

Rediscovery of *Achipteria setulosa*, with remarks on Japanese species of Achipteriidae and the proposal of species-groups (Acari, Oribatida)

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Abstract

The first detailed description of adults of *Achipteria setulosa* Golosova, 1981 with illustrations are provided, based on materials from central Japan. This species is placed in the subgenus *Achipteria* (*Izuachipteria*) Balogh & Mahunka, 1979. In addition, the species grouping of the known species in the genus *Achipteria* is briefly discussed, and three species-groups are proposed based on the structure of the lamellar complex. Furthermore, data on distribution, diversity and habitat ecology of all known species of Achipteriidae in Japan are presented, and a key is provided for the identification of recorded species in this country. The majority of achipteriid species found in Japan are known to be widely distributed in the vast areas of the northern hemisphere; only two species have restricted distributions in Japan. Most species of Achipteriidae in Japan are inhabitants of the litter of various forests, such as natural broad-leaved forests in high mountainous areas, soils of grasslands, wetlands and mosses growing on rocks.

Keywords

Achipteria, grassland on limestone, *Izuachipteria*, Japan, new record, species-group

Introduction

The oribatid mites belonging to the family Achipteriidae Thor, 1929 occur frequently, even sometimes with high numbers, in forest soils, litters, meadow soils, liverworts, bogs and at edges of lakes with mosses, but rarely found in arboreal habitats. Representatives of this family are diverse in both northern and southern hemispheres, but in the tropics, achipteriid species are mainly found at high elevations, for example, in cloud forest litter. Achipteriid species whose feeding habits have been studied are saprophages and mycophages that apparently feed opportunistically on available resources of fungi, algae and decaying plant material (Root et al. 2007, Seniczak and Seniczak 2007, Lindo et al. 2008, Norton and Behan-Pelletier 2009).

Some species of Achipteriidae are sensitive to environmental changes, including pollutants, and therefore, they may indicate changes in habitats. Several species of this family serve as intermediate hosts of tapeworms of the superfamily Anoplocephalata, which parasitize on wild and domestic animals (Rajski 1959, Denegri 1993, Seniczak and Seniczak 2007). The family is known from the Holarctic, Oriental and Neotropical regions with most species described from the North America, Europe, Central America and East Asia.

Currently, the family Achipteriidae Thor, 1929 includes seven genera, three subgenera, 90 species and four subspecies (Subías 2004, 2015). Among the genera, *Achipteria* Berlese, 1885 is largest in terms of species richness, and it includes two subgenera and 35 species (including two subspecies). Most known species belong to the nominotypical subgenus *Achipteria* (31 species, two subspecies).

Balogh and Mahunka (1979) proposed *Izuachipteria* and *Hokkachipteria* as new genera based on the character states of interlamellar setae, but Subías (2004) considered these as a subgenus of *Achipteria*. The main difference between subgenera *Achipteria* and *Izuachipteria* is size of interlamellar setae, which are long and thick, extending beyond basis of lamellar cusps in *A. (Achipteria)*, in contrast very short and slender interlamellar setae (or it is completely absent) in *A. (Izuachipteria)*. Only two species have hitherto been grouped into *A. (Izuachipteria)*, namely *A. (I.) imperfecta* (Suzuki, 1972) and *A. (I.) alpestris* (Aoki, 1973).

Eleven species of Achipteriidae have been recorded previously from Japan (Aoki 1959, 1961, 1970, 1973, 1976, Suzuki 1972, Fujikawa et al. 1993, Hirauchi and Aoki 1997, Maruyama 2003, Ohkubo et al. 2015).

The aim of the present work is to redescribe the morphology of a little known species, *A. setulosa* Golosova, 1981, which is found for the first time in Japan. This species has character states of the subgenus *Achipteria (Izuachipteria)*, therefore, we combine this species in the latter subgenus. Proposing the species grouping of the known species of *Achipteria sensu lato* along with review of the composition of the family Achipteriidae in Japan, with remarks on their biogeography, habitat ecology, and construction of an identification key to all known species from this country are the other goal of this study.

Material and methods

In total 64 specimens (26 males and 38 females) were collected from litter and soil of the grassland with *Saxifraga fortunei* Hook. f. var. *alpina* Nakai in the bottom of Senridou Doline, Maikomi-Daira (limestone area), Itoigawa City, Niigata Prefecture, Japan, 36°57'37"N, 137°48'10"E, alt. 695 m a.s.l., 03 September 2007, collected by I. Maruyama.

The morphological terminology used below is mostly that developed over many years by Grandjean (1932, 1952), and also that by Norton (1977), Norton and Behan-Pelletier (2009). The specimens were cleared in lactic acid and mounted on temporary slides to view the anterior, lateral and posterior aspects and then preserved in alcohol. A differential interference contrast microscope (Olympus BH 2) was used for investigation in transmitted light. Line drawings were made using a camera lucida attached to the compound microscope.

All measurements are given as a range, with the mean in parentheses. Body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate, to avoid discrepancies caused by different degrees of notogastral distension. Notogastral length was also measured in lateral aspect (when the dorsosejugal groove is discernable), from the anterior to the posterior edge; notogastral width refers to the maximum width in dorsal aspect. Setal formulas of the legs (including famulus) are given as numbers per segment for appendages (from trochanter to tarsus) and formulas of solenidia are given separately as number per podosomal segment.

Description

***Achipteria (Izuachipteria) setulosa* (Golosova, 1981), comb. n.**

[Japanese name: Maikomi-tsunobanedani]

Figs 1, 2

Achipteria setulosa Golosova, 1981: p. 148, fig. 1.

Achipteria setulosa: Pan'kov et al. 1997: p. 66; Bayartogtokh and Ryabinin 2012: p. 153.

Diagnosis. Large species, body length: 718–796 μm ; width: 480–576 μm ($n = 10$). Lamellar setae short, thin, smooth, inserted ventrally on cusps, not reaching tip of cusps; interlamellar setae short, thin, smooth, not reaching basis of lamellar cusps; sensilli long, club-shaped, epimeral regions III and IV with three setae each.

Measurement. Body length: 718–796 (759) μm ; width: 480–576 (543) μm ($n = 10$).

Integument. Body color dark brown, heavily sclerotized species with minute microtubercles on lateral part of podosoma, exobothridial and lenticular regions. Granular cerotegument (with minute round to conical granular structure) clearly evident at base of prodorsum and on mentum.

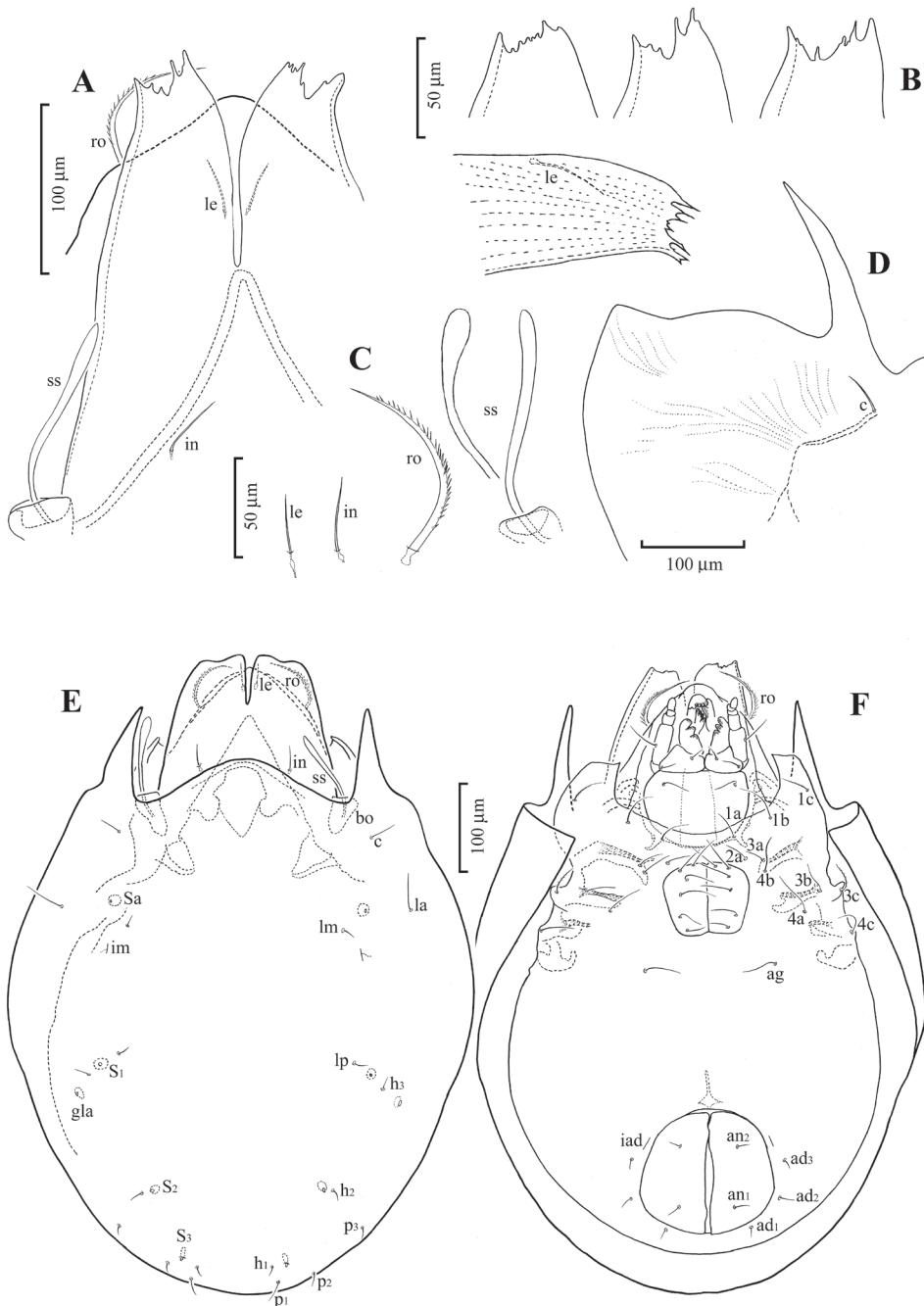


Figure 1. *Achipteria (Izuachipteria) setulosa* (Golosova, 1981). **A** Part of prodorsum showing flatly extended lamellae (after dissection) **B** Lamellar cusps, showing variation in arrangement of teeth on the anterior edge **C** Lamellar, interlamellar, rostral setae and sensillus showing variation of its head **D** Pteromorph showing its anterior projection and lateral corner (after dissection) **E** Dorsal view of body **F** Ventral view of body.

Prodorsum (Fig. 1A–C, E): Rostrum rounded, without horn-like anterior projection. Rostral setae (*ro*) long, barbed, curved inward, extending beyond tip of rostrum. Lamellae long and broad, fused medially; lamellar cusps nearly half as long as total length of lamellae, its anterior margin bending downwards, serrated irregularly as shown in Fig. 1A, B. Tutoria (*tu*) medium long, narrow, with free cusps distally. Lamellar setae (*le*) short (about 24 μm), thin, smooth, inserted ventrally on cusps, not exposed from cusps. Interlamellar setae (*in*) short, but slightly longer (about 35 μm) than lamellar setae, not reaching on base of lamellar cusps. Exobothridial setae not evident. Sensilli club-shaped, relatively long (about 102 μm), its head smooth (Fig. 1C). Bothridia nearly funnel-shaped, its opening exposed from anterior margin of notogaster.

Notogaster (Fig. 1D–F): Longer than wide, anterior and posterior margins broadly rounded. Lenticular region irregularly pentagonal, with diffuse margins, but weakly visible and lacking true lenticulus. Anterior projection of pteromorphs pointed, not reaching level of rostrum (Fig. 1D–F). Among 10 pairs of notogastral setae, *la* longest (35–42 μm), *c* next long setae (25–32 μm), other setae distinctly shorter (12–17 μm); relative length of mutual distances of setal pairs: $la-la > h_3-h_3 > c-c > p_3-p_3 > lp-lp > lm-lm > h_2-h_2 > p_2-p_2 > p_1-p_1 > h_1-h_1$. Four pairs of sacculi clearly developed; *Sa* located anterolaterally to setae *la*, *S*₁ between setae *lp* and *h*₃, *S*₂ anteriomedial of setae *h*₂, and *S*₃ anterolaterally to setae *h*₁. Lyrifissures *im* situated posterolaterally to setae *lm*. Openings of opisthonotal glands (*gla*) located posterolaterally to setae *h*₃.

Gnathosoma (Fig. 1F): Subcapitulum nearly as long as wide, smooth throughout; setae *h* 37 μm , *m* 17 μm , and *a* 15 μm , smooth. Chelicerae chelate-dentate (178 μm), cheliceral setae long, barbed, *cha* (64 μm) longer than *chb* (35 μm). Palps typical for family (104 μm), formula of setation: 0–2–1–3–10 including solenidion ω on tarsus.

Epimeral and lateral podosomal regions (Fig. 1F): Genal teeth rectangular, with pointed tip. Pedotecta I with pointed anteromedial end as seen in ventral view, and even more sharply pointed in lateral view. Apodemes *apo.2*, *apo.sj* and *apo.3* well developed. Epimeral regions III and IV with three setae each; epimeral setae 35–42 μm in length; *1c* and *3d* barbed, other setae smooth. Epimeral setal formula: 3–1–3–3. Custodia and discidia not clearly developed; circumpedal carinae poorly developed.

Anogenital region (Fig. 1F): Genital and aggenital setae long (36–43 μm), smooth; relative length of their mutual distances: $g_5-g_5 > g_4-g_4 \geq g_2-g_2 > g_3-g_3 > g_6-g_6 > g_1-g_1$. Anal and adanal setae (13–18 μm) smooth; mutual distances of an_1-an_1 and an_2-an_2 almost equal; relative distances between anal and adanal setae: $ad_1-ad_1 > an_1-an_1 > an_2-an_2 = an_1-an_1 > ad_1-ad_1 > ad_2-ad_2$. Adanal lyrifissures (*iad*) aligned, almost parallel to anterolateral margins of anal aperture.

Legs (Fig. 2): Lateral claws thinner than middle one, having small, but distinct serrations on dorsal edge (Fig. 2G). Setation of legs typical for genus, most setae finely barbed except few distal or ventral setae on tarsi, femora and trochanters. Solenidia φ_1 on tibiae I about 2.8 times as long as φ_2 ; setae *l'* on genua I and II markedly thick; setae *s* on tarsi II very thick, bearing several strong branches; genua IV curved, markedly longer than others. Formula of setation, including famuli: I (1-5-3-4-20), II (1-5-3-4-

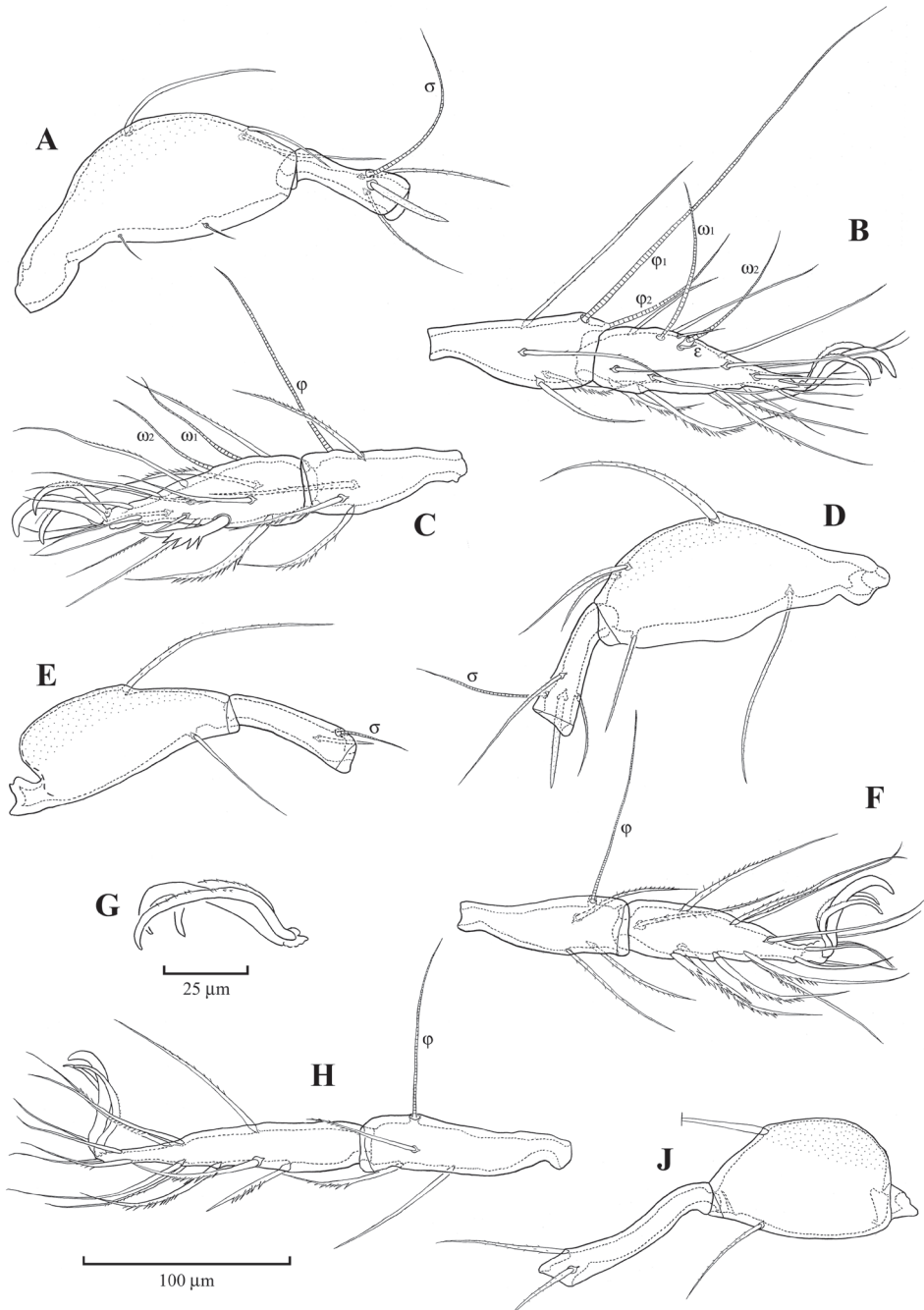


Figure 2. *Achipteria* (*Izuachipteria*) *setulosa* (Goloso, 1981). **A** Femur and genu of leg I (right, antiaxial aspect) **B** Tibia and tarsus of leg I (right, antiaxial aspect) **C** Tibia and tarsus of leg II (left, antiaxial aspect) **D** Femur and genu of leg II (left, antiaxial aspect) **E** Femur and genu of leg III (right, paraxial aspect) **F** Tibia and tarsus of leg III right, paraxial aspect) **G** Claws of leg IV **H** Tibia and tarsus of leg IV (right, antiaxial aspect) **J** Femur and genu of leg IV (right, antiaxial aspect).

Table 1. Homology of leg setation and solenidia of *Achipteria (Izuachipteria) setulosa* (Golosova, 1981)*

Legs	Trochanter	Femur	Genu	Tibia	Tarsus
I	v'	$d, (l), bv'', v''$	$(l), v', \sigma$	$(l), (v), \varphi_1, \varphi_2$	$(\overline{ft}), (tc), (it), (p), (u), (a), s, (pv), v', (pl), l'', e, \omega_1, \omega_2$
II	v'	$d, (l), bv'', v''$	$(l), v', \sigma$	$(l), (v), \varphi$	$(\overline{ft}), (tc), (it), (p), (u), (a), s, (pv), \omega_1, \omega_2$
III	l', v'	d, ev'	l', σ	$l', (v), \varphi$	$(\overline{ft}), (tc), (it), (p), (u), (a), s, (pv)$
IV	v'	d, ev'	d, l'	$l', (v), \varphi$	$\overline{ft}'', (tc), (p), (u), (a), s, (pv)$

*Roman letters refer to normal setae, e to famulus; Greek letters to solenidia; single prime (') marks setae on anterior and double prime (') setae on posterior side of the given leg segment; parentheses refer to a pair of setae.

15), III (2-2-1-3-15), IV (1-2-2-3-12); formula of solenidia: I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0); homology of setae and solenidia as indicated in Table 1.

Remarks. The character states of the specimens examined here accord well with those studied by Golosova (1981). Only the slight differences are the scarcely barbed sensilli in the Russian specimens (smooth in Japanese specimens), and number of epimeral setae (Russian specimens has fewer setae than Japanese ones). Until now, the present species was known only from the type locality, Kuril Islands in the Russian Far East. The original description, illustration and differential diagnosis of this species were not sufficient, and hence we present here some supplementary details.

Achipteria (I.) setulosa resembles the two other Japanese species, *A. (I.) alpestris* and *A. (I.) imperfecta* in having short and slender interlamellar setae. However, *A. (I.) alpestris* is different from *Achipteria (I.) setulosa* by the strongly-developed median horn-like projection of the rostrum, the relatively shorter sensilli, and much smaller body size. Another Japanese species, *A. (I.) imperfecta* has no interlamellar setae, relatively thick sensilli, different dentation of lamellar cusps, and much smaller body size.

Discussion

In the comprehensive checklist of oribatid mites of Japan, Fujikawa *et al.* (1993) presented eight species of *Achipteriidae* belonging to five genera, namely *Achipteria*, *Anachipteria*, *Parachipteria*, *Hokkachipteria* and *Izuachipteria*, but the two latter taxa are now considered as subgenera of *Achipteria*.

Most of *achipteriid* species found in Japan are known to be widely distributed in vast areas of the northern hemisphere. Thus, *Achipteria coleoptrata* (Linnaeus, 1758), *A. curta* Aoki, 1970, *A. nitens* (Nicolet, 1855), *Anachipteria achipteroides* (Ewing, 1913) and *Parachipteria punctata* (Nicolet, 1855) are widely distributed through Holarctic region. Some of these species were also recorded from the other biogeographic regions, e.g. in addition to their common distributions in Europe (everywhere), North America (USA and Canada), and Asia (Russian Far East, Siberia, Kazakhstan, Mongolia and Japan), *A. coleoptrata*, *A. curta* and *P. punctata* were reported from India,

Vietnam, subtropical part of China and Santa Helena islands (Wallwork 1977, Haq and Sumangala 2003, Wang et al. 2003, Chen et al. 2010). Two other species, such as *Anachipteria grandis* Aoki, 1966 and *Parachipteria distincta* (Aoki, 1959) have also fairly wide distributions in the Palearctic region. Only four species, *A. (I.) alpestris*, *A. (I.) imperfecta*, *A. (I.) setulosa* and *Parachipteria truncata* Aoki, 1970 have restricted distributions mainly in Japan, but two of these, (*A. (I.) imperfecta* and *A. (I.) setulosa*) have extended distributions in Taiwan and the Russian Far East (Aoki 1991, Ryabinin and Pan'kov 2002, Ohkubo et al. 2015, Subías 2015).

Among these species, *P. distincta* is most common species in Japan, which is ubiquitous in this country. Some other species, such as *A. curta*, *A. (I.) alpestris*, *A. (I.) imperfecta* and *An. grandis* are rather common, especially in its northern and central regions of the country. The other species (*A. coleoptrata*, *A. nitens*, *A. serrata*, *An. achipteroides*, *P. truncata*, *P. punctata*) are relatively rare, and known to be distributed only in one prefecture each. Most species of AchipterIIDae in Japan are the inhabitants of the litter of various forests, such as natural broad leaved forests in high mountainous areas, soils of grasslands, wetlands and mosses growing on rocks.

As mentioned above, *Achipteria sensu lato* is the largest genus of AchipterIIDae, and it encompasses diverse species in terms of morphological characters. Balogh and Mahunka (1979) attempted to classify species of *Achipteria* using the size of the interlamellar setae, but this proposal was not broadly accepted. In this sense, validity of the subgenus *Achipteria (Izuachipteria)* might not acceptable, but further detailed studies are required on the morphology of both adults and immature stages to clarify the status of this subgenus, which is beyond the scope of the present work.

The structure of lamellar complex is quite diverse in various species of *Achipteria*, e.g. some species have anteriorly narrowed, elongate triangular lamellae pointed distally with sharp lateral cusps, which is a typical lamellar complex for AchipterIIDae and an apomorphic character, according to Weigmann (2010). The other species have very broad lamellae distally with large cusps, which is a plesiomorphic character, according to the above-mentioned author. In case of the latter lamellar complex, the distal ends of lamellar cusps are mostly bent downwards, but in various species, these bending cusps are being either dentate or evenly rounded distally. Based on these different characters, it might be possible to establish at least two subgenera within the genus *Achipteria*. However, we do not do so, because of the below given reason.

As stated by Weigmann (2010) there are many genera of oribatid mites, creation of which were based upon single conspicuous character or some combination of characters, whose value for assessing phylogenetic relations is questionable. Moreover, Behan-Pelletier (2001) and Lindo et al. (2008) declared that the shapes of the lamellae vary extensively not only within the family AchipterIIDae, but even among different families of poronotic Brachypylina, and the polarity of these variations is unclear. They justified that proposing a separate generic taxon based on character of the lamellae is not appropriate.

Although it is not preferable to establish new subgeneric level taxa based on the characters of lamellar complex, it is suggested to classify the known species of *Achipteria* into three species-groups. The first species-group, which we call the *coleoptrata*-group, has

lamellar complex with anteriorly narrowed, elongate triangular lamellae pointed distally with sharp lateral cusps, but without medial cusps. Besides the type species, *A. coleoptrata*, this species-group includes such species as *A. bicarinata* Moskacheva, 1973, *A. borealis* (Banks, 1889), *A. cucullata* Moskacheva, 1973, *A. elegans* Schweizer, 1956, *A. holomonensis* Cancela da Fonseca & Stamou, 1987, *A. italica* (Oudemans, 1914), *A. oregonensis* Ewing, 1918, *A. quadridentata* (Willmann, 1951) and *A. sumatrensis* Willmann, 1931.

The second species-group, the *serrata*-group, has very broad lamellar complex, and the cusps are distally serrated with various dens or teeth. *Achipteria serrata* has strong serration on the distal end of lamellar cusps, and some other species with same character could be included in this group, e.g. *A. (I.) alpestris*, *A. curta*, *A. (I.) setulosa* and *A. catskillensis* Nevin, 1977.

The third group, the *nitens*-group, has similar structures of the lamellar complex to the *serrata*-group, but the distal end of lamellar cusps are not serrated, i.e. bluntly rounded or sometimes with pointed lateral tooth. This species-group includes *A. balearensis* Ermilov, Rybalov & Kemal, 2011, *A. clarencei* Nevin, 1977, *A. hasticeps* (Hull, 1914), *A. (I.) imperfecta*, *A. nitens* (Nicolet, 1855), *A. longesensillus* Schweizer, 1956, *A. longisetosa* Weigmann & Murvanidze, 2003 and *A. verrucosa* Rjabinin, 1974.

This grouping might be useful for further classification of *Achipteria* species, and it should mentioned here that we do not include some hitherto known species of *Achipteria* (e.g. *A. armata* (Banks, 1895), *A. hasticeps* (Hull, 1914), *A. languida* (Nicolet, 1855), *A. minuta* (Ewing, 1909), *A. moderator* Berlese, 1923 etc.) into any species-group, due to their unclear diagnostic characters.

It is evident that the large lamellar complex is for protecting the dorsal, lateral and anterior parts of the prodorsum and especially the anterior legs in redrawn position, but in some species of *Achipteria* the lamellar complex became distinctly smaller; the structure and function of different lamellar complexes are the interesting topics of the future studies.

In conclusion, the following key can be used to identify the adults of all known species of *Achipteriidae* in Japan.

A key to adults of known species of *Achipteriidae* in Japan

- 1 Octotaxic system expressed as four pairs of notogastral porose areas.....2
- Octotaxic system expressed as four pairs of notogastral saccules instead of porose areas (*Achipteria sensu lato*)3
- 2 A knife-like humeral projection of pteromorphs lacking (*Anachipteria*).....9
- Pteromorphs with a knife-like humeral projection (*Parachipteria*)10
- 3 Lamellar and interlamellar setae long, setae *le* extending beyond anterior tip of lamellar cusps; setae *in* not extending far beyond basis of lamellar cusps (*Achipteria (Achipteria)*)4
- Lamellar and interlamellar setae short, thin, sometimes setae *in* absent; setae *le* not reaching anterior tip of lamellar cusps; setae *in* not reaching basis of lamellar cusps *Achipteria (Izuachipteria)*7

- 4 Lamellar cusps rounded or with large lateral dens; sensilli long 5
- Lamellar cusps without lateral dens, but medially with 3–4 small dens; sensilli short *Achipteria (Achipteria) curta* Aoki, 1970
- 5 Notogastral setae well developed; lamellar cusps broad distally, concave medially, with few serrations or rounded distally 6
- Notogastral setae minute or represented by their alveoli; lamellar cusps with large, elongate-triangular lateral dens ... *A. (A.) coleoptrata* (Linnaeus, 1758)
- 6 Notogastral setae long, especially setae *c* and *la* very long; lamellar cusps with small lateral dens or blunt at tip; interlamellar setae extending beyond lamellar cusps; sensilli long, slender *A. (A.) nitens* (Nicolet, 1855)
- Notogastral setae *c* and *la* medium long, other setae very short; lamellar cusps with large lateral dens, concave medially and with few serrations; interlamellar setae not reaching tip of lamellar cusps; sensilli short, club-shaped *A. (A.) serrata* Hirauchi & Aoki, 1997
- 7 Interlamellar setae short, thin, but conspicuously developed; anterior margin of lamellar cusps distinctly serrated 8
- Interlamellar setae absent; anterior margin of lamellar cusps not serrated, but bluntly rounded *Achipteria (Izuachipteria) imperfecta* (Suzuki, 1972)
- 8 Rostrum with strongly-developed median horn-like projection; lamellar setae long, thick, reaching anterior end of cusps; body size relatively small (550–610 μm) *A. (I.) alpestris* (Aoki, 1973)
- Rostrum rounded, without median horn-like projection; lamellar setae short, thin, not reaching anterior end of cusps; body size large (718–796 μm) *A. (I.) setulosa* (Golosova, 1981)
- 9 Sensilli fusiform, long, extending far anterior to pedotecta I; lamellar cusps without medial dens; lamellar setae smooth *Anachipteria achipteroides* (Ewing, 1913)
- Sensilli club-shaped, short, not reaching level of the anterior end of pedotecta I; lamellar cusps with distinct medial dens; lamellar setae barbed *A. grandis* Aoki, 1966
- 10 Relatively small species with body length less than 450 μm ; notogastral porose areas large; notogaster without granular punctuations 11
- Relatively large species with body length greater than 550 μm ; notogastral porose areas small; notogaster with large granular punctuations *P. punctata* (Nicolet, 1855)
- 11 Lamellar cusps with blunt, but distinct medial dens, lateral dens large; region between medial and lateral dens of lamellar cusps deeply concaved; interlamellar setae extending beyond anterior end of lamellae *P. distincta* (Aoki, 1959)
- Lamellar cusps truncate, without medial dens; end of lamellar cusps not concaved, but convex, with few small teeth; interlamellar setae not reaching anterior end of lamellae *P. truncata* Aoki, 1976

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Phylogenetic analysis of the Australian trans-Bass Strait millipede genus *Pogonosternum* (Carl, 1912) (Diplopoda, Polydesmida, Paradoxosomatidae) indicates multiple glacial refugia in southeastern Australia

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Abstract

This study documents the first detailed phylogenetic analysis of an Australian paradoxosomatid millipede genus. Two mitochondrial genes (partial COI and 16S) as well as partial nuclear 28S rDNA were amplified and sequenced for 41 individuals of the southeastern Australian genus *Pogonosternum* Jeekel, 1965. The analysis indicates that five species groups of *Pogonosternum* occur across New South Wales, Victoria and Tasmania: *P. nigrovirgatum* (Carl, 1912), *P. adrianae* Jeekel, 1982, *P. laetificum* Jeekel, 1982 and two undescribed species. *P. coniferum* (Jeekel, 1965) specimens cluster within *P. nigrovirgatum*. Most of these five species groups exhibit a pattern of high intraspecific genetic variability and highly localized haplotypes, suggesting that they were confined to multiple Pleistocene refugia on the southeastern Australian mainland. The phylogenetic data also show that northwestern Tasmania was colonized by *P. nigrovirgatum*, probably from central Victoria, and northeastern Tasmania by an as yet undescribed species from eastern Victoria.

Keywords

Invertebrate, COI, 16S, 28S, genetic variability

Introduction

Pogonosternum Jeekel, 1965 is the most widespread and species-rich genus of the millipede tribe Antichiropodini Brölemann, 1916 in Victoria, with the five described species *Pogonosternum nigrovirgatum* (Carl, 1902), *P. coniferum* Jeekel, 1965, *P. adrianae* Jeekel, 1982, *P. laetificum* Jeekel, 1982 and the subspecies *P. nigrovirgatum infusum* Jeekel, 1982, all hitherto recorded from Victoria only. However, Jeekel (1982) and Mesibov and Churchill (2003) have recorded undescribed *Pogonosternum* species from Tasmania, and Car (2010) listed two undescribed *Pogonosternum* species from New South Wales.

Thus, *Pogonosternum* occurs on both sides of Bass Strait, which separates mainland Australia from Tasmania. The paradoxosomatid genus *Somethus* Chamberlin, 1920 also has a trans-Bass Strait distribution (Jeekel 2006), as do the paradoxosomatid species *Dicranogonus pix* Jeekel, 1982 and *Notodesmus scotius* Chamberlin, 1920 (Mesibov 2014).

Many soil invertebrates, including millipedes, have limited active dispersal capabilities. Phylogenetic studies of southeastern Australian soil invertebrates can give important insights into the impact of glacial periods during the Pleistocene (Byrne 2008, Endo et al. 2014, Garrick et al. 2004, Schultz et al. 2009, Sunnucks et al. 2006) and assist in identifying biogeographic barriers (Chapple et al. 2011). Unfortunately, phylogenetic studies of Australian millipedes are rare and restricted to a few taxa from a small number of localities (Adams and Humphreys 1993, Nistelberger et al. 2014, Wojcieszek and Simmons 2012). For the australiosomatine species *Orocladosoma kosciuskovagum* (Brölemann, 1913) from the Australian Alps a hypothesis of multiple glacial refugia has been proposed (Endo et al. 2014) to explain the results of such studies. Similarly, the australiosomatine genus *Somethus* in South Australia was found to have high morphological and genetic variability within species was discovered: it seems probable that isolation in multiple glacial refugia during the Pleistocene was the evolutionary driving force for this variability (Decker 2016).

The present study documents a molecular phylogenetic analysis of the antichiropodine genus *Pogonosternum*, using specimens from across the genus range, and with molecular evidence indicating past isolation in multiple Pleistocene refugia. Finally, the identity and origin of Tasmanian *Pogonosternum* populations are clarified.

Material and methods

Specimen collecting and preservation

Pogonosternum specimens were collected by hand in Victoria and New South Wales in August 2014 by the author, Karin Voigtländer and Robert Mesibov, and by Mesibov in Tasmania in May 2014 and May 2015 (Fig. 1). Most sites were searched for 1–5 hours with the aim of finding 1–3 adult males. At only a few localities were *Pogonosternum*

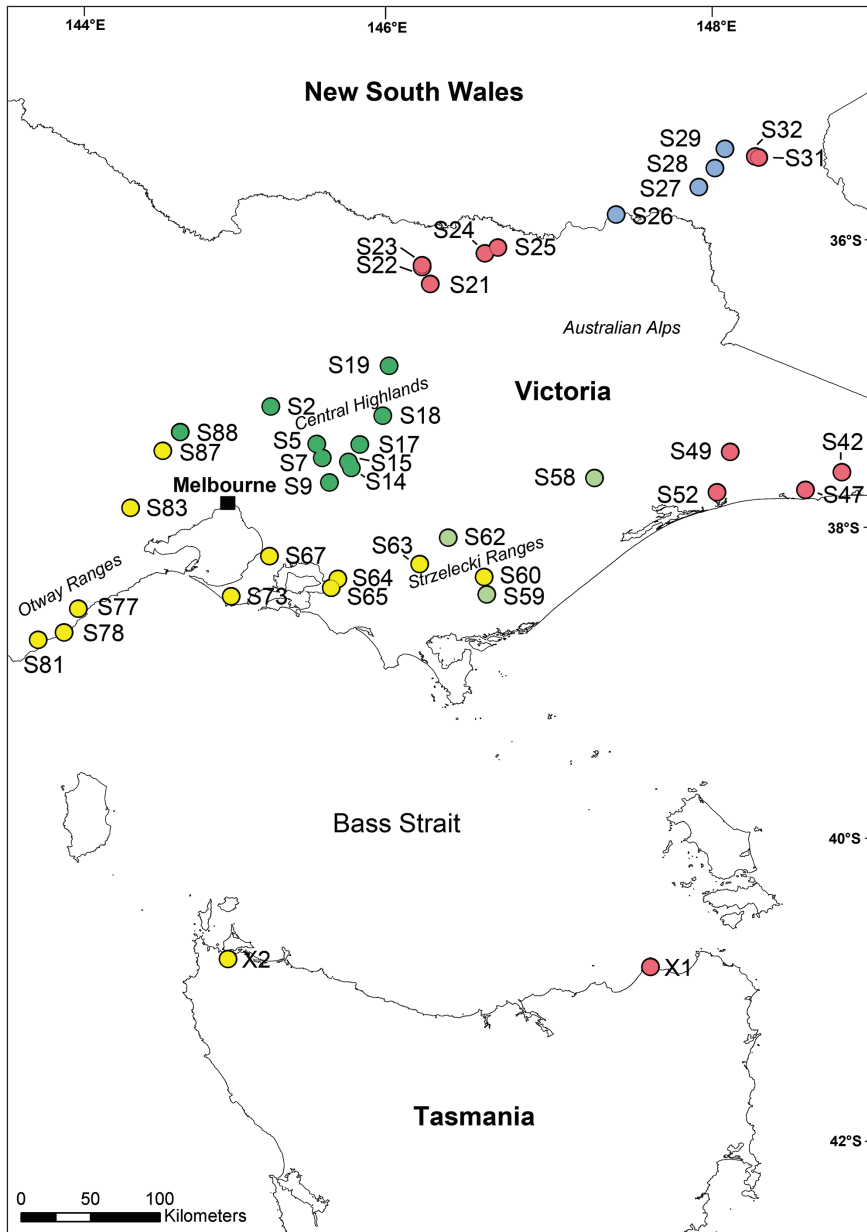


Figure 1. Map of Southeast Australia showing the distribution of *Pogonosternum* sampling sites with site numbers (see Table 1 and Suppl. material 1 for further details). *P. adrianae* (light green), *P. laetificum* (green), *P. nigrovirgatum* s. l./*coniferum* (yellow), *P. sp. A* (red), *P. sp. B* (blue).

found to be abundant. Specimens were killed and stored in 95% ethanol, with a change of ethanol after 1–2 months. Full details of locality, date, collector, collection number and coordinates (WGS84 decimal degrees) are provided in Suppl. material 1.

Illustrations

Maps were created with ArcGIS 10. The final phylogenetic trees were edited using Adobe Illustrator CS4.

Molecular analysis

DNA was extracted from 2–4 legs from each of 41 *Pogonosternum* specimens and from the three paradoxosomatid species *Archicladosoma magnum* Jeekel, 1984, *Somethus scopiferus* Jeekel, 2002 and *S. castaneus* (Attems, 1944), which were chosen as outgroups (Table 1). Total genomic DNA was extracted using the Qiagen DNAeasy Blood&Tissue kit following the standard protocol except that tissue was incubated for 48h.

Glom primer cocktail pairs (Decker 2016, Macek et al. 2014) were used to sequence a 618 bp fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. Primer pairs 28S D1a (Fw) and 28S D3b (Rv) (Dell’Ampio et al. 2009) were used to amplify 1225 bp of the D2 fragment and adjacent areas of D1 and D3 on the nuclear 28S ribosomal RNA gene.

For PCR protocol and all primer sequences (COI, 28S) see Decker (2016).

Primer pairs 16Sar (Fw) (5’-CGCCTGTTTAACAAAAACAT-3’) and 16Sbr (Rv) (5’-CCGGTCTGAACTCAGATCACGT-3’) (Simon et al. 1994) were used to sequence a 566 bp fragment of the large-subunit ribosomal RNA (16S) gene. The following thermocycling profile was used to amplify fragments of 16S: pre-denaturation at 94°C for 4 min 30 sec, 35 cycles of 30 sec at 94°C, 30 sec at 49°C and 50 sec at 72°C, and the final extension step for 5 min at 72°C.

All PCR mixes had a total volume of 10 µl comprising 1 µl template, 0.2 µM of each primer, 4x0.2 mM dNTPs [Peqlab], 1 x PCR Buffer containing 1.5 mM MgCl₂ [Peqlab], and 0.05u Polymerase [Peqlab].

All fragments were sequenced in both directions by the BiK-F Laboratory Centre, Frankfurt, Germany. All obtained sequences were checked via BLAST searches of GenBank; no contamination was discovered. The sequences were aligned by hand in ClustalX ver. 1.83 (Chenna et al. 2003) and uploaded to GenBank (Table 1).

Some homologisation problems in the 16S rRNA sequences arose mainly because of the highly variable expansion loops. As a result, selected alignment positions (272–297) were excluded from the 16S rRNA dataset for all further analyses using MEGA6.

The final alignments consisted of 618 bp of COI mtDNA, 540 bp of 16S rRNA and 1206 bp of 28S rRNA. The combined datasets after these exclusions consisted of 1158 bp for COI+16S. Individual partial alignments can be obtained from the author upon request. The alignment of the combined dataset can be found in the Suppl. material 2 as a FASTA file.

COI and 16S sequences were combined as a single dataset and incongruence assessed between the mtDNA intergenic spacer sequences with the incongruence length difference (ILD) test (Farris et al. 1994) implemented as the partition homogeneity test

Table 1. Site numbers, localities, GenBank accession numbers and repository accession numbers for all specimens analyzed. (See also Fig. 1) NMV = Museum Victoria, Melbourne, Victoria, Australia; QVMAG = Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia; SAM = South Australian Museum, Adelaide, Australia; SMNG = Senckenberg Museum of Natural History Görlitz, Görlitz, Germany; NSW = New South Wales; SA = South Australia; TAS = Tasmania; VIC = Victoria. See Suppl. material 1 for further details.

Species	Site No.	Locality	GenBank Acc. No. COI	GenBank Acc. No. 16S	GenBank Acc. No. 28S	Voucher
Outgroup						
<i>Somethus scopiferus</i> Jeekel, 2002		SA, Martin Washpool Conservation Park	KT948674	KU833272		SMNG VNR016931
<i>Somethus castaneus</i> (Atrems, 1944)		SA, Adelaide, Upper Sturt			KT964477	SAM OM2135
<i>Archicladosoma magnum</i> Jeekel, 1984		VIC, N Rawson	KT948681	KU833273		SMNG VNR016994
Ingroup						
<i>Pogonosternum adrianae</i>	S58	VIC, S Dargo	KU745235	KU745194	KU745185	NMV K-12203
<i>Pogonosternum adrianae</i>	S59	VIC, W Balook	KU745236	KU745195		NMV K-12204
<i>Pogonosternum adrianae</i>	S62	VIC, NE Moe	KU745237	KU745196	KU745186	NMV K-12207
<i>Pogonosternum coniferum</i>	S67	VIC, Langwarrin	KU745238	KU745197		NMV K-12212
<i>Pogonosternum coniferum</i>	S71	VIC, NE Cape Schandk	KU745239	KU745198		NMV K-12213
<i>Pogonosternum lactificum</i>	S2	VIC, NE Tyak	KU745240	KU745199		NMV K-12095
<i>Pogonosternum lactificum</i>	S5	VIC, SE Glenburn	KU745241	KU745200		NMV K-12096
<i>Pogonosternum lactificum</i>	S7	VIC, E Toolangi	KU745242	KU745201		NMV K-12101
<i>Pogonosternum lactificum</i>	S9	VIC, SE Healesville	KU745243	KU745202		NMV K-12102
<i>Pogonosternum lactificum</i>	S14	VIC, SE Narbethong	KU745244	KU745203	KU745187	SMNG VNR016987
<i>Pogonosternum lactificum</i>	S15	VIC, E Narbethong	KU745245	KU745204		SMNG VNR016988
<i>Pogonosternum lactificum</i>	S17	VIC, N Marysville	KU745246	KU745205		NMV K-12109
<i>Pogonosternum lactificum</i>	S18	VIC, S Eildon	KU745247	KU745206		NMV K-12110
<i>Pogonosternum lactificum</i>	S19	VIC, W Barjarg	KU745248	KU745207		NMV K-12176
<i>Pogonosternum lactificum</i>	S88	VIC, Mt Macedon	KU745249	KU745208		NMV K-13113
<i>Pogonosternum nigrovirgatum</i>	S60	VIC, SE Traralgon South	KU745250	KU745209	KU745188	NMV K-12205
<i>Pogonosternum nigrovirgatum</i>	S63	VIC, SW Trafalgar	KU745251	KU745210		NMV K-12208
<i>Pogonosternum nigrovirgatum</i>	S64	VIC, W Nyora	KU745252	KU745211		SMNG VNR016989
<i>Pogonosternum nigrovirgatum</i>	S65	VIC, SE The Gurdies	KT948680	KU745212	KT964478	NMV K-12211

Species	Site No.	Locality	GenBank Acc. No. COI	GenBank Acc. No. 16S	GenBank Acc. No. 28S	Voucher
<i>Pogonosternum cf. nigrovirgatum</i>	S77	VIC, NW Lorne	KU745253	KU745213		SMNG VNR016990
<i>Pogonosternum cf. nigrovirgatum</i>	S78	VIC, W Kennett River	KU745254	KU745214		NMV K-13114
<i>Pogonosternum cf. nigrovirgatum</i>	S81	VIC, N Apollo Bay	KU745255	KU745215	KU745189	NMV K-13115
<i>Pogonosternum cf. nigrovirgatum</i>	S83	VIC, SW Staughton Vale	KU745256	KU745216		SMNG VNR016991
<i>Pogonosternum nigrovirgatum</i>	S87	VIC, W Gisborne	KU745257	KU745217		NMV K-13116
<i>Pogonosternum cf. nigrovirgatum</i>	X2	TAS, S West Montagu	KU745258	KU745218		QVMAG:2015:23:1
<i>Pogonosternum</i> sp. A	S21	VIC, N Glenrowan	KU745259	KU745219		NMV K-12177
<i>Pogonosternum</i> sp. A	S22	VIC, NE Thoonia I	KU745260	KU745220		NMV K-12178
<i>Pogonosternum</i> sp. A	S23	VIC, NE Thoonia II	KU745261	KU745221		NMV K-12179
<i>Pogonosternum</i> sp. A	S24	VIC, SE Chiltern	KU745262	KU745222		SMNG VNR016992
<i>Pogonosternum</i> sp. A	S25	VIC, SSW Chiltern	KU745263	KU745223	KU745190	NMV K-12181
<i>Pogonosternum</i> sp. A	S31	NSW, E Talbingo I	KU745264	KU745224		NMV K-12187
<i>Pogonosternum</i> sp. A	S32	NSW, E Talbingo II	KU745265	KU745225		NMV K-12188
<i>Pogonosternum</i> sp. A	S42	VIC, NNW Bemm River	KU745266	KU745226		NMV K-12192
<i>Pogonosternum</i> sp. A	S47	VIC, E Orbost	KU745267	KU745227		NMV K-12195
<i>Pogonosternum</i> sp. A	S49	VIC, Buchan	KU745268	KU745228		NMV K-12197
<i>Pogonosternum</i> sp. A	S52	VIC, SW Nowa Nowa	KU745269	KU745229		NMV K-12199
<i>Pogonosternum</i> sp. A	X1	TAS, W Tomahawk	KU745270	KU745230	KU745191	SMNG VNR016986
<i>Pogonosternum</i> sp. B	S26	NSW, SE Holbrook	KU745271	KU745231		NMV K-12182
<i>Pogonosternum</i> sp. B	S27	NSW, W Tumbarumba	KU745272	KU745232		NMV K-12183
<i>Pogonosternum</i> sp. B	S28	NSW, NNE Tumbarumba	KU745273	KU745233	KU745192	SMNG VNR016993
<i>Pogonosternum</i> sp. B	S29	NSW, SE Badlow	KU745274	KU745234	KU745193	NMV K-12185

in PAUP* version 4.0b10 using a full heuristic search, 10 random taxon addition replicates, tree-bisection-reconnection (TBR) branch swapping, and with MaxTrees set to 100 (Swofford 2002). The best-fit model of nucleotide substitution for the individual COI and 16S dataset was determined by MrModelTest 2 (Nylander 2004). The best-fit model of nucleotide substitution selected using MrModelTest 2 was the General Time Reversible model with gamma distribution and proportion of invariant sites (Nei and Kumar 2000) for the individual COI and 16S dataset. The trees constructed from individual genes did not show significant conflicts in topology (nodes different among trees with support > 70% in ML) and no significant incongruence among the three genes was revealed by the ILD test ($P > 0.83$ in all of the pairwise comparisons), so the sequences were concatenated into a dataset containing 1158 characters for phylogenetic analysis.

The combined dataset of COI and 16S was analysed under maximum likelihood (ML) using MEGA6 (Tamura et al. 2011) and Bayesian inference (BI) using MrBayes version 3.2 (Ronquist et al. 2012). For ML analysis, three independent runs were performed with nodal support estimated from 1000 bootstrap (BP) pseudoreplicates using the best-fit model for the concatenated dataset. For Bayesian analysis, two independent runs were carried out with four differentially heated Metropolis-coupled Monte Carlo Markov chains for 10 000 000 generations started from a random tree and chains were sampled every 100 generations.

Multiple runs of ML and BI converged in trees with the same topology and similar likelihood score so that only the result of the first run is presented. The topology resulting from ML and BI analyses was largely congruent except for the arrangements of several terminal nodes with low support. Thus, results from the ML and BI analyses are shown together based on the ML tree with bootstrap (BP) and posterior probabilities (PP) of the major lineages shown on the corresponding branches with BP values > 70 (Fig. 2).

An appropriate DNA substitution model was determined for 28S under the Bayesian Information Criterion (BIC) in Modeltest implemented in MEGA 6 (Tamura et al. 2011). The lowest Bayesian Information Criterion score (BIC) was obtained for 28S rRNA (BIC 3875.11) with the Tamura 3-parameter model (Tamura 1992).

A phylogenetic hypothesis was inferred for COI+16S and 28S by using the maximum likelihood method conducted in MEGA6 (Tamura et al. 2011). The phylogenetic tree with the highest log likelihood (COI+16S: -7237.4280; 28S: -1831.9238) is shown (Figs 2, 3). Initial trees for the heuristic search were obtained by applying the neighbor-joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach (Tamura et al. 2004). A discrete Gamma distribution was used to model evolutionary rate differences among sites (five categories (+G, parameter = COI+16S: 0.2338)). The bootstrap consensus tree inferred from 1000 replicates (Felsenstein 1985) is here used as the best estimate of the phylogeny of the analyzed taxa (Figs 2, 3).

Mean uncorrected pairwise distances between terminals (transformed into percentages) were determined using MEGA6 (Tamura et al. 2011) and can be found in Suppl. material 3.

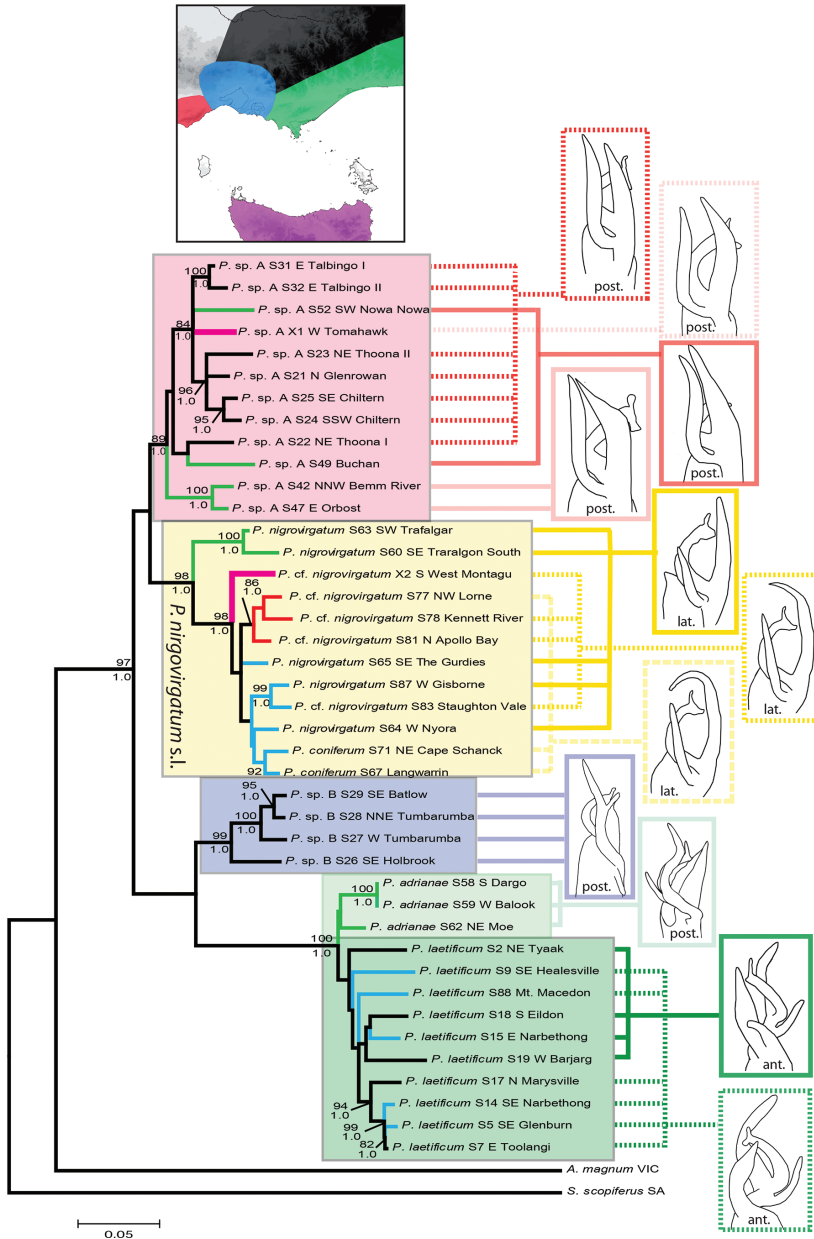


Figure 2. Maximum likelihood tree for the combined mitochondrial COI+16S dataset, 1000 bootstrap replicates, values below 70 not shown. The bootstrap values of ML and posterior probabilities of BI are given above and below the corresponding branches, respectively, for all major clades. Scale bar = substitutions per site. Coloured blocks indicate species groups. Color of branches refers to the major subregions shown in the map, Tasmanian branches thicker. General differences in male gonopod morphology are shown by sketches of the apical region of the right gonopod not drawn to scale. Coloured lines link those analysed specimens that have similar gonopod morphology. Posterior view = post.; lateral view = lat.; anterior view = ant.

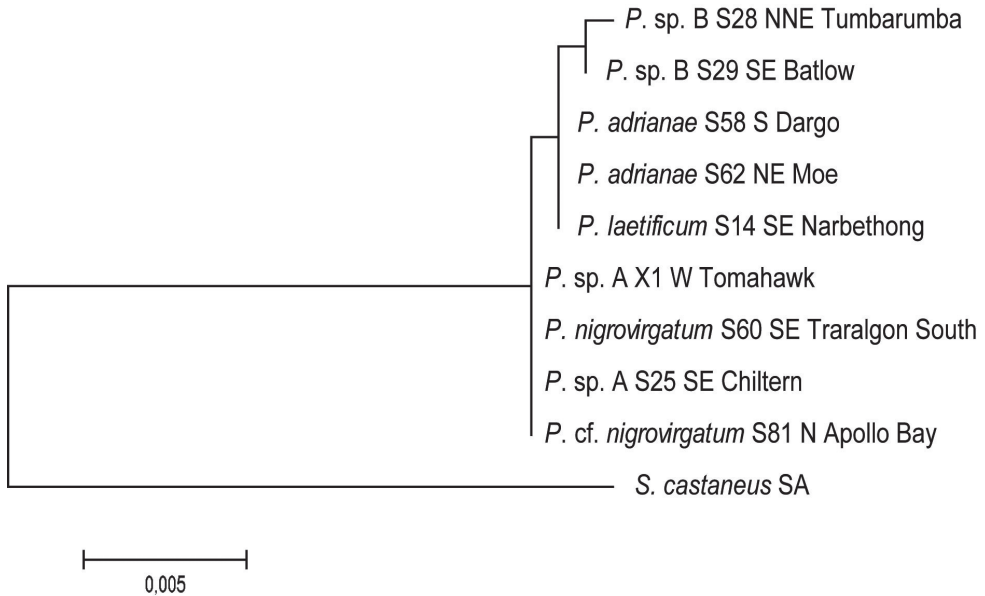


Figure 3. Maximum likelihood tree for the nuclear 28S dataset, 1000 bootstrap replicates, values below 70 not shown.

Results

Phylogenetic and distance analysis

The monophyly of the genus *Pogonosternum* is strongly supported (ML BP = 97; BI PP = 1.0) in the mitochondrial tree and shows five clades within *Pogonosternum*, resembling five species groups (Fig. 2).

One main clade includes three species from the mountainous area east and north-east of Melbourne: the undescribed species *Pogonosternum* sp. B (ML BP = 99; BI PP = 1.0), already mentioned by Car (2010) from New South Wales, *P. laetificum* (ML BP = 33; BI PP = 1.0) and *P. adrianae* (ML BP = 68; BI PP = 1.0), both not supported, the latter forming a sister clade (ML BP = 100; BI PP = 1.0) to *P. sp. B*. The latter two species show moderately large intraspecific distances ranging from 1.1 to 4.6% (*P. sp. B*) and 0.1 to 3.0% (*P. adrianae*), while *P. laetificum* shows high intraspecific distances (0.6–5.5%), even between geographically close (<10 km) populations.

Pogonosternum nigrovirgatum sensu lato with a trans-Bass Strait distribution formed a well-supported (ML BP = 89; BI PP = 1.0) sister clade to the new species *P. sp. A* (ML BP = 98; BI PP = 1.0) that also has a trans-Bass Strait distribution. *Pogonosternum* sp. A also occurs in New South Wales (Car 2010) and in northeast Tasmania (Mesibov & Churchill 2003). *Pogonosternum nigrovirgatum* s. l. occurs on mainland Australia (Otway Ranges to eastern Victoria) and in northwest Tasmania. *Pogonosternum coniferum* clusters with another form with intermediate gonopods (referred to as *P. cf. nigrovirgatum* in Fig. 2) between *P. nigrovirgatum* sensu stricto and *P. coniferum*.

Both *P. nigrovirgatum* s. l. and *P. sp. A* show high intraspecific distances ranging from 1.8 to 6.8% within *P. nigrovirgatum* s. l. and 1.1 to 5.9% within *P. sp. A*.

Within the *P. nigrovirgatum* s. l. species-group, the greatest genetic distances were observed between populations in the Strzelecki Ranges (S60, S63; ML BP = 100; BI PP = 1.0) and more western populations, with values ranging from 5.0 to 6.8%. Specimens from the Otway Ranges (S77, S78, S81) all formed a well-supported cluster (ML BP = 86; BI PP = 1.0). The Tasmanian specimen (X2) was distinct from both the Strzelecki Ranges (5.4–6.0%) and central and western Victorian specimens (3.7–3.8%). In the case of *Pogonosternum* sp. A the largest distances (4.2–5.8%) were between the Eastern Gippsland populations (S42, S47; ML BP = 100; BI PP = 1.0) and all other specimens. The status of the northeast Tasmanian specimen is not well resolved; it is closest to a population from Kosciuszko National Park (S31, 3.0%), the two forming a poorly supported sister clade with a specimen from Gippsland (S52; ML BP = 55; BI PP = 0.6).

All species show considerable intraspecific genetic distances and high phylogeographic structure, especially *P. laetificum*, and, except in the case of *P. adrianae*, no haplotypes are shared between different populations. Additional one to three sequenced specimens from eight sampling sites (S14, S15, S22, S58, S59, S78, S83, S87) always showed the same haplotype in *Pogonosternum* (data not published).

Interspecific distances within the genus *Pogonosternum* are moderately large, varying from 5.5% (*P. sp. A*–*P. nigrovirgatum* s. l.) to 10.4% (*P. nigrovirgatum* s. l.–*P. laetificum*), except *P. adrianae* to *P. laetificum* with only 2.9%.

Owing to the general lack of variability within the nuclear 28S rRNA dataset, the phylogenetic relationships among species were largely unresolved. Distances for 28S rRNA within *Pogonosternum* are very low, with a maximum of three base pair differences noted for *P. sp. B* (Fig. 3). Only the two condensed sister clades of *P. nigrovirgatum* + *P. sp. A* and *P. adrianae* + *P. laetificum*, as well as *P. sp. B* are shown.

Morphology

In a separate paper (Decker, in preparation), the morphology of the *Pogonosternum* species groups is described in detail and new species are described, based on the specimens used here and from ca 130 additional localities. Here I note briefly that several common morphological features were observed in the gonopods of *P. nigrovirgatum* s. l., *P. laetificum*, and *P. sp. A*: some specimens also showed intermediate states of those features (Fig. 2). It was found, however, when additional material was examined from each population that the morphology of each population was locally stable. It was only in rare cases in the Otway Ranges and NW Tasmania populations that two gonopod morphs occurred in one place.

Surprisingly, gonopod morphology did not appear to agree well with the phylogenetic tree (Fig. 2). Various gonopod forms were distributed with no apparent phylogeographical correlation. Only the species *P. adrianae* and *P. sp. B* showed stability in both gonopods and some other non-gonopodal characters over their distribution area, even when material from other museum collections was included (Decker, in preparation).

Discussion

Phylogenetic analysis

The mitochondrial tree (Fig. 2) shows five main clades, suggesting five species. *Pogonosternum coniferum* clustered within *P. nigrovirgatum*, and its taxonomic status needs re-examination (Decker, in preparation).

The 28S tree shows little or only little resolution at the species level (Fig. 3), but was useful in identifying sister clades. This result contrasts with that from a study of the paradoxosomatid genus *Somethus* in South Australia, in which the 28S gene was used successfully for species identification (Decker 2016). Future studies on other Australian Paradoxosomatidae will reveal if 28S is useful as a diagnostic nuclear gene at the species level.

Morphological variability

With the exception of *P. adrianae* and *P. sp. B*, *Pogonosternum* species show significant variability in gonopod form, with local morphs occurring throughout each species' distribution area.

Interestingly, *P. adrianae* is morphologically distinct (in size, spiracles, male tibio-tarsal brushes and gonopods, female coxal process) from *P. laetificum* despite their close genetic distance.

Gonopod variability was also documented for some species of *Somethus* in South Australia (Decker 2016) and *Stygiochiropus* Humphreys & Shear, 1993 from Western Australia (Humphreys and Shear 1993). Another good example of variability is seen in the trans-Bass Strait (eastern Victoria, NE Tasmania) paradoxosomatid millipede, *Dicranogonus pix*: while this species shows only slight variability in gonopods there is marked variation in the development of their paranota. Individuals with no paranota are separated from those with keels by a gap between the Kent and Furneaux Groups of islands (Mesibov 2014).

This study has shown that in the area of southern and southeast Australia, there are at least two genera, *Pogonosternum* and *Somethus* (Decker 2016), which both show variability in morphology and genetics. Poor sampling and too few specimens could lead to incorrect conclusions and unnecessary multiple species descriptions.

Multiple glacial refugia in southeastern Australia

The results indicate that there is high intraspecific genetic divergence, with high genetic distances and haplotype diversity in the mitochondrial genes between populations of *Pogonosternum*, even those adjacent to each other. The *P. laetificum* clade, which has been sampled extensively in the Central Highlands, shows particularly high intraspe-

cific genetic differences (mean genetic distance of 3.9%), apparently without corresponding geographic patterning, or morphological variation (Decker, in preparation).

The phylogenetic patterns with high intraspecific divergence, high genetic distances, and haplotype diversity with unique local haplotypes, resulting in long branches, shown by *Pogonosternum*, indicate multiple Pleistocene refugia according to Byrne (2008). These refugia provided suitably moist habitats in which species could persist during the dry, cold climate cycles of the Pleistocene period in southern Australia, while glaciation was limited to the alpine areas of the Great Dividing Range and Tasmania (Barrows et al. 2002). Moderate to high genetic diversity prior to these cycles can be assumed for poorly dispersing millipedes, through isolation by distance, and it is likely that populations were isolated within refugia, leading to further genetic diversification. In contrast, contractions to one or few major refugia during cold, arid periods would result in a low genetic diversity, few divergent lineages and low haplotype diversity, with few haplotypes in areas of postglacial recolonisation (Byrne 2008).

The phylogenetic patterns shown by *Pogonosternum* suggest that in Victoria and New South Wales there were large areas with multiple local refugia during the Pleistocene. No region in the study area on mainland Australia showed results which indicate rapid postglacial resettlement of *Pogonosternum*.

Evidence for multiple glacial refugia was also identified in the spirostreptidan millipede *Atelomastix bamfordi* Edward & Harvey, 2010 in Western Australia (Nistelberger et al. 2014) and for some species of *Somethus* in South Australia (Decker 2016). Similar phylogeographic patterns seem to occur in other soil invertebrates with limited dispersal capacities in southern Australia, for example flatworms (Sunnucks et al. 2006) and springtails (Garrick et al. 2004).

Endo et al. (2014) have suggested, however, that glacial periods have had less of an impact on the distribution and genetic diversity of invertebrate groups (Coleoptera, Orthoptera, Collembola, Diplopoda) in the Australian Alps than they have in alpine systems in the Northern Hemisphere.

However, further studies on genetic and morphological variability on a finer geographical scale could lead to a better understanding of the pattern and impact of isolation in multiple glacial refugia during the Pleistocene, also as an evolutionary driving force for morphological variability in some species.

Gippsland phylogeography

There is a notable high genetic distance gap within *P. nigrovirgatum* sensu lato between specimens from the Strzelecki Ranges (S60, S63), West Gippsland, and those sampled in the central and western regions in Victoria, but some specimens of adjacent populations from the latter (S64, S65) were morphologically indistinguishable from

specimens from the Strzelecki Ranges. A similar genetic gap was observed in *P. sp. A* for the populations in Eastern Gippsland east of Orbost (S42, S47) and all other populations. These two cases indicate that these areas may have been isolated for long periods from neighboring regions, possibly before the Pleistocene, perhaps during a marine incursion in the Gippsland Basin and other parts of southeast Australia close to the Miocene–Pliocene boundary (Dickinson et al. 2002).

Trans-Bass Strait distribution

The genus *Pogonosternum* shows a trans-Bass Strait distribution and most likely originated in mainland southeast Australia, since the highest species diversity is found on the mainland and the two Tasmanian branches occupy only very subordinate positions on the tree (Fig. 2). Tasmanian populations of this genus are restricted to the northeast and northwest corners of the Tasmanian mainland and neighboring islands, and presumably dispersed from Victoria when it was largely connected with Tasmania during the Pleistocene (Lambeck and Chappell 2001). Mitochondrial data suggest that the sequenced population of *P. nigrovirgatum* s. l. in northwest Tasmania was most likely derived from one in central Victoria or the Otway Ranges. While the results for *P. sp. A* from northeast Tasmania do not show a close relationship to coastal Victorian populations, analysis of 16S (data not included here) including sequences from two other localities in the western part of East Gippsland showed the Tasmanian specimen clustering with the latter. This indicates that the settlement of Tasmania by this species started in the Gippsland region. A remarkably similar distribution to that of *P. sp. A* across Bass Strait is also known for the paradoxosomatid millipedes *Dicranogonus pix* and *Notodesmus scotius* (Mesibov 2014).

Further studies using more sampling localities in Tasmania and its islands could indicate points of origin in Victoria and the timing of millipede settlement of Tasmania.

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Supplementary material 1

Full data of sequenced specimens

Authors: Peter Decker

Data type: Tab-delimited text file

Explanation note: Full details of sequenced specimens, including locality, date, collector, collection number and coordinates.

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Supplementary material 2

Alignment of combined dataset

Authors: Peter Decker

Data type: FASTA file

Explanation note: Alignment of the combined COI mtDNA and 16S rRNA dataset

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Supplementary material 3

P-distances of combined COI and 16S dataset

Authors: Peter Decker

Data type: CSV File

Explanation note: Mean uncorrected pairwise distances between terminals (transformed into percentages) of the combined COI mtDNA and 16S rRNA dataset.

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The millipede family Cryptodesmidae in Indochina (Diplopoda, Polydesmida)

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Abstract

In addition to two species of the diplopod family Cryptodesmidae already reported from Indochina, *Trichopeltis kometis* (Attems, 1938) and *Ophrydesmus anichkini* Golovatch, 2015, the fauna of that region is supplemented by three species: *Niponia nodulosa* Verhoeff, 1931, a millipede hitherto known only from southern Japan and Taiwan, is now recorded from Vietnam; *Trichopeltis cavernicola* **sp. n.** from Laos, the sixth species in that tropical Asian genus, is the first presumed troglobite to be described amongst the Asian cryptodesmids and shows several distinct troglomorphic features; and *Circulocryptus* **gen. n.**, monobasic, which joins the tribe Dyakryptini, but differs from all three contribal genera (two monobasic from Borneo, and another, oligotypic, from New Guinea) primarily in the gonopods of *C. faillei* **sp. n.**, from Vietnam, being especially elaborate and subcircular, the telopodites strongly twisted, and the sole-nomere lying much more basally.

Keywords

Diplopoda, Cryptodesmidae, taxonomy, new genus, new species, Vietnam, Laos

Introduction

In tropical or subtropical Asia and Australasia, the millipede family Cryptodesmidae currently comprises only 11 genera (including two that are dubious) and 34 species. Among them, only two genera and species, *Trichopeltis kometis* (Attems, 1938) (= *T. deharvengi* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2010) and *Ophrydesmus*

anichkini Golovatch, 2015, occur in Indochina, the former species being quite widespread in Vietnam, Laos and Cambodia, the latter species described from a single locality in southern Vietnam (Golovatch 2015, Golovatch and Akkari 2016).

This paper puts on record another three Cryptodesmidae found in Indochina. One represents a new genus and species from Vietnam. One more is a new species of a rather small tropical Asian genus from a cave in Laos, the first presumed troglobitic Asian cryptodesmid. The third species is common in southern Japan and Taiwan, being reported here for the first time from Indochina, in particular, northern Vietnam.

Material and methods

The types of both new species were collected by my French colleagues and friends Louis Deharveng and Anne Bedos, both from the Muséum national d'Histoire naturelle, Paris (MNHN), France, and Arnaud Faille, from the Bayerische Zoologische Staatssammlung, München (ZSM), Germany, and are now deposited in MNHN. The samples of *Niponia nodulosa* Verhoeff, 1931, were taken by friend Dmitri N. Fedorenko (Moscow, Russia), and are now housed in the Zoological Museum of the Moscow State University, Moscow (ZMUM), Russia. Focus stacking pictures were taken by Jonathan Brecko, of the Royal Museum for Central Africa, Tervuren (MRAC), Belgium.

Taxonomic part

Niponia nodulosa Verhoeff, 1931

Material. 1 ♂, 1 ♀ (ZMUM ♀ 3115), Vietnam, 25 km E of Hai Phong, Cat Ba Island, National Park, ca 10 km road-km NW of Cat Ba City, N20°47'56", E106°59'47", 10-24.X.2011, leg. D. Fedorenko.

Remarks. Based on material from Taiwan, this species has recently been redescribed and illustrated in due detail (Golovatch et al. 2011). It is common in southern Japan and Taiwan (Golovatch et al. 2011), erroneously reported also from continental China (Golovatch et al. 2010). The Vietnamese samples fully agree with the detailed account given by Golovatch et al. (2011).

Trichopeltis cavernicola sp. n.

<http://zoobank.org/61A071B5-A30A-49D4-B10D-A6833E8343D9>

Figs 1–7

Type material. Holotype ♂ (MNHN JC 367), Laos, Khammouane Prov., Ban Naden, Cave Tham Namlat, N17.504969°, E105.385598°, ca 180 m a.s.l., 09.11.2011, leg. L. Deharveng & A. Bedos (Lao 11-51).



Figures 1–3. Habitus of *Trichopeltis cavernicola* sp. n., ♂ holotype, dorsal, lateral and ventral views, respectively.

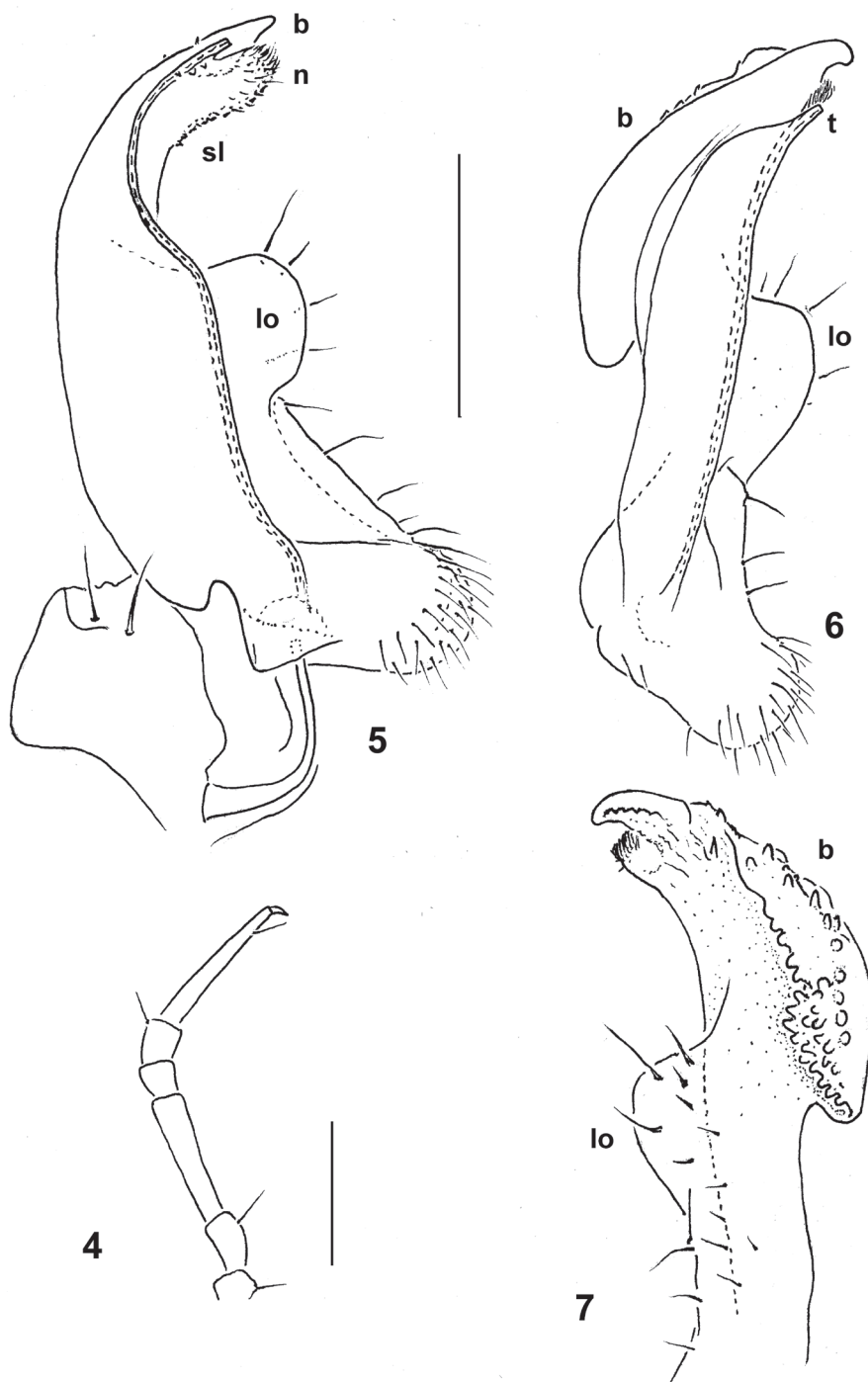
Name. To emphasize the cavernicolous and troglomorphic appearance of this new species; noun in apposition.

Diagnosis. Differs from congeners by the relatively gracile and slender body in which each midbody paratergite is clearly narrower than prozonite width, coupled

with the increasingly upturned postcollum paraterga and such obviously troglomorphic features as an unpigmented body, as well as the extremely long and slender legs and antennae. In addition, much of the distolateral part of an indistinctly tripartite gonopod telopodite is densely covered with wart-shaped knobs while the tip of the solenomere is vestigial and simple.

Description. Length ca 11 mm, width of midbody pro- and metazonae 0.8 and 1.7 mm, respectively. General coloration in alcohol entirely pallid, tegument mostly translucent (Figs 1–3).

Body with 20 segments (composed of collum plus 17 podous and one apodous rings, plus telson). In width, head \ll collum $<$ segment 2 $<$ 3 $<$ 4–17; thereafter body rapidly tapering towards telson. Head behind labrum very densely and clearly microgranulate and pilose; epicranial suture superficial, more distinct in vertigial region. Antennae unusually long and slender for a cryptodesmid (Figs 2, 3), barely clavate, not placed inside a groove, in situ reaching behind segment 3 when stretched laterally or ventrolaterally; in length, antennomere 2 $>$ 5=6 $>$ 3=4; antennomeres 5 and 6 each with a compact apicodorsal group of bacilliform sensilla. Interantennal isthmus about as broad as diameter of antennal socket. Tegument dull, clearly microgranulate almost throughout, only prozonae usually more finely shagreened. Dorsum from only slightly and regularly convex to increasingly flat towards midbody metazonae; paraterga mostly set at about upper 1/4 of body, very strongly developed (Figs 1–3), beginning with collum. Collum completely covering the head from above, biconvex, but clearly lobulate anteriorly (10+10 lobulations) and caudolaterally (5+5 lobulations, including lateralmost one shared with anterior row), but not mediocaudally; paraterga distinctly upturned as opposed to subhorizontal paraterga 2–7. Postcollum paraterga short and narrowly rounded laterally, on each side usually with 3–4 lateral, 4–5 anterior and 4–5 posterior lobulations, gradually, but increasingly upturned and elevated above dorsum towards segment 19 (Figs 1–3). Marginal lobulations on paraterga mostly rounded, relatively large and well separated from one another, lateral end of paraterga drawn caudad gradually, but increasingly on segments 15–19, produced behind rear tergal margin only on segments 18 and 19. Caudal row of lobulations on paraterga gradually diminished in size towards paratergal base to get transformed into 5+5 clearly smaller, subequal, subhorizontal, caudomarginal lobules, each of the latter bearing a smaller, narrowly rounded, subvertical tubercle/knob at base. Another two, more or less regular, transverse rows of 6–8+6–8 similar, almost sharp, subvertical knobs extending onto paraterga in front of mediocaudal row until about segment 15, followed by three irregular rows of similar knobs thereafter (Fig. 1). As a result, middle parts of metaterga 2–14 with three, of following metaterga with four, transverse, usually rather irregular rows of small, round, setigerous knobs/tubercles in addition to caudalmost, regular row of smaller lobules just in front of a microspiculate limbus. Tergal setae long and simple, mostly abraded, only a few retained on several caudal metaterga (Fig. 1). Neither axial line nor radii, nor pleurosternal carinae. Ozopores invisible, pore formula untraceable. Stricture dividing pro- and metazonae broad, shallow and microgranulate like adjacent metazonae. Epiproct (Figs 1–3) short, conical, subtruncate



Figures 4–7. *Trichopeltis cavernicola* sp. n., ♂ holotype: **4** leg 7, lateral view **5–7** left gonopod, mesal, submesal and sublateral views, respectively. Designations: **lo** lobe at midway of telopodite; **sl** solenomere branch; **t** tip of solenomere; **b** lateral branch; **n** setose lobule Scale bars: 0.2 mm.

at apex. Hypoproct (Fig. 3) subtrapeziform, 1+1 caudal setae clearly separated, borne on small knobs.

Sternites narrow (Fig. 3), sparsely setose, moderately impressed along main axis, clearly broadened only between coxae 7 and 9, respectively. Legs very long and slender, without modifications (Figs 1–4), ca 1.4–1.5 times as long as paratergal width (♂) (Figs 1–3); in length, femora = tarsi >> prefemora > coxae > postfemora and tibiae (Fig. 4); gonapophyses on coxae 2 small cones; neither adenostyles nor tarsal brushes. Gonopod aperture transversely ovoid, caudal and lateral margins thin, slightly elevated (Fig. 3).

Gonopods (Fig. 5–7) fairly complex, in situ held parallel to each other (Fig. 3). Telopodite only slightly curved caudad, vaguely tripartite. A short, simple, very sparsely setose, rounded lobe (**lo**) lying caudally at about midlength of telopodite and marking the end of the latter's stout half. A twice as slender acropodite subdivided into an irregularly shaped lateral branch (**b**), longest, subunciform apically and densely beset with wart-like knobs on lateral face, and a rather simple, suberect, mesal solenomere branch (**sl**) apically extended into a small, mesal, densely setose lobule (**n**) with an adjacent, minute, simple, rod-shaped solenomere proper (**t**). Neither an accessory seminal chamber nor a hairy pulvillus.

Remarks. *Trichopeltis* Pocock, 1894 (= *Otodesmus* Cook, 1896), formerly comprised six species that range from the Himalayas of India (Assam and Darjeeling District) and Myanmar to southern China, Indochina and Indonesia (Sumatra) (Golovatch et al. 2010, Golovatch and Akkari 2016).

The new species is not only the first clearly troglomorphic *Trichopeltis*, but also the first presumed troglobite among the Asian Cryptodesmidae. Similarly strongly cave-adapted cryptodesmids are exceptional, e.g. the highly troglomorphic *Peridontodesmella alba* Schubart, 1957, from several caves in São Paulo State, Brazil (Trajano et al. 2000).

Circulocryptus gen. n.

<http://zoobank.org/B7688BED-6280-4700-A7F3-F3CA32A02952>

Diagnosis. Cryptodesmidae with gonopod telopodite stout, subcircular, clearly twisted (= seminal groove mostly running on lateral face) and vaguely bipartite, supplied with a mesal prefemoral process at base; a considerable, spiniform, retrorse solenomere terminating a sigmoid seminal groove and placed near telopodite midway; neither an accessory seminal chamber nor a hairy pulvillus.

Name. To emphasize the subcircular gonopods; gender masculine.

Description. Small-sized Cryptodesmidae (adults about 1 cm long and 3 mm wide) with 20 segments (trunk composed of collum plus 17 podous and one apodous rings, plus telson); a flabellate collum covering the head from above. Antennae clearly clavate. Paraterga short and very broad, slightly declined, mostly squarish laterally, lobulate and/or radiate anteriorly, laterally and posteriorly; ozopores invisible, pore formula untraceable. Middle parts of metaterga with seriate transverse rows of abundant setigerous knobs/tubercles partly extending onto paraterga; tergal setae present,

simple; neither sternal cones nor leg modifications. Gonopod aperture subcordiform; gonopod telopodites in situ held parallel to each other, each vaguely bipartite and complex, with a mesal, parabasal, prefemoral process; basal part of telopodite clearly twisted and surmounted by a long, spiniform solenomere terminating a sigmoid seminal groove and situated at about telopodite midway. Neither an accessory seminal chamber nor a hairy pulvillus.

Type-species. *Circulocryptus faillei* sp. n.

Remarks. Globally, the *Cryptodesmidae* is a relatively small family that encompasses almost 40 genera and nearly 130 species and ranges from Mexico to Argentina in the Americas, occurring also in tropical Africa and tropical to subtropical Asia to Papua New Guinea and Japan in the East (Minelli 2015). Only three genera have hitherto been known in the entire family, in which the gonopod shows a distinct prefemoral process arising mesally near the origin of the seminal groove: *Astrolabius* Verhoeff, 1931, with 2 species from Papua New Guinea (Golovatch et al. 2010), *Dyakryptus* Hoffman, 1961, monobasic, from Eastern Malaysia, Sabah, Borneo (Hoffman 1961, 1980), and *Sarissocryptus* Hoffman, 1993, monobasic, from Eastern Malaysia, Sarawak, Borneo (Hoffman 1993). This process can be completely mesal (*Astrolabius*) or be twisted laterad (*Dyakryptus* and *Sarissocryptus*). Based of the above synapomorphy in gonopod structure, i.e. the presence of a basal prefemoral process, coupled with a coherent distribution pattern in Borneo and New Guinea, these three genera form the tribe Dyakryptini Hoffman, 1973 (Golovatch 2015). *Circulocryptus* gen. n. definitely joins this trio, but differs in the gonopods being especially elaborate and subcircular (versus far from so elaborate and not too strongly curved), the telopodites distinctly twisted basally (versus not twisted), and the solenomere lying much more basally, close to telopodite midlength (versus subapical). The range of Dyakryptini is thus considerably extended into continental SE Asia.

***Circulocryptus faillei* sp. n.**

<http://zoobank.org/BAAD23EF-944F-4698-BBE5-9FD3FF9E66A2>

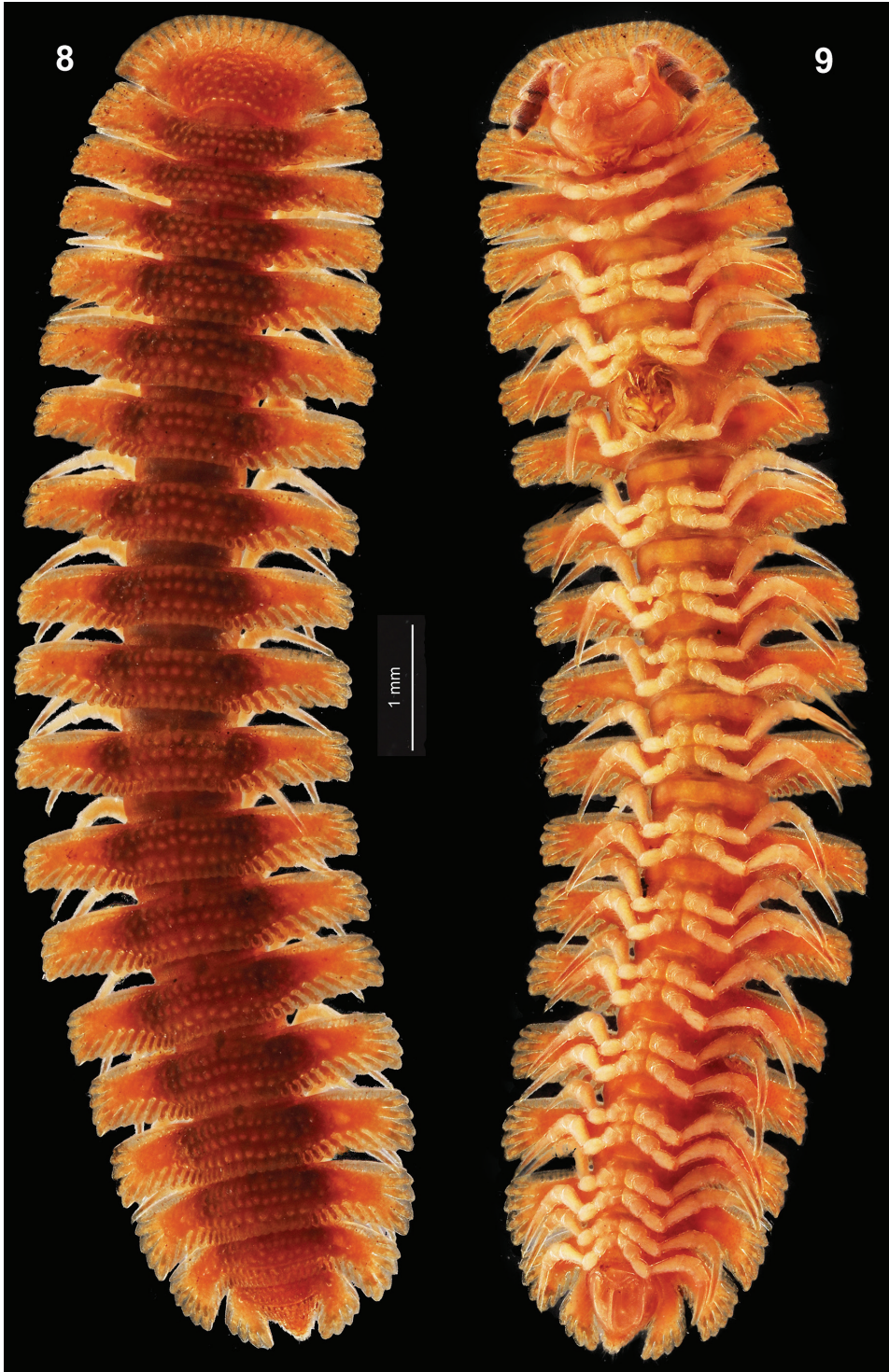
Figs 8–12

Type material. Holotype ♂ (MNHN JC 368), Vietnam, Khanh Hoa Prov., Cat Lam Distr., Suoi Cat community, Hon Ba Nature Reserve, road to Alexandre Yersin's monument in Hon Ba, 1350–1550 m a.s.l., mountain tropical rainforest, 14.XI.2013, leg. A. Faille (Vn No. 298).

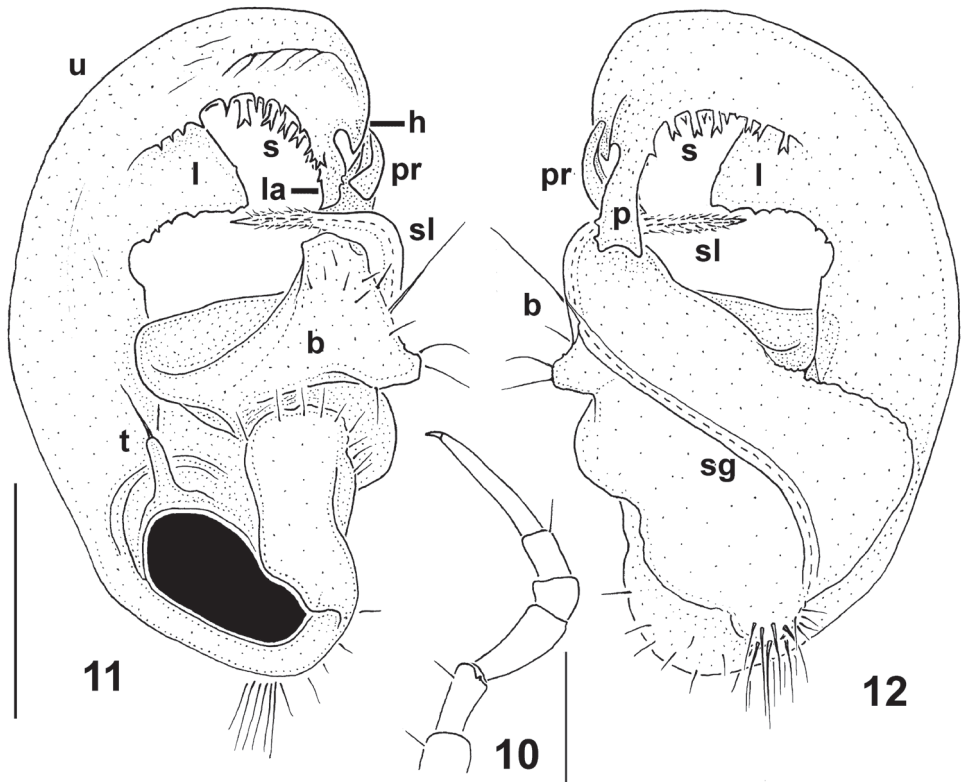
Name. Honours Arnaud Faille, the collector.

Description. Length ca 11 mm, width of midbody pro- and metazonae 1.2 and 2.9 mm, respectively. General coloration in alcohol red, but legs mostly somewhat lighter pink and antennomeres 5–7 increasingly infusate, red-brown to dark brown (Figs 8, 9).

Body with 20 segments. In width, head << collum < segment 2 < 3 < 4=15; thereafter body rapidly tapering towards telson.



Figures 8, 9. Habitus of *Circulocryptus faillei* sp. n., ♂ holotype, dorsal and ventral views, respectively.



Figures 10–12. *Circulocryptus faillei* sp. n., ♂ holotype: **10** leg 7, lateral view **11**, **12** left gonopod, mesal and lateral views, respectively. – Scale bars: 0.25 mm (10) and 0.2 mm (11, 12). Designations: **sg** seminal groove; **t** prefemoral process; **b** basal part of telopodite; **sl** solenomere; **pr** apical process of **b**; **u** distal half of telopodite; **i** midway lobe; **s** simple or bifid spinules; **p** lateral spatuliform process; **la** mesal subunci-form lappet; **h** ventral hook at base of **la**. NB: the large black spot in Fig. 11 is a condyle.

Head behind labrum very densely and clearly microgranulate; epicranial suture superficial, more distinct in vertigial region. Antennae short, clearly clavate (Fig. 9), C-shaped and placed mostly inside a groove; in length, antennomere 3 = 5 = 6 > 4 > 1 = 2 = 7; antennomeres 5 and 6 each with a compact apicodorsal group of bacilliform sensilla. Interantennal isthmus almost twice as broad as diameter of antennal socket. Tegument dull, clearly microgranulate almost throughout, only prozonae more finely shagreened. Dorsum moderately and regularly convex; paraterga mostly set at about upper 1/4 of body, very strongly developed (Figs 8, 9), beginning with collum, usually only slightly declined ventrad. Collum flabellate, completely covering the head from above, clearly radiate only anteriorly (12+12 long, apically setigerous radii), fore margin regularly convex, non-lobulated, but a distinctly and regularly emarginated caudal margin with 5+5 small setigerous lobulations; dorsal surface irregularly beset with small, dense, roundish, setigerous tubercles/knobs (Fig. 8). Postcollum paraterga very broad, each clearly broader than prozona; lateral edge mostly subquadrate, drawn

increasingly behind rear tergal margin only in segments 16–19; paraterga 19 produced as far behind as tip of epiproct. Fore margin/shoulder of paraterga straight, with numerous short radii, but lateral and caudal margins slightly, but sufficiently distinctly lobulated, lateral edge with an abbreviated anterolateral and 4 or 5 fully developed lateral lobulations; caudal edge increasingly poorly, but abundantly radiate and lobulate toward base. Mid-dorsal parts of metaterga typically with 3 transverse, more or less regular rows of small, rounded, low tubercles/knobs in front of 5–7+5–7 smaller lobulations forming a regular row at caudal margin between main axis and bases of paraterga; 1–2 rows of dorsal knobs growing increasingly obliterated when extended onto central parabasal parts of paraterga. Each marginal lobulation/radius and tergal tubercle normally surmounted by a short, poorly visible seta, these setae often being obliterated. Neither axial line nor pleurosternal carinae. Ozopores invisible, pore formula untraceable. Stricture dividing pro- and metazonae broad, shallow and microgranulate like adjacent metazonae, but shining. Epiproct (Figs 8, 9) short, conical, subtruncate at apex. Hypoproct (Fig. 9) subtrapeziform, 1+1 caudal setae clearly separated, borne on small knobs.

Sternites narrow (Fig. 9), sparsely setose, moderately impressed along main axis, somewhat or very clearly broadened only between coxae 7 and 9, respectively. Legs unmodified, long, but relatively stout (Figs 8–10), ca 1.4–1.5 times as long as paratergal width (♂); in length, tarsi > femora > prefemora and tibiae > coxae and postfemora (Fig. 10); gonapophyses on coxae 2 small cones (Fig. 9); neither adenostyles nor tarsal brushes. Gonopod aperture subcordiform, caudal and lateral margins slightly elevated (Fig. 9).

Gonopods (Figs 11, 12) very complex, in situ both held parallel to each other (Fig. 9). Telopodite subcircular, very strongly curved caudad, vaguely bipartite, at very base with a short, prefemoral, finger-shaped, trichostele-like process (**t**). Basal part (**b**) stout, extended terminally into a long, solid, spiniform, retrorse, laterally curved and densely pilose solenomere (**sl**), the latter at its base bearing a short, slightly curved, apical process (**pr**); seminal groove (**sg**) sigmoid, mostly running on lateral face of **b**, this being evidence of **b** torsion. Acropodite about half as long as telopodite, supplied with a subtriangular, midway, membranous lobe (**l**) and a large apical uncus (**u**) showing two caudal, parallel and strongly adjacent rows of simple or bifid spinules (**s**) before **u** branching into two peculiar apical structures, one a lateral spatuliform process (**p**) (in situ directed strongly laterad), the other a mesal subunciform lappet (**la**) with a smaller ventral hook (**h**) at base. Neither an accessory seminal chamber nor a hairy pulvillus.

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Contribution to the knowledge of Afrotropical Dryinidae, Embolemidae and Sclerogibbidae (Hymenoptera), with description of new species from Central African Republic and Uganda

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Abstract

An updated checklist of Dryinidae, Embolemidae and Sclerogibbidae from Central African Republic and Uganda is presented. The following new species of Dryinidae are described: from Central African Republic: *Anteon dzanganum* **sp. n.** (Anteoninae); from Uganda: *Anteon granulatatum* **sp. n.**, *A. kibalense* **sp. n.**, *A. makererense* **sp. n.**, *A. mubfs* **sp. n.** (Anteoninae); *Bocchus kibalensis* **sp. n.** (Bocchinae); *Dryinus kibalus* **sp. n.** (Dryininae); *Gonatopus kanyawarus* **sp. n.** (Gonatopodinae). The following species have been recorded for the first time from Central African Republic: Embolemidae: *Ampulicomorpha madecassa* Olmi, 1999a; *Embolemus capensis* Olmi, 1997; Dryinidae: *Aphelopus mediocarinatus* (Benoit, 1951d), *A. testaceus* Olmi, 1991, *A. wittei* Benoit, 1951c (Aphelopinae); *Anteon cautum* Olmi, 1994a, *A. evertsi* Olmi, 1989, *A. gutturnium* (Benoit, 1951b), *A. inflatrix* Benoit, 1951b, *A. kivuanum* (Benoit, 1951c), *A. semajanna* Olmi, Copeland & Guglielmino, 2015, *A. zairensis* Benoit, 1951d (Anteoninae); *Pseudodryinus townesi* (Olmi, 1984) (Dryininae); *Echthrodelpfax tauricus* Ponomarenko, 1970, *Gonatopus camerounensis* Olmi, 2011, *G. kolyadai* Olmi, 2007b, *Neodryinus antiquus* Benoit, 1954, *N. tussaci* Olmi, 2004b (Gonatopodinae); Sclerogibbidae: *Probethylus callani* Richards, 1939b; *Sclerogibba algerica* Benoit, 1963, *S. rapax* Olmi, 2005a. The following species have been recorded for the first time from Uganda: Embolemidae: *Ampulicomorpha magna* Olmi, 1996; Dryinidae: *Anteon cautum* Olmi, 1994a, *A. fisheri* Olmi, 2003,

A. hoyoi Olmi, 1984, *A. kivuanum* (Benoit, 1951c), *A. townesi* Olmi, 1984, *A. zairensis* Benoit, 1951d (Anteoninae); *Bocchus bini* Olmi, 1984 (Bocchinae); *Dryinus saussurei* (Ceballos, 1936) (Dryininae); *Echthrodolphax migratorius* Benoit, 1954, *Neodryinus tussaci* Olmi, 2004b (Gonatopodinae). The following further species has been recorded for the first time from Mali: *Sclerogibba algerica* Benoit, 1963 (Sclerogibbidae); from Ivory Coast: *Adryinus oweni* Olmi, 1984 (Gonatopodinae); from Cameroon and South Africa: *Gonatopus operosus* Olmi, 1993 (Gonatopodinae); from Democratic Republic of the Congo and Zambia: *Neodryinus antiquus* Benoit, 1954 (Gonatopodinae); from South Africa: *Anteon striatum* Olmi, 2005b (Anteoninae). Including the above new records, 23 species of Dryinidae (previously six), two species of Embolemidae (previously none) and three species of Sclerogibbidae (previously two) are now known from Central African Republic. For Uganda, 39 species of Dryinidae (previously 23), one species of Embolemidae (previously none) and four species of Sclerogibbidae (previously four) are now known. Additional new faunistic records are provided for Cameroon, Democratic Republic of the Congo, Ivory Coast, Mali, South Africa and Zambia.

Keywords

Chrysidoidea, new records, taxonomy, biogeography, Afrotropical Region

Introduction

Dryinidae and Embolemidae (Hymenoptera: Chrysidoidea) are parasitoids of Auchenorrhyncha (Hemiptera) (Guglielmino et al. 2013; Olmi 1996; Olmi et al. 2014). Sclerogibbidae (Hymenoptera: Chrysidoidea) are parasitoids of Embiidina (Olmi 2005a).

Afrotropical species of the above three families are poorly known. In recent years research investigation has been intensified in Burundi, Kenya, Madagascar, Mozambique and South Africa (mainly thanks to the efforts of Robert S. Copeland in Burundi and Kenya, Brian L. Fisher in Madagascar, Massimo Olmi in Mozambique and Simon van Noort in South Africa). The above inventory surveys resulted in the descriptions of many new species, and contributed to the publication of updated checklists (Azevedo et al. 2010 and Olmi 2007a, 2010 on Madagascar; Olmi and Copeland 2011 and Olmi et al. 2015 on Burundi and Kenya; Olmi et al. 2012 on Mozambique; Olmi 2006, 2007b, 2009 on South Africa). However, in spite of the above efforts, the fauna of dryinids, embolemids and sclerogibbids of many countries remains almost unknown.

In addition one of the authors (Simon van Noort) extended his research to two of the lesser known Afrotropical countries, Central African Republic and Uganda, where the number of recorded species was particularly low (in the Central Africa Republic, 6 species of Dryinidae, two species of Sclerogibbidae, no species of Embolemidae; in Uganda, 23 species of Dryinidae, one species of Embolemidae and four species of Sclerogibbidae). The subsequent study of the collected material has resulted in the discovery of eight new species described herein and, along with new distributional data for previously described species of these three families, has provided the opportunity to update the checklist of Dryinids, Embolemids and Sclerogibbids known from Central African Republic and Uganda.

Material and methods

Species descriptions follow the terminology used by Olmi (1984, 1994c, 1999b), Xu et al. (2013), Olmi and Virla (2014) and Olmi and Xu (2015). The measurements reported are relative, except for the total length (head to abdominal tip, without the antennae), which is expressed in millimetres. In the figures of male genitalia the right half is not included. The following abbreviations are used in the descriptions: POL distance between the inner edges of the two lateral ocelli; OL distance between the inner edges of a lateral ocellus and the median ocellus; OOL distance from the outer edge of a lateral ocellus to the compound eye; OPL distance from the posterior edge of a lateral ocellus to the occipital carina; TL distance from the posterior edge of the eye to the occipital carina.

Surveyed areas

The Dzanga-Sangha protected area was surveyed in Central African Republic. This area lies north of the equator and is located in the southwest triangle of the country (Sangha-Mbaéré Prefecture) bordered by Cameroon and the Republic of Congo. The Dzanga-Sangha protected area includes the Dzanga-Ndoki National Park (1220 km²), and the Dzanga-Sangha Dense Forest Special Reserve (3359 km²). The latter is a multiple use zone where logging, traditional hunting, safari hunting and extraction of plants are still allowed under controlled conditions. Annual rainfall is about 1500 mm, with average temperatures ranging between 25° and 29°Celsius. There are two peaks to the rainy season with highest precipitation occurring during the “long rains” from September to November and a second peak during the “short rains” in May and June (Carroll 1997). The eco-region is a part of the Guineo-Congolian lowland rain forest within the Guineo-Congolian regional centre of endemism (White 1983), characterized by the following species: *Entandrophragma congoense* (Meliaceae); *Pentaclethra eetveldeana* (Mimoseae); *Pericopsis elata* (Fabaceae); and *Gilbertiodendron dewevrei* (Fabaceae). The canopy can reach a height of 60 m. The understory is composed of shrubs, lianas and herbs. Harris (2002) recorded 1090 species of vascular plants in the reserve.

Three separate sites within the forest were sampled (named Camps 1-3). Camp 1 was situated at a marsh clearing, Mabéa Bai, in lowland rainforest 21.4km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510m, in the Dzanga-Ndoki National. The vegetation in the Bai marsh clearing is dominated by herbaceous plants including abundant sedges (Cyperaceae) and grasses (Graminae). Characteristic trees of the forest margin include *Lophira alata* and *Berlinia grandiflora*. Camp 2 was situated in lowland rainforest on the banks of the Sangha River in the Dzanga-Sangha Dense Forest Special Reserve, 12.7km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420m. The river is about 500 meters wide at this point and ranges from a depth of 20 cm at the end of the dry season (around March) to as much as 5 meters during the height of the rainy season

in September and October when the forests adjacent to the banks are flooded. This seasonally flooded forest has a complex architecture with 15–25 m trees forming a canopy with occasional emergent trees to 40 m with gaps less common; the understorey consists of small trees (5–10 m) with herbs and lianas common, whereas shrubs are almost absent (Harris 2002). Camp 3 was situated in lowland rainforest about 1 km from the banks of the Sangha River in the Dzanga-Ndoki National Park, 38.6km 173°S Lidjombo, 2°21.60'N, 16°09.20'E, 350m. Sampling was conducted in the seasonally inundated riparian forest (see above for species composition) and in mixed species terra firma forest above the flood plain. Details of the sampled habitats (including photographs of the sampling sites) and sampling effort conducted during the WWF expedition to Central African Republic are presented in Azevedo et al. 2015.

In Uganda surveys were undertaken within the vicinity of the Makerere University Biological Field Station (MUBFS) (0°33.798'N, 30°21.365'E, 1500 m) in the Kanyawara area of Kibale National Park where 12 main survey sites were sampled. The park is located in western Uganda, approximately 24 km from the eastern edge of the Ruwenzori Mountains and encompasses an area of 766 km² and an altitude varying between 1590 m in the north and 1100 m in the south (Chapman et al. 1997). Kibale forest is transitional between lowland rain forest and montane rain forest and is classified as a mid-altitude, moist, evergreen forest with a canopy height typically between 20 and 30 m, but with some trees exceeding 55 m (Chapman et al. 1997, Skorupa 1988, Struhsaker 1997, Wrangham et al. 1994). The park is dominated by moist evergreen forest (57%), with secondary regenerating forest (19%), woodland (4%), grassland (15%), lakes and wetlands (2%), and exotic tree plantations (1%) comprising the remainder (Chapman et al. 1997). Rainfall is bimodal with highest precipitation concentrated during March to May and September to November. Mean annual rainfall totals 1734 mm; mean maximum temperature is 23.7°C; mean minimum temperature is 15.5°C (Rhode et al. 2006). Chapman et al. (1997), Skorupa (1988), and Struhsaker (1997) provide further details of the Kanyawara area.

Sampling methods

The Malaise traps were constructed to the specifications of the Townes design (Townes 1972), and made with a fine-meshed netting (grid size of 0.2 mm), with black walls and a white roof. Yellow pan traps comprised plastic bowls of 165mm diameter x 40 mm depth, which were placed on the forest floor along a linear transect. Sweeping: The sweep net used for sampling was based on the design of Noyes (1982), with an opening area of c. 1300 cm², and a collecting bag constructed from fine-meshed netting with a grid size of 0.2 mm. The yellow pan trap collection method is indicated by the following abbreviation: YPT.

All types of the Afrotropical species of Dryinidae, Embolemidae and Sclerogibbidae have been examined. The specimens studied for this paper are deposited in the following collections:

AEIC	American Entomological Institute, Gainesville, Florida, USA.
AMNH	American Museum of Natural History, New York, NY, USA.
BMNH	The Natural History Museum, London, United Kingdom.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CASC	California Academy of Sciences, San Francisco, USA.
CNCI	Canadian National Collection of Insects, Ottawa, Canada.
IRSN	Institut Royal de Sciences Naturelles de Belgique, Bruxelles, Belgium.
MSNG	Museo Civico di Storia Naturale "Giacomo Doria" di Genova, Italy.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MOLC	Massimo Olmi collection, c/o Department of Plant Protection, University of Tuscia, Viterbo, Italy.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NMSA	Kwazulu-Natal Museum, Pietermaritzburg, KwaZulu-Natal, South Africa.
OLML	Oberösterreichisches Landesmuseum, Linz, Austria.
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.
SAMC	South African Museum, Cape Town, South Africa.;
USNM	National Museum of Natural History, Washington, DC, USA.
UKIC	Department of Entomology, University of Kentucky, Lexington, Kentucky, USA.

The descriptions of most of the new species are based on the study of a single specimen. Specimens of these families are rarely collected and are poorly represented in world collections. The authors are aware that descriptions of new taxa should normally be based on more individuals. However, on the basis of the experience and knowledge of the authors, the new species are sufficiently characterized to justify their descriptions.

Checklist of Dryinidae, Embolemidae and Sclerogibbidae from Central African Republic and Uganda

An asterisk (*) indicates that specimens are known only from Central African Republic or Uganda, double asterisk (**) indicates the species is newly recorded from Central African Republic or Uganda.

Family DRYINIDAE

Subfamily Aphelopinae Perkins, 1912

Genus *Aphelopus* Dalman

Aphelopus Dalman, 1823.

***Aphelopus himyarita* Olmi & van Harten**

Aphelopus himyarita Olmi & van Harten, 2006: 312.

Material examined. Published records. Olmi et al. (2015): **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 Km 53°NE Bayanga, 03°02'01"N 16°24'57"E, 510 m, 5–6.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 2♂♂ (SAMC); same locality label, 3–4.V.2001, 2♂♂ (SAMC); same locality label, 1–2.V.2001, 1♂ (SAMC); same locality label, 7–8.V.2001, 9♂♂, 3♀♀ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 22.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♀, 2♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kabarole District, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.871'S 30°21.355'E, 1495 m, 12–26.VIII.2008, Malaise trap, secondary mid-altitude rainforest, S. van Noort leg., 2♂♂, 1♀ (SAMC); same locality label, 0°33.408'S 30°22.603'E, 1587 m, Malaise trap, degraded mid-altitude rainforest, S. van Noort leg., 3♀♀, 1♂ (SAMC); same locality label, 2–12.VIII.2008, 0°33.784'S 30°22.617'E, 1500 m, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 2♀♀, 2♂♂ (SAMC); same locality label, 12–26.VIII.2008, 0°33.823'S 30°21.490'E, 1505 m, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Afrotropical, recorded from Cameroon, Central African Republic, Ivory Coast, Kenya, Madagascar, Nigeria, South Africa, Uganda and Yemen (Olmi and Copeland 2011; Olmi et al. 2015; Olmi and van Harten 2006).

***Aphelopus mediocarinatus* (Benoit)**

Antaphelopus mediocarinatus Benoit, 1951d.

Aphelopus mediocarinatus (Benoit): Olmi 1984: 60.

Material examined. Published records. Olmi (1984): **UGANDA: CENTRAL REGION:** Wakiso District, Entebbe (CNCI). **New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 03°02'01"N 16°24'57"E, 510 m, 3–4.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 1♀ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 22.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♂, 4♀♀ (SAMC); Reserve Speciale de Forêt Dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 13.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♀, 4♂♂ (SAMC).

Hosts. Cicadellidae Typhlocybinae (Guglielmino et al. 2013): in Mozambique (Niassa Province): *Molopopterus alfa* Dworakowska and *Empoasca* sp. Dworakowska; in Nigeria: *Empoasca* sp.

Distribution. Afrotropical, recorded from almost all sub-saharian countries, from Senegal to Somalia, in addition to Madagascar and Yemen (Olmi and Copeland 2011; Olmi et al. 2015; Olmi and van Harten 2006). Newly recorded from Central African Republic here.

Aphelopus testaceus Olmi**

Aphelopus testaceus Olmi, 1991: 112.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 7–8.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 1♂ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 22.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Democratic Republic of the Congo, South Africa, Tanzania and Yemen (Olmi and van Harten 2000, 2006). Newly recorded from Central African Republic here.

Aphelopus wittei Benoit**

Aphelopus wittei Benoit, 1951c: 16.

Material examined. Published records. Olmi (1990): **UGANDA: WESTERN REGION:** Kasese District, Ruwenzori Range, Misigo, 8550 ft., 2–3.VIII.1952, D.S. Fletcher leg., 3♂♂ (2 in BMNH, 1 in BPBM). **New records. CENTRAL AFRICAN REPUBLIC: NANA-MAMBÉRÉ PREFECTURE:** 60 km W Bouar, 05°45'N, 15°13'E, 660 m, 23.III.2010, J. Halada leg., 1♂ (OLML); **SANGHA-MBAÉRÉ PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 7–8.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 1♀, 4♂♂ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 22.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♀, 12♂♂ (SAMC); Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 6.V.2001, sweep, lowland rainforest, marsh clearing, CAR01-S48, S. van Noort leg., 1♂ (SAMC); Reserve Speciale de Forêt Dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 13.V.2001, sweep, lowland rainforest, S. van Noort leg., 1♀,

8♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kabarole District, Kibale Forest, Kanywara (RMNH); Kabarole District, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°34.405'N, 30°21.646'E, 1484 m, 12–26.VIII.2008, Malaise trap, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♂ (SAMC); same locality label, 00°33.891'N, 30°21.468'E, 1506 m, 12–26.VIII.2008, 1♀, 5♂♂ (SAMC); same locality label, 00°35.442'N, 30°21.741'E, 1465 m, 10.VIII.2008, sweep, primary mid-altitude rainforest, near stream, S. van Noort leg., 7♂♂ (SAMC); same locality label, 0°33.871'S 30°21.355'E, 1495 m, 12–26.VIII.2008, Malaise trap, secondary mid-altitude rainforest, S. van Noort leg., 2♂♂, 1♀ (SAMC); same locality label, 0°33.408'S 30°22.603'E, 1587 m, Malaise trap, degraded mid-altitude rainforest, S. van Noort leg., 3♂♂ (SAMC); same locality label, 2–12.VIII.2008, 0°33.784'S 30°22.617'E, 1500 m, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 1♀, 11♂♂ (SAMC); same locality label, 12–26.VIII.2008, 0°33.823'S 30°21.490'E, 1505 m, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 2♀♀, 2♂♂ (SAMC); same locality label, 2–12.VIII.2008, 0°33.836'S 30°21.700'E, 1523 m, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 2♀♀, 3♂♂ (SAMC).

Hosts. Cicadellidae Typhlocybinae (Guglielmino et al. 2013): in North Sudan: *Jacobiasca lybica* (Bergevin & Zanon); in Somalia: *Jacobiella facialis* (Jacobi).

Distribution. Afrotropical, recorded from almost all sub-saharian countries, from Senegal to Somalia, in addition to Madagascar and Yemen (Olmi and Copeland 2011; Olmi et al. 2015; Olmi and van Harten 2006). Newly recorded from Central African Republic here.

Subfamily Conganteoninae Olmi, 1984

Genus *Conganteon* Benoit

Conganteon Benoit, 1951c: 11.

Conganteon vulcanicum Benoit

Conganteon vulcanicus Benoit, 1951c: 12.

Material examined. Published record. Olmi et al. (2015): **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.891'N, 30°21.468'E, 1506 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Democratic Republic of the Congo, Kenya, Madagascar, Rwanda, South Africa, Uganda (Olmi 1984, 1994a; Olmi et al. 2015).

Subfamily Anteoninae Perkins, 1912**Genus *Anteon* Jurine**

Anteon Jurine, 1807: 302.

Anteon cautum* Olmi*

Anteon cautum Olmi, 1994a.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Réserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 17.V.2001, sweep, lowland rainforest, S. van Noort leg., 4♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.859'S 30°21.630'E, 1505 m, 5–12.VIII.2005, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Kenya, Madagascar and South Africa (Olmi 1994a, 2009; Olmi et al. 2015). Newly recorded from Central African Republic and Uganda here.

Anteon dzanganum* sp. n.

<http://zoobank.org/C58A5227-D69A-4416-B21E-3EA1412F26F5>

Figs 1A, 4

Type material. HOLOTYPE: ♀, **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE:** Réserve Spéciale de Forêt Dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 03°00.27'N, 16°11.55'E, 420 m, 11–17.V.2001, YPT, lowland rainforest, CAR01-Y26, S. van Noort leg. (SAMC).

Diagnosis. Female fully winged; head and mesosoma black, except mandible testaceous; head and scutum granulated and reticulate rugose; posterior surface of propodeum reticulate rugose, without longitudinal keels; forewing hyaline, without dark transverse bands or spots, with distal part of stigmal vein less than 0.5 as long as proximal part; segment 4 of protarsus slightly shorter than basal part of segment 5; segment 5 of protarsus (Figs 1A, 4D) with inner side curvilinear, with distinct apical region, basal part shorter than distal part, distal region very short and distal lamellae located near medial lamellae.

Description. Female. Fully winged; length 2.2 mm. Head black, except mandible testaceous; antenna testaceous, except dorsal side of segments 6–10 brownish; metasoma brown; legs testaceous. Antenna clavate; antennal segments in following proportions: 10:5:6:5:4:5:6:5.5:5.5:7. Head dull, granulated and reticulate rugose; frontal

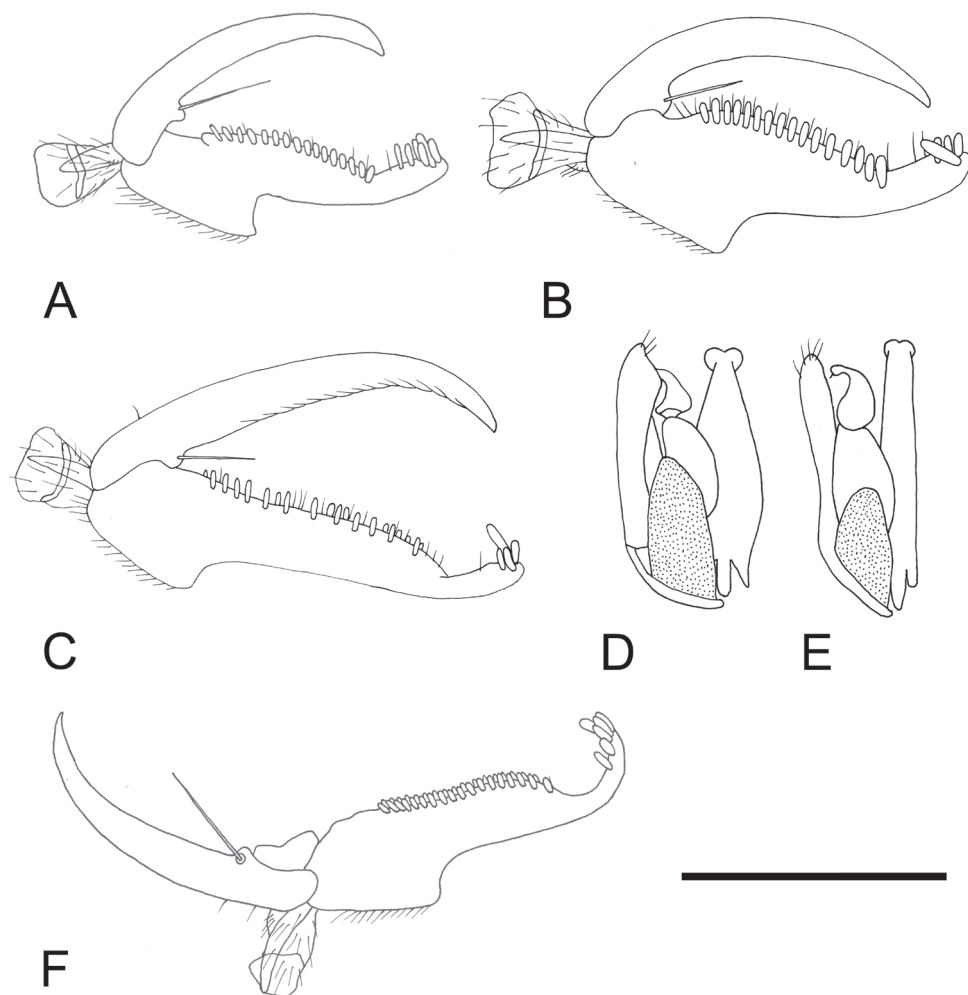


Figure 1. Chela of holotypes: **A** *Anteon dzanganum* **B** *A. kibalense* **C** *A. mubfs* **D** *A. zimbabwe*. Male genitalia of holotypes (right half removed): *A. granulatatum*; *A. makererense*. Scale bar: 0.26 mm (**A**); 0.28 mm (**B**); 0.22 mm (**C**); 0.13 mm (**D**, **E**); 0.40 mm (**F**).

line complete; face without two lateral keels around orbits and directed towards antennal toruli; occipital carina complete; POL = 6; OL = 3; OOL = 3; OPL = 4; TL = 4; greatest breadth of posterior ocelli about as long as OL. Pronotum dull, reticulate rugose; posterior surface longer than OPL (7:4) and shorter than scutum (7:14); pronotal tubercle reaching tegula. Scutum dull, granulated and reticulate rugose, except short unsculptured area near anterior margin. Notauli incomplete, reaching about 0.3 length of scutum. Scutellum and metanotum shiny, punctate, unsculptured among punctures. Mesopleuron and metapleuron dull, reticulate rugose. Propodeum dull, with transverse keel between dorsal and posterior surface; dorsal surface reticulate rugose; posterior surface reticulate rugose, without longitudinal keels. Forewing hyaline,

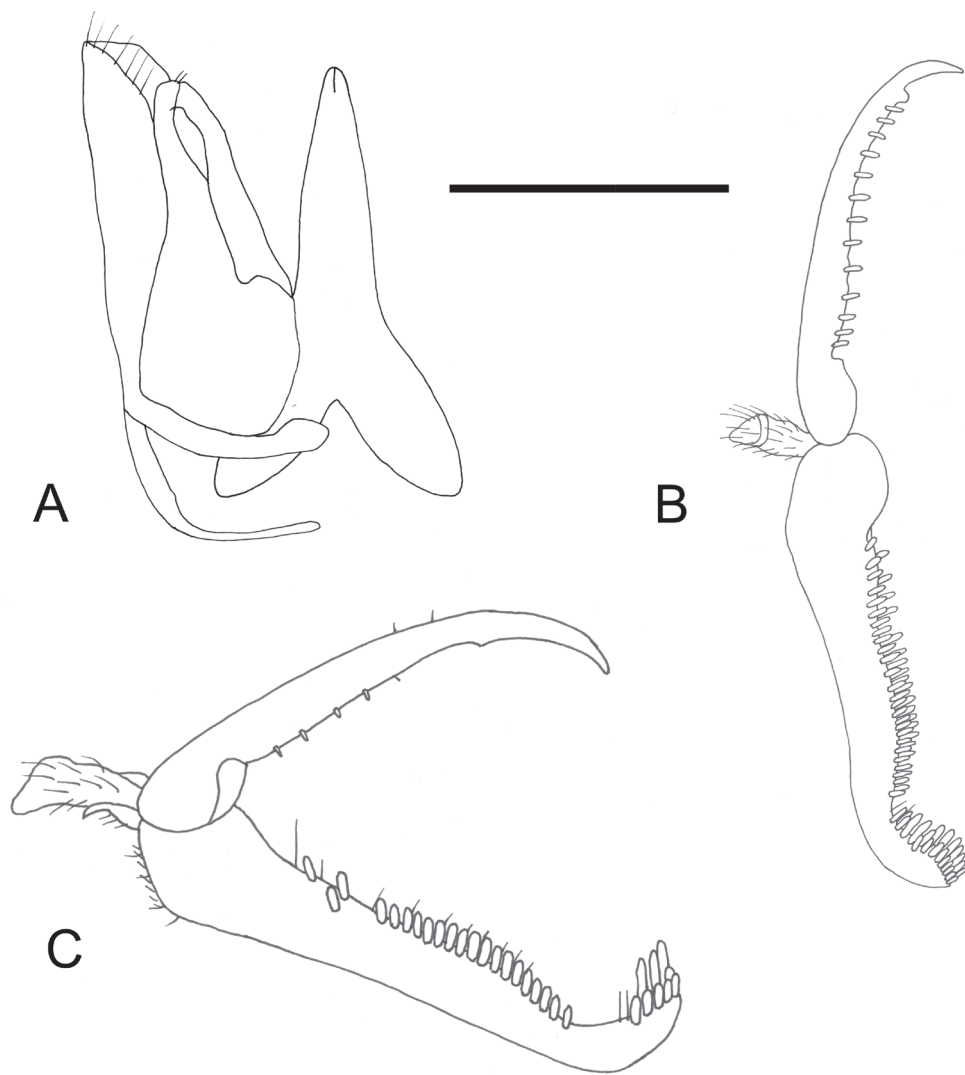


Figure 2. **A** male genitalia of *Bocchus kibalensis* (right half removed) **B, C** chelae of holotypes: **B** *Dryinus kibalus* **C** *Gonatopus kanyawarus*. Scale bar: 0.13 mm (**A**); 0.65 mm (**B**); 0.30 mm (**C**).

without dark transverse bands; distal part of stigmal vein much shorter than proximal part (2.5:9). Protarsal segments in following proportions: 5:2:3:4:13; segment 2 of protarsus produced into hook. Segment 4 of protarsus slightly shorter than basal part of segment 5 (4:6). Segment 5 of protarsus (Figs 1A, 4D) with basal part slightly shorter than distal part (6:7), with inner side curvilinear and with apical region distinct. Enlarged claw (Figs 1A, 4D) with proximal prominence bearing one long bristle. Segment 5 of protarsus (Figs 1A, 4D) with one row of 16 lamellae; distal apex with 6 lamellae. Tibial spurs 1/1/2.

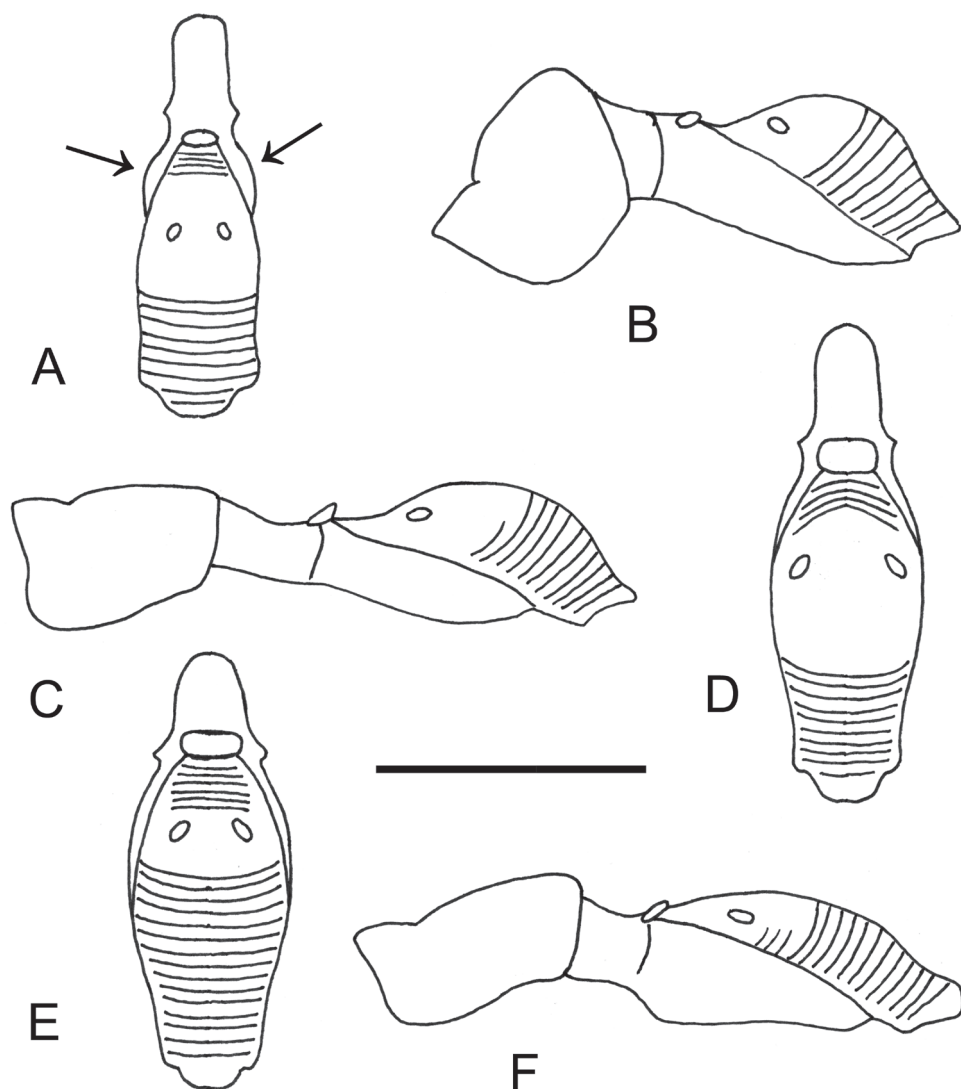


Figure 3. Mesosoma in dorsal (prothorax removed) and lateral view of holotypes: **A, B** *Gonatopus kanyawarus* (rounded protrusions of metanotum indicated by arrows) **C, D** *G. trochantericus* **E, F** *G. tulearensis*. Scale bar: 0.87 mm (**A, C, F**); 1.03 mm (**B**); 0.74 mm (**D**); 0.80 mm (**E**).

Male. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Anteon canabense* (Benoit, 1951b). The main differences regard the sculpture of the posterior surface of the propodeum and the colour (posterior surface of propodeum granulated, except few irregular keels near margins; head and mesosoma testaceous-reddish, occasionally partly darkened, in *A. canabense*; posterior surface

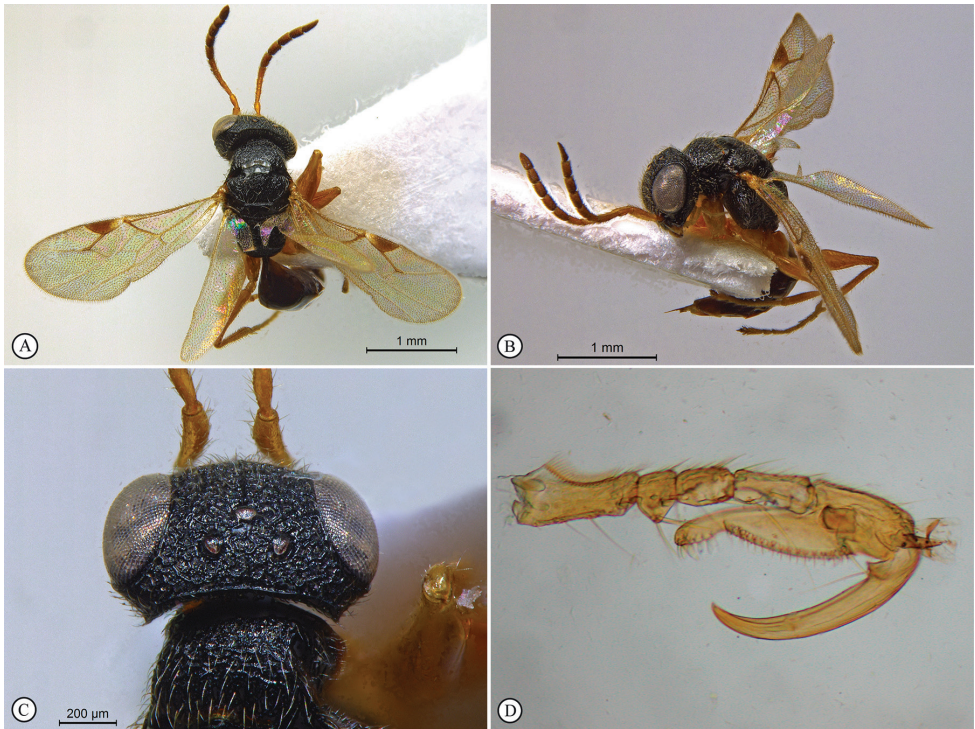


Figure 4. *Anteon dzanganum* sp. n. Holotype female. **A** habitus, dorsal view **B** habitus, lateral view **C** head, pronotum dorsal view **D** chela (slide mounted).

of propodeum reticulate rugose; head and mesosoma black, except mandible testaceous, in *A. dzanganum*).

Etymology. The species is named after the type locality, Dzanga-Ndoki National Park.

Hosts. Unknown.

Distribution. Central African Republic.

Anteon evertsi Olmi**

Anteon evertsi Olmi 1989: 159.

Material examined. New record. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 23.V.2001, sweep, lowland rainforest, S. van Noort leg., 4♂♂ (SAMC).

Hosts. Unknown.

Distribution. Cameroon, Gambia, Ivory Coast, Kenya (Olmi 1989; Olmi et al. 2015). Newly recorded from Central African Republic here.

Anteon fisheri Olmi**

Anteon fisheri Olmi, 2003: 24.

Material examined. New records. UGANDA: WESTERN REGION: Kibale Forest, Kanyawara (RMNH); Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°34.390'S 30°21.658'E, 1587 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Madagascar, South Africa (Azevedo et al. 2010; Olmi 2003, 2006). Newly recorded from Uganda here.

Anteon granulatum sp. n.*

<http://zoobank.org/7D0E3446-FDF4-4A96-8537-3CCE51AC202F>

Figs 1D, 5

Type material. HOLOTYPE: ♂, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.996'N, 30°21.262'E, 1495 m, 12–18.VIII.2005, UG05-M20, Malaise trap, secondary mid-altitude rainforest, S. van Noort leg. (SAMC).

Diagnosis. Male with clypeus not sculptured by longitudinal and subparallel keels; scutum completely granulated and slightly reticulate rugose; posterior surface of propodeum without longitudinal keels; paramere (Figs 1D, 5F) with small distal inner rounded process and proximal membranous process not provided with mosaic sculpture and sensorial setae; distal inner process of paramere with distal apex situated quite close to distal apex of paramere (Figs 1D, 5F).

Description. Male. Fully winged; length 1.7 mm. Head black, except mandible testaceous; antenna brown; mesosoma black; metasoma brown; legs testaceous. Antenna filiform; antennal segments in following proportions: 8:5:7:7:7:7:7:8. Head granulated; frontal line complete; face without lateral keels along orbits directed towards antennal toruli; occipital carina complete; POL = 6; OL = 3; OOL = 5; OPL = 3; TL = 4; greatest breadth of posterior ocellus slightly shorter than OPL (2:3). Scutum dull, completely granulated and slightly reticulate rugose. Notauli very short, hardly visible near anterior margin of scutum. Scutellum shiny, slightly granulated. Metanotum shiny, unsculptured. Propodeum completely reticulate rugose, with strong transverse keel between dorsal and posterior surface; posterior surface without longitudinal keels, with areolae about as large as those of dorsal surface. Forewing hyaline, without dark transverse bands or spots; distal part of stigmal vein much shorter than proximal part (1.5:6). Paramere (Figs 1D, 5F) with small distal inner rounded process; proximal membranous process without mosaic sculpture and sensorial setae. Tibial spurs 1/1/2.

Female. Unknown.

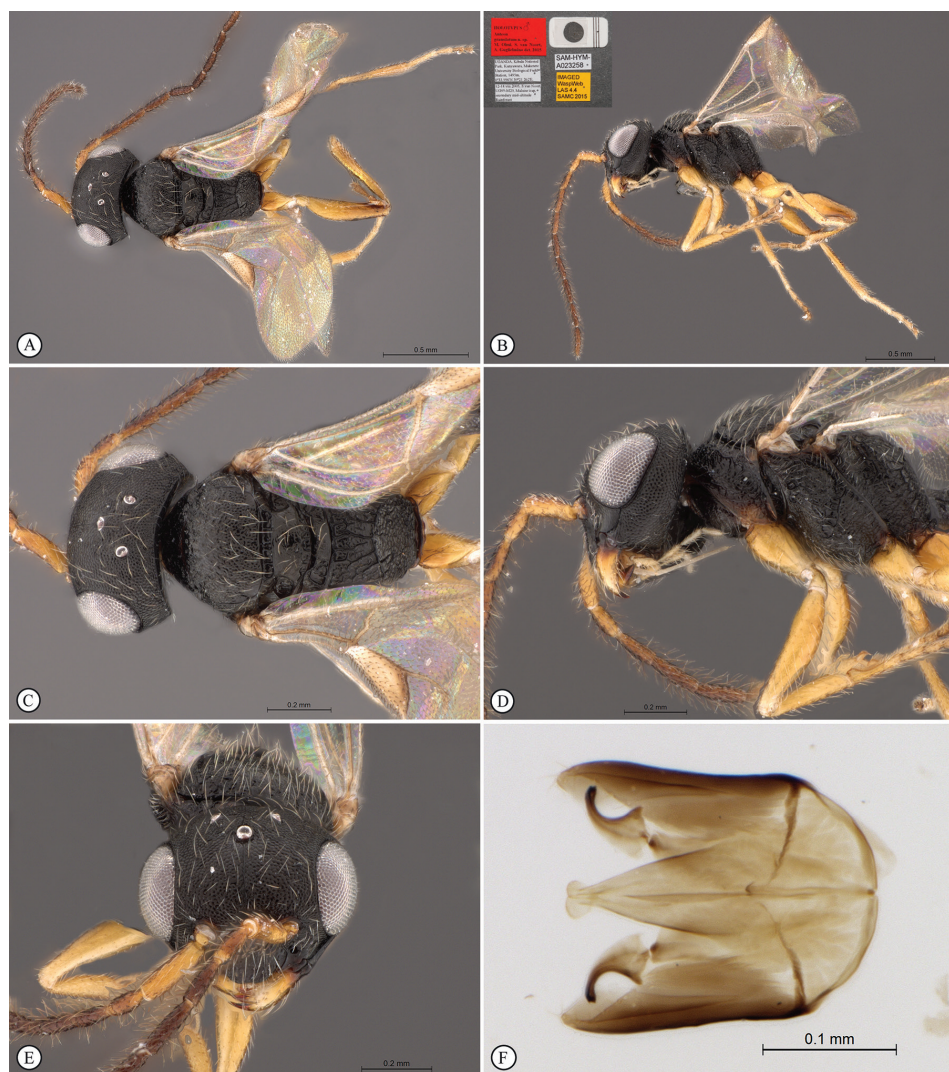


Figure 5. *Anteon granulatum* sp. n. Holotype male. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** male genitalia (slide mounted).

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Anteon cautum* Olmi, 1994a, *A. emeritum* Olmi, 1984, and *A. whartoni* Olmi, in Olmi & Copeland, 2011. The main difference regards the scutum sculpture: completely reticulate rugose and granulated in *A. granulatum*; not completely reticulate rugose, at most with small surface near anterior margin rugose in the other three species.

Etymology. The species is named after the head completely granulated.

Hosts. Unknown.

Distribution. Uganda.

Anteon gutturnium* (Benoit)**Xenanteon gutturnium* Benoit, 1951b.*Anteon gutturnium* (Benoit): Olmi 1984: 384

Material examined. Published records. Olmi (1984): **UGANDA: CENTRAL REGION:** Masaka District, Kawanda (BMNH, AMNH); Kampala District, Kampala, V.1938, H.C. Taylor leg., 1♀ (BMNH). **WESTERN REGION:** Bushenyi District, Bushenyi, III.1939, H.C. Taylor leg., 1♀ (BMNH). **New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Reserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 17.V.2001, sweep, lowland rainforest, S. van Noort leg., 3♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.836'N, 30°21.700'E, 1523 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 3♂♂ (SAMC); same locality label, 0°33.891'N, 30°21.468'E, 1506 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 2♂♂ (SAMC).

Hosts. Unknown.

Distribution. Afrotropical, recorded from almost all sub-saharian countries, from Senegal to Uganda (Olmi 1984, 2006; Olmi and Copeland 2011; Olmi et al. 2015), in addition to Madagascar (Azevedo et al. 2010). Newly recorded from Central African Republic here.

Anteon hoyoi* Olmi**Anteon hoyoi* Olmi, 1984: 390.

Material examined. New record. UGANDA: WESTERN REGION: Kasese District, Kibale National Park, Kanyawara, Makerere University Biological Field Station, 00°33.836'N, 30°21.700'E, 1523 m, 6.VIII.2008, sweep, primary mid-altitude rainforest, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Democratic Republic of the Congo (Olmi 1984). Newly recorded from Uganda here.

Anteon inflatrix* Benoit**Anteon inflatrix* Benoit, 1951b: 161.

Material examined. New record. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 4.V.2001, sweep, lowland rainforest, marsh clearing, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. South Africa (Olmi 1984, 2006). Newly recorded from Central African Republic here.

Anteon kawandanum Olmi

Anteon kawandanum Olmi, 1984: 374.

Material examined. Published records. Olmi (1984). **UGANDA: CENTRAL REGION:** Masaka District, Kawanda, V.1943, T.H.C. Taylor leg., holotype ♀ (BMNH); same locality label, 13.VII.1943, VII.1943, 15.VII.1943, 19.VII.1943, 5 paratypes ♂♂, 1 paratype ♀ (BMNH); same locality label, 1 paratype ♀, 1 paratype ♂ (AMNH). **EASTERN REGION:** Serere District, Serere, VII.1943, T.H.C. Taylor leg., 10 paratypes ♀♀ (BMNH); same locality label, 1 paratype ♀ (AMNH).

Hosts. Unknown.

Distribution. Afrotropical, recorded from almost all sub-saharian countries, from Gambia to Somalia (Olmi 1984, 2006), in addition to Madagascar (Azevedo et al. 2010).

Anteon kibalense sp. n.*

<http://zoobank.org/134FC47E-817B-4EE2-90EC-1046FC55605F>

Figs 1B, 6

Type material. HOLOTYPE: ♀, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.996'S 30°21.262'E, 1495 m, 29–31.VII.2005, UG05-Y06, YPT, secondary mid-altitude rainforest, S. van Noort leg. (SAMC). Paratypes: same locality label as holotype, 1 paratype ♀ (SAMC), 1 paratype ♀ (MOLC).

Diagnosis. Female fully winged; head and mesosoma black, except mandible brown; head completely reticulate rugose; posterior surface of propodeum reticulate rugose, without longitudinal keels, with areolae about as large as those of dorsal surface; forewing with two dark transverse bands, with distal part of stigmal vein less than 0.5 as long as proximal part; segment 4 of protarsus slightly shorter than basal part of segment 5; segment 5 of protarsus (Figs 1B, 6F) with inner side curvilinear, with distinct apical region, with basal part slightly shorter than distal part.

Description. Female. Fully winged; length 2.1–3.3 mm (holotype 2.8 mm). Head black, except mandible brown; antenna brown; mesosoma black; metasoma brown; legs brown, except articulations, trochanters, procoxa and mesocoxa testaceous. Antenna clavate; antennal segments in following proportions: 10:6:7:6:5:6:6:6:8. Head slightly convex, dull, completely reticulate rugose; frontal line complete; face without two lateral keels around orbits and directed towards antennal toruli; occipital carina complete; POL = 8; OL = 4; OOL = 6; OPL = 5; TL = 5; greatest breadth of posterior



Figure 6. *Anteon kibalense* sp. n. Holotype female. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** chela (slide mounted).

ocelli shorter than OPL (3:5). Pronotum anteriorly crossed by slight transverse impression, dull, with anterior surface transversely striate; posterior surface with anterior half transversely striate and posterior half slightly granulated, not striate; posterior surface shorter than scutum (7:14); pronotal tubercle reaching tegula. Scutum granulated, rugose and irregularly striate. Notauli absent. Scutellum shiny, unsculptured. Metanotum rugose. Propodeum with strong transverse keel between dorsal and posterior surface; dorsal surface dull, reticulate rugose; posterior surface dull, reticulate ru-

gose, without longitudinal keels, with areolae about as large as those of dorsal surface. Forewing with two dark transverse bands; distal part of stigmal vein much shorter than proximal part (4:9). Protarsal segments in following proportions: 8:3:4:6:16. Segment 4 of protarsus slightly shorter than basal part of segment 5 (6:7). Enlarged claw (Figs 1B, 6F) with proximal prominence bearing one long bristle. Segment 5 of protarsus (Figs 1B, 6F) with basal part slightly shorter than distal part (7:9), with one row of 16 lamellae; distal apex bent and with 5 lamellae. Tibial spurs 1/1/2.

Male. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Anteon zimbabwense* Olmi, 2005b. The main difference regards the segment 5 of the protarsus: with smaller lamellae and distal part slender in *A. zimbabwense* (Fig. 1F); with lamellae longer and distal part less slender in *A. kibalense* (Fig. 1B, 6F).

Etymology. The species is named after the type locality, Kibale National Park.

Hosts. Unknown.

Distribution. Uganda.

Anteon kivuanum (Benoit)**

Chelogyne kivuanus Benoit, 1951c: 13.

Anteon kivuanum Olmi, 1984: 363.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 4.V.2001, sweep, lowland rainforest, marsh clearing, S. van Noort leg., 3♂♂ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombi, 2°21.60'N, 16°03.20'E, 350 m, 23.V.2001, sweep, lowland rainforest, S. van Noort leg., 5♂♂ (SAMC); Reserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 17.V.2001, sweep, lowland rainforest, S. van Noort leg., 4♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kibale Forest, Kanyawara (RMNH); Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°34.390'S 30°21.658'E, 1587 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♀ (SAMC); same locality label, 0°33.836'N, 30°21.700'E, 1523 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 2♀♀, 2♂♂ (SAMC); same locality label, 0°33.891'N, 30°21.468'E, 1506 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 1♀, 1♂ (SAMC); same locality label, 0°33.996'S 30°21.262'E, 1495 m, 29–31.VII.2005, YPT, secondary mid-altitude rainforest, S. van Noort leg., 1♀, 1♂ (MOLC); same locality label, 0°33.784'S 30°21.617'E, 1500 m, 12–26.VIII.2008, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 1♂ (SAMC).

Hosts. Cicadellidae Iassinae (Guglielmino et al. 2013): in South Africa (Western Cape): *Iassomorpha drakensteini* (Naudé).

Distribution. Democratic Republic of the Congo, Kenya, Madagascar, South Africa and Yemen (Azevedo et al. 2010; Olmi 1984, 2006; Olmi and van Harten 2006; Olmi et al. 2015). Newly recorded from Central African Republic and Uganda here.

Anteon makererense* sp. n.

<http://zoobank.org/6B7329B0-3AB5-4CFB-9A8A-BA707C74FD5C>

Figs 1E, 7

Type material. HOLOTYPE: ♂, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.408'S 30°22.603'E, 1587 m, 30.VII–5.VIII.2005, UG05-M10, Malaise trap, degraded mid-altitude rainforest, S. van Noort leg. (SAMC).

Diagnosis. Male with head reticulate rugose and granulated; scutum with anterior third reticulate rugose and remaining surface sculptured by many longitudinal subparallel irregular keels; posterior surface of propodeum not provided with longitudinal keels; propodeum with strong transverse keel between dorsal and posterior surface; paramere (Figs 1E, 7F) without distal inner pointed or rounded process, slightly shorter than penis.

Description. Male. Fully winged; length 1.7 mm. Head black, except mandible testaceous; antenna brown, except segment 1 testaceous; mesosoma black; metasoma brown; legs testaceous-dark. Antenna filiform; antennal segments in following proportions: 9:4:4:4:4:4:4:5:7. Head completely reticulate rugose and granulated; frontal line complete; occipital carina complete; POL = 6; OL = 3; OOL = 4; OPL = 1.5; TL = 2; greatest breadth of posterior ocelli shorter than OL (2:3). Scutum dull, with anterior third reticulate rugose; remaining surface sculptured by many longitudinal subparallel irregular keels. Notauli very short, hardly visible near anterior margin of scutum. Scutellum and metanotum shiny, unsculptured. Propodeum with strong transverse keel between dorsal and posterior surface; dorsal surface reticulate rugose; posterior surface reticulate rugose, sculptured by areolae smaller than those of dorsal surface, without longitudinal keels. Forewing hyaline, without dark transverse bands or spots; distal part of stigmal vein much shorter than proximal part (2:6). Paramere (Figs 1E, 7F) without distal inner pointed process. Tibial spurs 1/1/2.

Female. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Anteon reunionense* Olmi, 1987. The main difference regards the sculpture of the scutum: with anterior half reticulate rugose and remaining surface unsculptured, or slightly granulated in *A. reunionense*; with anterior third reticulate rugose and remaining surface sculptured by many longitudinal subparallel irregular keels in *A. makererense*.

Etymology. The species is named after Makerere University.

Hosts. Unknown.

Distribution. Uganda.

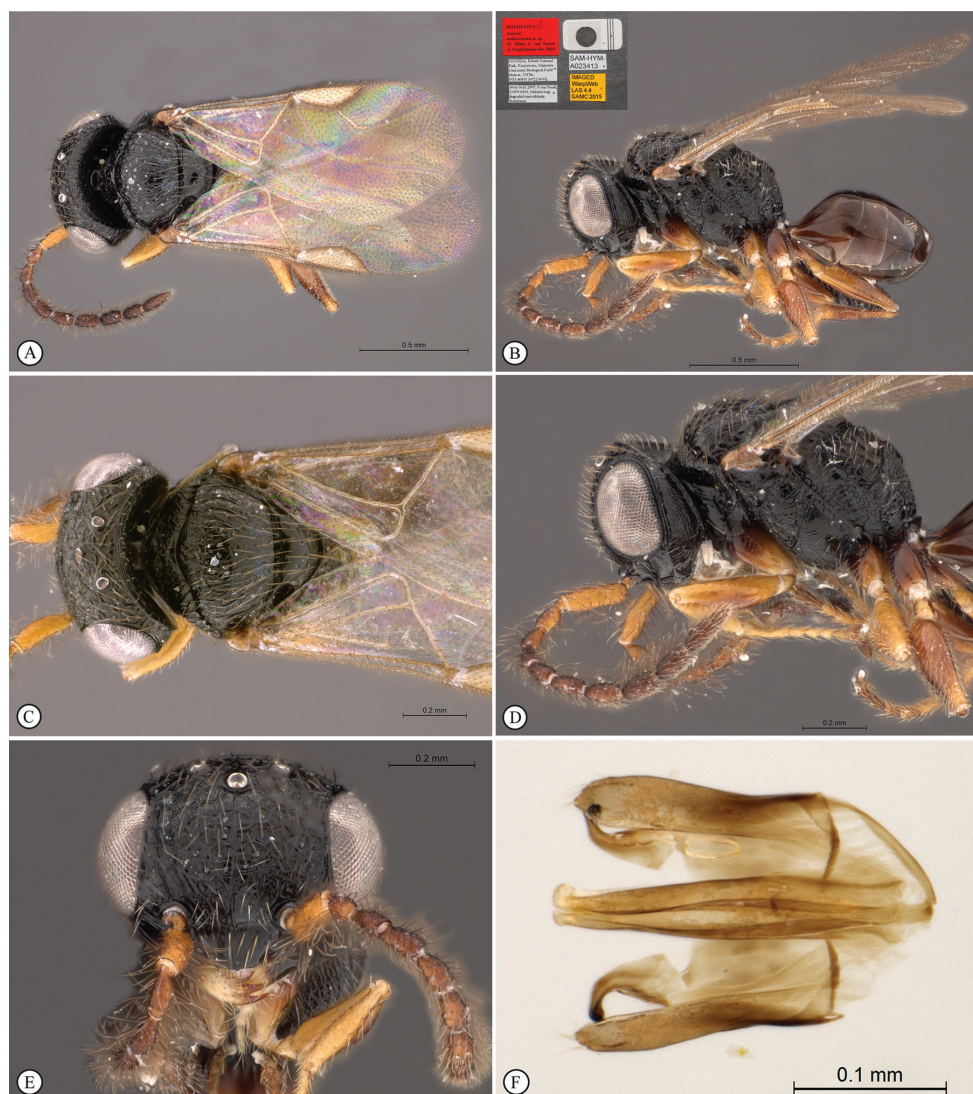


Figure 7. *Anteon makererense* sp. n. Holotype male. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** male genitalia (slide mounted).

Anteon mubfs sp. n.*

<http://zoobank.org/B07F8CE4-936A-41C1-9F99-F330182085B4>

Figs 1C, 8A–F

Type material. HOLOTYPE: ♀, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°35.405'S 30°21.646'E, 1484 m, 4–26.VIII.2008, UG08-KF10-Y02, YPT, primary mid-altitude rainforest, near stream, S. van Noort leg. (SAMC).

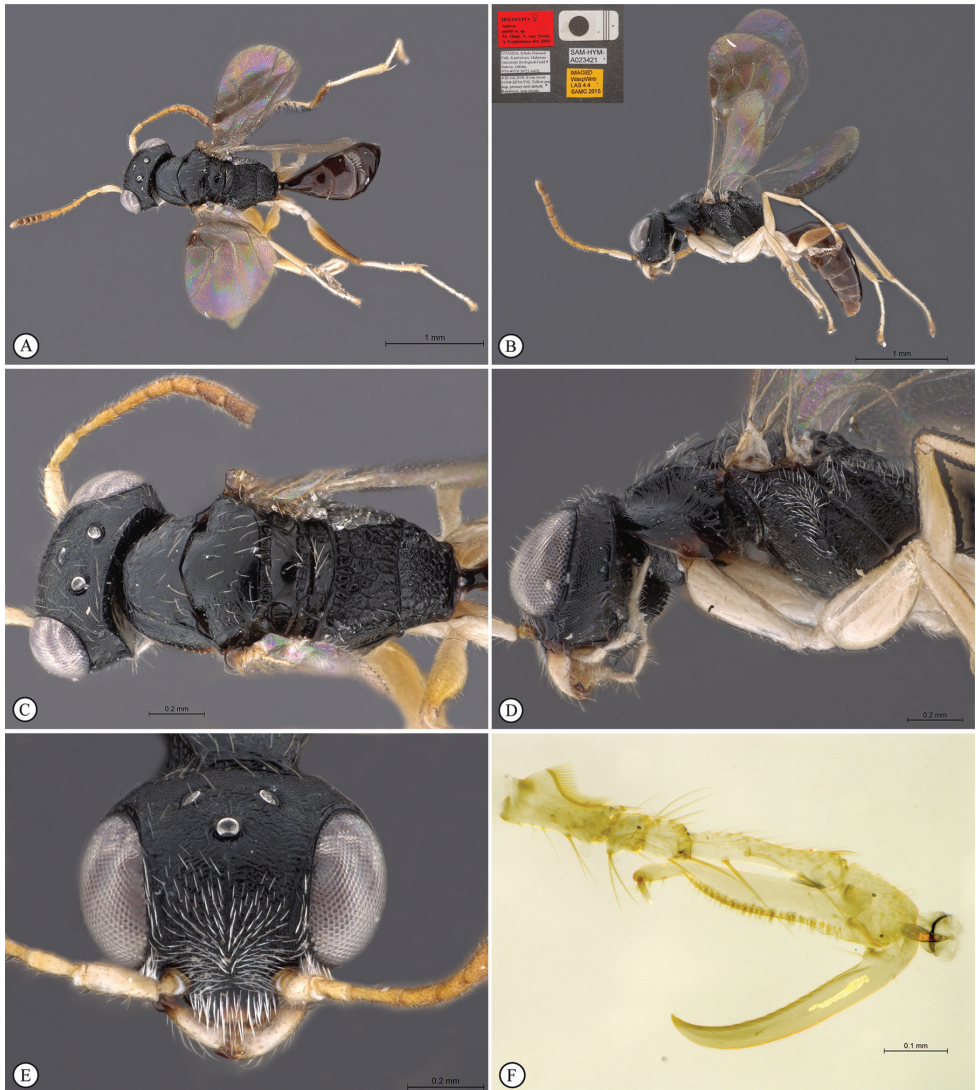


Figure 8. *Anteon mubfs* sp. n. Holotype female. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** chela (slide mounted).

Diagnosis. Female fully winged; head reticulate rugose, except vertex behind posterior ocelli and temple granulated; posterior surface of pronotum with raised carina on both anterior and lateral margins; posterior surface of propodeum reticulate rugose, without longitudinal keels; forewing with two dark transverse bands and distal part of stigmal vein less than 0.5 as long as proximal part; segment 4 of protarsus approximately longer than basal part of segment 5; segment 5 of protarsus (Figs 1C, 8F) with inner side curvilinear, with distinct apical region, with basal part shorter than distal part.

Description. Female. Fully winged; length 2.6 mm. Head black, except mandible and part of anterior half of clypeus testaceous; antenna testaceous; mesosoma black; metasoma brown; legs testaceous. Antenna clavate; antennal segments in following proportions: 8:6:7:6:5:5:6:6:8. Head dull, reticulate rugose, except vertex behind posterior ocelli and temple granulated; frontal line complete, partly continuing also behind the anterior ocellus; face with two lateral keels along orbits and directed towards antennal toruli; occipital carina complete; POL = 6; OL = 4; OOL = 4 OPL = 4; TL = 5; greatest breadth of posterior ocelli shorter than OPL (3:4). Pronotum with slight transverse anterior impression; anterior surface short, transversely striate, hidden behind head; posterior surface slightly shorter than scutum (11:14), shiny, granulated, except few irregular keels near anterior margin; posterior surface with raised carina on anterior and lateral margins; pronotal tubercle reaching tegula. Scutum shiny, slightly granulated, with some irregular keels on lateral surfaces. Notauli absent. Scutellum and metanotum shiny, unsculptured. Propodeum with transverse keel between dorsal and posterior surface; dorsal surface reticulate rugose; posterior surface reticulate rugose, with areolae about as large as those of dorsal surface, without longitudinal keels. Forewing with two dark transverse bands; distal part of stigmal vein much shorter than proximal part (4:9). Protarsal segments in following proportions: 6:2:3:10:18; protarsal segment 2 produced into hook; protarsal segment 4 much longer than basal part of protarsal segment 5 (10:5). Enlarged claw (Figs 1C, 8F) with a proximal prominence bearing one long bristle. Segment 5 of protarsus (Figs 1C, 8F) with basal part much shorter than distal part (5:13), with two rows of 8+12 lamellae; distal apex with 4 lamellae. Tibial spurs 1/1/2.

Male. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Anteon abditum* Olmi, 1994a. The main difference regards the shape of the pronotum: without raised carinae in *A. abditum*; with raised carina on anterior and lateral margins in *A. mubfs*.

Etymology. Named after the acronym of Makerere University Biological Field Station, where the holotype was collected. The field station is affectionately called “Mubfs” by those privileged to have experienced a stay there. Noun in apposition.

Hosts. Unknown.

Distribution. Uganda.

Anteon ngoyense Olmi

Anteon ngoyense Olmi, 2009: 451.

Material examined. Published record. Olmi et al. (2015: **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRE PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 Km 53°NE Bayanga, 03°02'01"N 16°24'57"E, 510 m, 4–5.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Central African Republic, South Africa, Uganda (Olmi et al. 2015).

Anteon semajanna Olmi, Copeland & Guglielmino**

Fig. 9

Anteon semajanna Olmi, Copeland & Guglielmino, 2015: 349.

Material examined. Published record. Olmi et al. (2015: **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°33.871'S 30°21.355'E, 1495 m, 12–26.VIII.2008, UG08-KF2-M12, Malaise trap, secondary mid-altitude rainforest, S. van Noort leg., 2 paratypes ♂♂ (SAMC). **New record. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21.60'N, 16°03.20'E, 350 m, 23.V.2001, sweep, lowland rainforest, S. van Noort leg., 2♂♂ (SAMC).

Hosts. Unknown.

Distribution. Kenya, Uganda (Olmi et al. 2015). Newly recorded from Central African Republic here.

Anteon striatum Olmi

Anteon striatum Olmi, 2005b: 233.

Material examined. Published record. Olmi (2005b): **UGANDA: CENTRAL REGION:** Mubende District, Mulange, XI.1922, R. Dummer leg., SAM-HYM-PO03772, holotype ♂ (SAMC). **New record. SOUTH AFRICA: KWAZULU-NATAL:** Karkloof, 29°19.1'S 30°15.5'E, 1325 m, 25.VII–25.IX.2005, Malaise trap, M. Mostovski leg., 1♂ (NMSA).

Hosts. Unknown.

Distribution. Uganda (Olmi 2005b). Newly recorded from South Africa here.

Anteon taylori Olmi*

Anteon taylori Olmi, 1984: 366.

Material examined. Published record. Olmi (1984): **UGANDA: CENTRAL REGION:** Masaka District, Kawanda, XI.1942, T.H.C. Taylor leg., holotype ♀ (BMNH).

Hosts. Unknown.

Distribution. Uganda (Olmi 1984).

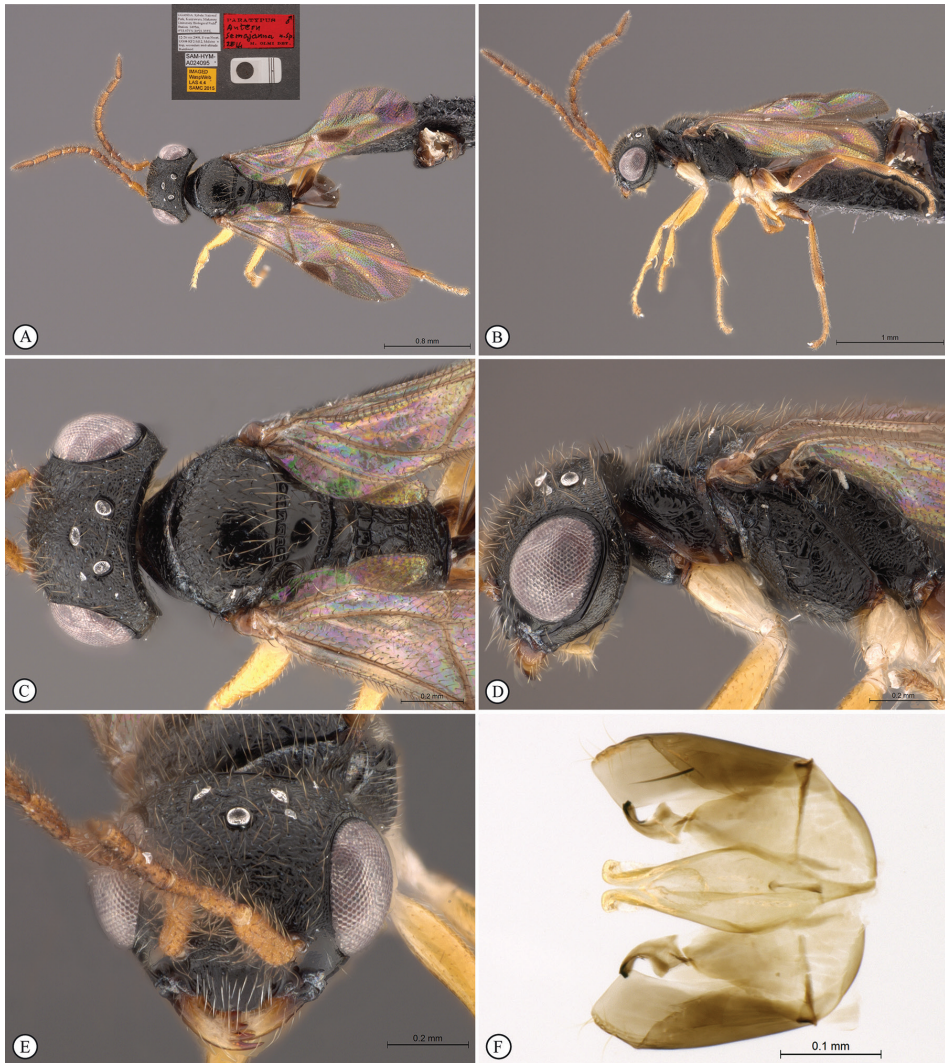


Figure 9. *Anteon semajanna* Olmi, Copeland & Guglielmino, 2015. Paratype male from Uganda, Kibale National Park. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** male genitalia (slide mounted).

Anteon townesi* Olmi*

Anteon townesi Olmi, 1984: 379.

Material examined. New record. UGANDA: WESTERN REGION: Kibale National Park, Kanyawara Makerere University Biological Field Station, 0°35.442'S 30°21.741'E, 1465 m, 10.VIII.2008, sweep, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Democratic Republic of the Congo and South Africa (Olmi 1984, 2006). Newly recorded from Uganda here.

Anteon ugandanum Olmi

Anteon ugandanum Olmi, 1984: 372.

Material examined. Published records. Olmi (1984): **UGANDA: CENTRAL REGION:** Masaka District, Kawanda, 16.VII.1943, T.H.C. Taylor leg., holotype ♀ (BMNH); same locality label, 15.VII.1943, VIII.1943, 2 paratypes ♀♀ (BMNH); same locality label, 9 paratypes (5♀♀, 4♂♂) (AMNH). **EASTERN REGION:** Serere District, Serere, VII.1943, T.H.C. Taylor leg., 6 paratypes ♀♀ (BMNH); Busoga Kingdom, Bussu, 1909, E. Bayon leg., 1♀ (MSNG).

Hosts. Unknown.

Distribution. Afrotropical, recorded from almost all sub-saharian countries, from Senegal and Mali to Kenya and Uganda (Olmi 1984, 2006; Olmi et al. 2015).

Anteon whartoni Olmi

Anteon whartoni Olmi, in Olmi & Copeland, 2011: 180.

Material examined. Published records. (Olmi et al. 2015): **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Reserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 17.V.2001, sweep, lowland rainforest, S. van Noort leg., 6♂♂ (5 in SAMC, 1 in MOLC); Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 4.V.2001, sweep, lowland rainforest, marsh clearing, S. van Noort leg., 2♂♂ (SAMC).

Hosts. Unknown.

Distribution. Central African Republic, Kenya (Olmi et al. 2015).

Anteon zairense Benoit**

Anteon zairense Benoit 1951d: 21.

Material examined. New records. **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Ndoki National Park, 38.6 km 173°S Lidjumbo, 2°21.60'N, 16°03.20'E, 350 m, 23.V.2001, sweep, lowland rainforest, S. van Noort leg., 6♂♂ (SAMC). **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara

Makerere University Biological Field Station, 0°33.784'S 30°21.617'E, 1500 m, 2–12.VIII.2008, Malaise trap, primary mid-altitude rainforest, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Afrotropical, recorded from Gabon to Kenya (Olmi et al. 2015), in addition to Madagascar (Azevedo et al. 2010). Newly recorded from Central African Republic and Uganda here.

Subfamily Bocchinae Richards, 1939a

Genus *Bocchus* Ashmead

Bocchus Ashmead, 1893: 91.

Bocchus bini Olmi**

Bocchus bini Olmi, 1984: 629.

Material examined. New record. UGANDA: WESTERN REGION: Ankole, Kichwamba, 23–29.IV.1968, 1♀, 1♂ (USNM); same locality label, 1♀ (AMNH).

Hosts. Unknown.

Distribution. Afrotropical, recorded from Ghana to Somalia and Yemen (Olmi and van Harten 2006; Olmi et al. 2015), in addition to Madagascar (Azevedo et al. 2010). Newly recorded from Uganda here.

Bocchus kibalensis sp. n.*

<http://zoobank.org/A1DB1304-4CB8-4463-B291-9AACB6EE5355>

Figs 2A, 10

Type material. HOLOTYPE: ♂, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.836'N, 30°21.700'E, 1523 m, 12–26.VIII.2008, UG08-KF8-M18, Malaise trap, primary mid-altitude rainforest, S. van Noort leg. (SAMC).

Diagnosis. Male with OPL slightly longer than POL; antennal segment 6 less than twice as long as broad; scutum and scutellum completely reticulate rugose; notauli absent; posterior surface of propodeum with median area crossed by numerous transverse keels.

Description. Male. Fully winged; length 2.9 mm. Head black, except mandible testaceous; antenna brown, except segments 1–2 ferruginous; mesosoma black; metasoma brown; legs brown, with articulations, tarsi and protibia testaceous. Antenna filiform; antennal segments in following proportions: 14:6:8:8:7:7:7:7:10; antennal

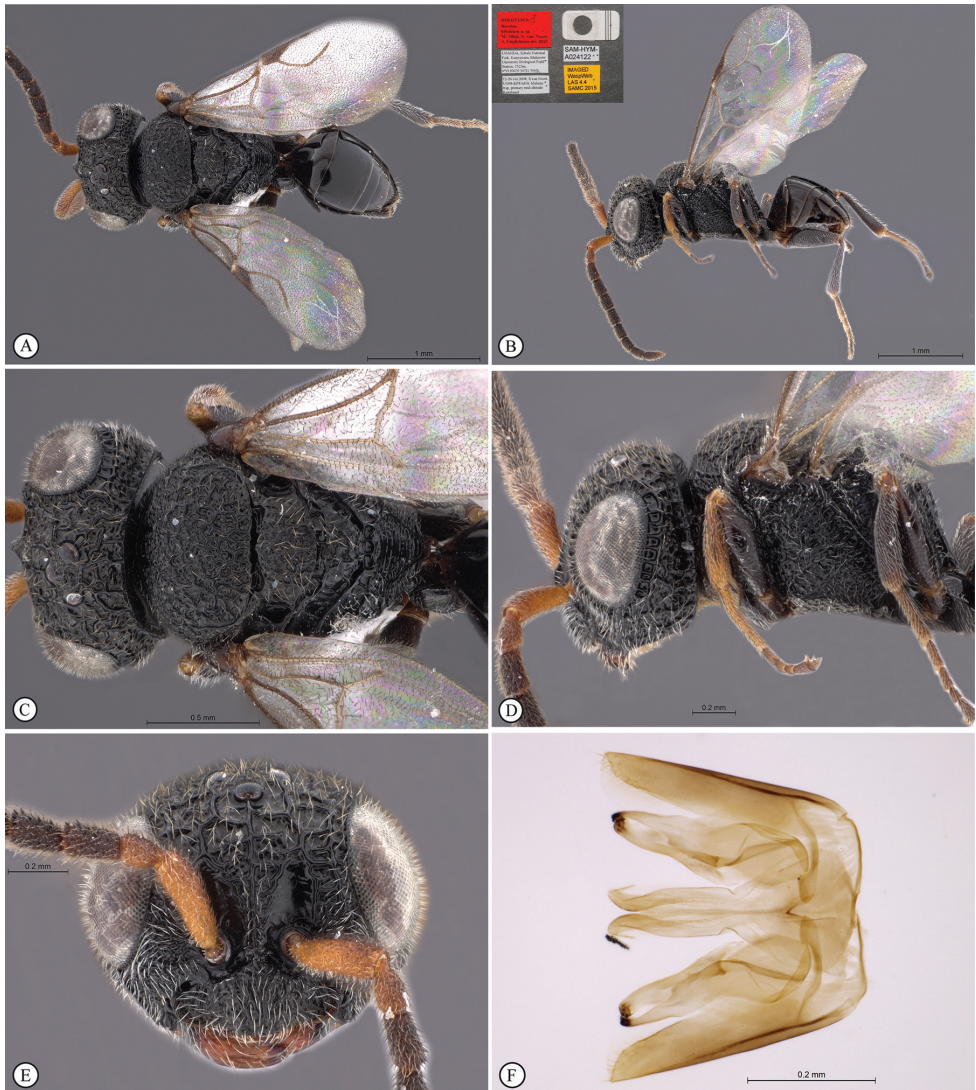


Figure 10. *Bocchus kibalensis* sp. n. Holotype male. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** male genitalia (slide mounted).

segment 6 less than twice as long as broad (7:5). Head convex, dull, covered with short hairs, completely reticulate rugose; clypeus reticulate rugose; frontal line complete, with pointed protrusion between antennal toruli; occipital carina complete; POL = 5; OL = 3; OOL = 7; OPL = 7; TL = 7; greatest breadth of posterior ocelli shorter than POL (4:5). Scutum, scutellum and metanotum dull, completely reticulate rugose. Notauli absent. Mesopleuron dull, reticulate rugose. Metapleuron dull, sculptured by numerous strong transverse keels. Propodeum with strong transverse keel between dorsal

and posterior surface; dorsal surface dull, reticulate rugose; posterior surface of propodeum with two complete longitudinal keels, median area crossed by many transverse keels and lateral areas completely reticulate rugose. Forewing hyaline, without dark transverse bands; distal part of stigmal vein about as long as proximal part. Genitalia as in Figs 2A, 10F. Tibial spurs 1/1/2.

Female. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Bocchus seyrigi* (Benoit, 1954). The main differences regard OPL/POL ratio (OPL slightly longer than POL in *B. kibalensis*; OPL more than twice as long as POL in *B. seyrigi*) and the sculpture of the median area of posterior surface of propodeum (crossed by many transverse keels in *B. kibalensis*; partly unsculptured in *B. seyrigi*).

Etymology. The species is named after the type locality, in Kibale National Park.

Hosts. Unknown.

Distribution. Uganda.

Subfamily Dryininae Haliday, 1833

Genus *Dryinus* Latreille

Dryinus Latreille, 1804: 176.

Dryinus aethiopicus (Olmi)

Mesodryinus aethiopicus Olmi, 1984: 1008.

Dryinus aethiopicus (Olmi): Olmi 2004a: 357.

Material examined. Published record. (Olmi 1984; Olmi and Copeland 2011; Olmi et al. 2015): **CENTRAL AFRICAN REPUBLIC: LOBAYE PREFECTURE:** Boukoko, 1 paratype ♀, 1 paratype ♂ (MNHN).

Hosts. In Central African Republic unidentified Dictyopharidae (Olmi 1984).

Distribution. Central African Republic, Kenya, Sierra Leone (Olmi 1984; Olmi and Copeland 2011).

Dryinus erraticus (Turner)

Neodryinus erraticus Turner, 1928: 149.

Dryinus erraticus (Turner): Carnegie 1975: 249.

Material examined. Published records. (Olmi et al. 2015): **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field

Station, 0°33.823'N, 30°21.490'E, 1505 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, S. van Noort leg., 1♀ (SAMC).

Hosts. Tropicoduchidae (Guglielmino et al. 2013): in South Africa and Swaziland: *Numicia viridis* Muir.

Distribution. Afrotropical, recorded from Angola, Democratic Republic of the Congo, Eritrea, Namibia, Somalia, South Africa, Swaziland, Tanzania, Uganda, Zimbabwe (Olmi 1984, 2006, 2009).

Dryinus kibalus* sp. n.

<http://zoobank.org/C8876DFD-C537-442D-AC60-D2C36A488D44>

Figs 2B, 11

Type material. HOLOTYPE: ♀, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.836'N, 30°21.700'E, 1523 m, 4–26.VIII.2008, UG08-KF8-Y07, YPT, primary mid-altitude rainforest, S. van Noort leg., 1♀ (SAMC).

Diagnosis. Female with head black, except mandible and clypeus testaceous; head flat, with posterior margin of vertex convex and TL more than twice as long as POL; head (dorsally viewed) provided with posterior ocelli placed behind imaginary straight line joining posterior edges of eyes; posterior ocelli almost touching occipital carina; head and scutum granulated and reticulate rugose, not sculptured by longitudinal keels or striae; pronotum black, except posterior collar ferruginous; posterior collar of pronotum present; propodeum black; segment 1 of protarsus slightly longer than segment 4; enlarged claw (Figs 2B, 11F) approximately as long as segment 5 of protarsus.

Description. Female. Fully winged; length 7.3 mm. Head black, except mandible and clypeus testaceous; antenna brown, except segments 1–2 and 10 testaceous, distal extremity of segment 4 and proximal third of segment 5 whitish; propleuron brown-black; pronotum black, except posterior collar ferruginous; rest of mesosoma black; metasoma brown-testaceous; legs testaceous. Antenna clavate; antennal segments in following proportions: 12:6:56:33:21:14:10:7:8:10; rhinaria present in segments 6–10. Head dull, granulated and reticulate rugose, without longitudinal keels; occipital carina complete; posterior ocelli almost touching occipital carina, situated just behind virtual straight line joining posterior edges of eyes; POL = 2; OL = 1.5; OOL = 12; OPL = 0.3; TL = 6; greatest breadth of posterior ocelli longer than POL (3:2). Pronotum dull, granulated, with numerous keels around disc, on lateral regions and anterior collar; pronotum crossed by slight anterior transverse impression and strong posterior transverse furrow; anterior collar little distinct; posterior collar long; pronotal tubercle not reaching tegula. Scutum granulated and reticulate rugose, not sculptured by longitudinal keels. Notauli incomplete, reaching about 0.8 length of scutum. Scutellum granulated, weakly rugose. Metanotum rugose. Propodeum reticulate rugose, without longitudinal keels on posterior surface; dorsal surface much longer than posterior surface. Forewing with two dark transverse bands; distal part of stigmal vein much longer than proximal



Figure 11. *Dryinus kibalus* sp. n. Holotype female. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** chela (slide mounted).

part (22:8). Protarsal segments in following proportions: 27:5:9:26:41. Segment 3 of protarsus produced into hook. Enlarged claw (Figs 2B, 11F) with one large subdistal tooth and one row of 13 lamellae. Segment 5 of protarsus (Figs 2B, 11F) with two rows of about 48 lamellae; distal apex with approximately 40 lamellae. Tibial spurs 1/1/2.

Male. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Dryinus undulatus* (Benoit, 1950b). The main difference regards the sculpture of the

head and scutum: granulated and reticulate rugose, not sculptured by longitudinal keels or striae, in *D. kibalus*; head granulated and with some longitudinal keels and scutum granulated and sculptured by many subparallel longitudinal keels in *D. undulatus*.

Etymology. The species is named after the type locality, Kibale National Park.

Hosts. Unknown.

Distribution. Uganda.

Dryinus saussurei (Ceballos)**

Lestodryinus saussurei Ceballos, 1936: 48.

Dryinus saussurei (Ceballos): Benoit 1954: 412.

Material examined. New record. UGANDA: **WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.836'N, 30°21.700'E, 1523 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, near stream, S. van Noort leg., 2♀♀ (SAMC).

Hosts. Unknown.

Distribution. Madagascar (Olmi 1984, 1994a), South Africa (Olmi 2006), Uganda. Newly recorded from Uganda here.

Dryinus shimbanus Olmi

Dryinus shimbanus Olmi, in Olmi & Copeland, 2011: 184.

Material examined. Published record. (Olmi et al. 2015): **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Sangha Dense Forest Special Reserve, 12.7 km 326°NW Bayanga, 03°00'27"N 16°11'55"E, 420 m, 14–15.V.2001, Malaise trap, lowland rainforest, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Kenya, Central African Republic (Olmi et al. 2015).

Dryinus turneri Olmi

Lestodryinus ampuliciformis Turner, 1928: 148 (preoccupied).

Dryinus turneri Olmi, Copeland & Guglielmino, 2015 (new name): 359.

Material examined. Published record. (Olmi 1984): **UGANDA: CENTRAL REGION:** Kampala District, Kampala, 1♀ (AEIC).

Hosts. Unknown.

Distribution. Recorded from many Afrotropical countries, from Nigeria to Somalia (Olmi and Copeland 2011).

***Dryinus ugandanus* (Olmi)**

Tridryinus ugandanus Olmi, 1984: 935.

Dryinus ugandanus (Olmi): Olmi 2006: 43.

Material examined. Published record. (Olmi 1984): **UGANDA: CENTRAL REGION:** Kampala District, Kampala, ♀ holotype (AEIC).

Hosts. Unknown.

Distribution. Recorded from Uganda, Sierra Leone and South Africa (Olmi 1984, 2006, 2009).

***Dryinus undulatus* (Benoit)**

Lestodryinus undulatus Benoit, 1950b: 226.

Dryinus undulatus (Benoit): Olmi 2004a: 357.

Material examined. Published records. (Olmi 1984; Olmi et al. 2015): **CENTRAL AFRICAN REPUBLIC: LOBAYE PREFECTURE:** 150 km NWW Mbaiki, 04°03'N, 17°02'E, 620 m, 14.VI.2009, J. Halada leg., 1♀ (OLL). **UGANDA: CENTRAL REGION:** Kampala District, Kampala, IV.1936, T.H.C. Taylor leg., 1♀ (BMNH).

Hosts. Lophopidae (Guglielmino et al. 2013): in Mozambique: *Elasmoscelis cimicoides* Spinola.

Distribution. Afrotropical, recorded from Burundi, Central African Republic, Democratic Republic of the Congo, Kenya, Mozambique and Uganda (Olmi et al. 2015).

Genus *Pseudodryinus* Olmi

Pseudodryinus Olmi, 1991: 365.

Pseudodryinus townesi* (Olmi)*

Thaumatodryinus townesi Olmi, 1984: 692.

Pseudodryinus townesi (Olmi): Olmi 1991: 369.

Material examined. Published records. (Olmi 1984, 1991): **UGANDA: CENTRAL REGION:** Kampala District, Kampala, ♀ holotype (AEIC); same locality label as holotype, 1♀ paratype (AMNH). **New record: CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRE PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 6.V.2001, sweep, lowland rainforest, marsh clearing, CAR01-S48, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Recorded from South Africa and Uganda (Olmi 1984). Newly recorded from Central African Republic here.

Subfamily Gonatopodinae Kieffer, in Kieffer & Marshall, 1906

Genus *Echthrodelpfax* Perkins

Echthrodelpfax Perkins, 1903: 36.

Echthrodelpfax migratorius Benoit**

Echthrodelpfax migratorius Benoit, 1954: 397.

Material examined. New record. UGANDA: CENTRAL REGION: Masaka District, Kawanda, X.1942, T. H. C. Taylor leg., 1♂ (BMNH).

Hosts. Delphacidae Delphacinae (Guglielmino et al. 2013): in Egypt: nymphs of *Sogatella furcifera* (Horváth) and *S. vibix* (Haupt); in Mozambique: *Sogatella petax* Fennah.

Distribution. Recorded from many Afrotropical countries, from the Cape Verde Islands, Niger and Senegal to Madagascar and Somalia, in addition to Oman and Egypt (Olmi 1984, 1994b, 2006; Olmi et al. 2015). Newly recorded from Uganda here.

Echthrodelpfax tauricus Ponomarenko**

Echthrodelpfax tauricus Ponomarenko, 1970: 432.

Material examined. New record. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 7.V.2001, sweep, lowland rainforest, marsh clearing, S. van Noort leg., 19♂♂ (18 in SAMC, 1 in MOLC).

Hosts. Delphacidae Delphacinae (Guglielmino et al. 2013): in the Afrotropical region: in the Cape Verde Islands: *Peregrinus maidis* (Ashmead); in Mozambique: *Nycheuma endymion* (Fennah), *Metadelpfax propinqua* (Fieber).

Distribution. Recorded from many Afrotropical countries (from the Cape Verde Islands to Somalia, including Madagascar and South Africa), in addition to many European countries, Oman, Yemen and the United Arab Emirates (Azevedo et al. 2010; Olmi 1999b, 2004c, 2005c, 2008; Olmi and van Harten 2000, 2006). Newly recorded from Central African Republic here.

Genus *Adryinus* Olmi

Adryinus Olmi, 1984: 1126.

***Adryinus bellicosus* (Benoit)**

Neodryinus bellicosus Benoit, 1950b: 227.

Adryinus bellicosus (Benoit): Olmi 1984: 1132.

Material examined. Published records. Olmi (1984): **UGANDA: CENTRAL REGION:** Mubende District, Namutamba, 2♀♀ (BMNH, AMNH); **WESTERN REGION:** Rukungiri District, Rujumbura County, Ruzumbura (= Rujumbura; Ruzhumbura; Ruzumbusa, misspellings in Olmi 1984) [00°40' 00" S, 029°52' 00" E], V.1939, T.H.C. Taylor leg., 1♀ (BMNH); **New record. UGANDA: WESTERN REGION:** Masindi District, Budongo Forest near Sonso, 01°45'N, 31°35'E, VI.1995, Th. Wagner leg., 1♀ (CNCI).

Hosts. Unknown.

Distribution. Recorded from Democratic Republic of the Congo, Uganda and Zimbabwe (Olmi 1984).

***Adryinus oweni* Olmi**

Adryinus oweni Olmi, 1984: 1135.

Material examined. Published record. Olmi (1984): **UGANDA: CENTRAL REGION:** Kampala District, Kampala, ♀ holotype (AEIC). **New record. IVORY COAST: BOUAKÉ DEPARTMENT:** Bouaké, 11.X.1980, Pitfall trap, 1♀ (AMNH).

Hosts. Unknown.

Distribution. Uganda (Olmi 1984). Newly recorded from Ivory Coast here.

Genus *Gonatopus* Ljungh

Gonatopus Ljungh, 1810: 161.

***Gonatopus nearcticus* (Fenton)**

Pachygonatopus nearcticus Fenton, 1927: 6.

Platygonatopus ugandanus Benoit, 1951a: 300 (synonymized by Olmi 1993).

Gonatopus nearcticus (Fenton): Olmi 1993: 80.

Material examined. Published records. Olmi (1984): **UGANDA: EASTERN REGION:** Busiki (=Namutumba) District, Bululo (= actually Bulule ?), 1909, E. Bayon leg., ♀ holotype of *Platygonatopus ugandanus* (MSNG); Serere District, Serere, VII.1943, T.H.C. Taylor leg., 1 ♀ (BMNH). **CENTRAL REGION:** Masaka District, Kawanda, V.1943, VI.1943, T.H.C. Taylor leg., 3 ♀♀, 3 ♂♂ (BMNH); same locality label, 1 ♀, 1 ♂ (AMNH).

Hosts. Cicadellidae (Guglielmino et al. 2013): in the Afrotropical region: in Namibia: *Paradorydium spatulatum* (Naudé); in South Africa: *Balclutha frontalis* (Ferrari) (= *B. rosea* (Scott)).

Distribution. Recorded from many countries of the Palearctic, Afrotropical and Nearctic Regions (Olmi et al. 2015); in Africa recorded from many sub-saharian countries, from Benin to South Africa and Ethiopia (Olmi 1984, 2006).

Gonatopus camerounensis Olmi**

Gonatopus camerounensis Olmi, 2011: 64.

Material examined. New record. **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE:** Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 03°02'01"N 16°24'57"E, 510 m, 6–7.V.2001, Malaise trap, lowland rainforest, marsh clearing, S. van Noort leg., 1 ♀ (SAMC).

Hosts. Unknown.

Distribution. Cameroon (Olmi 2011). Newly recorded from Central African Republic here.

Gonatopus guigliae (Benoit)

Digonatopus guigliae Benoit, 1951a: 298.

Gonatopus guigliae (Benoit): Olmi 1984: 1596.

Material examined. Published record. Benoit (1951a): **UGANDA: EASTERN REGION:** Busoga Kingdom, Bussu, 1910, E. Bayon leg., ♀ holotype (MSNG); same locality label as holotype, 1 ♀ paratype (MRAC) (collecting data have been wrongly reported as “Bussu - 1909” in the original description of Benoit (1951) (Penati & Olmi 2011)).

Hosts. Cicadellidae (Guglielmino et al. 2013): in Mozambique: *Exitianus zuluenensis* Ross ; in South Africa: *Exitianus natalensis* Ross and *E. taeniaticeps* (Kirschbaum).

Distribution. Recorded from Mozambique, South Africa and Uganda (Olmi 1984, 1998b, 2006).

***Gonatopus hyalinus* Olmi**

Gonatopus hyalinus Olmi, 1984: 1607.

Material examined. Published record. Olmi et al. (2015): **UGANDA: CENTRAL REGION:** Masaka District, Kawanda, VI.1943, T. H. C. Taylor leg., 1♀ (BMNH).

Hosts. Unknown.

Distribution. Recorded from Kenya, South Africa and Uganda (Olmi 1984, 2006; Olmi et al. 2015).

***Gonatopus incognitus* Olmi**

Gonatopus incognitus Olmi, 1984: 1613.

Material examined. Published record. Olmi (1984): **UGANDA: CENTRAL REGION:** Masaka District, Kawanda, 7.VII.1943, T.H.C. Taylor leg., ♀ holotype (BMNH).

Hosts. Cicadellidae (Guglielmino et al. 2013): in Burkina Faso: *Cicadulina similis* China; in Democratic Republic of the Congo: *Cicadulina mbila* (Naudé); in Nigeria: *Cicadulina storeyi* China; in South Africa: *Exitianus taeniaticeps* (Kirschbaum); in Tanzania: *Cicadulina bipunctata* (Melichar).

Distribution. Afrotropical, broadly spread from the Cape Verde Islands and Burkina Faso to Uganda, in addition to Madagascar, Yemen and Oman (Azevedo et al. 2010; Olmi 1984, 1994b, 1994a, 2006; Olmi and van Harten 2000).

Gonatopus kanyawarus* sp. n.

<http://zoobank.org/3DC58361-799F-4D33-BEBC-19557810BB35>

Figs 2C, 3A, 3B, 12

Type material. HOLOTYPE: ♀, **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.871'N, 30°21.355'E, 1495 m, 4–26.VIII.2008, UG08-KF2-Y03, YPT, primary mid-altitude rainforest, S. van Noort leg. (SAMC). Paratype: same locality label as holotype, 1♀ (SAMC).

Diagnosis. Female with temples without sharp carina; mesosoma black, except posterior third of scutum yellow; scutum less than twice as long as broad, with two lateral pointed apophyses; metanotum very hollow behind scutellum (Fig. 3B), with sides protruding (protrusions rounded) (Fig. 3A); meso-metapleural suture distinct and complete; mesopleuron without lateral pointed prominence; metathorax + propodeum without strong median furrow, shiny, with anterior surface sculptured by numerous longitudinal striae, unsculptured among striae; segment 1 of protarsus shorter



Figure 12. *Gonatopus kanyawarus* sp. n. Holotype female. **A** habitus, dorsal view **B** habitus lateral view (inset: data labels) **C** head, mesosoma dorsal view **D** head, mesosoma lateral view **E** head, anterior view **F** chela (slide mounted).

than segment 4; subapical tooth of enlarged claw situated very far from distal apex (Figs 2C, 12F).

Description. Female. Apterous; length 3.5–4.0 mm. Head brown-black, except mandible, clypeus, anterior half of face (with short stripe along orbits) and ventral side whitish; antenna brown, except segments 1–2 and proximal third of 3 whitish, segment 10 testaceous; mesosoma black, except posterior third of scutum yellow;

metasoma brown-testaceous; fore leg brown, except part of coxa, trochanter, stalk of femur, part of tibiae and part of chela testaceous; mid leg brown, except part of coxa, trochanter, part of femur and tibia, tarsus testaceous; hind leg brown, except distal extremity of coxa, trochanter, part of femur, tibia and tarsus testaceous. Antenna clavate; antennal segments in following proportions: 9:6:21:12:9:9:7:6:5:9. Head excavated, shiny, unsculptured; frontal line incomplete, absent in anterior third of face; occipital carina absent; POL = 2.5; OL = 2; OOL = 10. Palpal formula: 6/3. Pronotum crossed by strong transverse furrow, shiny, unsculptured. Scutum shiny, sculptured by numerous longitudinal striae, laterally with two strong pointed apophyses situated on sides of scutellum. Scutellum shiny, smooth, inclined. Metanotum very long, transversely striate and hollow behind scutellum (Fig. 3B), with sides protruding (protrusions rounded) (Fig. 3A). Metathorax + propodeum shiny, with anterior surface sculptured by numerous longitudinal striae, unsculptured among striae; posterior surface of propodeum, mesopleuron and metapleuron transversely striate. Meso-metapleural suture distinct and complete. Protarsal segments in following proportions: 17:3:6:20:31. Segment 3 of protarsus produced into hook. Enlarged claw (Figs 2C, 12F) with one small subapical tooth and one row of four small lamellae + one bristle. Segment 5 of protarsus (Figs 2C, 12F) with two rows of 1 (proximal) + 20 lamellae; distal apex with approximately 14 lamellae. Tibial spurs 1/0/1.

Male. Unknown.

Differential diagnosis. Because of the above diagnosis, the new species is similar to *Gonatopus trochantericus* (Benoit, 1954) and *G. tulearensis* Olmi, 2010. The main difference regards the metanotum (with sides protruding (rounded protrusions) in *G. kanyawarus* (Fig. 3A); with sides rounded and not protruding in the other two species (Figs 3D, E)).

Etymology. The species is named after the type locality, Kanyawara.

Hosts. Unknown.

Distribution. Uganda.

Gonatopus kolyadai Olmi**

Gonatopus kolyadai Olmi, 2007b: 224.

Material examined. New record. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Reserve Speciale de forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 11–12.V.2001, Malaise trap, lowland rainforest, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. South Africa (Olmi 2007b, 2009). Newly recorded from Central African Republic here.

***Gonatopus operosus* Olmi**

Gonatopus opacus Olmi, 1984: 1634 (preoccupied).

Gonatopus operosus Olmi, 1993: 80 (new name).

Material examined. Published record. Olmi (1984): **UGANDA: CENTRAL REGION**, Mukono district: Kyagwe (= Kyagur: mistake in original description) [00°25'00"N, 032°50'00"E], XI.1938, T.H.C. Taylor leg., ♀ holotype (BMNH). **New records. CAMEROON: SOUTH-WEST REGION:** 6 mi. S Kumba, 180 m, 1♀ (AMNH). **SOUTH AFRICA: WESTERN CAPE:** Die Dam, 24.II.2006, M. Olmi reared ex *Caffrolix cyclopia* (Cogan), 1♀ (MOLC). **UGANDA: WESTERN REGION:** Masindi District, Budongo Forest near Sonso, 01°45'N, 31°35'E, VI.1995, Th. Wagner leg., 1♀ (CNCI).

Hosts. Cicadellidae (Guglielmino et al. 2013): in South Africa: *Caffrolix cyclopia* (Cogan).

Distribution. Recorded from Uganda (Guglielmino and Olmi 2007; Olmi 1984). Newly recorded from Cameroon and South Africa here.

***Gonatopus taylori* Olmi**

Gonatopus taylori Olmi, 1984: 1628.

Material examined. Published records. Olmi (1984): **UGANDA: EASTERN REGION:** Sironko District, Bugusege (= Bugusaga, misspelt in Olmi 1984) [01°07'20"N, 034°15'55"E], XI.1938, T.H.C. Taylor leg., ♀ holotype (BMNH). **CENTRAL REGION:** Mubende District, Namutamba, 9.VII.1940, T.H.C. Taylor leg., 1♀ paratype (BMNH); **EASTERN REGION:** Mayuge district, Bugota [00°20'00"N, 033°37'00"E], 1♀ paratype (AMNH).

Hosts. Unknown.

Distribution. Recorded from Botswana, Ethiopia, Kenya, South Africa and Uganda (Olmi 1984; Olmi and Copeland 2011).

Genus *Neodryinus* Perkins

Neodryinus Perkins, 1905: 50.

Neodryinus antiquus* Benoit*

Neodryinus antiquus Benoit, 1954: 402.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE

Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 6.V.2001, sweep, lowland rainforest, marsh clearing, CAR01-S70, S. van Noort leg., 1♀ (SAMC). **DEMOCRATIC REPUBLIC OF THE CONGO: KATANGA:** Lubumbashi (= Elisabethville), 30.III.1939, 1♀ (IRSN). **ZAMBIA: LUSAKA PROVINCE:** Lusaka, 17.I.1980, Malaise trap, R.A. Beaver leg., 1♀ (AMNH).

Hosts. Unknown.

Distribution. Madagascar (Benoit 1954; Olmi 1984). Newly recorded from Central African Republic, Democratic Republic of the Congo and Zambia here.

Neodryinus tussaci Olmi**

Neodryinus tussaci Olmi, 2004b: 179.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 4.V.2001, sweep, lowland rainforest, marsh clearing, CAR01-S24, S. van Noort leg., 1♀ (SAMC). **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°34.390'N, 30°21.658'E, 1587 m, 4–26.VIII.2008, YPT, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Cameroon (Olmi 2004b). Newly recorded from Central African Republic and Uganda here.

Family EMBOLEMIDAE

Genus *Ampulicomorpha* Ashmead

Ampulicomorpha Ashmead, 1893: 79.

Ampulicomorpha magna Olmi**

Ampulicomorpha magna Olmi, 1996: 102.

Material examined. New records. UGANDA: WESTERN REGION: Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°33.996'N, 30°21.262'E, 1495 m, 3–5.VIII.2005, Malaise trap, secondary mid-altitude rainforest, UG05-M12, S. van Noort leg., 1♂ (SAMC).

Hosts. Unknown.

Distribution. Recorded from Gabon, Kenya, Malawi, South Africa, Zambia and Zimbabwe (Olmi and Copeland 2011). Newly recorded from Uganda here.

Ampulicomorpha madecassa* Olmi*

Ampulicomorpha madecassa Olmi, 1999a: 2.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombombo, 2°21'60"N 16°03'20"E, 350 m, 21–22.V.2001, Malaise trap, lowland rainforest, CAR01-M172, S. van Noort leg., 1♀ (SAMC).

Hosts. Unknown.

Distribution. Recorded from Madagascar (Olmi 1999a), Kenya and South Africa (Olmi et al. 2015). Newly recorded from Central African Republic here.

Genus *Embolemus* Westwood

Embolemus Westwood, 1833: 444.

Embolemus capensis* Olmi*

Embolemus capensis Olmi, 1997: 141.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombombo, 2°21'60"N 16°03'20"E, 350 m, 24–25.V.2001, Malaise trap, lowland rainforest, CAR01-M200, S. van Noort leg., 1♂ (SAMC); same locality label, 24–25.V.2001, CAR01-M204, 2♂♂ (SAMC); same locality label, 23–24.V.2001, CAR01-M189, 3♂♂ (SAMC); same locality label, 23–24.V.2001, CAR01-M193, 1♂ (SAMC); same locality label, 26–27.V.2001, CAR01-M227, 1♂ (SAMC); same locality label, 26–27.V.2001, CAR01-M226, 3♂♂ (1 in SAMC, 2 in MOLC); same locality label, 25–26.V.2001, CAR01-M211, 1♂ (SAMC); same locality label, 25–26.V.2001, CAR01-M212, 1♂ (SAMC); same locality label, 25–26.V.2001, CAR01-M215, 1♂ (SAMC); same locality label, 25–26.V.2001, CAR01-M214, 1♂ (SAMC).

Hosts. Unknown.

Distribution. Recorded from Burundi, Kenya, Madagascar, São Tomé and Príncipe, South Africa (Olmi 1997, Olmi and Copeland 2011).

Family SCLEROGIBBIDAE**Genus *Caenosclerogibba* Yasumatsu**

Caenosclerogibba Yasumatsu, 1958: 21.

***Caenosclerogibba probethyloides* Olmi**

Caenosclerogibba probethyloides Olmi, 2005a: 87.

Material examined. Published records. Olmi (2005a): **UGANDA: WESTERN REGION:** Mbarara District, 25 mi. S Mbarara, 10.XII.1957. Ex *Scelembia*, E. Ross reared, 1 ♀ paratype (CASC).

Hosts. Embiidina (Olmi 2005a): in Cameroon: *Heterembia* sp., *Holembia* sp.; in Ivory Coast: *Nodosembia* sp., *Parachirembia* sp., *Scelembia* sp., unidentified *Embiidae*, unidentified *Teratembiiidae*; in Kenya: *Oligotoma saundersii* (Westwood); in Tanzania: unidentified *Teratembiiidae*; in Uganda: *Scelembia* sp.

Distribution. Recorded from many Afrotropical countries (Cameroon, Ivory Coast, Kenya, Liberia, Madagascar, Tanzania, Uganda), in addition to Yemen (Olmi 2005a; Olmi et al. 2015).

Genus *Probethylus* Ashmead

Probethylus Ashmead, 1902: 270.

Probethylus callani* Richards*

Probethylus callani Richards, 1939b: 211.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAËRÉ PREFECTURE: Reserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 15–16.V.2001, Malaise trap, lowland rainforest, S. van Noort leg., 2♂♂ (SAMC); Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 2°21'60"N 16°03'20"E, 350 m, 21–22.V.2001, Malaise trap, lowland rainforest, CAR01-M173, S. van Noort leg., 1♂ (SAMC).

Hosts. Embiidina (Olmi 2005a): in the Afrotropical region: Congo: *Parthenembia* sp., *Plesembia* sp., *Dihybocercus collaris*; in Tanzania: *Rhagadochir vosseleri*.

Distribution. Recorded from many Nearctic, Neotropical and Afrotropical countries (Olmi 2005a). In Africa known from Angola, Democratic Republic of the Congo, Kenya, Nigeria, South Africa and Tanzania (Olmi 2005a; Olmi and Copeland 2011; Olmi et al. 2015).

Genus *Sclerogibba* Riggio & De Stefani-Perez

Sclerogibba Riggio & De Stefani-Perez, 1888: 19.

Sclerogibba algerica* Benoit*

Sclerogibba algerica Benoit, 1963: 84.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Dzanga-Ndoki National Park, Mabéa Bai, 21.4 km 53°NE Bayanga, 3°02.01'N, 16°24.57'E, 510 m, 1–7.V.2001, YPT, lowland rainforest, marsh clearing, S. van Noort leg., 1♀ (SAMC). **MALI: KOULIKORO REGION:** Katibougou, 2008, Malaise trap, D. Sommaggio leg., 1♂ (MOLC).

Hosts. Embiidina (Olmi 2005a): in Algeria: *Embia lesnei* Ross; in Tunisia: *Embia ramburi* (Rimsky-Korsakow). No hosts are known in the Afrotropical region.

Distribution. Recorded from Algeria and Tunisia (Olmi 2005a). Newly recorded from the Afrotropical region (Central African Republic and Mali).

***Sclerogibba crassifemorata* Riggio & De Stefani-Perez**

Sclerogibba crassifemorata Riggio & De Stefani-Perez, 1888: 146.

Material examined. Published record. Olmi (2005a): **CENTRAL AFRICAN REPUBLIC: HAUT-MBOMOU PREFECTURE:** Zemio, 05°45'N, 25°15'E, 6.III.1948, Neal A. Weber leg., 1♂ (AMNH).

Hosts. Embiidina (Olmi 2005a): in Algeria: *Embia lucasi* Ross. No hosts are known in the Afrotropical region.

Distribution. Recorded from many Palaearctic and Afrotropical countries (Olmi 2005a). In Africa known from Central African Republic, Kenya, Niger and Northern Africa (Olmi 2005a; Olmi and Copeland 2011).

***Sclerogibba impressa* Olmi**

Sclerogibba impressa Olmi, 2005a: 149.

Material examined. Published record. Olmi (2005a): **UGANDA: CENTRAL REGION:** Wakiso District, Entebbe, 3700', 14.V.1972, Malaise trap, H. Falke leg., 1♀ paratype (CNCI).

Hosts. Embiidina (Olmi 2005a). No hosts are known in the Afrotropical region. The unique hosts are known in the Philippines and Taiwan (*Aposthonia* species).

Distribution. Recorded from Afrotropical and Oriental countries (Olmi 2005a). In Africa known only from Kenya and Uganda (Olmi 2005a; Olmi and Copeland 2011; Olmi et al. 2015).

Sclerogibba rapax* Olmi*

Sclerogibba rapax Olmi, 2005a: 160.

Material examined. New records. CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE: Reserve Speciale de Forêt dense de Dzanga-Sangha, 12.7 km 326°NW Bayanga, 3°00.27'N, 16°11.55'E, 420 m, 15–16.V.2001, Malaise trap, lowland rainforest, S. van Noort leg., 2♂♂ (SAMC).

Hosts. Embiidina (Olmi 2005a): in Angola: *Machadoembia* sp., *Scelembia* sp.; in Cameroon: *Plesembia* sp.; in Democratic Republic of the Congo: *Scelembia* sp., *Plesembia* sp.; in Kenya: *Embia* (= *Dictyoploca*) *burensis* (Rimsky-Korsakov); in Malawi: *Embia* sp.

Distribution. Recorded from many Afrotropical and Oriental countries (Olmi 2005a). In Africa known from Angola, Cameroon, Democratic Republic of the Congo, Ghana, Kenya and Malawi (Olmi 2005a; Olmi and Copeland 2011; Olmi et al. 2015). Newly recorded from Central African Republic.

***Sclerogibba talpiformis* Benoit**

Sclerogibba talpiformis Benoit, 1950a: 133.

Material examined. Published records. Olmi et al. 2015: **CENTRAL AFRICAN REPUBLIC: SANGHA-MBAÉRÉ PREFECTURE:** Dzanga-Ndoki National Park, 38.6 km 173°S Lidjombo, 02°21.60'N, 16°03.20'E, 350 m, 24–25.V.2001, lowland rainforest, Malaise trap, S. van Noort leg., CAR01-M206, 1♂ (UKIC). **UGANDA: WESTERN REGION:** Kibale National Park, Kanyawara, Makerere University Biological Field Station, 0°34.405'N, 30°21.646'E, 1484 m, 16–26.VIII.2008, Malaise trap, primary mid-altitude rainforest, near stream, S. van Noort leg., 1♂ (SAMC).

Hosts. Embiidina (Olmi 2005a): in Ivory Coast: *Parachirembia* sp.; in South Africa: *Embia* sp.; in Zambia: *Embia* sp.

Distribution. Recorded from many countries of the world, excluding the Australian region (Olmi 2005a). In Africa known from Botswana, Burkina Faso, Cameroon, Central African Republic, Democratic Republic of the Congo, Gabon, Ivory Coast, Kenya, Madagascar, Mali, Mozambique, Namibia, South Africa, Uganda, Zambia, Zimbabwe, Yemen and Northern Africa (Azevedo et al. 2010; Olmi 2005a; Olmi and Copeland 2011; Olmi et al. 2015).

***Sclerogibba vagabunda* (Bridwell)**

Lithobiocerus vagabundus Bridwell, 1919: 36.

Sclerogibba vagabunda (Bridwell): Richards 1939b: 218.

Material examined. Published records. Olmi 2005a: **UGANDA: WESTERN REGION:** Mbarara District, 10 mi. SE Mbarara, 1300 m, Matured 19.I.1958, E. Ross reared, 1♂ (CASC).

Hosts. Embiidina (Olmi 2005a): in Kenya: *Chirembia* sp., *Gnathembia* sp., *Nava-siella* sp., *Cephalembia* sp.

Distribution. Recorded from many countries of the world, excluding the Neotropical Region (Olmi 2005a). In Africa known from Burundi, Kenya, Madagascar, Somalia, Tanzania, Togo, Uganda and Northern Africa (Olmi 2005a; Olmi and Cope-land 2011). Known also in Yemen (Olmi 2005a).

Discussion

The checklist of the Dryinidae, Embolemidae and Sclerogibbidae of Central African Republic and Uganda presented in this paper includes 23 species of Dryinidae, two species of Embolemidae and three species of Sclerogibbidae known from Central African Republic; 39 species of Dryinidae, one species of Embolemidae and four species of Sclerogibbidae known from Uganda. Seventeen species of Dryinidae, two species of Embolemidae and one species of Sclerogibbidae were newly recorded from Central African Republic; sixteen species of Dryinidae and one species of Embolemidae were reported for the first time in Uganda.

With 1827 species worldwide (Olmi and Xu 2015), Dryinidae is one of the three largest families in the Chrysidoidea, the other two being Chrysididae and Bethy- lidae. With the possible exception of Kenya, Madagascar, Mozambique and South Africa, the dryinid fauna of the Afrotropical Region, like that of many families of micro-Hyme- noptera, is poorly known. A comparison with the better known Afrotropical countries shows the following situation: in Madagascar 123 species of Dryinidae, six species of Embolemidae and seven species of Sclerogibbidae are recorded (Azevedo et al. 2010); in South Africa 174 species of Dryinidae (unpublished datum; 119 reported by Olmi (2006)), seven species of Embolemidae (unpublished datum; six reported by Olmi (2006)) and six species of Sclerogibbidae are recorded (Olmi 2005a); in Mozambique 45 species of Dryinidae (Olmi et al. 2012), no species of Embolemidae (unpublished datum) and three species of Sclerogibbidae are known (Olmi et al. 2015); in Kenya 76 species of Dryinidae, six species of Embolemidae and 12 species of Sclerogibbidae are reported by Olmi et al. (2015).

Hosts of Dryinidae are known for 12 of the 52 species reported in the presented checklists in this paper, but no new host associations were established during the recent inventory surveys conducted in Uganda and Central African Republic. No hosts of Embolemidae are known in the entire Afrotropical region. Host associations are better known for the Sclerogibbidae, mainly due to the rearing out of parasitized hosts car- ried out by Edward S. Ross: the hosts are known for seven of the eight species reported in the presented checklists, in one case as a result of rearing of adult wasps in Uganda.

Further baseline species inventory and establishment of host associations are required across the majority of the countries in the region to enable assessment of overall species richness and biology of the Afrotropical fauna for these families.

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Two new species of the ground beetle subgenus *Sadonebria* Ledoux & Roux, 2005 (Coleoptera, Carabidae, *Nebria*) from Japan and first description of larvae of the subgenus

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Abstract

Sadonebria Ledoux & Roux, 2005 is one of the more diverse subgenera of the genus *Nebria* Latreille, 1802 in East Asia, and its taxonomy remains unrevised at the subgeneric and specific levels. In this paper, two new species of this subgenus are described from Japan. *Nebria quinquelobata* sp. n. is described from Mt. Myôkô and is externally similar to *Nebria saeviens* Bates, 1883, to which specimens of this new species previously had been assigned. *Nebria yatsugatakensis* sp. n. is described from the Yatsugatake Mountains and is externally similar to locally adjacent species that had been recognized as *Nebria sadona* Bates, 1883 and were recently revealed as separate species. Both new species are distinguished by morphological (the shape of the endophallus) and morphometric (geometric morphometrics of the pronotum and aedeagus) features. For *N. yatsugatakensis*, the morphology of all larval instars is described based on specimens reared from eggs laid by collected adults. These results, together with previous studies of the species-level taxonomy of *Sadonebria* and larval morphology of other *Nebria* subgenera, suggest (i) the utility of geometric morphometrics in species-level taxonomy; (ii) the importance of larval secondary setae in the subgeneric taxonomy of the genus *Nebria*; and (iii) the presence of further cryptic species in *Sadonebria*.

Keywords

Cryptic species, endophallus, geometric morphometrics, larval morphology, male genitalia, *Nebria quinquelobata* sp. n., *Nebria sadona*, *Nebria yatsugataakensis* sp. n., taxonomy

Introduction

Sadonebria Ledoux & Roux, 2005 is an endemic East Asian subgenus of the genus *Nebria* Latreille, 1802 (Coleoptera, Carabidae). To date, 15 species-group taxa (13 species and two subspecies) have been described in this subgenus. Among the 15 taxa, *N. chinensis* Bates, 1872, which has developed hind wings, is widely distributed in China, Korea, and Japan (Farkač and Janata 2003). The remaining taxa, which have atrophied hind wings and are flightless, are endemic to Taiwan (*N. niitakana* Kano, 1930) and Japan (the remaining 13 taxa). Of the 13 Japanese taxa, nine were previously considered *N. sadona* Bates, 1883 due to marked similarities in external morphology but were recently separated based on the shape of the endophallus (a membranous inner sac everted from the aedeagus of male genitalia) (Sasakawa and Kubota 2006; Sasakawa 2008, 2009, 2010; Sasakawa and Toki 2011), a character that had been insufficiently examined by previous authors (e.g., Habu 1962; Uéno 1985). According to the latest comprehensive study by Sasakawa and Toki (2011), a major diversification of *Sadonebria* in the Japanese Archipelago occurred in the area east of Kinki, Honshu, where the species diversity of this group is highest (Fig. 1). However, taxonomic studies of *Sadonebria* in this area are still insufficient, and there are many localities from which no specimens have been examined. Moreover, the recent studies were predominantly based on comparative morphology of the single male genital character, and other morphological and genetic characters remain unexamined. It is important to address these issues to better understand the diversification of *Sadonebria* in the Japanese Archipelago.

In this paper, two new species of *Sadonebria* are described from the area east of Kinki, Honshu, Japan. As with the recently described species, the new species are separated from known species based on the shape of the endophallus. Here, in addition to comparative morphology of this genital character, geometric morphometrics of external and genital characters are also performed. This morphometric technique can effectively evaluate subtle morphological differences, which are difficult to detect by traditional morphometrics, and is now widely used for the analysis of morphometric data (e.g., Sha et al. 2016; Sasakawa 2016; Kosuda et al. 2016). Therefore, it may be useful for species-level taxonomy of *Sadonebria*, members of which have markedly similar external and genital (other than the endophallus) morphologies. For one of the new species, the morphology of all larval instars is also described based on specimens reared from eggs laid by collected adults; this is the first report of larval morphology for the subgenus *Sadonebria*. The implications of these results for the taxonomy of both the subgenus *Sadonebria* and the genus *Nebria* are discussed.

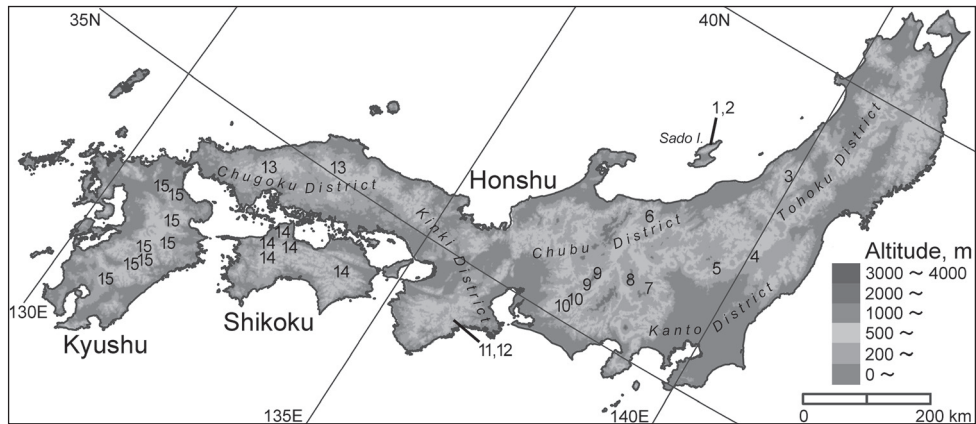


Figure 1. The distribution of *Nebria* (*Sadonebria*) spp. in the Japanese Archipelago; *N. chinensis* Bates, which is distantly related to the remaining species, and samples that are not identified by genital morphology are not included [modified from Sasakawa and Toki (2011)]. **1** *N. sadona sadona* Bates **2** *N. saevi* Bates **3** *N. asahina* Sasakawa **4** *N. nasuensis* Sasakawa **5** *N. sadona leechi* Bates **6** *N. quinquelobata* sp. n. **7** *N. chichibuensis* Sasakawa **8** *N. yatsugatakensis* sp. n. **9** *N. kiso* Sasakawa **10** *N. mikawa* Sasakawa **11** *N. sadona ohdaiensis* Nakane **12** *N. tenuicaulis* Sasakawa & Kubota **13** *N. jakuchisana* Sasakawa **14** *N. shikokuensis* Sasakawa; **15**: *N. trifida* Sasakawa.

Materials and methods

Morphological comparison and description

Information regarding comparisons of adults of related species was obtained from Sasakawa (2008, 2009), Sasakawa and Kubota (2006), and Sasakawa and Toki (2011), which describe key characters of the species, such as the male endophallus, based on their type materials (species other than *N. saevi*) or materials from the type locality (*N. saevi*). For *N. saevi*, the following additional materials from the type locality (Sado Island) were also examined: 5♂6♀, the upper reaches of the Kuchi river, Sado-shi, Niigata Prefecture, 10.vi.2010, Naoyuki Shibata leg. These specimens were also used in subsequent geometric morphometric analyses. Terminology of the male endophallus followed Sasakawa (2009).

To obtain larval specimens, adults of *N. yatsugatakensis* sp. n. were reared in plastic boxes (17.0 × 8.5 × 4.5 cm) following the technique described in Sasakawa (2011). The adults were collected at the type locality on 4–5 September 2010. Eggs were laid in the mud of rearing boxes from 5–15 September and were left in place until hatching. To simulate cooling autumn temperatures, the adults and eggs were reared under gradually decreasing temperatures: 18°C (5 September–10 October), 15°C (11–22 October), 10°C (23–26 October), and 5°C (27 October–3 November). The photoperiod was maintained at 8:16 h light:dark, and *Tenebrio molitor* larvae (cut into pieces) were provided as a food source. The eggs hatched between 30 October and 3

November and then were moved to Petri dishes (3.5 cm diameter, 1.0 cm high) filled with 0.5 cm moistened garden soil, after which they were reared at a constant temperature of 5°C or 10°C and checked daily for development. In total, 15 first-instar, 16 second-instar, and 14 third-instar specimens of *N. yatsugatakensis* sp. n. were obtained. For detailed morphological observations and measurements, five first-instar, four second-instar, and five third-instar specimens were dissected and mounted on permanent microscope slides in Euparal medium, according to the methods described by Grebennikov and Maddisio (2005). Other specimens were observed and preserved in 70% ethanol. The notation used for the setae and pores followed Bousquet and Goulet (1984) and Bousquet (1985).

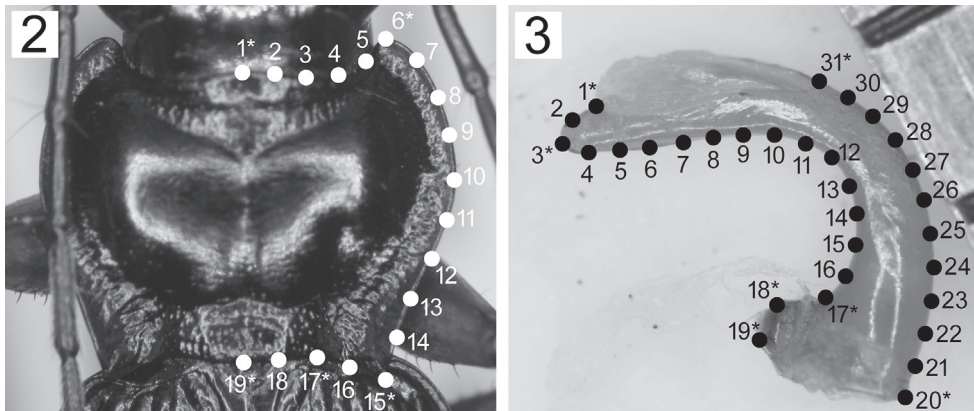
The examined specimens were deposited in the collections of the National Institute for Agro-Environmental Sciences, Tsukuba, Japan (NIAES), the Laboratory of Forest Zoology, Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo, Japan (FZUT), and those of the author (KS).

Geometric morphometrics

Geometric morphometrics were performed for the dorsal view of the pronotum and the left lateral view of the aedeagus of male genitalia using the following materials: *N. quinquelobata* sp. n., 3♂1♀, *N. saeviensi*, 5♂6♀; *N. yatsugatakensis* sp. n., 3♂6♀; and *N. chichibuensis* Sasakawa, 2010, 1♂2♀. The materials of species other than *N. saeviensi* are type series of each species. Scaled digital images were obtained using a charge-coupled device camera attached to the microscope, after adjusting the tilt in the horizontal direction of materials. The pronotum was maintained with the anterior and posterior ends (landmarks 6 and 15 in Fig. 2 and corresponding points of the left lateral side) in the same horizontal plane, and the aedeagus was placed such that the ventral margin (including sub-landmarks 5–10 in Fig. 3) near the membranous portion was maintained horizontally.

For the pronotum, five landmarks and 14 semi-landmarks were identified (Fig. 2). For the aedeagus, seven landmarks and 24 semi-landmarks were identified (Fig. 3). The coordinates were digitized using the software tpsDig version 2.17 (Rohlf 2013a). Using the software tpsRelw version 1.53 (Rohlf 2013b), the raw coordinates were converted to Procrustes coordinates, in which variations due to rotation, position, and size were removed with semi-landmarks being “slid” along the contours. Relative warp analysis and visualization of shape differences also were performed using this software.

To statistically evaluate shape differences, Procrustes ANOVA with 10,000 permutations was performed using the function procD.lm in the R package geomorph (Adams and Otárola-Castillo 2013). In both the pronotum and aedeagus analyses, all relative warp scores were included as response variables. For the pronotum, species, sex, and their interaction were included as explanatory variables. For the aedeagus, *N. chichibuensis* was excluded from the analysis because of its small sample size ($n=1$), and



Figures 2–3. Positions of landmarks (numbers with asterisks) and semi-landmarks (numbers without asterisks) on (2) a pronotum in the dorsal view and (3) an aedeagus in the right lateral view. Landmarks indicated in (2) are as follows: (1*) anterior end along the median line; (6*) apex of anterior angle; (15*) apex of posterior angle; (17*) proximal end of posterior angle; and (19*) posterior end along the median line. Landmarks indicated in (3) are as follows: (1*) apical end of membranous portion; (3*) aedeagal apex; (17*) basal end of ventral side of cylindrical part; (18*) apex of the prominence between landmarks 17 and 19; (19*) basal end of ventral side; (20*) basal end of dorsal side; and (31*) basal end of membranous portion. Semi-landmarks were plotted along the curvature at regular intervals between landmarks.

species was included as the explanatory variable. If needed, post hoc pairwise comparisons were performed using the Bonferroni-corrected significance level.

Results

Taxonomy

The two new species described here were distinguished from known species based on the shape of the endophallus. This result was complemented by that of geometric morphometrics, which is described later.

The two new species shared the following adult morphological character states. Habitus slender. Hind wings atrophied. Chaetotaxy as in other consubgeneric species (Sasakawa and Kubota 2006). Dorsal surface shiny and almost black; mouth appendages and antennae dark brown. Pronotum cordate and convex; lateral margins reflexed throughout; hind angle acute; laterobasal impression large and deep; median line impressed in the middle, reaching both the anterior and posterior margins; surface of central part almost smooth; surface of the anterior and posterior margins punctate; surface of the lateral margins sparsely punctate and/or shallowly, transversely wrinkled. Elytra oblong, widest behind the middle; four to seven dorsal pores on interval 3. Aedeagus slender and strongly arcuate, with simple apex. Endophallus stout, with four types of lobes on the surface, namely the laterobasal, lateroapical, dorsobasal, and dorsoapical lobes.

***Nebria (Sadonebria) quinquelobata* sp. n.**

<http://zoobank.org/AB3FF90A-C284-42D6-AFF9-1F228F14C999>

Figs 4, 8

Nebria saeviensi (part): Uéno (1985): 56, fig. 11.

Nebria (Orientonebria) saeviensi (part): Farkač and Janata (2003): 94.

Nebria (Sadonebria) saeviensi (part): Ledoux and Roux (2005): 824, fig. 621; Yoshitake et al. (2011): 38.

Type materials. Holotype: ♂ (NIAES), “X. 13, 1965 / Mt. Myoko / Niigata P. / K. BABA” [type locality: Mt. Myôkô, Myôkô-shi, Niigata Prefecture, Japan]. Paratypes: 2♂1♀ (NIAES), “Sasagamine [in Japanese] / S-Echigo / 28.VIII, 1966 / Col. K. Baba”.

Etymology. The specific name derives from the Latin adjectives *quinque-* (five of) and *lobatus*, *-a*, *-um* (with lobes) and refers to the ventral view of the male endophallus (Fig. 8c).

Diagnosis. Similar to *N. saeviensi* (Fig. 5) in having yellowish brown legs but distinguished by the shape of the endophallus (Figs 8, 9).

Description. *External structures:* Body length (including mandibles): ♂, 11.7–12.3 mm (mean ± SD: 12.0 ± 0.30 mm, n = 3); ♀, 13.1 mm (n = 1). Head with a reddish-brown patch between the eyes; pronotum reddish brown on the central part and dark brown at the lateral margins; head and other pronotal parts and elytra black; legs yellowish to light brown.

Male genitalia: Laterobasal lobes and lateroapical lobes both largely swollen and widely rounded, with the former slightly smaller than the latter; the dorsoapical lobe similar in size to the laterobasal lobe and bifurcated in a T shape at the apex; dorsobasal lobe distinct but smaller than the other lobes.

***Nebria (Sadonebria) yatsugatakensis* sp. n.**

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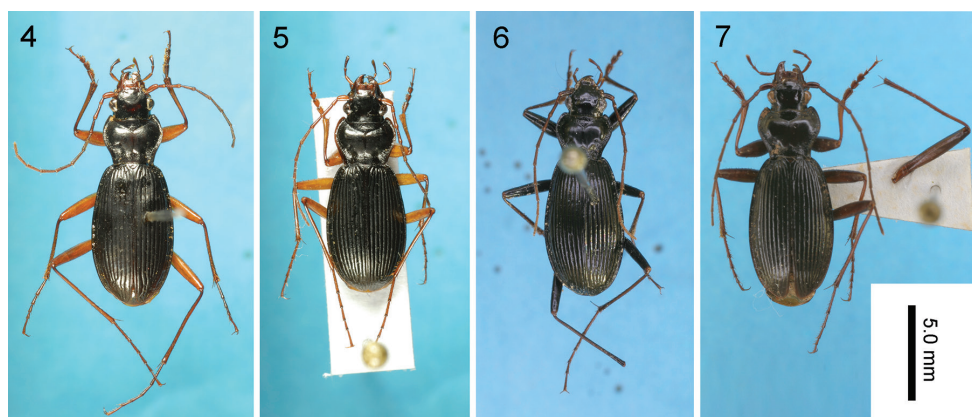
Figs 3, 7, 12–30

Nebria sadona (part): Uéno (1985): 56, fig. 10.

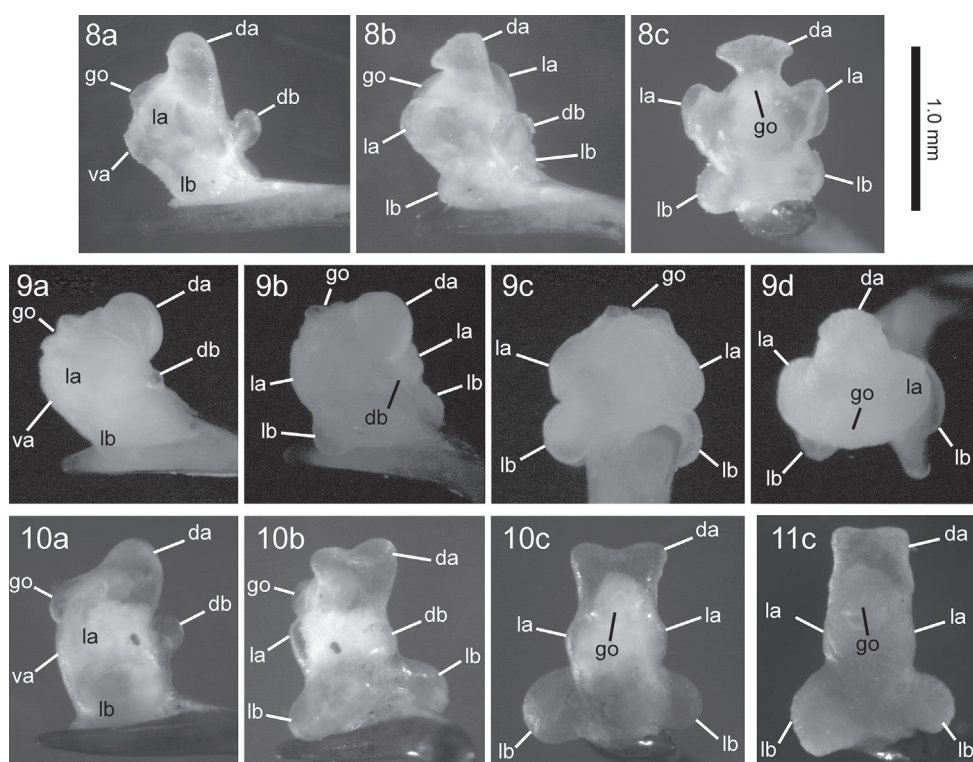
Nebria (Orientonebria) sadona (part): Farkač and Janata (2003): 94.

Nebria (Sadonebria) sadona (part): Ledoux and Roux (2005): 822, fig. 618; Yoshitake et al. (2011): 37.

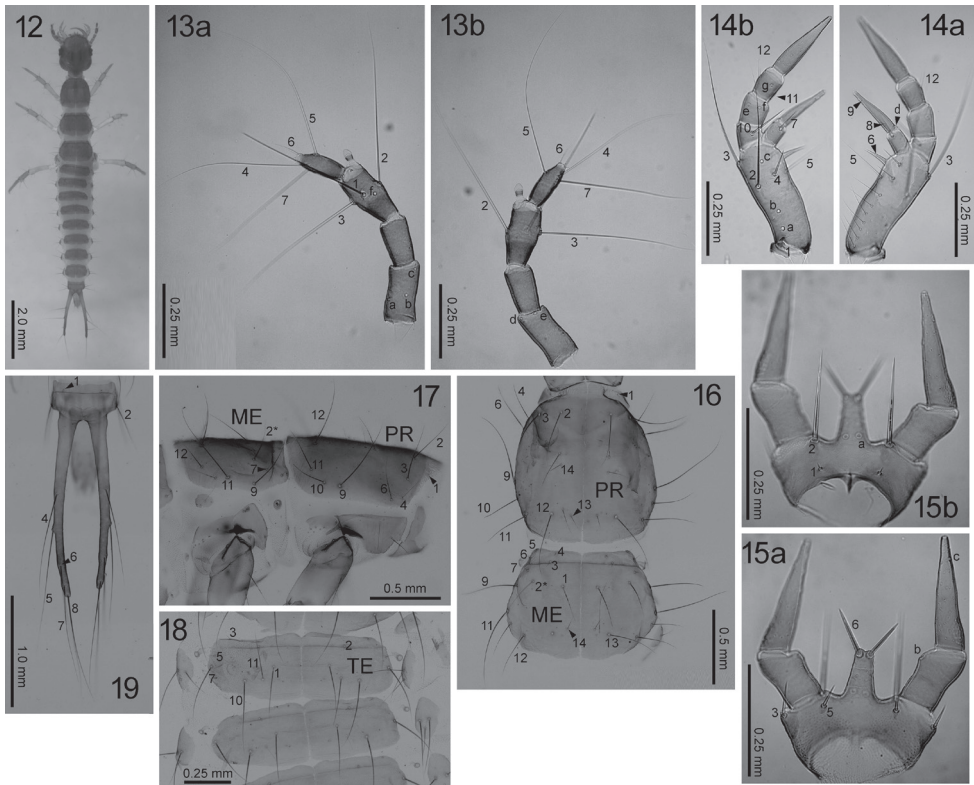
Type materials. Holotype: ♂ (FZUT), Tamagawa, Minoto, Chino-shi [the Yatsugatake Mountains], Nagano Prefecture, Japan (35°58'52.6"N, 138°18'29.4"E; ca. a.l.t. 1600 m), 4–5.ix.2010, K. Sasakawa leg. Paratypes (KS): 2♂6♀, same locality (2♀, 15–16.ix.2009, K. Sasakawa & H. Ikeda leg.; 2♂4♀, 4–5.ix.2010, K. Sasakawa leg). Larval specimens (KS) are not designated as type materials.



Figures 4–7. Dorsal view of *Nebria* (*Sadonebria*) spp. **4** *N. quinquelobata* sp. n., holotype male **5** *N. saeviensi*, male from type locality **6** *N. yatsugatakensis* sp. n., holotype male **7** *N. chichibuensis*, holotype male.



Figures 8–11. Left lateral view (**a**), left dorsolateral view (**b**), ventral view (**c**), and posterior view (**d**) of the endophallus of *Nebria* (*Sadonebria*) spp. **8** *N. quinquelobata* sp. n., holotype male **9** *N. saeviensi*, male from type locality **10** *N. yatsugatakensis* sp. n., holotype male **11** *N. chichibuensis*, holotype male. go, gonopore; da, dorsoapical lobe; db, dorsobasal lobe; va, ventroapical lobe; la, lateroapical lobe; lb, laterobasal lobe.

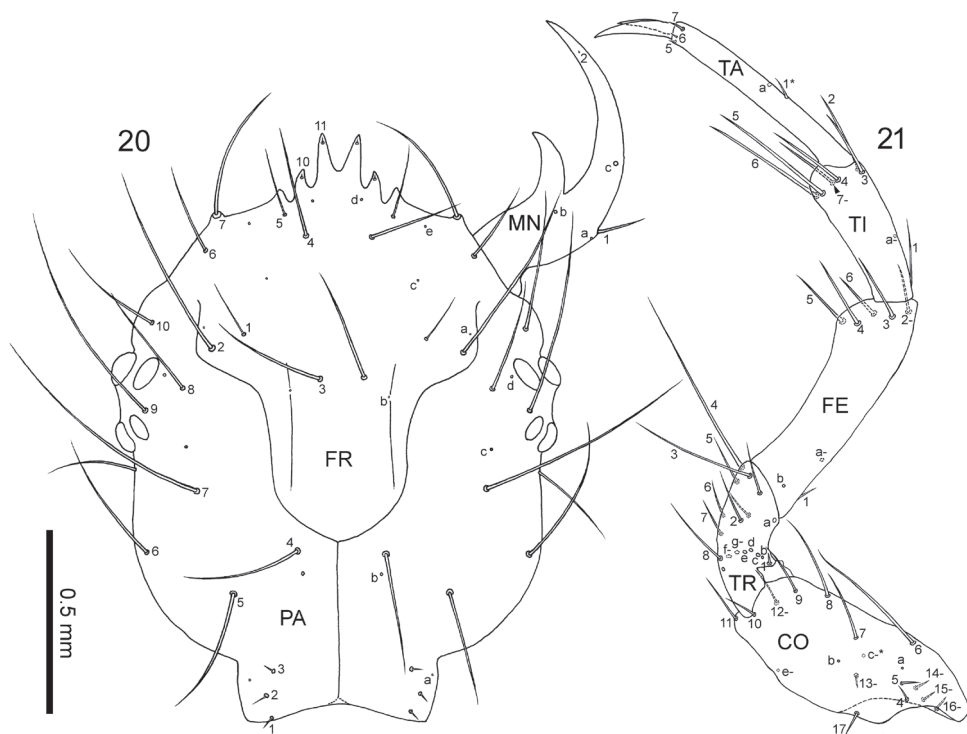


Figures 12–19. First-instar *N. yatsugatakensis* sp. n. **12** Dorsal view **13** antenna (**a** dorsal view; **b** ventral view) **14** maxilla (**a** dorsal view **b** ventral view) **15** labium (**a** dorsal view **b** ventral view) **16** prothorax and mesonotum, dorsal view **17** *Ditto*, right lateral view **18** tergites, dorsal view **19** urogomphi, dorsal view. ME, mesonotum; PR, prothorax; TE, first abdominal tergite. The homology of characters marked with an asterisk (*) is uncertain.

Etymology. The specific name is derived from the Yatsugatake Mountains, the type locality of the new species.

Diagnosis of adult. Similar to locally adjacent species, such as *N. chichibuensis* Sasakawa, 2010 (Figs 7, 11; see also Fig. 1), but distinguished by the shape of the endophallus (for example, the dorsoapical lobe is clearly Y-shaped in *N. yatsugatakensis* but not in *N. chichibuensis*). Distinguished from *N. sadona* by a pronotum line that reaches both the anterior and posterior margins, a feature that is absent in *N. sadona* near the anterior and posterior margins (Sasakawa 2008).

Description of adult. *External structures:* Body length (including mandibles): ♂, 11.7–12.9 mm (mean \pm SD: 12.2 \pm 0.58 mm, $n = 3$); ♀, 12.8–13.9 mm (mean \pm SD: 13.3 \pm 0.41 mm, $n = 6$). Head without a reddish-brown patch between eyes; pronotum entirely black, but lateral margins dark brown in some specimens; legs dark brown, except for the femora, which are brownish black.

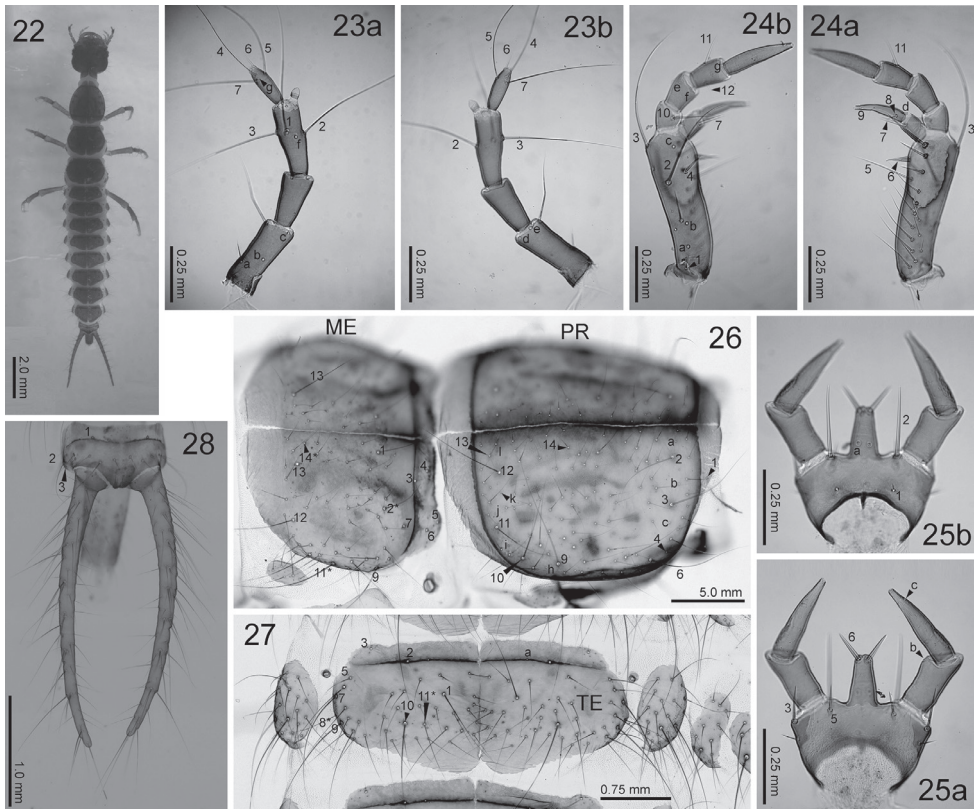


Figures 20–21. First-instar *N. yatsugatakensis* sp. n. **20** Head capsule, dorsal view **21** right foreleg, anterior view. CO, coxa; FE, femur; FR, frontale; MN, mandible; PA, parietale; TA, tarsus; TI, tibia; TR, trochanter. For the foreleg, the homology of characters marked with an asterisk (*) is uncertain, and characters with a hyphen (–) are present on the posterior side.

Male genitalia: Laterobasal lobes markedly swollen; laterapical lobes superficial; dorsoapical lobe large, similar in size to the laterobasal lobe, with the apex bifurcated in a Y shape; dorsobasal lobe distinct but smaller than the laterobasal and dorsoapical lobes.

Diagnosis of larvae. In older instars, distinguished from congeneric species by numerous setae on the entire surface of thoracic nota and abdominal tergites (see Discussion).

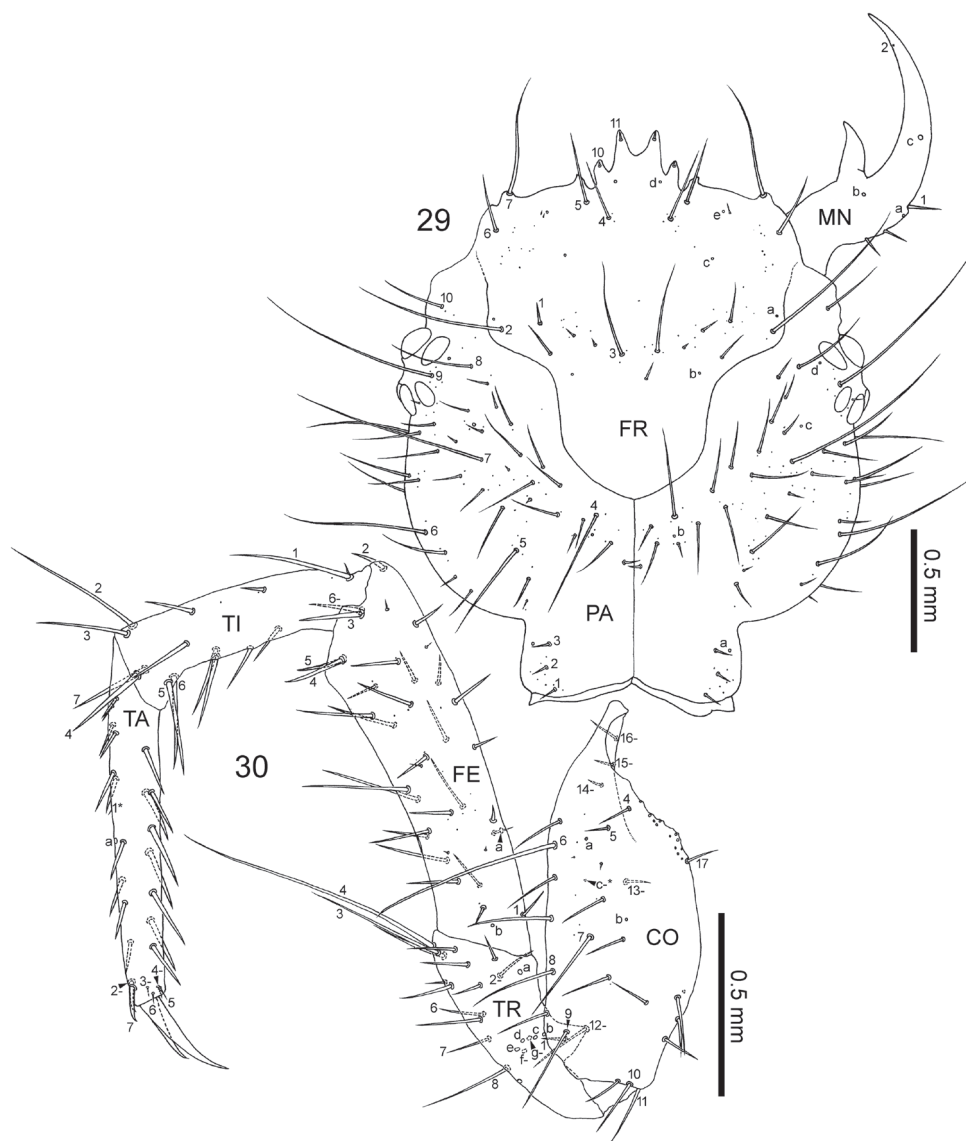
Description of larvae. *Characters present in all instars:* head capsule dark-brown to brownish black, with lighter ventral side; mouthpart appendages and legs brown to light-brown; urogomphi light- to dark-brown; other sclerites on thorax and abdomen gray to brownish-gray; membranous parts grayish white. Most primary setae and pores present, but at least the following ones absent: FR_8 , FR_9 , LA_4 , PR_7 , ME_2 , TE_4 , TE_6 , TE_9 , EM_1 , FR_p , PA_n , CO_d , TE_b , and PY_c . Head capsule oval, widest at stemmata. Frontale U-shaped at base, with posterior end at the level of basal 1/3 of head capsule; nasale prominent, with three pairs of large projections; adnasale sloping posterolaterally. Parietale with six stemmata; cervical groove absent; coronal suture present. Antennae longer than



Figures 22–28. Third-instar *N. yatsugatakensis* sp. n. **22** Dorsal view **23** antenna (**a** dorsal view **b** ventral view) **24** maxilla (**a** dorsal view **b** ventral view) **25** labium (**a** dorsal view **b** ventral view) **26** prothorax and mesonotum, right lateral view **27** tergite, dorsal view **28** urogomphi, dorsal view. ME, mesonotum; PR, prothorax; TE, first abdominal tergite. The homology of characters marked with an asterisk (*) is uncertain.

mandible; antenomeres I and III subequal in length, longer than II and IV. Mandible slender and arcuate, with sharp apex; terebra without tooth-like processes; retinaculum as long as the width of the mandible at the level of MN_1 and curved inward, with sharp apex. Maxilla with stipe as long as palpomeres III and IV combined; palpomere II and III subequal in length, shorter than IV, and longer than I; membranous notch absent. Labium with cordate prementum and elongated ligula; palpomere I longer than ligula but shorter than palpomere II. Thoracic nota and abdominal tergites transverse; notal carina of meso- and metanotum and abdominal tergal carina distinct. All legs with two unequal claws, with the anterior claw longer than the posterior one. Urogomphi slender, longer than head capsule.

Characters restricted to first-instar larvae: head width 1.16–1.22 mm (mean \pm SD: 1.20 ± 0.02 mm, $n = 5$). Urogomphi 1.59–1.72 mm (mean \pm SD: 1.66 ± 0.05 mm, $n = 5$). Secondary setae present on maxilla (9–11 for gMX), pronotum (one on central part, and one on posterior part), and abdominal epipleurite (one on central part).



Figures 29–30. Third-instar *N. yatsugatakensis* sp. n. **29** Head capsule, dorsal view **30** right foreleg, anterior view. CO, coxa; FE, femur; FR, frontale; MN, mandible; PA, parietale; TA, tarsus; TI, tibia; TR, trochanter. For the foreleg, the homology of characters marked with an asterisk (*) is uncertain, and characters with a hyphen (-) are present on the posterior side.

Head capsule with longitudinal, keel-like egg-bursters. Antennomere II almost cylindrical, subequal in length to IV. Maxillary palpomere III less than half the length of IV. Pronotum with indistinct notal carina. Urogomphi fused to tergite IX.

Characters restricted to older instars: Head width 1.50–1.52 mm (mean \pm SD: 1.51 ± 0.01 mm, $n = 4$) in second instar; 1.80–1.89 mm (mean \pm SD: 1.85 ± 0.04 mm,

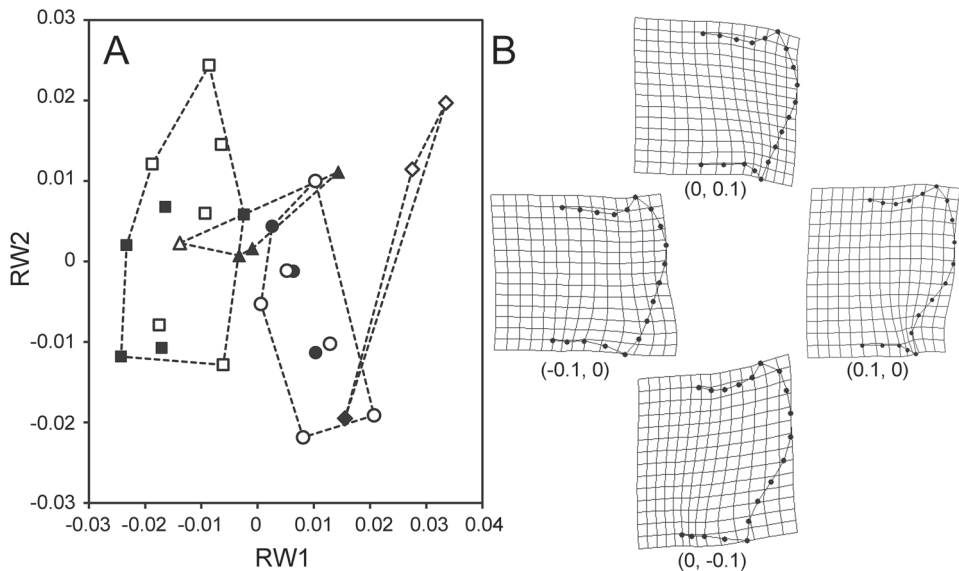


Figure 31. Scatter plot of RW1 and RW2 for the pronotum (A) and representations of extreme shape along each axis (B). Coordinates of each shape on the plot are presented in parentheses. Triangle- (△), circle- (○), square- (□), and diamond- (◇) marks denote *N. quinquelobata* sp. n., *N. yatsugatakensis* sp. n., *N. chichibuensis*, and *N. saeviens*, respectively. Black and white marks denote male and female, respectively. Broken lines represent connections along the margin of each species.

$n = 5$) in third instar. Urogomphi 2.08–2.27 mm (mean \pm SD: 2.19 ± 0.08 mm, $n = 4$) in second instar; 2.51–2.94 mm (mean \pm SD: 2.77 ± 0.16 mm, $n = 5$) in third instar. Secondary setae present on antennomere I (two on inner side), maxilla (14–19 for gMX, and two near MX_b), labium (one behind LA_3), frontale (absent or less than two near FRe and/or about three around FR_{1-3}), and epimeron (absent or less than two); parietale, thoracic nota, abdominal tergites, epusterna, epipleurites, pleurites, sterna, pygidium, urogomphi, legs except claws with numerous secondary setae on entire surface. Antennomere II longer than IV, with the distal end being distinctly wider than the proximal end. Maxillary palpomere III more than half the length of IV. Pronotum with notal carina distinct. Urogomphi not fused to tergite IX.

Remarks. For larvae reared at 5°C, the number of days (mean \pm SD) of the first and second instars were 25.50 ± 2.25 ($n = 16$) and 42.50 ± 1.87 ($n = 6$), respectively. For larvae reared at 10°C, the durations of first and second instars were 15.29 ± 0.61 ($n = 14$) and 22.13 ± 2.30 ($n = 8$).

Geometric morphometrics

Relative warp analyses generated 27 and 11 scores for the pronotum and the aedeagus, respectively. To visually capture the results, scatter plots based on the first two scores

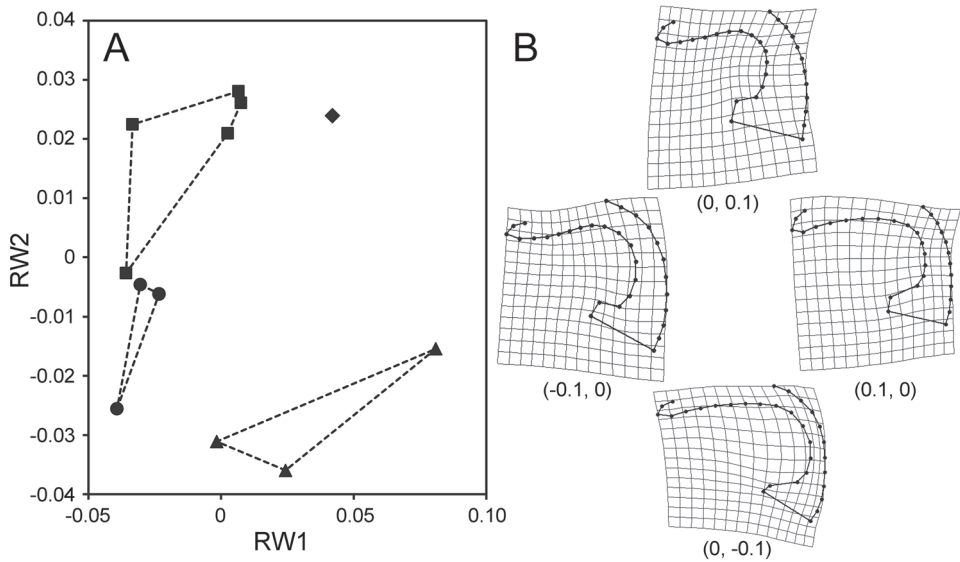


Figure 32. Scatter plot of RW1 and RW2 for the aedeagus (**A**) and representations of extreme shape along each axis (**B**). For explanations of the marks in **A** and of the numerals in parentheses in **B**, see the legend for Fig. 31.

were created (here referred to as RW1 and RW2). In the pronotum, RW1 accounted for 31.9% of the total variance and was mainly associated with the sinuation of the basal part of the lateral margin (landmarks 12–15). RW2 accounted for 20.0% of the total variance and was mainly associated with the sinuation of the lateral side of the posterior margin (landmarks 15–17) and relative size of the apical half. On the scatter plot, four species with overlapping areas were segregated (Fig. 31). Results of Procrustes ANOVA revealed significant effects of species ($F_{3,19} = 20949$, $p < 0.001$) and sex ($F_{1,19} = 12805$, $p = 0.022$) and no significant effects of the interaction term ($F_{3,19} = 1.39$, $p = 1.000$). Subsequent analysis with species as the only explanatory variable revealed that the overall difference was significant ($F_{3,23} = 37.56$, $p < 0.001$). Post hoc pairwise comparisons indicated that the differences between *N. quinquelobata* and *N. chichibuensis*, and between *N. yatsugatakensis* and *N. chichibuensis* were not significant ($F_{3,6} = 0.808$, Bonferroni-corrected $p = 0.225$; and $F_{3,8} = 0.625$, Bonferroni-corrected $p = 0.256$; respectively) but the other four between-species differences were significant (*N. saevi* vs. *N. quinquelobata*: $F_{3,11} = 0.871$, Bonferroni-corrected $p = 0.004$; *N. saevi* vs. *N. yatsugatakensis*: $F_{3,16} = 1.710$, Bonferroni-corrected $p < 0.001$; *N. saevi* vs. *N. chichibuensis*: $F_{3,10} = 1.761$, Bonferroni-corrected $p = 0.003$; *N. quinquelobata* vs. *N. yatsugatakensis*: $F_{3,9} = 0.874$, Bonferroni-corrected $p = 0.025$).

In the aedeagus, RW1 accounted for 48.8% of the total variance and was mainly associated with the relative size (length between landmarks 1 and 31) and the sinuation (curvature of landmarks 5–10) of the subapical portion. RW2 accounted for 30.0% of the total variance and was associated mainly with slenderness, particularly of the

basal half. On the scatter plot, four species were clearly segregated and did not overlap. Results of Procrustes ANOVA revealed that the overall difference was significant ($F_{3,7} = 2.586$, Bonferroni-corrected $p < 0.001$). Post hoc tests indicated that *N. quinquelobata* and *N. saeviensi* were significantly different ($F_{3,4} = 1.043$, Bonferroni-corrected $p = 0.045$), with *N. yatsugatakensis* being intermediate (vs. *N. saeviensi*: $F_{3,4} = 0.865$, Bonferroni-corrected $p = 0.101$; vs. *N. quinquelobata*: $F_{3,2} = 0.746$, Bonferroni-corrected $p = 0.256$).

Discussion

In *Sadonebria*, nine new species have recently been separated from known species based on differences in the shape of the endophallus (Sasakawa and Kubota 2006; Sasakawa 2008, 2009, 2010; Sasakawa and Toki 2011). These nine species were all previously recognized as *N. sadona*. In contrast, one of the new species described here, *N. quinquelobata*, had been recognized as *N. saeviensi*. The occurrence of this type of cryptic species (i.e., species that are clearly distinguishable only by the shape of the endophallus) in that other than *N. "sadona"* may indicate that other such cryptic species remain to be discovered in the subgenus. Future studies are needed to revise other consubgeneric species (e.g., *N. chinensis* Bates, 1872 and *N. niitakana* Kano, 1930), as well as other populations recognized as *N. saeviensi* (Yoshitake et al. 2011) based on the same morphological traits (endophallus of male genitalia). It is also important to assess the utility of this genital morphology for species-level taxonomy in other *Nebria* subgenera.

The results of geometric morphometrics complement those of the comparative morphology of the male endophallus. For example, morphometric values for both the pronotum and aedeagus were clearly different between *N. quinquelobata* and *N. saeviensi*, and these differences were statistically supported. Although the difference in the pronotum between *N. yatsugatakensis* and *N. chichibuensis* was not statistically supported, the two species were largely segregated on the scatter plot and only partially overlapped. In the analysis of the aedeagus, the two species are clearly segregated, and this difference was comparable to that between *N. quinquelobata* and *N. saeviensi*, for which the morphometric difference was statistically supported. Some of the statistical insignificances in the results of geometric morphometrics would be attributed to the small sample size of some species. Future studies need to address this issue by re-analysis using additional materials. Importantly, the geometric morphometrics performed here are based on external and genital structures that had been virtually neglected in recent studies of *Sadonebria*. Nevertheless, these results discriminate among very similar species, with an accuracy close to that of comparative morphology of the male endophallus. Thus, geometric morphometrics can provide insights into future studies of *Sadonebria* taxonomy. For example, geographic variation in widely-distributed species can be examined by this morphometric technique.

In the genus *Nebria*, larvae of species from the following 10 subgenera have been described [subgeneric taxonomy follows Ledoux and Roux (2005)]: *Alpaeonebria* Csiki, 1946; *Paranebria* Jeannel, 1937; *Boreonebria* Jeannel, 1937; *Nebria* Latreille, 1802; *Oreonebria* Daniel, 1903; *Paranebria* Jeannel, 1937; *Nebriola* Daniel, 1903; *Eunebria* Jeannel, 1937; *Tyrrhenia* Ledoux & Roux, 2005; and *Nippononebria* Uéno, 1955 (Emden 1942; Habu 1958; Kurosa 1959; Andersen 1970; Luff 1972, 1993; Spence et al. 1976; Arndt 1991; Šustek 1993; Huber and Molenda 2004). Compared with these species, the larvae of *N. yatsugatakensis* are unusual in that the thoracic nota and abdominal tergites of older instars have numerous secondary setae on the entire surface. In species of the other subgenera, thoracic nota and abdominal tergites of older instars have no or few secondary setae, described by Luff (1993) as a generic character of the genus *Nebria* (but this character was not described in species of *Alpaeonebria*, *Orientonebria*, *Paranebria*, *Tyrrhenia*, or *Nippononebria*). This unusual condition found in larval thoracic nota and abdominal tergites of *N. yatsugatakensis* could be an autapomorphy of *Sadonebria*, because the same character state was found in a field-collected larva that is probably another *Sadonebria* species, *N. shikokuensis* Sasakawa, 2011, based on morphological similarities and collection site (Sasakawa, unpublished data). To test this assumption, larvae of additional species of *Sadonebria* and the subgenus *Eonebria* Semenov & Znojko, 1928, the putative sister taxon of *Sadonebria* (Ledoux and Roux 2005), need to be examined. The results could provide insights into the subgeneric taxonomy of *Sadonebria*, as well as the taxonomic importance of larval secondary setae, which has not been addressed in the subgeneric taxonomy of the genus *Nebria*.

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The tiger beetles (Coleoptera, Carabidae, Cicindelinae) of Israel and adjacent lands

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Abstract

Based on field studies, museums collections and literature sources, the current knowledge of the tiger beetle fauna of Israel and adjacent lands is presented. In Israel eight species occur, one of them with two subspecies, while in the Sinai Peninsula nine species of tiger beetles are now known. In the combined regions seven genera from two tribes were found. The Rift Valley with six cicindelids species is the most specious region of Israel. *Cylindera contorta valdenbergi* and *Cicindela javeti azari* have localized distributions and should be considered regional endemics. A similarity analysis of the tiger beetles faunas of different regions of Israel and the Sinai Peninsula reveal two clusters of species. The first includes the Great Rift Valley and most parts of the Sinai Peninsula, and the second incorporates most regions of Israel together with Central Sinai Foothills. Five distinct adult phenological groups of tiger beetles can be distinguished in these two clusters: active all-year (three species), spring-fall (five species), summer (two species), spring-summer (one species) and spring (one species). The likely origins of the tiger beetle fauna of this area are presented. An annotated list and illustrated identification key of the Cicindelinae of Israel and adjacent lands are provided.

Keywords

Carabidae, tiger beetles, Cicindelinae, Israel, Lebanon, Jordan, Syria, Egypt, Sinai, Levant, Mediterranean, fauna, endemic, near-endemic, catalogue, key, distribution, phenology, faunogenesis

Introduction

The first data about tiger beetles of Palestine were published in the first third of the XXth century. In 1913 Sahlberg described from Wadi El Nawaime (modern Wadi en Nu'eima) *Cicindela littoralis aulicoides*. In 1934 Mandl recorded for the Palestine two subspecies of *Cicindela littoralis*: *C. l. winkleri* and *C. l. aulicoides*. The first species list of Palestinian Coleoptera including five species of tiger beetles was published by Bodenheimer in 1937. Around the same time, the first information about cicindelids of the Sinai Peninsula appeared and *Cicindela aulica* (Horn, 1931), *Cicindela littoralis aulicoides* (Mandl, 1934) and *Megacephala euphratica* (Schatzmayer, 1936) were recorded. Unfortunately, detailed locality data and collecting dates for specimens of these species were often incomplete.

A second wave of tiger beetles studies in the Levant was completed in the last third of XXth century. Alfieri (1976) published the catalogue of Egyptian Coleoptera with information about 11 species of tiger beetles, six of which were recorded for the Sinai Peninsula. The first data about Cicindelinae of Israel were published by Valdenberg (1983, 1985) and Nussbaum (1987). It should be noted that these papers also contained information about tiger beetles of the Sinai Peninsula. In all eight species were recorded from Israel and seven species for the Sinai. Unfortunately, in the paper by Nussbaum (1987) data about localities for several species given in the text and on the maps do not coincide.

Since the beginning of 2000 interest in the Cicindelinae of the Middle East has increased significantly (El-Moursy et al. 2001; Franzen 2001, 2007; Finkel et al. 2002; Wiesner 2002, 2005; Abdel-Dayem et al. 2003; Rittner 2003; Abdel-Dayem 2004, 2012; Chikatunov et al. 2006; Avgin and Özdikmen 2007; Franzen 2007; Avgin and Wiesner 2009; Ptashkovsky 2009; Deuve 2011, 2012; Abdel-Dayem and Kippenhan 2013; Jaskuła and Rewicz 2014). These studies revealed the presence of several species of tiger beetle previously unknown from the area. For example, *Habrodera nilotica* (Dejean, 1825), *Hypaetha singularis* (Chaudoir, 1876) and *Cephalota littorea* (Forskål, 1775) were recorded for the first time in Israel (Chikatunov et al. 2006). However, in the next publications these species were not included (Ptashkovsky 2009).

During the last decade, new information about the distribution of tiger beetles in different parts of the Levant has accumulated, and we include these new records here.

Material and methods

Specimens and data for this report come from the following museums and private collections:

TAU Tel Aviv University (Israel);

ZMUM Zoological Museum of Moscow State University (Moscow, Russia);

MPU Moscow State Pedagogical University (Moscow, Russia);

- SIZ** I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (Kiev, Ukraine);
cJW collection of Jürgen Wiesner (Wolfsburg, Germany);
cIOv collection of Igor' Ovsyannikov (Moscow, Russia).

The nomenclature of elytral pattern follows Acciavatti and Pearson (1989); the nomenclature of male internal sac follows Matalin (1998); the chorology follows Vigna Taglianti et al. (1999) with some additions; the regions of Israel and the Sinai Peninsula (Egypt) follow Nussbaum (1987). The similarity of the faunas of tiger beetles was calculated using complete linkage procedure (squared Euclidean distances).

The species included here that are not yet recorded from Israel are marked in the catalogue and in the key with a symbol (○).

Results and discussion

Catalogue of the tiger beetles of Israel and adjacent lands

Family Carabidae Latreille, 1802

Subfamily Cicindelinae Latreille, 1802

Tribe Cicindelini Latreille, 1802

Subtribe Cicindelina Latreille, 1802

Genus *Calomera* Motschulsky, 1862

***Calomera aulica aulica* (Dejean, 1831)**

General distribution. **Europe** - Greece; **Asia** - Lebanon, Israel, Jordan, Syria, Egypt (Sinai), Saudi Arabia, Arab Emirates, Oman, Yemen, Bahrain, Iran, Iraq, Pakistan; **Africa**: Cape Verde Islands, Senegal, Guinea Bissau, Mauritania, Morocco, Tunisia, Algeria, Libya, Sudan, Chad, Egypt, Somalia, Eritrea, Djibouti.

References. **ISRAEL** – Bodenheimer 1937: 108 (as *Cicindela*); Valdenberg 1983: 43, 46 (as *Cicindela*), 1985: 37 (as *Cicindela*); Cassola 1985: 56 (as *Lophyridia*); Nussbaum 1987: 9-10 (as *Cicindela*); Wiesner 1992: 151 (as *Lophyridia*); Puchkov and Matalin 2003: 99; Rittner 2003 (as *Lophyridia*); Ptashkovsky 2009: 8-9 (as *Lophyra*); **EGYPT (SINAI)** – Horn 1931: 162 (as *Cicindela*); Alfieri 1976: 1 (as *Cicindela*); Cassola 1984: 56 (as *Lophyridia*); Nussbaum 1987: 9-10 (as *Cicindela*); Wiesner 1992: 151 (as *Lophyridia*); Werner 2000: 98 (as *Lophyridia*); El-Moursy et al. 2001: 66 (as *Cicindela*); Abdel-Dayem et al. 2003: 205 (as *Lophyridia*); Puchkov and Matalin 2003: 103; Abdel-Dayem 2004: 74 (as *Lophyridia*).

Distribution (Figs 1, 2). **ISRAEL (INCLUDING STATE OF PALESTINE), Jordan Valley:** *Zor Deir Shaman*, 15.III.2005, I. Zonstein - 1♀; *Gesher*, 17.VIII.1939, H. Bytinski-Salz - 1♂ (both TAU); *Kinneret zone* (after Nussbaum 1987); **Dead Sea Area:** *Ne'ot HaKikkar*, 7.V.1980, leg. A. Valdenberg - 5♂♂ 7♀♀; 16.VII.1999, 13.VIII.1999,



Figure 1. Distribution of *Calomera aulica aulica* in Israel, Palestine and border areas of Jordan (open circles - records before year 1949, half-solid circles - records between years 1950–1999, solid circles - records after year 2000; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg)

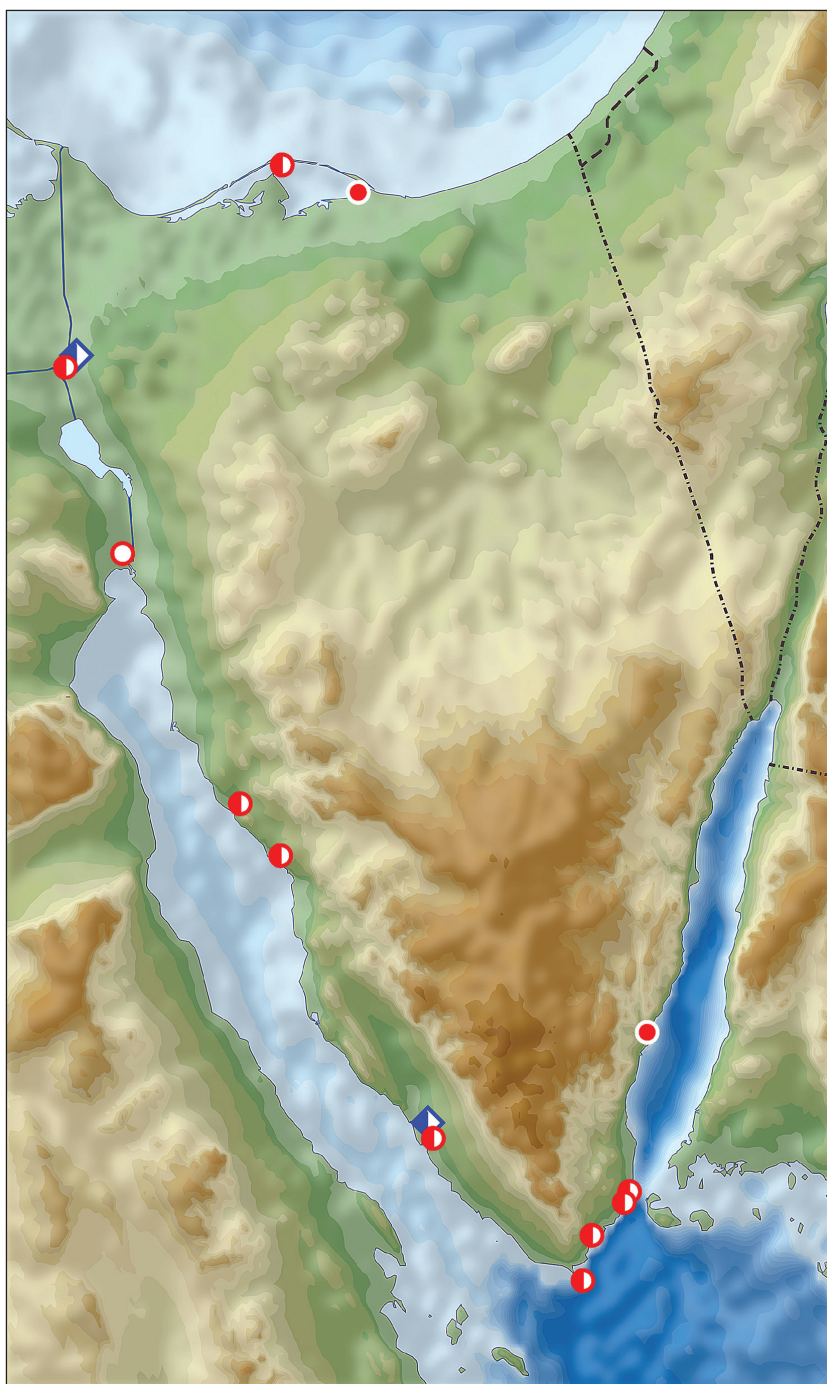


Figure 2. Distribution of *Calomera aulica aulica* (red circles) and *Calomera littoralis aulicoides* (blue rhombs) in Sinai Peninsula, Egypt (open symbols - records before year 1949, half-solid symbols - between years 1950–1999, solid symbols - records after year 2000; URL map source - https://upload.wikimedia.org/wikipedia/commons/5/59/Sinai_relief_location_map.svg).

11.IX.1999, and 12.XII. 1999, light trap BL, leg. I. Yarom & V. Kravchenko - 2♂♂ 7♀♀; *Sedom*, 15.VIII.1957, leg. J. Wahrman - 1♂ 2♀♀ (all TAU); *En Gedi*, 19-29.V.1989, leg. G. Müller - 1♀; *Qalya*, 28.VIII.1986, 28.6.1987, leg. Y. Nussbaum - 2♂♂ (both cJW); *Enot Qane* (after Nussbaum 1987); **Arava Valley:** *Be'er Ora*, 3.IV.1997, leg. V. Chikatunov - 3♂♂ 1♀; *En 'Iddan*, 15.VII.1999, leg. I. Yarom & V. Kravchenko - 1♂ 1♀ (all TAU).

JORDAN, Ma'Daba: *Callirhoe*, 7.VI.1942, leg. H. Bytinski-Salz - 2♀ (TAU).

EGYPT (SINAI), Northern Sinai: *Sabkhat al Bardawil*, 25.VIII.1967, leg. I. Margalit - 3♀♀; 24.VIII.1979, leg. A. Valdenberg - 1♂ 2♀♀ (TAU); *Ismailia* (after Alfieri 1976); *Zaranik Protectorate* (after El-Moursy et al. 2001; Abdel-Dayem et al. 2003; Abdel-Dayem 2004); **Sinai Mountains:** *20 km NE of Dahab*, saline land, 4.VIII.2008, leg. A. Sokolov - 4♂♂5♀♀ (MPU); **Southwestern Sinai:** *Suez* - 1♂ (ZMUM); *Nabeq*, 17.VIII.1971, leg. J. Kugler - 1♂ 2♀♀; 8.V.1980, leg. A. Valdenberg - 4♂♂ 6♀♀; *Ras al Tantur*, 5.VII.1957, leg. Ch. Lewinsohn - 2♂♂ 1♀, 17.VIII.1971, leg. M. Kaplan - 1♀ (all TAU); *15 km W Ofira*, Golf v. Elat, Straße von Tiran, 3.IV.1981, leg. G. Gerdes - 1♂ (cJW); *Wadi Gharandal*, 20.V.1969, leg. Tsabar - 1♂ (TAU); *Abu Zenima*, *Wadi Tayebbeh* (both after Alfieri 1976); *El Tor* (after Alfieri 1976; Abdel-Dayem et al. 2003; Abdel-Dayem 2004); *Ras Muhammad* (after Nussbaum 1987).

Calomera littoralis aulicoides (J. Sahlberg, 1913)

General distribution. Asia - Turkey, Israel, Jordan, Syria, Egypt (Sinai), Saudi Arabia, Iran, Iraq; Africa - Egypt.

References. ISRAEL – Sahlberg 1913: 3 (as *Cicindela*); Mandl 1934: 244-245 (as *Cicindela lunulata nemoralis aulicoides*), 1982: 93-94 (as *Lophyridia aulicoides*); Valdenberg 1983: 44, 47 (as *Cicindela*), 1985: 36 (as *Cicindela*); Nussbaum 1987: 11-12 (as *Cicindela*); Wiesner 1992: 149 (as *Lophyridia*); Puchkov and Matalin 2003: 100; Chikatunov et al. 2006: 293; **EGYPT (SINAI)** - Mandl 1934: 244-245 (as *Cicindela lunulata nemoralis aulicoides*), 1982: 94 (as *Lophyridia aulicoides*); Alfieri 1976: 2 (as *Cicindela lunulata aulicoides*); Wiesner 1992: 149 (as *Lophyridia*); Abdel-Dayem et al. 2003: 207 (as *Lophyridia*); Puchkov and Matalin 2003: 103; Abdel-Dayem 2004: 74 (as *Lophyridia*).

Distribution (Figs 2–3). **ISRAEL (INCLUDING STATE OF PALESTINE), Golan Heights:** *Hammat Gader*, 2.X.2002, leg. V. Kravchenko & V. Chikatunov - 1♀ (TAU); **Lower Galilee:** *Teverya*, 16.VI.1981, leg. A. Valdenberg - 1♀; *Kinneret*, 16.VI.1981, leg. A. Valdenberg - 3♂♂ 3♀♀; **Jordan Valley:** *Zor Deir Shaman*, Yarden bank, 32°02'30"N, 35°30'E, 15.III.2005, leg. L. Friedman & I. Zonstein - 3♂♂ 1♀ (TAU); *Allenby bridge* (after Mandl 1982); *Tomer, Ma'oz-Hayyim* (both after Nussbaum 1987); **Dead Sea Area:** *Yeriho*, Jordan, Palestine, 24.IV.27 - 1♀; *Enot Zuqim*, 13.III.1993, leg. V. Chikatunov - 2♂♂ 1♀, 9.VI.1997, leg. L. Friedman - 1♂, 1.II.1994, and 13.III.1994, leg. V. Chikatunov - 3♂♂ 2♀♀; *Ne'ot HaKikkar*, 19.IV.1999, 16.VII.1999, 13.VIII.1999, and 11.IX.1999, leg. I. Yarom

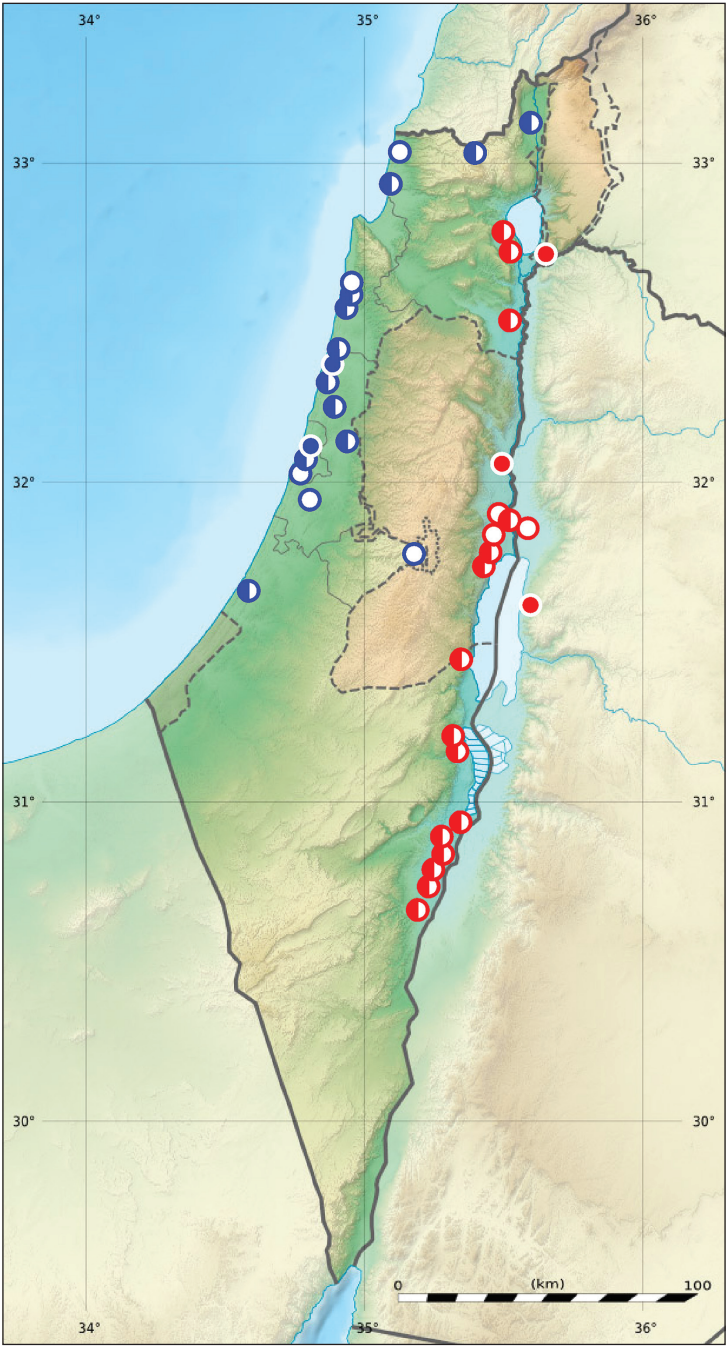


Figure 3. Distribution of two subspecies of *Calomera littoralis* in Israel, Palestine and border areas of Jordan (red circles – *C. l. aulicoides*, blue circles – *C. l. winkleri*, open circles - records before year 1949, half-solid circles – records between years 1950–1999, solid circles – records after year 2000; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg).

& V. Kravchenko - 17♂♂ 11♀♀; *Sedom*, 19.VIII.1957, J. Wahrman - 2♂♂; *Qalya*, 9.VI.1981, leg. A. Valdenberg - 4♂♂ 6♀♀ (all TAU); *En Gedi*, 1-13.V.1980, 19-29.V.1989, leg. G. Müller - 3♀♀; *Neve Zohar*, 24.VI.1987, leg. Y. Nussbaum - 1♂ (both cJW); *Wadi El Nawaime* [*Wadi en Nu'eima*] (after Sahlberg 1913); *Enot Qane* (after Nussbaum 1987); **Arava Valley**: *En Zin*, 30°53.60'N, 35°09.17'E, light trap BL, 12.X.1999, leg. I. Yarom & V. Kravchenko - 1♂; *Hazeva*, field school, 30°46.70'N, 35°14.25'E, light trap BL, 20.III.1999, 21.V.1999, leg. I. Yarom & V. Kravchenko - 1♂ 3♀♀; *En 'Iddan*, 20.VI.1995, leg. I. Yarom & A. Freidberg - 2♂♂ 1♀; 15.VII.1999, leg. I. Yarom & V. Kravchenko - 3♂♂ 4♀♀; *Nahal Shezaf*, 18.V.1999, 8.VI.1999, light trap, leg. I. Yarom & V. Kravchenko - 1♂ 1♀; *Nahal Neqarot*, 10.III.1999, leg. I. Yarom & V. Kravchenko - 1♀ (all TAU).

JORDAN, Al Balqā': *Al Maghtas*, 12.II.1942, leg. H. Bytinski-Salz - 1♂ 2♀♀ (TAU); **Ma'Dabā**: *Suwayma*, Dead Sea, 5.IV.2000, leg. G. & I. Zappi - 1♂1♀ (MPU).

EGYPT (SINAI), Northern Sinai: *Ismailia* (after Alfieri 1976); **Southwestern Sinai**: *El Tor* (after Alfieri 1976; Abdel-Dayem et al. 2003; Abdel-Dayem 2004).

Calomera littoralis winkleri (Mandl, 1934)

General distribution. **Europe** - Greece, Armenia, Azerbaijan; **Asia** - Cyprus, Turkey, Lebanon, Israel, Jordan, Syria, Iran, Iraq, Afghanistan, Turkmenistan.

References. **ISRAEL** – Mandl 1934: 240, 243, 245 (as *Cicindela*); Naviaux 1983: 82 (as *Lophyridia*), Valdenberg 1983: 44, 46 (as *Cicindela*), 1985: 36 (as *Cicindela*); Nussbaum 1987: 11, 13 (as *Cicindela*); Wiesner 1992: 151 (as *Lophyridia*); Puchkov and Matalin 2003: 101; Rittner 2003 (as *Cicindela*); Chikatunov et al. 2006: 293; Ptashkovsky 2009: 8-9 (as *Cicindela*).

Distribution (Fig. 3). **ISRAEL, Upper Galilee**: *Hula*, 23.VI.1952, leg. J. Wahrman - 5♂♂ 4♀♀; 8.III.1976, leg. M. Kaplan - 1♂; *Sasa*, 18.III.1951, leg. J. Wahrman - 1♀ (all TAU); **Northern Coastal Plain**: *Akko*, 7.VIII.1980, leg. A. Valdenberg - 3♂♂ 4♀♀; *Ma'agan Mikha'el*, 17-18.III.1979, 27.VI.1979, 26.III.1980, 24.IV.1980, 24.VI.1980, leg. A. Valdenberg - 17♂♂ 28♀♀; 4.VI.1983, leg. E. Sney-Dor - 2♂♂ 1♀; *Nahariyya*, 19.VI.1942, leg. H. Bytinski-Salz - 1♂ 2♀♀; *Dor*, Horvat Tantura, sea-shore, 13.IX.1949, leg. J. Wahrman - 1♀; *Zikhron Ya'aqov*, 29.VI.1998, leg. A. Traub - 3♀♀ (all TAU); **Central Coastal Plain**: *Hadera*, 28.III.2008, leg. G. Wizen - 1♂ 1♀; *Bat Yam*, 13.VII.1945, leg. H. Bytinski-Salz - 1♂ 3♀♀; *Hofit*, 21.IX.1994, leg. F. Kaplan & A. Freidberg - 1♀; *Mishmeret*, 3.VIII.1983, leg. A. Freidberg - 2♂♂ 3♀♀; *Qesarya*, 11.VII.1979, and 10.VIII.1979, leg. A. Valdenberg - 3♂♂ 4♀♀; *Tel Aviv*, 20.VI.1982, leg. A. Valdenberg - 1♂ 2♀♀; 12.IV.2003, leg. V. Kravchenko & V. Chikatunov - 4♂♂ 2♀♀; *Rosh Ha'Ayin*, 16.IV.1993, leg. A. Freidberg & F. Kaplan - 1♂ 1♀; *Rehovot*, 5.V.1942, leg. H. Bytinski-Salz - 3♂♂ 2♀♀ (all TAU); **South-ern Coastal Plain**: *Nitzanim*, 13.VII.1981, leg. A. Valdenberg - 3♂♂ 2♀♀ (TAU); **Judean Hills**: Jerusalem - 1♂ (after Mandl 1934: 40, Fig. 65).

Genus *Cephalota* Dokhtouroff, 1883

Cephalota (*Taenidia*) *zarudniana vartianorum* (Mandl, 1967)

General distribution. Asia - Israel, Syria, Iran, Iraq.

References. ISRAEL – Naviaux 1983: 78; Valdenberg 1983: 43 (as *Cicindela jarudniana vartianorum*), 45 (as *Cicindela jarudniana*), 1985: 37 (as *Cicindela jarudniana*); Nussbaum 1987: 9, 13 (as *Cicindela jarudniana*); Wiesner 1992: 177; Puchkov and Matalin 2003: 103; Chikatunov et al. 2006: 293 (as *Cephalota deserticola*); Ptashkovsky 2009: 8-9 (as *Cephalota deserticola*).

Distribution (Fig. 4). ISRAEL (INCLUDING STATE OF PALESTINE), **Dead Sea Area:** Yeriho, 24.IV.1927, leg. O. Theodor - 1♂; 'Enot Zugim, 1.II.1994, and 13.III.1994, leg. V. Chikatunov - 1♂ 2♀♀; Qalya, 6.V.1980, leg. A. Valdenberg - 2♂♂ 3♀♀; Ne'ot HaKikkar, 7.V.1980, leg. A. Valdenberg - 4♂♂; 28.IV.1984, leg. E. Shney-Dor - 2♀♀; 19.IV.1999, leg. I. Yarom & V. Kravchenko - 1♂1♀ (all TAU), 7.V.1980, leg. R. Naviaux - 1♀; V.1990, leg. Orbach - 1♂1♀ (both cJW).

Comments. References to *Cephalota zarudniana vartianorum* (Mandl, 1967) as *Cephalota deserticola* (Faldermann, 1836) (Chikatunov et al. 2006; Ptashkovsky 2009) were based on two mis-identified males from Qalya by K. Mandl. According to Franzen and Wiesner (1998) *C. deserticola* is distributed in the western part of Central Asia, as well as in Iran, Azerbaijan, Armenia and north-eastern Turkey.

(○) *Cephalota* (*Taenidia*) *littorea littorea* (Forskål, 1775)

General distribution. Asia - Egypt (Sinai), Saudi Arabia; Africa - Egypt, Sudan, Eritrea.

References. EGYPT (SINAI) - Forskål 1775: 77 (as *Cicindela*); Alfieri 1976: 2 (as *Cicindela*); Valdenberg 1983: 44, 46 (as *Cicindela*), 1985: 37 (as *Cicindela*); Nussbaum 1987: 9, 15 (as *Cicindela*); Gebert 1991: 176, 187; Wiesner 1992: 175; Werner 2000: 147; Abdel-Dayem et al. 2003: 199; Puchkov and Matalin 2003: 103; Rittner 2003; Abdel-Dayem 2004: 72.

Distribution (Fig. 5). EGYPT (SINAI), **Sinai Mountains:** Dahab, 9.V.1980, leg. A. Valdenberg - 1♂ 1♀; Ras-Burka, 5.IX.1976, leg. A. Freidberg - 1♂ (all TAU); Sun Pool (after Nussbaum 1987); **Southwestern Sinai:** Suez (after Forskål 1775; Gebert 1991); Nabeg, 8.V.1980, 17.VIII.1978, 31.V.1980, leg. A. Valdenberg - 25♂♂ 24♀♀; 29.V.1981, leg. A. Freidberg - 2♂♂ (all TAU); El Tor (after Alfieri 1976; Abdel-Dayem et al. 2003; Abdel-Dayem 2004); Ras Muhammad, 16.VIII.1978, leg. A. Valdenberg - 2♂♂ 1♀; (after Nussbaum 1987; Gebert 1991).

Comments. The specimen of *Cephalota littorea littorea* (Forskål, 1775) with label "Jerusalem" from Zoologisches Museum der Humboldt-Universität (Berlin) is mislabelled (see Gebert 1991). All subsequent records of this species from Israel (Wiesner 1992; Puchkov and Matalin 2003) are in error.



Figure 4. Distribution of *Cephalota zarudniana vartianorum* (orange triangles), *Cichindela javeti azari* (red circles) and *Cylindera contorta valdenbergi* (blue rhombs) in Israel, Palestine and border areas of Lebanon (open symbols - records before year 1949, half-solid symbols – records between years 1950–1999; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg).

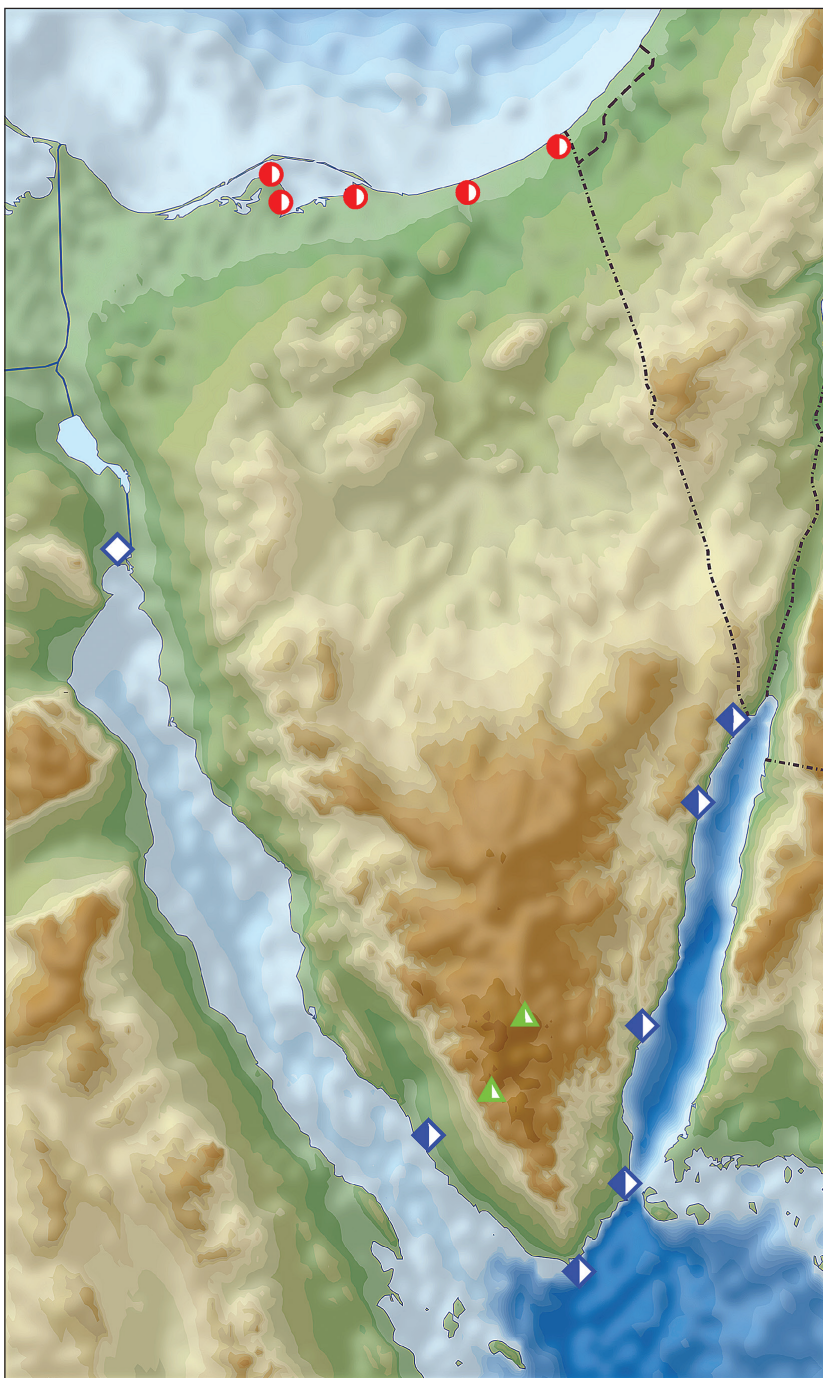


Figure 5. Distribution of *Cephalota tibialis tibialis* (red circles), *Cephalota littorea littorea* (blue rhombs) and *Habrodera nilotica nilotica* (green triangles) in Sinai Peninsula, Egypt (open symbols - records before year 1949, half-solid symbols – records between years 1950–1999; URL map source - https://upload.wikimedia.org/wikipedia/commons/5/59/Sinai_relief_location_map.svg).

In some publications (Abdel-Dayem et al. 2003; Abdel-Dayem 2004) *Cephalota circumdata* (Dejean, 1822) was recorded from the Sinai Peninsula (El Tor). However, the nominotypical subspecies of *C. circumdata* occurs along the Aegean, Marmora, Black and Mediterranean Sea coasts in the Greece, Bulgaria, western Turkey, and, probably Rumania (Franzen 1996; Cassola 1999; Gebert 1999); *C. c. cappadocica* Franzen, 1996 and *C. c. hattusae* Franzen, 1996 live along banks of the salt lakes in the central Turkey (Franzen 1996; Cassola 1999; Gebert 1999); *C. c. leonschaeferi* Cassola, 1970 occupies the Mediterranean sea coast in southern France (including Corsica) and north-western Italia (Gebert 1999); while *C. c. imperialis* Klug, 1834 records in the Italia (Sardinia and Sicilia), south-eastern Spain (including Balearic Islands), Tunisia and Algeria, but not in the Libya and Egypt (Gebert 1999). Most likely, the aberrant specimen of *C. littorea* was incorrectly identified as *C. circumdata*.

(○) *Cephalota (Taenidia) tibialis tibialis* (Dejean, 1882)

General distribution. Asia - Egypt (Sinai); Africa - Egypt.

References. EGYPT (SINAI) – Valdenberg 1983: 42, 47 (as *Cicindela*); Nussbaum 1987: 7, 12 (as *Cicindela*), 1985: 37 (as *Cicindela*); Gebert 1991: 179, 187; Wiesner 1992: 175; El-Moursy et al. 2001: 66 (as *Cicindela littorea*); Abdel-Dayem et al. 2003: 200; Puchkov and Matalin 2003: 103; Abdel-Dayem 2004: 72, 2012: 198.

Distribution (Fig. 5). EGYPT (SINAI), **Northern Sinai:** Yamit, 21.VI.1978, 14.VII.1981, leg. A. Valdenberg – 3♀♀ (TAU); Sabkhat al Bardawil, 7.VI.1977, 26.VII.1978, 31.VIII.1978, 7.VI.1980, leg. A. Valdenberg – 4♂♂ 7♀♀ (TAU); Arish (after Abdel-Dayem et al. 2003); Zaranik Protectorate (after El-Moursy et al. 2001; Abdel-Dayem 2004, 2012); Sabkhat al Shic (after Nussbaum 1987; Gebert 1991).

Genus *Cicindela* Linnaeus, 1758

Cicindela (s. str.) *javeti azari* Deuve, 2011

General distribution. Asia - Lebanon, Israel, Syria.

References. ISRAEL – Valdenberg 1983: 42, 48 (as *Cicindela campestris herbacea*), 1985: 37 (as *Cicindela campestris herbacea*); Nussbaum 1987: 7-8 (as *Cicindela herbacea*); Wiesner 1992: 127 (as *Cicindela herbacea*); Puchkov and Matalin 2003: 105 (as *Cicindela herbacea*); Rittner 2003 (as *Lophyridia herbacea*); Chikatunov et al. 2006: 293 (as *Cicindela herbacea*); Franzen 2007: 13 (as *Cicindela herbacea*); Ptashkovsky 2009: 8-9 (as *Lophyra herbacea*).

Distribution (Fig. 4). ISRAEL, **Upper Galilee:** Mt. Meron, 8.IV.1972, leg. D. Gerling – 1♀ (TAU); **Golan Heights:** Mezudat Nimrod, 8.V.1983, leg. E. Shney-Dor – 3♂♂ 1♀ (TAU); **Mt. Hermon:** 1900 m, 22.IV.1973, leg. D. Furth – 1♂; 2000 m, 9.VI.1992, leg. A. Freidberg – 1♂ 1♀ (all TAU).

LEBANON, Liban-Sud: Jezzin - 5♂♂ 11♀♀ (after Deuve 2011).

SYRIA, Dimashq: Bloudan (after Avgin and Wiesner 2009 - as *Cicindela thughurica* Franzen, 2007).

(○) *Cicindela* (s. str.) *herbacea herbacea* Klug, 1832

General distribution. Asia - Lebanon.

References. **LEBANON** – Wiesner 1992: 127; Puchkov and Matalin 2003: 105; Franzen 2007: 13; Deuve 2011: 129.

Distribution. **LEBANON, Liban-Nord:** Bcharré, Les Cèdres, VI. 1997 - 1♂1♀ (cIOv); Bcharré - 1♀ (after Franzen 2007); Tannourine - 1♀ (after Deuve 2011).

Comments. Until recently both these species were recorded from Syria, Lebanon and Israel by several authors as *Cicindela herbacea* Klug (Valdenberg 1983; Nussbaum 1987; Wiesner 1992; Puchkov and Matalin 2003; Chikatunov et al. 2006; Franzen 2007; Ptashkovsky 2009). However, according to recent data *C. herbacea* does not occur in Israel (Deuve 2011, 2012). The nominative subspecies occurs in Lebanon and Syria; *C. h. aleppensis* Deuve, 2012 is recorded from north-western Syria, while *C. h. perreaui* Deuve, 1987 and *C. h. colasi* Deuve, 2011 are found in Turkey - Tunceli and Adana Provinces, respectively. On the basis of the shape of pronotum (Figs 38 vs 39), white elytral pattern (Figs 54 vs 55), size of aedeagus and shape of it apex (Figs 93 vs 97), as well as shape of internal sack (Figs 94–96 vs 98–100) we consider all studied specimens from Israel to be *Cicindela javeti azari* Deuve, 2011 (type locality – Lebanon, Jezzine). It should be noted that the taxonomy of intraspecific forms within the ‘*campestris*’-group is complex, and additional studies are necessary.

Genus *Cylindera* Westwood, 1831

Cylindera (*Eugrapha*) *contorta valdenbergi* (Mandl, 1981)

General distribution. Asia – Israel, Egypt.

References. **ISRAEL** – Bodenheimer 1937: 108 (as *Cicindela*); Mandl 1981: 169 (as *Cicindela*); Naviaux 1983: 79; Valdenberg 1983: 43, 48 (as *Cicindela*), 1985: 29–30 (as *Cicindela*); Nussbaum 1987: 7, 10 (as *Cicindela*); Werner 1992: 22, 48, 74; Wiesner 1992: 195 (as *Cicindina*); Puchkov and Matalin 2003: 110; Rittner 2003 (as *Lophyridia*); Ptashkovsky 2009: 8–9 (as *Lophyridia*).

Distribution (Fig. 4). **ISRAEL, Northern Coastal Plain:** ‘Akko, 7.VIII.1980, leg. A. Valdenberg - 3♀♀; ‘Atlit, 5.VIII.1942, B. Feldman - 1♂; Ma’agan Mikha’el, 13.VII.1977, 9.IX.1978, 2.V.1979, 26.III.1980, VI.1980, leg. A. Valdenberg - 27♂♂ 53♀♀; 27.VII.1979, leg. J. Kugler - 2♂♂; 3.VI.1983, leg. E. Shney-Dor - 2♂♂ 7♀♀ (all TAU); VII.1987, leg. Y. Nussbaum - 1♀ (SIZ); 17.V.1980, leg. R. Naviaux - 1♀;

16.V.1986, leg. Y. Nussbaum - 5♂♂ 6♀♀ (both cJW); *Emeq Zevulun* (after Nussbaum 1987). **Central Coastal Plain:** *Bat Yam*, 13.VII.1945, leg. H. Bytinski-Salz - 1♂ 4♀♀ (TAU); *Qesariya*, *Zerufa* [*Tsrufa*] (both after Nussbaum 1987).

Genus *Habrodera* Motschulsky, 1862

(○) *Habrodera nilotica nilotica* (Dejean, 1825)

General distribution. **Asia** - Egypt (Sinai); **Africa** - Canary Islands (Grand Canary), Senegal, Ghana, Mali, Guinea, Equatorial Guinea, Sierra Leone, Nigeria, Central African Republic, Togo, Benin, Sudan, Egypt, Kenya, Congo, Zaire, Tanzania, Ethiopia, Malawi, Mozambique, South Africa.

References. ISRAEL – Chikatunov et al 2006: 293; **EGYPT (SINAI)** - Alfieri 1976: 2 (as *Cicindela*); Wiesner 1992: 165); Werner 2000: 138; Abdel-Dayem et al. 2003: 202; Puchkov and Matalin 2003: 103; Abdel-Dayem 2004: 74.

Distribution (Fig. 5). **EGYPT (SINAI), Sinai Mountains:** *Wadi Isla* (after Alfieri 1976; Abdel-Dayem et al. 2003; Abdel-Dayem 2004); *St. Katherine* (after Abdel-Dayem 2004).

Comments. Previously *Habrodera nilotica nilotica* (Dejean, 1825) was mistakenly referenced in the fauna of Israel (Chikatunov et al. 2006).

Genus *Hypaetha* LeCoute, 1857

(○) *Hypaetha singularis* (Chaudoir, 1876)

General distribution. **Asia** - Egypt (Sinai), Oman, Yemen; **Africa** - Egypt, Sudan, Somalia, Eritrea, Djibouti.

References. **EGYPT (SINAI)** - Valdenberg 1983: 43, 45 (as *Cicindela*), 1985: 37 (as *Cicindela*); Nussbaum 1987: 11, 13 (as *Cicindela*); Wiesner 1992: 219; Puchkov and Matalin 2003: 112.

Distribution (Fig. 9). **EGYPT (SINAI), Southwestern Sinai:** *Nabeq*, 8.V.1980, leg. A. Valdenberg - 1♂; *Ras Muhammad*, 16.VIII.1978, leg. A. Valdenberg - 2♂♂ 2♀♀ (all TAU).

Genus *Lophyra* Motschulsky, 1859

Lophyra (s. str.) *flexuosa flexuosa* (Fabricius, 1787)

General distribution. **Europe** - Portugal, Spain, Andorra, France, Italy, Switzerland; **Asia** - Israel, Egypt (Sinai); **Africa** - Morocco, Tunisia, Algeria, Libya, Egypt.

References. ISRAEL – Bodenheimer 1937: 108 (as *Cicindela*), Valdenberg 1983: 42, 48 (as *Cicindela flexosa*), 1985: 33 (as *Cicindela flexosa*); Nussbaum 1987: 9, 15 (as *Cicindela*); Wiesner 1992: 160; Puchkov and Matalin 2003: 112; Chikatunov et al. 2006: 293; Ptashkovsky 2009: 8-9; EGYPT (SINAI) – Alfieri 1976: 1-2 (as *Cicindela*); Nussbaum 1987: 9, 15 (as *Cicindela*); Wiesner 1992: 160; Abdel-Dayem et al. 2003: 203; Puchkov and Matalin 2003: 103; Abdel-Dayem 2004: 74.

Distribution (Figs 6, 9). **ISRAEL (INCLUDING STATE OF PALESTINE), Northern Coastal Plain:** 'Akko, 23.IV.1927, leg. O. Theodor - 1♀; Dor, 23.IV.1998, leg. A. Traub - 2♀♀; Haifa, 18.V.1996, leg. Hauser - 1♀; Ma'agan Mikha'el, 16.V.1978, 21.XI.1978, 18.XII.1978, 12.II.1979, 4.III.1979, 10.III.1979, 16.VI.1981, leg. A. Valdenberg - 31♂♂ 56♀♀; 16.IV.1983, leg. E. Shney-Dor - 1♂ 3♀♀ (all TAU); **Central Coastal Plain:** Bat Yam, 14.III.1940, 12.II.1941, leg. H. Bytinski-Salz - 2♂♂ 1♀; Hofit, 21.IX.1994, leg. A. Freidberg - 1♂; Holon, 4.V.1978, leg. A. Freidberg - 3♂♂ 2♀♀; Nahal Alexander, 32°24'N, 34°52'E, 15.V.2005, leg. I. Zonstein - 1♀; Rehovot, 18.III.1954, leg. J. Wahrman - 2♀♀ (all TAU); **Southern Coastal Plain:** Ashdod, sands, 29.II.1984, leg. A. Freidberg - 1♂; Nir 'Am, 21.III.1946, leg. H. Bytinski-Salz - 2♂♂ 3♀♀; Nizzanim, 5.III.1996, leg. A. Freidberg - 1♀; Yavne, 17.IV.1974, leg. D. Furth - 2♂♂; Ziqqim, 7.II.1996, leg. I. Yarom & A. Freidberg - 2♂♂ (all TAU); **Dead Sea Area:** Qumeran, 18.II.1997, leg. V. Chikatunov - 2♂♂; Yeriho, 23.VII.2002, leg. V. Kravchenko & V. Chikatunov - 1♂ 2♀♀ (all TAU); **Ara-va Valley:** 'En 'Iddan, 18.IV.1999, leg. I. Yarom & V. Kravchenko - 2♂♂ 1♀ (TAU); **Northern Negev:** Be'er Sheva, 1.IV.1946, leg. H. Bytinski-Salz - 2♀♀; Bor Mashash, 18.IV.1995, leg. A. Freidberg - 1♂ 1♀; Gevulot, 6.IV.1985, leg. E. Shney-Dor - 3♂♂ 5♀♀; Revivim, Park Golda, 26.III.1999, leg. A. Freidberg - 1♂ 1♀ (all TAU); **Central Negev:** Yeroham, 27.III.1966, leg. H. Bytinski-Salz - 4♂♂ 7♀♀; 25.IV.1973, 22.IV.1981, leg. J. Kugler - 1♂ 4♀♀; 19.III.1978, leg. M. Kaplan - 6♂♂ 5♀♀; 19.III.1978, leg. A. Freidberg - 6♂♂; Sede Boker, 8.VI.1987, leg. E. Shney-Dor - 1♂; Kadesh Barnea, 11.IV.1974, leg. D. Furth - 3♂♂ 2♀♀; 9.V.1979, leg. A. Valdenberg - 3♂♂ 6♀♀ (all TAU); **Southern Negev:** Elat, 14.VI.1981, leg. R. Keian - 1♀ (TAU).

EGYPT (SINAI), Northern Sinai: Sabkhat al Shic, 8.V.1981, leg. A. Valdenberg - 2♂♂ 2♀♀ (TAU); Ismailia (after Alfieri 1976); **Central Sinai Foothills:** Wadi Godirate [Gudeirat] (after Nussbaum 1987: Fig. 6; Abdel-Dayem 2004); **Southwestern Sinai:** Nabeg (after Abdel-Dayem 2004), Wadi Gharandal (after Alfieri 1976; Abdel-Dayem et al. 2003).

Genus *Myriochila* Motschulsky, 1858

Myriochila (s. str.) *melancholica melancholica* (Fabricius, 1798)

General distribution. **Europe** - Portugal, Spain, France, Italy, Malta, Albania, Greece, Georgia, Armenia, Azerbaijan; **Asia** - Cyprus, Turkey, Lebanon, Israel, Egypt (Sinai), Syria, Jordan, Saudi Arabia, Arab Emirates, Oman, Yemen, Bahrain, Kuwait, Iran,



Figure 6. Distribution of *Lophyra flexuosa flexuosa* in Israel and Palestine (open circles - records before year 1949, half-solid circles - records between years 1950–1999, solid circles - records after year 2000; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg).

Iraq, Kazakhstan, Kyrgyzstan, Tadzhikistan, Uzbekistan, Turkmenistan, Afghanistan, Pakistan (Punjab, Sind), India (Punjab, Haryana, Uttar Pradesh, Rajasthan, Madhya Pradesh, Maharashtra, Bihar, West Bengal), China (Xinjiang); **Africa** - Cape Verde Islands, Senegal, Morocco, Tunisia, Algeria, Libya, Egypt, Sierra Leone, Guinea, Guinea Bissau, Chad, Ivory Coast, Togo, Ghana, Nigeria, Cameroun, Equatorial Guinea, Central African Republic, Congo, Zaire, Kenya, Somalia, Ethiopia, Sudan, Tanzania, Malawi, Mozambique, Angola, Namibia, South Africa, Madagascar, Seychelles.

References. ISRAEL - Bodenheimer 1937: 108 (as *Cicindela*); Valdenberg 1983: 43, 46 (as *Cicindela*), 1985: 40 (as *Cicindela*); Nussbaum 1987: 9, 14 (as *Cicindela*); Wiesner 1992: 211; Finkel et al. 2002: 28; Puchkov and Matalin 2003: 114; Rittner 2003; Chikatunov et al. 2006: 293; Ptashkovsky 2009: 8-9; **EGYPT (SINAI)** - Nussbaum 1987: 9, 14 (as *Cicindela*); Abdel-Dayem et al. 2003: 208; Abdel-Dayem 2004: 75.

Distribution (Figs 7, 9). **ISRAEL (INCLUDING STATE OF PALESTINE), Upper Galilee:** *Tel Dan*, 25.VIII.1958, leg. J. Wahrman - 1♂; 23.VIII.2002, leg. V. Kravchenko & V. Chikatunov - 2♂♂; *Nahal Keziv*, 28.IX.1999, leg. M. Finkel - 1♂ 1♀; *Kefar Szold*, 5.V.1998, leg. R. Ortal - 1♂; *Hula*, 1.VI.1968, leg. H. Bytinski-Salz - 6♂♂ 3♀♀ (all TAU); **Lower Galilee:** *Teverya*, 3.VI.1961, leg. J. Wahrman - 4♂♂ 3♀♀; 24.V.1981, leg. A. Valdenberg - 3♂♂ 1♀; *Deganya*, 15.IX.1951, J. Wahrman - 3♂♂ (all TAU); **Golan Heights:** *Hammat Gader*, 23.VII.2002, 2.X.2002, leg. V. Kravchenko & V. Chikatunov - 5♂♂ 4♀♀ (TAU); **Northern Coastal Plain:** *Ma'agan Mikha'el*, 17.VI.1973, leg. D. Furth - 5♂♂ 7♀♀; 20.IV.1986, leg. A. Freidberg - 2♂♂ 3♀♀ (all TAU); **Central Coastal Plain:** *Herzliyya*, 20.V.2000, A. Freidberg - 2♀♀; *Bet Dagan*, 26.VIII.1981, leg. Q. Argaman - 2♂♂ 3♀♀; *Ramat Gan*, 3.VI.1985, leg. D. Gerling - 7♂♂ 5♀♀; *Rosh Ha'Ayin*, 15.X.1994, leg. V. Chikatunov - 3♂♂ 4♀♀; *Tel Aviv*, 2.IX.1974, leg. A. Freidberg & M. Kaplan - 57♂♂ 60♀♀; 15.VIII.2002, 12.IV.2003, leg. V. Kravchenko & V. Chikatunov - 2♂♂ 7♀♀; 24.VII.1948, H. Bytinski-Salz - 1♀ (all TAU); **Southern Coastal Plain:** *Nizzanim*, 23.VIII.2002, 5.X.2002, leg. V. Kravchenko & V. Chikatunov - 4♂♂ 4♀♀ (TAU); **Judean Desert:** *Nahal Perat (Wadi Qelt)*, 23.VII.2002, leg. V. Kravchenko & V. Chikatunov - 1♂ 2♀♀ (TAU); **Jordan Valley:** *Afqim*, 26.VIII.1971, leg. M. Kaplan - 2♂♂; *Ma'oz Hayyim*, 21.V.1977, leg. A. Valdenberg - 4♂♂ 2♀♀ (all TAU), from *Dan* to *Ne'ot HaKikkar* (after Nussbaum 1987); **Dead Sea Area:** *Yeriho*, 23.VII.2002, 5.X.2002, leg. V. Kravchenko & V. Chikatunov - 3♂♂ 4♀♀; *Qalya*, 6.V.1980, leg. A. Valdenberg - 3♂♂ 5♀♀ (all TAU); **Arava Valley:** *Gerofit*, 2.VIII.2002 and 5.X.2002, leg. V. Kravchenko & V. Chikatunov - 2♂♂ 4♀♀; *Hazeva*, 19.VII.1999, leg. I. Yarom & V. Kravchenko - 2♂♂ 3♀♀; 19.IX.1995, leg. A. Freidberg - 1♂ 1♀; *En 'Iddan*, 20.VI.1995, leg. A. Freidberg - 3♂♂ 1♀; *Yotvata*, 24.VIII.1989, leg. A. Eitam - 1♂; *Zuqim*, 22.VI.1999, leg. I. Yarom & V. Kravchenko - 1♂ 2♀♀; *Samar*, 29°50'N, 35°02'E, 26.IV.2007, leg. N. Ketner - 2♂♂ 2♀♀ (all TAU); **Northern Negev:** *Be'er Sheva*, 1.VIII.1945, leg. H. Bytinski-Salz - 2♂♂ 2♀♀; *Dimona*, 18.VIII.1957, leg. J. Wahrman - 1♂ 1♀; *Gevulot*, 18.V.1983, 6.VI.1984, 29.VIII.1987, leg. E. Shney-Dor - 11♂♂ 12♀♀; *Hazerim*, 31.VIII.1951, leg. J. Wahrman - 1♂ 1♀; *Retamim*, 12.VI.2002, 5.VI.2003, leg. V. Kravchenko &

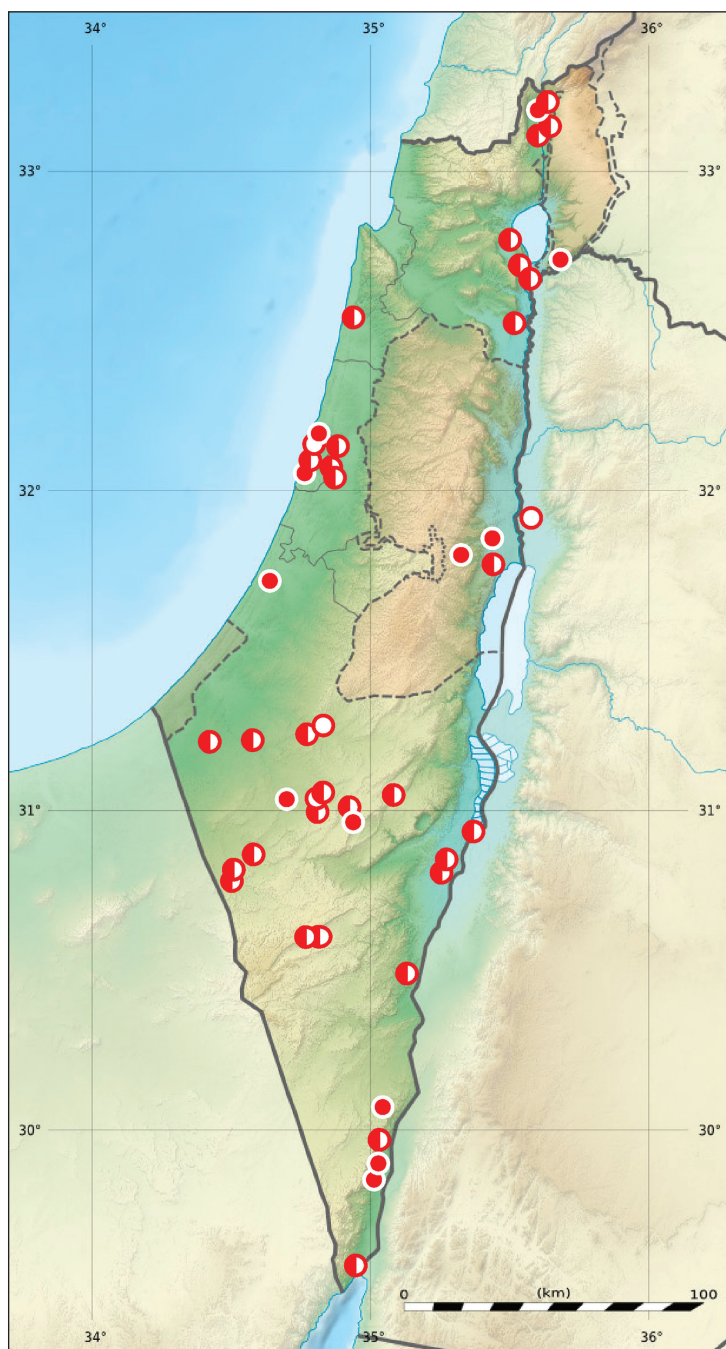


Figure 7. Distribution of *Myriochila melancholica melancholica* in Israel, Palestine and border areas of Jordan (open circles - records before year 1949, half-solid circles - records between years 1950–1999, solid circles - records after year 2000; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg).

V. Chikatunov - 2♂♂ 5♀♀; *Revivim*, 1.IV.1942, leg. H. Bytinski-Salz - 2♂♂ 2♀♀; 2.VIII.1958, leg. J. Kugler - 1♂ (all TAU); *Ze'elim*, 17.IX.1986, leg. Y. Nussbaum, 1♀ (cJW); **Central Negev:** *Mash'abbe Sade*, 23.VIII.1965, J. Wahrman - 3♂♂ 3♀♀; 27.VIII.1986, leg. A. Freidberg - 1♂ 1♀; *Yeroham*, 30.V.1957, leg. I. Yarkoni - 3♂♂ 1♀; *Tel Yeroham*, 19.XI.1959, leg. L. Fishelsohn - 1♂; *Ma'agar Yeroham*, 29.VII.2007, leg. L. Friedman - 1♂; 30°59.37'N, 34°53.87'E, 22.V.2008, leg. L. Friedman - 2♂♂ 2♀♀; *Makhtesh Ramon*, 9.VIII.1977, leg. A. Freidberg - 1♂; *Mizpe Ramon*, 4.VIII.1977, leg. D. Simon - 1♂; *Shivta*, 23.VI.1978, leg. A. Freidberg - 5♂♂ 6♀♀ (all TAU); *Qziot*, 8.IX.1986, leg. Y. Nussbaum - 2♂♂ (cJW); *Ezuz* (after Nussbaum 1987); **Southern Negev:** *Elat*, 6.IX.1974, leg. A. Freidberg - 2♂♂; *Shizzafon*, 12.VI.2002, 5.X.2001, leg. V. Kravchenko & V. Chikatunov - 1♂ 2♀♀ (all TAU).

Jordan, Al Balqā': *Al Maghtas*, 23.V.1942, H. Bytinski-Salz - 1♀ (TAU).

EGYPT (SINAI), Northern Sinai: *El Arish*, 15.VI.1968, leg. J. Kugler - 1♂ 2♀♀ (TAU; including after Abdel-Dayem et al. 2003; Abdel-Dayem 2004); **Southwestern Sinai:** *Ofira*, sewage, 2.V.1981, leg. A. Freidberg - 1♂ (TAU).

Tribe Megacephalini Laporte, 1834

Subtribe Megacephalina Laporte, 1834

Genus *Grammognatha* Motschulsky, 1850

Grammognatha euphratica euphratica Dejean in Latreille & Dejean, 1822

General distribution. **Europe** – Spain, Greece (Rhodes, Crete); **Asia** - Cyprus, Turkey, Lebanon, Israel, Jordan, Syria, Egypt (Sinai), Saudi Arabia, Arab Emirates, Kuwait, Oman, Yemen, Iran, Iraq, Pakistan; **Africa** - Morocco, Tunisia, Algeria, Libya, Egypt, Djibouti.

References. **ISRAEL** – Bodenheimer 1937: 108 (as *Megacephala*); Naviaux 1983: 75 (as *Megacephala*), Valdenberg 1983: 42, 47, 1985: 40 (as *Megacephala*); Nussbaum 1987: 8, 11 (as *Megacephala*); Wiesner 1992: 44 (as *M. euphratica nigra*); Franzen 2001: 89 (as *Megacephala*); Puchkov and Matalin 2003: 118 (as *Megacephala*); Rittner 2003 (as *Megacephala*); Chikatunov et al. 2006: 293 (as *Megacephala*); Ptashkovsky 2009: 8-9 (as *Megacephala*); **EGYPT (SINAI)** - Schatzmayr 1936: 6 (as *Megacephala*); Alfieri 1976: 1 (as *Megacephala*); Nussbaum 1987: 8, 11 (as *Megacephala*); Wiesner 1992: 44 (as *Megacephala euphratica nigra*); Werner 1999: 68 (as *Megacephala*); El-Moursy et al. 2001: 66 (as *Megacephala*); Franzen 2001: 88 (as *Megacephala*); Abdel-Dayem et al. 2003: 196; Puchkov and Matalin 2003: 118 (as *Megacephala*); Abdel-Dayem 2004: 73.

Distribution (Figs 8, 9). **ISRAEL (INCLUDING STATE OF PALESTINE), Northern Coastal Plain:** *Haifa* (after Franzen 2001); *Atlit*, 4.VI.1979, 1.V.1979, leg. A. Valdenberg - 2♀♀; 4.VI.1983, leg. E. Shney-Dor - 1♂; 32°42'N, 34°56'E, 17.V.1997, leg. E. Orbach - 1♂ 1♀ (all TAU), VI.1989, leg. E. Orbach - 1♂ (cJW); V.1989, not far from the coastal line, running to light, leg. E. Orbach - 2♂♂ (after Werner



Figure 8. Distribution of *Grammoglypha euphratica euphratica* in Israel and Palestine (open circles - records before year 1949, half-solid circles - records between years 1950–1999, solid circles - records after year 2000; map source - Eric Gaba Wikimedia Commons user: Sting and Wikimedia Commons user: NordNordWest, URL - https://upload.wikimedia.org/wikipedia/commons/7/7c/Israel_relief_location_map.jpg).

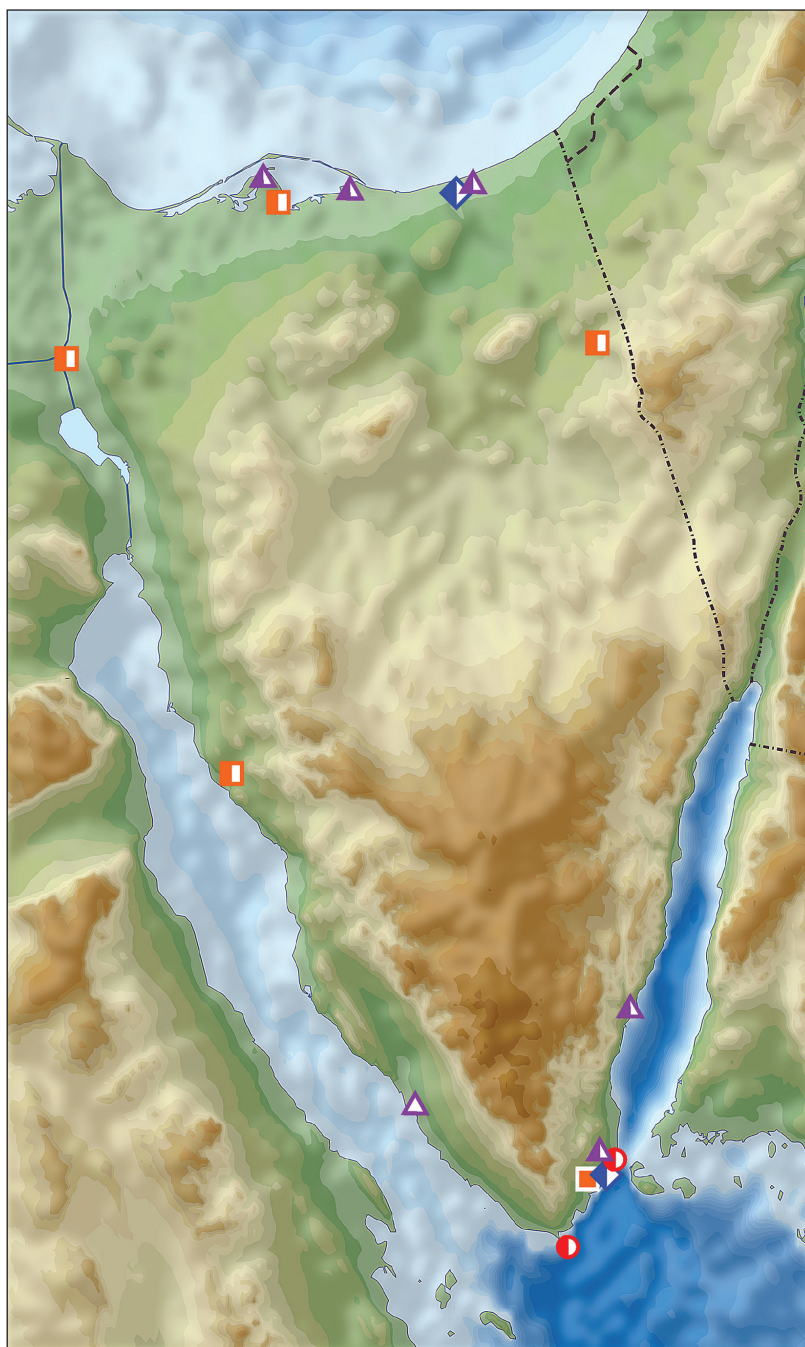


Figure 9. Distribution of *Hypaetha singularis* (red circles), *Myriochila melancholica melancholica* (blue rhombs), *Lophyra flexuosa flexuosa* (orange squares) and *Grammognatha euphratica euphratica* (lilac triangles) in Sinai Peninsula, Egypt (open symbols - records before year 1949, half-solid symbols – records between years 1950–1999; URL map source - https://upload.wikimedia.org/wikipedia/commons/5/59/Sinai_relief_location_map.svg).

1999); **Dead Sea Area:** *Bet Ha'Arava*, 5.IV.1941, leg. O. Theodor - 2♂♂ 2♀♀; *Jordan River*, near Dead Sea, 5.IV.1941, leg. O. Teodor - 1♀ (TAU); *'En Gedi*, 24.III.1958, leg. J. Kugler - 2♂♂; 15.III.65, leg. K. Yefenof - 1♀; *Ne'ot HaKikkar*, 15.II.1999, 19.IV.1999, leg. I. Yarom & V. Kravchenko - 3♂♂ 1♀; *Qalya*, 11.IV.1958, leg. M. Pener - 2♂♂ 1♀; *Sedom*, 6.V.1961, at night, leg. J. Wahrman - 1♂; *Shefekh Zohar*, 16.IV.1980, leg. J. Kugler - 1♀; *Zomet Zohar*, 17.IV.1997, leg. L. Friedman - 1♀ (all TAU); *Nawit Pools* (after Nussbaum 1987); **Arava Valley:** *Gerofit*, 23.IV.2003, 12.V.2003, 6.VI.2003, leg. D. Utshitel & V. Chikatunov - 3♂♂ 2♀♀ (TAU); **Southern Negev:** *Elat*, 30.VIII.1959, leg. L. Fishelsohn - 1♂ (TAU).

EGYPT (SINAI), Northern Sinai: *Sabkhat al Bardawil*, 23.III.1969, leg. A. Nitzan - 1♂♂ 2♀♀ (TAU); *Arish* (after Abdel-Dayem 2004); *Zaranik Protectorate* (after El-Moursy et al. 2001; Abdel-Dayem 2004); **Sinai Mountains:** *Dahab* (after Nussbaum 1987); **Southwestern Sinai:** *El Tor* (after Schatzmayr 1936; Alfieri 1976; Nussbaum 1987; Abdel-Dayem et al. 2003; Abdel-Dayem 2004); *Nabeq* (after Nussbaum 1987).

An identification key to the tiger beetles of Israel and adjacent lands

- 1(2) Anterior angles of pronotum projected towards the margin of prothorax (Figs 10, 45); the fourth joint of maxillary palpus shorter than the third one..... **Megacephalini** (*Grammognatha euphratica euphratica* Dejean, 1822)
- 2(1) Anterior angles of pronotum not projected towards the margin of prothorax (Figs 12–14); the fourth joint of maxillary palpus longer than the third one...
..... **Cicindelini 3**
- 3(4) Proepisterna prominent on pronotum so pronotopleural suture clearly visible dorsally (Fig. 42); anterior margin of pronotum with row of flat white setae
..... ***Hypaetha*** ((○) *Hypaetha singularis* (Chaudoir, 1876))
- 4(3) Proepisterna not prominent on pronotum so pronotopleural suture not visible dorsally (Figs 30–41, 43–44); anterior margin of pronotum glabrous **5**
- 5(6) Labrum with four submarginal setae (Fig. 29); middle and hind femora with numerous hooked setae along posterior margin, hind femora with sparse hooked setae (Fig. 64) ***Myriochila***
(s. str.) (*Myriochila* (s. str.) *melancholica melancholica* (Fabricius, 1798))
- 6(5) Labrum with at least six submarginal setae, except aberrant specimens with 3–5 setae (Figs 15–26, 28); femora without hooked setae along posterior margin..... **7**
- 7(8) Genae pilose (Figs 11, 14) **9**
- 8(7) Genae glabrous (Figs 12–13) **13**
- 9(10) Clypeus glabrous, anterior and posterior margins of each eye with group of white decumbent setae; labrum with 10 submarginal setae in a single row (Fig. 25); fourth antennomere of males with penicillus (Fig. 14); white elytral pattern with complete humeral lunule, long sinuate middle band

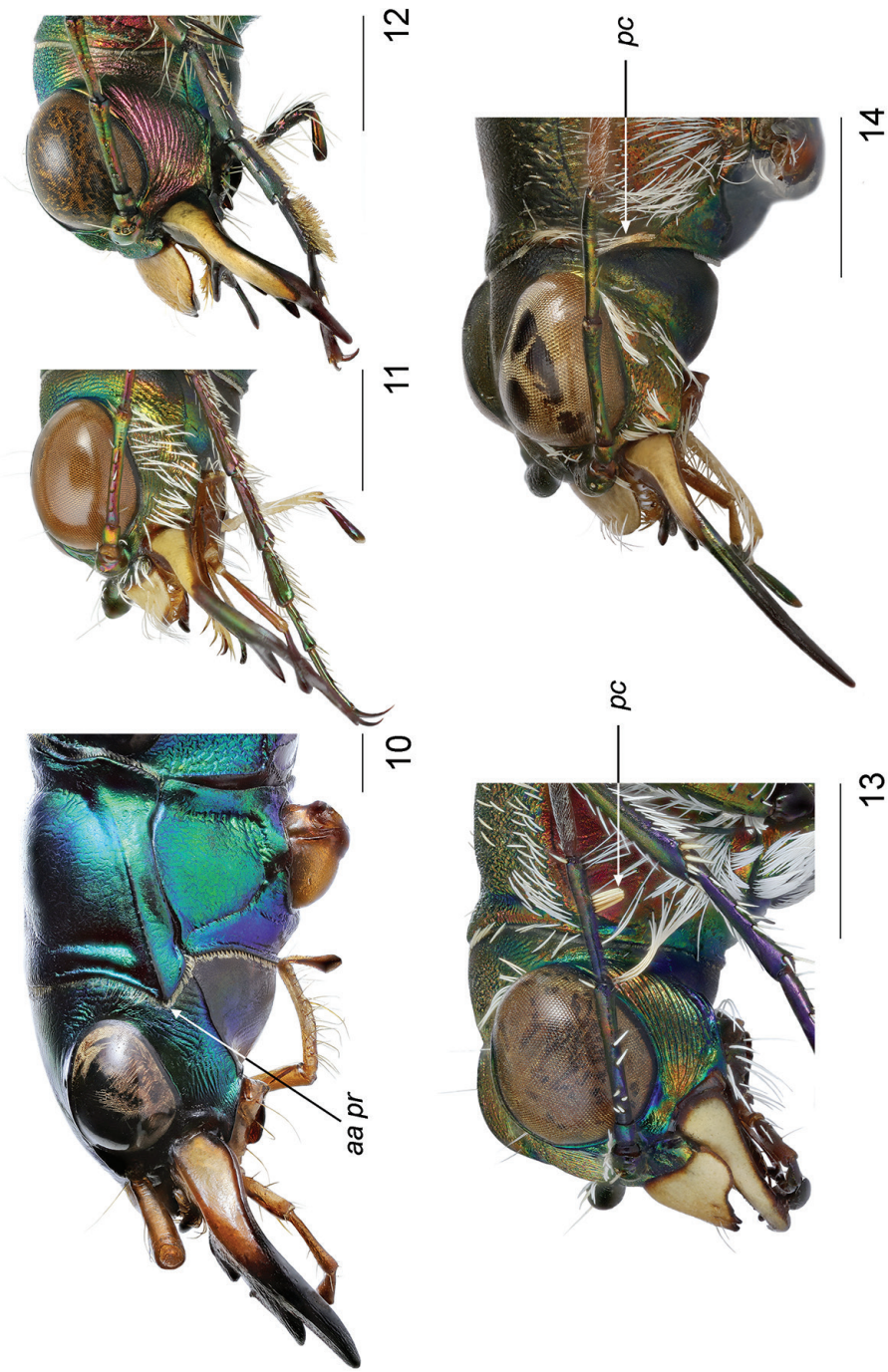
- and apical lunule coupling together via marginal and sutural bands (Fig. 56)..... ***Habrodera* ((○) *Habrodera nilotica nilotica* (Dejean, 1825))**
- 10(9) Clypeus pilose, anterior and posterior margins of each eye glabrous; labrum with several rows of numerous submarginal setae (Figs 15–18); fourth antennomere of males glabrous (Fig. 11); white elytral pattern without marginal and sutural bands (Figs 46–49) ***Calomera* 11**
- 11(12) Elytra dark brown with purple-bronze or green reflection (Fig. 46); pronotum 1.05–1.15 times as wide as long with straight parallel or slightly convergent lateral sides (Fig. 30); aedeagus straight, with long thin basal portion, apical lobe with distinct lateral flanges and small hook, without central groove (Figs 73, 77), ventro-apical bladder of internal sac short, right and left basi-lateral bladders very large (Figs 77, 81) ... ***Calomera aulica aulica* (Dejean, 1831)**
- 12(11) Elytra green sometimes with bronze or blue reflection (Figs 47–49); pronotum 1.15–1.35 times as wide as long with rounded distinctly convergent lateral sides (Figs 31–33); aedeagus curved, with short basal portion, apical lobe without lateral flanges and hook, but with clear central groove (Figs 74–76, 82–84), ventro-apical bladder of internal long, right and left basi-lateral bladders as small acicular areas (Figs 78–80, 82–84)..... ***Calomera littoralis* (Fabricius, 1787) 12a**
- 12a(12b) Left mandible with four teeth distal to apical molar (Fig. 16); pronotum narrow, 1.15–1.2 times wider than long (Fig. 31); aedeagus with small distinct bulge on the dorsal surface (Fig. 74); ventro-apical bladder of internal sac long and curved towards and on the left, apex of medial tooth blunt (Figs 74, 78, 82) ***Calomera littoralis aulicoides* (J.R. Sahlberg, 1913)**
- 12b(12a) Left mandible with three teeth distal to apical molar (Fig. 17–18); pronotum wide, 1.2–1.35 times wider than long (Figs 32–33); aedeagus without bulge on the dorsal surface (Figs 75–76); ventro-apical bladder of internal sac straight and not curved, apex of medial tooth sharp (Figs 75–76, 79–80, 83–84)..... **12c**
- 12c(12d) Labrum wider, 2.6–2.65 times as wide as long (Fig. 32), base of medial tooth of internal sac with one rarely two small additional spikes (Figs 75, 79, 83) ***Calomera littoralis winkleri* (Mandl, 1934)**
- 12d(12c) Labrum narrower, 2.35–2.45 times as wide as long (Fig. 33), base of medial tooth of internal sac smooth, without additional spikes (Figs 76, 80, 84)..... (○) ***Calomera littoralis nemoralis* (Olivier, 1790)**
- 13(14) Labrum tridentate with distinctly prominent apical teeth; mandibles with two teeth distal to apical molar (Fig. 26); scapus covered by numerous white decumbent setae (Figs 13, 26), fourth antennomere of males with penicillus (Fig. 13); posterior margin of each eye with group of white decumbent setae; white elytral pattern with basal dot and incomplete sutural band (Fig. 57).... ***Lophyra* (s. str.) (*Lophyra* (s. str.) *flexuosa flexuosa* (Fabricius, 1787))**
- 14(13) Labrum unidentate (Fig. 20–24, 28), in some species tridentate but with not or slightly prominent apical teeth only (Fig. 19); mandibles with three teeth

- distal to apical molar (Fig. 19–24); scapus glabrous (Figs 19–22, 28) or only with several sparse setae except apical ones (Figs 23–24), fourth antennomere of males glabrous (Fig. 11); posterior margin of each eye glabrous; white elytral pattern without basal dots and sutural band (Figs 50–55, 59) **15**
- 15(16) Head glabrous; scapus with apical setae only (Fig. 19–22, 28); lateral side of pronotum pilose (Figs 34–37, 43); white elytral pattern with long marginal band and long sinuate middle band (Figs 50–53, 59) **17**
- 16(15) Frons and vertex with long soft hairs, scapus with several setae except apical ones (Figs 23–24); lateral side of pronotum with soft sparse setae (Figs 38–39); white elytral pattern without marginal band and only with short slightly curved middle band (Figs 54–55) ***Cicindela* (s. str.) 25**
- 17(18) Anterior portion of apical lunule long, extending basal transverse portion of middle band (Fig. 59) ***Cylindera* (*Eugrapha*) (*Cylindera* (*Eugrapha*) *contorta valdenbergi* (Mandl, 1981))**
- 18(17) Anterior portion of apical lunule short, extending only apical portion of middle band (Figs 50–53) ***Cephalota* (*Taenidia*) 19**
- 19(20) Labrum tridentate, relatively short, no less than 2.3 times as wide as long (Fig. 19); pronotum 1.2–1.4 times wider than long (Fig. 34); mesepisternum entirely covered by white setae, densely in males and sparsely in females; white elytral pattern with relatively broad marginal band coupling with humeral and apical lunule as well as with middle band (Fig. 50), apical margin of elytra in sexes wide rounded, subtend practically right angle with sutural tooth (Figs 65–66); aedeagus with long thin gradually curved basal portion (Fig. 85) (○) ***Cephalota* (*Taenidia*) *tibialis tibialis* (Dejean, 1822)**
- 20(19) Labrum unidentate, relatively long, no more than 2.3 times as wide as long (Figs 20–22); pronotum 1.1–1.25 times wider than long (Figs 35–37); mesepisternum covered by white setae only along posterior margin and on the base; white elytral pattern usually with narrow marginal band or without it so in some specimens humeral lunule distinctly separated (Figs 51–53), apical margin of elytra at least in males subtend acute angle with sutural tooth (Figs 67–72); aedeagus with short thin basal portion (Figs 87, 89, 91) **21**
- 21(22) 4–11th antennomeres dark brown; elytra bright purple, 1.5–1.6 times as long as wide (Fig. 51), apical elytral margin in females narrowly rounded and subtend small right angle with sutural tooth (Fig. 67–68); aedeagus with broad blunt apex (Figs 87–88) (○) ***Cephalota* (*Taenidia*) *littorea littorea* (Forskål, 1775)**
- 22(21) 4–11th antennomeres light brown or yellowish; elytra greenish or greenish-blue sometimes with distinct golden-purple reflection, no less than 1.65 times as long as wide (Figs 52–53), apical elytral margin in both sexes subtend acute angle with sutural tooth (Figs 69–72); aedeagus with arrow-shaped apex (Figs 89–92) **23**
- 23(24) Labrum shorter, 2.0–2.2 times as wide as long (Fig. 21); lateral side of pronotum straight, slightly convergent to large posterior angles (Fig. 36); humeral

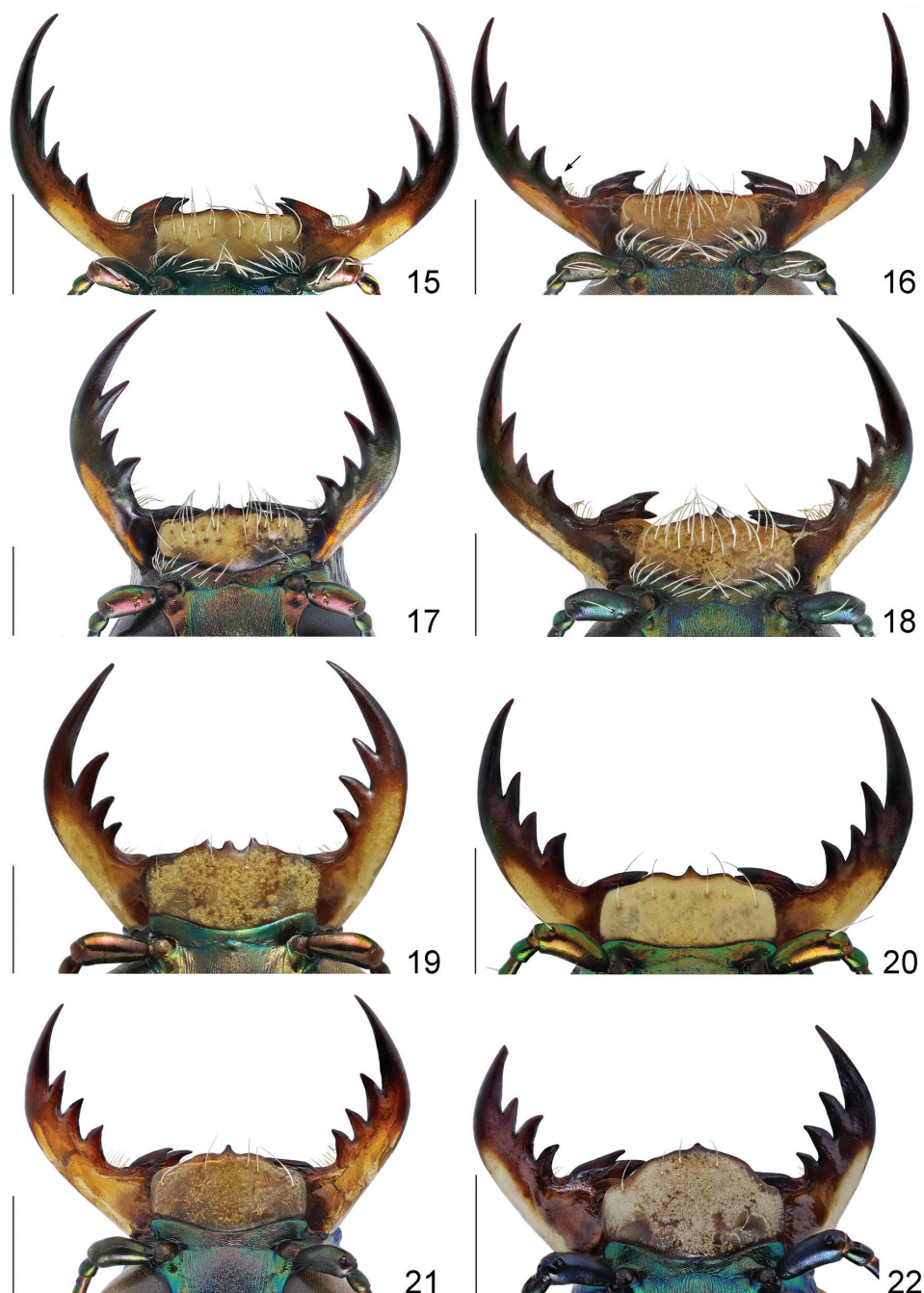
- lunule separated or narrowly coupled with marginal band (Fig. 52); aedeagus larger, with relatively long thin basal portion (Fig. 89) and short tapered apex (Fig. 90) ... ***Cephalota (Taenidia) zarudniana vartianorum* (Mandl, 1967)**
- 24(23) Labrum longer, 1.6–1.7 times as wide as long (Fig. 22); lateral side of pronotum slightly rounded, distinctly convergent to small posterior angles (Fig. 37); humeral lunule coupled with middle band via marginal band (Fig. 52); aedeagus smaller, with short thin basal portion (Fig. 91) and long tapered apex (Fig. 92).....(○) ***Cephalota (Taenidia) deserticola deserticola* (Faldermann, 1836)**
- 25(26) Pronotum with convex lateral sides gradually convergent to posterior angles, anterior margin same length or slightly longer than posterior one, notopleural suture looks like smooth border (Fig. 39); mesepisternum of female with small shallow pit and deep all along coupling sulcus, mesepimeron with groove along anterior margin (Fig. 63); middle band of white elytral pattern without oblique strip between transverse basal and circled apical portions, basal portion of apical lunule small (Fig. 55); aedeagus shorter, no more than 0.55 times as long as elytra (Fig. 97); basal and right ventro-lateral bladders of internal sac short (Figs 98–100)..... ***Cicindela* (s. str.) *javeti azari* Deuve, 2011**
- 26(25) Pronotum with straight lateral sides sharply convergent to posterior angles, anterior margin clearly longer than posterior one, notopleural suture looks like cut border (Fig. 38); mesepisternum of female with deep apically but shallow and indistinct basally coupling sulcus only, mesepimeron without groove along anterior margin (Fig. 62); middle band of white elytral pattern with distinct oblique strip between transverse basal and circled apical portions, basal portion of apical lunule large (Fig. 54); aedeagus longer, no less than 0.6 times as long as elytra (Fig. 93); basal and right ventro-lateral bladders of internal sac long (Figs 94–96).....(○) ***Cicindela* (s. str.) *herbacea herbacea* Klug, 1832**

Distribution

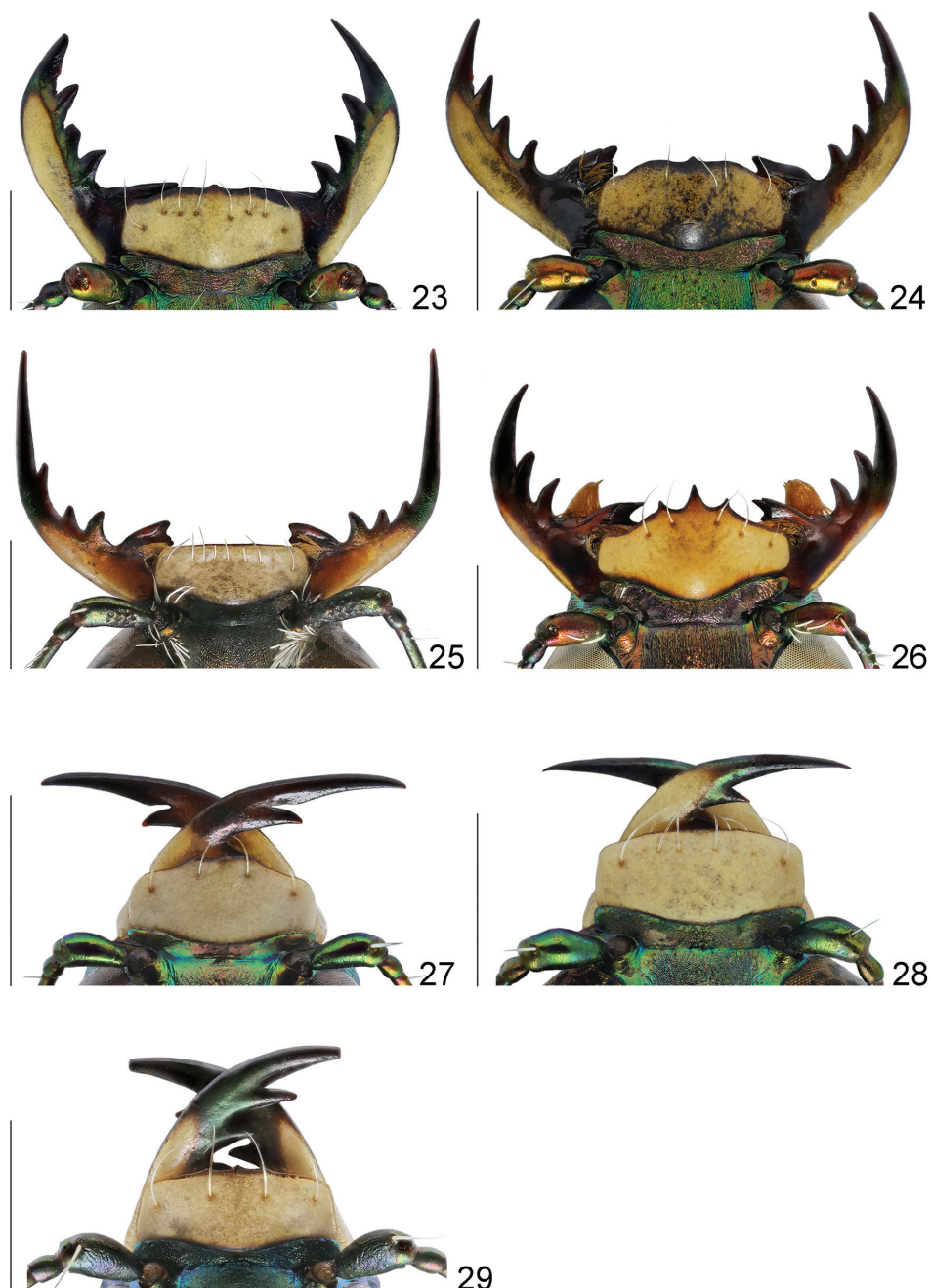
With these current records, eight species of tiger beetles, one of them with two sub-species, belonging to seven genera of two tribes are known from Israel (Table 1). The Rift Valley, including Jordan Valley, Dead Sea area and Arava Valley, with six cicindelids species is the most speciose region. The Coastal Plain is the second richest region with five species. The species richness gradually decreases from Northern (five species) through Central (four species) to Southern (three species) Coastal Plain. In the central densely populated areas of Israel, such as Samaria and Judea, the least number of tiger beetles species are recorded. Among all *M. melancholica melancholica* is the most common species observed in all regions of the country (Table 1, Fig. 7), while *L. flexuosa flexuosa* is the second most widespread species of tiger beetles absent only from northern (Galilee, Golan Heights) and central (Samaria, Judea) regions (Table 1, Fig. 6). *Lophyra flexuosa* (Fabricius, 1787) reaches the eastern limit of its distribution in Israel.



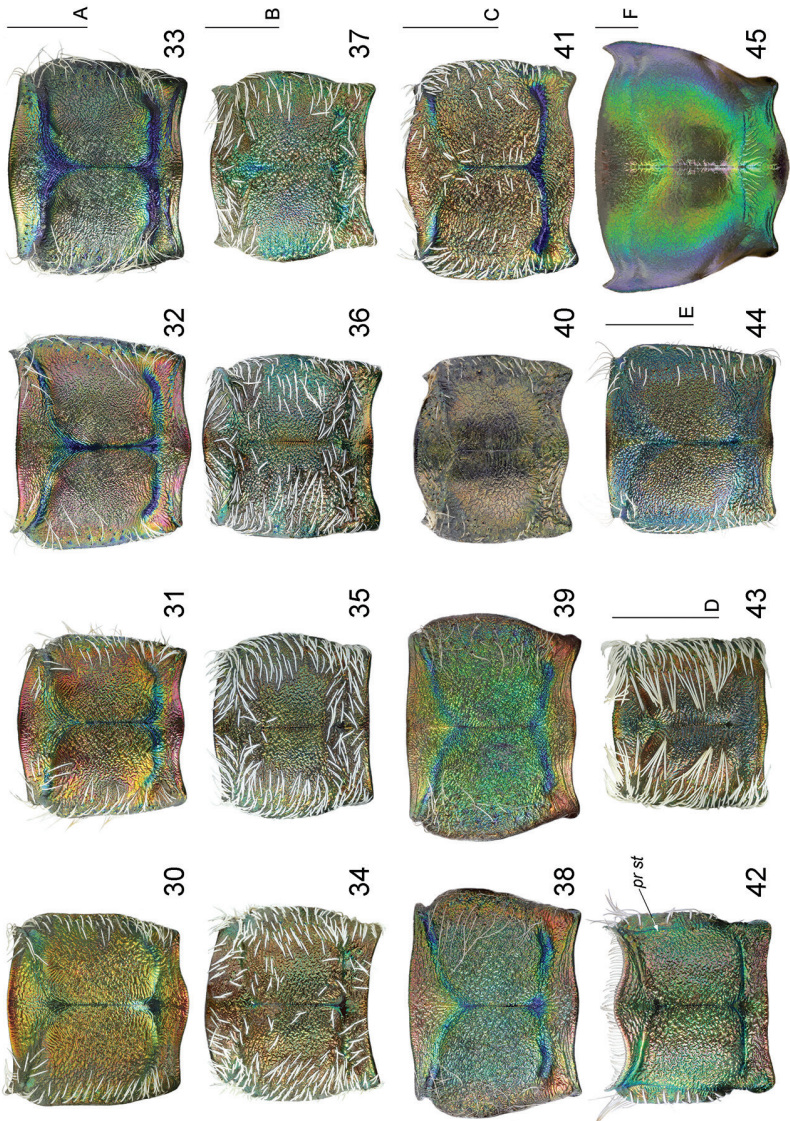
Figures 10–14. Head and pronotum of males, left lateral view: **10** *Grammognatha euphratica euphratica* **11** *Calomera aulica aulica* **12** *Cicindela javeti azari* **13** *Lophyrus flexuosus flexuosus* **14** *Habrodera nilotica*; aa pr – anterior angle of pronotum; pc – penicillus. Scale bars: 1 mm.



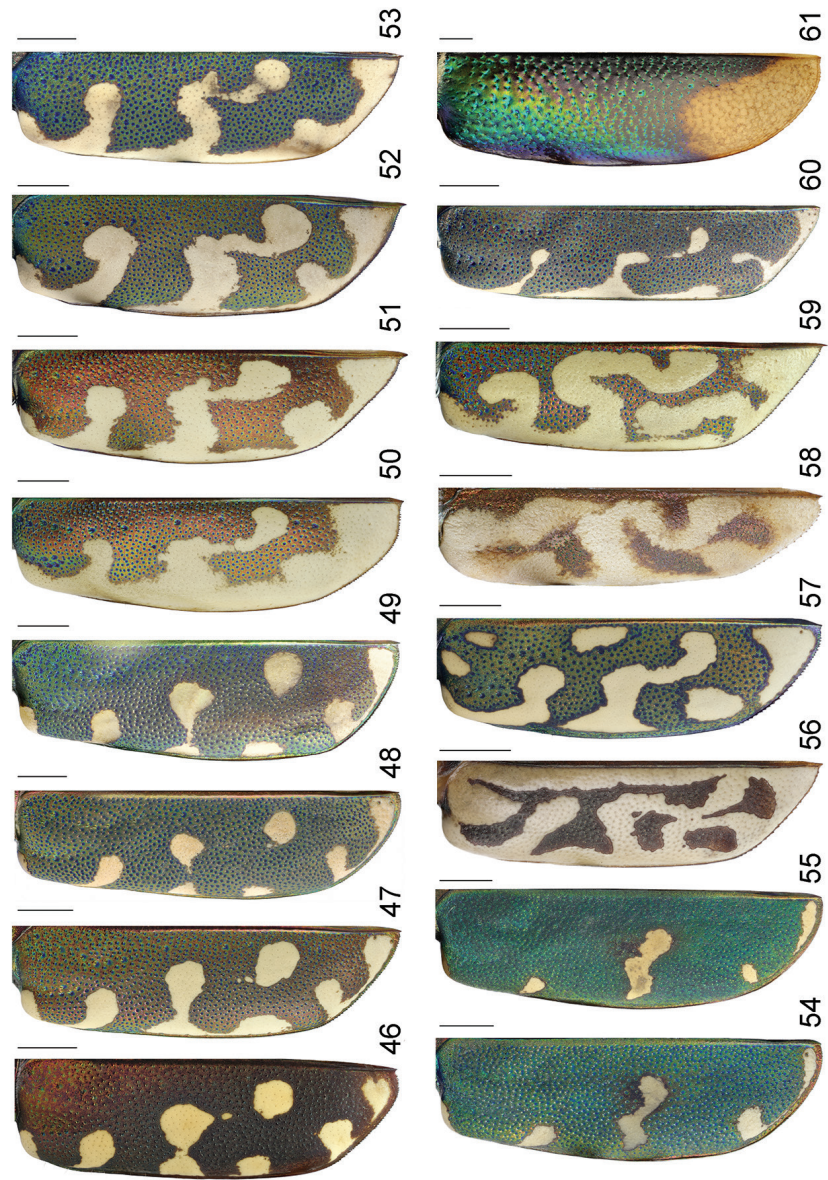
Figures 15–22. Labrum and mandibles of males, dorsal view: **15** *Calomera aulica aulica* **16** *Calomera littoralis aulicoides* **17** *Calomera littoralis winkleri* **18** *Calomera littoralis nemoralis* **19** *Cephalota tibialis tibialis* **20** *Cephalota littorea littorea* **21** *Cephalota zarudniana vartianorum* **22** *Cephalota deserticola deserticola*. Scale bars: 1 mm.



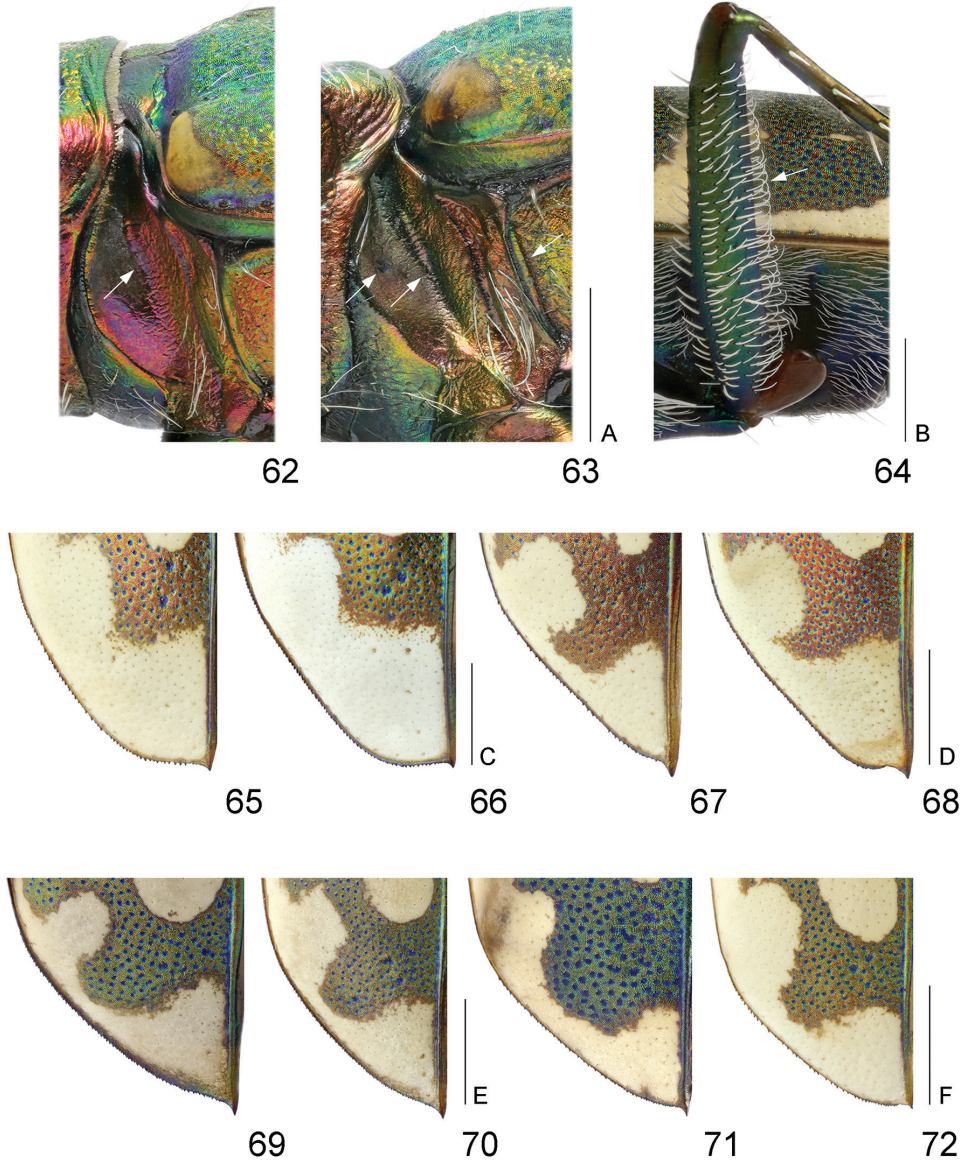
Figures 23–29. Labrum and mandibles of males, dorsal view: **23** *Cicindela herbacea herbacea* **24** *Cicindela javeti azari* **25** *Habrodera nilotica nilotica* **26** *Lophyra flexuosa flexuosa* **27** *Hypaetha singularis* **28** *Cylindera contorta valdenbergi* **29** *Myriochila melancholica melancholica*. Scale bars: 1 mm.



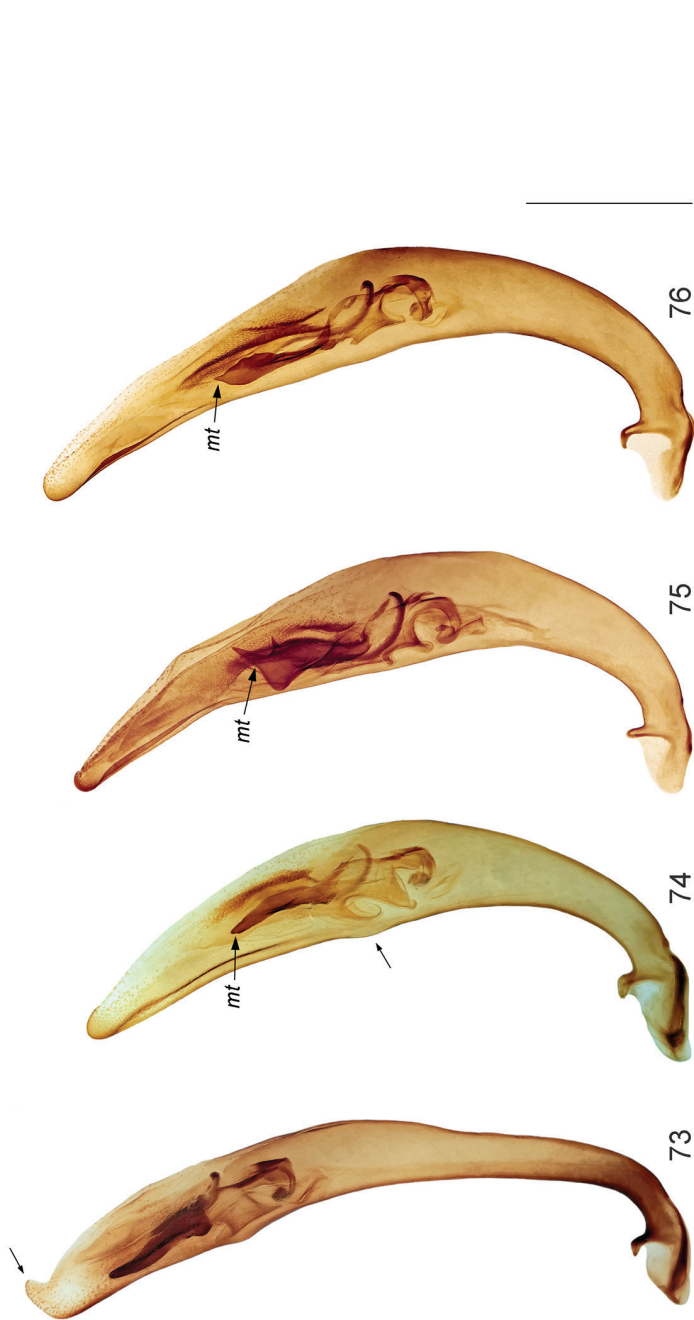
Figures 30–45. Pronotum of males, dorsal view: **30** *Calomera aulica aulica* **31** *Calomera littoralis aulicoides* **32** *Calomera littoralis winkleri* **33** *Calomera littoralis*
nemorialis **34** *Cephalota tibialis tibialis* **35** *Cephalota littorea littorea* **36** *Cephalota zarudniana varianorum* **37** *Cephalota deserticola deserticola* **38** *Cicindela herbacea*
herbacea **39** *Cicindela javeti azari* **40** *Habrodera nilotica nilotica* **41** *Lophyra flexuosa flexuosa* **42** *Hypaetha singularis* **43** *Cylindera contorta valdenbergi* **44** *Myriochila*
melancholica melancholica **45** *Grammognatha euphratica euphratica*; pr st - pronotopleural suture. Scale bars: 1 mm (30–33; A; 34–37; B; 38–41; C; 42–43; D; 44;
E; 45; F).



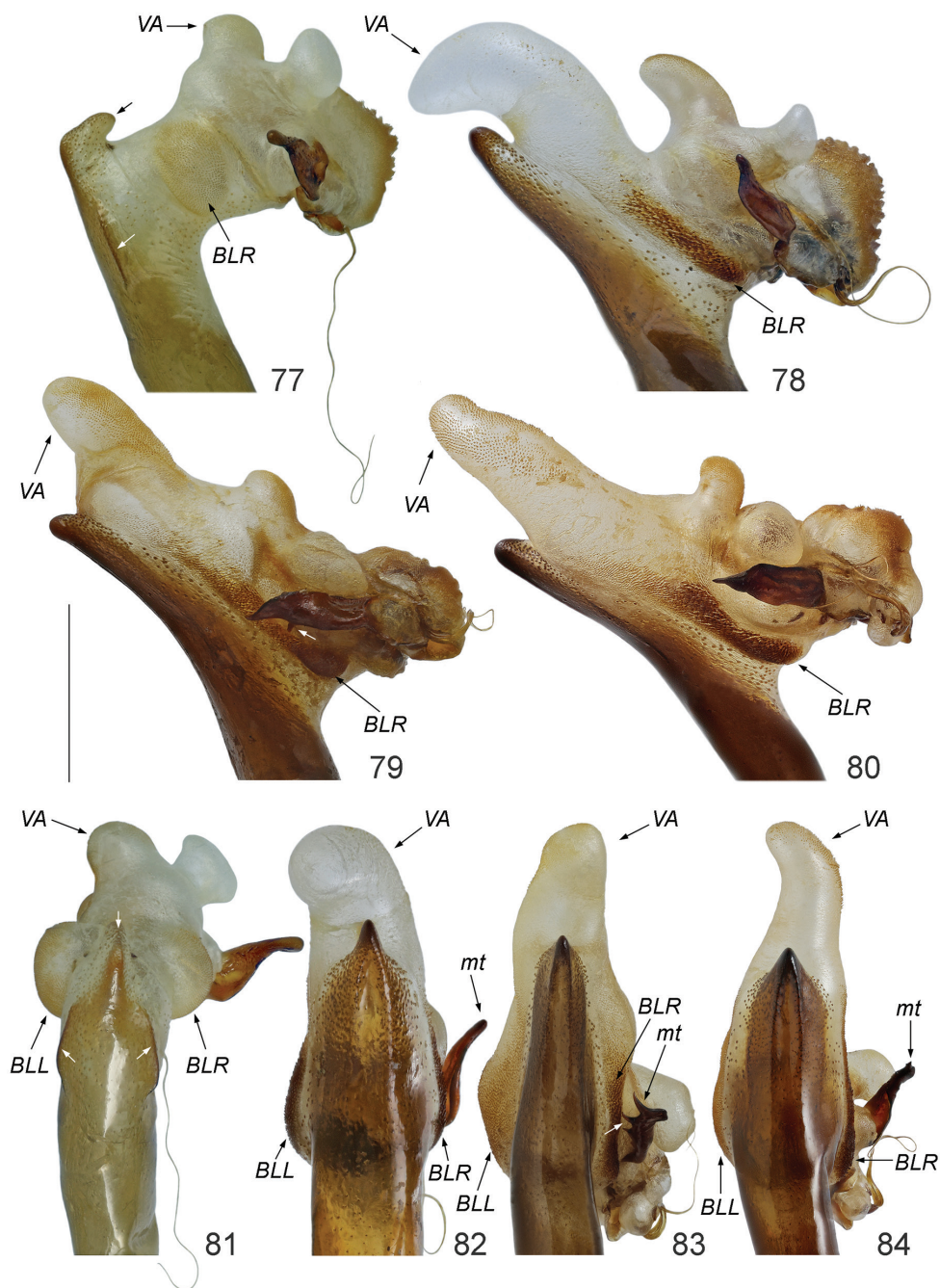
Figures 46–61. Left elytron of males, dorsal view: **46** *Calomera aulica aulica* **47** *Calomera littoralis aulicoides* **48** *Calomera littoralis winkleri*; **49** *Calomera littoralis nemoralis* **50** *Cephalota tibialis tibialis* **51** *Cephalota tiborea tiborea* **52** *Cephalota zarudniana varianorum* **53** *Cephalota deserticola deserticola* **54** *Cicindela herbacea herbacea* **55** *Cicindela javeti azari* **56** *Habrodera nilotica nilotica* **57** *Lophyra flexuosa flexuosa* **58** *Hypaetha singularis* **59** *Cylindera contorta valdenbergi* **60** *Myriochila melancholica melancholica* **61** *Grammognatha euphratica euphratica*. Scale bars: 1 mm.



Figures 62–72. Details of Cicindelinae: **62–63** mesoepisternal coupling sulcus **64** hind femora **65–72** apical part of left elytron **62** *Cicindela herbacea herbacea* **63** *Cicindela javeti azari* **64** *Myriochila melancholica melancholica* **65–66** *Cephalota tibialis tibialis* **67–68** *Cephalota littorea littorea* **69–70** *Cephalota zarudniana vartianorum* **71–72** *Cephalota deserticola deserticola* **64–65, 67, 69, 71** males **62–63, 66, 68, 70, 72** females. Scale bars: 1 mm (62–63: A; 64: B; 65–66: C; 67–68 D; 69–70: E; 71–72: F).



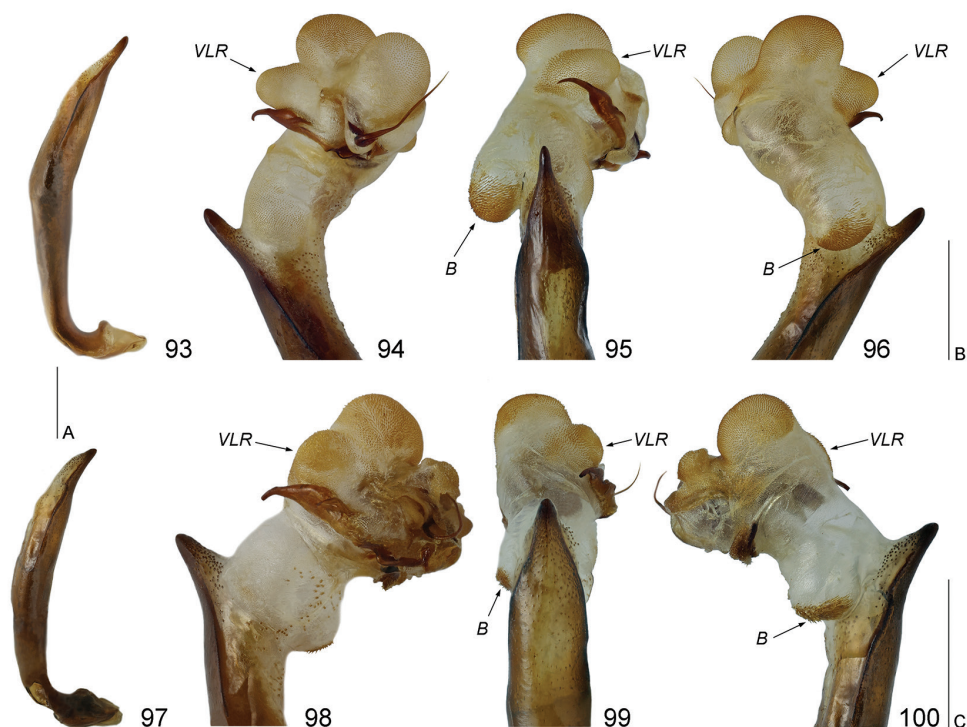
Figures 73–76. Acedeagus of *Calomera* spp., right lateral view: **73** *C. aulica aulica* **74** *C. littoralis aulicoides* **75** *C. littoralis winkleri* **76** *C. littoralis nemoralis*; *mt* – median tooth. Scale bar: 1 mm.



Figures 77–84. Internal sack of *Calomera* spp.: **77, 81** *C. aulica aulica* **78, 82** *C. littoralis aulicoides* **79, 83** *C. littoralis winkleri* **80, 84** *C. littoralis nemoralis* **77–80** right lateral view **81–84** dorsal view; BLR - basi-lateral right bladder; BLL - basi-lateral left bladder; VA – ventro-apical bladder; mt – median tooth. Scale bar: 1 mm.



Figures 85–92. Aedeagus of *Cephalota* spp.: **85–86** *Cephalota tibialis tibialis* **87–88** *Cephalota littorea littorea* **89–90** *Cephalota zarudhiana varianorum* **91–92** *Cephalota deserticola deserticola* **85, 87, 89, 90** aedeagus, left lateral view **86, 88, 91, 92** apex of aedeagus, ventral view. Scale bar: 1 mm.



Figures 93–100. Aedeagus and internal sac of *Cicindela* ssp.: **93–96** *C. herbacea herbacea* **97–100** *C. javeti azari* **93, 97** aedeagus **94–96, 98–100** internal sac **93, 96–97, 100** left lateral view **95, 99** dorsal view **94, 98** right lateral view **98–100** partly inflated); *B* - basal bladder; *VLR* – ventro-lateral right bladder. Scale bars: 1 mm (93, 97: A; 94–96: B; 98–100: C).

Three subspecies, *C. contorta valdenbergi*, *C. javeti azari* and *C. zarudniana var-tianorum*, are characterized by a restricted distribution in Israel (Fig. 4). The first two first subspecies should be considered as regional endemics.

The nominative subspecies of *Cylindera contorta* (F.-W., 1828) is widely distributed in Central Asia, some regions of Cis- and Transcaucasia as well as in the northern and western sides of the Black Sea from southern Russia to Romania (Wiesner 1992; Cassola 1999; Puchkov and Matalin 2003), however it is not known from Anatolia (Corel 1988; Cassola 1999; Puchkov and Matalin 2003; Avgin and Özdikmen 2007), Syria (Wiesner 1992; Puchkov and Matalin 2003; Avgin and Wiesner 2009; Jaskuła and Rewicz 2014), Jordan (Wiesner 1992; Puchkov and Matalin 2003), Iraq (Ali 1978; Wiesner 1992; Puchkov and Matalin 2003) and Saudi Arabia (Wiesner 1992; Cassola and Schneider 1997; Puchkov and Matalin 2003; Al Ahmadi and Salem 1999). The populations of *C. contorta valdenbergi* inhabit the Mediterranean coast from 'Akko (Northern Coastal Plain) to Bat Yam (Central Coastal Plain) in Israel (Nussbaum 1987; our data) as well as between Ras El Bar and Abu Qir in north-eastern Egypt (Alfieri 1976; Abdel-Dayem et al. 2003) are distinctly scattered and bound the south-western limit of the distributional area of *C. contorta* as a whole.

Table 1. The distribution of tiger beetles in different regions of Israel and the Sinai Peninsula.

Species/Subspecies	Choro- types	Israel										Siani (Egypt)									
		Galilee		Golan Heights (including Mt. Hermon)	Coastal Plain			Judea		Rift Valley			Negev			Northern Siani	Central Siani Foothills	Siani Mountains	Southwestern Sinai		
		Upper	Lower		Northern	Central	Southern	Judean Desert	Judean Hills	Jordan Valley	Dead Sea Area	Arava Valley	Northern	Central	Southern						
<i>Calomera aulica aulica</i>	SSS																				
<i>Calomera littoralis aulicoides</i>	NAA		•																		
<i>Calomera littoralis winkleri</i>	SAT	•																			
<i>Cephalota zarudniana varianorum</i>	INP																				
<i>Cephalota tibialis tibialis</i>	EGYP																				
<i>Cephalota littorea littorea</i>	NAA																				
<i>Cicindela javeiti azari</i>	LEVC	•																			
<i>Cylindera contorta valdenbergi</i>	CPND																				
<i>Habrodera nilotica nilotica</i>	AFT																				
<i>Hypaetha singularis</i>	NAA																				
<i>Lophyra flexuosa flexuosa</i>	WMA																				
<i>Myriochila melancholica melancholica</i>	AMC	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Gnamptognatha euphratica euphratica</i>	SMS																				
Total for localities		3	2	3	3		5	4	3	1	1	3	6	5	2	2	3	5	1	4	7
		4		3			5			2			6				3		9		
Total for regions		8(9)										9				9					

Chorotypes: AFT – Afrotropical, AMC – Afrotropical-Mediterraneo-Centralasiatic, INP – Irano-Palestinian, NAA – NE-African-Arabian, SAT – S-Anatolia-Turanian, SMS – S-Mediterraneo-Sindian, SSS – Saharo-Sahelo-Sindian, WMA – W-Mediterraneo-N-African, CPND – Coastal Plain-Nile Delta endemic, EGYP – Egyptian endemic, LEVC – C-Levntian endemic.

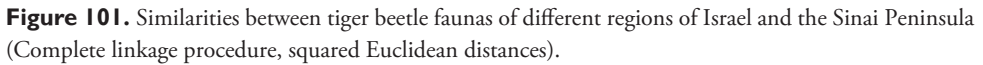
Cicindela javeti azari has a restricted distributional area and now is known only from southern Lebanon (Deuve 2011), southwestern Syria (Avgin and Wiesner 2009) as well as northern regions of Israel: Upper Galilee and Golan Heights (Nussbaum 1987; our data). Among three known subspecies (Deuve 2011) *C. javeti azari* inhabits the southern part of the species range area.

Cephalota zarudniana vartianorum lives from south-eastern Iran across Iraq and Syria to Jordan and Israel (Wiesner 1992; Puchkov and Matalin 2003). The Dead Sea Area is the western border of the distributional area both for this subspecies as well as for the species as a whole.

It should be noted that the three mentioned above subspecies were recorded in Israel only during XX century (Fig. 4), and the latest records are dated from the late 80's to the early 90's.

The Sinai Peninsula is the most diversity of tiger beetles region from all neighbouring territories by Israel because nine species live here, and *C. tibialis tibialis*, *C. littorea littorea*, *H. singularis* and *H. nilotica nilotica* are never really observe in Israel (*vs* Chikatinov et al. 2006). Among them *C. tibialis tibialis* is an endemic of Egypt and occurs along Mediterranean Sea coast in the Governorates Matrouh, Alexandria, Kafr el-Sheikh, Damietta, Port Said and North Sinai (Gebert 1991; Abdel-Dayem et al. 2003; Abdel-Dayem 2012). Moreover, *C. littorea littorea* is an regional near-endemic living along Red Sea coast in Egypt and Saudi Arabia (Gebert 1991; Cassola and Schneider 1997; Abdel-Dayem et al. 2003). Arabian-African *Hypaetha singularis* lives along Red Sea coast in Egypt, Sudan, Eritrea and Yemen, and on the shore of Gulf of Aden in Djibouti, Somalia and Yemen (Wranik et al. 1991; Werner 2000; Wiesner 2002, 2005) as well as on the littoral of Arabian Sea in Oman (Cassola and Rihane 1996). The Sinai localities are limited the northern border of the distribution area of this species. African *Habrodera nilotica nilotica* is widely distributed in Afrotropical Region (Wiesner 1992; Werner 2000). Two known localities from Sinai Mountains (Alferi 1976; Abdel-Dayem et al. 2003; Abdel-Dayem 2004) are limited the distribution range of this species to the east.

According to the analysis of the similarity between faunas of tiger beetle of natural regions of Israel and the Sinai Peninsula two large clusters are recognized (Fig. 101). First of them includes the faunas associated with southern part of the Great Rift Valley (Arava valley and Dead Sea area) and most part of the Sinai Peninsula, while the second combine most Israeli regions as well as Central Sinai Foothills. The last cluster diverges on the four groups. The fist combines assemblages of tiger beetles of the Mediterranean coastal habitats within the Northern and Central Coastal Plains. The communities typical for the arid habitats of the Negev Desert and the Central Sinai Foothills as well as for coastal habitats of the Southern Coastal Plain form the second group. The third group includes assemblages of the northern not seashore habitats of the Jordan Valley, Lower Galilee and Golan Heights. The last group is artificial, because the fauna of tiger beetles of Judea should be most similar to the fauna of the Dead Sea Area or the Northern Negev, while the fauna of tiger beetles of the Galilee, Jordan Valley and Golan Heights should be the most similar to each other. First of all, this discrepancy is due to a lack of data about tiger beetles of the central regions of Israel.



According to the literature data (Alfieri 1975; Nussbaum 1987; Abdel-Dayem et al. 2003) and the results of our own study some aspects of the phenology of tiger beetles both in Israel and on the Sinai Peninsula are discussed. The period of activity of the beetles but not the breeding period was analysed first of all. As a result, five groups of the tiger beetles were obtained (Table 2). Three species with the longer period of activity from January to November or from February to December belong to the all-year group. Five species, including two subspecies of *Calomera littoralis* (F., 1787), characterized by the prolonged period of activity from February to October-November, from March-April to November or from March to December and form the richest spring-fall group. Two species recorded only on the Sinai Peninsula with the period of activity from May to August-September are composed the summer group. At last, both the spring group (activity from February to May) and the spring-summer group (activity from February to August) contain a single species each.

It should be noted that the period of activity of some studied species does not correspond with the data of previous studies in Israel (Nussbaum 1987) and on the Sinai Peninsula (Alfieri 1975; Abdel-Dayem et al. 2003), as well as in the other parts of the distribution area (Jaskuła and Rewicz 2015; Jaskuła et al. 2015). For example, the activity of *C. aulica aulica*, *C. littoralis aulicoides*, *C. zarudniana vartianorum*, *C. contorta valdenbergi* and *G. euphratica euphratica* start one-two months earlier, while the activity of *C. aulica aulica*, *C. littoralis aulicoides*, *M. melancholica melancholica* and *G. euphratica euphratica* finish one-three, and in the case with *L. flexuosa flexuosa* even

Table 2. The phenology of tiger beetles in Israel (grey – our data; pink – after Nussbaum 1987) and in the Egypt (green – after Alfieri 1975; blue – after Abdel-Dayem et al. 2003).

<i>Cephalota zarudniana vartianorum</i>													Spring
<i>Grammognatha euphratica euphratica</i>			(Si)										Spring-summer
<i>Hypaetha singularis</i>					Si			Si					
						Si	Si						
<i>Cephalota littorea littorea</i>					Si	Si	Si	Si	Si				Summer
						(Si)		(Si)					
								(Si)					
<i>Cephalota tibialis tibialis</i>					Si	Si	Si	Si	Si				
		Si	Si	Si	Si	Si	Si	Si	Si	Si			
<i>Calomera littoralis aulicoides</i>													
<i>Calomera littoralis winkleri</i>													
<i>Cylindera contorta valdenbergi</i>													
<i>Cicindela javeti azari</i>													
<i>Myriochila melancholica melancholica</i>													
<i>Habrodera nilotica nilotica</i>				Si									
<i>Calomera aulica aulica</i>				(Si)	(Si)		(Si)	(Si)					
					Si				(Si)	Si			
		(Si)	(Si)	(Si)	(Si)	(Si)	(Si)	(Si)	(Si)	(Si)			
<i>Lophyra flexuosa flexuosa</i>					(Si)								
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	

Notes. Si – records only on the Sinai Peninsula, (Si) – records including the Sinai Peninsula. The density of the grey color corresponds with the frequency of the records of species (subspecies):

	1–3		4–6		7–9		10–12		13–15		16–18
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six months later comparing with the data of Nussbaum (1987). On the other hand, Nussbaum (1987) indicated longer period of activity of *C. littoralis winkleri* and *C. tibialis tibialis* as well as the later finish of the activity of *C. contorta valdenbergi* and *C. javeti azari* (Table 2).

Similarly, the periods of activity of *C. aulica aulica*, *L. flexuosa flexuosa* and *M. melancholica melancholica* in the central and southern Levant as well as on the Sinai Peninsula are appreciably longer than in the Maghreb region. So, in Tunisia *C. aulica aulica* records only in June and July (Jaskuła and Rewicz 2015), while in Israel it active from March to December and on the Sinai Peninsula from February to October (Table 2). Both in Tunisia and Morocco the period of activity of *L. flexuosa flexuosa* lasts from March-April to July (Jaskuła and Rewicz 2015; Jaskuła et al. 2015) but in Israel it continues from February to December (Table 2).

On the contrary, in Tunisia the activity of *G. euphratica euphratica* begins in March and ends in July (Jaskuła and Rewicz 2015) that is similar with the period of activity in Israel and on the Sinai Peninsula (Table 2), while in Morocco it takes only three months - from June to August (Jaskuła et al. 2015). The same situation is observed for different subspecies of *Cephalota littorea* (Forskål, 1775) as well as *C. littoralis*. In Tunisia *C. littorea gouditii* (Dejean, 1829) is active from May to October (Jaskuła and Rewicz 2015) while the period of activity of *C. littorea littorea* on the Sinai Peninsula lasts from May to September (Table 2). The activity of *C. littoralis littoralis* in Morocco is observed from April to October (Jaskuła et al. 2015) and in Tunisia from March to August (Jaskuła and Rewicz 2015), while the activity of *C. littoralis aulicoides* in Israel and on the Sinai Peninsula as well as *C. littoralis winkleri* in Israel occurs from February to October and from February to November, respectively (Table 2).

However, we must remember that the obtained data are compilative. The differences in the time and the density of sampling, the collection technics as well as the frequency of visit of the particular localities and habitats could really distort the real pattern.

Faunogenesis

The tiger beetle fauna of Israel as well as the Levant as a whole is complex. In geological time these areas were settled by species from different Mediterranean, African and Asiatic regions.

Unfortunately, the information about fossil Cicindelinae is extremely scant (Nagano et al. 1982). At present time South American *Oxycheilopsis cretacicus* Cassola & Werner, 2004 (Lower Cretaceous ca. 125 Ma) is the oldest known fossil tiger beetle (Cassola and Werner 2004). Three samples of fossil cicindelids are known from the northern Europe Baltic Amber (Oligocene ca. 23–34 Ma). Despite the identification ambiguity of the species, the genera were interpreted as the recent ones (Nagano et al. 1982; Röschmann 1999) as most known fossil Carabidae and other Coleoptera (Aleksiev 2013). All other fossil records of the tiger beetles from the Europe and northern

America (USA and Canada) are dated from the Quaternary period from Pleistocene to Holocene, and all other species are interpreted as recent (Nagano et al. 1982).

By analogy with other groups of carabid beetles (Kataev 1984, 2011; Casale and Vigna Taglianti 1999; Ruiz et al. 2012), we can assume that the genesis of the ancestral taxa of most recent cicindelids in the Mediterranean region began in late Paleogene – early Neogene (on the border of Oligocene – Miocene). According to data of DNA analysis the divergence processes of taxa of subtribe Cicindelina began *ca.* 15–25 Ma with most intensity between 2–10 Ma (Barracough and Vogler 2002; Pons et al. 2004; Tsuji et al. 2015). For example, the diversification of the species within *Cicindela hybrida* group started *ca.* 2 Ma (Cardoso and Vogler 2005), while the separation of the genus *Cosmodela* Rivalier, 1961 from other Cicindelinae took place *ca.* 2.2–5 Ma (López-López et al. 2015; Tsuji et al. 2015). Based on the fossil material we could be argued that at least 60,000–70,000 yrs. BP the recent species of tiger beetles were already presented both in the North America and in the Eurasia (Nagano et al. 1982).

The continental drift of the Arabian and Anatolian Plates, their collision and, as the result, closing the Neotethys Ocean during Oligocene-Miocene were the most important processes forming the Mediterranean Sea and the genesis of the terrestrial Mediterranean fauna. The Eurasian-African land-bridge formed during late Burdigalian – middle Serravallian *ca.* 12.5–18 Ma (Rögl 1998) initiated the species change/exchange between the Europe, Asia and Africa (Koufos et al. 2005). The territory of the Sinai Peninsula and the Levant free from the sea formed the first transit corridor. However, it was interrupted at least twice in Langhian (*ca.* 16–16.4 Ma) and in early Serravallian (*ca.* 13–13.3 Ma), while in Tortonian (*ca.* 11.6 Ma) the final connection of Arabian and Anatolian plates and isolation of the Mediterranean Sea took place (Rögl 1998, 1999). Because the Central and Southern Levant as well as the Sinai Peninsula were the part of the Arabian plate connected with the African continent (Rögl 1998; Popov et al. 2004; Robertson et al. 2012; Berra and Angiolini 2014) the African species *G. euphratica*, *H. nilotica*, *M. melancholica* and *L. flexuosa* could have colonized these territories before the other species.

The sharp decrease of the level of the Mediterranean Sea in Messinian (*ca.* 5.5–6 Ma) caused the formation of both numerous shallow enclosed saline basins and the land-bridges between Southern Europe and Northern Africa (Rögl and Steininger 1983). In our opinion during this time the active divergence and dispersion of such halophilic genera as *Cephalota*, *Calomera* and *Hypaetha* as well as the species of the subgenus *Eugrapha* occurred. All of them are arisen in the saline landscapes along the seashores of Para- and Neotethys in the Southern Russia as well as Central and Western Asia. From these regions the ancestors of the recent taxa probably dispersed through the Middle East, Arabian Peninsula and Anatolia to the Levant and the Sinai Peninsula, and some of them to Northern Africa. The second stream of the migration was possible along the Mediterranean coast of Southern Europe. Following this some species reached the Iberian Peninsula, and then the western regions of Northern Africa. In contrast *G. euphratica*, *M. melancholica*, *L. flexuosa* could be populated Southern Europe (Garcia-Reina et al. 2014), Western and Central Asia as well as Sind and some regions of South-Eastern Asia. Finally, possible during the last Glacial Period,

the ancestors of *C. javeti* and *C. herbacea* dispersed into the Levant from the Anatolia, a region characterized by a higher level of diversity of the species of the *Cicindela campestris* group (Cassola 1999; Franzen 2007; Deuve 2011, 2012; our unpublished data).

This proposed version of the biogeographical genesis of the fauna of tiger beetles of the Levant should be considered an initial hypothesis. Molecular analysis and more detailed paleontologic information are necessary to robustly reject or validate it.

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