular or plural nouns, hyphenated with a general area abbreviation (e.g., seta(e) "D-I", chalaza(e) "D-I", area(s) "D-I"), distinguished in detail with final Arabic numerals (non-subscript) if necessary (e.g., seta(e) "D-I1", seta(e) "D-I2"):

I = For describing a single seta, or the structure/location in which it resides [uni-setal]. If used for the



Figure 3. L_1 of *Antheraea compta*, the setal map, lateral view, with only the primary chaetotaxy coded. The setae of cephalic regions and legs T_{1-3} are not shown, proleg A_{10} displays the mesal surface, the ventral midline constitutes the bottom margin of A_{1-9} .

plural, for example, several setae within the designated area, then each seta is treated as an individual existing independently which could be objectively distinguished from others.

- II = For describing a pair of setae (n = 2), or the structure/location in which they reside collectively [bi-setal]. If used for the plural, for example, several setal pairs within the designated area, then each pair is treated as an individual existing independently which could be objectively distinguished from others.
- III = For describing a cluster of setae (n > 2), or the structure/location in which they reside collectively [multi-setal]. If used for the plural, for example, several setal clusters within the designated area, then each cluster is treated as an individual existing independently which could be objectively distinguished from others.
- IV = For describing uncertain condition on the designated structure/location [uni/bi/multi-setal].

Results

Morphology of preimaginal instars

Unless otherwise specified, numerical (metric) data was based on single normal individual in this chapter, and the fluorescence tests are only valid for naked eye vision.

Ova (Figs 4, 8A)

Tri-axial ellipsoid, ca. 3.71 mm (length) × 3.32 mm (width) \times 2.18 mm (height) (Fig. 4A–D). The micropylar zone is relatively flat, the external formation of rosette is combined by polygonal imprints of follicle cells (Fig. 4F, G). Other areas of the exochorion covered reticular crests [chorionic sculptures], walls generally heighted in ca. 18.7-30.4 µm and widened to ca. 27.1-34.8 µm, the begirded regions shaped into irregular subcircles with comparatively smooth surfaces in most cases (Fig. 4E), but in the circumferential zone of the ovum (except the micropylar zone) (Fig. 4B, C), some of such fragments and their walls formed into special spongiform (Fig. 4H), decorated as darker color (Figs 4A, 8A). The aeropyles (widths = ca. 2.32-12.1 µm) dispersedly located at intersections of the network except the micropylar part (Fig. 4E). Aeropyle crowns (widths = ca. 16.6–37.9 μ m) are not fully developed (incomplete or missing) and only localized to the vertices of the spongy polygons (Fig. 4I). The hydrophilic ovum shell is colored mostly opaque white under dry conditions, but becomes translucent after being sprayed with water causing the internal embryo to be visible (Fig. 4A), while the aeropyles are the major pathways for water desorption possibly (Fig. 4E). The chorionic interior is multihole mainly superimposed by lichen-like fillers (Fig. 4J), such minute lobes are hung loosely in more external (Fig. 4K), and stacked densely as multiple tiers in more internal (Fig. 4L). Chorionic thicknesses (excluding re-



Figure 4. Ova of *Antheraea compta*. **A.** Fertilized ovum; a: dry condition; b: wet condition; **B–D.** Unfertilized ovum (the flat zones are critically sunken); **B.** Micropylar side of the circumferential zone; **C.** Non-micropylar side of the circumferential zone; **D.** Flat zone; **E.** Flat zone; a: dry aeropyle; b: wet aeropyle; **F.** Micropylar zone; **G.** Micropylar zone, the center; **H.** Circumferential zone, spongiform fragments and their walls; **I.** Circumferential zone, spongiform fragments and their walls; **I.** Circumferential zone, spongiform fragments and their walls; **J.** Chorionic cross section; a: exochorion; b: exo-fillers; c: endo-fillers; d: endochorion; **K.** Chorionic exo-fillers; **L.** Chorionic endo-fillers 2 μm. Scale bars: 2 mm (**A**); 500 μm (**B**, **C**); 1 mm (**D**); 40 μm (**E**, **I**); 5 μm (**G**); 2 μm (**K**, **L**); 100 μm (**F**, **H**); 10 μm (**J**).

Larvae

L₁ (Figs 3, 5–7, 8A–C)

Head capsule is 1.78 mm width with shiny black appearance, whose anteclypeus is gray and longitudinally folded. Bearing 17 pairs of longer primary setae namely P1, P2, L1, AF1, AF2, F1, C1, C2, A1, A2, A3, O1, O2, O3, SO1, SO2 and SO3, they are pointed and with a smooth surface and sometimes slightly helical-shaped (Fig. 5A, D, E), seta P1 is the longest (length = 1.16 mm), seta F1 (length = $182.5 \mu m$) is the shortest. There are 4 other pairs of minute primary setae (lengths = ca. 7.4–8.1 μ m) erectly, i.e., MD1, MD2, MD3 and G1 which ended with rounded apexes (Fig. 5A, B, J). A total of 10 pairs of primary pores appeared on the head capsule, coded as Pb, La, AFa, Aa? [Pa?], Fa, Oa, Ob, SOa, MDa, and Ga (Fig. 5A–E), among them, the pores Fa (width = $21.1 \mu m$), Ob (width = 16.6 μ m) and SOa (width = 24.7 μ m) are slight raised (e.g., Fig. 5L), other ones are flat-bottomed or bowl pits with widths of ca. 9.4–12.5 µm (e.g., Fig. 5K, M-P), the deepest depression is pore Ga. A case was found that the sites of pores Pb are asymmetric, i.e., in the same specimen, they are respectively located on the inferolateral and superolateral sides to setae P2, but the former condition is normal. In addition, a few secondary setae and pores could be asymmetrically observed in individuals. S1 (width = 47.7 μ m), S2 (width = 46.3 μ m), S3 $(width = 58.9 \,\mu m), S4 (width = 50.3 \,\mu m), S5 (width = 48.1)$ and S6 (width = $46.7 \mu m$) have multiporous surface (e.g., Fig. 5I), their anisotropic wrinkles have observed on dry exuviae and alcohol-preserved specimens (Fig. 5A), but unclear if living larvae have the same feature. S1 and S6 are flatter, whereas S3 is the most elevated.

The antennal sclerites are mostly dark maroon linked with light gray antacoriae. The 2nd antennal segment is multiporous and elongated peanut-shaped, whose lower part of the sclerotized wall is embossed with slight reticular crests forming dense polygons, its longish ChS1 (length = 372.2 μ m) and ChS2 (length = 90.7 μ m) dotted dispersedly with tiny wall-pores (more obvious on ChS2) and standing lateroapically (Fig. 6A-C). Of the segment, BaS1 is dorsoapical, BaS2 and BaS3 are ventroapical, CaS1 (width = $13.2 \mu m$) is lateroproximal (Fig. 6D), CaS2 and CaS3 (widths = ca. $4.5-4.9 \mu m$) are lateroapical. Relatively, the 1st and 3rd segments of antenna have fewer pores on the walls, the latter is implanted distal BaS4, BaS5, BaS6 and StS (Fig. 6B, C). Antennal BaS1, BaS2 and BaS4 showing fingerprint-like surfaces (lined pores) and rounded tips with similar lengths of ca. 20.2-25.4 µm, alike epicuticle also observed on BaS3, BaS6 and BaS5, but the former two owning varying degrees of forky apexes (BaS3 usually has 2–4 forks and asymmetrically presents in a specimen, BaS6 is always bifurcated) with respective maximum lengths of 15.6 μ m and 8.7 μ m, BaS5 is an elevated pimple in 5.8 μ m height. The external surface of uniporous StS (length = 18.0 μ m) is smoother, exhibiting sharp or uni/bis-papilliform terminals.

The labral anterior surface is sepia, shiny, arrayed primary setae L1, L2, L3, M1, M2 and M3 in pairs with plane ends, seta M2 is the longest with 204.4 µm length and other ones are ca. 84.7-178.5 µm. The primary pores Ma, Mb and Mc are ca. $9.5-16.11 \mu m$ widths, the sizes one by one incrementally (Fig. 5F). The labral posterior surface [epipharynx] is off-white principally but the mid-notch [groove] is sepia. Except the smooth margin, other area covered by white and short denticulations densely, exhibiting pointed and flatted setae M4, M5 and L4 (lengths = $82.9-93.4 \mu m$), with a digitiform seta L5 in size ca. 56.8 μ m (length) × 24.3 μ m (width), they are aporous. Symmetrically paired pores Md, Me and Mf are obvious, the latter is the biggest up to 17.5 µm width, while other two are reduced to ca. 12.3-14.0 µm (Fig. 5G). Setae L1–5 and M1–5 are clear brown, pores Ma-f are campaniform.

Each mandible has 6 teeth (4 outer and 2 inner), primarily bears a pair of neighboring setae L1 (length = 295.9 μ m) and L2 (length = 134.2 μ m), with a pimple-like pore La (width = 27.8 μ m) which is surrounded by dense subcircular pits. The posterior condyle [postartis] is a prominent smooth knob (Fig. 5F, H).

The weakly sclerotized cardo is nearly a semicircle, the stipes forms a "F" shaped sclerite whose longer margin is lying medially and the arm points to the lateral side, its anterior and posterior edges respectively array the primary setae L1 (length = $202.2 \mu m$) and L2 (length = 213.3 μ m). Setae M1 (length = 218.3 μ m) and M2 (length = 90.2 μ m) could be invariably found on the apical margin of the incomplete annular sclerites, separately belongs to the palpifer and the 1st maxillary palpal segment; the latter has a striate-wrinkled top and connecting with the maxillary mesal lobe [galea], their medial junction zone (facing to the hypopharynx) is membranous and placing many toothed setae (Figs 6E, 7A-C). The sclerotized walls encircling maxillary palpus and mesal lobe are distally multiporous, the apical membranes of the latter and the 2nd-3rd segments of the former are knot-wrinkled (Fig. 7B, G, I). Maxillary palpal CaS1-4 are lateral, thereinto CaS1 and CaS2 are pits while CaS3 (height = $1.8 \mu m$) is elevated, but both forms are applicable to CaS4 (Fig. 7A, C, D, H). Each maxillary palpus ended with BaS1-8 (lengths = ca. 5.2-5.6 μ m) which have rounded tips and many campaniform olfactory pores (Fig. 7G). Dorsal sensilla of the 3rd maxillary palpal segment are rough, PIS1, PIS2 and PIS3 in widths of ca. 5.4-7.2 µm always surround the lateral to proximal sides of DiS (length = $11.8 \mu m$; widths = $6.6 \mu m$), distal morphology of the latter is alterable with 2-4 slight apical forks in different individuals and sometimes showing a sagittal concave midline (e.g., Fig. 7E, F). Each max-



Figure 5. L₁ of *Antheraea compta*. **A.** Ventrolateral view; a: head capsule; b: antenna; c: cervacoria; **B.** Head capsule, superolateral view; **C.** Head capsule, lateral view; **D.** Head capsule, superofrontal view; **E.** Head capsule, frontal view; a: frons; b: clypeus; a + b: frontoclypeus; c: anteclypeus; d: other area; **F.** Mouthpart (partly), frontal view; a: anteclypeus; b: labrum; c: mandible; **G.** Labrum, posterior view [epipharynx]; a: the smooth marginal area; b: the hirsute area; **H.** Mandible, the inner surface; a: inner teeth; b: posterior condyle; c: adductor; d: abductor; **I.** The external surface of S3, vertical view; **J–P.** Primary seta and pores of head capsule; **J.** Seta MD3, lateral view; **K.** Pore Pb, vertical view; **L.** Pore SOa, vertical view; **M.** Pore Aa? [Pa?], lateroapical view; **N.** Pore MDa, lateroapical view; **O.** Pore La. lateroapical view; **P.** Pore Ga, lateroapical view. Scale bars: 200 μm (**A**, **D**, **E**, **H**); 50 μm (**B**); 150 μm (**C**, **F**); 80 μm (**G**); 2 μm (**I**); 5 μm (**K**, **N**, **P**); 15 μm (**L**); 7 μm (**M**, **O**).



Figure 6. L_1 of *Antheraea compta*. **A–D**. Antennae. **A.** a: antacoriae; b–d: the 1st–3rd segments; **B.** a, b: the 2nd–3rd segments; **C.** a, b: the 2nd–3rd segment; **D.** a: the 2nd segment; **E.** Ventral view; a: head capsule; b: antenna; c: mandibles; d: stipites; e: palpifer; f–h: the 1st–3rd maxillary palpal segments; i: maxillary mesal lobe; j: postmentum; k: mentum; l: prementum (posterior); m: spinneret; n: prementum (anterior); o: hypopharynx; **F.** Ventrolateral view; a: mentum; b: prementum (posterior); **G.** Anterolateral view; a: prementum (anterior); b: the lateral lobe of spinneret; c: labial palpus; **H.** Lateral view; a: prementum (anterior); b: the medial lobes of spinneret; c: the lateral lobe of spinneret; **I.** Anteroventral view; a: prementum (anterior); b: hypopharynx; **J.** The lateral margin of hypopharynx (faces to the maxilla), lateral view; **K.** Legs T₁ (seta L2 is obscured), anterior view; a: coxae; b: femur; c: tibia; d: tarsus; e: pretarsus; f: secondary [subprimary?] seta; **L.** Pretarsus of leg T₁; **M.** Crochets of proleg A₄; ventral view;. Scale bars: 100 µm (**A**, **E**); 20 µm (**B**, **D**, **F–I**, **M**); 10 µm (**C**, **J**); 200 µm (**K**); 60 µm (**L**).



Figure 7. L_1 of *Antheraea compta*. **A.** Dorsolateral view; a–c: the 1st–3rd maxillary palpal segments; d: maxillary mesal lobe; **B.** Medial view; a: mandible; b: palpifer; c: the hirsute membranous zone between the 1st maxillary palpal segment and mesal lobe; d, e: the 2nd–3rd maxillary palpal segments; f: maxillary mesal lobe; g: hypopharynx; **C.** Lateral view; a: palpifer; b–d: the 1st–3rd maxillary palpal segments; **D.** Part of the apex of the lateral area of the 2nd maxillary palpal segment; **G.** The apex of the 3rd maxillary palpal segment; apical view; **H.** Ventromesal view; a, b: the 2nd–3rd maxillary palpal segments; c: maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary palpal segments; c: maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe; d: hypopharynx; **I.** Part of the apex of the maxillary mesal lobe, medioapical view. Scale bars: 40 µm (**A**–**C**); 4 µm (**D**, **G**); 10 µm (**F**); 5 µm (**F**, **I**); 20 µm (**H**).

illary mesal lobe arranging flat-topped ChS1, ChS2 and ChS3 from the lateral to medial, they are multiporous but such perforations of the former are more obvious and on the latter two are thinner. The lengths of ChS1 are unstable and the measurements based on a single specimen are 54.7 μ m and 84.9 μ m, ChS2 and ChS3 are special chisel shaped and ca. 37.8–41.2 μ m lengths. The elevated basal columns of StS1 and StS2 are relatively smooth (less pores) with lengths of ca. 23.6–27.8 μ m, their terminal dome topped cones are morphologically look like

the maxillary palpal BaS1–8, but lengthened to ca. 8.3– 9.0 μ m (Fig. 7I) with finer pores. For each maxillary mesal lobe, BaS1 is terminally uniporous and tapered (length = 14.2 μ m), while BaS2 is rough and reduced to a small wart (height = 3.4 μ m), and, an indeterminate shaped CaS (in the same larva, respectively crater-like and spine-like) was fixedly observed on the ventroapical margin and located close to StS1 (Fig. 7B, H). On the ventral area is a very large subcircle forming a slight protrusion with weak wave-like margins marked as CaS? (Fig. 7H), it is aporous and seems to only be observed at specific angles with certain light conditions, and its function is unclear.

The postmentum [submentum] is smooth and membranous largely, the proximolateral sclerite [submentales] is adjacent with the maxillary cardo, primary seta V1 (length = $104.1 \mu m$) is close to the border with the mentum, the latter is a semicircular membrane covered by minute noncellular processes (Fig. 6E, F). The prementum [stipulae] is lyre-shaped with most areas membranous, but a crescent sclerite is inlaid proximally of the posterior surface which abutted with the mentum, primary seta V2 (length = $14.6 \mu m$) is smooth and rounded. Campaniform pores Va, Vb and Vc are ca. 4.9-5.4 µm widths, always present on the posterolateral area of the prementum (Fig. 6F). The cleft spinneret is fleshy and semitransparent, whose linguiform medial lobes [glossae] are hirsute and the pliciform lateral lobes [paraglossae] are fine-grained surfacely (Fig. 6G, H). The distance between the two labial palpi is 238.8 µm, each of them dotted with many micropores but more remarkable on the lateral TrS (length = $47.2 \ \mu m$) and medial StS, the basal and setal parts of latter are respectively 16.5 µm and 68.0 μm lengths (Fig. 6G). The distal area of the hypopharynx is smooth but the posterior lingua is covered by numerous spines (Fig. 6I, J).

The setal map and related statistics are provided here (Fig. 3; Table 1). Grounded with bright yellow on $T_1 - A_{10}$ generally but the cervacoria and venter are lower saturation. The dorsal area of T₁ dotted with three black spots, one shown between the pair of scoli XD-III and other two exhibited on the dorsolateral respectively. Each of T₂-A₈ decorated two black dots along the dorsal midline, these segments have also lateral black stripes between the levels D and L. Level SV of A₀ lying a big black dapple on each side (divided along the dorsal and ventral midlines), while the anal shield, and the lateral surface of each proleg A₁₀ appearing as a large black patch shaping nearly semicircular, the latter structure distributed 13-18 bristles on the posterior to ventral margin. All thoracic and abdominal setae are translucent, to be the longest on scoli L-III of T₁. Scoli XD-III, D-III, and SD-III bear stout brown to black setae and the latter two have significantly elevated bases; other chalazae/scoli are developed with white setae. A pair of scoli D-III are medially fused on A₈, whose fusional characteristic is similar to the case of scoli XD-III and SD-III on the anterior margin of prothoracic shield on each side. Spiracle T_1 is the largest whereas spiracles $A_{1,8}$ are relatively small, all brownish colors. The paired sclerites of coxae are unclosed annular shaped and medially fused on T₁. Coxal setae L1 and L2 are respectively located on the antero/postero-terminal areas of the sclerite, other primary setae coded as M1, M2 and M3. The femur apically bears setae M4 and M5; each tibia has 6 setae labeled M6, M7, M8, M9, L3 and L4. On the top of the tarsus, setae M10, M11 and M12 are widened with slight longitudinal crests, seta L5 is a weak hair (Fig. 6K). A thick basal lobe is displayed on the pretarsus (Fig. 6L), sometimes there are secondary [subprimary?] setae occurring on legs T_{1,3}

Table 1. L_1 of *Antheraea compta*, a quantity statistic of chalazae/ scoli of the single side (divided along the dorsal and ventral midlines), and the numbers of primary setae borne on each them (in brackets). The "?" means inconclusive.

Structures\Segments	T ₁	T3	A ₁	A ₂	A ₃₋₆	A ₇	A ₈	A ₉	A ₁₀
Scoli D-III		1(8)	1(5)	1(4)	1(4)	1(4)	1(4)	1(4)	1(9?)
Chalazae D-I	2(1)		1(1)	1(1)	1(1)	1(1)	1(1)	1(1)	
Scolus XD-III	1(3-4)								
Scoli SD-III	1(4)	1(6)	1(4)	1(4)	1(4)	1(4)	1(4)	1(6)	
Scoli L-III	1(8–10)	1(6)	1(6)	1(6)	1(6)	1(6)	1(6)		
Chalazae L-I			1(1)	1(1)	1(1)	1(1)	1(1)		
Scoli SV-III	1(4–5)	1(3)							
Chalazae SV-I			1(1)	1(1)	2-3(1)	2(1)	2(1)	2(1)	
Chalazae V-I			2(1)	2(1)	1(1)	1(1)	1(1)	1(1)	4?(1)

(e.g., Fig. 6K). The plantae of prolegs are rosybrown in lateral view, each of them arranged dark maroon crochets in uniserial heteroideous mesoseries, the numbers are 23–27 (A_{3-6}) and 26–29 (A_{10}), such hooks have solid insides and longitudinally plicated epicuticle (Fig. 6M).

L₂ (Fig. 8D-F)

The primary chaetotaxy and related fusions are unchanged to L_1 . The head capsule (width = 2.61 mm) turned into sepia color with darker ocellar area. The antennal sclerotized parts are sienna connecting with golden antacoriae, the labrum, anteclypeus and frontoclypeus are bronzed. The cervacoria is lemon, the integumentary ground color of thorax-abdomen is largely pure or yellowish green but T₁ is always paler, the prothoracic shield (with scoli XD-III and SD-III) is gradually changing to light yellow with aquamarine scoli L-III. Chalazae SV-I of A1-2 and scoli SV-III and are blue to yellow-green, other scoli L-III, SD-III, and all scoli D-III owning ultramarine to blueviolet bases in smooth, but the proximal halves of the latter two borne on T₂-A₈ have shiny silvery appearance, the maximum size always showing on scoli SD-III of A_{2,7}. Some setae are elongated to form clubbed tips which displayed on scoli XD-III of T_1 , scoli D-III of T_2 (sometimes T_{2-3}) and A₂, as well as on all scoli SD-III and L-III, such special bristles lengthened on scoli D-III of T₂ to be longer than any others. Since this larval instar, secondary hairs beginning to obviously emerge from the cephalic regions and the venter of $T_1 - A_{10}$, accompanied by the harder observing on chalazae D-I, L-I, V-I and partial SV-I. Spiracles are surrounded by amber integumentary edges. The sclerites of legs $T_{1,3}$ are sepia, the distolateral surfaces of proleg bases of A3-6 developed many black dots with secondary setae, while prolegs A10 also stretched multidirectionally their marginal bristles. The lateral plate of each anal proleg is dyed with posterior ochre, central black and anterior yellow (sometimes displaying only the former two colors), the latter two colors usually corresponding multi-pitted surfaces, the feature similarly arises in the yellowish triangular area of the anal shield. The plantar colors of prolegs A_{3-6} and A_{10} are the same as L_1 , but the crochets rowed into uniserial homoideous mesoseries with the quantities of 26-30.



Figure 8. L_{1-6} of *Antheraea compta.* **A.** L_1 , newly hatched individual feeding on the eggshell, lateral view; **B.** L_1 , drinking water, dorsal view; **C.** L_1 , feeding on the edge of leaf (*Quercus yunnanensis*), lateral view; **D.** \bigcirc , L_2 , newly molted, lateral view; **E.** \bigcirc , L_2 , dorsal view; **F.** \bigcirc , L_2 , lateral view; **G.** \bigcirc , L_3 , dorsal view; **H.** \bigcirc , L_3 , lateral view; **I.** \bigcirc , L_4 , newly molted, A_{2-8} , lateral view; **J.** \bigcirc , L_4 , dorsal view; **K.** \bigcirc , L_4 , lateral view; **L.** \bigcirc , the late period of the 4th pre-molting, the dorsal area of T_2 , frontal view; **M.** \bigcirc , L_5 , dorsal view; **N.** \bigcirc , L_5 , lateral view; **O.** \bigcirc , L_5 , epicuticle of dry exuviae, the medial surface of scolus SD-III of A_1 ; **O.** a: spiny seta; b: shiny area; c: green integument; **P.** a: shiny area; b: green integument; **Q. R.** \bigcirc , L_6 , epicuticle of dry exuviae (sampling from co-coon), the clubbed setal apex of scolus D-III of T_3 ; **Q.** Centeral area; **R.** Marginal area. Scale bars: 3 mm (A–C, I, L); 5 mm (D–F); 1 cm (G, H, J, K); 2 cm (M, N); 200 µm (O); 30 µm (P); 4 µm (Q); 20 µm (R).



Figure 9. L_6 of *Antheraea compta*. **A.** \mathcal{S} , lateral view; **B.** \mathcal{S} , dorsal view; **C.** \mathcal{S} , frontal view; **D.** \mathcal{S} , posterior view; **E.** \mathcal{S} , anal prolegs, lateral view; **F.** \mathcal{S} , lateral margin of anal shield, dorsolateral view; **G.** \mathcal{S} , head and T_{1-2} , anterolateral view; **H.** \mathcal{S} , spiracle T_1 , vertical view; **I.** \mathcal{S} , legs T_{1-3} , ventral view; **J.** \mathcal{S} , proleg A_{10} , ventral view; **K.** \mathcal{S} , ventral view; a–c: A_{8-10} ; d: sexual gland; **L.** \mathcal{Q} , ventral view; **a**–c: A_{8-10} ; d: sexual gland; **M–T.** Latero-medioapical views; **M.** \mathcal{Q} , scolus D-III of T_2 ; **N.** \mathcal{Q} , scolus D-III of A_6 ; **O.** \mathcal{Q} , scoli D-III of A_8 (medially fused); **P.** \mathcal{Q} , scolus SD-III of A_6 ; **Q.** \mathcal{Q} , scolus SD-III of A_9 ; **R.** \mathcal{Q} , scolus L-III of A_6 ; **S.** \mathcal{S} , scolus SV-III of T_3 ; **T.** \mathcal{S} , chalaza SV-I of A_1 . Scale bars: 2 cm (**A**, **B**); 1 cm (**C**, **D**); 5 mm (**E**, **G**, **I**); 2 mm (**F**, **M–T**); 1.5 mm (**H**); 2.5 mm (**J–L**).

L₃ (Fig. 8G, H)

General morphology close to L_2 , but the head capsule is paler and widened to 3.73 mm. The flash basal parts have enlarged the volume further on scoli SD-III of A2-7, especially. Supplemented long setae with club-like apexes on scoli D-III of T₃-A₁, as well as on chalazae SV-I of A1-2 and scoli SV-III. Dense coryneform bristles initiating to present on the posterior zones of the middorsal A_{2-6} , colored as yellow vividly; they are minute and cross a transverse row combined by longer and pointed setae in the same color but borne on the anterior zones of A_{3-7} . Tricolored lateral plates of prolegs A₁₀ observed in most of L₂ now shared in all individuals. More secondary hairs are exhibited principally on ventral integument. Some of them are based on dollar spots, such dots originating since L₂ are now widely distributed to level L, gradually colored from black to light brown. The marginal setae of A₁₀ are pronouncedly elongated and orientated to the posterior side. The numbers of 50-55 crochets arranged as biordinal mesoseries on each planta.

 L_4 (Fig. 8I–L)

The macroscopic pattern is essentially same as L₃, but the 5.47 mm width head capsule begins to appear more yellowish in proportions, mainly enriched on its ventrolateral and frontal zones, but the dark sepia strip ornamented on ocellar areas are still visible. The color of cervacoria is more vivid, slanted, parallel dark olive-green streaks arising between the levels SD and L of A_{1-8} . For T_2-A_{10} , the venter is clearly darker than dorsa, the dense dark spots are developing to the level SD with some secondary hairs, and the coxal apexes of legs T_{2-3} are colored lightly like T_1 . The clubbed setal apexes already occur on the longer bristles on prolegs, starting from this instar, each lateral plate of anal prolegs shows a very minute black dot on the yellow tint area with relatively fixed position, and each lateral margin of the anal shield formed into vitreum, enveloping an internal dark brown band. Plantar crochets are still biordinal mesoseries but increased to numbers of 54–60. Take L_4 as an example, for a fresh larva or during the pre-molting, the oblate setal tip could be seen white translucent, whereas the silver-reflective zones of scoli are transparent just after ecdysis but fully colored after approximately about 18-22 hours (Fig. 8I, L).

L₅ (Fig. 8M–P)

Head capsule (width = 7.33 mm) is paler distinctly, but the distribution patterns of colors are basically the same as L_4 . The cephalic setae are more strongly developed, the dotted integument reaching the level D and all the secondary hairs turned into brownish to black with longer sizes. Parallel oblique stripes lying around spiracles A_{1-8} are more evident, each spiracle is outlined by pale aquamarine margin. Scoli XD-III and SD-III on each side of prothoracic shield are highly fuse to be a unified base outwardly. The band inlaid inside the vitric margin of anal shield is now darker. The shining silvery bases of scoli D-III of T_2-A_9 , and SD-III of T_2-A_8 are already spectacular (largest on scoli SD-III of A_{2-7} still), their epicuticles are extraordinary smooth in stark contrast to the green integument, the latter is densely covered noncellular processes (Fig. 80, P). Proleg plantae are surfaced with lateral dark gray and medial white with 61–64 crochets in biordinal mesoseries. Each of the lateral plates of prolegs A_{10} is constituted by the wrinkled bright yellow-green area, the smooth dark ochre posterior margin, and a narrow black stripe between the former two.

L₆ (Figs 8Q, R, 9, 10)

The final larval instar with giant body, head capsule is 10.32 mm width and the overall color pattern is near L_{s} but more pallid (Fig. 9C, G). Combined with the high-saturation goldenrod cervacoria and the pale lemon coxae, the front margin of T, forms a bright yellow annular zone, which showed intensely fluorescent enrichment under the excitation by UV 365 nm (Figs 9G, 10B). Fluorescence was not detected in the flash bases with the clubbed setae (Fig. 10C), but weakly appeared on the yellow-green regions of the central anal shield and the lateral plates of prolegs A_{10} (Fig. 10D), the wrinkles of the latter are more obvious than those during the prior stage (Fig. 9E). Both scoli XD-III and SD-III have different numbers of primary setae during L_{2,5} which appeared as short spines, but all of these are elongated into hair-like now (Fig. 9C, G). Similar to L_{2-5} , for all scoli, only partial setae on $T_1 - A_9$ have clubbed tips (Fig. 9M-T), statistic on the single larva displayed that most setal quantities of the corresponding sites are same as L₁, but that on 12 scoli are decreased and 2 scoli are increased (Table 2). The rod-like part of the clubbed seta is smooth helical, the flaky end is paved by shallow pits densely but strongly reflection (Fig. 8Q, R). There is a significant difference in general integumentary color, i.e., 2 \bigcirc are more yellowish than 3 \bigcirc , and the shiny scoli of females are tending to be purple-red but that of males look more purple-blue (Figs 9M–T, 10A). Observed the male sexual gland ["Herold's gland"] to be a slight mark localizing on ventral midline near to As/Ao boundary (Fig. 9K), the female sexual gland ["Ishiwata's gland"] arising as two pairs of dots on ventral A_g and A_g (Fig. 9L). Distinguished from L_s, the dark spots are added to the middorsal area except the prothoracic shield, and the secondary hairs are increased on the whole body at present, but except the sizes, the glassy margins of anal shield as well as the spiracles are morphologically almost unchanged (Fig. 9F, H). Vesicular processes were observed on the distomedial areas of each tibia and tarsus, and all the medial setae (both primary and secondary) of legs T_{1-3} form white thick spines (Fig. 9I), unfortunately, it lacked a leg observation for L_{2-5} . Plantae of A_{3-6} and A_{10} bear 59-65 crochets within biordinal mesoseries (e.g., Fig. 9J). The liquid feces after feeding ended (all larval instars fed from Q. yunnanensis) is bronzed mucus (Fig. 10E), after that, $1 \circlearrowleft$ was recorded the weight as 14.77 g.



Figure 10. L_6 of *Antheraea compta*. **A.** Lateral view; a: \Im ; b: \Im ; **B–D.** \Im , under 365 nm UV; **B.** Head and $T_1 - A_1$, ventrolateral view; **C.** A_7 , lateral view; **D.** A_{10} , lateral view; **E.** \Im , the last defecation [liquid defecation] from A_{10} , lateral view; **F.** \Im , spinning the peduncle of cocoon; **G.** \Im , spinning the external part [floss] of cocoon. Scale bars: 2 cm (**A**); 1 cm (**B**, **F**, **G**); 5 mm (**C**-**E**).

Table 2. L_6 of *Antheraea compta*, a statistic based on primary chalazae/scoli which have clubbed setae, with the format "short spines + elongated hairs (how many clubbed ones)". The "<" is lower, the "=" is same, and the ">" is higher than the normal value of the corresponding locations during L_1 (see Table 1). Merged cells means the scoli are medially fused.

Segments\Areas	SV-I/III	L-III	SD-III	XD/D-III	XD/D-III	SD-III	L-III	SV-I/III
T ₁	0 + 4(1) =	1 + 7(5) =	0 + 4(1) =	0 + 4(2) =	0 + 3(2) =	0 + 4(2) =	2 + 7(4) =	0 + 4(0) =
T ₂	0 + 1(1) <	4 + 2(2) =	3 + 3(3) =	5 + 3(3) =	5 + 3(3) =	3 + 2(2) <	4 + 2(2) =	2 + 1(1) =
T ₃	2 + 1(1) =	4 + 2(2) =	3 + 3(3) =	5 + 3(3) =	2 + 4(4) <	3 + 2(2) <	4 + 2(2) =	2 + 1(1) =
A ₁	0 + 1(1) =	4 + 2(2) =	3 + 1(1) =	3 + 2(2) =	1 + 1(1) <	4 + 1(1) >	$4 + 1(1)^{<}$	0 + 1(1) =
A ₂	0 + 1(1) =	3 + 1(1) <	3 + 1(1) =	2 + 2(2) =	3 + 1(1) =	2 + 2(2) =	4 + 2(2) =	0 + 1(1) =
A ₃		3 + 3(3) =	3 + 1(1) =	3 + 1(1) =	3 + 1(1) =	3 + 1(1) =	4 + 2(2) =	
A ₄		3 + 2(2) <	3 + 1(1) =	3 + 1(1) =	3 + 2(2) >	3 + 1(1) =	4 + 2(2) =	
A ₅		3 + 2(2) <	3 + 1(1) =	3 + 1(1) =	3 + 1(1) =	3 + 1(1) =	4 + 2(2) =	
A ₆		4 + 2(2) =	3 + 1(1) =	3 + 1(1) =	3 + 0(0) <	3 + 1(1) =	4 + 2(2) =	
A ₇		4 + 2(2) =	3 + 1(1) =	2 + 2(2) =	3 + 1(1) =	3 + 1(1) =	4 + 2(2) =	
A ₈		3 + 2(2) <	3 + 1(1) =	2 + 2(2) =	2 + 2(2) =	3 + 1(1) =	3 + 2(2) <	
A ₉			3 + 3(3) =	2 + 2(2) =	2 + 2(2) =	4 + 2(3) =		

Pupae (Figs 11, 12C)

The epicuticle is dark maroon to black except the translucent epicranial plate [frontoclypeus]. Females are larger (lengths: 3 C = 40.58 mm, 39.64 mm, 38.68 mm; $2 \ \bigcirc \bigcirc \bigcirc = 42.63 \text{ mm}, 44.48 \text{ mm}$) and heavier (weights of during overwintering diapause, measured on 06 Feb. 2023: 3 $\bigcirc \bigcirc \bigcirc \bigcirc = 8.16$ g, 7.46 g, 7.54 g; 2 $\bigcirc \bigcirc \bigcirc \bigcirc = 9.29$ g, 8.51 g) than males. The antennal margins in females are more flattened than males, the pair of antennae of the latter are not medially touching along the ventral midline, the maxillae and legs T_{1-2} are visible in both sexes (Fig. 11C, E). Spiracles T_1 is gapped on the boundary of T_1/T_2 (Fig. 11F), spiracle A_{2-7} are functional and large, but that of A_s is closed as a remnant. A pair of forewing tubercles [adult spurs] is rendered on the dorsolateral areas of T₂ specifically (Fig. 11F). The biserial larval scoli D-III had been reduced to smooth vestiges on pupal

stage, in only one case that such bulges on T_3-A_4 are obvious (Fig. 11H). The unsclerotized joints are junction zones between A_4/A_5 , A_5/A_6 , and A_6/A_7 , the tip of A_{10} is rounded without cremaster (Fig. 11G). Genital pores are navel-shaped scars apertured midventrally for males (A_9) and females (A_8 [ostium bursae] and A_9 [ostium oviductus]) (Fig. 11B, D).

Cocoons (Figs 10F, G, 12)

Large (max-lengths without peduncles: $3 \ \text{d} \ \text{d} = 63.49 \text{ mm}, 52.14 \text{ mm}, 56.44 \text{ mm}; 2 \ \text{Q} \ \text{Q} = 50.37 \text{ mm}, 60.41 \text{ mm})$, single layered (thicknesses = ca. 0.37–1.16 mm) and fully closed (no pre-formed exit), the external part was woven by floss for attaching to leaves (Fig. 10G), the general shape is irregular polyhedron but the silky pupal cell is prolate spheroid. White colored in dry environment (weak fluorescence under UV)



Figure 11. Pupae of *Antheraea compta*. **A.** a: \Diamond , lateral view; b: \Diamond , ventral view; c: \Diamond , dorsal view. d: \bigcirc , lateral view; e: \bigcirc , ventral view; f: \bigcirc , dorsal view; **B.** \Diamond , ventral view; a–d: A_{7-10} ; e: genital pore; **C.** \Diamond , head and T_{1-2} , ventrolateral view; **D.** \bigcirc , ventral view; a–d: A_{7-10} ; e: genital pore; **C.** \Diamond , head and T_{1-2} , ventrolateral view; **D.** \bigcirc , ventral view; a–d: A_{7-10} ; e: genital pore; **C.** \Diamond , head and T_{1-2} , ventrolateral view; **D.** \bigcirc , ventral view; a–d: A_{7-10} ; e: genital pore; **E.** \bigcirc , head and T_{1-2} , ventrolateral view; a: spiracle T_1 ; b: forewing tubercle; **G.** \Diamond , posterolateral view; a, b: A_{9-10} ; **H.** \Diamond , dorsolateral view; a–e: T_3-A_4 . Scale bars: 1 cm (**A**); 2 mm (**B**, **D**); 5 mm (**C**, **E**); 3 mm (**F–H**).

365 nm, barely visible) but metamorphosing into brown tones in wet (fluorescence disappeared). 2 \Im and 1 \bigcirc spun on erect vegetations with wide and loose peduncles of inferior structure (e.g., Figs 10F, 12A–C), 1 ♂ and $1 \stackrel{\bigcirc}{\downarrow}$ spun cocoons within fallen leaves and branches on the ground without peduncle (e.g., Fig. 12D). Each filament is a double-strand flat belt, wrinkles formed by longitudinal stretching could be observed on epi-sericin (Fig. 12F), the part of fibroin is combined by dense elongated fibers longitudinally to be almost non-porous within (less voids) (Fig. 12E). Microscopically surveyed three pieces (ca. 6.5-8.4 mm²) of silk-layer sliced from random sites of a cocoon, showing the external surface is rougher, the filaments are ca. 83.8–94.4 µm wide and ca. 4.7-9.3 µm thick (Fig. 12H). The internal surface [pupal cell] is smooth and flat relatively, widths of the filaments are ca. 56.4-92.8 µm with the thicknesses of ca. 2.3-3.9 µm (Fig. 12I). Many crystals (mainly calcium oxalate) granulated from the prepupal discharge liquor are scattered or concentrated in the silk-layer (Fig. 12G), due to gravity, the precipitation is more obvious in the outer surface of the cocoon that lies closer to the ground.

Rearing report

During my first expedition on Tibetan Nyingchi, $1 \ \mathcal{Q}$ of A. compta was collected on 28 Jun. 2021 from Mêdog 2122 m (Fig. 2), her 60 ova were hatched into 37 larvae in the experimental site in Kunming City of Yunnan Province, 1940 m, during mid Jul. to early Aug., these fresh L, rejected any Lauraceae, i.e., Cinnamomum camphora, Cinnamomum burmannii, Machilus spp., Lindera sp., Neolitsea sp., Litsea pungens and Litsea populifolia, moreover, Magnolia delavayi (Magnoliaceae), Prunus cerasoides (Rosaceae), Salix babylonica (Salicaceae) and Liquidambar formosana (Altingiaceae) were likewise not accepted. Finally, three individuals nibbled the leaves of Ouercus variabilis and Q. yunnanensis, but only one grew into the 3rd pre-molting with the latter, and because it was reared outdoors without a cage, this larva was preyed upon by a Myophonus caeruleus (Aves: Passeriformes, Muscicapidae).

After the first failed attempt, I recaptured 3 $\bigcirc \bigcirc$ adults with some males (Fig. 1) from the same natural habitat; during the rainy nights of 25–26 Jun. 2022, many large Quercus lamellosa were noticed at the site. Successively, 3 (coded as Gi, laid on 26 Jun.), 102 (coded as Gii, laid



Figure 12. Cocoons of *Antheraea compta*. **A–C**. \mathcal{J} , spun on the erect vegetation, lateral view; **A**. Original condition; **B**. Removed some leaves and branches; **C**. Opened; **D**. \mathcal{Q} , spun on the bottom of the net cage under a fallen leaf, lateral view [the underside]; **E**. \mathcal{J} , filaments of the external part, cross sectional view; a: transverse [horizontal] plane; b: diagonal plane; c: sagittal plane; **F**. \mathcal{J} , filament of the external part, vertical view; **G**. \mathcal{J} , the crystals precipitated from the prepupal discharge liquor, vertical view; **H**. \mathcal{J} , filaments of the external surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view; **I**. \mathcal{J} , filaments of the internal surface, vertical view. Scale bars: 3 cm (**A**–**D**); 10 µm (**E**); 20 µm (**F**); 2 µm (**G**); 100 µm (**H**, **I**).

on 25 Jun.-01 Jul.) and 16 (coded as Giii, laid on 26–30 Jun.) eggs severally into paper envelopes. Each of Gi and Giii was oviposited naturally into a single tier without longitudinal accumulation, Gii was the same condition in the early period but later heaped up to lump because of larger quantity and lack of available space for adult abdomen. The material was brought back to the same site in Kunming indoor and then grouped on three mesh pieces, a cotton pad was placed below with interval ca. 1 cm, water sprayed the ova every day, the circumambient air was ca. 17–21 °C with ca. 80–95% RH. This method helped prevent water from accumulating around the eggs; excess water drained through the mesh openings to the cotton pad below, while the space between helped ventilate the bottom of the eggs to prevent mold.

At Beijing Time 06:00 to 16:00 every day, 3 larvae of Gi hatched on 13 Jul. (ovum period 17 days), 81 larvae of Gii hatched during 12–19 Jul. (ordered as: 10, 27, 12, 5, 15, 6, 5, 1; ovum period 17–18 days) and 14 larvae of Giii hatched during 13–18 and 20 Jul. (ordered as: 3, 4, 3, 1, 1, 1, 1; ovum period 17–18 or 20 days, but the last individual was unhealthy and died on the day of hatching). Newly hatched L_1 usually fed on eggshells preferentially. Checking unhatched material on 31 Jul., 17 ova of Gii and 1 ovum of Giii were devoid of embryonic development and shriveled; mature embryos had died in 4 ova of Gii and 1 ovum of Giii.

Fresh L₁ were moved to a semi-open balcony for rearing, without cage protection. The plant stems were inserted into the bottle filled with water, and the bottleneck blocked with paper towels to prevent larval drowning. Some newly hatched individuals did not bite the leaves of Quercus schottkyana and Magnolia denudata within two days, so all larvae were given Q. yunnanensis, which was readily accepted. These caterpillars had weak positive phototaxis, usually did not climb to the apex of host plant and did not exhibit gregarious behavior, but there were often 2-5 scattered L, on a single leaf. They rested on the undersides of the leaves and moved to the edges only when feeding, if a branch had fresh terminal buds and thick mature leaves, newly hatched larvae did not distinguish between them, as they are perfectly capable of gnawing on harder leaves, which is apparently related to their larger head with powerful mandibular adductors. Although they did not have strict requirements for air humidity during the larval stage (kept in ca. 64-98% RH), the temperature should not exceed 28 °C, otherwise the larvae will die in large numbers. When the environment reached 26 °C, they usually unclasped the legs T_{1-3} and prolegs A_{3-5} from host plant and suspended in air to enhance ventilation for heat dissipation. This may cause many larvae to fall to the ground. The whole larval stage accompanied a strong need for drinking water, and the leaves must be sprayed with water several times each day to ensure normal development of caterpillars, except on rainy days.

A. compta is a rather difficult species to rear in captivity with a very high mortality in L_1 , in this study, only four individuals of Giii and five of Gii survived to the 1st pre-molting. However, two larvae within the latter group died during pharate and two died in early L_2 . In the five surviving L_2 , the individual "Giii1" was caged in outdoor and other four still fed semi-openly, until they cocooned respectively. Although the weather and nutritional conditions are identical, ontogenic time-consumptions are quite different in the same gender (Table 3).

Before entering each pre-ecdysis, larvae always moved away from their last feeding site. In late L_5 they cut the petiole to make the leaf fall to the ground or break it off completely to eliminate signs of feeding, which apparently helps to avoid some natural enemies which could find the caterpillar location by defoliation. Some individuals would sometimes entangle silk in selected locations to anchor themselves before shifting into apolysis state; such behavior was not consistent, but each of them always preferentially fed on their exuviae except the head capsule.

During L_{2-3} , larvae usually rested on the leaf midrib after a period of feeding of the lamina and secondary veins. For L_4 to medium L_5 they rested intermittently near the petiole and gradually nibbled along the midrib. Since late L_5 , the weight only allowed the activities on branches, before feeding a new leaf, the larva often first bit a large pit on the petiole and then ate along the basal area, if necessary, gnawed more gaps on midrib for further folding the leaf apex closer to itself. For mature larvae, feeding behavior mostly occurred at night, probably to avoid detection by birds. A continuous observation on single L_6 was recorded for reference (Suppl. material 1).

All larval instars were sensitive to light, i.e., in resting states, they always faced toward the side where the illuminance is higher (Suppl. material 2), and this behavior would draw predators' attention to the bright yellow ring on the front of T_1 , whose fluorescent was sufficient to indicate it plays a role in defensive warning. These caterpillars were extremely alert, and every slight shake would interrupt the feeding behavior. Under this state, larvae usually detached their legs T_{1-3} and prolegs A_3 (sometimes A_{3-4}) from the host plant, which may be an effective mimicry to make the lateral views more like leaves, sometimes clicking the mouthparts as a popping noise. The most alarmed individuals would swing from side to side, even triggering biting, whereas the special clubbed setae may help to enhance the spatial scope of tactile cue

Table 3. Developmental data of different individuals of Antheraea compta, fed from Quercus yunnanensis.

Stages\Codes	Giii1, 👌	Giii2, 👌	Giii3, 👌	Giii4, ♀	Gii1, ♀
Oviposited	30 Jun.	27 Jun.	28 Jun.	28 Jun.	25 Jun.
Hatched into L ₁	17 Jul.	14 Jul.	15 Jul.	15 Jul.	12 Jul.
1st pre-ecdysis	27 Jul.	25 Jul.	26 Jul.	26 Jul.	23 Jul.
Molted into L ₂	29 Jul.	27 Jul.	28 Jul.	28 Jul.	25 Jul.
2nd pre-ecdysis	05 Aug.	07 Aug.	08 Aug.	08 Aug.	06 Aug.
Molted into L ₃	07 Aug.	09 Aug.	10 Aug.	10 Aug.	08 Aug.
3rd pre-ecdysis	14 Aug.	16 Aug.	18 Aug.	18 Aug.	17 Aug.
Molted into L4	16 Aug.	18 Aug.	20 Aug.	20 Aug.	19 Aug.
4th pre-ecdysis	23 Aug.	26 Aug.	28 Aug.	30 Aug.	28 Aug.
Molted into L5	26 Aug.	29 Aug.	31 Aug.	01 Sep.	31 Aug.
5th pre-ecdysis	05 Sep.	10 Sep.	14 Sep.	15 Sep.	17 Sep.
Molted into L ₆	09 Sep.	15 Sep.	18 Sep.	19 Sep.	21 Sep.
Feeding ended	03 Oct.	09 Oct.	12 Oct.	16 Oct.	23 Oct.
Spun cocoon	04 Oct.	11 Oct.	13 Oct.	17 Oct.	24 Oct.

(Suppl. material 3). Even so, no secretions exude from the scoli under stimulated conditions, and no urticating reaction was detected on human skin after touch.

Larvae never left the host plant voluntarily if the leaves were plentiful. However, they quickly climbed or fell to the ground after feeding ended [liquid defecation] (happened at night usually), whereupon they were caged with upright living vegetation and dead leaves at the bottom for observation. Almost all individuals moved restlessly for about 24 hours before choosing a spinning location. The species undoubtedly constructs cocoons away from the host plant in the wild, either in low shrubs under the oak canopies or in the leaf litter on the ground.

The flight time in the natural habitat and captivity and reproductive behavior of adults will be recorded and published after the fresh adults emerge from existing pupae.

Discussion and conclusion

This article provides the first report of the complete life history of the enigmatic *A. compta*, whose lateral stripes of mature larvae are a feature close to that of North American *Antheraea oculea* (Neumoegen, 1883) (Tuskes et al. 1996: pl. 6; Lampe 2010: 121) and *A. polyphemus* (Bouseman and Sternburg 2002: 51; Hall 2021), the scale and distribution of the shiny silver spots closely resemble those in the Mexican *Antheraea montezuma* (Sallé, 1856) and *Antheraea meridiana* Naumann & Nogueira, 2021 (Paukstadt and Paukstadt 2020; Naumann and Nogueira 2021), while the tricolored lateral plate of anal proleg of Neotropical *A. godmani* (Nässig et al. 1996; Goossens et al. 2015) is similarly shared in *A. compta*. These observations preliminarily suggest that Himalayan *A. compta* should be assigned to the subgenus *Telea*.

Due to L₁ rejecting *Q. schottkyana* in captivity, it is inferred that Q. lamellosa is observed in the Tibetan habitat, and more cycle-cup oaks may not be the correct host plants to A. compta, namely the section Cyclobalanopsis. Additionally, in the eastern Himalayas, native specimens Quercus lodicosa, Quercus lanata, Quercus engleriana, Quercus semecarpifolia, Quercus aquifolioides, Quercus gilliana, Quercus rehderiana and Quercus senescens within the section Ilex, as well as Quercus acutissima of the section Cerris were also identified in recent works (Zhou and Sun 1996; Denk and Grimm 2009; Yang and Zhou 2015: 130; Lahiri et al. 2017), the three sections have been confirmed to form a monophyletic subgenus Cerris (Denk et al. 2017; Hipp et al. 2019). Because of the observed rejection of Q. variabilis (a single larva reluctantly ate a small gap, but did not continue), its sister taxon Q. acutissima would probably also be rejected. There is currently no experimental result on infrasubgeneric *Ilex* so it is uncertain whether *A. compta* can partially accept some species of the subgenus, but probably, Q. lodicosa and Q. lanata would be accepted as foods by such caterpillars; the former tree is common in southeastern Tibet and the latter is dominant from Mêdog to Tengchong County, Yunnan (bordered with Myanmar

Kanpaikti), all having humid mid-altitudinal distributions (Zhou et al. 1995). In any case, the above species are clearly distinguished from *Q. yunnanensis*, a deciduous oak within the subgenus *Quercus*. Another roburoid white oak *Quercus griffithii* is widely known in northeastern India (Negi and Naithani 1995: 50–53; Singh et al. 2009; Singh et al. 2015), likewise naturally occurring in mountains from northern Yungui Plateau to sections of Indochina (Huang et al. 1999; Menitsky 2005: 47–49), with a high probability to be a primary host to *A. compta* at the corresponding biotopes.

A. assamensis is a well-known Lauraceae feeder in the wild (Seidel and Peigler 2018; Devi et al. 2021) but accepted beech (Lampe 2010: 358) and oak (Crotch 1956: 55) in captivity. Interestingly, the current known hostplants of A. godmani are limited to oaks (Meister 2011: 148), while A. compta is also oligophagous and feeding on certain Quercus only. This means that the empty cocoons collected from Assam soalu trees Litsea monopetala and then sent to Peigler (1999) were actually spun by muga silkworms. Therefore, Jolly's (1981) conclusion that "A. compta is almost identical with A. assamensis [sic]" is completely incorrect, while native Indian material for study of chromosomes (Gupta and Narang 1981) and silk (Luikham et al. 2017) using the former name but based on Lauraceae host plants are surely misidentifications to A. assamensis or its sister species Antheraea castanea Jordan, 1910. In fact, no Indian author has ever provided an adult image to prove the true identity of so-called "A. compta", except Arora and Gupta (1979) who described a pinned male from the British India period. In recent years, there have been a few indigenous records from the country but limited to only checklists without reliable morphological description and often confusingly called "wild muga" or "oak tasar" (e.g., Bhatia et al. 2010; Devi et al. 2011; Kumar et al. 2016; Gogoi and Goswami 2016; CSB 2018; Marepally 2018: 4; Boro and Borah 2020; Kumar et al. 2020; Keisa et al. 2022). This confusion suggests that the current population of the species may be nearly extirpated because virtually no local researchers have actually collected A. compta. Coincidentally, in works in which illustrated moth photographs corresponding to the scientific names, no specimen of A. compta was recaptured in recent surveys of northeastern India (Gogoi et al. 2014; Kakati and Chutia 2009; Kalita and Dutta 2014; Lalhmingliani 2015; Sondhi et al. 2021a) or even its type-locality Meghalaya (Shangpliang and Hajong 2015a, 2015b), whereas also does not turn up in the long-term monitoring of the Himalayas and Indian subcontinent (Shubhalaxmi 2018; Chandra et al. 2019; Sondhi et al. 2021b). To date, no Chinese publications included this species, and no records from Bhutan, Nepal and Uttarakhand are available, whereas Schüssler (1933: 175) added Sikkim to the distribution without supporting data.

Actually, the moths flying in southeastern Tibet were separated taxonomically from Meghalaya *A. compta*, the former was named *Antheraea discata* Naumann & Löffler, 2015, whose type locality is the same as the origin of my material. Unfortunately, the authors of *A. discata* overlooked the study of specimens from mountainous Burma, and although they discovered some morphological and COI differences between Mêdog and Khasi Hills, the Myanmar samples are still crucial in resolving the phylogenetic relationships in this case. Unlike the natural barrier of the Assam Valley, the mountains of Sagaing-Kachin are connected to the Shillong Plateau and Himalayas, making it a logical corridor for the ancestral colonial activity of these moths. This suggests that the "species boundary" of A. discata is possibly fuzzy (transitional or gradual) or even not able to be located. Therefore, this paper rejects to use the name subjectively and treats it as "data-deficient" temporarily, however, it does not imply any effective taxonomic (synonymous) treatment for this taxon here. There is still a possibility in the future that the three ecoregional populations will be accepted as different species or subspecies to form a complex; the Sub-Himalayan genus Sinobirma Bryk, 1944 is a known case (Rougerie et al. 2012).

At present, the sources of published specimens of *A. compta* are localized within the following three restricted ecoregions of Indo-Malayan realm, the zoning based on Dinerstein et al. (2017):

- Meghalaya subtropical forests (Rothschild and Jordan 1899; Rothschild and Jordan 1901; Bouvier and Riel 1931: 53; Arora and Gupta 1979; Peigler 1999; Naumann and Löffler 2015).
- Northern triangle subtropical forests (Bryk 1944).
- Eastern Himalayan broadleaf forests (Naumann and Löffler 2015; Naumann and Nogueira 2021; this article).

Diverse evidence stresses the importance and necessity for conservation of wild *A. compta* in the current situation. As one of the central clues regarding the evolutionary history of the economically important genus *Antheraea*, its ecological and taxonomic significance is critical.

Larval feeding preference and morphological characters shared by the montane *A. godmani, A. montezuma* and *A. meridiana* with the Himalayan *A. compta* seemingly suggest that those Neotropical species are closer to the New World ancestor than are the Nearctic species (*A. polyphemus, A. oculea*). Three centuries of intense study of the genus *Antheraea* make more rigorous comparisons possible, and detailed phylogenetic studies on preimaginal morphologies and complete mitochondrial genomes of *A. compta* with related species are in preparation, to further confirm its evolutionary status.

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Supplementary material 1

Feeding schedule of Antheraea compta L₆

Author: Zhengyang Liu

Data type: table (.xlsx file)

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Supplementary material 2

Light sensitivity (the darker side = ca. 544-1185 Lux, the brighter side = ca. 9300-13600 Lux) of *Antheraea compta* L_6 (speed × 12)

Author: Zhengyang Liu

Data type: video (.mov file)

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Supplementary material 3

Defensive behavior of Antheraea compta L

Author: Zhengyang Liu

Data type: video (.mov file)

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- Link: https://doi.org/10.3897/dez.70.102952.suppl3

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Taxonomic review of the genus *Sinopanorpa* Cai & Hua, 2008 (Mecoptera, Panorpidae) with descriptions of two new species

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Abstract

The scorpionfly genus *Sinopanorpa* Cai & Hua, 2008 is endemic to the mountain regions of central China, currently consisting of four species: *Sinopanorpa tincta* (Navás, 1931), *S. digitiformis* Huang & Hua, 2008, *S. nangongshana* Cai & Hua, 2008, and *S. baokangensis* Wang, 2021. Here, the genus is taxonomically reviewed, with descriptions of two new species: *Sinopanorpa minshanicola* **sp. nov.** from the Minshan Mountains and *Sinopanorpa shennongjiaica* **sp. nov.** from the Shennongjia Mountains, increasing the species number of the genus to six. An updated key to species of *Sinopanorpa* is provided.

Key Words

biodiversity, China, Oriental Region, scorpionfly, Sinopanorpa, taxonomy

Introduction

The scorpionfly genus *Sinopanorpa* Cai & Hua, 2008 was erected with *Panorpa tincta* Navás, 1931 as its type species (Cai et al. 2008). The genus is mainly characterized by the wing membrane deeply yellow with sooty brown markings, male tergum VI without anal horns, basal part of male abdominal segment VII much thinner, and the gonostylus of male with the basal process modified as a sharp crescent blade.

Since the establishment of *Sinopanorpa*, the biology and morphology of *S. tincta* have been studied in many aspects. It completes one generation per year, with the adults emerging from late June to mid-September (Cai et al. 2008). The ovoid eggs with a ridge network on the chorion are deposited in clusters in a soil cavity (Ma et al. 2009). As in other species of Panorpidae (Byers and Thornhill 1983), the larvae of *S. tincta* are eruciform, with eight pairs of abdominal prolegs in addition to three pairs of thoracic legs (Chen and Hua 2011). The larvae possess a pair of compound eyes on the lateral side of the head, each consisting of approximately 40 ommatidia (Chen and Hua 2011).

The ommatidia of adult compound eyes in *S. tincta* are of the typical apposition type, each retinula consisting of eight retinula cells (Chen et al. 2012). Three dorsal ocelli are located on the vertex of the head, each having a corneal lens, a layer of corneagenous cells, and fused rhabdoms (Wei and Hua 2011). The mandibulate mouthparts are modified to feed on liquid food after the extra-oral digestion with hair brushes on the hirsute epipharynx, galea, labial palps, and hypopharynx (Huang and Hua 2011). The salivary glands exhibit a sexual dimorphism in that the male has six extremely elongate secretory tubules, but the female has only a short less-developed tube (Ma et al. 2011). The well-developed salivary glands of males are associated with their salivary secretions that are served as nuptial gifts to the females during mating. The spermatheca

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consists of a bean-shaped spermathecal reservoir and an elongated spermathecal duct (Yang and Hua 2021). The male reproductive system mainly comprises a pair of testes of three follicles, a pair of elongate vasa deferentia, and an ejaculatory sac in addition to the external genitalia. The vas deferens is highly coiled for its distal part into an epididymis and greatly expanded for its middle part into a well-developed seminal vesicle (Lyu and Hua 2017). According to recent phylogenetic analyses (Ma et al. 2012; Hu et al. 2015; Miao et al. 2019; Wang and Hua 2021), *Sinopanorpa* is confirmed to be monophyletic and forms a sister group with part of the paraphyletic genus *Panorpa*.

In this paper, we taxonomically reviewed the genus *Sinopanorpa* in the mountain regions of central China, and described two new species, raising the species number of the genus to six. An updated key to species of *Sinopanorpa* is provided.

Material and method

All the materials examined in this study are deposited in the Entomological Museum, Northwest A&F University, Yangling, Shaanxi, China (NWAU). Specimens were collected with collecting nets from the mountain regions in central China. Some type specimens were spread and pinned, and others were preserved in 75% or 95% ethanol. Specimens were dissected under a Nikon SMZ 1500 stereoscopic zoom microscope. The genitalia were macerated in cold 10% NaOH for 3-5 min and rinsed with distilled water. Habitus and ecological photographs were taken with a Nikon D7100 digital camera. Character images were taken using the scientific digital micrography system ZEISS SteREO Discovery.V20 equipped with the auto-montage imaging system AxioCam IC. All photographs were assembled with Adobe Photoshop CC 2015. A distribution map was generated by ArcGIS v.10.2 (ESRI, Redlands, USA) and was annotated in Adobe Illustrator CC. The localities in the map came from the collection labels of observed specimens and literature (Cai et al. 2008; Wang 2021).

Results

Genus Sinopanorpa Cai & Hua, 2008

Sinopanorpa Cai & Hua in Cai et al. 2008: 44.

Type species. *Panorpa tincta* Navás, 1931, by original designation.

Diagnosis. The genus *Sinopanorpa* can be readily distinguished from other genera of Panorpidae by the following characters: wing membrane deeply yellowish-brown with sooty brown markings; vein R_2 generally 3-branched; notal organ on the posterior margin of male tergum III less-developed; tergum VI of male without anal horns; abdominal segment VII much thinner, stalk-like for basal 1/3, but distinctly thicker for distal 2/3; gonostylus in male genitalia greatly elongated with well-developed pointed basal lobe; ventral parameres simple, with spines on inner side, extending over apex of gonocoxite; A6 bearing a bundle of dense hairs on the centre of T6 in males; and female medigynium with extremely elongated thin axis.

Distribution. China (Chongqing, Gansu, Hubei, Shaanxi, and Sichuan provinces) (Fig. 1).

Sinopanorpa tincta (Navás, 1931)

Panorpa tincta Navás, 1931: 75; Cheng 1957: 50; Chou et al. 1981: 2; Nie and Hua 2004: 190. Type locality: Huixian County, Gansu.

Panorpa statura Cheng, 1949: 148; Cheng 1957: 56. Synonymized by Hua and Peng 2005: 123. Type locality: Mt. Taibaishan, Shaanxi.

Sinopanorpa tincta, Cai et al., 2008: 45.

Diagnosis. This species differs from its congeners by the following characters: 1) gonostylus of male with median tooth blunt, and prominent basal lobe crescent spatula in shape; 2) ventral parameres shortened, only extending over apex of gonocoxite, with long comb-like spines along mesal margin on distal half; and 3) female medigynium narrow, with main plate nearly rectangular for basal 2/3, axis extending over 1/3 of its length beyond main plate.

Distribution. China (Gansu and Shaanxi provinces) (Fig. 1).

Sinopanorpa digitiformis Huang & Hua, 2008

Sinopanorpa digitiformis Huang & Hua in Cai et al. 2008: 48. Type locality: Shennongjia Mountains.

Diagnosis. This species can be differentiated from its congeners by the following characters: 1) abdominal segment VI of male markedly tapering towards apex in distal half; 2) basal lobe of gonostylus well-developed, with two acute distal hooks; 3) ventral parametes elongate, extending distinctly over basal lobe of gonostylus; and 4) main plate in female medigynium much shorter, only slightly longer than wide, with axis extending over half its length beyond main plate.

Distribution. China (Chongqing, Hubei, and Shaanxi provinces) (Fig. 1).

Sinopanorpa nangongshana Cai & Hua, 2008

Sinopanorpa nangongshana Cai & Hua in Cai et al. 2008: 51. Type locality: Mt. Nangongshan.

Diagnosis. This species can be readily differentiated from its congeners by the following characters: 1) posterior abdomen and male genitalia dark blackish brown; 2) ventral parameres greatly elongated, extending distinctly over median tooth of gonostylus; 3) basal lobe of gonostylus much narrower, with two short acute teeth at apex; and 4) main plate in female medigynium elongate, with thick axis extending half its length beyond main plate.



Figure 1. Species distribution map of the genus *Sinopanorpa* Cai & Hua, 2008. BK, Baokang (Hubei); BLG, Baligou (Hubei); DHB, Daheba Forest Park (Gansu); DJH, Dajiuhu (Hubei); FHS, Fenghuangshan (Shaanxi); FP, Foping (Shaanxi); HAB, Huang'anba (Chongqing); HC, Hengchong Nature Reserve (Hubei); HDT, Huoditang (Shaanxi); HLS, Hualongshan (Shaanxi); HX, Huixian (Gansu); HZZ, Houzhenzi (Shaanxi); JHP, Jiuhuping (Hubei); JLJ, Jialing River (Shaanxi); LHG, Laohegou (Sichuan); LJP, Liujiaping (Gansu); LP, Liping (Shaanxi); MCS, Micangshan (Sichuan); NGS, Nangongshan (Shaanxi); TB, Taibai (Shaanxi); TTH, Tongtianhe Forest Park (Shaanxi); TY, Tianyan (Hubei); XLS, Xiaolongshan (Gansu); ZBS, Zibaishan (Shaanxi); ZQ, Zhuque Forest Park (Shaanxi).

Distribution. China (Shaanxi Province) (Fig. 1).

Sinopanorpa baokangensis Wang, 2021

Sinopanorpa baokangensis Wang, 2021: 1. Type locality: Baokang, Hubei.

Diagnosis. This species can be distinguished from its congeners by the following characters: 1) male gonostylus with greatly developed simple acute basal lobe, extending beyond median tooth; 2) male ventral parameres moderately elongate, extending over base of basal lobe; and 3) female medigynium with main plate slightly longer than wide, with axis slender, two times as long as main plate.

Distribution. China (Hubei Province) (Fig. 1).

Sinopanorpa minshanicola sp. nov.

https://zoobank.org/56273B3C-54B7-41F3-9565-AB22F8B72F09 Figs 2, 3

Type specimens. *Holotype* $\stackrel{\circ}{\circ}$ (NWAU), CHINA, Sichuan Province, Pingwu County, Laohegou (32°29'17"N, 104°43'17"E, 1800 m), 20 July 2017, leg. Yuan Hua & Kai Gao. *Paratypes*: $3\stackrel{\circ}{\circ} 2\stackrel{\circ}{\circ}$ (NWAU), CHINA, Sichuan Province, Pingwu County, Laohegou (32°29'17"N, 104°43'17"E, 1800 m), 14 July 2022, leg. Yuan Hua; $2\stackrel{\circ}{\circ} 2\stackrel{\circ}{\circ}$ (NWAU), CHINA, Sichuan Province, Pingwu County, Laohegou (32°29'17"N, 104°43'17"E, 1650–1900 m), 6

July 2021, leg. Yuan Hua; 3♂ 5♀(NWAU), CHINA, Gansu Province, Wenxian County, Liujiaping (32°48'30"N, 104°46'43"E, 2080 m), 25 June 2019, leg. Kai Gao & Zhi-Chao Jia.

Diagnosis. The new species can be readily recognized from its congeners by the following characters: 1) vertex with a dark transverse band across ocellar triangle; 2) ventral parameres of male shortened, only extending slightly over basal lobe of gonostylus; 3) basal process of gonostylus short, simple, acute, but non-furcated; and 4) female medigynium elongate, with axis half its length out of main plate.

Etymology. The specific epithet is derived from the type locality, Minshan, and the Latin *-cola* (dwell).

Description. Male (Fig. 2A). Head mostly yellowish brown. Rostrum faint yellow, with a pair of darkish longitudinal stripes laterally. Maxillary and labial palps yellowish brown, with distal segment dark brown. Antenna filiform, blackish brown. Ocellar triangle black. A dark transverse band across ocellar triangle to eyes (Fig. 2C).

Pronotum dark brown, with short black setae along anterior margin (Fig. 2D). Meso- and metanotum blackish brown. Pleura and sterna pale. Legs yellowish brown, with distal parts of tarsomeres dark brown.

Forewing length 15.96–16.70 mm, width 3.84– 3.92 mm. Forewing membrane light yellow, with markings pale brown; pterostigma prominent, orange yellow; apical band broad, covering whole apical part; pterostigmal band complete, with basal and distal branches equal



Figure 2. *Sinopanorpa minshanicola* sp. nov. A. Male adult, dorsal view; B. Female adult, dorsal view; C. Male head, frontal view; D. Male head and thorax, dorsal view; E. Male abdomen, lateral view. Scale bars: 5 mm (A, B); 1 mm (C–E). ms, mesonotum. mt, metanotum. pr, pronotum.

in width; marginal spot elongate-rectangular, extending from costa to R_{4+5} ; basal band almost complete, across whole wing; basal spot absent; R_2 three-branched; R_3 arising from middle of pterostigmal band (Fig. 2A). Hindwing similar to forewing in pattern, but marginal spot and basal band absent. Forewings with 7–9 jugal bristles, hindwings with 2–3 frenular bristles.

Abdominal segments I–IV (A1–A4) black in terga, pale yellow in sterna, and pale in pleura with spiracles clearly visible. Notal organ on posterior margin of tergum III (T3) less-developed, with postnatal organ on tergum IV very small near anterior margin. A5 pale yellow. A6 reddish yellow, greatly elongated, two times as long as A5, without anal horns. A patch of golden hairs along mid T6. A7 much thinner in basal 1/3 than in distal 2/3, with a cluster of hairs on anterio-dorsal corner of distal part (Fig. 2E). A8 longer than A7, slightly constricted for basal 1/4.

Genital bulb long elliptic (Fig. 3A–C). Epandrium (tergum IX) broad at base, narrowing towards apex with a shallow apical emargination; a pair of cerci protruding subapically from under epandrium (Fig. 3C). Hypandrium (sternum IX) almost without basal stalk; hypovalves broad, extending beyond apex of gonocoxites, mesal margin of distal half bearing numerous barb spines. Two hypovalves almost parallel, with apex blunt (Fig. 3A). Gonocoxite with two small dark apical spots. Gonosty-lus elongate, slender, longer than gonocoxite, smoothly curved outwards; median tooth blunt, roughly at basal 1/3; basal lobe extremely developed, prominent, strongly

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sclerotized in apical half, assuming a stout elongate spine (Fig. 3E). Ventral parameres slender, finger-like, extending over basal lobe of gonostylus, distal half with dense long spines along mesal margins, shorter towards apical part. Aedeagus simple, with paired ventral and dorsal valves (Fig. 3B).

Female (Fig. 2B). Head dark yellow. Thorax dark black dorsally, light yellow laterally. Forewing length 16.30–16.76 mm, width 3.88–4.00 mm. Wing pattern similar to that of male, but markings vaguer, marginal spot absent. In hindwings, markings indistinct, basal band completely absent. A1–A4 dark black in terga, light yellow in sterna; A5–A7 yellowish brown dorsally, with a longitudinal thin mesal line.

Subgenital plate broad at base, gradually narrowing towards apex, with bluntly rounded apex, apical part bearing long setae (Fig. 3D). Medigynium (genital plate) very broad, main plate longer than wide, with a pair of posterior arms roughly forming a broad U-shape; axis elongate, extending half its length beyond main plate (Fig. 3F, G).

Distribution. China (The Minshan Mountains in Gansu and Sichuan provinces).

Habitat. Numerous adults of the new species were collected from late June to the end of July at the edges of coniferous and broad-leaf mixed forests, with dense subshrubs in the Minshan Mountains. At the type locality, adults are often found in moist microhabitats, especially rich on the alpine shrub or understory in broad-leaved


Figure 3. *Sinopanorpa minshanicola* sp. nov. A. Male genitalia, ventral view; B. Male genitalia, with hypovalves removed, ventral view; C. Male genitalia, dorsal view; D. Female terminalia, ventral view; E. Male gonostylus, dorsal view; F, G. Female medigynium, ventral and dorsal views. Scale bars: 0.5 mm. ax, axis. bp, basal process. ce, cercus. ep, epandrium. gcx, gonocoxite. gs, gonostylus. hv, hypovalve. mp, main plate. pa, posterior arm. pm, paramere. sgp, subgenital plate.

forests with an altitude ranging from 1600 to 2100 m above sea level (Fig. 1).

Sinopanorpa shennongjiaica sp. nov.

https://zoobank.org/F361CD43-9169-4FE0-AAC1-7E41EE040CCA Figs 4, 5

Type specimens. *Holotype* ♂ (NWAU), CHINA, Hubei Province, Shennongjia Nature Reserve, Tianyan (31°42'58"N, 110°21'35"E; 1800 m), 1 July 2018, leg. Kai Gao & Yu-Ru Yang. *Paratypes*: 1 ♂ 2♀ (NWAU), CHINA, same data as for the holotype; 2♀ (NWAU), CHINA, Hubei Province, Shennongjia, Dalongtan (31°29'39"N, 110°18'10"E; 2200 m), 3 July 2018, leg. Kai Gao & Yu-Ru Yang; 8♂ 6♀ (NWAU), CHINA, Hubei Province, Shennongjia, Jiuhuping (31°30'32"N, 110°20'57"E; 1850 m), 3 July 2018, leg. Kai Gao & Yu-Ru Yang; 2♀ (NWAU), CHINA, Hubei Province, Shennongjia, Jiuhuping (31°30'32"N, 110°20'57"E; 2200 m), 4 July 2018, leg. Kai Gao & Yu-Ru Yang; 6♂ 6♀ (NWAU), CHINA, Hubei Province, Shennongjia, Jiuhuping (31°30'32"N, 110°20'57"E; 2200 m), 4 July 2018, leg. Kai Gao & Yu-Ru Yang; 6♂ 6♀ (NWAU), CHINA, Hubei Province, Shennongjia, Jiuhuping (31°30'32"N, 110°20'57"E; 2200 m), 4 July 2018, leg. Kai Gao & Yu-Ru Yang; 6♂ 6♀ (NWAU), CHINA, Hubei Province, Shennongjia, Jiuhuping (31°30'32"N, 110°20'57"E; 1900 m), 18 July 2019, leg. Kai Gao.

Diagnosis. The new species can be differentiated from its congeners by the following characters: 1) vertex

with ocellar triangle black, but without transverse band; 2) male tergum VI and female terga VI–IV orange; 3) ventral parameres of male greatly elongated, extending distinctly over median tooth of gonostylus to apical forth; 4) gonostylus with basal lobe well-developed and split into two separate acute elongate hooks; and 5) female subgenital plate with X-shaped ridge over whole length, and medigynium with slender axis non-expanded anteriorly.

Etymology. The specific epithet is derived from the type locality, *Shennongjia*, by using the adjective form of the locality name with the fuffix *-ica*.

Description. Male (Fig. 4A). Head yellowish brown; eyes dark; ocellar triangle black; vertex and frons yellowish brown. Antennae darkish brown, filiform with 44–45 segments. Rostrum, labrum, and maxillae light brown; mandibles reddish brown with tips dark brown; maxillary palp light yellow except apical part dark brown.

Thorax blackish brown dorsally, pale yellow or yellowish brown laterally. Pronotum with 12 setae along anterior margin. Legs yellow, except joints from tibia to claws dark brown to black, claws serrate with six teeth.

Forewing length 15.32–16.34 mm, width 3.78– 3.94 mm. Forewing membrane deeply yellow, with markings faint grayish brown; pterostigma prominent,



Figure 4. *Sinopanorpa shennongjiaica* sp. nov. A. Male adult, dorsal view; B. Female adult, dorsal view; C. Male head, frontal view; D. Male head and thorax, dorsal view; E. Male abdomen, lateral view. Scale bars: 5 mm (A, B); 1 mm (C–E). pr, pronotum. ms, mesonotum. mt, metanotum.



Figure 5. *Sinopanorpa shennongjiaica* sp. nov. A. Male genitalia, ventral view; B. Male genitalia, with hypovalves removed, ventral view; C. Male genitalia, dorsal view; D. Female terminalia, ventral view; E. Male gonostylus, dorsal view; F, G. Female medigynium, ventral and dorsal views. Scale bars: 0.5 mm. ax, axis. bp, basal process. ce, cercus. ep, epandrium. gcx, gonocoxite. gs, gonostylus. hv, hypovalve. mp, main plate. pa, posterior arm. pm, paramere. sgp, subgenital plate.

orange. Apical band broad; pterostigmal band prominent, with complete basal and distal branches equal in width; marginal spot absent or elongate, extending from R_1 to R_{2+3} ; basal band complete, broad; basal spot absent. R_2 3-branched. Hindwings similar to forewings, but marginal spot and basal band absent (Fig. 4A).

Terga I–IV blackish brown, A5 yellowish brown; A6 orange reddish brown, A7–A9 yellowish brown. Sterna I–V pale yellow, pleura pale with dark longitudinal stripes. Notal organ on posterior margin of T3 less-developed. A6 subcylindrical, at least two times as long as A5, with a cluster of hairs on mid protuberance of tergum, without anal horns. A7 prominently thinner for basal 1/3, then suddenly swollen dorsad for distal 2/3, with a cluster of short hairs along anterodorsal corner of distal part (Fig. 4E).

Genital bulb rounded (Fig. 5A–C). Epandrium (tergum IX) broad at base, gradually narrowing towards apex, with apex shallowly emarginated; a pair of cerci protruding subapically from under epandrium (Fig. 5C). Hypandrium (sternum IX) with basal stalk very short; hypovalves broad, split from base of hypandrium, extending to apex of gonocoxite, almost parallel, bearing long setae on inner margin of distal half (Fig. 5A). Gonocoxites yellowish brown, with two black

Key to species of Sinopanorpa Cai & Hua, 2008

Updated from Cai et al. 2008 and Wang 2021.

1	Male ventral parameres short, extending slightly over apex of gonocoxites at most
_	Male ventral parameres elongate, extending distinctly beyond median tooth of gonostylus
2	Basal process of male gonostylus with distal tooth smaller than basal tooth; paramere with long comb-like spines o
	inner margin; female medigynium with axis greatly divergent at baseS. tinct
-	Male gonostylus with basal process simple, not furcated distally; female medigynium elongate, with axis half its lengt
	out of main plate S. minshanicola sp. no
3	Male gonostylus with basal process bifurcated basally
-	Male gonostylus with basal process simple, not bifurcated basally
4	Basal process of male gonostylus with two teeth almost equal in size; female medigynium with axis slightly divergent
	female medigynium with apodemes of axis divergent apicallyS. digitiformi
-	Basal process of male gonostylus separate completely as two lobes from base; median tooth of gonostylus acute
	female subgenital plate with X-shaped ridge over whole length, and medigynium with slender axis not expanded anter
	orlyS. shennongjiaica sp. no
5	Basal process of male gonostylus well-developed, pointed, median tooth indistinct; female medigynium with stout pos
	terior arms longer than half length of main plateS. baokangensi
-	Male gonostylus with basal process only slightly developed, bifurcated distally; female medigynium with posterior pol
	tion wider than half width of main plateS. nangongshan

Discussion

Species of the genus *Sinopanorpa* are found in high elevation habitats ranging from 1600 to 2200 m above sea level in the Qingling, Minshan, Bashan, and Shennongjia mountains. Numerous adults were often found in the summer on the alpine shrub or understory at the edges of coniferous and broad-leaf mixed forests, with dense subshrubs. Their microhabitats are usually situated in considerably cool and moist valleys in the mountain top regions with high elevation and high precipitation. Therefore, we assume that they are typical cool-adapted insects. The cool-adapted preference of *Sinopanorpa* species is similar to that of *Cerapanorpa*, which has been reported as a cold-adapted genus of Panorpidae (Gao and Hua 2019, 2021; Gao et al. 2020, 2022). The cool-adapted preference makes the genus *Sinopanorpa* an ideal model to investigate the speciation and phylogeographic pattern of cold-adapted insects. In an ongoing study, we are investigating the distribution patterns of the Panorpidae in China,

spots at apex. Gonostylus elongate, curved outwards, almost as long as gonocoxite, with one pointed mesal tooth and two prominent acute basal lobes (Fig. 5E). Ventral parameres greatly elongate, extending distinctly over median tooth to distal forth of gonostlylus, without distinct spines along inner margins, with apices slightly convergent. Aedeagus black (Fig. 5B).

Female. Forewing length 16.64–17.12 mm, width 3.94–4.10 mm. Wings generally similar to those of male, but marginal spot present (Fig. 4B). Terga I–III black, corresponding sterna pale; T4 reddish brown, with lateral margins black; T5–T9 reddish brown.

Subgenital plate narrow, with an X-shaped ridge (Fig. 5D). Medigynium broad, nearly rectangular from above; main plate two times as long as wider, with a pair of posterior arms in U-shape. Axis elongate, slender, extending half its length beyond main plate, not expanded at anterior end (Fig. 5F, G).

Distribution. China (Hubei Province).

Habitat. This species is distributed in the Shennongjia Mountains. In the type locality, all specimens were captured on herbaceous groundcover, with elevations ranging from 1800 to 2200 m. Suitable microhabitats are moist and cool valleys during the imaginal flight period. trying to discover the centers of biodiversity, and areas of endemism, and exploring the key factors in the speciation.

The discovery of Sinopanorpa minshanicola sp. nov. and S. shennongjiaica sp. nov. increases the species number of the genus to six. The six species are disproportionately distributed in central China's mountain regions, including the Qinling, Minshan, Bashan, and Shennongjia mountains (Fig. 1). The widespread species Sinopanorpa tincta (Navás, 1931) is located in the Qinling, Bashan and Minshan mountains. It is noteworthy that the specimens of Sinopanorpa from Sichuan and southern Gansu provinces previously identified as S. tincta by Wang (2021) are treated as S. minshanicola sp. nov. herein. Nevertheless, the other species are all geographically restricted. Sinopanorpa minshanicola sp. nov. is likely endemic to the Minshan Mountains, whereas S. digitiformis Huang & Hua, 2008, S. nangongshana Cai & Hua, 2008, S. baokangensis Wang, 2021 and S. shennongjiaica sp. nov. are all distributed in the microhabitats of eastern Bashan Mountains, including Shenongjia. Further phylogeographic analyses are needed to clarify the causes of the disproportionate distribution pattern of *Sinopanorpa*.

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<u> PENSOFT</u>,



A morphology-based revision and phylogenetic analysis of the *Pterostichus macrogenys* species group (Coleoptera, Carabidae) and implications for differentiation of the species group

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Abstract

The *Pterostichus macrogenys* species group is an endemic subterranean Japanese carabid clade that provides intriguing material for studying morphological differentiation, speciation and interspecific relationships. However, its diversity remains not fully explored. We investigated specimens from northern Tohoku District, an area where knowledge of this species group is notably limited. Our research led to the description of three new species: *P. namahage* **sp. nov.**, *P. kamurosanus* **sp. nov.** and *P. atsumidakensis* **sp. nov.** We also updated distribution records for three known species: *P. asahinus* Habu & Baba, 1960; *P. kitakamisanus* Sasakawa, 2005; and *P. chokaisanus* Sasakawa, 2009. This report includes both the expanded distribution ranges of the known species and the discovery of a new sympatric species pair (*P. chokaisanus* and *P. asahinus*). We conducted a morphological phylogenetic analysis of all but one species, for which no male specimens were available, accounting for a total of 42 species within the group. The resulting phylogenetic tree implies that the initial differentiation of this species group originated on the Sea of Japan side, in the northern part of their current distribution, followed by dispersion to other areas and subsequent differentiation. Additionally, our findings indicate that sympatric species of varying body sizes are distantly related phylogenetically. These insights into the differentiation process align with regional distribution patterns of species-level diversity and sympatric sites.

Key Words

character evolution, cryptic species, endophallus, Japan, male genitalia, morphological phylogeny, *Nialoe*, sympatric occurrence, synapomorphy, taxonomy

Introduction

The *macrogenys* species group is an endemic subterranean Japanese carabid clade belonging to the *Pterostichus* subgenus *Nialoe* Tanaka, 1958 (s. lat. i.e. *Nialoe* sensu Sasakawa 2021). Members of this species group are medium to large (body length 12–20 mm) and characterised by a large head with long mandibles, a flattened body and relatively simple secondary sexual characteristics on the male last abdominal segment (Sasakawa 2009; Sasakawa et al. 2020). All species have atrophied hind wings, limiting their dispersal ability.

Marked regional differentiation is recognised and about 40 species-group taxa with limited distributions are known in mountainous areas north of the Kinki District, Honshu. These species appear very similar externally and are mainly distinguished by the genital morphology of males. Sympatric occurrences, consistent with reproductive isolation, have been confirmed amongst some species and differences in body and/or male genital size are observed amongst species in sympatry (Sasakawa et al. 2020). Hence, the *macrogenys* species group is of interest for studying morphological differentiation, speciation and interspecific relationships.

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On the other hand, several fundamental aspects regarding the diversity of this species group, crucial for comprehensive study, remain unresolved. One such aspect is the insufficient knowledge about species-level diversity in certain regions. Particularly since Sasakawa (2009), there have been no new species discoveries or new reports on the distribution of known species from the northern Tohoku District, located in the northern part of the group's range (Fig. 1). This situation contrasts with other areas, where new species and new distributions of known species are being reported (southern Tohoku District: e.g. Sasakawa and Itô (2017, 2022); Sato (2021); Kanto District: e.g. Morita et al. (2013); Sato et al. (2014); Ohkawa (2018); Chubu District: e.g. Morita and Ohkawa (2010); Toda (2012); Ito and Ogai (2015); Sasakawa and Inoue (2021)).



Figure 1. Distribution of the *macrogenys* species group in the Tohoku District and northern part of Niigata Prefecture (the Chubu District), based on collection sites of type specimens and specimens identified by the endophallus. 1. *Pterostichus orionis* Jedlička, 1962; 2. *P. shirakamisanus* Sasakawa, 2005; 3. *P. shirakamisan* Sasakawa, 2009; 4. *P. namahage* sp. nov.; 5. *P. tanakai* Ishida, 1964; 6. *P. kitakamisanus* Sasakawa, 2005; 7. *P. chokaisanus* Sasakawa, 2009; 8. *P. kurikomasanus* Sasakawa, 2005; 9. *P. kamurosanus* sp. nov.; 10. *P. takadateyamanus* Sasakawa, 2009; 11. *P. atsumidakensis* sp. nov.; 12. *P. gassanus* Sasakawa, 2009; 13. *P. awashimaensis* Sasakawa & Itô, 2022; 14. *P. shinbodakensis* Sasakawa & Itô, 2017; 15. *P. asahinus* Habu & Baba, 1960; 16. *P. eboshiyamanus* Sasakawa, 2009; 17. *P. monolineatus* Sasakawa, Mitsuduka & Itô, 2020; 18. *P. yahikosanus* Sasakawa, 2009; 19. *P. tateishiyamanus* Sasakawa & Itô, 2017; 20. *P. ohsawacavus* Sasakawa, 2005; 21. *P. adatarasanus* Sasakawa, 2005. Red letters denote the type localities of each species. White circles indicate where the specimens examined in this study were collected.

Another unresolved aspect involves the incomplete understanding of phylogenetic relationships amongst species. Within the subgenus *Nialoe* (s. lat.), which includes the *macrogenys* species group, phylogenetic relationships amongst species groups have been examined both morphologically (Sasakawa 2005a) and molecularly (Sasakawa and Kubota 2009). However, the phylogenetic understanding within each species group is only partial. To date, within-group phylogenetic relationships have been examined only for two species groups (the *asymmetricus* and *raptor* species groups; Sasakawa (2005b) and Sasakawa et al. (2017), respectively), based on morphological data. The inference of sister-species relationships, based on morphology, has also been examined in only a few species.

In this paper, we describe new species of the *macrogenys* species group and report updated distribution records of known species, based on specimens recently collected from the northern Tohoku District. As mentioned earlier, no reports on the species group have been published from this area since Sasakawa (2009). These findings serve to bridge a gap in our understanding of the species group's diversity and, although preliminary, allow for an analysis of the overall diversity of the species group for the first time. We, therefore, conducted a morphological phylogenetic analysis of nearly all members of the species group and evaluated the regional distribution of species-level diversity. We discuss these results in the context of the species group's differentiation process.

Materials and methods

Sample collection and comparative morphology

Of the specimens examined, one was hand-collected alive during a field survey and the others were collected using subterranean baited traps similar to those in Yoshida (2012). Silkworm pupa powder was used as an attractant. Saturated salt brine, which is suitable for preserving samples for taxonomic studies (Sasakawa 2007), was used as a preservative. For each collection site, the Military Grid Reference System (**MGRS**) and lat/log values are provided. Holotypes of the new species are deposited in the collection of the National Museum of Nature and Science, Tsukuba, Japan (**NSMT**). The other specimens are in the authors' collection.

Male specimens were primarily identified by the morphology of the endophallus, which was everted and fully inflated by injecting toothpaste from the base of the aedeagus. Females were identified by matching their external morphological features with those of identified males from the same collection site. Information on the morphology of related species was obtained from Sasakawa (2005c, 2009), Sasakawa and Itô (2017 and 2022), Sasakawa et al. (2020) and scaled photos of the *Pterostichus kitakamisanus* holotype male, which were taken during a study by Sasakawa (2005c). The homology and terminology of the endophallus followed Sasakawa et al. (2020). Following Sasakawa et al. (2020), three body lengths were measured: those from the mandible apices (**BLm**), anterior margin of the labrum (**BLI**) and clypeal apex (**BLc**) to the elytral end. The Japanese names of some species reported here are given in of Suppl. material 1: table S1.

Morphological phylogeny and regional species-level diversity

Phylogenetic trees were constructed using maximum parsimony analysis with TNT version 1.6 (Goloboff and Morales 2023). All but one of the 42 members of the species group were included as the ingroup taxa. The exception was P. awashimaensis Sasakawa & Ito, 2022, for which no male specimens have been obtained to date. Pterostichus (Nialoe) micropoides Yin, Shi & Liang, 2021 was used as the outgroup taxon; this species is a member of the opacipennis species group (= Koreonialoe sensu Yin, Shi & Liang, 2021), which is thought to be the sister clade to the macrogenys species group. Twelve adult morphological characters (ten male genital, one female genital and one female external) were examined (Tables 1 and 2). The evaluation and coding of character states were based on morphological descriptions in this study, published literature and some unpublished data. Character states without available data were coded with "?". The analysis was performed with the following parameter settings: Analyze > "Traditional search"; Starting trees > "Wagner trees" with "random seed" = 1 and 100 replicates; Swapping algorithm > "tree bisection reconnection (TBR)" with 10 trees saved per replication; default parameter settings for all other factors. All characters were, thus, treated as "non-additive" (unordered as per PAUP*) and given equal weight. Bootstrap values were calculated using 'standard' and 'absolute frequencies' options with 1000 replicates.

Synapomorphies and autapomorphies were mapped on the strict consensus tree derived from the obtained trees, based on the list of these character state changes (found under Optimize > Synapomorphies > List common synapomorphies in the TNT output). Each synapomorphy was designated as "some trees" or "all trees" in the TNT output and they are here referred to as "possible" and "unambiguous" synapomorphies, respectively. In addition, maximum and minimum values of BLc, serving as an index of body size, which is considered to contribute to sympatric occurrence, were shown on the consensus tree for each species. For most species, the values of males were used, but in seven species, P. akitai, P. koheii, P. momuranus, P. nagasawai, P. nakamiyorinus, P. omiensis and P. shojii, the values of pooled male and female data were used due to the unavailability of sex-specific values. Maximum and minimum BLc values of male, female and pooled male and female of each taxon were given in of Suppl. material 1: table S2.

Table 1. Character evaluation and coding.

Character ID: Character: Evaluation and coding

1: Right paramere: (0) almost straight, short; (1) with apical part strongly bent ventrally; (2) with apical part strongly bent ventrally and large in size; (3) with apical part strongly bent ventrally, large in size, wide in dorsal view.

2: Basal half of aedeagus: (0) uniformly arcuate, rather than sharply bent; (1) sharply bent at aedeagal basal 1/3.

3: Apical half of aedeagus: (0) not swollen at ventral side of central part, with apical part wide and weakly protruding in dorsal view; (1) not swollen at ventral side of central part, with the apical part narrow and strongly protruding in dorsal view; (2) swollen at ventral side of central part, with apical part narrow and strongly protruding in dorsal view.

4: Left pigmented band: (0) not sclerotised; (1) weakly sclerotised; (2) strongly sclerotised.

5: Right pre-apical lobe: (0) not distinctly protruding, virtually absent; (1) small in size, conical or hemispherical in shape, directed dorsally or dorso-apically, with dorsal contour not continuous with that of connected part of endophallus; (2) large in size, cylindrical-shape, directed apically, with dorsal contour continuous with that of connected part of endophallus; (3) large in size, apically hooked cylindrical-shape, directed apically, with dorsal contour continuous with that of connected part of endophallus; (3) large in size, apically hooked cylindrical-shape, directed apically, with dorsal contour continuous with that of connected part of endophallus.

6: Basal part of left pre-apical lobe: (0) not protruding; (1) weakly protruding; (2) largely protruding.

7: Apical part of left preapical lobe: (0) simple, without protrusions; (1) with one protrusion directed apically; (2) bifidly protruding apically; (3) largely protruding laterally, with the apex bifurcated or T-shaped.

8: Middle part of left apical lobe: (0) almost straight, not bent; (1) uniformly bent, not forming a corner outwards of bending part; (2) sharply bent, forming a distinct corner outwards of bending part.

9: Apical part of left apical lobe: (0) simple, not bifurcated; (1) bifurcated, with two apices different in size; (2) bifurcated, with two apices same size.

10: Surface of left apical lobe: (0) not sclerotised; (1) weakly sclerotised; (2) strongly sclerotised.

11: Vaginal pigmentation: (0) absent; (1) present.

12: Adhesive hairs on female tarsal segment 1: (0) absent; (1) present.

Table 2. Character matrix for phylogenetic analysis.

Taxon	Characters [†]	Source
P. adatarasanus	0002100000?0	Sasakawa (2005c); Sasakawa et al. (2020)
P. akitai	012?????????	Morita (2004)
P. asahinus	300a30310200	Sasakawa (2005c) [‡] ; Sasakawa et al. (2020) [‡]
P. atsumidakensis	100130110100	this study
P. chokaisanus	000a121220?0	Sasakawa (2009); Sasakawa et al. (2020); this study
P. eboshiyamanus	0002100010?0	Sasakawa (2009); Sasakawa et al. (2020)
P. fukube	012?????????	Sugimura (2005)
P. gassanus	0002102110?1	Sasakawa (2009); Sasakawa et al. (2020); Itô, unpublished data (character 12)
P. gujoensis	012?????????	Toda (2012)
P. isolatus	011000000??	Sasakawa (2005c); Morita et al. (2013)
P. iwakiensis	000110200000	Sasakawa (2009); Sasakawa et al. (2020)
P. kamurosanus	000110100010	this study
P. kitakamisanus	000a10200010	Sasakawa (2005c); this study
P. koheii	0020100020?0	Sasakawa (2005c); Morita and Hirasawa (1996)
P. kuraiyamanus	012?10???0??	Morita and Ohkawa (2010)
P. kurikomasanus	000210000010	Sasakawa (2005c); Sasakawa et al. (2020)
P. macrogenys	000212210011	Sasakawa (2005c); Sasakawa and Itô (2018)
P. miyazawai	012?003100??	Morita and Ohkawa (2009)
P. momuranus	01200????0??	Morita et al. (2013)
P. monolineatus	0002100000?0	Sasakawa et al. (2020)
P. nagasawai	002??????0??	Ito and Ogai (2015)
P. nakamiyorinus	01100????0??	Morita et al. (2013)
P. namahage	0002010200??	this study
P. ohosawacavus	0000102100?0	Sasakawa (2005c); Sasakawa and Itô, unpublished data (character 12)
P. omiensis	0120????????	Sekine and Nakase (2022)
P. orionis	000110100000	Sasakawa (2005c)
P. shikatai	012?????????	Toda (2012)
P. shinbodakensis	2002303102??	Sasakawa and Itô (2017)
P. shirakamisan	000110111000	Sasakawa (2009)
P. shirakamisanus	000110100010	Sasakawa (2005c)
P. shojii	012?????????	Sugimura (2006)
P. sumondakensis	000210210011	Sasakawa (2005c)
P. takadateyamanus	100120110100	Sasakawa (2009); Sasakawa and Itô (2015); Sasakawa et al. (2020)
P. tanakai	000110100010	Sasakawa (2005c)
P. tateishiyamanus	0001102220?0	Sasakawa and Itô (2017)
P. todai todai	0110???????0	Morita and Kanie (1997); Sugimura (2002)
P. todai toyoshimai	012?????????	Sugimura (2002)
P. toyodai	012????????0	Morita and Kurosa (1998)

Taxon	Characters [†]	Source
P. uedaorum	012???????0	Morita and Hirasawa (1996)
P. yahikosanus	000210100010	Sasakawa (2009); Sasakawa and Itô (2015)
P. yamizosanus	000110200010	Sasakawa (2005c)
P. yorikoae	0120??????0	Sugimura (2007)
P. micropoides	0000010000?	Yin et al. (2021)

[†] a: polymorphic character state, 1 and 2, which is coded as "(12)" in date for TNT.

[‡] as P. falcispinus Sasakawa, 2005.

Regional species-level diversity was assessed by the number of species per Prefecture. This was achieved by compiling collection records from published literature and one unpublished data source.

Results

New species descriptions

Three species described here are similar and share the following adult morphology:

Dorsal habitus. Medium-sized (ca. 13–17 mm) macrocephalic species. Surface glossy, not opaque; head reddish-black; pronotum and elytra reddish-brown, with pronotum darker; appendages dark brown to reddish-brown.

Head. Large, widest at tempora. Mandibles long, hooked at apex, left mandible larger and more hooked than right. Frontal grooves shallow. Tempora strongly swollen, widest part wider than pronotal posterior margin, anterior–posterior length more or less longer than anterior–posterior length of eye. Surfaces of labrum, frons and tempora smooth. Antennal segment 1 with one seta; segment 2 with one or more setae; segment 3 with apical ring of six or seven setae; pubescence absent on segments 1–3, but present on other segments. Eyes weakly convex, with anterior–posterior length exceeding half-length of antennal segment 1. Mentum with pair of medial setae and pair of longitudinal depressions; mentum tooth bifid; submentum with two setae on each side.

Pronotum. Cordate-shaped, widest slightly behind apical 1/5. Anterior angles produced, with widely rounded apices. Hind angles with apices narrowly rounded, not denticulate. Posterior margin more or less emarginated medially and arcuate laterally. Median line distinctly impressed in middle area. Laterobasal impression single each side, shallow, as both impressions connected by transverse grooved area. Anterior marginal setae at widest pronotal point; posterior marginal setae near hind angles.

Elytra. Almost parallel-sided, less convex. Basal margin at interval 3–5 concave; shoulders distinct, not denticulate. Apices rounded. Basal transverse line connecting anterior ends of elytral intervals distinct; scutellar-stria present; striae distinct; intervals less convex. One setigerous puncture on stria 1 at level of posterior end of scutellum. Two setigerous punctures on interval 3, anterior one slightly in front of middle, posterior one between posterior almost 1/4 to posterior 1/5, both adjoining stria 2. Hind wings completely atrophied.

Abdominal ventral sides. Sterna 4–6 with pair of setae; sternum 7 with pair of setae in male, two pairs of setae in female. Sternum 7 of male more or less concave, forming secondary sexual characteristic.

Legs. Ventral side of first tarsomere of female forelegs without adhesive hairs in species for which female specimens were available for examination. Fifth tarsomere of hind legs without setae on the ventral side.

Male genitalia. Aedeagus stout, bent at basal 1/3, without tubercles. Endophallus short, stout, strongly bent ventrally. Left paramere subquadrate.

Female genitalia. Vagina almost spherical. Apophyses of seminal canal and median oviduct fully sclerotised.

Pterostichus (Nialoe) namahage Sasakawa & Mitsuduka, sp. nov.

https://zoobank.org/589C7C23-CC4B-4DC7-B92A-473A42F766B3 Figs 2A, 4A–D, 6A

Type material. *Holotype*, ♂, Haraikawa, Honzanmonzen, Funagawaminato, Oga-shi, Akita Prefecture, Japan (MGRS: 54SUK92241 16384; 39.89067718°N, 139.73961047°E), 28. v–30. vi. 2022, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2A).

Description. *Body length (mm)*. ♂ (n = 1), BLm 13.15, BLI 12.32, BLc 11.96.

Head. Mandibular surface with several short wrinkles at middle. Anterior–posterior length of tempora slightly longer than anterior–posterior length of eye. Surface of clypeus smooth. Antennal segment 2 with two setae. Mentum tooth shallowly bifid; width between paired apices three times anterior–posterior length between level of mentum apices to level of innermost part of median notch.

Pronotum. Lateral margin arcuate on apical 4/5, only slightly sinuate on basal 1/5. Anterior margin emarginated, with contour arched more strongly than curvature of apical 4/5 of lateral margin. Posterior margin slightly emarginated at median area and slightly arcuate at lateral areas, with curvatures of both the same as curvature of basal 1/5 of lateral margin. Hind angles slightly acute. Median line absent near anterior margin and in front of transverse grooved area between laterobasal impressions. Transverse grooved area between laterobasal impressions concave to same degree as laterobasal impressions. Surface including laterobasal impressions smooth.

Elytra. Scutellar-stria not connected to stria 1. One setigerous puncture in front of level of posterior end of scutellum. Posterior setigerous punctures on interval 3 slightly in front of posterior 1/4.

Abdominal ventral sides. Sternum 7 of male moderately concave, with degree of concavity greater than that



Figure 2. Habitus dorsal view of the *macrogenys* species group. A. *Pterostichus namahage* sp. nov. holotype male from Haraikawa; B. *P. kamurosanus* sp. nov. holotype male from Ariya; C. *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi; D. *P. asahinus* male from Momoyake.

of convexity of median area of sterna; shape of concave area transverse ellipse; posterior margin of ellipse corresponding to posterior margin of sternum; anterior–posterior length of concave area slightly longer than 1/2 anterior–posterior length of sternum 7; transverse, major axis of ellipse about 1.4 times that of longitudinal minor axis; area corresponding to minor axis of ellipse posterior to major axis slightly raised.

Male genitalia. Endophallus with gonopore directed basal-ventrally; left pigmented band weakly sclerotised; distinct right preapical lobe absent, but corresponding area

slightly swollen; left preapical lobe with basal part protruding left-laterally; left apical lobe short, not bent, bifurcated (Fig. 4A–D). Relative sizes of lobes: right apex of bifurcated left apical lobe apex \approx basal protrusion of left preapical lobe >> left apex of bifurcated left apical lobe apex. Right paramere short, straight, with apex rounded (Fig. 6A).

Female. Unknown.

Etymology. The specific name is a noun in apposition and derives from Namahage, which is a famous folk event held on the Oga Peninsula, where the type specimen was collected.

Pterostichus (Nialoe) kamurosanus Sasakawa & Mitsuduka, sp. nov.

https://zoobank.org/EC64C14A-C5A7-4161-BA26-77958C62BD19 Figs 2B, 4E–H, 6B, 7A, B

Type materials. *Holotype*, \Diamond , Ariya, alt. 403 m, Kaneyama-machi, Yamagata Prefecture, Japan (MGRS: 54SVJ49358 06377; 38.90482277°N, 140.41594335°E), 18. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2B). *Paratypes*, 4 \heartsuit , same data as the holotype; $2 \Diamond 2 \heartsuit$, Kamuro Forest Road, alt. 416 m, Ariya, Kaneyama-machi, Yamagata Prefecture, subterranean baited trap, Y. Mitsuduka leg. ($1 \diamondsuit$, 15–29. ix. 2015; $1 \Huge{} 2 \Huge{} 2, 5.$ vii–21. viii. 2017).

Description. Body length (mm). \Diamond (n = 3), BLm 14.46–15.97, 15.19 \pm 0.64, BLI 13.15–14.43, 13.84 \pm 0.54, BLc 12.70–13.95, 13.37 \pm 0.52; \Diamond (n = 6), BLm 14.19–15.08, 14.58 \pm 0.46, BLI 13.10–13.63, 13.34 \pm 0.27, BLc 12.60–13.21, 12.89 \pm 0.31.

Head. Mandibular surface wrinkled with individual variation: short rudimentary wrinkles on both lateral sides, wrinkles on one lateral side, no wrinkles on either lateral side. Anterior–posterior length of tempora 1.7–1.8 times anterior–posterior length of eye. Surface of clypeus smooth in females, but irregular and slightly uneven in males. Antennal segment 2 with one or two setae, varying individually. Mentum tooth deeply bifid; width between paired apices apparently less than three times anterior– posterior length between level of mentum apices to level of innermost part of median notch.

Pronotum. Lateral margin arcuate for apical 3/4, only slightly sinuate for basal 1/4; anterior margin emarginated, with contour arched more strongly than curvature of apical 3/4 of lateral margin; posterior margin emarginated at median area and arcuate at lateral areas, with curvature of median area distinctively greater than that of basal 1/4 of pronotal lateral margin and that of lateral areas same or only slightly greater than basal 1/4 of pronotal lateral margin; hind angles right-angled to slightly acute. Median line disappearing near pronotal anterior margin; in holotype male, posterior end disappears in front of transverse grooved area between laterobasal impressions, while in paratype female, posterior end reached pronotal posterior end. Transverse grooved area between laterobasal impressions concave to same degree as laterobasal impressions. Surface including laterobasal impressions smooth in most specimens; in some specimens, several punctations sparsely present near posterior ends of laterobasal impressions.

Elytra. Scutellar-stria connected smoothly to stria 1 in most specimens; in some specimens, scutellar-stria disappears before connecting with stria 1, but its hypothetical extension smoothly connects to stria 1. One setigerous puncture on stria 1 at level of posterior end of scutellum. Posterior setigerous punctures on interval 3 at posterior 1/5–1/4.

Abdominal ventral sides. Sternum 7 of male very shallowly concave, with degree of concavity matching that of median area of sterna; shape of concavity transverse ellipse, but indistinct due to shallowness; posterior margin of ellipse aligns with sternum posterior margin; anterior– posterior length of concavity about 0.6 times anterior– posterior length of sternum 7; transverse, major axis of ellipse about 1.5 times that of longitudinal minor axis; area corresponding to minor axis very weakly raised, except near anterior and posterior ends.

Male genitalia. Endophallus with gonopore directed basal-ventrally; left pigmented band weakly sclerotised; right pre-apical lobe indistinct, only weakly swollen; left pre-apical lobe protrudes apically at apical part; left apical lobe short, not bifurcated (Fig. 4E–H). Relative sizes of lobes: apical protrusion of left preapical lobe > left apical lobe apex >> right pre-apical lobe. Right paramere short, straight, with rounded apex (Fig. 6B).

Female genitalia. Innermost part of vagina with pigmentation (Fig. 7A, B).

Etymology. The specific name is an adjective, derived from the Japanese noun Kamurosan, which refers to Mt. Kamuro, where the type specimens were collected and the Latin adjectival suffix *-anus* (m), which means, when attached to a noun, "pertaining to".

Pterostichus (Nialoe) atsumidakensis Sasakawa & Mitsuduka, sp. nov.

https://zoobank.org/76E0733E-1D9A-472E-BBFC-6BEFAD64DBD2 Figs 2C, 4I–L, 6C–E, 7C, D

Type material. *Holotype*, ♂, Take-no-koshi, Yuatsumi, Tsuruoka-shi, Yamagata Prefecture, Japan (MGRS: 54SUH79821 75877; 38.62327968°N, 139.61944580°E), 2–24. vi. 2022, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2C). *Paratype*, 1♀, same data as the holotype.

Description. *Body length (mm).* \mathcal{J} (n = 1), BLm 16.54, BL1 14.91, BLc 14.36; \mathcal{Q} (n = 1), BLm mm, BLl 14.62, BLc 14.09.

Head. Mandibular surface smooth, except for right mandible of the paratype female, which has several short wrinkles at middle. Anterior–posterior length of tempora about twice anterior–posterior length of eye. Surface of clypeus irregularly uneven. Antennal segment 2 with four setae in the holotype male, with one seta on left and two on right in the paratype female. Mentum tooth deeply bifid; width between paired apices apparently less than three times anterior–posterior length between level of mentum apices to level of innermost part of median notch.

Pronotum. Lateral margin arcuate on apical 3/4, only slightly sinuate on basal 1/4. Anterior margin emarginated, with contour arched more strongly than curvature of apical 3/4 of lateral margin. Posterior margin emarginated at median area and arcuate at lateral areas, with curvature of median area distinctly greater than that of basal 1/4 of pronotal lateral margin and with that of lateral areas to same degree or slightly stronger than basal 1/4 of pronotal lateral margin. Hind angles right-angled to slightly acute. Median line absent near pronotal anterior margin and in front of transverse grooved area between laterobasal impressions. Concavity of transverse grooved area between laterobasal impressions weaker than that of laterobasal

impressions. Surface smooth, except for laterobasal impressions; laterobasal impressions sparsely punctate.

Elytra. Scutellar-stria not connected to stria 1. One setigerous puncture on stria 1 at level of posterior end of scutellum in the holotype male, slightly in front of posterior end in the paratype female. Posterior setigerous punctures in front of posterior 1/4.

Abdominal ventral sides. Sternum 7 of male fairly concave, with degree of concavity obviously greater than the convexity of median area of sterna; shape of concavity transverse ellipse; posterior margin of ellipse corresponding to posterior margin of sternum; anterior–posterior length of concavity 0.7 times anterior–posterior length of sternum 7; transverse, major axis of ellipse about 1.7 times that of longitudinal minor axis; middle of minor axis slightly raised for half the length of minor axis.

Male genitalia. Endophallus with gonopore directed basally; left pigmented band slightly sclerotised; right pre-apical lobe short, stout, hooked at apex; left pre-apical lobe small, protruding left laterally; left apical lobe slender, slightly bent, with weakly sclerotized surface (Fig. 4I–L). Relative sizes of lobes: right pre-apical lobe > left apical lobe; and right pre-apical lobe > left pre-apical lobe (size difference between left apical and pre-apical lobes could not be determined unambiguously because of shape difference). Right paramere bent at acute angle at apical 1/3 (Fig. 6C–E).

Female genitalia. Innermost part of vagina without pigmentations (Fig. 7C, D).

Etymology. The specific name is an adjective and derives from the Japanese noun Atsumidake, which refers to Mt. Atsumi, where the type specimens were collected and the Latin adjectival suffix *-ensis* (m), which means, when attached to a locality name, "from the locality".

New distribution records

Pterostichus (Nialoe) asahinus Habu & Baba, 1960 Figs 2D, 4M–P, 6F–H

Materials examined. 1♂, Momoyake, alt. 1030 m, Yurihonjô-shi, Akita Prefecture, Japan (MGRS: 54SVJ26680 29227; 39.1091115°N, 140.15197046°E), 24. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg.

Notes. The body lengths (mm) of the specimen are BLm 16.38, BLI 14.60 and BLc 14.06. This specimen was collected together with *P. chokaisanus*, which is to be recorded below. This is the first report of the sympatric occurrence of this species pair and provides evidence that they are reproductively isolated distinct species. Although the comparison was based on a single male for each species, a body-size difference was observed between the two species, with *P. asahinus* larger than *P. chokaisanus*. This collection record is the northernmost distribution record of the species and the first record for Akita Prefecture.

Pterostichus (Nialoe) chokaisanus Sasakawa, 2009 Figs 3A, B, 5A–H, 6I, J

Materials examined. $1 \stackrel{\circ}{\circ} 2 \stackrel{\circ}{\circ}$, Momoyake, alt. 1030 m, Yurihonjo-shi, Akita Prefecture, Japan (MGRS: 54SVJ26680 29227; 39.1091115°N, 140.15197046°E), 24. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg. (Figs 3A, 5A–D, 6I); $1\stackrel{\circ}{\circ}$, Zaô-chûô-kôgen, Zaô-onsen Spa, Yamagata-shi, Yamagata Prefecture, Japan (MGRS: 54SVH49227 23449; 38.15750459°N, 140.42046179°E), 1–6. ix. 2020, subterranean baited trap, Y. Mitsuduka leg. (Figs 3B, 5E–H, 6J).

Notes. The endophallus of the Zaô-chûô-kôgen specimen could not be inflated sufficiently due to changes in the membranous part (Fig. 5E–H), but the specimen was identified unambiguously as *P. chokaisanus*, based on species-specific structures of the endophallus. The body lengths (mm) of the Momoyake specimens (3/2/2) are BLm 14.91/14.24/14.94, BLI 13.65/13.08/13.68 and BLc 13.18/12.56/13.21; and those of the Zaô specimen are BLm 14.20, BLI 12.83 and BLc 12.40. The Zaô-chûôkôgen specimen is the southernmost distribution record of this species.

Pterostichus (Nialoe) kitakamisanus Sasakawa, 2005 Figs 3C, D, 5I–N, 6K–M

Material examined. 1∂, Ôdateminami, Ayukawahama, Ishinomaki-shi, Miyagi Prefecture, Japan (MGRS: 54SWH4527440885; 38.31492752°N, 141.51788663°E), 28. vii. 2022, hand-collected from soil, Y. Mitsuduka leg (Figs 3C, 5I–L, 6K, L).

Notes. The identification was based on comparison with the P. kitakamisanus holotype male, which is labelled "JA-PAN; Iwate-ken/Miyako-shi/Genbeidaira/ 30.VIII-10.IX. 2002/Y. Kawahara leg" (Figs 3D, 5M, N, 6M). Although the apex of the left pre-apical lobe was not confirmed to be the same structure as that of the holotype due to failure to evert it, all other structures of the endophallus, parameres and external morphology were identical to those of the holotype. In particular, the left pre-apical lobe directed left laterally is a character state found only in P. kitakamisanus amongst the known taxa of the macrogenys species group and provides definitive evidence for our species identification. The body lengths (mm) of the specimen are BLm 15.11, BLI 14.13 and BLc 13.63. This collection record is the southernmost record of the species. Judging from its known collection sites, P. kitakamisanus is likely distributed widely in the Kitakami Mountains.

Morphological phylogeny

Eighty most-parsimonious trees with a score of 40 were obtained. The strict consensus tree had many unresolved nodes with low bootstrap values, but some relationships were still recognised (Fig. 8). The species



Figure 3. Habitus dorsal view of the *macrogenys* species group. A. *Pterostichus chokaisanus* male from Momoyake; B. *P. chokaisa-nus* male from Zaô-chûô-kôgen; C. *P. kitakamisanus* male from Ôdateminami; D. *P. kitakamisanus* holotype male from Genbeidaira.

P. takadateyamanus, P. atsumidakensis, P. shinbodakensis and *P. asahinus* formed a clade, supported by three possible synapomorphies. Within this clade, *P. shinbodakensis* and *P. asahinus* were sister taxa, supported by one unambiguous and one possible synapomorphy. A polytomy was formed by *P. shinbodakensis* + *P. asahinus, P. atsumidakensis* and *P. takadateyamanus. Pterostichus chokaisanus* and *P. tateishiyamanus* were sister taxa, supported by one unambiguous and one possible synapomorphy.

Pterostichus ohsawacavus, P. sumondakensis, P. gassanus and P. macrogenys formed another clade, supported by two possible synapomorphies. Within this clade, *P. sumondakensis*, *P. gassanus* and *P. macrogenys* formed a polytomic clade, supported by one unambiguous synapomorphy and was sister to *P. ohsawacavus*.

Eighteen taxa, including P. nagasawai, P. koheii, P. isolatus, P. nakamiyorinus, P. todai todai, P. momuranus, P. omiensis, P. shikatai, P. shojii, P. todai toyoshimai, P. miyazawai, P. toyodai, P. uedaorum, P. kuraiyamanus, P. gujoensis, P. fukube, P. yorikoae and P. akitai, formed a clade, supported by one unambiguous and two possible synapomorphies. Within this clade, 16



Figure 4. Endophallus of *Pterostichus namahage* sp. nov. holotype male from Haraikawa (A-D), *P. kamurosanus* sp. nov. holotype male from Ariya (E-H), *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi (I-L) and *P. asahinus* male from Momoyake (M-P). Fully inflated endophallus in left lateral (A, E, I, M), apical (B, F, J, N), right lateral (C, G, K, O) and basal part in dorsal and apical part in ventral (D, H, L, P) views. Abbreviations: go – gonopore; lal – left apical lobe; lpb – left pigmented band; lpl – left pre-apical lobe; rpl – right pre-apical lobe.

species, except for *P. nagasawai* and *P. koheii*, formed a clade supported by one unambiguous synapomorphy, with *P. isolatus*, *P. nakamiyorinus* and *P. todai todai* forming another clade supported by one unambiguous synapomorphy.

Regional species-level diversity

The highest number of species, totalling nine, was observed in Yamagata and Niigata Prefectures, followed by six in Akita, Nagano and Gifu Prefectures. There were



Figure 5. Endophallus of *Pterostichus chokaisanus* male from Momoyake (**A–D**), *P. chokaisanus* male from Zaô-chûô-kôgen (**E–H**), *P. kitakamisanus* male from Ôdateminami (**I–L**) and *P. kitakamisanus* holotype male from Genbeidaira (**M**, **N**). Fully inflated endophallus in left lateral (**A**, **E**, **I**, **M**), apical (**B**, **F**, **J**, **N**), right lateral (**C**, **G**, **K**) and basal part in dorsal and apical part in ventral (**D**, **H**, **L**) views.

four in Fukushima and Tochigi Prefectures, three in Miyagi Prefecture and one or two in the remaining Prefectures. Overall, there were more species on the Sea of Japan side than on the Pacific side and the central part had a higher number of species than the northern and southern regions of the distribution (Fig. 9).

Discussion

We describe three new species and report new distribution records for three known species, thereby updating their distribution ranges and documenting a new sympatric species pair. Together with the first morphological



Figure 6. Right paramere of *Pterostichus namahage* sp. nov. holotype male from Haraikawa (**A**), *P. kamurosanus* sp. nov. holotype male from Ariya (**B**), *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi (**C–E**), *P. asahinus* male from Momoyake (**F–H**), *P. chokaisanus* male from Momoyake (**I**), *P. chokaisanus* male from Zaô-chûô-kôgen (**J**), *P. kitakamisanus* male from Ôdateminami (**K**, **L**) and *P. kitakamisanus* holotype male from Genbeidaira (**M**). Left lateral (**A–C, F, I–K**), right lateral (**L, M**), apical part in apical and basal part in ventral (**D, G**) and apical part in dorsal (**E, H**) views.

phylogenetic analysis performed in this study, these findings provide important insights into the diversification process of this species group.

Despite many unresolved nodes in the resultant strict consensus tree, several notable species relationships were unveiled. For instance, in the two clades-one consisting of P. takadateyamanus, P. atsumidakensis, P. shinbodakensis and P. asahinus and the other comprising P. ohsawacavus, P. sumondakensis, P. gassanus and P. macrogenys-the basal clade species (P. takadateyamanus and P. atsumidakensis in the former and P. ohsawacavus in the latter) exhibited fewer apomorphic traits and were localised to a narrow area on the Sea of Japan side. Conversely, species with more apomorphic traits had a wider distribution across various mountains. This pattern implies that initial differentiation of these clades occurred on the Sea of Japan side, followed by dispersal to other regions and geographical differentiation. A similar pattern was observed in the clade composed of western 18 species, although at the supraspecific level rather than at species level. Members of this clade are allopatrically distributed over a wide area to the west of the species group's distribution. Considering that the two species of the basal clades-P. nagasawai and P. koheii-are distributed more towards the east than most other members of the clade, it is assumed that this clade of 18 species dispersed from the east and subsequently differentiated.

Our assumptions regarding the differentiation and dispersal processes of these three clades align with the overall distribution patterns of the species group. Higher species diversity was observed on the Sea of Japan side than on the Pacific side and the highest diversity was in the central part of the distribution on the Sea of Japan side. Even though prefectural boundaries do not necessarily align with geographical barriers (such as mountain ranges or rivers) and are thus artificial, the spatial distribution of species diversity would not significantly change the observed distribution pattern. Interpreting the number of species in Nagano and Gifu Prefectures requires caution. This is because some species pairs that are close in distribution and very similar in morphology have not had their endophallus structure compared-a procedure that is critical for confirming their status as distinct species. Therefore, the actual number of species in these two Prefectures might be less than currently recognised. Considering the species' phylogeny, character evolution and distribution of diversity, it appears the macrogenys species group initially differentiated on the Sea of Japan



Figure 7. Genital membranous part of a *Pterostichus kamurosanus* sp. nov. paratype female from Ariya (**A**, **B**) and the *P. atsumidak-ensis* sp. nov. paratype female from Take-no-koshi (**C**, **D**). Dorsal (**A**, **C**) and ventral (**B**, **D**) views in everted condition of the vagina. Abbreviations: am – apophysis of the median oviduct; as – apophysis of the seminal canal; p – pigmentation on the innermost part of the vagina. Note that the two apophyses (am and as) are viewed through the membranous vagina.

side, likely near Yamagata and Niigata prefectures and, subsequently, dispersed and diverged in other areas. This hypothesis aligns with the fact that most species in the basal clades of the *opacipennis* species group, thought to be the sister clade to the *macrogenys* species group (Sasakawa 2005a; Sasakawa and Kubota 2009), are found in north-eastern China, the northern part of the Korean Peninsula and Russian Primorye (Yin et al. 2021). These regions are located almost directly across the Sea of Japan from the presumed initial differentiation area of the *macrogenys* species group (around Yamagata and Niigata Prefectures). This distribution pattern implies that the presence/formation of the Sea of Japan may have been associated with the origin of the *macrogenys* species group. The obtained phylogenetic tree revealed that sympatric species of different body sizes were not sister taxa. In almost all instances, the sympatric species belonged to separate clades and were phylogenetically distant. The exception to this pattern is *P. asahinus* and *P. takadateyamanus*, which belong to the same clade, but these two species were not sister taxa within that clade. These patterns imply an ancient origin of bodysize differences that contribute to species sympatry. This hypothesis is supported by the fact that all known sympatric sites are located on or near the Sea of Japan side in the northern part of the current distribution, which is considered the initial differentiation area of the species group.

Key to species of the *macrogenys* species group (for males)

Currently, it is virtually impossible to identify species based solely on female specimens. Usually, females are identified, based on conspecific males from the same collection site. Therefore, a key is presented here for males only. Information about species that have not been covered in our previous studies was obtained from the



Figure 8. The strict consensus tree of 80 most parsimonious trees. Syn- and autapomorphies are indicated by the squares on branches, where the numbers in the squares indicate character ID and numbers above the squares indicate character-state change. Black and white squares indicate "unambiguous" and "possible" apomorphies, respectively. Numbers in parentheses below the branches indicate bootstrap values (where > 50%). Horizontal bars at tips of the tree indicate body length of each species. Numbers in the square brackets after species name indicate that the species were collected at site coded as the same number in Figs 1 and 9. Dashed lines, which connect species and have the code (i)–(v), indicate that the species occur sympatrically at sites with the same code in Fig. 9.



Figure 9. Distribution of species diversity of the *macrogenys* species group, based on collection records. Collection sites for each species are indicated by the numbers used as species identifiers in Figs 1, 8. The codes (i)–(v) for sympatric sites are the same as those used in Fig. 8. Two uppercase letters indicate the following abbreviations for prefectures in Japan: AI – Aichi; AK – Akita; AO – Aomori; CB – Chiba; FI – Fukui; FS – Fukushima; GI – Gifu; GU – Gunma; IB – Ibaraki; IS – Ishikawa; IT – Iwate; MG – Miyagi; NA – Nagano; NI – Niigata; NR – Nara; SI – Shiga; ST – Saitama; SZ – Shizuoka; TC – Tochigi; TY – Tokyo; TM – Toyama; YG – Yamagata; YN – Yamanashi.

original description of each species. For body lengths, male values are given, except for *P. akitai*, *P. koheii*, *P. momuranus*, *P. nagasawai*, *P. nakamiyorinus*, *P. omiensis* and *P. shojii*; values of pooled male and female data are provided for these seven species. Abbreviations: BLc, body lengths measured from the clypeal apex to the elytral; PW/PA, pronotum width at widest part / pronotum anterior margin width.

1	Right paramere strongly bent at apical 1/3, forming C-shape in left lateral view (e.g. Fig. 6C, F)
-	Right paramere almost straight in lateral view; even if curved, not forming C-shape in left lateral view (e.g. Fig. 6A,B)5
2	Width at widest part of apical 1/3 of right paramere in dorsal view > 1.5 times width of basal 1/3 of right paramere in
	lateral view (e.g. Fig. 6F, H). Left apical lobe hooked, distinctly sclerotised (e.g. Ial in fig. 40)
-	lateral view (e.g. Fig. 6C, E). Left apical lobe only weakly sclerotised (e.g. lal in Fig. 4K)
3	Widest part of apical 1/3 of right paramere in dorsal view located behind half of dorsal view of right paramere apical 1/3 (Sasakawa and Itô 2017; fig. 16) BL c 1/4 3 mm. Mount Shinbodaka
_	Widest part of apical 1/3 of right paramere in dorsal view located before half of dorsal view of right paramere apical
	1/3 (Fig. 6H). BLc 12.5–16.1 mm. Asahi and Iide Mountains, Mount Chokaisan and adjacent areas
	P. asahinus Habu & Baba
4	Right paramere with dorsum of apical margin concave (Sasakawa et al. 2020: 7 in fig. 5C); left ventrolateral margin of
	apical part almost straight in left lateral view (Sasakawa et al. 2020: 5 in fig. 5C). Right pre-apical lobe straight, not hooked
_	(Sasakawa et al. 2020; rpl in fig. 50). BLC 12.0–13.9 mm. Mount Takadateyama
-	left lateral view (Fig. 6C). Right pre-apical lobe hooked apically (rpl in Fig. 4I–K). BLc 14.36 mm. Mount Atsumidake
	P. atsumidakensis sp. nov.
5	Left lateral margin of aedeagus constricted at subapical part, forming narrow apical part in ventral view (e.g. Sugimura
	(2005): fig. 2b)
-	Left lateral margin of aedeagus not constricted but slightly arcuate at subapical part (e.g. Morita and Hirasawa (1996):
6	tigs 10a and 11a)
-	Apical part of right paramere more or less modified i.e. parrowed apically (e.g. Morita and Hirasawa (1996); fig. 12a)
	truncate with sharp corner(s) (e.g. Toda (2012): fig. 12) or with a small projection on apical margin (Sekine and Nakase
	2022: fig. 9)
7	Right paramere not bent in lateral views; contour of ventral side in lateral view almost straight (e.g. Morita and Ohkawa
	(2009): fig. 5). Aedeagus with tubercle on ventral side near middle (e.g. Morita and Ohkawa (2009): fig. 3). Posterior
	margin of sternum 7 with small, shallow notch at middle (e.g. Morita and Ohkawa (2009): fig. 2)
-	Pronotal laterobasal impressions shallow with deep wide transverse wrinkles: $PW/PA < 1.15$ BL c. 12.5–14.2 mm. Shi-
0	rabiso-tôge Pass, on ridgeline between Mounts Odakayama and Oikeyama
_	Pronotal laterobasal impressions rather deep, with shallow transverse wrinkles; PW/PA > 1.15. BLc 12.9 mm. Abe-tôge
	Pass, on south-eastern ridgeline of Mount HakkôreiP. toyodai Morita & Kurosa
9	Right paramere strongly constricted at bending part; in lateral view, width at bending part less than half that of widest
	part of basal part (Ito and Ogai 2015: rp in fig. 5). Posterior margin of sternum / with emargination, width of which
	bercle on ventral side near middle: in lateral view, curvature of contour of tubercle greater than that of dorsal contour
	of aedeagal bending part (Ito and Ogai 2015: I and r in fig. 5). BLc 12.4–13.2 mm. Sugadaira-kôgen Highland, on the
	north-western slope of Mount Azuyamasan
-	Right paramere not conspicuously constricted at bending part, with width at bending part more than half that of widest
	part of basal part. Posterior margin of sternum 7 weakly emarginated or not emarginated; even if emarginated, width
	of emargination less than half that between pair of setae near posterior margin (e.g. Morita et al. (2013): fig. 11c).
	than that of dorsal contour of aedeagal bending part (e.g. Sugimura (2005): fig. 2a)
10	Pronotum widest at apical < 1/10 (Morita et al. 2013: fig. 11a). BLc 12.57–13.85 mm. Nakamiyori, i.e. Mount Shiba-
	kusayama and neighbouring mountain slopes
-	Pronotum widest at apical 1/6–1/5. BLc > 13.87 m 11
11	Contour of aedeagal apical 2/3 in dorsal view bent to right (Morita et al. 2013: fig. 10). Ventral contour of aedeagal api-
	cal 2/3 in lateral views bent at apical 1/4 of total length of aedeagus, rather than uniformly bent throughout apical 2/3
	(Morita et al. 2013: lig. 5). Posterior margin of sternum 7 simply rounded, not emarginated (Morita et al. 2013: lig. 4). BLC 14.14–16.86 mm. Mount Momurayama and neighbouring areas. P. momuranus Morita. Obkawa & Kuribara
_	Contour of aedeagal apical 2/3 in dorsal view not bent, directed posteriorly (e.g. Morita and Hirasawa (1996); fig. 18b).
	Ventral contour of aedeagal apical 2/3 in lateral views uniformly bent throughout (e.g. Morita and Hirasawa (1996): fig.
	18a)
12	Ventral side of aedeagal subapical part with transverse wrinkles (e.g. Sugimura (2005): fig. 2b). Sternum 7 weakly and
	transversely raised near middle (e.g. Sugimura (2005): fig. 2h)
-	transversely near middle (e.g. Morita (2004): figs 1 2)

13 -	Apical margin of left paramere widely emarginate (Sugimura 2005: fig. 2d). Pronotum widest at apical 1/6 (Sugimura 2005: fig. 3a). BLc 14.4–16.3 mm. Mounts Fukubegatake and Kôkasan <i>P. fukube</i> Sugimura Apical margin of left paramere slightly arcuate (Sugimura 2007: fig. 2d). Pronotum widest at apical 1/4 (Sugimura 2005: figs 1a, b). BLc 12.2–14.8 mm. Midori-dani Valley on north-western foot of Mount loganayama and Mount Shagatateyma <i>P. yorikoae</i> Sugimura
14	Terminal lamella of aedeagus shorter, with length less than twice width of base (Morita 2004: fig. 6). Elytral marginal setigerous punctures 12 or more. Sternum 7 weakly concave (Morita 2004: figs 1, 2). BLc 14.25–15.43 mm. Mount Oikedake
-	Terminal lamella of aedeagus longer, with length more than twice width of base (Morita and Hirasawa 1996: figs 18b , 19b). Elytral marginal setigerous punctures 11 or less. Sternum 7 deeply concave (Morita and Hirasawa 1996: figs 16, 17). BLc 13.87–15.53 mm. Mounts Iwôzen and Hakusan <i>P. uedaorum</i> Morita & Hirasawa
15	Apex of right paramere gradually narrowed along mid-line (e.g. Morita and Hirawasab (1996): fig. 12d). Ventral con- tour of aedeagal apical 2/3 in lateral views bent at apical 1/4 of total length of aedeagus, rather than uniformly bent throughout apical 2/3 (e.g. Morita et al. (2013): fig. 12c)
-	Apex of right paramere not gradually narrowed along mid-line, but either bent ventrally with narrow apex (e.g. Morita and Ohkawa (2010): fig. 9), with a small projection (Sekine and Nakase 2022: fig. 9) or truncate (e.g. Toda (2012): fig. 12)
16	Right lateral contour of aedeagal apical part in dorsal view straight (Morita et al. 2013: fig. 12d). PW/PA > 1.1. BLc 11.35–12.00 mm. Mount Tashiroyama
_	Right lateral contour of aedeagal apical part in dorsal view more or less bent to right (Morita and Hirasawa 1996; figs 12b, 13b). PW/PA < 1.1. BLc 12.54–14.15 mm. Mounts Yatsugatake, Daibosatsurei, Akagunayama and Hakutai
17	Right paramere with a small projection on apical margin (Sekine and Nakase 2022: fig. 9). Aedeagus with tubercle on ventral side near middle (Sekine and Nakase 2022: figs 6, 7). Elytral marginal setigerous punctures 15. BLc 13.0–
-	Right paramere without projection on apical margin and either bent ventrally with narrow apex (e.g. Morita and Ohkawa (2010): fig. 9) or truncate (e.g. Toda (2012): fig. 12)
18	Right paramere apical 1/3 bent ventrally; apical 1/3 directed approximately perpendicular to mid-line of basal 2/3, gradually narrowed apically (Morita and Ohkawa 2010: fig. 9). BLc 13.28–15.57 mm. Mount Kuraiyama
_	Right paramere truncate apically, forming two (ventral and dorsal) corners in lateral views (e.g. Toda (2012): fig. 12) 19
19	Pronotal laterobasal impressions not wrinkled (Toda 2012: fig. 6). Sternum 7 transversely raised near middle (Toda 2012: fig. 7). BLc 13.45–15.46 mm. Sakamoto-tôge Pass and Miyama-shônyûdô Cave in mountainous areas on left bank of Yoshidagawa River
-	Pronotal laterobasal impressions more or less wrinkled (e.g. Toda (2012): fig. 13). Sternum 7 not raised transversely near middle
20	Aedeagus without tubercle on ventral side near middle (Morita and Kanie 1997: fig. 3; Sugimura 2002: fig. 3a). Angles of two corners of truncate apex of right paramere in lateral views differ, with ventral corner acute and dorsal corner ob-
	tuse, forming diamond shape in lateral views (Morita and Kanie 1997: fig. 5; Sugimura 2002: fig. 3d). Posterior margin of sternum 7 only slightly or not emarginated at middle; even if emarginated, width of emargination less than 1/3 width between pair of setae near posterior margin (Morita and Kanie 1997: fig. 2; Sugimura 2002: fig. 3f). BLc 14.1–15.6 mm. Mount Enasan
-	Aedeagus with tubercle on ventral side near middle (e.g. Sugimura (2002): fig. 4a). Angle of two corners of truncate apex of right paramere in lateral views almost equal, forming square shape in lateral views (e.g. Sugimura (2002): fig. 4d). Posterior margin of sternum 7 with an emargination, width of which more than half that between pair of setae near parterior margin (a.g. Sugimura (2002): fig. 4f).
21	Terminal lamella of aedeagus longer, with length more than twice width of base (Toda 2012: figs 9, 10). Pronotum laterobasal impressions with wrinkles at proximal anterior part, but not near base (Toda 2012: fig. 13). BLc 12.30–14.31
-	Terminal lamella of aedeagus shorter, with length less than twice width of base (e.g. Sugimura (2002): fig. 4a, b). Proportum laterobasal impressions with wrinkles pear base $Bl c > 14.5 \text{ mm}$
22	Sternum 7 with several wrinkles near posterior margin on outside of pair of setae (Sugimura 2006: fig. 2g). Pronotum widest at apical 1/5.1. BLc 16.30–16.81 mm Mount Shirakusavama
-	Sternum 7 not wrinkled near posterior margin on outside of pair of setae. Pronotum widest at apical 1/6. BLc 14.6– 15.2 mm. Mount Kisokomagatake
23	Aedeagus with middle dorsal side convex (Sasakawa et al. 2020: 1 in fig. 7C, D). Left pigmented band sclerotised from base to apex, with same degree as aedeagus and positioned on exactly left lateral side (Sasakawa et al. 2020: 1, 2, 4)

	in fig. 7C, D). BLc 12.81–13.98 mm. Northern part of Abukuma Mountains
	P. monolineatus Sasakawa, Mitsuduka & Itô
-	Aedeagus with middle dorsal side not convex (e.g. Sasakawa et al. (2020): 1 and 2 in fig. 7B). Left pigmented band, if
	present, positioned on left ventrolateral rather than lateral side (e.g. Sasakawa et al. (2020): lpb in fig. 7B), with degree
	of chitinisation varying amongst species
24	Base of left pre-apical lobe swollen and protruding left laterally in dorsal view (e.g. lpl in Fig. 5B, D, F, H)
-	Base of left pre-apical lobe not swollen (e.g. Ipl in Fig. 4E–H)
25	Left apical lobe smoothly bent near middle, without corner outwards of bending part (Sasakawa and Ito 2018: figs 3, 5). BLc
	13.1–18.6 mm. Joshin'etsukokkyo Mountains, Nikko Mountains, Nasu Mountains, Okuchichibu Mountains, Tanzawa Moun-
	Laft apical lobe charply best near middle, forming dictingt corpor outwards of bonding part (o.g. lal in Fig. 5P). Place
_	13.0 mm
26	Left apical lobe bifid apically (Sasakawa et al. 2020: Ial in fig. 3A–C). BLc 11.5–13.1 mm. Mounts Chôkaisan, Gassan, Funagatayama and Zaôsan
-	Left apical lobe not bifid (Ial in Fig. 4A–C). BLc 12.0 mm. Oga Peninsula P. namahage sp. nov.
27	Left apical lobe large, bifid; length between larger of left apical lobe apices and left pre-apical lobe apex in lateral views
	longer than width of aedeagus at ostium in lateral views (Sasakawa 2009: Ial in fig. 11). BLc 15.0 mm. Shirakami Moun- tains
_	Left apical lobe with length between left apical lobe apex (or apices) and left pre-apical lobe apex in lateral views shorter
	than half width of aedeagus at ostium in lateral views (e.g. Fig. 4E, F)
28	Apex of right preapical lobe directed left laterally (rpl in Fig. 5I–N). BLc 13.6–15.0 mm. Kitakami Mountains
_	Apex of right pre-apical lobe not directed left laterally (e.g. Fig. 4E–G)
29	Endophallus and gonopore directed ventroposteriorly (Sasakawa et al. 2020: fig. 3D, E). BLc 13.6–15.0 mm. Mount
	Kurikomayama
_	Endophallus and gonopore directed ventrally/anteriorly (e.g. Figs 4, 5)
30	BLc ≥ 15.5 mm
-	BLc < 15.0 mm
31	Left apical lobe gradually narrows towards apex and moderately bent (Sasakawa 2005c: fig. 10). BLc 15.5 mm. Mount
	SumondakeP. sumondakensis Sasakawa
-	Left apical lobe cylindrical, not narrowed towards apex and strongly bent (Sasakawa et al. 2020: Ial in fig. 6A, B). BLc
	16.4–17.6 mm. Mount Gassan and Azuma Mountains
32	Left apical lobe sharply bent near middle, forming distinct corner outwards of bending part; apical part bifid, with two apices same size (Sasakawa and Itô 2017: lal in figs 21, 22). BLc 12.2–12.9 mm. Mount Tateishiyama
-	Left apical lobe bent at the base (not at the middle) (e.g. Sasakawa (2005c): fig. 8) or not bent (e.g. Sasakawa (2005c):
	fig. 2)
33	Left pre-apical lobe bifid apically (e.g. Sasakawa et al. (2020): lpl in fig. 6C–E)
-	Left pre-apical lobe not bifid (e.g. Sasakawa et al. (2020): Ipl in fig. 5D, E)
34	BLc < 13.5 mm Left pigmented band absent or weakly sclerotised
-	BLC 14.7 mm. Left pigmented band weakly scierotised (Sasakawa 2005c: fig. 9). Mount Yamizosan
25	Left nigmented band cheant (Secologica) fig. 8) Develout surface of bady reddich brown. Die 12.2 mm. Ober
30	Leit pigmented band absent (Sasakawa 2005c: lig. 8). Dorsal surface of body reddish-brown. BLc 13.3 mim. Onsa-
	Warshortyddo Cave
-	12.82 mm. Southern part of Abukuma Mountains and porth western foot of lide Mountains P iwakiensis Sasakawa
36	Ventral contour of left pre-apical lobe widely emarginate at middle in left lateral view (e.g. Sasakawa et al. (2020): Inl in
50	fig 5D F)
_	Ventral contour of left pre-apical lobe arcuate, not emarginate at middle in left lateral view (e.g. Sasakawa et al. (2020):
	Ipl in fig. 7A, B)
37	Left pre-apical lobe with posteriorly directed protrusion at ventroposterior end (e.g. Sasakawa (2005c): lpl in fig. 2).
	Degree of chitinisation of left pigmented band weaker than that of aedeagus near ostium (e.g. Fig. 4E)
_	Ventroposterior end of left pre-apical lobe widely rounded, without apically narrowed protrusion (Sasakawa et al. 2020:
	Ipl in fig. 5D, E). Degree of chitinisation of left pigmented band same as that of aedeagus near ostium (Sasakawa et al.
	2020: Ipb in fig. 5D, E). BLc 12.7–12.9 mm. Mounts Adatarayama and TakadateyamaP. adatarasanus Sasakawa
38	Right pre-apical lobe about same size as protrusion at ventroposterior end of left pre-apical lobe (Sasakawa 2005c: fig.
	2). BLc 12.1–12.6 mm. Mount Hakkôdasan
-	Right pre-apical lobe rudimentary, with size apparently smaller than that of protrusion at ventroposterior end of left
	pre-apical lobe (Fig. 4E–H). BLc 12.7–14.0 mm Mount KamurosanP. kamurosanus sp. nov.

39	Left pre-apical lobe with single, hooked protrusion at ventroposterior end (Sasakawa 2005c: fig. 4). BLc 12.8–14.6 mm.
	Mounts Akitakomagatake, Iwatesan and HachimantaiP. tanakai Ishida
_	Left pre-apical lobe with simple, unhooked protrusion (e.g. Sasakawa (2009): lpl in fig. 17) or without protrusions (Sa-
	sakawa et al. 2020: IpI in fig. 7A and B). BLc ≤ 12.6 mm
40	Left pre-apical lobe without protrusions (Sasakawa et al. 2020: Ipl in fig. 7A, B). BLc 11.8–12.4 mm. Eboshiyama Hills,
	located in the north between lide and Azuma Mountains P. eboshiyamanus Sasakawa
_	Left pre-apical lobe simple, unhooked protrusion (e.g. Sasakawa (2009): lpl in fig. 17)
41	Left pigmented band strongly sclerotised (Sasakawa 2009: lpb in fig. 17). Pronotum less cordate, with PW/PA being
	1.15. Dorsal surface of body reddish-brown (Sasakawa 2009: fig. 8). BLc 12.6 mm. Mount Yahikosan
_	Left pigmented band weakly sclerotised (Sasakawa 2005c: fig. 3). Pronotum cordate, with PW/PA being 1.24. Dorsal
	surface of body black. BLc 11.7 mm. Shirakami Mountains

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Supplementary material 1

Proposed Japanese name for species treated in the present study and BLc (mm) of each taxon, compiled from published literature and the authors' unpublished data

Authors: Kôji Sasakawa, Yoshiji Mitsuduka Data type: docx

- Explanation note: **table S1.** Proposed Japanese name for species treated in the present study. **table S2.** BLc (mm) of each taxon, compiled from published literature and the authors' unpublished data. The value is given as minimum–maximum values, except when the value was from one individual only or was not obtained from the data sources. In these cases, the single value and "NA" instead of value is provided, respectively.
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PENSOFT.



Explosive radiation versus old relicts: The complex history of Ethiopian Trechina, with description of a new genus and a new subgenus (Coleoptera, Carabidae, Trechini)

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https://zoobank.org/8D3E277C-424C-440B-8FE8-78085239C2A2

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Abstract

The trechine beetle fauna (Coleoptera, Carabidae) of the Ethiopian Highlands is known to be highly diverse in species, and many species groups were recognized to be characterized by unusual character states of external and genital morphology. Earlier authors described several genera and subgenera of Ethiopian Trechina endemic to certain high mountains of the country. However, the relationships of these species groups and their evolutionary history are unknown so far. Here, we present the first molecular phylogenetic analysis of Ethiopian Trechina, detect several synonymic names under *Trechus* sensu lato, and introduce two new species groups to the country's fauna: the monotypic genus *Baehria* Schmidt & Faille, **gen. nov.**, with the type species *B. separata* **sp. nov.** from Mt. Choke in northern Ethiopia, and the *Trechus* subgenus *Abunetrechus* Schmidt & Faille, **subgen. nov.**, with the type species *T. bipartitus* Raffray, 1885; this subgenus includes three species of northern Ethiopia. We show that the composition of the Ethiopian fauna is based on multiple events of immigration, which started simultaneously with or some million years after the Oligocene-Early Miocene orogenic events north and south of the Rift Valley. Our results support the habitat island hypothesis for the evolution of the Ethiopian highland fauna. We found no evidence for an alternative hypothesis assuming a close connection of the Trechina immigration to Ethiopia and Pleistocene cooling. We, thus, conclude that the geomorphological development rather than the climatic changes are the main drivers of the diversification of the high-altitude Trechina fauna in Ethiopia.

Key Words

Abunetrechus, Baehria, biogeography, checklist, mountains of East Africa, new species, new synonymy, phylogeny, Trechus

Introduction

The biogeographic and evolutionary history of the Trechini fauna of Ethiopia is complex and poorly understood. Members of two trechine subtribes are known to occur in the country. Within the subtribe Trechodina, the genus *Pachydesus* Motschulsky is a typical element of the southern African fauna, and two species were found in Ethiopia so far (Basilewsky 1974; Merene et al. 2023). Similarly, only two species of *Trechodes* Blackburn occur in Ethiopia; the genus belongs to Trechodina and is widely distributed in tropical-subtropical regions of Africa, Madagascar, Indochina, the Philippines and Australia (Casale and Laneyrie 1982; Magrini et al. 2005; Faille et

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al. 2021). Another Trechodina genus, *Perileptus* Schaum, has a distribution similar to *Trechodes* but also occurs in the warm temperate zone of the Palearctic region. Four species of *Perileptus* are noted for the Ethiopian fauna (Casale and Laneyrie 1982; Deuve 2004; Merene et al. 2023). Based on our field investigations in Ethiopia, species of *Pachydesus*, *Perileptus*, and *Trechodes* have their habitats along brooks and rivers at lower and medium elevations, with the highest occurrences of *Pachydesus* at altitudes up to 3200 m.

Most of the Trechini species of the Ethiopian fauna belong to the megadiverse Holarctic genus *Trechus* Clairville (in the widest sense) of the subtribe Trechina and have their occurrences restricted to afromontane and afroalpine environments (Fig. 1). Molecular phylogenetic analyses have shown that the taxon *Trechus* (sensu lato) is polyphyletic (Faille et al. 2010, 2013). However, so far, the systematic position of the Ethiopian and East African representatives has not been addressed.

In the mountains of East Africa, several *Trechus* (sensu lato) lineages occur in widely separated high-altitude habitats ("mountains islands"): 21 species are placed in the subgenera *Elgonophyes* Jeannel, *Elgonotrechus* Jeannel, and *Trechus* s. str. on Mt. Elgon, two species of the subgenus *Meruitrechus* Jeannel on Mt. Meru, and 64 species are placed in the subgenera *Abyssinotus* Quéinnec & Ollivier, *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti, *Minitrechus* Vigna Taglianti & Magrini, and *Trechus* s. str.) in the Ethiopian Highlands (Jeannel 1954a; Casale and Laneyrie 1982; Geginat 1995, 2008; Pawłowski 2003; Vigna Taglianti and Magrini 2010; Ortuño and Novoa 2011; Magrini et al. 2012; Schmidt and Faille 2018; Quéinnec et al. 2021).

The eyeless Trechini species *Nunbergites aethiopicus* Pawłowski & Stachowiak, 1991, is special to the country's fauna. This species was found in the Simien Mountains (Fig. 1) and is considered closely related to *Neotrechus* J. Müller of the subtribe Trechina from the eastern Mediterranean region (Pawłowski and Stachowiak 1991).

Four additional Trechini genera and a total of 13 species were described from the mountains of northern Ethiopia just recently (Quéinnec et al. 2021): *Aethiopsis* Quéinnec & Ollivier, from Mt. Abune Yosef, and *Afrotrechus* Quéinnec & Ollivier, *Deuveopsis* Quéinnec & Ollivier, and *Nilotrechus* Quéinnec & Ollivier from Mt. Choke (Fig. 1). Based on morphological character analyses, the authors conclude that the hypothesis of phylogenetic relationships between these genera and Trechodina is debatable.

Overall, these data indicate that the Ethiopian Highlands might be considered a hotspot of Trechini diversity,



Figure 1. Map of Ethiopia showing the main topographic features of the country. Seven prominent volcanic massifs which are discussed in the text are highlighted. The base map was downloaded from www.freeworldmaps.net (01-07-2023).

not only in terms of species numbers but also lineage diversity. Remarkably, in some Trechini genera, several species seem to be highly endemic to single Ethiopian volcanos (Quéinnec et al. 2021). However, phylogenetic relationships among Ethiopian Trechini species and species groups are largely unknown, and taxonomic concepts are in flux (Ortuño and Novoa 2011; Schmidt and Faille 2018). Also, the biogeographical history and evolution of the East African high-altitude Trechini fauna are rarely known. Related questions are part of a persisting controversial debate (Jeannel 1954b; Mani 1968; Ortuño and Novoa 2011; Schmidt and Faille 2018; Quéinnec et al. 2021).

In recent years, a more intensive field investigation of the diversity, ecology and distribution of the high-altitude ground beetle fauna of Ethiopia was performed by authors of the present study. As a result, several new synonymies could be detected, and two additional, previously unrecognized trechine species groups were identified and are described in this paper. Most importantly, representatives of all Ethiopian Trechus (s. l.) species groups and the genera recently described by Quéinnec et al. (2021) became available for molecular analysis. Based on this material, we present the first dated phylogeny of the Ethiopian species. Using sequence fragments of two mitochondrial and two nuclear ribosomal genes, we aimed at answering the following questions: Are species groups recently described by Quéinnec et al. (2021) representatives of Trechina or Trechini? How many independent immigration events caused the Ethiopian high-altitude trechine fauna to emerge? When did immigration of Palearctic trechine taxa occur – in the course of the Late Cenozoic cooling or, alternatively, in response to the major orogenic events in East Africa, starting in the Oligocene?

Materials and methods

Materials

Specimens used for the morphological studies are listed in the respective Material sections of the relevant taxa, below. Specimens included in the molecular phylogenetic analyses are listed in Suppl. material 1. Taxonomy and identification of Ethiopian *Trechus* species and species groups follow Jeannel (1927), Pawłowski (2001, 2003), Ortuño and Novoa (2011), Schmidt and Faille (2018) and Quéinnec et al. (2021). Institutional codes used in the taxonomic treatment are as follows:

- CAF Arnaud Faille working collection, Stuttgart, Germany;
- **CSCHM** Joachim Schmidt working collection, later to be deposited in the Zoologische Staatssammlung, Munich;
- MNHN Muséum National d'Histoire Naturelle, Paris;
- UARK University of Arkansas Arthropod Collection;
- NHMAA Natural History Museum, Addis Ababa University.

Morphological studies

Specimens were examined by stereomicroscope Leica M205-C. The photographs were taken with a Leica DFC450 digital camera using a motorised focussing drive, light base Leica TL5000 Ergo, diffused light with Leica hood LED5000 HDI, subsequently processed with Leica LAS application software, and enhanced with CorelDRAW Graphics Suite X5.

Body size was measured from the tip of mandibles in opened position to the apex of the longer elytron. The width of the head was measured across the widest portion including compound eyes. The width of pronotum and the width of elytra were measured at their widest points. The length of pronotum was measured along the median line. The widths of pronotal, apical and basal margins were measured between the tips of the apical and basal angles, respectively. The length of elytra was measured from the tip of the scutellum to the apex of the longer elytron. The length of the hind tibia was measured along its maximum length including its basal joint. The length of aedeagal median lobe was measured across the longest distance without consideration of the sagittal aileron. The following abbreviations were used in the species descriptions:

Length of aedeagal median lobe;
Length of elytra;
Width of elytra;
Width of head;
Length of pronotum;
Width of pronotal apical margin;
Width of pronotal basal margin;
Width of pronotum;
Length of hind tibia.

Molecular data acquisition

Specimens used for the molecular study were collected alive by hand in the field and preserved in absolute ethanol. Genomic DNA was isolated from whole specimens using a non-destructive extraction protocol (Rowley et al. 2007) and the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). The specimens were then dry mounted on a card, male genitalia extracted and included in a drop of water-soluble dimethyl hydantoin formaldehyde resin (DMHF) on a transparent card beneath the specimen. Vouchers and DNA samples are deposited in the collections of the State Museum of Natural History, Stuttgart (CAF, SMNS). In the phylogenetic analyses, we included 55 specimens belonging to 49 species of Ethiopian Trechini, including representatives of all genera and subgenera described so far (Suppl. material 1). We complemented this data set with representatives of Trechodina and Trechus subgenera from Tanzania (Meruitrechus Jeannel) and Yemen (Arabotrechus Mateu), as well as representatives of all the lineages and clades of Trechus Clairville and allied genera identified in Faille et al. (2013).

	Baehria gen. nov.		<i>Trechus</i> (s. l.) <i>Abunetrechus</i> subg. nov.		<i>Trechus</i> (s. l.) subgen. <i>Abyssinotus</i>		Trechus (s. l.) subgen. Minitrechus	
	Stem	Crown	Stem	Crown	Stem	Crown	Stem	Crown
Ac	15.19 (9.86–21.13)	2.13 (1.03-3.27)	10.67 (6.83–14.62)	3.62 (1.52-5.96)	n.a.	17.5 (13.01–22.23)	n.a.	16.57 (12.44–21.04)
ac+sr	22.87 (15.9-30.08)	4.19 (2.12-6.85)	17.74 (12.93-22.96)	6.01 (3.02–9.36)	n.a.	26.22 (21.51-30.96)	n.a.	22.87 (20.89–24.00)

Table 1. Node ages (My) and 95% HPD (height posterior density) of high-altitude trechine groups endemic to Ethiopia obtained from BEAST2 based on the concatenated data set. For calibration, two age constraints (ac) were implemented or combined with available substitution rates (sr) (see text, for details).

The sampling includes most of the type species of the genera treated in this paper, including *Trechus*. Other genera of uncertain affinities were also included: *Anchotrechus* Jeannel from the Canary Islands, *Paratrechus* Jeannel and *Oxytrechus* Jeannel from Ecuador, *Duvaliomimus* Jeannel from New Zealand, *Tasmanorites* Jeannel from Tasmania, *Bhutanotrechus* Uéno from Bhutan, *Agonotrechus* Jeannel from Nepal, *Trechisibus* Motschulsky from Chile. We used Anillini and Bembidiini as outgroups. Two species of Patrobini were selected to root the tree since they are known to belong to the subfamily Trechinae but are outside the group revised in the present study (Maddison et al. 2019).

We amplified three DNA fragments, two mitochondrial (the 5' end of cytochrome c oxidase subunit 1, cox1 and a fragment containing the 5' end of large ribosomal unit plus the Leucine transfer plus the 3' end of NADH dehydrogenase subunit 1, rrnL+trnL+nad1; ca 740 bp) and two nuclear (large and small ribosomal unit, LSU and SSU rRNA). For the primers used, see Suppl. material 2, and for the general PCR conditions, see Faille et al. (2010). Sequences were assembled and edited with Bioedit v. 7.0 (Hall 1999) and Geneious Prime 2019.2.3 (Kearse et al. 2012). New sequences have been deposited in GenBank database, with accession numbers indicated in Suppl. material 1. A few sequences were taken from Faille et al. (2010, 2011, 2013, 2014) and Fresneda et al. (2019) (Suppl. material 1).

We aligned the sequences using the online version of MAFFT v.7 (Katoh et al, 2019) using the L-INS-i algorithm and default parameters. Maximum likelihood analyses were conducted on the concatenated alignment using RAxML v.7.2 (Stamatakis 2006), with thorough bootstraps, 20 runs, 500 reps, and a GTR+I+G evolutionary model (Stamatakis 2006, 2014). We used the default values for other parameters of the search (Stamatakis 2014).

Divergence time estimations were performed based on the concatenated data set, partitioned by genes and codons using BEAST2 v.2.6.7 (Bouckaert et al. 2019). We specified HKY substitution models, a birth-death prior, and a relaxed log-normal clock. To calibrate the tree, we implemented two age constraints: c1, upper age range of 24 Mya for the *Trechus* clade of southern Ethiopia based on the maximum age of the Bale Mountains (Abbate and Bruni 2015) (uniform distribution); c2, a minimum age of 98 Mya for the Trechini stem group based on the earliest fossil of that group (log-normal distribution M=2, S=1.105, offset=99). The oldest trechini fossils are known from Burmese amber (coll. D.R. Maddison and coll. A. Faille; data will be published by A. Faille and co-workers elsewhere). The amber is dated as about 98.79 ± 0.62 Ma (earliest Cenomanian; Shi et al. 2012). We also used the rates estimated for the same gene fragments in a previous work on Carabidae, all with a normal distribution and a standard deviation of 0.3 (i.e. 0.0016 changes/branch/ Ma for 16S; 0.0013 for 28S; and 0.0145 for COI; Andújar et al. 2012). Two dating approaches were performed: i) using the age constraints only, and ii) including age constraints and available rates. Six (i) and three (ii) runs were performed, each with 100 million generations, and a thinning range of 10,000. Replicate runs were then combined with BEAST2 LogCombiner v.2.6.7 by re-sampling logs and trees from the posterior distributions at a lower frequency (ii) and using a burn-in of 10% for each data-set, resulting in a final set of ~18,000 (i) and ~27,000 trees (ii). Convergence and stationary levels were verified with Tracer v1.7.1 (Rambaut et al. 2018). We annotated the tree information with TreeAnnotator v.2.6.7 and visualized it with FigTree v.1.4.2.

Results

In accordance with previous molecular phylogenetic studies on Trechinae (Faille et al. 2013, 2021; Maddison et al. 2019), we recovered a monophyletic Trechini clade with Trechodina forming the sister clade of Trechina. The genus *Oxytrechus* is sister to the remaining Trechina, and the Tasmanian *Tasmanorites* together with the Chilean representative of *Trechisibus* form a well-supported clade. These two taxa are sister clade to the remaining Trechina. Inside this large clade of Trechina, the main clades found in Faille et al. (2013) are largely recovered: the Isotopic clade (Clade 2 in Faille et al. 2013), the Pyrenean hypogean clade (Clade 1.1 in Faille et al. 2013), the *Epaphius* clade, the Dinaro-Alpine clade (Clade 1.3.2.1 in Faille et al. 2013) and the *Trechus* clade (Clade 1.3.2.2 in Faille et al. 2013).

Phylogeny of Ethiopian Trechina

The Ethiopian high-altitude trechine fauna consists of at least three isolated clades, all of which cluster within Trechina (Figs 2, 3). Because *Nungbergites* was not available to our study, the systematic position of this taxon remains to be tested.

The monotypic genus *Baehria* gen. nov. from Mt. Choke in northern Ethiopia (see below, for description) forms a well-supported clade together with the Trechina







Figure 3. Subtree of the ultrametric time-calibrated phylogeny of Trechini beetles as shown in Fig. 2 (see there for details). Collapsed, colored clades refer to previous results of Faille et al. (2013). Clades which include Ethiopian *Trechus* (sensu lato) species are highlighted by different colors (see text for details).

genera *Duvaliomimus* from New Zealand and *Paratrechus* from South and Central America (in the following the BDP clade). Based on our dataset, the sister group of this clade is formed by the Palearctic "isotopic clade" of Trechina (Faille et al. 2013), although with low support (Fig. 2).

All other Ethiopian high-altitude trechine species cluster within the megadiverse genus *Trechus* (sensu lato). Within the genus *Trechus*, *Abunetrechus* subgen. nov. (see below, for description) is a member of a well-supported clade which includes the monotypic *Anchotrechus* Jeannel from Tenerife, the monotypic *Arabotrechus* Mateu from Yemen, as well as the subgenus *Meruitrechus* Jeannel with two species from Mt. Meru, Tanzania (in the following the "AAMA clade"). The tree shows low supported basal branching of *Abunetrechus* subgen. nov. within the AAMA clade (Fig. 3).

The remaining Ethiopian *Trechus* (s. l.) form two clades that strictly separate the northern and southern Ethiopian faunas (Fig. 3). A sister relationship of the northern and southern Ethiopian clades is not supported by our tree. Moreover, the results do not support a close relationship of these two clades with any of the Holarctic *Trechus* (s. l.) lineages.

The southern Ethiopian *Trechus* clade includes all species known to occur in the Bale and Arsi Mountains and the Gughe Highlands, south and west of the Rift Valley. The two species from the Gughe Highlands form a separate lineage within one of the two main clades of South Ethiopian *Trechus* (Fig. 3). This clade comprises only species with markedly small body size (Schmidt and Faille 2018). The taxa *Archeotrechus* and *Minitrechus* are closely related and representatives of a terminal clade within southern Ethiopian *Trechus* (s. 1.) (Fig. 3).

Our phylogenetic analyses show a similar picture for the trechine fauna of the highlands in northern Ethiopia. Samples of this clade originated from the Abune Yosef Massif, Guassa Plateau, and Mt. Choke. Based on the dated tree, all of the Trechini genera and subgenera recently described by Quéinnec et al. (2021) cluster within the northern Ethiopian *Trechus* (s. l.) clade (Fig. 3); these are *Abyssinotus, Abayopsis, Abyssiniopsis, Aethiopsis, Afrotrechus, Deuveopsis*, and *Nilotrechus*.

The systematic positions of the *Trechus* (s. l.) species from the Simien Mountains in northern Ethiopia and of *T. aethiopicus* Alluaud, 1918 from the mountains near Addis Abeba remain unknown due to the lack of molecular material.

Noteworthy, among the Palearctic species groups, both the monotypic genera *Anchotrechus* Jeannel from Tenerife, and *Speotrechus* Jeannel from France, are nested within *Trechus* (s. l.) in our phylogeny.

Molecular dating of the Trechina species groups endemic to Ethiopia

Stem and crown group ages of the trechines endemic to Ethiopia, as calculated with BEAST2 using two different dating approaches, are summarized in Table 1.

Taxonomic results

Baehria Schmidt & Faille, gen. nov.

https://zoobank.org/71FD62CE-3922-4927-9A70-E94D7DD7A7A0 Figs 4–15

Type species. *Baehria separata* sp. nov., herewith designated.

Diagnosis. Representative of subtribe Trechina due to presence of bidentate mandibles (absence of retinacle) and dorsally closed aedeagal median lobe (Jeannel 1926). Comparatively large trechines characterized by robust head, large mandibles, small but markedly protruded eyes, smooth, markedly convex tempora, cordiform pronotum, straight pronotal basal margin with large, rectangular to acute laterobasal angles, slender elytra, short metepisternum, reduced hindwings, moderately slender antenna and legs, protibia with a complete longitudinal groove on external surface, presence of a row of long adhesive hairs on apical margins of 4th tarsomeres which are as long as the 5th tarsomeres, and by a markedly slender median lobe of aedeagus, which possesses a small, slightly sclerotized endophallic copulatory piece. The new genus is particularly distinguished from other representatives of Trechina by unusual chaetotaxy of head capsule and elytra as follows: clypeus plurisetose, each side with 3-5 setae; submentum with three setae each side; anterior elytral discal seta located in the 4th interval, adjoined to the 4th stria.

Etymology. The new genus name is given *in memoriam* of our dear friend and colleague, the distinguished entomologist Martin Baehr, Munich (10.03.1943– 17.04.2019).

Description. Head: Large and robust, without pilosity. Mandibles large, moderately slender, with bidentate dentition pattern as shown in Fig. 8. Labrum with apical margin moderately emarginated, with six setae near apical margin. Clypeus each side with three or four setae (Figs 5, 7; seldom only two setae at one of the sides). Eyes moderately small, as long as or slightly shorter than tempora, markedly convexly protruded (Figs 5, 7). Two supraorbital setae each side in normal position for Trechina. Supraorbital furrows unevenly bent in posterior half, markedly deep in front and middle portions, slightly flatter near insertion of posterior supraorbital seta. Tempora markedly convex, markedly wrinkled to the neck, smooth. Mid of head convexly elevated, with a distinct transverse depression between supraorbital area and neck (Figs 5, 7). Antennae slender, with third antennomere longest, 1/9-1/10 longer than first respectively fourth antennomere, and with second antennomere about 2/3 of length of third. Suborbital seta present. Apical tooth of mentum bifid, sensory pits of mentum present; submentum with three setae each side (Fig. 9).

Prothorax: Pronotum rather small, without pilosity, moderately transverse, cordate, broadest distinctly before middle, with lateral margin markedly concave before base, and with basal margin slightly smaller than apical margin (Figs 4, 6). Disc moderately convex. Anterior margin straight or slightly concave in middle with anterior angles small but distinct, rounded, moderately protruded. Basal margin straight along internal 3/4, with laterobasal angles slightly shifted posteriad. Lateral margin convexly rounded in anterior 2/3 and concave towards laterobasal angles, latter large, rectangular or sharp at tip, sometimes slightly protruded laterally. Marginal gutter moderately broad throughout. Median longitudinal impression sharply incised, disappearing near apex, somewhat deepened before base. Anterior and posterior transverse impressions shallow and smooth. Laterobasal foveae large, internally and externally (towards lateral gutter) distinctly sloped, without punctures but with fine transversal wrinkles. Lateral and laterobasal setae present, with the former situated at or slightly anterad of maximum width of pronotum. Proepisternum glabrous and smooth.

Pterothorax: Elytra without pilosity, long and very slender ovate, very slightly convex or flattened in middle of disc, in dorsal view broadest distinctly posterad middle, shoulders flatly rounded (Fig. 13), apical sinuation distinct, apex rounded with the indication of a very obtuse apical angle. Striae 1-8 complete, moderately deep impressed, impunctate, intervals moderately convex, parascutellar stria free, 1/6-1/9 of length of elytra. Recurrent preapical stria deep, long, in most specimens reaching the apex of the fifth stria. Parascutellar seta present. Anterior discal seta located in the 4th interval, adjoined to the 4th stria, located near the end of the anterior elytral 5th (Fig. 13); second discal seta located at the 3rd stria about at elytral middle (in most specimens, the posterior setiferous pore together with the 3rd stria is switched into the 4th interval); posterior discal seta (= subapical seta near the end of 3rd stria) present, located about 1/9 of elytral length from elytral apex; subapical seta of the recurrent stria isolated, distinctly removed from this stria by distance of 2-3 diameters of the setiferous pore. Number and positions of the setae of the marginal umbilicate series as in Trechus s. str. Metepisternum very short, glabrous and smooth, with outer margin about as long as anterior margin.

Legs: Moderately long and robust. Protibia distinctly dilated towards apex, straight, with longitudinal groove on dorsal surface complete, and with several fine setae on anterior surface near apex (Fig. 12). Two basal protarsomeres of males dilated and dentoid at the inner apical border (Fig. 10). Fourth pro-, meso- and metatarsomeres each with a row of long adhesive hairs on apical margins which are as long as the 5th tarsomeres (Figs 10, 11).

Male genitalia (Figs 14, 15): Aedeagal median lobe markedly elongated, slender tube-like, in lateral view slightly sinusoidal, with apex distinctly bent upwardly, simple, with apical lamella insignificant; basal bulb rather small with large sagittal aileron. Endophallus with a small, very slightly sclerotized copulatory piece. Parameres with 3-4 apical setae.

Distribution. So far only known from Mt. Choke in northern Ethiopia (Fig. 1).

Relationships and identification. Based on the molecular data, Baehria gen. nov. is representative of a well-supported clade comprising Duvaliomimus Jeannel from New Zealand and Paratrechus Jeannel from South and Central America (Fig. 2). Apart from a general "Duvalius-like" appearance, the three genera share some common features like the large size, cordate pronotum, rounded head with salient temples, and pubescent protibiae. Baehria gen. nov. differs from both these genera by the presence of three or four setae instead of two on each side of the clypeus, and by the position of the anterior discal seta on elytra: in Baehria gen. nov., this seta inserts in the 4th interval instead on the 3rd stria in Duvaliomimus and on the 5th stria in Paratrechus. Baehria gen. nov. differs additionally from Paratrechus by the simple apex of the aedeagal median lobe, which is button-like shaped in Paratrechus (Jeannel 1928; Barr 1982; Townsend 2010).

Baehria separata Schmidt & Faille, sp. nov.

https://zoobank.org/430BB485-1056-462B-8088-FF992DE5F947 Figs 4-15

Type material. Holotype male, with label data: Ethiopia, Amhara, Mt. Choke, crater valley, alt. 3780-3900 m, 10°42'12"N, 37°50'58"E, 27.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Paratypes: 39 males, 54 females, same data as holotype (CAF, CSCHM, NHMAA); 2 males, Mt. Choke, crater valley, alt. 3700-3800 m, 10°41'14"N, 37°50'07"E, 24.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM); 6 males, 7 females, Mt. Choke, western crater valley, alt. 3500–3600 m, 10°41'00"N, 37°50'35"E, 01.V.2022, leg. J. Schmidt, Yeshitla M., (CSCHM).

Additional material. 3 males, 3 females, W-slope Mt. Choke, alt. 3370 m, 10°38'07"N, 37°45'51"E, 23.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 6 males, 7 females, W-slope Mt. Choke, alt. 3700-3900 m, 10°42'17"N, 37°50'29"E, 25.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 43 males, 31 females, W-slope Mt. Choke, "Shoa Kidaneberet" valley, alt. 3700-3800 m, 10°39'08"N, 37°49'45"E, 8.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 10 males, 10 females, N-slope Mt. Choke, alt. 3800-3950 m, 10°43'16"N, 37°51'15"E, 26.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM); 18 males, 20 females, N-slope Mt. Choke, alt. 3750-3850 m, 10°43'51"N, 37°52'15"E, 09.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 3 males, 2 females, N-slope Mt. Choke, above Gumadur, alt. 3750-3850 m, 10°44'10"N, 37°53'48"E, 05.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 1 male, N-slope Mt. Choke, N of Waber, alt. 3450-3600 m, 10°44'48"N, 37°46'22"E, 07.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 13 males, 5 females, Mt. Choke, eastern crater valley, alt. 3700-3800 m, 10°42'59"N, 37°54'13"E, 06.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM).



Figures 4–7. *Baehria separata* Schmidt & Faille, gen. nov., sp. nov., dorsal aspect of body (4, 6) and head (5, 7) of paratypes; 4, 5. Male; 6, 7. Female. The small white circles in Figs 5 and 7 mark the insertion points of the clypeal setae.

Etymology. The specific epithet refers to the markedly separated distributional area of the taxon, which is, based on current knowledge, far away from its next relatives. It is built by the past participle of the Latin verb *separare*.

Description. See description of genus.

Body length: 6.9–7.5 mm (Ø = 7.19 mm, n = 20). *Proportions* (n = 20): PW/HW = 1.18–1.25 (Ø = 1.21); PW/PL = 1.30–1.38 (Ø = 1.34); PW/PBW = 1.48–1.54 (Ø =



Figures 8–15. *Baehria separata* Schmidt & Faille, gen. nov., sp. nov. 8. Left and right mandible, dorsal aspect; 9. Ventral aspect of head; the small white circles mark the insertion points of the setae on submentum; 10. Right male protasomeres, left latero-ventral aspect; 11. Left male metatarsomeres, right lateral aspect; 12. Right male protibia, dorsal aspect; 13. Anterior part of elytra and pronotal base; the arrows point to the insertions of the anterior elytral discal setae; 14. Aedeagus, left lateral aspect; 15. Aedeagus, dorsal aspect.

1.50); PBW/PAW = 0.92–1.00 (Ø = 0.96); EW/PW = 1.42– 1.48 (Ø = 1.45); EL/EW = 1.46–1.56 (Ø = 1.51).

Colour: Dark brown to blackish, moderately shiny in both sexes; palpi light brown, labrum and scapus reddish

brown, basal 3/4 of femora light brown; antennal base in some specimens more widely brightened.

Microsculpture: Same in males and females. Head with deeply engraved, rather large, almost isodiametric

sculpticells on disc and supraorbital area, slightly smaller sculpticells on clypeus. Pronotum with moderately deep engraved, slightly transverse sculpticells on disc and markedly deep engraved sculpticells near base; the sculpticells are somewhat smaller than on head disc. Elytral intervals with more finely engraved sculpticells which are more transverse than on pronotum.

Aedeagus. Proportion EL/AL (n = 10): 2.40–2.64 (\emptyset = 2.52). Median lobe in lateral view unevenly bent, dorsally with a distinct concavity before middle (Fig. 14), in dorsal view not or very slightly broadened before apex (Fig. 15).

Differential diagnosis. See Diagnosis and Identification sections of the genus, above.

Distribution and geographical variability. The type series was collected on the western side of the crater valley of Mt. Choke. Additional populations were collected on the north eastern side of the crater valley and on northern and western slopes of Mt. Choke. Specimens of these populations differ +/- distinctly from those of the type series and from each other by the curvature of the aedeagal median lobe, the number of lightened basal antennomeres, and the depth of the engraving of the elytral microsculpture. Slight differences were also found in the DNA sequence segments of the three investigated specimens representing three different populations (Fig. 2; Suppl. material 1). Further morphological and molecular genetic studies are needed to answer the question of whether certain populations represent species.

Habitat. Specimens of *Baehria separata* gen. nov., sp. nov. have been found in stone packs traversed by running water in small steep streams in the afroalpine zone, together with Dytiscidae beetles (Fig. 16). Based on this finding, *Baehria separata* gen. nov., sp. nov. seems to be adapted to a rheophilic way of life.

Trechus Clairville, 1806

Abunetrechus Schmidt & Faille, subgen. nov.

https://zoobank.org/608E14D6-39EC-4CEC-97C9-68870B659966

Type species. *Trechus bipartitus* Raffray, 1885, herewith designated.

Diagnosis. Representative of Trechina and *Trechus* s. l. sensu Jeannel (1926, 1927, 1928) due to presence of bidentate mandibles (absence of retinacle), dorsally closed aedeagal median lobe, well-developed compound eyes, protibia glabrous on anterior surface, presence of two elytral dorsal setae situated in third interval, elytral intervals glabrous, 4+2+2 pattern of umbilicate setae, and two basal tarsomeres of male dilated. Externally, *Abunetrechus* subgen. nov. reminders a non-specialised high-altitude *Trechus* of moderate body size, short mandibles, antenna and legs, moderately large eyes, rounded humeri, short metepisternae and hindwings reduced to short stubs. *Trechus* sensu lato, *Abunetrechus* subgen. nov. is characterized by the combination of following character states: bisetose clypeus (Figs 18,

20, 22), smooth tempora, pronotum with fully rounded laterobasal angles and with laterobasal setae markedly protruded anteriorly (Figs 18, 20, 21), elytral striae 3 and 4 merging at level of the anterior discal seta (Fig. 23), elytral preapical seta of the third interval present and situated about at level of the elytral apical tenth, protibia with longitudinal groove on external surface; aedeagus with two moderately sclerotized portions of the endophallus arranged one behind the other in apical half of the median lobe (Figs 24–29).

Etymology. The subgenus name combines the name of the Abune Yosef Massif in northern Ethiopia, where the species of this subgenus occur, with the name of the genus *Trechus*.

Description. Head: Size averaged for Trechus sensu lato, without pilosity. Mandibles short, with dentition pattern as in Trechus sensu stricto. Labrum with apical margin moderately emarginated, with six setae near apical margin. Clypeus each side with one long seta (Figs 18, 20, 22; very seldom with an additional very fine seta situated interior of one of the primary setae). Eyes moderately large, convexly protruded, more than two times as long as tempora, latter moderately convex (Figs 18, 20, 22). Two supraorbital setae each side in normal position for Trechus. Supraorbital furrows moderately deep and almost evenly bent throughout. Tempora moderately convex, markedly wrinkled to the neck, smooth. Mid of head convexly elevated. Antennae short, with third antennomere slightly longer than pedicellus. Suborbital seta present. Apical tooth of mentum truncate or slightly bifid, sensory pits of mentum present but very small; submentum with 4-7 setae.

Prothorax: Pronotum with size averaged for Trechus sensu lato, without pilosity, slightly transverse, broadest distinctly before middle, with lateral margin completely rounded towards base, and with laterobasal angles indistinct. Basal margin (between insertion points of laterobasal setae) distinctly broader than apical margin. Disc markedly convex. Anterior margin slightly or moderately concave with anterior angles shortly rounded, moderately protruded. Basal margin straight or slightly convex in middle and with outer quarters markedly shifted anteriorly towards lateral margin (Figs 18, 20, 21). Lateral margin convexly rounded throughout; laterobasal angle fully rounded or marked as a very small blunt tooth. Marginal gutter very narrow throughout. Median longitudinal impression slightly incised, disappearing near apex and base, not deepened within area of posterior transverse impression. Anterior and posterior transverse impressions very shallow, smooth or (posterior transverse impression) sometimes finely wrinkled. Laterobasal foveae rather small, moderately impressed, smooth. Lateral and laterobasal setae present, with the former situated near maximum width of pronotum. Proepisternum glabrous and smooth.

Pterothorax: Elytra without pilosity, slender ovate, markedly domed towards disc, not flattened in middle of disc, in dorsal view broadest slightly posterad middle, shoulders flatly rounded, apical sinuation very slightly developed or indistinct, apex rounded or marked as an obtuse apical angle. Parascutellary stria short to moderately





Figure 16. North-exposed slope on Mt. Choke with *Erica* forest and a steep small brook at an altitude of 3600 m during dry season (May, 2022). The stone pack in the brook is habitat of *Baehria separata* Schmidt & Faille, gen. nov., sp. nov.: the beetles were collected between the stones along which the water flows (in order to find the beetles, the creek bed was partially dug up).

long, free; striae 1-8 almost complete, moderately deep impressed in middle of disc, less deeply towards sides, disappearing near base, crenulated, striae 3 and 4 merging at level of the anterior discal seta; intervals slightly convex. Recurrent preapical stria deep, long, connected with the apex of the fifth stria. Parascutellar seta present. Anterior discal seta situated at merging point of the 3rd and 4th stria, near the end of the anterior elytral 5th (Fig. 23); second discal seta located at the 3rd stria somewhat behind elytral middle; posterior discal seta (= subapical seta near end of 3rd stria) present, located about 1/10 of elytral length from elytral apex; subapical seta of the recurrent stria isolated, removed from this stria by distance of 1-2 diameters of the setiferous pore. Number and positions of the setae of the marginal umbilicate series as in Trechus s. str. Metepisternum very short, glabrous and smooth, with outer margin about as long as anterior margin.

Legs: Short and moderately robust. Protibia distinctly dilated towards apex, straight, glabrous, with longitudinal groove on dorsal surface complete. Two basal protarsomeres of males dilated and dentoid at the inner apical border. Chaetotaxy as in *Trechus* sensu stricto.

Male genitalia (Figs 24–29): Aedeagal median lobe moderately large, in lateral view markedly curved, with apical lamella short, latter with distinct terminal capitu-

lum; basal bulb and saggital aileron averaged. Endophallus with a moderately large, moderately sclerotized folding structure (copulatory piece) in the shape of a halfopen cylinder or cone which is located in apical half of the median lobe and directed to its longitudinal axis, and with the open part of the copulatory piece facing ventrad. Apicad of this piece, an additional slightly more strongly sclerotized folding structure is developed which is shaped as a small plate (best visible in lateral view); the basal part of this piece. Parameres with 2–4 apical setae.

Remarks. In his redescription of *Trechus bipartitus*, Jeannel (1927) noted the presence of a single copulatory piece which is characterized by a long sinusoidal appendix. However, in his figure of the left lateral view of the copulatory piece (Jeannel 1927: 195) he merged the more strongly sclerotized folding structure near median lobe apex with the more basad located larger copulatory piece which leads to the impression of a single, very long piece.

Distribution. Northern Ethiopia Plateau (Fig. 1): Three species are known so far, two from Mt. Abune Yosef (*T. bipartitus* Raffray, *T. lalibelae* Quéinnec & Ollivier) and one from the Guassa Plateau (*T. habeshaicus* Quéinnec & Ollivier).

Relationships and identification. Based on the molecular data, Abunetrechus subgen. nov. is representative of a clade comprising Anchotrechus Jeannel from Tenerife, the Trechus subgenus Arabotrechus Mateu from Yemen, and the Trechus subgenus Meruitrechus Jeannel from Mt. Meru, Tanzania (Fig. 3; in the following called the AAMA clade). Abunetrechus subgen. nov. differs from all species groups of the AAMA clade by bisetose clypeus. A quadrisetose clypeus was hypothesized plesiomorphic character state in Trechini (Schmidt et al. 2021). Within this tribe, a bisetose clypeus is also developed in the genus Omalodera Blanchard from Chili, the Caucasian genus Alanorites Belousov of the Neotrechus Phyletic Series, and two Epaphiopsis Uéno species occurring in the central Himalaya (Belousov 1998; Naito 2023). However, this character state has to be considered homoplasic because none of these taxa cluster within Trechus sensu lato (Faille et al. 2013, 2021; Maddison et al. 2019, see Fig. 2 in this paper). Abunetrechus subgen. nov. additionally differs from all other species of the AAMA clade by rounded pronotal laterobasal angles, from Meruitrechus by presence of the elytral preapical seta of the third interval, the isodiametric sculticells on elytra less deeply engraved, and eight striae well marked, from Anchotrechus by smaller and stouter body, glabrous elytra and much shorter aedeagal median lobe, and from Arabotrechus by the smaller body size, presence of a second discal setae (missing in Arabotrechus, as well as in T. aethiopicus and some species of Elgonotrechus Jeannel. Abunetrechus subgen. nov. shares the elytral striae 3 and 4 merging at level of the anterior discal seta with Arabotrechus (based on a single investigated specimen; larger series would be necessary to confirm the stability of this character).
Trechus (Abunetrechus) bipartitus Raffray, 1885

Figs 17, 18, 23-25

Trechus bipartitus Raffray, 1885: 318; locus typicus: "col du mont Abouna-Yousef (4024 m)".

Trechus bipartitus: Jeannel 1927: 194.

Trechus bipartitus: Pawłowski 2003: 157.

Trechus bipartitus: Ortuño and Novoa 2011: 137.

Trechus (s. str.) bipartitus: Quéinnec et al. 2021: 20.

Type material. Not studied. The lectotype was designated by Quéinnec et al. (2021). Identification is based on the redescriptions of the species, including habitus and male genital figures of the type specimens, presented by Jeannel (1927) and Quéinnec et al. (2021), as well as on comprehensive material collected at the type locality (see below).

Additional material. 6 males, 9 females, Ethiopia, Amhara, Mt. Abuna Yosef, N-slope, 3800–3950 m, 12°07'52"N, 39°11'39"E, 4.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 6 males, 12 females, ditto, S-slope, 3850–3900 m, 12°07'29"N, 39°11'21"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM, NHMAA); 5 males, 2 females, ditto, S-slope, 3700–3850 m, 12°09'10"N, 39°09'35"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Additions to the species description. Mature species with elytra including suture blackish brown (Quéinnec et al. 2021: "suture distinctly brown shiny"; this information is probably based on confusion with *T. habeshanicus*). Body length 4.1–4.7 mm (Quéinnec et al. 2021: "> 4.5 mm"). Length of aedeagus 0.98–1.05 mm. PW/PL=1.29–1.37; n=20 (Quéinnec et al. 2021: PW/PL=1.6; this value is very probably based on a measurement error). PW/TL = 1.06-1.15; n = 20. EL/AL = 2.15-2.46; n = 10.

Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Abune Yosef Mountains of the northern Ethiopian Highlands.

Habitat. As in *T. (Abunetrechus) lalibelae* Quéinnec & Ollivier (see below).

Trechus (Abunetrechus) lalibelae Quéinnec & Ollivier Figs 19, 20, 26, 27

Trechus (Abunetrechus) lalibelae: Quéinnec et al. 2021: 21; locus typicus: Mt. Abuna Yosef, 12°08'32"N, 39°10'59"E.

Type material. Not studied. Identification is based on the original description, including habitus and male genital figures of the type specimens (Quéinnec et al. 2021), as well as on comprehensive material collected at the type locality (see below).

Additional material. 13 males, 11 females, Ethiopia, Amhara, Mt. Abuna Yosef, N-slope, 3800–3950 m, 12°07'52"N, 39°11'39"E, 4.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (SCHM, NHMAA); 1 male, 1 female, ditto, S-slope, 3850–3900 m, 12°07'29"N, 39°11'21"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Ye-shitla M., Yitbarek W. (CSCHM); 1 male, ditto, S-slope, 3700–3850 m, 12°09'10"N, 39°09'35"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Additions to the species description. Body length 4.2–5.1 mm (Quéinnec et al. 2021: 4.8–5.1 mm). Length of aedeagus 0.98-1.02 mm. PW/PL = 1.24-1.30; n = 20. PW/TL = 0.99-1.04; n = 20. EL/AL = 2.39-2.65; n = 10.

Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Abune Yosef mountains of the northern Ethiopian Highlands.

Habitat. Specimens of *T. lalibelae* were found syntopic with *T. bipartitus* and *T. sublaevis* Raffray under stones and in humus and rotten plant material near brooks in the afroalpine zone.

Trechus (Abunetrechus) habeshanicus Quéinnec & Ollivier

Figs 21, 22, 28, 29

Trechus (Abunetrechus) habeshanicus: Quéinnec et al. 2021: 23; locus typicus: Guassa Plateau 10°17'19"N, 39°48'13"E.

Type material. Not studied. Identification is based on the original description, including habitus and male genital figures of the type specimens (Quéinnec et al. 2021), as well as on comprehensive material collected at the type locality (see below).

Additional material. 98 exx. (males, females), Ethiopia, Amhara, northern Guassa Plateau, near Guassa Comm. Lodge 3330 m, 10°17'17"N, 39°47'54"E, 18.V.2022, leg. J. Schmidt, Yeshitla M. (CAF, CSCHM, NHMAA); 360 exx. (males, females), ditto, "Aste wuha" 3400 m, 10°24'N, 39°48'E, 19.V.2022, leg. J. Schmidt, Yeshitla M. (CAF, CSCHM, NHMAA); 11 exx. (males, females), ditto, "Yegana Natural Forest", river valley, 3125 m, 10°26'03"N, 39°47'16"E, 20.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM).

Additions to the species description. Mature species with elytra blackish brown, and with suture and first interval reddish brown lightened in most specimens (Quéinnec et al. 2021: "suture distinctly darkened"; this information is probably based on confusion with *T. bipartitus*). Body length 4.1–5.0 mm (Quéinnec et al. 2021: 4.1–4.3 mm). Length of aedeagus 0.70–0.80 mm. PW/PL = 1.28-1.38; n = 20. PW/TL = 1.08-1.13; n = 20. EL/AL = 3.00-3.33; n = 10.

Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Guassa Plateau of the northern Ethiopian Highlands.

Habitat. Specimens of *T. habeshanicus* were found syntopic with *T. guassaensis* (Quéinnec & Ollivier) and two hitherto undescribed *Trechus* species in humus and rotten plant material along brooks in the afromontane zone.



Figures 17–20. *Trechus* subgenus *Abunetrechus* nov., dorsal aspect of body (17, 19), head and pronotum (18, 20). 17, 18. *T. bipartitus* Raffray; 19, 20. *T. lalibelae* Quéinnec & Ollivier. The small white circles in Figs 18 and 20 mark the insertion points of the clypeal setae.



Figures 21–23. *Trechus* subgenus *Abunetrechus* nov., dorsal aspect of body (21) and head (22), and anterior part of left elytron (23). 21, 22. *T. habeshaicus* Quéinnec & Ollivier; 23. *T. bipartitus* Raffray. The small white circles in Fig. 22 mark the insertion points of the clypeal setae; the arrow in Fig. 23 points to the insertion of the anterior elytral discal seta.

Revised key to species of Abunetrechus subgen. nov.

Remarks. Quéinnec et al. (2021) proposed a key to the species of their *Trechus* (s. str.) *bipartitus* group, which includes the three species we here assigned to the subgenus *Abunetrechus* nov. For species' differentiation, the authors used total body length, proportions of the pronotum and

coloration patterns of the elytra. However, we found that these character states are unsuitable due to high intraspecific variability. In addition, the pronotal proportion value was probably erroneously presented by Quéinnec et al. (2021; see Additions to the species descriptions, above).

1	Body more slender, with shoulders more gently rounded (Fig. 19	and with appendages slightly longer: tibiae about as long as width of
	pronotum (PW/TL < 1.05). Endemic to Mt. Abune Yosef	Trechus (Abunetrechus) Ialibelae Quéinnec & Ollivier
-	Body more robust, with shoulders broader (Figs 17, 21) and with	h appendages shorter: tibiae distinctly shorter than width of pronotum
	(PW/TL > 1.05	

2	Aedeagal median lobe much smaller (length: 0.70–0.80 mm; E	L/AL > 2.9), its ventral margin almost evenly curved from base to apex
	(lateral view, Fig. 28). Endemic to the Guassa Plateau	Trechus (Abunetrechus) habeshaicus Quéinnec & Ollivier
-	Aedeagal median lobe larger (length: 0.98–1.05 mm; EL/AL <	2.5), its ventral margin almost straight near apex (lateral view, Fig. 24).
	Endemic to Mt. Abune Yosef	Trechus (Abunetrechus) bipartitus Jeannel



Figures 24–29. *Trechus* subgenus *Abunetrechus* nov., aedeagus in left lateral aspect (24, 26, 28) and dorsal aspect (25, 27, 29). 24, 25. *T. bipartitus* Raffray; 26, 27. *T. lalibelae* Quéinnec & Ollivier; 28, 29. *T. habeshaicus* Quéinnec & Ollivier.

Subgenus Minitrechus Vigna Taglianti & Magrini, 2010

Type species. T. gypaeti Vigna Taglianti & Magrini, 2010.

New synonymy. Archeotrechus Magrini, Quéinnec & Vigna Taglianti, 2012 (type species: *T. relictus* Magrini, Quéinnec & Vigna Taglianti, 2012), syn. nov.

Remarks. Based on the molecular data, all *Trechus* species known to occur in the mountains of southern Ethiopia (Bale and Arsi Mountains, Gughe Highlands), form a monophyletic clade (Fig. 3). This clade includes species characterized by widely differing body sizes, shapes, and proportions, and by many other morphological characters, including elytral chaetotaxy, the number of dilated male protarsomeres, and the extent of the dorsal opening of the aedeagal median lobe. Similar character states can likewise be found in *Trechus* sensu lato species occurring in northern Ethiopia which, however, do not cluster within the south Ethiopian clade. At the current state of knowledge, a morphological definition of this clade together with a differential diagnosis with respect to other species groups of *Trechus* sensu lato cannot be presented here and require more comprehensive morphological investigations.

For the monophyletic southern Ethiopian *Trechus* clade, the oldest valid species group name is *Minitrechus* Vigna Taglianti & Magrini, which was given for a very tiny, depigmented species from Mt. Enkuolo (Vigna Taglianti and Magrini 2010). The subgenus *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti was described two years later for a likewise tiny and depigmented species from the Bale Mountains, which is additionally characterized by a very wide dorsal opening of aedeagus (Magrini et al. 2012). In our phylogeny, the type species of both of these subgenera cluster together within

one of the two main clades of South Ethiopian Trechus, both of which are highly supported by the molecular data (Fig. 3). Consequently, the status of Archeotrechus as a separate subgenus within Trechus sensu lato can no longer be maintained.

A complete list of species we propose to summarize within the subgenus Minitrechus, is shown in the checklist of the Ethiopian Trechini species, see Discussion, below.

Trechus (Minitrechus) patrizii Jeannel Figs 30-35

Trechus Patrizzi [sic!] Jeannel, 1960: 265; locus typicus: "mont Chillálo".

Trechus Patrizii Jeannel (1960): 266.

Trechus patrizii Jeannel: Casale and Laneyrie (1982): 125.

Trechus (s. str.) patrizzii [sic!] Jeannel: Lorenz (2005): 186.

Trechus patrizii Jeannel: Ortuño and Novoa (2011): 135.

Trechus (s. str.) oromiensis Magrini, Quéinnec & Vigna Taglianti, 2012: 26; locus typicus: Oromia Province, Bale massif, South of Goba, alt. about 3200 m.

Trechus patrizii Jeannel: Schmidt and Faille (2018): 37.

Trechus oromiensis Magrini et al.: Schmidt and Faille (2018): 37.

Trechus (s. str.) patrizii Jeannel: Quéinnec et al. 2021: 65.

Trechus (s. str.) oromiensis Magrini et al.: Quéinnec et al. 2021: 65.

New synonymy. Trechus patrizii Jeannel, 1960 = Trechus oromiensis Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.

Type material examined. Trechus patrizii Jeannel: Holotype female, with label data "TYPE" (printed on red card), "A.O.I. Arussi occ. / Reg. Aselle m. 2600 ca / pend. M.te Cillalo / S. Patrizi 20:27.4.38", "Trechus / patrizii nov. / R. Jeannel det., 19" in UARK (Fig. 30).

Paratype male, with label data "A.O.I. Arussi occ. / Torr. Asciabacá / S. Patrizi 28.IV.38 / m 2500", "Trechus / patrizii n.", "Lectotype / E. Quéinnec dés. 1994" (printed on red card), "Trechus / patrizii / MNHN Paris" (printed and handwritten on red card) in MNHN (Fig. 32).

Remarks. Jeannel (1960: 266) stated that the type specimen is deposited in the S.L. Straneo collection. Significant parts of the Straneo collection together with the T. patrizii specimen cited by Jeannel (1960) are now preserved in the UARK (M. Pavesi, pers. comm. 2018). The above cited T. patrizii specimen from the UARK collection has thus to be considered the holotype of T. patrizii, while the (unpublished) lectotype designation made by E. Quéinnec for the specimen preserved in the MNHN has to be considered unjustified.

Trechus oromiensis Magrini et al.: Type material not studied. Identification is based on the detailed description of this distinctive taxon and comprehensive material from the type locality (see Schmidt and Faille 2018).

Additional material. For comprehensive material studied see our previous paper (Schmidt and Faille 2018). Note that in this study, T. oromiensis Magrini, Quéinnec & Vigna Taglianti was erroneously treated as a distinct

species. In the meantime, the following additional material was available for us: Ethiopia, Oromia, SE-slope of Mt. Chillalo, Dhaba village, alt. 3200 m, 19.II.2020, 7.861644°N, 39.27711°E, leg. J. Schmidt, C. Wirkner, Yeshitla M. (1 female: CSCHM); ditto, Bale Mts., Web river N Dinsho, alt. 3000 m, 5.II.2019, 07°07'18"N, 39°46'03"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (12 specimens: CSCHM); ditto, Bale Mts., forest remain W Dinsho, alt. 3100 m, 8.II.2019, 07°06'16"N, 39°44'46"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (12 specimens: CSCHM); ditto, Bale Mts., Sebsebe Washia Forest, Salgen Valley, alt. 2720-2800 m, 3.II.2019, 07°02'08"N, 39°36'06"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (7 specimens: CSCHM); ditto, Bale Mts., Sebsebe Washia Forest, Salgen Valley, alt. 3130 m, 4.II.2019, 07°02'08"N, 39°36'06"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (30 specimens: CSCHM); ditto, Bale Mts., Angeso Valley S Goba, alt. 3050 m, 5.II.2020, 6.932923°N, 39.951341°E, leg. J. Schmidt, C. Wirkner, Yeshitla M., Yitbarek W. (53 specimens: CSCHM); ditto, Bale Mts., Shaya Valley SW Goba, alt. 3100-3150 m, 6.II.2020, 6.991843°N, 39.884397°E, leg. J. Schmidt, C. Wirkner, Yeshitla M., Yitbarek W. (15 specimens: CSCHM).

Justification of the new synonymy. Jeannel (1960) noted for his T. patrizii the absence of pronotal basolateral setae as diagnostic character. Up to today, T. patrizii is considered the only Ethiopian species bearing this particular character (for development of this character state in T. amharicus Ortuño & Novoa, for which absence of pronotal basolateral setae was likewise determined, see Quéinnec et al. 2021). However, based on re-investigation of the type material of T. patrizii, we found that a pore is present in the normal position for the basolateral seta both sides of the pronotum (Figs 30, 31). Very probably, absence of these setae is based on preservation artefacts. The T. patrizii type specimens correspond in all external and genital diagnostic characters with the many specimens we previously identified as T. oromiensis Magrini et al. from the Bale Mts, Mt. Enkuolo and from the type locality of T. patrizii, Mt. Chillalo (Schmidt and Faille 2018). In far most of these specimens, the pronotal basolateral seta is present but lost on one or both sides in very few cases (Figs 32, 33; Schmidt and Faille 2018: 38, figs 58-60). Consequently, we conclude junior synonymy for the taxon T. oromiensis Magrini, Quéinnec & Vigna Taglianti under T. patrizii Jeannel.

Diagnosis. Within the Trechus fauna of the Bale and Arsi Mountains, T. patrizii is easily recognized by absence of the posterior elytral discal seta (Schmidt and Faille 2018). Beside T. patrizii, absence of the posterior elytral discal seta is also characteristic for T. amharicus Ortuño & Novoa and T. aethiopicus Alluaud. Trechus patrizii differs from T. amharicus by two male protarsomeres dilated, by presence of an apical disc on aedeagal median lobe, and by very differently sclerotized endophallus (for comparison see Ortuño and Novoa 2011: 134, fig. 3b, d, and Schmidt and Faille 2018: 37, figs 64-66). Trechus patrizii differs from T. aethiopicus by the pronotum with



Figures 30–35. *Trechus (Minitrechus) patrizii* Jeannel, type labels (**29**, **31**) and pronotum (**31**, **33–35**). **30**, **31.** Holotype, female (UARK); **32**, **33.** Paratype, female (MNHN); **34.** Specimen from Mt.Chillalo, locus typicus of *T. patrizii*; **35.** Specimen from Goba, Bale Mts, locus typicus of *T. oromiensis* Magrini, Quéinnec & Vigna Taglianti. The arrows in Figs 32, 33 point to the insertion pores of the seta on laterobasal angles of pronotum (setae are lacking).

smaller laterobasal angles, and by the copulatory piece of the endophallus, which is long and spine-like (short and tube-like in *T. aethiopicus*, see Jeannel 1927: 197, figs 598, 599).

Relationships. Based on the molecular data, *T. patrizii* is representative of a well-supported clade comprising

also *T. hagenia* Schmidt & Faille, *T. mekbibi* Schmidt & Faille, and *T. bastianinii* Magrini & Sciaky, all endemic to the Bale Mountains (Fig. 3). Within this clade, *T. patrizii* is identified sister species of *T. bastianinii*.

Distribution. Occurrences of *T. patrizii* are known from the northern slope of the Bale Mountains as well as

from the northerly adjacent Arsi volcanos Chillalo, Encuolo, and Kaka (Schmidt and Faille 2018; Fig. 1).

Habitat. Based on our field work data, *T. patrizii* is an epedaphic-hemiedaphic species adapted to shadowed and moderately humid soil conditions at altitudes of about 2500–3300 m (Schmidt and Faille 2018). It was found under large stones and by sifting leaf litter in mesophilic *Hagenia* forests and layers of humus shadowed by shrubs and rock faces. It was also found in large numbers in humid soils on shadowed places along mountain streams.

Discussion

Diversity, distribution, and taxonomic reorganization of the Ethiopian Trechina

Our phylogenetic tree shows that all high-altitude trechine species of Ethiopia belong to the subtribe Trechina, contradicting a recent hypothesis that suggests relationships of some afroalpine species with Trechodina (Quéinnec et al. 2021). Consequently, particular morphological character states of the mandibles which are Trechodina-like developed, e.g., in *Aethiopsis, Afrotrechus, Deuveopsis, Nilotrechus*, have to be considered homoplasic. Trechodina representatives occurring in Ethiopia (*Pachydesus, Perileptus* and *Trechodes*) are restricted to areas below the high montane zone.

Based on the molecular phylogenetic analyses, the species group diversity of the Ethiopian high-altitude trechines is lower than the taxonomic and morphological data suggest. Within Trechina, we identified only four isolated species groups. Because Nunbergites and several Trechus (s. l.) species from the Simien Mountains are not included in the analyses, the actual Trechina species group diversity might be slightly higher. However, seven species groups were recently described by Quéinnec et al. (2021) from Mt. Abune Yosef, Mt. Choke and the Guassa Plateau (Abayopsis, Abyssiniopsis, Abyssinotus, Aethiopsis, Afrotrechus, Deuveopsis, Nilotrechus). All of them form a single terminal clade within Trechus (s. l.). For this clade, we propose the name Abyssinotus Quéinnec & Ollivier because it is the first of the species group names introduced in the paper of Quéinnec et al. (2021). The resulting synonymy is summarized in the revised checklist of the Ethiopian Trechini species (below).

Distribution of *Abyssinotus*, in the new sense, is restricted to the mountains north of the Rift Valley. Unfortunately, we could not include species known to occur in the Simien Mountains in our molecular phylogenetic analyses. These mountains are the highest in Ethiopia and situated north of Mt. Abune Yosef and Mt. Choke where *Abyssinotus* is distributed. Pawłowski (2003) suggested close relationships of species occurring in the latter mountains with those from the Simien. In our opinion, there is a high probability that most, if not all, of the *Trechus* (s. 1.) species described from the Simien Mountains belong to *Abyssinotus*. However, at the current state of knowledge and with the lack of a phylogenetic analysis, we decided to list these species under *Trechus* subgenus *incertae sedis* (see checklist of the Ethiopian Trechini species, below).

Two of the species groups described from the Bale and Arsi mountains, namely *Archaeotrechus* and *Minitrechus* (Vigna Taglianti and Magrini 2010; Magrini et al. 2012), also form a single terminal clade within *Trechus* (s. l.) in our phylogeny. This highly species-rich clade is endemic to the southern Ethiopian highlands, and we proposed the subgeneric name *Minitrechus* Vigna Taglianti & Magrini for it, due to priority (see checklist of the Ethiopian Trechini species, below). Morphologically, this subgeneric name might be misleading, because *Minitrechus*, in the new sense, besides many tiny species, also includes particularly large ones, such as *T. rotundicollis* (Basilewsky), which is characterized by a body length of up to 7 mm (Basilewsky 1974).

Because the branching pattern of *Abyssinotus* and *Minitrechus* with other lineages of *Trechus* (s. l.) remains unresolved in our phylogeny, the relationships of these subgenera remain unknown. The monotypic *Speotrechus* Jeannel, from the mountains of central France, clusters with *Abyssinotus*, however, with low support. Based on the current data a sister relationship of *Abyssinotus* and *Minitrechus* cannot be excluded.

We could further identify two additional, hitherto unknown Trechina species groups within the Ethiopian fauna which are both endemic to the northern part of the country. One of these, Abunetrechus subgen. nov., clusters within Trechus (s. l.) and includes three species from Mt. Abune Yosef and the Guassa Plateau. For the type species of Abunetrechus subgen. nov., T. bipartitus, Jeannel (1927) proposed the group of T. bipartitus which, however, is polyphyletic in our analyses because T. sublaevis Raffray is placed within the subgenus Abyssinotus. Abunetrechus subgen. nov. is not related to any of the other Ethiopian Trechus clades but represents an isolated lineage within the AAMA clade of Trechus (s. l.). Members of this clade (Abunetrechus, Anchotrechus, Meruitrechus, resp. Arabotrechus) are characterized by disjunct distributions across widely separated mountains of North and East Africa (Ethiopia, Tenerife, Tanzania, resp. Yemen). Further studies are necessary to elucidate the affinities with the rich trechine fauna of the Elgon Massif.

One of the most surprising results of our study is the finding of Baehria gen. nov. in the Choke Mountain of northern Ethiopia. Besides Nunbergites (a genus with uncertain taxonomic position), Baehria gen. nov., is the only known Trechina taxon that clusters outside the megadiverse Trechus (s. 1.). The New Zealand endemic Duvalionimus is placed as sister group to Baehria gen. nov., and both these groups together are next related to Paratrechus from the mountains of northern South America. Given these findings, we assume Baehria gen. nov. to be a relic of a species group which was widely distributed on Earth during deep times. However, it is possible that further, so far unidentified members of that clade exist, e.g., in East and Southeast Asia, where the Trechina fauna is particularly rich in lineages but phylogenetically poorly known. Therefore, the sister group relationship of Baehria gen. nov. and Duvaliomimus, as shown by

our molecular data, should be considered as a preliminary hypothesis. Interestingly, both genera, Duvaliomimus and Paratrechus, were regarded as completely isolated among the respective regional Trechine faunas (Jeannel 1930, 1931; Barr 1982; Townsend 2010). Jeannel (1928) even erected a new "série phylétique" for each of the two genera. Future analyses including Trechina taxa from the whole distribution area of the subtribe may solve the question of whether lineages exist which are likewise members of the BDP clade and closer related to the Ethiopian Baehria gen. nov. We consider our results as preliminary with respect to the distribution and species diversity of Baehria gen. nov. in Ethiopia. Currently, the genus includes a single species which is distributed on Mt. Choke. Due to the very particular habitat of this species (see section Habitat in species description), and its rheophilic way of life, additional species of the genus could have been overseen by earlier explorers but may occur, e.g., along streams in the afroalpine zone of the Simien Mountains.

Revised checklist of the Ethiopian Trechini species

Our phylogenetic findings and the identification of new taxa result in comprehensive taxonomic changes in the recently published checklist of Ethiopian Trechini species (Quéinnec et al. 2021). The revised checklist is shown below. For references of original descriptions and details of the species' distribution in Ethiopia see Merene et al. (2023).

SUBTRIBE TRECHINA S. STR.

Genus *Baehria* Schmidt & Faille, gen. nov. *B. separata* Schmidt & Faille, sp. nov.

Genus Nunbergites Pawłowski & Stachowiak, 1991 N. aethiopicus Pawłowski & Stachowiak, 1991

Genus Trechus Clairville, 1806

- Subgenus *Abunetrechus* Schmidt & Faille, subgen. nov. *A. bipartitus* Raffray, 1885
 - A. habeshaicus Quéinnec & Ollivier, 2021
 - A. lalibelae Quéinnec & Ollivier, 2021

Subgenus Abyssinotus Quéinnec & Ollivier, 2021

- = Abayopsis Quéinnec & Ollivier, 2021, syn. nov.
- = Abyssiniopsis Quéinnec & Ollivier, 2021, syn. nov.
- = Aethiopsis Quéinnec & Ollivier, 2021, syn. nov.
- = Afrotrechus Quéinnec & Ollivier, 2021, syn. nov.
- = Deuveopsis Quéinnec & Ollivier, 2021, syn. nov.
- = Nilotrechus Quéinnec & Ollivier, 2021, syn. nov.
- A. abunaensis (Quéinnec & Ollivier, 2021), comb. nov.
- A. abyssinicus (Quéinnec & Ollivier, 2021), comb. nov.
- A. afroalpinus (Quéinnec & Ollivier, 2021), comb. nov.
- A. amharicus Ortuño & Novoa, 2011
- A. basilewskianus (Geginat, 2008): 124
- = *A. minutus* (Basilewsky, 1974)

- A. bunae (Quéinnec & Ollivier, 2021), comb. nov.
- A. chioriae (Quéinnec & Ollivier, 2021), comb. nov.
- A. chokensis Pawłowski, 2001
- A. delantae (Quéinnec & Ollivier, 2021), comb. nov.
- A. dimorphicus Pawłowski, 2001
- A. gigas Pawłowski, 2001
- A. guassaensis (Quéinnec & Ollivier, 2021), comb. nov.
- A. lastaensis (Quéinnec & Ollivier, 2021), comb. nov.
- A. lobeliae (Quéinnec & Ollivier, 2021), comb. nov.
- A. meneliki (Quéinnec & Ollivier, 2021), comb. nov.
- A. niloticus (Quéinnec & Ollivier, 2021), comb. nov.
- A. reebae (Quéinnec & Ollivier, 2021), comb. nov.
- A. sabae Quéinnec & Ollivier, 2021
- A. salomon Quéinnec & Ollivier, 2021
- A. sublaevis Raffray, 1885
- A. wolloi (Quéinnec & Ollivier, 2021), comb. nov.

Subgenus Minitrechus Vigna Taglianti & Magrini, 2010

- = Archeotrechus Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.
- M. abalkhasimi Schmidt & Faille, 2018
- M. adaba Schmidt & Faille, 2018
- M. angavoensis Schmidt & Faille, 2018
- M. baleensis (Basilewsky, 1974)
- M. balesilvestris Schmidt & Faille, 2018
- M. bastianinii Magrini & Sciaky, 2006
- M. batuensis Magrini & Sciaky, 2006
- M. bombi Schmidt & Faille, 2018
- M. chillalicus Jeannel, 1936
- *= M. robini* (Basilewski, 1974)
- M. clarkeianus (Basilewsky, 1974)
- M. colobus Schmidt & Faille, 2018
- M. culminicola Jeannel, 1936
- M. depressipennis Schmidt & Faille, 2018
- M. dodola Schmidt & Faille, 2018
- M. ericalis Magrini, Quéinnec & Vigna Taglianti, 2013
- M. fisehai Schmidt & Faille, 2018
- M. gallorites Jeannel, 1936
- M. grandipennis Schmidt & Faille, 2018
- M. gugheensis Jeannel, 1950
- M. gypaeti Vigna Taglianti & Magrini, 2010
- *M. hagenia* Schmidt & Faille, 2018
- M. haggei Schmidt & Faille, 2018
- M. harenna Schmidt & Faille, 2018
- M. harryi Schmidt & Faille, 2018
- M. iridescens Schmidt & Faille, 2018
- M. kosso Quéinnec & Ollivier, 2021
- M. mattisi Schmidt & Faille, 2018
- M. mekbibi Schmidt & Faille, 2018
- M. minitrechus Schmidt & Faille, 2018
- M. nanulus Schmidt & Faille, 2018
- M. nigrifemoralis Schmidt & Faille, 2018
- M. oppositus Schmidt & Faille, 2018
- M. patrizzii Jeannel, 1960
- = M. oromiensis Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.
- M. relictus Magrini, Quéinnec & Vigna Taglianti, 2012
- M. rira Schmidt & Faille, 2018
- M. rotundicollis (Basilewsky, 1974)

M. sanettii Schmidt & Faille, 2018
M. scotti Jeannel, 1936
M. tragelaphus Schmidt & Faille, 2018
M. transversicollis Schmidt & Faille, 2018
M. wiersbowskyi Schmidt & Faille, 2018

Trechus subgenus incertae sedis T. aethiopicus Alluaud, 1918 T. ambarasensis Jeannel, 1954 T. buahitensis Jeannel, 1954 T. degienensis Jeannel, 1954 T. loeffleri Magrini & Sciaky, 2006 T. martelluccii Magrini & Sciaky, 2006 T. peynei Magrini & Sciaky, 2006 T. pilosipennis Jeannel, 1954 T. raffrayanus Jeannel, 1954 T. rougemonti (Basilewsky) = T. derougemonti Geginat, 2017 T. schimperanus Jeannel, 1954 T. simienensis Jeannel, 1954

SUBTRIBE TRECHODINA JEANNEL

Genus Pachydesus Motschulsky, 1864 = Plocamotrechus Jeannel, 1926 P. aethiopicus Basilewsky, 1974 P. rufipes clarkei Basilewsky, 1972

Genus *Perileptus* Schaum, 1860 = *Ochthephilus* Nietner, 1857 [preocc.]

Subgenus Parablemus G. Müller, 1939 P. latimargo G. Müller, 1939

Subgenus Perileptus s. str. *P. africanus aethiopicus* Jeannel, 1935 *P. ledouxi* Deuve, 2004

Subgenus *Pyrrotachys* Sloane, 1896 = *Pyrrhotachys* Jeannel, 1926 [unav.] *P. testaceus* Putzeys, 1870

Genus *Trechodes* Blackburn, 1901 *T. lebioderus* (Chaudoir, 1876) *T. lucanerii* Magrini, Sciaky & Bastianini, 2005

Historical biogeography

Based on the dated phylogenetic tree, the evolution of the Ethiopian high-altitude fauna started during the Oligocene or Early Miocene, simultaneous with or some million years after the onset of large-scale mountain building in the area which was caused by extensive volcanism about 30 Mya (Hofmann et al. 1997; Table 1). The oldest Trechina lineages endemic to Ethiopia are the *Trechus* subgenera *Abyssinotus* and *Minitrechus*. The trechine phylogeny supports the geological data which show somewhat younger ages for the volcanism on the Somali Plateau in southern Ethiopia (ca. 24 Mya for the Bale Basalts; Abbate and Bruni 2015). Crown ages of southern Ethiopian *Minitrechus* are about 1–3.5 My younger than those of *Abyssinotus*, depending on the dating approach (Table 1). Altogether, these data support the hypothesis of the immigration of ancestral *Trechus* originating from the Cenozoic Boreal. Subsequent diversification takes place as a result of the geomorphological development of the Ethiopian Highlands and the related large-scale development of habitats characterized by extratropical climates (Schmidt and Faille 2018).

Crown ages of the endemic Trechus subgenus Abunetrechus subgen. nov. and Baehria gen. nov. from northern Ethiopian are much younger than Minitrechus and Abyssinotus, and estimated to a period between the Miocene-Pliocene and the Pliocene-Quaternary boundaries, depending on the dating approach (Table 1). However, the evolution of these groups started much earlier. Abunetrechus subgen. nov. separated from the AAMA clade about 10.7 or 17.7 Mya, and Baehria gen. nov. from the BDP clade about 15.2 or 22.9 Mya. However, these stem group data have to be treated with caution because we have no information on the stem group evolution, which might have taken place exclusively in the Ethiopian Highlands. Alternatively, additional lineages might exist or might have existed which are stem group members of Abunetrechus subgen. nov. or Baehria gen. nov., and which are or were distributed outside Ethiopia. Consequently, our dating in both these groups does not provide certain evidence for the respective onset of species group evolution within the Ethiopian Highlands.

Taxonomic remarks on Trechina species groups occurring outside Ethiopia

Earlier studies have proven that Trechus (s. l.) sensu auctorum represents a polyphyletic assemblage of Trechina (Faille et al. 2013; Maddison et al. 2019). However, a highly species-diverse, monophyletic terminal clade was identified by these studies and by our present phylogenetic analyses, including Trechus (s. str.) (= clade 1.3.2.2 in Faille et al. 2013) as well as several additional Trechus lineages containing the Ethiopian Abunetrechus subgen. nov., Abyssinotus sensu novo, and Minitrechus sensu novo (Figs 2, 3). Our results also show that two species groups which, based on the currently accepted taxonomy, are considered independent genera outside of Trechus (s. l.), are, in fact, ingroup members of this megadiverse genus. One of these groups is the monotypic taxon Anchotrechus Jeannel from Tenerife, a member of the AAMA clade of Trechus (s. l.). The other one is the monotypic Speotrechus Jeannel from central France, with unknown relationships within Trechus (s. l.) (Fig. 3). Based on these results, we propose the following taxonomic changes:

Genus *Trechus* Clairville, 1806: Subgenus *Anchotrechus* Jeannel, 1927, stat. nov. Subgenus *Speotrechus* Jeannel, 1922, stat. nov.

Conclusions

Our phylogeny of the Ethiopian Trechini beetles shows that the composition of the high-altitude fauna is based on multiple events of immigration which started during the Oligocene or Early Miocene. These results support the habitat island hypothesis proposed by Schmidt and Faille (2018) for the evolution of the Ethiopian highland Trechina fauna. Based on this hypothesis, immigration by flight-active ancestors and subsequent diversification of the trechines occurred almost immediately after the development of extratropical habitats in the course of the Oligocene-Early Miocene volcanism and the resulting uplift of high mountains in the area. In contrast, we found no evidence supporting the alternative hypothesis of a Trechina evolution in Ethiopia aided by Pleistocene cooling (Jeannel 1954b; Mani 1968; Ortuño and Novoa 2011). In the two most species-diverse clades, Abyssinotus and Minitrechus, diversification started long before the Pliocene and Quaternary periods and continued since then. We, thus, assume that the geomorphological formation of the highlands and the associated development of the local climates were the main drivers of the diversification of the high-altitude Trechina fauna in Ethiopia, rather than the late Cenozoic changes of the global climates.

Up to today, 79 species of Trechina beetles have been described from the Ethiopian Highlands (see species' checklist above). However, this number represents probably only a part of the actual number of species occurring in the country. From our fieldwork, we are aware of several undescribed species (descriptions will be presented elsewhere), and large parts of the Highlands are greatly understudied by carabidologists. All but one of the Ethiopian Trechina species are endemic to single volcanic mountains or valley systems along high mountain slopes, and those mountains with altitudes ≥4000 m a.s.l. are particularly species-rich areas (see summary in Quéinnec et al. 2021). Trechus patrizii is the only species known to occur on the Arsi Volcanoes as well as in the Bale Mts. We, therefore, assume that the Cenozoic uplift of the volcanic massifs on both sides of the Rift Valley led to massive, if not explosive, radiation of the regional carabid beetle fauna as it was likewise described from other volcanic mountains of lower latitudes, e.g. the Canary Islands (Contreras-Díaz et al. 2007) and Hawaii (Liebherr 2015). It remains unknown whether the phylogenetic position of the enigmatic new genus Baehria contrasts with this scenario. Future studies using a larger taxon sampling are required to show whether Baehria gen. nov. is a relic of a moderately old Trechina lineage with its ancestor having immigrated to the Ethiopian Highlands at about the same time as the ancestors of the highly species diverse Abyssinotus and Minitrechus.

Given the limited taxon and gene sampling our evolutionary scenarios have to be considered preliminary. Also, the results of our study do not allow for conclusions concerning the relationship between the species diverse North Ethiopian *Trechus* clade (*Abyssinotus*) and the likewise diverse South Ethiopian clade (*Minitrechus*). It remains open whether the evolution of these groups results from a single Oligocene-Early Miocene immigration event from the Cenozoic Boreal. Alternatively, independent immigrations of two ancestral trechines into two separated volcanic areas of the country, which were uplifted at different times, are possible. Especially species of the Simien Mountains in Ethiopia, including the enigmatic genus *Nunbergites*, representatives of the diverse Trechina fauna from the Elgon Massif, and additional Holarctic Trechina lineages need to be included in future molecular analyses to better understand the relationships of the Ethiopian lineages. Moreover, using a larger number of molecular markers may improve the resolution of the more basal branches in the phylogenetic tree.

Evidence emerged from our study regarding the taxonomic positions of most of the trechine groups known to occur in Ethiopia. We could reject an earlier hypothesis of potential relationships of some of the highland trechines with Trechodina (Quéinnec et al. 2021). Further, we could show that the species group diversity is much lower than suspected by earlier authors. Consequently, morphological character states which were used to define species groups on subtribal, genus or subgenus levels, for the Ethiopian high-altitude fauna are often unsuitable to define natural groups, e.g. bidentate or tridentate mandibles, patterns of chaetotaxy and pilosity, the number of dilated male protarsomeres and the extent of the dorsal closure of the aedeagal median lobe (e.g., Pawłowski 2003; Vigna Taglianti and Magrini 2010; Magrini et al. 2012; Quéinnec et al. 2021). In fact, the molecular data demonstrate that the high morphological diversity in both, the northern and the southern Ethiopian Trechus clades, Abyssinotus and Minitrechus, are the result of independent morphological radiations within these clades. These radiations might have been fostered by i) the absence or very limited presence of additional hygrophilic ground beetles in the high-altitude forests of Ethiopia, such as Nebriini, Patrobini, Platynini and Pterostichini, and ii) interspecific concurrence. The latter argument is supported by the fact that up to eight Abyssinotus species can be found syntopically, e.g., along slopes of Mt. Choke (own unpubl. data). Within trechine beetles, this is a unique ecologic-faunistic phenomenon, supporting Jeannel's observation on the abundance of Trechus on Mount Elgon (Jeannel 1950). Detailed morphological studies, intensive fieldwork and a significant extension of the molecular databases are required to test these hypotheses and to understand the evolution of the high diversity of Trechina species and their morpho-types in the Ethiopian Highlands.

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Supplementary material 1

Material used in the study with voucher IDs, locality data, and accession numbers of the sequences

Authors: Arnaud Faille, Sylvia Hofmann, Yeshitla Merene, David Hauth, Lars Opgenoorth, Yitbarek Woldehawariat, Joachim Schmidt

Data type: docx

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Link: https://doi.org/10.3897/dez.70.107425.suppl1

Supplementary material 2

Primers used for DNA amplification and sequencing

Authors: Arnaud Faille, Sylvia Hofmann, Yeshitla Merene, David Hauth, Lars Opgenoorth, Yitbarek Woldehawariat, Joachim Schmidt

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PENSOFT.



Phylogeny of genus *Sichuana* Shen & Yin, 2020 (Orthoptera, Tettigoniidae, Tettigoniinae) with four new species from Sichuan, China

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Abstract

Four new species of *Sichuana* Shen & Yin, 2020 are described based on morphological comparison and molecular analysis: *S. planicercata* **sp. nov.**, *S. curvicercata* **sp. nov.**, *S. longilamina* **sp. nov.** and *S. magnicerca* **sp. nov.** Specimens showed some intraspecific variation of male tegmina and subgenital plates. The genes *COI* and 16S were used to analyze the genetic distance between species and *COI* was used to analyze the phylogenetic relationship of *Sichuana*.

Key Words

Drymadusini, genetic distance, revision, variation, veins

Introduction

The genus *Sichuana* Shen & Yin, 2020 (Tettigoniinae, Drymadusini) is endemic to Sichuan, China (Yin et al. 2020). It is comprised of two species, *S. cryptospina* Shen & Yin, 2020 and *S. feicui* He, 2020, in Wenchuan County and Mao County of western Sichuan (He et al. 2020). It is characterized by the following character states: lateral carina distinct in the metazona but faintly indicated on the prozona; prosternum with a pair of spines; female tegmina slightly longer than the length of the pronotum; male cerci strongly incurved in the middle, the apices are acute, and there is an inner tooth in the basal area of the male cerci.

After morphological comparison, we revised the diagnosis of *Sichuana* and described four new species: *S. planicercata* sp. nov., *S. curvicercata* sp. nov., *S. longilamina* sp. nov. and *S. magnicerca* sp. nov. We analyzed the genetic distances among species using the mitochondrial genes *COI* and 16S and did a phylogenetic analysis of the genus based on *COI*.

Materials and methods

Specimens and equipment

The specimens were collected in western Sichuan, China. They (including holotypes) are deposited in the collection of the Department of Plant Protection of Sichuan Agricultural University (**SICAU**), Chengdu, China (Jun-Jie Gu, Curator).

Photographs were taken using a SZX16 microscope system (Olympus, Tokyo, Japan), or a Cannon D550 with a 50 mm lens, composing by cellSens Dimension 3.2 software. The images were digitally stacked composites of approximately 20 focal planes using Helicon Focus 6 (http://www.heliconsoft.com accessed on 12 May 2022).

Anatomical abbreviations

Wing venation nomenclature is based on the interpretation of Béthoux and Nel (2002) and Chivers et al. (2017): CuA, anterior cubitus; CuP, posterior cubitus; CuPaα, an-

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terior branch of first posterior cubitus; CuPa β , posterior branch of first posterior cubitus; CuPb, second posterior cubitus; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; ScA, anterior subcosta; ScP, posterior subcosta. "Handle" describes the strong crossvein appearing as a main vein between the origin of CuA + CuPa α and CuPa β .

DNA extraction and amplification.

Genomic DNA was extracted from the muscles of one hind leg using a CWBIO Universal Genomic DNA Kit by the manufacturer's instructions. The molecular markers selected for this paper were mitochondrial cytochromec o xidase subunit I gene (*COI*) and the mitochondrial large-subunit rRNA gene (16S). The primers used are shown in Table 1 (Xiong and Kocher 1991; Pan et al. 2006). GenBank accession numbers are showed in Table 2.

Table 1. Primer sequences.

Target genes	Sequences
COI	COBL TYTCAACAAAYCAY AARGATATTGG
	COBU TAAACTTCWGGRTGWCCAAARAATCA
16S	16Sa CGCCTGTTTATCAAAAACAT
	16Sb CTCCGGTTTGAACTCAGATCA

The *COI* and 16S sequences isolated from all samples were used for phylogenetic assay (Table 2) (Yin et al. 2020; Liu et al. 2018). All fragments were trimmed using Seqmen in DNAstar (Echeverry et al. 2017), and were aligned in MEGA11 by ClustalW (Tamura et al. 2021).

Genetic distance analysis

COI and 16S were used for this analysis (Table 2). Estimation of genetic distance was conducted by MAGE11.

Table 2. GenBank accession number.

Taxon	COI	168	Reference
Sichuana magnicerca	OQ799533	OQ801125	this study
sp. nov. 1			
S. magnicerca sp. nov. 2	OQ799537	OQ801126	this study
S. magnicerca sp. nov. 3	OQ799534	OQ801127	this study
S. magnicerca sp. nov. 4	OQ799532	OQ801128	this study
S. magnicerca sp. nov. 5	_	OQ801129	this study
S. longilamina sp. nov.	OQ799531	OQ801133	this study
S. feicui	OQ799536	OQ801124	this study
S. planicercata sp. nov. 1	OQ799525	OQ801130	this study
S. planicercata sp. nov. 2	OQ799526	OQ801131	this study
S. planicercata sp. nov. 3	OQ799527	OQ801132	this study
S. planicercata sp. nov.4	OQ799528	_	this study
S. curvicercata sp. nov.1	OQ799529	OQ801121	this study
S. curvicercata sp. nov.2	OQ799530	OQ801122	this study
S. curvicercata sp. nov. 3	_	OQ801123	this study
S. cryptospina 1	MT161464	_	Yin et al. 2020
S. cryptospina 2	MT161465	-	Yin et al. 2020
Mongolodectes huangxinleii	MT161460	_	Yin et al. 2020
Atlanticus fengyangensis	MG787210	_	Liu et al. 2018

We selected "compute pairwise distances" for comparing *Sichuana* species and used the "bootstrap method" with 1000 bootstrap replicates in the variance estimation method, then analyzed the data by the Kimura-2-parameter model.

Molecular phylogenetic analysis

COI was used for this analysis (Table 2). *M. huangxinleii* Liu, Xu & Zhang, 2015 and *A. fengyangensis* Liu, 2013 were used as outgroups. In all three datasets, the species of *Sichuana* Yin & Shen, 2020 were treated as ingroups. Phylogenetic analysis was conducted using MrBayes 3.2.7 (Ronquist et al. 2012) for Bayesian inference (BI) and IQ-tree 1.6.2 (Nguyen et al. 2015) for maximum-likelihood (ML). In the BI analysis, four chains were run for 1,000,000 generations, sampling every 1,000 generations and taking the first 25% of the trees as burn-in. In the ML analysis, the best model obtained by IQ-tree1.6.2 was TVM+F+I, a total of 10000 ultrafast bootstrap replicates were executed before a thorough ML search.

Species distribution map

The satellite maps were sourced from the National Platform for Common Geospatial Information Services (https://www.tianditu.gov.cn/) and edited with ArcGIS 10.8 (Esri 2011). The distribution of *Sichuana* species is shown in Fig. 1.

Results

Systematics

Orthoptera: Tettigoniidae: Tettigoniinae: Drymadusini

Genus Sichuana Shen & Yin, 2020

Emended diagnosis. Differs from all other Drymadusini genera in China by its male cercus being strongly incurved at or after its middle with acute apex, with a basal inner tooth (Figs 2, 6, 9, 12); median carina faintly indicated in prozona and absent in metazona; male tegmen about twice as long as pronotum; and female tegmen equal to or slightly longer than pronotum. Furthermore, Sichuana differs from Uvarovina Ramme, 1939, Ptosoproctus Shen, Yin & He, 2021, and Eulithoxenus Bey-Bienko, 1951 by its prosternum with a pair of spines (Figs 4, 8, 11, 14). Differs from Atlanticus Scudder, 1894, Eulithoxenus, Ptosoproctus, and Uvarovina by its ovipositor being decurved (Figs 2, 6, 9, 12). Differs from Atlanticus, Eulithoxenus, Mongolodectes Bey-Bienko, 1951, Paratlanticus Ramme, 1939, Ptosoproctus, and Uvarovina by its lateral carina being distinct in metazona and faintly indicated on prozona (Figs 2, 6, 9, 12). Differs from Kansua Uvarov, 1933, Paratlanticus, Ceraeocercus Uvarov, 1910 by dorsal side of protibia only



S. magnicerca sp. nov. S. cryptospina S. longilamina sp. nov. S. planicercata sp. nov. S. curvicercata sp. nov.

Figure 1. A. Distribution of *Sichuana* species in Sichuan Province, China; B, C. Enlarged version of *Sichuana* species distribution; B. *S. planicercata* sp. nov. and *S. curvicercata* sp. nov.; C. *S. longilamina* sp. nov. and *S. magnicerca* sp. nov. (circles, squares and triangles represent the three clades on the phylogenetic tree).

with external spurs, and dorsal side of mesotibia with spurs on both sides. Differs from *Kansua* Uvarov, 1933 by its smooth pronotum (Heller and Liu 2016; Liu 2013; Liu 2015; Liu et al. 2019; Shen et al. 2021).

Type species. Sichuana cryptospina Shen & Yin, 2020.

Sichuana planicercata Gu, Zheng & Yue, sp. nov.

https://zoobank.org/B79B73BD-FB84-485C-B8CA-B4A8E54FAAE4

Material examined. *Holotype:* \mathcal{J} , Xiaojin County, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province, China, (30°59'31"N, 102°21'39"E, alt., ca. 2700 m), coll. Cheng-Jie Zheng and Yuan Wei, VIII-2022. *Paratypes*:10 \mathcal{J} 5 \mathcal{Q} , same data as in holotype.

Diagnosis. Differs from all other *Sichuana* species by its male tenth abdominal tergite with a pair of very short round projections at posterior margin (Fig. 2F); male cercus without distinct curve upward or downward (Fig. 2E, F, H), inner tooth far above the top of cercus in lateral view (Fig. 2 H); and lacuna of female tenth abdominal tergite rounded and deep, reaching to or near posterior margin of ninth abdominal tergite (Fig. 2G).The related species *S. curvicercata* sp. nov. with narrower lateral field of male tegmen and simple male tenth abdominal tergite, thus being similar to *S. planicercata* sp. nov. (Fig. 6I, F).

Etymology. The specific epithet is derived from a combination of the Latin '*plani*' meaning flat, and '*cercus*', describing the male cerci not bent ventrally or dorsally. Chinese name: 平尾川螽.

Measurements (mm). Body (head to tip of abdomen): 32.4–33.86♂, 34.22–35.83♀; pronotum: 8.26–8.98♂, 7.86–8.46♀; tegmen: 15.39–16.21♂, 7.96–9.35♀; mirror

of right tegmen (from fore to hind): 4.23-4.423; hind wing: 6.12-6.903, 5.43-5.762; protibia: 8.86-9.363, 8.85-10.312; profemur: 7.68-8.043, 7.92-8.532; mesotibia: 9.18-10.583, 9.96-11.282; mesofemur: 8.47-9.013, 8.48-9.4222; metatibia: 21.09-22.713, 22.39-23.2422; metafemur: 21.61-22.713; 22.98-23.7622; ovipositor: 20.82-21.43.

Description. Male. Body, large. Frons flat, slightly oblique. Frontal fastigium and clypeofrontal sulcus black. Face light-colored. Occiput convex. Vertical fastigium broad, slightly wider than scape. Median ocellus visible. Compound eyes broadly round and bulging outwards, surrounded by black coloration that extends backward to form a band. Antennae inserted at the inner sides of the compound eyes, scapus robust, much thicker than pedicel, flagellum tapers toward the apex, covered with short setae (Fig. 2A–D).

Pronotum saddle-shaped, smooth, nearly equal to profemur in length. Disc of prozona with a broadly obtuse concavity in the middle of each side, anterior margin of pronotum slightly concave and posterior margin blunt, median carina faintly indicated in prozona, absent in metazona, lateral carina distinct in metazona, faintly indicated in prozona. Lateral lobe of pronotal length greater than depth, with a light-colored stripe along the lateral margin, sometimes not obvious, humeral sinus obvious (Fig. 2A-D). Prosternum with a pair of small cone-shaped spines (Fig. 4E). Mesosternum with a pair of triangular lobes, nearly equal in width to height. Metasternum with a pair of rounded triangular lobes, width distinctly greater than height (Fig. 4E). Thoracic auditory spiracle elongated and elliptical, partially covered by lateral lobe of pronotum.



Figure 2. A–D. Body of *Sichuana planicercata* sp. nov. A, B. Male holotype; C, D. Female paratype; A, C. Dorsal view; B, D. Lateral view; E. Male terminal abdomen with artificially unfurled cerci in dorsal view for showing inner tooth; F. Male terminal abdomen in dorsal view; G. Female terminal abdomen in dorsal view; H. Male terminal abdomen in lateral view; I. Male left tegmen in lateral view.

Tegmen approximately equal to, or slightly shorter than, twice length of pronotum, with clear longitudinal and cross veins. Tegmen folded downward along the M+CuA, flat dorsal field with a transverse lacuna in the middle. Tegmen almost the same width as the metazona disc from base to middle, then gradually narrowing in dorsal view. Lateral field of the tegmen slightly broadened (Fig. 2I). ScA weak and short, very close to anterior margin, ended at or before the middle of the anterior margin. ScP strong, with 4–6 branches. R forked to RA and RP very distally or without distinct dichotomy (Fig. 3B), sometimes distally fused with ScP then separated immediately (Fig. 3A). M+CuA separated to M and CuA after the origin of the handle, but the position of their separation is unstable. M forked to MA and MP distally (Fig. 3A–F). Stridulatory file with about 20 teeth (Fig. 4G). Mirror on right tegmen pentagonal, its length greater than its width (Fig. 3B, D, F). Hind wing rudimentary.

Legs. Prothoracic leg: genicular lobes of pro- and mesothoracic leg usually unarmed on both sides, sometimes armed with 1–2 spinules; dorsal procoxa with a long spine; profemur with 0–2 external black spinules and 1–4 internal black spinules ventrally; protibia with a slit-like tympanum on both sides; protibia with 2–3 external spurs dorsally, with 4–5 spurs on each side ventrally; protibia with an external apical spur dorsally and a pair of apical CuA+CuPaq

A

C

ScF RA

RP

MA

MP

ScP

RA

RI

MA

MP



CuA+CuPaq CuA+CuPaa 4mm 4mm E F ScA ScA Scl ScP R CuPby uPb RA RF CuP RP uPaf CuPal MF CuA+CuPaq CuA+CuPaa MP 4mm 4mm

Figure 3. A-F. Tegmina of Sichuana planicercata sp. nov. in dorsal view. A, C, E. Left tegmina; B, D, F. right tegmina.

spurs ventrally. Mesothoracic leg: mesofemur with 1-4 external black spinules and 0-2 internal black spinules ventrally; mesotibia with 2-4 external spurs and 3-4 internal spurs dorsally, with 5-6 spurs on each side ventrally; mesotibia with an internal apical spur dorsally and with a pair of apical spurs ventrally. Metathoracic leg: metafemur with sparse black spinules on each side ventrally; metatibia with a row of spines of different sizes on each side dorsally, with a row of sparse tiny spurs on each side ventrally, progressively denser toward apex; metatibia with a pair of apical spurs dorsally, with two pairs of apical spurs ventrally, one pair distinctly larger.

The apical area of the tenth abdominal tergite with a wide and pileous lacuna in the middle, covered with many tiny granular protrusions; posterior margin of tenth abdominal tergite with a shallow notch at the middle of the posterior margin, sides of which form a pair of very short round projections (Fig. 2F). Cercus conical and pileous, strongly incurved after the middle of itself, apex acute, not bent toward dorsal or ventral side. Presence of a hook-like and incurved inner tooth at base of cercus, tapering and curving from base to apex; inner teeth far

above top of cercus in lateral view (Fig. 2E, F, H). Subgenital plate length greater than width, slightly beyond cercus; with lateral carinae, middle part of posterior margin with a deep notch; width of notch varies; stylus slender and longer than notch (Fig. 4A-C). Epiproct triangular. Titillator L-shaped, with 2-3 rows of larger denticles, gradually decreasing from base to apex in apical portion (Fig. 4F).

Female. Generally similar to male, but body slightly larger. Tegmen slightly longer or shorter than pronotum, extending to the third abdominal tergum (Fig. 2B, D). Hindwing micropterous, longer than half of pronotum. Cercus conical and pileous. Tenth abdominal tergite with a wide rounded deep lacuna in the middle, reaching to or near posterior margin of ninth abdominal tergite (Fig. 2G). Subgenital plate nearly trapezoid, its width greater than length, middle of posterior margin with a wide notch (Fig. 4D). Ovipositor slightly shorter than metafemur, straight or slightly decurved distally (Fig. 2B, D).

Remarks. S. planicercata sp. nov., can be assigned to Sichuana Shen & Yin, 2020 by its median carina faintly indicated in the prozona and absent in the metazona;



Figure 4. *Sichuana planicercata* sp. nov. A–C. Male subgenital plate; D. Female subgenital plate; E. Thorax in ventral view; F. Titillator; G. Stridulatory file on underside of male left tegmen.

lateral carina distinct in metazona, faintly indicated in prozona; prosternum with a pair of spines; male tegmina mesopterous, far exceeding pronotum; male cerci conical, strongly incurved at middle, apex acute, and with an inner tooth placed in basal area.

S. planicercata sp. nov. is similar to *S. curvicercata* sp. nov., but differs distinctly by: male cerci not bending ventrally or dorsally, while those of *S. curvicercata* sp. nov. are curved ventrally with apex pointing dorsally; a hook-like inner tooth that tapers and curves from base to apex, extending far above the top of cerci in lateral view, while *S. curvicercata* sp. nov. having almost the same thickness overall and suddenly sharp and incurved at apex, slightly above the top of the cerci in lateral view; the posterior margin of the male tenth abdominal tergite has a shallow notch at the middle of the posterior margin, and its sides form a pair of very short round projections, while that of *S. curvicercata* sp. nov. is without protrusion, only a wide and shallow notch at the middle (Figs 2E, F, 6E, F); denticles on the apical portion of the titillator of *S.*

planicercata sp. nov. are fewer and sparser than those of *S. curvicercata* sp. nov. and are relatively larger (Figs 4F, 8F); *S. planicercata* sp. nov. has slightly more stridulatory teeth than *S. curvicercata* sp. nov., and the spacing of the teeth of *S. planicercata* sp. nov. is slightly narrower than that of *S. curvicercata* sp. nov. (Figs 4G, 8G); and female tenth abdominal tergite has a wide rounded deep lacuna in the middle that reaches the posterior margin of the ninth abdominal tergite, while that of *S. curvicercata* sp. nov. has a wide trapezoidal projection at the posterior margin (Figs 2G, 6G).

S. planicercata sp. nov. differs from *S. feicui* He, 2020 and *S. cryptospina* Shen & Yin, 2020 by the following character states: the lateral field of the male tegmina is only slightly broadened; in the male tegmina, M+CuA is separated to M and CuA after the origin of the handle; the male cerci are strongly incurved after their middle; a hook-like inner tooth is far above the top of the cerci in lateral view; and the pair of projections at the posterior margin of the male's tenth abdominal tergite is very short

and inconspicuous. These two species also differ from *S. planicercata* sp. nov. in the shape of the inner teeth, the denticles on the titillator, the morphology of the female tenth abdominal tergite, the shape of the stridulatory file, and the number of stridulatory teeth.

Sichuana curvicercata Gu, Zheng & Yue, sp. nov.

https://zoobank.org/EA8A23D6-8FDD-46B0-9CC0-C6FF514353C6

Material examined. *Holotype*: 3, Yonghong village, Dawei town, Xiaojin County, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province, China (30°58'6"N, 102°38'16"E, alt., ca. 2800 m), coll. Cheng-Jie Zhengand Yuan Wei, VIII-2022. Paratypes: 103 12, same data as in holotype (Fig. 5).

Diagnosis. Differs from all other *Sichuana* species by male tenth abdominal tergite without projections at posterior margin (Fig. 6F); male cercus gradually curved ventrally with apex pointing dorsally (Fig. 6E, F, H), inner tooth thick and nearly straight, suddenly sharp and incurved at apex (Fig. 6E); female tenth abdominal tergite with a wide trapezoidal projection at posterior margin (Fig. 6G).

Etymology. The specific epithet is derived from a combination of the Latin '*curvi*' meaning curved and 'cercus', describing the male cerci curved ventrally with the apex pointing dorsally. Chinese name: 弯尾川螽.

Measurements (mm). Body (head to tip of abdomen): 25.36-26.77, 27.28, pronotum: 6.98-7.26, 7.44, tegmen: 11.70-12.42, 7.08, mirror of right tegmen (from fore to hind): 3.88-3.96; hind wing: 4.39-4.62, 4.79; protibia: 6.24-7.23, 7.6; profemur: 6.45-6.86, 7.28; mesotibia: 7.24-7.72, 9.32; mesofemur: 6.26-7.10, 8.16; metatibia: 16.33-17.19, 19.92; metafemur: 17.56-17.8, 20.96; ovipositor: 17.64.

Description. Male. *Body* size medium. Frons flat, slightly oblique. Frontal fastigium and clypeofrontal sulcus black. Face light-colored. Occiput convex. Vertical fastigium broad, slightly wider than scape. Median ocellus visible. Compound eyes broadly round and bulging outwards, surrounded by black coloration that extends backward to form a black band. Filiform antennae inserted at the inner side of the compound eyes, scapus robust, much thicker than pedicel, flagellum taper toward the apex, covered with short setae (Fig. 6A–D).

Pronotum saddle-shaped, smooth, nearly equal to profemur in length. Disc of prozona with a broadly obtuse concavity in the middle of each side, anterior margin of pronotum slightly concave and posterior margin blunt, median carina faintly indicated in prozona, absent in metazona, lateral carina distinct in metazona, faintly indicated in prozona. Lateral lobe of pronotal length greater than depth, with a light-colored stripe along the lateral margin, sometimes not obvious, humeral sinus obvious (Fig. 6A– D). Prosternum with a pair of small cone-shaped spines



Figure 5. Sichuana curvicercata sp. nov. A. Adult female; B-D. Adult male.



Figure 6. A–D. Body of *Sichuana curvicercata* sp. nov. A, B. Male holotype; C, D. Female paratype; A, C. Dorsal view; B, D. Lateral view; E. Male terminal abdomen with artificially unfurled cerci in dorsal view for showing inner tooth; F. Male terminal abdomen in dorsal view; G. Female terminal abdomen in dorsal view; H. Male terminal abdomen in lateral view; I. Male left tegmen in lateral view.

(Fig. 8E). Mesosternum with a pair of triangular lobes, nearly equal in width to height. Metasternum with a pair of rounded triangular lobes, width distinctly greater than height (Fig. 8E). Thoracic auditory spiracle elongated and elliptical, partially covered by lateral lobe of pronotum.

Tegmen approximately equal to or slightly shorter than twice length of pronotum, with clear longitudinal and cross veins. Tegmen folded downward along M+CuA, dorsal field flat, with a transverse lacuna in the middle. Tegmen almost the same width with disc of metazona from basic until middle, and then gradually narrowing in dorsal view. Lateral field of tegmen slightly broadened (Fig. 6I). ScA weak and short, very close to anterior margin, ending at or before middle of anterior margin. ScP strong, with 5–7 branches. R without distinct dichotomy. M+CuA separated into M and CuA after intersection of handle and M+CuA, slightly after middle of tegmen. M separated into MA and MP after origin of handle but the position of their separation is unstable (Fig. 7A–F). Stridulatory file with about 18 teeth (Fig. 8G). Mirror on right tegmina pentagonal, length greater than width (Fig. 7B, D, F). Hind wing rudimentary.

Legs. Prothoracic leg: genicular lobes armed with 1–2 internal spinules and externally unarmed. Dorsal side of procoxa with a long spine. Profemur with 2–4 internal black spinules ventrally; protibia with a slit-like auditory tympanum on both sides; protibia with 0–3 external spurs dorsally, with 4–5 spurs on each side ventrally; protibia with an external apical spur dorsally and with a pair of apical spurs ventrally. Mesothoracic leg:



Figure 7. A-F. Tegmina of Sichuana curvicercata sp. nov. in dorsal view. A, C, E. Left tegmina; B, D, F. Right tegmina.

genicular lobes armed with 0-2 spinules on each side. Mesofemur with 2–4 external black spinules and 0-2 internal black spinules ventrally; mesotibia with 2–4 external spurs and 3–4 internal spurs dorsally, with 5–6 spurs on each side ventrally; mesotibia with an internal apical spur ventrally and a pair of apical spurs dorsally. Metathoracic leg: genicular lobes unarmed; metafemur with sparse black spinules on each side ventrally; metatibia with a row of spines of different sizes on each side dorsally, with a row of sparse tiny spurs on each side ventrally, progressively denser toward apex; metatibia with a pair of apical spurs dorsally and two pairs ventrally, one of which is distinctly larger.

The apical area of the tenth abdominal tergite with a wide and pileous lacuna in the middle, covered with many tiny granular protrusions. The tenth abdominal tergite with a wide and shallow notch in the middle of the posterior margin (Fig. 6F). Cercus conical and pileous, strongly incurved at middle; cercus curved ventrally after the middle, with the apex pointing dorsally. With a thick and nearly straight inner tooth at the base of the cercus, almost the same thickness overall, its apex abruptly thin and incurved; inner tooth slightly above the top of cercus in lateral view (Fig. 6E, F, H). Subgenital plate length greater than width, with lateral carinae, middle part of posterior margin with a deep notch, width of notch varies; stylus slender and longer than notch (Fig. 8A–C). Epiproct triangular. Titillator L-shaped, with 5–6 rows of dense denticles or more, gradually decreasing from base to apex on apical portion (Fig. 8F).

Female. Generally similar to male, but body slightly larger. Tegmen shorter than pronotum, extending to the third abdominal tergum (Fig. 6B, D). Hindwing micropterous, longer than half of pronotum. Cercus conical and pileous. The posterior margin of tenth abdominal tergite with a wide trapezoidal projection (Fig. 6G). Subgenital plate nearly trapezoid, width nearly equal to length, middle of posterior margin with a wide notch (Fig. 8D). Ovipositor slightly shorter than metafemur, slightly decurved distally (Fig. 6B, D).

Remarks. S. curvicercata sp. nov. is similar to S. planicercata sp. nov., but is distinct by: male cerci gradually



Figure 8. *Sichuana curvicercata* sp. nov. A–C. Male subgenital plate; D. Female subgenital plate; E. Thorax in ventral view; F. Titillator; G. Stridulatory file on underside of male left tegmen.

curved ventrally with the apex pointing dorsally, while those of S. planicercata sp. nov. do not bend ventrally or dorsally; the inner tooth is nearly straight and almost fo same thickness overall and is suddenly sharp and incurved at apex, while that of S. planicercata sp. nov. is tapering and curving from base to apex and is far above the top of the cerci in lateral view; the posterior margin of the male tenth abdominal tergite only with a wide and shallow notch in the middle of the posterior margin, while that of S. planicercata sp. nov. has a pair of very short and inconspicuous projections (Figs 2E, F, 6E, F); denticles on the apical portion of titillator of S. planicercata sp. nov. are fewer and sparser than those of S. curvicercata sp. nov. and are relatively larger (Figs 4F, 8F); S. curvicercata sp. nov. with slightly fewer stridulatory teeth than S. planicercata sp. nov., and the spacing of the teeth of S. curvicercata sp. nov. is slightly wider than that of S. planicercata sp. nov. (Figs 4G, 8G); female tenth abdominal tergite with a wide trapezoidal projection at the posterior margin, while that of S. planicercata sp. nov. have a wide rounded deep lacuna in the middle (Figs 2G, 6G).

S. curvicercata sp. nov. differs from S. feicui He, 2020 and S. cryptospina Shen & Yin, 2020 by: the lateral field of the male tegmina is slightly broadened; in male tegmina, M+CuA separate to M and CuA after the origin of the handle; the posterior margin of the male tenth abdominal tergite is without projections; male cerci are curved ventrally with the apex pointing dorsally. Furthermore, *S. curvicercata* sp. nov. differs from *S. feicui* by its male cerci strongly incurved at the middle. These two species also differ from *S. curvicercata* sp. nov. in the shape of the inner teeth, the denticles on the titillator, the morphology of the female tenth abdominal tergite, the shape of the stridulatory file, and the number of stridulatory teeth.

Sichuana longilamina Gu, Zheng & Yue, sp. nov.

https://zoobank.org/0B23FBDC-D40A-4AE2-957A-982FB4F64E4D

Material examined. *Holotype*: ∂, Guergou, Li County, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province, China, (31°30'29"N, 102°58'35"E, alt., ca. 2400 m), coll. Cheng-Jie Zhengand Yuan Wei, VIII-2022. *Paratypes*: 1♀, same data as in holotype.

Diagnosis. Differs from all other *Sichuana* species by notch of tenth abdominal tergite of male trapezoidal (Fig.



Figure 9. A–D. Body of *Sichuana longilamina* sp. nov. **A**, **B**. Male holotype; **C**, **D**. Female paratype; **A**, **C**. Dorsal view; **B**, **D**. Lateral view; **E**. Male terminal abdomen with artificially unfurled cerci in dorsal view for showing inner tooth; **F**. Male terminal abdomen in dorsal view; **G**. Female terminal abdomen in dorsal view; **H**. Male terminal abdomen in lateral view; **I**. Male left tegmen in lateral view.

9 F); male cercus strongly incurved at an acute angle and pointing dorsally (Fig. 9E, F, H), inner tooth pointing dorsally (Fig. 9E); apex of male subgenital plate elongate, the long styli about one-third of length of subgenital plate (Figs 9H, 11C); notch of female tenth abdominal tergite trapezoidal (Fig. 9G).

Etymology. The specific epithet is derived from a combination of the Latin 'longus' meaning long and 'lamina' meaning plate, to describe its male subgenital plate which is distinctly longer than the cerci. Chinese name:长板川螽.

Measurements (mm). Body (head to tip of abdomen): 27.7♂, 31.38♀; pronotum: 8.36♂, 8.6♀; tegmen: 17.42♂,

8.76 \bigcirc ; mirror of right tegmen (from fore to hind): 4.34 \Diamond ; hind wing: 7.82 \Diamond , 5.54 \bigcirc ; protibia: 7.58 \Diamond , 10 \bigcirc ; profemur: 7.4 \Diamond , 8.5 \bigcirc ; mesotibia: 9.42 \Diamond , 10.94 \bigcirc ; mesofemur: 8.52 \Diamond , 9.62 \bigcirc ; metatibia: 21.12 \Diamond , 26.28 \bigcirc ; metafemur: 20.98 \Diamond ; 25.64 \bigcirc ; ovipositor: 23.34.

Description. Male. *Body* size medium. Frons flat, slightly oblique. Frontal fastigium and clypeofrontal sulcus black. Face light-colored. Occiput convex. Vertical fastigium broad, slightly wider than scape. Median ocellus visible. Compound eye broadly round and bulging outwards, surrounded by black coloration extending backward to form a band. Filiform antennae inserted on the inner sides of the compound eyes, scapus robust,



Figure 10. A, B. Tegmina of Sichuana longilamina sp. nov. in dorsal view. A. Left tegmen; B. Right tegmen.

much thicker than pedicel, flagellum tapers toward the apex, covered with short setae (Fig. 9A–D).

Pronotum saddle-shaped, smooth, nearly equal to profemur in length. Disc of prozona with a broadly obtuse concavity in the middle of each side, anterior margin of pronotum slightly concave and posterior margin blunt, median carina faintly indicated in prozona, absent in metazona, lateral carina distinct in metazona, faintly indicated in prozona. Lateral lobe of pronotal length greater than depth, with a light-colored stripe along the lateral margin, sometimes not obvious, humeral sinus obvious (Fig. 9A-D). Prosternum with a pair of longer cone-shaped spines (Fig. 11A). Mesosternum with a pair of acute triangular lobes, height greater than width. Metasternum with a pair of rounded triangular lobes, width distinctly greater than height (Fig. 11E). Thoracic auditory spiracle elongated and elliptical, partially covered by lateral lobe of pronotum.

Tegmen slightly shorter than twice the length of pronotum, with clear longitudinal and cross veins. Tegmen folded downward along the M+CuA, the dorsal field flat, with a transverse lacuna in the middle. Tegmen almost the same width as disc of metazona from base to the middle, then gradually narrowing in dorsal view. Lateral field of the tegmen distinctly broadened (Fig. 9I). ScA weak, very close to anterior margin, ending at the middle of the anterior margin or fused with branch of ScP. ScP strong, with 3-5 branches. R forked to RA and RP distally, RA very close to ScP, sometimes distally fused with ScP (Fig. 10B). M+CuA branched to M and CuA before intersection of handle and CuA, slightly before middle of tegmen. M forked to MA and MP before the origin of the handle, but position of their separation unstable (Fig. 10A, B). Stridulatory file with about 34 teeth (Fig. 11E). Mirror on right tegmina pentagonal, length greater than width (Fig. 10B). Hind wing rudimentary.

Legs. Prothoracic leg: genicular lobes armed with 1–2 internal spinules and externally unarmed. Dorsal procoxa with a long spine. Profemur with 2–4 internal black spinules ventrally; protibia with a slit-like auditory tympanum on both sides; protibia with 2 external spurs dorsally, with 5 spurs on each side ventrally; protibia with an external apical spur dorsally and with a pair of apical

spurs ventrally. Mesothoracic leg: genicular lobes armed with 0–1 external spinule and 1 internal spinule; mesofemur with 2–3 external black spinules and 0–2 internal black spinules ventrally; mesotibia with 2 external spurs and 3 internal spurs dorsally, with 5 spurs on each side ventrally; mesotibia with an internal apical spur dorsally and with a pair of apical spurs ventrally. Metathoracic leg: genicular lobes unarmed; metafemur with sparse black spinules on each side ventrally; metatibia with a row of spines of different sizes on each side dorsally, with a row of sparse tiny spurs on each side ventrally, progressively denser toward the apex; metatibia with a pair of apical spurs dorsally, with two pairs of apical spurs ventrally, one pair distinctly larger.

The apical area of the tenth abdominal tergite with a wide lacuna in the middle covered with many tiny granular protrusions. The posterior margin of the tenth abdominal tergite with a trapezoidal notch at the middle, its sides forming a pair of round, blunt lobes (Fig. 9E, F). Cercus conical and pileous, strongly incurved at an acute angle after its middle and points dorsally, apex acute; with a hook-like, incurved inner tooth placed at base of cercus, tapering and curving from the base to the apex and pointing dorsally (Fig. 9E, F, H). Subgenital plate length greater than width, with lateral carinae, middle posterior margin with a deep notch, apex of subgenital plate elongate, far beyond cercus; stylus slender, about one-third the length of subgenital plate, longer than notch (Fig. 11C). Epiproct triangular. Titillator L-shaped, with 2-3 rows of denticles, and denticles on upper part of the apical portion distinctly larger than those on the lower part (Fig. 11D).

Female. Generally similar to male, but body slightly larger. Tegmen shorter than pronotum, extending to the third abdominal tergum (Fig. 9C, D). Hindwing micropterous, longer than half of the pronotum. Cercus conical and pileous. The apical area of the tenth abdominal tergite with a wide depression in the middle, near the posterior margin of ninth abdominal tergite. Tenth abdominal tergite with a U-shaped excision in the middle of posterior margin, sides of excision form a pair of round blunt projections (Fig. 9G). Subgenital plate nearly trapezoid, width greater than length, middle of posterior margin



Figure 11. *Sichuana longilamina* sp. nov. A. Thorax in ventral view; B. Female subgenital plate; C. Male subgenital plate; D. Titillator; E. Stridulatory file on underside of male left tegmen.

with a wide notch (Fig. 11B). Ovipositor slightly shorter than metafemur, slightly decurved distally (Fig. 9C, D).

Remarks. S. longilamina sp. nov. differs from S. feicui He, 2020, S. cryptospina Shen & Yin, 2020, S. planicercata sp. nov. and S. curvicercata sp. nov. by the following: pair of cone-shaped spines on prosternum more slender; pair of lobes on mesosternum acutely triangular, height greater than width (Fig. 11 A); male cerci strongly incurved at an acute angle slightly after their middle and gradually curved dorsally (Fig. 9E, F, H); apex of male subgenital plate extended far beyond cerci (Figs 9H, 11C); styli longer, about one-third the length of subgenital plate (Fig. 11C). Furthermore, S. longilamina sp. nov. differs from S. planicercata sp. nov. and S. curvicercata sp. nov. by: tenth abdominal tergite with a pair of round blunt projections on posterior margin; in male tegmina M+CuA branching to M and CuA before origin of handle; lateral field of male tegmina distinctly broadened.

These four species also differ from *S. longilamina* sp. nov. in the shape of the inner teeth, the denticles on the titillators, the morphology of the tenth abdominal tergite, the shape of the stridulatory file, and the number of stridulatory teeth.

Sichuana magnicerca Gu, Zheng & Yue, sp. nov. https://zoobank.org/532D02B3-2225-46C3-9DC9-2EB1918373A2

Material examined. *Holotype*: ♂, Zagunao town, Li County, Ngawa Tibetan and Qiang Autonomous Prefecture, Sichuan Province, China, (31°27'33"N, 103°10'52"E, alt., ca. 2000 m), coll. Cheng-Jie Zheng and Yuan Wei, VIII-2022. *Paratypes*: 8♂ 11♀, same data as in holotype.

Diagnosis. Differs from all other *Sichuana* species by notch of male tenth abdominal tergite U-shaped; large and long male cercus beyond subgenital plate (Fig. 12F, H), inner tooth small, inserted in the most basal part of cercus (Fig. 12E); notch of female tenth abdominal tergite V-shaped (Fig. 12G). The related species *S. cryptospina* Shen & Yin, 2020 with a pair of projections covering the inner tooth at male tenth abdominal tergite, male cercus at an obtuse angle, and broader lateral field of male tegmen, thus being similar to *S. magnicerca* sp. nov. (Fig. 12).

Etymology. The specific epithet is derived from a combination of the Latin '*magnus*' meaning huge and '*cercus*', to describe its male cerci, large and longer than the subgenital plate. Chinese name: 巨钩川螽.



Figure 12. A–D. Body of *Sichuana magnicerca* sp. nov. A, B. Male holotype; C, D. Female paratype; A, C. Dorsal view; B, D. Lateral view; E. Male terminal abdomen with artificially unfurled cerci in dorsal view for showing inner tooth; F. Male terminal abdomen in dorsal view; H. Male terminal abdomen in lateral view; I. Male left tegmen in lateral view.

Measurements (mm). Body (head to tip of abdomen): 30.78–33.02 $^{\circ}$, 35.1–37.34 $^{\circ}$; pronotum: 8.16–9.04 $^{\circ}$, 8.82–9.7 $^{\circ}$; tegmen: 15.84–17.57 $^{\circ}$, 8.14–8.92 $^{\circ}$; mirror of right tegmen (from fore to hind): 4.39–4.64 $^{\circ}$; hind wing: 8.23–8.39 $^{\circ}$, 5.28–5.78 $^{\circ}$; protibia: 8.12–9.14 $^{\circ}$, 9.5–10.58 $^{\circ}$; profemur: 7.68–8.34 $^{\circ}$, 8.04–8.98 $^{\circ}$; mesotibia: 9.42–10.12 $^{\circ}$, 10.52–11.74 $^{\circ}$; mesofemur: 8.44– 9.39 $^{\circ}$, 9.1–10.18 $^{\circ}$; metatibia: 22.24–24.43 $^{\circ}$, 24.36– 27.76 $^{\circ}$; metafemur: 23.02–24.88 $^{\circ}$; 24.48–27.54 $^{\circ}$; ovipositor: 21.48–24.39.

Description. Male. *Body* size medium. Frons flat, slightly oblique. Frontal fastigium and clypeofrontal sulcus black. Face light-colored. Occiput convex. Vertical fastigium broad, slightly wider than scape. Median ocel-

lus visible. Compound eyes broadly round and bulging outwards, surrounded by black coloration that extending backward to form a band. Filiform antennae inserted at inner sides of the compound eyes, scapus robust, much thicker than pedicel, flagellum tapering toward apex, covered with short setae (Fig. 12A–D).

Pronotum saddle-shaped, smooth, nearly equal to profemur in length. Disc of prozona with a broadly obtuse concavity in the middle of each side, anterior margin of pronotum slightly concave and posterior margin blunt, median carina faintly indicated in prozona, absent in metazona, lateral carina distinct in metazona, faintly indicated in prozona. Lateral lobe of pronotal length greater than depth, with a light-colored stripe along the lateral



Figure 13. A-D. Tegmina of Sichuana magnicerca sp. nov. in dorsal view. A, C. Left tegmina; B, D. Right tegmina.

margin, sometimes not obvious, humeral sinus obvious (Fig. 12A–D). Prosternum with a pair of cone-shaped spines (Fig. 14). Mesosternum with a pair of triangular lobes, nearly equal in width to height. Metasternum with a pair of rounded triangular lobes, width distinctly greater than height (Fig. 14E). Thoracic auditory spiracle elongated and elliptical, partially covered by lateral lobe of pronotum.

Tegmen approximately equal to or slightly shorter than twice the length of pronotum, with clear longitudinal and cross veins. Tegmen folded downwards along M+CuA, the dorsal field flat, with a transverse lacuna in middle. Tegmen almost same width as disc of metazona from base to middle, and then gradually narrowing in dorsal view. Lateral field of tegmen distinctly broadened (Fig. 12I). ScA weak, very close to anterior margin, ending at or before middle of anterior margin. ScP strong, with 5-6 branches. R usually forked to RA and RP after middle of tegmen, in a few examples very distally (for example, Fig. 13D). M+CuA forked to M and CuA before origin of handle. M usually very close to RP (Fig. 13A, C, D), or fused with RP then separateing immediately (Fig. 13B). Stridulatory file with about 33 teeth (Fig. 14G). Mirror on right tegmen pentagonal, length greater than width (Fig. 13B, D). Hind wing rudimentary.

Legs. Prothoracic leg: genicular lobes armed with 1–2 internal spinules, unarmed externally. Dorsal surface of procoxa with a long spine; profemur with 3–5 internal black spinules ventrally; protibia with a slit-like auditory tympanum on both sides; protibia with 2–4 external spurs dorsally, with 5 spurs on each side ventrally; protibia with an external apical spur dorsally and a pair of apical spurs ventrally. Mesothoracic leg: genicular lobes armed with

1–2 spinules on each side; mesofemur with 2–3 external black spinules and 0–2 internal black spinules ventrally; mesotibia with 2–3 external spurs and 3–5 internal spurs dorsally, with 5 spurs on each side ventrally; mesotibia with an internal apical spur dorsally and a pair of apical spurs ventrally. Metathoracic leg: genicular lobes unarmed. Metafemur with sparse black spinules on each side ventrally; metatibia with a row of spines of different sizes on each side dorsally, with a row of sparse tiny spurs on each side ventrally, progressively denser toward the apex; metatibia with a pair of apical spurs dorsally, with two pairs of apical spurs ventrally, one pair of which distinctly larger than the other.

Apical area of the tenth abdominal tergite with a slight pileous lacuna covered with many tiny granular protrusions. Posterior margin of tenth abdominal tergite with U-shaped notch in middle, sides of notch which form a pair of round blunt projections (Fig. 12E, F). Cercus large and long, extending beyond subgenital plate, conical and pileous, strongly incurved after middle, apex acute and slightly upturned. With a small, hook-like and incurved inner tooth at basal-most part of the cercus, tapering and curving from base to apex, invisible in lateral view (Fig. 12E, F, H). Subgenital plate length greater than width, with lateral carinae, middle part of posterior margin with a deep notch, width of notch varying among individuals; stylus slender and longer than notch (Fig. 14A-C). Epiproct triangular. Titillator L-shaped, with only one row of denticles, gradually getting larger from base to apex on apical portion (Fig. 14F).

Female. Similar to male, but body slightly larger. Tegmen shorter than pronotum, extending to the third abdominal tergum (Fig, 12B, D). Hindwing micropterous,



Figure 14. *Sichuana magnicerca* sp. nov. A–C. Male subgenital plate; D. Female subgenital plate; E. Thorax in ventral view; F. Titillator; G. Stridulatory file on the underside of the male left tegmen.

longer than half of pronotum. Cercus conical and pileous. Tenth abdominal tergite depressed downward in middle, and with a V-shaped notch at middle of posterior margin, its sides forming a pair of round blunt projections (Fig. 12G). Subgenital plate nearly trapezoid, nearly equal in width to length, middle of posterior margin with a wide notch (Fig. 14D). Ovipositor slightly shorter than metafemur, slightly decurved distally (Fig. 12B, D).

Remarks. *S. magnicerca* sp. nov. is similar to *S. cryp-tospina* Shen & Yin, 2020, but differs distinctly by: male cerci large and long, extending beyond subgenital plate, while those of *S. cryptospina* are relatively shorter and smaller, not extending beyond subgenital plate; the inner tooth is small and placed at the basal-most part of the cerci, while that of *S. cryptospina* is relatively larger and longer, and is placed at the sub-basal area of the cerci (Fig. 12E, F, H); the apical portion of the titillator of *S. magnicerca* sp. nov. has only 1 row of denticles that are aligned

vertically, while that of *S. cryptospina* has 1–2 rows that are aligned diagonally (Fig. 14F); and the female tenth abdominal tergite is depressed downward in the middle and has a V-shaped notch, while that of *S. cryptospina* has a U-shaped notch (Fig. 12G).

S. magnicerca sp. nov. differs from S. feicui He, 2020, S. planicercata sp. nov., S. longilamina sp. nov. and S. curvicercata sp. nov. by its large and long male cerci, which extend beyond the subgenital plate. Furthermore, S. magnicerca sp. nov. differs from S. planicercata sp. nov. and S. curvicercata sp. nov. by: tenth abdominal tergite with a pair of round blunt projections on posterior margin; in male tegmina M+CuA branching to M and CuA before origin of handle; and lateral field of male tegmina distinctly broadened. It differs from S. feicui by its male cerci strongly incurved after middle. It differs from S. longilamina sp. nov. by male subgenital plate not extended beyond cerci, and male cerci incurved at an obtuse angle. These four species also differ from *S. magnicerca* sp. nov. in shape of the inner teeth, denticles on the titillators, morphology of female tenth abdominal tergite, shape of stridulatory file, and the number of stridulatory teeth.

Genetic distanceanalysis

The mean of the sequence divergences for *COI* among species of *Sichuana* Shen & Yin, 2020 ranged from a low of 2.208% to a high of 15.688% (Table 3). The sequence divergences for *COI* between most species are greater than 8%. While only *S. planicercata* sp. nov. and *S. curvicercata* sp. nov. show low sequence divergences between them (2.208%), this is still significantly greater than the intraspecific mean of sequence divergence. Relative to *COI*, the genetic distance analysis using 16S shows lower sequence divergence at all levels (Table 4).

Molecular phylogenetic results

The results of the ML and BI analyses are almost identical (Fig. 15). *S. feicui* He, 2020 appears at the earliest position and is sister of all other *Sichuana* species. The rest consist of two clades. The clade containing *S. magnicerca* sp. nov., *S. cryptospina* Shen & Yin, 2020 and *S. longilamina* sp. nov. is sister of the clade containing *S. planicercata* sp. nov. and *S. curvicercata* sp. nov. *S. longilamina* sp. nov. is the sister group of the clade containing

 Table 3. Sequence divergences for COI among species of Sichuana.

Species	COI sequence divergences (%)						
	S. planicercata	S. magnicerca	S. longilamina	S. feicui	S. curvicercata	S. cryptospina	
S. planicercata	0.586						
S. magnicerca	13.620	0.847					
S.longilamina	13.150	10.738	_				
S .feicui	15.391	15.688	14.407	-			
S. curvicercata	2.208	10.671	13.103	14.393	0.305		
S. cryptospina	13.563	8.760	11.000	17.214	12.686	0.152	

 Table 4. Sequence divergences for 16S among species of Sichuana.

Species	16S sequence divergences (%)					
	S. planicercata	S. magnicerca	S. longilamina	S. feicui	S. curvicercata	
S. planicercata	0.127					
S. magnicerca	3.989	0.000				
S. longilamina	3.177	2.126	-			
S. feicui	5.828	4.945	3.719	-		
S. curvicercata	0.830	3.652	3.245	5.900	0.254	

S. magnicerca sp. nov. and *S. cryptospina*. In the ML tree, samples of *S. curvicercata* sp. nov. resolved as the sister of the clade containing *S. planicercata* sp. nov. and other samples of *S. curvicercata* sp. nov. In contrast, these two species are well resolved in the BI tree.

Discussion

Morphological variation within species

Variation in wing shape and venation is documented in various groups of fossil orthopterans and their relatives (Zessin 1987; Béthoux 2008; Gu et al. 2010, 2011, 2014, 2021). However, this is rarely addressed in extant orthoptera. The venation of Sichuana shows different degrees of intraspecific variation. For instance, the end of ScA, the dichotomous position of M, the dichotomous position of R and the fusion of some longitudinal veins are unstable among individuals, even in the left and right tegmina of an individual (Figs 3, 7, 10, 13), including structures associated with R. For instance, in S. planicercata sp. nov., R sometimes fuses distally with ScP and is separated immediately (Fig. 3A), R usually forks into RA and RP distally, but sometimes R is unbranched (Fig. 3B). In S. magnicerca sp. nov. RP sometimes fuses with M and separated immediately (Fig. 13B). M also shows significant variation between individuals, mainly in the position of its forking to MA and MP. However, the bifurcation of R and M is usually stable in fossil ensiferans (Gu et al. 2009, 2014, 2021; Wang et al. 2016). Therefore, more documentation on wing venation within species of extant orthopterans would help us better understand wing morphology and provide a reference for classification of extinct orthopterans.

The male subgenital plate of *Sichuana* also shows different degrees of variation between individuals. The shape and width of the notch on its posterior margin vary between individuals, especially in *S. planicercata* sp. nov. (Figs 4, 8, 11, 14).

Molecular analysis

Genetic distance analysis shows that sequence divergences for *COI* between most species of *Sichuana* are greater than 8% (Table 3). While the sequence divergence between *S. planicercata* sp. nov. and *S. curvicercata* sp. nov. is significantly smaller, about 2.208%, it's still significantly greater than the intraspecific mean of sequence divergence. Generally, the genetic distance within a species is much smaller than between species (Hebert et al. 2003b). Previous studies have shown that *COI* intraspecific divergences are rarely greater than 2% and most are less than 1% in insects (Avise 2000; Hebert et al. 2003a, b). Although there is a small amount of difference between the results from the BI and ML methods, the molecular phylogenetic analysis resolved these samples as six lineages with a high supporting rate. This is



0.04

Figure 15. The gene trees of Sichuana. A. BI phylogenetic tree; B. ML phylogenetic tree.

consistent with results from morphological comparison. Therefore, assigning these specimens to four new species of *Sichuana* is justified.

Conclusion

Based on the morphological and molecular analysis above, we described four new species of *Sichuana* Shen & Yin, 2020, *S. planicercata* sp. nov., *S. curvicercata* sp. nov., *S. longilamina* sp. nov. and *S. magnicerca* sp. nov., and refined the diagnosis of the genus. This large sample suggests that variation in wing venation and the male subgenital plate is common within species in this genus.

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PENSOFT.



Comparative morphology of the larval mouthparts among six species of Notodontidae (Insecta, Lepidoptera), with discussions on their feeding habits and pupation sites

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Abstract

Larval mouthparts are significant organs for the individual development, morphologically related with feeding habits, and providing valuable characters for taxonomy and phylogenetic analysis. In previous studies, larval mouthparts revealed two identifying characters of Notodontidae. However, the evolutionary driving force and exact definition of these structures remain unsatisfactory. In this study, the larval mouthparts of *Euhampsonia cristata* (Butler, 1877), *Fentonia ocypete* (Bremer, 1861), *Phalera assimilis* (Bremer & Grey, 1853), *Nerice davidi* Oberthür, 1881, *Cerura erminea* (Esper, 1783) and *Furcula furcula* (Clerck, 1759) are morphologically observed and compared using scanning electron microscopy (SEM). The larval mouthparts of the six species are commonly equipped with paired maxillary sacs, congruent with the previous descriptions. However, the larval mouthparts of *N. davidi* are peculiar for bearing toothed mandibles, providing an exception of Notodontidae. Otherwise, the mouthparts exhibit morphological diversity and the related feeding and pupation habits are briefly discussed.

Key Words

labral notch, mandible, maxillary sac, sensillum, spinneret

Introduction

Larvae, the juveniles of holometabolous insects, are considered feeding devices that turn smaller embryos into larger individuals (Hart and Strathmann 1995). With respect to Lepidoptera, the larvae mainly feed on plant organs and are able to cause great losses to agriculture and forestry (van Emden 1957; Zacharuk and Shields 1991), or produce silk as a fiber resource for our textile industry (Stehr 1987; Wagner 2005). In fact, both of plant attacking and silk producing processes are inevitably undertaken by their feeding apparatus, which are commonly called mouthparts (Chapman 2013; Tong et al. 2021; Zhang et al. 2022).

Larval mouthparts are generally of the mandibulate type, representing a ground plan of biting and chewing mechanisms in insects (Chapman and de Boer 1995). Mouthparts are usually structurally associated with feeding habits (Stehr 1987; Smith and Capinera 2005) and morphologically diverse among insect lineages (Grebennikov and Scholtz 2004; Beutel et al. 2008; Neugart et al. 2009; Beutel et al. 2010; Jiang and Hua 2015). Mouthpart characters have been utilized in previous phylogenetic analyses (McCabe 1988; Godfrey et al. 1989; Miller 1991). However, the detailed morphological comparisons are far less satisfactory in previous studies, especially in Notodontidae.

Notodontidae represent a large family of Lepidoptera, comprising approximately 3800 recognized species assigned to 734 genera across the world (Pan 2008; Schintlmeister 2013). Adults of Notodontidae are usually called trifid noctuid moths and are frequently considered serious pests because some of their larvae attack the leaves of

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fruit trees. Larvae of Notodontidae are commonly called prominents for their remarkably larger head capsules and noticeably modified anal prolegs (Wagner 2005). Previously, larvae of Notodontidae were reported to be identified by two mouthpart modifications, which are shared by 154 species in 90 genera of Notodontidae (Godfrey et al. 1989). Later, counter-examples on mandibles were also discovered in two species of *Nerice* (Dolinskaya 2008). However, "Why these mandibles become morphologically different during development?" and "What exactly the stipital lobes really are?" still remain unanswered hitherto.

In this study, larval mouthparts of *Euhampsonia cristata* (Butler, 1877), *Fentonia ocypete* (Bremer, 1861), *Phalera assimilis* (Bremer & Grey, 1853), *Nerice davidi* Oberthür, 1881, *Cerura erminea* (Esper, 1783), *Furcula furcula* (Clerck, 1759) are morphologically observed and compared using scanning electron microscopy, in order to discover more morphological characters for larval taxonomy.

Materials and methods

The female adults were collected under light traps, with the detailed collection information listed in Table 1. Fertilized eggs were obtained from a wild-captured female, confined in a paper box, at room temperature $(26 \pm 1 \text{ °C})$. The eggs were kept in plastic boxes with wet absorbent cotton to keep humidity. After emergence, the larvae were fed with fresh leaves of the specific host plant (Table 2). Photographs were taken with a Nikon D810 digital camera (Nikon, Tokyo, Japan). Voucher specimens were kept at the Entomological Museum of Shenyang Agricultural University (SYAU).

For scanning electron microscopy, the final instar larvae were fixed in Dietrich's solution (formalin: 95% ethanol: glacial acetic acid: distilled water = 6: 15: 1: 80, v/v), which was heated up to 70 °C and boiled for 1 min then left to stand for 12 h under hood before being preserved in 75% ethanol (Jiang and Hua 2015). Five individuals of each species were dissected under a Leica EZ4HD Stereoscopic Zoom Microscope, serially dehydrated in a graded ethanol, replaced by tertiary butanol, freeze-drying for 3 h, spotter-coated with gold, before examined under a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 5 kV.

Results

Feeding habits and pupation sites

The larvae are all herbivorous, feeding on leaves of peculiar host plants (Table 2). The larvae of *E. cristata*, *F. ocypete*, *P. assimilis* feed on *Quercus mongolica* (Fig. 1A–C), while those of *N. davidi* feed on *U. pumila* (Fig. 1D), and the larvae of *C. erminea* and *F. furcula* feed on *Populus* sp. (Fig. 1E, F).

All first instar larvae prefer to chew on the ventral surface of host leaves, while the mature larvae usually bite Table 1. Sample information of the larvae of Notodontidae.

Species	Localities	Dates
Euhampsonia cristata	Sankuaishi Mountain	vii-30-2019
(Butler, 1877)	(41°36'N, 124°16'E)	
Fentonia ocypete	Sankuaishi Mountain	vii-30-2019
(Bremer, 1861)	(41°36'N, 124°16'E)	
Phalera assimilis	Guanmen Mountain	vii-8-2019
(Bremer & Grey, 1853)	(40°49'N, 123°34'E)	
Nerice davidi	Houshi Mountain	vii-21-2020
Oberthür, 1881	(41°40'N, 124°26'E)	
Cerura erminea	Hehuogou Mountain	viii-6-2020
(Esper, 1783)	(41°11'N, 123°15'E)	
Furcula furcula	Shenyang Agricultural University	viii-5-2021
(Clerck, 1759)	(40°48'N, 123°33'E)	

on the edge of leaves (Fig. 1). The larvae of *P. assimilis* live gregariously, whereas the larvae of the other five species are solitary. The mature larvae usually hold on the twigs and leaves, and bite on the leaf edge (Fig. 1A–C).

When fully grown, the larvae stop feeding, build a cocoon and finally step into a prepupal period. The sites of pupation and ways of cocoon spinning varied significantly among the six species. The mature larvae of *E. cristata*, *F. ocypete*, *N. davidi* and *P. assimilis* usually build cocoons in soil. The larvae of *C. erminea* and *F. furcula* secrete a thickened cocoon covering the bark.

Larval mouthparts of *Euhampsonia cristata* (Butler, 1877)

The mouthparts are of the mandibulate type, consisting of a labrum, a pair of mandibles, and a maxilla-labial complex (Fig. 2A–G).

The labrum is V-shaped, possessing six pairs of setae: three pairs of medial setae (MS1, MS2, MS3) and three pairs of lateral setae (LS1, LS2, LS3). Two lateral setae (LS1, LS2) are significantly longer than the mesal setae. The epipharynx is furnished with three pairs of sensilla chaetica (SC1, SC2, SC3) and a digitiform sensillum at the lateral area (Fig. 2B).

The paired mandibles are heavily sclerotized, almost spherical each with a smooth cutting edge but without incisor cusps (Fig. 2C–E). Each mandible bears two long setae on the external surface.

The maxilla-labial complex consists of paired maxillae, a pair of labial palps, and a spinneret (Fig. 2F, G). Each maxilla is composed of a cardo, stipes, galea, maxillae sac and a two-segmented maxillary palp. The cardo bears two long setae. The stipes bears a sensillum chaeticum. The maxilla is remarkably equipped with a protuberant maxillary sac on the inner surface of the galea (Fig. 2F). The labial palp is furnished with a prominent sensillum styloconicum and a short sensillum chaeticum (Fig. 2G). The spinneret is situated between the bases of the labial palps and is generally tubular, gradually tapering towards the apex, and longitudinally depressed on the dorsal surface of the distal end (Fig. 2G). The role of the spinneret is to release the silk secreted by the larval silk glands.


Figure 1. The mature larvae in habitus of the six species in Notodontidae. A. Euhampsonia cristata; B. Fentonia ocypete; C. Phalera assimilis; D. Nerice davidi; E. Cerura erminea; F. Furcula furcula.

Larval mouthparts of *Fentonia ocypete* (Bremer, 1861)

(Fig. 3A–G).

The larval mouthparts of *F. ocypete* are morphologically remarkable for the shape and setae of the labrum, the sensilla on the epipharynx, and the structure of the spinneret

The labrum is longitudinally split, with a pair of lateral lobes overlapped in the middle (Fig. 3A). The labrum possesses six pairs of setae: three pairs of medial setae (MS1, MS2, MS3) and three pairs of lateral setae (LS1, LS2, LS3). The mesal setae (MS1) are located at the base, and the lateral setae (LS1, LS2) are more prominent than the mesal setae. The epipharynx possesses two pairs of sensilla chaetica similar in length (SC1, SC2). The epipharynx is also furnished with a semispherical sensillum digitiformium on the lateral area and an epipharyngeal sensillum at the basal part (Fig. 3B).

The paired mandibles have a smooth cutting edge and a ridge on the inner side (Fig. 3C–E). Each mandible bears two long setae situated on the basal part of the outer surface.

The maxilla-labial complex is morphologically similar to those of *E. cristata* (Fig. 3F, G) with paired maxillae, a pair of labial palps, except for the structure of spinneret (Fig. 3G). The spinneret is dorsal-ventrally depressed, with the distal opening slightly separated (Fig. 3G).

Larval mouthparts of *Phalera assimilis* (Bremer & Grey, 1853)

The mouthparts of *P. assimilis* are morphologically similar to those of *E. cristata* except for the detailed characters on epipharynx, mandibles and spinneret (Fig. 4A–G).

The labrum is V-shaped and bears six pairs of setae, with LS1 and LS2 slightly longer than the others (Fig. 4A). The epipharynx is equipped with three sensilla chaetica along the mesal notch (SC1, SC2, SC3), a sensillum digitiformium at the lateral margin (SD), and an epipharyngeal sensillum arranged on the central region (Fig. 4B).

The paired mandibles also have a smooth cutting edge and a ridge on the inner side (Fig. 4C–E). Each mandible also bears two long setae situated on the external surface.

The maxillary sac is also elongate and hirsute (Fig. 4F). The spinneret is comparative short, with the distal opening dorsal-ventrally depressed (Fig. 4G).

Larval mouthparts of *Nerice davidi* Oberthür, 1881

The mouthparts of *N. davidi* differ significantly from those of the other species in terms of the shape of the labrum, setal length, sensilla on the epipharynx, structure of the spinneret (Fig. 5A–G), and especially the teeth on the mandibles.



Figure 2. Larval mouthparts of *Euhampsonia cristata* (Butler, 1877). A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–3; median seta; MP, maxillary palp; MxS, maxillary sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes.

The labrum is equipped with a shallow notch, which is not extented to the center (Fig. 5A). The labrum also possesses six pairs of setae with LS2 slightly longer than others. The epipharynx bears three pairs of sensilla chaetica (SC1, SC2, SC3) on each ventrolateral margin, a sensillum digitiformium along the lateral margin, and an epipharyngeal sensillum in the central area (Fig. 5B).

The paired mandibles are heavily sclerotized and peculiar for bearing six blunt dentitions (T1–T6) on the distal margin (Fig. 5C–E). Each mandible bears two prominent setae on the external surface. The maxilla-labial complex also has a pair of maxillary sacs (Fig. 5F). The labial palp has a sensillum styloconicum and a sensillum chaeticum that are generally similar in length (Fig. 5G). The spinneret situated between the bases of the labial palps is dorsal-ventrally depressed (Fig. 5G).

Larval mouthparts of *Cerura erminea* (Esper, 1783)

The mouthparts of *C. erminea* are morphologically similar to those of *E. cristata* with the exception of the setal



Figure 3. Larval mouthparts of *Fentonia ocypete* (Bremer, 1861). A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–2; median seta; MP, maxillary palp; MxS, maxillary sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes.

length, sensilla on the epipharynx, and the structure of the spinneret (Fig. 6A–G).

The labrum is furnished with a longitudinal notch in the middle (Fig. 6A) and six pairs of setae on the external surface. The lateral setae (LS2) and mesal setae (MS2) are slightly longer than the others. The epipharynx bears three sensilla chaetica (SC1, SC2, SC3), which are gradually shorter from distal pairs to basal pairs. The epipharynx is also equipped with a small sensillum digitiformium and an epipharyngeal sensillum (Fig. 6B).

The paired mandibles are heavily sclerotized and furnished with a smooth cutting edge (Fig. 6C–E). Each mandible also bears two prominent setae on the exterior surface. The maxillary sacs are certified to be hollow and occasionally cut open (Fig. 6F). The spinneret is short, dorsal-ventrally depressed, with the distal opening widely separated (Fig. 6G).

Larval mouthparts of *Furcula furcula* (Clerck, 1759)

The mouthparts of *F. furcula* are morphologically similar to those of *C. erminea* with the structure of spinneret (Fig. 7A–G).

The labrum is V-shaped and furnished with six pairs of setae, with the medial setae (MS1, MS3) noticeably



Figure 4. Larval mouthparts of *Phalera assimilis* (Bremer & Grey, 1853). A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–3; median seta; MP, maxillary palp; MxS, maxillary sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes.

shorter than the others (LS1, LS2, LS3, MS2). The epipharynx also possesses three pairs of sensilla chaetica (SC1, SC2, SC3), all of which are similar in length. A digitiform and an epipharyngeal sensillum are present at the lateral margin and central region. (Fig. 7B).

The paired mandibles are heavily sclerotized, with a smooth cutting edge and two long setae on the external surface of each mandible (Fig. 7C–E).

The maxilla-labial complex also has a pair of maxillary sacs (Fig. 7F). The spinneret is unique and different from others, it is lamellar and broad-flat. (Fig. 7G).

Discussion

Mouthpart apparatuses of the final instar larvae of *E. cristata, F. ocypete, P. assimilis, N. davidi, C. erminea,* and *F. furcula* were morphologically compared for the first time, using scanning electron microscopy. Based on our morphological comparison, the larval maxillary sac is confirmed to be shared by all the six species. The labral notches, setal arrangements, and spinnerets exhibit morphological diversity among the six species. The toothed mandibles were also confirmed in the mature larvae of *N. davidi*.



Figure 5. Larval mouthparts of *Nerice davidi* Oberthür, 1881. A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–3; median seta; MP, maxillary palp; MxS, maxillary sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes; T1–6, tooth.

Mandibles, the essential components of mandibulate mouthparts, varied morphologically among lineages that have diverse feeding habits (Chapman and de Boer 1995; Chapman 2013). The mandibles usually possess sharp apical cusps in predacious larvae (Michat 2010; Lawrence et al. 2011; Cao and Liu 2013), or bear morphologically diverse molar regions for filtering or grinding in saprophagous larvae (Jiang and Hua 2015). With respect to the phytophagous larvae, the mandibles are equipped with smooth cutting edges in the leaf-feeding caterpillars in some Saturniidae (Bernays and Janzen 1988), furnished with dentate cusps in the concealed feeding larvae in Lycaenidae, Gelechiidae, Cossidae, Carposinidae, or Tortricidae (Liu et al. 2011; Song et al. 2014; Abd El-Ghany and Faucheux 2021), or combined cutting edges and dentate cusps in some Saturniidae (Zhang et al. 2022). In Notodontidae, the larval mandibles are peculiar for being serrate in the first instar but smooth in the later stages (Miller 1991; Dolinska-ya 2008). The morphological differences are helpful for



Figure 6. Larval mouthparts of *Cerura erminea* (Esper, 1783). A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–3; median seta; MP, maxillary palp; MxS, maxillary sac; OB, An occasional broken of the sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes.

the first-instar larvae chewing on leaf surfaces, and more suitable for the mature larvae cutting and biting on leaf edges (Liu et al. 2023). In this study, the serrated mandibles of the mature larvae of *N. davidi* are quite different from all the other known larvae in Notodontidae (Miller 1991; Dolinskaya 2008), but very similar to the stem chewing larvae of *Sericinus montela* (Wang and Jiang 2023) or to the polyphagous larvae of *Spodoptera exigua* (Li et al. 2008). The atypical morphological differences on larval mandibles may imply potential enigmatic feeding strategy of *N. davidi*. Maxillae of Notodontidae are peculiar for bearing paired "stipital lobes" on the maxillary complex, which represents another identifying character for the family (Godfrey et al. 1989). These characters were reported to be shared by more than 143 species of Notodontidae (Miller 1991; Dolinskaya 2008), but were never reported in the other larvae in Lepidoptera (Albert 1980; Grimes and Neunzig 1986; Godfrey et al. 1989; Li et al. 2018). Based on our morphological investigation under electron microscopy, the so-called "stipital lobes" are internally hollow. From a perspective of location, it is difficult to



Figure 7. Larval mouthparts of *Furcula furcula* (Clerck, 1759). A. Labrum; B. Epipharynx; C. Left mandible, inner view; D. Right mandible, inner view; E. Left mandible external view; F. Maxilla-labial complex; G. Magnification of the spinneret. Ca, cardo; Es, epipharyngeal sensillum; Ga, galea; LN, labral notch; LP, labial palp; LS1–3, lateral seta; MS1–3; median seta; MP, maxillary palp; MxS, maxillary sac; SC, sensillum chaeticum; SD, sensillum digitiformium; SS, sensillum styloconicum; Sp, spinneret; St, stipes.

Table 2. Relationships between	en larval mouthparts and habits.
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Species name	mandibles	Labral notch	Type of spinnerets	Host plants	Pupation sites
Euhampsonia cristata (Butler, 1877)	smooth	V-shape	Longitudinal depressed	Quercus mongolica (Fagaceae)	In soil
Fentonia ocypete (Bremer, 1861)	smooth	Deep	Longitudinal depressed	Quercus mongolica (Fagaceae)	In soil
Phalera assimilis (Bremer & Grey, 1853)	smooth	V-shape	Depressed tupular	Quercus mongolica (Fagaceae)	In soil
Nerice davidi Oberthür,1881	toothed	Shallow	Depressed tupular	Ulmus pumila (Ulmaceae)	In soil
Cerura erminea (Esper, 1783)	smooth	V-shape	Broadly depressed	Populus sp. (Salicaceae)	Cocoon on bark
Furcula furcula (Clerck, 1759)	smooth	V-shape	Broadly depressed	Populus sp. (Salicaceae)	Cocoon on bark

say that these structures are located on the stipes. For these reasons, the structures should be defined as "maxillary sac" rather than "stipital lobe". These sacs seem to form seals between the mandibles and maxillae, assisting to hold leaf tissue within the oral cavity while the mandibles are acting (Godfrey et al. 1989; Miller 1991).

Spinneret usually form into a tube-like structure that produces silk in immature insects (Capinera 2008), and varies in shapes among insect lineages (Grimes and Neunzig 1986; Lin 2002; Li et al. 2008; Liu et al. 2011; Chen and Hua 2014; Zhang et al. 2014; Zhou et al. 2015; Liu et al. 2018). In Lepidoptera, the spinnerets are normally tubular in Cossidae, Gelechiidae, Carposinidae, Tortricidae and Lasiocampidae (Liu et al. 2011; Men and Wu 2016; Rana and Mohankumar 2017; Xu et al. 2017; Song et al. 2018; Abd El-Ghany and Faucheux 2021), rudimentary but bearing paired flake lobes in some Saturniidae (Zhang et al. 2022). In this study, the larval spinnerets of Notodontidae are longitudinally depressed in E. cristata, F. ocypete, P. assimilis and N. davidi that usually pupate in the soil (Pei 1988; Li et al. 2003; Zeng and Ji 2018), broadly depressed in C. erminea and F. furcula, which usually built thickened cocoons covering the bark (Pan 2013) (Table 2). The structural differences among the six species are very likely related to silk secreting or cocoon spinning behaviors (Craig 1997; Zalucki et al. 2002; Sorensen et al. 2006).

The labral notches of phytophagous insects are usually morphologically adapted to peculiar food resources (Chapman and de Boer 1995). The labral notches are shallow in the tunneling species in some Cossidae, Gelechiidae and Carposinidae (Liu et al. 2011; Song et al. 2014; Xu et al. 2017; Abd El-Ghany and Faucheux 2021), deeply split in the leaf biting larvae of Sphingidae, Noctuidae, Saturniidae, and some Notodontidae (Cardoso et al. 2017; Rana and Mohankumar 2017; Venancio et al. 2020), or even diverse among congeneric larvae of Saturniidae that exhibit divergent feeding habits (Zhang et al. 2022). In this study, the labral notches are morphologically similar between larvae of C. erminea and F. furcula attacking Populus sp. (Table 2), and E. cristata and P. assimilis consuming leaves of Quercus mongolica (Table 2). The labral notch of F. ocypete, however, is much deeper than those of all the other species in Notodontidae (Miller 1991; Dolinskaya 2008).

In fact, larvae of *F. ocypete* are quite peculiar not only for the deep split labral notches, but also for the setae on the labrum and the sensilla on the epipharynx. In general, the lepidopterous larvae usually possess six pairs of setae on the labrum (Lin 1997, 2002; Li et al. 2008; Chen and Hua 2014; Men and Wu 2016; Chen et al. 2018; Li et al. 2018), and three pairs of sensilla chaetica on the epipharynx (Liu et al. 2011; Men and Wu 2016; Chen et al. 2018; Li et al. 2018). The larvae of *F. ocypete* also have six pairs of setae on the labrum but the MS1 are shorter than others and located on the base, and two pairs of sensilla chaetica on the apex of epipharynx. The atypical morphological features of *F. ocypete* imply its peculiar taxonomic status or enigmatic living habits, which still need further observations.

Different from other agricultural pest species, larvae of Notodontidae are more frequently discovered on trees in forest ecosystems (Pei 1988; Wu and Fang 2003; Wang 2005; Xue et al. 2005; Liu et al. 2011; Pan 2013; Zeng and Ji 2018). For better inhabiting the relatively complicated ecosystem, larvae of Notodontidae not only employ dramatically diverse defensive strategies to avoid being attacked (Ruxton et al. 2005; Liu et al. 2023), but also possess structurally specialized mouthparts for feeding more efficiently, similar to other forest-dwelling larvae in Saturniidae (Zhang et al. 2022). Based on our previous observations, the serrate mandibles are more valuable for the first-instar larvae chewing on the leaf surface (Liu et al. 2023). On the other hand, the mesally smooth mandibles are more suitable for the mature larvae cutting the hardened leaf edges of woody plants (Fig. 1). Moreover, the toothed mandibles of mature larvae in *N. davidi*, as an exception of Notodontidae, are very likely adapted to the rough and wrinkled leaves or other tissues of their host plant *U. pumila*.

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PENSOFT.



Taxonomic study of the tribe Campsomerini (Hymenoptera, Scoliidae) from northern Vietnam, with the description of a new species and a checklist of Vietnamese scoliid wasps

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Abstract

The tribe Campsomerini (Hymenoptera: Scoliidae) from northern Vietnam was studied, resulting in the finding of three species and six subspecies belonging to five genera. Three genera (*Megacampsomeris* Betrem, 1928 (with *M. shillongensis* (Betrem, 1928)), *Micromerialla* Betrem, 1964 (with *M. marginella marginella* (Klug, 1810)) and *Phalerimeris* Betrem, 1967 (with *P. phalerata phalerata* (de Saussure, 1858))) and three species (*Sericocampsomeris flavomaculata* Gupta & Jonathan, 1989, *Campsomeriella (Annulimeris) annulata* (Fabricius, 1793) and *C. (Campsomeriella) collaris* (Fabricius, 1775)) are recorded for the first time from Vietnam. One new species, *Sericocampsomeris vietnamica* Pham & van Achterberg, **sp. nov.** is described and illustrated. Identification keys to the genera, species and subspecies of the tribe Campsomerini from northern Vietnam and to the species of *Sericocampsomeris* Betrem, 1941 are presented. Lastly, we provide a checklist with 13 species and subspecies of Scoliidae from Vietnam.

Key Words

checklist, hairy wasp, key, new record, Oriental region, Scoliinae, Sericocampsomeris

Introduction

The family Scoliidae Latreille, 1802, is a group of solitary aculeate wasps belonging to the superfamily Vespoidea and is distributed worldwide. They are commonly known as digger wasps, hairy wasps or scarab-hunter wasps and are parasitoids of scarab larvae (Coleoptera, Scarabaeidae). There are about 560 species in 43 genera belonging to two subfamilies: Proscoliinae and Scoliinae. Proscoliinae, represented by a single genus, *Proscolia* Rasnitsyn, 1977 with two known species, is recorded from the South Palearctic Region, being known only from Armenia and Greece.

The Scoliinae, consisting of about 558 species distributed amongst 42 genera in two tribes, Campsomerini Betrem, 1965 and Scoliini Latreille, 1802 is recorded throughout the world, predominantly in tropical and subtropical regions (Day et al. 1981; Osten 2005; Girish Kumar and Pham Ph 2015; Liu et al. 2021a; Taylor and Barthélémy 2021).

Members of the Scoliidae are readily distinguished from other families of Hymenoptera by two primary characters: 1 - The wing membrane beyond the closed cells is closely striolate; and 2 - The mesosternum and metasternum form a flat plate overlying the bases of the mid- and hind coxae (Krombein 1978; Gupta and Jonathan 2003).

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Males and females usually show a high degree of sexual dimorphism, differing in the number of antennal segments, often in wing venation, body-form and colour. While females are relatively easy to distinguish to genus and species, males are, in general, difficult to identify as they are very similar in external morphological characters (Gupta and Jonathan 2003; Liu et al. 2021b).

From North to South, Vietnam has a 3444 km long coastline and a 4639 km long land boundary. Known as a country of mega-biodiversity, it consists of subtropical and warm-temperate climate in the north and a tropical climate in the south. Northern Vietnam, especially, is within the Indo-Burma biodiversity hotspot and has, climatically, more or less warm-temperate characteristics and is expected to be a primary biodiversity centre (Pham Ph and Girish Kumar 2015). Unfortunately, diversity and taxonomic studies conducted in the country are few and fragmentary. This is most probably due to protracted wars in the past and the lack of Vietnamese entomologists. This lack of information includes the Scoliidae. The Vietnamese scoliid wasps were previously treated by Betrem (1928) in his monograph of the Indo-Australian Scoliidae with zoogeographical considerations, based mainly on specimens deposited in the Natural History Museum at Paris. Betrem (1941), Bradley and Betrem (1967), Gupta and Jonathan (2003), Liu et al. (2021a), Taylor and Barthélémy (2021) and Chen et al. (2022) listed scoliid species from Vietnam, but likely the references in the last five papers are based on Betrem (1928, 1941) only. Khuat et al. (2013) recorded an undetermined scoliid species from Ha Noi as Campsomeris sp.

Here, we study the taxonomy of the tribe Campsomerini (Hymenoptera, Scoliidae) from northern Vietnam, describe and illustrate a new species and provide a key to the genera, species and subspecies of the tribe from northern Vietnam and an identification key to all *Sericocampsomeris* species. The goal of this paper is to provide new species and genera records for Vietnam and to considerably enhance the current knowledge on the scoliid wasp fauna of Vietnam; we also present a checklist of Scoliidae from the country.

Materials and methods

Specimens were collected using sweep nets and Malaise traps at localities in the following provinces in northern Vietnam: Ha Noi, Hai Phong, Hoa Binh, Lang Son, Lao Cai, Nam Dinh, Quang Ninh, Thanh Hoa, Thai Binh and Vinh Phuc. Adult morphological characters were observed and described from pinned and dried specimens with the aid of a stereoscopic microscope. Betrem (1928, 1941), Gupta and Jonathan (2003) and Liu et al. (2021b) were used to accomplish identifications to all taxon levels.

Our identification key to species of the genus *Sericocampsomeris* Betrem, 1941 was constructed, based on Vietnamese specimens and the original descriptions of *S. degaullei*, *S. stygia* and *S. punctata* by Betrem (1928), Gupta and Jonathan (2003) and Chen et al. (2022), respectively.

A checklist of Scoliidae from Vietnam was constructed using publications of Betrem (1928, 1941), Bradley and Betrem (1967), Gupta and Jonathan (2003), Osten (2005), Danilov and Dubatolov (2021), Liu et al. (2021a), Taylor and Barthélémy (2021) and Chen et al. (2022).

Photographic images were taken using a Nikon SMZ800N microscope camera and a Canon SD3500 IS camera.

Specimens examined, including the holotype and the paratype of the new species are deposited in the Institute of Ecology and Biological Resources (**IEBR**), Vietnam Academy of Science and Technology, Ha Noi, Vietnam.

Abbreviations used in the text are as follows: Metasomal tergum = T(x), x being the tergum number, Metasomal sternum = $S(\gamma)$, γ being the sternum number.

Results and discussion

Order Hymenoptera Family Scoliidae Latreille, 1802 Subfamily Scoliinae Latreille, 1802 Tribe Campsomerini Betrem, 1965

Key to the genera, species and subspecies of Campsomerini from northern Vietnam

(females of Micromeriella Betrem and Megacampsomeris Betrem unknown).

- 3 Larger species, 30–33 mm; lateral carina of propodeum extended beyond spiracle; dorso-median area of propodeum truncate posteriorly, posterior surface of propodeum with dense punctures; vertex behind posterior ocelli with dense punctures (Fig. 6C); mesopleural crest sharp; metasoma black, except yellow T5, T2–T4 with yellow spots laterally; mesosoma with black setae (Fig. 6D)....... Sericocampsomeris Betrem (S. rubromaculata rubromaculata (F. Smith, 1855))

Erect setae on occiput, scapula, dorsal surface of pronotum and anterior part of mesoscutum red-brown (Fig. 2D)
 Campsomeriella collaris quadrifasciata (Betrem, 1928)

- 6 Head elliptical in anterior view, maximum width ≈ 1.3× its height; front impunctate, with large, flat, triangular area in front of anterior ocellus; declivity of vertex conspicuously sloping and temples receding dorsally...... Campsomeriella Betrem 7
- 7 S6 and S7 without copulatory brushes; base of volsella covered with sparse and short setae (Fig. 1B) Campsomeriella (Annulimeris) annulata annulata (Fabricius, 1793)

Campsomeriella Betrem, 1941

Campsomeries subgenus Campsomeriella Betrem, 1941: 86. Campsomeriella Betrem, 1967: 25.

Type species. Scolia thoracica Fabricius, 1787.

Campsomeriella (Annulimeris) annulata annulata (Fabricius, 1793)

Fig. 1A, B

Tiphia annulata Fabricius, 1793: 225.

Campsomeris servillei Lepeletier, 1845: 501.

Scolia annulata (Fabricius): F. Smith 1855: 100.

Elis (Dielis) annulata (Fabricius): de Saussure and Sichel 1864: 196. *Elis aglaea* Cameron, 1901: 19.

Campsomeris annulata (Fabricius): Rohwer 1921: 88.

Campsomeris (Dielis) annulata (Fabricius): Betrem 1928: 94-95.

Campsomeris (Phalerimeris) annulata (Fabricius): Bradley1964: 9.

- Campsomeriella (Annulimeris) annulata (Fabricius): Betrem 1967: 25–29.
- Campsomeris (Campsomeriella) annulata annulata (Fabricius): Tsuneki 1972: 18–19.

Campsomeriella (Annulimeris) annulata (Fabricius): Krombein 1979: 1317.

Specimens examined. VIETNAM: Thai Binh: 1 ♂, Hong Minh, Hung Ha, 24.vi.2013, Coll. Phong Huy Pham. Ha Noi: 4 ♂♂, Co Nhue 2, Bac Tu Liem, 13.xii.2015, Coll. Phong Huy Pham. Hoa Binh: 6 ♂♂, Tan Thanh, Luong Son, 1–30.viii.2018, Malaise traps, Coll. Phong Huy Pham.

Diagnosis. Male. Body length 11–16 mm. Front largely impunctate, with large, flat, triangular area in front of anterior ocellus; declivity of vertex conspicuously sloping and temples receding dorsally; antennal segment not distinctly crenulate; S6 and S7 without copulatory brushes; base of mandible, clypeus laterally, dorsal surface of pronotum, callosity, scapula, broad stripe narrowly interrupted medially on the scutellum, large spot on metanotum medially, small apical stripe on inner surface of first femur, apical half on the outer surface of all femora, outer surface of first and second tibiae and outer surface of first and fifth fore tarsal segments yellow; T1-T5 with apical yellow bands, covering about one-third of T1, T4 and T5 and about one-half of T2 and T3 (Fig. 1A); apical yellow bands on S2-S4 broadly interrupted medially; metasoma with blue reflections; erect vestiture white, except black on two last metasomal segments; wings lightly infumated; base of volsella covered with sparse and short setae (Fig. 1B).

Female. Unknown.

Distribution. Vietnam (new record): Ha Noi, Hoa Binh, Thai Binh (Fig. 8A). Elsewhere: Bhutan, China, India, Indonesia, Japan, Korea, Malaysia, Myanmar, Nepal, Philippines (Betrem 1928; Gupta and Jonathan 2003; Girish Kumar and Pham Ph 2015; Liu et al. 2021a; Taylor and Barthélémy 2021).

Campsomeriella (Campsomeriella) collaris collaris (Fabricius, 1775) Fig. 2A–C

Tiphia collaris Fabricius, 1775: 354.

Tiphia thoracica Fabricius, 1798: 254.

Colpa parvula Lepeletier, 1845: 548.

Elis (Dielis) thoracica (Fabricius): Bingham 1897: 99.

Elis (Dielis) fimbriata (Burmeister): Bingham 1897: 99.

- Campsomeris (Campsomeris) collaris (Fabricius): Betrem 1928: 126.
- Campsomeris (Campsomeriella) collaris (Fabricius): Betrem 1941: 89.
- Campsomeris (Campsomeriella) collaris collaris (Fabricius): Bradley 1964: 12.

Campsomeriella (Campsomeriella) collaris collaris (Fabricius): Betrem 1967: 29.

Specimens examined. VIETNAM: Thai Binh: 1 \mathcal{Q} , Phuong Huy Pham; Dong Minh and Dong Hoang, Tien Hai, 27.vii.2017, 2.ix.2017 Coll. Phong Huy Pham; $2 \bigcirc \bigcirc +3$ ♂♂, Hong Minh, Hung Ha, 25.vi.2013, 10.vii.2017, Coll. Phong Huy Pham. Hoa Binh: 1 ♀, Thanh Nong, Kim Boi, 5.viii.2017, Coll. Phong Huy Pham; 1 ♀, My Tan, Tan Thanh, Luong Son, 27.vi.2019, Coll. Phong Huy Pham. Thanh Hoa: $3 \bigcirc \bigcirc +4 \oslash \odot$, Sam Son town, 22.vi.2016, 26– 28.vii.2020, Coll. Phong Huy Pham; $2 \stackrel{\frown}{\downarrow} + 2 \stackrel{\frown}{\circ}$, Hai Tien, Hoang Hoa, 1.vi.2022, Coll. Phong Huy Pham. Ha Noi: Coll. Phong Huy Pham; $2 \mathfrak{Q} \mathfrak{Q} + 3 \mathfrak{Z}$, Lien Mac, Bac Tu Liem, 26.viii.2017, 19.viii.2017, 22.x.2017, 6.vii.2019, Coll. Phong Huy Pham; $2 \bigcirc \bigcirc$, Van Hoa, Ba Vi, 8.i.2020, Coll. Phong Huy Pham; $6 \ \downarrow + 2 \ \Diamond$, Co Nhue 2, Bac Tu Liem, 12.xii.2015, 05.i.2016, 12.xii.2022, 1.i.2023, Coll. Phong Huy Pham; $2 \ \bigcirc \ \bigcirc \ + 2 \ \bigcirc \ \bigcirc \ \bigcirc$, Minh Khai, Bac Tu Liem, iii-vi.2019, Malaise traps, Coll. Phong Huy Pham; 1 Å, Thuy Xuan Tien, Chuong My, Malaise trap, Coll. Phong Huy Pham. Vinh Phuc: $3 \bigcirc \bigcirc$, Me Linh Station for biodiversity, Me Linh, 2.vi.2018, Coll. Phong Huy Pham. Nam Dinh: 1 \bigcirc , Xuan Thuy National Park, Xuan Thuy, 3.ix.2016, Coll. Phong Huy Pham. Quang Ninh: 1 ♂, Bai Chay, Ha Long, 14.vi.2020, Coll. Phong Huy Pham.

Diagnosis. Female. Body length 14–21 mm. Vestiture black, except greyish on clypeus, front and antennal scape; occiput, dorsal surface of pronotum, scapula and anterior part of mesoscutum with dense, erect white setae; wings dark brown, with conspicuously blue reflections (Fig. 2A).

Male. Body length 10–15 mm. S6 and S7 with copulatory brushes; metasoma with light blue reflections; broad stripe along lateral margin of clypeus, base of mandible, dorsal surface of pronotum, scapula dorsally and posteriorly, stripe on callosity, tegula anteriorly; moderately large band on scutellum narrowly interrupted medially, rather small median spot on metanotum, stripe on apical half of all femora, outer surface of all tibiae and outer surface of first and fifth fore tarsal segments yellow; T1–T4 with apical yellow bands, covering almost entire T1, more than three-fourths of T2, more than one-half of T3 and approximately one-half of T4 (Fig. 2B); a pair of rather small yellow spots on S2, S3 and S5 posterolaterally; erect



Figure 1. Campsomeriella (Annulimeris) annulata annulata (Fabricius, 1793), male. A. Habitus, dorsal view; B. Genitalia, ventral view.



Figure 2. *Campsomeriella (Campsomeriella) collaris collaris* (Fabricius, 1775) and *Campsomeriella (Campsomeriella) collaris quadrifasciata* (Fabricius, 1798). A–C. C. (C.) *collaris collaris*; D–F. C. (C.) *collaris quadrifasciata* (A, D. Habitus, female, dorsal view; B, E. Habitus, male, dorsal view; C, F. Genitalia, ventral view).

vestiture white, except black on S5–S7; S6 and S7 with long, dense black setae; wings lightly infumated; base of volsella covered with dense and long setae (Fig. 2C).

Distribution. Vietnam (new record): Ha Noi, Hoa Binh, Nam Dinh, Quang Ninh, Thai Binh, Thanh Hoa, Vinh Phuc (Fig. 8B). Elsewhere: Bangladesh, India, Nepal, Sri Lanka (Betrem 1928; Krombein 1978; Gupta and Jonathan 2003; Liu et al. 2021a; Taylor and Barthélémy 2021).

Campsomeriella (Campsomeriella) collaris quadrifasciata (Fabricius, 1798) Fig. 2D–F

Scolia quadrifasciata Fabricius, 1798: 231.

Campsomeris quadrifasciata Fabricius: Betrem 1928: 336.

Campsomeris (Campsomeriella) quadrifasciata Fabricius: Betrem 1941: 89.

- Campsomeris (Campsomeriella) collaris quadrifasciata Fabricius: Betrem and Bradley 1964: 19.
- *Campsomeriella (Campsomeriella) collaris quadrifasciata* Fabricius: Betrem 1967: 29.

Specimens examined. VIETNAM: Thai Binh: 13 $\bigcirc \bigcirc$, Hong Minh, Hung Ha, 25.vi.2013, 10.vii.2017, Coll. Phong Huy Pham. Thanh Hoa: 1 $\bigcirc + 2 \checkmark \checkmark$, Sam Son town, 22.vi.2016, 26–28.vii.2020, Coll. Phong Huy Pham; 2 \checkmark , Hai Tien, Hoang Hoa, 1.vi.2022, Coll. Phong Huy Pham: Ha Noi: 1 $\bigcirc + 1 \checkmark$, Nghia Do, Cau Giay, 04.i.2016, 16.vii.2017, Coll. Phong Huy Pham; 1 $\bigcirc + 2 \checkmark \checkmark$, Red river bank, Long Bien, 13.ix.2015, Coll. Phong Huy Pham; 1 \bigcirc , Lien Mac, Bac Tu Liem, 19.viii. 2017, 22.x.2017, Coll. Phong Huy Pham; 8 $\bigcirc \bigcirc + 2 \checkmark \circlearrowright$, Co Nhue 2, Bac Tu Liem, 05.i.2016, 13.xii.2015, 21.xii.2022, Coll. Phong Huy Pham. Lang Son: 1 \bigcirc , Huu Lien, Huu Lung, 13.vi.2018, Coll. Phong Huy Pham.

Diagnosis. Female. Body length 14–22 mm. Vestiture black, except greyish-white on clypeus, front and antennal scape; occiput, dorsal surface of pronotum, scapula and anterior part of mesoscutum with dense, erect red-brown setae; wings dark brown, with light blue reflections (Fig. 2D).

Male. Body length: 10–14 mm. S6 and S7 with copulatory brushes; metasoma with light blue reflections; broad stripe along lateral margin of clypeus, base of mandible, very narrow stripe on scapula posteriorly, very small spot on callosity, tegula anteriorly, small stripe on apical half of fore femur, outer surface of mid-femur apically, small spot on hind femur apically, outer surface of fore and mid-tibiae, large stripe on apical half of hind tibia and outer surface of first and fifth fore tarsal segments yellow; apical yellow bands on T1–T4, covering about one-half of T1, T2 and T4 and about one-third of T3 (Fig. 2E); a pair of small yellow spots on S2 and S3 posterolaterally, sometimes on S4; erect vestiture white, except black on two last metasomal segments; wings lightly infumated; base of volsella covered with dense and long setae (Fig. 2F).

Distribution. Vietnam: Ha Noi, Lang Son, Thanh Hoa, Thai Binh (Fig. 8C). Elsewhere: China, Indonesia, Malaysia, Myanmar, Thailand (Betrem 1928, 1941; Gupta and Jonathan 2003).

Campsomeriella collaris (Fabricius) is a polytypic taxon that is widely distributed primarily in the Oriental region. The species consists of three subspecies, *C. collaris collaris* (Fabricius), *C. collaris quadrifasciata* (Fabricius) and *C. collaris insularis* Gupta & Jonathan, 2003 (Osten 2005). These subspecies are distinguished, in females, by differences in the colour of the erect setae on the head and mesosoma and reflections on wings and in males, by the difference in yellow spots.

In northern Vietnam, *C. collaris collaris* (Fabricius) and *C. collaris quadrifasciata* (Fabricius) are the most common and recognised scoliid species because of the entirely black body in females, the dark brown wings and erect white or red-brown setae on the occiput, scapula and anterior part of the mesoscutum; and the very large yellow bands on T1–T3 in males of *C. collaris collaris* (Fabricius).

Campsomeriella collaris collaris was originally described from India by Fabricius (1775) as Tiphia collaris. Krombein (1979) stated that the subspecies occurs only in Sri Lanka and southern India. Gupta and Jonathan (2003) showed the subspecies being common and widely distributed in the Indian subregion and recorded it occurring in Nepal and Bangladesh. Betrem (1928) recorded only C. collaris quadrifasciata from northern and central Vietnam. Liu et al. (2021a, 2021b) recorded C. (C.) collaris from China without recognition of subspecies. Judging from the key characters and images, these specimens should be classified as C. (C.) collaris quadrifasciata. Taylor and Barthélémy (2021) recorded it from Hong Kong. In this present study, the first author found that populations collected at the same locality, for example, Thai Binh and Thanh Hoa, would key to both C. collaris collaris and C. collaris quadrifasciata. We hypothesise

that *C. collaris* populations are variable in colour in India, Nepal, Bangladesh to Vietnam and China and that recognition of both subspecies is probably not warranted as indicated in Liu et al. (2021a, 2021b). Future research is needed to better understand the colour variation of this species in a larger geographical context.

Some small female specimens (14–15 mm body length) have dense greyish setae on the occiput, scapula and anterior part of the mesoscutum, suggesting that variation in the colour of setae on the body is at least partly related to overall size.

Khuat et al. (2013) recorded a scoliid as *Campsomeris* sp. from Ha Noi. The specimens (two females and two males collected at Bai Giua Song Hong, Long Bien district in 2012) would key to *C. collaris quadrifasciata*.

Megacampsomeris Betrem, 1928

Campsomeris subgenus *Megacampsomeris* Betrem, 1928: 138. *Megacampsomeris* Betrem: Betrem in Betrem and Bradley 1972: 164.

Type-species. Tiphia grossa Fabricius, 1804.

Megacampsomeris shillongensis (Betrem, 1928) Fig. 3A, B

Campsomeris (Megacampsomeris) shillongensis Betrem, 1928: 155–156. Campsomeris (Megacampsomeris) lindenii Lepeletier: Betrem 1928: 151–152.

Megacamposeris shillongensis (Betrem): Betrem in Betrem and Bradley 1972: 164.

Specimens examined. VIETNAM: Lao Cai: 2 ♂♂, Cat Cat, Sa Pa, 21.ix.2017, Coll. Phong Huy Pham.

Diagnosis. Male. Body length 16-18 mm. Frontal spatium densely punctate, with small impunctate area posteriorly at the middle; hind tibial spur white; antenna reddish-brown; base of mandible, clypeus, scrobe, large spot on gena, scapula, dorsal surface of pronotum, callosity, small spot at posterior corners of mesoscutum, tegula anteriorly, fore coxa, stripe on outer surface of all femora, outer surface of fore and mid-tibiae and outer surface of first fore tarsal segment yellow; apical yellow bands on T1-T4 narrow, about onethird of T1 and about one-fifth of T2-T4 (Fig. 3A); S2-S4 with small apical yellow bands, that on S2, interrupted narrowly and those on S3 and S4 interrupted more widely; erect vestiture goldish-white, except black on three last metasomal segments; wings yellowish, lightly infuscated at apex; genitalia with paramere moderately long and stout, base of volsella with dense and long setae, distance between base of these setae less than their own diameter (Fig. 3B).

Female. Unknown.

Distribution. Vietnam (new record): Lao Cai (Fig. 8D). Elsewhere: India, Myanmar, Nepal (Betrem 1928; Gupta and Jonathan 2003; Girish Kumar and Pham Ph 2015).

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Figure 3. Megacampsomeris shillongensis (Betrem, 1928), male. A. Habitus, dorsal view; B. Genitalia, ventral view.

Micromeriella Betrem, 1964

Campsomeris subgenus Micromeris Betrem in Bradley 1964: 186. Micromeriella Betrem Betrem in Bradley 1972: 166.

Type species. Scolia marginella KIug, 1810.

Micromeriella marginella marginella (KIug, 1810) Fig. 4A–C

Scolia marginella Klug, 1810: 214.

Elis (Campsomeris) hirsuta de Saussure, 1858: 234.

Elis (Dielis) hirsuta de Saussure: Saussure and Sichel 1864: 216.

Elis (Dielis) marginella (KIug): de Saussure and Sichel 1864: 186.

Scolia hirsuta (de Saussure): Dalla Torre 1897: 163.

- Campsomeris (Campsomeris) marginella marginella (Klug): Betrem 1928: 135.
- Campsomeris (Campsomeriella) marginella marginella (Klug): Betrem 1941: 90.

Campsomeris (Micromeris) marginella marginella (Klug): Bradley and Betrem 1968: 329.

Micromeriella marginella (Klug): Betrem and Bradley 1972: 119. *Micromeriella marginella marginella* (Klug): Bradley 1974: 443.

Specimens examined. VIETNAM: Ha Noi: 1 ♂, Lien Mac, Bac Tu Liem, 27.viii.2017, Coll. Phong Huy Pham; 1 ♂, Long Bien, 12.xii.2015, Coll. Phong Huy Pham. Thai Binh: 2 ♂♂, Hong Minh, Hung Ha, 10.vii.2017, Coll. Phong Huy Pham. Thanh Hoa: 2♂, Hai Tien, Hoang Hoa, 1.vi.2022, Coll. Phong Huy Pham.

Diagnosis. Male. Body length 7–10 mm. Metasoma with faint blue reflections dorsally; flagellum brown; clypeus, except for large black spot medially, base of mandible (Fig. 4B), scapula, tiny spot on callosity, small spot on tegula anteriorly, stripe on scutellum medially, small median spot on metanotum posteriorly, about one-third of anterior surface of fore coxa beneath, small stripe on apical half of all femora and outer surface of hind tibia, outer surface of fore and mid-tibiae, outer surface of fore tarsus and mid-basitarsus yellow; T1–T5 with apical yellow bands, that on T1, moderately emarginate anteromedially

and covering about one-third of T1, those on T2–T4, conspicuously emarginate anteromedially and covering onehalf of T2–T4, that on T5, not emarginate anteriorly (Fig. 4A); S2–S4 with narrow apical yellow bands, that on S4, interrupted medially or reduced to spot posterolaterally; erect vestiture white, sparse on metasoma and moderately dense on head and mesosoma; two last metasomal segments with black setae; tomentum silvery, relatively sparse on head and side of mesosoma; wings hyaline; genitalia with paramere stout; base of volsella with sparse and long setae (Fig. 4C).

Female. Unknown.

Distribution. Vietnam (new record): Ha Noi, Thai Binh (Fig. 8E). Elsewhere: China, India, Sri Lanka, Taiwan (Betrem 1928; Gupta and Jonathan 2003; Liu et al. 2021a).

Micromeriella marginella is widely distributed in the Oriental region. The species ranges from Sri Lanka through India to Southeast Asia and also in China and Taiwan. There have been seven subspecies recorded for M. marginella, namely M. marginella marginella (Klug), M. m. bariensis (Tsuneki, 1972), M. m. billitonensis (Tullgren, 1904), M. m. formosana (Betrem, 1928), M. m. modesta (F. Smith, 1855), M. m. terinata (F. Smith, 1858) and M. m. thainana (Tsuneki, 1972). Osten (2005) did not recognise M. m. bariensis, M. m. billitonensis and M. m. thainana. The seven subspecies are distinguished by the difference in yellow marks on the body in males and by alteration of apical yellow bands on the metasomal terga in females. These characters are likely insufficient to retain the subspecies as valid taxa.

Phalerimeris Betrem, 1967

Campsomeris subgenus Phalerimeris Betrem in Bradley and Betrem 1967: 294.

Phalerimeris Betrem: Bradley 1974: 460.

Type species. *Elis (Campsomeris) phalerata* de Saussure, 1858.



Figure 4. *Micromeriella marginella marginella* (Klug, 1810), male. A. Habitus, dorsal view; B. Head, frontal view; C. Genitalia, ventral view.

Phalerimeris phalerata phalerata (de Saussure, 1858) Fig. 5A–C

Elis (Campsomeris) phalerata de Saussure, 1858: 233.

Elis (Dielis) phalerata de Saussure: de Saussure and Sichel 1864: 201.

Elis (Dielis) iris Lepeletier: Magretti 1892: 247.

Campsomeris albopilosa Rohwer, 1911: 480.

Campsonleris (Dielis) phalerata phalerata (de Saussure): Betrem 1928: 103.

Campsomeris lindenii (Lepeletier): Yano 1932: 317.

Campsomeris (Phalerimeris) phalerata (de Saussure): Betrem in Bradley and Betrem 1967: 294.

Phalerimeris phalerata phalerata (de Saussure): Bradley 1974: 460.

Specimens examined. VIETNAM: Quang Ninh: $3 \ Q \ Q$, Yen Tu National Park, Uong Bi, 27.vi.2013, Coll. Phong Huy Pham; $2 \ Collocolor \ Dots \ Do$

Diagnosis. Female. Body length 12–20 mm. Front with deep punctures in front of anterior ocellus; lateral carina of propodeum extended beyond spiracle; forewing yellowish and hyaline, with first submarginal cell almost entirely covered with short setae and with a large black

spot subapically; legs ferruginous; antenna black; mandible often red-brown; T1–T3 with narrow yellow bands apically; apical fringes on T1–T4 reddish-golden; erect vestiture and tomentum reddish-golden, except black on two last metasomal segments (Fig. 5A).

Male. Body length 10-13 mm. Antenna and legs wholly black; metasoma with faint blue reflections; clypeus, except for large black spot medially, base of mandible, lower part of inner eye orbit, scrobe, elongate mark on gena, scapula, callosity, tiny mark on mesoscutum posterolaterally, small spot on tegula anteriorly, narrow band on scutellum anteriorly, large median spot on metanotum, anterior side of fore coxa, apical mark on fore and hind femora beneath, narrow stripes above and below on mid-femur, outer surfaces of fore and mid-tibiae and outer surface of first fore tarsi yellow; apical yellow bands on T1-T4, covering less than one-half of their length (Fig. 5B); S2-S4 with narrow apical yellow bands, that on S4, broadly interrupted medially; erect vestiture pale white, except black on two last metasomal segments and some black setae on T5 apically; wings hyaline, slightly infumated at apex; forewing without dark mark subapically; base of volsella with sparse setae, distance between bases of these setae more than their own diameter (Fig. 5C).

Distribution. Vietnam (new record): Ha Noi, Hoa Binh, Nam Dinh, Quang Ninh, Thai Binh (Fig. 8F). Elsewhere: Bhutan, China, India, Indonesia, Malaysia, Myanmar, Nepal, Taiwan, Thailand (Betrem 1928; Gupta and Jonathan 2003; Girish Kumar and Pham Ph 2015; Liu et al. 2021a; Taylor and Barthélémy 2021).

Phalerimeris phalerata is widely distributed in the Oriental region and ranges from Sri Lanka, India and Nepal, eastwards to Southeast Asia and also into China and Taiwan.



Figure 5. *Phalerimeris phalerata phalerata* (de Saussure, 1858). A. Habitus, female, dorsal view; B. Habitus, male, dorsal view; C. Genitalia, ventral view.

Three subspecies have been recorded P. phalerata phalerata (de Saussure), P. p. turneri (Betrem, 1928) and P. p. bankanensis (Betrem, 1928). Osten (2005) did not recognise the last subspecies. In females, these three subspecies are distinguished, based on apical fringes on the metasomal terga and the yellow bands on T1 and T2. In P. p. phalerata, the apical fringes on T1-T4 are reddish-golden, the apical fringe on T5 and setae on T6 are black and the yellow bands on T1 and T2 are narrow and continuous in the middle area. In P. p. turneri, the apical fringes on T1-T5 and setae on T6 are reddish-golden and the yellow bands on T1 and T2 are moderately broad and continuous in the middle area. In P. p. bankanensis, the apical fringes on T1-T5 and setae on T6 are reddish-golden and the yellow bands on T1 and T2 are rather narrow and interrupted in the middle. The males of all three subspecies are very similar (de Saussure 1858; Betrem 1928; Gupta and Jonathan 2003).

In some female specimens of *P. phalerata phalerata* from North Vietnam, the apical yellow bands on T1 and T2 are narrow, about one-third the length of T1 and one-fifth that of T2 and continuous in the middle area. The apical yellow band on T3 is also narrow, but interrupted in the middle. The apical fringe on T5 includes both median black and lateral yellow setae and setae on T6 are entirely black. Therefore, the population of this species in northern Vietnam shows variation suggesting that *P. p. turneri* should be synonymised with *P. p. phalerata*.

Sericocampsomeris Betrem, 1941

Campsomeris subgenus *Sericocampsomeris* Betrem, 1941: 91. *Sericocampsomeris* Betrem: Betrem and Bradley 1972: 12.

Type species. Scolia stygia Illiger, 1802.

Sericocampsomeris flavomaculata Gupta & Jonathan, 1989

Fig. 6A, B

Sericocampsomeris flavomaculata Gupta and Jonathan, 1989: 53.

Specimens examined. VIETNAM: Ha Noi: 3 33, Lien Mac, Bac Tu Liem, 27.viii.2017, 4.ix.2017; 3 33, Red

River Bank, Long Bien, 13.ix.2015, 13.xi.2015; Coll. Phong Huy Pham.

Diagnosis. Male. Body length 17-21 mm. Clypeus broadly impunctate medially, with coarse, dense punctures laterally and posteriorly; frontal spatium with small, contiguous punctures; mesosoma moderately densely and shallowly punctate; clypeus black; scapula, tiny spots on posterolateral corners of mesoscutum, apical bands on T1-T5 and S2-S4, spots on S2 and S3 anterolaterally and small spots on S5 and S6 posterolaterally yellow; apical yellow bands on T1-T3 broad, covering more than one-half of their length, that on T1, broadly interrupted medially, those on T2 and T3, deeply and broadly emarginate, those on T4 and T5, covering less than one-half of their length and narrowly emarginate medially (Fig. 6A); yellow bands on S2-S5 narrowly interrupted medially; vestiture white, except black on T6 and T7; tomentum on head and mesosoma silvery; wings yellowish, forewing slightly infumated apically; base of volsella with dense and long setae; outer margin of paramere with dense and long setae medially; inter margin with sparse and short setae medially (Fig. 6B).

Female. Unknown.

Distribution. Vietnam (new record): Ha Noi (Fig. 8G). Elsewhere: China (Hong Kong), India, Nepal (Gupta and Jonathan 1989, 2003; Taylor and Barthélémy 2021; Chen et al. 2022).

Sericocampsomeris rubromaculata rubromaculata (F. Smith, 1855)

Fig. 6C, D

Scolia rubromaculata F. Smith, 1855: 99.

Elis (Campsomeris) bicolor de Saussure, 1858: 233.

Elis (Dielis) rubromaculata (F. Smith): de Saussure and Sichel 1864: 196.

Elis (Dielis) bicolor de Saussure: de Saussure and Sichel 1864: 186.

- Scolia bicolor (de Saussure): Dalla Torre 1897: 148.
- Scolia (Elis) rubromaculata F. Smith: Tullgren 1904: 468.
- Campsomeris (Dielis) rubromaculata rubromaculata (F. Smith): Betrem 1928: 119.

Campsomeris (Dielis) bicolor (de Saussure): Betrem 1928: 121.

Campsomeris rubromaculata (F. Smith): Betrem 1932: 415.

Campsomeris (Sericocampsomeris) rubromaculata rubromaculata (F. Smith): Betrem 1941: 95.

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Figure 6. Sericocampsomeris flavomaculata Gupta & Jonathan, 1989 and Sericocampsomeris rubromaculata rubromaculata (Smith, 1855). A, B. S. flavomaculata, male; C, D. S. rubromaculata rubromaculata, female (A, D. Habitus, dorsal view; B. Genitalia, ventral view; C. Head, frontal view).

Sericocampsomeris rubromaculata rubromaculata (F. Smith): Betrem in Betrem and Bradley 1972: 12.

Specimens examined. VIETNAM: Ha Noi: $2 \ \bigcirc \ \bigcirc$, Lien Mac, Bac Tu Liem, 27.viii.2017; $1 \ \bigcirc$, My Dinh, Nam Tu Liem, 16.x.2015, Coll. Phong Huy Pham. Thai Binh: $2 \ \bigcirc \ \bigcirc$, Dong Hoang, Tien Hai, 2.viii.2018; $3 \ \bigcirc \ \bigcirc$, Hong Minh, Hung Ha, 20–25.vi.2013, 25.x.2019, Coll. Phong Huy Pham. Nam Dinh: $1 \ \bigcirc$, Xuan Thuy National Park, Xuan Thuy 23.v.2016, Coll. Phong Huy Pham. Vinh Phuc: $1 \ \bigcirc$, Ngoc Thach, Me Linh, 31.v.2019, Coll. Phong Huy Pham. Lang Son: $1 \ \bigcirc$, Lang Son city, 23.iv.2022, Coll. Phong Huy Pham.

Diagnosis. Female. Body length 30–33 mm. Lateral carina of propodeum extending beyond spiracle; dorso-median area of propodeum not triangularly protruded posteriorly, posterior surface of propodeum with dense punctures; vertex behind posterior ocelli with dense punctures (Fig. 6C); mesopleural crest sharp; mandible usually with red-brown spots; T2 and T3 with a pair of yellow spots posterolaterally, T2 and T3 reddish-brown anteriorly, T5 yellow, T4 almost entirely yellow, S3–S6 reddish-brown; erect vestiture black, except whitish on scrobe and frons; occiput and gena with blackish-grey setae; apical fringes and setae on T3–T5 and S3–S5 reddish-golden; T6 with reddish-golden setae; wings dark brown, with violet reflections (Fig. 6D).

Male. Unknown.

Distribution. Vietnam: Ha Noi, Lang Son, Nam Dinh, Thai Binh, Vinh Phuc (Fig. 8H). Elsewhere: China, Indonesia, Malaysia, Myanmar (Betrem 1928; Gupta and Jonathan 2003; Liu et al. 2021a; Chen et al. 2022).

Sericocampsomeris vietnamica Pham & van Achterberg, sp. nov.

https://zoobank.org/CCA7D1C8-1B23-41C1-8E72-CA2169C7661F Fig. 7A-F

Specimens examined. *Holotype.* ♂, VIETNAM: Hai Phong, Cat Ba National Park, Cat Hai district, 20°47'50"N, 107°4'15"E, 7 m alt., 17.ii.2016, Coll. Phong Huy Pham (IEBR). *Paratype.* 1♂, same place, date and collector as holotype (IEBR).

Diagnosis. Sericocampsomeris vietnamica belongs to the genus Sericocampsomeris because of the following combination of characters: Body length 21–24.5 mm; frontal spatium densely punctate; frontal fissura present, extending up to anterior ocellus; anterior ocellus distinctly larger than posterior ocelli and set in a broad and shallow pit; wings yellowish and hyaline, forewing with two recurrent veins; integument black; clypeus marked with yellow; mandible, scapula, scutellum and metanotum entirely black; hind tibial spur black; metasoma with yellow bands on apical tergites and sternites; vestiture yellowish-white



Figure 7. *Sericocampsomeris vietnamica* Pham & van Achterberg, sp. nov., holotype, male. A. Head, frontal view; B. Mesosoma, dorsal view; C. Metasoma, dorsal view; D. Metasoma, ventral view; E. Habitus, dorsal view; F. Genitalia, ventral view.

mixed with black; paramere slender, outer margin moderately angled medially, rounded apically, inner margin substraight, dorsal surface with dense and long setae, ventral surface with sparse and short setae; volsella with setae, moderately dense basally and sparse ventrally (for diagnosis of male *Sericocampsomeris*, see Betrem (1941) (page 92), Betrem and Bradley (1972) (page 12), Gupta and Jonathan (2003) (page 58), Liu et al. (2021b) (pages 146 and 159) and Taylor and Barthélémy (2021) (pages 20 and 42)).

This new species is similar to S. flavomaculata and S. stygia by having clypeus impunctate medially, with dense punctures posteriorly; frontal spatium densely and distinctly punctate; frontal fissure present, extending to anterior ocellus; anterior ocellus distinctly larger than posterior ocelli and set in a broad and shallow pit; scutellum and metanotum without longitudinal carina medially; dorso-median area of propodeum without distinct tubercle medially; T1-T3 with yellow bands apically. The new species is easily distinguished from S. flavomaculata and S. stygia by the following characters: head, scape, mesoscutum, scutellum and metanotum densely, coarsely, deeply punctate; clypeus sparsely punctate laterally and anteriorly; anterior margin of clypeus dark yellow; scapulae, scutellum and metanotum entirely black; T4 without yellow band apically; apical yellow bands on S2 and S3 narrow, broadly interrupted medially; head and mesosoma with yellowish setae; wings yellowish; metasoma with conspicuous blue reflections.

Description. Male. Body length 21–24.5 mm (holotype: 22.5 mm); forewing length 20–21 mm (holotype: 20 mm).

Colour. Black, except yellow on anterior margin of clypeus; tegula testaceous (Fig. 7A, B); T1–T3 with yellow bands apically, that on T1, very narrow and broadly interrupted medially, covering about one-sixth of T1, that on T2, narrowly emarginate medially, covering less than one-half of T2, that on T3, covering about one-fourth of T3 (Fig. 7E); apical yellow bands on S2 and S3 narrow, broadly interrupted medially; metasoma with conspicuous blue reflections (Fig. 7C).

Vestiture. Yellowish-white, except black on two last metasomal segments (Fig. 7D), T5 with yellowish-white setae mixed black setae; tomentum silvery (Fig. 7C). Wings hyaline, yellowish, forewing slightly infumated subapically, with two recurrent veins (Fig. 7E).

Head. Clypeus rugose on apical half, impunctate medially, sparsely punctate laterally and anteriorly, densely punctate posteriorly (Fig. 7A); frontal spatium densely and distinctly punctate, with small tubercle between antennal sockets (Fig. 7A); frontal fissura weakly impressed, extending to anterior ocellus; front with a few scattered punctures; vertex with weak groove near hind ocelli elongated to inner eye margin; scape, vertex and gena with dense punctures; anterior ocellus distinctly larger than posterior ocelli and set in a broad and shallow pit.

Mesosoma. Scapula, mesoscutum, metanotum and dorsal propodeum with dense, coarse, deep punctures, interspaces much smaller than puncture diameter; scute-llum with punctures separated by about their diameter (Fig. 7B); scutellum and metanotum moderately convex, without longitudinal carina medially; mesopleuron and metapleuron densely punctate; lateral carina of propodeum distinctly prominent and long, extending beyond spiracle; dorso-median area of propodeum without being distinctly tuberculate medially.

Metasoma. Metasoma moderately densely and coarsely punctate (Fig. 7C, E); two-thirds of S1 densely and coarsely punctate anteriorly; median tubercle on S2 moderately risen anteriorly; S7 with longitudinal carina medially (Fig. 7D).

Genitalia (Fig. 7F). Brown; paramere glabrous, dorsal surface with dense and long setae, ventral surface with sparse and short setae, outer margin with a few short setae, moderately-angled medially, rounded apically, inner margin sub-straight; base of volsella covered with moderately dense and long setae, with dense punctures; lamina volsellaris sparsely punctate, interspaces larger than puncture diameter, with sparse and short setae ventrally



Figure 8. Distribution of the Scoliid species from northern Vietnam. A. Campsomeriella (Annulimeris) annulata annulata (Fabricius, 1793);
B. Campsomeriella (Campsomeriella) collaris collaris (Fabricius, 1775);
C. Campsomeriella (Campsomeriella) collaris quadrifasciata (Fabricius, 1798);
D. Megacampsomeris shillongensis (Betrem, 1928);
E. Micromeriella marginella marginella (Klug, 1810);
F. Phalerimeris phalerata phalerata (de Saussure, 1858);
G. Sericocampsomeris flavomaculata Gupta and Jonathan, 1989;
H. Sericocampsomeris rubromaculata rubromaculata (Smith, 1855);
I. Sericocampsomeris vietnamica Pham & van Achterberg, sp. nov.

(Fig. 7F); aedeagus with eight teeth, apical teeth conspicuously reduced. Female. Unknown. **Etymology.** The species name refers to the country of origin, Vietnam.

Distribution. Vietnam: Hai Phong Province (Fig. 8I).

Identification key to species of Sericocampsomeris Betrem

Key to females (females of *S. flavomaculata* Gupta & Jonathan, 1989, *S. punctata* Liu & Chen, 2022, and *S. vietnamica* Pham & van Achterberg, sp. nov. are not known).

- 1 Metanotum and dorso-median area of propodeum sparsely punctate; T2 and T3 reddish-brown anteriorly; T2 and T3 with large yellow spots laterally; apical fringes on T2–T5 and S3–S6 reddish-golden; metasomal setae back and reddish-gold; (China, India, Indonesia, Malaysia, Myanmar, Vietnam)......S. *rubromaculata* (F. Smith, 1855)
- 2 Scapula and upper margin of clypeus with golden setae; metasoma with dark brown setae, except T6 with reddish-brown setae; T3 with large yellow mark covering almost its dorsum; (China, Vietnam) S. degaullei (Betrem, 1928)
- Scapula, clypeus and metasoma with black setae; metasoma black, except small yellow spots on T2 and T3 laterally; (Bangladesh, Bhutan, India, Indonesia, Malaysia, Myanmar).....S. stygia (Illiger, 1802)

Key to males

1	T1–T3 with yellow bands apically	2
-	T1-T3 without yellow bands apically; T3 reddish-yellow partly or predominantly	5

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2	Head and mesosoma densely, coarsely and deeply punctate; T4 without apical yellow band; apical yellow band on T1 very narrow, about one-fifth × length of T1 and broadly interrupted medially; setae on head and mesosoma yellowish; (Vietnam)
-	Head and mesosoma sparsely to densely punctate; T4 with apical yellow band, apical yellow band on T1 absent or present, in latter case, that is large, at least one-third of length of T1; colour of setae on head and mesosoma variable
3	Clypeus and legs with yellow spots; scutellum and metanotum with broad yellow bands medially; band on T1 not emar- ginate and uninterrupted, band on T2 shallowly emarginate, band on T3 not emarginate
-	Clypeus and legs without yellow spots; scutellum and metanotum entirely black; band on T1 emarginate or interrupted, bands on T2 and T3 deeply emarginate
4	Clypeus without yellow band apically; scapula yellow; T1 with broad yellow band interrupted medially, bands on T2 and T3 very broad and deeply emarginate medially; T5 with yellow band apically; (China (Hong Kong), India, Nepal, Vietnam)S. flavomaculata Gupta & Jonathan, 1989
-	Clypeus with yellow band apically; scapula black; T1 with yellow band uninterrupted medially, bands on T2 and T3 moderately broad and narrowly emarginate medially, T5 without yellow band apically; (China)
5	Scutellum and metanotum with longitudinal carina medially; T1 and T2 entirely black; wings infuscate; metasomal setae dark brown, except reddish brown on T4–T7
-	Scutellum and metanotum without longitudinal carina medially; T1 and T2 almost reddish-yellow; wings yellowish to brownish; metasomal setae pale yellow, except black on T5–T7S. rubromaculata (F. Smith, 1855)

The genus Sericocampsomeris Betrem was described as a subgenus of Campsomeris and raised to generic level by Betrem and Bradley (1972). Betrem (1941) recorded 10 species for the genus (as Campsomeris (Sericocampsomeris)). Gupta and Jonathan (1989) recorded eight species and described one new species, S. flavomaculata Gupta and Jonathan. Osten (2005) listed S. degaullei Betrem, 1928 (with two subspecies, S. degaullei degaullei Betrem, 1928 and S. d. rubropilosa Betrem, 1941); S. rubromaculata (F. Smith, 1855) (with five subspecies, S. rubromaculata rubromaculata (F. Smith, 1855); S. r. beharensis (Betrem, 1928); S. r. bomeana (Cameron, 1902); S. r. hainanensis (Betrem, 1928); and S. r. pseudoindica (Betrem, 1928)) and S. stygia (Illiger, 1802) and omitted S. flavomaculata Gupta and Jonathan (also see Taylor and Barthélémy (2021)). Gupta and Jonathan (2003), after reexamining Megacampsomeris bella that was originally described by Bingham (1897) as *Elis* (*Dielis*) bella, moved it to Sericocampsomeris. Osten (2005) retained it in Megacampsomeris. Schulten et al. (2011) raised the subgenus Bellimeris of Megacampsomeris to the generic level and included M. bella. Kim (2020) produced characteristics of the genus Bellimeris, which consists of only B. bella and B. stoetzneri after studying and describing the male of the latter. Liu et al. (2021b) listed B. bella as Megacampsomeris bella. Recently, Chen et al. (2022) reviewed the genus Sericocampsomeris from China, recognised three species and described a new species. Altogether, including the new species described in this study, six species have been retained in Sericocampsomeris. The genus is mainly distributed in the Oriental region and ranges from Sri Lanka, India and Nepal to Southeast Asia and southern China. Four Vietnamese species have been recorded, three, S. vietnamica Pham & van Achterberg, sp. nov., S. flavomaculata and S. rubromaculata in the present study and one, S. degaullei in Betrem (1928).

A checklist of Scoliidae from Vietnam

Family Scoliidae Latreille, 1802 Subfamily Scoliinae Latreille, 1802

Campsomerini Betrem, 1965

Campsomeriella Betrem, 1941

Campsomeris - subgenus *Campsomeriella* Betrem, 1941: 86. *Campsomeriella* Betrem, 1967: 25.

Type species. Scolia thoracica Fabricius, 1787.

Campsomeriella collaris quadrifasciata (Fabricius, 1798)

Scolia quadrifasciata Fabricius, 1798: 231.

Campsomeris aureicollis Lepeletier, 1845: 132.

- Campsomeris quadrifasciata Fabricius: Betrem 1928: 336.
- Campsomeris (Campsomeriella) quadrifasciata Fabricius: Betrem 1941: 89.
- Campsomeriella (Campsomeriella) collaris quadrifasciata Fabricius: Betrem 1967: 29.

Distribution. China, India, Indonesia, Laos, Malaysia, Philippines, Singapore, Thailand, Vietnam: Ha Noi, Quang Ninh(?), Quang Tri, southern Vietnam (Betrem 1928).

Betrem (1928) recorded this subspecies from Vietnam as *Campsomeris aureicollis* Lepeletier, 1845, but Osten (2005) synonymised it under *Campsomeriella collaris quadrifasciata* (Fabricius, 1798). Specimens are known from Tien Yen (possibly Tien Yen District, Quang Ninh Province), Tonkin, Hanoi (both males and females), Cochin-china: Annam (currently central Vietnam, Kuang-Tri (possibly Quang Tri Province currently) (Betrem 1928).

Campsomeriella sauteri berlandi (Betrem, 1928)

Campsomeris sauteri berlandi Betrem, 1928: 123.

- *Campsomeris (Campsomeriella) sauteri* Betrem: Betrem 1941: 88.
- *Campsomeriella* (*Campsomeriella*) quadrifasciata sauteri Betrem: Betrem 1967: 29.

Distribution. Vietnam: Cochin-China (currently southern Vietnam) (Betrem 1928).

Colpacampsomeris Betrem, 1941

Campsomeris subgenus Colpacampsomeris Betrem, 1941: 101.

Colpacampsomeris Betrem: Betrem in Bradley 1974: 445.

Type species. Scolia indica de Saussure, 1855.

Colpacampsomeris indica (de Saussure, 1855)

Scolia (Lacosi) indica de Saussure, 1855: 46.

- Scolia ignita Smith, 1855: 101.
- Scolia (Discolia) indica de Saussure: de Saussure and Sichel 1864: 119.
- Scolia indica de Saussure: Dalla Torre 1897: 165.
- *Campsomeris* (*Dielis*) *indica* (de Saussure): Betrem 1928: 116.
- Campsomeris (Dielis) assamensis Betrem, 1928: 111
- *Campsomeris (Colpacampsomeris) indica* (de Saussure): Betrem 1941: 101.
- Capmsomeris (Colpacampsomeris) indica assamensis Betrem: Betrem 1941: 102.
- *Campsomeris* (*Colpacampsomeris*) *indica indica* (de Saussure): Betrem in Bradley and Betrem 1967: 308.
- *Colpacampsomeris indica indica* (de Saussure): Betrem in Bradley 1974: 445.

Distribution. Bangladesh, India, Myanmar, Malaysia, Sri Lanka, Vietnam: Cochin China (southern Vietnam) (Betrem 1941; Bradley and Betrem 1967; Gupta and Jonathan 2003).

Sericocampsomeris Betrem, 1941

- Campsomeris subgenus Sericocampsomeris Betrem, 1941: 91.
- Sericocampsomeris Betrem: Betrem and Bradley 1972: 12.

Type species. Scolia stygia Illiger, 1802.

Sericocampsomeris degaullei (Betrem, 1928)

Campsomeris degaullei Betrem, 1928: 121.

Campsomeris (*Sericocampsomeris*) *degaullei* Betrem: Betrem 1941: 93.

Distribution. China, Vietnam: Tonkin (currently northern Vietnam): Ha Noi, Tuyen Quang (Betrem 1928; Liu et al. 2021a; Chen et al. 2022).

Betrem (1928) described this subspecies, based on females collected from northern Vietnam (Ha Noi and Tuyen Quang).

Sericocampsomeris rubromaculata (Smith, 1855)

Scolia rubromaculata Smith, 1855: 99.

Elis (Campsomeris) bicolor de Saussure, 1858: 233.

- *Elis (Dielis) rubromaculata* (Smith): de Saussure and Sichel 1864: 196.
- *Elis (Dielis) bicolor* de Saussure: de Saussure and Sichel 1864: 186.
- Scolia bicolor (de Saussure): de Saussure 1897: 148.

Scolia (Elis) rubromaculata Smith: Tullgren 1904: 468.

Campsomeris rubromaculata (Smith): Betrem 1928: 119.

- Campsomeris (Dielis) bicolor (de Saussure): Betrem 1928: 121.
- Campsomeris (Sericocampsomeris) rubromaculata rubromaculata (Smith): Betrem 1941: 95.
- Sericocampsomeris rubromaculata rubromaculata (Smith): Betrem in Betrem and Bradley 1972: 12.

Distribution. China, India, Indonesia, Malaysia, Myanmar, Vietnam: Ha Noi (Betrem 1928; Gupta and Jonathan 2003; Liu et al. 2021a; Chen et al. 2022).

Scoliini Latreille, 1802

Austroscolia Betrem, 1927

Scolia (Austroscolia) Betrem, 1927: xcviii.

Type species. Scolia ruficeps Smith, 1855.

Austroscolia ruficeps (Smith, 1855)

Scolia capitata Guérin-Méneville, 1838: 248 (not Fabricius, 1804).

Scolia ruficeps Smith, 1855: 111.

Scolia westermanni de Saussure, 1858: 212.

Triscolia nigropilosa Micha, 1927: 100.

Triscolia tenggerana Micha, 1927: 100.

Triscolia viridiaenea Micha, 1927: 100.

- Triscolia ruficeps impressifrons Micha, 1927: 100.
- Scolia (Triscolia) capitata Guérin-Méneville: de Saussure and Sichel 1864: 47.

Triscolia ruficeps (Smith): Micha 1927: 96.

- Scolia (Austroscolia) ruficeps Smith: Betrem 1927: xcviii.
- Austroscolia ruficeps Smith: Bradley and Betrem 1967: 319.

Distribution: China, India, Indonesia, Malaysia, Myanmar, Philippines, Vietnam: Indochine: Sai Gon (currently Ho Chi Minh City) (Betrem 1941; Taylor and Barthélémy 2021).

Carinoscolia Betrem, 1927

Scolia - subgenus Carinoscolia Betrem, 1927: xcvii. Carinoscolia Betrem: Bradley and Betrem 1967: 293.

Type species. Scolia opalina Smith, 1858.

Carinoscolia yunnanensis (Betrem, 1941)

Scolia (Carinoscolia) junnanensis Betrem, 1928: 188. Scolia (Carinoscolia) yunnanensis Betrem: Betrem 1941: 116.

Distribution. China, Japan, Laos, Vietnam: Annam (currently central Vietnam) (Betrem 1928; Taylor and Barthélémy 2021; Liu et al. 2021a)

Megascolia Betrem, 1964

- Scolia subgenus Triscolia de Saussure and Sichel: Betrem 1927: xcvii.
- Scolia subgenus Triscolia (section Triscolia) de Saussure and Sichel: Betrem 1928: 228.
- Scolia subgenus Triscolia (section Megascolia Betrem), Betrem, 1928: 239.

Megascolia Betrem: Betrem and Bradley 1964: 437.

Type species. Scolia procer Illiger, 1802.

Megascolia (Regiscolia) azurea azurea (Christ, 1791)

Scolia azurea Christ, 1791: 256.

- Scolia rubiginosa Fabricius, 1793: 230.
- Scolia ornata Lepeletier, 1845: 517.
- Scolia magnifica de Saussure, 1859: 175.
- Scolia (Triscolia) rubiginosa Fabricius: Bingham 1897: 76–77.
- Triscolia azurea azurea Christ: Micha 1927: 117.
- Scolia (Triscolia) azurea rubiginosa Fabricius: Betrem 1928: 231.
- Scolia (Triscolia) azurea christiana Betrem & Guiglia, 1958: 96.
- Megascolia (Regiscolia) azurea christiana Betrem & Guiglia: Betrem and Bradley 1964: 444.

Distribution. Bangladesh, Bhutan, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand, Vietnam: Tonkin (currently northern Vietnam): Thuong Lam (possibly being a location in Ha Noi currently), Annam (currently central Vietnam): An-Ninh nahe Quang-Tri (Quang Tri Province), Cochin-China (currently southern Vietnam): Nha Trang (currently belonging to Khanh Hoa Province) (Betrem 1928; Gupta and Jonathan 2003; Taylor and Barthélémy 2021; Liu et al. 2021a).

Betrem (1928) recorded this subspecies under *Scolia* azurea rubiginosa Fabricius, 1793.

Megascolia (Regiscolia) azurea cochinensis (Betrem, 1928)

Scolia azurea cochinensis Betrem, 1928: 232.

Megascolia (Regiscolia) azurea cochinensis Betrem: Betrem and Bradley 1964: 444.

Distribution. Vietnam: Cochin-China (currently southern Vietnam) (Betrem 1928; Gupta and Jonathan 2003).

Scolia Fabricius, 1775

Scolia Fabricius, 1775: 355.

Scolia - subgenus Lacosi Guérin-Méneville, 1839: 243.

Lisoca Costa, 1858: 8. *Scolia* - subgenus *Discolia* de Saussure: de Saussure and Sichel 1864: 55.

Scolia - subgenus *Scolia* Fabricius: Betrem 1927: xcviii. *Scolia* Fabricius: Betrem and Bradley 1964: 89.

Type species. Scolia quadripustulata Fabricius, 1775.

Scolia (Discolia) binotata Fabricius, 1804

Scolia binotata Fabricius, 1804: 244. Scolia sexpustulata Klug, 1805: 243. Scolia quadripustulata humeralis de Saussure, 1864: 321. Scolia barmanica Magretti, 1892: 242. Scolia burmanica Dalla Torre, 1897: 150. Scolia cucullata Bingham, 1897: 82. Scolia humeralis Bingham, 1897: 81. Scolia quadripustulata formosensis Betrem, 1928: 150. Scolia quadripustulata kancisarensis Betrem, 1928: 318.

Distribution. Bhutan, China, India, Japan, Laos, Malaysia, Myanmar, Singapore, Sri Lanka, Vietnam: Tonkin: Than-Moi (possibly Lang Son Province currently), Cochin-China: Kompong (possibly a location in Khanh Hoa Province currently) (Betrem 1928; Taylor and Barthélémy 2021; Liu et al. 2021a).

Betrem (1928) recorded this species from Vietnam under the subspecies *Scolia* 4-*pustulata barmanica* Magretti, 1892 and *Scolia* 4-*pustulata humeralis* de Saussure, 1864.

Scolia (Discolia) decorata desidiosa Bingham, 1896

Scolia desidiosa Bingham, 1896: 424.

Scolia (Scolia) decorata desidiosa Bingham: Betrem 1928: 321.

Scolia (Scolia) histrionica histrionica Betrem, 1941: 63. *Scolia (Discolia) desidiosa*, Bingham: Betrem 1947: 86.

Distribution. Bhutan, China, India, Myanmar, Taiwan, Vietnam: Tonkin (currently northern Vietnam) (Betrem 1928; Danilov and Dubatolov 2021).

Danilov and Dubatolov (2021) listed this subspecies under *Scolia* (*Discolia*) *histrionica* (Fabricius, 1787) from Vietnam, Mongolia and Thailand, based on specimens deposited in the collection of the Siberian Zoological Museum, Russia.

Scolia (Discolia) superciliaris sauteri Betrem, 1928

Scolia (Discolia) sauteri Betrem, 1928: 277. Scolia superciliaris sauteri Betrem: Betrem 1941: 137.

Distribution. China, Taiwan, Vietnam: Cochin-China (currently southern Vietnam), Tonkin (currently northern Vietnam) (Betrem 1928).

Scolia (Discolia) superciliaris staudingeri Betrem, 1928

Scolia (Scolia) sauteri staudingeri Betrem, 1928: 278.

- Scolia (Scolia) superciliaris staudingeri Betrem: Betrem 1941: 135.
- *Scolia* (*Discolia*) *superciliaris staudingeri* Betrem: Betrem and Bradley 1964: 92.

Distribution. China, India, Myanmar, Nepal, Taiwan, Vietnam: Annam (currently central Vietnam) (Betrem 1928; Gupta and Jonathan 2003).

Betrem (1928) described this subspecies, based only on males collected from central Vietnam.

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<u>PENSOFT</u>.



Two new species of *Deuterophlebia* Edwards, 1922 from Southwestern China (Diptera, Deuterophlebiidae)

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Abstract

The family Deuterophlebiidae is considered the most plesiomorphic Diptera family, with striking morphology and life history. In this study, we provide detailed descriptions and figures of two new species from Southwestern China: *Deuterophlebia pseudopoda* **sp. nov.** and *Deuterophlebia pachychaeta* **sp. nov.**, along with genetic distances of COI sequences between the seven known Chinese species of *Deuterophlebia* Edwards, 1922. The two new species can be identified by the adults' male terminalia, head structures, male and female antennae and mesothoracic spines or abdominal projections of the pupae. As a result, China is currently the country with the highest *Deuterophlebia* species diversity.

Key Words

aquatic insects, barcoding, COI, genetic identification, mountain midge

Introduction

Deuterophlebiidae (or mountain midge) is a monotypic family in the order Diptera. Members of this family show unique morphology and living habits. In contrast to other dipteran groups, the larvae of *Deuterophlebia* Edwards, 1922 have paired pseudopodia and live in torrent streams; adults mate at sunrise, male adults die immediately after mating, while females shed their wings, go back to the water and lay eggs (Courtney 1989; Zheng et al. 2022). This kind of specialized taxon and its living history has attracted more and more attention and studies in recent years.

The biogeographic and phylogenetic status of the family is still enigmatic (Courtney 1994; Zheng et al. 2022). In the latest phylogenetic topology based on mitochondrial sequences, Deuterophlebiidae was considered the earliest branching lineage of Diptera, a sister group of all other dipterans (Zhang et al. 2022). This result differs from previous inferences, which usually consider Blephariceridae and Deuterophlebiidae as sister groups (Courtney 1991). Obviously, many questions are still waiting for answers in the systematic study of this family. Up to 2022, there were 14 named species in this family, eight species reported from the Palearctic Region (Kitakami 1938; Jedlička and Halgoš 1981; Courtney 1994; Sofi et al. 2020) and six from the Nearctic realm (Pennak 1945, 1951; Shewell 1954; Kennedy 1958, 1960; Courtney 1989, 1990). China was a blank area in the distribution maps (Courtney 1994). In 2022, five species were reported from Southwestern and Eastern China, bringing some new insights into the diversity and biogeography of Deuterophlebiidae (Zheng et al. 2022). Encouraged by that, extensive investigations were carried out, and it was hypothesized that China is possibly the center of the diversity of Deuterophlebiidae. More studies on these Chinese species can provide more information on their evolution and dispersal.

During a trip in Yunnan Province of southwestern China, some *Deuterophlebia* adults and pupae were collected. After careful examination, they were recognized as two new species. We presented detailed images of their adults and pupae, described them in detail and compare them with the known species using COI and morphological characters, including some that have not been mentioned before.

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Materials and methods

Pupae were hand-picked from the surface of stones underwater. Adults were found floating nearby the banks of creeks. Specimens were examined under a stereomicroscope (Nikon SMZ 745T). Habitus of pupae and adults were photographed using a SONY a7R II camera with a LAOWA 25 mm 5× macro lens. Details of heads and legs were studied by dissection and treatment in 10% NaOH (30 °C, 30 min), observed and photographed with a camera (Nikon 50i) coupled on a microscope. Terminology mainly follows that of Courtney (1994). All specimens were preserved in 85% ethanol and deposited in the Diptera collection of College of Life Sciences, Nanjing Normal University and School of Grain Science and Technology, Jiangsu University of Science and Technology.

To associate the pupae and winged stages, total genomic DNA was extracted from the abdomen of specimens using Animal Genomic DNA Kit (TsingKe Biotech Co., Beijing, China). The mitochondrial gene cytochrome coxidase subunit I fragment was PCR-amplified using the Premix Taq (Takara Bio Inc., Beijing, China) with forward primer LCO1490 (5'-GGTCAACAAATCATAAAGA-TATTGG-3') and reverse primer HCO2198 (5'-TA-AACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994). PCR conditions included initial denaturation at 94 °C for 5 min, 40 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 40 s, with a final extension at 72 °C for 10 min (Zheng et al. 2022). Sequences were aligned using Muscle, and the K2P genetic distances were estimated in MEGA11 (Tamura et al. 2021). The intraspecific genetic distances were lower than 0.01. The sequence of each species has been uploaded to GenBank (Table 1) with the same specimen information as for the holotype of each species.

 Table 1. GenBank accession numbers of COI sequences used in this research.

Species	GenBank Accession Number
D. sinensis Zheng et al., 2022	ON637906
D. yunnanensis Zheng et al., 2022	ON637909
D. alata Zheng et al., 2022	ON637916
D. acutirhina Zheng et al., 2022	ON637914
D. wuyiensis Zheng et al., 2022	ON637910
D. pseudopoda sp. nov.	OR064529 (this study)
D. pachychaeta sp. nov.	OR064528 (this study)

Results

Deuterophlebia pseudopoda sp. nov.

https://zoobank.org/E1B5D9F5-9797-4350-815F-197CEBE47826

Description. Male adults. Body length ca. 2.2-2.6 mm (n=5), uniformly brownish black (Fig. 1). Head brownish black, flattened, nearly trapezoidal, width ca. 0.50 mm, folded backward under thorax, hidden in dorsal view (Fig. 1). Head densely covered with microtrichia. Median



Figure 1. Male adult of D. pseudopoda sp. nov. Scale bar: 1.0 mm.

clypeal lobe slightly convex, semicircle shaped, with around 20 sharp setae (Fig. 2A). Mouthparts in form of an invaginated tubule, oral region depressed (Fig. 2A, B). Edges of oral region (or mouth opening) ridged, convex medially on ventral ridge, forming a blunt mental tooth (Fig. 2A, B). Postgena and oral region with sparser microtrichia than other regions, a pair of tentorial pits present on each side of oral region (Fig. 2A, B). Compound eyes glabrous, width ca. 0.18 mm, distance between eyes ca. 0.30 mm (Fig. 2A).

Antennae 8.5–10.0 mm (n=5) (Fig. 2A, C). Scape oval shaped, pedicel globular, both covered with microtrichia (Fig. 2A, C). Flagella four segmented, flagellomeres I–III slender cylindrical, each with a subapical tubercle on front margin, bearing 9–12, 6–9 and 4–6 digitiform setae respectively (Fig. 2C). Flagellomere IV flattened and elongated, broader than flagellomeres I–III, narrowed gradually, with curved hair-like setae on the anterior side of basal half, apical half generally glabrous but bearing 4–5 clusters of curved hair-like setae, apex slightly expanded with some curved hair-like setae (Fig. 2C). Antennal ratio: 4.0: 2.0: 5.0: 3.0: 3.0: 238.0 (Figs 1, 2C). Flagellomere IV about 14× combined length of five basal antennal articles or about 4× body length (Fig. 1).

Thorax uniformly brownish black, densely covered with microtrichia (Fig. 1). Pronotum almost hidden, mesonotum strongly expanded (Fig. 1). Wings ca. 4.0 mm, uniformly set with dark micro-tubercles, grayish translucent, cubital area greatly enlarged, costal margin slightly thickened (Fig. 1). Outer margin fringed with soft hairlike setae, denser and longer on cubital margin (Fig. 1). Veins radially arranged, pale and inconspicuous (Fig. 1). Halteres transparent, ca. 0.35 mm (Fig. 1).

Legs brownish black, slender, sharing similar chaetotaxy with four types of setae: (1) microtrichia, densely covered on all segments; (2) sharp macrotrichia, sparsely on dorsal margin of femora and tibiae; (3) long capitate setae, ventrally on tarsomeres I–IV of each leg, distal half of ventral edge of all tibiae, surrounding the top of foreand midtibiae, and also densely arranged radially on each empodium; (4) digitiform setae, 1–3 pairs for each tarsomere (Fig. 2D–F). In all legs, coxae much broader than trochanters, coxae about twice the length of trochanters (Fig. 2D–F). In foreleg, femur: tibia: tarsus = 9.0: 14.0: 14.0; femur slightly flattened, tibia slender, cylindrical,



Figure 2. Male adult of *D. pseudopoda* sp. nov.: **A.** Head (ventral view); **B.** Oral region (ventral view); **C.** Flagellomeres; **D.** Foreleg; **E.** Midleg; **F.** hindleg; **G.** Terminalia (dorsal view). Abbreviations: cp, median clypeal lobe; pd, pedicel; fl, flagellomere; or, oral region; mt, mental tooth; pg, postgena; co, coxa; tr, trochanter; fe, femur; tb, tibia; ts, tarsomere; em, empodium; dp, dorsal plate; gc, gonocoxite; gs, gonostylus; ad, aedeagus. Scale bars: 0.1 mm (**A, C, G**); 0.05 mm (**B**); 0.5 mm (**D**–**F**).

and gradually broader apically; tarsomere I: II: III: IV: V = 6.4: 2.3: 1.4: 1.4: 1.0, tarsomeres I–IV cylindrical, tarsomere V conical; empodium shell-shaped, length subequal to tarsomere V; claw slender, tapered, shorter than empodium (Fig. 2D). Midleg shortest among all legs, similar to foreleg, femur: tibia: tarsus = 8.0: 10.5: 12.0, tarsomere I: II: III: IV: V = 6.0: 1.9: 1.1: 1.1: 1.0 (Fig. 2E). In hindleg, femur: tibia: tarsus of hindleg = 10.0: 13.5: 10.0, tarsomere I: II: III: IV: V = 3.5: 1.5: 1.2: 1.0 (Fig. 2F).

Abdomen brownish black, densely covered with microtrichia, nine segmented, tapering posteriorly (Fig. 1). First two segments strongly fused with each other, paler and shorter than others (Fig. 1). Segment VIII in form of a short chitin ring (Fig. 1). Sternite IX almost glabrous, fused with dorsal plate, connected with gonocoxite (Fig. 2G). Gonocoxite with posterior projection which length subequal to gonostylus (Fig. 2G). Gonostylus subequal to the dorsal plate in length, flattened, oval-shaped, flexor surface with numerous curved sharp setae (Fig. 2G). Dorsal plate parallel-sided, posterior margin slightly depressed without cleft with some stout curved setae on margin (Fig. 2G). Aedeagus in form of a smooth tube, length subequal to gonostylus and dorsal plate (Fig. 2G).

Female adult. Body length ca. 2.0 mm (n = 1). Besides sexual differences, generally similar to the males except following features (Fig. 3A–D).



Figure 3. Female adult of D. pseudopoda sp. nov.: A. Head (ventral view); B. Foreleg; C. Midleg; D. Hindleg. Scale bars: 0.1 mm.

Head width ca. 0.36 mm (Fig. 3A). Median clypeal lobe strongly protruded medially with ca. 20 setae (Fig. 3A). Oral region located near anterior margin of head (Fig. 3A). Compound eyes more prominent than males (Fig. 3A). Antenna ca. 0.3 mm. Scape slender oval shaped, pedicel globular, both scape and pedicel covered with microtrichia and bearing several sharp setae (Fig. 3A). Flagellomere I slender cylindrical, flagellomeres II–III slender oval shaped, flagellomere IV dripping shaped, strongly narrowed basally (Fig. 3A). Each of flagellomeres I–III bearing ca. 5 digitiform setae apically, flagellomere IV with 4 sharp setae. Antennal ratio ca. 7.0: 3.0: 10.0: 4.0: 5.0: 4.0 (Fig. 3A). Legs sharing similar chaetotaxy and exhibiting three types of setae, chaetotaxy similar to males but without capitate setae (Fig. 3B–D). In foreleg and midleg, femur: tibia: tarsus = 1.0: 2.0: 1.3, tarsomere I: II: III: IV: V = 1.0: 0.8: 0.8: 0.8: 2.4. (Fig. 3B, C) In hindleg, femur: tibia: tarsus = 1.0: 1.7: 1.1, tarsomere I: II: III: IV: V = 1.0: 0.9: 0.9: 0.9: 2.7 (Fig. 3D). Claws of all legs similar, paired, stout and curved, with a blunt protrusion in the middle (Fig. 3B–D). Empodium in form of a long and hairy spine, subequal to the length of claw (Fig. 3B–D).

Male pupae. Pupae flattened oval shaped, length 2.3 mm (n = 2), width 1.6 mm. Dorsal integument dark brown, divided into 11 segments (Fig. 4A, B).



Figure 4. Pupae of *D. pseudopoda* sp. nov.: **A.** Male pupa (dorsal view); **B.** Male pupa (ventral view); **C.** Female pupa (dorsal view); **D.** Female pupa (ventral view). Scale bars: 1.0 mm.



Figure 5. Pupa of *D. pseudopoda* sp. nov.: A. Thoracic spine (dorsal view); B. Gill (ventral view); C. Posterior end (ventral view). Abbreviation: pp, posterolateral projections. Scale bars: 0.1 mm.

Prothorax fused with mesothorax, forming a conical segment with a median suture (Fig. 4A, B). Mesothoracic lateral margins each with a sharp spine and a gill (Figs 4A, B, 5A, B). Spines ca. 0.4 mm, slightly curved, dark brown, originated from a round base (Fig. 5A, B). Ventral gills light to dark brown, length subequal to the dorsal spines, hand-shaped and consisting of three filaments: posterior filament shorter, pointing backward; anterior two filaments similar in shape, twisted and light in color apically (Fig. 5A, B). Metathorax completely surrounded by mesothorax and first abdominal segment (Fig. 4A, B). Abdominal segments I–II with a pair of anterolateral projections, each projection pointing forward and bearing ca. 13 spines (Fig. 4A, B). Segments VI-VII with a pair of posterolateral projections, projections foot-shaped and each bearing ca. 8 spines (Fig. 5C). Segment VIII shieldshaped, surrounded by segments VII and IX (Fig. 4A, B).

Adult structures visible on ventral side (Fig. 4A, B). Head present directly below mesothorax; antennal sheaths in form of a large elliptic ring, surrounding body 2.0 times (Fig. 4A, B). Leg sacs extended to posterior end of antennal ring, strongly expanded apically.

Abdominal segments III–V with a pair of black adhesive discs (Fig. 4A, B).

Female pupae. Length ca. 2.2 mm (n = 2), width ca. 1.5 mm (Fig. 4C, D). Dorsal morphology similar to male except for smaller mesothorax (Fig. 4C, D). Gender can be identified through the absence of antennal ring, apex of female leg sheaths not expanded (Fig. 4C, D).

Material examined. *Holotype:* male adult, China: Yunnan Province, Gongshan County, Dulongjiang Township, Dulongjiang River, 27°50'14.16"N, 98°19'54.2"E, 1470 m a.s.l., 4.II.2023, Xuhongyi Zheng leg. *Paratypes:* 6 male adults, 1 female adult, 2 male pupae, 2 female pupae, same locality and data as holotype.

Diagnosis. Male adults of *Deuterophlebia pseudopoda* sp. nov. can be identified by their terminalia: gonostylus short, length of gonostylus subequal to the gonocoxite and dorsal plate; posterior margin of dorsal plate slightly depressed but without a median cleft (Fig. 2G). Such a terminalia differs from the 19 named *Deuterophlebia* species (Courtney 1990, 1994; Zheng et al. 2022). The shape of their heads is also distinct among known species: median clypeal lobe slightly convex, inner side of compound eye without a protruded corner (Fig. 2A) (Courtney 1990, 1994; Zheng et al. 2022).

Female adults of *D. pseudopoda* sp. nov. can be recognized through a combination of the pronounced median clypeal lobe, chaetotaxy of antennae, and shape of flagella (Fig. 3A). Compared to other species, its pronounced median clypeal lobe is similar to *D. oporina* Courtney, 1994 and *D. nipponica* Kitakami, 1938, but can be differentiated from them by its antenna: flagellomeres I–III bearing ca. 5 digitiform setae respectively, flagellomere IV with only 4 sharp setae, antennal ratio = 7.0: 3.0: 10.0: 4.0: 5.0: 4.0 (Courtney 1990, 1994; Zheng et al. 2022).

Pupae can be easily identified by their foot-shaped posterolateral projections of abdominal segments VI– VII (Fig. 5C). This feature is absent in the 15 species with clear pupal stage (Courtney 1990, 1994; Zheng et al. 2022). They can also be separated from other species by their single mesothoracic spines, gills consisting of three filaments, and absence of conspicuous thoracic ridges (Figs 4A–D, 5A, B) (Courtney 1990, 1994; Zheng et al. 2022).

Etymology. The specific epithet "*pseudopoda*" means "pseudopodia", refers to the pseudopodia-like lateral projections of pupal abdominal segments VI–VII.

Distribution. China (Yunnan Province).

Deuterophlebia pachychaeta sp. nov.

https://zoobank.org/99503019-F78C-49B5-B602-8CE1D53BD96A

Description. Male adults. Body length ca. 3.0 mm (n = 2), uniformly brownish black. Head brownish black, flattened and nearly trapezoidal, width ca. 0.50 mm (Fig. 6A). Head densely covered with microtrichia. Median clypeal lobe slightly convex, semicircle shaped with around 20 sharp setae (Fig. 6A). Mouthparts in form of an invaginated tubule, oral region depressed (Fig. 6A, B). Edges of oral region (or mouth opening) ridged, forming a protruded angle on inner side of each eye (Fig. 6A, B). Ventral ridge of oral region convex medially and forming a blunt mental tooth (Fig. 6A, B). Postgena and oral region with microtrichia but more sparse than other regions, a pair of tentorial pits present on each side of oral region (Fig. 6A, B). Compound eyes glabrous, width ca. 0.13 mm, distance between eyes ca. 0.30 mm (Fig. 6A).

Antennae ca. 13.0 mm (n=5) (Fig. 6A, C). Scape oval shaped, pedicel globular, both scape and pedicel covered with microtrichia (Fig. 6A, C). Flagella four segmented, flagellomeres I–III slender cylindrical, each with a sub-apical tubercle on front margin and bearing 8–10 digitiform setae (Fig. 6C). Flagellomere IV flattened and elongated, with curved hair-like setae on the anterior side of basal half, apical half generally glabrous but bearing 4–5 clusters of curved hair-like setae, apex slightly expanded with some curved hair-like setae (Fig. 6C). Antennal ratio ca. 4.0: 2.0: 5.0: 3.0: 287.0, flagellomere IV about 17× combined length of five basal antennal articles or about 4× body length (Fig. 6C).

Thorax brownish black, densely covered with microtrichia. Mesonotum strongly expanded. Wings ca. 5.5 mm, shape, venation and other features similar to *D. pseudopoda* sp. nov. (Fig. 1).

Legs brownish black, slender, three pairs sharing similar chaetotaxy exhibiting four types of setae: (1) microtrichia, densely covered on all segments; (2) sharp macrotrichia, sparsely on dorsal margin of femora and tibiae; (3) long capitate setae, on ventral side of tarsomere I-IV of each leg, distal half of ventral edge of all tibiae, surrounding the top of fore- and midtibiae, and also densely arranged radially on each empodium; (4) digitiform setae, 1-3 pairs for each tarsomere (Fig. 6D-F). In foreleg, femur: tibia: tarsus = 11.0: 17.0: 16.0; femur slightly flattened, tibia slender cylindrical and gradually broader apically; tarsomere I: II: III: IV: V = 8.5: 2.0: 2.0: 1.5: 0.8, tarsomeres I-IV cylindrical, tarsomere V conical; empodium shell-shaped, length subequal to tarsomere V; claw slender tapered, shorter than empodium (Fig. 2B) (Fig. 6D). Midleg shortest among all legs, features generally similar to foreleg, femur: tibia: tarsus = 10.0: 12.5: 14.0, tarsomere I: II: III: IV: V = 8.5: 2.0: 2.0: 1.5: 0.8 (Fig. 6E). In hindleg, femur: tibia: tarsus of hindleg = 14.0: 17.0: 11.0, tarsomere I: II: III: IV: V = 3.0: 2.0: 2.0: 1.5: 0.8 (Fig. 6F).

Abdomen brownish black, densely covered with microtrichia, nine segmented, tapering posteriorly. Segment VIII in form of a short chitin ring, sternite IX almost glabrous, connected with dorsal plate and gonocoxite (Fig. 6G). Gonocoxite with posterior projection ca. 1/2 length of gonostylus (Fig. 6G). Gonostylus subequal dorsal plate, flattened, slender oval shaped, flexor surface with numerous curved sharp setae (Fig. 6G). Dorsal plate parallel-sided, posterior margin slightly depressed with a median cleft and some stout setae on margin (Fig. 6G). Aedeagus in form of a smooth tube, length subequal to gonostylus, longer than dorsal plate (Fig. 6G).

Female adult. Body length ca. 2.3 mm (n = 1). Besides sexual differences, generally similar to the males except following features (Fig. 7A–D).

Head width ca. 0.40 mm (Fig. 7A). Median clypeal lobe slightly convex with ca. 20 setae (Fig. 7A). Oral region located near anterior margin of head, postgena and oral region with microtrichia but more sparse than other regions (Fig. 7A). Compound eyes more prominent than males (Fig. 7A). Antenna ca. 0.3 mm. Scape slender ovalshaped, pedicel globular, both scape and pedicel covered with microtrichia with several sharp setae (Fig. 7A). Flagellomere I slender cylindrical, flagellomeres II–III slender oval shaped, flagellomere IV dripping shaped (Fig. 7A). Flagellomeres I–IV bearing 2, 4, 10 and 2 digitiform setae apically respectively, flagellomere III–IV with 1 and 4 sharp setae respectively (Fig. 7A). Antennal ratio = 7.0: 4.0: 10.0: 5.0: 5.0: 4.0 (Fig. 7A).

Legs sharing similar chaetotaxy and exhibiting three types of setae, chaetotaxy similar to males but without capitate setae (Fig. 7B–D). In all legs, coxae about twice longer and broader than trochanters, femora slightly



Figure 6. Male adult of *D. pachychaeta* sp. nov.: **A.** Head (ventral view); **B.** Oral region (ventral view); **C.** Flagellomeres; **D.** Foreleg; **E.** Midleg; **F.** Hindleg; **G.** Terminalia (dorsal view). Scale bars: 0.1 mm (**A**, **C**, **G**); 0.05 mm (**B**); 0.5 mm (**D**–**F**).


Figure 7. Female adult of *D. pachychaeta* sp. nov.: A. Head (ventral view); B. Foreleg; C. Midleg; D. Hindleg. Scale bars: 0.1 mm.

flattened, tibiae and tarsomeres slender cylindrical (Fig. 7B–D). In foreleg and midleg, femur: tibia: tarsus = 1.0: 2.0: 1.5, tarsomere I: II: III: IV: V = 1.2: 0.8: 0.8: 0.8: 2.4 (Fig. 7B, C). In hindleg, femur: tibia: tarsus = 1.0: 1.7: 1.1, tarsomere I: II: III: IV: V = 1.0: 0.8: 0.8: 0.8: 2.4 (Fig. 7D). Claws of all legs similar, paired, stout and curved, with a blunt protrusion in the middle (Fig. 7B–D). Empodium in form of a long and hairy spine, subequal to the length of claw (Fig. 7B–D).

Male pupae. Pupae flattened oval shaped, length 2.8 mm (n = 2), width 2.0 mm (Fig. 8A, B). Dorsal integument dark brown, divided into 11 segments (Fig. 8A, B).

Prothorax fused with mesothorax, forming a conical segment with a median suture (Fig. 8A, B). Mesothoracic lateral margins each with a pair of sharp spines and a gill (Figs 8A, B, 9A, B). Spines ca. 0.4 mm, expanded basally, slightly curved, dark brown, originated from a round base (Fig. 9A). Ventral gills light to dark brown, length subequal



Figure 8. Pupae of *D. pachychaeta* sp. nov.: A. Male pupa (dorsal view); B. Male pupa (ventral view); C. Female pupa (dorsal view); D. Female pupa (ventral view). Scale bars: 1.0 mm.



Figure 9. Male pupa of D. pachychaeta sp. nov.: A. Thoracic spine (dorsal view); B. Gill (ventral view). Scale bar: 0.1 mm.

to the dorsal spines, each including four filaments: posterior filament single and short, pointing backward; anterior three gill filaments on a common base, similar in shape, slender and twisted; second and third filaments fused at base (Fig. 9B). Metathorax completely surrounded by mesothorax and first abdominal segment (Fig. 8A, B).

Abdominal segment I and II similar, each with a pair of anterolateral projections, each projection pointing forward and bearing ca. 18 spines (Fig. 8A, B). Lateral margins of segments VI and VII with several spines on both dorsal and ventral sides. Segment VIII shield-shaped, surrounded by segments VII and IX (Fig. 8A, B).

Adult structures visible on ventral side (Fig. 8B). Head present below mesothorax; antennal sheaths in form of a large elliptic ring, surrounding body 2.0 times (Fig. 8B). Leg sacs extended to posterior end of antennal ring, strongly expanded apically. Abdominal segments III–V each with a pair of black adhesive discs (Fig. 8B).

Female pupae. Length ca. 2.8 mm (n = 1), width ca. 2.0 mm (Fig. 8C, D). Dorsal morphology similar to male except for smaller mesothorax (Fig. 8C, D). Gender can be identified through the absence of antennal ring, apex of female leg sheaths not expanded (Fig. 8C, D).

Material examined. *Holotype*: male adult, China: Yunnan Province, Nujiang Lisu Autonomous Prefecture, Gongshan County, Dulongjiang Township, Dulongjiang River, 27°50'14.16"N, 98°19'54.2"E, 1470 m a.s.l., 4.II.2023, Xuhongyi Zheng leg. *Paratypes*: 1 male adult, 2 male pupae, same locality and data as holotype; 1 female adult dissected from a pupa, Yunnan Province, Nujiang Lisu Autonomous Prefecture, Fugong County, 26°57'17.32"N, 98°52'3.04"E, 1265 m a.s.l., 3. VII. 2022, leg. Xuhongyi Zheng, Zhenxing Ma, Zhiteng Chen & Pengxu Mu.

Diagnosis. Male adults of *Deuterophlebia pachychaeta* sp. nov. can be identified by their head shape and

chaetotaxy of antennae (Fig. 6A, C). Following the keys of Courtney (1994) and Zheng et al. (2022), males of this species, which are similar to *D. mirabilis* Edwards, 1922, *D. blepharis* Courtney, 1994 and *D. sinensis* Zheng et al., 2022, can be separated from other Asian species by their relatively long antennae (longer than 8.0 mm), and postgena covered with microtrichia (Fig. 6B). Chaetotaxy on flagellomeres can be used to differentiate those four similar species: in the new species, there were ca. 8–10 digtiform setae on each of flagellomeres I–III (Fig. 6A, C) (Courtney 1990, 1994; Zheng et al. 2022).

Female adults of *D. pachychaeta* sp. nov. can be recognized through a combination of the smooth median clypeal lobe, chaetotaxy of antennae, and shape of flagella (Fig. 7A). Its smooth and convex median clypeal lobe is similar to *D. mirabilis* Edwards, 1922, *D. blepharis* Courtney, 1994, *D. sinensis* Zheng et al., 2022, *D. yunnanensis* Zheng et al., 2022 and *D. wuyiensis* Zheng et al., 2022, but can be differentiated from them by its antenna: flagellomeres I–IV bearing ca. 2, 4, 10 and 2 digitiform setae respectively, flagellomere IV with additionally 4 sharp setae; antennal ratio = 7.0: 4.0: 10.0: 5.0: 5.0: 4.0 (Fig. 7A) (Courtney 1990, 1994; Zheng et al. 2022).

Pupae can be identified by their mesothoracic spines: there are two spines on each side, expanded basally (Fig. 9A, B). Compared with the 15 species with a clear pupal stage (Courtney 1990, 1994; Zheng et al. 2022), only *D. acutirhina* Zheng et al., 2022 has similar basally expanded spines, but less expanded than in the new species. They can also be distinguished by the absence of abdominal dots (Zheng et al. 2022).

Etymology. The specific epithet "*pachychaeta*" is a combination of the words *pachy* and *chaeta*, which refers to its thickened spines on pupal mesothorax.

Distribution. China (Yunnan Province).

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Keys to Asian Deuterophlebia

Key to male adults

Modified from the key by Zheng et al. 2022. Among the 15 Asian species, *D. tyosenensis* and *D. wuyiensis* are not included since male adults of them remain unknown.

1	Antennal length 7 mm or less, length of flagellomere IV approximately 3× the body length	
_	Antennal length 8 mm or more, length of flagellomere IV approximately 4× the body length	
2	Median clypeal lobe convex	D. oporina
_	Median clypeal lobe indistinct	
3	Flagellomere I with more than 10 digitiform setae	D. alata
_	Flagellomere I with fewer than 10 digitiform setae	D. brachyrhina
4	Dorsal plate without a median cleft	D. pseudopoda sp. nov.
_	Dorsal plate with a median cleft	5
5	Mid-tibiae dorsally glabrous at the top	D. acutirhina
-	Mid-tibiae with capitate setae around top	6
6	Postgena with microtrichia	7
_	Postgena glabrous	
7	Compound eyes with microtrichia between ommatidia	D. blepharis
_	Compound eyes glabrous	
8	8–10 digitiform setae on each of flagellomeres I–III	D. pachychaeta sp. nov.
_	Flagellomere I–III with less than 8 digitiform setae	9
9	Oral region with microtrichia	D. mirabilis
_	Oral region glabrous	D. sinensis
10	Flagellomere I with more than 10 digitiform setae	D. sajanica, D. bicarinata
_	Flagellomere I with 10 or fewer digitiform setae	
11	Hind-tibiae covered with sharp setae on dorsal margin	D. yunnanensis
_	Hind-tibiae glabrous on dorsal margin	D. nipponica

Key to pupae

Modified from the key by Zheng et al. 2022. Contains nine known species with previously described pupal stage and two new species from this work.

1	Mesothorax with lateral outgrowths	D. alata
_	Mesothorax without lateral outgrowths	
2	Abdominal tergites VI–VII with posterolateral projections	D. pseudopoda sp. nov.
_	Abdominal tergites VI–VII without posterolateral projections	
3	Mesothorax without spines on anterolateral margin	D. nipponica
_	Mesothorax with spines on anterolateral margin	
4	Mesothorax with one pair of spines on anterolateral margin	
_	Mesothorax with two pairs of spines on anterolateral margin	
5	Abdominal tergites with dark bands	D. bicarinata
-	Abdominal tergites without dark bands	D. sajanica, D. yunnanensis
6	Abdominal tergites with dark bands	D. wuyiensis
_	Abdominal tergites without dark bands	
7	Abdominal tergites with a pair of large dark dots	D. acutirhina
_	Abdominal tergites without obvious larger dark dots	
8	Mesothoracic spines expanded basally	D. pachychaeta sp. nov.
_	Mesothoracic spines not expanded basally	
9	Gills with elongated posterior filaments	D. sinensis
_	Gills with indistinct posterior filaments	D. tyosenensis

Molecular study

We sequenced a fragment of the COI gene of the two new species in this study and analyzed them together with the other five Chinese species. One female adult, one male adult and one pupa were sequenced for each species, since the intraspecific distances are under 0.01, we submit only one sequence of male adult for

Values	D. sinensis	D. yunnanensis	D. alata	D. acutirhina	D. wuyiensis	D. pseudopoda sp. nov.
D. yunnanensis	0.086					·
D. alata	0.154	0.164				
D. acutirhina	0.154	0.159	0.148			
D. wuyiensis	0.175	0.167	0.156	0.155		
D. pseudopoda sp. nov.	0.129	0.127	0.154	0.158	0.154	
D. pachychaeta sp. nov.	0.118	0.091	0.160	0.163	0.169	0.131

Table 2. Values of K2P genetic distance among the DNA barcodes (COI).

each species with the collecting information same as for the holotype.

Interspecific genetic distances are 0.086-0.175 (Table 2). Two of them are under 0.10, one is between D. sinensis and D. yunnanensis, the other is between D. pachychaeta and D. yunnanensis. Morphologically, male adults of the three species share several common characters, including relatively long antennae (longer than 8 mm), similar models of head (flattened and nearly trapezoidal, median clypeal lobe slightly convex) and terminalia (relatively slender, dorsal plate with a median cleft). Pupae and female adults of the three species also show similarity, as mentioned above and in Zheng et al. 2022. As a result, we consider them as closely related species, possibly belonging to the same clade, which may also contain D. mirabilis. A reliable phylogenetic tree reconstructed by more specimens and molecular data may provide support for this hypothesis.

Biological notes

Specimens were collected from Dulong River, in the dry season, water was ca. 20 m wide and 2–3 m deep, unshaded, containing stones of various sizes (Fig. 10). Water temperature was lower than 10 °C. All pupae and adults of these two new species were collected at the same locality. Pupae were collected in torrent areas where the water depth was ca. 0.4 m and we could hardly stand (Fig. 10). Pupae were tightly attached to the stone surfaces with their abdominal discs. Dead adults were found floating near the river bank. These biological aspects are similar to other known *Deuterophlebia* species.

Discussion

The two new species in this study enrich the Chinese diversity of Deuterophlebiidae, making China the area with the most *Deuterophlebia* species. At present, China holds half of the Asian species, including seven only reported from China and *D. mirabilis*, the type species of the genus that has been collected from Xinjiang Province in the last century (Brodsky 1930; Courtney 1994).

Morphologically, *Deuterophlebia pseudopoda* sp. nov. has more apomorphies than *D. pachychaeta* sp. nov. Both shapes of genitalia (stout, length of gonostylus subequal to the gonocoxite and dorsal plate, dorsal plate without median cleft) and head (nearly trapezoidal, without protruded corners near eyes, median clypeal lobe slightly



Figure 10. Habitat stream of *D. pseudopoda* sp. nov. and *D. pachychaeta* sp. nov.

convex) of *D. pseudopoda* sp. nov. are unique among *Deuterophlebia* members (Fig. 2A, G). Its pupae have a prominent autapomorphy: the posterolateral projections on abdominal segments VI–VII (Fig. 5C). Through extensive examination and comparison in recent years, we found that the pupal stage is the easiest for species identification, although most species have a male adult as holotype. All seven Chinese species have their pupal structures described.

In an overview of the distribution map of Deuterophlebiidae (Fig. 11, modified from Courtney 1994 and Zheng et al. 2022), a Himalayan bias can be easily identified. Taking into account the biogeography, the Dulongjiang area (the type locality of the two new species) can be considered as part of the Himalayas (Zhu and Yan 2002). Thus, at least six species can be found in the Himalayas, including *D. mirabilis*, *D. blepharis*, *D. brachyrhina*, *D. oporina* (Courtney 1994; Zheng et al. 2022), and the two new species in this study. In addition, *D. brachyrhina* and *D. oporina*, which are considered sister to the remaining Deuterophlebidae species, also have their distributions restricted to the Himalayas



Figure 11. Distribution of Asian Deuterophlebia spp.

(Courtney 1994). This could indicate a Himalayan origin of the genus and family.

However, there are two issues with this hypothesis. One is that the formation of the Himalayas was much later than the origin of early dipteran members. The former event happened about 50 million years ago, but the fossils of early flies can already be found in Cretaceous ambers (about 100 million years ago) (Borkent and Grimaldi 2004; Poinar 2019). The emergence of Deuterophlebiidae, which is possibly the earliest extant fly lineage, can be traced back to the Triassic period (Wiegmann et al. 2011; Zhang et al. 2022). Additionally, the absence of species in Europe remains unexplained. In contrast, the Nearctic realm, which is much farther to the Himalayas than to Europe, hosts six species (Courtney 1994; Zheng et al. 2022).

In conclusion, the possibility of a Himalayan origin is low. At the present time, the only thing we can be sure of is that the Himalayas and its surroundings are one of the speciation centers of *Deuterophlebia* because it harbors the highest diversity and the most plesiomorphic species of the genus. Western North America with six species is another center (Courtney 1990, 1994). A plausible explanation of the Himalayan diversity of *Deuterophlebia* is the unique geography here. Those rapidly raised mountains and distinct climates created abundant streams and diverse habitats, coupled with the geographical barriers of the mountains and habitat changes, possibly accelerated the speciation of Himalayan mountain midges.

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