

Revision of the *Austrelatus papuensis* group with descriptions of 42 new species from New Guinea (Coleoptera, Dytiscidae, Copelatinae)

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Abstract

The *Austrelatus papuensis* group is the second species group of the New Guinean representatives of the recently described genus *Austrelatus* Shaverdo et al., 2023. The group is mainly defined by distinct scale- and/or spinula-like surface structures of the dorsal sclerite of the median lobe. The species group already contains four described species and 42 new species and one subspecies treated here: *Austrelatus aiyurensis* sp. nov., *A. asteios* sp. nov., *A. bewaniensis* sp. nov., *A. bosaviensis* sp. nov., *A. bundunensis* sp. nov., *A. centralensis* sp. nov., *A. craterensis* sp. nov., *A. decoris* sp. nov., *A. dekai* sp. nov., *A. epicharis* sp. nov., *A. flavocapitatus* sp. nov., *A. fuscus* sp. nov., *A. herzogensis* sp. nov., *A. inconstans* sp. nov., *A. iriatoi* sp. nov., *A. kalibumi* sp. nov., *A. kebarensis* sp. nov., *A. kokodensis* sp. nov., *A. leptos* sp. nov., *A. loloki* sp. nov., *A. lopintolensis* sp. nov., *A. madangensis* sp. nov., *A. maindai* sp. nov., *A. mamberamo* sp. nov., *A. mianminensis* sp. nov., *A. miltokarens* sp. nov., *A. noiadi* sp. nov., *A. normanbyensis* sp. nov., *A. ohu* sp. nov., *A. posmani* sp. nov., *A. procerus* sp. nov., *A. pseudogestroi* sp. nov., *A. pseudomianminensis* sp. nov., *A. robustus* sp. nov., *A. sararti* sp. nov., *A. sumokedi* sp. nov., *A. wanangensis* sp. nov., *A. wasiorensis* sp. nov., *A. wasurensis* sp. nov., *A. weigeli* sp. nov., *A. yamurensis* sp. nov., *A. yeretuar* sp. nov., *A. xanthocephalus nabirensis* ssp. nov. A checklist and identification key to New Guinean species of the group are provided and important diagnostic characters are illustrated. Data on the species distributions and habitat preferences are given.

Key words: Australasia, Dytiscidae, New Guinea, new species, species group, taxonomy



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Introduction

The genus *Austrelatus* Shaverdo et al., 2023 has been recently described for 62 Australasian species, 37 of which are known from New Guinea. The New Guinean *Austrelatus* species include *A. clarki* (Sharp, 1882), *A. fumato* Shaverdo et al., 2023, and *A. setiphallus* Shaverdo et al., 2023 with rather distinct morphology of the male genitalia, as well as 32 species of the *A. neoguineensis* group (Shaverdo et al. 2023). The remained four species of New Guinean *Austrelatus* are *A. luteomaculatus* (Guignot, 1956), *A. gestroi* (Régimbart, 1892), *A. papuensis* (J. Balfour-Browne, 1939), and *A. xanthocephalus* (Régimbart, 1899) that have distinct scale- and/or spinula-like surface structures of the dorsal sclerite of the median lobe. Therefore, they were placed into the *A. papuensis* group introduced by Shaverdo et al. (2023) and defined here in detail. Based on this special character of the male genitalia, the Solomon Islands species *A. baranensis* (Hájek, Shaverdo, Hendrich & Balke, 2021), *A. bougainvillensis* (Hájek, Shaverdo, Hendrich & Balke, 2021), and *A. kietensis* (Hájek, Shaverdo, Hendrich & Balke, 2021) and the Moluccan species *A. sibelaemontis* (Hájek, Hendrich, Hawlitschek & Balke, 2010), *A. ternatensis* (Régimbart, 1899), and *A. wallacei* (J. Balfour-Browne, 1939) are also considered to belong to the *A. papuensis* group (Shaverdo et al. 2023). At present, the *A. papuensis* group is the largest species group of *Austrelatus*, because 42 new species from New Guinea described here also belong to it, which increases its species number to 52.

The present work is aimed to define in detail the *A. papuensis* group, describe its new representatives, and provide a key to their identification as well as information on their distributions and habitats.

Materials and methods

The present work is based on material from the following collections:

- BMNH** The Natural History Museum, London, UK
- CAS** Collection of Anders Skale, Gera, Germany
- CLH** Collection of Lars Hendrich, Munich, Germany (property of NHMW)
- HNHM** Hungarian Natural History Museum, Budapest, Hungary

IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
KSP	Kelompok Serranga Papua Collection, UNCEN, Jayapura, Papua, Indonesia
MNHN	Muséum national d'Histoire naturelle, Paris, France
MTD	Museum für Tierkunde, Dresden, Germany
MZB	Museum Zoologicum Bogoriense, Cibinong, West Java, Indonesia
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
NMPC	Národní muzeum, Prague, Czech Republic
RMNH	Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZSM	SNSB-Zoologische Staatssammlung München, Munich, Germany

All specimen data are quoted as they appear on the labels attached to the specimens. Label text is cited using quotation marks; comments in square brackets are ours, including hw (handwritten). All holotypes and paratypes are provided with corresponding red printed labels. Administrative divisions of Indonesia and Papua New Guinea follow information from Wikipedia (2021a, b, c).

The methods used to study and illustrate morphology follow those of Shaverdo et al. (2023). In female descriptions, as “matt forms” we indicate females with the pronotum and elytra very densely covered with fine longitudinal striae. For most of the species, the median lobe should be dissected to study structure of its ventral sclerite in detail. Terminology of the median lobe sclerites follows that of Shaverdo et al. (2023) where the illustrations (fig. 4 on p. 15 and fig. 5 on p. 16) can be consulted. In the female descriptions, “as male” is with an exclusion of the male characters of the pro- and mesoleg, i.e., protibiae, pro- and mesotarsi, and proclaws are not modified in females. The species descriptions are given in the alphabetic order. Arrangement of the figures follows the species order in the key to simplify use of the key and affinity notes. The morphological illustrations are followed by distributional maps and habitats photos.

The following abbreviations were used in the descriptions: **DBE** – minimum distance between eyes; **PL** – pronotal length (along midline from anterior to posterior margins); **PW** – pronotal width at level of posterior margin; **TL** – total length, measured from front of head to apex of elytra; **TL-H** – total length minus head length, measured from anterior margin of pronotum to apex of elytra; **MW** – maximum width of body measured at right angle to TL.

Results

Austrelatus papuensis group

The group is represented in New Guinea by 46 species (Table 1), 42 of which are new and described below.

The diagnostic characters of the group are mainly those of the median lobe:

- median lobe of aedeagus with dorsal and ventral sclerites not separated medially, pressed together;
- dorsal and ventral sclerites each divided into two lobes in apical half;

- dorsal sclerite more strongly sclerotised than partly membranous ventral one, ventral lobes (especially left one) each with a differently developed lateral sclerotised area;
- apexes of lobes of dorsal and ventral sclerites without strong modification, elongate, more or less pressed together;
- surface of left and right lobes of dorsal sclerite in apical half with numerous scale- and/or spinula-like structures distinctly visible in lateral views;
- elytron with number of striae and degree of their development very variable among species and within one species: (0–11)+(0–1) meaning (dorsal striae)+(submarginal stria); usual patterns 11+1, (10–11)+(0–1), and 6+(0–1).

The other morphological characters of the group representatives are in correspondence with the diagnosis and morphological description of the genus (Shaverdo et al. 2023) that can be supplemented with some general characters of the surface sculpture of the head and pronotum and more detailed description of the ventral surface sculpture, which is similar in all studied New Guinean species:

Table 1. Checklist, body size, number of elytral striae, and distribution of the *Austrelatus papuensis* group species. IN: Indonesia, PNG: Papua New Guinea, EHL: Eastern Highlands, NCD: National Capital District, SHL: Southern Highlands.

	Species	TL, mm	Elytral striae	Distribution
1	<i>A. aiyurensis</i> sp. nov.	6.5–7.6	11+0	PNG: EHL
2	<i>A. asteios</i> sp. nov.	5.7–6.6	11+1	IN: West Papua: Manokwari
3	<i>A. bewaniensis</i> sp. nov.	6.9–7.8	11+1	IN: Papua: Biak Numfor, Sarmi, Jayapura; PNG: Sandaun
4	<i>A. bosaviensis</i> sp. nov.	7.25–8.3	11+1	PNG: SHL
5	<i>A. bundunensis</i> sp. nov.	7.1–7.9	(0–10)+(0–1)	PNG: Morobe
6	<i>A. centralensis</i> sp. nov.	7–8	(6–10)+1	PNG: Central
7	<i>A. craterensis</i> sp. nov.	6.4	11+0	PNG: Simbu
8	<i>A. decoris</i> sp. nov.	5.9	11+1	IN: Papua: Mimika
9	<i>A. dekai</i> sp. nov.	6.45–7.7	(10–11)+(0–1)	IN: Papua: Mimika, Pegunungan Bintang, Yahukimo; PNG: SHL
10	<i>A. epicharis</i> sp. nov.	5.1–6.35	11+1	IN: Papua: Aru Islands, Mimika, Nabire, Yahukimo; West Papua: Kaimana, Raja Ampat; PNG: SHL, Central
11	<i>A. flavocapitatus</i> sp. nov.	5.4–6.1	(10–11)+1	PNG: East Sepik
12	<i>A. fuscus</i> sp. nov.	6.4	10+1	PNG: Central
13	<i>A. gestroi</i> (Régimbart, 1892)	5.8–6.8	(10–11)+1	PNG: Central, Morobe, NCD, ?East New Britain
14	<i>A. herzogensis</i> sp. nov.	5.65–6.7	(10–11)+0	?IN: West Papua: Yapen Islands; PNG: East Sepik, Madang, Morobe
15	<i>A. inconstans</i> sp. nov.	6.7–8.2	(0–10)+(0–1)	IN: Papua: Nabire, Puncak; West Papua: Kaimana, Teluk Wondama
16	<i>A. iriatoi</i> sp. nov.	4.95–5.55	11+1	IN: Papua: Puncak
17	<i>A. kalibumi</i> sp. nov.	6.1–6.7	(10–11)+0	IN: Papua: Nabire
18	<i>A. kebarensis</i> sp. nov.	5.1–5.7	6+1	IN: West Papua: Manokwari
19	<i>A. kokodensis</i> sp. nov.	5.6–5.65	11+(0–1)	PNG: Central
20	<i>A. leptos</i> sp. nov.	4.4–4.5	0+0	PNG: Sandaun
21	<i>A. loloki</i> sp. nov.	5	11+1	PNG: NCD
22	<i>A. lopintolensis</i> sp. nov.	4.7	6+1	IN: West Papua: Raja Ampat (Waigeo)
23	<i>A. luteomaculatus</i> (Guignot, 1956)	5.55–6.6	6+(0–1)	PNG: Gulf, Madang, Morobe
24	<i>A. madangensis</i> sp. nov.	6.8–8.15	(10–11)+1	PNG: EHL, East Sepik, Madang
25	<i>A. maindai</i> sp. nov.	5.4–5.7	11+1	IN: Papua, Sarmi

	Species	TL, mm	Elytral striae	Distribution
26	<i>A. mamberamo</i> sp. nov.	7.5–7.9	11+1	IN: Papua: Mamberamo Raya
27	<i>A. mianminensis</i> sp. nov.	5.6–6.4	11+1	PNG: Sandaun, ?Madang
28	<i>A. miltokarenos</i> sp. nov.	7.3–8.2	(6–11)+1	PNG: Morobe
29	<i>A. noiadi</i> sp. nov.	7.9	11+1	IN: Papua: Mamberamo Raya
30	<i>A. normanbyensis</i> sp. nov.	6.5–7	6+1	PNG: Milne Bay Province (Normanby Island)
31	<i>A. ohu</i> sp. nov.	4.35–5	6+(0–1)	PNG: Madang
32	<i>A. papuensis</i> (Balfour-Browne, 1939)	6.9–7.8	(10–11)+1	PNG: Central, EHL, Morobe
33	<i>A. posmani</i> sp. nov.	7–7.7	11+1	PNG: Central
34	<i>A. procerus</i> sp. nov.	4.5–4.55	(0–6)+0	IN: West Papua: Sorong
35	<i>A. pseudogestroi</i> sp. nov.	6.9	11+1	PNG: NCD
36	<i>A. pseudomianminensis</i> sp. nov.	5.3–5.5	11+1	IN: Papua: Puncak
37	<i>A. robustus</i> sp. nov.	7.45–7.9	11+1	PNG: Central, Madang
38	<i>A. sararti</i> sp. nov.	5.7	11+1	IN: West Papua: Teluk Wondama (Wandammen)
39	<i>A. sumokedi</i> sp. nov.	4.85	11+1	IN: Papua: Mimika
40	<i>A. wanangensis</i> sp. nov.	5.3	11+1	PNG: Madang, Sandaun
41	<i>A. wasiorensis</i> sp. nov.	5.95–6.4	11+1	IN: West Papua: Teluk Wondama (Wandammen)
42	<i>A. wasurensis</i> sp. nov.	5.4–6.3	11+1	IN: Papua: Merauke
43	<i>A. weigeli</i> sp. nov.	6.4–6.6	11+1	PNG: East New Britain
44	<i>A. yamurensis</i> sp. nov.	5.6–5.8	6+0	IN: West Papua: Kaimana
45	<i>A. yeretuar</i> sp. nov.	4.8–5.55	11+1	IN: Papua: Nabire
46	<i>A. xanthocephalus</i> (Régimbart, 1899)	4.7–7.1	6+(0–1)	IN: West Papua: Fak-Fak, Manokwari, Raja Ampat, Sorong, South Manokwari, South Sorong, Tambrauw
46a	<i>A. xanthocephalus nabirensis</i> ssp. nov.	6.1–7.1	(0–6)+0	IN: Papua: Nabire

Head with a row of coarse setiferous punctures along inner margin of each eye and a short row or just a few punctures at frontal angle of each eye; a longer punctural row forms a more or less strongly impressed fronto-clypeal depression at each head side. Pronotum with a row of setiferous punctures along pronotal margins, absent in posterior middle, generally less distinct when striae present; disc of pronotum with distinct or indistinct, short or long longitudinal median scratch.

Ventral side with very fine punctation, almost invisible on metaventricle and metacoxae and more distinct but sparse on abdominal ventrites; abdominal ventrite 6 with distinct punctation, sparse medially and forming denser area at each lateral side; prosternum without microreticulation, smooth medially, with very sparse punctation; metaventricle and metacoxae with distinct microreticulation; on abdominal ventrites microreticulation slightly finer; metacoxal plates with numerous, distinctly impressed, longitudinal striae, abdominal ventrites 1 and 2 with numerous, long, longitudinal striae; on abdominal ventrites 3 and 4 striae turn to middle, sometimes almost horizontal, sparser or absent medially and more distinct laterally; abdominal ventrites 5 and 6 usually without striae, abdominal ventrite 5 sometimes with oblique striae at its anterior margin, abdominal ventrite 6 very seldom with a few small striae at its sides, e.g., for the *A. papuensis* group, it was observed in *A. decoris* sp. nov., *A. inconstans* sp. nov., and *A. procerus* sp. nov.

Species descriptions

1. *Austrelatus aiyurensis* sp. nov.

<https://zoobank.org/EF4E1E21-62E2-4B81-98F0-801AC03DBD1B>

Figs 29, 80, 107

Type locality. PAPUA NEW GUINEA: Eastern Highlands Province, Aiyura, 06°21.131'S, 145°54.398'E, 1670 m a.s.l.

Type material. Holotype: male "3189" [green label], "Papua New Guinea: Eastern Highlands, Aiyura, 1670m, 5.iv.2006, 06.21.131S 145.54.398E, Balke & Sagata (PNG 32)" (ZSM). **Paratypes:** 2 males, 3 females with the same label as the holotype (NHMW, ZSM). 2 males "Papua New Guinea: Eastern Highlands, Aiyura creek, 1670m, 20.iv.2006, 06.21.131S 145.54.398E, John & Balke (PNG 70)" (ZSM).

Description. Body size and form: Beetle large, oblong-oval to elongate (Fig. 29).

Measurements: TL 6.5–7.6 mm, TL-H 5.9–6.95 mm, MW 2.9–3.6 mm, TL/MW 2.11–2.24; PL 0.9–1.1 mm, PW 2.6–3.05 mm, PL/PW 0.35–0.36; DBE 1.15–1.3 mm, DBE/PW 0.43–0.44. **Holotype:** TL 7.6 mm, TL-H 6.95 mm, MW 3.6 mm, TL/MW 2.11; PL 1.1 mm, PW 3.05 mm, PL/PW 0.36; DBE 1.3 mm, DBE/PW 0.43.

Colouration: Dorsally piceous, usually with yellowish red head, pronotal sides and at elytral apex between striae (Fig. 29).

Head yellowish red to brown, narrowly darker behind eyes. Pronotum brown to piceous on disc and reddish to yellowish red on sides, especially at anterior angles; in teneral species, gradually paler (to yellowish red) to sides. Elytron brown to piceous, without basal band, sometimes with small, faint, reddish spot at shoulder, but broadly yellow between striae in apical 1/2, sometimes even to shoulder spot laterally, and reddish along suture. Scutellum reddish to brown. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side brown, yellowish red to reddish on head, prosternum, lower margin of metacoxae and medially and laterally on abdominal ventrites 1–4. **Note:** the holotype is a sequenced specimen; such specimens are usually darker.

Surface sculpture: Elytron with 11 complete striae, submarginal stria absent: 11+0 (Fig. 29).

Head usually without or with single striae between eyes, with more or less regular, dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (usually diameter of punctures equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with numerous striae, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae; submarginal stria absent. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum narrowly rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws long, subequal in length. Median lobe of aedeagus robust, with two lobes of dorsal sclerite subequal in length, with pointed apices and covered with scale-like structures; left dorsal lobe distinctly concave subapically, with long, narrow apical crest and apex

slightly thickened at its tip, also with lateral side concave medially, above this concavity with small convex area covered with spinula-like structures; right dorsal lobe with large, elongate membranous area medially; lobes of ventral sclerite pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe with relatively broad, elongate sclerotised area, with pointed apex, situated in left part of lobe and mostly visible in left lateral view; membranous right part of left ventral lobe conjoined with sclerotised area and has apical tuft of long setae; right ventral lobe membranous, long and relatively broad. Parameres with dense, long setae occupying slightly more than half of dorsal margin (Fig. 80).

Female: Some females with more numerous striae on head and pronotum than in males.

Variability. There is a variation in body shape, dorsal colouration and striation described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures, e.g., *A. centralensis* sp. nov. and *A. normanbyensis* sp. nov. However, it is well-recognisable by its elytral colouration without basal band, 11+0 elytral striation, relatively narrow body shape, and median lobe with left dorsal lobe distinctly concave subapically and having convex area with spinula-like structures medially.

Etymology. The species is named after Aiyura creek. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Eastern Highlands Province. The species is known only from the type locality (Fig. 107).

Habitat. The species was collected in rest pools of a temporary stream.

2. *Austrelatus asteios* sp. nov.

<https://zoobank.org/D024C45D-C054-4087-B4FD-C97B7CF02FEF>

Figs 57, 105, 108

Type locality. INDONESIA: West Papua Province: Manokwari Regency, Kebar, 0°48'27.9"S, 133°03'33.3"E, 584 m a.s.l.

Type material. Holotype: male "Indonesia: Papua Barat, Kebar, shaded deep sandy irrigation roadside ditches, 584m, 6.xi.2013," "-0.80775253 133.05923529, UNIPA Team (BH031)" (MZB). **Paratypes:** 102 males, 78 females with the same label as the holotype, one male with an additional green text label "6249" (MZB, NHMW, ZSM). 1 male, 1 female "Indonesia: Papua Barat, Kebar Valley, 596m, 6.v.2015, -0,8406 133,2682, UNIPA Team (BH059)" (ZSM). 1 female "IN: West Papua: Manokwari Reg., on road Manokwari-Kebar, near Munbrani vill., ca. 600 m, 8.V., 00°46'21"S 133°22'53"E, roadside ditch (2015-WP36)" (NHMW). 5 males, 4 females "Indonesia: Papua, Manokwari, 140m, 8.ii.2006, 00.55.752S 133.54.448E, UNIPA Team (BH 09)", one male with an additional green label "4248" (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 57).

Measurements: TL 5.7–6.6 mm, TL-H 5.1–5.95 mm, MW 2.7–3.2 mm, TL/MW 2.06–2.12; PL 0.8–0.95 mm, PW 2.3–2.7 mm, PL/PW 0.35–0.36; DBE 0.85–1 mm, DBE/PW 0.37–0.38. **Holotype:** TL 6.15 mm, TL-H 5.55 mm, MW 2.9 mm, TL/MW 2.12; PL 0.9 mm, PW 2.5 mm, PL/PW 0.36; DBE 0.95 mm, DBE/PW 0.38.

Colouration: With piceous elytra and pronotum, yellowish red head, pronotal sides, and elytral basal band and yellowish between striae laterally (Fig. 57).

Head yellowish red medially, narrowly piceous behind eyes and brownish anteriorly. Pronotum piceous on disc and broadly yellowish red on sides, especially at anterior angles. Elytron piceous, with rather broad yellowish red basal band, usually extending between striae, especially laterally and yellowish between striae laterally and sometimes additionally apically, seldom whole elytron slightly yellowish, with distinct basal band. Scutellum reddish to piceous. Antennae, other head appendages, and pro- and mesolegs yellow, metalegs slightly darker proximally and distinctly distally. Ventral side yellowish red, darker on metaventrite, metacoxal plates and two last abdominal ventrites.

Surface sculpture: Elytron with 11 complete dorsal striae, submarginal stria present, long: 11+1 (Fig. 57).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures usually equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with numerous, sparse striae on lateral parts, only middle of disc without striae, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae, striae 1 and 2, seldom 1–3, less strongly impressed dorsally; submarginal stria present, long, often reaching ½ of elytral length. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, strongly convex medially; blade of prosternal process narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, subequal in length. Median lobe of aedeagus rather robust, apically thick, with two lobes of dorsal sclerite with broadly pointed apices, more or less straight and subequal in length; left dorsal lobe with lateral margin not beaded, rather strongly concave at its apical 1/4; lateral side of left dorsal lobe completely covered with tiny spinulae situated in groups on scale-like structures; right dorsal lobe covered with large scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, slightly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with curved apex and slightly sclerotised part distinctly shorter, with dense setae apically; right ventral lobe longer than left one, partly sclerotised, with apex curved left and covered with setae sometimes distinctly sticking out in left lateral view. Parameres with dense, relatively long setae occupying slightly more than half of dorsal margin (Fig. 105).

Female: As males.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body shape and size and general shape of the median lobe, it is similar and probably closely related to *A. epicharis* sp. nov. but differs from it in paler elytral colouration, more robust median lobe, and left dorsal lobe of the median lobe with apex thicker and lateral margin more strongly concave apically and therefore ventral lobes more visible in left lateral view. See also under *A. yeretuar* sp. nov.

Etymology. The species name is a Greek adjective meaning “nice, pretty” and refers to the nice yellowish red dorsal pattern of the species.

Distribution. Indonesia: West Papua Province: Manokwari Regency (Fig. 108).

Habitat. The species was collected in shaded, deep, sandy irrigation roadside ditches.

3. *Austrelatus bewaniensis* sp. nov.

<https://zoobank.org/7D8151FC-9022-4367-89A1-B72A6096CFA5>

Figs 36, 86, 108

Type locality. PAPUA NEW GUINEA: Sandaun Province, Bewani Mts, 03°05.130'S, 141°10.227'E, 200–300 m a.s.l.

Type material. Holotype: male “Papua New Guinea: Sandaun, Bewani Stn., stream@base of Bewani Mts., 200–300m, 12.iv.2006, nr. 03.05.130S 141.10.227E, Balke & Sagata (PNG 37)” (MZB). **Paratypes: PNG: Sandaun:** 4 males, 2 females with the same labels as the holotype (MZB, NHMW, ZSM). 2 females “Papua New Guinea: Sandaun, Bewani Stn., forest puddles @ base of Bewani Mts., 300 m, 12.iv.2006, nr. 03.05.130S 141.10.227E, Balke & Sagata (PNG 38)”, one with an additional green label “3215” (ZSM). **IN: Papua: Jayapura Regency:** 1 male “Dutch New Guinea: Humbolt Bay [Yos Sudarso Bay] Dist. Pukusam Dist. West of Tami River. Vi.1937.” (BMNH). **Sarmi Regency:** 1 male, 1 female “Indonesia: Papua, Sarmi, Waaf, N Foja Mts, waterfall in forest, 120m, 23.ix.2014, -2,3317 138,7500, Tim UNCEN: Balke & Menufandu (Pap031)”, male with “6465” [green text] (ZSM). 2 males, 4 females “Indonesia: Papua, Foja Mountains N foot, N Waaf vill., pondok, 150m, 4.-7.vi.2016,” “-2.06142 138.743949, Sumoked (Pap061)” (NHMW, ZSM). **Biak Numfor Regency:** 1 male “Indonesia: Papua, Biak, Nimbotong Nimbokramp, 110m 21.iv.2006, Tindige leg.”, “3157” [green label] (ZSM). 1 male “Indonesia: Papua, Biak, Nimbotong Nimbokramp, 110m 21.iv.2006, Tindige”, “1325” [green label] (ZSM). 3 males, 4 females “Indonesia: Papua, Biak, Nimbotong Nimbokramp, 110m 21.iv.2006, Tindige” (NHMW, ZSM).

Additional material. IN: Papua: Pegunungan Bintang Regency: 1 male “Indonesia: Papua, Dekai, upper Brazza, 273m, 2./3.vi.2015, -4,741084724 139,654211075976, Sumoked (Pap044)” (ZSM). **Note:** a teneral specimen.

Description. Body size and form: Beetle large, oblong-oval (Fig. 36).

Measurements: TL 6.9–7.8 mm, TL-H 6.35–7.1 mm, MW 3.25–3.6 mm, TL/MW 2.12–2.23; PL 0.95–1.15 mm, PW 2.85–3.2 mm, PL/PW 0.33–0.37; DBE 1.2–1.3 mm, DBE/PW 0.4–0.42. **Holotype:** TL 7.5 mm, TL-H 6.8 mm, MW 3.4 mm, TL/MW 2.21; PL 1.15 mm, PW 3.1 mm, PL/PW 0.37; DBE 1.3 mm, DBE/PW 0.42.

Colouration: Dorsally piceous, with yellowish red to reddish head, pronotal sides, and elytron with narrow, often faint yellowish red to reddish basal band and yellow apex (Fig. 36).

Head yellowish red to reddish, narrowly darker behind eyes. Pronotum piceous on disc and gradually paler (to yellowish red) to sides. Elytron piceous, with narrow yellowish red to reddish basal band, sometimes broadened between striae making base of elytron yellowish red or sometimes basal band faint, very narrow or even absent; elytral apex broadly or narrowly yellowish

red, seldom broadened between striae making elytron yellowish red laterally or even in apical 1/2, striae brown to piceous. Scutellum yellowish red to brown. Antennae, other head appendages, and pro- and mesolegs yellowish red to reddish, metalegs darker, all legs darker distally. Ventral side reddish brown, paler on prosternum.

Surface sculpture: Elytron with 11 dorsal striae, stria 1 shortly reduced basally, submarginal stria present: 11+1 (Fig. 36).

Head without strioles, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with few to several strioles posterolaterally, more numerous in females, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae: stria 1 shortly reduced basally, seldom striae 1–3 reduced basally; submarginal stria present. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia more or less straight: its ventral margin slightly curved proximally. Proclaws long, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe without distinct median concavity and its whole apical 1/2 broad, more or less evenly tapering to small, curved downwards, slightly truncate apex bearing crest; scale-like structures of left dorsal lobe large in its apical 1/2; right dorsal lobe shorter than left one, broad, with pointed apex and membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, not visible in left lateral view due to broad, not concave left dorsal lobe; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying slightly more than half of dorsal margin (Fig. 86).

Female: Trimorphic: 1) as male but with much more numerous pronotal strioles, 2) matt, with pronotum and elytron very densely covered with fine longitudinal strioles, and 3) less matt with strioles partly absent on pronotal and elytral discs, sometimes completely absent on elytron, but with strong dorsal punctation and microreticulation, especially on elytron.

Variability. There is a variation in dorsal colouration and striolation as described above. The male from Dekai (see Additional material) is teneral but most likely belongs to *A. bewaniensis* sp. nov. It is not *A. dekai* sp. nov. according to shape of the male proclaws and median lobe though the latter is difficult clearly to interpret due to weak sclerotisation. However, the specimen differs from all other specimens of *A. bewaniensis* sp. nov. in reduced elytral striation: dorsal stria 1 almost completely reduced, present only as single striole in apical 1/2, striae 3, 5, 7, 9 absent in basal 1/2 and present in apical one as striae or strioles. More material from the area is necessary to clarify specimen affiliation and range of elytral striation variability of the species.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is distinguished by rather dark dorsal colouration and 11+1 elytral striation, and, especially, left dorsal lobe of the median lobe without median concavity and its apical 1/2 covered with large scale-like structures, very broad, evenly tapering to small, curved downwards, slightly truncate apex bearing crest.

Etymology. The species is named after Bewani Mountains. The name is an adjective in the nominative singular.

Distribution. Indonesia: Papua Province and Papua New Guinea: Sandaun Province (Fig. 108).

Habitat. The species was collected in the different forest water bodies: a stream, puddles, and near a waterfall.

4. *Austrelatus bosaviensis* sp. nov.

<https://zoobank.org/66A2C27D-5AE8-434A-8F22-5CC9FD46A9F0>

Figs 31, 82, 107

Type locality. PAPUA NEW GUINEA: Southern Highlands Province, Bosavi Mt, 06°28'S, 142°50'E, 700 m a.s.l.

Type material. Holotype: male "Collection Naturhistorisches Museum Basel", "Papua New Guinea S. Highlands Prov. L.Cizek lgt.", "Mt Bosavi, 700m 142°50'E 6°28'S 20–27.VI.1999" (NHMB). **Paratypes:** 18 males, 16 females with the same labels as the holotype (NHMB, NHMW, ZSM).

Description. Body size and form: Beetle large, oblong-oval (Fig. 31).

Measurements: TL 7.25–8.3 mm, TL-H 6.65–7.5 mm, MW 3.5–4.1 mm, TL/MW 2.02–2.07; PL 1.05–1.3 mm, PW 3.05–3.6 mm, PL/PW 0.34–0.36; DBE 1.2–1.4 mm, DBE/PW 0.39. **Holotype:** TL 8.2 mm, TL-H 7.4 mm, MW 3.95 mm, TL/MW 2.08; PL 1.25 mm, PW 3.45 mm, PL/PW 0.36; DBE 1.35 mm, DBE/PW 0.39.

Colouration: Dorsally piceous, with reddish head, pronotal sides and elytral basal band (Fig. 31).

Head dark yellowish red to reddish, narrowly darker behind eyes. Pronotum dark brown to piceous on disc and sometimes gradually paler (to dark yellowish red) to sides or sides broadly reddish, in contrast to piceous disc. Elytron dark brown to piceous, with narrow, dark yellowish red to reddish basal band differently developed: short, present in shoulder area, faint or distinct at whole base length. Scutellum reddish brown to piceous. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs darker, all legs darker distally. Ventral side reddish brown, darker on posterior margins of abdominal ventrites 1–5 and on abdominal ventrite 6.

Surface sculpture: Elytron with 11 complete striae, submarginal stria present: 11+1 (Fig. 31).

Head without strioles, with dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (usually diameter of punctures larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with strioles posterolaterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 shortly or distinctly reduced basally, sometimes absent in basal 1/2; submarginal stria present. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia slightly modified: its ventral margin slightly curved proximally. Proclaws long and straight, subequal in length, anterior claw medially thicker than posterior one and due to this with a shallow subproximal incision on its inner margin. Median lobe of aedeagus very robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe very strongly concave medially, with apical 1/2 very broad and apex slightly rounded and bearing small but rather distinct crest; right dorsal lobe shorter, narrower, more or less evenly tapering to pointed apex, with small membranous area medially; lobes of ventral sclerite mostly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 (visible in left lateral view) and long, thread-like apical 1/2 (not visible); less sclerotised right part long and broad, with its apical part densely covered with long setae (partly visible in left lateral view); right ventral lobe mostly sclerotised, long and broad (partly visible in left lateral view). Parameres with dense, long setae occupying slightly more than half of dorsal margin (Fig. 82).

Female: As male.

Variability. There is an insignificant variation in dorsal colouration described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is very similar to *A. robustus* sp. nov. and differs from it in narrower, straighter male anterior claw with inner margin incision situated more proximally and distinctly broader apical 1/2 of the left dorsal lobe of the median lobe. See also under *A. robustus* sp. nov.

Etymology. The species is named after Bosavi Mountain. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Southern Highlands Province, Bosavi Mt area (Fig. 107).

Habitat. Unknown.

5. *Austrelatus bundunensis* sp. nov.

<https://zoobank.org/5E16A2A5-B1ED-44FF-A81F-306748A53480>

Figs 11, 12, 64, 107

Type locality. PAPUA NEW GUINEA: Morobe Province, Herzog Mts, Bundun, 06°51.598'S, 146°37.07'E, 700–800 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Morobe, Herzog Mts., Bundun, 700–800m, 2.iv.2006, 06.51.598S 146.37.07E, Balke & Sagata (PNG 27)" (ZSM). **Paratypes:** 16 males, 10 females with the same label as the holotype, three males additionally with green labels "3198", "3199", and "3228" (NHMW, ZSM). 1 male "3237" [green label], "Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 250m, 31.iii.2006, 06.30.270S 146.59.581E, Balke & Sagata (PNG 24)" (ZSM). 1 female "3208" [green label], "Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 460m, 31.iii.2006, 06.32.736S 146.59.616E, Balke & Sagata (PNG 26)" (ZSM).

Description. Body size and form: Beetle large, with oblong-oval habitus (Figs 11, 12).

Measurements: TL 7.1–7.9 mm, TL-H 6.5–7.1 mm, MW 3.4–3.7 mm, TL/MW 2.08–2.14; PL 1–1.15 mm, PW 2.9–3.25 mm, PL/PW 0.34–0.35; DBE 1.2–1.3 mm, DBE/PW 0.4–0.41. **Holotype:** TL 7.7 mm, TL-H 7 mm, MW 3.7 mm, TL/MW 2.08; PL 1.1 mm, PW 3.2 mm, PL/PW 0.34; DBE 1.3 mm, DBE/PW 0.41.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and basal band on elytron (Figs 11, 12).

Head yellow to yellowish red, narrowly dark brown behind eyes. Pronotum dark brown to piceous on disc and gradually paler (to yellow) on sides. Elytron dark brown to piceous, with narrow yellow to yellowish red basal band, sometimes with yellowish red apex, seldom yellowish red line along suture too. Scutellum yellowish red to brown. Antennae, other head appendages, and pro- and mesolegs yellow to yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown.

Surface sculpture: Dorsal elytral striation very variable, submarginal stria usually absent or present as a short stria or few short striae apically: (0–10)+(0–1) (Figs 11, 12).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with striae laterally, with punctation and microreticulation slightly finer than on head. Elytron with striation very variable: from without striae, with three puncture lines, with up to ten dorsal striae (as in holotype), of which striae 3, 5–10 usually complete, striae 1 and 2 always strongly reduced basally; submarginal stria usually absent or present as a short stria or few short striae apically. Elytron with punctation distinctly finer than on pronotum and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum narrowly rounded anteriorly, distinctly convex medially; blade of prosternal process relatively broad.

Male: Protibia more or less straight, not modified. Proclaws long, slightly curved, subequal in size and form. Median lobe of aedeagus robust, with two lobes of dorsal sclerite unequal in length and shape, both covered with scale-like structures; left dorsal lobe broader apically and shorter than right dorsal lobe, with a distinct median concavity and its whole apical 1/2 narrowed, its proximal part very large, and its apex more or less straight, with a distinct crest; right dorsal lobe with apex pointed and membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area (visible as a triangular in left lateral view) and less sclerotised right part (visible in left lateral view); sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe long and broad. Parameres with dense, long setae occupying slightly more than half of dorsal margin (Fig. 64).

Female: Probably dimorphic: all females from the type locality (PNG27) are matt. The only female without this dense striolation is from the locality PNG26, where it was the only specimen collected. It is characterised by the reduced

elytral striae (3 more or less complete dorsal striae, with some striae between them) and presence of numerous striae on the pronotal sides.

Variability. The species is very variable in the elytral striation, as described above, within and among populations. The holotype is with 10+1 elytral striae. Most specimens from the type locality (PNG27) have such striation but some of them have stria reduction, one specimen up to 5 dorsal striae. Only male from the locality PNG24 is without elytral striae. The female from the locality PNG26 is 3 more or less complete dorsal striae, with some striae between them.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. inconstans* sp. nov. in size, body form, and dorsal colouration, but distinctly differs from it in shape of the median lobe and simple male proclaws. Also, the species is very similar to *A. miltokarenos* sp. nov. in median lobe shape but has some differences: apex of left dorsal lobe straighter, with stronger apical crest (in left lateral view) and right dorsal lobe with longer, more curved apex and ventral opening broader (in right lateral view). Additionally, *A. bundunensis* sp. nov. distinctly differs from *A. miltokarenos* sp. nov. by presence of a yellowish red basal band on elytron and its smaller, more oval body.

Etymology. The species is named after its type locality, Bundun. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Morobe Province, Herzog Mts (Fig. 107).

Habitat. The species was collected in small forest pools.

6. *Austrelatus centralensis* sp. nov.

<https://zoobank.org/0083CB16-F998-465B-AB5D-F16D690BAC5F>

Figs 20, 71, 107

Type locality. PAPUA NEW GUINEA: Central Province, 09°25'47.5"S, 147°32'59.1"E, 755 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Central, 755 m 28.x.2009, S9 25 47.5 E147 32 59.1, Sagata (PNG229)" (ZSM). **Paratypes: PNG: Central:** 10 males, 6 females with the same label as holotype (NHMW, ZSM). 1 male, 4 females "Papua New Guinea: Central, Moroka area, Kailaki Wareaga ridge, 768 m, 27.x.2009, S9 25 42.4 E147 31 06.8, Sagata (PNG227)" (ZSM). 2 males "Papua New Guinea: Central, Moreguina [10°00'57"S, 148°28'27"E] 16.viii.2008 Posman (PNG183) (ZSM). 1 male "Papua New Guinea: Central, Moreguina 18.viii.2008 Posman (PNG184)" (ZSM). 1 male, 1 female "Papua New Guinea: Central, Kokoda Trek, 320m, i.2008, [09°]19.236S 147 31.791E, Posman, (PNG 168)" (ZSM). 2 females "Papua New Guinea: Central, Kokoda Trek, 980m, i.2008, [09°]15.933S 147 36.590E, Posman, (PNG 169)" (ZSM). **NCD:** 2 males "Papua New Guinea: National Capital District, Varirata NP, 600m, 16.xii.2007, 09.26.13S 147.22.09E, Balke & Sagata (PNG 159)", one male with an additional green label "2847" (ZSM).

Description. Body size and form: Beetle large, with oblong-oval habitus (Fig. 20).

Measurements: TL 7–8 mm, TL-H 6.3–7.2 mm, MW 3.3–3.8 mm, TL/MW 2.11–2.12; PL 1–1.2 mm, PW 2.9–3.4 mm, PL/PW 0.35–0.36; DBE 1.15–1.35 mm, DBE/PW 0.4. **Holotype:** TL 7.6 mm, TL-H 6.8 mm, MW 3.6 mm, TL/MW 2.11; PL 1.1 mm, PW 3.1 mm, PL/PW 0.36; DBE 1.25 mm, DBE/PW 0.4.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and basal band on elytron (Fig. 20).

Head yellowish red to red, narrowly piceous behind eyes. Pronotum piceous on disc and gradually paler (to yellowish red) on sides, especially at anterior angles. Elytron piceous, with yellowish red to red basal band, which can be distinct or faint, narrower or broader, especially between striae, sometimes due to this elytron reddish laterally; often with yellowish brown apex. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown medially and yellowish red on pro- and metaventrite and abdominal ventrites.

Surface sculpture: Dorsal elytral striation variable, usually with six dorsal striae and stria 1 reduced in basal 1/2, submarginal stria present: (6–10)+1 (Fig. 20).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with striae laterally (few at posterolateral angles to rather numerous but sparse on sides), with punctation slightly denser and finer than on head and microreticulation fine. Elytron usually with six dorsal striae and some striae between them, sometimes developed into complete and/or partly complete striae: up to ten dorsal striae; stria 1 always absent in basal 1/2; submarginal stria present, sometimes reduced to short apical striae. Elytron with very fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum broadly rounded anteriorly, distinctly convex medially; blade of prosternal process relatively narrow.

Male: Protibia more or less straight, not modified; its ventral margin can be slightly curved proximally. Proclaws relatively short, subequal in length, anterior claw slightly thicker and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite distinctly narrowed to pointed apices and covered with scale-like structures; left dorsal lobe longer than right lobe, slightly concave subapically and medially, with apex slightly curved downwards; right dorsal lobe with small membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area (not visible in left lateral view) and less sclerotised right part (visible in left lateral view); sclerotised area with elongate and broad basal 1/2 and long, hair-like apical 1/2; less sclerotised right part long and broad, with its apical part with a tuft of long setae; right ventral lobe long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin; more distally situated setae longer than more proximal ones (Fig. 71).

Female: As male.

Variability. There is a variation in the elytral striation and colouration described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. inconstans* sp. nov. and *A. bundunensis* sp. nov. in size, body form, and dorsal colouration, but distinctly differs from them in median lobe with dorsal sclerite lobes distinctly narrowed to pointed apex and elytral striae always present.

Etymology. The species is named after Central Province. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Central Province (Fig. 107).

Habitat. Unknown.

7. *Austrelatus craterensis* sp. nov.

<https://zoobank.org/3AC4CFFC-3749-4CA1-B01D-E0DD4431E6F0>

Figs 28, 79, 107

Type locality. PAPUA NEW GUINEA: Simbu Province, Crater Mts, ca. 06°34'53.5"S, 145°05'26.7"E.

Type material. Holotype: male "386" [green label], "PNG: Crater Mts ii.2003, Sagata, MB 386" (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 28).

Measurements: Holotype: TL 6.4 mm, TL-H 5.75 mm, MW 3.1 mm, TL/MW 2.07; PL 1 mm, PW 2.8 mm, PL/PW 0.36; DBE 1.2 mm, DBE/PW 0.43.

Colouration: Dorsally yellowish-reddish brown, with darker head and pronotum (Fig. 28).

Head brown, gradually paler (to reddish) anteriorly, narrowly darker behind eyes. Pronotum dark brown on disc and gradually paler (to reddish) to sides. Elytron uneven yellowish-reddish brown due to strongly developed yellowish red colouration between striae. Scutellum brown. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs darker, all legs darker distally. Ventral side brown.

Surface sculpture: Elytron with 11 complete striae, submarginal stria absent: 11+0 (Fig. 28).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with striae on sides, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae, stria 1 shortly reduced basally; submarginal stria absent. Elytron with fine, relatively dense punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws long, slightly curved, subequal in length. Median lobe of aedeagus robust, with two lobes of dorsal sclerite unequal in length and shape, both covered with scale-like structures; left dorsal lobe more or less evenly tapering to apex, its apex straight, with small but distinct incision and crest; right dorsal lobe with apex pointed and membranous area medially; lobes of ventral sclerite, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view, with sclerotised areas (since there is only the holotype, we could not dissect the median lobe to study structure of the ventral sclerite lobes in detail). Parameres with dense, long setae occupying distinctly more than half of dorsal margin (Fig. 79).

Female: Unknown.

Affinities. The species is well distinguishable by its uniform, yellowish-red-dish brown elytral colouration, 11+0 elytral striation and smaller body size from species with similar structures of the median lobe: usually, these species have TL > 6.5 mm, e.g., *A. inconstans* sp. nov.; additionally, the left dorsal lobe of the median lobe of *A. craterensis* sp. nov. has a very characteristic apex with small but distinct incision and crest.

Etymology. The species is named after Crater Mountains. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Simbu Province. The species is known only from the type locality (Fig. 107).

Habitat. Unknown.

8. *Austrelatus decoris* sp. nov.

<https://zoobank.org/52BB9A5B-7448-40A1-8784-FCA429991CC4>

Figs 27, 78, 107

Type locality. INDONESIA: Papua Province: Mimika Regency, 04°15'07.3"S, 136°38'36.2"E, 149 m a.s.l.

Type material. Holotype: male "7889" [green text], "Indonesia: Papua, Kabupaten Mimika, Timika, 149m, 25–30.v.2017,", "-4.252020° 136.643384°, B. Sumoked (Pap68-Bob06)" (MZB).

Description. Body size and form: Beetle medium-sized, elongate (Fig. 27).

Measurements: Holotype: TL 5.9 mm, TL-H 5.3 mm, MW 2.72 mm, TL/MW 2.17; PL 0.95 mm, PW 2.4 mm, PL/PW 0.4; DBE 1.05 mm, DBE/PW 0.53.

Colouration: Dorsally dark brown, with paler head, pronotal sides and elytral base and apex (Fig. 27).

Head reddish, narrowly piceous behind eyes and darker posteromedially. Pronotum dark brown on disc and gradually paler (reddish) on sides. Elytron dark brown, reddish basally, laterally and apically, also with faint reddish colouration between striae so that elytron not looking uniformly dark brown. Scutellum reddish brown. Antennae, other head appendages, and legs reddish, darker distally. Ventral side brown.

Surface sculpture: Elytron with 11 complete, relatively strongly impressed striae, submarginal stria present: 11+1 (Fig. 27).

Head without strioles, with distinct, dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (diameter of punctures slightly larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without strioles, with punctation finer than on head and fine microreticulation. Elytron with 11 complete, relatively strongly impressed striae, submarginal stria present. Elytron with fine punctation and distinct microreticulation. Abdominal ventrite 6 with distinct punctation, sparse medially and forming denser area at each lateral side and with some strioles medially of this area.

Structures: Head large and broad. Pronotum relatively long, its lateral margins rounded, very slightly convergent anteriorly. Base of pronotum slightly narrower than base of elytron, therefore, habitus outline discontinuous. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia slightly modified; its ventral margin curved proximally. Proclaws relatively long, subequal in length, anterior claw slightly thicker and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite unequal in length, covered with scale-like structures; left dorsal lobe with lateral margin slightly concave medially, with apex truncate and slightly curved downwards, having distinct crest; right dorsal lobe broad, shorter than left lobe, with pointed apex and membranous area medially; lobes of ventral sclerite mostly sclerotised, pressed together between lobes of dorsal sclerite, almost invisible in lateral view: tip of setation of less membranous part of left ventral lobe distinctly sticking out (since there is only the holotype, we could not dissect the median lobe to study structure of the ventral sclerite lobes in detail, see e.g., *A. inconstans* sp. nov.). Parameres with long and dense setae occupying approximately half of dorsal margin; more distally situated setae longer than more proximal ones (Fig. 78).

Female: Unknown.

Affinities. The species is well-recognisable by its elongate, slightly discontinuous habitus, almost uniformly reddish brown dorsal colouration, strong elytral striation, and characteristic shape of the median lobe.

Etymology. The species name is a Latin adjective meaning elegant and refers its elongate, slightly discontinuous habitus, with rounded pronotal sides.

Distribution. Indonesia: Papua Province: Mimika Regency. The species is known only from the type locality (Fig. 107).

Habitat. Unknown.

9. *Austrelatus dekai* sp. nov.

<https://zoobank.org/1DE615B8-46C6-4985-929B-4DF5AD73B16D>

Figs 32, 83, 107

Type locality. INDONESIA: Papua Province: Yahukimo Regency, Dekai, upper Brazza, 04°44'27.9"S, 139°39'15.2"E, 273 m a.s.l.

Type material. Holotype: male "Indonesia: Papua, Dekai, upper Brazza, 273m, 2./3.vi.2015, -4,741084724 139,654211075976, Sumoked (Pap044)" (MZB). **Paratypes: IN: Papua: Yahukimo Regency:** 11 males, 13 females with the same label as the holotype, 2 males and 2 females with additional green text labels "7214", "7215", "7216" and "7217", respectively (MZB, NHMW, ZSM). **Pegunungan Bintang Regency:** 4 males, 4 females "Indonesia: Papua, S Ok Sibil, tributary of Digul Riv, 359m, 9.vi.2015, -5,05718389526009 140,722535848617, Sumoked (Pap051)" (MZB, NHMW, ZSM). **Mimika Regency:** 1 male "Indonesia: Papua, Kabupaten Mimika, Timika, 149m, 25–30.v.2017, 04°15.092'S 136°38.597'E, B. Sumoked (Pap68-Bob06)" (ZSM). 1 male, 1 female "Indonesia: Papua, Kabupaten Mimika, Timika, 149m, 25–30.v.2017," "4.252020° 136.643384°, B.Sumoked (Pap68-Bob06)", with additional green text labels "7887" and "7888", respectively (ZSM). **PNG: SHL:** 1 male, 1 female "Collection Naturhistorisches Museum Basel", "Papua New Guinea S. Highlands Prov. L. Cizek lgt.", "Mt Bosavi, 700m 142°50'E 6°28'S 20–27.VI.1999" (NHMB).

Additional material. 7 males "New Guinea XII-1942 W.G.Bodenstein" (ZSM). Note: teneral specimens.

Description. Body size and form: Beetle large, oblong-oval (Fig. 32).

Measurements: TL 6.45–7.7 mm, TL-H 5.8–6.95 mm, MW 3.1–3.7 mm, TL/MW 2–2.08; PL 1–1.2 mm, PW 2.8–3.4 mm, PL/PW 0.35–0.36; DBE 1.15–1.35 mm, DBE/PW 0.39–0.41. **Holotype:** TL 7.2 mm, TL-H 6.5 mm, MW 3.6 mm, TL/MW 2; PL 1.15 mm, PW 3.2 mm, PL/PW 0.36; DBE 1.25 mm, DBE/PW 0.39.

Colouration: Dorsally piceous, with yellowish red to reddish head, pronotal sides and usually elytral basal band (Fig. 32).

Head yellowish red to reddish, narrowly darker behind eyes. Pronotum dark brown to piceous on disc and gradually paler (to yellowish red) to sides. Elytron brown to piceous, without basal band or with narrow, yellowish red to reddish basal band, often short, present in shoulder area, faint. Scutellum brown. Antennae, other head appendages, and pro- and mesolegs yellowish red to reddish, metalegs darker, all legs darker distally. Ventral side reddish brown.

Surface sculpture: Elytron with 10 or 11 differently reduced striae, submarginal stria present or absent: (10–11)+(0–1) (Fig. 32).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum without striae, with punctation finer than on head and microreticulation fine. Elytron with 10 or 11 differently reduced dorsal striae: stria 1 usually completely reduced, sometimes more or less complete or present as striae in apical 1/2, striae 2 and 3 usually reduced basally, striae 5, 7, and 10 usually interrupted in basal 1/2; submarginal stria absent or present, seldom as complete stria, usually as apical striae. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process broad, weakly convex.

Male: Protibia slightly modified: its ventral margin slightly curved proximally. Proclaws long and straight, subequal in length, anterior claw thicker medially than posterior one. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe distinctly broader and longer than right dorsal lobe; left dorsal lobe with a distinct median concavity and its whole apical 1/2 narrowed, its apex straight, without distinct crest, sometimes with a weak crest due to small, very shallow tip concavity, more or less evenly rounded; right dorsal lobe with apex pointed and membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but visible in left lateral view; left ventral lobe consists of two parts (partly visible in left lateral view): left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe partly sclerotised, long and broad, curved at apex. Parameres with long and dense setae occupying approximately half of dorsal margin; more distally situated setae longer and denser than more proximal ones (Fig. 83).

Female: Dimorphic: as male, shiny, and matt, with pronotum and elytron very densely covered with fine longitudinal striae. Matt forms present in two populations, more numerous than shiny ones: e.g., ratio shiny to with striae is 11:2 in the type locality. Only matt forms are known from the locality "Pap051".

Variability. There is a variation in dorsal colouration and striolation described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. inconstans* sp. nov., *A. bundunensis* sp. nov. and *A. miltokarenos* sp. nov. but differs from them in smaller body size, male anterior proclaw long, straight but thicker medially than posterior one and narrower apical 1/2 of the left dorsal lobe of the median lobe.

Etymology. The species is named after its type locality, Dekai Village. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province and Papua New Guinea: Southern Highlands Province (Fig. 107).

Habitat. The species was collected side pools of a forest stream.

10. *Austrelatus epicharis* sp. nov.

<https://zoobank.org/13F8C1E4-59CB-428B-BB42-0C5FCBF963BF>

Figs 56, 106, 108, 109, 110, 115

Type locality. INDONESIA: Papua Province: Nabire Regency, Nabire, Wanggar, Kali Bumi.

Type material. Holotype: male “W.-Neuguinea /Paniai Prov./ Wanggar- Kali Bumi / IR 14 30.9 & 1.10.90 leg: Balke & Hendrich” (ZSM). **Paratypes: IN: Papua: Nabire Regency:** 14 males, 20 females with the same label as the holotype (CLH, ZSM). 3 males, 8 females “IR 90#14: West New Guinea, Nabire→Wanggar, 100m, 30.ix.1990, Balke” (ZSM). 2 males, 8 females “Irian: Nabire – Ikaga [sic! Ilaga], “KM 35”, Seitenstr. nach K. Cemara, 1991, leg. M. Balke” (ZSM). 8 males, 8 females “West New Guinea/Paniai Prov./IR 23 track Nabire-Illaga km 34 near Topo, 120m, 23.7.1991 leg: Balke & Hendrich” (ZSM). 4 males, 1 female “IRIAN JAYA: Nabire Prov. rd. Nabire – Illaga, Km 35 Kali Cemara, 100m, 27.9.1997 (IR97#6)” (NHMW). 7 males, 6 females “IRIAN JAYA: Nabire Prov. rd. Nabire – Illaga, Km 35 Kali Cemara, 100m, 23.10.1997 (IR97#14)” (NHMW). **Mimika Regency:** 1 female “Indonesia: Papua, Kabupaten Mimika, Timika, 149m, 25–30.v.2017, 04°15.092'S 136°38.597'E, B. Sumoked (Pap68-Bob06)” (ZSM). 9 males, 4 females “Indonesia: Papua, Kabupaten Mimika, 24m, 25–30.v.2017, S 04°30.330”, “E 136°46.53”, B. Sumoked (Pap69-Bob07)” (ZSM). **Yahukimo Regency:** 2 males, 4 females “Indonesia: Papua, Dekai, upper Brazza, 273m, 2./3. vi.2015, -4,741084724 139,654211075976, Sumoked (Pap044)”, one male with an additional green text label “7221” (ZSM). **Aru Islands Regency:** 2 males “INDONESIA: Aru Islands, Trangan, 1km E of Ngalgull, 6°48'S 134°4'E, 29.vii.1994, 90m, A.H. Kirk-Spriggs.”, “A.H.Kirk-Spriggs Maluku Tenggara Coll. NMW.Z.1994.061”, “Temporary/Sago pools, Primary mixed forest.” (CLH, ZSM). 1 female “INDONESIA: Aru Islands, Trangan, 1km E of Ngalgull, 6°48'S 134°4'E, 23–28.vii.1994, 90m, A.H. Kirk-Spriggs.”, “A.H.Kirk-Spriggs Maluku Tenggara Coll. NMW.Z.1994.061”, “Temporary/Sago pools, Primary mixed forest.” (CLH, ZSM). 1 male “INDONESIA, SE Moluccas ARU ISLS, WOKAM Isl. 17 km NE Wakua vill. 1.-7.ii.2022, S. Jákl leg.”, “coll. Jiří HÁJEK National Museum Prague, Czech Republic” (NMPC). 1 male “INDONESIA, SE Moluccas ARU ISLS, WOKAM I. 17 km NE Wakua vill. 1–7.II.2022, St. Jakl leg.”, “coll. Jiří HÁJEK National Museum Prague, Czech Republic” (NMPC).

West Papua: Kaimana Regency: 1 male, 3 females “INDONESIA W-PAPUA 50km SE Kaimana, Triton bay, vic. Kamaka vill. S3°49'50"/E134°11'27", 10–50m, 02.-05. II.2011 A. Skale (006)” (ZSM). 1 male “INDONESIA: W-PAPUA vic. Kaimana, road 17 km NE, S3°31'41"/E133°40'51", 50m, 31.I.2011 A Skale (003)”, “4431” [green label] (ZSM). 47 males, 60 females “IRIAN JAYA: Fak Fak dist. Lake Yamur area, IV.1998 ca. 50 – 100m, Waldtümpel” (NHMW). **Raja Ampat Regency: Waigeo:** 2 males, 3 females “W-PAPUA Raja Ampat Prov. Waigeo Isl., Lopintol 0°07'54"S, 130°53'45"E 11.i.2004 leg. A.Skale UWP” (CAS). 1 male “760” [green label], “W Papua: Raja Ampat, Waigeo, Lopintol, 11/2005, A. Skale, MB760” (ZSM). 1 female “762” [green label], “W Papua: Raja Ampat, Waigeo, Lopintol, 11/2005, A. Skale, MB 762” (ZSM). **Batanta:** 1 male “W-PAPUA Raja Ampat Pr. Yensawai Batanta, 9 km W Ross-River 0°49'23"S 130°35'52"E 17.I.2004 leg. A.Weigel UWP KL” (CAS). 1 male, 1 female “Indonesia: Papua, Batanta Selatan, Wailebet, 100m, 17.ii.2006, inland 00.53.957S 130.39.951E, Tindige & Prativi (BH 15)”, with additional green labels “4252” and “4253” (ZSM). 1 male “Indonesia: Papua, Batanta Selatan, Wailebet, 20m, 16.ii.2006, 00.54.003S 130.39.296E (BH 14)” (ZSM). 6 males, 2 females “Indonesia: Papua, Batanta Utara, 20m, 14.ii.2006, 00.50.125S 130.42.856E (BH 12)” (ZSM). 1 male, 1 female “W-PAPUA, Raja Ampat Pr. Waywesar/Batanta 2 km E, 0°45'17"S 130°48'06"E 18.I.2004, leg. A. Weigel” (CAS). 11 males, 21 females “W-PAPUA Raja Ampat Prov. Batanta Isl. bor., 9 km W Yensawai, Ross-River 0°49'23"S, 130°35'52"E 17.I.2004 leg. A. Skale” (CAS, NHMW). 4 males “W-PAPUA Raja Ampat Prov. Batanta Isl. bor., Yensawai, 0°48'05"S, 130°40'36"E 15.-18.I.2004 leg. A.Skale” (CAS, NHMW). 1 female “W-PAPUA Raja Ampat Prov. Batanta Isl. bor., Arefl, 0°47'24,5"S, 130°42'10"E 16.I.2004 leg. A.Skale” (CAS). 7 males, 2 females “W-PAPUA Raja Ampat Prov. Batanta Isl. bor., Waywesar, 0°45'26"S, 130°46'55"E 12.-15.I.2004 leg. A.Skale UWP” (CAS, NHMW). **Salawati:** 2 males “W-PAPUA Raja Ampat Prov. Salawati Isl. Or., 2–4 km N Kalobo 01°00'56"S, 131°04'58"E 28.I.2004 leg. A.Skale” (CAS). 1 male, 1 female “W-PAPUA Raja Ampat Prov. 1 km E Kalobo, Wajir Island 01°00'S, 131°04'E 26.I.2004 leg. A.Skale UWP/UWS” (CAS). **Misool:** 23 males, 19 females “Indonesia: West Papua, Raja Ampat, Misool, v.2015, -1.799575° 129.950446, Prativi” (NHMW, ZSM). **PNG: SHL:** 4 males, 1 female “Collection Naturhistorisches Museum Basel”, “Papua New Guinea S. Highlands Prov. L.Cizek lgt.”, “Mt Bosavi, 700m 142°50'E 6°28'S 20–27.VI.1999” (NHMB, NHMW, ZSM). **Central:** 6 males, 5 females “Papua New Guinea: Central, Tapini, 870m, 29.x.2007, 08.20.511S 146.59.824E Kinibel (PNG 161)”, one male and one female additionally with green labels “2854” and “2853”, respectively (NHMW, ZSM).

Additional material. 2 males (teneral) “Papua New Guinea: Southern Highlands Province, Tari to Komo, Hides Gas basecamp, 1200m, 13.v.2006, 05.55.223'S 142.46.090'E, Balke (PNG 60)”, one male additionally with a green label “3231” (ZSM).

Description. Body size and form: Beetle small to medium-sized, oblong-oval (Fig. 56).

Measurements: TL 5.1–6.35 mm, TL-H 4.55–5.8 mm, MW 2.45–3.1 mm, TL/MW 2.04–2.8; PL 0.8–0.95 mm, PW 2.1–2.65 mm, PL/PW 0.35–0.38; DBE 0.85–1.1 mm, DBE/PW 0.4–0.42. **Holotype:** TL 5.6 mm, TL-H 5.1 mm, MW 2.75 mm, TL/MW 2.04; PL 0.85 mm, PW 2.4 mm, PL/PW 0.35; DBE 0.95 mm, DBE/PW 0.4.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and elytral basal band and apical spot (Fig. 56).

Head yellowish red medially, narrowly piceous behind eyes and brownish anteriorly. Pronotum piceous on disc and broadly yellowish red on sides, especially at anterior angles. Elytron piceous, with distinct yellowish red basal band, usually not reaching shoulders and suture; elytron usually with yellow spot apically sometimes slightly extending laterally. Scutellum reddish to piceous. Antennae, other head appendages, and pro- and mesolegs yellow, metalegs slightly darker proximally and distinctly distally. Ventral side reddish brown, darker on metaventrite, metacoxal plates and two last abdominal ventrites.

Surface sculpture: Elytron with 11 complete dorsal striae, submarginal stria present, long: 11+1 (Fig. 56).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures usually equal to and smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with several or rather numerous, sparse striae on lateral parts, sometimes only middle of disc without striae, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae, sometimes strongly impressed, sometimes less, sometimes stria 1 or striae 1 and 2, seldom 1–3, less strongly impressed dorsally; submarginal stria present, long, often reaching ½ of elytral length. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, strongly convex medially; blade of prosternal process narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite with broadly pointed apexes, more or less straight and subequal in length; left dorsal lobe with lateral margin not beaded, slightly concave its apical 1/2; lateral side of left dorsal lobe completely covered with tiny spinulae situated in groups on scale-like structures; right dorsal lobe covered with large scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, slightly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with curved apex and slightly sclerotised part distinctly shorter, with dense setae apically; right ventral lobe longer than left one, partly sclerotised, with apex curved left and covered with setae sometimes distinctly sticking out in left lateral view. Parameres with long and dense setae occupying approximately half of dorsal margin; more distally situated setae longer and denser than more proximal ones (Fig. 106).

Female: As males.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body shape and size and general shape of the median lobe, it is similar and probably closely related to *A. asteios* sp. nov. but differs from it in paler elytral colouration, more robust median lobe, and left dorsal lobe of the median lobe with apex thicker and lateral margin more strongly concave apically and therefore ventral lobes more visible in left lateral view. See also under *A. yeretuar* sp. nov.

Notes on Copelatinae of the Aru Islands. *Austrelatus epicharis* sp. nov. is the second copelatine species described from the Aru Islands. The first one is *Copelatus haemorrhoidalis* Régimbart, 1883, which was described based on a single female. We have studied habitus photos of the holotype (RMNH. INS.1487394), which is deposited in the Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands (RMNH), and compared them with images and specimens of *A. epicharis* sp. nov. We believe that they are two different species since 1) thought *C. haemorrhoidalis* has 11+1 elytral striae, striae 2, 4, 6, 8 are reduced in the apical 1/2, and *A. epicharis* sp. nov. never demonstrates elytral stria reduction; 2) *C. haemorrhoidalis* has less prominent yellowish red dorsal colouration and a V-shaped brown spot on head, but head of *A. epicharis* sp. nov. is always uniformly yellowish red medially (Figs 56, 58). Most likely, *C. haemorrhoidalis* belongs to the genus *Austrelatus* but it will be possible to determine with certainty when males of the species are found. Besides these two species, there are two more copelatine species found in the material recently collected from the Aru Islands. They are represented by three females, two of which belong to the *A. neoguineensis* group and one is most likely a *Copelatus* species. Thus, Copelatinae fauna of the Aru Islands includes four different species with the certain record of *A. epicharis* sp. nov. For three other species, more material is necessary to clarify their taxonomic position.

Etymology. The species name is a Greek adjective meaning “beautiful, graceful” and refers to striation and nice yellowish red dorsal pattern of the species.

Distribution. The species is widely distributed in Indonesian part of New Guinea including the small islands; it is also known from Central and SHL provinces of PNG (Fig. 108).

Habitat. All specimens on the track Nabire to Ilaga were collected in shallow (up to 20 cm water depth), shaded or at least partly shaded forest pools and road-side ditches, rich in rotten leaves and twigs (Figs 109, 110). The type specimens were collected in shallow, exposed and flooded meadow puddles and oxbows along Kali (= River) Bumi at Wanggar (Fig. 115). Few specimens were also found in water-filled track hollows. On the Aru Islands, the species was collected in temporary Sago swamp pools, surrounded by primary mixed forest.

11. *Austrelatus flavocapitatus* sp. nov.

<https://zoobank.org/95679550-737D-4E55-8AD5-80A6C66AA0B2>

Figs 46, 95, 108

Type locality. PAPUA NEW GUINEA: East Sepik Province, Lembena, 04°56.859'S, 143°57.379'E, 335 m a.s.l.

Type material. **Holotype:** male “Papua New Guinea: East Sepik, Lembena, 335m, 10.ix.2009, 04 56.859S 143 57.379E, Ibalim & Pius (PNG251)” (ZSM). **Paratypes:** 3 males, 2 females with the same label as the holotype (NHMW, ZSM). 3 males, 3 females “Papua New Guinea: East Sepik, Lembena, 198m, 3.ix.2009, 04.56.974S 143.56.995E, Ibalim & Pius (PNG241)” (NHMW, ZSM). 3 females “Papua New Guinea: East Sepik, Lembena, 198m, 3.ix.2009, 04 46 [!] 974S 143.56.995E, Ibalim & Pius (PNG243)” (ZSM). 2 males “Papua New Guinea: East Sepik, Lembena, 136m, 3.ix.2009, 04 56.911S 143.56.870E, Ibalim & Pius (PNG244)” (ZSM). 1 male, 6 females “Papua New Guinea: East Sepik, Lembena, 117m, 8.ix.2009,

04.57.513S 143.57.296E, Ibalim & Pius (PNG248)", one male and four females with additional green text labels "6001", "5999", "6000", "6002", and "6003", respectively (ZSM). 1 male, 2 females "Papua New Guinea: East Sepik, Lembena, 110m, 10.ix.2009, 04.57.512S 143.57.366E, Ibalim & Pius (PNG249)", male with a green text label "6033" (ZSM). 2 females "Papua New Guinea: East Sepik, Lembena, 335m, 10.ix.2009, 04.56.859S 143.59.375E, Ibalim & Pius (PNG250)" (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 46).

Measurements: TL 5.4–6.1 mm, TL-H 5–5.4 mm, MW 2.65–2.9 mm, TL/MW 2.04–2.1; PL 0.85–0.9 mm, PW 2.3–2.5 mm, PL/PW 0.36–0.37; DBE 0.9–0.95 mm, DBE/PW 0.38–0.39. **Holotype:** TL 5.5 mm, TL-H 5 mm, MW 2.7 mm, TL/MW 2.04; PL 0.85 mm, PW 2.35 mm, PL/PW 0.36; DBE 0.9 mm, DBE/PW 0.38.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and basal band and large apical spot on elytron (Fig. 46).

Head yellowish red, narrowly piceous behind eyes. Pronotum piceous on disc and yellowish red on sides, especially at anterior angles. Elytron piceous, with distinct, rather broad, yellowish red basal band and large, often laterally extending yellow spot on apex. Scutellum reddish to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs distinctly darker, especially distally. Ventral side reddish brown to brown, paler on pro- and metaventrite and abdominal ventrites 1–3.

Surface sculpture: Elytron with (10–11)+1 striae, sometimes striae differently reduced or interrupted (Fig. 46).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without or with few striae posterolaterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 differently reduced, often absent in basal 1/2 and present as few striae in apical 1/2, seldom completely absent, striae 2 and 3 reduced or interrupted basally, striae 5–7, 9 and 10 sometimes shortly reduced or interrupted basally; submarginal stria present, sometimes reduced to few striae apically. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw thicker subapically than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, more or less straight, with very broadly pointed apices, apex of left dorsal lobe slightly curved downwards; left dorsal lobe with lateral side covered with numerous, distinct, strong spinula-like structures; lateral margin apically without surface structures, smooth; right dorsal lobe covered with scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved to right and membranous right part long, thin, apically covered with setae sometimes visible in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with long and dense setae occupying approximately half of dorsal

margin; more distally situated setae longer and denser than more proximal ones (Fig. 95).

Female: As males but with stronger dorsal punctation and microreticulation and usually more numerous pronotal striae.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe not completely covered by spinula-like structures, upper lateral margin without spinulae, smooth in left lateral and ventral views. Based on shape of the median lobe, it is similar to *A. mianminensis* sp. nov. and especially to *A. pseudomianminensis* sp. nov. (in having lateral margin of left dorsal lobe with edge, below which spinula-like structures situated, more sharp, prominent) but differs from them in more bright dorsal colouration: yellowish red head and lateral sides of pronotum, elytron with broad yellowish red basal band and large apical spot, as well as in less striolated elytron: (10–11)+1 striae, stria 1 strongly reduced basally (visible in traces in apical 1/2), sometimes completely absent, the other striae can be differently reduced. See also under *A. maindai* sp. nov. and *A. kokodensis* sp. nov.

Etymology. The species name is a combination of the Latin words *flavus* (yellow) and *capitatus* (heaving a head) and refers to the distinct yellowish head colouration of the species. The species name is an adjective in the nominative singular.

Distribution. Papua New Guinea: East Sepik Province. The species is known only from Lembena area (Fig. 108).

Habitat. Unknown.

12. *Austrelatus fuscus* sp. nov.

<https://zoobank.org/C206C98D-7EBE-4FFE-9797-BFA24340800B>

Figs 50, 99, 108

Type locality. PAPUA NEW GUINEA: Central Province, Kokoda, 08°53.481'S, 147°43.648'E, 410 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Northern, Kokoda, 410m, i.2008, 53.481S 147.43.648E, Posman, (PNG 174)" (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 50).

Measurements: Holotype: TL 6.4 mm, TL-H 5.8 mm, MW 3.1 mm, TL/MW 2.07; PL 0.9 mm, PW 2.7 mm, PL/PW 0.33; DBE 0.95 mm, DBE/PW 0.35.

Colouration: Dorsally almost uniformly piceous (Fig. 50).

Head dark brown, reddish posteriorly between eyes and anteromedially, narrowly piceous behind eyes. Pronotum piceous, dark brown on sides, reddish at anterior angles. Elytron piceous, yellowish red apically, slightly extending laterally. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs distinctly darker, especially distally. Ventral side piceous, with paler prosternum.

Surface sculpture: Elytron with 10+1 striae; submarginal stria present as weak apical striae (Fig. 50).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures

equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with single striae at posterior angles, with punctation slightly finer than on head and microreticulation fine. Elytron with ten dorsal striae, striae 1 and 2 absent in basal 1/3, striae 4 and 5 can be interrupted basally, stria 10 reduced and interrupted basally; submarginal stria present only as very weak apical striae. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively short, subequal in length, anterior claw thicker and more curved subapically than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed apices; whole lateral side of left dorsal lobe with large but shallow concavity, covered with numerous large spinula-like structures getting longer and denser towards lateral margin and shorter towards dorsal side where they replaced by scale-like structures; lateral margin slightly concave apically so that apex of left dorsal lobe slightly curved upwards; right dorsal lobe covered with large scale-like structures, with small, indistinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved to right and membranous right part long, thin, apically covered with setae visible in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with dense, rather short setae occupying more than half of dorsal margin (Fig. 99).

Female: Unknown.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body size and dark dorsal colouration, it is similar to *A. kalibumi* sp. nov., *A. herzogensis* sp. nov., *A. mianminensis* sp. nov., and *A. pseudomianminensis* sp. nov. but differs from them in left dorsal lobe of the median lobe with large, shallow concavity and surface of left dorsal lobe completely covered by surface structures. It is also similar to *A. sararti* sp. nov. but differs from it in larger body size, elytron with 10, not 11, dorsal striae, and left dorsal lobe of the median lobe with concavity and large, long spinula-like structures. See also under *A. wasiorensis* sp. nov.

Etymology. The species name is a Latin adjective meaning “dark, dusky” and indicates the dark elytral colouration of the species.

Distribution. Papua New Guinea: Central Province. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

13. *Austrelatus gestroi* (Régimbart, 1892)

Figs 52, 101, 108

Copelatus gestroi Régimbart 1892: 991 (orig. descr.); Régimbart (1899: 303); Zimmermann (1919: 202, 1920: 139); Guignot (1956: 55); Guéorguiev

(1968: 14); Guéorguiev and Rocchi (1993: 159); as objective synonym of *Copelatus neogestroi* Balke in Shaverdo et al. (2008: 50).

Copelatus neogestroi Balke in Shaverdo et al. (2008: 50) as replacement name for *C. gestroi* Régimbart, 1892; Nilsson and Hájek (2023: 53).

Austrelatus gestroi (Régimbart, 1892): Shaverdo et al. (2023: 6).

Type locality. PAPUA NEW GUINEA: Central Province, Rigo District, ca. 09°46'51.6"S, 147°50'24"E.

Type material. Lectotype: male "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea Mus. Genua", "Copelatus Gestroi Reg." [hw], "Coll. Mus. Vindob." (NHMW).

Paralectotypes: 2 males, 6 females "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea Mus. Genua" (NHMW). 1 male "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea Mus. Genua", "Copelatus Gestroi Reg." [hw] (NHMW). 1 male "N. Guinea Rigo *Luglio 1889* L.Loria" [hw], "Neu Guinea Mus. Genua" (NHMW). 2 males "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Cotype" [red], "Regimbart det., 1891: COPELATUS (s. str.) Gestroi – Reg." [partly hw] (ZSM). 2 males "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea 7407" [partly hw], "Copelatus Gestroi Rg det. Gschwendt." [hw], "Staatl. Museum für Tierkunde, Dresden" (MTD). 2 females "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea 7407" [partly hw], "Staatl. Museum für Tierkunde, Dresden" (MTD). 3 males, 2 females "N. GUINEA MER. RIGO *Luglio 1889* L.Loria", "Neu Guinea 8947" [partly hw], "Staatl. Museum für Tierkunde, Dresden" (MTD). 1 male "N. GUINEA MER. RIGO *Luglio 1889* L.LORIA", "Regimbart det., 1891: COPELATUS (s. str.) Gestroi – Reg." [partly hw], "EX TYPUS" (IRSNB). 21 exs. "N. GUINEA MER. RIGO *Luglio 1889* L.Loria" (MNHN); these paralectotypes are from the collections of Régimbart (1 ex.), Legros (1 ex.), Guignot (2 ex.), Oberthür (17 exs.), some of them with the hand written labels indicating *C. gestroi*; median lobes of the specimens were not studied. 1 male "N. GUINEA MER. KELESI Nov. Dic. 1890 L.LORIA", "MUSEUM PARIS COLL MAURICE REGIMBART 1908", "MNHN, Paris EC29239 [with QR code]" (MNHN).

Additional material. 1 male "Neu Guinea" [hw by ?Zimmermann], "Samml. A. Zimmermann" (ZSM). 1 male [only aedeagus glued on pined triangular, beetle probably lost] "Penis *C. gestroi*" [hw by ?Zimmermann], "Samml. A. Zimmermann" (ZSM).

PNG: NCD: 1 male "2846", "Papua New Guinea: National Capital District, Varirata NP, 600m, 16.xii.2007, 09.26.13S 147.22.09E, Balke & Sagata (PNG 159)" (ZSM). 4 males, 5 females "Stn. No. 196", "Papua: Pt. Moresby Brown R. Rd., 15.III.1965", "M.E. Bacchus. B.M. 1965-120" (BMNH, NHMW). 1 male, 4 females "Stn. No. 195", "Papua: Pt. Moresby Brown R. Rd., 15.III.1965", "M.E. Bacchus, B.M. 1965-120" (BMNH). 2 males, 3 females "Stn. No. 206", "Papua: Loloki c. 10 m. N. of Pt. Moresby, 19.III.1965.", "M.E. Bacchus. B.M. 1965-120" (BMNH). 4 males, 10 females "Stn. No. 208", "Papua: Loloki, c. 10 m. N. of Pt. Moresby 19.III.1965.", "M.E. Bacchus. B.M. 1965-120" (BMNH, NHMW). 5 males, 3 females "Stn. No. 207a", "Papua: Moitaka, c. 7 m. N. of Pt. Moresby. 17.III.1965", "M.E. Bacchus. B.M. 1965-120" (BMNH, NHMW). 1 male, 1 female "4881 New Guinea Port Moresby Dist 24.iii.1956 E.S. Brown" [partly hw], "Pres. By Com.Inst.Ent. B.M. 1958-79" (BMNH). **Morobe:** 2 males, 1 female "Stn. No. 103", "New Guinea: Morobe Dist., Finisterre Mts., Mt. Abilala, c.9,000 ft. 19–22.xi.1964.", "M.E. Bacchus. B.M. 1965-120" (BMNH).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 52).

Measurements: TL 5.8–6.8 mm, TL-H 5.45–6.2 mm, MW 2.9–3.3 mm, TL/MW 2–2.06; PL 0.85–0.95 mm, PW 2.45–2.8 mm, PL/PW 0.34–0.35; DBE 0.9–

1 mm, DBE/PW 0.35–0.37. **Lectotype:** TL 6.4 mm, TL-H 5.8 mm, MW 3.15 mm, TL/MW 2.03; PL 0.9 mm, PW 2.6 mm, PL/PW 0.35; DBE 0.9 mm, DBE/PW 0.35.

Colouration: With piceous elytra and pronotum and yellowish red posterior margin of head, pronotal sides, and elytral basal band and apex (Fig. 52).

Head almost completely brownish or piceous, often paler, to yellowish red posteriorly and anteriorly and darker medially. Pronotum dark brown to piceous on disc and broadly yellowish red on sides, especially at anterior angles. Elytron dark brown to piceous, with yellowish red basal band differently developed: distinct, relatively broad or rather narrow, often notched at posterior margin (expanding between striae), seldom reduced near suture and distinct at shoulders; elytron broadly yellow apically, this yellow colouration usually extending between striae, especially laterally (up to elytral 1/2). Scutellum reddish to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, especially distally. Ventral side reddish brown to brown, darker on coxal plates and abdominal ventrites 4–6.

Surface sculpture: Elytron with (10–11)+1 striae (Fig. 52).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to and larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with few to several striae at posterior angles or more numerous laterally (in females), with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 usually reduced to striae in apical 1/2, sometimes completely absent; striae 2 and 3 usually absent in basal 1/4 and additionally interrupted, sometimes uneven dorsal striae interrupted basally, especially striae 5 and 7; submarginal stria present, well-developed. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, subequal in length, anterior claw thicker and more curved at its apex than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite with broadly pointed apexes, left straight, right slightly curved to left; left dorsal lobe slightly longer than right dorsal lobe, distinctly narrowed to apex in its apical 1/2; lateral side of left dorsal lobe in whole apical 1/2 narrowly and shallowly concave under lateral margin that looks like a bead, covered with large scale-like structures towards dorsal side and smaller scale-like structures towards apex and on lateral margin, with numerous small spinula-like structures in concavity and less numerous large, short spinula-like structures medially; right dorsal lobe covered with large scale-like structures, with small, indistinct median membranous area; lobes of ventral sclerite sclerotised, long, broad, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with slightly curved apex and broad slightly sclerotised part rounded apically; right ventral lobe longer than left one, slightly sclerotised, with long curved apex visible in left lateral view. Parameres with dense, relatively long setae occupying approximately half of dorsal margin, with single the most proximal setae standing separately (Fig. 101).

Female: As males but with stronger dorsal punctation and microreticulation and more numerous pronotal striae.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on dorsal colouration and general shape of the median lobe, it is similar to *A. asteios* sp. nov., *A. epicharis* sp. nov., *A. wasurensis* sp. nov., and *A. yeretuar* sp. nov. but differs from them in larger body size and left dorsal lobe of the median lobe with narrow, shallow, concavity under the lateral margin and different organisation of the surface structures. It is also very similar to *A. pseudogestroi* sp. nov., see its affinities.

Distribution. Papua New Guinea: Central (Rigo, Kapakapa, Hula and Kelesi in Régimbart (1892: 991; 1899: 303), Angabanga River as Paumomu River in Régimbart (1899: 303)), Morobe, National Capital District, East New Britain (Kokopo as Herbertshöhe in Zimmermann (1919: 202)) provinces (Fig. 108). The East New Britain record needs to be confirmed.

Habitat. The species was collected in Varirata NP in small, shallow and shaded forest pools rich in rotten leaves.

14. *Austrelatus herzogensis* sp. nov.

<https://zoobank.org/A70BB204-8306-43EA-8A9A-1B5E336F3E9A>

Figs 43, 92, 108

Type locality. PAPUA NEW GUINEA: Morobe Province, Herzog Mts, backroad to Wagau, 06°46.717'S, 146°38.953'E, 100 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Morobe, Herzog Mts., backroad to Wagau, 100m, 3.iv.2006, 6 46.717S 146 38.953E, Balke & Sagata (PNG 29)" (ZSM). **Paratypes: PNG: Morobe:** 1 male, 7 females with the same label as the holotype (NHMW, ZSM). 1 male "Papua New Guinea: Morobe, Herzog Mts., backroad to Wagau, 100m, 3.iv.2006, Balke & Sagata (PNG 29)", "3216" [green label] (ZSM). 5 males, 7 females "Stn. No. 158", "New Guinea: Morobe Distr., Gusap, Markham, Valley c.90 m W. of Lae. 1,000ft. 27–30.i.1965", "M.E. Bacchus B.M. 1965-120" (BMNH, NHMW). 1 male, 1 female "Stn. No. 162", "New Guinea: Morobe Distr., Gusap, Markham, Valley c.90 m W. of Lae. 1,000ft. 27–30.i.1965", "M.E. Bacchus B.M. 1965-120" (BMNH). 1 female "Stn. No. 161", "New Guinea: Morobe Distr., Gusap, Markham, Valley c.90 m W. of Lae. 1,000ft. 27–30.i.1965", "M.E. Bacchus B.M. 1965-120" (BMNH). 1 male, 6 females "Stn. No. 114", "New Guinea: Morobe Distr., Markham R. Valley. Gusap, c.90 m. W. of Lae. 1000ft. 3.xii.1964", "M.E. Bacchus B.M. 1965-120" (BMNH). **Madang:** 3 males, 7 females "Papua New Guinea: Madang, middle ramu [Ramu River], Akaraski, 50m, 12.iii.2007, 05.04.787S 144.43.137E, Kinibel (PNG 157)", two males with additional green labels "2881" and "2882" (NHMW, ZSM). **East Sepik:** 1 male, 2 females "Papua New Guinea East Sepik Province Amboin Patrol Post Karawari Lodge 7 Jan. 1983, A.C.Messer" (ZSM). **IN: West Papua: Yapen Islands Regency:** 1 male "Irian Jaya: Japen Isl. W Serui, Panduamin ca. 100m, 19.2.1999 leg. Riedel" (NHMW).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 43).

Measurements: TL 5.65–6.7 mm, TL-H 5.75–6.1 mm, MW 2.8–3.2 mm, TL/MW 2.02–2.09; PL 0.8–0.95 mm, PW 2.3–2.7 mm, PL/PW 0.33–0.37; DBE

0.85–1 mm, DBE/PW 0.37. **Holotype:** TL 6.3 mm, TL-H 5.75 mm, MW 3.05 mm, TL/MW 2.07; PL 0.95 mm, PW 2.6 mm, PL/PW 0.37; DBE 0.95 mm, DBE/PW 0.37.

Colouration: Dorsally piceous, with yellowish red posterior part of head, pronotal sides, especially anterolaterally, broad, basal band and large, apical spot on elytron (Fig. 43).

Head piceous, yellowish red posteriorly, between eyes; sometimes yellowish red to brown, piceous behind eyes and two spots in middle. Pronotum piceous, with yellowish red sides, often only in anterolateral half. Elytron piceous, with broad, distinct, yellowish red basal band and large, yellow spot apically that usually slightly extending laterally. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs slightly darker, especially distally. Ventral side brown, with paler prosternum and abdominal ventrites.

Surface sculpture: Elytron with (10–11)+0 striae; stria 1 usually strongly reduced, striae 2 and 3 sometimes reduced basally (Fig. 43).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (diameter of punctures usually larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without striae or with few striae posterolaterally or in females, with numerous striae laterally; with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 often present as striae in apical 1/2 or sometimes completely absent, striae 2 and 3 usually absent in basal 1/4 or present as striae, stria 10 reduced at shoulder; submarginal stria absent. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, more or less straight and evenly tapering to broadly pointed apices, tip of left dorsal lobe apex with kind of small incision, not completely pointed; left dorsal lobe with lateral side modified: with distinct, median concavity of triangular shape, covered with numerous, very distinct, strong and long spinula-like structures; lateral margin apically without surface structures, smooth; right dorsal lobe covered with scale-like structures, with median membranous area; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave apically, with apex pointed and slightly curved to right and membranous right part with long, thin, upwardly curved apex sometimes sticking out in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with dense, long setae occupying approximately half of dorsal margin, with single the most proximal setae standing separately (Fig. 92).

Female: As males but usually with stronger elytral punctation and microreticulation and pronotum with numerous striae occupying sides completely so that only disc without striae. Interestingly, some females have pronotum with lateral margin slightly to distinctly concave at anterior angles.

Variability. There is a variation in dorsal colouration and striation as described above.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe. Based on body size and shape and shape of the median lobe with the characteristic median, triangle concavity of the left dorsal lobe, it is very similar to *A. kalibumi* sp. nov. but differs from it in elytron with broad and distinct, yellowish red basal band and slightly differently shaped median lobe, with its apical part distinctly shorter and apex of the left dorsal lobe less pointed. See also under *A. sararti* sp. nov.

Etymology. The species is named after Herzog Mts. The name is an adjective in the nominative singular.

Distribution. According to the studied material, the species has a disjunct areal: all specimens except one are from Papua New Guinea: Madang, Morobe and East Sepik provinces and only one male (its identification is sure) is known from Yapen Island of Indonesia (Fig. 108). Further sampling activities are necessary to show whether the species is indeed distributed in western part of New Guinea or the Yapen specimen is mislabelled.

Habitat. In the Herzog Mts, the species was collected in shallow and shaded forest pools rich in rotten leaves.

15. *Austrelatus inconstans* sp. nov.

<https://zoobank.org/82127944-30E0-4F34-B7E8-5247BA54FCBD>

Figs 13–15, 65, 107, 109–113

Type locality. INDONESIA: Papua Province: Nabire Regency, road Nabire-Enarotali, 54th km, 03°29.51'S, 135°43.91'E, 750–800 m a.s.l.

Type material. Holotype: male “West New Guinea/Paniai Prov./IR 19 track Nabire-Ilaga km 54 Basecamp, 750–800m, 16.-27.7.1991 leg: Balke & Hendrich” (ZSM). **Paratypes: IN: Papua: Nabire Regency:** 52 males, 36 females with the same label as the holotype (MZB, NHMW, ZSM). 9 males, 9 females “IR 19-W, New Guinea, Track Nabire-Ilaga KM 54, basecamp, 750–800m, 16.-27.vii.1991 Balke & Hendrich leg.” (NHMW). 41 males, 12 females “W.-Neuguinea/Paniai Prov. Strasse Nabire-Ilaga km 54 700m, 22.-25.9.1990/IR 11 leg: Balke & Hendrich” (NHMW, ZSM). 6 males, 3 females “West New Guinea/Paniai Prov./IR 20 track Nabire-Ilaga KM 59, ca.750m, 18.7.1991 leg: Balke & Hendrich leg.” (ZSM). 17 males, 3 females “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 65, 29.8.1996, 250m (96 # 6)” (NHMW). 1 male “West New Guinea/Paniai Prov./IR 23 track Nabire-Ilaga km 34 near Topo, 120m, 23.7.1991 leg: Balke & Hendrich” (ZSM). 2 males “IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 27.9.1997 (IR97#6)” (NHMW). 1 male, 3 females “IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 23.10.1997 (IR97#14)” (NHMW). 1 male “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 38 18.9.1996, 150m (96 # 26)” (NHMW). 2 males “West New Guinea/Paniai Prov./IR 18 River n. Nabire, 2m, 15.7.1991 leg: Balke & Hendrich leg.” (ZSM). 54 males, 36 females “West New Guinea/Paniai Prov./IR 22 track Nabire-Ilaga km 62 250m, 24.7.1991, forest pools leg: Balke & Hendrich” (NHMW, ZSM). 1 female “IRIAN JAYA: Kabup. Nabire rd. Nabire – Ilaga, km 62 200m, IX.1998 leg. Konyorah (62)” (NHMW). 23 males, 2 females “West New Guinea/Paniai Prov./IR 21 track Nabire-Ilaga km 65 Kali Utowa, 250m, 18.&19.7.1991 leg: Balke & Hendrich” (NHMW, ZSM). 9 males, 10

females “IR 23-W. New Guinea, track Nabire-Illaga KM 62, 250m, 24.vii.1991 Balke & Hendrich leg.” (NHMW). 12 males, 13 females “West New Guinea/Paniai Prov./ IR 21 track Nabire-Illaga km 65 Kali Utowa, 250m, 18.&19.7.1991 leg: Balke & Hendrich” (ZSM). 5 males, 3 females “IR 21-W. New Guinea, track Nabire-Illaga KM 65, Kali Utowa, 250m, 18.-19.vii.1991 Balke & Hendrich leg.” (ZSM). 1 male, 1 female “Indonesia: Papua, Road Nabire-Enarotali KM 55, 774m, 22.x.2011, 03 29.796S 135 43.885E, UNCEN team (PAP09)”, “5127” [green text] and “5126” [green text], respectively (ZSM). 1 male “5136” [green text], “Indonesia: Papua, Road Nabire-Enarotali KM 62, 340m, 22.x.2011, 03.31.684S 135.42.802E, Uncen (PAP11)” (ZSM). 4 males “W.-Neuguinea /Paniai Prov./ Wanggar- Kali Bumi / IR 14 30.9 & 1.10.90 leg: Balke & Hendrich” (ZSM). 1 male, 1 female “IR 90#14: West New Guinea, Nabire→Wanggar, 100m, 30.ix.1990, Balke” (ZSM). **Puncak Regency:** 2 males, 1 female “Indonesia: Papua, Rouaffer, Iratoi, hill in forest, 164m, 6.ix.2014, -3,2403 137,332 (Pap028)”, one male and female with additional green text labels “6476” and “6475”, respectively (ZSM). **West Papua: Kaimana Regency:** 1 male “INDONESIA: W-PAPUA vic. Kaimana, road 18 km NE S3°31'11"/E 133°40'15", 50–80m 21.-25.II.2011 leg. A.Skale (014)” (CAS). **Teluk Wondama Regency:** 1 male “Indonesia: Irian Jaya, Wandammen, Wasior, DMP, 7.-10.I.2001, Riedel, MB 54”, “54” [green label] (ZSM). 1 female “Indonesia: West Papua, DMP, Wasior, 7.-10.i.2001, Riedel leg.” (ZSM). 5 males, 2 females “IRIAN JAYA, Wandammen Bay, Wasior, KM 38, Sararti, 100-200 m, 7.-9.I.2001, leg. A. RIEDEL” (SMNS).

Description. Body size and form: Beetle large, with oblong-oval habitus (Figs 13–15).

Measurements: TL 6.7–8.2 mm, TL-H 6–7.3 mm, MW 3.2–3.9 mm, TL/MW 2.09–2.14; PL 0.95–1.25 mm, PW 2.8–3.5 mm, PL/PW 0.34–0.36; DBE 1.1–1.4 mm, DBE/PW 0.39–0.41. **Holotype:** TL 7.6 mm, TL-H 6.8 mm, MW 3.55 mm, TL/MW 2.14; PL 1.15 mm, PW 3.2 mm, PL/PW 0.36; DBE 1.3 mm, DBE/PW 0.41.

Colouration: With piceous elytra and pronotum and bright yellowish red head, pronotal sides, and basal band on elytron; sometimes yellowish red colouration can be more strongly developed on elytron (Figs 13–15).

Head yellow to yellowish red, narrowly piceous behind eyes. Pronotum dark brown to piceous on disc and gradually paler (to yellow) on sides. Elytron dark brown to piceous, with very distinct yellow to yellowish red basal band, often with yellowish or reddish apex, sometimes also yellow laterally and between striae up to so that whole elytron yellow, with darker disc. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red to yellowish brown, metalegs darker, all legs darker distally. Ventral side reddish brown.

Surface sculpture: Dorsal elytral striation very variable, submarginal stria usually absent or present as a short stria or few short striae apically: (0–10)+(0–1) (Figs 13–15).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without striae, with punctation finer than on head and sometimes with longitudinal wrinkles laterally; microreticulation finer than on head. Elytron with striation very variable: from without striae, with three or four puncture lines, which have often some striae instead of punctures; with up to ten dorsal striae (as in holotype), of which uneven striae usually complete, striae 1 and 2 always reduced basally; submarginal stria usually absent

or present as a short stria or few short striae apically. Elytron with fine punctation and microreticulation. Abdominal ventrite 6 with distinct punctation, sparse medially and forming denser area at each lateral side, with few striae laterally.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum broadly rounded anteriorly, distinctly convex medially; blade of prosternal process broad.

Male: Protibia modified: thinner proximally and broader medially and distally due to its curved ventral margin. Proclaws relatively short, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite unequal in length and shape, both covered with scale-like structures; left dorsal lobe distinctly broader and longer than right dorsal lobe; left dorsal lobe with a distinct median concavity and its whole apical 1/2 narrowed, its basal part very large, and its apex very slightly curved downwards, with a small crest; right dorsal lobe with apex pointed and membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area (not visible in left lateral view) and less sclerotised right part (visible in left lateral view); sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2, which apex can be visible at median lobe apex; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe long and broad. Parameres with dense, long setae occupying slightly more than half of dorsal margin (Fig. 65).

Female: Dimorphic: as male, shiny, and matt, with pronotum and elytron very densely covered with fine longitudinal striae. Matt forms present in almost every population, usually less numerous than shiny ones: e.g., ratio shiny to with striae is 23:13 in the type locality.

Variability. The species is very variable in the elytral striation and colouration, as described above, within and among populations. The holotype is characteristic: piceous, with yellowish red head, pronotal sides, and basal band on elytron, and with 10+1 elytral striae. All specimens from the type locality (IR19) have such colouration but most of them have some stria reduction up to six dorsal striae. In the neighbour population (locality IR21), almost all specimens have elytra without striae and approximately half of them have yellow elytral colouration strongly developed. From Papua Province (Kaimana, Wandammen, and Iratoi) only striated and dark specimens are recorded.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. bundunensis* sp. nov. in size, body form, and dorsal colouration, but distinctly differs from it in shape of the median lobe and modified male proclaws.

Etymology. The species name is a Latin adjective meaning inconsistent and indicates very variable elytral striation of the species.

Distribution. Indonesia: West Papua Province and western part of the Papua Province (Fig. 107).

Habitat. Most specimens were collected in shallow (up to 20 cm water depth), shaded or at least partly shaded forest pools and puddles of different size, rich in rotten leaves and twigs, as, for example, a small forest pool at the 62 km of the Nabire-Ilaga track (Figs 109–113). Few specimens were also found in water-filled track hollows on forest tracks.

16. *Austrelatus iriatoi* sp. nov.

<https://zoobank.org/50C03E00-528C-4E51-A5AC-630B8FDCC9EF>

Figs 25, 76, 107

Type locality. INDONESIA: Papua Province: Puncak Regency, Iratoi, Rouaffer River, 3°14'25.1"S, 137°19'58.7"E, 164 m a.s.l.

Type material. Holotype: male "Indonesia: Papua, Rouaffer, Iratoi, hill in forest, 164m, 6.ix.2014, -3,2403086 137,3329744 (PAP028)" (KSP). **Paratypes:** 7 males, 9 females with the same label as the holotype, two males with additional labels with green text "6471" and "6472" (MZB, NHMW, ZSM).

Description. Body size and form: Beetle small, elongate (Fig. 25).

Measurements: TL 4.95–5.55 mm, TL-H 4.5–5.1 mm, MW 2.25–2.5 mm, TL/MW 2.2–2.23; PL 0.75–0.85 mm, PW 2–2.3 mm, PL/PW 0.36–0.38; DBE 0.87–0.95 mm, DBE/PW 0.41–0.44. **Holotype:** TL 5.45 mm, TL-H 4.8 mm, MW 2.45 mm, TL/MW 2.23; PL 0.8 mm, PW 2.22 mm, PL/PW 0.36; DBE 0.95 mm, DBE/PW 0.43.

Colouration: Dorsally piceous, with yellowish red head, pronotal sides and elytral basal band and apex (Fig. 25).

Head yellowish red, narrowly darker behind eyes. Pronotum piceous on disc and gradually paler (to yellowish red) to sides. Elytron piceous, with distinct yellowish red basal band and yellow apically, especially between striae. Scutellum reddish to brown. Antennae, other head appendages, and pro- and mesolegs yellow to yellowish red, metalegs darker, all legs darker distally. Ventral side brown, reddish brown on head, pro- and metaventrite and medially on abdominal ventrites.

Surface sculpture: Elytron with 11 complete striae, submarginal stria present: 11+1 (Fig. 25).

Head without strioles, with dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with few strioles at posterior margin to several strioles at anterior and posterior margins, with punctation finer than on head and microreticulation fine. Elytron with 11 complete striae, stria 10 shortly reduced basally; submarginal stria present, long. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process narrow.

Male: Protibia more or less straight, not modified; its ventral margin can be slightly curved proximally. Proclaws very long, straight, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed apexes; left dorsal lobe with lateral margin slightly concave apically and lateral side slightly concave medially, covered laterally with numerous distinct spinula-like structures and dorsally with less numerous scale-like structures, lateral margin without surface structures, smooth; right dorsal lobe covered with scale-like structures; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, concave apically, with apex pointed and slightly curved; right ventral lobe longer than left lobe, with narrow sclerotised area on right margin,

membranous part with long, thin, upwardly curved apex distinctly sticking out in left lateral view. Parameres with dense, long setae occupying distinctly more than half of dorsal margin; on small area proximally shorter and sparser, with several the most proximal setae standing separately (Fig. 76).

Female: Only matt forms present.

Affinities. The species is similar to *A. sumokedi* sp. nov. in elongate habitus and dorsal colouration and striation, but differs from it in larger body size, very long, straight male proclaws, and in median lobe structure: slender and more pointed left lobe apex of dorsal sclerite and larger spinula-like structures of left dorsal lobe. In shape and surface structure of the median lobe and long, straight male proclaws, the species is also similar to *A. ohu* sp. nov. but it is larger than the latter, has more elytral striae and slightly differently shaped left dorsal lobe of the median lobe and its spinula-like structures more numerous.

Etymology. The species is named after Iriatoi. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province: Puncak Regency. The species is known only from the type locality (Fig. 107).

Habitat. The species was collected in small, shallow and shaded forest pools rich in rotten leaves.

17. *Austrelatus kalibumi* sp. nov.

<https://zoobank.org/36ECD2F5-D604-4866-8FE5-5502AB718BCC>

Figs 42, 91, 108, 109, 115

Type locality. INDONESIA: Papua Province: Nabire Regency, Wanggar, Bumi River.

Type material. Holotype: male "W.-Neuguinea /Paniai Prov./ Wanggar- Kali Bumi / IR 14 30.9 & 1.10.90 leg: Balke & Hendrich" (ZSM). **Paratypes:** 63 males, 29 females with the same label as the holotype (NHMW). 16 males, 8 females "West New Guinea/Paniai Prov./IR 23 track Nabire-Illaga km 34 near Topo, 120m, 23.7.1991 leg: Balke & Hendrich" (MZB, CLH, ZSM). 11 males, 8 females "Irian: Nabire – Ikaga [sic! Ilaga], "KM 35", Seitenstr. nach K. Cemara, 1991, leg. M. Balke" (ZSM). 1 female "Indonesia: Papua, Road Nabire-Enarotali KM 35, r. Topo, 130m, 22.x.2011, 03 28.727S 135.38.734E, Uncen (PAP09A)" (ZSM). 1 female "Indonesia: Papua, Road Nabire-Enarotali KM 62, 340m, 22.x.2011, 03.31.684S 135.42.802E, Uncen (PAP11)", "5144" [green text] (ZSM). 6 males, 2 females "IR 90#14: West New Guinea, Nabire→Wanggar, 100m, 30.ix.1990, Balke" (ZSM). 1 male "IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 27.9.1997 (IR97#6)" (NHMW). 1 female "IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 27.9.1997 (IR97#5)" (NHMW). 1 female "IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 23.10.1997 (IR97#14)" (NHMW). 1 male, 2 females "IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 38 18.9.1996, 150m (96 # 26)" (NHMW). 1 female "IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 90 1.9.1996, 150m (96 # 11)" (NHMW). 4 females "IRIAN JAYA: Kabup, Nabire 30km S Nabire, Kali Cemara, 150m, 15.8.1998 (CE 1)" (NHMW). 2 males, 2 females "IRIAN JAYA: Kabup, Nabire 30km S Nabire, Kali Cemara, 150m, 15.8.1998 (CE 2)" (NHMW).

Additional material. 1 female "Indonesia: Papua, Road Nabire-Enarotali KM 62, 340m, 22.x.2011, 03.31.684S 135.42.802E, Uncen (PAP11)" (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 42).

Measurements: TL 6.1–6.7 mm, TL-H 5.5–6.05 mm, MW 2.85–3.25 mm, TL/MW 2.06–2.14; PL 0.85–1 mm, PW 2.4–2.7 mm, PL/PW 0.35–0.37; DBE 0.9–1 mm, DBE/PW 0.37–0.38. **Holotype:** TL 6.3 mm, TL-H 5.7 mm, MW 3 mm, TL/MW 2.1; PL 0.95 mm, PW 2.6 mm, PL/PW 0.37; DBE 0.95 mm, DBE/PW 0.37.

Colouration: Dorsally piceous, with yellowish red pronotal sides, especially anterolaterally, and large yellowish red spot on elytral apex (Fig. 42).

Head piceous, paler (sometimes to yellowish red) posteriorly, between eyes, seldom also anteriorly. Pronotum piceous, with yellowish red sides, often only in anterolateral half. Elytron piceous, with large, yellow spot apically that usually slightly extending laterally. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs distinctly darker, especially distally. Ventral side piceous, with slightly paler prosternum.

Surface sculpture: Elytron with (10–11)+0 striae; stria 1 usually strongly reduced, stria 2 reduced basally (Fig. 42).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures fine and weakly impressed (diameter of punctures usually smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum without striae or in females, with numerous striae laterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 often completely absent or present as few tiny striae in apical 1/2, stria 2 usually absent in basal 1/4 or present as striae, stria 3 sometimes shortly reduced basally, stria 10 reduced at shoulder or interrupted; submarginal stria absent. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, more or less straight and evenly tapering to broadly pointed apices; left dorsal lobe with lateral side modified: with distinct, median concavity of triangular shape, covered with numerous, very distinct, strong and long spinula-like structures; lateral margin apically without surface structures, smooth; right dorsal lobe covered with scale-like structures, with median membranous area; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave apically, with apex pointed and slightly curved to right and membranous right part with long, thin, upwardly curved apex sometimes sticking out in left lateral view; right ventral lobe longer than left lobe, with narrow sclerotised area on right margin. Parameres with dense, relatively long setae occupying approximately half of dorsal margin (Fig. 91).

Female: As males but with stronger elytral punctation and microreticulation and pronotum with striae, usually numerous, occupying complete sides so that only disc without them.

Variability. There is a variation in dorsal striolation as described above.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe. Based on body size and shape and shape of the median lobe with the characteristic median, triangle concavity of the left dorsal lobe, it is very similar

to *A. herzogensis* sp. nov. but differs from it in dark elytron, without yellow basal band and slightly differently shaped median lobe, with its apical part distinctly longer. See also under *A. sararti* sp. nov.

Etymology. The species is named after the Bumi River (= Kali), near Wanggar, Nabire. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province: Nabire and Paniai regencies (Fig. 108).

Habitat. Specimens at the type locality were collected in shallow, exposed and flooded meadow and oxbows along Kali (=River) Bumi at Wanggar (Fig. 115). All specimens on the track Nabire to Ilaga at km 34 (Topo), were collected in shallow (up to 20 cm water depth), shaded or at least partly shaded forest pools and road side ditches, rich in rotten leaves and twigs (Fig. 109).

18. *Austrelatus kebarensis* sp. nov.

<https://zoobank.org/B1EAE5A2-5896-4CF5-AA81-6A0A843B6767>

Figs 17, 69, 107

Type locality. INDONESIA: West Papua Province: Manokwari Regency, road from Kebar to Manokwari, 0°48'05.0"S, 133°19'20.6"E, 331 m a.s.l.

Type material. Holotype: male "Indonesia: Papua Barat, Kebar to Manokwari, 1h from Kebar, limestone creek and roadside pools," "331m, 8.xi.2013, -0.8013 133.3223, Unipa team (BH035)" (KSP). **Paratypes:** 2 males, 2 females with the same label as the holotype, one male additionally with a green text label "6245" (MZB, NHMW, ZSM). 2 males, 3 females "Indonesia: Papua Barat, Sausapor-Fef, 157m, 30.ix.2014, -0,6975004 132,072253 (BH044)", one male additionally with a green text label "6485" (ZSM). 1 female "Indonesia: Papua Barat, Kebar Valley, 596m, 6.v.2015, -0,8406 133,2682, Unipa team (BH059)" (ZSM). 2 females "Indonesia: Papua Barat, lowland Manokwari, 66m, 8.v.2015, -0,7433 133,3975, Unipa team (BH065)" (ZSM). 1 male, 1 female "Indonesia: Papua Barat, Manokwari to Kebar, forest stream, 302m, 3.xi.2013, -0.8005 133.3321, Unipa team (BH023)", with two additional green text labels "6222" and "6221", respectively (ZSM). 2 males, 1 female "Indonesia: Papua, Manokwari, 140m, 8.ii.2006, 00.55.752S 133.54.448E, Tindige & Balke (BH 09)" (ZSM). 1 male, 3 females "Indonesia. West Papua Manokwari distr., Utai. riv. Arfak Mts., 500m 14.xii.2012 J. Horák leg." (NMPC).

Description. Body size and form: Beetle medium-sized, oblong-oval to elongate (Fig. 17).

Measurements: TL 5.1–5.7 mm, TL-H 4.6–5.2 mm, MW 2.4–2.65 mm, TL/MW 2.13–2.15; PL 0.8–0.9 mm, PW 2.1–2.3 mm, PL/PW 0.37–0.39; DBE 0.87–1 mm, DBE/PW 0.41–0.44. **Holotype:** TL 5.6 mm, TL-H 5.2 mm, MW 2.6 mm, TL/MW 2.15; PL 0.9 mm, PW 2.3 mm, PL/PW 0.39; DBE 1 mm, DBE/PW 0.44.

Colouration: Dorsally piceous, with yellowish red head, pronotal sides, basal band and apex of elytron (Fig. 17).

Head yellowish red to red, narrowly piceous behind eyes. Pronotum piceous on disc and gradually paler (to yellowish red) to sides. Elytron piceous, with distinct, broad yellowish red basal band and largely yellow apex, especially between striae. Scutellum reddish brown. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown.

Surface sculpture: Elytron with six dorsal striae and a submarginal stria: 6+1 (Fig. 17).

Head without striae, with distinct, relatively sparse punctation (spaces between punctures 1–5× size of punctures); punctures relatively fine (diameter of punctures more or less equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without striae, with punctation finer than on head and microreticulation distinct. Elytron with six dorsal striae; stria 1 can be shortly reduced basally; striae 5 and sometimes 6 shortly reduced basally or present only in apical 1/2; submarginal stria present. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins slightly convergent anteriorly. Base of prosternum rounded anteriorly, distinctly convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with large, broad scale-like structures; left dorsal lobe with lateral margin concave apically and with subapical crest, apex broadly pointed and slightly curved upwards; lobes of ventral sclerite partly sclerotised, subequal in length, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, its apex pointed and curved; right ventral lobe more membranous, slightly longer than left lobe, with apex pointed and slightly curved. Parameres with dense, long setae occupying more than half of dorsal margin; on small area proximally shorter and sparser (Fig. 69).

Female: As male.

Variability. There is an insignificant variation in the elytral striation and colouration.

Affinities. In body size and shape and dorsal colouration, the species is similar to *A. yamurensis* sp. nov. but distinctly differs from it in the median lobe without submedian knob-like modification of the left dorsal lobe and 6 complete dorsal elytral striae.

Etymology. The species is named after Kebar Village. The name is an adjective in the nominative singular.

Distribution. Indonesia: West Papua Province: Manokwari Regency (Fig. 107).

Habitat. The species was collected in different water bodies: in a limestone creek, roadside pools and a forest stream.

19. *Austrelatus kokodensis* sp. nov.

<https://zoobank.org/86FB2431-F900-47CC-B647-848205871595>

Figs 49, 97, 108

Type locality. PAPUA NEW GUINEA: Central Province, Kokoda, 08°53.481'S, 147°43.648'E, 410 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Northern, Kokoda, 410m, i.2008, 53.481S 147.43.648E, Posman, (PNG 174)" (ZSM). **Paratypes:** 1 male, 2 females with the same label as the holotype (NHMW, ZSM).

Description. Body size and form: Beetle medium-sized, rather elongate (Fig. 49).

Measurements: TL 5.6–5.65 mm, TL-H 5.1–5.2 mm, MW 2.6–2.65 mm, TL/MW 2.11–2.17; PL 0.8–0.85 mm, PW 2.25–2.3 mm, PL/PW 0.34–0.37; DBE 0.9–0.95 mm, DBE/PW 0.4–0.41. **Holotype:** TL 5.6 mm, TL-H 5.2 mm, MW 2.65 mm, TL/MW 2.11; PL 0.85 mm, PW 2.3 mm, PL/PW 0.34; DBE 0.95 mm, DBE/PW 0.41.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and basal band and large apical spot on elytron (Fig. 49).

Head yellowish red, narrowly piceous behind eyes. Pronotum piceous on disc and yellowish red on sides, especially at anterior angles. Elytron piceous, with distinct, rather broad, yellowish red basal band and large, yellow spot on apex often extending between striae and laterally. Scutellum reddish brown to brown. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs distinctly darker, especially distally. Ventral side reddish brown to brown, paler on pro- and metaventrite and abdominal ventrites 1–3.

Surface sculpture: Elytron with 11+(0–1) striae (Fig. 49).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to and larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with several striae or more numerous (in females) laterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, striae 1 and 10 usually shortly reduced basally, stria 1 additionally can be interrupted; submarginal stria absent or present as few tiny striae apically. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw thicker subapically than posterior one and due to this with a shallow median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed, more or less straight apices; lateral side of left dorsal lobe covered with numerous, small spinula-like structures; lateral margin slightly concave apically, without surface structures, smooth; right dorsal lobe covered with large scale-like structures, with large, distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave apically, with apex pointed and slightly curved and membranous right part with long, thin, upwardly curved apex sometimes sticking out in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with relatively dense and long setae occupying approximately half of dorsal margin (Fig. 97).

Female: As males but with stronger dorsal punctation and microreticulation and more numerous pronotal striae.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe not completely covered by spinula-like structures, upper lateral margin without spinulae, smooth in left lateral and ventral views. Based on body size and dorsal colouration, it is similar to *A. flavocapitatus* sp. nov. but differs from it in more elongate habitus, left dorsal lobe of the median lobe with small spinu-

la-like structures and its apical part slender and more elongate. See also under *A. luteomaculatus* and *A. maindai* sp. nov.

Etymology. The species is named after Kokoda Village. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Central Province. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

20. *Austrelatus leptos* sp. nov.

<https://zoobank.org/354B356F-655A-4BCF-9183-0B6A08E01F46>

Figs 1, 59, 107

Type locality. PAPUA NEW GUINEA: Sandaun, Bewani Stn., ca 03°05.130'S, 141°10.227'E, 300 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Sandaun, Bewani Stn., forest puddles @ base of Bewani Mts., 300 m, 12.iv.2006, nr. 03.05.130S 141.10.227E, Balke & Sagata (PNG 38)", "3210" [green label] (ZSM). **Paratypes:** 1 female with the same label as the holotype (ZSM).

Description. Body size and form: Beetle small, distinctly elongate, rather slender (Fig. 1).

Measurements: TL 4.4–4.5 mm, TL-H 4 mm, MW 1.9 mm, TL/MW 2.32–2.37; PL 0.7–0.75 mm, PW 1.8–1.85 mm, PL/PW 0.38–0.42; DBE 0.9 mm, DBE/PW 0.49–0.5. **Holotype:** TL 4.5 mm, TL-H 4 mm, MW 1.9 mm, TL/MW 2.37; PL 0.75 mm, PW 1.8 mm, PL/PW 0.42; DBE 0.9 mm, DBE/PW 0.5.

Colouration: Dorsally yellowish brown to brown, with distinct yellow basal band on elytron and paler head and pronotal sides; both specimens slightly teneral (Fig. 1).

Head yellowish to yellowish brown, narrowly darker behind eyes. Pronotum brown on disc and paler (yellowish brown to yellow) on sides. Elytron brown, with distinct yellow basal band. Scutellum yellowish to brown. Antennae, other head appendages, and pro- and mesolegs yellowish to yellowish brown, metalegs darker, all legs darker distally. Ventral side yellowish to yellowish brown. Most likely, beetles are darker when more mature.

Surface sculpture: Elytron without striae: 0+0, with three or four indistinct puncture lines (Fig. 1).

Head without strioles, with distinct, uneven punctation (spaces between punctures 1–5× size of punctures); punctures fine (diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinctly impressed. Pronotum with short, weak strioles along posterior margin but mainly at posterior angles, with punctation finer and sparser than on head and microreticulation distinct. Elytron without striae, with three or four indistinct puncture lines (first line near suture sometimes reduced) and separate large punctures between them. Elytron with very fine, sparse punctation and distinct microreticulation.

Structures: Head large and broad. Pronotum slightly trapezoid, its lateral margins subparallel. Base of prosternum broadly rounded anteriorly, slightly convex medially; blade of prosternal process broad.

Male: Protibia straight, not modified. Proclaws long, slightly curved, subequal in size and form. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with scale-like structures; left dorsal lobe with lateral margin slightly concave apically and with some spinula-like structures medially in left lateral view; apex of left dorsal lobe straight, broadly pointed; left lobe of ventral sclerite with elongate, narrow sclerotised area visible in left lateral view, its apex slightly curved upwards; right lobe of ventral sclerite membranous, with long, thin, upwardly curved apex distinctly sticking out in left lateral view. Parameres with relatively dense and long setae occupying more than half of dorsal margin (Fig. 59).

Female: As male.

Variability. There is an insignificant variation in the colouration and dorsal punctation described above.

Affinities. The species is very distinct due to its small size, elongate, slender habitus, colouration, elytra without striae, and shape of the median lobe.

Etymology. The species name is a Greek adjective meaning “thin, fine, slender” and indicates small, elongate habitus of the species.

Distribution. Papua New Guinea: Sandaun Province. The species is known only from the type locality (Fig. 107).

Habitat. The species was collected in forest puddles.

21. *Austrelatus loloki* sp. nov.

<https://zoobank.org/EA370DAB-AC2D-4EFC-9361-94D07609E02A>

Figs 23, 74, 107

Type locality. PAPUA NEW GUINEA: National Capital District: ca. 16 km N from Port Moresby, Loloki River.

Type material. Holotype: male “Stn. No. 208”, “Papua: Loloki c. 10 m. N. of Pt. Moresby, 19.III.1965.”, “M.E. Bacchus. B.M. 1965-120” (BMNH).

Description. Body size and form: Beetle small, with oblong-oval habitus (Fig. 23).

Measurements: Holotype: TL 5 mm, TL-H 4.5 mm, MW 2.4 mm, TL/MW 2.08; PL 0.75 mm, PW 2.1 mm, PL/PW 0.36; DBE 0.8 mm, DBE/PW 0.38.

Colouration: Dorsally dark brown, elytron with faint yellowish shoulder spot and apicolaterally (Fig. 23).

Head dark brown, narrowly piceous behind eyes and paler on clypeus and posteromedially. Pronotum dark brown on disc and reddish on sides. Elytron dark brown, paler basally, with faint yellowish shoulder spot, yellow at apex and narrowly laterally in more than apical 1/2. Scutellum reddish brown. Antennae, other head appendages, and legs yellowish brown, darker distally. Ventral side brown.

Surface sculpture: Elytron with 11 complete, relatively strongly impressed striae, submarginal stria present: 11+1 (Fig. 23).

Head with few striae between eyes, with distinct, rather dense punctation (spaces between punctures 1–5× size of punctures); punctures relatively coarse (diameter of punctures slightly larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum complete covered with sparse but distinct striae absent at anterior angles, with punctation finer than on head and microreticulation distinct. Elytron with 11 complete, relatively strongly impressed striae, submarginal stria present, long. Elytron with fine punctation and distinct microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively short, slightly curved, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with scale-like structures; left dorsal lobe with lateral margin slightly concave medially, with apex truncate and slightly curved downwards; right dorsal lobe narrowed subapically, with broad, rounded apex; lobes of ventral sclerite elongate, mostly sclerotised, almost invisible in lateral view. Parameres with rather short and sparse setae occupying slightly more than half of dorsal margin (Fig. 74).

Female: Unknown.

Affinities. The species is well-recognisable by its smaller size, uniform, brown dorsal colouration, strong elytral striation and striolation of head and pronotum, and characteristic shape of the median lobe and paramere setation.

Etymology. The species is named after Loloki River. The name is a noun in the nominative singular standing in apposition.

Distribution. Papua New Guinea: National Capital District. The species is known only from the type locality (Fig. 107).

Habitat. Unknown.

22. *Austrelatus lopintolensis* sp. nov.

<https://zoobank.org/42A389E2-FBDD-4483-A76F-BD6D141B13FB>

Figs 3, 66, 107

Type locality. INDONESIA: West Papua Province: Raja Ampat Regency, Waigeo Island, Lopintol, Bajon River, 0°07'S, 130°53'E.

Type material. Holotype: male "MB759" [green label], "W-PAPUA Raja Ampat Prov. Waigeo Isl., Lopintol, Bajon River, 0°07'S, 130°53'E 11.I.2004 leg. A.", "W Papua: Raja Ampat, Waigeo, Lopintol, 11i2004, A. Skale, MB 759" (MZB).

Paratype: 1 male "W-PAPUA Raja Ampat Prov. Waigeo Isl., Lopintol 0°07'54"S, 130°53'45"E 11.I.2004 leg. A. Skale UWP" (CAS).

Description. Body size and form: Beetle small, elongate (Fig. 3).

Measurements: TL 4.7–4.85 mm, TL-H 4.3–4.35 mm, MW 2.1–2.2 mm, TL/MW 2.21–2.24; PL 0.7–0.75 mm, PW 1.9–2 mm, PL/PW 0.37–0.38; DBE 0.9–0.95 mm, DBE/PW 0.47–0.48. **Holotype:** TL 4.7 mm, TL-H 4.3 mm, MW 2.1 mm, TL/MW 2.24; PL 0.7 mm, PW 1.9 mm, PL/PW 0.37; DBE 0.9 mm, DBE/PW 0.47.

Colouration: With dark brown elytra and paler head and pronotal sides; yellow basal band on elytron distinct (Fig. 3).

Head reddish, narrowly darker behind eyes. Pronotum dark brown on disc and gradually paler (to yellowish red) to sides. Elytron dark brown, with distinct yellowish red basal band and pale brown apex. Scutellum brown. Antennae, other head appendages, and pro- and mesolegs yellow, metalegs darker, all legs darker distally. Ventral side yellowish red.

Surface sculpture: Elytron with six dorsal striae and a submarginal stria: 6+1 (Fig. 3).

Head without striae, with distinct, uneven punctation (spaces between punctures 1–5× size of punctures); punctures relatively fine (diameter of punctures more or less equal to diameter of microreticulation cells); microreticulation dis-

tinct. Pronotum without striae, with punctation sparser and microreticulation finer than on head. Elytron with six dorsal striae, striae 1–4 complete, stria 5 reduced basally, stria 6 reduced apically. Elytron with fine punctation and microreticulation.

Structures: Head large and broad. Pronotum trapezoid, its lateral margins slightly convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively short, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with scale-like structures; left dorsal lobe with lateral margin thickened apically in kind of bead or crest and concave medially, which gives median lobe calla-like shape; this apical crest of left dorsal lobe with small but distinct numerous spinula-like structures; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, its apex sharply pointed and curved upwards; right ventral lobe more membranous, longer than left lobe, with pointed apex. Parameres with dense, long setae occupying more than half of dorsal margin, proximally shorter and sparser (Fig. 66).

Female: Unknown.

Affinities. In body size and shape, elytral striation and dorsal colouration, the species is similar to *A. procerus* sp. nov. and *A. ohu* sp. nov. but distinctly differs from them by its calla-like shape of the median lobe and complete, more strongly impressed elytral striae.

Etymology. The species is named after its type locality, Lopintol. The name is an adjective in the nominative singular.

Distribution. Indonesia: West Papua Province: Raja Ampat Regency, Waigeo Island (Fig. 107).

Habitat. The species was collected in a shaded side pool of a larger river.

23. *Austrelatus luteomaculatus* (Guignot, 1956)

Figs 18, 19, 70, 107

Copelatus luteomaculatus Guignot 1956: 53; Guéorguiev 1968: 21; Guéorguiev and Rocchi 1993: 159; Nilsson and Hájek 2023: 50.

Austrelatus luteomaculatus (Guignot, 1956): Shaverdo et al. 2023: 7.

Type locality. PAPUA NEW GUINEA: Madang Province, Astrolabe Bay, Stephansort, 05°26'38.4"S, 145°44'47.8"E.

Type material. Holotype: male "N. Guinea Biró 97.", "Stephansort Astrolabe B", "Holotypus 1956 ♂ *Copelatus luteomaculatus* Guignot" [label with red frame, partly hw by Guignot], "Type" [red label], "Dr F. Guignot det., 1955 *Copelatus luteomaculatus* sp.n. HoloType ♂" [partly hw by Guignot] (HNHM). **Paratypes:** 1 female "N. Guinea Biró 97.", "Stephansort Astrolabe Bai // 18.V. [hw on reverse side]", "♀", "Paratype" [red label with black frame] (MNHN); 2 males "N. Guinea Biró 1898", "Simbang Huon Golf // IX.17. [hw on reverse side]", "♂", "Paratype" [red label with black frame] (MNHN); 2 females "N. Guinea Biró 1898", "Simbang Huon Golf // IX.17. [hw on reverse side]", "Paratypus 1956 *Copelatus luteomaculatus* Guignot" [label with red frame, partly hw by Guignot] (HNHM).

Additional material. PNG: Morobe: 2 males, 1 female “Papua New Guinea: Morobe, Patep, 700m, 20.xi.2006, 06.58.267S 146.37.895E, Balke & Kinibel (PNG 105)” (NHMW, ZSM). 1 female “Papua Neuguinea Morobe Provinz Wau Ecology Institute”, “Wau Station 1217m 15.4.1999 073386S 1467083E leg. M.Schaarschmidt/H.Deumer A.Michalczyk” (ZSM). 2 males, 3 females “Papua New Guinea: Morobe, Herzog Mts., Bundun, 700–800m, 2.iv.2006, 06.51.598S 146.37.07E, Balke & Sagata (PNG 27)” (NHMW, ZSM). 2 males “Papua New Guinea: Morobe, Herzog Mts., backroad to Wagau, 100m, 3.iv.2006, Balke & Sagata (PNG 29)” (ZSM). 1 male “3236” [green label], “Papua New Guinea: Morobe, Huon Pen., rd to Kwapsanek, 250m, 31.iii.2006, 06.30.270S 146.59.581E, Balke & Sagata (PNG 24)” (ZSM). 1 female “Papua New Guinea: Morobe, Sattelberg, Iunjaing, 840m, 16.x.2009, 06.27.239S 147.42.531E, Idaho (09) (PNG209)” (ZSM). 25 males, 16 females “Papua New Guinea: Morobe, Menyamy, coffee garden, 1000m, 14.xi.2006, 07.13.714S 146.01.260E, Balke & Kinibel (PNG 99)”, two males with green labels “3225” and “3226” (NHMW, ZSM). 6 males, 8 females “Stn. No. 114”, “New Guinea: Morobe Distr., Markham R. Valley. Gusap, c.90 m. W. of Lae. 1000ft. 3.xii.1964”, “M.E. Bacchus B.M. 1965-120” (BMNH, NHMW). 3 males, 8 females “Stn. No. 158”, “New Guinea: Morobe Distr., Gusap, Markham Valley. c.90 m. W. of Lae. 1,000 ft. 27-30.i.1965”, “M.E. Bacchus B.M. 1965-120” (BMNH, NHMW). 2 males, 1 female “Stn. No. 159”, “New Guinea: Morobe Distr., Gusap, Markham Valley. c.90 m. W of Lae. 1,000 ft. 27-30.i.1965”, “M.E. Bacchus B.M. 1965-120” (BMNH). 1 male, 1 female “Stn. No. 160”, “New Guinea: Morobe Distr., Gusap, Markham Valley. c.90 m. W. of Lae. 1,000 ft. 27-30.i.1965”, “M.E. Bacchus B.M. 1965-120” (BMNH). 1 male, 4 females “Stn. No. 161”, “New Guinea: Morobe Distr., Gusap, Markham Valley. c.90 m. W. of Lae. 1,000 ft. 27-30.i.1965”, “M.E. Bacchus B.M. 1965-120” (BMNH). 1 female “Stn. No. 131”, “New Guinea: Morobe Distr., Lae-Bulolo Rd., 30.xii.1964.”, “M.E. Bacchus B.M. 1965-120” (BMNH). 8 males, 11 females “Stn. No. 127”, “New Guinea: Morobe Distr., Bulolo, 2,070ft. 28.xii.1964.”, “M.E. Bacchus B.M. 1965-120” (BMNH, NHMW). **Madang:** 2 males “Papua New Guinea: Madang, Mt Tapo, 180m, ii.2008, 5.24.11.00S 145.36.17.16E, BRC leg. (PNG 178)” (ZSM). 1 male, 2 female “Papua New Guinea: Madang, Brahmin, 150m, 26IX2002, 5 44.953S 145 20.844E Balke & Sagata (PNG 024)” (ZSM). **Gulf:** 2 males “Papua New Guinea: Gulf, 1500m, 13.xi.2006, 07.11.721S 145.54.746E, Balke & Kinibel (PNG 95)”, one male with a green label “4244” (ZSM).

Description. Body size and form: Beetle medium-sized, with oblong-oval habitus (Figs 18, 19).

Measurements: TL 5.55–6.6 mm, TL-H 5.1–6 mm, MW 2.7–3.2 mm, TL/MW 2.06–2.07; PL 0.8–0.95 mm, PW 2.3–2.8 mm, PL/PW 0.34–0.35; DBE 0.85–1.01 mm, DBE/PW 0.36–0.39. **Holotype:** TL 6.2 mm, TL-H 5.6 mm, MW 3 mm, TL/MW 2.07; PL 0.9 mm, PW 2.6 mm, PL/PW 0.35; DBE 1 mm, DBE/PW 0.39.

Colouration: Dorsally piceous, with yellowish red head, pronotal sides, basal band and apex of elytron (Figs 18, 19).

Head yellow to red, narrowly piceous behind eyes and darker on clypeus. Pronotum piceous, with yellow to red anterior angles and relatively narrowly on sides, darker to posterolateral angles. Elytron piceous, with bright yellow to red basal band and largely yellow apex, especially between striae. Scutel-

lum reddish to piceous. Antennae, other head appendages, and pro- and meso-legs yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown, yellowish red on head, pro- and metaventrite. The holotype is a teneral specimen, therefore, distinctly paler.

Surface sculpture: Elytron with six dorsal striae and with or without submarginal stria: 6+(0–1) (Figs 18, 19).

Head without strioles, with distinct, relatively sparse punctation (spaces between punctures 2–5× size of punctures); punctures very fine (diameter of punctures smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with strioles laterally (few at posterolateral angles to rather numerous but sparse on sides), with punctation slightly denser than on head and microreticulation fine. Elytron with six dorsal striae; striae 1, 5, and 6 reduced basally; striae 1 and 5 sometimes more strongly reduced and present only in apical 1/2; sometimes with single strioles between striae; submarginal stria absent or present, sometimes as fine strioles apically. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum narrowly rounded anteriorly, distinctly convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively short, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length; left dorsal lobe gradually tapering, covered with very dense spinula-like structures except for thickened lateral margin, with apex rounded and more or less straight; right dorsal lobe covered with large scale-like structures, without membranous area medially; lobes of ventral sclerite partly sclerotised, subequal in length, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, well-visible in left lateral view, its apex pointed and curved; right ventral lobe more membranous, slightly longer than left lobe, with apex pointed and slightly curved. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 70).

Female: As male.

Variability. There is an insignificant variation in the elytral striation and colouration.

Affinities. In colouration and in shape and surfaces structure of the median lobe, the species is similar to *A. flavocapitatus* sp. nov. and *A. kokodensis* sp. nov. but differs from them in larger size, lesser elytral striation and dorsal sclerite shape of the median lobe. *Austrelatus flavocapitatus* sp. nov. has 10 dorsal elytral striae and left lobe of the dorsal sclerite with more concave lateral margin and apex gently curved downwards (with more straight lateral margin and apex gently curved upwards in *A. luteomaculatus*). *Austrelatus kokodensis* sp. nov. has 11 dorsal elytral striae and left dorsal lobe with more concave lateral margin (with more straight lateral margin in *A. luteomaculatus*). Two latter species have right lobe of the dorsal sclerite with membranous area medially, which is lacking in *A. luteomaculatus*.

Distribution. Papua New Guinea: Madang, Morobe, and Gulf provinces (Fig. 107).

Habitat. The species was collected in shallow and shaded forest pools.

24. *Austrelatus madangensis* sp. nov.

<https://zoobank.org/BF54D803-7FAF-4A4C-B253-09057B90BF79>

Figs 38, 39, 88, 108

Type locality. PAPUA NEW GUINEA: Madang Province, Wannang, 05°17.235'S, 145°06.160'E, 230 m a.s.l.

Type material. Holotype: male “Papua New Guinea: Madang, Wannang, 230m 3.x.2008, 05.17.235S 145.06.160E, Posman (PNG188)” (ZSM). **Paratypes:** **PNG: Madang:** 12 males, 12 females with the same labels as the holotype, one of males additionally with a green label “3765” (NHMW, ZSM). 2 males, 1 female “Papua New Guinea: Madang, Wannang, 270m, 31.x.2008, 05.15.458S 145.02.389E, Posman, (PNG187)”, males with additional green labels “4171” and “3792” (ZSM). 1 male “Papua New Guinea: Wanang I, river, 25.ix.2013, Boukal, 44/2013” (NHMW). 1 female “Ibisca Niugini, PNG 2-4.xii.2012 Wannang -5,227670193 145,0797424”, “FIT-WAN-T-8/8-d16 / Plot 20 / P0707 Vial 22371-CODYTI” (ZSM). 1 male, 1 female “Papua New Guinea: Wanang, Kusa, 24.ix.2013, Boukal, 39/2013” (ZSM). 1 male “Papua New Guinea: Wanang - Kusa, Digitam, 24.ix.2013, Boukal, 40/2013” (ZSM). 4 males, 3 females “PNG Madang Province OHU Village, 14.1.2001 leg.: Lukas Cizek Coll. HENDRICH” (CLH). 1 female “Papua New Guinea: Madang, Madang, Ohu Village, 160m, 30.iv.2006, 05.13.923S 145.40.763E, Balke & Manaono (PNG 49) (ZSM). 1 male, 1 female “Papua New Guinea: Madang, Usino, 260m, 15.iii.2007, 05.31.125S 145.25.316E, Kinibel (PNG 158)” (ZSM). 6 males, 7 females “Papua New Guinea: Madang, Akameku-Brahmin, Bismarck Range, 250–500m, 25.xi.2006, nr 05.47.026S 145.24.131E, Balke & Kinibel (PNG 115)” (NHMW, ZSM). 1 female “Ibisca Niugini, PNG 7–9.xi.2012 Mount Wilhelm 200m -5,739897251 145,3297424 MW0200 / P0866 Vial 07444” (ZSM). 1 male “Ibisca Niugini, PNG 1–3.xi.2012 Mount Wilhelm 200m”, “-5,739897251 145,3297424 FIT-MW200-T-4/8-d08 / P0863 Vial 07369-CODYTI” (ZSM). 1 male “Papua New Guinea Madang Prov. 2002 Hulcr”, “coll. Jiří Hájek National Museum Prague, Czech Republic” (NMPC). 3 males, 3 females “Papua New Guinea: Madang, Adelbert Mts., Keki to Sewan, 650m, 7.v.2006, 04.41.802S 145.25.460E, Balke (PNG 54)”, one male with an additional green label “3202” (NHMW, ZSM). 1 male “Papua New Guinea: Madang, Adalbert [sic!] Mts., Keki, 850m, 4.v.2006, nr 04.42.300S 145.25.089E, Balke & Manaono (PNG 52)”, “3206” [green label] (ZSM). 1 male, 1 female “Papua New Guinea: Madang, Keki – Sewan, Adalbert [sic!] Mts., 700m, 30.xi.2006, nr 04.41.802S 145.25.460E, Binatang Boys (PNG 120)” (NHMW, ZSM). 1 male “N. Guinea Biró 97.”, “Stephansort Astrolabe B.”, “♂”, “pauensis Balf.-Br.” [hw, Guignot], “MUSEUM PARIS 1960 Coll. F.GUIGNOT” [pink label], “MNHN, Paris EC29237 [with QR code]” (MNHN). **East Sepik:** 2 males “Papua New Guinea: East Sepik, Lembena, 198m, 3.ix.2009, 04.56.974S 143.56.995E, Ibalim & Pius (PNG241)” (ZSM). 1 male, 2 females “Papua New Guinea: East Sepik, Lembena, 198m, 3.ix.2009, 04 46 [!] 974S 143.56.995E, Ibalim & Pius (PNG243)” (ZSM). 1 female “Papua New Guinea: East Sepik, Lembena, 127m, 3.ix.2009, 04 56.953S 143 56.614E, Ibalim & Pius (PNG246)” (ZSM). 9 males, 9 females “Papua New Guinea: East Sepik, Lembena, 117m, 8.ix.2009, 04 57.513S 143 57.296E, Ibalim & Pius (PNG248)”, four males and one female with additional green text labels “5989”, “5991”, “5992”, “5993”, and “5990”, respectively (ZSM). 6 males, 2 females “Papua New Guinea: East Sepik, Lembena,

110m, 10.ix.2009, 04.57.512S 143.57.366E, Ibalim & Pius (PNG249)” (ZSM). 2 males, 1 female “Papua New Guinea: East Sepik, Lembena, 335m, 10.ix.2009, 04.56.859S 143.59.375E, Ibalim & Pius (PNG250)” (ZSM). 2 females “Papua New Guinea: East Sepik, Lembena, 335m, 10.ix.2009, 04 56.859S 143 57.379E, Ibalim & Pius (PNG251)” (ZSM). 1 male “Papua New Guinea: East Sepik, Lembena, 335m, 10.ix.2009, 04 56.921S 143 57.478E, Ibalim & Pius (PNG252)” (ZSM). 2 males, 1 female “Papua New Guinea: East Sepik, Prince Alexander Mts., Wewak-Angoram, 300m, 21.iv.2006, 03.42.129S 143., Balke (PNG 46)”, female with a green label “3222” (ZSM). **EHL:** 1 male “6438”, “Papua New Guinea: Eastern Highlands, Bena – pass to Goroka valley, 1550m, 5.iv.2006, 06.14.567S 145.29.634E, Balke & Sagata (PNG33)” (ZSM).

Description. Body size and form: Beetle large, oblong-oval (Figs 38, 39).

Measurements: TL 6.8–8.15 mm, TL-H 6.2–7.35 mm, MW 3.25–4 mm, TL/MW 2.04–2.09; PL 1–1.2 mm, PW 2.9–3.55 mm, PL/PW 0.34–0.35; DBE 1.15–1.35 mm, DBE/PW 0.37–0.4. **Holotype:** TL 7.6 mm, TL-H 6.8 mm, MW 3.7 mm, TL/MW 2.08; PL 1.15 mm, PW 3.25 mm, PL/PW 0.35; DBE 1.2 mm, DBE/PW 0.37.

Colouration: Elytron yellowish red to reddish brown between striae, piceous on pronotal disc, with yellowish red head and pronotal sides (Figs 38, 39).

Head yellowish red, narrowly darker behind eyes. Pronotum brown to piceous on disc and gradually paler (to yellowish red) to sides. Elytral colouration varies: usually yellowish red to reddish brown between striae and piceous on striae, sometimes narrowly brown to piceous on disc, seldom elytron brown to piceous, with yellowish red basal band and yellow apex or apical 1/2. Scutellum yellowish red to brown. Antennae, other head appendages, and pro- and mesolegs yellowish red to reddish, metalegs darker, all legs darker distally. Ventral side brown, paler on prosternum and posteriorly and laterally on metacoxal plates and abdominal ventrites.

Surface sculpture: Elytral striation varies: usually elytron with 11 dorsal striae, stria 1 or striae 1–3 reduced in basal 1/2, sometimes stria 1 absent and other reduced or interrupted in basal 1/2, submarginal stria present: (10–11)+1 (Figs 38, 39).

Head without striae, with rather sparse punctation (spaces between punctures 1–5× size of punctures); punctures rather fine (usually diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without or with striae posterolaterally, more numerous in females, with punctation finer than on head and microreticulation fine. Elytral striation varies: usually elytron with 11 dorsal striae, stria 1 or striae 1–3 absent in basal 1/2, sometimes more striae (e.g., striae 5–7, 9) reduced basally or differently interrupted; maximal reduction with stria 1 absent and almost all other striae absent or interrupted in basal 1/2; submarginal stria present, sometimes as apical striae. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia more or less straight: its ventral margin slightly curved proximally. Proclaws long, subequal in length, anterior claw thicker apically and more strongly curved downwards than posterior one and due to this with a subapical

incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe slightly concave medially, its whole apical 1/2 broad, more or less evenly tapering to rather large, curved downwards, truncate apex bearing broad crest; right dorsal lobe shorter than left one, broad, with pointed apex and membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, slightly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae (sometimes visible at apex); right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 88).

Female: Dimorphic: as male, but with much more numerous pronotal striae and distinctly denser punctation and stronger microreticulation on pronotum and elytron, and matt, with pronotum and elytron very densely covered with fine longitudinal striae. Interestingly, the matt forms are characteristic only for the populations with male specimens having reduced elytral striae, e.g., ones of Adelbert and Alexander Mts or Ohu Village. In latter population, the normal form is also present but less numerous: ratio shiny to with striae is 1:3.

Variability. There is a strong variation in dorsal colouration and striolation as described above. As mentioned above, specimens with reduced elytral striae are observed in three regions: Ohu Village and, especially Adelbert and Alexander Mts. Beetles from the two latter regions also have larger, broader, and more robust habitus and sturdier median lobe of aedeagus.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, in shape of the median lobe, it is similar to *A. mamberamo* sp. nov. and differs from it in more pale elytral colouration and apex of left dorsal lobe of the median lobe shorter, with more vertical, broader crest. See also under *A. mamberamo* sp. nov.

Etymology. The species is named after Madang Province where it is largely distributed. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Madang, Eastern Highlands and East Sepik provinces (Fig. 108).

Habitat. Unknown.

25. *Austrelatus maindai* sp. nov.

<https://zoobank.org/E25F8356-6F8B-454C-B882-48957BC20320>

Figs 47, 96, 108, 114

Type locality. INDONESIA: Papua Province: Sarmi Regency, Waskey, 01°58'17.0"S, 138°50'56.9"E, 70 m a.s.l.

Type material. Holotype: male "Indonesia: Papua, Sarmi area, 70m, 25.ix.2014, -1.9713908 138.8491402, Tim UNCEN: Balke & Menufandu (Pap032)" (KSP).

Paratypes: 2 males, 1 female with the same label as the holotype, one male with an additional green text label "6469" (MZB, ZSM). 1 male "Indonesia: Papua, Sarmi, Waaf, N Foja Mts, waterfall in forest, 120m, 23.ix.2014, -2.3317793, 138.7500472, Tim UNCEN: Balke & Menufandu (Pap031)", "6467" [green text]

(ZSM). 1 male "Indonesia: Papua, Foja Mountaints N foot, N Waaf vill., pondok, 150m, 4.-7.vi.2016," "-2.06142 138.743949, Sumoked (Pap061)" (NHMW). 1 male, 1 female "Indonesia: West Papua, Sarmi Dest, Tor riv. Togonfo vill. 2°15'07.03"S 138°51'25.89"E, 80 m, hollowed log with water, 25.v.2019, leg. Bretschneider Exp." (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 47).

Measurements: TL 5.4–5.7 mm, TL-H 4.95–5.25 mm, MW 2.6–2.7 mm, TL/MW 2.04–2.11; PL 0.8–0.85 mm, PW 2.3–2.4 mm, PL/PW 0.35; DBE 0.9–0.95 mm, DBE/PW 0.38–0.4. **Holotype:** TL 5.5 mm, TL-H 5.1 mm, MW 2.7 mm, TL/MW 2.04; PL 0.85 mm, PW 2.4 mm, PL/PW 0.35; DBE 0.9 mm, DBE/PW 0.38.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and basal band and large apical spot on elytron (Fig. 47).

Head yellowish red, narrowly piceous behind eyes. Pronotum piceous on disc and yellowish red on sides, especially at anterior angles. Elytron piceous, with distinct, rather broad, yellowish red basal band and large, often extending between striae and laterally, yellow spot on apex. Scutellum reddish brown to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs distinctly darker, especially distally. Ventral side reddish brown to brown, paler on pro- and metaventricle and abdominal ventrites 1–3.

Surface sculpture: Elytron with 11+1 striae (Fig. 47).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to and larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with several striae posterolaterally or in females, more numerous laterally, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae, striae 1 and 10 usually shortly reduced basally; submarginal stria present. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw thicker subapically than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed, more or less straight apices; lateral side of left dorsal lobe with large but shallow, subapical concavity, covered with numerous, small spinula-like structures; lateral margin slightly concave apically, without surface structures, smooth; right dorsal lobe covered with large scale-like structures, with very small, indistinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved to right and membranous right part with long, thin, upwardly curved apex distinctly projecting in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with dense, long setae occupying distinctly more than half of dorsal margin; setae on small area proximally shorter and sparser, several most proximal setae standing separately (Fig. 96).

Female: As males but with stronger dorsal punctation and microreticulation and more numerous pronotal striae.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe not completely covered by spinula-like structures, upper lateral margin without spinulae, smooth in left lateral and ventral views. Based on body size and shape and dorsal colouration, it is similar to *A. flavocapitatus* sp. nov. and *A. kokodensis* sp. nov. but differs from them in left dorsal lobe of the median lobe with large lateral concavity.

Etymology. The species is named after our colleague Tobias Mainda, a great naturalist and next-generation rove beetle expert. The specific epithet is a substantive in the genitive case.

Distribution. Indonesia: Papua Province: Sarmi Regency (Fig. 108).

Habitat. In Foja Mts, the species was collected from small puddles near a waterfall in forest. The specimens from Togonfo were sampled from a water-filled hollow in a tree trunk (Fig. 114).

26. *Austrelatus mamberamo* sp. nov.

<https://zoobank.org/0A2FE69A-DF08-46F5-BCC6-4F8BC9CEC018>

Figs 40, 89, 108

Type locality. INDONESIA: Papua Province: Mamberamo Raya Regency, Rouffaer Mts, Noiadi, ca. 02°46'S, 137°46'E, 150–200 m a.s.l.

Type material. Holotype: male "IRAN JAYA: Jayapura Prov. Mamberamo, Rouffaer Mts., Noiadi, 150–200m 17.3.1999, leg. Riedel" (NHMW). **Paratypes:** 1 male with the same label as the holotype (NHMW).

Description. Body size and form: Beetle large, oblong-oval (Fig. 40).

Measurements: TL 7.5–7.9 mm, TL-H 6.8–7.3 mm, MW 3.6–3.9 mm, TL/MW 2.03–2.08; PL 1.1–1.15 mm, PW 3.3–3.45 mm, PL/PW 0.33; DBE 1.3–1.35 mm, DBE/PW 0.39. **Holotype:** TL 7.5 mm, TL-H 6.8 mm, MW 3.6 mm, TL/MW 2.08; PL 1.1 mm, PW 3.3 mm, PL/PW 0.33; DBE 1.3 mm, DBE/PW 0.39.

Colouration: Dorsally piceous, with reddish brown head and reddish pronotal sides, elytral basal band and apex (Fig. 40).

Head reddish brown, narrowly darker behind eyes. Pronotum piceous on disc and gradually paler (to reddish) to sides. Elytron piceous, with narrow yellowish red to reddish basal band and yellowish red spot on apex. Scutellum reddish brown to piceous. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs darker, all legs darker distally. Ventral side piceous, paler on prosternum and posteriorly on metacoxal plates and abdominal ventrites.

Surface sculpture: Elytron with 11 dorsal striae, stria 1 reduced to striae in apical 1/2, some other striae reduced or interrupted basally, submarginal stria present: 11+1 (Fig. 40).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum without or with few striae posterolaterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae: stria 1 absent on basal 1/2 and reduced to striae in apical 1/2, striae 2 and 3 strongly reduced basally, sometimes striae 5–7 shortly reduced basally;

submarginal stria present, long. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia modified: thinner proximally and broader medially and distally due to its curved ventral margin. Proclaws long, subequal in length, anterior claw thicker apically and more strongly curved downwards than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe slightly concave medially, its whole apical 1/2 broad, more or less evenly tapering to rather large, elongate, curved downwards, truncate apex bearing broad crest; right dorsal lobe shorter than left one, broad, with pointed apex and membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, slightly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae (sometimes visible at apex); right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 89).

Female: Unknown.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, in shape of the median lobe, it is similar to *A. madangensis* sp. nov. and differs from it in elytron darker, with narrow, yellowish red basal band and apex of left dorsal lobe of the median lobe more elongate, with more transverse, narrower crest. See also under *A. madangensis* sp. nov. and *A. noiadi* sp. nov.

Etymology. The species is named after the Mamberamo Raya Regency. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province: Mamberamo Raya Regency. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

27. *Austrelatus mianminensis* sp. nov.

<https://zoobank.org/0C7A4E92-B360-4057-B2F4-64E348F98101>

Figs 44, 93, 108

Type locality. PAPUA NEW GUINEA: Sandaun Province, Mianmin, 04°53'17.5"S, 141°34'07.1"E, 670 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Sandaun, Mianmin, 670m 20.x.2008, 4.53.292S 141.34.118E, Ibalim (PNG 191)" (ZSM). **Paratypes:** **PNG: Sandaun:** 22 male, 36 female with the same label as the holotype (NHMW, ZSM). 1 male, 1 female "Papua New Guinea: Sandaun, Mianmin (pool), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 193)" (ZSM). 1 male, 1 female "Papua New Guinea: Sandaun, Mianmin (pool), 1080m, 24.x.2008, 04.55.780S 141.38.185E, Ibalim (PNG 196)", male with an additional green label "3771" (ZSM). 2 males, 2 females "Papua New Guinea: Sandaun, Mianmin (river) 700m,

21.x.2008, 04.52.858S 141.31.706E Ibalim (PNG 197)", one male with an additional green label "3786" (ZSM). 8 males, 14 females "Papua New Guinea: Sandaun, Mianmin (pool), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 198)" (NHMW, ZSM). 7 males, 7 females "Papua New Guinea: Sandaun, Mianmin, 670m, 22.x.2008, 04.53.329S 141.35.263E S. Ibalim PNG189" (NHMW, ZSM). 5 males, 1 female "Papua New Guinea: Sandaun, Mianmin area, >700m, 7.i.2010, Ibalim & Pius (PNG231)", two males with additional green text labels "6017" and "6018" (ZSM). 1 male "Papua New Guinea: Sandaun, Mianmin, Fak River, 775m, 13.xi.2003, 4.53.53.00S 141.36.39.40E, K. Sagata (WB31)", "4197" [green label] (ZSM).

Additional material. PNG: Madang: 1 male, 4 females "Papua New Guinea: Madang, Trans Gogol, 30 m, ii.2008, 5 18.0915S 145 36.4532E, BRC leg. (PNG 179)" [teneral specimens] (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 44).

Measurements: TL 5.6–6.4 mm, TL-H 5.2–5.8 mm, MW 2.8–3.1 mm, TL/MW 2–2.07; PL 0.8–0.9 mm, PW 2.3–2.6 mm, PL/PW 0.34–0.35; DBE 0.9–0.95 mm, DBE/PW 0.36–0.39. **Holotype:** TL 6 mm, TL-H 5.5 mm, MW 2.9 mm, TL/MW 2.07; PL 0.85 mm, PW 2.5 mm, PL/PW 0.34; DBE 0.9 mm, DBE/PW 0.36.

Colouration: Dorsally piceous, with yellowish red to reddish brown head, anterior angles of pronotum, and yellow to yellowish red spot on elytral apex (Fig. 44).

Head yellowish red to reddish brown, narrowly piceous behind eyes. Pronotum piceous, yellowish red to reddish brown in anterior of sides, sometime more, sometimes less extending. Elytron piceous, with yellow to yellowish red apical spot, sometimes rather small and rounded, sometimes larger or even slightly extending laterally. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red to reddish brown, metalegs darker, especially distally. Ventral side piceous, with brown prosternum.

Surface sculpture: Elytron with 11+1 striae; stria 1 often differently reduced (Fig. 44).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to or larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with distinct striae laterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 usually weakly impressed, often absent in basal 1/2 or present as striae, maximal reduction to few striae in apical 1/2, striae 2 and 10 can be shortly reduced basally; submarginal stria present. Elytron with fine but distinct punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw thicker at its apex than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, more or less straight, with very broadly pointed apices, apex of left dorsal lobe slightly curved downwards; left dorsal lobe with lateral side covered with numerous, distinct, strong spinula-like structures; lateral margin apically without surface structures, smooth; right dorsal lobe covered with scale-like structures, with distinct median membranous

area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved to right and membranous right part long, thin, apically covered with setae sometimes visible in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with dense, long setae occupying slightly more than 1/2 of dorsal margin (Fig. 93).

Female: As males but with stronger dorsal punctation and microreticulation and pronotum with striae, usually numerous, occupying sides completely so that only disc without striae.

Variability. There is a variation in dorsal colouration and striation as described above.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe not completely covered by spinula-like structures, upper lateral margin without spinulae, smooth in left lateral and ventral views. Based on body size and shape and dorsal colouration and striation, it is similar to *A. kalibumi* sp. nov. but differs from it in paler head colour and median lobe without concavity of its left dorsal lobe. See also under *A. pseudomianminensis* sp. nov., *A. flavocapitatus* sp. nov. and *A. sararti* sp. nov.

Etymology. The species is named after Mianmin area. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea. The species is mainly known from Mianmin area of the Sandaun Province; five teneral specimens, most likely belonged to the species, are recorded from Madang Province (Fig. 108).

Habitat. In the Mianmin area, the species was collected from a forest pool and a river side pool.

28. *Austrelatus miltokarenos* sp. nov.

<https://zoobank.org/7AD55950-D944-45DC-B20D-AA5DD62DEC53>

Figs 22, 73, 107

Type locality. PAPUA NEW GUINEA: Morobe Province, Garaina, 07°52.516'S, 147°10.427'E, 770 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Garaina, 770m, vi.2008 07.52.516S 147.10.427E Ibalim & Sosanika (PNG219)" (ZSM). **Paratypes:** 2 males, 4 females with the same label as the holotype (NHMW, ZSM). 1 female "Papua New Guinea: Garaina, 770m, 25.vi.2008, 07 50.859S 147 08.614E, Ibalim & Sosanika, (PNG222)" (ZSM)

Description. Body size and form: Beetle large, elongate (Fig. 22).

Measurements: TL 7.3–8.2 mm, TL-H 6.5–7.4 mm, MW 3.3–3.8 mm, TL/MW 2.16–2.21; PL 1.1–1.25 mm, PW 2.95–3.45 mm, PL/PW 0.36–0.37; DBE 1.25–1.4 mm, DBE/PW 0.41–0.42. **Holotype:** TL 8.2 mm, TL-H 7.4 mm, MW 3.8 mm, TL/MW 2.16; PL 1.25 mm, PW 3.45 mm, PL/PW 0.36; DBE 1.4 mm, DBE/PW 0.41.

Colouration: Dorsally piceous, with yellowish red head and pronotal sides (Fig. 22).

Head yellowish red, narrowly piceous behind eyes. Pronotum reddish brown to piceous on disc and gradually paler on sides, to yellowish red at anterior angles. Elytron piceous, seldom with faint, small reddish spot(s) at shoulder and/or reddish along suture. Scutellum reddish to piceous. Antennae, other head appendages, and legs yellowish red to red, darker distally. Ventral side reddish brown to brown.

Surface sculpture: Dorsal elytral striation variable, usually with ten complete and partly reduced striae, submarginal stria present: (6–11)+1 (Fig. 22).

Head without striae, with relatively sparse punctation (spaces between punctures 2–5× size of punctures); punctures relatively fine (diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with striae laterally, with punctation finer than on head and microreticulation fine. Elytron with striation variable, usually with ten dorsal, complete or partly reduced, striae, sometimes with six striae with some striae between them and stria 1 reduced basally (as in holotype), seldom with 11 stria, stria 1 short, present only medially; submarginal stria long, distinct. Elytron with very fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum rounded anteriorly, distinctly convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws very long, slightly curved, subequal in size, anterior claw with slight median incision of its inner margin subapically, thinner apically. Median lobe of aedeagus robust, with two lobes of dorsal sclerite subequal in length and shape, both covered with scale-like structures; left dorsal lobe slightly shorter and apically broader than right dorsal lobe, with a distinct median concavity and its whole apical 1/2 narrowed, its proximal part very large, and its apex slightly curved downwards, with a distinct crest; right dorsal lobe with apex pointed and membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area (visible as a triangular in left lateral view) and less sclerotised right part (visible in left lateral view); sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 73).

Female: As male, except for more numerous pronotal striae, sometimes absent only on disc.

Variability. There is a variation in the elytral striation and colouration described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. bundunensis* sp. nov. in simple male proclaws and shape of the median lobe but differs from it in larger and elongate body, absence of basal elytral band and slightly different structure of median lobe sclerites: see under *A. bundunensis* sp. nov. Also see under *A. xanthocephalus*.

Etymology. The species name is a combination of the Greek words *miltos* (red lead, red) and *karenon* (head), meaning red-headed and refers to the distinct yellowish red head colouration of the species. The species name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Morobe Province (Fig. 107).

Habitat. Unknown.

29. *Austrelatus noiadi* sp. nov.

<https://zoobank.org/7D938245-BF30-4A60-A053-823D76F0CFDB>

Figs 37, 87, 108

Type locality. INDONESIA: Papua Province: Mamberamo Raya Regency, Rouffaer Mts, Noiadi, ca. 02°46'S, 137°46'E, 150–200 m a.s.l.

Type material. Holotype: male "IRAN JAYA: Jayapura Prov. Mamberamo, Rouffaer Mts., Noiadi, 150–200m 17.3.1999, leg. Riedel" (NHMW).

Description. Body size and form: Beetle large, oblong-oval (Fig. 37).

Measurements: Holotype: TL 7.9 mm, TL-H 7.1 mm, MW 3.8 mm, TL/MW 2.08; PL 1.1 mm, PW 3.3 mm, PL/PW 0.33; DBE 1.3 mm, DBE/PW 0.39.

Colouration: Elytron piceous in basal 1/2 and yellowish red between striae in apical 1/2 and laterally, with narrow, faint, reddish basal band; head reddish brown, pronotal sides reddish (Fig. 37).

Head reddish brown, narrowly darker behind eyes. Pronotum piceous on disc and gradually paler (to reddish) to sides. Elytron piceous basally on disc and yellowish red between striae in apical 1/2 and laterally, with narrow, faint, reddish basal band, partly conjoined with yellowish red lateral area. Scutellum reddish. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs darker, all legs darker distally. Ventral side piceous, paler on prosternum and posteriorly on abdominal ventrites.

Surface sculpture: Elytron with 11 dorsal striae, stria 1 reduced basally, submarginal stria present: 11+1 (Fig. 37).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with striae posterolaterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae: stria 1 reduced basally, striae 2 and 3 interrupted basally; submarginal stria present. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively long, subequal in length, anterior claw thicker subapically and slightly more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe without concavity, its whole apical 1/2 more or less evenly tapering to small, slightly curved downward and truncate apex bearing small crest; right dorsal lobe shorter than left one, broad, with pointed apex and membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, slightly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and

broad, with its apical part densely covered with long setae (sometimes visible at apex); right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 87).

Female: Unknown.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, in shape of the median lobe, it is similar to *A. mamberamo* sp. nov. and differs from it in elytron paler apically, male anterior proclaw thicker subapically, with median incision of its inner margin, and apex of left dorsal lobe of the median lobe distinctly shorter, with smaller crest.

Etymology. The species is named after Noiadi Village. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province: Mamberamo Raya Regency. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

30. *Austrelatus normanbyensis* sp. nov.

<https://zoobank.org/5925A873-F633-4CCE-9E68-8D7F46852F2C>

Figs 21, 72, 107

Type locality. PAPUA NEW GUINEA: Milne Bay Province, Normanby Island, Sewa Bay, Sibonai, 10°02.418'S, 150°58.461'E, 35 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Milne Bay, Normanby Isl., Sewa Bay, Sibonai, 35 m", "30.vi.2017, 10°02.418'S 150°58.461'E, Riedel", "8722" [green text] (MZB). **Paratypes:** 3 males with the same label as holotype and additional labels with green text "8723", "8724" and "8727" (NHMW, SMNK, ZSM). 6 males, 4 females "Papua New Guinea: Milne Bay Prov., Normanby Isl., Sewa Bay, Sibonai", "10°02.418'S 150°58.461'E, 35 m, beaten & hand-collected", "30-VI-2017 – position 1, A. Riedel." (NHMW, SMNK, ZSM). 3 males, 4 females "Papua New Guinea: Milne Bay Prov., Fergusson Isl., Salamo area, Dei Dei", "09°39.386'S 150°52.460'E to 09°39.230'S 150°52.586'E, 110 m", "beaten & hand-collected, 28-II-2017 – position 1 to 2, A. Riedel." (NHMW, SMNK, ZSM). 1 male "Papua New Guinea: Milne Bay, Fergusson Isl., Salamo area, Dei Dei", "110 m, 28.iii.2017, 09°39.230'S 150°52.586'E, Riedel", "8729" [green text] (SMNK).

Description. Body size and form: Beetle large, with oblong-oval habitus (Fig. 21).

Measurements: TL 6.5–7 mm, TL-H 5.8–6.3 mm, MW 3.1–3.4 mm, TL/MW 2.06–2.12; PL 1–1.1 mm, PW 2.7–3 mm, PL/PW 0.36–0.37; DBE 1.1–1.2 mm, DBE/PW 0.4–0.41. **Holotype:** TL 6.9 mm, TL-H 6.1 mm, MW 3.25 mm, TL/MW 2.12; PL 1 mm, PW 2.8 mm, PL/PW 0.36; DBE 1.15 mm, DBE/PW 0.41.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and broad basal band on elytron (Fig. 21).

Head yellowish red, narrowly piceous behind eyes. Pronotum piceous, yellowish red on sides, broader at anterior angles. Elytron piceous, with yellowish red broad basal band, often with yellowish on apex, sometimes expanded between striae laterally. Scutellum piceous. Antennae, other head appendages, and legs yellowish red, legs darker distally. Ventral side reddish brown, with paler prosternum.

Surface sculpture: Elytron with six dorsal striae, stria 1 reduced in basal 1/2, submarginal stria present: 6+1 (Fig. 21).

Head without strioles, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with several strioles at posterolateral angles, with punctation finer than on head and microreticulation fine. Elytron with 6 dorsal striae, stria 1 absent in basal 1/2, submarginal stria present, sometimes only apically. Elytron with very fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum broadly rounded anteriorly, distinctly convex medially; blade of prosternal process narrow.

Male: Protibia straight, not modified. Proclaws relatively short, subequal in length, anterior claw slightly thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite subequal in length, with pointed apices and covered with scale-like structures; left dorsal lobe concave medially, with apex curved downwards, with small apical crest; right dorsal lobe with membranous area medially; lobes of ventral sclerite sclerotised, pressed together between lobes of dorsal sclerite, but partly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area (not visible in left lateral view) and less sclerotised right part (visible in left lateral view); sclerotised area with elongate and broad basal 1/2 and long, hair-like apical 1/2; less sclerotised right part long and broad, with a tuft of long setae; right ventral lobe long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin; more distally situated setae longer than more proximal ones (Fig. 72).

Female: As male.

Variability. There is a variation in the elytral striation and colouration described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. inconstans* sp. nov., *A. bundunensis* sp. nov. and *A. centralensis* sp. nov. in body form and dorsal colouration, but differs from them in smaller size and median lobe with narrow, distinctly bent downwards apex of left dorsal lobe.

In addition to *A. normanbyensis* sp. nov., one more *Austrelatus* species, *A. garainensis* Shaverdo et al., 2023, is known from Normanby Island (see below). The species belongs to the *A. neoguineensis* species group, representatives of which have a differently shaped male median lobe without surface sculptures (Shaverdo et al. 2023). The species is distinctly smaller in size than *A. normanbyensis* sp. nov. and has 11 complete dorsal striae on the elytron.

Etymology. The species is named after Normanby Island. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Milne Bay Province, Normanby and Ferguson islands (Fig. 107).

Habitat. Unknown.

31. *Austrelatus ohu* sp. nov.

<https://zoobank.org/8DC9BEF8-E230-4BA7-B355-EF946F14FEA1>

Figs 4, 67, 107

Type locality. PAPUA NEW GUINEA: Madang Province, 15 km southwest of Madang, Ohu Village.

Type material. Holotype: male “PNG Madang Province OHU Village, 14.1.2001 leg.: Lukas Cizek Coll. HENDRICH” (NHMW). **Paratypes:** 11 males, 21 females with the same label as the holotype (CLH, NHMW, ZSM). 1 male “NEW GUINEA 25 km. N Madang 3 km. W Sempi 27 I 1989 leg. M.&R. HOŁYŃSKI” (ZSM).

Description. Body size and form: Beetle small, elongate (Fig. 4).

Measurements: TL 4.35–5 mm, TL-H 3.9–4.25 mm, MW 1.9–2.23 mm, TL/MW 2.24–2.29; PL 0.7–0.8 mm, PW 1.73–1.95 mm, PL/PW 0.39–0.42; DBE 0.8–0.95 mm, DBE/PW 0.46–0.5. **Holotype:** TL 4.8 mm, TL-H 4.25 mm, MW 2.1 mm, TL/MW 2.29; PL 0.75 mm, PW 1.95 mm, PL/PW 0.39; DBE 0.9 mm, DBE/PW 0.46.

Colouration: Dorsally dark brown, with yellowish red head, pronotal sides and basal band on elytron (Fig. 4).

Head yellowish red, narrowly darker behind eyes. Pronotum brown to dark brown on disc and gradually paler (to yellowish red) to sides. Elytron brown to dark brown, with distinct yellowish red basal band and often yellow apex. Scutellum yellowish red to brown. Antennae, other head appendages, and pro- and mesolegs yellowish to yellowish red, metalegs darker, all legs darker distally. Ventral brown. Specimens slightly to strongly teneral.

Surface sculpture: Elytron with six dorsal striae and usually with submarginal stria: 6+(0–1) (Fig. 4).

Head without strioles, with distinct, sparse punctation (spaces between punctures 2–5× size of punctures); punctures relatively fine (diameter of punctures more or less equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without strioles, with punctation as on head and microreticulation distinct. Elytron with six dorsal striae, sometimes striae 1, 3, 5, and 6 shortly reduced basally and/or interrupted, stria 1 can be more strongly reduced; submarginal stria present, seldom absent or represented by tiny strioles. Elytron with fine punctation and microreticulation.

Structures: Head large and broad. Pronotum slightly trapezoid, its lateral margins subparallel. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws very long, straight, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed apexes; left dorsal lobe with lateral margin slightly concave apically and lateral side slightly concave medially, covered laterally with numerous distinct spinula-like structures and dorsally with less numerous scale-like structures, lateral margin without surface structures, smooth; right dorsal lobe covered with scale-like structures; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, concave apically, with apex pointed and slightly curved; right ventral lobe longer than left lobe, with narrow sclerotised area on right margin, membranous part with long, thin, upwardly curved apex distinctly sticking out in left lateral view. Parameres with relatively dense and long setae occupying distinct-

ly more than half of dorsal margin; setae on small area proximally shorter and sparser, with several most proximal setae standing separately (Fig. 67).

Female: Only matt, strongly striolated form known.

Variability. There is an insignificant variation in the elytral striation.

Affinities. In body size and shape, elytral striation and dorsal colouration, the species is similar to *A. procerus* sp. nov. and *A. lopintolensis* sp. nov. but distinctly differs from them by its long, straight male proclaws and shape of the median lobe. See also under *A. iriatoi* sp. nov.

Etymology. The species is named after its type locality, Ohu Village. The name is a noun in the nominative singular standing in apposition.

Distribution. Papua New Guinea: Madang Province (Fig. 107).

Habitat. Unknown.

32. *Austrelatus papuensis* (Balfour-Browne, 1939)

Figs 34, 35, 85, 108

Copelatus papuensis Balfour-Browne 1939: 86; Guignot (1956: 52, 55); Guéorguiev (1968: 10); Guéorguiev and Rocchi (1993: 159); Nilsson and Hájek (2023: 65).

Austrelatus papuensis (Balfour-Browne, 1939): Shaverdo et al. (2023: 7).

Type locality. PAPUA NEW GUINEA: Central Province, Kokoda, 08°52'28.4"S, 147°44'16.1"E, ca. 365 m a.s.l. Note: In Balfour-Browne (1939: 87), it is given as "♂ holotype, ♀ allotype, 14 ♂♂ and 10 ♀♀ paratypes, Papua: Kokoda, 1200ft., v.1933 (*Miss Chesman*) (British Museum, 1933-577)."

Type material. Holotype: male "♂" [hw, next to beetle], "Type" [round label with red frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Copelatus papuensis, B-B. ♂ TYPE" [hw by J. Balfour-Browne], "Manuscript name" [printed in red], "Holotype" [red label] (BMNH). **Paratypes:** 1 female "♀" [hw, next to beetle], "Type" [round label with red frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Copelatus papuensis, B-B. ♀ TYPE" [hw by J. Balfour-Browne] (BMNH). 1 male "♂" [hw, next to genitalia], "Type" [round label with yellow frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Copelatus papuensis, B-B. ♂" [hw by J. Balfour-Browne] (BMNH). 8 males, 7 females "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Type" [round label with yellow frame], "Copelatus papuensis, B-B. ♂ [or ♀]" [hw by J. Balfour-Browne] (BMNH). 1 male "Under stones: river side.", "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Type" [round label with yellow frame], "Copelatus papuensis, B-B. ♂" [hw by J. Balfour-Browne] (BMNH). 1 female "♀" [hw, next to beetle], "Type" [round label with yellow frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Copelatus papuensis, B-B. ♀" [hw by J. Balfour-Browne] (BMNH). 1 female "♀" [hw, next to beetle], "Type" [round label with yellow frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Copelatus papuensis, B-B. ♀" [hw by J. Balfour-Browne], "measured J. Parkin 73" (BMNH). 1 male "♂" [hw, next to beetle], "Type" [round label with yellow frame], "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw

on reverse side], "Copelatus papuensis, B-B. ♂" [hw by J. Balfour-Browne] (BMNH). 1 male "PAPUA: Kokoda. 1,200ft. v.1933. L.E.Cheesman. B.M.1933-577.", "57" [hw on reverse side], "Type" [round label with yellow frame], "Copelatus papuensis, B-B. ♂" [hw by J. Balfour-Browne], "measured J. Parkin 72" (BMNH).

Additional material. PNG: Morobe: 188 males, 98 females "Papua New Guinea: Garaina, 720m, vi.2008 07 51.032S 147 07.007E Ibalim & Sosanika (PNG216)" (NHMW, ZSM). 32 males, 33 females "Papua New Guinea: Garaina 800m, vi.2008 07.53.091S 147.07.915E Ibalim & Sosanika, PNG217" (NHMW, ZSM). 16 males, 9 females "Papua New Guinea: Garaina, 770m, vi.2008 07.52.516S 147.10.427E Ibalim & Sosanika (PNG219)", one of males additionally with a green label "4074" (NHMW, ZSM). 4 males, 1 female "Papua New Guinea: Garaina, 800m, 27.vi.2009 (PNG220) 7.52.669S 147.07.196E Ibalim & Sosanika", one of males additionally with a green label "3845" (ZSM). 19 males, 11 females "Papua New Guinea: Garaina, 770m, 25.vi.2008, 07 50.859S 147 08.614E, Ibalim & Sosanika, (PNG222)" (NHMW, ZSM). 1 female "Papua New Guinea: Garaina, 820m, 24.vi.2008 07.52.287S 147.06.297E, Ibalim & Sosanika, (PNG224)" (ZSM). **EHL:** 1 male, 1 female "Papua New Guinea: Eastern Highlands, Bena Brigde, Unggai Bena, 1393m, 27.viii.2005, K.Sagata, (WB136)" (ZSM).

Description. Body size and form: Beetle large, oblong-oval or elongate (Figs 34, 35).

Measurements: TL 6.9–7.8 mm, TL-H 6.35–7.1 mm, MW 3.25–3.6 mm, TL/MW 2.12–2.23; PL 0.95–1.15 mm, PW 2.85–3.2 mm, PL/PW 0.33–0.37; DBE 1.2–1.3 mm, DBE/PW 0.4–0.42. **Holotype:** TL 7.5 mm, TL-H 6.8 mm, MW 3.4 mm, TL/MW 2.21; PL 1.15 mm, PW 3.1 mm, PL/PW 0.37; DBE 1.3 mm, DBE/PW 0.42.

Colouration: Elytron yellowish red to reddish brown between striae, narrowly piceous on pronotal and elytral discs, with yellowish red head and pronotal sides (Figs 34, 35).

Head yellowish red, narrowly darker behind eyes. Pronotum piceous on disc and gradually paler (to yellowish red) to sides. Elytron narrowly brown to piceous on disc, with yellowish red basal band broadened at shoulder area, yellow apex, and usually intensive yellowish red colouration between striae, striae brown to piceous. Scutellum yellowish red to brown. Antennae, other head appendages, and pro- and mesolegs yellowish red to reddish, metalegs darker, all legs darker distally. Ventral side reddish brown, paler on prosternum and abdominal ventrites.

Surface sculpture: Elytron with 10–11 dorsal striae, striae 1–3 reduced in basal 1/2, submarginal stria present: (10–11)+1 (Figs 34, 35).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with few to several striae posterolaterally, more numerous in females, with punctation finer than on head and microreticulation fine. Elytron with 10 or 11 dorsal striae: striae 1–3 reduced in basal 1/2, stria 1 strongly to completely reduced, striae 5 and 9 can be interrupted; submarginal stria present, often as apical striae. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly, seldom rounded so that pronotal base slightly broader than that of elytra. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws long, subequal in length, anterior claw thicker subapically and often more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe without distinct median concavity and its whole apical 1/2 more or less evenly tapering to elongate, slightly curved, evenly or unevenly narrowly rounded apex bearing small crest; right dorsal lobe shorter, with membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, slightly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 85).

Female: Dimorphic: as male but with more numerous pronotal striae and matt, with pronotum and elytron very densely covered with fine longitudinal striae. Matt forms seldom; in the studied material, known only from the PNG219 population, with ratio shiny to with striae is 7:3.

Variability. There is a variation in dorsal colouration and striolation described above as well as in shape of left dorsal lobe apex of the median lobe: more or less rounded and curved even within one population. Less rounded, curved apex is characteristic of the holotype.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is similar to *A. posmani* in shape of the median lobe and differs from it in weaker elytral striation, with striae 1–3 reduced in basal 1/2 and stria 1 sometimes absent, male anterior proclaw with median incision of its inner margin, and apex of left dorsal lobe of the median lobe broader, with more distinct crest. See also under *A. posmani* sp. nov.

Distribution. Papua New Guinea: Central, Morobe, and Eastern Highlands provinces (Fig. 108). According to Guignot (1956: 52), the species occurs also in Madang Province, Stephansort, Astrolabe Bay; however, this record has not been confirmed. During our study of Guignot's collection in MNHN, the specimen, on which the records were based, has been found and identified as *A. madangensis* sp. nov. (see above).

Habitat. Unknown.

33. *Austrelatus posmani* sp. nov.

<https://zoobank.org/098A9F81-BDCA-49E6-BAFF-B64AA2DE553D>

Figs 33, 84, 108

Type locality. PAPUA NEW GUINEA: Central Province, Moreguina, 10°00'57"S, 148°28'27"E.

Type material. Holotype: male "Papua New Guinea: Central, Moreguina 16.viii.2008 Posman (PNG183)" (ZSM). **Paratypes:** 1 male with the same label as the holotype (ZSM).

Description. Body size and form: Beetle large, oblong-oval (Fig. 33).

Measurements: TL 7–7.7 mm, TL-H 6.3–6.9 mm, MW 3.4–3.6 mm, TL/MW 2.06–2.14; PL 1–1.2 mm, PW 2.9–3.15 mm, PL/PW 0.35–0.38; DBE 1.15–1.2 mm, DBE/PW 0.38–0.4. **Holotype:** TL 7 mm, TL-H 6.3 mm, MW 3.6 mm, TL/MW 2.06; PL 1 mm, PW 2.9 mm, PL/PW 0.35; DBE 1.15 mm, DBE/PW 0.4.

Colouration: With almost completely yellowish red elytron, yellowish red head and pronotal sides (Fig. 33).

Head yellowish red, narrowly darker behind eyes. Pronotum piceous on disc and broadly yellowish red on sides. Elytron yellowish red due to strongly developed basal band and colouration between striae, piceous on small part of disc, on striae and very narrowly on sides. Scutellum yellowish red. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown, paler on prosternum and abdominal ventrites.

Surface sculpture: Elytron with 11 complete, strongly impressed dorsal striae, submarginal stria present: 11+1 (Fig. 33).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (usually diameter of punctures equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with striae laterally, mainly at posterior margin, with punctation slightly finer than on head and microreticulation fine. Elytron with 11 complete, strongly impressed dorsal striae: stria 1 shortly reduced basally; submarginal stria present, long. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly, distinctly rounded so that pronotal base slightly broader than that of elytra. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process broad.

Male: Protibia more or less straight: its ventral margin very slightly curved proximally. Proclaws long, slightly curved, subequal in length, anterior claw thicker at its apex than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus robust, with two lobes of dorsal sclerite covered with scale-like structures, with their apexes broadly pointed; left dorsal lobe without distinct median concavity and its whole apical 1/2 relatively narrow, more or less evenly tapering to elongate, straight apex bearing small crest; right dorsal lobe shorter, with small membranous area medially; lobes of ventral sclerite partly sclerotised, pressed together between lobes of dorsal sclerite, slightly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 and long, thread-like apical 1/2; less sclerotised right part long and broad, with its apical part densely covered with long setae; right ventral lobe partly sclerotised, long and broad. Parameres with dense, long setae occupying approximately half of dorsal margin (Fig. 84).

Female: Unknown.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is distinguished by yellow colouration and strong striation of its elytra. It is similar to *A. papuensis* in shape of the median lobe and differs from it in stronger elytral striation, male anterior proclaw thicker at its apex than posterior one and with subapical incision of its inner margin, and apex of left dorsal lobe of the median lobe narrower, with crest weaker. See also under *A. papuensis* sp. nov.

Etymology. The species is named after its collector A. Posman. The name is a noun in the genitive case.

Distribution. Papua New Guinea: Central Province. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

34. *Austrelatus procerus* sp. nov.

<https://zoobank.org/C6D50444-65C7-49B4-B2F5-0AF9A04CA0B5>

Figs 2, 60, 107

Type locality. INDONESIA: West Papua Province: Sorong Regency, road Sorong-Teminabuan, 01°08'08.6"S, 131°54'00.1"E, 130 m a.s.l.

Type material. Holotype: male "Indonesia: Papua Barat, Sorong-Teminabuan, 130 m, 2.x.2014, -1,1357267 131,9000149, UNIPA team (BH047)" (KSP).

Paratypes: 2 females "Indonesia: Papua Barat, Sorong-Teminabuan, 50 m, 2.x.2014, -1,1092904 131,6125645, B. Sumoked (BH046)", with two green text labels "6453" and "6454", respectively (MZB, ZSM).

Description. Body size and form: Beetle small, distinctly elongate (Fig. 2).

Measurements: TL 4.5–4.55 mm, TL-H 4.1 mm, MW 2–2.05 mm, TL/MW 2.22–2.25; PL 0.7–0.75 mm, PW 1.83–1.9 mm, PL/PW 0.38; DBE 0.85–0.9 mm, DBE/PW 0.47. **Holotype:** TL 4.5 mm, TL-H 4.1 mm, MW 2.05 mm, TL/MW 2.22; PL 0.75 mm, PW 1.9 mm, PL/PW 0.38; DBE 0.9 mm, DBE/PW 0.47.

Colouration: Elytra piceous, head and pronotum paler; yellow basal band on elytron distinct and broad (Fig. 2).

Head yellowish red, narrowly darker behind eyes. Pronotum dark brown on disc and gradually paler (to yellowish red) to sides. Elytron piceous, with broad yellow basal band and yellow apex. Scutellum yellowish red. Antennae, other head appendages, and pro- and mesolegs yellowish to yellowish red, metalegs darker, all leg darker distally. Ventral side yellowish to yellowish red.

Surface sculpture: Elytron without striae or with 6 weakly impressed striae, submarginal stria absent: (0–6)+0 (Fig. 2).

Head without striae, with distinct, uneven punctation (spaces between punctures 1–5× size of punctures); punctures fine (diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without or with short, weak striae on sides, with punctation sparser than on head and microreticulation distinct. Elytron without striae, with four puncture lines, or as in holotype, with six weakly impressed striae: striae 2 and 4 complete, other striae strongly reduced, especially basally. Elytron with fine, sparse punctation and distinct microreticulation. Abdominal ventrite

6 with distinct punctation sparse medially and forming denser area at each lateral side, with few striae laterally.

Structures: Head broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process short and broad.

Male: Protibia straight, not modified. Proclaws long, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with scale-like structures; left dorsal lobe with lateral margin concave apically, with its side concave subapically and medially, and with some spinula-like structures medially in left lateral view; apex of left dorsal lobe straight, with thickened tip; left lobe of ventral sclerite with elongate, narrow sclerotised area, with its apex visible in left lateral view; right lobe of ventral sclerite membranous. Parameres with relatively long and dense setae occupying distinctly more than half of dorsal margin; more distally situated setae denser and longer than more proximal ones (Fig. 60).

Female: As male, but elytron without striae and pronotum with numerous, weak striae on its sides.

Variability. There is a variation in the elytral striation described above: the holotype has elytron with 6 dorsal striae and both females are without elytral striae.

Affinities. The species is similar to *A. leptos* sp. nov. in small size, elongate habitus, and dorsal colouration, but differs from it in sturdier habitus, convergent anteriorly pronotal lateral margins, elytron with striae and broader yellow basal band, and different shape of the median lobe and male proclaws.

Etymology. The species name is a Latin adjective meaning slender, and indicates the elongate habitus of the species.

Distribution. Indonesia: West Papua Province: Sorong Regency. The species is known only from the type locality (Fig. 107).

Habitat. The species was collected in small forest pools rich in rotten leaves.

35. *Austrelatus pseudogestroi* sp. nov.

<https://zoobank.org/B222C677-92BA-47E9-AB57-E3135B282E2E>

Figs 53, 102, 108

Type locality. PAPUA NEW GUINEA: National Capital District Province, Port Moresby, Brown River Road situated nearby to the suburbs Morata and Waigani.

Type material. Holotype: male "Stn. No. 195", "Papua: Pt. Moresby Brown R. Rd., 15.III.1965", "M.E.Bacchus, B.M. 1965-120" (BMNH).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 53).

Measurements. Holotype: TL 6.9 mm, TL-H 6.2 mm, MW 3.3 mm, TL/MW 2.09; PL 0.95 mm, PW 2.7 mm, PL/PW 0.35; DBE 1 mm, DBE/PW 0.37.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and elytral basal band and apex (Fig. 53).

Head almost completely yellowish red, narrowly piceous behind eyes and with V-shaped, brown spot medially. Pronotum piceous on disc and broadly yellowish red on sides, especially at anterior angles. Elytron piceous, with rather broad yellowish red basal band; elytron broadly yellow apically, usually extend-

ing between striae, especially laterally (up to elytral half). Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, especially distally. Ventral side piceous, with paler prosternum.

Surface sculpture: Elytron with 11+1 striae, striae 1–3 reduced basally (Fig. 53).

Head without strioles, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures usually equal to and smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum without strioles, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, stria 1 absent in basal 1/2 and interrupted in apical 1/2; striae 2 and 3 absent in basal 1/4 and additionally interrupted basally; submarginal stria present, well-developed. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long; anterior claw shorter, thicker and more curved than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus relatively broad, with two lobes of dorsal sclerite with narrowly rounded apexes, left straight, right slightly curved to left; left dorsal lobe slightly longer than right dorsal lobe, distinctly narrowed to apex in its apical 1/3; lateral side of left dorsal lobe covered with large scale-like structures towards dorsal side and smaller scale-like structures towards apex, with numerous small spinula-like structures on slightly beaded lateral margin and numerous large, short spinula-like structures medially; right dorsal lobe covered with large scale-like structures, with small median membranous area; lobes of ventral sclerite sclerotised, long, broad, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with curved apex and broad slightly sclerotised part rounded apically; right ventral lobe distinctly longer than left one, slightly sclerotised, with long curved apex visible in left lateral view. Parameres with dense, long setae occupying distinctly more than half of dorsal margin; on small area proximally very distinctly shorter and sparser (Fig. 102).

Female: Unknown.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on dorsal colouration and general shape of the median lobe, it is similar to *A. asteios* sp. nov., *A. epicharis* sp. nov., *A. wasurensis* sp. nov., and *A. yeretuar* sp. nov. but differs from them in larger body size and left dorsal lobe of the median lobe with narrow, shallow, concavity under the lateral margin and different organisation of the surface structures. In body size, shape and colouration, it is very similar to *A. gestroi* sp. nov. but differs from it in the elytron with a broader yellowish red basal band and different shape of the median lobe: the left dorsal lobe is broader and its apical part is distinctly shorter.

Etymology. The species is named after its similarity to *A. gestroi*. The name is a noun in the nominative singular standing in apposition.

Distribution. Papua New Guinea: National Capital District. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

36. *Austrelatus pseudomianminensis* sp. nov.

<https://zoobank.org/352382ED-8FBA-4E4C-940C-D57E39B82C64>

Figs 45, 94, 108

Type locality. INDONESIA: Papua Province: Puncak Regency, Iratoi, Rouaffer River, 3°14'25.1"S, 137°19'58.7"E, 164 m a.s.l.

Type material. Holotype: male "Indonesia: Papua, Rouaffer, Iratoi, hill in forest, 164m, 6.ix.2014, -3,2403086 137,3329744, UNCEN team (PAP028)" (KSP).

Paratypes: 2 females with the same label as the holotype (MZB, ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 45).

Measurements: TL 5.3–5.5 mm, TL-H 4.95–5.1 mm, MW 2.6–2.7 mm, TL/MW 2.04–2.06; PL 0.75–0.8 mm, PW 2.3 mm, PL/PW 0.33–0.35; DBE 0.85 mm, DBE/PW 0.37. **Holotype:** TL 5.5 mm, TL-H 5.05 mm, MW 2.7 mm, TL/MW 2.04; PL 0.8 mm, PW 2.3 mm, PL/PW 0.35; DBE 0.85 mm, DBE/PW 0.37.

Colouration: Dorsally piceous, with yellowish red to reddish brown head, anterior angles of pronotum, and yellow spot on elytral apex (Fig. 45).

Head yellowish red to reddish, narrowly piceous behind eyes. Pronotum piceous, yellowish red to reddish on anterior half of sides. Elytron piceous, with large yellow apical spot, slightly extending laterally. Scutellum reddish to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs distinctly darker, especially distally. Ventral side piceous, with brown prosternum.

Surface sculpture: Elytron with 11+1 complete, rather strongly impressed striae (Fig. 45).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with distinct striae broadly laterally, only disc without them, with punctation finer than on head and microreticulation fine. Elytron with 11 complete, rather strongly impressed dorsal striae, stria 10 shortly reduced basally; submarginal stria present. Elytron with fine and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw thicker at its apex than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, more or less straight, with very broadly pointed apices, apex of left dorsal lobe slightly curved downwards; left dorsal lobe with lateral side covered with numerous, distinct, strong spinula-like structures; lateral margin apically without surface structures, smooth; right dorsal lobe covered with scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved to right and membranous right part long, thin, apically covered with setae sometimes visible in left lateral view; right ventral lobe with narrow sclerotised area on right margin.

Parameres with dense, long setae occupying approximately half of dorsal margin; more distally situated setae longer than more proximal ones (Fig. 94).

Female: As males but with stronger dorsal punctation.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe not completely covered by spinula-like structures, upper lateral margin without spinulae, smooth in left lateral and ventral views. Based on shape of the median lobe, it is very similar to *A. mianminensis* sp. nov. but differs from it in smaller body size, elytral striae complete and rather strongly impressed, more numerous pronotal striae, and smaller median lobe, with the lateral margin of left dorsal lobe with edge, below which spinula-like structures situated, more sharp, prominent. See also under *A. flavocapitatus* sp. nov. and *A. sararti* sp. nov.

Etymology. At the beginning, the species was considered to belong to *A. mianminensis* sp. nov. due to their similarity. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: Papua Province: Puncak Regency. The species is known only from the type locality (Fig. 108).

Habitat. The species was collected in small and shaded forest pools rich in rotten leaves.

37. *Austrelatus robustus* sp. nov.

<https://zoobank.org/0747FD25-78D8-4E39-8E01-6BD1DC547A62>

Figs 30, 81, 107

Type locality. PAPUA NEW GUINEA: Madang Province, Highway near Madang, 05°24.405'S, 145°38.213'E, 80 m a.s.l.

Type material. Holotype: male "Papua New Guinea: Madang, Highway nr. Madang, ford, 80m, 26.xi./2.-3.xii.1994, 05.24.405S 145.38.213E, Binatang Boys, (PNG 117)" (ZSM). **Paratypes: PNG: Madang:** 1 male with the same label as the holotype (NHMW). **Central:** 1 male "Papua New Guinea: Central, Myola, 1110m, i.2008, [09]12.630S 147 31.880E, Posman (PNG 177)", "4119" [green label] (ZSM).

Description. Body size and form: Beetle large, oblong-oval (Fig. 30).

Measurements: TL 7.45–7.9 mm, TL-H 6.8–7.1 mm, MW 3.75–3.9 mm, TL/MW 1.99–2.03; PL 1.1–1.2 mm, PW 3.35–3.6 mm, PL/PW 0.33–0.33; DBE 1.3–1.45 mm, DBE/PW 0.39–0.4. **Holotype:** TL 7.45 mm, TL-H 6.8 mm, MW 3.75 mm, TL/MW 1.99; PL 1.1 mm, PW 3.35 mm, PL/PW 0.33; DBE 1.3 mm, DBE/PW 0.39.

Colouration: Dorsally piceous, with reddish head, pronotal sides and elytral base and apex (Fig. 30).

Head red, narrowly darker behind eyes. Pronotum brown on disc and gradually paler (to dark yellowish red) to sides, especially at anterior angles. Elytron dark brown to piceous, with short, faint, dark yellowish red to reddish basal band present on shoulder area and with yellowish red apex, sometimes more developed laterally. Scutellum dark brown. Antennae, other head appendages, and pro- and mesolegs reddish, metalegs darker, all legs darker distally. Ventral side dark brown, sometimes paler medially and on abdominal ventrites.

Surface sculpture: Elytron with 11 complete striae, submarginal stria present: 11+1 (Fig. 30).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (usually diameter of punctures larger than diameter of microreticulation cells); microreticulation distinct. Pronotum with few striae on sides, with punctation finer than on head and microreticulation fine. Elytron with 11 complete striae, striae 1 and 10 usually shortly reduced basally; submarginal stria present. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia modified: thinner proximally and broader medially and distally due to its curved ventral margin. Proclaws relatively long, subequal in length, anterior claw thicker subapically and more strongly curved downwards than posterior one and due to this with a distinct median incision on its inner margin. Median lobe of aedeagus very robust, with two lobes of dorsal sclerite covered with scale-like structures; left dorsal lobe very strongly concave medially, with apical 1/2 very broad and apex slightly rounded and bearing small but rather distinct crest; right dorsal lobe shorter, narrower, more or less evenly tapering to pointed apex, with small membranous area medially; lobes of ventral sclerite mostly visible in left lateral view; left ventral lobe consists of two parts: left sclerotised area and less sclerotised right part; sclerotised area with elongate and broad basal 1/2 (visible in left lateral view) and long, thread-like apical 1/2 (not visible); less sclerotised right part long and broad, with its apical part densely covered with long setae (partly visible in left lateral view); right ventral lobe mostly sclerotised, long and broad (partly visible in left lateral view). Parameres with dense, long setae occupying slightly more than half of dorsal margin, with proximal setae shorter (Fig. 81).

Female: Unknown.

Variability. There is an insignificant variation in dorsal colouration described above.

Affinities. The species belongs to the large species with robust median lobe, covered mainly with scale-like structures. Among them, it is very similar to *A. bosaviensis* sp. nov. and differs from it in broader male anterior claw with median inner margin incision and narrower apical 1/2 of the left dorsal lobe of the median lobe. See also under *A. bosaviensis* sp. nov.

Etymology. The species name is a Latin adjective meaning “hard and strong like oak” and indicates the large, broad, robust habitus and median lobe of the species.

Distribution. Papua New Guinea: Madang and Central provinces (Fig. 107).

Habitat. In Madang, the species was collected at a stream ford.

38. *Austrelatus sararti* sp. nov.

<https://zoobank.org/E8A96AB9-9877-4834-B567-53D5AA379FEF>

Figs 48, 98, 108

Type locality. INDONESIA: West Papua: Teluk Wondama Regency, Wasior, Sararti 100–200 m a.s.l.

Type material. Holotype: male “Irian Jaya: Wandammen Bay, Wasior, Sararti 100–200 m, 7.-9.I.2001, leg A. Riedel” (SMNS).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 48).

Measurements: Holotype: TL 5.7 mm, TL-H 5.1 mm, MW 2.75 mm, TL/MW 2.07; PL 0.85 mm, PW 2.35 mm, PL/PW 0.36; DBE 0.95 mm, DBE/PW 0.4.

Colouration: Dorsally almost uniformly piceous (Fig. 48).

Head dark brown, slightly paler posteriorly, narrowly piceous behind eyes. Pronotum piceous, dark brown on sides, brown at anterior angles. Elytron piceous, slightly paler apically. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs reddish brown, metalegs darker, especially distally. Ventral side dark brown.

Surface sculpture: Elytron with 11+1 striae (Fig. 48).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with several striae laterally, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, striae 1 and 10 usually shortly reduced basally, striae 1 additionally interrupted; submarginal stria present, long. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws long, rather straight, subequal in length, anterior claw thicker subapically than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite relative narrow, subequal in length; apex of left dorsal lobe curved upwards, rounded; left dorsal lobe with lateral margin distinctly concave apically and with lateral side covered with large scale-like structures and at lateral margin medially additionally with small spinula-like structures; right dorsal lobe with broadly pointed apex, covered with large scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, concave subapically, with apex pointed and slightly curved and membranous right part long, thin, apically covered with setae slightly visible in left lateral view; right ventral lobe with narrow sclerotised area on right margin. Parameres with dense, long setae occupying slightly more than half of dorsal margin, with proximal setae shorter (Fig. 98).

Female: Unknown.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body size and dark dorsal colouration, it is similar to *A. kalibumi* sp. nov., *A. herzogensis* sp. nov., *A. mianminensis* sp. nov., and *A. pseudomianminensis* sp. nov. but differs from them in almost uniformly piceous elytron colouration and median lobe of different shape and surface of left dorsal lobe completely covered by surface structures. See also under *A. fuscus* sp. nov. and *A. wasiorenensis* sp. nov.

Etymology. The species is named after Sararti Village. The name is a noun in the nominative singular standing in apposition.

Distribution. Indonesia: West Papua Province: Teluk Wondama Regency. The species is known only from the type locality (Fig. 108).

Habitat. Unknown.

39. *Austrelatus sumokedi* sp. nov.

<https://zoobank.org/3E4E5A70-038C-4919-8FCE-64E15538F846>

Figs 24, 75, 107

Type locality. INDONESIA: Papua Province: Mimika Regency, 04°30.330'S, 136°46.53'E, 24 m a.s.l.

Type material. Holotype: male "Indonesia: Papua, Kabupaten Mimika, 24m, 25–30.v.2017, S 04°30.330", "E 136°46.53', B. Sumoked (Pap69-Bob07)" (KSP).

Description. Body size and form: Beetle small, elongate (Fig. 24).

Measurements: Holotype: TL 4.85 mm, TL-H 4.4 mm, MW 2.2 mm, TL/MW 2.21; PL 0.7 mm, PW 1.9 mm, PL/PW 0.37; DBE 0.81 mm, DBE/PW 0.43.

Colouration: With yellowish red head, brownish pronotum with yellowish red sides and dark brown elytra, with broad yellowish red basal band and yellowish apically and laterally (Fig. 24).

Head yellowish red, narrowly darker behind eyes. Pronotum brown on disc, darker on anterior and posterior margins and gradually paler (to yellowish red) to sides. Elytron dark brown, with broad yellowish red basal band and broadly yellow apically and laterally in apical 1/2. Scutellum reddish. Antennae, other head appendages, and legs yellowish red, legs darker distally. Ventral side reddish brown, darker on metacoxal plates.

Surface sculpture: Elytron with 11 complete striae, submarginal stria present: 11+1 (Fig. 24).

Head without strioles, with distinct, dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without strioles, with punctation slightly sparser and finer than on head and microreticulation fine. Elytron with 11 complete striae; submarginal stria present, long. Elytron with very fine, sparse punctation and fine microreticulation.

Structures: Head broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively broad.

Male: Protibia straight, not modified. Proclaws relatively short, slightly curved, subequal in length. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, covered with scale-like structures; left dorsal lobe with lateral margin concave apically, with straight, thick, and rounded apex, and scale-like structures with tiny spinulae covering whole lateral surface; right dorsal lobe broad, tapering to broadly pointed apex; lobes of ventral sclerite subequal in length, visible apically in left lateral view; left ventral lobe with elongate, narrow sclerotised area, with its apex slightly curved; right ventral lobe mostly membranous. Parameres with rather sparse and short setae especially proximally; setae occupying almost whole dorsal margin (Fig. 75).

Female: Unknown.

Affinities. The species is similar to *A. iriatoi* sp. nov. in elongate habitus and dorsal colouration, but differs from it in smaller body size, simple, slightly

curved male proclaws (straight in *A. iriatoi* sp. nov.), and in median lobe structure: thicker and more rounded left lobe apex of dorsal sclerite and smaller and differently organised spinula-like structures of left dorsal lobe.

Etymology. The species is dedicated to the collector and our friend Bob Sumoked (Tomohom, Sulawesi). The species name is a noun in the genitive case.

Distribution. Indonesia: Papua Province: Mimika Regency. The species is known only from the type locality (Fig. 107).

Habitat. Unknown.

40. *Austrelatus wanangensis* sp. nov.

<https://zoobank.org/4B2DE3F6-CF50-4BEA-B0AF-16CACE3B645B>

Figs 26, 77, 107

Type locality. PAPUA NEW GUINEA: Madang Province, Wanang Village, Wanang River.

Type material. Holotype: male “PNG: Madang, Wanang Vill., Wanang Riv., 25.IX.13, #44 leg., D. Boukal” [hw, H. Shaverdo], “6442” [green text label] (ZSM).

Paratypes: PNG: Sandaun: 2 females “Papua New Guinea: Sandaun, Toricelli Mts., 2h walk fr Sibilanga Stn, 350m, 19.iv.2006, 03.39.121S 142.29.991E, Balke (PNG 44), one with an additional green label “3234” (ZSM).

Description. Body size and form: Beetle small, elongate (Fig. 26).

Measurements: Holotype: TL 5.3 mm, TL-H 4.9 mm, MW 2.35 mm, TL/MW 2.25; PL 0.85 mm, PW 2.15 mm, PL/PW 0.4; DBE 0.9 mm, DBE/PW 0.42.

Colouration: Dorsally brown, with yellowish red head, pronotal sides and broadly on elytral base, sides and apex (Fig. 26).

Head yellowish red, narrowly darker behind eyes. Pronotum brown on disc and gradually paler (to yellowish red) to sides. Elytron brown, with broad yellowish red basal band, conjoined with yellowish red lateral side and apex, so that only elytral disc brown. Scutellum yellowish red. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side brown.

Surface sculpture: Elytron with 11 complete striae, submarginal stria present: 11+1 (Fig. 26).

Head without striae, with dense punctation (spaces between punctures 1–3× size of punctures); punctures coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with few striae at middle of lateral sides, with punctation finer than on head and microreticulation fine. Elytron with 11 complete striae, stria 10 shortly reduced basally; a submarginal stria present, long. Elytron with fine, relatively dense punctation and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, relatively long, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length, anterior claw with very slight median incision of its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length, with broadly pointed apices; left dorsal lobe with lateral margin slightly

concave apically and lateral side slightly concave medially, covered laterally with numerous distinct spinula-like structures and dorsally with less numerous scale-like structures, lateral margin without surface structures, smooth; right dorsal lobe covered with scale-like structures; lobes of ventral sclerite partly sclerotised, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, concave apically, with apex pointed and slightly curved; right ventral lobe longer than left lobe, with narrow sclerotised area on right margin, membranous part with long, thin, upwardly curved apex distinctly sticking out in left lateral view. Parameres with relatively dense and long setae occupying more than half of dorsal margin; proximally shorter and sparser, with several the most proximal setae standing separately (Fig. 77).

Female: As male but with more numerous pronotal striae on sides and less developed yellow colouration of elytron, absent laterally.

Affinities. The species is very similar to *A. iriatoi* sp. nov. in elongate habitus, dorsal colouration and striation and shape and surface structure of the median lobe, but differs from it in slightly curved male proclaws (straight in *A. iriatoi* sp. nov.) and left dorsal lobe of the median lobe with shorter and less concave apex and its surface structures slightly differently situated.

Etymology. The species is named after Wanang Village. The name is an adjective in the nominative singular.

Distribution. Papua New Guinea: Sandaun and Madang provinces (Fig. 107).

Habitat. At the Sibilnaga Station, the species was collected in small and shallow forest pools rich in rotten leaves.

41. *Austrelatus wasiorensis* sp. nov.

<https://zoobank.org/D16D6B61-C218-4429-9C68-71E916EA1FD1>

Figs 51, 100, 108

Type locality. INDONESIA: West Papua: Teluk Wondama Regency, Wasior, Sararti 100–200 m a.s.l.

Type material. Holotype: male “Irian Jaya: Wandammen Bay, Wasior, Sararti 100–200 m, 7.-9.I.2001, leg A. Riedel” (SMNS). **Paratypes:** 2 males, 1 female “Irian Jaya, Wandammen Bay, Wasior, KM 38, Sararti, 100–200 m, 7.-9.I.2001, leg A. Riedel” (NHMW, SMNS). 1 female “Irian Jaya, Wandammen Bay, Wasior, blok, 200 m, 8.I.2001, leg A. Riedel” (SMNS). 1 female “53” [green label], “Indonesia: West Papua, DMP, Wasior, 7.-10.I.2001, Riedel leg.” (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 51).

Measurements: TL 5.95–6.4 mm, TL-H 5.4–5.9 mm, MW 2.9–3.2 mm, TL/MW 1.99–2.05; PL 0.75–1 mm, PW 2.4–2.7 mm, PL/PW 0.31–0.37; DBE 0.95–1.05 mm, DBE/PW 0.39–0.41. **Holotype:** TL 6.15 mm, TL-H 5.55 mm, MW 3.1 mm, TL/MW 1.99; PL 0.9 mm, PW 2.55 mm, PL/PW 0.35; DBE 1.05 mm, DBE/PW 0.41.

Colouration: Dorsally piceous, with reddish head, pronotal sides and elytral apex (Fig. 51).

Head reddish, slightly darker narrowly behind eyes. Pronotum piceous, with reddish sides. Elytron piceous, reddish apically, sometimes with small, yellow spot at apex, seldom with faint reddish basal spots medially. Scutellum brown to piceous. Antennae, other head appendages, and pro- and mesolegs reddish,

metalegs slightly darker, especially distally. Ventral side brown, darker on posterior margins of abdominal ventrites 3–5 and on abdominal ventrite 6.

Surface sculpture: Elytron with 11+1 striae (Fig. 51).

Head without striae, with rather dense punctation (spaces between punctures 1–3× size of punctures); punctures rather coarse (diameter of punctures usually equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with numerous striae mainly laterally, with few very tiny striae on disc, with punctation finer than on head and microreticulation fine. Elytron with 11 dorsal striae, striae 10 and 11 shortly reduced basally; submarginal stria present, sometimes as apical striae. Elytron with fine punctation and relatively distinct microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum broadly rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, curved, anterior claw slightly longer than posterior. Median lobe of aedeagus with two lobes of dorsal sclerite with broadly pointed apices; left dorsal lobe slightly longer than right dorsal lobe; lateral side of left dorsal lobe subapically with narrow, shallow concavity, covered with numerous large, short spinula-like structures and towards apex and dorsal side with scale-like structures; lateral margin slightly concave at apical tip; right dorsal lobe covered with large scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with apex elongate, rather straight and pointed and broad membranous part apically covered with setae not visible in left lateral view; right ventral lobe with relatively broad sclerotised area on right margin. Parameres with rather short and sparse setae occupying approximately half of dorsal margin (Fig. 100).

Female: As males but with stronger dorsal punctation and microreticulation and more numerous pronotal striae.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body size and dark dorsal colouration, it is similar to *A. kalibumi* sp. nov., *A. herzogensis* sp. nov., *A. mianminensis* sp. nov., and *A. pseudomianminensis* sp. nov. but differs from them in left dorsal lobe of the median lobe with narrow, shallow, subapical concavity and surface of left dorsal lobe completely covered by surface structures. It is also similar to *A. fuscus* sp. nov. and *A. sararti* sp. nov. but differs from them in anterior proclaw simple, without median incision and left dorsal lobe of the median lobe with subapical concavity and large, but short spinula-like structures.

Etymology. The species is named after Wasior District. The name is an adjective in the nominative singular.

Distribution. Indonesia: West Papua Province: Teluk Wondama Regency (Fig. 108).

Habitat. Unknown.

42. *Austrelatus wasurensis* sp. nov.

<https://zoobank.org/84581F99-E0A5-4280-9212-62CD5A7153DC>

Figs 54, 103, 108, 116

Type locality. INDONESIA: Papua Province: Merauke Regency, Wasur, -07.6756°S, 140.4526°E, 20 m a.s.l.

Type material. Holotype: male “Indonesia: Papua, Merauke, Wasur, pools, 20m, 15–16.x.2011, -7.6756° 140.4526°, UNCEN team (PAP02)” (KSP). **Paratypes:** 17 males, 12 females with the same label as the holotype, one male and one female with additional labels with green text “5012” and “5013”, respectively (MZB, NHMW, ZSM).

Additional material. 1 female “7887” [green text], “Indonesia: Papua, Kabupaten Mimika, Timika, 149m, 25–30.v.2017,” “-4.252020° 136.643384°, B. Sumoked (Pap68-Bob06)” (ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval (Fig. 54).

Measurements: TL 5.4–6.3 mm, TL-H 4.9–5.8 mm, MW 2.6–3 mm, TL/MW 2.08–2.14; PL 0.8–0.9 mm, PW 2.2–2.6 mm, PL/PW 0.35–0.36; DBE 0.85–1 mm, DBE/PW 0.39–0.4. **Holotype:** TL 6.2 mm, TL-H 5.5 mm, MW 2.9 mm, TL/MW 2.14; PL 0.9 mm, PW 2.5 mm, PL/PW 0.36; DBE 1 mm, DBE/PW 0.4.

Colouration: Piceous, with reddish head, pronotal anterior angles, and elytral basal band (Fig. 54).

Head almost completely reddish, narrowly piceous behind eyes and sometimes with obscure, V-shape, brownish spot medially. Pronotum piceous, reddish at anterior angles and sometimes on sides. Elytron piceous, with reddish basal band, sometimes rather distinct, sometimes obscure; elytral apex shortly yellow. Scutellum piceous. Antennae, other head appendages, and pro- and mesolegs yellowish brown, metalegs darker, especially distally. Ventral side piceous, with paler prosternum.

Surface sculpture: Elytron with 11 complete dorsal striae, submarginal stria present, long: 11+1 (Fig. 54).

Head without strioles, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures usually equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with several strioles at lateral margins, more numerous in females, with punctation finer than on head and microreticulation fine. Elytron with 11 complete, relatively strongly impressed dorsal striae; submarginal stria present, long, reaching more than half of elytral length. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum narrowly rounded anteriorly, strongly convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long; anterior claw shorter, thicker and more curved than posterior one and due to this with a median incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite with broadly pointed apexes, more or less straight; left dorsal lobe slightly longer than right dorsal lobe, with not beaded, slightly concave at its apical 1/3 lateral margin; lateral side of left dorsal lobe completely covered with numerous large, single spinula-like structures; right dorsal lobe covered

with large scale-like structures, with small, indistinct median membranous area; lobes of ventral sclerite sclerotised, long, broad, slightly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with curved apex and broad slightly sclerotised part rounded apically; right ventral lobe distinctly longer than left one, slightly sclerotised, with long, thin apex. Parameres with dense, relatively long setae occupying distinctly more than half of dorsal margin; proximally shorter and sparser, several most proximal setae standing separately (Fig. 103).

Female: As males but with stronger dorsal punctation and microreticulation and more numerous pronotal strioles, in some specimens covering whole pronotum.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body shape and size and general shape of the median lobe, it is similar to *A. asteios* sp. nov., *A. epicharis* sp. nov., and *A. yeretuar* sp. nov. but differs from them in darker dorsal colouration, with usually indistinct, reddish basal band of the elytron and in median lobe with large, single spinulae on surface of its left dorsal lobe.

Etymology. The species is named after Wasur. The name is an adjective in the nominative singular.

Distribution. Indonesia: Papua Province: Merauke Regency (Fig. 108) but according to the additional material, it might have broader distribution in Papua.

Habitat. At the type locality, the species was collected in shallow pools rich in rotten leaves and surrounded by wet savannah forest (Fig. 116). The species co-occurs with *Austrelatus clarkii* (Sharp, 1882) and numerous Bidessini species.

43. *Austrelatus weigeli* sp. nov.

<https://zoobank.org/CC3AC79B-9373-4739-AF02-851A0CE9F193>

Figs 41, 90, 108

Type locality. PAPUA NEW GUINEA: East New Britain Province, 30 km SW Kokopo, Arabam, 04°35.75'S, 152°06.84'E, 200 m a.s.l.

Type material. Holotype: male "PNG: E New Britain Prov. 30km SW Kokopo, Arabam, 200m 04°35'75"S, 152°06'84"E 21.II-04.III.2000 leg. A. Weigel KL" (ZSM). **Paratypes:** 1 male, 1 female with the same label as the holotype (NHMW, ZSM).

Description. Body size and form: Beetle medium-sized, oblong-oval to elongate (Fig. 41).

Measurements: TL 6.4–6.6 mm, TL-H 5.7–5.95 mm, MW 2.99–3.1 mm, TL/MW 2.08–2.2; PL 0.95–1 mm, PW 2.5–2.6 mm, PL/PW 0.37–0.39; DBE 1.1–1.2 mm, DBE/PW 0.44–0.46. **Holotype:** TL 6.45 mm, TL-H 5.8 mm, MW 3.1 mm, TL/MW 2.08; PL 0.95 mm, PW 2.6 mm, PL/PW 0.37; DBE 1.15 mm, DBE/PW 0.44.

Colouration: With almost completely yellowish red elytron, yellowish red head and pronotal sides (Fig. 41).

Head yellowish red, narrowly darker behind eyes. Pronotum piceous on disc and broadly yellowish red on sides. Elytron yellowish red due to strongly devel-

oped basal band and colouration between striae; seldom piceous, with broad yellowish red basal band and yellowish red colouration between striae apically. Scutellum brownish. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs brown, all legs darker distally. Ventral side brown, paler on prosternum and metaventrite and darker on abdominal ventrites.

Surface sculpture: Elytron with 11 complete, strongly impressed dorsal striae, submarginal stria present: 11+1 (Fig. 41).

Head with few striae between eyes, with relatively sparse punctation (spaces between punctures 1–5× size of punctures); punctures fine (diameter of punctures smaller than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with numerous but sparse striae absent in middle and anterolaterally, with punctation sparser than on head and microreticulation fine. Elytron with 11 complete strongly impressed dorsal striae, stria 10 shortly reduced basally, sometimes with few small striae between striae; submarginal stria present. Elytron with fine, sparse punctation and fine microreticulation.

Structures: Head relatively large and broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum narrowly rounded anteriorly, convex medially; blade of prosternal process broad.

Male: Protibia straight, not modified. Proclaws relatively long, subequal in length, anterior claw thicker apically and slightly more strongly curved downwards than posterior one and due to this with a subapical incision on its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length; left dorsal lobe slightly longer than right one, with broadly pointed and curved upwards apex; its lateral side with strong, elongate concavity subapically under upper lateral margin and covered with numerous, small but distinct scale-like structures bearing small spinulae; lateral margin and apex covered with small scale-like structures without spinula, lateral concavity covered with rather large scale-like structures; right dorsal lobe with broad, straight, pointed apex and covered with rather large scale-like structures, without membranous area on lateral side; lobes of ventral sclerite partly sclerotised, long, subequal in length, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, with apex pointed and slightly curved to right; right ventral lobe with narrow, rather weak sclerotised area on right margin. Parameres with dense, long setae occupying distinctly more than half of dorsal margin; on small area proximally shorter and sparser, several most proximal setae standing separately (Fig. 90).

Female: As male but darker: elytron piceous, with broad yellowish red basal band and yellowish red colouration between striae apically.

Affinities. The species belong to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe. However, it can be distinguished from them by yellowish red colouration and 11+1 complete, strongly impressed striae of its elytron and elongate, subapical concavity on the lateral side of the left dorsal lobe.

Etymology. The species is named after our colleague Andreas Weigel, a specialist for xylophagous beetles, who collected the type series. The specific epithet is a substantive in the genitive case.

Distribution. Papua New Guinea: East New Britain Province. The species is known only from the type locality (Fig. 108).

Habitat. The species was collected in small forest pools.

44. *Austrelatus yamurensis* sp. nov.

<https://zoobank.org/76F8B7F4-72DF-49E3-A656-53B732667A97>

Figs 16, 68, 107

Type locality. INDONESIA: West Papua Province: Kaimana Regency, Fakfak District, Lake Yamur area, 50–100 m a.s.l.

Type material. Holotype: male "IRIAN JAYA: Fak Fak dist. Lake Yamur area, IV.1998 ca. 50 – 100m, Waldtümpel" (NHMW). **Paratypes:** 3 males with the same label as the holotype (MZB, NHMW, ZSM).

Description. Body size and form: Beetle medium-sized, elongate (Fig. 16).

Measurements: TL 5.6–5.8 mm, TL-H 5–5.1 mm, MW 2.45–2.6 mm, TL/MW 2.23–2.29; PL 0.9 mm, PW 2.3 mm, PL/PW 0.39; DBE 0.95 mm, DBE/PW 0.41.

Holotype: TL 5.8 mm, TL-H 5.1 mm, MW 2.6 mm, TL/MW 2.23; PL 0.9 mm, PW 2.3 mm, PL/PW 0.39; DBE 0.95 mm, DBE/PW 0.41.

Colouration: Dorsally piceous, with yellowish red head and anterolateral pronotal angles, broad yellow basal band and large yellow apical spot on elytron (Fig. 16).

Head yellowish red, narrowly darker behind eyes. Pronotum piceous, with yellowish red anterior angles and narrowly on sides. Elytron piceous, with distinct, broad yellow basal band and large yellow apical spot. Scutellum yellowish red to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs darker, all legs darker distally. Ventral side reddish brown. All specimens except for the holotype are teneral.

Surface sculpture: Elytron with six dorsal striae but looks like with 5 dorsal striae due to stria 6 strongly reduced and weakly impressed; submarginal stria absent: 6+0 (Fig. 16).

Head without striae, with distinct, relatively sparse punctation (spaces between punctures 1–5× size of punctures); punctures relatively fine (diameter of punctures more or less equal to diameter of microreticulation cells); microreticulation distinct. Pronotum without striae, with punctation finer than on head and microreticulation distinct. Elytron with six dorsal striae, but stria 6 strongly reduced and weakly impressed, present as short stria or separate striae only in apical 1/2 near stria 5; dorsal striae weakly impressed; striae 1 and 5 absent in basal 1/2; submarginal stria absent. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins slightly convergent anteriorly. Base of prosternum narrowly rounded anteriorly, distinctly convex medially; blade of prosternal process relatively narrow.

Male: Protibia straight, not modified. Proclaws relatively long, slightly curved, subequal in length; anterior claw slightly thicker subapically than posterior one, with weak median incision of its inner margin. Median lobe of aedeagus with two lobes of dorsal sclerite covered with large, thick scale-like structures; left dorsal lobe slightly longer than right one, with apex broadly pointed and curved upwards, strong subapical crest, lateral margin concave apically, lateral groove, and with characteristic submedian knob-like modification; lobes of ventral sclerite partly sclerotised, subequal in length, long, partly visible in left lateral view; left ventral lobe with elongate, narrow sclerotised area, its apex pointed and curved; right ventral lobe more membranous, with apex pointed and slightly curved. Parameres with dense, relatively long setae occupying more than half of dorsal margin (Fig. 68).

Female: Unknown.

Variability. There is an insignificant variation in the elytral striation.

Affinities. In body size and shape and dorsal colouration, the species is similar to *A. kebarensis* sp. nov. but distinctly differs from it in its characteristic shape of the median lobe, with submedian knob-like modification of the left dorsal lobe, and only five complete dorsal elytral striae.

Etymology. The species is named after its type locality, Lake Yamur area. The name is an adjective in the nominative singular.

Distribution. Indonesia: West Papua Province: Kaimana Regency, Fakfak District. The species is known only from the type locality (Fig. 107).

Habitat. The species was collected in a forest pool.

45. *Austrelatus yeretuar* sp. nov.

<https://zoobank.org/3C7AF79D-E9AB-48DC-A146-3097A3509C83>

Figs 55, 104, 108

Type locality. INDONESIA: Papua Province: Nabire Regency, Yeretuar, 10 m a.s.l.

Type material. Holotype: male "IRIAN JAYA: Kabup. Nabire Wandammen penins., Yeretua 10m, 17.-20.8.1998 (WA 18) (KSP). **Paratypes:** 8 males, 8 females with the same label as the holotype (MZB, NHMW, ZSM).

Description. Body size and form: Beetle small, elongate or oblong-oval (Fig. 55).

Measurements: TL 4.8–5.55 mm, TL-H 4.3–5 mm, MW 2.25–2.65 mm, TL/MW 2.09–2.21; PL 0.7–0.8 mm, PW 2–2.35 mm, PL/PW 0.34–0.38; DBE 0.85–0.95 mm, DBE/PW 0.4–0.44. **Holotype:** TL 5.2 mm, TL-H 4.6 mm, MW 2.35 mm, TL/MW 2.21; PL 0.8 mm, PW 2.1 mm, PL/PW 0.38; DBE 0.9 mm, DBE/PW 0.43.

Colouration: With piceous elytra and pronotum and yellowish red head, pronotal sides, and elytral basal band (Fig. 55).

Head yellowish red medially, narrowly piceous behind eyes and brownish anteriorly. Pronotum piceous on disc and broadly yellowish red on sides, especially at anterior angles. Elytron piceous, with rather narrow yellowish red basal band, usually not reaching shoulders and suture; elytron sometimes with narrow yellow spot apically. Scutellum brownish to piceous. Antennae, other head appendages, and pro- and mesolegs yellowish red, metalegs slightly darker, especially distally. Ventral side brownish, with paler prosternum and darker posterior margins of ventrites.

Surface sculpture: Elytron with 11 complete dorsal striae, submarginal stria present, long: 11+1 (Fig. 55).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively fine (diameter of punctures usually equal to or smaller than diameter of microreticulation cells); microreticulation distinct. Pronotum with sparse striae on lateral parts, only disc without striae, with punctation finer than on head and microreticulation fine. Elytron with 11 complete dorsal striae, striae 1–3 less strongly impressed, especially anteriorly; submarginal stria present, long, often reaching more than ½ elytral length. Elytron with fine punctation and microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins convergent anteriorly. Base of prosternum rounded anteriorly, strongly convex medially; blade of prosternal process narrow.

Male: Protibia straight, not modified. Proclaws relatively long, simple, subequal in length. Median lobe of aedeagus slender, apically thin, with two lobes of dorsal sclerite with broadly pointed apices, straight, subequal in length; left dorsal lobe with lateral margin not beaded, slightly concave at its apical 1/2; lateral side of left dorsal lobe completely covered with tiny spinulae situated in groups on scale-like structures; right dorsal lobe covered with large scale-like structures, with distinct median membranous area; lobes of ventral sclerite partly sclerotised, long, slightly visible in left lateral view; left ventral lobe with elongate, strong sclerotised area, with curved apex and slightly sclerotised part distinctly shorter, with dense setae apically; right ventral lobe longer than left one, partly sclerotised, with apex curved left and covered with setae usually distinctly sticking out in left lateral view. Parameres with long and dense setae occupying approximately half of dorsal margin; more distally situated setae longer and denser than more proximal ones, with single most proximal setae standing separately (Fig. 104).

Female: As males.

Affinities. Although the species is relatively small, it belongs to the medium-sized species with median lobe of the aedeagus that has scale- and spinula-like structures on the left dorsal lobe and among them, to the species with surface of left dorsal lobe completely covered by scale- and spinula-like structures in left lateral and ventral views. Based on body shape, dorsal colouration and general shape of the median lobe, it is similar and probably closely related to *A. asteios* sp. nov. and *A. epicharis* sp. nov. but differs from them in smaller body size and median lobe median lobe slender and its apex distinctly narrower in left lateral view. After first examination of the specimens of these three species, we thought to consider them as one species with two subspecies in Manokwary Regency (with sturdier median lobe) and Wandammen Peninsula (with slenderer median lobe). However, after further study, it was decided to treat them as separate species since there are other morphological differences. Material from the gap areas needs to confirm this decision.

Distribution. Indonesia: Papua Province: Nabire Regency. The species is known only from the type locality (Fig. 108).

Habitat. The species was collected in different forest pools and puddles, rich in rotten leaves.

46. *Austrelatus xanthocephalus* (Régimbart, 1899)

Figs 5–8, 61, 62, 107

Copelatus xanthocephalus Régimbart 1899: 293; Zimmermann (1919: 200, 1920: 144); Guignot (1956: 55); Guéorguiev (1968: 25); Guéorguiev and Rochi (1993: 160); Nilsson and Hájek (2023: 50).

Austrelatus xanthocephalus (Régimbart, 1899): Shaverdo et al. (2023: 7).

Type locality. According to Régimbart (1899: 293), “Nouvelle-Guinée (A. Raffray, coll. du Muséum de Paris)”. The types labels say “Nouvelle-Guinée (Amberbaki) A. Raffray 1878”. “Amberbaki” is most likely Amberbaken District (Indonesia: West Papua Province: Tambrau Regency).

Type material. Lectotype: male [small, red, square label], “2795 78” [round label, hw], “Nolle [illegible, probably short form from Nouvelle] Guinée” [hw], “MUSEUM PARIS COLL. MAURICE REGIMBART 1908”, “MUSÉUM PARIS Nouvelle-Guinée (Amberbaki) A. Raffray 1878”, “SYNTYPE” [red label], “SYNTYPE Copelatus xanthocephalus Régimbart, 1899”, “MNHN, Paris EC14220 [barcode]”, “Lectotype *Copelatus xanthocephalus* Régimbart, 1899 des. H. Shaverdo 2023” [red label] (MNHN) (Fig. 7). **Paralectotype:** 1 female “2795 78” [round label, hw], “Nolle [illegible, probably short form from Nouvelle] Guinée Raffray” [hw], “MUSEUM PARIS COLL. MAURICE REGIMBART 1908”, “xanthocephalus Rég” [hw], “MUSÉUM PARIS Nouvelle-Guinée (Amberbaki) A. Raffray 1878”, “SYNTYPE” [red label], “SYNTYPE Copelatus xanthocephalus Régimbart, 1899”, “MNHN, Paris EC14219 [barcode]”, “Paralectotype *Copelatus xanthocephalus* Régimbart, 1899 des. H. Shaverdo 2023” [red label] (MNHN) (Fig. 8).

Additional material. IN: West Papua: Raja Ampat Regency: Waigeo: 2 males “Indonesia: Papua, Waigeo, Waifoi, Mt.Nok, 500m, 11.ii.2006, 00.05.076S 130.44.586E, Tindige & Balke (BH 11)” (ZSM). 1 male, 1 female “Indonesia: Papua, Waigeo, Waifoi, < 50m, 10.ii.2006, 00.06.088S 130.42.855E, Tindige & Balke (BH 10)” (ZSM). 1 male “N.Dutch New Guinea Waigeu, Camp Nok. 2,500ft. vi.1938. L.E.Cheesman. B.M. 1938-593.” (BMNH). 9 male, 9 females “Irian Jaya: Sorong Prov. Waigeo Isl., Kabui Bay Wawiay, 14.-15.11.1996 0–250m, leg. A.Riedel” (NHMW, ZSM). 1 male, 1 female “Indonesia: Papua, Waigeo, Waifoi, Mt.Nok, 500m, 11.ii.2006”, “00 05.076S 130 44.586E, Tindige & Balke (BH 11)”, “7594” and “7595” respectively [labels with green text] (ZSM). 6 males, 1 female “N.Dutch New Guinea Waigeu, Mt.Nok. Camp 2. (Buffelhorn.) vi.1938. L.E.Cheesman. B.M. 1938-593.” (BMNH, NHMW). **Batanta:** 26 males, 22 females “Indonesia: Papua, Batanta Selatan, Wailebet, 100m, 17.ii.2006, inland 00.53.957S 130.39.951E, Tindige & Prativi (BH 15)”, one male and one female with additional green labels “4256” and “4254”, respectively (NHMW, ZSM). 5 males, 4 females “W-PAPUA Raja Ampat Pr. Yensawai Batanta, 9 km W Ross-River 0°49'23"S 130°35'52"E 17.I.2004 leg. A. Skale (CAS). 10 males, 3 females “Indonesia: Papua, Batanta Utara, 20m, 14.ii.2006, 00.50.125S 130.42.856E, Tindige & Balke, (BH 12)” (MZB, NHMW, ZSM). 5 male, 3 females “Indonesia: Papua, Batanta Selatan, Wailebet, 280m, 17.ii.2006, inland 00.53.957S 130.39.951E, Tindige & Prativi (BH 16)” (NHMW, ZSM). **Salawati:** 6 male, 2 females “Indonesia: Papua, Salawatti Utara, 100–250m, 18.ii.2006, 00.57.954S 130.40.531E, Tindige & Balke (BH 18)” (NHMW, ZSM). **Sorong Regency:** 1 female “Indonesia: Papua Barat, Sorong-Sausapor, 300m, 29.ix.2014, -0,7629653 131,6177023, B. Sumoked (BH041)” (ZSM). 4 males, 4 females “Indonesia: Papua Barat, Sausapor-Fef, 157m, 30.ix.2014, -0,6975004 132,072253, B. Sumoked (BH044)”, one male and two females additionally with green text labels “6484”, “6486”, and “6487”, respectively (ZSM). 6 males, 5 females “Indonesia: Papua Barat, Sorong-Teminabuan, 50m, 2.x.2014, -1,1092 131,6125, B. Sumoked (BH046)”, two males additionally with labels with green text “6448” and “6449” (ZSM). 3 males “Indonesia: West Papua, Malawor 50m 28.i.2001 Riedel leg.” (ZSM). 1 male “58” [green label], “Indonesia: Irian Jaya, Malawor, 28.i.2001, Riedel, MB 58” (ZSM). **South Sorong Regency:** 3 males, 1 female “Indonesia: Papua Barat, Sorong-Teminabuan, 130m, 2.x.2014, -1,1357267 131,9000149, B.Sumoked (BH047)”, one male additionally with label with green text “6488” (ZSM). **Manokwari Regency:** 2 males, 2 females “Indonesia: Papua Barat, Kebar to Manokwari, 1h from Kebar, limestone creek and roadside pools”, “331m, 8.xi.2013, -0.80138488 133.32238254, UNIPA team (BH035)”, one male with an

additional label with green text “6246” (ZSM). 1 male, 3 females “Indonesia: Papua Barat, Kebar Valley, 596m, 6.v.2015, -0,840623751282691 133,268257565796, UNIPA team (BH059)” (ZSM). 2 males “Indonesia: Papua Barat, Tamrau Mts N of Kebar, forest stream, 750m, 7.xi.2013, -0.7831 133.0721, UNIPA team (BH033)” (ZSM). 6 males, 10 females “Indonesia: Papua Barat, Kebar to Aibogar, forest stream, 644m, 4.xi.2013, -0,8533 132,8713 UNIPA Team (BH024)” (ZSM). 35 males, 23 females “Indonesia: Papua Barat, Kebar to Aibogar, slow forest stream, 503m, -0,8624 132,8299 UNIPA team (BH025)”, two males additionally with labels with green text “6219” and “6220” (NHMW, ZSM). 2 males, 3 females “Indonesia: Papua Barat, Fumato, forest stream, 820m, -0.90427148 132.71981431 UNIPA team (BH027)” (ZSM). 10 males, 2 females “IN: WP: Manokwari Reg., nr Testega Vill., ca. 1200 m, forest puddles, 03.V.2015, 01°22'11"S, 133°35'34"E UNIPA team (2015-WP25)” (NHMW). 1 male “IN: WP: Manokwari Reg., Testega, ca. 1000 m, forest streams, 1.V.2015, 01°22'54"S, 133°35'44"E, leg. Shaverdo (2015-WP18)” (NHMW). 1 female “IN: WP: Manokwari Reg., nr Testega Vill., ca. 1200 m, forest puddles, 03.V.2015, 01°22'15"S, 133°35'37"E UNIPA team (2015-WP23)” (NHMW). 1 female “IN: WP: Manokwari Reg., nr Testega Vill., ca. 1200 m, puddles in streambed, 03.V.2015, 01°22'11"S, 133°35'34"E UNIPA team (2015-WP24)” (NHMW). 22 males, 10 females “Indonesia: Papua Barat, Testega, 1212m, 3.v.2015, -1,36869 133,5908, UNIPA team (BH054)”, two males with additional labels with green text “7229” and “7228” (ZSM). 2 males, 1 female “IRIAN JAYA: Manokwari Iba 1300m 7.-8.4.1993 leg. A. Riedel” (NHMW). 3 females “Indonesia: Papua Barat, lowland Manokwari, 66m, 8.v.2015, -0,7433 133,3975, UNIPA team (BH065)” (ZSM). **South Manokwari Regency:** 1 male, 3 females “Indonesia: Papua, Ransiki-Anggi, 1160m, 30.i.2006, 01.25.536S 134.02.456E, Tindige & Balke (BH 03)” (MZB, ZSM). **Fakfak Regency:** 2 males, 2 females “West New Guinea / Fak-Fak / IR 27 Kali Mati, 4km N of Fak-Fak 260 m, 8. & 9.8.1991 leg. Balke & Hendrich” (CLH, ZSM). 1 male “Indonesia: Fak Fak, 800m, 23.ii.2008, Tindige, (FakFak)” (ZSM). 1 male “1323” [green label], “Indonesia: Irian Jaya Barat, Fak Fak, 310m, 23.ii.2006, Tindige” (ZSM). 1 male “Indonesia: Irian Jaya Barat, Fak Fak, 310m, 23.ii.2006, 2.53.756S 132.18.074E, Tindige, (FakFak)” (ZSM).

Description. Body size and form: Beetle small to large, with habitus oblong-oval to more or less elongate (Figs 5–8).

Measurements: TL 4.7–7.1 mm, TL-H 4.3–6.5 mm, MW 2.3–3.3 mm, TL/MW 2.04–2.15; PL 0.78–1.1 mm, PW 2.05–3 mm, PL/PW 0.37–0.38; DBE 0.9–1.3 mm, DBE/PW 0.43–0.45. **Lectotype** (measured from photo): TL 6.11 mm, TL-H 5.5 mm, MW 2.84 mm, TL/MW 2.15; PL 0.9 mm, PW 2.42 mm, PL/PW 0.37; DBE 1.08 mm, DBE/PW 0.45.

Colouration: Dorsally piceous, with reddish head and pronotal sides (Figs 5–8).

Head yellowish red to dark red, narrowly piceous behind eyes. Pronotum dark brown to piceous on disc and gradually paler on sides, to yellowish red at anterior angles. Elytron almost always piceous, seldom with faint, small reddish spot(s) at shoulder and/or reddish along suture. Scutellum reddish to piceous. Antennae, other head appendages, and legs yellowish red to red, darker distally. Ventral side reddish brown to brown.

Surface sculpture: Elytron with 6+(0–1) striae, submarginal stria usually absent (Figs 5–8).

Head without striae, with relatively dense punctation (spaces between punctures 1–3× size of punctures); punctures relatively coarse (diameter of punctures larger than or equal to diameter of microreticulation cells); microreticulation distinct. Pronotum with striae (sometimes numerous) mainly at posterolateral angles, sometimes at posterior margin except for its middle, with punctation and microreticulation finer than on head. Elytra with a stable striation: six complete dorsal striae; submarginal stria usually absent, seldom present as a short stria or few short striae apically. Elytra with punctation finer than on pronotum and fine microreticulation.

Structures: Head relatively broad. Pronotum trapezoid, its lateral margins distinctly convergent anteriorly. Base of prosternum rounded anteriorly, convex medially; blade of prosternal process relatively narrow.

Male: Protibia more or less straight, not modified; its ventral margin can be slightly curved proximally in larger specimens. Proclaws short, slightly curved, subequal in size and form. Median lobe of aedeagus with two lobes of dorsal sclerite subequal in length and shape, thin in apical 1/2, with slightly thickened, pointed apices in lateral view, both densely covered with striola-like structures; usually left dorsal lobe slightly longer than right lobe, sometimes they of equal length, seldom left dorsal lobe slightly shorter than right lobe; apex of left dorsal lobe with hook-like tip, which placed into spoon-like tip of right lobe apex; lobes of ventral sclerite well-developed, mostly membranous, both with elongate sclerotised areas basally, distinctly shorter than dorsal lobes, broad, placed freely and well-visible ventrally, slightly visible laterally. Parameres with dense, long setae occupying distinctly more than half of dorsal margin; on small area distally longer and denser, proximal setae distinctly shorter and sparser (Figs 61, 62).

Female: As male, but with more numerous pronotal striae.

Variability. The species is very variable in body size. The smallest specimens are those from the islands (TL 4.7–5.5 mm). The medium-sized beetles are from Sorong (TL 5.1–5.8 mm), Kebar (TL 5.6–6.9 mm), Fumato (TL 5.8–6.1 mm), Manokwari (TL 5.9–6.2 mm), Anggi (TL 5.3–5.4 mm), and Fakfak (TL 5.8–6.5 mm). The largest specimens are from Testega (TL 6.6–7.1 mm). The variability in a relative length of lobes of dorsal sclerite of the median lobe is observed: most specimens have left dorsal lobe slightly longer than right lobe or equal to it (Figs 61C, 62E), only few specimens from Waigeo and Kedar have left dorsal lobe slightly shorter than right lobe, which is also characteristic for the lectotype (Fig. 62B, D).

Affinities. The nominative subspecies differs from *A. xanthocephalus nabirensis* ssp. nov. by its striated elytra, simple male protibia and usually smaller size. The species is similar to *A. miltokarenos* sp. nov. in body shape and colouration but differs from it in its smaller size, less striated elytra and completely different shape of the median lobe.

Distribution. Indonesia: West Papua Province (Fig. 107).

Habitat. The species was collected in many different water bodies: forest puddles and streams, a limestone creek and different roadside pools.

46a. *Austrelatus xanthocephalus nabirensis* ssp. nov.

<https://zoobank.org/6E6BF65B-8692-427B-8067-63D2CE80F66F>

Figs 9, 10, 63, 107, 111, 112, 113

Type locality. INDONESIA: Papua Province: Nabire Regency, road Nabire-Enarotali, 54th km, 03°29.51'S, 135°43.91'E, 750–800 m a.s.l.

Type material. Holotype: male “West New Guinea/Paniai Prov./IR 19 track Nabire-Ilaga km 54 Basecamp, 750–800m, 16.-27.7.1991 leg: Balke & Hendrich” (ZSM). **Paratypes:** 14 males, 12 females with the same label as the holotype (MZB, NHMW, ZSM). 11 males, 10 females “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 65, 29.8.1996, 250m (96 # 6)” (NHMW). 1 female “IRIAN JAYA: Nabire Prov., road Nabire – Ilaga, km 54, 26./27.8.1996, 750–800m (96 # 2)” (NHMW). 3 males “IRIAN JAYA: Nabire Prov., Nabire – Ilaga, km 54, 26.9.1997, 750m (# 4)” (NHMW). 1 male, 1 female “IRIAN JAYA: Nabire Prov., rd. Nabire - Ilaga, km 54, 03°29'51"S 135°43'91"E 750m, IV.1998”, “Restpfütze eines Baches” (NHMW). 4 males “Irian Jaya: Nabire distr., road Nabire-Ilaga, km 54, 03.29'517"S 135.43'913"E, 750m, iv.1998,” (ZSM). 1 female “IRIAN JAYA: Nabire Prov. rd. Nabire – Ilaga, Km 35 Kali Cemara, 100m, 27.9.1997 (IR97#6)” (NHMW). 1 male “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, Km 54, 30.8.1996, 750m (96 # 9)” (NHMW). 1 female “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, Km 54, 10.9.1996, 800m (96 # 20)” (NHMW). 5 males, 7 females “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 54, 10.9.1996, 900m (96 # 19)” (NHMW). 1 female “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 80, 1.9.1996, 200m (96 # 10)” (NHMW). 6 males “W.-Neuguinea/Paniai Prov. Straße Nabire-Ilaga km 54 700m, 22.-25.9.1990/IR 11 leg: Balke & Hendrich” (ZSM). 2 males, 2 females “IR90-11: W. New Guinea, Trek Nabire-Ilaga, km55, 19–25.ix.1990, Balke” (ZSM). 1 male “IR 19-W, New Guinea, Track Nabire-Ilaga KM 54, basecamp, 750–800m, 16.-27.vii.1991 Balke & Hendrich leg.” (ZSM). 4 males, 3 females “West New Guinea/Paniai Prov./IR 20 track Nabire-Ilaga KM 59, ca.750m, 18.7.1991 leg: Balke & Hendrich” (CLH, ZSM). 3 males, 1 female “West New Guinea/Paniai Prov./IR 24 track Nabire-Ilaga km 54 Basecamp, 750m, 25.7.1991 leg: Balke & Hendrich” (ZSM). 2 male, 2 females “IR #91-7 (IR 24). West New Guinea, Nabire-Ilaga km 54, basecamp 750m, 25. & 27.vii.1991, Balke” (ZSM). 1 male, 1 female “IR 23-W. New Guinea, track Nabire-Ilaga KM 62, 250m, 24.vii.1991 Balke & Hendrich leg.” (ZSM). 15 males, 5 females “West New Guinea/Paniai Prov./IR 22 track Nabire-Ilaga km 62 250m, 24.7.1991, forest pools leg: Balke & Hendrich” (CLH, ZSM). 6 males, 5 females “Indonesia: Papua, Road Nabire-Enarotali KM 55, 774m, 22.x.2011, 03 29.796S 135 43.885E, UNCEN team (PAP09)”, one male with an additional label with green text “5128” (ZSM). 4 males, 2 females “Indonesia: Papua, Road Nabire-Enarotali KM 52, 555m, 23.x.2011, 03.30.107S 135.42.971E, UNCEN team (PAP17)” (MZB, KSP, ZSM). 1 male “Indonesia: Papua, Road Nabire-Enarotali KM 60, 640m, 22.x.2011, 03.30.474S 135.42.611E, UNCEN team (PAP10)” (ZSM). 1 male “Indonesia: Papua, Road Nabire-Enarotali KM 62, 340m, 22.x.2011, 03.31.684S 135.42.802E, UNCEN team (PAP11)”, “5143” (ZSM).

Additional material. 1 male “IRIAN JAYA: Paniai Prov. road Nabire – Ilaga, km 54, 10.9.1996, 900m (96 # 19)” (NHMW).

Description. Body size and form: Beetle medium-sized to large, with oblong-oval habitus (Figs 9, 10).

Measurements: TL 6.1–7.1 mm, TL-H 5.6–6.6 mm, MW 2.9–3.5 mm, TL/MW 2.03–2.1; PL 0.95–1.15 mm, PW 2.6–3.05 mm, PL/PW 0.36–0.38; DBE 1.1–1.3 mm, DBE/PW 0.41–0.43. **Holotype:** TL 6.9 mm, TL-H 6.2 mm, MW 3.3 mm, TL/MW 2.09; PL 1.1 mm, PW 2.9 mm, PL/PW 0.38; DBE 1.2 mm, DBE/PW 0.41.

Colouration: As in nominative subspecies: dorsally piceous, with reddish head and pronotal sides (Figs 9, 10).

Surface sculpture: As in the nominative subspecies except for elytron usually without striae, with 3 rows of punctures or striae, seldom with six dorsal striae; submarginal stria absent: (0–6)+0 (Figs 9, 10).

Structures: As in the nominative subspecies.

Male: Protibia modified: thinner proximally and broader medially and distally due to its curved ventral margin. Proclaws short, slightly curved, subequal in size and form. Median lobe of aedeagus and parameres as in the nominative subspecies except for left dorsal lobe never shorter than right lobe; it may be slightly longer than right lobe or of equal length (Fig. 63).

Female: Dimorphic: as male, but with more numerous pronotal striae and sometimes elytral striae between puncture lines or striae, and matt forms.

Variability. There is an insignificant variation in the elytral striation: from all listed specimens, only seven have striated elytra. It is interesting that one male from the locality 96#19 (see “Additional material”) has shape of the median lobe different from those of the other males of the same locality: it is broader in ventral view and has very thin, forceps-like apexes of the dorsal sclerite lobes. The specimen also has striated elytra. It is most likely that this median lobe shape is a type of teratology or variation rather than this specimen being a new distinct species. However, more material from the area is necessary to clarify the matter.

Affinities. The subspecies differs from the nominative subspecies by its elytra without striae, modified male protibia, and larger size.

Etymology. The subspecies is named after Nabire Regency. The name is an adjective in the nominative singular.

Distribution. Indonesia: Papua Province. The subspecies is known only from the area of the Nabire-Enarotali road (Fig. 107).

Habitat. Most specimens around Nabire at km 54–62 of the Nabire-Illaga track were collected in shallow (up to 20 cm water depth), shaded or at least partly shaded forest pools and puddles of different size, rich in rotten leaves and twigs (Figs 111–113). Few specimens were also found in water-filled track hollows on forest tracks and puddles remained in dried up streambeds.

Key to species of *Austrelatus papuensis* group of New Guinea

The key is based mostly on male characters, since many species are rather similar in external morphology (for females, in internal morphology as well) and in most cases, the male genitalia (especially median lobe) need to be studied for reliable species identification. However, female identification is possible and for that, males and females from the same locality should not be separated for identification. If co-occurring species are not numerous (2–4 species), successful identifications of the females in association with the males of the same locality is highly possible.

A strong variability in the elytral striae is characteristic for the representatives of this group. Therefore, some species are placed twice or more in the key and their species dichotomies are composed so that they present all possible striae numbers. It is advisable also to use, if possible, several specimens of the same population for identification.

Numbers in square brackets placed before the species names refer to the species number above in the systematic account.

- 1 Without elytral striae, with 2–4 rows of punctures or striae.....**2**
- With elytral striae.....**6**
- 2 Beetle small, TL 4.4–4.55 mm, elongate, with subparallel elytral sides (Figs 1, 2)**3**
- Beetle larger, TL > 6.5 mm, elongate-oval (Figs 5–15)**4**
- 3 Beetle slender, with pronotal sides subparallel. Elytron without striae, with a narrower yellow basal band (Fig. 1). Male proclaws subequal in size and form. Male genitalia as in Fig. 59[20] **A. leptos sp. nov.**
- Beetle sturdier, with pronotal sides convergent anteriorly. Elytron with (0–6)+0 striae, with a broader yellow basal band (Fig. 2). Male anterior proclaw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Male genitalia as in Fig. 60 [34] **A. procerus sp. nov.**
- 4 Elytron uniformly dark brown to piceous, rarely with indistinct reddish brown basal spots. Elytron with (0–6)+0 striae: usually without striae, with 3 rows of punctures or striae and seldom with 6 dorsal striae; submarginal stria absent. TL 6.1–7.1 mm (Figs 9, 10). Median lobe more slender, especially apically (Fig. 63).....[46a] **A. xanthocephalus nabirensis ssp. nov.**
- Elytron with a distinct reddish yellow basal band. Elytral striation very variable: (0–10)+(0–1) striae. TL 6.7–8.2 mm. Median lobe robust**5**
- 5 Median lobe as in Fig. 64: left lobe of dorsal sclerite with a stronger median concavity, its apical 1/2 broader, apical crest larger. Male proclaws subequal in size and form. Elytron with narrower yellowish red basal band and yellowish red apex. TL 7.1–7.9 mm (Figs 11, 12) [5] **A. bundunensis sp. nov.**
- Median lobe as in Fig. 65: left lobe of dorsal sclerite with a weaker median concavity, its apical 1/2 narrower, apical crest smaller. Male anterior proclaw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Elytron with broader yellowish red basal band and sometimes additionally yellowish red laterally, apically and between striae. TL 6.7–8.2 mm (Figs 13–15) [15] **A. inconstans sp. nov.**
- 6 Elytron with 6+(0–1) striae, sometimes with small striae or reduced striae in-between **7**
- Elytron with (10–11)+(0–1) striae..... **19**
- 7 Beetle smaller, TL ≤ 6 mm, elongate, almost parallel-sided. Elytron with a yellowish red basal band **8**
- Beetle larger, usually TL > 6 mm, elongate-oval. Elytron with or without a yellowish red basal band **12**
- 8 Beetle smaller, TL ≤ 5 mm..... **9**
- Beetle larger, TL 5.1–5.8 mm **11**
- 9 Elytron with (0–6)+0 striae; if present, striae weakly impressed, partly reduced. TL 4.5–4.55 mm (Fig. 2). Male genitalia as in Fig. 60 [34] **A. procerus sp. nov.**
- Elytron with 6+(0–1) striae; striae more strongly impressed, complete or some of them shortly reduced basally..... **10**

- 10 Elytron with 6+1 striae; stria 5 shortly reduced basally. TL 4.7 mm (Fig. 3). Male anterior proclaw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe as in Fig. 66: left lobe of dorsal sclerite broader, more strongly developed, with a subapical crest, which gives median lobe calla-like shape [22] **A. *lopintolensis* sp. nov.**
- Elytron with 6+(0–1) striae; sometimes striae 1, 3, 5 and 6 shortly reduced basally, stria 1 can be more strongly reduced. TL 4.35–5 mm (Fig. 4). Male proclaws very long, straight. Median lobe as in Fig. 67: left lobe of dorsal sclerite narrower, especially apically, without crest [31] **A. *ohu* sp. nov.**
- 11 Elytron with 6+0 striae but looks like with 5 dorsal striae due to stria 6 strongly reduced, weakly impressed and slightly visible only apically; striae 1 and 5 reduced in basal 1/2; submarginal stria absent (Fig. 16). Median lobe as in Fig. 68: left lobe of dorsal sclerite with a distinct submedian knob-like modification [44] **A. *yamurensis* sp. nov.**
- Elytron with 6+1 striae: striae more strongly impressed, striae 1, 5, and 6 sometimes reduced basally, submarginal stria present (Fig. 17). Median lobe as in Fig. 69: left lobe of dorsal sclerite without such modification [18] **A. *kebarensis* sp. nov.**
- 12 Elytron with a yellowish red basal band **13**
- Elytron uniformly piceous, without a distinct yellowish red basal band, seldom with reddish basal spots or reddish basally **17**
- 13 Beetle smaller, TL 5.55–6.6 mm. Elytron with 6+(0–1) striae: striae more weakly impressed, striae 1, 5 and 6 reduced basally (Figs 18, 19). Median lobe as in Fig. 70: left lobe of dorsal sclerite not concave medially [23] **A. *luteomaculatus***
- Beetle usually larger, TL \geq 6.3 mm. Elytron with 6+(0–1) striae: striae more strongly impressed, stria 1 reduced in basal 1/2, sometimes with additional striae or striae in-between. Median lobe with left lobe of dorsal sclerite concave medially **14**
- 14 Median lobe as in Fig. 71: apex of left dorsal lobe narrow, pointed, without crest. Elytron with (6–9)+1 striae: submarginal stria sometimes present as traces. TL 7–8 mm (Fig. 20) [6] **A. *centralensis* sp. nov.**
- Median lobe: apex of left dorsal lobe broader, with crest **15**
- 15 Median lobe as in Fig. 65: left lobe of dorsal sclerite with a weak median concavity and very small apical crest. Elytral striation very variable: (0–10)+(0–1) striae. Elytron sometimes yellowish red laterally, apically and between striae additionally to yellowish red basal band. TL 6.7–8.2 mm (Figs 13–15) [15] **A. *inconstans* sp. nov.**
- Median lobe: left lobe of dorsal sclerite with a strong median concavity and larger apical crest. Elytron with yellowish red basal band and yellowish apically **16**
- 16 Beetle larger, TL 7.1–7.9 mm. Elytron with (0–10)+(0–1) striae and narrower yellowish red basal band (Figs 11, 12). Median lobe as in Fig. 64: apex of left dorsal lobe broad, rather straight [5] **A. *bundunensis* sp. nov.**
- Beetle smaller, TL 6.5–7 mm. Elytron with 6+1 striae and broad yellowish red basal band (Fig. 21). Median lobe as in Fig. 72: apex of left dorsal lobe narrower, distinctly bent downwards [30] **A. *normanbyensis* sp. nov.**

- 17 Beetle larger, TL 7.3–8.2 mm. Elytron with (6–11)+1 striae (Fig. 22). Median lobe as in Fig. 73: left lobe of dorsal sclerite concave medially..... [28] **A. *miltokarenos* sp. nov.**
- Beetle smaller, TL 4.7–7.1 mm. Elytron with (0–6)+(0–1) striae. Median lobe as in Figs 61–63: left lobe of dorsal sclerite not concave medially **18**
- 18 Elytron with 6+(0–1) striae. Beetle usually smaller, TL 4.7–7.1 mm (Figs 5–8). Protibia simple or seldom slightly modified. Median lobe as in Figs 61, 62: usually left dorsal lobe longer than right one, seldom other way around[46] **A. *xanthocephalus***
- Elytron almost always without striae, very seldom with 6+0 striae. Beetle usually larger, TL 6.1–7.1 mm (Figs 9, 10). Protibia modified: thinner proximally and broader medially and distally due to its curved ventral margin. Median lobe as in Fig. 63: dorsal lobes equal or left lobe slightly longer than right one..... [46a] **A. *xanthocephalus nabirensis* ssp. nov.**
- 19 Beetle smaller, TL < 5.5 mm, elongate**20**
- Beetle larger, TL > 5.5 mm, mostly elongate-oval.....**23**
- 20 Elytron dark brown, paler basally and apically, with faint yellowish red shoulder spot. Elytron with 11+1 striae. TL 5 mm (Fig. 23). Median lobe as in Fig. 74: left lobe of dorsal sclerite apically thick, ventral sclerite not visible in left lateral view [21] **A. *loloki* sp. nov.**
- Elytron with a distinct yellowish red basal band. Median lobe: left lobe of dorsal sclerite apically thin, ventral sclerite visible in left lateral view.....**21**
- 21 Beetle smaller, TL 4.9 mm (Fig. 24). Male genitalia as in Fig. 75: median lobe narrower in ventral view, its left dorsal lobe with thicker and more rounded apex and surface completely covered with scale-like structures with tiny spinulae in left lateral view[39] **A. *sumokedi* sp. nov.**
- Beetle larger, TL 5–5.5 mm (Figs 25, 26). Male genitalia: median lobe broader in ventral view, its left dorsal lobe with narrower apex and surface covered with larger spinula-like structures, absent on smooth upper lateral margin in left lateral view.....**22**
- 22 Male proclaws very long, straight. Median lobe as in Fig. 76: apex of left dorsal lobe longer and more concave in left lateral view [16] **A. *iriatoi* sp. nov.**
- Male proclaws distinctly shorter, slender, slightly curved. Median lobe as in Fig. 77: apex of left dorsal lobe shorter and less concave in left lateral view [40] **A. *wanangensis* sp. nov.**
- 23 Beetle with habitus elongate, slightly discontinuous between pronotum and elytra; pronotum large and long, with slightly rounded sides; TL 5.9 mm (Fig. 27). Male genitalia as in Fig. 78: median lobe robust, its left dorsal lobe thick, with a curved downwards apex and distinct apical crest[8] **A. *decoris* sp. nov.**
- Beetle elongate-oval; pronotum usually shorter, distinctly continuous with elytra. If median lobe similar, then beetle larger, TL > 6.3 mm; or, if beetle smaller, median lobe more slender, its left dorsal lobe thin, with evenly concave lateral margin, apex pointed or slightly rounded**24**
- 24 Beetle larger, TL > 6.5 mm, except for *A. craterensis* (TL 6.4 mm). Median lobe sturdier, its left dorsal lobe thick, often with a curved downwards apex and small apical crest, laterally evenly tapering or differently concave; surface of left dorsal lobe often smoother due to scale-like structures.....**25**

- Beetle smaller, TL < 6.5 mm, seldom TL up to 6.7 mm. Median lobe more slender, its left dorsal lobe thin, with evenly concave lateral margin, with apex pointed or slightly rounded; surface of left dorsal lobe often more rough due to distinct predominant spinula-like structures.....**38**
- 25 Beetle smaller, TL 6.4 mm (Fig. 28). Median lobe as in Fig. 79: left lobe of dorsal sclerite evenly tapering, its apex straight, with small but distinct incision and crest[7] **A. craterensis sp. nov.**
- Beetle larger, TL > 6.5 mm. Median lobe: left lobe of dorsal sclerite often with a curved downwards apex and small apical crest but without incision, laterally evenly tapering or differently concave.....**26**
- 26 Median lobe as in Fig. 80: left lobe of dorsal sclerite distinctly concave apically; its apex narrow, with a long crest; ventral sclerite visible only in small apical part in left lateral view. TL 6.5–7.6 mm. Elytron with 11+0 striae: dorsal striae complete, always evidently 11. Elytron piceous, without a yellowish red basal band, yellowish apically (Fig. 29) [1] **A. aiyurensis sp. nov.**
- Median lobe: left lobe of dorsal sclerite with a distinct median concavity and its whole apical 1/2 narrowed or broadened, or without distinct median concavity and its whole apical 1/2 evenly tapering; apex of left dorsal lobe broad, with a small crest or without it; ventral sclerite not visible or visible in whole apical 1/2 in left lateral view**27**
- 27 Median lobe: left lobe of dorsal sclerite with very strong median concavity, its apical 1/2 very broad. Elytron with 11+1 striae: stria 1 reduced basally, submarginal stria present. Elytron piceous, with narrow, sometimes short and faint yellowish red basal band.....**28**
- Median lobe: left lobe of dorsal sclerite with a distinct median concavity and its whole apical 1/2 narrowed or without distinct median concavity and its whole apical 1/2 evenly tapering. Elytron with (0–10)+(0–1) striae; with or without a yellowish red basal band**29**
- 28 Male anterior proclaw thicker and more strongly curved downwards. Male protibia distinctly modified: thinner proximally and broader medially and distally due to its curved ventral margin. Median lobe as in Fig. 81: left lobe of dorsal sclerite with apical 1/2 narrower. TL 7.45–7.9 mm (Fig. 30) [37] **A. robustus sp. nov.**
- Male anterior proclaw narrower, straight. Male protibia slightly modified. Median lobe as in Fig. 82: left lobe of dorsal sclerite with apical 1/2 broader. TL 7.25–8.3 mm (Fig. 31) [4] **A. bosaviensis sp. nov.**
- 29 Median lobe: left lobe of dorsal sclerite with a distinct median concavity and its whole apical 1/2 narrowed.....**30**
- Median lobe: left lobe of dorsal sclerite without distinct median concavity and its whole apical 1/2 more or less evenly tapering**33**
- 30 Median lobe as in Fig. 83: left lobe of dorsal sclerite with apical 1/2 narrower and apex straight, without distinct crest, sometimes with a weak crest due to small, very shallow tip concavity, more or less evenly rounded. Elytron with (10–11)+(0–1) striae; with or without yellowish red basal band. TL 6.45–7.7 mm (Fig. 32)..... [9] **A. dekai sp. nov.**
- Median lobe: left lobe of dorsal sclerite with apical 1/2 broader and apex slightly curved downwards, with a small but distinct crest, slightly truncate or broadly pointed**31**

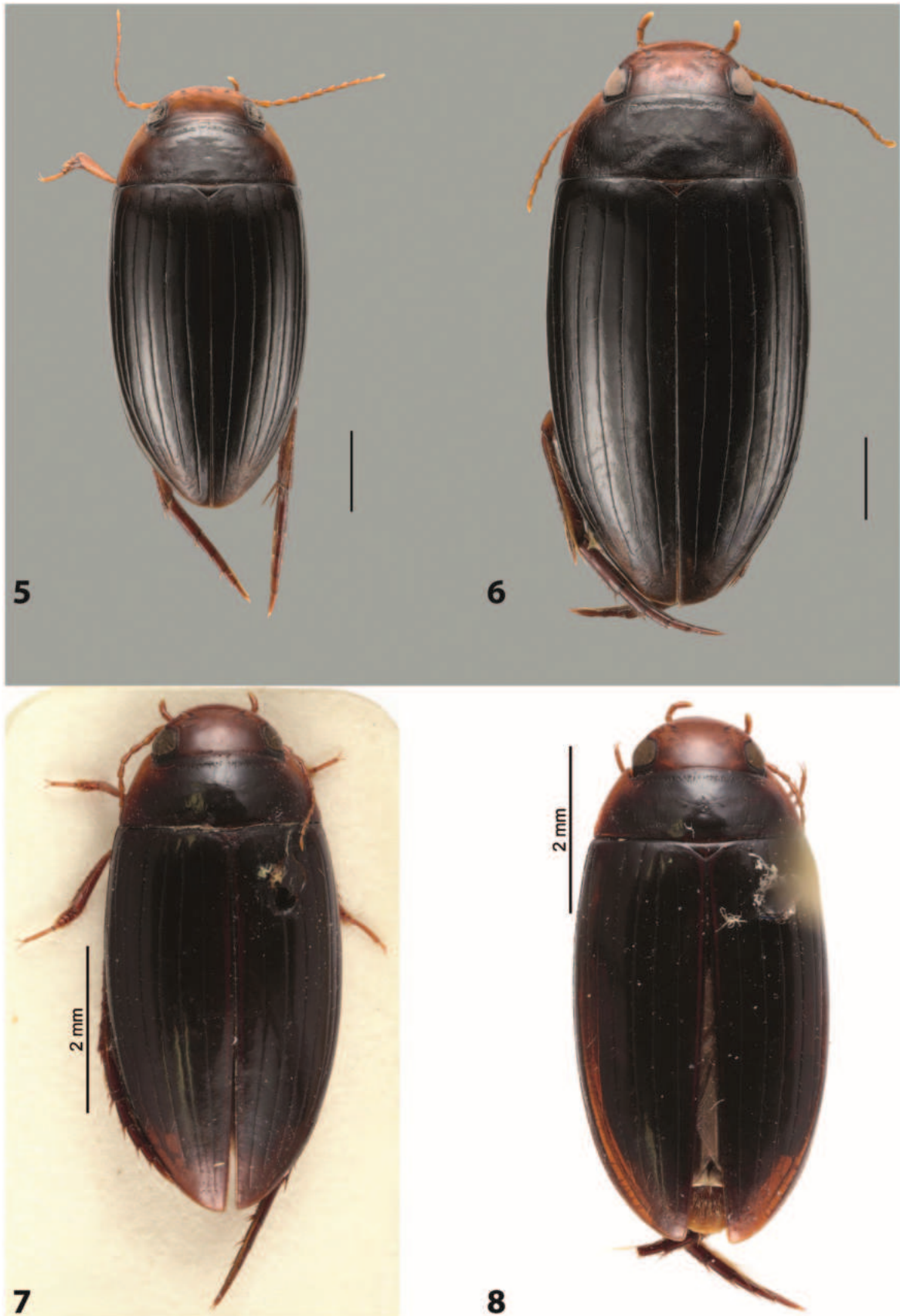
- 31 Median lobe as in Fig. 65: left lobe of dorsal sclerite with a weaker median concavity, its apical 1/2 narrower, apical crest smaller. Elytral striation very variable: (0–10)+(0–1) striae. Elytron often yellowish red laterally, apically, and between striae additionally to yellowish red basal band. TL 6.7–8.2 mm (Figs 13–15).....[15] **A. *inconstans* sp. nov.**
- Median lobe: left lobe of dorsal sclerite with a stronger median concavity, its apical 1/2 broader, apical crest larger**32**
- 32 Elytron with (6–11)+1 striae, without yellowish red basal band. TL 7.3–8.2 mm (Fig. 22). Median lobe as in Fig. 73: left lobe of dorsal sclerite with apical 1/2 narrower and right dorsal lobe shorter [28] **A. *miltokarenos* sp. nov.**
- Elytron with (0–10)+(0–1) striae, with yellowish red basal band. TL 7.1–7.9 mm (Figs 11, 12). Median lobe as in Fig. 64: left lobe of dorsal sclerite with apical 1/2 broader and right dorsal lobe longer
.....[5] **A. *bundunensis* sp. nov.**
- 33 Median lobe: apex of left dorsal lobe elongate, almost straight, evenly or unevenly rounded or broadly pointed, with a small crest**34**
- Median lobe: apex of left dorsal lobe broader, slightly truncate and curved downwards, with more distinct crest**35**
- 34 Elytron with 11+1 striae: dorsal striae complete, only stria 1 shortly reduced basally. TL 7–7.7 mm (Fig. 33). Male anterior proclaw thicker at its apex than posterior one and with slight subapical incision of its inner margin. Median lobe as in Fig. 84: apex of left dorsal lobe narrower, with weaker crest[33] **A. *posmani* sp. nov.**
- Elytron with (10–11)+1 striae: striae 1–3 reduced in basal 1/2, stria 1 strongly to completely reduced. TL 6.9–7.8 mm (Figs 34, 35). Male anterior proclaw thicker subapically and more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe as in Fig. 85: apex of left dorsal lobe broader, with more distinct crest [32] **A. *papuensis***
- 35 Median lobe as in Fig. 86: left lobe of dorsal sclerite broad and flat, with broader and more rounded scale-like structures and small, short apex. TL 6.9–7.8 mm. Elytron with 11+1 striae: stria 1 shortly reduced basally (Fig. 36)..... [3] **A. *bewaniensis* sp. nov.**
- Median lobe: left lobe of dorsal sclerite distinctly narrower, with narrower scale-like structures and larger, more elongate apex**36**
- 36 Male anterior proclaw thicker subapically and slightly more strongly curved downwards than posterior one and due to this with a median incision on its inner margin. Median lobe as in Fig. 87: left lobe of dorsal sclerite with shorter, more rounded apex. TL 7.9 mm (Fig. 37)
.....[29] **A. *noiadi* sp. nov.**
- Male anterior proclaw thicker apically and more strongly curved downwards than posterior one, with subapical incision on its inner margin. Median lobe: left lobe of dorsal sclerite with longer apex**37**
- 37 Median lobe as in Fig. 88: apex of left dorsal lobe shorter, with more vertical, broader crest. Elytron often yellowish red due to strongly developed, broad basal band and lateral and apical yellowish colouration; usually with 11+1 striae, seldom with a strong stria reduction: dorsal

- striae present only in apical part and some of them as strioles, stria 1 can be absent. TL 6.8–8.15 mm (Figs 38, 39) [24] ***A. madangensis* sp. nov.**
- Median lobe as in Fig. 89: apex of left dorsal lobe more elongate, with more transverse, narrower crest. Elytron darker, with narrow yellowish red basal band; with 11+1 striae: striae 1–3 reduced in basal 1/2, stria 1 can be reduced to apical strioles. TL 7.5–7.9 mm (Fig. 40)..... [26] ***A. mamberamo* sp. nov.**
- 38 Median lobe: left lobe of dorsal sclerite with a distinct, deep surface concavity under upper lateral margin in left lateral view **39**
- Median lobe: left lobe of dorsal sclerite without such lateral concavity or with shallow one..... **41**
- 39 Median lobe as in Fig. 90: left lobe of dorsal sclerite with subapical, elongate concavity. Elytron yellowish or with yellow basal band, with 11+1 complete, strongly impressed striae. TL 6.4–6.6 mm (Fig. 41) [43] ***A. weigeli* sp. nov.**
- Median lobe: left lobe of dorsal sclerite with concavity situated more medially, of triangular shape. Elytron with (10–11)+0 striae: stria 1 strongly reduced basally (visible in traces in apical 1/2), sometimes completely reduced, stria 2 or striae 2 and 3 usually reduced basally..... **40**
- 40 Elytron without yellowish red basal band, piceous, yellowish red apically. TL 6.1–6.7 mm (Fig. 42). Median lobe as in Fig 91, with its apical part distinctly longer [17] ***A. kalibumi* sp. nov.**
- Elytron with a broad yellowish red basal band, piceous, yellowish red apically. TL 5.65–6.7 mm (Fig. 43). Median lobe as in Fig 92, with its apical part distinctly shorter [14] ***A. herzogensis* sp. nov.**
- 41 Median lobe: surface of left dorsal lobe not completely covered by spinula-like structures in apical 1/2, upper lateral margin without spinulae, smooth, especially medially, in left lateral and ventral views **42**
- Median lobe: surface of left dorsal lobe completely covered by spinula-like structures in apical 1/2 including median part in left lateral and ventral views **46**
- 42 Elytron without yellowish red basal band, with a yellow apical spot **43**
- Elytron with a yellowish red basal band **44**
- 43 Beetle larger, TL 5.6–6.4 mm. Elytron with 11+1 striae but stria 1 usually weakly impressed or differently reduced (Fig. 44). Median lobe as in Fig. 93: lateral margin of left dorsal lobe with weak edge, below which spinula-like structures are situated [27] ***A. mianminensis* sp. nov.**
- Beetle smaller, TL 5.3–5.5 mm. Elytron with 11+1 complete, strongly impressed striae (Fig. 45). Median lobe as in Fig. 94: lateral margin of left dorsal lobe with more sharp and prominent edge, below which spinula-like structures are situated [36] ***A. pseudomianminensis* sp. nov.**
- 44 Median lobe as in Fig. 95: left dorsal lobe covered with larger spinula-like structures, its apex slightly curved downwards. TL 5.4–6.1 mm, TL/MW 2.04–2.1 (Fig. 46)..... [11] ***A. flavocapitatus* sp. nov.**
- Median lobe: left dorsal lobe covered with smaller spinula-like structures, its apex more or less straight **45**

- 45 Median lobe as in Fig. 96: lobes of dorsal sclerite broader, left dorsal lobe with a shallow surface concavity in left lateral view. Beetle more oval: TL 5.4–5.7 mm, TL/MW 2.04–2.11 (Fig. 47).....[25] **A. *maidai* sp. nov.**
- Median lobe as in Fig. 97: lobes of dorsal sclerite narrower, left dorsal lobe without concavity in left lateral view. Beetle more elongate: TL 5.6–5.65 mm, TL/MW 2.11–2.17 (Fig. 49).....[19] **A. *kokodensis* sp. nov.**
- 46 Elytron without yellowish red basal band, piceous, sometimes yellowish red apically.....**47**
- Elytron with a yellowish red basal band.....**49**
- 47 Beetle smaller, TL 5.7 mm. Elytron with 11+1 striae (Fig. 48). Median lobe as in Fig. 98: left lobe of dorsal sclerite without concavity, covered with small spinula-like structures..... [38] **A. *sararti* sp. nov.**
- Beetle larger, TL 5.95–6.4 mm. Median lobe: left lobe of dorsal sclerite with shallow concavity, covered with large spinula-like structures.....**48**
- 48 Elytron with 10+1 striae: submarginal stria present as weak apical strioles (Fig. 50). Median lobe as in Fig. 99: left lobe of dorsal sclerite with a shallow, large, median concavity, covered with large, long spinula-like structures..... [12] **A. *fuscus* sp. nov.**
- Elytron with 11+1 striae (Fig. 51). Median lobe as in Fig. 100: left lobe of dorsal sclerite with a shallow, narrow, subapical concavity, covered with large, short spinula-like structures..... [41] **A. *wasiorensis* sp. nov.**
- 49 Elytron with (10–11)+1 striae, striae 1–3 reduced basally, often stria 1 present only apically as strioles, sometimes completely reduced. Median lobe: lateral margin of left dorsal lobe beaded. Beetle usually larger, TL 5.8–6.9 mm.....**50**
- Elytron with 11+1 complete striae, seldom stria 1 reduced basally. Median lobe: lateral margin of left dorsal lobe simple, not beaded. Beetle usually smaller, TL 4.8–6.6 mm.....**51**
- 50 Elytron with narrower yellowish red basal band. TL 5.8–6.8 mm (Fig. 52). Median lobe as in Fig. 101: left lobe of dorsal sclerite narrower and narrowed to apex in its apical 1/2..... [13] **A. *gestroi***
- Elytron broader with yellowish red basal band. TL 6.9 mm (Fig. 53). Median lobe as in Fig. 102: left lobe of dorsal sclerite broader and narrowed to apex in its apical 1/3..... [35] **A. *pseudogestroi* sp. nov.**
- 51 Elytron piceous, usually with a short, median reddish basal band. TL 5.4–6.3 mm (Fig. 54). Median lobe as in Fig. 103: surface of left dorsal lobe with large, single spinulae..... [42] **A. *wasurensis* sp. nov.**
- Elytron usually with a distinct yellowish red basal band. TL 5.7–6.6 mm. Median lobe: surface of left dorsal lobe with tiny spinulae situated in groups on scale-like structures.....**52**
- 52 Beetle smaller, TL 4.8–5.5 mm (Fig. 55). Male genitalia as in Fig. 104: median lobe slender, its apex distinctly narrower in left lateral view..... [45] **A. *yeretuar* sp. nov.**



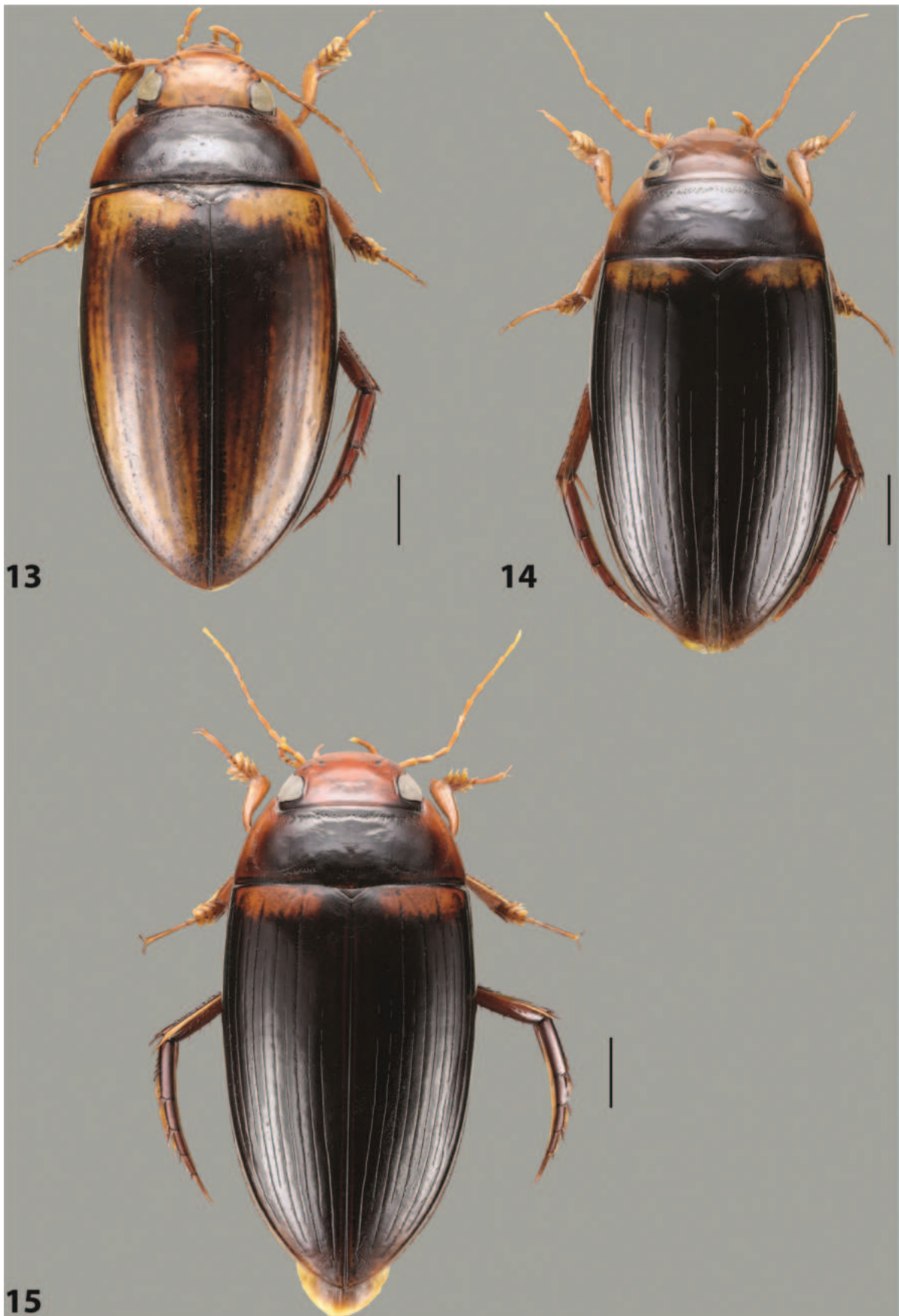
Figures 1–4. Habitus and colouration of the holotypes of 1 *Austrelatus leptos* sp. nov. 2 *A. procerus* sp. nov. 3 *A. lopintolensis* sp. nov. 4 *A. ohu* sp. nov. Scale bars: 1 mm.



Figures 5–8. Habitus and colouration of **5** *Austrelatus xanthocephalus* (Régimbart, 1899), Ransiki - Anggi (BH03) **6** *A. xanthocephalus*, Testega (BH054) **7** *A. xanthocephalus*, lectotype **8** *A. xanthocephalus*, paralectotype. **7** and **8** photographs by Christophe Rivier (MNHN). Scale bars: 1 mm (**5**, **6**).



Figures 9–12. Habitus and colouration of **9** *Austrelatus xanthocephalus nabirensis* ssp. nov., holotype, without elytral striae **10** *A. x. nabirensis* ssp. nov., with elytral striae **11** *A. bundunensis* sp. nov., without elytral striae **12** *A. bundunensis* sp. nov., holotype, with elytral striae. Scale bars: 1 mm.



Figures 13–15. Habitus and colouration of **13** *Austrelatus inconstans* sp. nov., without elytral striae **14** and **15** *A. inconstans* sp. nov., holotype, with elytral striae. Scale bar: 1 mm.



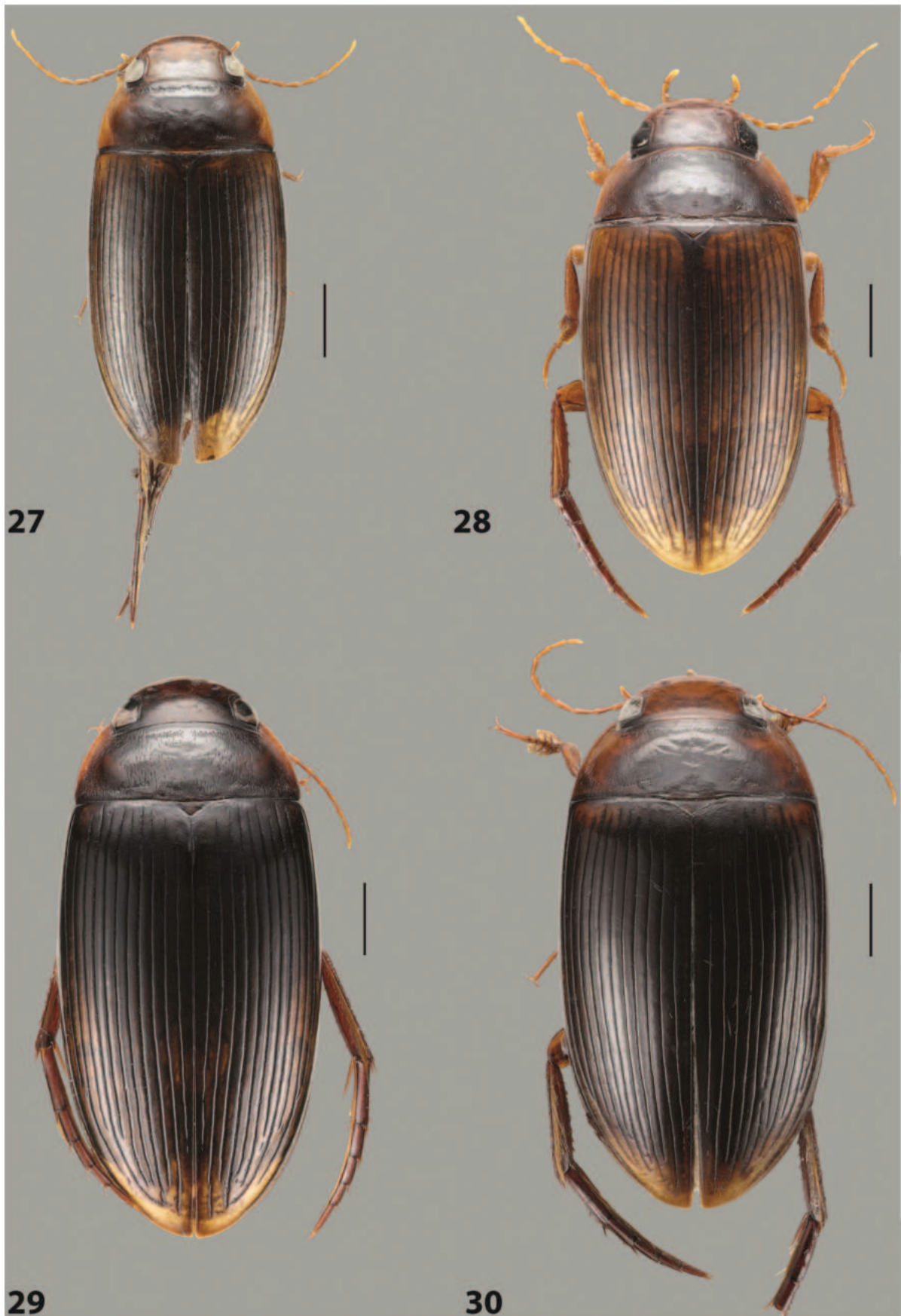
Figures 16–19. Habitus and colouration of **16** *Austrelatus yamurensis* sp. nov., holotype **17** *A. kebarensis* sp. nov., holotype **18** *A. luteomaculatus* (Guignot, 1956), lectotype **19** *A. luteomaculatus*. Scale bar: 1 mm.



Figures 20–22. Habitus and colouration of **20** *Austrelatus centralensis* sp. nov., paratype **21** *A. normanbyensis* sp. nov., holotype **22** *A. miltokarenos* sp. nov., holotype. Scale bar: 1 mm.



Figures 23–26. Habitus and colouration of the holotypes of **23** *Austrelatus loloki* sp. nov. **24** *A. sumokedi* sp. nov. **25** *A. iriatoi* sp. nov. **26** *A. wanangensis* sp. nov. Scale bar: 1 mm.



Figures 27–30. Habitus and colouration of the holotypes of **27** *Austrelatus decoris* sp. nov. **28** *A. craterensis* sp. nov. **29** *A. aiyurensis* sp. nov. **30** *A. robustus* sp. nov. Scale bars: 1 mm.



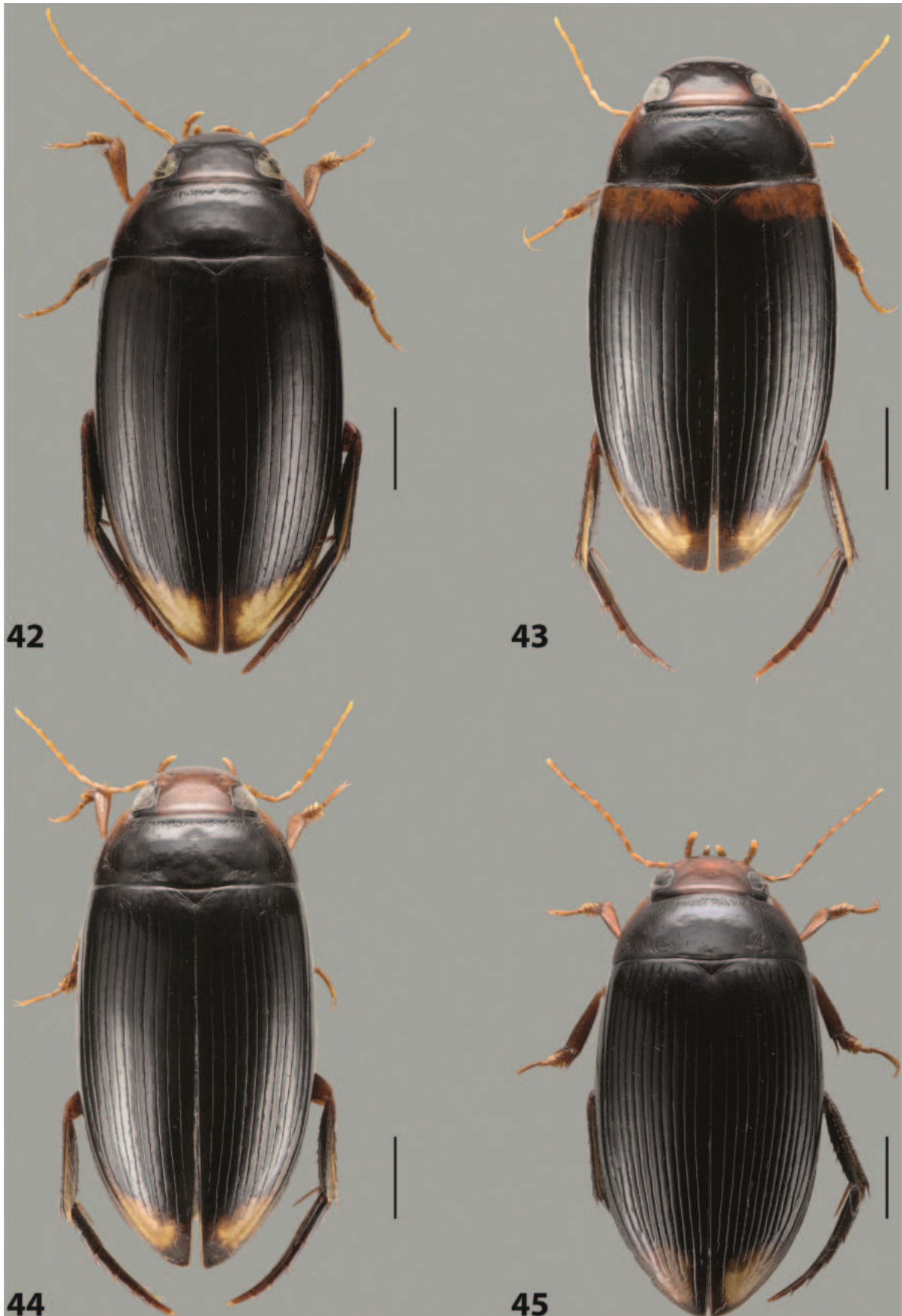
Figures 31–33. Habitus and colouration of the holotypes of **31** *Austrelatus bosaviensis* sp. nov. **32** *A. dekai* sp. nov. **33** *A. posmani* sp. nov. Scale bars: 1 mm.



Figures 34–37. Habitus and colouration of **34** *Austrelatus papuensis* (J. Balfour-Browne, 1939) **35** *A. papuensis*, holotype **36** *A. bewaniensis* sp. nov., holotype **37** *A. noiadi* sp. nov., holotype. Scale bars: 1 mm.



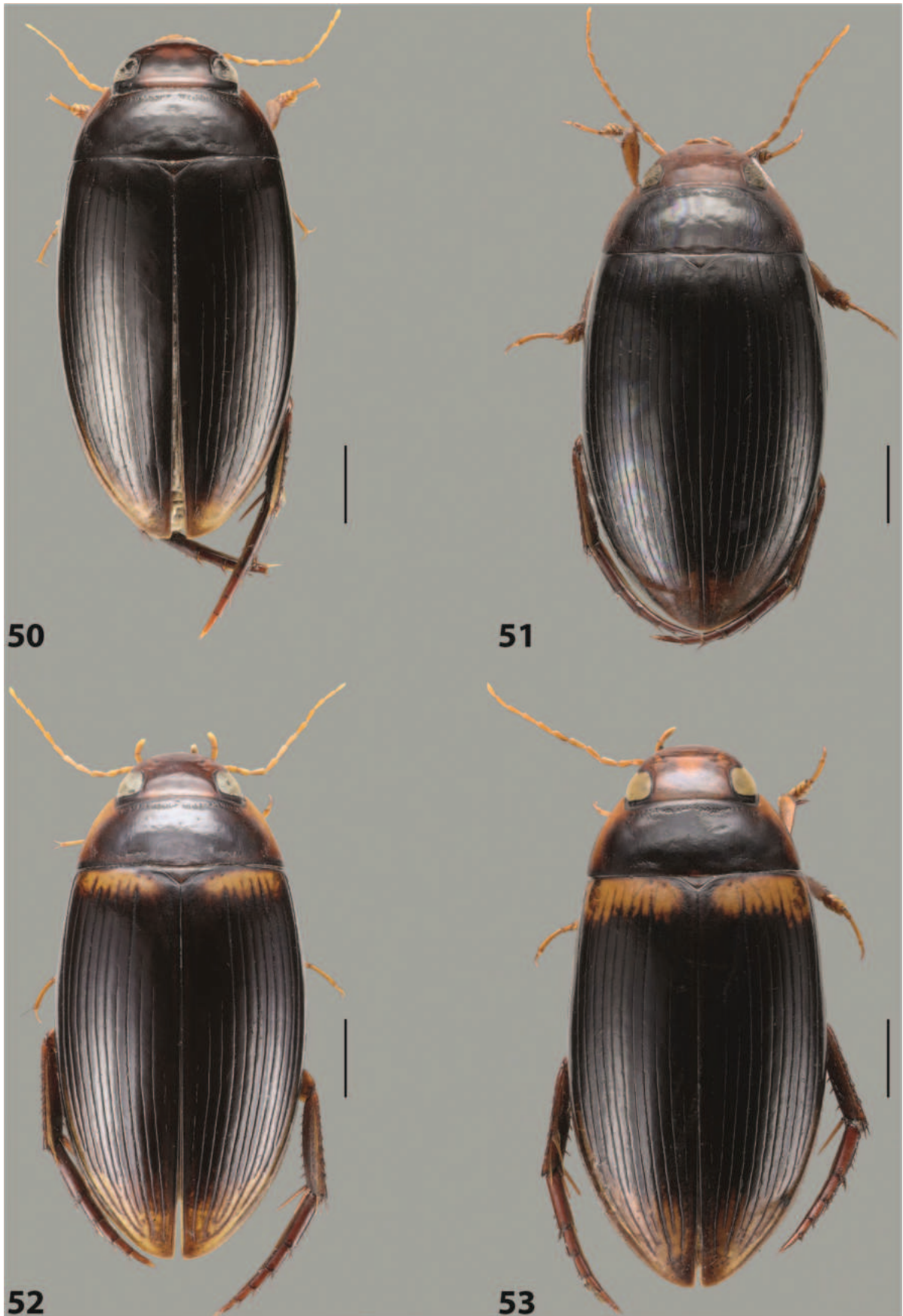
Figures 38–41. Habitus and colouration of **38** *Austrelatus madangensis* sp. nov. **39** *A. madangensis* sp. nov., holotype **40** *A. mamberamo* sp. nov., holotype **41** *A. weigeli* sp. nov., holotype. Scale bars: 1 mm.



Figures 42–45. Habitus and colouration of the holotypes of **42** *Austrelatus kalibumi* sp. nov. **43** *A. herzogensis* sp. nov. **44** *A. mianminensis* sp. nov. **45** *A. pseudomianminensis* sp. nov. Scale bars: 1 mm.



Figures 46–49. Habitus and colouration of the holotypes of **46** *Austrelatus flavocapitatus* sp. nov. **47** *A. maindai* sp. nov. **48** *A. sararti* sp. nov. **49** *A. kokodensis* sp. nov. Scale bars: 1 mm.



Figures 50–53. Habitus and colouration of **50** *Austrelatus fuscus* sp. nov., holotype **51** *A. wasiorenensis* sp. nov., holotype **52** *A. gestroi* (Régimbart, 1892) **53** *A. pseudogestroi* sp. nov., holotype. Scale bars: 1 mm.



Figures 54–57. Habitus and colouration of the holotypes of **54** *Austrelatus wasurensis* sp. nov. **55** *A. yeretuar* sp. nov. **56** *A. epicharis* sp. nov. **57** *A. asteios* sp. nov. Scale bars: 1 mm.

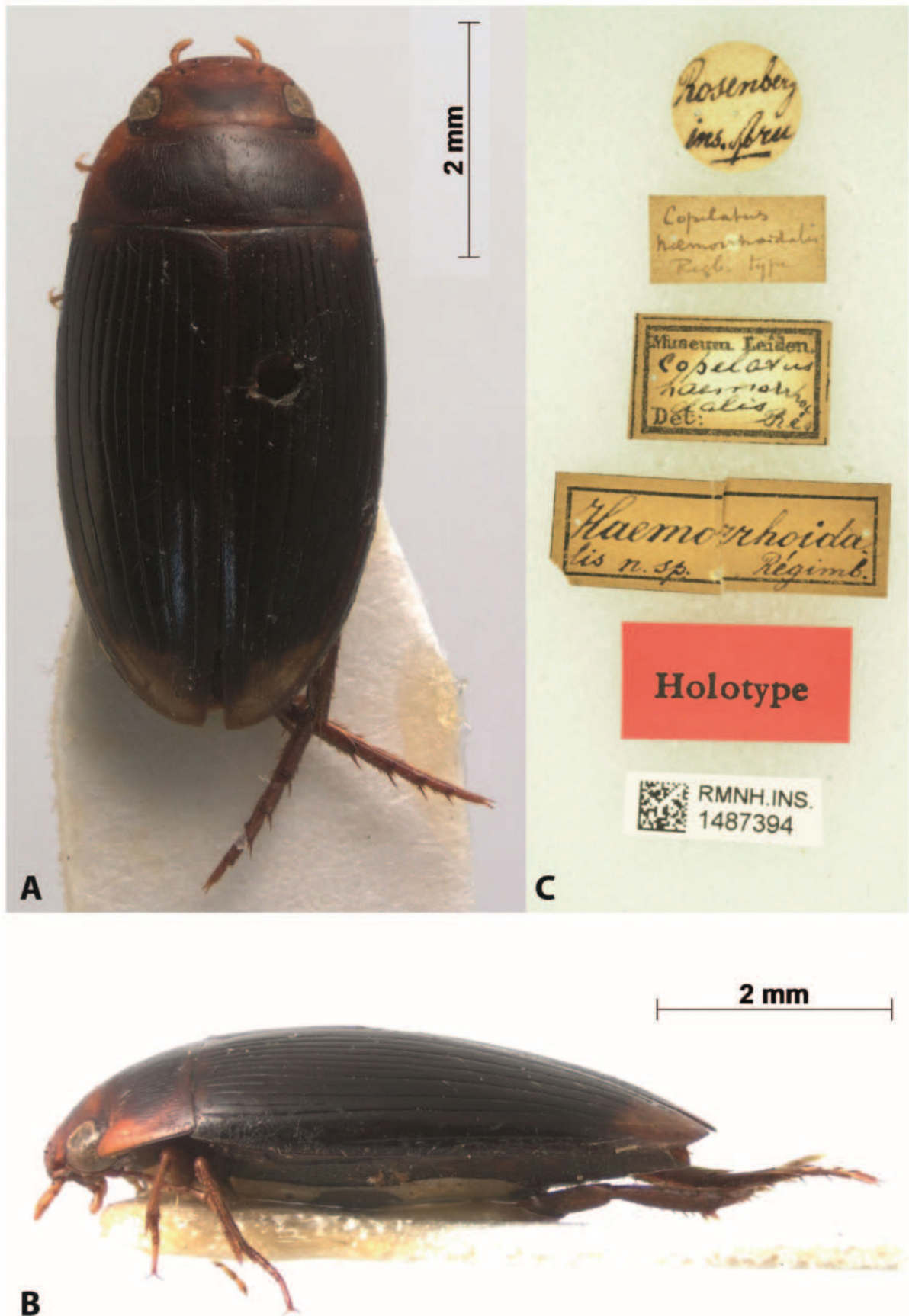


Figure 58. *Copelatus haemorrhoidalis* Régimbart, 1883, holotype (RMNH.INS.1487394), female **A** dorsal view **B** lateral view **C** labels. Photographs by Yvonne van Dam (RMNH).



Figure 59. *Austrelatus leptos* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 60. *Austrelatus procerus* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 61. *Austrelatus xanthocephalus* (Régimbart, 1899), Ransiki - Anggi (BH03), median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 62. *Austrelatus xanthocephalus* (Régimbart, 1899), median lobe **A, C** left lateral view **B, D, E** ventral view **A, B** Kebar (BH035) **C, D** lectotype, photographs by Ch. Rivier (MNHN) **E** Testega (BH054). Scale bar: 1 mm (**A, B, E**).



Figure 63. *Austrelatus xanthocephalus nabirensis* ssp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 64. *Austrelatus bundunensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 65. *Austrelatus inconstans* sp. nov., paratype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 66. *Austrelatus lopintolensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 67. *Austrelatus ohu* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

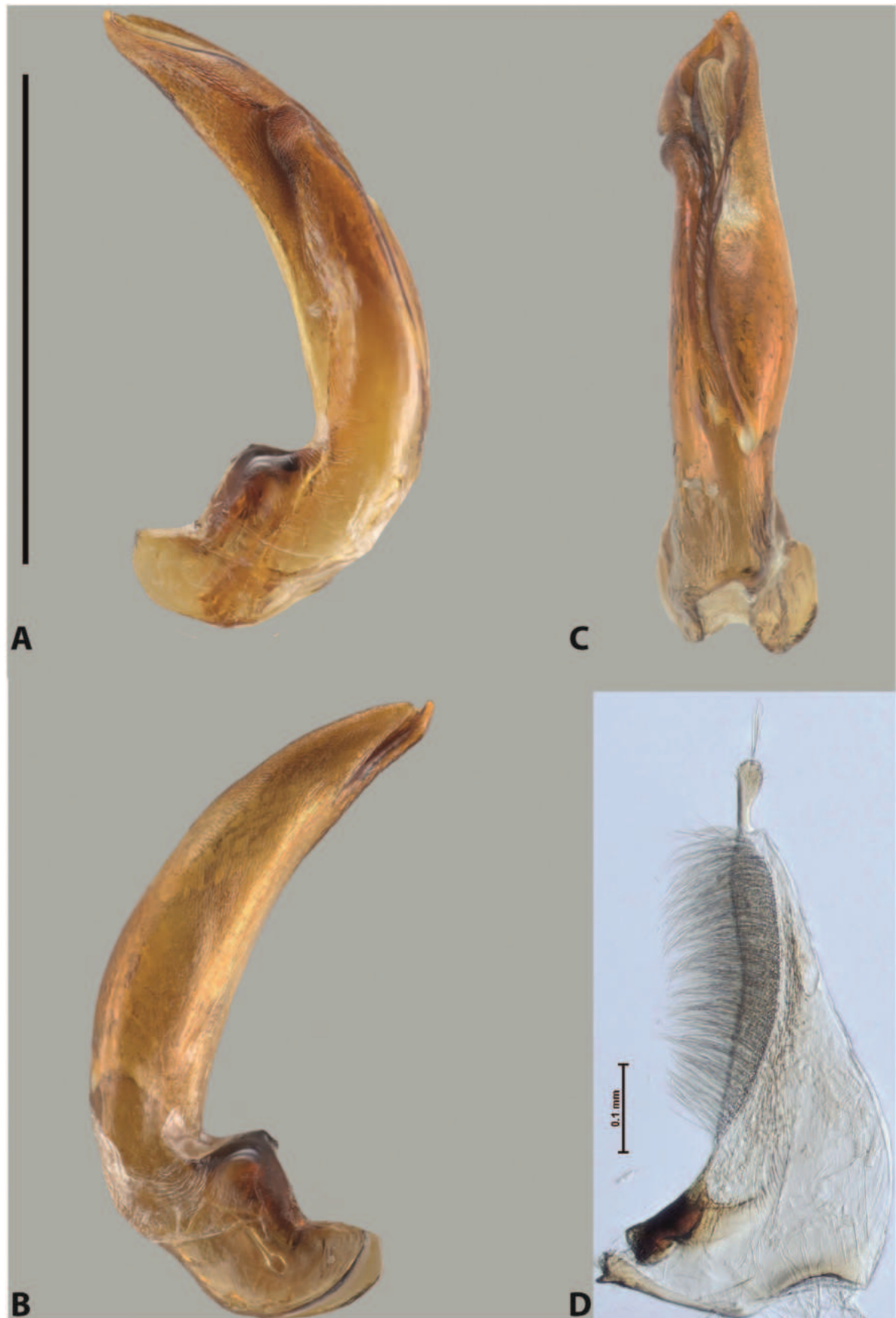


Figure 68. *Austrelatus yamurensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 69. *Austrelatus kebarensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 70. *Austrelatus luteomaculatus* (Guignot, 1956), median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 71. *Austrelatus centralensis* sp. nov., paratype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

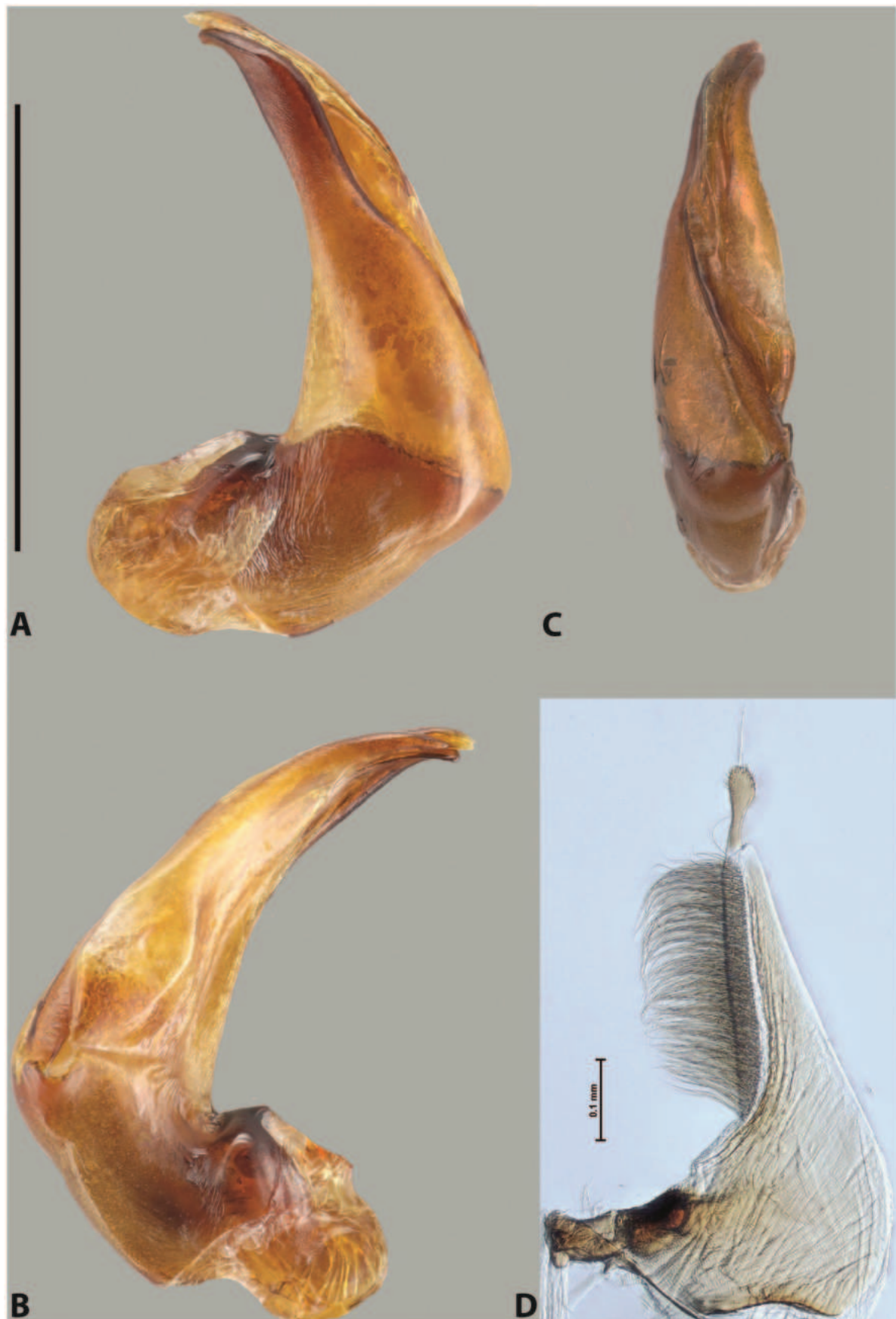


Figure 72. *Austrelatus normanbyensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

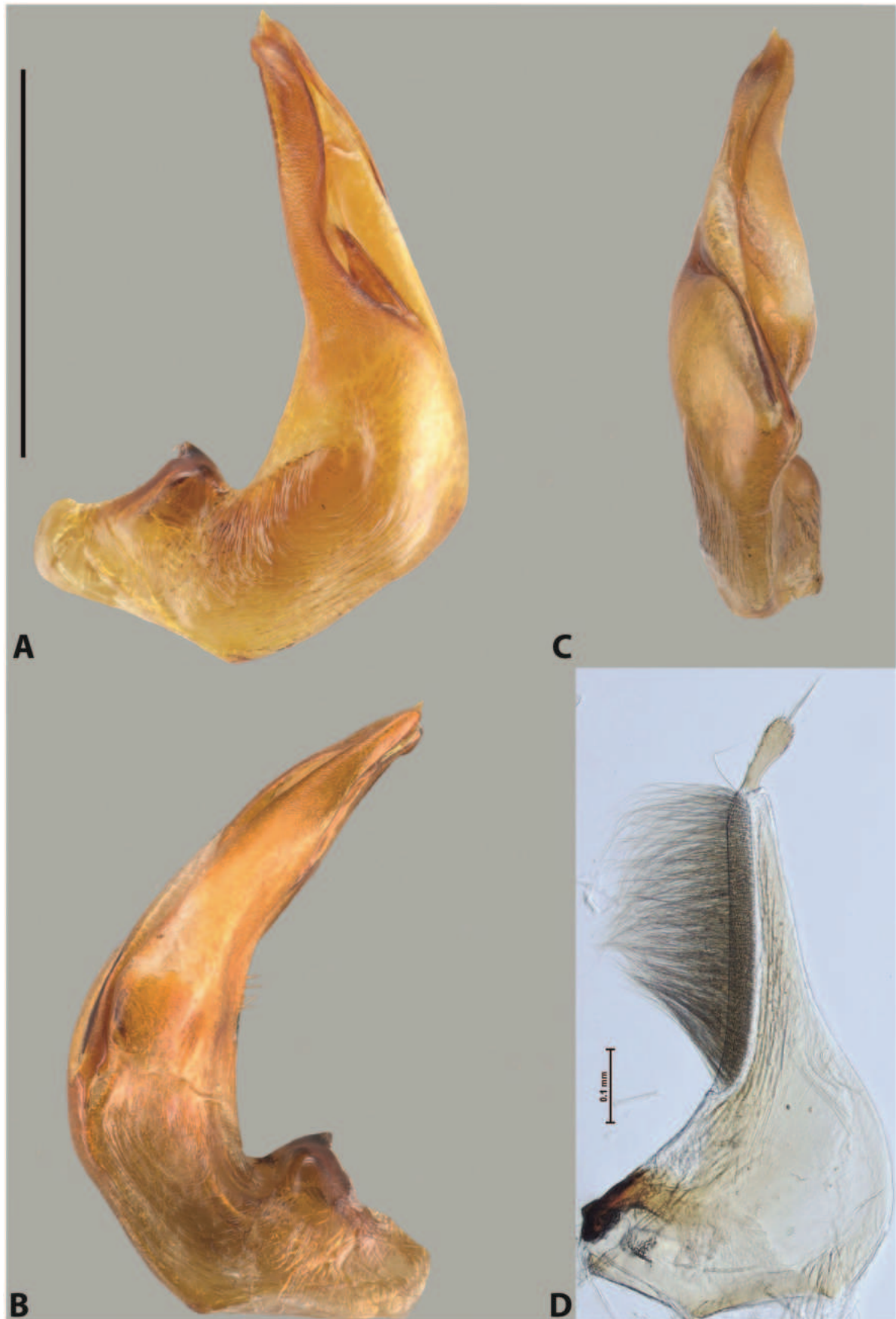


Figure 73. *Austrelatus miltokarenos* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 74. *Austrelatus loloki* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

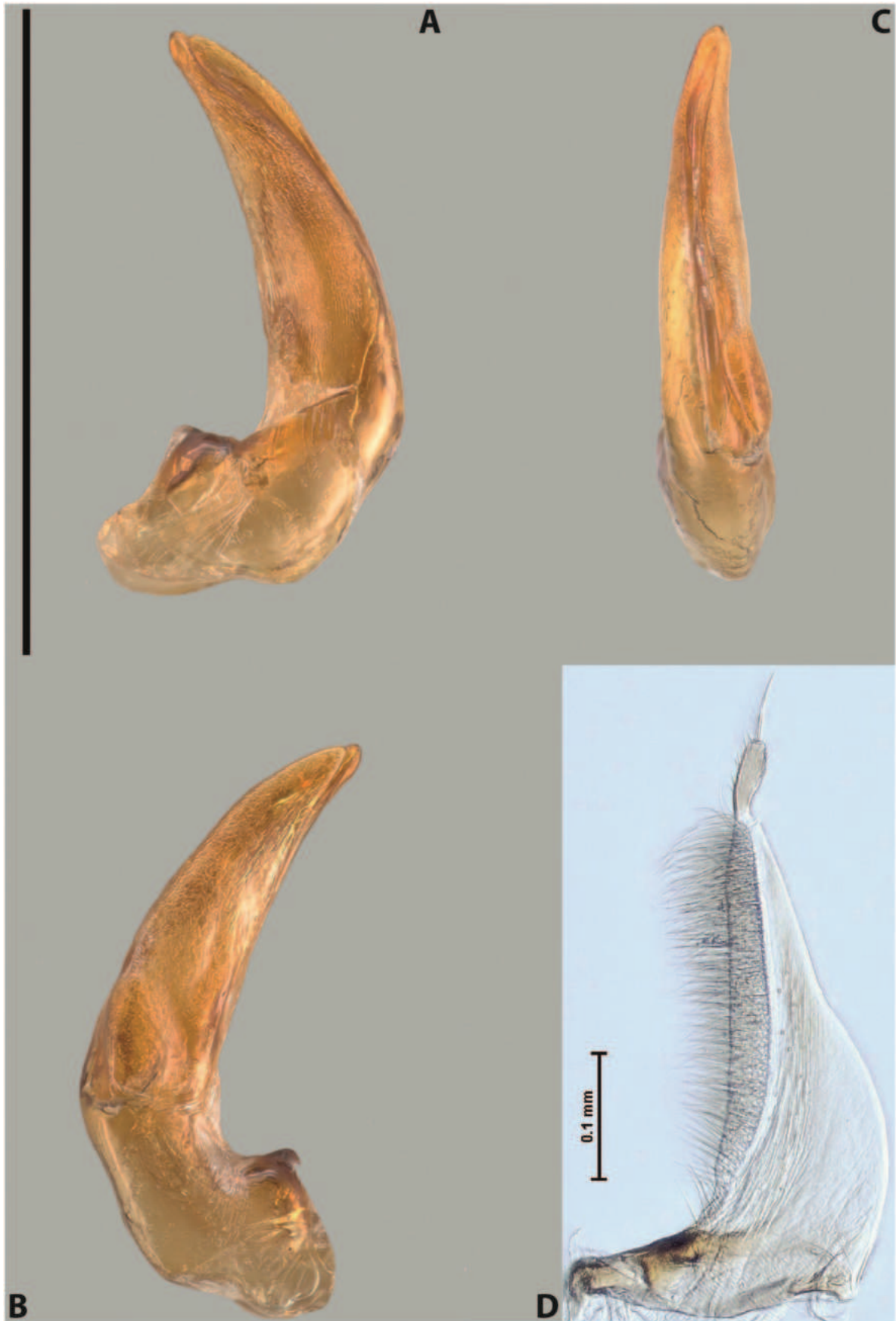


Figure 75. *Austrelatus sumokedi* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 76. *Austrelatus iriatoi* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 77. *Austrelatus wanangensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 78. *Austrelatus decoris* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 79. *Austrelatus craterensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

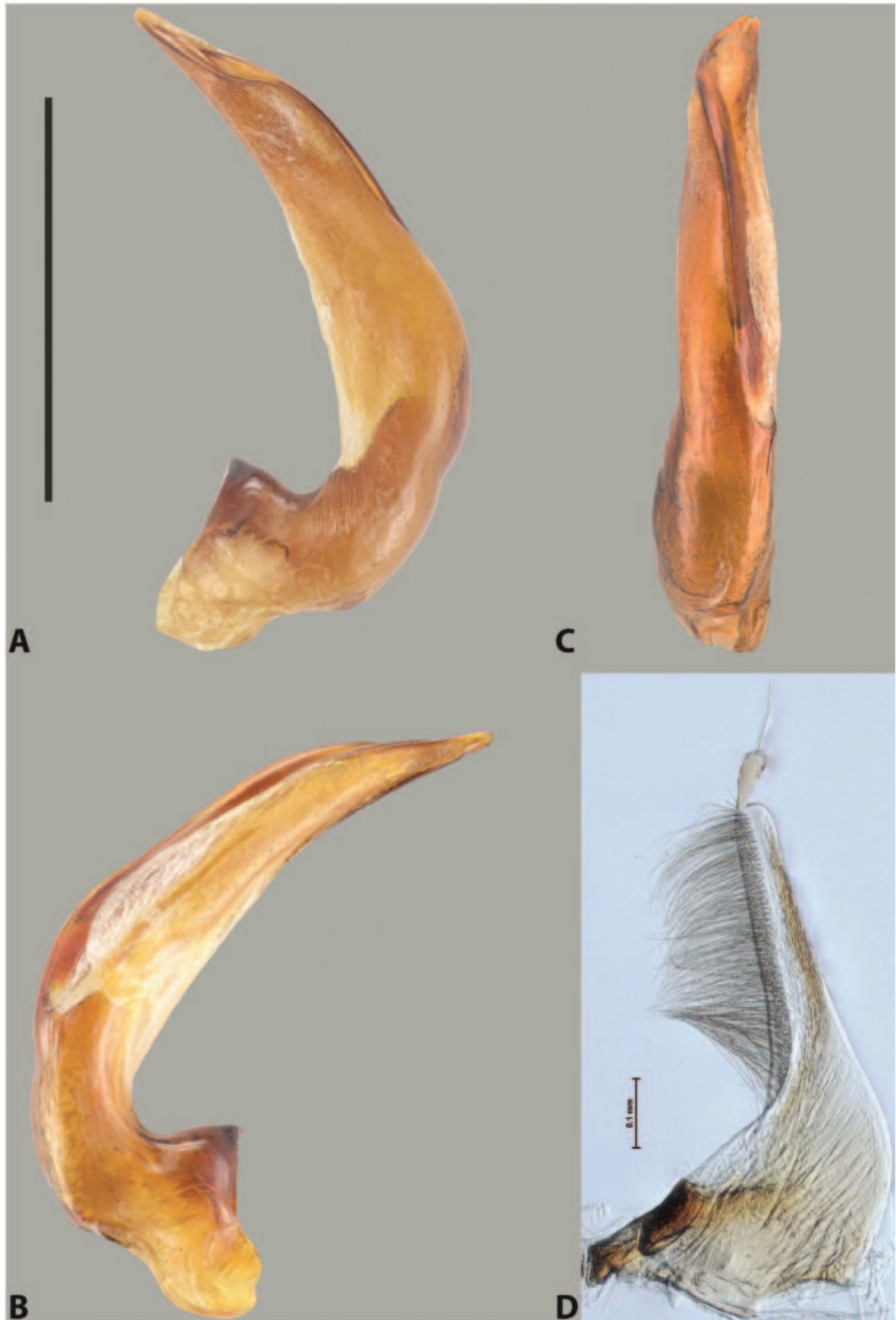


Figure 80. *Austrelatus aiurensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 81. *Austrelatus robustus* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 82. *Austrelatus bosaviensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 83. *Austrelatus dekai* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

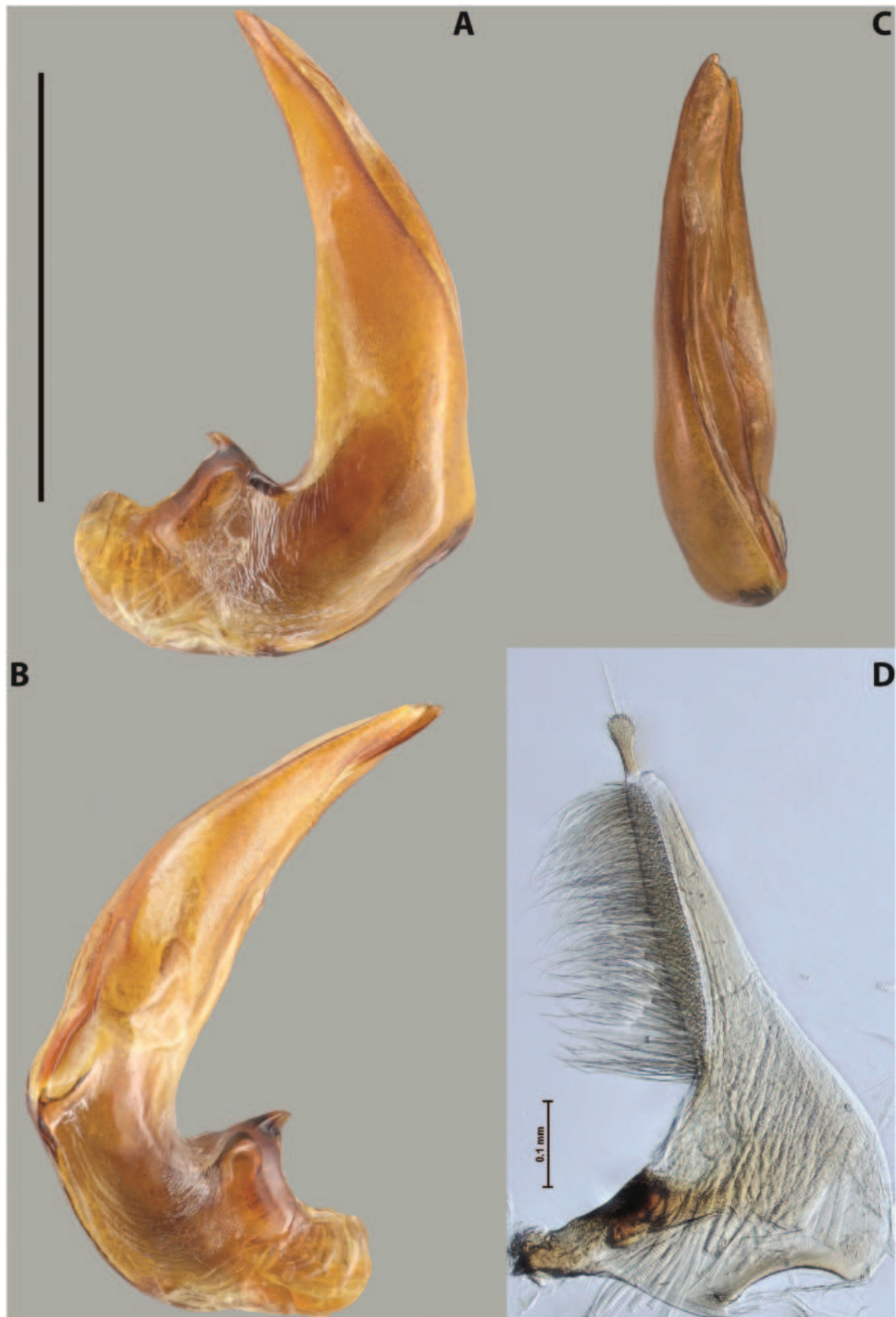


Figure 84. *Austrelatus posmani* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 85. *Austrelatus papuensis* (J. Balfour-Browne, 1939), median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 86. *Austrelatus bewaniensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 87. *Austrelatus noiadi* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 88. *Austrelatus madangensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 89. *Austrelatus mamberamo* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 90. *Austrelatus weigeli* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 91. *Austrelatus kalibumi* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

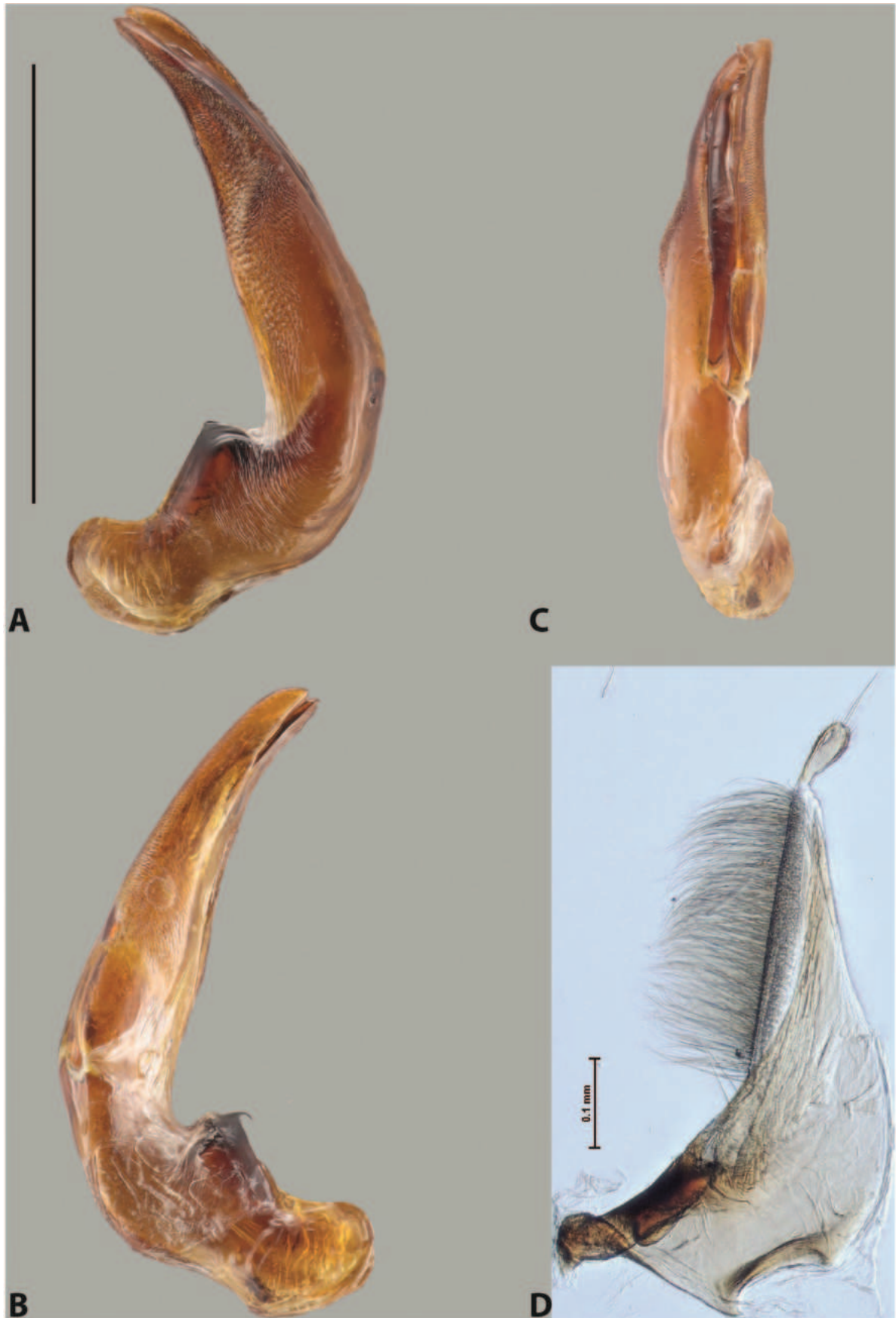


Figure 92. *Austrelatus herzogensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

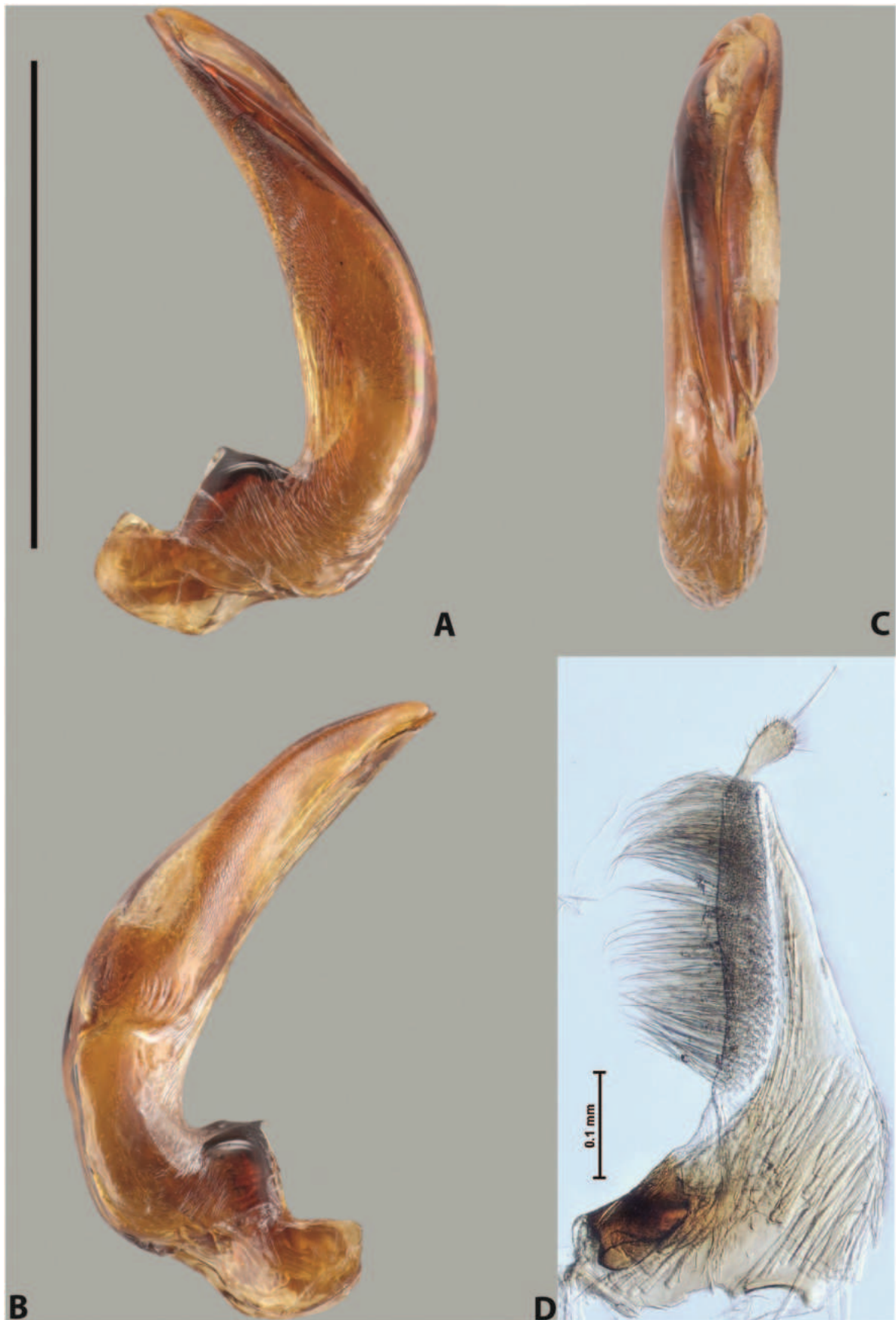


Figure 93. *Austrelatus mianminensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

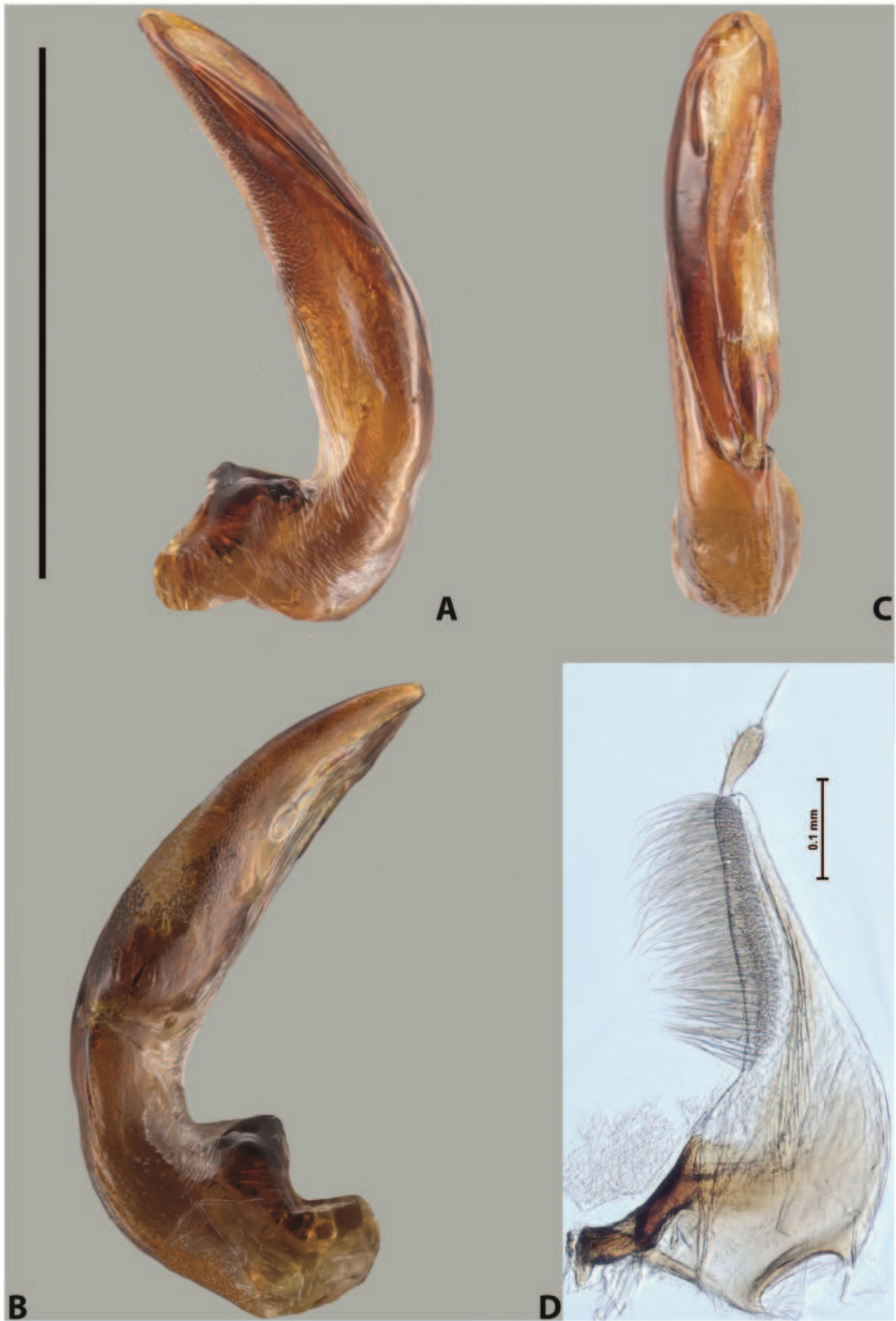


Figure 94. *Austrelatus pseudomianminensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

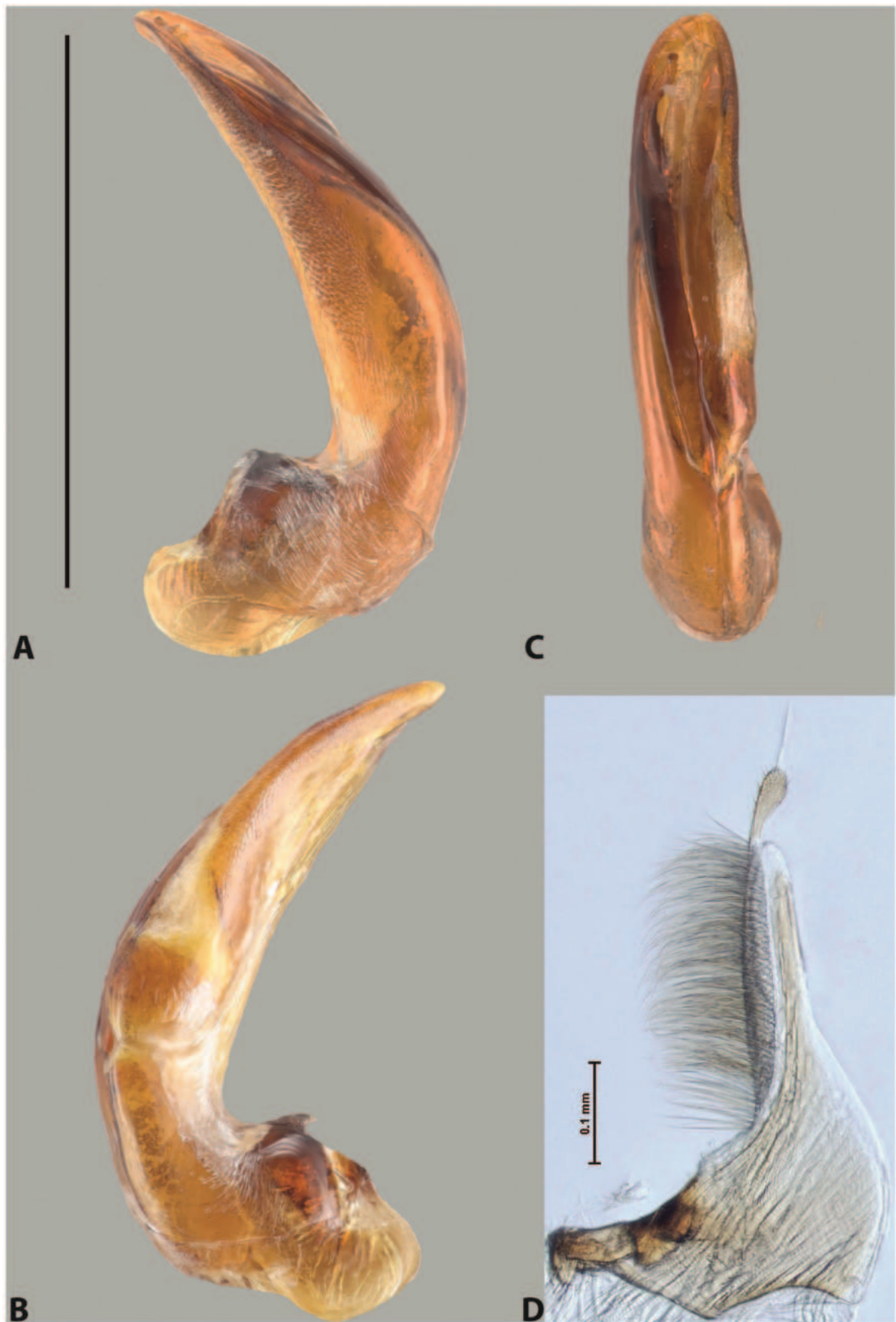


Figure 95. *Austrelatus flavocapitatus* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 96. *Austrelatus maindai* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

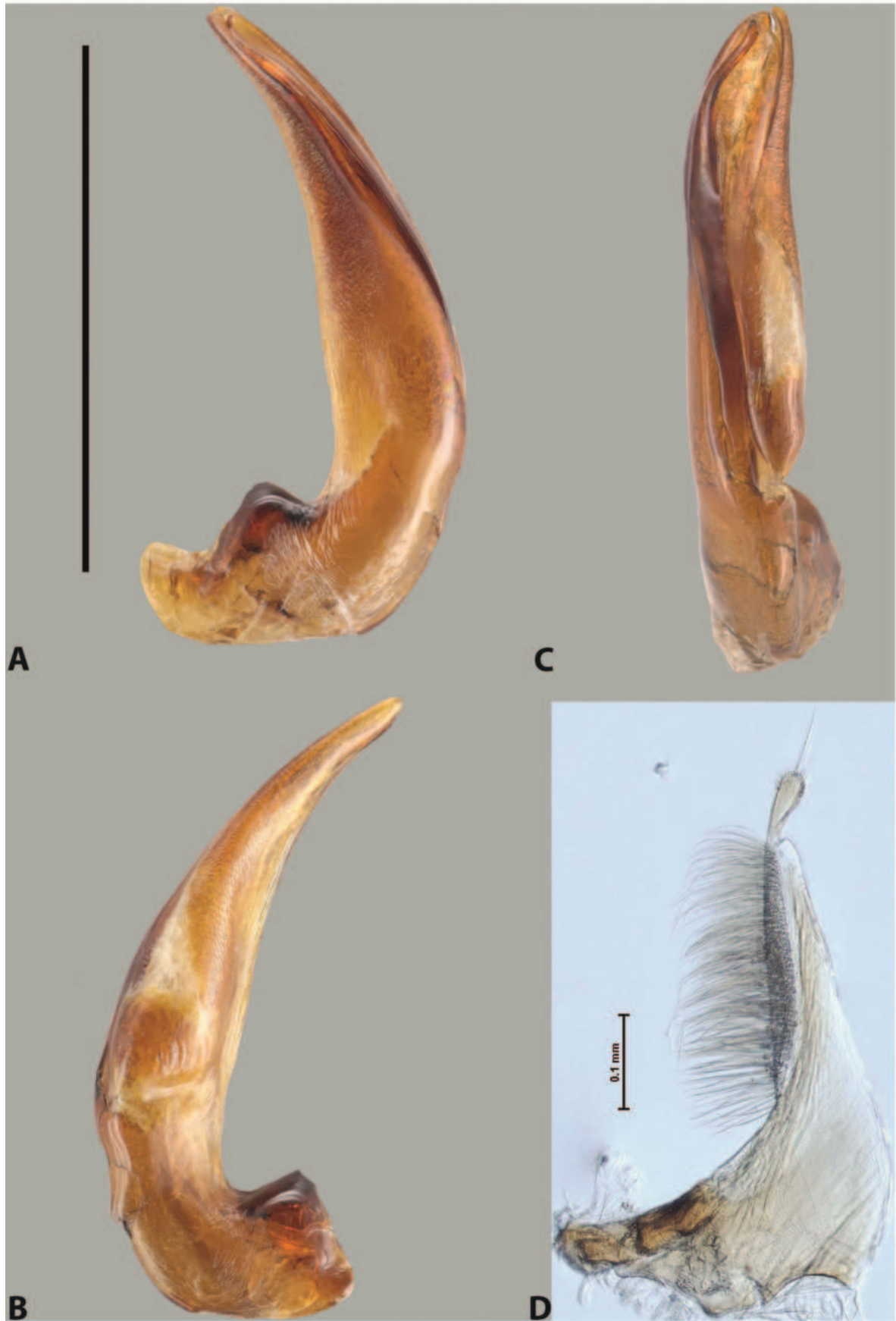


Figure 97. *Austrelatus kokodensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 98. *Austrelatus sararti* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 99. *Austrelatus fuscus* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 100. *Austrelatus wasiorensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

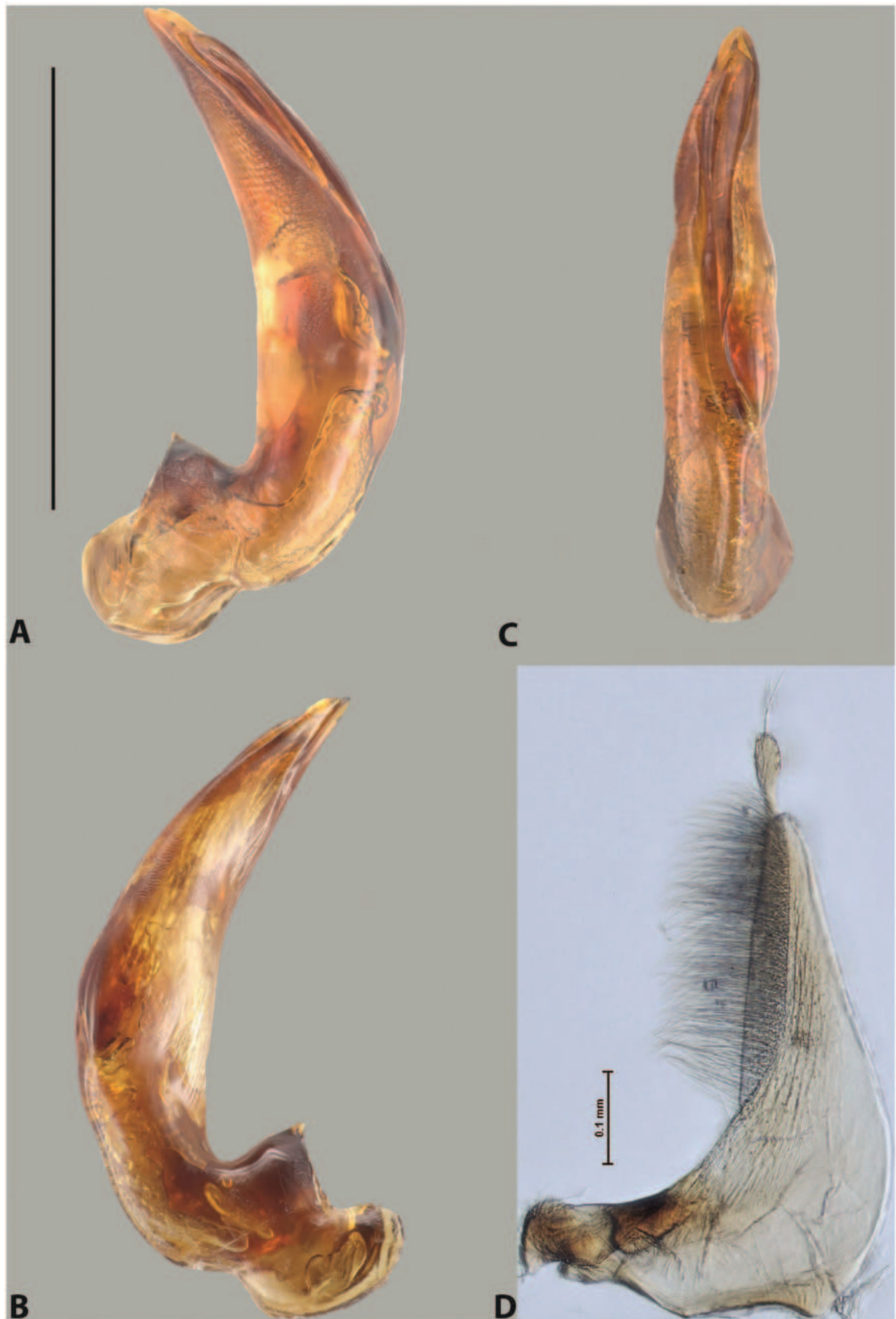


Figure 101. *Austrelatus gestroi* (Régimbart, 1892), lectotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

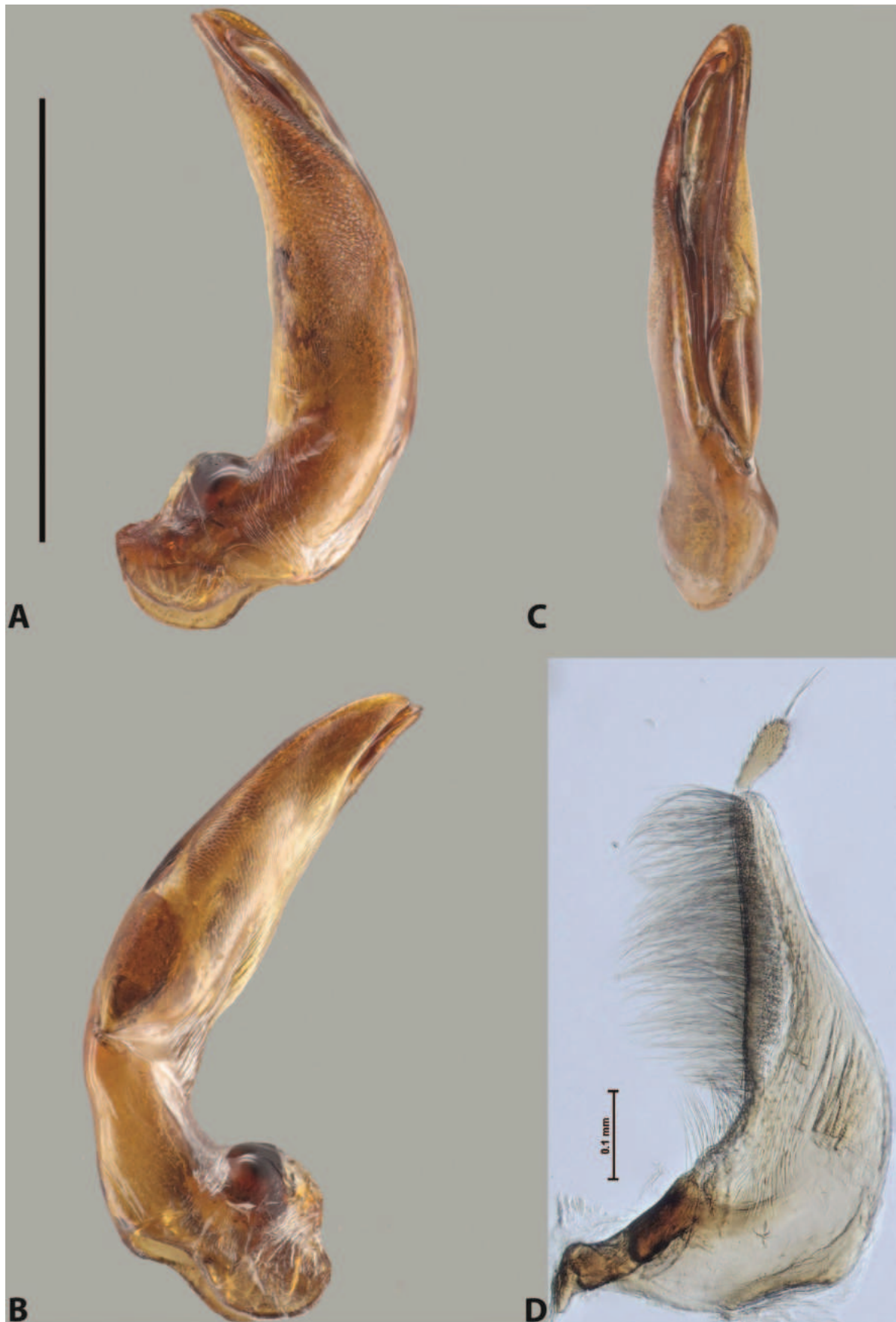


Figure 102. *Austrelatus pseudogestroi* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 103. *Austrelatus wasurensis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 104. *Austrelatus yeretuar* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 105. *Austrelatus asteios* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).

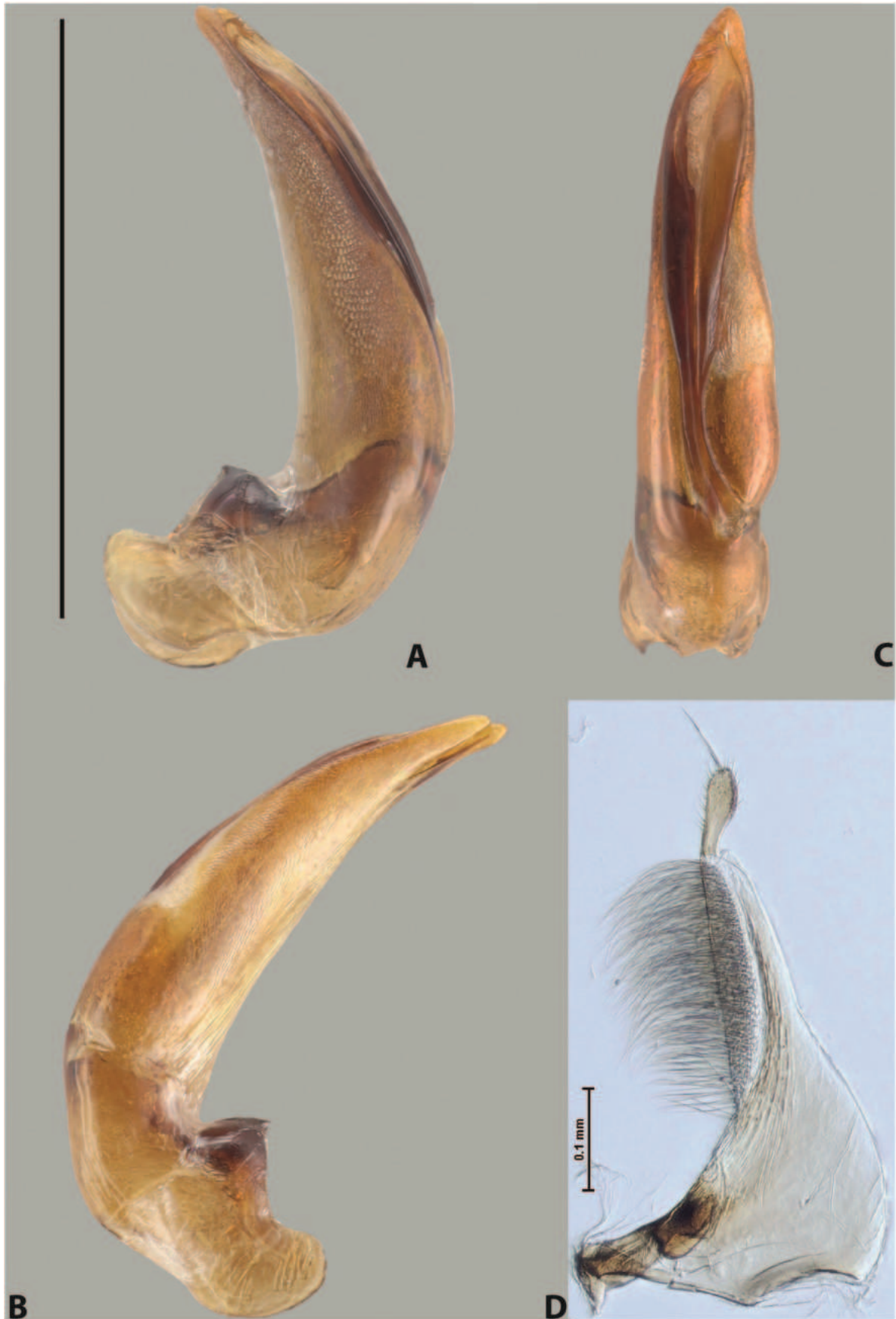


Figure 106. *Austrelatus epicharis* sp. nov., holotype, median lobe **A** left lateral view **B** right lateral view **C** ventral view **D** left paramere in external view. Scale bar: 1 mm (**A–C**).



Figure 107. Map of New Guinea showing distribution of 23 *Austrelatus* species and one subspecies.



Figure 108. Map of New Guinea showing distribution of 23 *Austrelatus* species.



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Figures 109, 110. Habitats of *Austrelatus* species **109** *A. epicharis* sp. nov., *A. kalibumi* sp. nov., and *A. inconstans* sp. nov.: Papua Province, Nabire Regency, track Nabire – Ilaga, km 34 (Topo), roadside ditch rich in rotten leaves **110** *A. epicharis* sp. nov. and *A. inconstans* sp. nov.: track Nabire – Ilaga, km 35, partly shaded roadside ditch. Photographs by MB.



Figures 111, 112. Habitats of *Austrelatus xanthocephalus nabirensis* ssp. nov. and *A. inconstans* sp. nov. Papua Province, Nabire Regency, track Nabire – Ilaga, km 54, shaded, temporary and small pools in primary rainforest, rich in rotten debris. Photographs by LH.



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114

Figures 113, 114. Habitats of *Austrelatus* species **113** *A. xanthocephalus nabirensis* ssp. nov. and *A. inconstans* sp. nov.: Papua Province, Nabire Regency, track Nabire – Ilaga, km 54–62, exposed to sun, temporary puddle in rainforest clearing **114** *A. maindai* sp. nov.: Sarmi Regency, Tor River, Togonfo, water filled tree trunk. Photographs by MB.



Figures 115, 116. Habitats of *Austrelatus* species **115** type locality of *A. epicharis* sp. nov. and *A. kalibumi* sp. nov.: Papua Province, Nabire Regency, Wanggar, flooded meadows and shallow oxbows near Bumi River **116** *A. wasurensis* sp. nov. and *A. clarkii* (Sharp, 1882): Papua Province, Merauke Regency, Wasur, shallow, almost dry pools in wet savannah forest. Beetles hiding deep in mud and rotten leaves. Photographs by MB.

- Beetle larger, usually TL > 5.5 mm. Male genitalia: median lobe sturdier, its apex broader in left lateral view**53**
- 53 Beetle paler: elytron piceous, with a distinct, broad yellowish red basal band and yellowish between striae laterally, sometimes additionally apically, seldom whole elytron slightly yellowish. TL 5.7–6.6 mm (Fig. 57). Male genitalia as in Fig. 105: median lobe sturdier, left dorsal lobe with apex thicker and lateral margin more strongly concave apically and therefore ventral lobes more visible in left lateral view [2] ***A. asteios* sp. nov.**
- Beetle darker: elytron piceous, with a distinct yellowish red basal band and apical spot. TL 5.1–6.35 mm (Fig. 56). Male genitalia as in Fig. 106: median lobe slender, left dorsal lobe with apex thinner and lateral margin more straight apically and therefore ventral lobes less visible in left lateral view [10] ***A. epicharis* sp. nov.**

Notes on other *Austrelatus* species from New Guinea

Austrelatus clarki (Sharp, 1882)

During the study of Régimbart's collection in MNHN, a female specimen indicated as "*Copelatus vagestriatus* Rég." was found: 1 female "NeuGuinea", "vagestriatus Rég. n. sp. typ." [hw, Régimbart], "MUSEUM PARIS COLL MAURICE REGIMBART 1908", "MNHN, Paris EC29238 [with QR code]" (MNHN).

Zimmermann (1919: 199) described *Copelatus vagestriatus* with a note "(Rég. in litt.)" and clearly wrote that he based the description on the only female from the Berlin-Dahlem collection. With the discovery of the additional specimen with the similar labels in the Paris collection, it is obvious that Régimbart used at least these two specimens to indicate his unpublished species. Similar to the holotype, the newly found female also belongs to *A. clarki* but, having seven dorsal and one submarginal striae on the elytron, is more striated than the holotype.

Austrelatus garainensis Shaverdo et al., 2023

First record from Normanby Island: 1 male, 2 females "Papua New Guinea: Milne Bay Prov., Normanby Isl., Sewa Bay, Sibonai", "10°02.418'S 150°58.461'E, 35 m, beaten & hand-collected", "30-VI-2017 – position 1, A. Riedel." (SMNK, ZSM).

Austrelatus kaszabi (Guignot, 1956)

During the study of Guignot's collection in MNHN, nine additional paratypes of *Copelatus kaszabi* Guignot, 1956 were found: 1 male "Stephansort Astrolabe B", "N. Guinea Biró 97.", "♂", "Paratype" [red label with black frame]; 1 male, 7 females "N. Guinea Biró 1898", "Simbang Huon Golf // IX.17. [hw on reverse side]", "Paratype" [red label with black frame]. As well as one paratype in IRSNB: 1 male "N. Guinea Biro 1898", "Simbang Huon Golf", "♂", "Paratype" [red label with black frame].

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability







All of the data that support the findings of this study are available in the main text.

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An island in a sea of sand: a first checklist of the herpetofauna of the Serra da Neve inselberg, southwestern Angola

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Abstract

The Serra da Neve inselberg in Namibe Province, southwestern Angola is the second highest peak of Angola with an elevation of 2489 m. It remains one of the least explored regions in the country, despite several endemic species having been recently described from this inselberg. Here we provide an inventory of the amphibian and reptile species occurring in Serra da Neve and compare its fauna with that of the surrounding habitats at lower elevations. We also examine the phylogenetic affinities of the inselberg taxa. A total of 59 herpetological taxa were recorded for the Serra da Neve inselberg and its immediate surroundings. These include 11 species of amphibians, belonging to nine genera and seven different families, and 48 species of reptiles, belonging to 32 genera and 12 families. Of these, one amphibian and seven reptiles from seven different genera are strictly endemic, making the inselberg the richest region in southwestern Africa with respect to strict endemics, with one endemic reptile taxa per 127 km². Not surprisingly, most of the recorded taxa belong to clades that are endemic, or at least strongly associated, with southern Africa, but two are representatives of central African clades, and another two are more closely related to eastern African highland taxa. We also provide comments on the threats to the conservation of this endemic-rich inselberg.

Key words: Amphibians, Angola, biodiversity, conservation, endemism, inselberg, reptiles, Southwestern Africa, taxonomy

Introduction

Inselbergs are isolated mountains/rock outcrops which rise more or less abruptly above a plain. Scattered across all continents, these rock outcrops are usually important biodiversity hotspots, serving as refugia for diverse plant and animal taxa (Porembski and Barthlott 2000; Burke 2005; Brand et al. 2011; Bayliss et al. 2014; Porembski et al. 2017). Acting as islands, inselbergs are usually separated and



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isolated from each other in a way similar to oceanic islands (MacArthur and Wilson 2001). Due to their isolation and geomorphologic delimitation from the surroundings, for some groups they represent partly independent ecosystems that are especially suitable for comparative research on the structure and dynamics of floral and faunal communities (Porembski and Barthlott 2000). Their microclimatic conditions and habitats, which usually differ from those in the surrounding lowlands, allow inselbergs to support unique biological communities and high levels of endemism (Simmons et al. 1998; Porembski and Barthlott 2000; Burke 2001, 2003, 2005; Porembski 2007; Michael et al. 2008; Brand et al. 2011, 2019; Bayliss et al. 2014). In addition, they are excellent models for studying aspects of island ecology, geographical differentiation and mechanisms influencing diversity. Due to their topography, Inselbergs are typically not used for agriculture and, except for some instances of tourism, have not been transformed by human activities. They thus constitute almost pristine habitats with special importance for conservation, and usually provide favorable conditions for flora and fauna, concerning availability of water, shade, and refuge (Porembski and Barthlott 2000).

The study of African inselbergs and other “sky-islands” has been a topic of great interest in recent years for a broad scope of scientists, from conservation biologists to systematists. This is especially true for East-African Afromontane inselberg regions, as in the case of Mount Namuli and Mount Mabu in Mozambique (e.g., Timberlake et al. 2009; Portik et al. 2013a, 2013b; Bayliss 2014) or Mount Mulanje in Malawi (Curran et al. 2012). Due to this interest, in recent years several new endemic animal species, such as amphibians (Ceríaco et al. 2018; Conradie et al. 2018), reptiles (Branch et al. 2005; Branch and Bayliss 2009; Branch and Tolley 2010; Portik et al. 2013b; Branch et al. 2014, 2019; Marques et al. 2019, 2020, 2023a, 2023b), invertebrates (Congdon et al. 2010; Daniels and Bayliss 2012; Bilton 2014; Daniels et al. 2014, 2020), and mammals (Monadjem et al. 2010; Taylor et al. 2012; Simmons et al. 2021) have been described from inselbergs across Africa. Several studies have also provided inventories of the herpetofauna (Michael et al. 2008; Kirchhof et al. 2010; Conradie et al. 2016a; Bittencourt-Silva et al. 2020) and plant diversity (Rabari-manarivo et al. 2019; Porembski and Barthlott 2000; Burke 2003; Kandziora et al. 2022; Brand et al. 2019) of these inselbergs across the continent.

In contrast to East-African Afromontane inselberg studies, xeric southwestern African inselbergs have been largely neglected in the fauna studies (Elzen 1983; Griffin 2000), with most focusing only on flora and vegetation (Porembski and Barthlott 2000), and, more recently, on carnivores (Rapson et al. 2013). Northwestern Namibia and west-central Angola form an area with a considerable diversity and number of inselbergs. Surrounded by desert and savanna habitats, southwestern African inselbergs are usually rocky outcrops of diverse geology and origins that contrast with the intervening habitats (Goudie and Viles 2015). Both reptile diversity and endemism are high in rocky areas in Angola and Namibia (Bauer et al. 2023).

The landscape of southwestern Angola is characterized by the presence of isolated mountain-like rocky outcrops of subvolcanic origin mostly composed of gneisses, migmatites and granites (Pereira 1977). One of the most impressive southwestern Angolan inselbergs is Serra da Neve. Located at the northern limit of Namibe Province, southwestern Angola, and with a basal area of approximately 630 km², Serra da Neve is the second highest peak of Angola, with an elevation of

2489 m (Pereira 1977). It lies in what Mendelsohn and Huntley (2023) define as “the southern escarpment landscape”, an area ranging from the Coporolo River in Benguela Province, Angola, to the Huab River in Namibia. The inselberg is covered by a Miombo forest habitat, contrasting with the surrounding lowland habitats, which are mainly dominated by Namibian woodland savanna and arid areas of Namib Desert (Grandvaux-Barbosa 1970). Although its biodiversity is still poorly known, and systematic surveys have only recently begun, the inselberg is already known to harbor an impressive number of strictly endemic species of amphibians and reptiles, such as *Poyntonophrynus pachnodes* Ceriaco, Marques, Bandeira, Agarwal, Stanley, Heinicke, Blackburn & Bauer, 2018, *Cordylus phonolithos* Marques, Ceriaco, Stanley, Bandeira, Agarwal & Bauer, 2019, *Lygodactylus baptistai* Marques, Ceriaco, Buehler, Bandeira, Janota & Bauer, 2020, *Afroedura praedicta* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie, 2021, and *Acontias mukwando* Marques, Parrinha, Tiutenko, Lopes-Lima, Bauer & Ceriaco, 2023 (Ceriaco et al. 2018; Marques et al. 2019, 2020, 2023b; Branch et al. 2021), with at least three other reptile species currently being described (MPM unpubl. data; DP unpubl. data).

Currently, no data for other taxonomic groups exist, but recent multidisciplinary surveys have also uncovered interesting and cryptic diversity within those, which will result in a better understanding of the taxonomic diversity, biogeographic patterns, and endemism of Serra da Neve. In this context, the main objective of this study is to provide a first description of Serra da Neve herpetofauna, and more specifically to 1) to provide an inventory of the occurring species as well as list taxa that have not yet been recorded, but which may be present; 2) to compare the fauna present on the inselberg with that of the surrounding lower elevation habitats; 3) to examine the phylogeographic affinities of the inselberg taxa; 4) to compare the level of endemism of Serra da Neve with other regions in Angola and southern Africa; and 5) to present a first glimpse into the major conservation threats that the inselberg herpetofauna may be facing.

Materials and methods

Three herpetological surveys of Serra da Neve and its surrounding areas have been carried out since 2016. The first survey was conducted from 18 to 22 November 2016, the second one from 26 to 28 February 2019, and the third one from 26 October to 6 November 2022. A total of eight main sites were surveyed (Table 1, Fig. 1). The combination of sites was chosen to maximize the types

Table 1. Sampling localities in and around the Serra da Neve inselberg, and respective latitude, longitude, and elevation data.

Localities	Latitude, Longitude	Elevation (m)	Map (see Fig. 1)
Road to Quilengues	-13.8159, 13.3264	587	1
N'Dolondolo	-13.8133, 13.1362	681	2
Mamué	-13.8003, 13.1229	701	3
Maylowe	-13.8355, 13.2755	798	4
2 km N of Maylowe	-13.8280, 13.2625	820	5
Basecamp 1	-13.7770, 13.2591	1488	6
Lutala Crater	-13.7325, 13.1841	1567	7
Catchi	-13.7627, 13.2564	1590	8

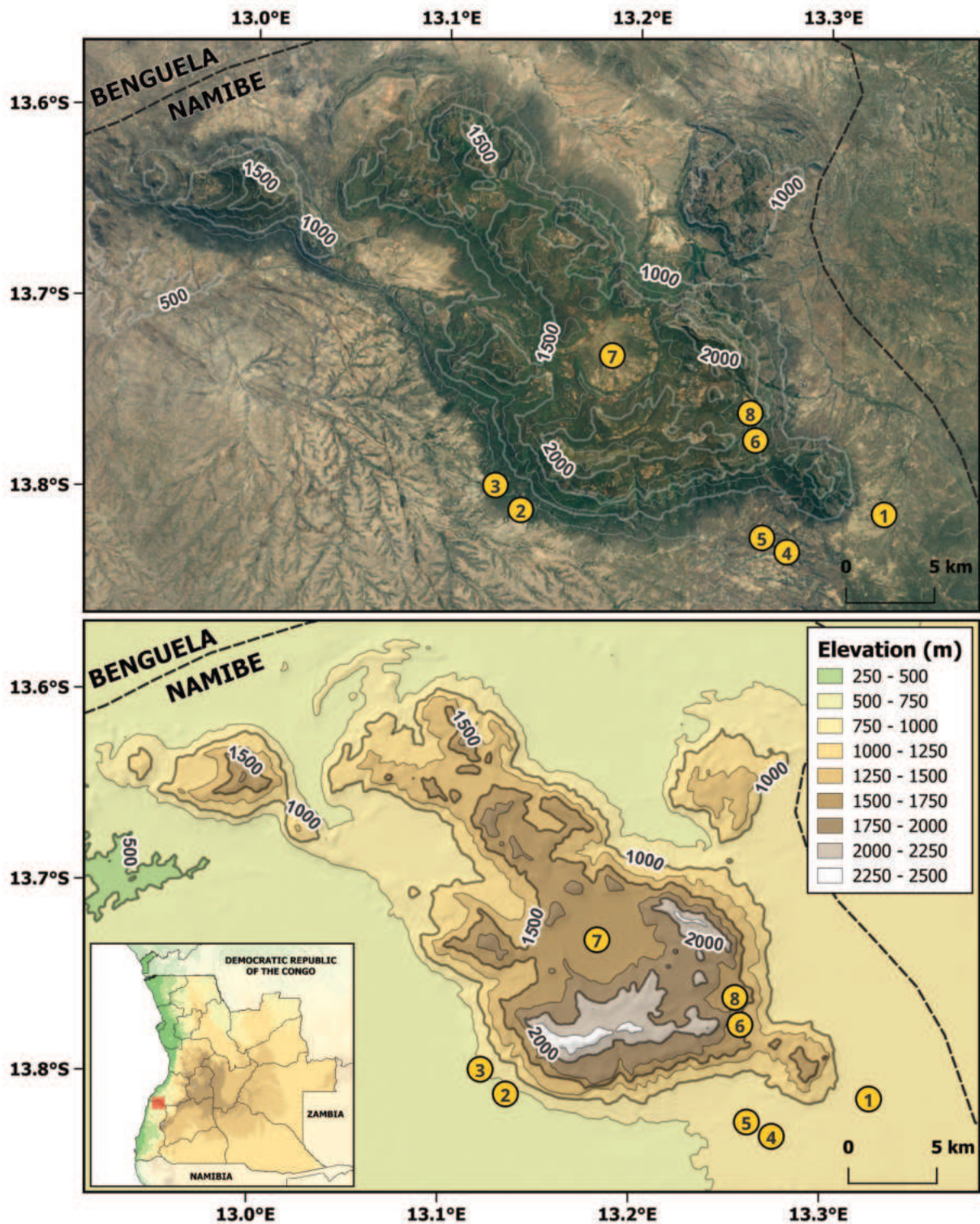


Figure 1. Map of the sampling localities in Serra da Neve and its surroundings; contour lines represent elevation in meters above sea level. Localities 1 road to Quilengues 2 N'Dolondolo 3 Mamué 4 Maylowe 5 2 km N of Maylowe 6 base-camp 1 7 Lutala Crater 8 Catchi.

of habitats surveyed, including rocky outcrops, woodlands, open grasslands, streams, and ponds, and to capture different elevations from the base to the top of Serra da Neve. Locality data are presented in decimal degrees using the WGS-84 map datum, and elevation is presented as meters above sea level.

The areas surrounding the base of Serra da Neve are all dominated by relatively dense Mopane (*Colophospermum mopane*) woodlands on sandy soil (Fig. 2a–d; Huntley 2023). This habitat dominates the landscape around Maylowe village and extends for a considerable radius around Serra da Neve. The Mopane trees can be seen up to ~ 1100 m elevation on the inselberg, where they are replaced by a largely intact Miombo woodland that dominates the landscape at higher elevations. Still, at the base of Serra da Neve, some areas have interesting vegetation and geological characteristics that are worth mentioning. The N'Dolondolo area, while still dominated by Mopane woodlands, is considerably more humid than other areas near Maylowe, especially due to its



Figure 2. Lowland habitats in the near surroundings of the Serra da Neve inselberg **a** Mopane habitat, **b** Mopane habitat in the vicinity of Maylowe **b** dry Mopane habitat, 2 km N of Maylowe **c** sandy areas with Mopane leaf litter near Maylowe **d** dry riverbed near Maylowe **e, f** N'Dolondolo **g, h** riparian vegetation in Mamué. Photographs by LMPC (**a**), AT (**b–d**) and IA (**e–h**).



Figure 3. Highland habitats in Serra da Neve inselberg **a** Miombo woodland in the vicinity of Catchi **b** preserved Miombo woodlands on the way to Lutala **c** agricultural crops on the way to Lutala **d** disturbed landscape, vicinity of Catchi **e** Miombo woodland with granite outcrops, vicinity of Catchi **f** riparian vegetation on the way to Lutala crater **g, h** sparse Miombo savanna habitat at Lutala crater. Photographs by LMPC (**a–c**) and AT (**d–h**).

sulphurous hot water spring, and its soil is less sandy, with outstanding granite outcrops present (Fig. 2e, f). Further north-west from N'Dolondolo, but still at the base of Serra da Neve, the Mamué area already presents a more complex habitat, with Mopane still present, but the landscape dominated by streams and associated riparian vegetation that extends downward from Serra da Neve, with large waterfalls (Fig. 2g, h).

As elevation rises, the landscape becomes completely dominated by what Grandvaux-Barbosa (1970) described as sparse Miombo woodlands, with the presence of *Brachystegia* and *Julbernardia* trees, and the soil becomes rockier

and with the conspicuous presence of large granite outcrops (Barker et al. 2015). At an elevation of ~ 1490 meters, near Basecamp 1, the area is still well-preserved, without much anthropogenic degradation. There is almost no grass, but different types of bushes (*Combretum* spp.) are present and there is a considerable accumulation of leaf-litter below the tree canopy. This type of habitat is continuous throughout the largest part of the inselberg above 900 m (pers. Obs.). The closest areas (~ 100 km) where this type of vegetation occurs are in the margins of the Escarpment around Cubal, Chongoroi and Quilengues, and then further inland in Cangandala, in the Queve and Kwanza River valleys (Grandvaux-Barbosa 1970). Catchi (1590 m), an important collecting locality in these surveys, is a small village and human impacts on the landscape are notable, as most of the plateau around the village is grazed and transformed into corn and maize plantations, or cattle pastures, with the Miombo woodlands restricted to the steeper slopes around the village. A small stream, with its respective riverine gallery, passes through the Catchi plateau, adding to the complexity of the landscape. In the main crater of the inselberg near Lutala village (1567 m), tree density is notably lower, forming an open Miombo savanna with herbaceous undergrowth, and fewer shrubs and granite outcrops in contrast to other areas of the mountain (Fig. 3).

Specimens were collected using pit fall traps, long-nooses, rubber bands, or by hand during both diurnal and nocturnal visual encounter surveys. Pit falls were set in two different sites in a dry riverbed near Maylowe, Serra da Neve base. Each pit fall consisted of a line of four buckets, active for three days (3–5 Nov 2024). All specimens were euthanized following Villanova University animal care and use protocol #1866, preserved in 10% buffered formalin in the field, and then gradually transferred to 70% ethanol for long term storage. Liver tissues were extracted before formalin fixation and preserved in 95% ethanol. Voucher specimens were deposited in the herpetological collections of the California Academy of Sciences, USA (**CAS**); Florida Museum of Natural History, USA (**UF**); Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Portugal (**MUHNAC/MB**), Museu de História Natural e da Ciência da Universidade do Porto, Portugal (**MHNC-UP/REP**), and a subset of specimens were deposited in the reference collection of Instituto Nacional da Biodiversidade e Áreas de Conservação (**INBAC**) in Luanda, Angola. In some cases, species identifications were further confirmed by sequencing the mitochondrial 16S ribosomal RNA gene.

Results

A total of 59 herpetological taxa were recorded for the Serra da Neve inselberg and its immediate surroundings. These include 11 species of amphibians, belonging to nine genera and seven different families, and 48 species of reptiles, belonging to 32 genera and 12 families. No crocodylians were recorded in the area. The families Scincidae and Gekkonidae were those represented by the largest number of species (14 and 10, respectively). Among the recorded species, 22 were found exclusively in the lowland areas of the inselberg base and 14 in the highlands, while 23 species were recorded throughout the study area (Table 2). Eight species are strictly endemic to the Serra da Neve inselberg, and 23 additional species are regional endemics to southwestern Angola and central and northwestern Namibia (Table 2).

Table 2. Synoptic table listing all recorded species, with notes on elevational distribution and endemism. Lowland localities include Mamué, Maylowe and its surroundings, N'Dolondolo, and the road to Quilengues (below 1000 m above sea level), while highland localities refer to Catchi, Basecamp 1, and Lutala Crater (> 1000 m above sea level; see Table 1 for further details).

Taxa	Serra da Neve lowlands	Serra da Neve highlands	Strict endemic	Regional endemic (southwestern Angola and central and northwestern Namibia)
AMPHIBIA				
Anura				
Family Pipidae				
Genus <i>Xenopus</i>				
<i>Xenopus petersii</i>	x	x		
Family Bufonidae				
Genus <i>Poyntonophrynus</i>				
<i>Poyntonophrynus grandisonae</i>	x			x
<i>Poyntonophrynus pachnodes</i>		x	x	
Genus <i>Sclerophrys</i>				
<i>Sclerophrys pusilla</i>	x	x		
Family Microhylidae				
Genus <i>Phrynomantis</i>				
<i>Phrynomantis annectens</i>	x			
Family Arthroleptidae				
Genus <i>Leptopelis</i>				
<i>Leptopelis anchietae</i>		x		x
Family Ptychadenidae				
Genus <i>Ptychadena</i>				
<i>Ptychadena anchietae</i>	x			
Family Phrynobatrachidae				
Genus <i>Phrynobatrachus</i>				
<i>Phrynobatrachus natalensis</i>	x	x		
Family Pyxicephalidae				
Genus <i>Amietia</i>				
<i>Amietia angolensis</i>		x		
Genus <i>Tomopterna</i>				
<i>Tomopterna ahli</i>	x			
<i>Tomopterna tuberculosa</i>	x	x		
REPTILIA				
Testudines				
Family Testudinidae				
Genus <i>Kinixys</i>				
<i>Kinixys belliana</i>	x	x		
Genus <i>Stigmochelys</i>				
<i>Stigmochelys pardalis</i>	x			
Squamata				
Family Gekkonidae				
Genus <i>Afroedura</i>				
<i>Afroedura praedicta</i>		x	x	
Genus <i>Hemidactylus</i>				
<i>Hemidactylus benguellensis</i>	x	x		x
Genus <i>Chondrodactylus</i>				
<i>Chondrodactylus pulitzerae</i>	x	x		x
Genus <i>Lygodactylus</i>				
<i>Lygodactylus baptistai</i>	x	x	x	
<i>Lygodactylus nyaneke</i>	x			x

Taxa	Serra da Neve lowlands	Serra da Neve highlands	Strict endemic	Regional endemic (southwestern Angola and central and northwestern Namibia)
Genus <i>Pachydactylus</i>				
<i>Pachydactylus caraculicus</i>	x			x
<i>Pachydactylus maiatoi</i>	x	x		x
<i>Pachydactylus</i> cf. <i>punctatus</i>	x			
Genus <i>Rhoptropus</i>				
<i>Rhoptropus</i> aff. <i>barnardi</i>	x	x		x
<i>Rhoptropus</i> aff. <i>montanus</i>		x	x	
Family Lacertidae				
Genus <i>Heliobolus</i>				
<i>Heliobolus crawfordi</i>	x			x
Genus <i>Pedioplanis</i>				
<i>Pedioplanis haackei</i>	x			x
<i>Pedioplanis serodioi</i>	x			x
Family Cordylidae				
Genus <i>Cordylus</i>				
<i>Cordylus phonolithos</i>	x	x	x	
Family Gerrhosauridae				
Genus <i>Cordylosaurus</i>				
<i>Cordylosaurus subtessellatus</i>	x			
Genus <i>Gerrhosaurus</i>				
<i>Gerrhosaurus</i> sp.		x		
Genus <i>Matobosaurus</i>				
<i>Matobosaurus maltzahni</i>	x	x		
Family Scincidae				
Genus <i>Acontias</i>				
<i>Acontias mukwando</i>		x	x	
Genus <i>Mochlus</i>				
<i>Mochlus sundevallii</i>	x			
Genus <i>Panaspis</i>				
<i>Panaspis cabindae</i>	x			
<i>Panaspis mocamedensis</i>	x			
<i>Panaspis</i> sp. 1	x	x	x	
<i>Panaspis</i> sp. 2		x	x	
Genus <i>Sepsina</i>				
<i>Sepsina copei</i>	x			x
Genus <i>Trachylepis</i>				
<i>Trachylepis albopunctata</i>	x	x		
<i>Trachylepis ansorgii</i>	x	x		x
<i>Trachylepis binotata</i>	x			x
<i>Trachylepis bouri</i>		x		x
<i>Trachylepis chimbana</i>	x	x		x
<i>Trachylepis huilensis</i>		x		x
<i>Trachylepis laevis</i>	x	x		x
Family Chamaeleonidae				
Genus <i>Chamaeleo</i>				
<i>Chamaeleo dilepis</i>		x		

Taxa	Serra da Neve lowlands	Serra da Neve highlands	Strict endemic	Regional endemic (southwestern Angola and central and northwestern Namibia)
Family Agamidae				
Genus <i>Agama</i>				
<i>Agama aculeata</i>	x			
<i>Agama schacki</i>	x	x		x
Serpentes				
Family Typhlopidae				
Genus <i>Afrotyphlops</i>				
<i>Afrotyphlops schlegeli petersii</i>	x			
Family Leptotyphlopidae				
Genus <i>Leptotyphlops</i>				
<i>Leptotyphlops cf. scutifrons</i>		x		
Family Pythonidae				
Genus <i>Python</i>				
<i>Python natalensis</i>	x			
Family Viperidae				
Genus <i>Bitis</i>				
(Subgenus <i>Macrocerastes</i>)				
<i>Bitis (Macrocerastes) gabonica</i>		x		
Genus <i>Causus</i>				
<i>Causus nasalis</i>	x			x
Family Lamprophiidae				
Genus <i>Boaedon</i>				
<i>Boaedon variegatus</i>	x	x		x
Genus <i>Hemirhagerrhis</i>				
<i>Hemirhagerrhis viperina</i>	x	x		x
Genus <i>Lycophidion</i>				
<i>Lycophidion hellmichi</i>	x	x		x
Genus <i>Psammophis</i>				
<i>Psammophis subtaeniatus</i>	x	x		
<i>Psammophylax tritaeniatus</i>		x		
Family Colubridae				
Genus <i>Dasypeltis</i>				
<i>Dasypeltis scabra</i>	x			
Genus <i>Telescopus</i>				
<i>Telescopus semiannulatus polystictus</i>	x			

Endemicity levels

Serra da Neve currently harbors a total of eight strictly endemic herpetological species (one amphibian and seven reptiles, from seven different genera). We consider strictly endemic taxa to be those currently only known to occur within the area defined by the base of the Serra da Neve inselberg (see Fig. 1). These include one species of bufonid frog *Poyntonophrynus pachnodes* (family Bufonidae), one cordylid lizard, *Cordylus phonolithos* (family Cordylidae), three geckos, *Lygodactylus baptistai*, *Afroedura praedicta*, and *Rhoptropus aff. montanus* (family Gekkonidae), and three skinks, *Acontias mukwando*, *Panaspis* sp. 1,

and *Panaspis* sp. 2 (family Scincidae). No strictly endemic snakes or chelonians are known from Serra da Neve. Besides the strictly endemic taxa, the inselberg hosts a number of other regional highland endemics, such as *Leptopelis anchietae* (Bocage, 1873), *Trachylepis huilensis* (Laurent, 1964), *Trachylepis ansorgii* (Boulenger, 1907), *Trachylepis bouri* Ceriaco, Marques, Parrinha, Tiutenko, Weinnell, Butler & Bauer, 2024, and *Pachydactylus maiatoi* Marques, Parrinha, Ceriaco, Brennan, Heinicke & Bauer, 2023, all associated with the highland areas of southwestern Angola.

When numbers of strictly endemic taxa on Serra da Neve and the other southwestern African highlands are compared, the inselberg stands amongst the richest in the region (Table 3; Bauer et al. 2023; Becker et al. 2023). Serra da Neve hosts a total of seven strictly endemic reptile species, the highest level of endemism in the country. The Huíla Escarpment and Plateau in southwestern Angola (with an approximate area of 18000 km²), harbor only five strictly endemic reptile species (Table 3; Bauer et al. 2023; Becker et al. 2023). All other inselbergs, both in Angola and Namibia, have a maximum of two strictly endemic species (Table 3; Bauer et al. 2023; Becker et al. 2023). Serra da Neve's strictly endemic numbers are even more striking when considering its area. With an approximate area of 630 km², Serra da Neve is undoubtedly the richest region in southwestern Africa with respect to strict endemics per unit of area, with one endemic reptile taxa per 127 km² (Table 3; Bauer et al. 2023), and much more similar to or higher than those found on endemic-rich oceanic islands (Ceriaco et al. 2022; Bauer et al. 2022), or South American table mountains, known as "tepuis" (Recoder et al. 2020; Fouquet et al. 2023).

Biogeographic affinities

Not surprisingly, most of the recorded taxa belong to clades endemic to, or at least strongly associated, with southern Africa. The exceptions are *Bitis* (*Macrocerastes*) *gabonica* (Duméril, Bibron & Duméril, 1854), *Panaspis cabindae* (Bocage, 1866) *Acontias mukwando*, and *Lygodactylus baptistai*, of which the first two are representatives of central African clades, and the latter two are more closely related to eastern African highland taxa. The subgenus *Macrocerastes*, of which large-bodied vipers such as *Bitis nasicornis* (Shaw, 1792), *B. rhinoceros* (Schlegel, 1855), *B. parviocula* (Böhme, 1977) and *B. gabonica* are members, is a group predominantly associated with central African habitats (Barlow et al. 2019; Ceriaco et al. 2020a), even if some of these species have some populations in southern (*B. gabonica*) and eastern Africa (*B. parviocula*). Within this group, is *B. heraldica* (Bocage, 1889), a species endemic to the Angolan central highlands, and the only member of the subgenus which is small-bodied (Ceriaco et al. 2020a). The specimen of *B. gabonica* from Serra da Neve represents the southwestern-most record of the subgenus in the continent.

A similar distribution pattern can also be observed for *Panaspis cabindae* and the putative new species *Panaspis* sp. 1 (MPM unpubl. data). Although the genus *Panaspis* is relatively diverse and widely distributed in southern Africa (Medina et al. 2016), the distribution of *P. cabindae* ranges from southwestern Republic of the Congo and the Democratic Republic of the Congo southwards to central and southwestern Angola through woodlands associated with the Angolan Escarpment (Ceriaco et al. 2020b). The putative new species *Panaspis* sp. 1 belongs to

Table 3. Comparison of herpetofaunal endemicity levels between Angolan and Namibian inselbergs. Data from Bauer et al. (2023) and Becker et al. (2023).

Country	Inselberg / Highlands	Strictly endemic species (Amphibians / Reptiles)	Strictly highland but not strictly endemic (Amphibians / Reptiles)
Namibia	Brandberg	- / -	- / 2
	Erongo Mts	- / -	- / 1
	Spitzkoppe	- / -	- / 1
	Swakop-Kahn inselbergs	- / -	- / 3
	Central Highlands	- / 1	- / 4
	Tiras Mountains	- / 1	- / 3
	Huns-Orange Mts	- / -	- / 3
	Baynes-Otjihipa	- / 1	- / -
	Entedeka Mts	- / -	- / -
	Karasberg	- / 1	- / 3
	Klein Karasberg	- / -	- / 1
	Nubib Mts	- / 1	- / 2
	Aus Mts	-	- / 1
	Otavi Highlands	- / 2	- / -
	Huab Outliers	- / -	- / 1
	Brukkaros	- / -	- / -
	Onder-Rooirand	- / -	- / 1
	Interior Plateau	- / 1	- / -
	Namuskluft Mts	- / -	1 / 1
	south Otjihipa Mts	- / -	- / -
	Waterberg Plateau	- / 2	- / -
	Skerpioenkop	- / -	- / 1
	Central Group south to Karasberg exclusive of desert inselbergs	- / -	- / 1
	Naukluft Mts	- / -	- / 1
	Tsaris Mts	- / -	- / 1
	Gamsberg	- / -	- / 1
	Rantberge	- / -	- / 1
Central Plateau	- / -	- / 1	
Rooikoppe	- / -	- / 1	
Auas Mountains	- / -	- / 1	
Angola	Namba	1 / 1	/ -
	Serra da Neve	1 / 7	1 / 4
	Huíla Escarpment and Plateau	2 / 5	1 / 4
	Central Plateau	2 / 1	1 / 6
	Pungo Andongo	- / 1	- / -
	Mt. Moco	- / 1	- / 1
	Mombolo	- / 1	
	Congulu Escarpments	3 / -	2

the same Central African lineages as *P. cabindae*, the same clade as the species from the Gulf of Guinea Oceanic islands (Ceríaco et al. 2020b; MPM unpubl. data).

On the other hand, *Lygodactylus baptistai* belongs to a lineage comprising East African species (Marques et al. 2020). As part of the *A. occidentalis* species

complex, a group whose distribution covers most of southern Africa, *A. mukwando* is more closely related to *A. percivali*, a species endemic to the Eastern Arc Mountains of northeastern Tanzania and southeast Kenya, than to other lineages of the complex occurring in Namibia and Angola (Marques et al. 2023b). This pattern is also present in the new species *Panaspis* sp. 2, currently under description (MPM unpubl. data). Among the taxa with southern African affinities there are particularly arid-adapted lizards, which are mostly restricted to the dry lowlands of the inselberg, such as *Pedioplanis haackei* Conradie, Measey, Branch & Tolley, 2012, *Pedioplanis serodioi* Parrinha, Marques, Heinicke, Khalid, Parker, Tolley, Childers, Conradie, Bauer & Ceriaco, 2021, *Heliobolus crawfordi* Marques, Ceriaco, Heinicke, Chehouri, Conradie, Tolley & Bauer, 2022, and *Pachydactylus caraculicus* Fitzsimons, 1959. On the other hand, the more mesic highlands of the inselberg also support taxa that are typically associated with the highlands of the Escarpment and the Central Plateau, such as *Trachylepis ansorgii*, *Trachylepis huilensis*, *Psammophylax tritaeniatus* (Günther, 1868), and *Leptopelis anchietae*.

Taxonomic accounts

Amphibia, Anura

Family Pipidae Gray, 1825

Genus *Xenopus* Wagler, 1827

Xenopus petersii Bocage, 1895

Fig. 4a, b

Records. Catchi, small stream near basecamp [-13.7630, 13.2513, 1595 m] (MUNHAC/MB04-001066); Maylowe, inside a well [-13.8349, 13.2765, 803 m] (MUNHAC/MB04-001067–001091).

Comments. Traditionally considered as a subspecies of *Xenopus laevis* (Daudin, 1802), Furman et al. (2015) reclassified all central and western Angolan populations as *X. petersii*. Frétey et al. (2018) designated as lectotype of the species a specimen collected by José d'Anchieta in Benguela Province, Angola. This species is known from several localities in southwestern regions of the country (see Marques et al. 2018) and the Serra da Neve population is within the expected distribution range of *X. petersii* in the province.

Family Bufonidae Gray, 1825

Genus *Poyntonophrynus* Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green & Wheeler, 2006

Poyntonophrynus grandisonae (Poynton & Haacke, 1993)

Fig. 4c

Records. N'Dolondolo [-13.8133, 13.1362, 889 m] (CAS 262731, 262732; UF 184185–184187; INBAC/AMB 10337, 10339).

Comments. These are the first specimens of *P. grandisonae* collected since the original description by Poynton and Haacke (1993) and used by Ceriaco et al. (2018) to provide the first molecular data for *P. grandisonae*. The natural



Figure 4. **a, b** *Xenopus petersii* **c** *Poyntonophrynus dombensis* **d** *Poyntonophrynus pachnodes* **e** *Sclerophrys pusilla* **f** *Phrynomantis annectens* **g** *Leptopelis anchietae* **h** *Phrynobatrachus natalensis*. Photographs by AT (**a, b, e, g, h**); LMPC (**c, f**) and IA (**d**).

history and distribution of this species remain poorly known. The species is endemic to Angola and restricted to the southwestern regions of Namibe Province. It is associated with xeric vegetation in low-elevation areas (Marques et al. 2018; Baptista et al. 2023).

***Poyntonophrynus pachnodes* Ceríaco, Marques, Bandeira, Agarwal, Stanley, Bauer, Heinicke & Blackburn, 2018**

Fig. 4d

Records. Basecamp 1 [-13.7770, 13.259, 1488 m] (UF 184183, 184184, 190278, 190279; CAS 262730, INBAC/AMB 10209; INBAC/LMPC 1262–1264; MUHNAC/MB04-000999, 001092).

Comments. This recently described species is only known from Serra da Neve and considered a strict endemic (Ceríaco et al. 2018; Baptista et al. 2023). Additional material for this species was collected from the type locality by the second expedition to the inselberg in 2019. This highland specialist was found in an area with moist soil under leaf-litter and rocks, at elevations greater than 1000 m. Recent research by Baptista et al. (2023) provided new data regarding the phylogenetic relationship of this Serra da Neve endemic, indicating that it is closely related to the arid-adapted *P. dombensis* and *P. damaranus*.

Genus *Sclerophrys* Tschudi, 1838

***Sclerophrys pusilla* (Mertens, 1937)**

Fig. 4e

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 263036, 263037; INBAC/AMB 10206); vic. N'Dolondolo [-13.8087, 13.1352, 731 m] (CAS 263025, 263030); N'Dolondolo [-13.8133, 13.1362, 593 m] (UF 187174); Maylowe [-13.8342, 13.2767, 803 m] (UF 190289; MUNHAC/MB04-001093); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB04-001094).

Comments. The species has a wide distributional range in central and southern Angola (Marques et al. 2018). The Angolan population was for some time treated as *Sclerophrys maculata* (Hallowell, 1854), until Poynton et al. (2016) established that *S. maculata* is restricted to West Africa, while *S. pusilla* is mainly distributed across eastern and southern Africa, including Angola. This species is common in Serra da Neve and its surroundings. It is usually found near leaf litter.

Family Microhylidae Günther, 1858

Genus *Phrynomantis* Peters, 1867

***Phrynomantis annectens* Werner, 1910**

Fig. 4f

Records. N'Dolondolo [-13.8004, 13.1362, 897 m] (UF 187250, 187251; INBAC/AMB 10344); Maylowe [-13.8342, 13.2767, 803 m] (UF 190275).

Comments. Endemic to southwestern Africa from southwestern Angola southwards through Namibia to the arid regions of northern South Africa (Marques et al. 2018; Channing and Rödel 2019). In Angola, *P. annectens* is restricted to the coastal lowlands of the country (Marques et al. 2018). The species is frequently associated with inselbergs and other rocky outcrops in arid regions (Channing 2001; Channing and Rödel 2019). Our specimens were found inside crevices at the base of Serra da Neve. Ceriaco et al. (2021) discussed the taxonomic and nomenclatural history of *P. annectens* and provided an additional record for the country.

Family Arthroleptidae Mivart, 1869

Genus *Leptopelis* Günther, 1859

***Leptopelis anchietae* (Bocage, 1873)**

Fig. 4g

Records. Catchi, near small stream [-13.7630, 13.2514, 1595 m] (MUNHAC/MB04-001095, 001096).

Comments. An Angolan endemic, distributed throughout much of the western half of the country (Marques et al. 2018; Becker et al. 2023). The collected specimens were heard croaking from a small bush at night, a common event especially after rain. Considered a cryptic species complex by several authors (Perret 1976; Schiøtz 1999). Becker et al. (2023) did not record the species in Serra da Neve.

Family Ptychadenidae Dubois, 1987

Genus *Ptychadena* Boulenger, 1917

***Ptychadena anchietae* (Bocage, 1867)**

Records. N'Dolondolo [-13.8004, 13.1362, 897 m] (CAS 263024; UF 187280; INBAC/AMB 10308).

Comments. The species is broadly distributed from western to eastern Angola and is widespread extraliminally (Marques et al. 2018; Channing and Rödel 2019), typically associated with savanna and grassland habitats.

Family Phrynobatrachidae Laurent, 1941

Genus *Phrynobatrachus* Günther, 1862

***Phrynobatrachus natalensis* (Smith, 1849)**

Figs 4e, 5a

Records. Mamué riparian area [-13.8004, 13.1246, 732 m] (UF 187249); Catchi, small stream near basecamp [-13.7630, 13.2513, 1595 m] (MUNHAC/MB04-001097–001146).

Comments. The species, as currently understood, is likely to contain multiple undescribed cryptic species across its large distribution in the savanna and grassland regions of sub-Saharan Africa (Zimkus et al. 2010). Based on newly

generated molecular data (LMPC unpub. data), we conclude that the population from Serra da Neve belongs to the same lineage as topotypical populations in South Africa. The specimens were collected on the margins of small streams, both in the lowlands and highlands of the inselberg.

Family Pyxicephalidae Bonaparte, 1850

Genus *Amietia* Dubois, 1987

***Amietia angolensis* (Bocage, 1866)**

Fig. 5b

Records. Catchi, small stream near basecamp [-13.7630, 13.2513, 1595 m] (MUNHAC/MB04-001147–001154).

Comments. Formerly considered a widespread species in western and central Africa, is now restricted to Angola (Channing and Baptista 2013; Channing et al. 2016). The species was frequently encountered in the rocky margins of small streams and ponds at the top of the inselberg.

Genus *Tomopterna* Duméril & Bibron, 1841

***Tomopterna ahli* (Deckert, 1938)**

Fig. 5c

Record. Maylowe [-13.8342, 13.2767, 803 m] (UF 190305).

Comments. Ceríaco et al. (2016) provided the first record of this species for Angola as *Tomopterna damarensis* Dawood & Channing, 2002. Heinicke et al. (2017a) used morphological and mtDNA data to show that this species is broadly distributed in Angola and Namibia and suggested that some records of *Tomopterna* from southern Angola could correspond to this species. Channing and Becker (2019) showed that *Tomopterna ahli* was a senior synonym of *T. damarensis*. All Angolan specimens previously assigned to *T. damarensis* (Ceríaco et al. 2016, Heinicke et al. 2017a; Marques et al. 2018) should thus be referred to as *T. ahli*.

***Tomopterna tuberculosa* (Boulenger, 1882)**

Fig. 5d

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 263038, 263039); Mamwé riparian area [-13.8006, 13.1230, 706 m] (UF 187293); N'Dolondolo [-13.8133, 13.1362, 681 m] (UF 187294); Maylowe [-13.8342, 13.2767, 803 m] (MUNHAC/MB04-001155); Catchi, basecamp [-13.7627, 13.2562, 1597 m] (MUNHAC/MB04-0011556).

Comments. The species has a wide distribution in western Angola (Marques et al. 2018). These specimens represent the first record of the species in Namibe Province since those that were reported by Bocage (1895). *Tomopterna tuberculosa* appears to occur in sympatry with *T. ahli* at Serra da Neve and across the southwestern areas of Namibe Province.

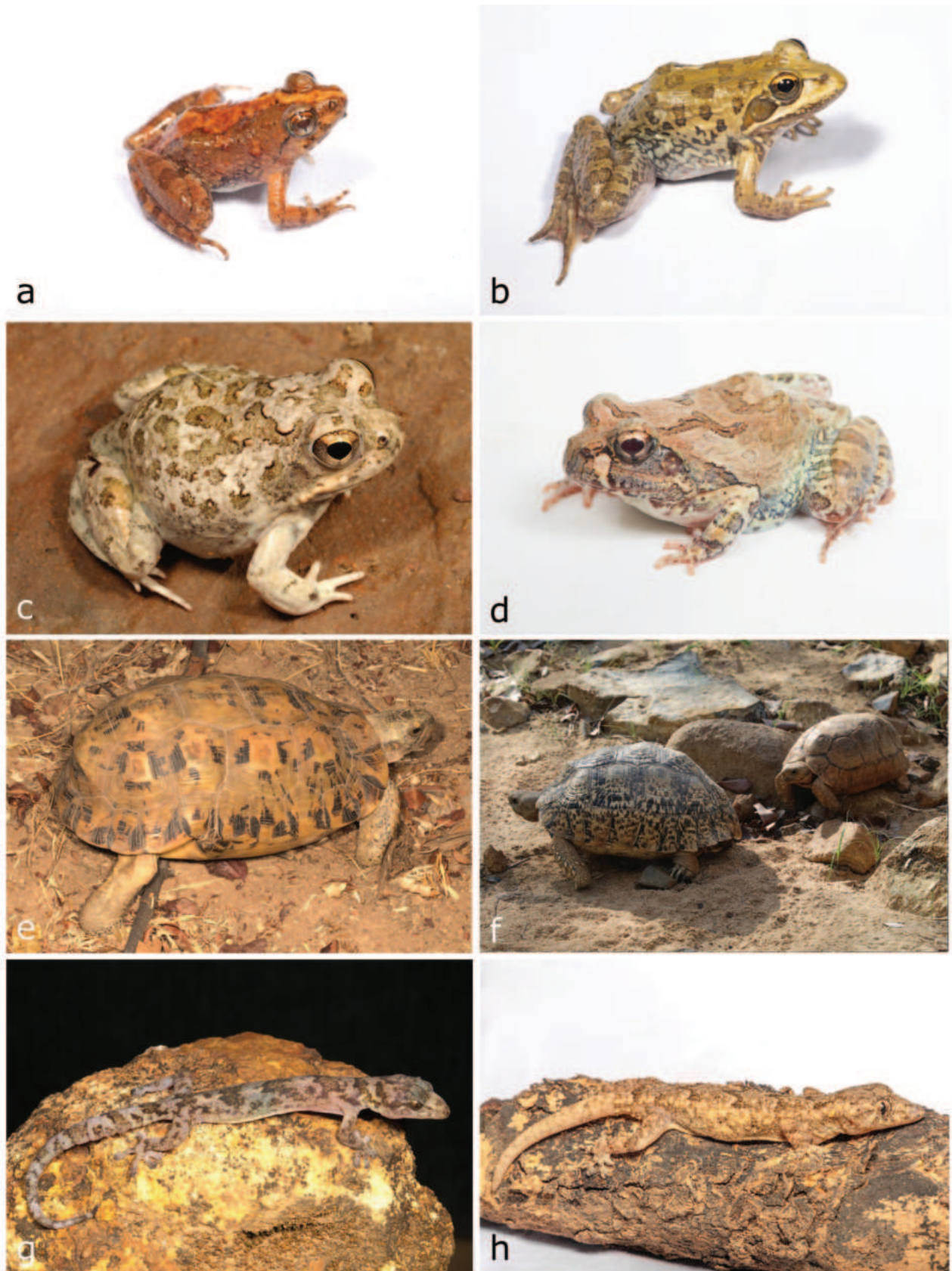


Figure 5. **a** *Phrynobatrachus natalensis* **b** *Amietia angolensis* **c** *Tomopterna ahli* **d** *Tomopterna tuberculosa* **e** *Kinixys belliniana* **f** *Stigmochelys pardalis* **g** *Afroedura praedicta* **h** *Hemidactylus benguellensis*. Photographs by AT (**a**, **b**, **d**, **h**) and LMPC (**c**, **e**–**g**).

Reptilia, Testudines
Family Testudinidae Batsch, 1788
Genus *Kinixys* Bell, 1827

***Kinixys belliana* Gray, 1863**

Fig. 5e

Records. Catchi surroundings [-13.7577, 13.2543, 1576 m] (MUNHAC/MB03-001548, 001549 only tissue); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001550, only tissue).

Comments. A wide-ranging species from eastern Africa to southwestern and central Angola. Historically, the taxonomic status of *Kinixys* populations in Angola has been uncertain (for further discussion see Marques et al. 2018), although according to the most recent sub-Saharan Africa chelonian phylogeny (Fritz et al. 2022), the Angolan material should be assigned to *Kinixys belliana*. This species is frequently consumed a delicacy by the Mucubal tribe at the base of Serra da Neve (pers. obs.).

Genus *Stigmochelys* Gray, 1873

***Stigmochelys pardalis* (Bell, 1828)**

Fig. 5f

Record. 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001551, only tissue).

Comments. *Stigmochelys pardalis* is a large-bodied species occurring from northern Somalia southwards through eastern Africa to South Africa, and westwards to Namibia and Angola (Marques et al. 2018). The species has been recorded in the southern provinces of the country (Marques et al. 2018).

Reptilia, Squamata
Family Gekkonidae Gray, 1825
Genus *Afroedura* Loveridge, 1944

***Afroedura praedicta* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie, 2021**

Fig. 5g

Records. Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/ MB03-001552–001554).

Comments. This recently described species is only known from the Serra da Neve inselberg and is considered a strict endemic (Branch et al. 2021; Conradie et al. 2023). This highland specialist was found in vertical walls of large granite boulders at night. A juvenile (MUNHAC/ MB03-001552) was collected in rock crevices near a communal laying site with dozens of hatched eggs.

Genus *Hemidactylus* Goldfuss, 1820

Hemidactylus benguellensis Bocage, 1893

Fig. 5h

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 263367–263372); N'Dolondolo [-13.8133, 13.1362, 681 m] (CAS 263536–263540; UF 187202; INBAC/AMB 10237, 10245); vic. N'Dolondolo [-13.8068, 13.1351, 754 m] (CAS 263549); Maylowe [-13.8342, 13.2767, 803 m] (CAS 266144); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001555, 001556); MPLA post near Catchi [-13.7618, 13.2514, 1614m] (MUNHAC/MB03-001799); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001557, 001558).

Comments. The species is endemic to southwestern Angola and northern Namibia (Marques et al. 2018; Ceríaco et al. 2020c; Lobón-Rovira et al. 2021). Although *H. benguellensis* appears to be very common in the Angolan Escarpment areas, it has also been found in more coastal environments in southwestern Namibe Province (Lobón-Rovira et al. 2021). The species is strongly associated with rupicolous habitats.

Genus *Chondrodactylus* Peters, 1870

Chondrodactylus pulitzerae (Schmidt, 1933)

Fig. 6a

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 266367–CAS 266369, 266371; INBAC/AMB 10200); N'Dolondolo [-13.8133, 13.1362, 681 m] (CAS 266370); Maylowe [-13.8342, 13.2767, 803 m a.s.l.] (CAS 266114); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001559–001565); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001566–001568).

Comments. The genus has recently been reviewed by Heinz et al. (2021). The species is quite widespread in Angola (Marques et al. 2018; Heinz et al. 2021), and it occurs at different elevations on Serra da Neve and its surrounding areas.

Genus *Lygodactylus* Gray, 1864

Lygodactylus baptistai Marques, Ceríaco, Buehler, Bandeira, Janota & Bauer, 2020

Fig. 6b

Records. Mamué riparian area [-13.8008, 13.1235, 715 m] (CAS 263557), [-13.8004, 13.1246, 748 m] (CAS 263551); MPLA post near Catchi [-13.7618, 13.2514, 1614 m] (MUNHAC/MB03-001569–001571); near Ondjili, between Catchi and Lutala crater (MUNHAC/MB03-001572).

Comments. This recently described species is only known from the Serra da Neve inselberg and is considered a strict endemic. The species was recently described from the inselberg by Marques et al. (2020). *Lygodactylus baptistai* appears to be the single representative of this lineage in southwestern Africa. Morphologically it is also more similar to those species found on inselbergs of



Figure 6. **a** *Chondrodactylus pulitzerae* **b** *Lygodactylus baptistai* **c** *Lygodactylus nyaneka* **d, e** *Pachydactylus caraculicus* (adult and juvenile) **f** *Pachydactylus maiatoi* **g** *Pachydactylus* cf. *punctatus* **h** *Rhoptropus* aff. *barnardi*. Photographs by AT (**a, d, e, g**); IA (**b, f**) and LMPC (**c, h**).

Mozambique such as *L. rex* Broadley, 1963 and *L. regulus* Portik, Travers, Bauer & Branch, 2013 (Portik et al. 2013b) than to the other species known from Angola, *L. angolensis* Bocage, 1896 and *L. nyaneka* Marques, Ceriaco, Buehler, Bandeira, Janota & Bauer, 2020, both restricted to Miombo forested areas, or *L. lawrencei* Hewitt, 1926, an arid zone specialist.

***Lygodactylus nyaneka* Marques, Ceriaco, Buehler, Bandeira, Janota & Bauer, 2020**

Fig. 6c

Record. Mamué riparian area [-13.8008, 13.1235, 715 m] (CAS 263556).

Comments. A recently described species from the central and southwestern regions of the country and neighboring northern Namibia, with records from Epupa Falls (Marques et al. 2020). The individual collected from Serra da Neve occurs in sympatry with the strictly endemic *L. baptistai*.

Genus *Pachydactylus* Wiegmann, 1834

***Pachydactylus caraculicus* FitzSimons, 1959**

Fig. 6d, e

Records. N'Dolondolo [-13.8133, 13.1362, 681 m] (CAS 10283, 10347); Maylowe [-13.8342, 13.2767, 803 m] (CAS 266145; MUNHAC/MB03-001573); 2 km N of Maylowe [-13.8280, 13.2616, 804 m] (MUNHAC/MB03-001574); 2 km N of Maylowe, rock outcrops near basecamp [-13.8280, 13.2646, 8020 m] (MUNHAC/MB03-001575–001581).

Comments. The species is known from southwestern Angola and northwestern Namibia (Marques et al. 2018). It is part of a diverse and primarily rupicolous “northwestern clade” of *Pachydactylus* (Bauer and Lamb 2005; Heinicke et al. 2011), sister to *P. angolensis* Loveridge, 1944 and *P. maiatoi* (Heinicke et al. 2017b; Marques et al. 2023a). Usually found in crevices and cracks of granitic boulders.

***Pachydactylus maiatoi* Marques, Parrinha, Ceriaco, Brennan, Heinicke & Bauer, 2023**

Fig. 6f

Records. N'Dolondolo [-13.8133, 13.1362, 681 m] (CAS 266484, 266485); Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 266486); Maylowe [-13.8355, 13.2755, 798 m] (MUNHAC/MB03-001246); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001247); 2 km N of Maylowe [-13.8289, 13.2625, 820 m] (MUNHAC/MB03-001248).

Comments. Heinicke et al. (2017b) identified putative species-level diversity within the *Pachydactylus angolensis* group. Based on a combination of morphological, meristic and DNA sequence data, it was possible to separate two different taxa, a “coastal” and “inland” form of *P. angolensis* group. Marques et al. (2023a) described the inland form as *P. maiatoi*. The recently described species appears to be restricted to southwestern Angola, namely in the inland

regions of Namibe Province and along the highlands associated with the Escarpment in Huíla Province. This species is usually found under rocks in areas with some vegetation, in highland regions.

***Pachydactylus cf. punctatus* Peters, 1854**

Fig. 6g

Records. 2 km N of Maylowe [-13.8289, 13.2625, 820 m] (MUNHAC/MB03-001582–001591).

Comments. *Pachydactylus punctatus* is a widespread species complex extending from South Africa northwards to Malawi, the former Katanga Province of the Democratic Republic of the Congo and southern Angola (Marques et al. 2018). In Angola itself, Heinz (2011) noted the presence of four species-level divergent lineages. As the taxonomy and nomenclature of this group is still in a state of flux, we opt here to simply refer our specimens to *P. cf. punctatus*, until the ongoing revision of the group is complete.

Genus *Rhoptropus* Peters, 1869

***Rhoptropus aff. barnardi* Hewitt, 1926**

Fig. 6h

Records. N'Dolondolo [-13.8133, 13.1316, 681 m] (MUNHAC/MB03-001592–001595); vic. N'Dolondolo [-13.8113, 13.1365, 699 m] (MUNHAC/MB03-001596–001603); Basecamp 1 [-13.7770, 13.2591, 1488 m] (MUNHAC/MB03-001604–001610); Maylowe [-13.8355, 13.2755, 798 m] (CAS 266105–10, 266130–32, 266134–37, 266156; MUNHAC/MB03-001611–001620); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (CAS 266127; MUNHAC/MB03-001621, 001622); near Basecamp 1 [-13.7770, 13.2591, 1488 m] (MUNHAC/MB03-001623–001633; CAS 266164–68); Catchi surroundings [-13.7619, 13.2568, 1585 m] (MUNHAC/MB03-001634–001688); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001689–001693); MPLA post near Catchi [-13.7618, 13.2514, 1614 m] (MUNHAC/MB03-001694); 2 km N of Maylowe [-13.8289, 13.2625, 820 m] (MB03-001695–001705).

Comments. Recent surveys in southwestern Angola revealed undescribed cryptic diversity associated with *Rhoptropus barnardi* (Ceríaco et al. 2016; Kuhn 2016; Butler et al. 2019; Lobón-Rovira et al. 2022). The specimens collected in Serra da Neve belong to an undescribed Angolan endemic with affinities to *Rhoptropus barnardi* Hewitt, 1926 and *R. biporosus* FitzSimons, 1957, which is widespread in southwestern Angola, from sea level to an elevation of more than 2000 m. A revision of the genus is being prepared (DP unpubl. data).

***Rhoptropus aff. montanus* Laurent, 1964**

Fig. 7a

Records. Catchi surroundings [-13.7618, 13.2514, 1614 m] (MUNHAC/MB03-001706–001708).

Comments. Three specimens of an unknown species of *Rhoptropus* were collected in a riparian area during our last expedition in 2022. This lineage is currently being described in a separate paper, and is endemic to the highlands of the inselberg (DP unpubl. data). It has affinities to *Rhoptropus montanus* Laurent, 1964, another montane endemic from the Huila Plateau in southwestern Angola (Laurent 1964).

Family Lacertidae Oppel, 1811

Genus *Heliobolus* Fitzinger, 1843

***Heliobolus crawfordi* Marques, Ceriaco, Heinicke, Chehouri, Conradie, Tolley & Bauer, 2022**

Fig. 7b, c

Records. N'Dolondolo [-13.8133, 13.1316, 681 m] (CAS 266267–266269, 266271, 266273, 266275; INBAC/AMB 10335); near Maylowe [-13.8113, 13.3222, 879 m] (CAS 266120, 266121, 266146; INBAC/LMPC 1220, 1221; MHNC-UP/REP 869–871); 2 km N of Maylowe [-13.8280, 13.2416, 804 m] (MUNHCA/MB03-001709–001713).

Comments. Endemic to Angola and restricted to the central coastal regions of the country, including the surroundings of Serra da Neve (Marques et al. 2022). It is absent from higher elevations in Serra da Neve but abundant in the surrounding lowlands.

Genus *Pedioplanis* Fitzinger, 1843

***Pedioplanis haackei* Conradie, Measey, Branch & Tolley, 2012**

Fig. 7d

Records. Dirt road to the top of the mountain, near Maylowe [-13.8328, 13.2652, 794 m] (MHNC-UP/REP 634-635, CAS 266123); Dirt road to Quilengues [-13.8159, 13.3264, 892 m] (MHNC-UP/REP 645); vic. N'Dolondolo [-13.8086, 13.13521, 731 m] (CAS 264757, 264765); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001714–001716).

Comments. This species is endemic mainly to Namibe Province, usually occurring near granite outcrops on sandy areas (Conradie et al. 2012; Parrinha et al. 2021). It was only found in the lowland arid plains of Serra da Neve surroundings, in Mopane habitats, but not in the Miombo-dominated areas at higher altitudes.

***Pedioplanis serodioi* Parrinha, Marques, Heinicke, Khalid, Parker, Tolley, Childers, Conradie, Bauer & Ceriaco, 2021**

Fig. 7e

Records. Dirt road to the top of the mountain, near Maylowe [-13.8328, 13.2652, 794 m] (MHNC-UP/REP 636; CAS 266122); Dirt road to Quilengues [-13.8159, 13.3264, 892 m] (MHNC-UP/REP 637, 638); Maylowe [-13.8355, 13.2755, 798 m] (MHNC-UP/REP 639, 646); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001717–001756).

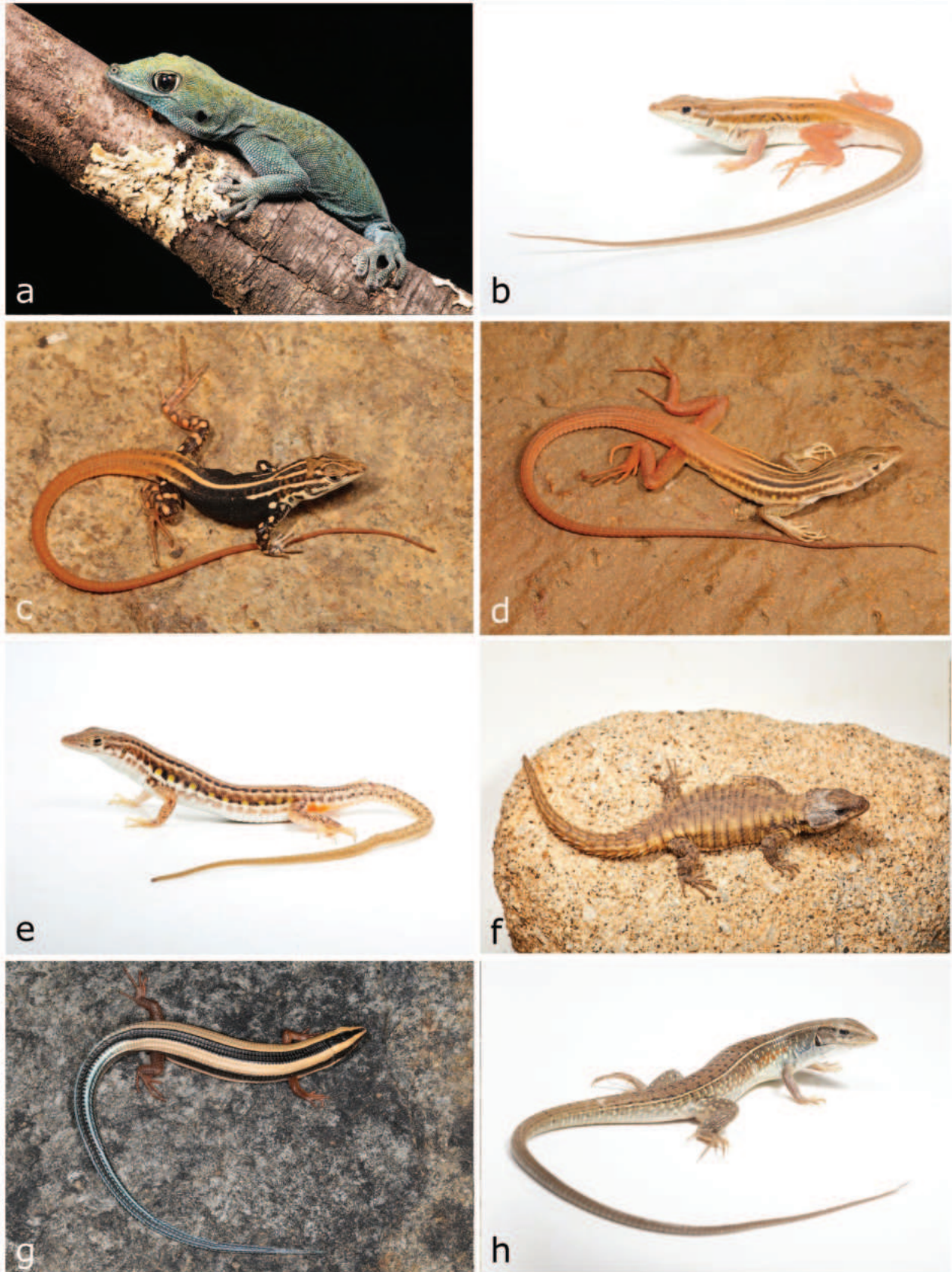


Figure 7. **a** *Rhoptropus* aff. *montanus* **b** *Heliobolus crawfordi* (adult) **c** *Heliobolus crawfordi* (juvenile) **d** *Pedioplanis haackei* **e** *Pedioplanis serodioi* **f** *Cordylus phonolithos* **g** *Cordylosaurus subtessellatus* **h** *Gerrhosaurus* sp. Photographs by AT (**a**, **b**, **e**, **f**, **h**) and LMPC (**c**, **d**, **g**).

Comments. This recently described species (Parrinha et al. 2021) is widely distributed through the lowlands of southwestern Angola, from central Benguela Province to western Cunene Province, with exception of the more xeric areas of southwestern Namibe Province. As with other lacertids, this species was only recorded from the arid lowlands of the inselberg.

Family Cordylidae Fitzinger, 1826

Genus *Cordylus* Laurenti, 1768

***Cordylus phonolithos* Marques, Ceriaco, Stanley, Bandeira, Agarwal & Bauer, 2019**

Fig. 7f

Records. vic. N'Dolondolo [-13.8068, 13.1351, 752 m] (CAS 263581; INBAC/AMB 10272); Rock outcrops near Catchi [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001757-001765).

Comments. This recently described species is only known from the Serra da Neve inselberg and is considered a strict endemic. *Cordylus phonolithos* was recently described from the inselberg by Marques et al. (2019). It is genetically divergent and morphologically distinguished from the closely related Angolan Escarpment dwelling *Cordylus machadoi* Laurent, 1964 and the low-elevation species *C. namakuiyus* Stanley, Ceriaco, Bandeira, Valério, Bates & Branch, 2016. This species is found in cracks in granite boulders, but sometimes can be seen basking outside or even crossing paths on the ground.

Family Gerrhosauridae Fitzinger, 1843

Genus *Cordylosaurus* Gray, 1866

***Cordylosaurus subtessellatus* (Smith, 1844)**

Fig. 7g

Records. vic. Dolondolo [-13.8087, 13.1352, 731 m] (CAS 263031); Mamué riparian area [-13.8003, 13.1229, 710 m] (INBAC/AMB 10326).

Comments. The species is known from southwestern Angola through western Namibia and into western parts of South Africa (Marques et al. 2018). In Angola, *C. subtessellatus* has been recorded from the coastal areas of Benguela and Namibe provinces (Marques et al. 2018). It is commonly found basking in granite outcrops and hidden in crevices.

Genus *Gerrhosaurus* Wiegmann, 1828

***Gerrhosaurus* sp.**

Fig. 7h

Records. Catchi surroundings [-13.7577, 13.2543, 1576 m] (MUNHAC/MB03-001766-001778).

Comments. The Serra da Neve population belongs to a genetic clade that also occurs in the plateau areas of central and southeastern Angola, already signaled by Butler et al. (2019) and Conradie et al. (2016b, 2022) (LMPC unpub. data).

Genus *Matobosaurus* Bates & Tolley, 2013

Matobosaurus maltzahni (De Grys, 1938)

Fig. 8a

Records. N'Dolondolo [-13.8133, 13.1362, 681 m] (INBAC/AMB 10280); Rock outcrops near Catchi [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001779); 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001780).

Comments. The species is known from the northwestern regions of Namibia to the southwestern regions of Angola, where it occurs in the western lowlands of Namibe and Benguela provinces and neighboring Huíla Province (Marques et al. 2018). It occurs in a variety of micro-habitats, from rock outcrops to woodlands. The specimen MUNHAC/MB03-001780 was found at night, sleeping inside a hollow trunk of a Mopane tree.

Family Scincidae

Genus *Acontias* Cuvier, 1816 “1817”

Acontias mukwando Marques, Parrinha, Tiutenko, Lopes-Lima, Bauer & Ceríaco, 2023

Fig. 8b

Records. Catchi, Miombo woodland near basecamp [-13.7660, 13.2587, 1674 m] (MUHNAC/MB03-001522–24).

Comments. This recently described species is only known from the Serra da Neve inselberg and considered a strict endemic. It was found hiding under rocks and active on leaf-litter in Miombo-dominated landscapes (Marques et al. 2023b).

Genus *Mochlus* Günther, 1864

Mochlus sundevallii (Smith, 1849)

Record. 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (specimen not collected).

Comments. This species occurs throughout southern Africa (Marques et al. 2018). The specimen was seen active at dusk, under a cattle fence made from dead Mopane trees, in sandy soil with some Mopane leaf litter.

Genus *Panaspis* Cope, 1868

Panaspis cabindae (Bocage, 1866)

Records. Mamué riparian area [-13. 8015, 13.1206, 665 m] (CAS 263550, 263553–263555; UF 187242; INBAC/AMB 10317, 10320).

Comments. The distribution area of this species extends from central Africa to the central highlands in Angola, reaching its southern limit in the forest margins below the Escarpment in southeastern Namibe Province (Ceríaco et al. 2020b). The species appears to be absent from more xeric and desertic areas of the southwestern regions of Namibe Province, where it is replaced by its congener *Panaspis mocamedensis*. In Serra da Neve, the species was found under leaf-lit-

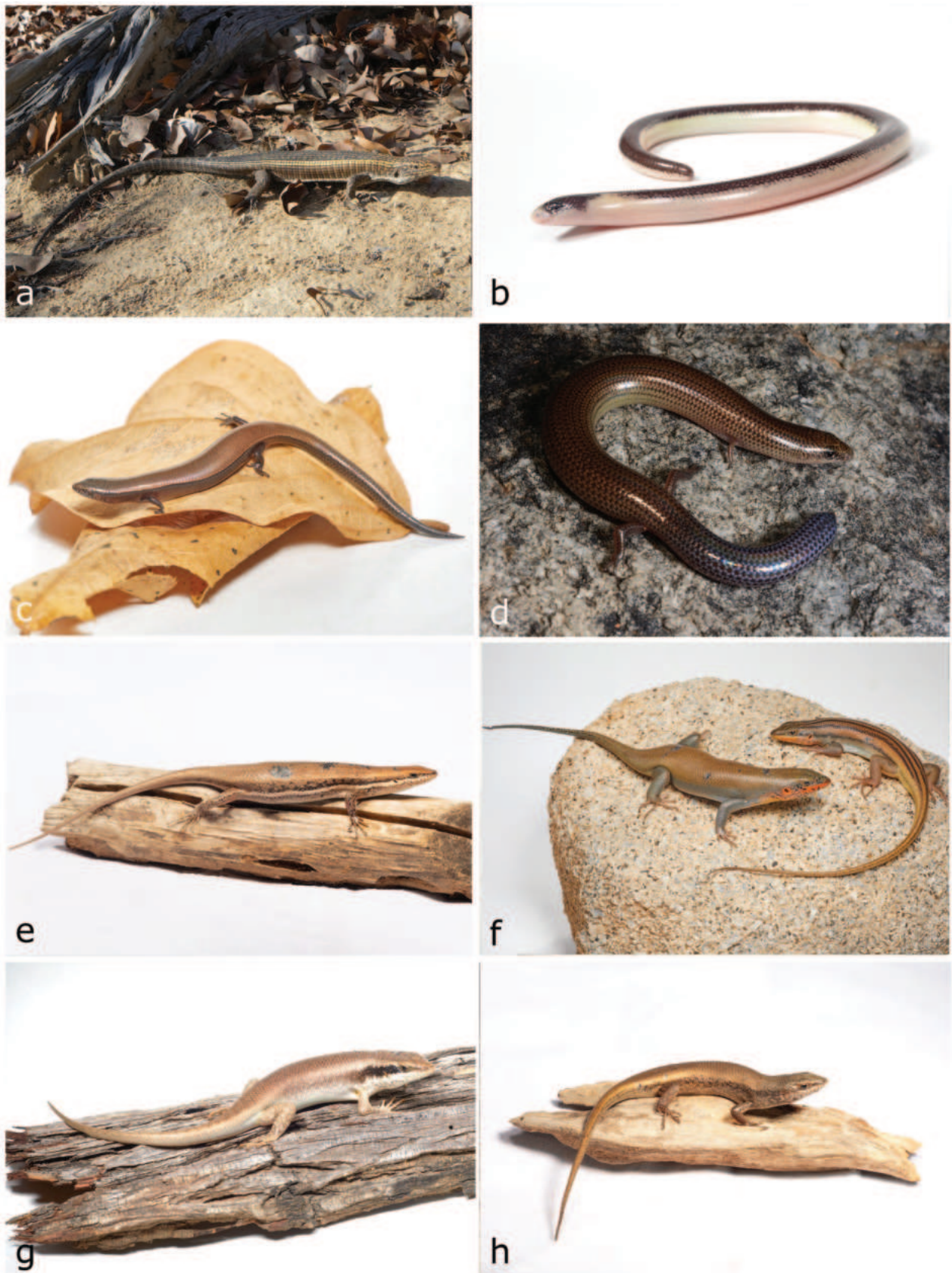


Figure 8. **a** *Matobosaurus maltzahni* **b** *Acontias mukwando* **c** *Panaspis* sp. 1 **d** *Sepsina copei* **e** *Trachylepis albopunctata* **f** *Trachylepis ansorgii* **g** *Trachylepis binotata* **h** *Trachylepis bouri*. Photographs by AT (**a–c**, **e–h**); LMPC (**d**).

ter, in dense Miombo woodlands. In Serra da Neve the species occurs in more humid lowlands, tendentially preferring more forested areas with deeper leaf litter.

***Panaspis mocamedensis* Ceríaco, Heinicke, Parker, Marques & Bauer, 2020**

Records. 2 km N of Maylowe [-13.8280, 13.2625, 820 m] (MB03-001532, 001533).

Comments. *P. mocamedensis* is endemic to Namibe Province (Ceríaco et al. 2020b). This species tendentially prefer more open and dry micro-habitats than their Angolan congeners.

***Panaspis* sp. 1**

Fig. 8c

Records. Rock outcrops near Catchi [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001525, 001526); Catchi, basecamp [-13.7627, 13.2562, 1597 m] (MUNHAC/MB03-001528); 2 km N of Maylowe [-13.8280, 13.2625, 820 m], (MUNHAC/MB03-001529–001531); Dry riverbed, 2 km N of Maylowe [-13.8265, 13.2601, 720 m] (MUNHAC/MB03-001534).

Comments. A new species is currently being described (MPM unpubl. data), only known from the Serra da Neve inselberg, where it is assumed to be endemic. *Panaspis* sp. 1 belongs to the same Central African lineages as *P. cabinda* and is part of the same clade as the Gulf of Guinea Oceanic islands species (Ceríaco et al. 2020b; MPM unpubl. data). This species shows some ecological adaptability occurring in both Miombo woodlands in the higher elevation areas but also in the arid Mopane lowlands (MPM unpubl. data). It was recorded in sympatry with *P. mocamedensis* in the lowlands of the inselberg.

***Panaspis* sp. 2**

Record. MPLA post near Catchi [-13.7618, 13.2514, 1614 m] (MUNHAC/MB03-1527).

Comments. A new species is currently being described (MPM unpubl. data); similarly to *Panaspis* sp. 1, it is known only from Serra da Neve. The single collected specimen was found under a log near to a riparian gallery. *Panaspis* sp. 2 present phylogenetic and biogeographic affinities with *P. annettesabinae* from the highlands of Ethiopia (Colston et al. 2020; MPM unpubl. data).

Genus *Sepsina* Bocage, 1866

***Sepsina copei* Bocage, 1873**

Fig. 8d

Records. Mamué riparian area [-13.8015, 13.1206, 665 m] (CAS 263918–263921); vic. N'Dolondolo [-13.8086, 13.1352, 731 m] (CAS 263916).

Comments. This species is endemic to Angola. It occurs in western coastal regions, from Luanda to Namibe Province.

Genus *Trachylepis* Fitzinger, 1843

Trachylepis albopunctata (Bocage, 1867)

Fig. 8e

Records. Rock outcrop near Basecamp 1 [-13.7864, 13.2575, 1596 m] (CAS 263560); Basecamp 1 [-13.7770, 13.2591, 1488 m] (MUNHAC/MB03-001384, 001516; INBAC/LMPC 1265); Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001468, 001469, 001486–001498, 001500–001502, 001504–001508); 2 km N of Maylowe [-13.8280, 13.2625, 818 m] (MUHNAC/MB03-001509); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001499, 001503).

Comments. The species is widely distributed in Angola, except for the south-eastern areas of the country, where it is replaced by *Trachylepis damarana* (Peters, 1870). The Angolan population was long identified as *Trachylepis varia* (Peters, 1867), but recent reviews by Weinell and Bauer (2018) and Ceriaco et al. (2024) validated the specific status of *albopunctata*.

Trachylepis ansorgii (Boulenger, 1907)

Fig. 8f

Records. Maylowe [-13.8357, 13.2763, 800 m] (MUHNAC/MB03-001396, 001397); Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 263567; UF 187313); Rock outcrop near Basecamp 1 [-13.7865, 13.2572, 1594 m] (UF 187314); vic. N'Dolondolo [-13.8104, 13.1361, 713 m] (CAS 263545); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001472, 001475, 001477, 001478, 001482); Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001473, 001474, 001479–001481, 001485); 2 km N of Maylowe [-13.8280, 13.2625, 818 m] (MUHNAC/MB03-001476); Lutala crater, near airstrip [-13.7325, 13.1841, 1567 m] (MUHNAC/MB03-1484).

Comments. Butler et al. (2019) presented the first topotypical material since the taxon was originally described by Boulenger (1907). According to the molecular results of Butler et al. (in press) and Ceriaco et al. (2024), *T. ansorgii* is a valid species, distinct from *T. sulcata*. *Trachylepis ansorgii* is restricted to the highlands of Angola, mostly distributed from Malanje to northern Huíla Province, while *T. sulcata* seems to occur in the southwestern regions of the country, with records for southern Namibe and southwestern Huíla provinces (Ceriaco et al. 2024). The material collected from Serra da Neve is the first evidence of *T. ansorgii* in Namibe Province and the southernmost record of the species, emphasizing the species restriction to areas of high elevations.

Trachylepis binotata (Bocage, 1867)

Fig. 8g

Records. Maylowe [-13.8357, 13.2763, 800 m] (CAS 266149); 2 km N of Maylowe [-13.8280, 13.2625, 818 m] (MUHNAC/MB03-001453, 001454).

Comments. This large arboreal skink occurs across all southwestern Angola. *Trachylepis binotata* is usually associated with Mopane woodland habitats and was widely recorded in the country (Marques et al. 2018; Ceríaco et al. 2024). In our study area, it was only found in the Mopane-dominated localities at the base of the inselberg.

***Trachylepis bouri* Ceríaco, Marques, Parrinha, Tiutenko, Weinell, Butler & Bauer, 2024**

Fig. 8h

Records. Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001511); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001512).

Comments. This newly described species is endemic to southwestern Angola. It is associated with rock outcrops, especially along the Escarpment (Ceríaco et al. 2024).

***Trachylepis chimbana* (Boulenger, 1887)**

Fig. 9a

Records. vic. N'Dolondolo [-13.8105, 13.1361, 707 m] (CAS 263542, 263543, 263544); near dirt road to top of the mountain, N of Maylowe [-13.8105, 13.2581, 1502 m] (CAS 263562, 263563); Maylowe [-13.8355, 13.2755, 798 m] (MUNHAC/MB03-001387); 2 km N of Maylowe [-13.8280, 13.2625, 818 m] (MUNHAC/MB03-001518); Catchi surroundings [-13.7619, 13.2569, 1585 m] (MUNHAC/MB03-001514); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001515, 001519).

Comments. *Trachylepis chimbana* is one of the most taxonomically challenging species of the genus. This Angolan endemic had been confused by several authors (Schmidt 1933; Hellmich 1957a, b; Laurent 1964) with other taxa, such as *Trachylepis bocagii* or *T. wahlbergi*. Ceríaco et al. (2024) restricted *T. chimbana* to northern Namibe and southern Benguela provinces. This species is primarily rupicolous and was found mainly on granite outcrops.

***Trachylepis huilensis* (Laurent, 1964)**

Fig. 9b

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (CAS 263565; UF 187310; MUNHAC/MB03-001388, 001516); Rock outcrop near Basecamp 1 [-13.7877, 13.2572, 1600 m] (UF 187311), [-13.7865, 13.2572, 1594 m] (CAS 263558), [-13.7881, 13.2571, 1612 m] (CAS 263559); Catchi surroundings [-13.7619, 13.2569, 1585 m] (MUNHAC/MB03-001467, 001470, 001471, 001517).

Comments. This taxon was originally described as a subspecies of *T. bayonii* by Laurent (1964). Butler et al. (2019) provided the first evidence that *huilensis* should be considered a full species, rather than a subspecies. Based on newly

obtained molecular and morphological data, Ceríaco et al. (2024) found that the species is more widespread than originally known. It is associated with the highlands of the Leba Escarpment in Huíla Province and the Serra da Neve inselberg.

***Trachylepis laevis* (Boulenger, 1907)**

Fig. 9c

Records. vic. N'Dolondolo [-13.8105, 13.1361, 713 m] (CAS 263541; UF 187308); Rock outcrop near Basecamp 1 [-13.7881, 13.2571, 1612 m] (CAS 263582); vic. Catci, granite boulders near basecamp [-13.7646, 13.2601, 1603 m] (MUHNAC/MB03-001463–001465).

Comments. This conspicuous species is common in southwestern Angola and neighboring Namibia (Marques et al. 2018; Ceríaco et al. 2024). It is usually seen basking on granite outcrops.

Family Chamaeleonidae Rafinesque, 1815

Genus *Chamaeleo* Linnaeus, 1758

***Chamaeleo dilepis* Leach, 1819**

Fig. 9d

Records. Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001781–001782).

Comments. *Chamaeleo dilepis* is a species complex distributed throughout southern and eastern Africa (Tilbury 2010). Marques et al. (2018) opted to identify all Angolan records as *C. dilepis quilensis* and showed its large distribution throughout the country. More recently, Main et al. (2022) provided evidence of several divergent lineages that may warrant a species-level status. For this paper and until the taxonomy of the group is clarified, we simply refer to the Serra da Neve populations as *C. dilepis*.

Family Agamidae Gray, 1827

Genus *Agama* Daudin, 1802

***Agama aculeata* Merrem, 1820**

Fig. 9e

Records. Maylowe [-13.8342, 13.2767, 803 m] (CAS 266138, 266139).

Comments. *Agama aculeata* is a ground-dwelling agamid commonly found in higher altitudes in southern Angola (Marques et al. 2018). In Namibe Province the species is restricted to areas closely associated with inselbergs and with the Great Escarpment, being replaced by *A. anchietae* in lower altitudes (Marques et al. 2018).

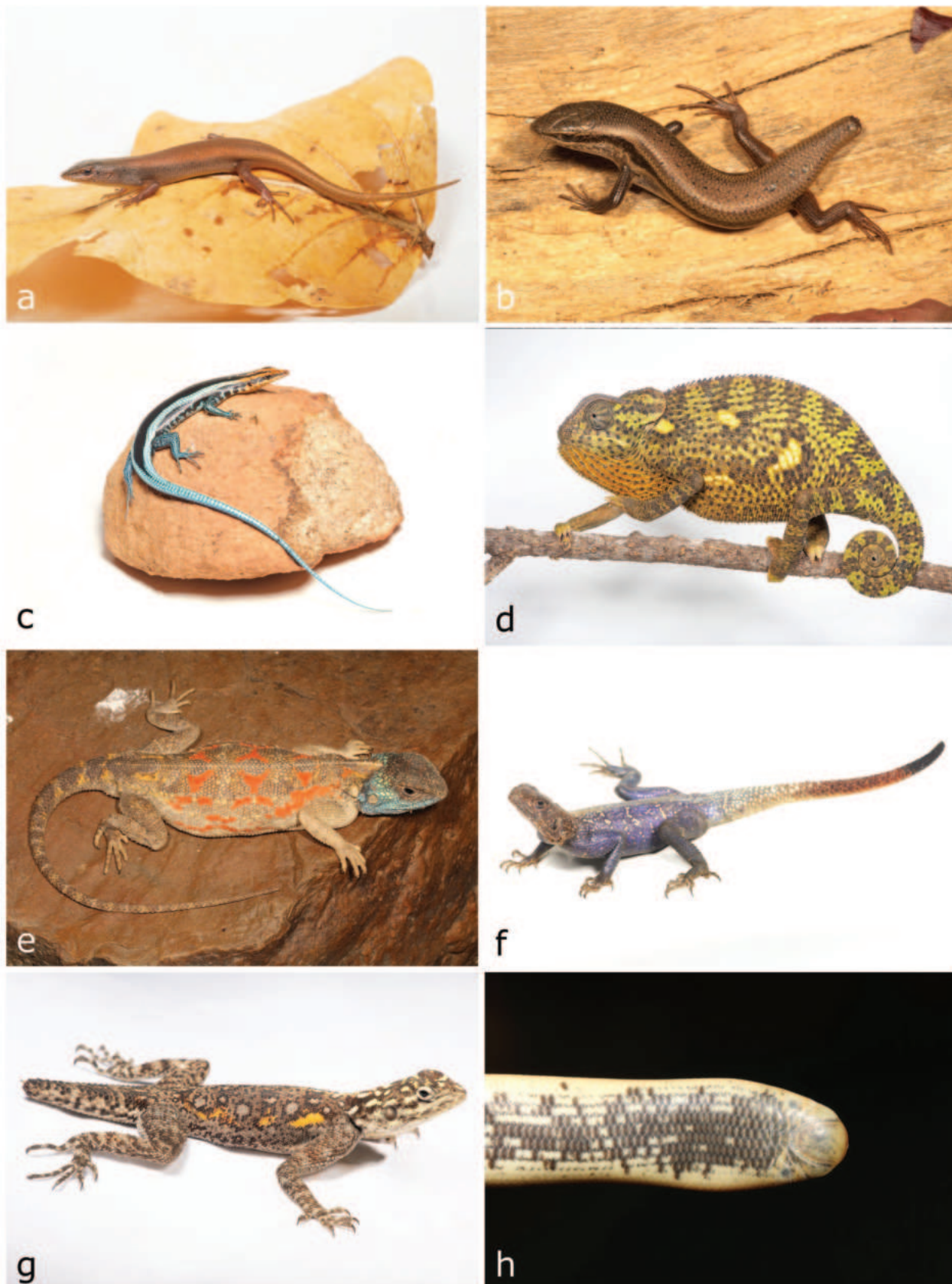


Figure 9. **a** *Trachylepis chimbana* **b** *Trachylepis huilensis* **c** *Trachylepis laevis* **d** *Chamaeleo dilepis* **e** *Agama aculeata* **f** *Agama schacki* (male) **g** *Agama schacki* (female) **h** *Afrotrophlops schlegeli petersii*. Photographs by AT (**a**, **c**, **d**, **f**, **g**) and LMPC (**b**, **e**, **h**).

***Agama schacki* Mertens, 1938**

Fig. 9f, g

Records. Rock outcrop near Basecamp 1 [-13.7865, 13.2572, 1594 m] (CAS 263035), [-13.7881, 13.2571, 1612 m] (INBAC/AMB 10233); N'Dolondolo [-13.8133, 13.1362, 681 m] (INBAC/AMB 10302, 10303); vic. N'Dolondolo [-18.8105, 13.1361, 707 m] (CAS 263026); Maylowe [-13.83424, 13.27669, 803 m] (CAS 266128, CAS 266129; INBAC/LMPC 1169; MUNHAC/MB03-001783); Catchi surroundings [-13.7620, 13.2569, 1584 m] (MUNHAC/MB03-001784); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001785–001796); 2 km N of Maylowe [-13.8280, 13.2616, 804 m] (MUNHAC/MB03-001797); Serra da Neve base, 2 km N of Maylowe, rock outcrops near basecamp [-13.8280, 13.2625, 820 m] (MUNHAC/MB03-001798).

Comments. Originally described by Mertens (1938) as a subspecies of *Agama planiceps* Peters, 1862, *A. schacki* was shown to be a distinct species by Butler et al. (in press), based on molecular data. Marques et al. (2018) had already considered *A. schacki* as a full species and restricted its distribution to the Escarpment area in western Huíla and eastern Namibe and Benguela provinces. The species is strongly associated with higher elevations, being replaced by *A. planiceps* in lowland areas of southern Namibe Province.

Family Typhlopidae

Genus *Afrotyphlops* Broadley & Wallach, 2009

***Afrotyphlops schlegeli petersii* (Bocage, 1873)**

Fig. 9h

Record. Mamué riparian area [-13.8015, 13.1206, 665 m] (CAS 266467).

Comments. The *Afrotyphlops schlegeli* species complex is, as most of the other members of this genus, a taxonomic and nomenclatural conundrum. The validity of *petersii* as a distinct taxon, endemic to southwestern Angola and Namibia, was supported by Roux-Estève (1974). Marques et al. (2018) considered the Angolan population simply as *A. schlegeli*. Given the significant geographic separation between the Angolan population and the topotypical population in Mozambique, as well as the morphological differences noted by Roux-Estève (1974), we treat the Angolan populations as a distinct subspecies until a more comprehensive review of the group is undertaken. This taxon appears to be associated with higher elevation and montane areas (Marques et al. 2018). The collected specimen had been killed by locals who regard it as highly venomous.

Family Leptotyphlopidae

Genus *Leptotyphlops* Fitzinger, 1843

***Leptotyphlops cf. scutifrons* (Peters, 1854)**

Record. vic. Mamué [-13.7877, 13.1257, 1600 m] (CAS 264756).

Comments. *Leptotyphlops scutifrons* is widely distributed in southern Africa. It was recorded from several localities in the Angolan Plateau (Broadley and

Broadley 1999; Conradie et al. 2016b; Marques et al. 2018). Although some historical records may refer to *Namibiana latifrons* (Sternfeld, 1908) (Marques et al. 2018), our specimen agrees almost completely with the diagnosis of *L. scutifrons* that was provided by Broadley and Broadley (1999). Nevertheless, this taxon should be treated as a species complex with multiple divergent lineages (Adalsteinsson et al. 2009). In Angola, it is mostly restricted to the highlands of the Escarpment and Central Plateau (Marques et al. 2018).

Family Pythonidae Fitzinger, 1826

Genus *Python* Daudin, 1803

***Python natalensis* Smith, 1833**

Fig. 10a

Record. Maylowe [-13.8342, 13.2767, 803 m] (photographic record, specimens not collected).

Comments. This species is widely distributed throughout southern Angola (Marques et al. 2018). The skin in the photograph is held by local Mucubal people in the town of Maylowe, where it was killed.

Family Viperidae Opperl, 1811

Genus *Bitis* Gray, 1842

Subgenus *Macrocerastes* Reuss, 1939

***Bitis (Macrocerastes) gabonica* (Duméril, Bibron & Duméril, 1854)**

Fig. 10b

Record. Catchi surroundings [precise locality unknown] (MUNHAC/MB03-001535).

Comments. The Gaboon viper is an African viperid with a primarily west and central African distribution, while some populations extend marginally into northern Zambia. Isolated populations exist from southern South Sudan, Kenya, Tanzania, and the KwaZulu-Natal region of eastern South Africa (Spawls et al. 2023; Marques et al. 2018). In Angola, the species has been recorded mainly in northern and central areas of the country, with the southwestern-most record in Central Benguela (Marques et al. 2018). The Serra da Neve population thus represents the southwestern-most record of the species and the first record for Namibe Province. Our specimen was killed by locals when crossing a path early in the morning. The local name for this species is M'buta, which is also used for other large viperids such as the Puff-adder, *Bitis arietans* Merrem, 1820 (Ceríaco and Marques 2021).

Genus *Causus* Wagler, 1830

***Causus nasalis* Stejneger, 1893**

Fig. 10c

Records. Mamué riparian area [-13.8006, 13.1230, 706 m] (CAS 263034; IN-BAC/AMB 10324).



Figure 10. **a** *Python natalensis* (skin) **b** *Bitis* (*Macrocerastes*) *gabonica* **c** *Causus nasalis* **d** *Boaedon variegatus* **e** *Hemirhagerrhis viperina* **f** *Lycophidion hellmichi* **g** *Psammophis subtaeniatus*. Photographs by LMPC (a, c, f); AT (d, e, g) and DP (b).

Comments. Bocage (1895) suggested that Angolan populations of *Causus resimus* (Peters, 1862) belonged to a new variety, which he named *angolensis*. This decision was supported, according to the author, by morphological differences between the Angolan populations and the nominotypical form. A few years earlier, Stejneger (1893) had already described what he called *Causus nasalis* from “West Africa” based on a specimen collected during the United States Eclipse Expedition to West Africa in 1890. Since Stejneger did not know the exact collection locality of the type, he assumed that it was “Cunga” [most likely Fazenda Cunga, on the banks of the Kwanza River, Luanda Province]. A label bearing this information accompanied another specimen (USNM 16074), which we examined, and which is currently labelled as paratype in the collections of the National Museum of Natural History, Smithsonian Institution, USA (USNM). Neither *nasalis* nor *angolensis* has been commented upon by subsequent authors. The recently collected specimens from Serra da Neve could represent this distinct Angolan population, considering not only its morphological differences but also its geographic isolation from the rest of the known distribution of the topotypical form. Our specimens agree entirely with the morphological description provided by both Stejneger (1893) and Bocage (1895). Given this, we here recognize *C. nasalis* as a valid species for Angola, endemic to the coastal areas of the country, from Luanda to Namibe provinces.

Family Lamprophiidae Fitzinger, 1843

Genus *Boaedon* Duméril, Bibron & Duméril. 1854

***Boaedon variegatus* Bocage, 1867**

Fig. 10d

Records. vic. N’Dolondolo [-13.8105, 13.1361, 707 m] (CAS 263027); Catchi, basecamp [-13.7627, 13.2562, 1597 m] (MUNHAC/MB03-001536).

Comments. This species is a southwestern African endemic, distributed from the coastal areas of Kwanza Sul Province in Angola southwards to Namibia (Hallermann et al. 2020).

Genus *Hemirhagerrhis* Boettger, 1896

***Hemirhagerrhis viperina* (Bocage, 1873)**

Fig. 10e

Records. Basecamp 1 [-13.7770, 13.2591, 1488 m] (UF 187211); vic. N’Dolondolo [-13.8105, 13.1361, 291 m] (CAS 263028), [-13.8109, 13.1351, 705 m] (CAS 263032); N’Dolondolo [-13.8133, 13.1362, 681 m] (INBAC/AMB 10279, 10298); Catchi, rock outcrops near basecamp [-13.7653, 13.2571, 1645 m] (MUNHAC/MB03-001537, 001538), [-13.7659, 13.2582, 1671 m] (MUNHAC/MB03-001539); Catchi, basecamp [-13.7627, 13.2562, 1597 m] (MUNHAC/MB03-001540, 001541).

Comments. This species is restricted to southwestern Angola and northern Namibia (Marques et al. 2018). It is relatively common across its range, where it is usually found during the day in rocky outcrops.

Genus *Lycophidion* Fitzinger, 1843

Lycophidion hellmichi Laurent, 1964

Fig. 10f

Records. Mauué riparian area [-13.8006, 13.1230, 706 m] (CAS 263033); Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001542, 001543).

Comments. This recently collected material represents the first Angolan specimens of this species collected since its original description by Laurent (1964). The species appears to be endemic to southwestern Angola, from Benguela to Namibe Province and to northwestern Namibia. Our specimen from Serra da Neve was collected in the middle of its currently known distribution (Marques et al. 2018). A specimen from northwestern Namibia was assigned to this species by Broadley (1991, 1996). A very similar species, *L. namibianum* Broadley, 1991, which occurs in northwestern Namibia and southern Namibe Province (Broadley 1991, 1996; Lobón-Rovira et al. 2022), is distinguished from *L. hellmichi* by the lack of contact of the post-nasal with the first labial (in contact in *L. hellmichi*). Our specimens agree with the holotype in both coloration and the contact between post-nasal and first supralabial (Laurent 1964). The specimens from Catchi are adult male and female collected while copulating.

Genus *Psammophis*

Psammophis subtaeniatus Peters, 1882

Fig. 10g

Records. Maylowe [-13.8342, 13.2767, 803 m] (CAS 266140); Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001544); 2 km N of Maylowe [-13.8280, 13.2625, 803 m] (MUNHAC/MB03-001545).

Comments. Species restricted to dry shrublands and savannas, particularly Mopane woodland, and widely distributed from southern Angola and northern Namibia eastwards through Botswana, Zambia and Zimbabwe to western Mozambique (Marques et al. 2018). Specimen MUNHAC/MB03-001545 was collected on sandy substrate near a rocky outcrop while active at night.

Genus *Psammophylax* Fitzinger, 1843

Psammophylax tritaeniatus (Günther, 1868)

Fig. 11a

Record. Catchi surroundings [-13.7620, 13.2569, 1585 m] (MUNHAC/MB03-001546).

Comments. This species occurs in mid to high-elevation areas throughout southern and eastern Africa (Spawls et al. 2018). Previous records from Angola are from high-elevation areas of the Escarpment (Marques et al. 2018). This specimen represents the first record for Namibe Province and the westernmost record for *P. tritaeniatus*. Further sampling across the species range may reveal additional cryptic diversity (Keates et al. 2019).

Family Colubridae

Genus *Dasypeltis* Wagler, 1830

***Dasypeltis scabra* (Linnaeus, 1758)**

Fig. 11b

Record. N'Dolondolo [-13.8133, 13.1362, 681 m] (CAS 263023).

Comments. Following the key provided by Bates (2023), our specimen completely conforms with *Dasypeltis scabra*. Marques et al. (2018) provided a map of the distribution of this widespread species in Angola.

Genus *Telescopus* Wagler, 1830

***Telescopus semiannulatus polystictus* Mertens, 1954**

Fig. 11c

Records. vic. N'Dolondolo [-13.8105, 13.1361, 707 m] (CAS 263029); 2 km N of Maylowe [-13.8280, 13.2625, 803 m] (MUNHAC/MB03-001547).

Comments. The collected specimens exhibit more than 60 dark blotches on the back. This fits in the range attributed to the subspecies *polystictus* rather than to the nominotypical form (20–50 blotches according to Branch 1998). This is the first confirmed record for Angola of this subspecies that is otherwise known from neighboring Namibia.



Figure 11. **a** *Psammophylax tritaeniatus* **b** *Dasypeltis scabra* **c** *Telescopus semiannulatus polystictus*. Photographs by DP (a) and LMPC (b, c).

Discussion

Serra da Neve is situated in one of the most herpetologically rich areas not only in Angola, but in Southwest Africa more broadly (Marques et al. 2018). Due to its close proximity to the high elevation areas of the Angolan Escarpment, in combination with the surrounding lowland xeric areas of Namibe and Benguela provinces, the inselberg combines two distinct faunas: one associated with the Angolan highlands (with some Zambezan or Congolian affinities), and one with the desert areas extending from the Namib desert in Namibia to Benguela Province in Angola.

Despite its small area, the number of species recorded from the Serra da Neve inselberg is high, especially when strictly endemic species are considered. The number of Serra da Neve endemics is almost the same as in other biodiversity hotspots in the region, such as the Angolan Central Plateau and the Huíla Escarpment, whose areas are many times the size of the inselberg. These numbers are also considerably higher than those found on other similar inselbergs in Namibia. Whether these differences are related to the geomorphological and biogeographic characteristics of Serra da Neve, isolation, or simply reflect a bias due to poor sampling in other inselbergs, remains to be tested. Despite the already high number of recorded herpetological taxa for Serra da Neve and surrounding areas, several other taxa are expected to occur in the area, given their habitat preferences and known distribution ranges (Marques et al. 2018). Although amphibian diversity is lower in more arid than in mesic areas, several other xeric-tolerant species, such as *Poyntonophrynus dombensis* (Bocage, 1895) and *Sclerophrys regularis* (Reuss, 1833), are expected to occur in Serra da Neve and nearby lowlands. The lack of records of members of the family Hyperoliidae, such as representatives of the *Hyperolius angolensis* Ahl, 1931 or *H. benguellensis/nasutus* species complexes, may be because none of our sampling events occurred in the peak of the rainy season. The habitats in the higher areas of the inselberg are similar to those where these species are found in other parts of the country. Other common rocket-frogs, such as *Ptychadena oxyrhynchus* (Smith, 1849) may also be expected in the study area. The same applies to certain squamate groups, such as representatives of the lacertid genera *Ichnotropis* and *Nucras*, amphisbaenids, rock monitors (*Varanus albigularis angolensis* Schmidt, 1933), or tree agamas of the genus *Acanthocercus*. To our surprise, despite the relatively high diversity of geckos in the area, we did not record the ubiquitous *Hemidactylus mabouia* (Moreau de Jonnès, 1818), a species commonly found around human settlements. This may be another sign of the isolation from routes of regular human movements on and around the inselberg. Other species of geckos, such as the recently described *Kolekanos spinicaudus* Lobón-Rovira, Conradie, Baptista & Pinto, 2022, *Rhoptropus benguellensis* Mertens, 1938, and *Pachydactylus* cf. *oreophilus* McLachlan & Spence, 1967 may be present in the northern surrounding areas of the inselberg. Snake records always tend to be limited, especially during such short-term surveys and, therefore, many other species are expected to occur in the area, such as *Amblyodipsas polylepis* (Bocage, 1873), *Aparallactus capensis* Smith, 1849, *Atractaspis bibronii* Smith, 1849, *Dispholidus typus* (Smith, 1828), *Prosymna* sp., *Philothamnus* sp., *Naja anchietae* Bocage, 1879, and *N. nigricincta* Bogert, 1940 in both the lowland and highland areas; *Bitis arietans*, *B. caudalis* (Smith, 1839), and *Aspidelaps lubricus* (Laurenti, 1768) in the lowlands; and *Crotaphopeltis hotamboeia*

(Laurenti, 1768), *Dendroaspis polylepis* Günther, 1864, *Elapsoidea* sp., and *Thelotornis capensis oatesi* (Günther, 1881) in the highlands. The discovery of other unexpected and undescribed taxa cannot be ruled out, as seen from the recent descriptions of such species as *Acontias mukwando* and *Lygodactylus baptistai*.

The remoteness of Serra da Neve and the lack of good accesses to its base and summit have served so far as a guarantee of its preservation. Furthermore, the ruggedness, elevation, and climatic conditions of the inselberg may deter human settlement and concomitant large-scale habitat alterations. In oceanic islands, topographic and climatic conditions are known to have prevented land-cover changes, despite the presence of humans (Norder et al. 2020). This seems to apply to inselbergs such as Serra da Neve as well. A quick comparison with Mount Moco, an inselberg of similar elevation and with similar number of human inhabitants seems to confirm this idea: Mount Moco is much less rugged than Serra da Neve, and much easier access by the local population has led to a considerable land-use change (Powell et al. 2023). Due to its remoteness, Serra da Neve is unlikely to suffer from activities such as mining, that traditionally cause degradation of inselbergs (Porembski et al. 2016).

Landscape changes are clearly visible on the different plateaus of Serra da Neve, especially around human settlements with large agricultural fields and cattle pastures. Human-caused fires were observed during our fieldwork. The presence of livestock, such as cows, goats, and pigs were also noticeable, but no rodent species associated with humans, such as rats, were observed or collected in an ongoing small mammals survey. Traditional hunting is common, targeting ungulates and birds, but not reptiles. However, chameleons and snakes are seen as dangerous and are usually killed when encountered, as it was the case of our specimens of *Bitis gabonica*, *Telescopus semiannulatus polystictus*, *Psammophylax tritaeniatus*, and *Lycophidion hellmichi*. At the base of the inselberg, tortoises, such as *Kinixys*, are consumed or traded as a delicacy. The remaining amphibians and reptiles are usually neglected by the local human population. Pollution is noticeable in a few water bodies due to its use by humans and cattle and may pose a threat to some amphibians.

Serra da Neve was identified as a potential conservation area by both the scientific community (Huntley and Matos 1992; Huntley 2010; Pinto et al. 2023) and the Angolan authorities. The present checklist, even though it is focused only on amphibians and reptiles, unambiguously shows its conservation importance and interest, not only due to its high number of endemic taxa, but also to its taxonomic diversity. Similar checklists are currently being prepared for other taxonomic groups, such as birds and mammals (Marks pers. comm. November 2022; Ferguson pers. comm. November 2022). This is particularly important in the current scenario of climate change, as inselbergs in xeric areas can serve as important biodiversity retreats (Burke 2003).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MPM, LMPC. Data curation: MPM. Formal analysis: MPM, DP, MLL, AMB, AT, LMPC. Funding acquisition: AMB, LMPC. Investigation: MPM, DP, LMPC, AT, AMB. Methodology: MPM, DP, MLL, LMPC. Project administration: LMPC, AMB. Software: MLL. Supervision: LMPC, AMB. Writing – original draft: MPM, DP. Writing – review and editing: AMB, MLL, LMPC, AT.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Phylogenetic evidence suggests the non-validity of the Iberian land snail genus *Tartessiberus* and confirms its synonymy with *Iberus* (Helicidae)

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Abstract

The monospecific genus *Tartessiberus* was described in the year 2021 including a single species (*T. cilbanus*). However, its description relied solely on morphological and anatomical data. In the present work, we use a fraction of the mitochondrial DNA cytochrome oxidase subunit I (COI), 16S ribosomal RNA (16S rRNA) and the nuclear large ribosomal subunit (LSU) to clarify its validity through phylogenetic positioning. Knowledge of the distribution of this species is also improved by citing new locations and expanding the geographical range to approximately 200 km². Additionally, a morphometric analysis of 259 shells is presented for comparisons with shells of the *Iberus marmoratus* complex and testing the power of conchological features as a tool for specimen identification. The relatively high conchological variability found for *T. cilbanus*, together with the discovery of populations with intermediate conchological features between *T. cilbanus* and other closely related taxa, suggest that the determination of this species should be based on genetic criteria. Our molecular analyses demonstrate that *T. cilbanus* belongs to the *Iberus* genus, and thus, we proceed to update its taxonomic status to *Iberus cilbanus* **comb. nov.**, and, thus, to consider *Tartessiberus* from now on as a junior synonym of *Iberus*.

Key words: Andalusia, Gastropoda, Helicidae, Iberian Peninsula, land snails, morphometrics, new combination, Spain, *Tartessiberus*, taxonomy

Introduction

The Iberian Peninsula is unquestionably a flora and fauna biodiversity hotspot (Orme et al. 2005) and contains an impressive diversity of land snails (Cadevall and Orozco 2016). The traditional determination of land snail species has typically been carried out based on morphological characters such as shell and genitalia. However, plenty of morphological traits are known to be of limited



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use in assessing land snail diversity at the species level (Gould and Woodruff 1986). It is not surprising that the use of genetic molecular tools has allowed for a better delimitation and more accurate understanding of biodiversity, in snail species too (Pfenninger et al. 2006). Molecular analyses are most useful in the detection of cryptic species that have passed unnoticed (Pfenninger and Magnin 2001; Nantararat et al. 2019; Liétor et al. 2024), and avoid cutting rather than lumping of species when purportedly different taxa are in fact only lineages without sufficient genetic differentiation to be considered separate species (Elejalde et al. 2008). Nevertheless, there are groups of taxa that have high genetic variability, and therefore caution is needed when interpreting genetic divergence.

Despite the importance of carrying out genetic analysis for species delimitation, still several land snail species, or even genera, are described solely based on anatomical and/or morphological approaches. A recent example is the description of *Tartessiberus cilbanus* Altaba & Ríos Jiménez (2021), a new monospecific genus endemic from southern Spain. The description and delimitation of this genus were entirely based on morphological and anatomical traits (genitalia, shell, and radula morphology), in comparison to closely related species of the tribe Allognathini. The fact that the morphology of this new species was intermediate between those of the genera *Iberus* Montfort, 1810 and *Allognathus* Pilsbry, 1888 directed the authors to create a new genus for the species. Despite morphological characters being useful for discerning within-population variance, they should be complemented with molecular analyses to complete taxonomic evidence when possible.

Tartessiberus cilbanus is linked to a number of snail populations located in the Sierra de Grazalema Natural Park (Cadiz Province, southwestern Spain), which were traditionally assigned to *Iberus loxanus* (A. Schmidt, 1855) because their shells fit within the pattern of variation of this species. However, *I. loxanus* exhibits a great conchological variation (Liétor 2014). Moreover, genetic analyses situated *I. loxanus* snails in phylogenetically separated clades, mixed with other supposed species (Elejalde et al. 2008). Elejalde et al.'s (2008) phylogenetic study not only showed that *I. loxanus* was a polyphyletic taxon, but also that several supposed species of *Iberus* (including *I. loxanus*) are different morphotypes of the same species [*I. marmoratus* (A. Férussac, 1821)]. However, Elejalde et al. (2008) did not include specimens attributable to *T. cilbanus* in their study. Hence, the phylogenetic position of this monospecific genus remained unknown.

The objective of this work is to analyse the phylogenetic position of *T. cilbanus*, providing molecular analyses of specimens sampled in various locations of its potential distribution area. The determination of its validity has important implications for cataloguing the Iberian land snail diversity and understanding the speciation processes in gastropods in the Iberian Peninsula.

Materials and methods

Field sampling

We carried out a field sampling systematically covering all the calcareous mountain ranges of the potential distribution area of *T. cilbanus*, according to

Altaba and Ríos Jiménez (2021). As a result, 11 field locations were sampled (Suppl. material 1: table S1) which allowed us to define a precise distribution area for the taxon (Fig. 1).

Morphometrics

We measured 259 *T. cilbanus* shells. Measurements of shell morphometrics were conducted following López-Alcántara et al. (1985). Always the same researcher (JL) measured with a digital calliper (accuracy 0.01 mm): the largest and the smallest diameter (\emptyset) of the shell, shell height, and major and minor external \emptyset of the peristome. According to these data, we estimated the shell and peristome area, by considering that both the shell and the peristome may resemble an ellipse, applying the formula $\text{area} = \pi \times [(\text{major } \emptyset)/2] \times [(\text{minor } \emptyset)/2]$. On the basis of these measurements, we estimated a subsequent set of morphological ratios: shell height/major \emptyset of the shell (as an indicator of shell globosity, more globose shells having a higher ratio); major \emptyset of the shell/minor \emptyset of the shell (as an indicator of shell circularity, so that the closer this ratio is to unity, the greater the degree of circularity of the shell); major external \emptyset of the peristome/minor external \emptyset of the peristome (as an indicator of peristome circularity); percentage of the total surface of the shell occupied by the peristome [calculated as $(\text{peristome area} \times 100)/\text{shell area}$].

We carried out statistical comparisons between morphometric measurements with those of the two taxa closely related both phylogenetically and geographically (*I. marmoratus loxanus* and *I. marmoratus marmoratus*) with ANOVA tests when the variables were homoscedastic and normally distributed, otherwise using the Kruskal-Wallis test. In addition, a Principal Components Analysis (PCA) was carried out to determine the overlap in the morphospace between the populations of the described species and those of both *I. marmoratus* ssp. The variables used to place each population into the morphospace were the averages of the largest \emptyset and the height of the shells along with the average percentage of the total surface of the shells occupied by the peristome. These variables were shown to be adequate because more than 92% of the variance of the grouped data was explained by accumulating the first two principal components (PC).

Molecular analysis

Three specimens (codes A2, A3, and AH1) were sacrificed by drowning and a tissue sample was extracted for molecular analyses, stored in absolute ethanol and maintained at -20 °C. Specimen A3 was collected 660 m north from the type locality shown by Altaba and Ríos Jiménez (2021).

Genomic DNA was extracted using QIAGEN DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. The total alignment comprises all known *Iberus* sequences from Genbank ($N = 141$) including *Iberellus* sp. and two outgroup taxa, (*Rossmassleria sicanooides* (Kobelt, 1881) and *Eremina dillwyniana* (L. Pfeiffer, 1853) (Suppl. material 1: table S2).

We firstly used the primers LCO and HCO (Folmer et al. 1994) to amplify the mitochondrial cytochrome oxidase I (COI) gene, but amplifications were sometimes problematic, and therefore we designed specific primers for *Iberus*

(F: ATAAYGTTATTGTTACTGCYCATGCATTYG, R: AGATGTTGRTAYARAATRG-GRTCYCC ~600 pb). We used primers (F: CGCCTGTTTATCAAAAACAT, R: CCGGTCTGAACTCAGATCACGT) from Palumbi (1996) to amplify a 480 bp of the mitochondrial 16S ribosomal RNA (16S rRNA), and primers (F: CTAGCTGC-GAGAATTAATGTGA, R: ACTTTCCTCACGGTACTTG) from Wade et al. (2006) to amplify and sequence a ~900 pb fraction of the nuclear gene large ribosomal subunit (LSU). Sequences were edited with Sequencher v.5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA), and checked for potential contaminants using GenBank's BLASTn search (Altschul et al. 1990). Sequences were edited in Seaview v.4.2.11 (Gouy et al. 2010) and aligned with MAFFT (Katoh et al. 2002) in the CIPRES platform (Miller et al. 2010).

Phylogenetic tree reconstructions for the three concatenated gene fragments (total length 1984 bp) were performed using maximum likelihood (ML) and Bayesian inference (BI), through RAxML v.7.0.4 (Silvestro and Michalak 2012) and MrBayes v.3.2, (Ronquist and Huelsenbeck 2003), respectively. The Akaike Information Criterion (AICc) and partition scheme was implemented in PartitionFinder v.2.1.1 (Lanfear et al. 2016), using a 'greedy' search (Lanfear et al. 2012) to select the best fit evolutionary model for each partition. The resulting models and partitions were GTR+I+G (COI pos1), F81+I (COI pos2), GTR+I+G (COI pos3), GTR+I+G (16S rRNA) and HKY+G (LSU).

From the BI analysis, two independent runs (each with four Markov chains for 10×10^7 generations) were performed. Trees and parameters were sampled every 1000 generations. A majority-rule consensus tree was estimated by combining results from duplicated analyses, after discarding 25% of the total samples as burn-in. ML searches were conducted under GTRGAMMA and support was assessed by using 1000 bootstrapped replicates. All phylogenetic analyses were performed in the CIPRES platform (Miller et al. 2010). The consensus tree was visualised and rooted using FigTree v.1.4.4 (Rambaut 2018), and later prepared as a graphic with the software Inkscape v.1.0.1 (<http://www.inkscape.org>).

Results

Phylogenetic analyses and genetic distances

The phylogenetic analyses recovered three well-supported clades for the genus *Iberus* with *Tartessiberus* included within the tree topology, a clear indication that this later genus cannot be valid. Sequences of *T. cilbanus* specimens were grouped in the centre clade, with *I. rositai*, *I. loxanus*, *I. marmoratus* and *Iberus* sp. (Fig. 1). The *T. cilbanus* clade was strongly supported in both the ML and BI analyses. Analyses of the nuclear gene tree placed the three samples within the same *Iberus* clade (data not shown) as the mitochondrial data did. GenBank blast searches of the nuclear fragment matched 99.81% with *I. rositai*, *I. marmoratus*, *I. loxanus* and *I. cobosi*.

Genetic divergence between *T. cilbanus* and the rest of the closely associated taxa remained high, with a minimum divergence of 7.5% and a maximum of 10.9% for the COI and 3% and 5.8% for the 16S rRNA gene fraction (Table 1). Genetic divergence within individuals from the *T. cilbanus* clade was high, as the A2 and A3+AH1 had a genetic distance between them of 7.1% and 3.4%

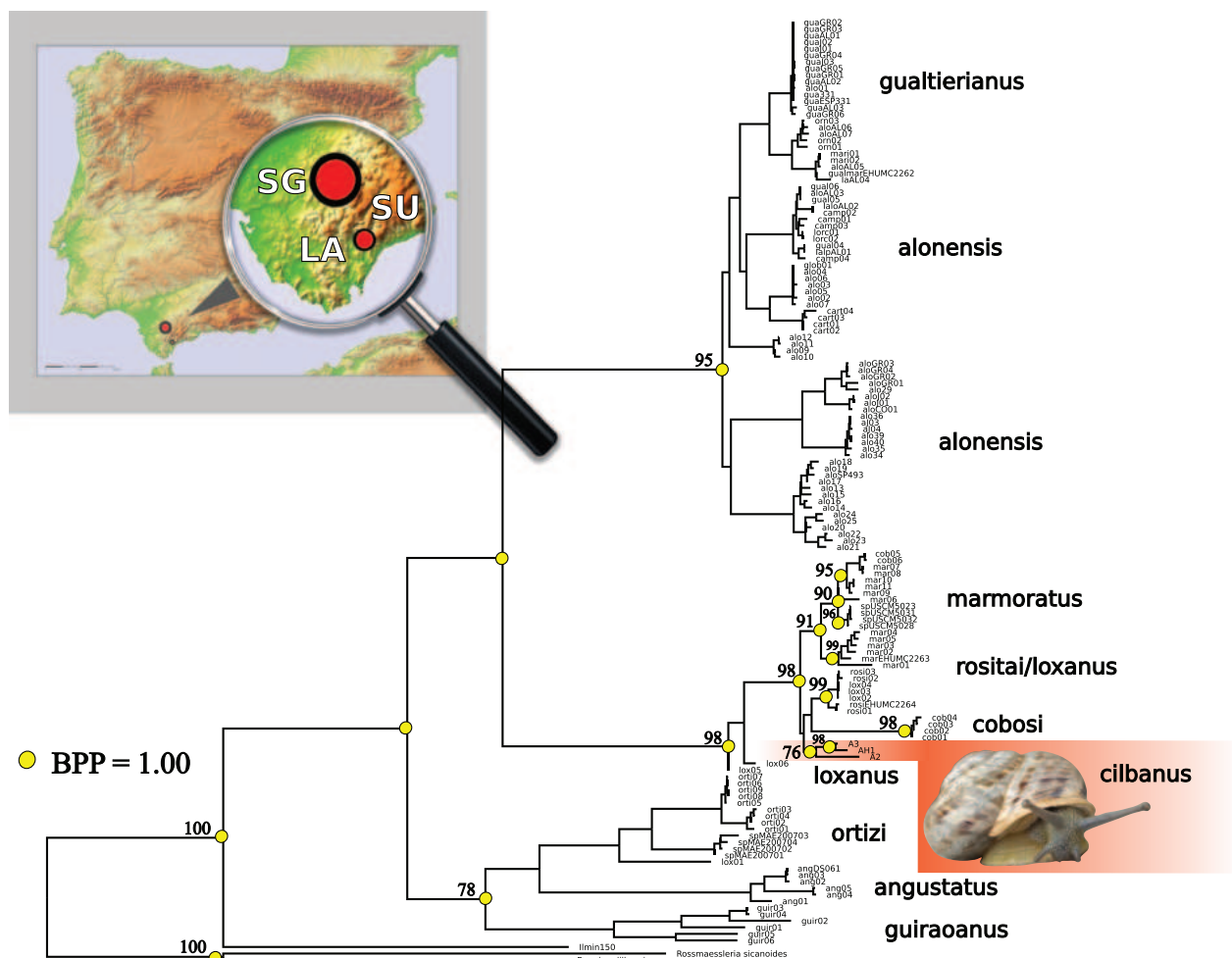


Figure 1. Top left: Map of the western provinces of Andalusia (Southern Spain) showing the geographic location (in red-filled circles) of the two known populations for *T. cilbanus*. Acronyms on map: SG (Sierra de Grazalema Natural Park, Cadiz), LA (Los Alcornocales Natural Park, Cadiz), SU (Sierra de la Utrera, Malaga). Right: maximum likelihood tree of *Iberus*. Values by nodes represent bootstrap values for the ML analyses (> 75%) and BI posterior probabilities (BPP = 1) (represented by yellow-filled circles) are shown for all major clades and for *T. cilbanus* and closely related taxa. *T. cilbanus* clade is shown in red.

Table 1. *P*-uncorrected distances for the taxa of the clade closely associated with *T. cilbanus*, COI (lower matrix) and 16S rRNA (upper matrix).

	<i>T. cilbanus</i>	<i>I. cobosi</i>	<i>I. loxanus</i>	<i>I. marmoratus</i>	<i>I. rositai/loxanus</i>
<i>T. cilbanus</i>	–	5.80%	3.07%	4.99%	3.25%
<i>I. cobosi</i>	10.90%	–	4.74%	5.76%	5.04%
<i>I. loxanus</i>	10.45%	12.73%	–	4.28%	2.58%
<i>I. marmoratus</i>	8.23%	11.13%	10.65%	–	4.19%
<i>I. rositai/loxanus</i>	7.48%	10.09%	10.18%	7.73%	–

for the COI and 16S rRNA, respectively. Overall, the mean genetic divergence within *T. cilbanus* was 5.6% (COI) and 2.3% (16S rRNA). Meanwhile, within other closely related species, genetic divergences were: *I. cobosi*, 0.9% (COI), 0.13% (16S rRNA); *I. loxanus* 05+06, 0.9% (COI), 1.3% (16S rRNA); *I. marmoratus*+sp, 4.1% (COI), 2.4% (16S rRNA); *I. rositai*+*loxanus*, 1.8% (COI), 0.09% (16S rRNA).

Distribution

As expected, most locations for *T. cilbanus* were from the Cadiz Province. Nevertheless, a new locality was found in the Sierra de la Utrera massif (province of Malaga, southern Spain), a karstic habitat ecologically analogous to that of its main distribution region in the Grazalema Natural Park (Fig. 1). The specimens from Sierra de la Utrera showed shell sizes below standard for the species (318 mm² of average shell area ($N = 19$), significantly lower than 424 mm² for the remaining *T. cilbanus* ($N = 240$); p -value = 0.000009 for one-way ANOVA plus post hoc Tukey test). Moreover, our field samplings improved the knowledge of the distribution of this species with new locations that extend its distribution range to approximately 200 km². The altitudinal range is also more precisely determined, to the interval from 314 to 1257 m a.s.l. (Suppl. material 1: table S1).

Morphology

Suppl. material 1: fig. S1 shows a series of specimens of *T. cilbanus* covering its range of conchological variability, which is complemented with images of living specimens in situ (Fig. 2) and their habitats (Fig. 3).

The first factor of the PCA (PC1, Fig. 4) combined major shell \emptyset and shell height, thus being assignable to a gradient of shell size which increases from left to right along the x-axis. PC1 best captured the morphological variability of the shells, with 60.51% of the variance of the morphometric data. The second factor (PC2, Fig. 4), a gradient of the percentage of the shell surface that is occupied by the peristome (increasing from bottom to top along the y-axis), grouped the populations more weakly, explaining 32.26% of the data variance. The PCA showed that *T. cilbanus* occupies a position in the two-dimensional space separated from the subspecies of the *I. marmoratus* complex, which show very similar shells. Still, some overlap between *T. cilbanus* and the other two taxa may be found (Fig. 4).

Suppl. material 1: table S3 summarises the morphometric data of 259 shells of *T. cilbanus* from eight sampling locations. Most morphometric parameters measured in the shells of *T. cilbanus* significantly exceeded those of the two subspecies of the *I. marmoratus* complex, which are phylogenetically and geographically closely related. The shells of *T. cilbanus* were wider, taller, more globose, and with a larger area than those of the *I. marmoratus* ssp. The peristome of *T. cilbanus* was larger and, therefore, had a greater area, which is also manifested in a greater relative area with respect to the total area of the shell, in comparison to *I. marmoratus* ssp. The only morphometric parameters that did not show statistical differences among the three taxa compared were the circularity of both the shells and the peristomes (Suppl. material 1: table S4).

During the sampling, we found populations composed of dwarf-sized specimens with intermediate conchological characteristics between *T. cilbanus* and other taxa of the *I. marmoratus* complex that surround the Grazalema Natural Park. These populations were found in the distribution margins of *T. cilbanus*, pointing to possible genetic introgression in the north (Algodonales, Cadiz Province), as well as in the south (Casares, Malaga Province). Fig. 5 shows some shells of specimens from both populations. The major and minor average shell and peristome diameters, as well as the average shell height, were

found to be significantly lower in the two aforementioned dwarf populations than in *T. cilbanus* (p-value < 0.00001, Kruskal Wallis plus 2-tailed multiple comparison H test).

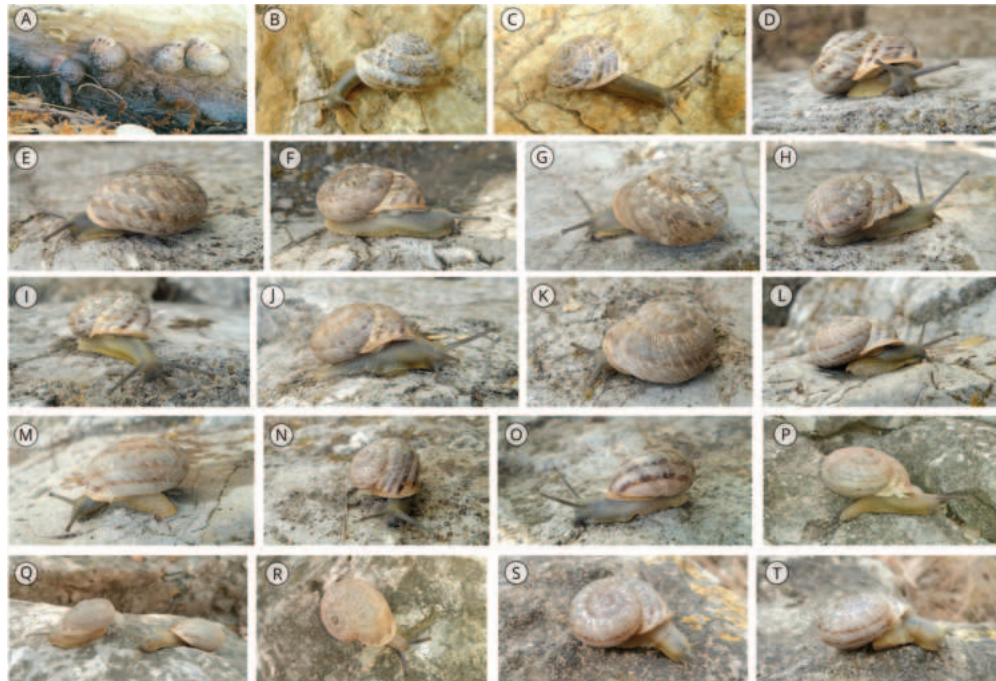


Figure 2. Live specimens of *T. cilbanus* from Cadiz Province photographed in situ **A–I** Grazalema town ring road, Grazalema Natural Park **J–O** Benaocaz, Grazalema Natural Park **P–T** next to the Caldereto neighborhood, Ubrique, Grazalema Natural Park.



Figure 3. Habitats of *T. cilbanus*. **A–E** Grazalema Natural Park, Cadiz Province (**A** Llanos del Apeo, Los Alamos **B** Puerto de las Palomas **C** Grazalema town ring road **D** Caldereto neighborhood, Ubrique **E** 'El Cintillo' viewpoint, Benaocaz) **F** Sierra de la Utrera, Manilva, Casares, Malaga Province.

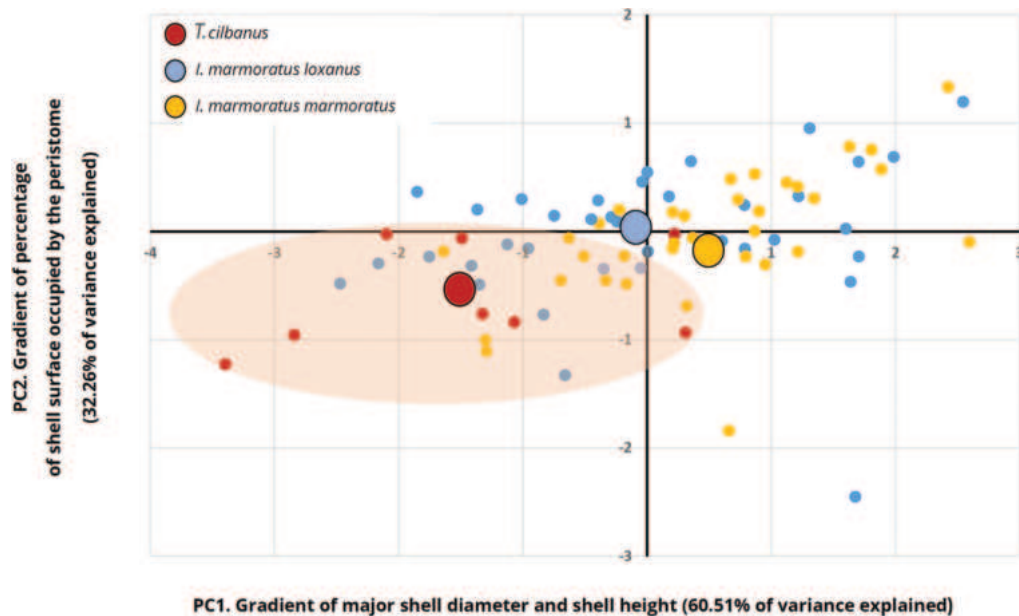


Figure 4. Distribution of *T. cilbanus* (8 localities), *I. marmoratus loxanus* (35 localities) and *I. marmoratus marmoratus* (36 localities) in the bidimensional space generated by the two first PC of a PCA analysis. Each point in the graph represents a single sampling locality. Coordinates of centroids for each species have been calculated as the average X and Y coordinates of the points included in the corresponding clouds. *T. cilbanus* cloud has been highlighted in light red.

Discussion

Altaba and Ríos Jiménez (2021) defined the genus *Tartessiberus* on the basis of morphological and anatomical traits (genitalia, shell and radula). Our genetic study on *Tartessiberus* is yet another example of how genetic tools may further contribute to define taxonomic levels in snails (e.g., Gould and Woodruff 1986; Pfenninger and Magnin 2001; Haase and Bisenberger 2003; Teshima et al. 2003; Pfenninger et al. 2006; Nantararat et al. 2019). In our study, the three sequenced individuals ascribed to *T. cilbanus* grouped within the genus *Iberus*. Therefore, we can unequivocally affirm that snails believed to be *T. cilbanus* are indeed *Iberus* land snails. Furthermore, the genetic distances with other lineages within the closely related clades and its monophyly, with no shared haplotypes to other taxa, suggest the validity of *Iberus cilbanus* comb. nov. (*I. cilbanus* hereafter). However, the notable intraspecific divergence found for *I. cilbanus* suggests the need for subsequent studies on a larger number of samples to determine whether we are dealing with one or several taxa.

The position of *I. cilbanus* as an independent lineage rules out that this clade could be mistaken for any of its closely related species. Our findings, consequently, provide a study case highlighting the importance of genetic analysis to correctly assign taxonomic value when describing species or even genera, although Altaba and Ríos Jiménez (2021) did correctly describe a new species without molecular tools.

In addition to the phylogenetic position, we rely on genetic divergence to ascertain the high genetic differentiation between *I. cilbanus* and its sister clade (Fig. 1). The genetic threshold for considering separated species may be, to some degree, arbitrary. Davison et al. (2009) proposed a 4% threshold for establishing limits between land snail species (with a relatively high rate of error). However, Köhler and Johnson (2012) suggested at least 6% genetic distance for the COI based on their

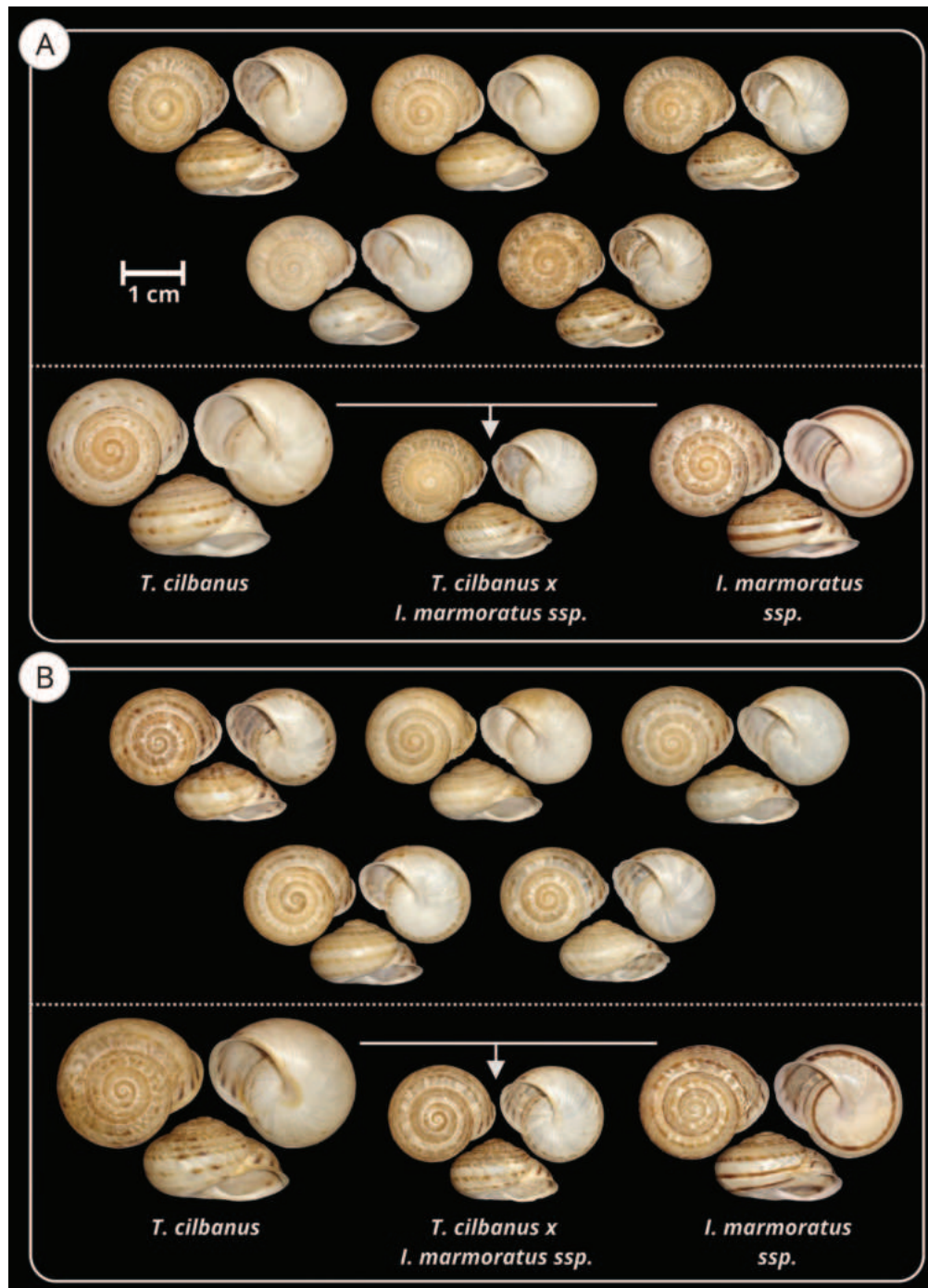


Figure 5. Photographic series of intermediate specimens between *T. cilbanus* and *I. marmoratus* ssp. **A** Hermitage of Virgencita, Algodonales, Sierra de Lijar (Cadiz Province) **B** Sierra Crestellina, Casares (Malaga Province). Below each photographic series, a tentative composition with the parents and an intermediate specimen in a central position is displayed. Selected shells of *I. marmoratus* ssp. come from the closest locations where sampling material was available: Cueva del Gato, Benaolan (Malaga Province) for series A and Gaucin Castle (Malaga Province) for series B.

study in insular land snails, which showed up to 6% variance within species and at least 6% variance between species inhabiting different islands. Moreover, for molluscs, the divergence between congeneric species typically is over 8% (67.5% of cases), with only 15% of pairs of congeneric species showing distances between 4 and 8% (Hebert et al. 2003). But there are known exceptions in some groups and, therefore, this data alone should be treated with caution. Despite these numbers,

we are aware that there is no cut-off point to species delimitation based on genetic distances per se, and we enter the conundrum of 'how long is a piece of string'. Nevertheless, the presence of a clear, strongly supported clade, morphologically differentiated from other *Iberus* species and subspecies, the high genetic divergence, as well as moderate geographical separation, firmly support the validity of a distinct *Iberus* species (i.e., *I. cilbanus*). *Iberus cilbanus* showed a morphology on average well differentiated from *I. marmoratus* spp. (see Fig. 5), the nearest taxon geographically speaking. Their distribution is also separated, although there are a few contact areas. Its reduced distribution range (200 km²) and the existence of some fragmented isolated populations (in Sierra de la Utrera) suggest that some conservation considerations might be necessary for this species.

The existence of the genus *Tartessiberus* would not only imply an unusually young genus (~ 5 Ma versus *Iberus* at 18.5 Ma; Neiber et al. 2021) but also the paraphyly of *Iberus*, suggesting the need for immense taxonomic changes. One other genus, *Pseudotachea* C. R. Boettger, 1909, remains positioned within the *Iberus* clade though Neiber et al. (2021) suggest its synonymization with *Iberus*. Therefore, with *Tartessiberus* and *Pseudotachea* synonymized with *Iberus*, the latter remains monophyletic, which implies an ancient evolutionary lineage and origin for the Iberian Peninsula.

Our field observations and captive breeding trials (unpublished data) have found that individuals and populations of different species of the genus *Iberus* tend to show dwarfism tendencies as a possible consequence of hybridization. Further studies will be necessary to determine if the smaller population of Sierra de la Utrera is undergoing a process of introgression by *I. marmoratus marmoratus* or, alternatively, if the small size is a local adaptive response or a symptom of phenotypic plasticity. Further genetic sequencing will corroborate possible hybridization between these species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.


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Author contributions

Conceptualization: JL, MJJ, GMR. Data curation: MJJ, PAJ, ART, JL, IGL. Formal analysis: IGL, MJJ, JL. Funding acquisition: GMR, MJJ. Methodology: IGL, MJJ, JL, ART, PAJ. Supervision: JL. Validation: MJJ. Writing - original draft: MJJ, GMR. Writing - review and editing: ART, IGL, JL, MJJ, GMR.

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Data availability

All data generated or analysed during this study are included in this published article (Supporting information).

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Supplementary material 1

Supporting information

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Data type: docx

Explanation note: **figure S1**. Photographic series showing the range of variability for the shells of *T. cilbanus* (Cadiz): 1–11: Grazalema town ring road, Grazalema Natural Park; 12–20: Next to the Caldereto neighborhood, Ubrique, Grazalema Natural Park; 21–24: Llanos del Apeo, Los Alamos, Grazalema Natural Park; 25–39: ‘El Cintillo’ viewpoint, Benaocaz, Grazalema Natural Park; (Malaga); 40: Sierra de la Utrera, Manilva, Casares. **table S1**. Sampling locations for *T. cilbanus*. **table S2**. Samples used in the phylogenetic analyses. GenBank voucher abbreviations, species names, localities, coordinates and GenBank accessions. **table S3**. Morphometric parameters and ratios measured for *T. cilbanus* ($N = 259$). **table S4**. Morphometric comparisons between *T. cilbanus* and the two taxa of the *marmoratus* complex which inhabit the surrounding areas. K: Kruskal Wallis plus 2-tailed multiple comparison H test; A: one-way ANOVA plus post hoc Tukey test (HSD) for the comparisons between *T. cilbanus* and *I. marmoratus marmoratus* and *I. marmoratus loxanus*, respectively; ns: non-significant.

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Link: <https://doi.org/10.3897/zookeys.1201.117318.suppl1>

The ectoparasitoid wasp *Heterospilus sicanus* (Marshall, 1888) (Hymenoptera, Braconidae, Doryctinae) as a natural enemy of *Gastrallus pubens* Fairmaire, 1875 (Coleoptera, Ptinidae) in Italy

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Abstract

Heterospilus sicanus (Marshall, 1888) is redescribed and illustrated based on the holotype of *Dendrosoter sicanus* Marshall, 1888 and on recently collected material from its type locality (Sicily, Italy). Previous host records for this species are unreliable. Here, the host of *H. sicanus*, the rare ptinid beetle *Gastrallus pubens* Fairmaire, 1875, is recorded for the first time, having been reared in a historic library in Palermo, Italy. *Heterospilus sicanus* is compared with the similar species *Telebolus* (= *Heterospilus*) *corsicus* Marshall, 1888, which was described in the same monograph from Corsica (France), and it is also redescribed and illustrated. *Atoreuteus ceballosi* Docavo Alberti, 1960, **syn. nov.** is synonymised under *Heterospilus sicanus* (Marshall, 1888), and *Hormiopteris* (= *Rhaconotus*) *ollivieri* Giraud var. *flava* Fahringer, 1931, **syn. nov.** is a junior synonym of *Heterospilus cephi* Rohwer, 1925. A key for determination of the Western Palaearctic *Heterospilus* species with a striate vertex is provided and the distributions of *H. sicanus* and *H. corsicus* are discussed.

Key words: Bookworm, diagnosis, Ichneumonoidea, parasitoid, redescrptions, taxonomy

Introduction

The family Braconidae is a vast group within the order Hymenoptera, comprising more than 20,000 recognised species (Yu et al. 2016). Together with the family Ichneumonidae it constitutes one of two recent families of Ichneumonoidea, the vast majority of which are parasitoids (Wharton 1993).

The braconid subfamily Doryctinae is renowned for its exceptional genera and species richness and diversity, including more than 2000 described species distributed globally across almost 200 genera (Shenefelt and Marsh 1976; Marsh 1993, 2002; Belokobylskij et al. 2004a, 2004b; Belokobylskij and Maetô 2009; Yu et al. 2016). Doryctines, for the most part, are idiobiont ectoparasitoids on

the larvae of xylophagous and bark-boring Coleoptera. Some members of this group also parasitise the larvae of Lepidoptera and Hymenoptera (Symphyta), while a few genera are known to be phytophagous (Ramírez and Marsh 1996; Wharton and Hanson 2005; Zaldívar-Riverón et al. 2007, 2014). Additionally, in certain cases, they function as parasitoids (perhaps endoparasitoids) of adult Embioptera or have been observed inhabiting termite nests (Shaw and Edgerly 1985; Wharton 1993; Kistner et al. 2000; Belokobylskij 2002).

Within this subfamily, the genus *Heterospilus* Haliday, 1836, belonging to the tribe Heterospilini, stands out as one of the largest and most hyperdiverse braconid genera, with already more than 400 species described and many more to be described (Marsh et al. 2013; Yu et al. 2016; Ghahari et al. 2022). In total, 21 species of *Heterospilus* of 45 Palaearctic species are known in Europe, while more than 340 species have been described from the New World (Nearctic and mainly Neotropics) and 37 species from the Oriental region; only one species has been described from Australia and none from the Afrotropical region (Yu et al. 2016; Belokobylskij and Ku 2021).

Species of *Heterospilus* are idiobiont ectoparasitoids known for their exceptionally diverse range of primarily endophytic hosts (Belokobylskij and Maeto 2009; Yu et al. 2016), primarily targeting stem-boring Coleoptera of various families, including Anobiidae, Buprestidae, Cerambycidae, Chrysomelidae (mainly Bruchinae), Curculionidae (including Scolytinae), Languriidae, Mordellidae, and Ptinidae. Additionally, they also parasitise Lepidoptera species of the families Cosmopterigidae, Gelechiidae, Prodoxidae and Pyralidae, and even stem-boring Hymenoptera of the family Cephidae. In addition, a few species have been reared from nests of Crabronidae (Hymenoptera) (Marsh 1982; Shaw 1995; Marsh and Melo 1999; Cabrera et al. 2002).

In this study we provide an illustrated redescription and updated diagnosis of *Heterospilus sicanus* (Marshall, 1888), discovered in the frass, holes, and tunnels created by *Gastrallus pubens* Fairmaire, 1875 (Coleoptera: Ptinidae) in books seriously infested by this book-boring beetle during inspections in the “Ottavio Ziino” Law History Library of the Law Department at the University of Palermo (Sicily, Italy). *Heterospilus sicanus* is compared with the congeneric *Telebolus* (= *Heterospilus*) *corsicus* Marshall, 1888, which is also redescribed and illustrated, and *Atoreuteus ceballosi* Docavo Alberti, 1960 is here synonymised under *H. sicanus* (Marshall, 1888). Finally, a key for the determination of the Western Palaearctic *Heterospilus* species with a striate vertex is included and the distributions of *H. sicanus* and *H. corsicus* are discussed.

Materials and methods

The terminology employed in this work for the morphological features, measurements, and wing venation nomenclature follows Belokobylskij and Maeto (2009), with the terminology for wing venation by van Achterberg (1993) shown in parentheses. Images were taken using a Leica DM series compound microscope (Leica, Benzheim, Germany) and a Leica DFC series mounted camera with Leica Application Suite software (LAS EZ 3.4.0, Leica, Switzerland), and with a Canon SLR EOS 5DSR with either a 65 mm macro lens or a Mitutoyo 10× lens in combination with a 70–130 mm macro lens, mounted on a stand

with an automated Z-stepper (the Natural History Museum, London, UK). All insect photos were integrated using the freeware CombineZP (Hadley 2011) or Helicon Focus and processed in Adobe Photoshop CS4.

Abbreviations of specimen depositories

The specimens (including types) examined in this study have been deposited in the following collections.

HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain;
NHMUK	the Natural History Museum, London, UK;
NHMW	Naturhistorisches Museum, Wien, Austria;
SAAF-UNIPA	Department of Agricultural, Food and Forest Science, University of Palermo, Palermo, Italy;
ZISP	Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

Taxonomy

Class Hexapoda Blainville, 1816

Order Hymenoptera Linnaeus, 1758

Family Braconidae Nees, 1811

Subfamily Doryctinae Foerster, 1863

Tribe Heterospilini Fischer, 1981

Genus *Heterospilus* Haliday, 1836

The original description of *Dendrosoter sicanus* Marshall, 1888: 242, translated from French, is as follows:

“Head transverse, largely dark brown as well as the thorax; the rest of the body tawny; abdomen black towards the tip. Vertex high, gibbous, without frontal protuberances, finely wrinkled crosswise; eye and stemmaticum smooth. Ocelli sunk in the head, the front one placed on the slope of the forehead. Frontal excavation very shallow and poorly determined. Orbits and genae fawn. Antennae as long as the body, slender, blackish with ferruginous base, with 20 antennal segments. Thorax granular, slightly shiny. Mesonotum dark brown; its crenulated furrows converging towards a deep, rough dimple. Metanotum fawn, slightly shiny, granular irregularly streaked lengthwise on its anterior part, roughly reticulated in rear, with several high lines which cross in all directions. Wings slightly smoky, veins and stigma brown; second cubital cell receiving the recurrent vein; vein posterior non-interstitial. Legs fairly short and thick, testaceous. Abdomen as long as the head and thorax, and wider than the latter, tawny, becoming more and more blackish towards the end, last segment pale; first segment in truncated triangle, twice wider at the tip than at the base, bicarinated and high in the middle, depressed on the side edges, leathery, dull, longitudinally streaked. Second suture erased, even on the sides. Second segment very linearly wrinkled at the base, smooth and shiny on the rest of its surface, as well as all the following ones. Ovipositor as long as the abdomen. Male unknown. Long. 2–3.5 mm.”

Marshall (1897: 127) additionally noted (here translated from French), “This species [*D. sicanus*], like the others, is variable as to the size and the colours. I received from Genoa two ♀ which are much darker than the type, and one of which is only half the size indicated. In other aspects their features agree with those of *D. sicanus*. Homeland: add, Italy (Genoa), sent from Mr Mantero.”

Mantero (1904: 28) elaborated on the Italian specimens (here translated from Italian): “Belvedere, July 1891 (Solari). The Ligurian specimens, also cited by Marshall (1897) have a darker colour than the type.”

***Heterospilus sicanus* (Marshall, 1888)**

Figs 1–5

Dendrosoter sicanus Marshall, 1888: 243.

Heterospilus sicanus: Tobias 1971: 194; 1976: 35; Shenefelt and Marsh 1976: 1312; Yu et al. 2016.

Atoreuteus ceballosi Docavo Alberti, 1960: 33, syn. nov.

Heterospilus ceballosi: Shenefelt and Marsh 1976: 1302; Yu et al. 2016.

Type material examined. Holotype of *Dendrosoter sicanus*: female, Italy, “Type” (round with red border), “*sicanus* Marsh. (Sicily)” (handwriting), “Marshall coll. 1904–120”, “Almost certainly type of *Dendrosoter sicanus* Msh., G. Nixon, 25.I.38” (handwriting by G. Nixon), “This is definitely type of *Dendrosoter sicanus* Marshall. Paul M. Marsh, VI–17–71” (handwriting by P. Marsh), “B.M. Type Hym. 3c.1751”, “NHMUK 010880780” (NHMUK, London). **Holotype of *Atoreuteus ceballosi*:** female, Spain, “Tenerife, Bajamar, 8.V.1901”, “♀”, “*Atoreuteus ceballosi* Docavo n. sp.”, “Tipo”, “*Heterospilus* ♀ *ceballosi* Doc., det. Papp J., 1983”, “MNCN Cat. Typos N 11.246” (MNCN, Madrid).

Additional material examined. Italy: Sicily, “Ottavio Ziino” Law History Library of the Law Department of the University of Palermo, 5.VI.2023 (E. Peri, S. Savoldelli, C. Jucker and S. Guarino), 18 females, 15 males (SAAF-UNIPA); Sicily, Vittoria, IX – X.1899 (G. Mantero), 1 female (ZISP). Russia: Crimea, Sebastopol, 5.V.1917 (W. Pliginski), 8 females with the same label of the latter (ZISP).

Redescription. Female (holotype). Body length 2.6 mm; fore wing length 2.3 mm.

Head. Head not depressed, its width 1.6× median length, 1.1× width of mesoscutum. Head behind eyes weakly convex anteriorly, evenly and roundly narrowed posteriorly. Transverse diameter of eye 1.2× longer than temple (dorsal view). Ocelli small, in almost equilateral triangle. POL 1.3× Od, 0.35× OOL. Diameter of antennal socket equal to distance between sockets, twice distance between socket and eye. Eye with sparse and short setae, without emargination opposite antennal sockets, 1.2× as high as broad. Malar space 0.7× height of eye, 1.2× basal width of mandible. Face convex, its width 1.2× height of eye and almost equal to height of face and clypeus combined. Malar suture absent. Clypeus with distinct lower flange. [Hypoclypeal depression covered by glue.] Occipital carina complete dorsally, ventrally joining hypostomal carina distant from base of mandible. Head below eyes (front view) roundly narrowed. Hypostomal flange distinct but narrow.

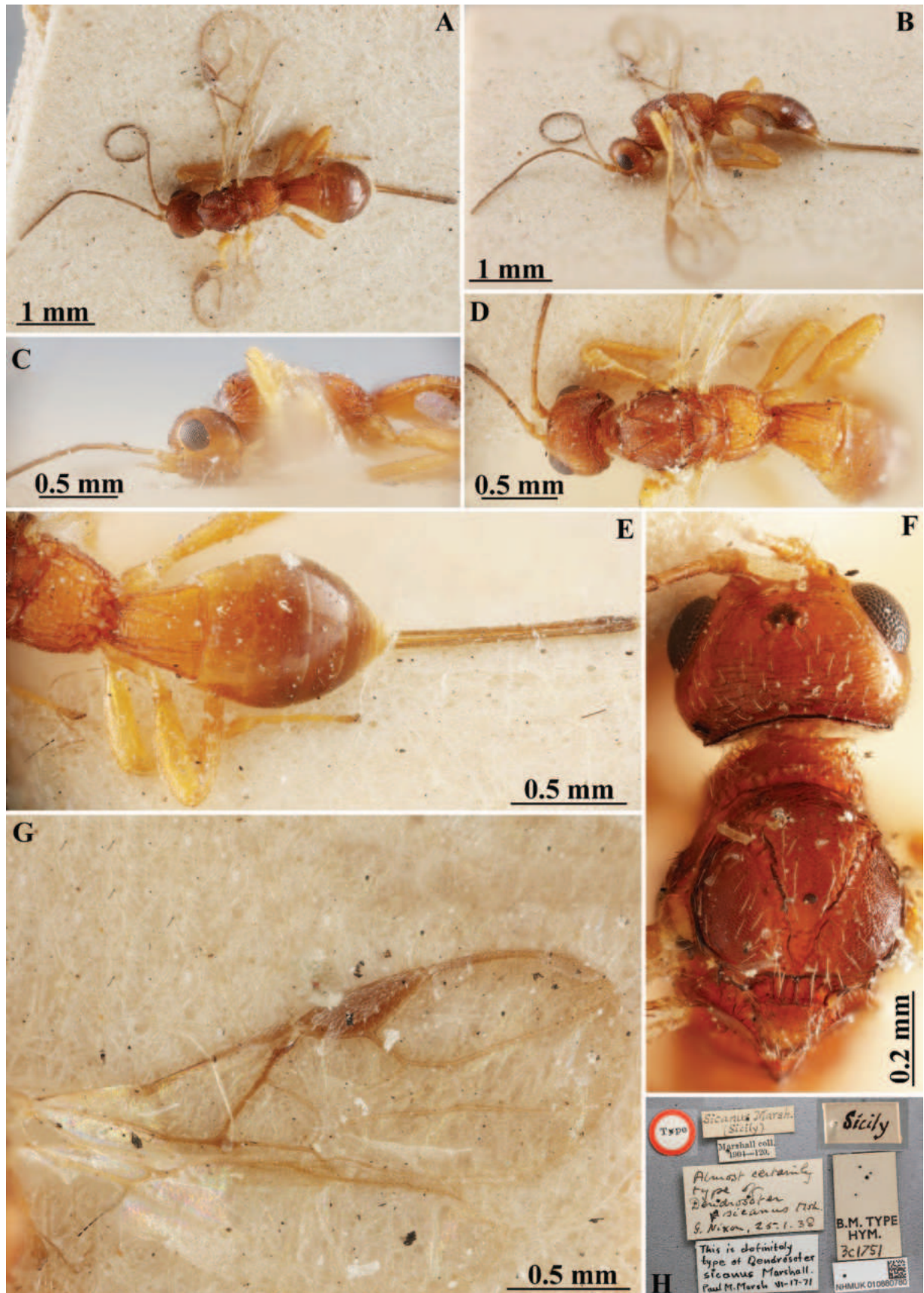


Figure 1. *Heterospilus sicanus* (Marshall, 1888) (female, holotype) **A** habitus, dorsal view **B** habitus, lateral view **C** head, mesosoma and base of metasoma, lateral view **D** head, mesosoma and base of metasoma, dorsal view **E** propodeum, metasoma and ovipositor, dorsal view **F** head and mesoscutum, dorsal view **G** wings **H** labels.

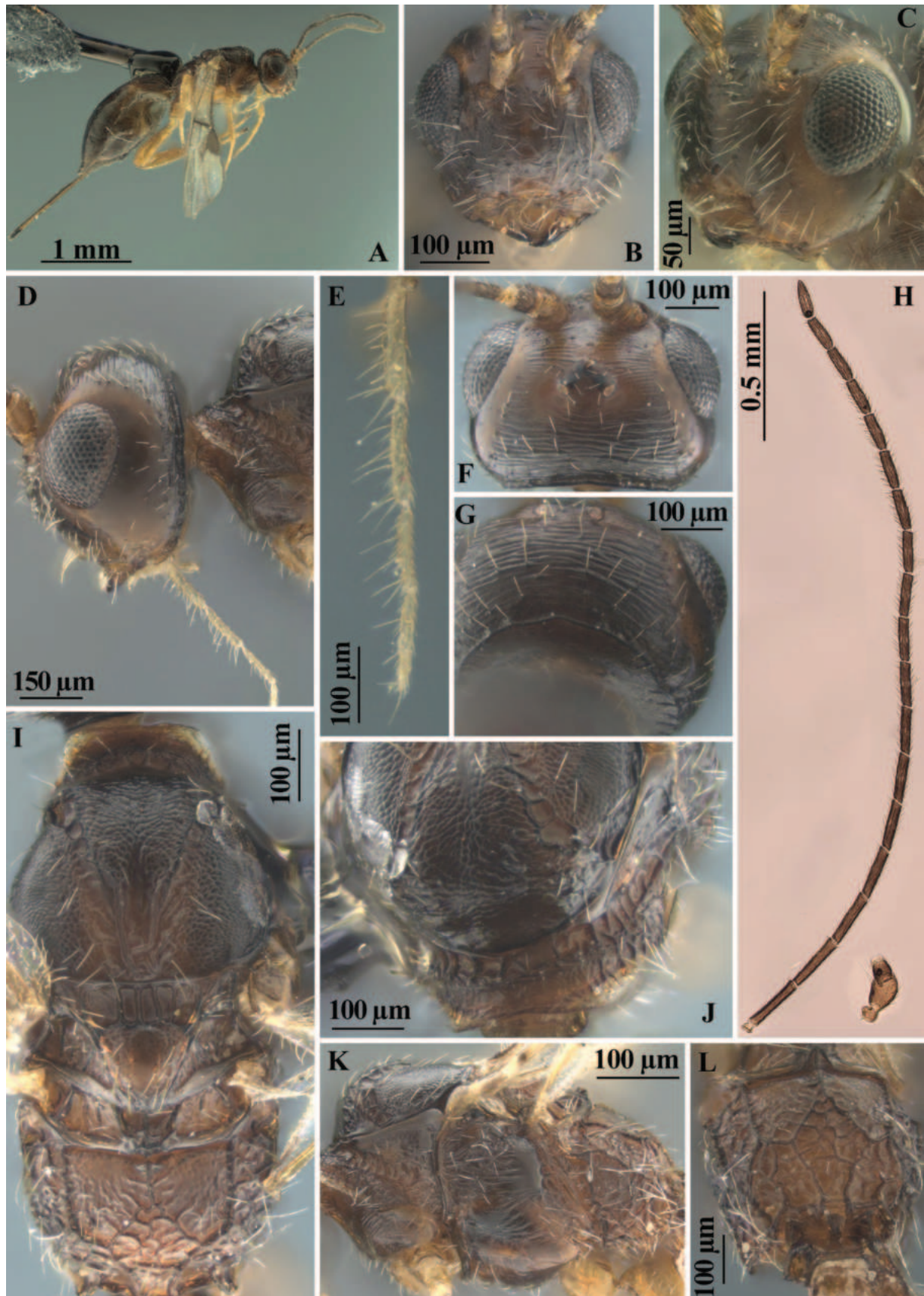


Figure 2. *Heterospilus sicanus* (Marshall, 1888) (female) **A** habitus, lateral view **B–D** head, frontal, antero-lateral and lateral view **E** maxillary palp **F, G** head, dorsal and postero-dorsal view **H** antenna **I** mesosoma, dorsal view **J** pronotum, antero-dorsal view **K** mesosoma, lateral view **L** propodeum, dorsal view.

Antennae. Antenna slender, filiform, 20-segmented, almost as long as body. Scape rather short and thick, 1.5× longer than its maximum width. First flagellar segment slender, almost straight, subcylindrical, 5.5× longer than apical width, almost as long as second segment. Penultimate segment 3.3× longer than wide, 0.6× as long as first segment, 0.9× as long as apical segment; the latter pointed apically and without spine.

Mesosoma. Mesosoma not depressed dorso-ventrally, its length 1.6× maximum height. Pronotal neck rather long, dorsally without convex lobe, with rather distinct submedial pronotal carina; side of pronotum with distinct, almost straight, and rather wide submedial oblique crenulate furrow. Mesoscutum highly and perpendicularly elevated above pronotum, maximum width of mesoscutum 1.3× its median length. Median lobe of mesoscutum (dorsal view) protruding forwards, weakly convex anteriorly, with distinct and almost pointed anterolateral corners. Notauli wide, rather deep, densely and coarsely crenulate. Prescutellar depression deep, wide, with 4 carinae, finely sculptured between carinae, ~ 0.3× as long as wide, 0.45× as long as scutellum. Scutellum convex, with fine lateral carinae, its width 1.1× median length. Subalar depression rather deep, wide, sparsely and coarsely rugose-striate. Precoxal sulcus deep, almost straight, rugulose, running along anterior 0.6 of lower part of mesopleuron. Metanotal tooth (lateral view) relatively long, wide, distinctly pointed apically. Metapleural lobe rather large, more or less wide, rounded posteriorly. Propodeum (lateral view) regularly convex-roundly slanted from base to apex, without lateral tubercles; propodeal spiracle small.

Wings. Fore wing 3.0× longer than its maximum width, 0.9× as long as body. Pterostigma 3.0× longer than wide. Radial vein (r) arising before middle of pterostigma, distance from base of pterostigma to radial vein (r) 0.85× distance from radial vein (r) to apex of pterostigma. Radial (marginal) cell not shortened. Metacarp (1-R1) 1.2× longer than pterostigma. First radial abscissa (r) almost as long as maximum width. Second radial abscissa (3-SR) as long as first abscissa (r), 0.25× as long as the straight third abscissa (SR1), 0.5× as long as trace of first radiomedial vein (2-SR). Trace of first radiomedial vein (2-SR) 2.3× longer than second radiomedial vein (r-m), 4.0× longer than recurrent vein (m-cu). Recurrent vein (m-cu) distinctly postfurcal. First medial abscissa (1-SR+M) curved. Discoidal (discal) cell 1.6× longer than its width. Distance (1-CU1) from nervulus (cu-a) to basal vein (1-M) ~ 0.5 of nervulus (cu-a) length; nervulus (cu-a) straight and almost perpendicular to longitudinal anal vein (1-1A). Mediocubital vein (M+CU1) almost straight. Parallel vein (CU1a) distinctly curved subbasally. Brachial (subdiscal) cell widely open distally, brachial vein (CU1b) absent. Hind wing 4.2× longer than wide. First abscissa of costal vein (C+SC+R) 1.2× longer than second abscissa (1-SC+R); second abscissa (1-SC+R) strongly sclerotised. Last costal abscissa (SC+R1) 0.8× as long as first (C+SC+R) and second (1-SC+R) abscissae combined. Radial vein (SR) strongly desclerotised. Medial (basal) cell narrow, almost parallel-sided in its apical half, its length ~ 11.0× maximum width, almost 0.3× length of wing. First abscissa of mediocubital vein (M+CU) 0.8× as long as second abscissa (1-M). Recurrent vein (m-cu) unsclerotised, almost interstitial, straight, very weakly oblique toward base of wing.

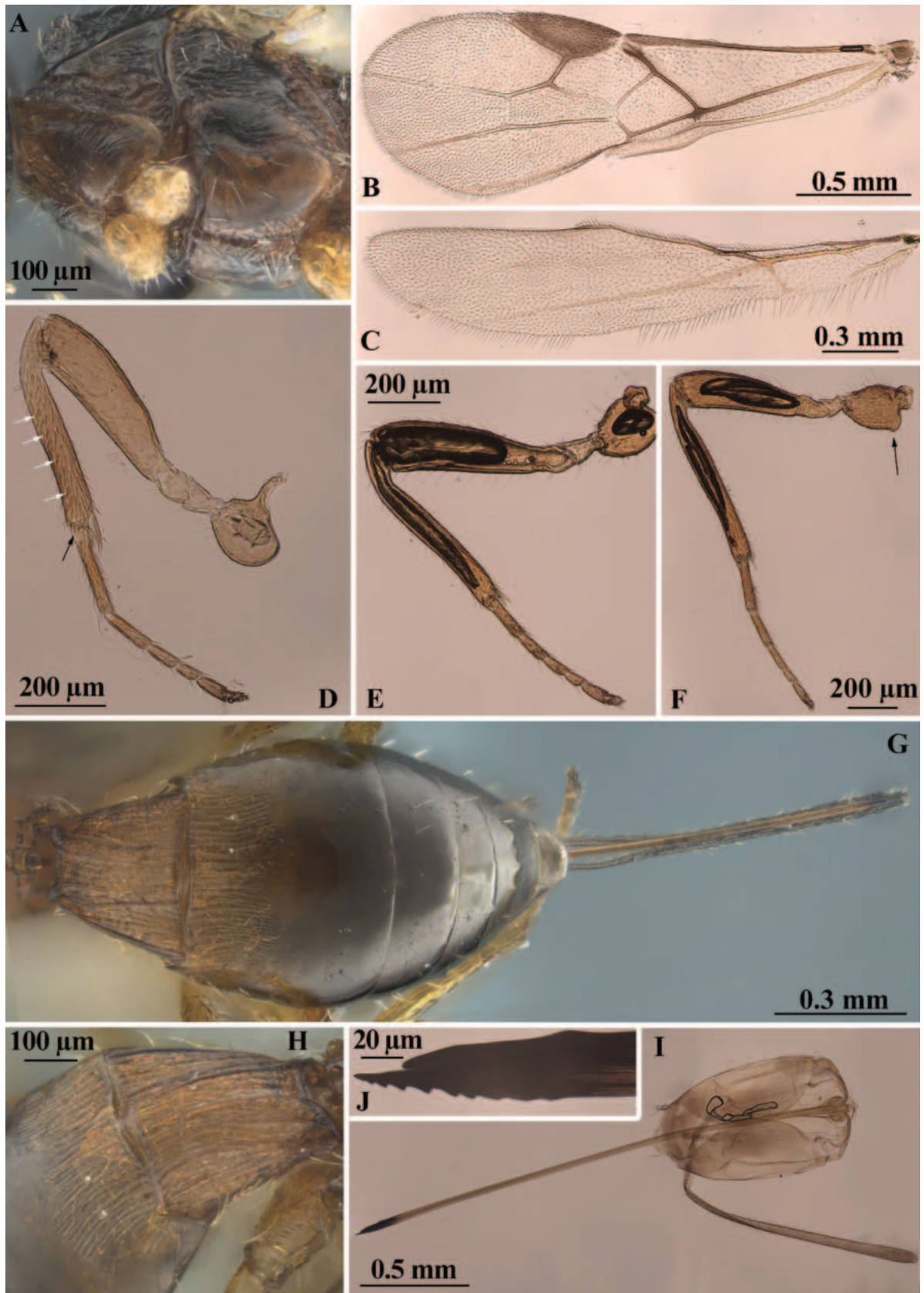


Figure 3. *Heterospilus sicanus* (Marshall, 1888) (female) **A** mesosoma, ventro-lateral view **B** fore wing **C** hind wing **D** fore leg (white arrows indicate short stout spines on its front tibia surface and black arrow those on the apical part) **E** middle leg **F** hind leg (black arrow indicates a distinct antero-ventral basal tubercle on the coxa) **G** metasoma, dorsal view **H** first tergite, dorso-lateral view **I** ovipositor and one of its sheaths **J** ovipositor apex.

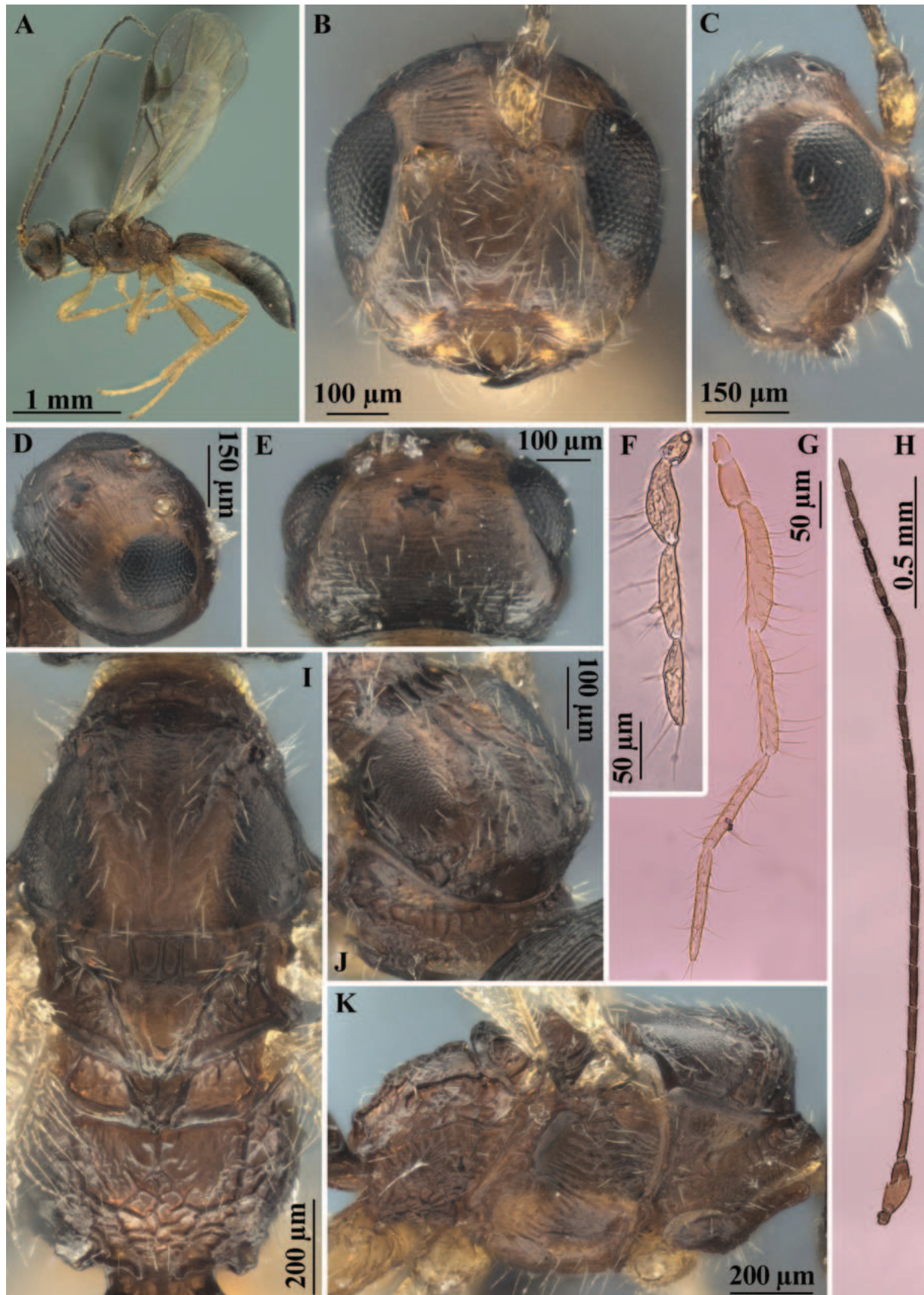


Figure 4. *Heterospilus sicanus* (Marshall, 1888) (male) **A** habitus, lateral view **B** head, front view **C** head, lateral view **D** head dorso-lateral view **E** head dorsal view **F** labial palpus **G** maxillary palpus **H** antenna **I** mesosoma, dorsal view **J** pronotum, antero-dorsal view **K** mesosoma, lateral view.

Legs. Fore tibia with several rather slender spines arranged in longitudinal line. Hind coxa with basoventral tubercle, 1.3× longer than its maximum width. Hind femur rather wide, without dorsal protuberance, 3.5× longer than wide. Hind tarsus 0.9× as long as hind tibia. Basitarsus not thickened, without ventral keel, 0.5× as long as second–fifth segments combined. Second tarsal segment 0.7× as long as basitarsus, 1.6× longer than fifth segment (without pretarsus).

Metasoma. Metasoma 0.9× as long as head and mesosoma combined, 1.8× longer than its maximum width. First segment with short acrosternite. First tergite with not high but rather distinct and wide median area, with distinct dorsope, without spiracular tubercles; tergite distinctly and almost linearly widened from base to apex. Length of first tergite equal to its apical width, 1.4× length of propodeum; maximum width of tergite ~ 2.0× its minimum width. Median length of second tergite 0.45× its basal width, 0.8× length of third tergite. Combined length of second and third tergites 0.9× basal width of second tergite, 0.7× their maximum width. Second suture present, but fine, usually weakly curved laterally. Third tergite without transverse furrow. Ovipositor sheath rather slender, 0.8× as long as metasoma, 1.1× longer than mesosoma, 0.4× as long as body, 0.5× as long as fore wing.

Sculpture and pubescence. Vertex entirely distinctly and rather densely transversely striate, partly with very fine additional reticulation between striae; frons entirely densely and distinctly transversely striate [face covered in glue]; temple smooth. Mesoscutum densely and distinctly granulate, medioposteriorly with two posteriorly convergent carinae. Scutellum granulate. Mesopleuron entirely rugose-striate. Metapleuron entirely distinctly rugose-reticulate. Propodeum with rather wide, short and finely granulate-coriaceous basolateral areas, weakly delineated by carinae; areola finely delineated; basal carina 0.8× as long as anterior fork of areola; posterior 0.7 of propodeum irregularly rugose-reticulate. Hind coxa densely granulate, transversely striate dorsally. Hind femur finely and densely granulate-coriaceous. First tergite with rather distinct and posteriorly convergent dorsal carinae, densely and distinctly longitudinally striate, with fine and dense additional reticulation between striae. Second tergite mostly distinctly longitudinally striate, laterally smooth over rather wide area, rugulose postero-medially. Remaining tergites smooth. Vertex almost entirely with rather dense, short and semi-erect setae arranged in rows. Mesoscutum with rather dense, relatively long and semi-erect pale setae at wide area along notauli and scattered across lobes, all lobes narrowly glabrous medially. Hind tibia dorsally with short, sparse, semi-erect setae; length of these setae ~ 0.3× maximum width of hind tibia.

Colour. Body reddish brown, vertex, mesonotum, and posterior half of metasoma dark reddish brown. Antenna dark brown, four basal segments pale brown. Palpi yellow. Legs entirely pale brown. Ovipositor sheath mainly brown, black apically. Fore wing very faintly infusate. Pterostigma almost entirely brown.

Variation. Head width 1.4–1.6× median length. Transverse diameter of eye 1.1–1.3× longer than temple (dorsal view). Malar space 0.6–0.7× height of eye. Hypoclypeal depression round, its width 0.7–0.8× distance from margin of depression to margin of eye, 0.4–0.5× width of face. Face mainly smooth. Antennae 20-segmented. First flagellar segment 4.5–5.5× longer than its apical width. Penultimate segment 3.0–3.3× longer than wide. Mesosoma length

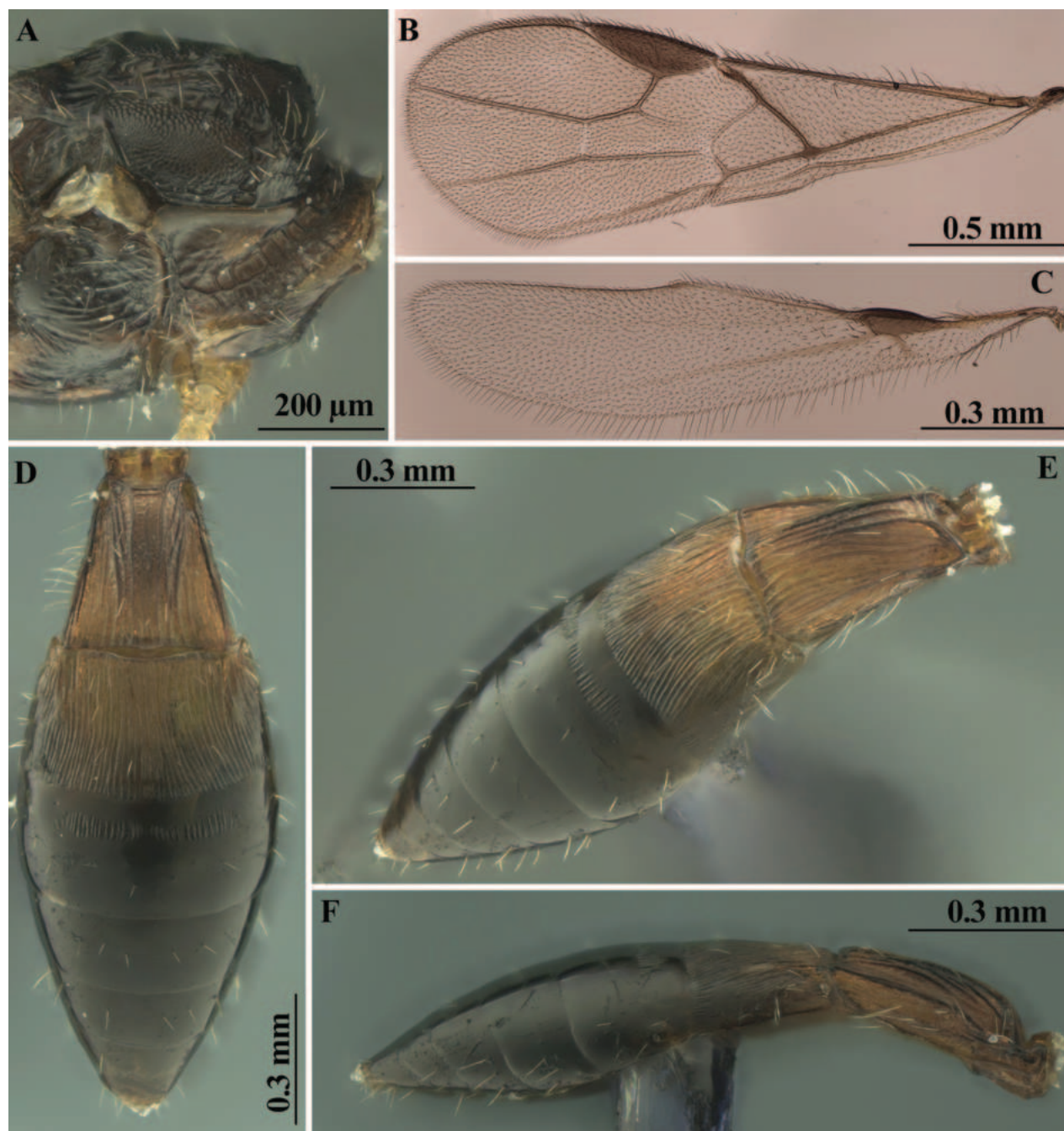


Figure 5. *Heterospilus sicanus* (Marshall, 1888) (male) **A** pronotum and propleuron, dorso-lateral view **B** fore wing **C** hind wing **D** metasoma, dorsal view **E** metasoma dorso-lateral view **F** metasoma, lateral view.

1.6–1.7× maximum height. Maximum width of mesoscutum 1.2–1.3× its median length. Mesopleuron sometimes smooth in small submedial area. Basal carina of propodeum 0.8–1.0× as long as areola anterior fork. Wings. Pterostigma 2.8–3.6× longer than wide. Second radial abscissa (3-SR) 1.0–1.3× as long as first abscissa (r), 0.25–0.30× as long as third abscissa (SR1), 0.5–0.7× as long as trace of first radiomedial vein (2-SR). Discoidal (discal) cell 1.6–1.8× longer than its width. Legs. Hind femur 3.5–3.8× longer than wide. Hind tibia dorsal setae 0.3–0.4× maximum width of hind tibia. First metasomal tergite 1.3–1.4× longer than propodeum. Median length of second tergite 0.40–0.45× its basal width, 0.7–0.8× length of third tergite. Ovipositor sheaths 0.7–0.9× as

long as metasoma, 1.1–1.2× longer than mesosoma. Body mainly dark reddish brown, sometimes ventrally distinctly paler. Legs entirely pale brown or yellow, anterior half of metasoma often yellow or pale reddish brown. Fore wing very faintly infusate. Pterostigma brown or pale brown.

Male. Body length 2.6–2.8 mm; fore wing length 2.1 mm. Antennae slender, filiform, 21-segmented, approximately as long as body. Hind wing with relatively small, complex, brown stigma-like enlargement, its length 0.7–0.8× distance from base of wing to base of enlargement. Length of first metasomal tergite 1.1× its apical width. Second tergite entirely striate. Median length of second tergite 0.75× its anterior width, 1.2× length of third tergite. Third tergite with shallow and crenulate transverse furrow in anterior one-third. Body mainly brown to dark brown, anterior third of metasoma paler. Otherwise similar to female.

Host. Until recently, the only reported host of this species was *Cryphalus piceae* (Ratzeburg, 1837) (Coleoptera, Curculionidae, Scolytinae) (Tobias 1971; Kenis et al. 2004; Wegensteiner et al. 2015). However, the first author checked material assigned to this species deposited in the collection of the Zoological Institute RAS (St Petersburg, Russia) determined by Dr V. I. Tobias as *H. sicanus* (Marshall) (Tobias 1971). This sample comprised seven females and ten males with the label: “Teberda, Sev. Kavkaz [North Caucasus, Karachay-Cherkess Republic], on *Cryphalus piceae*, T. Guryanova [leg], 24 VI [19]64”, “*Dendrosotinus sicanus* Marsh., Tobias det. 1965”. Our redetermination of these specimens showed that they actually belong to another genus and species, *Dendrosotinus (Gildoria) similis* Boucek, 1955. Thus, the host of *H. sicanus* was unknown before this study and *Gastrallus pubens* Fairmaire, 1875 (Coleoptera, Anobiidae) is the first and only known host of *H. sicanus*.

Distribution. According to Taxapad, the world catalogue of Ichneumonoidea (Yu et al. 2016), besides Italy (Sicily), *H. sicanus* has also been recorded in Spain (Falco Gari et al. 1993), Croatia (Papp 1977), Serbia (Brajkovic 1989), and Hungary (Papp 1984); however, at least some of these records require confirmation. In Russia, this species has only been found in Crimea (new record; see ‘Additional material examined’), whereas its records from the North Caucasus of Russia (Tobias 1971, 1976) were erroneous (for details see ‘Remarks’ under the ‘Hosts’ section).

Comparative diagnosis. *Heterospilus sicanus* (Marshall) is very similar to *H. corsicus* (Marshall, 1888), but differs from the latter by having the head behind the eyes convex anteriorly and roundly narrowed posteriorly (evenly roundly narrowed posteriorly in *H. corsicus*), eyes setose, transverse diameter in dorsal view 1.1–1.3× length of temple (glabrous, transverse diameter 1.5–1.6× length of temple in *H. corsicus*), antenna slender (thickened in *H. corsicus*), mesosoma 1.6–1.7× longer than its height (1.8× in *H. corsicus*), medial lobe of mesoscutum without pointed anterolateral corners (with pointed corners in *H. corsicus*), radial vein (r) of fore wing arising slightly before middle of pterostigma (almost from or behind middle in *H. corsicus*), setae on dorsal side of hind tibia short, ~ 0.3× as long as maximum width of tibia (long, 0.5–0.7× in *H. corsicus*), and pterostigma almost entirely brown (yellow in *H. corsicus*).

Western Palaearctic *Heterospilus* species with an almost entirely sculptured vertex can be differentiated using the key below.

***Heterospilus corsicus* (Marshall, 1888)**

Fig. 6

Telebolus corsicus Marshall, 1888: 202.

Heterospilus corsicus: Shenefelt and Marsh 1976: 1303; Yu et al. 2016.

Caenophanes cingulatus Szépligeti, 1900: 213.

Heterospilus cingulatus: Shenefelt and Marsh 1976: 1302; Belokobylskij and Tobias 1986: 33 (as synonym); Yu et al. 2016.

Type material examined. *Holotype of Telebolus corsicus*: female, France (Corsica), "Type" (round with red border), "Corsica", "B.M. Type Hym. 3c.188", "*corsicus* Marsh.", "Marshall coll. 1904–120.", "B.M. Type Hym. *Telebolus corsicus* Marshall 1888". "NHMUK010880788" (NHMUK, London). *Holotype of Caenophanes cingulatus*: female, "Szóváta, Csiki", "Transsylvania", "Holotypus ♀ *Caenophanes cingulatus* Szép., 1900 sp. n. / des/ Papp J. 1967", "Hym. Typ. N 598. Museum Budapest", "*Heterospilus cingulatus* Sz., det. Papp J., 1983" (HNHM).

Redescription. Female (holotype). Body length 2.6 mm; fore wing length 1.8 mm.

Head. Head not depressed, its width 1.5× median length, 1.3× width of mesoscutum. Head behind eyes evenly and roundly narrowed. Transverse diameter of eye 1.6× longer than temple (dorsal view). Ocelli small, in almost equilateral triangle. POL almost equal to Od, 0.4× OOL. Diameter of antennal socket 1.3× distance between sockets, 1.8× distance between socket and eye. Eye without setae, with shallow emargination opposite antennal sockets, 1.2× as high as broad. Malar space 0.5× height of eye, 1.3× basal width of mandible. Face convex, its width 1.15× height of eye and 1.3× height of face and clypeus combined. Malar suture absent. Clypeus with short lower flange. Hypoclypeal depression rather small and suboval, its width 0.7× distance from edge of depression to eye, 0.35× width of face. Occipital carina complete dorsally, joining hypostomal carina ventrally distant from upper base of mandible. Head below eyes distinctly and weakly-roundly narrowed. Hypostomal flange distinct but narrow.

Antenna. Antenna weakly thickened, filiform, 21-segmented, slightly longer than body. Scape rather long and thick, 1.5× longer than its maximum width. First flagellar segment weakly thickened, weakly curved, subcylindrical, 4.5× longer than its apical width, almost as long as second segment. Penultimate segment 2.7× longer than wide, 0.6× as long as first segment, 0.9× as long as apical segment; the latter pointed apically and without spine.

Mesosoma. Mesosoma not depressed, its length 1.8× maximum height. Pronotal neck rather long, dorsally weakly convex, but without convex lobe and pronotal carina; side of pronotum with rather shallow, weakly curved and wide submedian oblique and sparsely crenulate furrow. Mesoscutum highly and roundly elevated above pronotum (lateral view), maximum width of mesoscutum 1.3× its length (dorsal view). Median lobe of mesoscutum (dorsal view) weakly protruding forwards, without anterolateral corners, distinctly convex anteriorly. Notauli rather narrow, deep, sparsely and finely crenulate. Prescutellar depression deep, long, with median carina, finely and irregularly sculptured, 0.5× as long as wide, 0.55× as long as scutellum. Scutellum convex, with fine lateral carinae, its basal width almost equal to median length. Subalar depression rather deep, wide, sparsely and coarsely striate. Precoxal sulcus rather deep, almost

straight, distinctly crenulate, running along anterior 0.6 of lower part of mesopleuron. Metanotal tooth (lateral view) rather long, wide, more or less pointed apically. Metapleural lobe rather long, more or less wide, rounded apically. Propodeum (lateral view) regularly convex-roundly slanted from base to apex, without lateral tubercles; propodeal spiracle small.

Wings. Fore wing 3.5× longer than its maximum width, 0.7× as long as body. Pterostigma 3.5× longer than wide. Radial vein (r) arising almost from middle of pterostigma, distance from base of pterostigma to radial vein (r) almost equal to distance from radial vein (r) to apex of pterostigma. Radial (marginal) cell not shortened. Metacarp (1-R1) 1.3× longer than pterostigma. First radial abscissa (r) 0.75× as long as maximum width of pterostigma. Second radial abscissa (3-SR) twice longer than first abscissa (r), 0.35× as long as the straight third abscissa (SR1), 0.7× as long as the trace of first radiomedial vein (2-SR). Trace of first radiomedial vein (2-SR) 2.2× longer than second radiomedial vein (r-m), 2.2× longer than recurrent vein (m-cu). Recurrent vein (m-cu) postfurcal. First medial abscissa (1-SR+M) almost straight. Discoidal (discal) cell 1.6× longer than wide. Nervulus (cu-a) almost interstitial, straight and subperpendicular. Mediocubital vein (M+CU1) almost straight. Parallel vein (CU1a) very weakly curved subbasally. Brachial (subdiscal) cell widely open distally, brachial vein (CU1b) absent. Hind wing with 5.5× longer than wide. First abscissa of costal vein (C+SC+R) 1.5× longer than second abscissa (1-SC+R); second abscissa (1-SC+R) strongly sclerotised. Last costal abscissa (SC+R) 0.75× as long as first (C+SC+R) and second (1-SC+R) abscissae combined. Radial vein (SR) very strongly desclerotised. Medial (basal) cell narrow, almost parallel-sided to weakly narrowed in apical half, its length 8.5× maximum width, ~ 0.3× length of wing. First abscissa of mediocubital vein (M+CU) almost as long as second abscissa (1-M). Recurrent vein (m-cu) unsclerotised, almost interstitial, straight, distinctly oblique toward base of wing.

Legs. Fore tibia with several slender spines arranged in narrow stripe. Hind coxa with basoventral tubercle, ~ 1.4× longer than its maximum width. Hind femur relatively narrow, without dorsal protuberance, 4.0× longer than wide. Hind tarsus 0.9× as long as hind tibia. Basitarsus not thickened, without ventral keel, 0.5× as long as second–fifth segments combined. Second tarsal segment 0.7× as long as basitarsus, 1.3× longer than fifth segment (without pretarsus).

Metasoma. Metasoma 0.9× as long as head and mesosoma combined, almost twice as long as its maximum width. First tergite with rather high and wide median area, with small dorsope, without spiracular tubercles; tergite strongly and almost linearly widened from anterior to posterior apex. Length of first tergite 0.85× its apical width, a little larger than length of propodeum; maximum width of tergite 2.5× its minimum width. Median length of second tergite 0.4× basal width of second tergite, 0.7× length of third tergite. Combined length of second and third tergites 0.9× basal width of second tergite, 0.7× their maximum width. Second suture distinct, distinctly curved laterally. Third tergite without sculptured transverse furrow. Ovipositor sheaths 0.8× as long as metasoma, 1.1× longer than mesosoma, 0.4× as long as body, 0.6× as long as fore wing.

Sculpture and pubescence. Vertex rather finely and densely transversely striate with additional rugulosity between striae; frons mostly finely and densely transversely striate. Face mainly smooth, rugose medially; temple finely striate above, but mostly smooth. Mesoscutum densely and rather finely granulate, with two carinae medioposteriorly. Scutellum finely granulate. Mesopleuron entirely finely

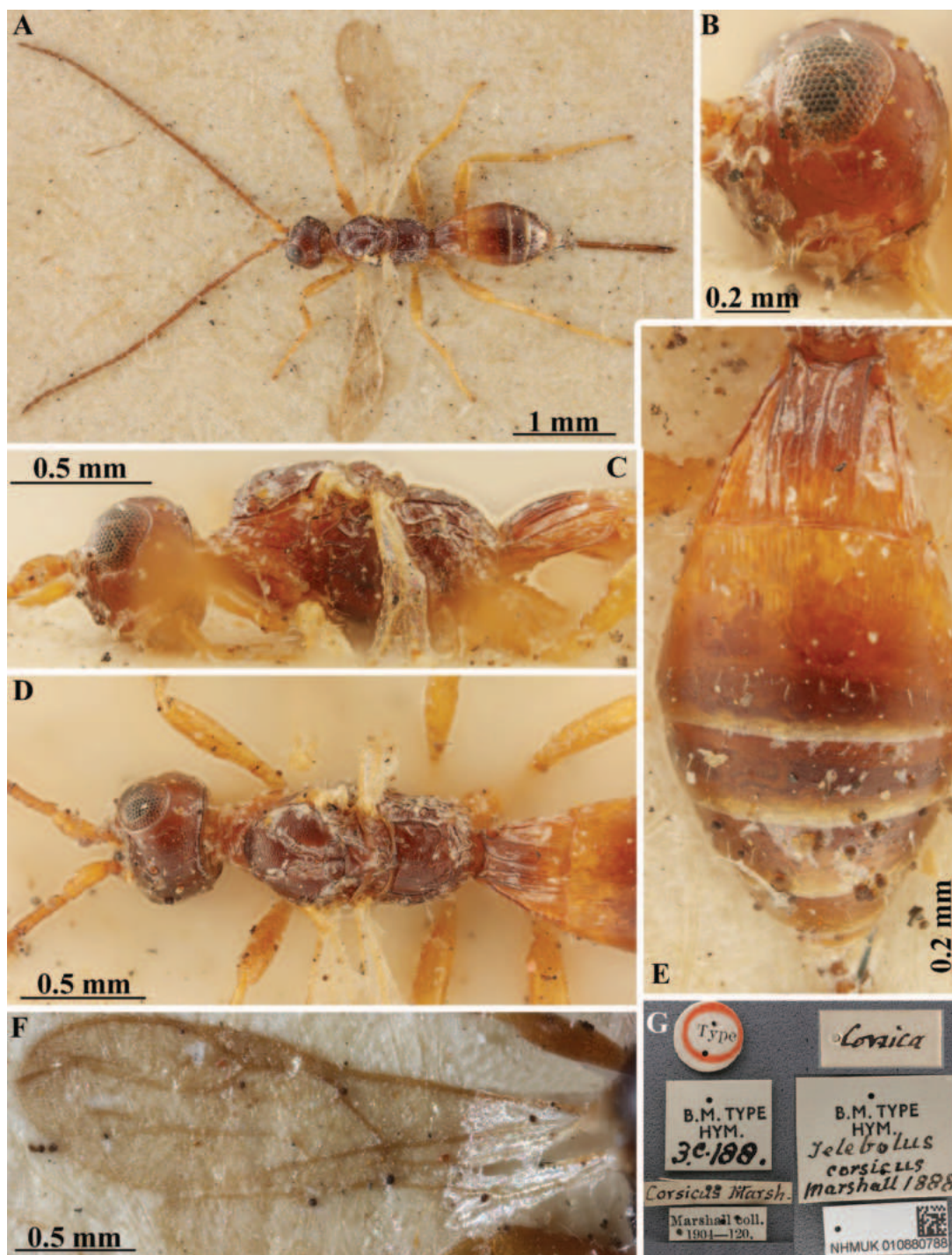


Figure 6. *Heterospilus corsicus* (Marshall, 1888) (female, holotype) **A** habitus, dorsal view **B** head, lateral view **C** head, mesosoma and base of metasoma, lateral view **D** head, mesosoma and base of metasoma, dorsal view **E** metasoma, dorsal view **F** wings **G** labels.

reticulate-granulate. Metapleuron entirely and rather distinctly rugose-reticulate. Propodeum with rather wide and finely granulate-coriaceous basolateral areas, distinctly delineated by carinae; areola indistinctly delineated by carinae; basal carina relatively long, 0.8× as long as anterior fork of areola; posterior 0.7 of propodeum coarsely and irregularly rugose-reticulate. Hind coxa densely granulate, coarsely transversely striate dorsally. Hind femur finely coriaceous. First tergite with rather distinct and convergent posteriorly dorsal carinae, distinctly longitudinally striate,

with very fine, partly indistinct ground sculpture. Second tergite entirely densely and distinctly longitudinally striate. Remaining tergites smooth. Vertex partly with rather sparse and relatively long setae, almost glabrous medially. Mesoscutum with sparse, rather long and semi-erect pale setae arranged almost in one line along notauli and marginally, all lobes widely glabrous medially. Metapleuron widely glabrous medially. Hind tibia dorsally with relatively long, sparse and semi-erect setae; length of these setae 0.5–0.7× maximum width of hind tibia.

Colour. Body dark reddish brown, almost black; pronotum pale reddish brown; first (except its dark medio-anterior half), second and anterior half of third metasomal tergites pale brown with reddish tint. Antenna dark reddish brown, paler basally. Palpi yellow. Legs pale brown. Ovipositor sheath almost black. Fore wing faintly infusate. Pterostigma yellow.

Distribution. France (Corsica), Italy, Hungary, Romania, Bulgaria, Moldova, Crimea (Yu et al. 2016).

Remarks. The records of this species for Lithuania, Kazakhstan, Korea, and the Russian Far East by Belokobylskij and Tobias (1986) were erroneous due to the unclear understanding of this species before the study of the holotype.

Host. Unknown.

Key to the Western Palaearctic species of *Heterospilus* with distinctly sculptured vertex

- 1 Metasoma behind third tergite striate anteriorly on fourth or fourth and fifth tergites **2**
 - Metasoma entirely smooth behind third tergite; often third tergite also smooth **6**
- 2 Fore wing strongly shortened, reaching at maximum to middle of metasoma; wing venation in distal half of fore wing strongly reduced. [Europe (rarely), Turkey, Iran, Mongolia]
 - H. hemipterus* (Thomson, 1892) (*Lituania brachyptera* Jakimavicius, 1968)**
 - Fore wing not shortened, complete, prolonged behind posterior end of metasoma; wing venation in distal half of fore wing complete as usual for *Heterospilus* **3**
- 3 First metasomal tergite relatively long, its length not less than posterior width. Often only fourth tergite striate anteriorly. Vertex often less distinctly striate. Body slender and slim **4**
 - First metasomal tergite short, its length distinctly shorter than posterior width. Fourth and fifth tergites always striate anteriorly. Vertex distinctly and coarsely transversely striate. Body robust **5**
- 4 Second tergite shorter, its medial length ~ 0.3× anterior width. Sculpture of first two tergites distinctly striate, less infilled with rugosity. Ovipositor projecting just more than 0.6× length of metasoma, just more than 1.1× length of hind tibia. Body predominantly reddish brown. [Europe, Russia (widely), western and central Asia, China, Korea, Japan] ***H. leptosoma* Fischer, 1960**
 - Second tergite longer, its medial length ~ 0.4× anterior width. Sculpture of first two tergites less regular, more rugulose. Ovipositor shorter, projecting 0.3–0.5× length of metasoma, 0.7–1.1× length of hind tibia. Body usually extensively dark. [UK, Sweden, China (?)] ***H. fuscexilis* M. Shaw, 1997**

- 5 Ovipositor sheaths distinctly shorter than metasoma, 0.4–0.6× as long as metasoma. Body often predominantly brownish yellow or light reddish brown. [Holarctic]
***H. cephi* Rohwer, 1925 (*H. testaceus* Telenga, 1941; *H. rubicundus* Fischer, 1960; *Rhaconotus ollivieri* (Giraud) var. *flava* Fahringer 1931, syn. nov.)**
- Ovipositor sheaths slightly shorter than or almost equal to metasoma, 0.7–1.0× as long as metasoma. Body often predominantly reddish brown to light reddish brown with often dark propodeum and first metasomal tergite. [Europe, Russia (widely), Turkey, Israel, Iran, Kazakhstan, Mongolia, China, Korea, Japan].....
 ***H. tauricus* Telenga, 1941 (*H. graeffei* Fischer, 1960)**
- 6 Second metasomal tergite striate only on its anterior one–third or quarter. Suture between second and third tergites absent. Mesopleuron smooth over wide median area. [Portugal (Madeira), Israel, Russia (Crimea)].....
 ***H. divisus* (Wollaston, 1858)**
- Second metasomal tergite striate or striate-rugulose over anterior fourth–fifths or entirely. Suture between second and third tergites present but sometimes rather weak. Mesopleuron usually rugose-reticulate over wide median area **7**
- 7 Head behind eyes (dorsal view) weakly convex in anterior half and roundly narrowed in posterior half; transverse diameter of eye 1.1–1.3× longer than temple. Mesosoma 1.5–1.6× longer than maximum height. Medial lobe of mesoscutum without or with indistinct anterolateral corners. Radial vein (r) of fore wing arising before middle of pterostigma. [Spain, Italy, Croatia, Hungary, Russia (Crimea)] ***H. sicanus* (Marshall, 1888) (*Atoreuteus ceballosi* Docavo Alberti, 1960, syn. nov.)**
- Head behind eyes (dorsal view) evenly and rather distinctly roundly narrowed; transverse diameter of eye 1.5–2.0× longer than temple. Mesosoma 1.8–2.0× longer than maximum height. Medial lobe of mesoscutum usually with distinct pointed anterolateral corners. Radial vein (r) of fore wing arising from or slightly behind middle of pterostigma **8**
- 8 Malar space 0.5–0.6× height of eye, 1.2–1.3× basal width of mandible. Occipital carina ventrally joining hypostomal carina. Precoxal sulcus distinctly crenulate. Second segment of hind tarsus 1.3–1.5× longer than fifth segment (without pretarsus). Third metasomal tergite without transverse furrow. Mesopleuron entirely reticulate-granulate. Basal carina of propodeum relatively long. Pterostigma yellow or light brown. [France (Corsica), Italy, Hungary, Romania, Bulgaria, Moldova, Ukraine] ***H. corsicus* (Marshall, 1888) (*Caenophanes cingulatus* Szépligeti, 1900)**
- Malar space 0.4× height of eye, equal to basal width of mandible. Occipital carina obliterated below and not joining hypostomal carina ventrally. Precoxal sulcus smooth. Second segment of hind tarsus almost 2.0× longer than fifth segment (without pretarsus). Third metasomal tergite with crenulate transverse furrow in anterior one–third. Mesopleuron smooth over lower three–fifths. Basal carina of propodeum very short. Pterostigma brown. [Spain] ***H. marchi* (Docavo Albert, 1960)**

Discussion

The species *Dendrosoter sicanus* Marshall, 1888 and *Telebolus corsicus* Marshall, 1888 both actually belonging to the genus *Heterospilus*, were described in the same year and in the same book (Marshall 1888) and have never subsequently been redescribed or compared with each other. The diagnostic characters of these species were relatively badly designated and the reliable determination of these taxa as well as stable differences between the species subsequently caused certain difficulties. This study with illustrated redescrptions of the type material, together with the preparation of a key for determination of the European *Heterospilus* species with a sculptured vertex, should help to avoid errors in their identification.

The holotype (female) of *Atoreuteus ceballosi* Docavo Albert, 1960, studied by the first co-author in MNCN (Madrid, Spain), is morphologically very similar to *H. sicanus* (Marshall, 1888), which allowed us to synonymise the first name under the second as a new synonym. Also in the same Museum (MNCN), the holotype of *Atoreuteus* (= *Heterospilus*) *marchi* Docavo Albert, 1960, described from Spain (female, with labels "Barcelona, 27.V.1896", "♀", "*Atoreuteus marchi* Docavo n. sp.", "Holotip", "*Heterospilus* ? *tauricus* Tel., det. Papp J., 1983", "MNCN Cat. Typos N 11.489"), was examined, which helped us to evaluate the status of this species as closely related to *H. corsicus* (Marshall, 1888). The first co-author has also studied the single specimen (female) in NHMW (Wien, Austria) of the form *Hormiopterus* (= *Rhaconotus*) *ollivieri* Giraud var. *flava* Fahringer 1931 (Fahringer 1931; Shenefelt and Marsh 1976) (with labels: "*Hormiopterus ollivieri* (sic!) Gr. var *flava* m." (handwriting by Fahringer), "ollivieri (sic!) Fer. (sic!), det. Fahringer", but without any geographic information), which turned out to be a new junior synonym of *Heterospilus cephi* Rohwer, 1925.

The discovery of *H. sicanus* in the frass, holes, and tunnels of rare books damaged by *Gastrallus pubens* Fairmaire (Coleoptera: Ptinidae), with its illustrated redescription and updated diagnosis, and its comparison with the morphologically similar *H. corsicus* sheds light on these rare and barely studied doryctine species. The inclusion of digital photographs and the key for determination of the Western Palaearctic species of *Heterospilus* with distinctly sculptured vertex have also helped to improve the precise species identification of these taxa. This accurate identification of parasitoids is crucial for effective and sustainable pest management programmes. In fact, *Heterospilus sicanus* could be a potential biological control agent against *G. pubens*, which is an emerging threat to librarians and archivists in Italy and across Europe given the destructive larval activity of the beetles, which causes serious damages to books, especially ancient.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: EP, CJ, GC, SS, SAB, SG, GRRB. Data curation: SAB. Investigation: GC, GRRB, SAB, CJ, SG, SS, EP. Methodology: EP, SS, SG, GRRB, GC, SAB. Supervision: SS, CJ. Writing - original draft: GC, SAB, SG. Writing - review and editing: GRRB, SS, CJ, EP.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Checklist of hosts, illustrated geographical range, and ecology of tick species from the genus *Ixodes* (Acari, Ixodidae) in Russia and other post-Soviet countries

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Abstract

Hard ticks (Acari: Ixodidae) are the economically and ecologically most important blood-sucking arthropod vectors that can transmit disease agents under temperate climate. In this group, the highest number of species (currently nearing 270) belongs to the genus *Ixodes*. For this review, more than 400 papers related to this genus in the context of Russia were checked for data on the host records, locations of collection, as well as ecology of assigned tick species. This monograph compensates for the lack of a similarly comprehensive English-language overview of *Ixodes* species in the region of Russia for nearly half century, and also makes a large set of data easily available for international readers, which is especially important if the original source is difficult to access from outside this country. In addition, the data from a significant number of papers on this topic available only in the Russian language are made accessible through this work.

Key words: Acari, Aves, Ixodidae, Mammalia, Reptilia, subgenus, taxonomy



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Introduction

Russia is the largest country of the globe, covering nearly one third of the territory of Eurasia and 1/8th of the entire Earth's landmass. It belongs to the Palearctic Zoogeographic Region (Guglielmo et al. 2023). The ecosystems of Russia are very diverse, including polar deserts, tundra, forest tundra, taiga, mixed and broad-leaved forests, forest steppe, steppe, semi-desert, and subtropics. At least 1100 species of terrestrial vertebrates are known to occur in this country, of which 65% of the territory is considered virtually untouched by economic and other human activities (CBD 2023).

With such a vast area, the broad spectrum of suitable habitats and vertebrate hosts in the background, the tick fauna of Russia was extensively studied. Although there was an enormous collection of data published in English (Anastos 1957), because it is more than half a century old, it is outdated. Moreover, the most well-known source describing the taxonomic diversity of Ixodidae Koch in this country and its nearby regions was compiled decades ago (Filippova 1977;

1997), and is only available in the Russian language. This book on ixodid species in Russia included 34 *Ixodes* Latreille species, which is updated to 37 by adding species with more recent data, as exemplified by *Ixodes prokopjevi* Eme-lyanova and *I. ghilarovi* Filippova & Panova, as well as *I. turdus* Nakatsudi with its first and single record (Bolotin and Kolonin 1979). Recent work has also been published including a list of hard tick species known to be indigenous in Russia (Guglielmone et al. 2023) with indications of tick species of other post-Soviet countries. However, the latter does not consider their specific locations or host records and various distinctive features of biology relevant to certain regions. Less studied species (some often known exclusively from these territories by single or a limited number of findings) are also reviewed here in more detail, in particular with the addition of precise data on their type specimens.

The need was recognized for a comprehensive work that would contain data and references from the last decades, written in English, which would thus be accessible by experts and anyone interested in the current ixodid fauna and its supportive hosts in the vast geographical and biotope range of Russia, as well as several other post-Soviet territories. In this review the authors tried to compensate for this scarcity of fresh information on hard ticks occurring in Russia and former states of the Soviet Union, targeting the most species-rich genus, *Ixodes*. Although the checklist and georeferenced data might still contain gaps, this work is also intended to be used as baseline data for the unfolding quest to discover and to describe not-yet-known ixodid species in this extensive geographical range.

Materials and methods

The relevance of publications used in this review was searched in databases using the keywords of *Ixodes* species, their hosts, and locality or region. The following databases were used: Library of the Russian Academy of Sciences (including its department at the Zoological Institute of the Russian Academy of Sciences), Springer Link, Web of Science, Zoological Record, Google Scholar, and CyberLeninka – the Russian scientific electronic library. However, a limited number of works was excluded from consideration and inclusion in the review due to the absence of scientific background and/or indeterminate data. Similarly, papers with repetitive data (i.e., not adding new tick-host associations, geographical locations to existing literature data) are not cited.

The same databases were used for searching and estimating the data on *Ixodes* from the post-Soviet territories, reviewed in this checklist: Russia, Belarus, Ukraine, Moldova, Georgia, Azerbaijan, Armenia, Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, and Tajikistan. The Baltic states (Estonia, Latvia, and Lithuania) were excluded from the consideration due to the availability of recently updated tick checklists, as well as the well-studied tick fauna (Paulauskas et al. 2010; Kitrytė and Baltrūnaitė 2023), which is also very similar to the tick fauna of neighboring Belarus and northwestern Russia.

Within Prostriata (genus *Ixodes*), tick species names are arranged according to their subgenera and are used sensu Guglielmone et al. (2014). The Latin names of tick species are written according to Guglielmone et al. (2023). The only exception is *Ixodes filippovae* Černý which we consider a synonym of *Ixodes crenulatus* Koch according to Filippova (1958a, 1977). The names of host species are written in accordance with their international English names, as well as the current

Latin names using the online databases, such as ASM Mammal Diversity Database (<https://www.mammaldiversity.org/index.html>) as well as Avibase (<https://avibase.bsc-eoc.org/>) and Reptile Database (<http://www.reptile-database.org/>).

Systematics

Class Arachnida

Order Ixodida

Family Ixodidae Koch, 1844

Genus *Ixodes* Latreille, 1795

Subgenus *Ceratixodes* Neumann, 1902: 115

Ixodes uriae White, 1852

Ixodes uriae White, 1852: 208.

Ixodes jacksoni Hoogstraal, 1967: 37.

Ixodes fimbriatus Kramer & Neumann, 1883: 527; Neumann 1911: 29.

Ixodes borealis Kramer & Neumann, 1883: 526; Neumann 1911: 29.

Ixodes hirsutus Birula, 1895: 353; Arthur 1963: 152.

Ixodes putus (Pickard-Cambridge, 1876): 260; Neumann 1899: 125; Schulze 1938: 12.

Ixodes putus procellariae Schulze, 1930: 123; Zumpt 1952: 12.

Recorded hosts. Aves: auks - birds of the family Alcidae, namely: *Alca torda* Linnaeus (razorbill), *Cephus grylle* Linnaeus (black guillemot), *Fratercula arctica* Linnaeus (common puffin), *Uria aalge* (Pontoppidan) (common guillemot), *Uria lomvia* Linnaeus (Brünnich's guillemot) (Filippova 1977).

Occasional hosts include *Fratercula cirrhata* (Pallas) (tufted puffin) and also various species of gulls and kittiwakes (Laridae): *Rissa brevirostris* (Bruch) (red-legged kittiwake), *R. tridactyla* (Linnaeus) (black-legged kittiwake) (Karpovich 1970; Dietrich et al. 2012), as well as fulmars (Procellariidae) – *Fulmarus glacialis* Linnaeus (northern fulmar) and cormorants (Phalacrocoracidae) – *Phalacrocorax capillatus* (Temminck and Schlegel) (Japanese cormorant), *Urile pelagicus* (Pallas) (pelagic cormorant), *Urile urile* (Gmelin) (red-faced cormorant) (Lvov et al. 1972b, 1975; Filippova 1977; Dietrich et al. 2012; Duron et al. 2014). A single atypical case of parasitism on *Motacilla alba* Linnaeus (white wagtail) (Motacillidae) was also reported (Karpovich 1970).

Recorded locations (Fig. 1). Murmansk seacoast (Russia): islands and sea-shores of the White Sea and also the Barents Sea (Karpovich 1971), namely: the Kuvshin Island and Kharlov Island (Karpovich 1970), Podpakhta Bay (Bekleshova et al. 1970), Dvorovaya Bay (Flint and Kostyko 1967), Seven Islands Reserve (Belopolskaya 1952; Karpovich 1973). **The Far East (Russia):** Mosolova Bay (the northern coast of the Strait of Tartary) (Savitskaya 1975), Bering Island (Lvov et al. 1975; Dietrich et al. 2012), Ptichy Island and Starichkov Island (Dietrich et al. 2012), Iony Island (Lvov et al. 1975), Kuril Islands (Lvov et al. 1975; Dietrich et al. 2012), Tyuleniy Island (Karpovich 1971; Lvov et al. 1972a; Filippova 1977), Sakhalin (Lvov et al. 1972a), Commander Islands (Dietrich et al. 2012).

Ecology and other information. *Ixodes uriae* is the only representative of the subgenus *Ceratixodes* in the tick fauna of Russia and the northern hemisphere



Figure 1. Map of Russia and neighboring countries showing the locations where *Ixodes uriae* was reported.

in general. As a nidicolous parasite of seabirds living in colonies, it is a species with a circumpolar distribution, occurring on oceanic coasts and islands of both the northern and southern hemispheres, from the polar regions to the subtropical zone (Wilson 1967; Filippova 1977).

In the northern hemisphere, this tick species is strongly associated with seabirds of the family Alcidae. The high degree of nest conservativity of these birds contributes to supporting a considerable number of ticks in bird colonies, which use the same places for many years (Karpovich 1971). The occasional hosts of *I. uriae* usually become involved in its life cycle in mixed bird colonies, where nests of typical and atypical hosts are located very close to each other (Violovich 1962b). In absence of auks, it may also use, for example, cormorants as exclusive hosts, as reported on the Kuril Islands (Lvov et al. 1975; Dietrich et al. 2012). In the southern hemisphere it was noted that penguins (Spheniscidae) are more typical hosts; this can be explained by similarities in the habits of these birds to those of puffins and guillemots.

There were noted rare records of adults from Carnivora: Mustelidae, and nymphs from Rodentia: Muridae (Eley 1977; Jaenson and Jensen 2007; Baggs et al. 2011; Guglielmone et al. 2020) and even humans (Karpovich 1971; Keirans and Lacombe 1998; Martyn 1998; Smith et al. 2006; Jaenson and Jensen 2007).

Subgenus *Eschatocephalus* Frauenfeld, 1853: 55

Ixodes simplex Neumann, 1906

Ixodes simplex Neumann, 1906: 197.

Ixodes audyi Kohls, 1955: 1; Clifford et al. 1973: 489.

Ixodes spiculae Arthur, 1956: 180.

Ixodes pospelovae Emchuk, 1955: 606; Beaucournu 1966: 495.

Ixodes chiropterorum Babos & Janisch, 1958: 389; Beaucournu 1966: 495.



Figure 2. Map of Russia and neighboring countries showing the locations where *Ixodes simplex* was reported.

Recorded hosts. Mammalia: *Myotis blythii* Tomes (lesser mouse-eared bat), *Miniopterus schreibersii* (Kuhl) (common bent-wing bat), *Nyctalus leisleri* (Kuhl) (lesser noctule) (Filippova 1977).

Recorded locations (Fig. 2). Russia: Krasnodar Krai – outskirts of Sochi (Emchuk 1955; Filippova 1972). **Ukraine:** eastern Carpathians – outskirts of Solotvyn and Rakhiv (Emchuk 1955; Filippova 1972). **Azerbaijan:** outskirts of Şahbuz and Hadrut (Emchuk 1955; Filippova 1972).

Ecology and other information. *Ixodes simplex* is a tick species specialized for bats as hosts (Filippova 1977). This species is mainly monoxenous and can be found usually on the common bent-wing bat although some other species of the Chiroptera may also act as hosts, especially which share colonies with its main host (Beaucournu 1967). Some rare cases of human infestation are also recorded (Okino et al. 2010; Péter et al. 2021).

***Ixodes vespertilionis* Koch, 1844**

Ixodes vespertilionis Koch, 1844b: 232.

Ixodes longipes Lucas: Neumann 1901: 249.

Ixodes pagurus Neumann, 1911: 28.

Ixodes nodulipes (Kolenati): Neumann 1911: 28.

Ixodes troglodytes Schmidt in Frauenfeld: Neumann 1901: 249.

Eschatocephalus gracilipes Frauenfeld: Estrada-Peña 1989: 165.

Eschatocephalus nodulipes Santos Dias: Santos Dias 1961: 229.

Eschatocephalus seidlitzii Koch: Neumann 1911: 30.

Eschatocephalus frauenfeldi Koch: Neumann 1901: 249.

Eschatocephalus seidlitzii Koch: Neumann 1901: 249.

Eschatocephalus vespertilionis (Koch): Neumann 1901: 249.

Eschatocephalus exaratus (Kolenati): Neumann 1901: Santos Dias 1961: 229.

Eschatocephalus flavipes (Koch): Doss and Anastos 1977: 34.

Recorded hosts. Mammalia: *Eptesicus serotinus* (Schreber) (serotine bat), *Myotis blythii* (lesser mouse-eared bat) (Filippova 1977), pond bat *Myotis dasycneme* (Boie) (Starikov et al. 2017b), Daubenton's bat *Myotis daubentonii* (Kuhl) (Orlova et al. 2011), *Myotis myotis* (Borkhausen) (greater mouse-eared bat) (Filippova 1977), *Myotis mystacinus* (Kuhl) (whiskered bat) (Bobkova 2003), *Nyctalus noctula* (Schreber) (common noctule), *Pipistrellus pipistrellus* (Schreber) (common pipistrelle), *Rhinolophus ferrumequinum* (Schreber) (greater horseshoe bat), *Rhinolophus hipposideros* (Bechstein) (lesser horseshoe bat), *Rhinolophus mehelyi* Matschie (Mehely's horseshoe bat) (Filippova 1977).

Recorded locations (Fig. 3). Russia: Udmurtia (Orlova et al. 2011), Voronezh Oblast (Usmsnskiy pine forest), (Khitsova and Sherstyanykh 2014), Novosibirsk Oblast (resort Lake Karachi) (Fedorov 2016), Khanty-Mansi Autonomous Okrug (outskirts of the urban locality Mortka) (Starikov et al. 2017b), Krasnodar Krai (Sochi National Park) (Romashin 2021), Stavropol Krai (Tsapko 2019). **Ukraine:** Ivano-Frankivsk Oblast, Chernivtsi Oblast, Ternopil Oblast, Zakarpattia Oblast, Crimea (Bobkova 2003). **Moldova:** Codru Reserve (Dniester-Prut interfluve) (Uspenskaya 1987). **Georgia:** Abkhazia (Kerbabaev 2011). **Azerbaijan:** Shusha, Hadrut (Filippova 1972). **Armenia:** Meghri (Ogandzhanyan 1949). **Kyrgyzstan:** Chüy Valley (Fedorova 2012a). Turkmenistan: rural localities Ahcha-Kuima and Mollagara (Dubinin and Bregetova 1952). **Tajikistan:** northern spurs of the Zarafshan Range (Filippova 1972).

Ecology and other information. *Ixodes vespertilionis* Koch is a species of ixodid ticks associated with bats as typical hosts (Filippova 1977), mostly from the families Rhinolophidae and Vespertilionidae. Usually, *I. vespertilionis* can be found in caves inhabited by bats. Occasional findings in Central Russia and Siberia are considered to result from accidental transportation.

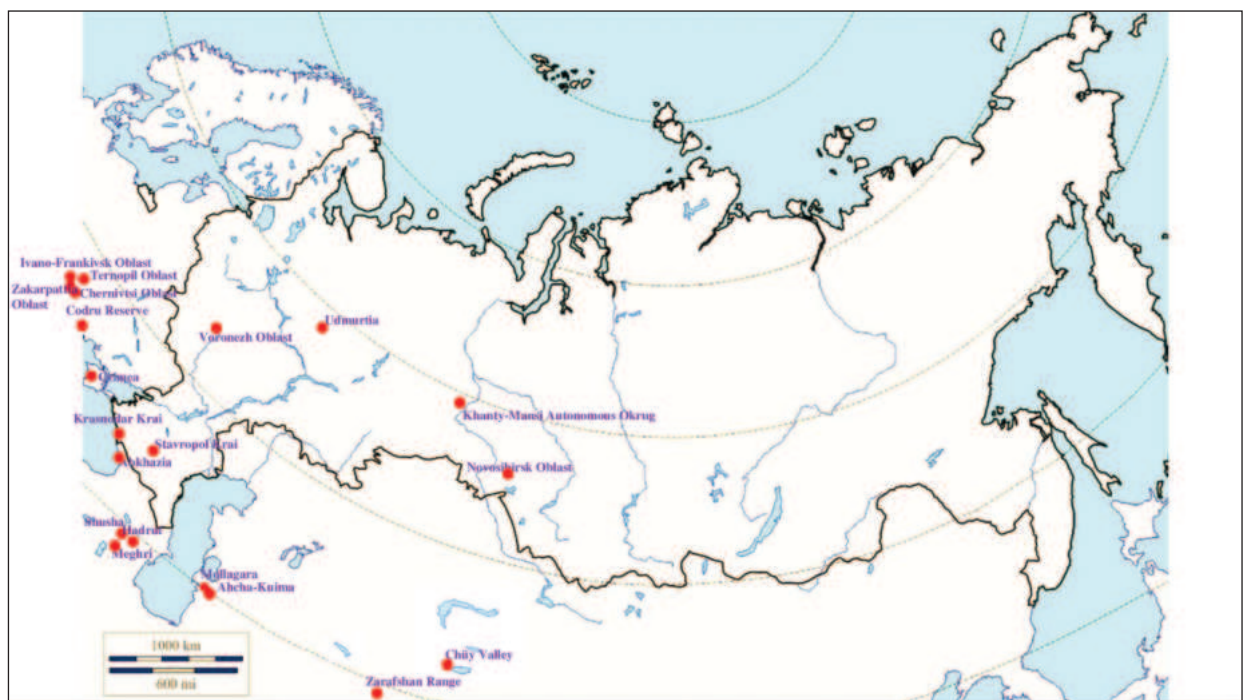


Figure 3. Map of Russia and neighboring countries showing the locations where *Ixodes vespertilionis* was reported.

Subgenus *Filippoviella* Apanaskevich, Greiman & Fedorov, 2024: 229

Ixodes ghilarovi Filippova & Panova, 1988

Ixodes ghilarovi Filippova & Panova, 1988: 212.

Recorded hosts. Mammalia: *Apodemus flavicollis* Melchior (yellow-necked field mouse), *Chionomys gud* Satunin (Caucasian snow vole), *Chionomys nivalis* (Martins) (European snow vole), *Microtus daghestanicus* (Shidlovsky) (Daghestan pine vole), *Nothocricetulus migratorius* (Pallas) (grey dwarf hamster), *Sorex raddei* Satunin (Radde's shrew) (Filippova and Panova 1989; Filippova and Stekol'nikov 2007).

Recorded locations (Fig. 4). Russia: Dagestan – the valley of the Akhtychay River which is the right tributary of the Samur River near the confluence of these rivers, ~ 1000 m a.s.l. and at the same location near rural locality Khnov, ~ 1700 m a.s.l.; the valley of the Avar Koysu River, ~ 1000 m a.s.l. (Filippova and Panova 1989); Kabardino-Balkaria, Bezengi gorge – 1550–2500 m a.s.l. and Karachay-Cherkessia – 1900–2200 m a.s.l. (Filippova and Stekol'nikov 2007). **Georgia:** Mtskheta-Mtianeti region, Kazbegi Municipality, outskirts of the hamlet Suatsi, 2200 m a.s.l. (Filippova and Panova 1989).

Ecology and other information. *Ixodes ghilarovi* is the second representative of the subgenus *Filippoviella* in the Palearctic tick fauna together with *I. trianguliceps* but known at the current moment exclusively from several locations of the Caucasus (Filippova and Panova 1988). The species was found only in rocky biotopes on the slopes containing xerophilous herbaceous-shrub vegetation consisting of many endemics of Southern Dagestan (Filippova and Panova 1989).

Further investigations of this poorly studied tick species are of undoubted interest. *Ixodes ghilarovi* has certain common structural features with the African



Figure 4. Map of Russia and neighboring countries showing the locations where *Ixodes ghilarovi* was reported.

species *I. alluaudi*, for example the presence of auriculae, especially visible in nymphs of both species (Filippova 2010); molecular analysis is also necessary to obtain more data on interspecific connections of these ticks and inside the subgenus in general. The host-parasite relations of *I. ghilarovi* and its distribution and habitats are probably wider than it is known today. The seasonality of *I. ghilarovi* and its role as a vector of tick-borne infections remain unknown.

The type specimens of *I. ghilarovi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: nymph; Russia, 25, Daghestan, Samur Mt. Range, near Akhty Village, River Akhtychay valley, ~ 1000 m a. s. l., *Chionomys gud*, Sat., 24.5.1980, coll. I.V. Panova; FBM 610a, 610b and the paratypes: 4 nymphs; FBM I610a, I610b. Description – Filippova and Panova 1989: 419–421 (female, larva; male unknown) (Filippova 2008).

***Ixodes trianguliceps* Birula, 1895**

Ixodes trianguliceps Birula, 1895: 358.

Ixodes nivalis Rondelli, 1928: 85; Pomerantsev 1950: 84.

Ixodes tenuirostris Neumann, 1901: 286.

Endopalpiger heroldi Schulze, 1939: 35; Černý 1959: 156.

Recorded hosts. Mammalia: *Alexandromys oeconomicus* (Pallas) (tundra vole), *Apodemus agrarius* (Pallas) (striped field mouse) (dominates as the host in the Udel'ny forest park in St. Petersburg, according to Tretyakov (2009), *Apodemus flavicollis* (yellow-necked field mouse), *Apodemus sylvaticus* (Linnaeus) (wood mouse), *Apodemus uralensis* Pallas (Ural field mouse), *Arvicola amphibius* (Linnaeus) (European water vole), *Chionomys gud* (Caucasian snow vole), *Chionomys nivalis* (European snow vole), *Craseomys rufocanus* (Sundevall) (grey red-backed vole), *Cricetus cricetus* (Linnaeus) (European hamster), *Crocidura leucodon* (Hermann) (bicolored shrew), *Crocidura suaveolens* (Pallas) (lesser white-toothed shrew), *Eutamias sibiricus* (Laxmann) (Siberian chipmunk), *Lasiopodomys gregalis* (Pallas) (narrow-headed vole), *Lepus europaeus* Pallas (European hare), *Lepus timidus* Linnaeus (mountain hare), *Micromys minutus* (Pallas) (harvest mouse), *Microtus agrestis* (Linnaeus) (short-tailed field vole), *Microtus arvalis* (Pallas) (common vole), *Microtus majori* (Thomas) (Major's pine vole), *Microtus socialis* (Pallas) (social vole), *Microtus subterraneus* (de Selys-Longchamps) (European pine vole), *Mus musculus* Linnaeus (house mouse), *Mustela nivalis* Linnaeus (least weasel), *Myodes glareolus* (Schreber) (bank vole), *Myodes rutilus* (Pallas) (northern red-backed vole), *Myopus schisticolor* (Lilljeborg) (wood lemming), *Neomys anomalus* Cabrera (Mediterranean water shrew) (Filippova 1977), *Neomys fodicens* (Pennant) (Eurasian water shrew) (Lutta 1968), *Nyctalus noctula* (common noctule), *Ochotona alpina* (Pallas) (alpine pika), *Prometheomys schaposchnikowi* Satunin (long-clawed mole vole), *Rattus norvegicus* (Berkenhout) (brown rat), *Sciurus vulgaris* Linnaeus (red squirrel), *Sicista betulina* Pallas (northern birch mouse), *Sorex araneus* Linnaeus (common shrew), *Sorex caecutiens* Laxmann (Laxmann's shrew), *Sorex daphaenodon* Thomas (Siberian large-toothed shrew) (Filippova 1977), *Sorex isodon* Turov (taiga shrew) (Sapegina 1980), *Sorex minutus* Linnaeus (Eurasian pygmy shrew), *Sorex minutissimus* Zimmermann (Eurasian least shrew) (Filippova 1977), *Sorex roboratus* Hollister (flat-skulled shrew)

(Shtilmark 1963; Sapegina 1980), *Spermophilus suslicus* (Güldenstädt) (speckled ground squirrel), *Vulpes vulpes* (Linnaeus) (red fox) (Filippova 1977).

Aves: *Anthus trivialis* (Linnaeus) (tree pipit), *Carduelis carduelis* (Linnaeus) (European goldfinch), *Dendrocopos major* (Linnaeus) (great spotted woodpecker), *Emberiza citronella* Linnaeus (yellowhammer), *Nucifraga caryocatactes* (Linnaeus) (Eurasian nutcracker), *Strix uralensis* Pallas (Ural owl), *Turdus viscivorus* Linnaeus (mistle thrush) (Filippova 1977).

Reptilia: *Zootoca vivipara* (viviparous lizard) (Lichtenstein) (Filippova 1977).

Recorded locations (Fig. 5). Russia: North Karelia – Cape Kartesh (Stanyukovich and Fedorov 2022); Karelia (Lutta 1968) including the village Malaya Gomselga (southern Karelia) (Bespyatova and Bugmyrin 2015; Bespyatova et al. 2019), St. Petersburg (Tretyakov 2009), Leningrad Oblast (Sukhomlinova 1977), Novgorod Oblast (Grigoryeva and Tretyakov 1998), Pskov Oblast – the village Gogolevo (own data, unpublished), Kaliningrad Oblast, the Vistula Spit (own data, unpublished); Tver Oblast (Schipanov and Makhanko 2018), Tula Oblast (Kozlova et al. 2014), Perm Oblast (Korenberg et al. 2015), Eastern Upper Volga (Egorov et al. 2016), Krasnodar Krai and the Caucasus (Shatas 1957; Filippova and Stekol'nikov 2007), Kurgan Oblast (Starikov and Starikova 2021), Tyumen Oblast (Bragina et al. 2013), Omsk Oblast (Rar et al. 2014, 2020), Kemerovo Oblast (Kovalevsky et al. 2018), Western Sayan (Shtilmark 1963), Eastern Sayan (Schluger 1961), Khamar-Daban ridge (Vershinina 1988). **Belarus** (Arzamasov 1963). **Ukraine:** Crimea (Filippova 2010), Polesia (Podobivskyi and Fedonyuk 2017). **Moldova:** north and central Moldova (Uspenskaya et al. 2006). **Georgia:** the village Bakuriani and the Roki Tunnel (Djaparidze 1960). **Armenia:** the whole territory (Ogandzhanyan 1960). **Azerbaijan:** the south of the country (Ogandzhanyan 1960).

Ecology and other information. *Ixodes trianguliceps* Birula has a wide geographical distribution in the Palaearctic region, occurring from the coast of Lake



Figure 5. Map of Russia and neighboring countries showing the locations where *Ixodes trianguliceps* was reported.

Baikal to Western Europe (Filippova 2010; Estrada-Peña et al. 2018). In the north it reaches northern Karelia and the Scandinavian Peninsula (Fedorov and Leonovich 2021). Also, an isolated southern population of this species was found in the Crimean Peninsula (Filippova 2010) although in other parts of Ukraine it is present in forest zones, such as Polesia (Podobivskiy and Fedonyuk 2017).

The population that was supposed to be isolated in the mountain systems of the Caucasus (Filippova 2010) now seems to be more expanded, as proved by the recent finding in Turkey (Bolu and Kars province, the north of Turkey) (Keskin and Selçuk 2021). The Kars province is located near the border with Georgia, where this species was known before (Djaparidze 1960) and, therefore, the ticks reported from there are probably part of the same Caucasian population.

The map of findings of this tick species in Russia clearly illustrates that it lives in a broad range of forest biotopes throughout a vast territory including the zonal and mountain deciduous and mixed forest of the European type and forests of southern and middle-taiga types. Along the southern border of the largest part of the range in Russia, *I. trianguliceps* occurs in the forest-steppe zone, populating shrubby and forested biotopes. This distinctly correlates with the main habitats of shrews and rodents, because the presence of these small mammals together with well-developed soil litter, plays an important role in the abundance of ticks in the landscape, as it is known that shrews of the genus *Sorex* are the most preferable host for larvae (Randolph 1975).

Interestingly, *I. trianguliceps* was also reported from two bat species (*Myotis myotis* in Poland (Siuda et al. 2009) and *Nyctalus noctula* in Russia, as well as several bird species and one reptile species (Filippova 1977). These animals are non-typical and occasional hosts for this tick species. The single cases of parasitism on these host species can be a clear indication that *I. trianguliceps* is predominantly an exophilic species, because it is unlikely that ticks could contact bats and birds in a burrow. Findings of this tick species in micropores of burrow tunnels in Belarus in winter (Arzamasov 1963) demonstrate only the ability of its larvae to remain active even during winter.

Phylogenetic trees inferred from the concatenated nucleotide sequences of 10 protein-coding genes of the mitochondrial genome of *I. trianguliceps*, together with consideration of its morphology, justified to establish the new subgenus *Filippoviella* and include there *I. trianguliceps* together with aforementioned *I. ghilarovi* (Apanaskevich et al. 2024) both of which used to belong to the subgenus *Exopalpiger*.

Subgenus *Ixodes* Latreille, 1795: 179

***Ixodes apronophorus* Schulze, 1924**

Ixodes apronophorus Schulze, 1924: 281.

Ixodes arvicolae Warburton, 1926: 55; Morel and Pérez 1978: 201.

Ixodes arvalis Karpov & Popov, 1944: 75; Morel and Pérez 1978: 201.

Ixodes dorrien-smilhi Turk: Morel and Pérez 1978: 201.

Ixodes dorriensmithi Turk: Morel and Pérez 1978: 201.

Recorded hosts. Mammalia: *Alexandromys oeconomus* (tundra vole), *Apodemus agrarius* (striped field mouse), *Apodemus flavicollis* (yellow-necked field mouse),

Apodemus sylvaticus (wood mouse), *Arvicola amphibius* (European water vole), *Cricetus cricetus* (European hamster), *Craseomys rufocanus* (grey red-backed vole), *Erinaceus europaeus* Linnaeus (European hedgehog), *Eutamias sibiricus* (Siberian chipmunk), *Lasiopodomys gregalis* (narrow-headed vole), *Lepus timidus* (mountain hare), *Micromys minutus* (Eurasian harvest mouse), *Microtus arvalis* (common vole), *Microtus agrestis* (Linnaeus) (short-tailed field vole), *Mus musculus* (house mouse), *Mustela nivalis* (least weasel), *Mustela sibirica* Pallas (Siberian weasel), *Myodes glareolus* (bank vole), *Myodes rutilus* (northern red-backed vole), *Myopus schisticolor* (wood lemming), *Neomys fodiens* (Eurasian water shrew), *Nothocricetulus migratorius* (grey dwarf hamster), *Ondatra zibethicus* (Linnaeus) (muskrat), *Rattus rattus* (Linnaeus) (black rat), *Sicista betulina* (northern birch mouse), *Sorex araneus* (common shrew), *Sorex caecutiens* (Laxmann's shrew), *Sorex daphaenodon* (Siberian large-toothed shrew), *Sorex isodon* (taiga shrew), *Sorex minutus* (Eurasian pygmy shrew), *Sorex roboratus* (flat-skulled shrew), *Talpa europaea* Linnaeus (European mole), *Vulpes vulpes* (red fox) (Filippova 1977).

Aves: *Anas crecca* Linnaeus (Eurasian teal) (Adamovich 1968), *Gallinula chloropus* (Linnaeus) (common moorhen) (Filippova 1977), *Motacilla alba* (white wagtail), *Turdus merula* Linnaeus (common blackbird) (Adamovich 1968).

Recorded locations (Fig. 6). Russia: Arkhangelsk Oblast (Olenev 1931a), Karelia (Lutta 1976), Saint-Petersburg (Tretyakov 2009), Leningrad Oblast (Sukhomlinova 1977), Vologda Oblast, Tver Oblast (Filippova 1977; Belova et al. 2008), Moscow Oblast (Mosolov 1961), the whole territory of the Upper-Volga (Egorov et al. 2016), Samara Oblast (Kirillova and Kirillov 2008a), Bryansk Oblast (Adamovich 1968), Voronezh Oblast, Nyzhny Novgorod Oblast (Solovyov 1966), Chuvash Republic (Petrov et al. 1967), Krasnodar Krai (Kalita and Pelipeychenko 1957; Shevchenko et al. 1960), Kabardino-Balkaria (Bittirova et al. 2019), Dagestan (Aliev et al. 2012), Perm Krai, Chelyabinsk Oblast (Filippova 1958a),



Figure 6. Map of Russia and neighboring countries showing the locations where *Ixodes apronophorus* was reported.

Ekaterinburg (Chernousova and Tolkachyov 2009), Omsk Oblast (Znamenskiy district and Bolsheukov district) (Sabitova et al. 2023), Khanty-Mansiysk (Popov 1967), Surgut (Petukhov et al. 2018), Novosibirsk Oblast (Novosibirsk and Toguchinsky District) (Mal'kova and Bogdanov 2004), Tyumen Oblast – Nyzhnevartovsk (Starikov et al. 2017a), Kurgan Oblast (Starikov and Starikova 2021), Salekhard (Starikov et al. 2017a), Tomsk Oblast (Chainsky District) (Mal'kova and Bogdanov 2004), Kemerovo Oblast, Altai Krai, Altai Republic (Bogdanov and Yakimenko 2016), Krasnoyarsk Krai – Podkamennaya Tunguska River and the rural locality Bolshoy Kemchug (Voltsyt 1997). **Ukraine:** Volyn Polesie (Adamovich 1968), outskirts of Kyiv (Akimov and Nebogatkin 2013), Cherkassy Oblast (Nikitchenko 2011), the North-Western seacoast of the Black Sea (Rusev 2009). **Belarus:** throughout the whole territory (Subbotina and Osmolovsky 2022). **Moldova:** reedbeds of the lower reaches of the Prut River (Uspenskaya et al. 1984). **Kazakhstan:** Jambyl Region (Galuzo 1950), Jetisu Region – outskirts of Taldykorgan and Jarkent, Almaty Region – outskirts of Sarkand and Almaty (Golov 1933; Sorokoumov 1937; Ushakova and Fedosenko 1972; Ushakova et al. 1976). **Kyrgyzstan:** outskirts of Bishkek, Tokmak Reserve (Grebenyuk 1966), Chuy Valley (Kharadov et al. 2013).

Ecology and other information. *Ixodes apronophorus* has a wide distribution in the Northern Palearctic from the Atlantic coast to Eastern Siberia. Its geographical range generally coincides with the distribution of the water vole, its most frequent host, as both the tick and its common host prefer swampy and humid places for living, especially near water bodies.

***Ixodes eldaricus* Djaparidze, 1950**

Ixodes eldaricus Dzhaparidze, 1950: 117.

Ixodes tatei Arthur, 1959: 108; Clifford et al. 1973: 489.

Recorded hosts. Aves: *Alectoris chukar* (Gray) (chukar partridge), *Anthus campestris* (Linnaeus) (tawny pipit), *Athene noctua* (Scopoli) (little owl), *Chroicocephalus ridibundus* (Linnaeus) (black-headed gull), *Coccothraustes coccothraustes* (Linnaeus) (hawfinch), *Coloeus monedula* (Linnaeus) (western jackdaw), *Curruca communis* (Latham) (common whitethroat), *Emberiza bruniceps* Brandt (red-headed bunting), *Galerida cristata* (Linnaeus) (crested lark), *Lullula arborea* (Linnaeus) (woodlark), *Luscinia svecica* (Linnaeus) (bluethroat), *Melanocorypha bimaculata* (Ménétrés) (bimaculated lark), *Monticola solitarius* (Linnaeus) (blue rock thrush), *Oenanthe* sp. (wheatear), *Passer domesticus* (Linnaeus) (house sparrow), *Perdix perdix* (grey partridge), *Petronia petronia* (Linnaeus) (rock sparrow), *Phoenicurus erythronotus* (Eversmann) (Eversmann's redstart), *Phylloscopus griseolus* (Blyth) (sulphur-bellied warbler), *Pica pica* (Linnaeus) (Eurasian magpie), *Sitta tephronota* Sharpe (Eastern rock nuthatch), *Turdus merula* (common blackbird) (Filippova 1977).

Mammalia: *Crocidura leucodon* (bicolored shrew), *Meriones persicus* (Blanford) (Persian jird), *Mus musculus* (house mouse), *Nesokia indica* (Gray) (short-tailed bandicoot rat), grey dwarf hamster *Nothocricetulus migratorius* (Pallas), *Rattus pyctoris* (Hodgson) (Turkestan rat), *Rhinolophus mehelyi* (Mehely's horseshoe bat) (Filippova 1977).

Recorded locations (Fig. 7). Russia: Dagestan and North Osetia-Alania (Shatas 1957; Filippova 1977). **Ukraine:** Crimean Peninsula, in particular the Tarkhankut Peninsula and the Kara Dag (Filippova 1974). **Georgia:** the Shiraki Plain and the Vashlovani Nature Reserve (Djaparidze 1950, 1960). **Armenia:** Vayots Dzor Province – the rural locality Herher (Ogandzhanyan 1959). **Azerbaijan:** Karabakh Plateau – Lachin District and Hadrut District, Adzhynokhur Steppe (Ogandzhanyan 1959; Filippova 1977). **Kazakhstan:** Dzungarian Alatau (Ushakova et al. 1976) and Trans-Ili Alatau (Filippova 1977). **Kyrgyzstan:** Terskey Ala-too Range (Filippova 1974). **Turkmenistan:** the Kopet Dagh – the valley of the Chandyr River, Magtymguly, Gökdepe District, outskirts of Ashgabat, Köytendag Range, Bayramaly (Kerbabaev 1960; Kochkareva et al. 1971; Berdyev 1973; Scherbinina 1973). **Uzbekistan:** Termez (Filippova 1977). **Tajikistan:** Hisar Range, Varzob gorge, outskirts of Dushanbe (Filippova 1977).

Ecology and other information. *Ixodes eldaricus* is a little studied endophilic tick species which is mainly a parasite of ground-feeding birds although nymphs and larvae, besides birds, were also found on small mammals – rodents and shrews. It usually inhabits deciduous mountain forests and shrub thickets in mountain river valleys. The vertical distribution range of its occurrence varies from 300 (Ashgabat) to 1800 m (Terskey Ala-too Range and Hisar Range) a. s. l. (Filippova 1977).

Briefly described by a female from the east of Georgia (type locality: the Shiraki Plain), *I. eldaricus* was later found in Armenia and Azerbaijan, and the male, nymph descriptions were based on the material from Azerbaijan (Ogandzhanyan 1959). The holotype female described from the grey partridge is stored at the Institute of Zoology of Ilia State University. The above findings from post-Soviet territories are known from the Crimea, as well as the Caucasus and Central Asia. The majority of samples are stored at the collection of the Zoological Institute of the Russian Academy of Sciences.



Figure 7. Map of Russia and neighboring countries showing the locations where *Ixodes eldaricus* was reported.

Additionally, it is important to note that in Crimea this tick species is considered disappearing (Nebogatkin 1998) due to anthropogenic pressure followed by destruction of its habitats and decline in its host populations (Uspensky 2021).

***Ixodes kashmiricus* Pomerantsev, 1948**

Ixodes kaschmiricus Pomerantsev, 1948: 132; Filippova 1969: 675.

Ixodes persulcatus kaschmiricus Pomerantsev, 1948: 132; Filippova 1969: 675.

Recorded hosts. Mammalia: *Apodemus sylvaticus* (wood mouse), *Canis familiaris* Linnaeus (dog), *Ovis aries* Linnaeus (sheep) (Filippova 1977).

Recorded locations (Fig. 8). Kyrgyzstan: the Tien Shan – northern and eastern slopes of the Terskey Ala-too range (gorges Ulken-Kokpak and Chon-Dzhargylchak) (Filippova 1969).

Ecology and other information. *Ixodes kashmiricus* is a tick species with a disjunctive relict range limited by the Tien Shan in Kyrgyzstan as well as India (Filippova 1977) and Pakistan (Numan et al. 2022). In Kyrgyzstan the tick was found mainly in the mid-altitude vertical zone of the mountains at the lower border of the forest at the altitude of 2000 and 2500 m a. s. l. Cases of parasitism on humans have been recorded (Hoogstraal 1970).

Phylogenetic analysis of mitochondrial and nuclear genes showed that *I. kashmiricus* belongs to the *I. ricinus* group (Kovalev et al. 2018) and clusters with such members of the *I. ricinus* group as *I. apronophorus* and *I. kazakstani* (Numan et al. 2022).

The type specimens are stored at the Zoological Institute of the Russian Academy of Sciences and include the lectotype - female; [India], Kashmir,



Figure 8. Map of Russia and neighboring countries showing the locations where *Ixodes kashmiricus* was reported.

Vardvan Maru River, northern tributary of Chinab River, 10–13. V.1910, coll. S.P. Trubetskoi; AL I533, as well as the paralectotype - male; AL 533a. *Ixodes kashmiricus* (see: Filippova 1969: 677). Description – Filippova 1977: 292–296 (female, male, nymph, larva) (Filippova 2008). Originally the tick was named *I. persulcatus kaschmiricus* (lapsus).

***Ixodes kazakstani* Olenev & Sorokoumov, 1934**

Recorded hosts. Mammalia: *Apodemus sylvaticus* (wood mouse) (Filippova 1977), *Canis familiaris* (domestic dog) (Kovalev et al. 2018), *Dryomys nitedula* (Pallas) (forest dormouse), *Lepus tolai* Pallas (tolai hare), *Mus musculus* (house mouse), *Nothocricetulus migratorius* (grey dwarf hamster) (Filippova 1977).

Aves: *Phasianus colchicus* Linnaeus (common pheasant) (Filippova 1977).

Recorded locations (Fig. 9). **Kazakhstan:** Betpak-Dala – the valley of the Chu River (Ushakova 1961), Tian Shan – the valley of the Ili River (Ushakova 1958; Kovalev et al. 2018), outskirts of Jarkent (Olenev and Sorokoumov 1934; Pomerantsev 1950). **Kyrgyzstan:** the Issyk-Kul basin (Filippova 1958b; Kovalev et al. 2018), the valley of the Talas River (Olenev and Sorokoumov 1934; Pomerantsev 1950; Grebenyuk 1966; Lyashko 1973; Kovalev et al. 2018).

Ecology and other information. *Ixodes kazakstani* is a tick species with a disjunctive relict range limited by Southeastern Kazakhstan and neighboring territories of Kyrgyzstan (Filippova 1977). The patchy arrangement of its range can be explained, above all, by associations of this tick mainly with the animals dwelling in tugai forests which also create humidity conditions in the soil suitable for this tick species (Filippova 1958b). Also, there are some cases of parasitism on livestock and humans (Lyashko 1973; Filippova 1977). On livestock it was found in few numbers among mass parasitism of other tick species.



Figure 9. Map of Russia and neighboring countries showing the locations where *Ixodes kazakstani* was reported.

Phylogenetic analysis of mitochondrial and nuclear genes showed that *I. kazakstani* belongs to the *I. ricinus* group (Kovalev et al. 2018) and clusters with such members of the *I. ricinus* group as *I. apronophorus* and *I. kashmiricus* (Numan et al. 2022). *Ixodes kazakstani* can presumably exemplify links between Nearctic and Palearctic species, so further studies of genetic sequences of *I. kazakstani* are necessary to understand better evolutionary connections between more tick species in the *I. ricinus* group.

The type specimens are stored at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; Kazakhstan, Jarkent, collected from human dress, 20.VI.1932, coll. Kirin; AL I536. Description - Filippova 1977: 283–290 (female, male, nymph, larva) (Filippova 2008).

***Ixodes laguri* Olenov, 1929**

Ixodes laguri Olenov, 1929a: 489.

Ixodes redikorzevi lagurae Olenov: Olenov 1931b: 62.

Ixodes laguri armeniacus Kirshenblat, 1938: 46; Morel and Pérez 1978: 201.

Ixodes laguri colchicus Pomerantsev, 1946: 1; Morel and Pérez 1978: 201.

Ixodes laguri slovacicus Cerny, 1960: 178; Morel and Pérez 1978: 201.

Recorded hosts. Mammalia: *Allactaga major* (Kerr) (great jerboa), *Allocricetulus eversmanni* (Brandt) (Eversmann's hamster), *Apodemus sylvaticus* (wood mouse), *Chionomys nivalis* (European snow vole), *Cricetus cricetus* (European hamster), *Dryomys nitedula* (forest dormouse), *Ellobius talpinus* (Pallas) (northern mole vole), *Erinaceus europaeus* (European hedgehog), *Glis glis* (Linnaeus) (European edible dormouse), *Hemiechinus auratus* (Gmelin) (long-eared hedgehog), *Lagurus lagurus* (Pallas) (steppe lemming), *Marmota bobak* (Müller) (bobak marmot), *Martes martes* (Linnaeus) (European pine marten), *Microtus arvalis* (common vole), *Microtus socialis* (social vole), *Meles meles* (Linnaeus) (European badger), *Meriones meridianus* (Pallas) (midday jird), *Mesocricetus brandti* (Pallas) (Turkish hamster), *Mesocricetus raddei* (Nehring) (Ciscaucasian hamster), *Mus musculus* (house mouse), *Mustela eversmannii* (Lesson) (steppe polecat), *Mustela nivalis* (least weasel), *Nothocricetulus migratorius* (grey dwarf hamster), *Pygeretmus pumilio* (Kerr) (dwarf fat-tailed jerboa), *Rattus rattus* (black rat), *Spalax microphthalmos* Gueldenstaedt (greater blind mole-rat), *Spermophilus citellus* (Linnaeus) (European ground squirrel), *Spermophilus fulvus* (Lichtenstein) (yellow ground squirrel), *Spermophilus pygmaeus* (Pallas) (little ground squirrel), *Spermophilus suslicus* (speckled ground squirrel), *Spermophilus xanthopyrmnus* (Bennett) (Asia Minor ground squirrel), *Stylodipus telum* (Lichtenstein) (thick-tailed three-toed jerboa), *Vormela peregusna* (Güldenstädt) (marbled polecat), *Vulpes corsac* (Linnaeus) (Corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977).

Recorded locations (Fig. 10). Russia: Samara Oblast (Kirillova and Kirillov 2008b), Rostov Oblast (Stakheev and Panasyuk 2016), Krasnodar Krai (Popov et al. 2019), Stavropol Krai (Tsapko 2019), Volgograd Oblast, Astrakhan Oblast (Nelzina et al. 1955), Kalmyk Republic (Sandzhiev et al. 2006), Chechnya (Baisarova 2021), Dagestan (Musaev et al. 2019) and North Osetia-Alania (Filippova 1977). **Ukraine:** Kyiv (Omeri and Moysak 2013), Odesa Oblast (Rusev 2008), Kherson Oblast, Chernivtsi Oblast, Ternopil Oblast, Luhansk Oblast, Donetsk



Figure 10. Map of Russia and neighboring countries showing the locations where *Ixodes laguri* was reported.

Oblast, the Crimean Peninsula, particularly in the Syvash (Filippova 1958a; Emchuk 1960; Sklyar 1970; Andryushchenko et al. 2005; Evstafiev 2017). **Moldova:** Bălți Steppe, Bugeac Steppe (Filippova 1977) and Tiraspol (Kravchenko 2014). **Georgia:** Abkhazia (Shaposhnikova and Sakhno 2012), Imereti (Sukhiashvili et al. 2020), Lagodekhi Nature Reserve (Djaparidze 1960). **Armenia:** Lori Province – Nalband and the valley of the river Hrazdan (Filippova 1977). **Azerbaijan:** Talysh (Pomerantsev 1950), the Nakhchivan Autonomous Republic – the Zangezur Mountains (Kadatskaya and Shirova 1963; Filippova 1977). **Kazakhstan:** West Kazakhstan Region (Pomerantsev 1950; Levit 1957; Filippova 1977), Kyzylorda Region (Loseva 1963), Kostanay Region, Akmola Region (Ushakova 1961, 1962). **Turkmenistan:** the Kopet Dagh (Kerbabaev 1961).

Ecology and other information. *Ixodes laguri* is a tick species which is mainly a nidicolous parasite of rodents and small and medium carnivores, first of all ground squirrels. It is present usually in zonal and mountainous steppes at the altitude of 1500 m a.s.l. This tick species is less common in desert and semi-desert biotopes (Filippova 1977).

Filippova (1977) states that the tick has four subspecies – *I. laguri laguri*, *I. I. armeniacus*, *I. I. colchicus* and *I. I. slovacicus*. The differential characters of the female and the male of *I. I. slovacicus* are based on comparison with characters of the other subspecies in Pomerantsev (1950) but some of them, such as the genital aperture and chaetotaxy of the scutum and the hypostome and the coxa 1, are not characterized precisely enough (Filippova 1977).

According to Filippova (1977), *I. laguri laguri* can be found in Moldova, Ukraine, Kazakhstan, as well as in the south of Russia; *I. I. armeniacus* is distributed in the Caucasus – North Ossetia-Alania, Dagestan, Georgia, Armenia and Azerbaijan; *I. I. colchicus* is known from the western spurs of the Greater Caucasus, the now abandoned rural locality Babuk-Aul; *I. I. slovacicus* was described from the south-east of Slovakia.

The type specimens of *I. laguri* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. I. armeniacus*: the lectotype, female; Armenia, Nalband, from *Mesocricetus brandti* Nehr., 9.9.1936; AL I558 and the paralectotype, male; AL I556, description – Filippova 1977: 384 (female, male, nymph; larva unknown). (Filippova 2008), as well as *I. I. colchicus*: the lectotype, male; Western Caucasus, near Babuk-Aul, *Glis glis* L., 30.9.1935, coll. V. K. Popov, det. B. Pomerantsev: *I. I. colchicus*, type; AL I554a; paralectotypes: 2 females; AL I554a, description – Filippova 1977: 384 (female, male; nymph and larva unknown) (Filippova 2008).

***Ixodes nipponensis* Kitaoka & Saito, 1967**

Recorded hosts. Mammalia: *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Microtus fortis* (Büchner) (reed vole), *Myodes rutilus* (northern red-backed vole) (Filippova 1977).

Recorded locations (Fig. 11). Russia: Primorsky Krai – the Lake Khasan, the Poyma River, the Partizansky District, outskirts of urban localities Posyet, Kraskino, Slavyanka and cities Vladivostok and Nakhodka, near the village Rechitsa (Filippova 1969; Filippova and Belyaev 1970; Allenov et al. 2015).

Ecology and other information. *Ixodes nipponensis* is a tick species found in Russia in the south and south-west of the Primorsky Krai and also in the Korean peninsula and Japan (Filippova 1977). In Russia it was reported mainly from murine rodents, although in the Republic of Korea it was also observed on lizards (Kim et al. 2018) and cattle, goats, dogs, horses, and birds in Japan (Kitaoka and Saito 1967; Yamaguti et al. 1971).



Figure 11. Map of Russia and neighboring countries showing the locations where *Ixodes nipponensis* was reported.

Multiple cases of parasitism on humans have been recorded (Nakatsukase and Hatsushika 1985; Paik et al. 1989; Cho et al. 1995; Chu et al. 1997; Ryu et al. 1998; Ko et al. 2002).

***Ixodes occultus* Pomerantsev, 1946**

Recorded hosts. Mammalia: *Crocidura suaveolens* (lesser white-toothed shrew), *Diplomesodon pulchellum* (Lichtenstein) (piebald shrew), *Meriones libycus* Lichtenstein (Libyan jird), *Meriones meridianus* (midday jird), *Meriones persicus* (Persian jird), *Mustela nivalis* (least weasel), *Nothocricetulus migratorius* (grey dwarf hamster), *Rhombomys opimus* (Lichtenstein) (great gerbil), *Spermophilopsis leptodactylus* (Lichtenstein) (long-clawed ground squirrel), *Vormela peregusna* (marbled polecat) (Filippova 1977).

Reptilia: *Gloydius halys* (Pallas) (Halys pit viper) (Filippova 1977).

Recorded locations (Fig. 12). **Kazakhstan:** Mangystau Region – the Mangyshlak Peninsula (Kaluzhenkova et al. 1961) and the Ustyurt Plateau; Kyzylorda Region (Filippova 1958a; Loseva 1963; Maslennikova and Ushakova 1971), Jambyl Region – the Moynkum Desert (Maslennikova and Ushakova 1971), Almaty Region – the foothills of the Dzungarian Alatau: the Sholak and Katutau mountains, the deserts Taukum and Saryesik-Atyrau (Ushakova 1960; Maslennikova et al. 1964; Ushakova et al. 1976). **Turkmenistan:** distributed everywhere – the southern Ustyurt, the Octumkumy Desert, the Üñüzaňrýsy and Türkmenbaşy Plateau, the Meshed and Saynaksan Desert, the Karakum Desert (Pomerantsev 1950; Kerbabaev 1961; Kochkareva et al. 1971); Hojagala (Berdjev and Annaev 1997). **Uzbekistan:** the Pistalitau Ridge and the rural locality Tashrabat (Maslennikova and Ushakova 1971).

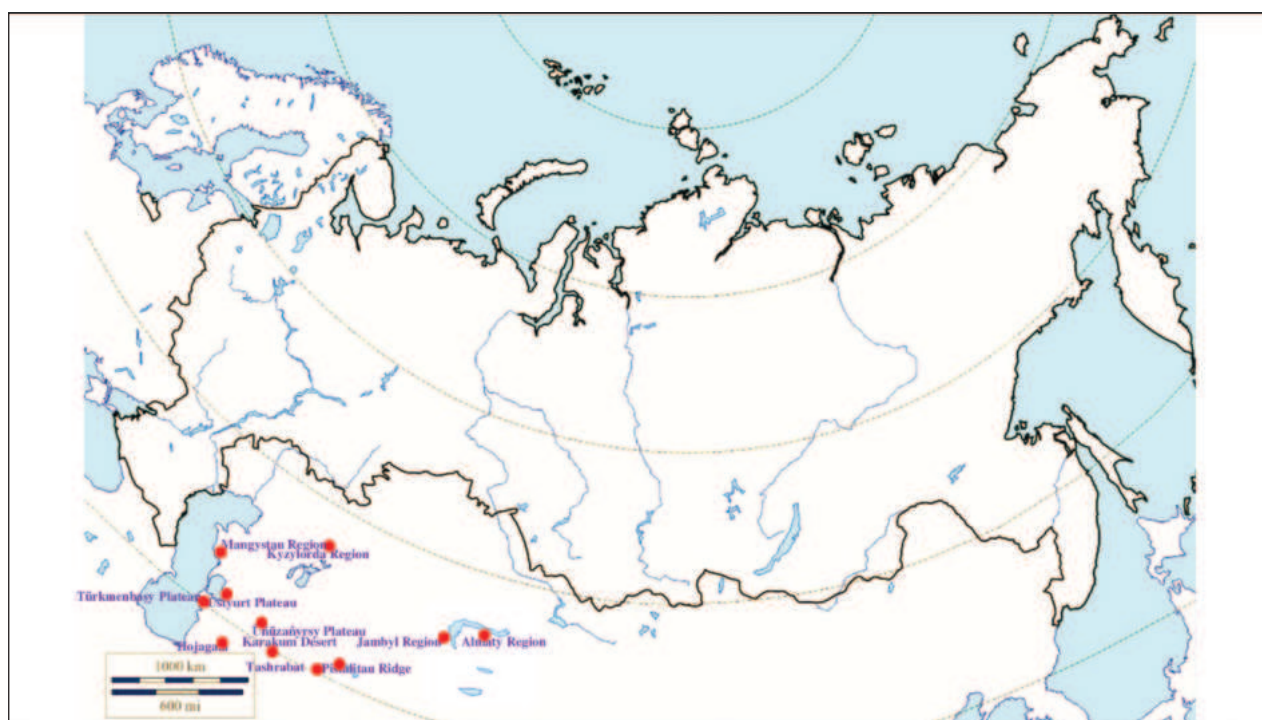


Figure 12. Map of Russia and neighboring countries showing the locations where *Ixodes occultus* was reported.

Ecology and other information. *Ixodes occultus* is a tick species inhabiting deserts. It is mainly a nidicolous parasite of gerbils and jirds (subfamily Gerbillinae), first of all, the great gerbil, as well as of those small mammals which also use long and deep burrows of great gerbils as shelters (Filippova 1977). Some predators which have strong trophic relationships with gerbils and regularly contact with their colonies act as secondary hosts for this tick species.

The type specimen of *I. occultus* is deposited at the Zoological Institute of the Russian Academy of Sciences and includes the holotype: male; Turkmenia, Repetek, *Rhombomys opimus*, 5.10.1937, coll. B.I. Pomerantsev, type; AL I550. Description – Filippova 1977: 365–371 (female, male, nymph, larva) (Filippova 2008).

***Ixodes pavlovskiy* Pomerantsev, 1946**

Recorded hosts. Aves: *Acrocephalus dumetorum* Blyth (Blyth's reed warbler), *Acrocephalus schoenobaenus* (Linnaeus) (sedge warbler), *Anas platyrhynchos* Linnaeus (mallard), *Anthus trivialis* (tree pipit), *Calliope calliope* (Pallas) (Siberian rubythroat), *Carduelis carduelis* (European goldfinch), *Carpodacus erythrinus* (Pallas) (common rosefinch), *Chloris chloris* (Linnaeus) (European greenfinch) *Columba livia* Gmelin (rock dove), *Corvus cornix* Linnaeus (hooded crow), *Corvus corone* Linnaeus (carrion crow), *Coturnix coturnix* (Linnaeus) (common quail), *Crex crex* (Linnaeus) (corn crane), *Curruca communis* (Latham) (common whitethroat), *Curruca curruca* (Linnaeus) (lesser whitethroat), *Cyanopica cyanus* Pallas (azure-winged magpie), *Emberiza calandra* Linnaeus (corn bunting), *Emberiza citrinella* Linnaeus (yellowhammer), *Emberiza leucocephalos* Gmelin (pine bunting), *Emberiza spodocephala* Pallas (black-faced bunting), *Ficedula hypoleuca* (Pallas) (European pied flycatcher), *Fringilla coelebs* Linnaeus (Eurasian chaffinch), *Fringilla montifringilla* Linnaeus (brambling), *Lanius collurio* Linnaeus (red-backed shrike), *Locustella lanceolata* (Temminck) (lanceolated warbler), *Luscinia luscinia* (Linnaeus) (thrush nightingale), *Luscinia svecica* (Linnaeus) (bluethroat) *Parus major* Linnaeus (great tit), *Passer montanus* (Linnaeus) (Eurasian tree sparrow), *Pastor roseus* (Linnaeus) (rosy starling), *Phoenicurus phoenicurus* (Linnaeus) (common redstart), *Phylloscopus fuscatus* (Blyth) (dusky warbler), *Phylloscopus trochiloides* (Sundevall) (greenish warbler), *Pica pica* (Eurasian magpie), *Sitta europaea* Linnaeus (Eurasian nuthatch), *Sturnus vulgaris* Linnaeus (common starling), *Sylvia borin* (garden warbler), *Tetrao urogallus* (western capercaillie), *Tetrastes bonasia* (hazel grouse), *Turdus iliacus* Linnaeus (redwing), *Turdus philomelos* Brehm (song thrush), *Turdus pilaris* Linnaeus (fieldfare), *Turdus ruficollis* Pallas (red-throated thrush), *Turdus viscivorus* (mistle thrush) (Filippova 1977; Moskvitina et al. 2014).

Mammalia: *Alexandromys oeconomus* (tundra vole), *Apodemus agrarius* (striped field mouse), *Arvicola amphibius* (European water vole), *Cruseomys rufocanus* (grey red-backed vole), *Cricetus cricetus* (European hamster), *Eutamias sibiricus* (Siberian chipmunk), *Lepus timidus* (mountain hare), *Microtus agrestis* (short-tailed field vole), *Microtus arvalis* (common vole), *Mus musculus* (house mouse), *Myodes glareolus* (bank vole), *Myodes rutilus* (northern red-backed vole), *Neomys fodiens* (Eurasian water shrew), *Nothocricetulus migratorius* (grey dwarf hamster), *Ochotona alpina* (Alpine pika), *Sciurus vulgaris* (red squirrel), *Sicista betulina* (northern birch mouse), *Sicista subtilis* (Pallas) (southern



Figure 13. Map of Russia and neighboring countries showing the locations where *Ixodes pavlovskyi* was reported.

birch mouse), *Sorex araneus* (common shrew), *Sorex minutus* (Eurasian pygmy shrew), *Sorex roboratus* (flat-skulled shrew), *Stenocranius gregalis* (Pallas) (narrow-headed vole) (Filippova 1977).

Recorded locations (Fig. 13). Russia: Tomsk Oblast (Kovalev et al. 2015), Novosibirsk Oblast, Altai Republic (Tkachev et al. 2017), Altai Krai, Kemerovo Oblast, Krasnoyarsk Krai, Khakassia, northern spurs of the Western Sayan, Amur Oblast, Khabarovsk, Primorsky Krai – the Sikhote-Alin (Filippova 1969; Sapagina and Ravkin 1969; Filippova and Panova 1998), Russky Island (Nikitin et al. 2021). **Kazakhstan:** East Kazakhstan Region (Tkachev et al. 2017; Perfilyeva et al. 2020), Abai Region, Jetisu Region (Filippova 1977), Tarbagatai Mountains, Dzungarian Alatau, Küngöy Ala-Too Range (Ushakova et al. 1976; Filippova and Panova 1998). **Kyrgyzstan:** Küngöy Ala-Too Range (Filippova and Panova 1998), Terskey Ala-too (Fedorova 2017).

Ecology and other information. *Ixodes pavlovskyi* is a tick species distributed in Western Siberia, the Far East, Eastern Kazakhstan, and Kyrgyzstan (Filippova 1977; Fedorova 2017), as well as in China (Guo et al. 2016) and Japan (Nakao et al. 1992; Guglielmone et al. 2023). It more often prefers birds as hosts, as well as small mammals although some cases of human and livestock infestation are also recorded. Its preferred habitats include usually coniferous and deciduous forests, undergrowth, as well as motley grass (Filippova 1977).

Often it can be found in the same biotopes together with *I. persulcatus* with complete coincidence of the seasons of activity of both species at each ontogenetic stage (Filippova 1999) and where their hybridization can also occur (Kovalev et al. 2015; Rar et al. 2019).

In certain areas of Siberia *I. pavlovskyi* outnumbers *I. persulcatus* and also other tick species due to the high abundance of ground-feeding birds, especially in urban landscapes with habitats suitable for ticks like parks and cemeteries. So, for example, in the city of Tomsk in Western Siberia *I. pavlovskyi* dominates

everywhere in the city and its outskirts (Romanenko 2011). Probably eventually over time *I. persulcatus* was gradually replaced by *I. pavlovskyi* because it is too difficult for adult *I. persulcatus* to find its preferred hosts, namely mammals (Romanenko and Leonovich 2015).

Filippova and Panova (1998) recognize two subspecies in Russian populations of this tick, namely *I. pavlovskyi pavlovskyi* and *I. pavlovskyi occidentalis* which differentiation is based on morphological features between western and eastern specimens.

The type specimens of *I. pavlovskyi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. pavlovskyi*, Pomerantsev (Pomerantsev 1946: 11), the holotype: female; [Russia], DVK [Primorskii Terr.], Imanskii Forestry, hazel, 2.9.1932, type; AL 1513. Description – Filippova 1977: 305–312 (female, male, nymph, larva); as well as *I. pavlovskyi* subsp. *occidentalis* (Filippova and Panova 1998: 396–411 – female, male, nymph, larva) the holotype: female; Russia, western foothills of Kuznetskii Ala Tau, basin of upper Tom River, environs of Mezhdurechensk, from vegetation, flagging, 24.5.1972, coll. E.D. Chigirik, det. N.A. Filippova; AL 11016 and finally *I. pavlovskyi* subsp. *pavlovskyi* (Filippova and Panova 1998: 396–411, female, male, nymph, larva), the holotype (the same as the holotype of the species): see *I. pavlovskyi* (Filippova 2008).

***Ixodes persulcatus* Schulze, 1930**

Ixodes persulcatus Schulze, 1930: 294.

Ixodes ricinus miyazakiensis Kishida: Morel and Pérez 1978: 201.

Ixodes persulcatus diversipalpis Schulze, 1930: 294; Pomerantsev 1950: 43.

Ixodes persulcatus cornuatus Olenov: Pomerantsev 1950: 43.

Ixodes sachalinensis Filippova: Kolonin 1981: 49.

Recorded hosts. The spectrum of hosts of *I. persulcatus* is extremely broad both systematically and ecologically and includes more than 200 species of mammals and 100 species of birds (Shilova and Clabovskii 1968). Rarely it can parasitize reptiles – lizards of the family Lacertidae (Ravkin 1969). Literally almost all mammals and birds inhabiting various types of forests and their derivative biotopes can act as hosts for *I. persulcatus*. Larvae and nymphs parasitize more often small and medium-sized mammals, such as shrews, hedgehogs, rodents, and lagomorphs, as well as ground-feeding and ground-nesting birds. Adults usually feed on large and medium-sized mammals – ungulates, carnivores, lagomorphs. Humans and domestic animals can also be hosts for this tick species (Filippova 1977).

Distribution in Russia and other post-Soviet countries (Fig. 14). The range of *I. persulcatus*, like no other Palearctic species, is extended in the latitudinal direction by a continuous strip, covering a significant part of the taiga forest zone in Eurasia between 21°–66° latitude in the northern hemisphere from the Scandinavian Peninsula, the Baltic states, Belarus and Ukraine in the west where it is present sporadically to the east up to the Pacific coast including the Kamchatka Peninsula and the Sakhalin Island and further to the north-east of China, the Korean Peninsula and Japan (Filippova 1977; Wang et al. 2023). This tick belongs to the tick fauna of the next post-Soviet countries: Estonia, Latvia,

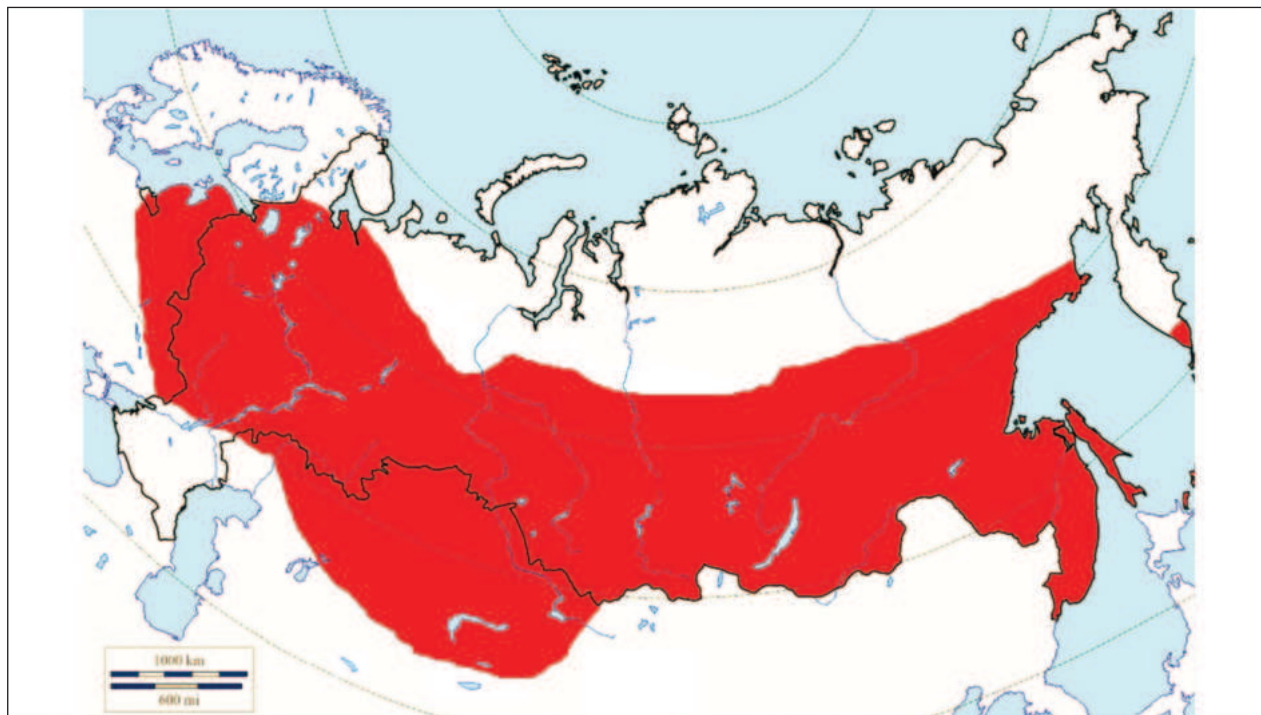


Figure 14. Map of Russia and neighboring countries showing the locations where *Ixodes persulcatus* was reported.

Lithuania, Belarus, Russia, Ukraine, Kazakhstan, Kyrgyzstan (Guglielmone et al. 2023). The presence of *I. persulcatus* in Ukraine outside the south-west border of the taiga was mentioned by Filippova (1977), although the possibility of permanent populations existing there was disputed by Nebogatkin (1993). Therefore, this probably exemplifies transportation by migratory birds.

Ecology and other information. *Ixodes persulcatus* is an exophilic tick species widely distributed in the northern Palearctic along the forest zone. It may use almost all mammals and birds living in its biotopes; therefore, it is one of the most important vectors of a broad range of tick-borne pathogens. Since it can also transmit tick-borne encephalitis virus, together with *I. ricinus* it has the greatest medical and veterinary significance among other ticks of the genus *Ixodes* in the Palearctic. Another important fact is that *I. persulcatus* is a very aggressive species toward humans (Uspensky 1993) and, therefore, this species represents especially high medical-epidemiological risks.

The most significant part of the range of *I. persulcatus* stretches across the territory of Russia where we can observe the full spectrum of biotopes where *I. persulcatus* can be found. There are a lot of published works about its ecology in different regions which depend on the climatic region and biotic-abiotic conditions in it.

This tick prefers various types of forest and forest-steppe biotopes, especially taiga forests and their derivatives, i.e., mixed forests and bushes (both plain and mountainous), up to 2000 m a.s.l., like in the Tian Shan. In other words, it can inhabit any herbaceous forest and forest-steppe biotope with the level of humidity high enough for reproduction and supporting the life cycle, even in urban landscapes (Filippova 1977). In the Dzungarian Alatau there were some observations of occurring in steppe regions bordering forests and parasitizing the unusual host, namely the grey marmot *Marmota baibacina* Kastschenko (Bibikov et al. 1961). Permanent and stable populations of *I. persulcatus* exist in some areas adjacent

to cities within its range and even inside these cities on condition that the suitable forest environment together with hosts, such as wild animals of different sizes and stray dogs are present. Examples of such cities are Saint Petersburg, Petrozavodsk, Novosibirsk, Tomsk, Irkutsk, and Vladivostok (Uspensky 2017).

Several studies attest the changing boundaries of the ranges of *I. persulcatus*. It is assumed that ticks of the *I. persulcatus* group appeared and evolved in forest biotopes similar to modern relict forests of the Ussuri type and the taiga of the mountains of Southern Primorye, Southern Siberia, and the Korean Peninsula in the Pliocene. The wide ecological niche of *I. persulcatus* was formed during the formation of the species in the process of its adaptation to various landscape and climatic conditions. This allowed the species to gradually expand its range in the northwestern direction in the Holocene (Filippova 2017). An increase in air temperature by one or several degrees in a particular region near the boundaries of its range was probably the main driver of its expanding distribution. The fact of finding *I. persulcatus* populations in Sweden (Jaenson et al. 2016) and even in the Magadan Oblast in the north-east of Russia where it was absent before (Yamborko et al. 2015) are good examples of the distribution expansion in several directions and confirm the tendency which continues.

In Russia, high numbers of observations show noticeable changes in the distribution of *I. persulcatus* in certain regions. In Karelia the range expansion of *I. persulcatus* to the north is noted in relation to general climate warming (Bugmyrin et al. 2013). A similar observation was also recorded in the Komi Republic (Glushakova et al. 2011). The range expansion of this tick species in Arkhangelsk Oblast and Western and Central Siberia to the north is confirmed both by the results of their records and by the data on tick bites and morbidity in the human population, not only in places which were free from ticks before (Pogodina 2021). Besides that, there are some data about the range expansion of *I. persulcatus* to the north in the Republic of Sakha (Yakutia). The reasons causing these changes are under evaluation but climate change, anthropogenic pressure in natural landscapes as well as the number of vertebrate animals are among the most influential factors. At the same time, it is also possible that inadvertent dispersal of ticks by timber material transported from tick-infested areas may be in part responsible for this phenomenon (Danchinova et al. 2006). Although other factors are not excluded, it is believed that climate changes have made the greatest contribution to the increase in areas primarily for TBE foci in the northern regions of the country. But despite all this, as a result of the same changes, the southwestern part of the range of *I. persulcatus* in Belarus and the Baltic countries has decreased (Pogodina 2021).

Often it can be found in the same biotopes together with *I. ricinus* in Europe and *I. pavlovskyi* in Siberia with complete or partial coincidence of the seasonal activity of these species at each ontogenetic stage (Ushakova and Filippova 1968; Bolotin et al. 1977; Filippova 1999). In zones of sympatry their hybridization can occur, and their hybrids can also transmit tick-borne encephalitis virus and probably other pathogens (Kovalev et al. 2015; Rar et al. 2019; Belova et al. 2023). Under laboratory conditions, interspecific hybridization between *I. ricinus* and *I. persulcatus* was successfully conducted as well. F1 hybrid ticks were completely sterile, as revealed by unsuccessful attempts of their subsequent hybridization with ticks of the parent generation (Balashov et al. 1998). In *I. persulcatus* and *I. ricinus*, any morphological barrier to crossing is undoubtedly

absent and then sterility of the F1 hybrid generation is probably a quite significant factor limiting the population size of both species in their sympatric areas. Hybrid ticks also have morphological features allowing to differentiate them at preimaginal and imaginal stages (Bugmyrin et al. 2015, 2016). Moreover, some studies were conducted in the Southern Primorye (Filippova 2002) in sympatric zones of *I. persulcatus* and *I. pavlovskyi occidentalis*, due to the close cohabitation of both species. These showed that in case of these two species there are distinct morphological barriers which are manifested in the fitting of organs involved in mating, in particular their size proportions. According to the result of the studies, mating and hybridization of different tick species are possible only in the next combination: female *I. pavlovskyi* and male *I. persulcatus*. Whereas in case of the reverse combination, the parameters of the genital aperture of the female exceed those of the largest width of the hypostome in the male.

There is an excellent summary on the questing behavior of *I. persulcatus* in the monograph by Filippova (1985). In brief, the ticks climb onto the vegetation in quest of a host. When the host approaches, the tick spreads its first pair of legs and, upon contact with the host, become attached. From time to time, ticks perform vertical migrations and go even into the soil litter for rehydration. Horizontal movements of ticks towards trails used by potential hosts are also possible, as well as crawling onto a nearby animal. Ticks react to humans by spreading their first legs from distances of ~ 15–20 m. At short distances, ticks also react to a heat source. In general, a similar pattern of questing behavior is used by other exophilic ticks of the genus *Ixodes*.

In *I. persulcatus* there is an important signaling mechanism causing a morphogenetic diapause – a developmental delay which is the response of ticks to the duration of the diurnal photoperiod (Belozarov 1976). Moreover, *I. persulcatus* has a behavioral diapause of non-engorged adult ticks, which is not connected with photoperiodic regulation (Korenberg et al. 2021). But as the studies in the Kirov Oblast and Udmurt Republic showed, in more warmer areas, an increased proportion of engorged larvae and nymphs develop without the diapause and the reason for this is the early activation and, as a result, their mass feeding on hosts in the first half of summer. The factors determining the diapause of engorged larvae and nymphs in the compared regions practically do not differ (Korotkov 2008). The correlation of the tick number varies, depending on the type of biotope, as well as temperature and humidity and also many other abiotic factors. For example, in boreal taiga forests of Karelia mainly *I. persulcatus* dominates (except the southwestern part where the mass species is *I. ricinus*) (Bugmyrin et al. 2013). The beginning of adult *I. persulcatus* activity also differs in different regions depending on the sum of abiotic factors listed above. For example, in the Far East the seasonal peak in the number of larvae is observed in the third decade of May – second decade of July, whereas in the European part of its range in the third decade of July (Belozarov 1976; Filippova 1977; Balashov 1998; Korenberg et al. 2013). In the territory from the Volga River to Primorye the average activity of adult ticks varies from 60 to 140 days (Korenberg et al. 1974). The boundaries of the range of the tick are determined mainly by the combination of photo- and hygrothermal factors. The general indicators of warmth and moisture along the range of this tick species vary widely. The fundamental ecological niche of *I. persulcatus* with the broad scope of its preferred conditions allows it to adapt to the wide diversity of biotopes in the forest zone.

Some type specimens of *I. persulcatus* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. persulcatus* subsp. *diversipalpis* (Schulze 1930: 300), lectotype: male; [Russia, Primorskii Terr.], lower Amur River, 8 km of Vyatskoe Vill., 26.VI.1910, coll. Soldatov, det. N.O. Olenev: *I. ricinus ovatus*; AL I266, as well as the paralectotypes: 1 female, 1 male; AL I266a. *I. persulcatus* (see: Filippova 1969: 677). Description – Filippova 1977: 316–327 (female, male, nymph, larva) (Filippova 2008). But Filippova (1969) also states that re-examination of the type material of the above subspecies demonstrated that the specimens used for describing differences of this subspecies are damaged in some morphologically important parts (not noticed before), and the key morphological characters that were previously thought to distinguish the subspecies are not specific enough and can be found in ticks throughout their entire geographical range.

***Ixodes redikorzevi* Olenev, 1927**

Ixodes redikorzevi Olenev, 1927: 219.

Recorded hosts. Mammalia: *Apodemus agrarius* (striped field mouse), *Apodemus mystacinus* (Danford and Alston) (eastern broad-toothed field mouse), *Apodemus uralensis* (Ural field mouse), *Arvicola amphibius* (European water vole), *Chionomys nivalis* (European snow vole), *Chionomys roberti* (Thomas) (Robert's snow vole), *Cricetus cricetus* (European hamster), *Crocidura leucodon* (bicolored shrew), *Crocidura suaveolens* (lesser white-toothed shrew), *Dryomys nitedula* (forest dormouse), *Erinaceus europaeus* (European hedgehog), *Glis glis* (European edible dormouse), *Hemiechinus auratus* (long-eared hedgehog), *Lepus europaeus* (European hare), *Marmota bobak* (bobak marmot), *Martes martes* (European pine marten), *Meles meles* (European badger), *Meriones libycus* (Libyan jird), *Meriones meridianus* (midday jird), *Meriones persicus* (Persian jird), *Meriones tamariscinus* (Pallas) (tamarisk jird), *Meriones tristrami* Thomas (Tristram's jird), *Mesocricetus auratus* Waterhouse (golden hamster), *Mesocricetus raddei* (Ciscaucasian hamster), *Microtus arvalis* (common vole), *Microtus majori* (Major's pine vole), *Microtus socialis* (social vole), *Mus musculus* (house mouse), *Mustela eversmannii* (steppe polecat), *Mustela nivalis* (least weasel), *Nesokia indica* (short-tailed bandicoot rat), *Nothocricetulus migratorius* (grey dwarf hamster), *Rattus norvegicus* (brown rat), *Rattus pyctoris* (Turkestan rat), *Rattus rattus* (black rat), *Rhombomys opimus* (great gerbil), *Sciurus anomalus* Gmelin (Caucasian squirrel), *Sciurus vulgaris* (red squirrel), *Sicista betulina* (northern birch mouse), *Sicista subtilis* (southern birch mouse) *Spalax giganteus* Nehring (giant blind mole-rat), *Spalax microphthalmos* Gueldenstaedt (greater blind mole-rat), *Spermophilopsis leptodactylus* (long-clawed ground squirrel), *Spermophilus pygmaeus* (little ground squirrel), *Sorex araneus* (common shrew), *Vormela peregusna* (marbled polecat) *Vulpes vulpes* (red fox) (Filippova 1977).

Aves: *Alauda arvensis* Linnaeus (Eurasian skylark), *Alectoris chukar* (chukar partridge), *Anthus campestris* (tawny pipit), *Anthus pratensis* (Linnaeus) (meadow pipit), *Coccothraustes coccothraustes* (hawfinch), *Columba livia* (rock dove), *Emberiza calandra* (corn bunting), *Emberiza schoeniclus* (Linnaeus) (common reed bunting), *Erithacus rubecula* (Linnaeus) (European robin),

Galerida cristata (crested lark), *Garrulus glandarius* (Linnaeus) (Eurasian jay), *Lullula arborea* (woodlark), *Melanocorypha calandra* (Linnaeus) (calandra lark), *Mergus serrator* Linnaeus (red-breasted merganser), *Oenanthe hispanica* (Linnaeus) (western black-eared wheatear), *Oenanthe isabellina* (Temminck) (Isabelline wheatear), *Oenanthe lugens* (Lichtenstein) (mourning wheatear), *Oenanthe oenanthe* (Linnaeus) (northern wheatear), *Oenanthe picata* (Blyth) (variable wheatear), *Phylloscopus collybita* (Vieillot) (common chiffchaff), *Phylloscopus fuscatus* (dusky warbler), *Pica pica* (Eurasian magpie), *Pterocles orientalis* (Linnaeus) (black-bellied sandgrouse), *Saxicola torquatus* (Linnaeus) (African stonechat), *Sturnus vulgaris* (common starling), *Turdus merula* (common blackbird), *Turdus philomelos* (song thrush), *Turdus ruficollis* (red-throated thrush) (Filippova 1977).

Reptilia: *Darevskia chlorogaster* (Boulenger) (greenbelly lizard) (Orlova et al. 2022), *Lacerta agilis* Linnaeus (sand lizard) (Filippova 1977), *Lacerta strigata* Eichwald (Caucasus emerald lizard) (Orlova et al. 2023), *Pseudopus apodus* (Pallas) (Pallas's glass lizard) (Filippova 1977).

Recorded locations (Fig. 15). Russia: Rostov Oblast (Khametova et al. 2018), Krasnodar Krai, Stavropol Krai, Kalmyk Republic, Chechnya, Dagestan, and North Osetia-Alania (Shatas 1957; Shevchenko et al. 1960; Zaytsev and Popova 1967; Tiflova 1974; Filippova 1977; Abdulmagomedov et al. 2017; Zaytseva et al. 2022). **Ukraine:** Odesa Oblast (Bugeac Steppe), Kherson Oblast (Black Sea Biosphere Reserve), Poltava Oblast, Chernivtsi Oblast, Dnipropetrovsk Oblast, Luhansk Oblast, Donetsk Oblast, widely distributed in the Crimean Peninsula (Emchuk 1960; Emchuk 1967; Sklyar 1970; Filippova 1977). **Moldova:** the north of the country (Uspenskaya et al. 2006). **Georgia:** outskirts of Kutaisi and Tbilisi and the Lagodekhi Nature Reserve, as well as the seacoast of the Black Sea (Kirschenblatt 1936; Djaparidze 1960; Filippova 1977). **Armenia:** outskirts of



Figure 15. Map of Russia and neighboring countries showing the locations where *Ixodes redikorzevi* was reported.

Yerevan and most of the rest of the territory (Zilfyan et al. 1960; Tiflova 1974). **Azerbaijan:** Zagatala State Reserve, Hadrut District, and the Mil plain (Tiflova 1974), outskirts of the Bilasuvar, the Sara Peninsula (Kirschenblatt 1936), Talysh (Pomerantsev 1950), Nakhchivan Autonomous Republic (Kadatskaya and Shirova 1963; Filippova 1977). **Kazakhstan:** West Kazakhstan Region, Kyzylorda Region, North Kazakhstan Region, Jambyl Region, Turkistan Region, Abai Region (Loseva 1963; Popova and Sokolova 1963). **Kyrgyzstan:** outskirts of Bishkek, Chüy Valley, Talas Valley, Issyk-Kul Basin, Terskey Ala-too Range (Filippova 1958b; Grebenyuk 1966; Filippova 1977). **Turkmenistan:** foothills of the Uly Balkan and the Kopet Dag; the Kugitangtau Range (Kochkareva et al. 1971; Filippova 1977). **Uzbekistan:** outskirts of Tashkent, foothills of the Chatkal Range, Qurama Mountains, the Hisar Range, the Kugitangtau Range and Karakalpakstan – the Ustyurt Plateau and the lower reaches of the Amu Darya River (Kuklina 1967; Uzakov 1972; Filippova 1977). **Tajikistan:** Hisar Range - Varzob gorge, outskirts of Dushanbe – the Ramit State Nature Reserve, Vakhsh Range, Peter the First Range (Lotozky 1951; Sosnina 1957; Filippova et al. 1966; Kochkareva et al. 1971; Filippova 1977).

Ecology and other information. *Ixodes redikorzevi* is a tick species which is mainly a parasite of rodents, shrews, and small carnivores, as well as of dendrophilic ground-feeding birds and rarely reptiles (Filippova 1977). According to Tiflova (1974), this species is considered exophilic and can be found in significant numbers on dendrophilic birds. In the absence of mammalian and avian hosts, *I. redikorzevi* can parasitize lizards in significant numbers (Orlova et al. 2022). It usually inhabits mountain deciduous forests and steppes located nearby.

Beyond the post-Soviet territories considered above, the range of this tick covers also Eastern Europe, Turkey, Israel, as well as Afghanistan (Filippova 1977) and China (Yin et al. 2010).

At the current moment it is still questionable whether *I. redikorzevi* is a synonym of *I. acuminatus* or not. Kolonin (2009) considers this species a synonym of *I. acuminatus*, but Guglielmone et al. (2010) regard it as provisionally valid. As it was fairly noted by Guglielmone et al. (2014) this question can be solved by comparison of the type specimens of both species. Moreover, Pomerantsev (1950) described by females two subspecies: *I. redikorzevi redikorzevi* and *I. redikorzevi emberizae*. Later the other subspecies *I. redikorzevi theodori* was described although Filippova comments (1977) that the authors had quite little material during descriptions but the differences in size and shape of some characters are visible and it is necessary to compare more specimens from more locations of its large area of distribution.

Ixodes redikorzevi redikorzevi occurs in Ukraine, the Transcaucasus and Tajikistan according to Pomerantsev (1950); and *I. redikorzevi emberizae* can be found in Lankaran and the Hisar Range in Tajikistan. Later the other subspecies, *I. redikorzevi theodori* was described from the Middle East (Warburton 1927).

The type specimens of *I. redikorzevi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; [former] Tavricheskaya Province (Crimea), Yaman-Kala, near Baidar, 25.10.1924, coll. V. Shnitnikov, AL I338 and the paralectotype of *I. redikorzevi emberizae* female; AL I522. Description – Pomerantsev 1950: 63 (female; male unknown); Filippova 1977: nymph, larva (Filippova 2008).

***Ixodes ricinus* (Linnaeus, 1758)**

- Acarus ricinus* Linnaeus, 1758: 616.
Ixodes reduvius (Linnaeus): Neumann 1911: 12.
Ixodes sanguisugus (Linnaeus): Morel and Pérez 1978: 201.
Ixodes vulgaris (Fabricius): Neumann 1911: 12.
Ixodes holsatus (Fabricius): Nuttall and Warburton 1911: 285.
Ixodes megathyreus Leach: Neumann 1911: 12.
Ixodes bipunctatus Risso: Neumann 1911: 12.
Ixodes trabeatus Audouin: Neumann 1911: 12.
Ixodes marginalis Hahn: Oudemans 1896: 191.
Ixodes sciuri Koch: Neumann 1911: 12.
Ixodes fuscus Koch: Neumann 1911: 12.
Ixodes sulcatus Koch: Neumann 1911: 12.
Ixodes rufus Koch: Neumann 1901: 249.
Ixodes lacertae Koch: Neumann 1911: 12.
Ixodes pustularum Mégnin: Neumann 1911: 12.
Ixodes vicinus Yerrill: Oudemans 1896: 191.
Ixodes fodiens Murray: Neumann 1904: 444.
Ixodes nigricans Neumann: Schulze 1939: 1.
Ixodes areolaris Olenov: Pomerantsev 1950: 37.

Recorded hosts. The host spectrum of *I. ricinus* is extremely broad both systematically and ecologically, including literally almost all mammals and birds of its geographical range, rarely even reptiles inhabiting the same biotopes with the tick. The fact of mass parasitism of immature stages on lizards of the Lacertidae family, in particular species of the genus *Darevskia* in the Caucasus (Kidov et al. 2013; Orlova et al. 2022) in habitats where they outnumber small mammals probably brightly demonstrates that *I. ricinus* is a generalist tick capable to use almost any available terrestrial vertebrates as hosts. Overall, the list of hosts consists of more than 300 species of mammals, birds and reptiles which have been recorded (Gern et al. 2002). Humans and domestic animals can also be hosts for the tick (Filippova 1977).

Distribution (Fig. 16). The distribution of *I. ricinus* in Russia includes almost the whole territory of its European part excluding subpolar tundra areas (see the map) (Filippova 1977; Kahl and Gray 2023) and due to climate changes, the distribution of this tick species becomes wider (Gray et al. 2009; Yasyukevich et al. 2009). *Ixodes ricinus* is part of the tick fauna of the following post-Soviet countries: Estonia, Latvia, Lithuania, Belarus, Russia, Ukraine, Moldova, Georgia, Azerbaijan, Armenia, Turkmenistan, and Kazakhstan (Guglielmone et al. 2023). In Kazakhstan a little number of specimens were found in the northern part of West Kazakhstan Oblast (Maikanov 2012). In Turkmenistan the tick was also recorded in few numbers in the western foothills of the Kopet-Dag (Kerbabaev 1960) which probably could be transported there by migratory birds.

Ecology and other information. *Ixodes ricinus* is an exophilic tick species widely distributed in Europe, mostly inhabiting deciduous and mixed forest zones in both plain and mountainous areas, as well as forest-steppes bordering them. It also occurs in city parks and gardens (Gray 1998). In addition, it can be found in North Africa (Arthur 1965). In Ukraine *I. ricinus* colonized and reached

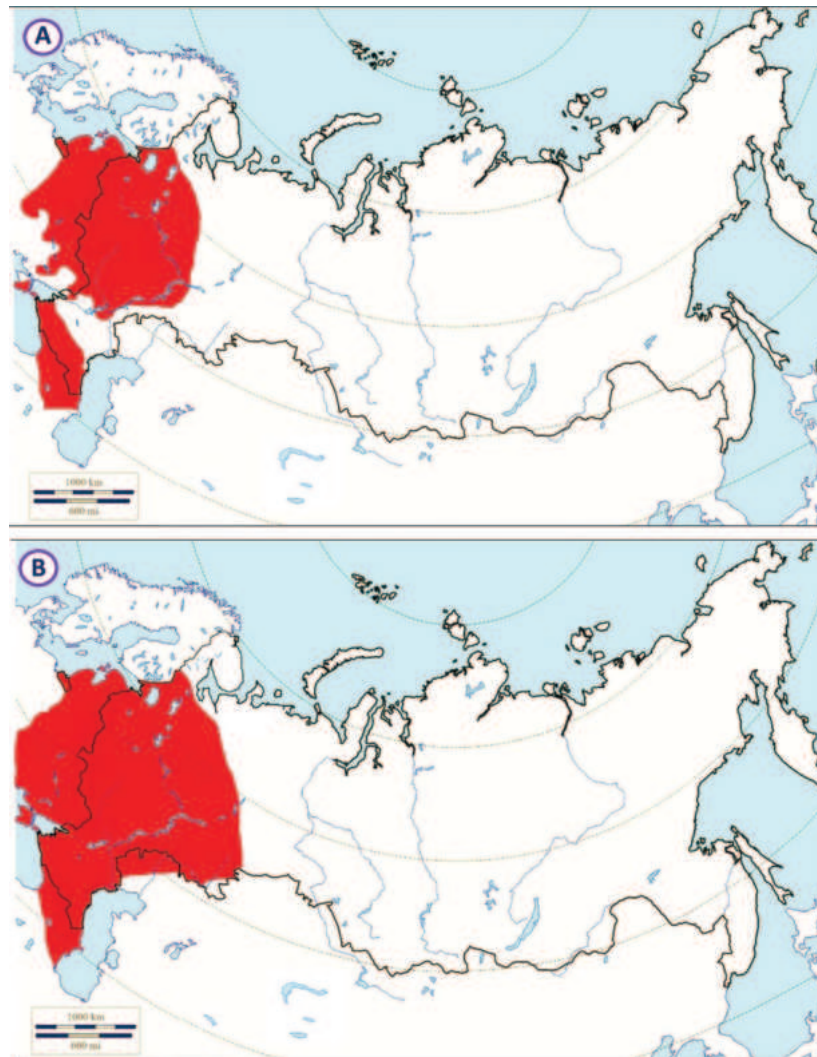


Figure 16. Map of Russia and neighboring countries showing the locations where *Ixodes ricinus* was reported: **A** before 1975 **B** from 1976.

a high abundance in artificial forest plantations of the Askania-Nova Nature Reserve surrounded from all sides by steppes for a period of less than 80 years (Emchuk 1972). In urban areas with conditions able to support tick populations, for example, Minsk or Kyiv, *I. ricinus* usually dominates among other tick species, especially among members of the genus *Ixodes* (Uspensky 2017). This tick species uses almost all forest vertebrate animals as hosts and, together with *I. persulcatus*, it is one of the most important vectors of a broad spectrum of tick-borne pathogens, first of all, tick-borne encephalitis virus (Filippova 1977).

Often it can be found in the same biotope with *I. persulcatus*, often exhibiting complete or partial coincidence of seasonal activity at each ontogenetic stage (Filippova 1999). In zones of sympatry their hybridization can occur, and although hybrid offspring are incapable of reproduction (Bugmyrin et al. 2015), they can still transmit tick-borne encephalitis virus and probably other pathogens (Kovalev et al. 2016; Belova et al. 2023). The absence of any morphological barrier for copulation was discovered in geographical points of probably the secondary sympatric zone (Filippova 2002) of *I. persulcatus* and *I. ricinus* in the north-west of the East European Plain (Balashov et al. 1998). However, in some areas of this sympatric zone, for example, in southern Kare-

lia, its slight shrinking has recently been noted due to the withdrawal of *I. ricinus* from territories where it used to live (Bespyatova and Bugmyrin 2021).

Due to the high epidemiological significance and wide distribution of *I. ricinus* and its regular contacts with humans and domestic animals, its biology and life cycle were more extensively studied than in case of any other species of its genus inhabiting the same territories. As a species, *I. ricinus* probably appeared approximately 8–12 thousand years ago when deciduous and mixed forests formed in the southeast of Europe and the Mediterranean, as well as in the northern and northeastern slopes of the Greater Caucasus, when current environmental conditions of these territories have begun to shape. And the climate there was also milder than in Siberian taiga forests where *I. persulcatus* evolved (Filippova 2017).

It was revealed that in a certain region the duration of tick activity period and the number of adult ticks depend on spring and summer temperatures and air humidity (Korotkov et al. 2015; Korenberg et al. 2021). Females and larvae usually attach to hosts when the air near the soil warms up from +2 to +30 °C, and in the case of nymphs from +2 to +22 °C. The relative humidity of the surrounding air has to be higher than 60% for an extended period of time (Sirotkin and Korenberg 2018). It is absolutely important for ticks to receive the necessary amount of warmth to complete their metamorphosis at each stage within a strictly defined period of time (Korenberg et al. 2013). As a consequence, the seasonal activity of all stages of *I. ricinus* is more extended than in the case of *I. persulcatus*, and engorged ticks begin oviposition or metamorphosis without strict dependence on the photoperiod. Therefore, in the southern range of distribution (the Mediterranean, Central Europe, the Caucasus) ticks initiate activity in the end of March – the beginning of April (Korenberg et al. 2021), whereas in Eastern European regions – in April (Medvedev et al. 2016; Korenberg et al. 2021). *Ixodes ricinus* also uses a diapause as a biological mechanism, although due to warmer conditions in the majority of its distribution range, no more than 10–20% of ticks at each stage undergo such an interruption of development (Korenberg and Kovalevsky 1977; Korenberg et al. 2016).

***Ixodes sachalinensis* Filippova, 1971**

Ixodes sachalinensis Filippova, 1971: 236; Kolonin 1981: 49.

Ixodes persulcatus diversipalpis Schulze, 1930: 294; Pomerantsev 1950: 43.

Ixodes persulcatus cornuatus Olenev: Pomerantsev 1950: 43.

Recorded hosts. Mammalia: *Lepus timidus* (mountain hare) (Filippova 1977).

Recorded locations (Fig. 17). Russia: the Sakhalin Island, Sachalin Oblast, the rural locality Khomutovo (Filippova 1971).

Ecology and other information. *Ixodes sachalinensis* is a tick species known only by the single finding from Sakhalin. It was collected from a mountain hare together with 79 females, 15 males and 7 nymphs of *I. persulcatus* (Filippova 1971).

Kolonin (2009) and Camicas et al. (1998) consider *I. sachalinensis* a synonym of *I. persulcatus*, but Barker and Murrell (2004) and Guglielmone et al. (2009, 2010) recognize this species as valid.

The type specimen is deposited at the Zoological Institute of the Russian Academy of Sciences and includes the holotype: female; [Russia], Sakhalin, near Khomutovo Vill., *Lepus timidus*, 27.5.1950, [coll.: unknown]; AL 1729 (Filippova 2008).

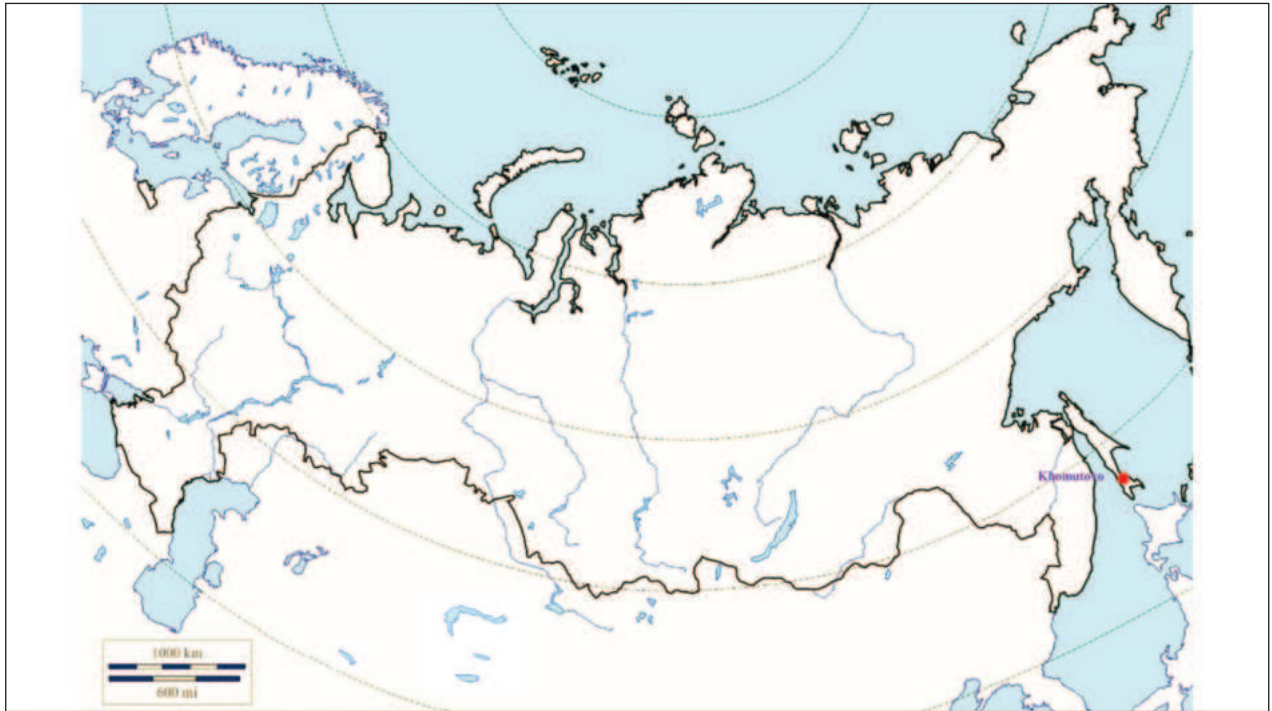


Figure 17. Map of Russia and neighboring countries showing the locations where *Ixodes sachalinensis* was reported.

Subgenus *Ixodiopsis* Filippova, 1957: 31.

Ixodes angustus Neumann, 1899

Ixodes angustus Neumann, 1899: 136.

Recorded hosts. Mammalia: *Alexandromys oeconomicus* (tundra vole), *Craseomys rufocanus* (grey red-backed vole), *Eutamias sibiricus* (Siberian chipmunk), *Mus musculus* (house mouse), *Myodes rutilus* (northern red-backed vole), *Ochotona alpina* (alpine pika), *Rattus norvegicus* (brown rat), *Sicista caudata* Thomas (long-tailed birch mouse), *Sorex araneus* (common shrew), *Sorex minutus* (Eurasian pygmy shrew) (Filippova 1977).

Recorded locations (Fig. 18). Russia: outskirts of Magadan and the lower reaches of the Kukhtui River, Okhotsky district – the northernmost points of record of *I. angustus* in the Palearctic (Belyaev 1963); Kamchatka Peninsula – outskirts of the villages Tigil and Ust-Khayryuzovo (Pomerantsev 1950), the valley of the Kamchatka River to Ust-Kamchatsk (Serdjukova 1956), the eastern coast of the Kamchatka peninsula to Petropavlovsk-Kamchatsky (Speranskaya 1958), the valley of the rivers Avacha and Pinachevskaya (Paramonov et al. 1966); Middle Outer Manchuria (Filippova 1977); Sovetsko-Gavansky district (Emelyanova and Koshkin 1962); Sikhote-Alin (Belyaev and Filippova 1976); Sakhalin – Novoaleksandrovka (former Konuma), the valley of the Lyutoga River (Pomerantsev 1950) and the Cape Patience (Skrynnik 1950; Asanuma 1951; Violovich 1958, 1960; Savitsky and Okuntsova 1967; Timofeeva and Kon'kova 1971); Kuril Islands – Simushir (Pomerantsev 1950; Violovich 1958, 1960; Timofeeva and Kon'kova 1971).

Ecology and other information. *Ixodes angustus* occurs in the Palearctic predominantly on the East Asian coast and also in the Nearctic – Canada and the USA (Filippova 1977). In the Russian Far East in Outer Manchuria, the islands



Figure 18. Map of Russia and neighboring countries showing the locations where *Ixodes angustus* was reported.

and along the main ridges of the Sikhote-Alin it inhabits a wide range of biotopes: various types of mixed and broad-leaved forests in mountains and valleys, as well as tundra and rocks, stone outcrops, coastal biotopes, meadow and river valleys (Speranskaya 1958; Violovich 1958; Emelyanova and Koshkin 1962; Belyaev 1963; Paramonov et al. 1966; Savitsky and Okuntsova 1967; Belyaev and Filippova 1976).

Ixodes angustus is considered a nidicolous ectoparasite of rodents and shrews because it was found not only on hosts but also in their burrows (Filippova 1977), although there are documented cases on this species biting humans without contacts with burrows (Cooley 1946). As a parasite which is connected with rodents, and, like other rodent ticks, *I. angustus* plays a role in supporting natural foci of tick-borne infections such as anaplasmosis (Yambrko and Eremeeva 2014) and the Lyme disease (Peavey et al. 2000).

Although hyperparasitism is not common in *Ixodes* ticks, *I. angustus* belongs to a small number of species of the genus, in which this phenomenon was recorded (Durden et al. 2018), when a male was feeding from a female attached to a red squirrel *Tamiasciurus hudsonicus*. The other *Ixodes* species in which males have been recorded to attach and feed on engorging conspecific females include *I. holocyclus* in Australia and *I. pilosus* in South Africa (Oliver et al. 1986).

***Ixodes pomerantzevi* Serdjukova, 1941**

Ixodes pomerantzevi Serdjukova, 1941: 519.

Recorded hosts. Mammalia: *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Erinaceus amurensis* Schrenk (Amur hedgehog), *Eutamias sibiricus* (Siberian chipmunk), *Microtus fortis* (reed vole), *Myodes rutilus*

(northern red-backed vole), *Sorex araneus* (common shrew) (Filippova 1977), *Sorex caecutiens* (Laxmann's shrew), *Sorex unguiculatus* Dobson (long-clawed shrew), (individual specimens ((Okulova et al. 1986), *Rattus norvegicus* (brown rat), *Tscherskia triton* (De Winton) (greater long-tailed hamster) (Filippova 1977).

Recorded locations (Fig. 19). Russia: Sikhote-Alin – outskirts of Dal’ny Kut (the northernmost point of finding (Filippova 1977), valley of the Dorozhnaya River, Dalnegorsk, Ussurisky (former Komarovskii) Nature Reserve; coast of the Sea of Japan – outskirts of the villages Terney, Dukhovo, Kamenka, Lazovsky nature reserve, Fokino (former Promyslovka), the bays Razboynik and Linda; the coast of the Peter the Great Gulf: Kedrovaya Pad Nature Reserve, the rural localities Barabash and Posyet (Serdjukova 1941; Pomerantsev 1950; Slonov 1961; Khudyakov 1963; Belyaev and Filippova 1976).

Ecology and other information. *Ixodes pomerantzevi* is a relict species occurring on the East Asian coast (Filippova 1977) and in Russia its distribution is limited to a few locations in Outer Manchuria (a.k.a. Primorsky Krai) in the Russian Far East (Tsapko 2020). It is also known to occur in Korea (Kim et al. 2009a, 2010, 2011) and China (Guo et al. 2016). Predominantly it can be found in coniferous and broad-leaf forests, or secondary forests and bush thickets, as well as rock and stone outcrops among trees in the Sikhote-Alin and on the coast of the Sea of Japan (Belyaev and Filippova 1976).

Luh and Woo (1950) supposed that *I. pomerantzevi* is possibly a synonym of *Ixodes angustus*; Filippova (1977) considered it as valid and in the last list of valid tick species names, it is also considered valid (Guglielmone et al. 2020).

Ixodes pomerantzevi is a nidicolous tick species, an ectoparasite of rodents, hedgehogs, and shrews (Filippova 1977).

The type specimen of *I. pomerantzevi* is deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; [Russia], DVK



Figure 19. Map of Russia and neighboring countries showing the locations where *Ixodes pomerantzevi* was reported.

[Primorskii Terr.], Suputinskii [Komarovskii or Ussuriskii] Nature Reserve, from *Myodes rufocanus*, 9–13.VI.1939, coll. B.I. Pomerantsev; AL I502. Description – Filippova 1977: 128–132 (female, male - unknown, nymph, larva) (Filippova 2008).

Ixodes stromi Filippova, 1957

Ixodes stromi Filippova, 1957: 864.

Recorded hosts. Mammalia: *Alticola argentatus* (Severtzov) (silver mountain vole), *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Crocidura* sp. (shrew), *Lasiopodomys gregalis* (narrow-headed vole), *Microtus arvalis* (common vole), *Mustela* sp. (weasel), *Myodes centralis* (Miller) (Tien Shan red-backed vole), *Nothocricetulus migratorius* (grey dwarf hamster), *Ochotona macrotis* (Günther) (large-eared pika), *Rattus pyctoris* (Turkestan rat) (Filippova 1977).

Recorded locations (Fig. 20). Russia: Western Sayan (Arumova and Dineva 1973). **Kazakhstan:** Tarbagatai Mountains (Afnas'eva 1959), Dzungarian Alatau (Ushakova and Fedosenko 1963; Ushakova et al. 1976), Trans-Ili Alatau (Ushakova and Fedosenko 1963). **Kyrgyzstan:** Kyrgyz Ala-Too Range (Fedorova 2012b), Terskey Alatau (Fedorova 2012b), Chuy Valley – found in 1966 (Grebnyuk 1966), was not found in the same territories in 2018 (Fedorova 2021). **Tajikistan:** Peter the First Range (Filippova 1977), Varzob gorge (Sosnina 1954 – here *I. stromi* was incorrectly identified as *I. trianguliceps* because the new species was described by Filippova in 1957b).

Ecology and other information. *Ixodes stromi* is a tick species only indigenous to southern Siberia in Russia (Tsapko 2020). The main part of its distribution spans in Kazakhstan and Middle Asia. In all territories of its range,

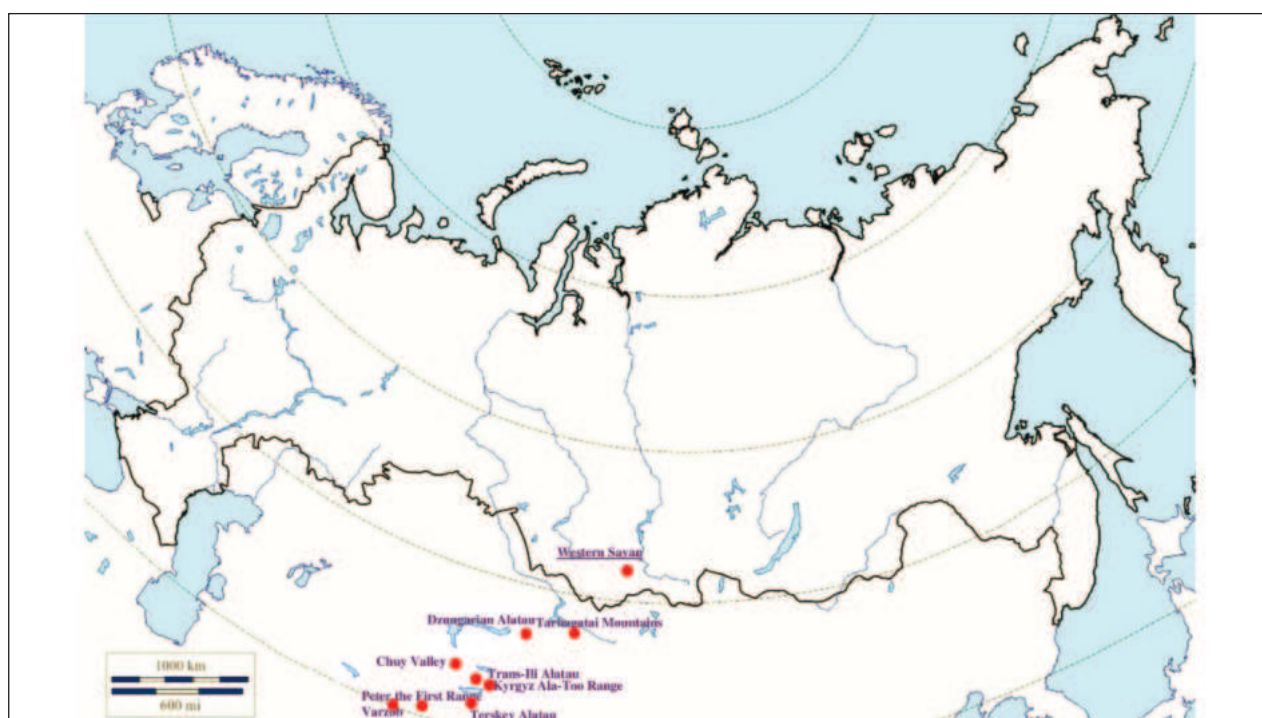


Figure 20. Map of Russia and neighboring countries showing the locations where *Ixodes stromi* was reported.

it is confined to the forest-meadow and forest-steppe belt of medium-altitude mountains, to stony and rocky habitats, which are insolated and, therefore, have a warmer microclimate (Filippova 1967).

This species is nidicolous and uses rodents, shrews, and small carnivores as hosts at all stages. It is considered a rare species reaching small individual number (Filippova 1977).

The type specimens of *I. stromi* are known from Kyrgyzstan and stored at the Zoological Institute of the Russian Academy of Sciences: the lectotype: the nymph; Kyrgyzstan, Tien Shan, Kungei Ala Tau Mt. Range, Ch-Aksu Canyon, talus, from *Clethrionomys frater* (synonym of *Myodes centralis*), 11.VIII.1953, coll. N.A. Filippova; AL I78. The paralectotypes: 6 larvae; FBM I586, I876; 6 larvae; FBM I873, I875. Description – Filippova 1977: 122–127 (female, nymph, larva; male unknown) (Filippova 2008).

Subgenus *Monoixodes* Emelyanova & Kozlovskaya, 1967: 489.

***Ixodes maslovi* Emelyanova & Kozlovskaya, 1967**

Ixodes maslovi Emelyanova & Kozlovskaya, 1967: 489.

Recorded hosts. To date hosts of this tick species are unknown (Guglielmone et al. 2014).

Recorded locations (Fig. 21). Russia: Khabarovsk Krai – Khekhtsir Range and the rural locality Vyatskoye (Emelyanova and Kozlovskaya 1967); Krasnoyarsk Krai – Kozulsky District, the village Bolshoy Kemchug (Voltsyt 1997).

Ecology and other information. *Ixodes maslovi* is an almost unstudied tick known and described from two findings of its male and female (Emelyanova and Kozlovskaya 1967), as well as the nymph (Voltsyt 1997).

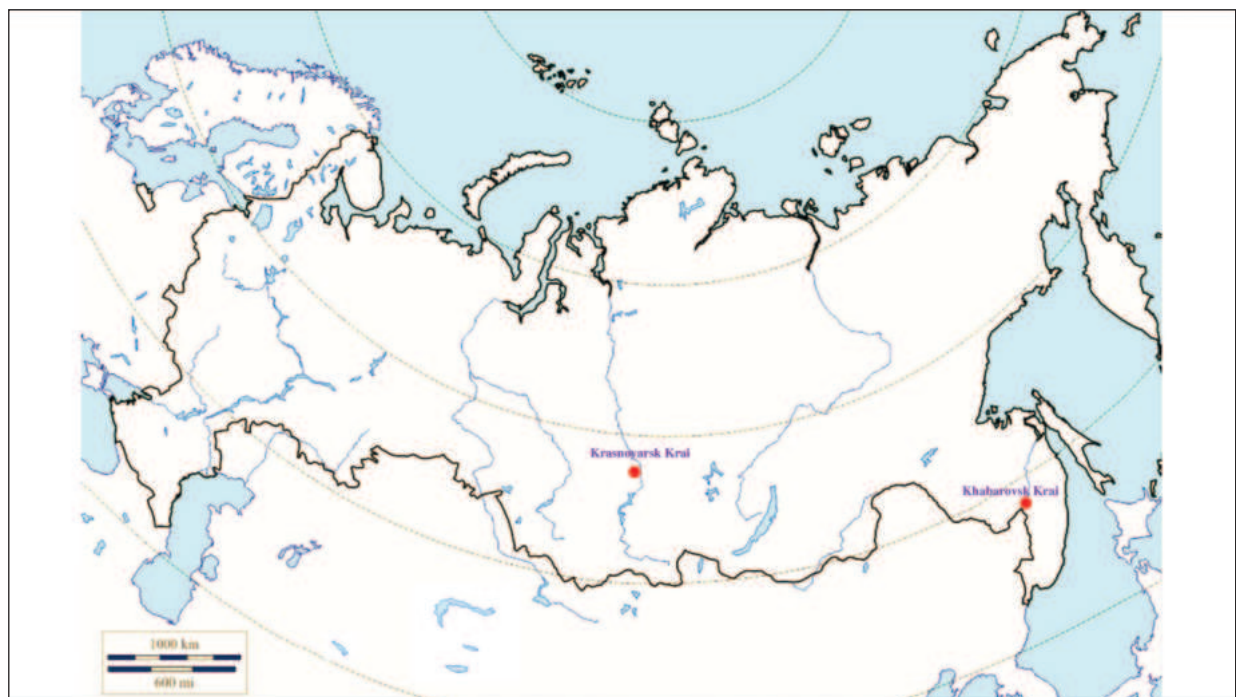


Figure 21. Map of Russia and neighboring countries showing the locations where *Ixodes maslovi* was reported.

Camicas et al. (1998) and Kolonin (2009) regard *I. maslovi* as an abnormal form of *I. persulcatus* although Filippova (1977) and Guglielmone et al. (2020) consider *I. maslovi* a valid taxon.

The type specimens are deposited at the Zoological Institute of the Russian Academy of Sciences – the holotype: male; [Russia], environs of Khabarovsk, Khehtsir Mt. Range, 12.VI.1964, collected from vegetation by O.L. Kozlovskaya; FBM I1412; the paratype: female; FBM I1413. Description – Filippova 1977: 248–251 (female, male); Voltsit 1997: 265–268 (nymph; larva unknown) (Filippova 2008).

Subgenus *Pholeoixodes* Schulze, 1942: 630.

***Ixodes arboricola* Schulze & Schlottke, 1929**

Ixodes arboricola Schulze & Schlottke: Morel and Pérez 1973: 275.

Ixodes arboricola muscicapae Schulze, 1930: 3; Haarløv 1962: 425.

Ixodes strigicola Schulze & Schlottke: Haarløv 1962: 425.

Ixodes dryadis Schulze & Schlottke: Haarløv 1962: 425.

Ixodes passericola Schulze: Haarløv 1962: 425.

Ixodes arboricola bogatschevi Kirshenblat, 1936: 93; Haarløv 1962: 425.

Ixodes lagodechiensis Dzshaparidze, 1950: 117; Kolonin 1981: 84.

Recorded hosts. Aves: *Accipiter gentilis* (Linnaeus) (northern goshawk), *Acrocephalus scirpaceus* (Hermann) (Eurasian reed warbler), *Aegithalos caudatus* (Linnaeus) (long-tailed tit), *Aegolius funereus* (Linnaeus) (boreal owl), *Athene noctua* (little owl), *Certhia brachydactyla* Brehm (short-toed treecreeper), *Certhia familiaris* Linnaeus (Eurasian treecreeper), *Chloris chloris* (European greenfinch), *Coloeus monedula* (Linnaeus) (western jackdaw), *Columba palumbus* Linnaeus (common wood pigeon), *Coracias garrulus* Linnaeus (European roller), *Corvus frugilegus* Linnaeus (rook), *Curruca communis* (common white-throat), *Cyanistes caeruleus* (Linnaeus) (Eurasian blue tit), *Dendrocopos major* (great spotted woodpecker), *Emberiza citrinella* (yellowhammer), *Erithacus rubecula* (European robin), *Falco peregrinus* Tunstall (peregrine falcon), *Falco tinnunculus* Linnaeus (common kestrel), *Ficedula albicollis* (Temminck) (collared flycatcher), *Ficedula hypoleuca* (European pied flycatcher), *Garrulus glandarius* (Eurasian jay), *Glaucidium passerinum* (Linnaeus) (Eurasian pygmy owl), *Hirundo rustica* Linnaeus (barn swallow), *Lophophanes cristatus* (Linnaeus) (crested tit), *Motacilla alba* (white wagtail), *Muscicapa striata* (Pallas) (spotted flycatcher), *Parus major* (great tit), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Periparus ater* (Linnaeus) (coal tit), *Phoenicurus ochruros* (Gmelin) (black redstart), *Phoenicurus phoenicurus* (common redstart), *Phylloscopus trochilus* (Linnaeus) (willow warbler), *Picus canus* Gmelin (grey-headed woodpecker), *Poecile montanus* (Conrad von Baldenstein) (willow tit), *Poecile palustris* (Linnaeus) (marsh tit), *Pyrrhula pyrrhula* (Linnaeus) (Eurasian bullfinch), *Remiz pendulinus* (Linnaeus) (Eurasian penduline tit), *Riparia riparia* (Linnaeus) (sand martin), *Serinus serinus* (Linnaeus) (European serin), *Sitta europaea* (Eurasian nuthatch) (Filippova 1977; Keve et al. 2022), western rock nuthatch *Sitta neumayer* Michahelles (Ogandzhanyan 1984), *Spinus spinus* (Linnaeus) (Eurasian siskin), *Strix aluco* Linnaeus (tawny owl), *Sturnus vulgaris* (common starling), *Troglodytes troglodytes* (Linnaeus) (Eurasian wren),



Figure 22. Map of Russia and neighboring countries showing the locations where *Ixodes arboricola* was reported.

Turdus merula (common blackbird), *Turdus philomelos* (song thrush), *Tyto alba* (Scopoli) (barn owl), *Upupa epops* Linnaeus (Eurasian hoopoe) (Filippova 1977; Keve et al. 2022).

Recorded locations (Fig. 22). **Russia:** Southern Primorskyi Krai (Pogranichny District, Vladivostok, Nakhodka, Putyatın Island) (Emelyanova and Gordeeva 1969; Emelyanova 1972; Bolotin 2000). **Ukraine:** outskirts of Kyiv (Nebogatkin 2014), Dnipropetrovsk Oblast (the rural locality Andriivka), Crimea (Olenivka and Alushta) (Filippova 1977). **Belarus:** Białowieża Forest, Minsk, Gomel Oblast (the village Markovskoye) (Gembetsky 1966, 1972). **Armenia:** Syunik Province (former Goris Province) (Ogandzhanyan 1984). **Azerbaijan:** Karabakh (Kirschenblatt 1936). **Georgia:** Lagodekhi Nature Reserve (Djaparidze 1960). **Kyrgyzstan** (Fedorova 2012a).

Ecology and other information. *Ixodes arboricola* is an endophilic parasite, mainly of birds from ecological groups nesting in tree holes and nest boxes and also even in ground burrows (Filippova 1977). Also, certain cases of this species infesting bats in tree holes have been recorded (Arthur 1963).

The interesting feature of its distribution is the disjunctivity, which is confirmed by the discovery of this species in the areas quite distant from each other – western and central Europe, North Africa, Transcaucasia, western Asia, and the Far East in Russia (Estrada-Peña et al. 2018) and China (Chen et al. 2010).

***Ixodes cornutus* Lotozky, 1956**

Ixodes cornutus Lototsky, 1956: 27.

Ixodes rugicollis Schulze & Schlottko: Morel and Aubert 1975: 99.

Recorded hosts. Mammalia: *Mustela erminea* Linnaeus (stoat) (Filippova 1977).



Figure 23. Map of Russia and neighboring countries showing the locations where *Ixodes cornutus* was reported.

Recorded locations (Fig. 23). Tajikistan: Peter the First Range, the source of the Divansu River, close to the Oshanin glacier (Filippova 1977).

Ecology and other information. *Ixodes cornutus* is a species described from two identical females (Lotozky 1956) that were found in Tajikistan, in the eastern part of Peter the First Range, by the source of the Divansu River (the basin of the Surkhob River), near the Oshanin glacier, on a stoat.

The type specimen of *I. cornutus* is deposited at the Zoological Institute of the Russian Academy of Sciences (Lotozky 1956: 27). Lectotype: female; 38 [Tajikistan, the Peter the First Mt. Range], the source of the Divansu River, the ancient moraine of the Oshanin glacier, *Mustela erminea*, ad.; male; 4.VII.1954; AL 1845. Description – Filippova 1977: 178 (female; male, nymph, larva unknown) (Filippova 2008).

***Ixodes crenulatus* Koch, 1844**

Ixodes crenulatus Koch, 1844c: 39; Morel and Pérez 1973: 275.

Note. Tick names are used sensu Guglielmone et al. (2014) in this review. Thus, this species is not synonymous with *I. canisuga* Johnston as suggested by Filippova (1977) based on their morphological similarities and because the latter is not known to occur in Russia. *Ixodes crenulatus* was erroneously synonymized with *I. kaiseri* Arthur (Sonenshine et al. 1969), as clarified later (Filippova and Uspenskaya 1973).

Recorded hosts. Mammalia: *Allactaga major* (Kerr) (great jerboa), *Allactaga sibirica* (Forster) (Mongolian five-toed jerboa), *Allocricetulus evermanni* (Brandt) (Eversmann's hamster), *Apodemus sylvaticus* (wood mouse), *Canis aureus* Linnaeus (golden jackal), *Canis familiaris* (domestic dog), *Canis lupus* Linnaeus (gray wolf), *Cricetulus barabensis* (Pallas) (Chinese striped hamster),

Ellobius talpinus (northern mole vole), *Erinaceus europaeus* (European hedgehog), *Felis catus* Linnaeus (domestic cat), *Felis lybica* Forster (African wildcat), *Hemiechinus auratus* (long-eared hedgehog), *Homo sapiens* Linnaeus (human), *Lasiopodomys gregalis* (narrow-headed vole), *Lepus tolai* (tolai hare), *Marmota baibacina* (gray marmot), *Marmota bobak* (bobak marmot), *Marmota caudata* (Geoffroy) (long-tailed marmot), *Marmota kastschenkoi* Stroganov and Yudin (forest-steppe marmot), *Marmota menzbieri* (Kashkarov) (Menzbier's marmot), *Marmota sibirica* (Tarbagan marmot), *Meles meles* (Eurasian badger), *Microtus arvalis* (common vole), *Mustela eversmanii* (steppe polecat), *Mustela nivalis* (least weasel), *Myodes glareolus* (bank vole), *Myospalax myospalax* (Siberian zokor), *Nothocricetulus migratorius* (grey dwarf hamster), *Nyctereutes procyonoides* (Gray) (common raccoon dog), *Ochotona dauurica* (Pallas) (Daurian pika), *Ochotona pallasii* (Gray) (Pallas's pika), *Otocolobus manul* (Pallas) (Pallas's cat), *Ovis aries* (domestic sheep), *Phodopus sungorus* (Pallas) (winter white dwarf hamster), *Procyon lotor* (Linnaeus) (raccoon), *Spermophilus dauricus* Brandt (Daurian ground squirrel), *Spermophilus pygmaeus* (little ground squirrel), *Spermophilus relictus* (Kashkarov) (relict ground squirrel), *Spermophilus suslicus* (speckled ground squirrel), *Vulpes corsac* (corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977; Litvinov and Sapegina 2003; Kalyagin et al. 2005, 2008).

Aves: *Emberiza cia* Linnaeus (rock bunting), *Oenanthe isabellina* (isabelline wheatear) (Filippova 1977).

Recorded locations (Fig. 24). **Russia:** Tula Oblast (Myasnikov and Kateлина 1964), Kursk Oblast (Lgovsky District), Voronezh Oblast (Kamennaya Steppe Nature reserve), Rostov Oblast (Aksay), Republic of Kalmykia (Derbetovsky District, Sarpinsky District), Volgograd Oblast (Gorodishchensky, Derbetovsky and Sarpinsky District) (Denisov 2010, 2019), Kabardino-Balkaria



Figure 24. Map of Russia and neighboring countries showing the locations where *Ixodes crenulatus* was reported.

(tract Khaimasha) (Bittirova et al. 2019), Dagestan (Aliev et al. 2007), Astrakhan Oblast, Stavropol Krai (Filippova 1977), Saratov Oblast (Turtseva 2007; Denisov 2010, 2019; Porshakov et al. 2020), Yekaterinburg (Milintsevich et al. 2016), Tyumen Oblast (Glazunov and Zotova 2014), Kurgan Oblast (Starikov and Starikova 2021), Novosibirsk Oblast (Suzunsky, Karasuksky and Maslyaninsky District) (Davydova and Lukin 1969), Omsk Oblast (Tarasevich et al. 1971), Kemerovo Oblast (Kalyagin et al. 2005, 2008; Kovalevsky et al. 2018); Altai Krai (Oberth et al. 2015) (Sovetsky District, the village Kokshi) (Filippova 1977), Altai Republic (Shebalinsky District, the village Cherga) (Litvinov and Sapagina 2003), Tuva (Glazunov and Zotova 2014; Filippova 1977), Transbaikal (villages Borgoy, Kyakhta, Selenge and Borzinsky District) (Filippova 1977); Amur Oblast (village Krasny Vostok), Southern Outer Manchuria (Khankaysky District (Kolonin 1986; Bolotin 2000). **Ukraine:** outskirts of Kyiv (Akimov and Nebogatkin 2016), Zakarpattia Oblast and Western Ukraine in general (Podobivskyi and Fedonyuk 2017), Cherkasy Oblast, Dnipropetrovsk Oblast, Askania-Nova Nature Reserve, Striltsivskyi Steppe Nature Reserve, Kharkiv Oblast (Tokarsky and Zorya 2007), Lugansk Oblast (Kuznetsov and Bondarev 2007) (including Khomutovs'kyi Steppe) (Filippova 1977), the north-western sea coast of the Black Sea (Rusev 2009), Crimea (Evstafiev 2017) – plain and mountainous lands (Filippova 1977). **Belarus:** Viciebsk Voblasts (Subbotina and Osmolovsky 2022), Białowieża Forest (Filippova 1977), considered rare (Bychkova et al. 2015). **Moldova:** Lozova, Ivancea, Leova, reedbeds of the low Dniester and Pruth (Filippova 1977; Uspenskaya et al. 2006). **Georgia:** Samegrelo-Zemo Svaneti, Imereti (Sukhiashvili et al. 2020). **Armenia:** Aragats mountain range (Dilbaryan and Poghosyan 2018). **Kazakhstan:** through the whole territory of Kazakhstan (Filippova 1977) and plus recent findings in the next regions: West Kazakhstan Region (Tanitovsky and Maikanov 2018), Almaty Region (Bibikov and Bibikova 2010), Pavlodar Region (Amirova et al. 1989), the north of Betpak-Dala (Rapoport et al. 2017), Jambyl Region (Kyrgyz Ala-Too Range, Talas Alatau) (Sarsenbaeva et al. 2016). **Kyrgyzstan:** Tian Shan in general (Abdikarimov et al. 2018) and its certain ranges and valleys including Kyrgyz Ala-Too Range (Akyshova et al. 2022) and Terskey Ala-too Range (Fedorova 2012b); Chuy Valley (Fedorova 2021). **Turkmenistan:** Krasnovodsk Peninsula, Daşoguz, the foothills of The Köpet Dag, Badhyz State Nature Reserve, Karakum Desert (Kochkareva et al. 1971), Serhetabat (former Kushka) (Filippova 1977). **Uzbekistan:** Tashkent Region (Muratbekov 1954). **Tajikistan:** outskirts of the rural locality Jilikul (Filippova 1977), Tigrovaya Balka (Manilova and Shakhmatov 2008).

Ecology and other information. *Ixodes crenulatus* is among the tick species that have the most extensive ranges comparing to other representatives of its family within Russia (Tsapko 2020).

It is a typical nidicolous parasite of mammals and in the Asian part of its range as the main hosts it uses species of marmots of the genus *Marmota* (with a predominance of gray marmot) and such representatives of predatory mammals as badgers, steppe polecats, red and corsac foxes. The composition of the main host spectrum from different orders (rodents and predatory mammals) finds an explanation in close connections of topical and trophic relationships of marmots and predators. All of them have burrows of medium diameter, complex design, with a nesting chamber, remote from the entrance, which

provides the stability of the microclimate, where ticks find suitable conditions. The above species of carnivores often use the burrows of their prey, marmots, and small carnivores, facilitating the exchange of ticks not only between individual burrows, but also between remote host settlements (Filippova 2011).

This tick species is considered rare, for example, only few findings were mentioned in the Astrakhan Oblast (Zimina et al. 1965; Zimina et al. 1996) and Saratov Oblast (Denisov 2019). In most of the recognized range, *I. crenulatus* coexists with the closely related *I. kaiseri*. These species not only inhabit the same territory and the same biotopes but can also parasitize one host individual at the same time (Tsapko 2017). Therefore, it is necessary to consider that accurate identification of these species is required and there is always a chance of their misidentification.

According to some suggestions (Emelyanova 1979), *I. crenulatus* is probably a species group, or at least has remarkable intraspecific variations involving morphotypes (Filippova and Panova 2000).

***Ixodes hexagonus* Leach, 1815**

Ixodes hexagonus Leach, 1815: 397; Morel and Pérez 1973: 275.

Ixodes autumnalis Leach: Neumann 1911: 17.

Ixodes erinacei Audouin: Neumann 1911: 17.

Ixodes auricularis Robineau-Desvoidy: Morel and Pérez 1973: 275.

Ixodes sexpunctatus Koch: Neumann 1911: 17.

Ixodes vulpis Pagenstecher: Neumann 1911: 17.

Ixodes erinaceus Audouin: Neumann 1911: 17.

Recorded hosts. Mammalia: *Bos taurus* Linnaeus (cattle), *Canis familiaris* (domestic dog), *Erinaceus europaeus* (European hedgehog), *Felis catus* (domestic cat), *Lutra lutra* (Linnaeus) (Eurasian otter), *Meles meles* (Eurasian badger), *Mustela erminea* (stoat), *Mustela nivalis* (least weasel), *Mustela putorius* Linnaeus (European polecat), *Oryctolagus cuniculus* (Linnaeus) (European rabbit), *Ovis aries* (sheep), *Rattus norvegicus* (brown rat), *Vulpes vulpes* (red fox) (Filippova 1977).

Aves: *Turdus merula* (common blackbird) (Filippova 1977).

Recorded locations (Fig. 25). Ukraine: outskirts of Kyiv, Khmelnytskyi Oblast (Levytska et al. 2021), the North-Western seacoast of the Black Sea (Rusev 2009), Zakarpattia Oblast (the rural locality Malyi Berezhny) (Filippova 1961).

Ecology and other information. *Ixodes hexagonus* is a typical nidicolous parasite of carnivores and hedgehogs. It has certain morphological similarities to *I. crenulatus* and *I. kaiseri* and has common sympatric zones with this species along its range (Filippova 1999). Ukraine is the only country of the former Soviet Union, on the territory of which this European species is present in the tick fauna (Filippova 1977). In general *I. hexagonus* was detected quite rarely in Ukraine, and almost always in the west of Ukraine and mainly from hedgehogs (Kolonin 2009). Akimov and Nebogatkin (2016) assumed that it can be found in the vicinity of Kyiv, and eventually it was confirmed by Levytska et al. (2021). Rare occasional human bites have been recorded (Rosický and Weiser 1952; Arthur 1963; Bursali et al. 2012).



Figure 25. Map of Russia and neighboring countries showing the locations where *Ixodes hexagonus* was reported.

Ixodes kaiseri Arthur, 1957

Ixodes kaiseri Arthur, 1957: 578; Morel and Aubert 1975: 99.

Ixodes bakonyensis Babos: Morel and Aubert 1975: 99.

Ixodes vulpinus Babos: Morel and Aubert 1975: 99.

Recorded hosts. Mammalia: *Canis familiaris* (domestic dog), *Erinaceus concolor* Martin (southern white-breasted hedgehog), *Erinaceus europaeus* (European hedgehog), *Erinaceus roumanicus* Barrett-Hamilton (northern white-breasted hedgehog), *Felis chaus* Schreber (jungle cat), *Felis lybica* (African wildcat), *Hyaena hyaena* (Linnaeus) (striped hyena), *Hystrix indica* Kerr (Indian crested porcupine), *Lepus europaeus* (brown hare), *Mustela eversmanii* (steppe polecat), *Meles meles* (Eurasian badger), *Nyctereutes procyonoides* (common raccoon dog), *Vulpes corsac* (corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977; Tsapko 2017).

Recorded locations (Fig. 26). Russia: southwestern peripheries of the Central Russian Upland and also Rostov Oblast (Khametova et al. 2018) and Stavropol Krai (Tsapko 2017) and the North Caucasus – the outskirts of Grozny (Chechnya) (Filippova 1977, 1999; Tsapko 2017, 2020) and Nogaysky District (Dagestan) (Tsapko 2017). **Ukraine:** outskirts of Kyiv (Akimov and Nebogatkin 2016) and the south of Ukraine, in particular Askania-Nova Nature Reserve (Filippova 1977), the North-Western seacoast of the Black Sea (Matyukhin 2017), Crimea (Filippova 1977). **Moldova:** Lozova, Ivancea, Doibani, Leova, Etulia, reedbeds of the low Dniester and Pruth (Filippova 1977; Uspenskaya et al. 2006). **Georgia:** the outskirts of Tbilisi, Lagodekhi Nature Reserve (Filippova 1977), Eldari Steppe (Tsapko 2017). **Armenia:** Gegharkunik Province (rural locality Geghamashen) (Tsapko 2017), Aragats



Figure 26. Map of Russia and neighboring countries showing the locations where *Ixodes kaiseri* was reported.

mountain range (Dilbaryan and Poghosyan 2018). **Azerbaijan:** Mil plain (Filippova and Uspenskaya 1973), Beylagan District, Zangilan District, Aghjabadi District, Martuni Province, Shaki District (Tsapko 2017). **Kazakhstan:** West Kazakhstan Region, Dzungarian Alatau – outskirts of the rural locality Topolëvka and the Koxsu district (Ushakova et al. 1976; Filippova 1999). **Kyrgyzstan** (Fedorova 2012b).

Ecology and other information. *Ixodes kaiseri* is a typical nidicolous parasite of carnivores and also hedgehogs and porcupines which is morphologically very similar to *I. crenulatus* and has common sympatric zones with this species along its range (Filippova 1999). Its range itself is patchy and disjunctive areas of sympatry for both of these species are found in southeastern Europe - Romania, Moldova, Ukraine, including the Crimean Peninsula as well as in Russia - the southwestern extremities of the Central Russian Upland and the Northern Caucasus; then after a long gap - in Western Kazakhstan and again after a big gap - in the Dzungarian Alatau (Filippova 1999). Judging by literature, it is also known from Egypt and Israel (Arthur 1957, 1960, 1965). As Filippova and Uspenskaya (1973) assumed, its distribution in the Middle East and also other parts of Asia can be wider than it is known at present, which was already confirmed by the findings of this tick species in Turkey (Orkun and Karaer 2018) and Xinjiang in China (Zhao et al. 2019) near the border with Kazakhstan and the Dzungarian Alatau and hence, it is possible that the sympatry of these two species is more widespread. This is also supported by literature data, because until the 1970s in the territory of the former USSR *I. kaiseri* was not differentiated from *I. hexagonus* and *I. crenulatus* (Emelyanova 1979; Filippova 1999).

These species not only inhabit the same territory and inhabit the same biotopes in some places but can also parasitize one host individual at the same time (Tsapko 2017). It is also important to note that according to Filippova's

opinion (1999), the territorial signs of the ranges of these two species, their biotope and host-parasite relationships indicate that the range of *I. crenulatus* (which is predominantly connected with marmots and their burrows in steppe and forest-steppe zones) over the most part of its distribution has a Central Asian origin, while the range of *I. kaiseri* (mainly the parasite of carnivores and occurring in their burrows) is supposedly of European origin.

***Ixodes lividus* Koch, 1844**

Ixodes lividus Koch, 1844: 234; Morel and Pérez 1973: 275.

Ixodes bavaricus Schulze & Schlottke, 1929: 95.

Ixodes plumbeus bavaricus Schulze & Schlottke: Morel and Pérez 1973: 275.

Ixodes plumbeus obotriticus Schulze & Schlottke: Morel and Pérez 1973: 275.

Ixodes (Pholeoixodes) hirundinicola Schulze: Kolonin 1981: 19.

Recorded hosts. Aves: *Alauda arvensis* (Eurasian skylark), *Delichon urbicum* (Linnaeus) (common house martin), *Merops apiaster* Linnaeus (European bee-eater), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Riparia diluta* (Sharpe & Wyatt) (pale martin), *Riparia riparia* (sand martin) (Filippova 1977; Tagiltsev et al. 1984; Rusev 2009; Bolshakova et al. 2019; Kovalevsky et al. 2019).

Mammalia: *Mus musculus* (house mouse) (Filippova 1977).

Recorded locations (Fig. 27). Russia: Curonian Spit (Kaliningrad Oblast) (Filippova 1961), Karelia (Bobrovskikh 1979), Leningrad Oblast, (Zolotov and Buker 1976), Moscow Oblast (Glashchinskaya-Babenko 1956), Ryazan Oblast (Filippova 1977), Ivanovo Oblast (Mayorova 2004), Saratov Oblast (Korneev



Figure 27. Map of Russia and neighboring countries showing the locations where *Ixodes lividus* was reported.

et al. 2018), Kuybyshev Reservoir (Republic of Tatarstan) (Lvov et al. 2014), Voronezh Oblast (Gaponov and Tewelde 2021), Tymen Oblast (Starikov et al. 2017b), Kurgan Oblast (Starikov and Starikova 2021), Omsk Oblast (Tagiltsev et al. 1984; Yakimenko et al. 1991), Tomsk Oblast, Kemerovo Oblast (Kovalevsky et al. 2019), Novosibirsk Oblast (Yakimenko et al. 2013), Irkutsk Oblast (Danchinova et al. 2007), Ikatsky Ridge (Republic of Buryatia), Zabaykalsky Krai (Emelyanova et al. 1963), Republic of Tuva (Kholodilov et al. 2019), Sakha (Yakutia) (Shadrina et al. 2011), Khabarovsk Krai (Volkov and Chernykh 1977). **Ukraine:** Zakarpattia Oblast, Kaniv Nature Reserve (Cherkasy Oblast), (Emchuk 1960), Danube Biosphere Nature Reserve (Odessa Oblast) (Emchuk 1960; Didyk 2013), Kyiv (Akimov and Nebogatkin 2002), delta of the Dniestr River (Rusev 2009). **Belarus:** Gomel Region, Minsk Region (Gembetsky 1972). **Moldova:** banks of the Dniestr River (Movila et al. 2008). **Kazakhstan:** Atyrau Region (Pomerantsev 1950; Levit 1957), Kostanay Region (Makhmetov 1961), Pavlodar Region (Amirova et al. 1989), Akmola Region (Filippova 1961; Ushakova 1962).

Ecology and other information. *Ixodes lividus* is a specific nidicolous ectoparasite of the sand martin, *Riparia riparia*. Also, it has been collected from birds and house mice which occasionally could visit sand martin's nests such as house sparrows and common house martins.

Due to the wide distribution of its main host, this tick species also occurs in a vast geographical range and can be characterized by having a trans-Palaearctic distribution. The locations of findings in Russia and the neighboring countries listed above reflect the general pattern of its distribution on a map so we can suppose that this tick can be found in the north of the Palaearctic almost everywhere in habitats of the sand martin.

***Ixodes prokopjevi* (Emel'yanova, 1979)**

Pholeoixodes prokopjevi Emel'yanova, 1979: 14.

Recorded hosts. Mammalia: Daurian hedgehog *Mesechinus dauuricus* (Sundevall) (Emelyanova 1979).

Recorded locations (Fig. 28). Russia: Transbaikal (Emelyanova 1979).

Ecology and other information. *Ixodes prokopjevi* is an extremely poorly studied tick species initially described based on the male holotype from steppes of north-eastern Mongolia; its paratypes, larvae and nymphs, are noted as originating from the outskirts of the lake Baruun Shavart Nuur in Eastern Mongolia, as well as females and nymphs from the south-eastern Transbaikal without any indications of certain points of findings (Emelyanova 1979).

Kolonin (2009) states that this species should be considered a synonym of *I. crenulatus* but Guglielmone et al. (2010, 2014) recognize it as a valid species.

The Daurian hedgehog was recorded as a host, but we can assume that carnivores, lagomorphs, and rodents are also hosts of this tick species, as in case of *I. crenulatus*, another representative of the subgenus *Pholeoixodes* and the most similar species to this tick. The distribution area and ecology of *I. prokopjevi*, as well host-parasite relationships and their role in transmission of vector-borne infections remain unknown.



Figure 28. Map of Russia and neighboring countries showing the locations where *Ixodes prokopjevi* was reported.

Ixodes subterraneus Filippova, 1961

Ixodes subterraneus Filippova, 1961: 226. Morel and Pérez 1973: 275.

Pholeioxodes arboricola koskinae Emel'yanova: Kolonin 1981: 20.

Pholeioxodes arboricola deserta Emel'yanova: Kolonin 1981: 20.

Recorded hosts. Aves: *Athene noctua* (little owl), *Carduelis carduelis* (European goldfinch), *Coracias garrulus* (European roller), *Coturnix coturnix* (common quail), *Galerida cristata* (crested lark), *Falco naumanni* Fleischer (lesser kestrel), *Oenanthe hispanica* (western black-eared wheatear), *Oenanthe isabellina* (isabelline wheatear), *Oenanthe oenanthe* (northern wheatear), *Parus major* (great tit), *Passer ammodendri* Gould (saxaul sparrow), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Pastor roseus* (rosy starling), *Petronia petronia* (rock sparrow), *Pica pica* (Eurasian magpie), *Sturnus vulgaris* (common starling), *Turdus ruficollis* (red-throated thrush) (Filippova 1977).

Recorded locations (Fig. 29). Russia: Transbaikalia (Barguzin Valley, Cape Ryty) (Emelyanova 1972, as *I. arboricola*). **Kazakhstan:** Mangyshlak Peninsula (Maslennikova and Ushakova 1971), Jambyl Region (Kokuzek), Trans-Ili Alatau, Syugaty Valley (Maslennikova and Stogov 1974), Almaty Region (lower reaches of the Ili River) (Ushakova 1958, as *Ixodes* sp.), Dzungarian Alatau (Ushakova et al. 1976). **Kyrgyzstan:** Jalal-Abad Region (Bazar-Korgon District), the valley of the river Naryn (Grebenyuk 1966). **Turkmenistan:** Krasnovodsk plateau, outskirts of Geok Tepe, Kara Kala, Ashgabat, Tejen, Bayramaly, highland Badhyz (Filippova 1961; Kochkareva et al. 1971; Scherbinina 1973). **Tajikistan:** southern spurs of the Hisar Range – the vicinity of Hisar (Filippova 1977).

Ecology and other information. *Ixodes subterraneus* is a parasite of birds nesting in ground burrows (Filippova 1977). The main part of its distribution



Figure 29. Map of Russia and neighboring countries showing the locations where *Ixodes subterraneus* was reported.

lies in Kazakhstan and Middle Asia, the lesser part in Transbaikalia (Russia) (Filippova 1977). This tick species can be found in foothill dry steppes, as well as near and in deserts. This species was originally named *I. subterraneus* in Filippova (1961) but amended to *I. subterraneus* in Filippova (1977).

Subgenus *Scaphixodes* Schulze, 1941: 491

Ixodes berlesei Birula, 1895

Ixodes berlesei Birula, 1895: 353.

Recorded hosts. Aves: *Apus pacificus* (Latham) (Pacific swift), *Corvus frugilegus* Linnaeus (rook), *Falco rusticolus* Linnaeus (gyrfalcon), *Falco tinnunculus* Linnaeus (common kestrel), *Monticola solitarius* (blue rock thrush), *Montifringilla nivalis* (Linnaeus) (white-winged snowfinch), *Phoenicurus erythrogastrus* (Güldenstädt) (Güldenstädt's redstart), *Phoenicurus ochruros* (black redstart), *Phoenicurus erythronotus* (Eversmann's redstart), *Plectrophenax nivalis* (Linnaeus) (snow bunting), *Prunella collaris* (Scopoli) (alpine accentor), *Sturnus vulgaris* (common starling), *Tichodroma muraria* (Linnaeus) (wallcreeper) (Filippova 1977; Voltsyt 1997).

Recorded locations (Fig. 30). **Russia:** Dagestan (Filippova 1977), Western Siberia – Salair Ridge, Kuznetsk Alatau (Chunihin 1967), Eastern Siberia – banks of the Angara River (Birula 1895) and Buryatia (Ikatsky Ridge) (Emelyanova et al. 1963), Bering Island (Voltsyt 1997). **Kazakhstan:** Trans-Ili Alatau (Grebenyuk 1966). **Kyrgyzstan:** Aksay Valley (Grebenyuk 1966). **Turkmenistan:** outskirts of Ashgabad (Filippova 1977). **Tajikistan:** Hisar Range, Varzob gorge (Ivanov 1945; Lotozky 1945).

Ecology and other information. *Ixodes berlesei* is a little studied nidicolous tick occurring in the Greater Caucasus, as well as in Middle Asia and Siberia.



Figure 30. Map of Russia and neighboring countries showing the locations where *Ixodes berlesei* was reported.

There is one report about a finding of this tick on the Bering Island belonging to the Commander Islands in the Bering Sea, a female and three larvae collected 26 August 1990 from a snow bunting and deposited at the collection of the Zoological Museum of Moscow State University (Voltsyt 1997). The author states that the date of the tick collection indicates the presence of a permanent population of this species on the island because in the end of August birds usually already are prepared for the autumn migration after the breeding period, and, therefore, ticks could not have been transported there from the continent. Hence, we could assume that probably the real distribution of this tick is much wider and includes mountainous areas not only in a warmer and temperate climate but also in cooler tundra and other climatically similar landscapes. The snow bunting as a host of this species also was registered for the first time. Overall, its hosts include birds nesting usually in rocks and feeding on the ground and during the flight (Filippova 1977).

The type specimen is deposited at the Zoological Institute of the Russian Academy of Sciences - holotype: female; 683, [Russia, Siberia] Angara, 1867, Chekanovskii, type; AL 1528. Description – Filippova 1977: 230–236 (female, nymph, larva; male unknown) (Filippova 2008).

***Ixodes caledonicus* Nuttall, 1910**

Ixodes caledonicus Nuttall, 1910: Nuttall 1910: 408.

Ixodes caledonicus sculpturatus Schulze, 1929: 60; Arthur 1963: 53.

Ixodes gussevi Reznik, 1958: 457; Filippova and Panova 1975: 339.

Recorded hosts. Aves: *Apus pacificus* (Pacific swift), *Corvus corax* Linnaeus (common raven), *Corvus cornix* (hooded crow), *Columba livia* (common pigeon),

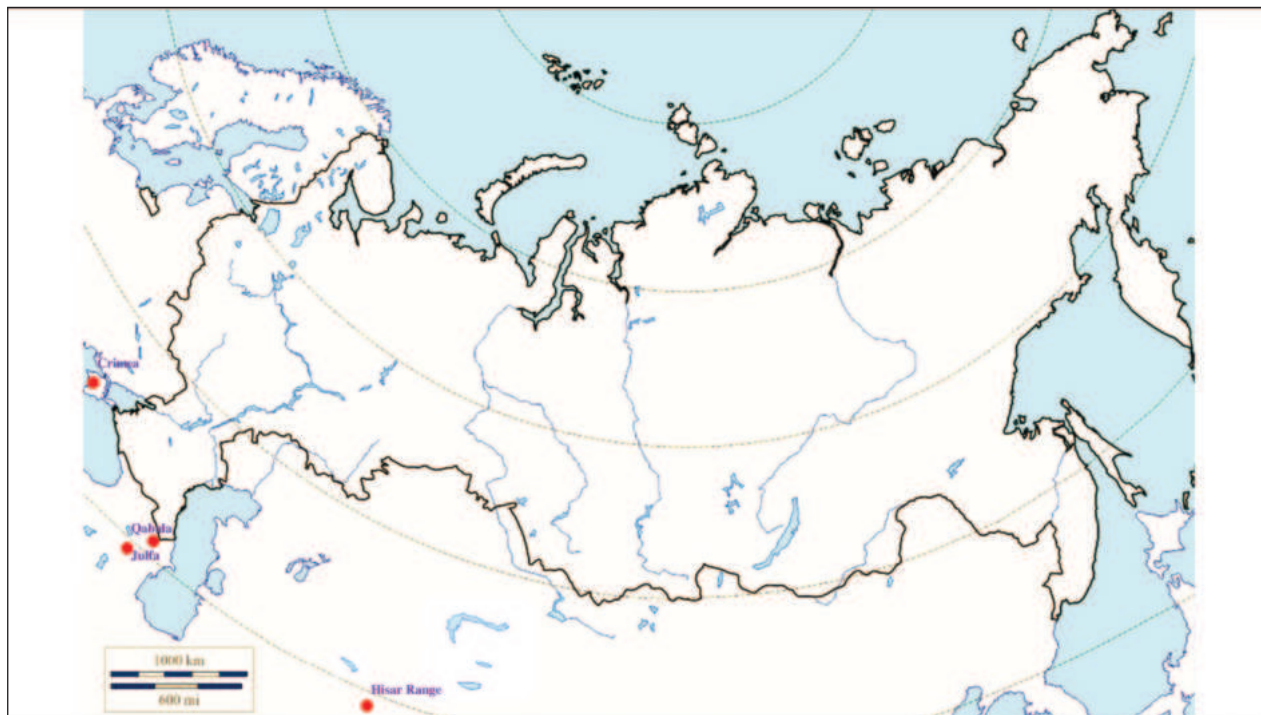


Figure 31. Map of Russia and neighboring countries showing the locations where *Ixodes caledonicus* was reported.

Coloeus monedula (western jackdaw), *Falco peregrinus* (peregrine falcon), *Monticola solitarius* (blue rock thrush), *Oenanthe oenanthe* (Northern wheatear), *Petronia petronia* (rock sparrow), *Phoenicurus* sp. (redstart), *Tachymarptis melba* (Linnaeus) (Alpine swift) (Filippova 1977; Bolotin and Kolonin 1979).

Recorded locations (Fig. 31). **Russia:** valley of the Zerkalnaya River (Bolotin and Kolonin 1979). **Ukraine:** Crimean Peninsula, in particular the Tarkhankut Peninsula and the cape Kazantyp (Emchuk 1960; Filippova 1977). **Azerbaijan:** Qabala (Reznik 1958), Julfa (Filippova and Panova 1975). **Tajikistan:** Hisar Range (Filippova and Panova 1975).

Ecology and other information. *Ixodes caledonicus* is a little studied nidicolous tick species occurring in Europe as well as Western and Middle Asia. In Crimea this species is very rare and never has been found after 1980 (Nebogatkin 1998). Its hosts are birds that usually nest in rocks, feed on the ground, or feed and drink during flight (Filippova 1977).

Ixodes semenovi Olenev, 1929

Ixodes semenovi Olenev, 1929: 489.

Recorded hosts. Aves: *Prunella collaris* (alpine accentor), *Pyrrhocorax pyrrhocorax* (Linnaeus) (red-billed chough) (Filippova 1977).

Recorded locations (Fig. 32). **Kazakhstan:** Tian Shan – the northern slope of the Kyrgyz Ala-Too Range, the source of the river Merke (Jambyl Region) (Olenev 1929b). **Kyrgyzstan:** Terskey Ala-too Range (Grebnyuk 1961, 1966).

Ecology and other information. *Ixodes semenovi* is a very rare species in the post-Soviet territories known only from Kazakhstan and Kyrgyzstan, from

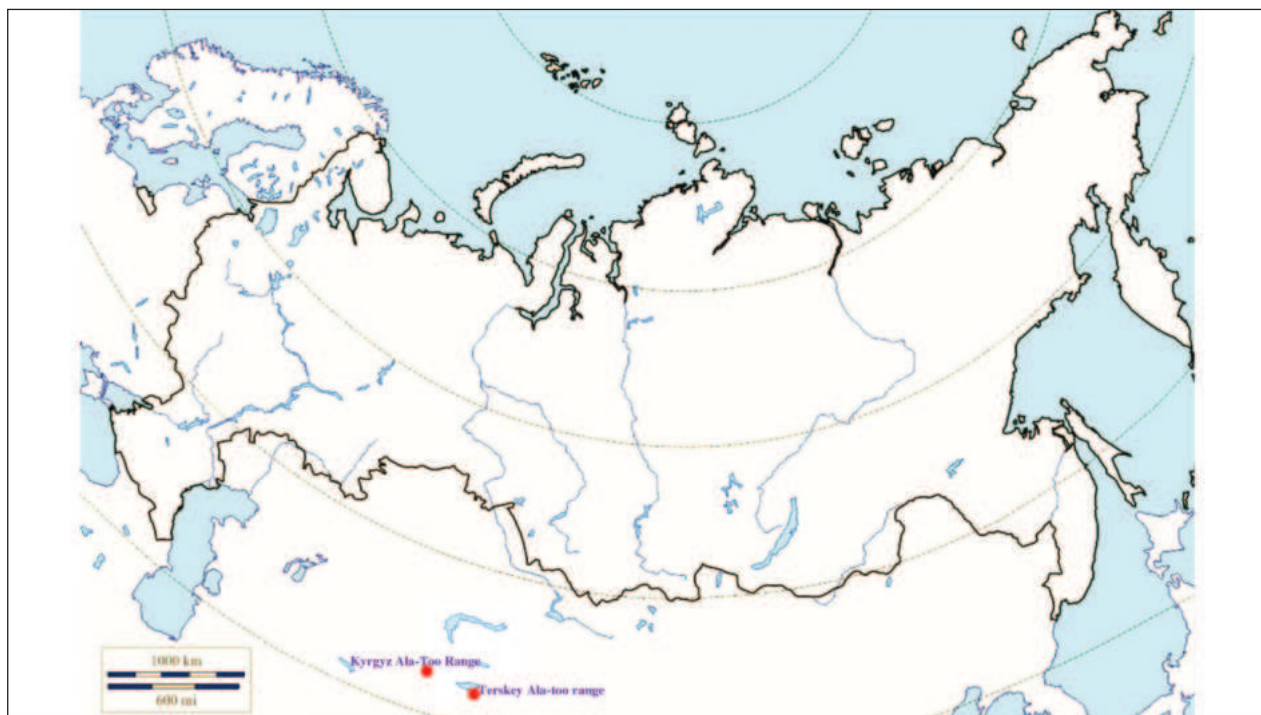


Figure 32. Map of Russia and neighboring countries showing the locations where *Ixodes semenovi* was reported.

the Tian Shan, where it inhabits rocks at an altitude of 2000 m a. s. l. (Filippova 1977). The type specimen of *I. semenovi* is deposited at the Zoological Institute of the Russian Academy of Sciences: the holotype - female; Mi[ddle] Asia, Aleksandrovskii Mt. Range [Kirgizskii Ala Tau], source of Merke River, Aral-Tyube, from *Accentor collaris*, 4.VII.1929, coll. I.A. Portenko; AL 1549. Description – Filippova 1977: 219–223 (female, male, nymph; larva unknown) (Filippova 2008).

***Ixodes signatus* Birula, 1895**

Ixodes signatus Birula, 1895: 353.

Ixodes arcticus Osborn: Cooley and Kohls 1945: 201.

Ixodes parvirostris Neumann: Neumann 1904: 444.

Ixodes eudyptidis v. *signata* Birula: Neumann 1911: 21.

Recorded hosts. Aves: *Phalacrocorax carbo* (Linnaeus) (great cormorant), *Urile pelagicus* (pelagic cormorant), *Urile penicillatus* (Brandt) (Brandt's cormorant), *Urile urile* (red-faced cormorant) (Filippova 1977).

Recorded locations (Fig. 33). Russia: islands: Furugelm Island, Tyuleniy Island, the Kuril Islands – Paramushir, Urup and Makanrushi, the Commander Islands – the Kamen Ariy and the Bering Island (Kirschenblatt 1936; Pomerantsev 1950; Violovich 1958, 1962a; Leonova et al. 1971; Timofeeva et al. 1971, 1974; Lvov et al. 2014b); mainland – Primorsky Krai (Lazovsky District) (Kozlovskaya et al. 1968).

Ecology and other information. *Ixodes signatus* is a nidicolous tick species occurring in several archipelagos and separate islands of the Russian Far East,

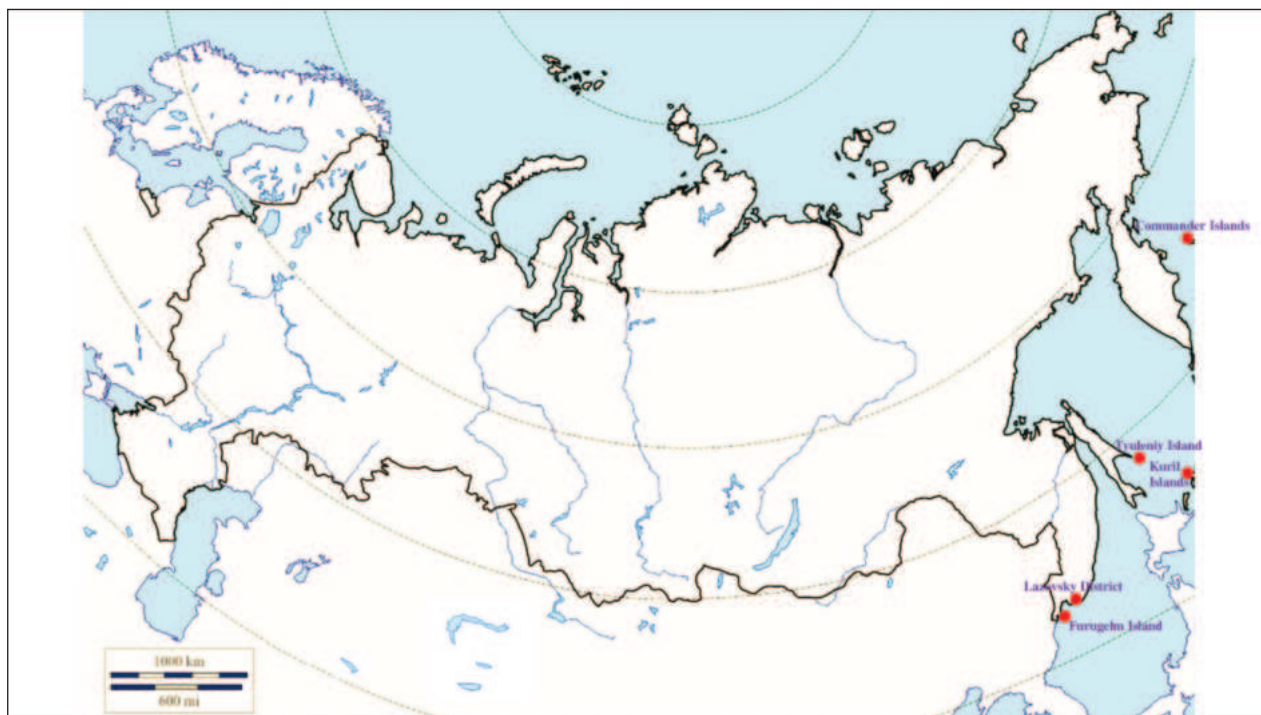


Figure 33. Map of Russia and neighboring countries showing the locations where *Ixodes signatus* was reported.

as well as in Japan and the west coast of North America together with the Pacific islands nearby (Filippova 1977). It inhabits mostly coastal rocks being an obligate parasite of cormorants. Other birds, for example the Siberian thrush *Geokichla sibirica* (Pallas), are considered occasional hosts (Violovich 1962a). Findings in the mainland Eurasia are probably occasional cases of transportation (Kozlovskaya et al. 1968).

The type specimens of *I. signatus* are deposited at the Zoological Institute of the Russian Academy of Sciences (Filippova 2008) and include the lectotype: female; [Aleut Islands], Unalashka, 1846, coll. Voznesenskii, type; AL I358; paralectotypes: 8 females, 1 nymph, AL I358a; 2 females; CB I3170, I3171. Description – Filippova 1977: 204–210 (female, male, nymph, larva).

***Ixodes unicavatus* Neumann, 1908**

Ixodes unicavatus Neumann, 1908: 109; Schulze 1941: 491.

Ixodes tauricus Vshivkov & Filippova, 1957: 553; Gilot and Beaucournu 1973: 131.

Recorded hosts. Aves: *Gulosus aristotelis* (European shag) (Linnaeus) (Filippova 1977).

Recorded locations (Fig. 34). Ukraine: Crimean Peninsula, in particular the Tarkhankut Peninsula, The Kara Dag, the Kerch Peninsula, the cape Kazantyp (Emchuk 1960; Filippova 1977).

Ecology and other information. *Ixodes unicavatus* is an endophilic tick occurring in Europe primarily in coastal areas of the Atlantic Ocean and which can be found in its hosts' nests and under stones near them (Filippova 2007). It uses mostly cormorants - the European shag *Gulosus aristotelis* and the great

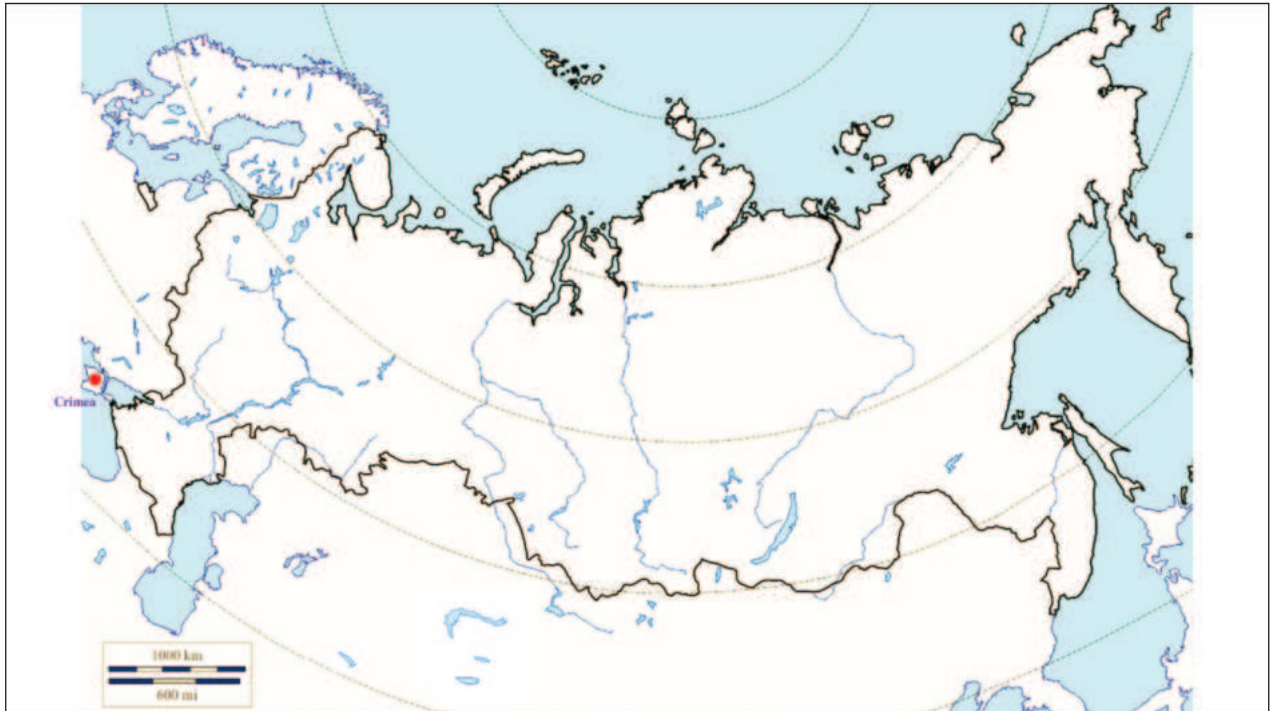


Figure 34. Map of Russia and neighboring countries showing the locations where *Ixodes unicavatus* was reported.

cormorant *Phalacrocorax carbo* as hosts (Schulze 1932; Arthur 1963; Guiguen et al. 1987; Kolonin 2008). In Crimea, this species has been known from a little number of specimens (Serdjukova 1956; Emchuk 1960).

Subgenus *Trichotoixodes* Reznik, 1961: 276.

***Ixodes brunneus* Koch, 1844**

Ixodes brunneus Koch, 1844a: 232.

Ixodes californicus Banks, 1904: Keirans and Clifford 1978: 54.

Ixodes kelloggi Nuttall & Warburton, 1907: Cooley and Kohls 1945: 205.

Recorded hosts. Aves: *Lanius collurio* (red-backed shrike) (Filippova 1977)

Recorded locations (Fig. 35). Ukraine: Crimea – Sudak City Municipality, the village Perevalivka (Filippova 1977).

Ecology and other information. *Ixodes brunneus* is a tick occurring mainly in the Americas being predominantly a parasite of passerine birds (Filippova 1977). The only record in Crimea on a red-backed shrike is considered a case of accidental introduction (Tsapko 2020).

***Ixodes frontalis* (Panzer, 1798)**

Acarus frontalis Panzer, 1798: 59, 23; Koch 1844a: 234.

Ixodes pallipes (Fabricius): Arthur 1963: 111.

Ixodes pari Leach, 1815: 399; Neumann 1911: 18.

Ixodes sturni Pagenstecher: Neumann 1901, 249.



Figure 35. Map of Russia and neighboring countries showing the locations where *Ixodes brunneus* was reported.

Ixodes avisugus Berlese: Neumann 1899: 107.

Ixodes apronatus Kirshenblat, 1934: 257; Arthur 1963: 111.

Ixodes sigalasi Lamontellerie, 1954: 561; Lamontellerie 1965: 87.

Recorded hosts. Aves: *Alectoris chukar* (chukar partridge), *Caprimulgus europaeus* Linnaeus (European nightjar), *Chloris chloris* (European greenfinch), *Corvus frugilegus* (rook), *Curruca communis* (common whitethroat), *Curruca curruca* (lesser whitethroat), *Erithacus rubecula* (European robin), *Falco tinnunculus* (common kestrel), *Fringilla coelebs* (Eurasian chaffinch), *Fringilla montifringilla* (brambling), *Garrulus glandarius* (Eurasian jay), *Hippolais icterina* (Vieillot) (icterine warbler), *Lanius collurio* (red-backed shrike), *Luscinia luscinia* (thrush nightingale), *Luscinia megarhynchos* (Brehm) (common nightingale), *Muscicapa striata* (spotted flycatcher), *Oenanthe hispanica* (western black-eared wheatear), *Oenanthe isabellina* (isabelline wheatear), *Parus major* (great tit), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Petronia petronia* (rock sparrow), *Phoenicurus phoenicurus* (common redstart), *Phylloscopus trochilus* (willow warbler), *Phasianus colchicus* (common pheasant), *Pica pica* (Eurasian magpie), *Regulus regulus* (Linnaeus) (goldcrest), *Saxicola rubetra* (Linnaeus) (whinchat), *Streptopelia turtur* (Linnaeus) (European turtle dove), *Turdus iliacus* (redwing), *Turdus merula* (common blackbird), *Turdus philomelos* (song thrush), *Turdus torquatus* Linnaeus (ring ouzel), *Turdus viscivorus* (mistle thrush) (Filippova 1977).

Mammalia: *Meriones libycus* (Libyan jird) (Tsapko and Kotti 2017).

Recorded locations (Fig. 36). Russia: Kurgan Oblast – the rural locality Ketovo (Ruzsky 1929), Stavropol Krai (Reznik 1950; Guseva 1962; Tiflova et al. 1970), Krasnodar Krai; Chechnya (Marutyan 1963; Baisarova 2021), Dagestan (Gusev and Guseva 1960). **Ukraine:** Poltava Oblast (Olenev 1931a), Odesa Oblast, Mykolaiv Oblast, Kherson Oblast (Rusev 2009), Crimea (Filippova 1977). **Belarus:** Pripyatsky National Park (Tsvirko 2008). **Moldova:** Codru (Morozov et al. 2022),



Figure 36. Map of Russia and neighboring countries showing the locations where *Ixodes frontalis* was reported.

Olănești (Filippova 1977), Chishinau (Morozov and Proka 2012). **Armenia:** Syunik Province (former Goris Province) (Ogandzhanyan 1984). **Azerbaijan:** Alazani River (Ter-Vartanov et al. 1956), Lankaran (Filippova 1977), Shaki District (Tsapko and Kotti 2017). **Georgia:** Kutaisi, Lagodekhi, Dedoplistsqaro (Kirschenblatt 1936; Djaparidze 1960), Guria (Sukhiashvili et al. 2020). **Turkmenistan:** outskirts of Magtymguly, Aydere (Berdyev and Annaev 1997).

Ecology and other information. *Ixodes frontalis* is an exophilic tick species parasitizing primarily dendrophilic birds (Filippova 1977). It is relatively widely distributed throughout Europe, Western Asia, as well as North Africa (Filippova 1977; Estrada-Peña et al. 2018). *Ixodes frontalis* is rare in most of its range. However, the place of mass reproduction of this species was discovered in Dagestan near the Sulak River in a big colony of rooks (Gusev and Guseva 1960). Under the nests in the rookery, a high, uncountable number of larvae of these ticks was observed. Often there were up to 5,000 individuals per m² (Tsapko 2023).

Single collections of *I. frontalis* from mammals are known as exceptions. In Europe, adults were found on representatives of the mustelid family (Guglielmone et al. 2014). In the Shaki District of Azerbaijan (2 km north of the village of Şirinbulaq, 31 Oct 1956), two nymphs were taken from two Libyan jird *Meriones libycus* (collections of R.B. Kosminsky and R.S. Karandina) (Tsapko and Kotti 2017). In addition, certain cases of attachments to humans are known (Gilot et al. 1997).

***Ixodes turdus* Nakatsudi, 1942**

Ixodes turdus Nakatsudi, 1942: 287.

Recorded hosts. Aves: *Turdus pallidus* Gmelin (pale thrush) (Bolotin and Kolinin 1979).



Figure 37. Map of Russia and neighboring countries showing the locations where *Ixodes turdus* was reported.

Recorded locations (Fig. 37). Russia: Primorsky Krai, Nadezhdinsky District, the right shore of the Razdolnaya River (Bolotin and Kolonin 1979).

Ecology and other information. *Ixodes turdus* is a bird-associated tick species that can be found usually in East Asia, especially in Nepal, Korea, and Japan (Takahashi and Chunikhin 1972; Clifford et al. 1975; Ishiguro et al. 2000; Kim et al. 2009b; Sato et al. 2021). The single case of finding *I. turdus* in the Far East of Russia is considered a result of transportation (Bolotin and Kolonin 1979). Some occasions of parasitism on humans (Woo et al. 1990; Kadosaka and Hasegawa 1996), as well as on wild boars (Chae et al. 2017) are also recorded.

Discussion

The territory of Russia and other post-Soviet countries reviewed here occupies a significant part of the Palearctic and its *Ixodes* tick fauna comprises in total approximately 37 species belonging to ten subgenera (Table 1). Some of these species are endemic. A significant ratio of these *Ixodes* species have a broad distribution area, as exemplified by *I. ricinus*, *I. persulcatus*, *I. trianguliceps*, *I. apronophorus*, *I. crenulatus*, *I. kaiseri*, *I. laguri*, *I. redikorzevi*, *I. eldaricus*, *I. frontalis*, and *I. lividus*. Moreover, the geographical range of some of these species also continues further to the west (into Europe) and to the south and east (to other parts of Asia).

Tick species like *I. ricinus* and *I. persulcatus* are able to live in a broad range of forest and forest-steppe biotopes and parasitize literally any vertebrate hosts among mammals, birds, and in some cases reptiles available in their habitats. Further species listed above parasitize species of those ecological groups of higher vertebrates which are widely distributed within the limits of the reviewed territories and even outside of them (like shrews, rodents, carnivores, and passerines), so this could explain the wide distribution of these species together

with the presence of suitable hosts and biotopes. On the other hand, five tick species – *I. stromi*, *I. semenovi*, *I. signatus*, *I. uriae*, *I. occultus* – have more limited distribution areas, occurring only in certain habitats where they are specialized to parasitize an ecologically restricted range of hosts. There are at least five tick species (*I. angustus*, *I. pomerantzevi*, *I. nipponensis*, *I. kashmiricus*, *I. redikorzevi*) which have geographical ranges extending far beyond post-Soviet territories, and these also occur in neighboring and more distant countries sharing a similar fauna. The distribution areas of six further species (*I. berlesei*, *I. caledonicus*, *I. arboricola*, *I. subterraneus*, *I. simplex*, *I. vespertilionis*) cannot be defined more precisely, due to the limited number of their findings in locations distantly separated from each other. It is important to note here that these ticks are nidicolous parasites of birds and bats, therefore can be transported by their hosts to new habitats in other locations during migration, although it is not necessary that they will establish and form sustainable populations there. The distribution area of the tick *I. pavlovskyi* is also disjunct and populated by two different subspecies. Finally, there are four tick species known exclusively from the reviewed territories and certain locations by a very few records and their real distribution areas and biology are poorly studied, namely *I. cornutus*, *I. ghilarovi*, *I. maslovi*, and *I. prokopjevi*.

It is still questionable whether or not *I. brunneus* and *I. turdus* are indigenous in the examined geographical area. There have been no confirmations of stable populations of these two species in the locations where both species were found on migratory birds; both are known from these territories by single specimens outside their main distribution areas. Therefore, we suspect that these two tick species do not belong to the tick fauna of Russia and post-Soviet territories.

Among the reviewed *Ixodes* species, from the point of view of host preferences, there are both generalists and specialists. Rodents of the families Muridae and Cricetidae, as well as passerine birds, harbor the highest number of *Ixodes* species in the reviewed territories (Table 2). All these groups live almost everywhere in a great variety of biotopes, often in significant numbers, therefore playing an important role in diverse ecosystems and also having epidemiological significance as reservoirs of multiple tick-borne pathogens. Among the ticks in this review, 15 species parasitize murine rodents and 14 passerine birds (Table 2). Shrews (family Soricidae) also include a relatively high number of species which are ubiquitous and serve as typical hosts for certain *Ixodes* species, predominantly from the subgenera *Filippoviella* and *Ixodiopsis*.

In general, 18 *Ixodes* species are typically parasites of mammals from various taxonomic and ecological groups, 12 species prefer birds as hosts. Altogether, six species are generalists and therefore can parasitize virtually any available warm-blooded host species. All these species belong to the subgenus *Ixodes*. Ticks from other subgenera can attach to and feed from atypical hosts occasionally. Specific parasites of reptiles among *Ixodes* species are not known to occur in the reviewed territories, but some of the generalist species can parasitize these hosts, especially in the absence of their preferred ones. Sometimes even mass parasitism of *Ixodes* species can be observed on reptiles, as in the case of *I. redikorzevi*. Last, we can note that hosts of *I. maslovi* are still unknown, and the exact host range of *I. cornutus*, *I. ghilarovi*, *I. prokopjevi*, and *I. sachalinensis* also remains to be clarified.

Table 1. The list of *Ixodes* subgenera and species according to post-Soviet countries.

Tick subgenus	Tick species	Russia	Belarus	Ukraine	Moldova	Georgia	Armenia	Azerbaijan	Kazakhstan	Kyrgyzstan	Uzbekistan	Turkmenistan	Tajikistan
Ceratixodes	<i>I. uriae</i>	+											
Eschatocephalus	<i>I. simplex</i>	+		+				+					
	<i>I. vespertilionis</i>	+		+	+	+	+	+		+		+	+
Filippoviella	<i>I. ghilarovi</i>	+				+							
	<i>I. trianguliceps</i>	+	+	+	+	+	+	+					
Ixodes	<i>I. apronophorus</i>	+	+	+	+				+	+			
	<i>I. eldaricus</i>	+		+		+	+	+	+	+	+	+	+
	<i>I. kazakstani</i>								+	+			
	<i>I. kashmiricus</i>									+			
	<i>I. laguri</i>	+		+	+	+	+	+	+			+	
	<i>I. nipponensis</i>	+											
	<i>I. occultus</i>								+		+	+	
	<i>I. pavlovskyi</i>	+							+	+			
	<i>I. persulcatus</i>	+	+	+					+	+			
	<i>I. redikorzevi</i>	+		+	+	+	+	+	+	+	+	+	+
	<i>I. ricinus</i>	+	+	+	+	+	+	+	+			+	
	<i>I. sachalinensis</i>	+											
Ixodiopsis	<i>I. angustus</i>	+											
	<i>I. pomerantzevi</i>	+											
	<i>I. stromi</i>	+							+	+			+
Monoixodes	<i>I. maslovi</i>	+											
Pholeoixodes	<i>I. arboricola</i>	+	+	+	+	+	+	+		+			
	<i>I. cornutus</i>												+
	<i>I. crenulatus</i>	+	+	+	+	+	+		+	+	+	+	+
	<i>I. hexagonus</i>			+									
	<i>I. kaiseri</i>	+		+	+	+	+	+	+	+			
	<i>I. lividus</i>	+	+	+	+				+				
	<i>I. prokopjevi</i>	+											
	<i>I. subterraneus</i>	+							+	+		+	+
Scaphixodes	<i>I. signatus</i>	+											
	<i>I. berlesei</i>	+							+	+		+	+
	<i>I. caledonicus</i>	+		+				+					+
	<i>I. unicavatus</i>			+									
	<i>I. semenovi</i>								+	+			
Trichotoixodes	<i>I. brunneus</i> *			+									
	<i>I. frontalis</i>	+	+	+	+	+	+	+				+	
	<i>I. turdus</i> *	+											
Total number of species		29	8	18	11	11	10	11	16	15	4	10	9
Total number of subgenera		9	4	6	5	5	5	6	4	5	2	5	5

* non-indigenous (transported) tick species in the reviewed territories.

Table 2. The list of *Ixodes* tick subgenera and species according to host taxa recorded in post-Soviet countries.

Tick subgenus	Tick species	Host taxonomic groups	
<i>Ceratixodes</i>	<i>I. uriae</i>	Aves:	
		Charadriiformes – Alcidae, Laridae;	
		Suliformes – Phalacrocoracidae; Procellariiformes – Procellariidae	
<i>Eschatocephalus</i>	<i>I. simplex</i>	Mammalia: Chiroptera	
	<i>I. vespertilionis</i>	Mammalia: Chiroptera	
<i>Filippoviella</i>	<i>I. ghilarovi</i>	Mammalia: Eulipotyphla – Soricidae; Rodentia – Cricetidae, Muridae	
	<i>I. trianguliceps</i>	Mammalia: Eulipotyphla – Soricidae; Rodentia – Cricetidae, Muridae, Sminthidae	
<i>Ixodes</i>	<i>I. apronophorus</i>	Mammalia: Eulipotyphla – Erinaceidae, Soricidae, Talpidae; Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae; Lagomorpha – Leporidae; Carnivora – Canidae, Mustelidae	
		<i>I. eldaricus</i>	Aves: Galliformes; Passeriformes; Strigiformes
			Mammalia: Eulipotyphla – Soricidae; Rodentia – Cricetidae, Muridae
			<i>I. kazakstani</i>
	Mammalia: Lagomorpha – Leporidae; Rodentia – Cricetidae, Muridae, Gliridae		
	<i>I. kashmiricus</i>		
		<i>I. laguri</i>	Mammalia: Eulipotyphla – Erinaceidae; Rodentia – Cricetidae, Gliridae, Dipodidae, Muridae, Sciuridae, Spalacidae; Carnivora – Canidae, Mustelidae
			<i>I. nipponensis</i>
	<i>I. occultus</i>		Mammalia: Eulipotyphla – Soricidae; Rodentia – Cricetidae, Muridae, Sciuridae
<i>I. pavlovskyi</i>		Aves: Anseriformes;	

Tick subgenus	Tick species	Host taxonomic groups
<i>Ixodes</i>	<i>I. pavlovskyi</i>	Columbiformes;
		Galliformes;
		Gruiformes;
		Passeriformes
		Mammalia:
		Eulipotyphla – Soricidae;
		Lagomorpha – Leporidae, Ochotonidae;
	Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae	
	<i>I. persulcatus</i>	Any mammalian and avian hosts (rarely reptilian) available
	<i>I. redikorzevi</i>	Aves:
Anseriformes;		
Columbiformes;		
Galliformes;		
Passeriformes;		
Pteroclitiformes		
Mammalia:		
Eulipotyphla – Erinaceidae, Soricidae;		
Lagomorpha – Leporidae;		
Rodentia – Cricetidae, Gliridae, Muridae, Sciuridae, Sminthidae, Spalacidae		
Carnivora – Canidae, Mustelidae		
Reptilia:		
Squamata – Lacertidae		
<i>I. ricinus</i>	Mammalia, Aves, Reptilia	
<i>I. sachalinensis</i>	Mammalia:	
Lagomorpha – Leporidae		
<i>Ixodiopsis</i>	<i>I. angustus</i>	Mammalia:
		Eulipotyphla – Soricidae;
		Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae;
		Lagomorpha – Ochotonidae
	<i>I. pomerantzevi</i>	Mammalia:
		Eulipotyphla – Erinaceidae, Soricidae;
Rodentia – Cricetidae, Muridae, Sciuridae		
<i>I. stromi</i>	Mammalia:	
	Eulipotyphla – Soricidae;	
	Rodentia – Cricetidae, Muridae;	
	Lagomorpha – Ochotonidae;	
Carnivora – Mustelidae		
<i>Monoixodes</i>	<i>I. maslovi</i>	Unknown
<i>Pholeioxodes</i>	<i>I. arboricola</i>	Aves:
		Accipitriformes;
		Bucerotiformes;
Columbiformes;		
Passeriformes;		
Piciformes;		
Strigiformes;		
Falconiformes		
<i>I. cornutus</i>	Mammalia:	
Carnivora – Mustelidae		

Tick subgenus	Tick species	Host taxonomic groups
<i>Pholeoixodes</i>	<i>I. crenulatus</i>	Mammalia: Eulipotyphla – Erinaceidae; Rodentia – Cricetidae, Muridae, Sciuridae, Pálcaidé; Lagomorpha – Ochotonidae, Leporidae; Carnivora – Canidae, Felidae, Mustelidae, Procyonidae
	<i>I. hexagonus</i>	Mammalia: Eulipotyphla – Erinaceidae; Lagomorpha – Leporidae; Carnivora – Canidae, Felidae, Mustelidae
	<i>I. kaiseri</i>	Mammalia: Eulipotyphla – Erinaceidae; Rodentia – Hystricidae; Lagomorpha – Leporidae; Carnivora – Canidae, Felidae, Hyaenidae, Mustelidae
	<i>I. lividus</i>	Aves: Passeriformes; Coraciiformes
	<i>I. prokopjevi</i>	Mammalia: Eulipotyphla – Erinaceidae
	<i>I. subterraneus</i>	Aves: Galliformes; Passeriformes; Strigiformes; Falconiformes
<i>Scaphixodes</i>	<i>I. signatus</i>	Aves: Phalacrocoracidae – Phalacrocoracidae
	<i>I. berlesei</i>	Aves: Apodiformes; Passeriformes; Falconiformes
	<i>I. caledonicus</i>	Aves: Apodiformes; Columbiformes; Passeriformes; Falconiformes
	<i>I. unicavatus</i>	Aves: Suliformes – Phalacrocoracidae
	<i>I. semenovi</i>	Aves: Passeriformes
<i>Trichotoixodes</i>	<i>I. brunneus</i> *	Aves: Passeriformes
	<i>I. frontalis</i>	Aves: Caprimulgiformes; Columbiformes; Galliformes; Passeriformes; Falconiformes
	<i>I. turdus</i> *	Aves: Passeriformes

* non-indigenous (transported) tick species in the reviewed territories.

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Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

Denis Fedorov: writing, data curation, methodology. Sándor Hornok: conceptualization, writing, methodology.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Platyintybia, a new genus of Apalochrini (Coleoptera, Melyridae, Malachiinae) from China

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Abstract

A new genus of malachiine Melyridae, *Platyintybia* **gen. nov.**, is described based on several male-specific characters, along with description of its type species, *Platyintybia zhongshanensis* **sp. nov.**, from China. A new combination, *Platyintybia sarawakensis* (Champion, 1921), **comb. nov.**, is proposed after examining the type specimen; this species is newly recorded from China. A key to the genera of Chinese Apalochrini is provided for the first time.

Key words: key to genera, new combination, new species, soft-winged flower beetles, taxonomy



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Introduction

Apalochrini is one of the monophyletic tribes of malachiine Melyridae, characterized by a shortened pedicel, which is almost concealed in the scape. This tribe comprises more than 40 genera from all over the world, with new genera still being described in the past few years (Evers 1987; Tshernyshev 2015a, 2015b, 2016a, 2020a, 2020b, 2020c, 2021a, 2021b, 2021c; Liu et al. 2020, 2021; Tshernyshev and Shcherbakov 2020). The genera of Apalochrini are distinguished by different combinations of characters of the antenna, head, pronotum, elytra, legs, etc., in males (Evers 1987; Tshernyshev 2015b). Members of this tribe mostly inhabit areas close to water bodies, like streams, lakes, salt lakes, and even oceans (Liu et al. 2021). Larvae and adults of Apalochrini are predators or scavengers, feeding on smaller or dead creatures, and sometimes can be collected on flowers (Horne et al. 2000; Liu et al. 2021; Zhenhua Liu pers. obs.).

In China, 12 genera and 43 species of Apalochrini have been recorded so far. The genera are *Intybia* Pascoe, 1866, *Laius* Guérin-Meneville, 1830, *Myrmecospectra* Motschulsky, 1858, *Protocollops* Evers, 1991, *Troglocollops* Wittmer, 1965, *Dromanthomorphus* Pic, 1921, *Mimapalochrus* Tshernyshev, 2015, *Pectapalochrus* Tshernyshev, 2016, *Apalochrus* Erichson,

1840, *Hadrocnemus* Kraatz, 1895, *Opisthpalochrus* Evers, 1987, and *Spinapalochrus* Pic, 1919 (Major 2007; Tshernyshev 2015a; Tong et al. 2022, 2023; Liu et al. 2023). About half of the species of Apalochrini that occur in China belong to the genus *Intybia*, which is characterized by simple, 5-segmented front tarsi, a dilated scape and antennomere 3 with antennomere 3 highly modified, and a pronotum that is unbeaded along the margin (Liu et al. 2020). Recently, we collected several specimens from Guangdong and Fujian, China. These specimens are similar to *Intybia* but differ in several characters of the male from the current definition of that genus; thus, a new genus is described here.

Materials and methods

Materials examined in this study are deposited in the following institutions:

IZGAS Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, China

FAF Fujian Academy of Forestry, Fuzhou, China

BMNH The Natural History Museum, London, United Kingdom

Specimens for dissections were cleared in 5% solution of KOH for about 12 h at room temperature. The abdomen with the aedeagus was transferred to a cavity slide, and the aedeagus was separated from the abdomen using a hooked, fine dissecting needle. Specimens are mounted on Goodrich cards using white emulsion glue, and the genitalia and terminal abdominal segments are preserved in genitalia vials with glycerol.

Layered images of specimens and male genitalia were captured using the Canon 7D DSLR camera mounted on a Wemacro Focus Stacking Rail, with Canon MPE-65 mm macro lens, Mitutoyo 5× and 10× objective lens, and dual-headed flash, with the aid of Helicon Remote (v. 3.9.10 M) and WeMacro Control software. The images were stacked in Helicon Focus v. 8.1.1 software and edited in Photoshop CC 2022.

The morphological terms used in this paper follow Lawrence and Ślipiński (2013). The following standard measurements are used in this study: body length—from apical edge of clypeus to apex of abdomen; pronotal length—median line from anterior margin to posterior margin; pronotal width—maximum width of pronotum; elytral length—from base of scutellum to elytral apex along suture; elytral width—maximum width across the elytra.

Taxonomy

***Platyintybia* Liu, gen. nov.**

<https://zoobank.org/FBC2C1DF-3811-41A8-B075-1ED269D208FB>

扁角囊花萤属

Type species. *Platyintybia zhongshanensis* Liu & Wang sp. nov.

Etymology. The genus name is a combination of the Latin word *platys* and the genus name *Intybia*; *platys* means broad, referring to the modified terminal antennomere in male. Gender feminine.

Diagnosis. This genus can be recognized from other genera of Apalochrini by combination of the following male specific characters: antenna with scape and antennomere 3 dilated and modified, antennomere 11 enlarged and flattened; head with pair of concavities on head between eyes; front tarsi 4-segmented, without comb on tarsomere 2. It can also be separated from *Collops* Erichson, 1840 and some species of *Notointybia* Liu, Ślipiński & Pang, 2020, which also with 4-segmented front tarsi, by having lateral margins of the pronotum without a bead.

Description. Length about 2.7mm.

Male. Head and pronotum black, elytra black with pair of large white spots at about basal fourth and pair of smaller white spots at about anterior fourth; antenna yellow with base of scape and terminal segment black; ventral surface mostly black, abdomen orange with lateral areas more or less black. Vestiture comprising double row of dense, short, whitish setae and sparser, longer, black bristles.

Head subtriangular, widest across eyes; vertex with pair of large concavities besides eyes; frons flattened dorsally, moderately constricted in front of eyes. Dorsal surface covered with dense, short, depressed whitish setae, sparser between antennal insertions and absent on concavities. Eyes relatively large, distinctly protruding laterally, finely faceted. Antenna 11-segmented, laterodorsally inserted on frons; scape and antennomere 3 dilated and modified; antennomere 11 flattened and expanded. Maxillary palps with terminal palpomere dilated, cupped, and apical surface depressed; labial palps with terminal palpomere conical.

Pronotum longer than wide, widest at about middle; lateral margins slightly curved, moderately constricted at base, without lateral carina; posterior margin nearly truncate. Disc finely, densely punctate, smoother at middle, posterior area with shallow transverse depression, covered with dense, depressed setae. Prosternum short, with deep incision anteriorly between pronotum and prosternum. Procoxal cavities transverse, continuous at middle, externally open. Procoxae projecting, with protrochantins exposed. Scutellum with visible part subtrapezoidal, posterior margin almost truncate.

Elytra with dorsal surfaces finely and densely punctate, covered with dense, depressed, whitish setae and longer, sparse, black setae posteriorly; epipleura incomplete, extending to abdomen. Meso- and metaventrite without distinct punctuation, covered with dense depressed setae; metaventrite moderately dilated, with short discrimen; metepisternum broad at base, not extending to posterior margin of metaventrite ventrally. Mesocoxae subtriangular, projecting, with exposed trochantins. Metacoxae subtriangular, sharply narrowed laterally. Legs with femora slightly dilated at about basal third; tibiae slender, covered with dense, short setae along inner edge; hind tibiae slightly curved; tarsal formula 4-5-5, with basal tarsomeres slightly prolonged ventrally.

Abdomen with 6-segmented ventrites, freely articulated, gradually narrowed to posterior. Tergite VIII transverse, subtrapezoidal, with pair of anterior struts; sternite VIII nearly divided, weakly connected by membrane at middle (Fig. 4). Aedeagus slender and curved, with apex upwardly curved; endophallus with 1 slender sclerite and a few short sclerites around it.

Female. Similar to male in body shape and colouration, but antenna with basal and apical segments simple, head without concavity on vertex, and front tarsi 5-segmented.

Distribution. China (Fujian, Guangdong); Malaysia (Borneo).

***Platyintybia zhongshanensis* Liu & Wang, sp. nov.**

<https://zoobank.org/DBE66FE1-0C63-4B64-ACFC-2C58C0DEB831>

Figs 1, 3, 4

中山扁角囊花萤

Etymology. The species name is derived from Zhongshan, a city of Guangdong Province in South China, where Kongxia, the type locality of the new species, is located.

Material examined. Holotype: CHINA—Guangdong Prov. • ♂: Zhongshan, Kongxia Village; 22.39510°N, 113.46785°E; 30 May 2023; net sweeping on grasses near stream; Zhenhua Liu leg.; IZGAS COL0001.

Diagnosis. The new species resembles *Platyintybia sarawakensis* in the shape of the basal antennomeres and aedeagus, but it can be easily recognized from the latter by the transverse basal spot and a much smaller subapical spot on the elytra (Fig. 1A). It also differs from *P. sarawakensis* in the following characters in males: apical antennomere more rounded (Fig. 3C); front tibiae distinctly slender (Fig. 3D); tergite VIII with posterior margin less emarginate (Fig. 4C); penis less curved laterally (Fig. 4A, F), apex of penis more depressed ventrally (Fig. 4B, G), the shape of long sclerite in inner sac (Fig. 4B, G).

Description. Length 2.7 mm.

Male. Antenna mostly yellow, with base and inner edge of scape and apical antennomere black. Legs with middle and hind legs black; front leg with basal half of femora and base of tibiae black, apex of tibiae and apical tarsomere dark brown, remaining parts yellow. Elytra with basal spots whitish and transverse, not extending to lateral or inner suture; subapical spots much smaller, more or less yellowish. Abdominal ventrites mostly orange-red, with lateral areas black.

Head about 1.1 times as wide as pronotum; concavities on head almost extending to anterior margin of eyes; width of vertex between concavities about 1.1 times as wide as concavity across middle of eyes. Dorsal surface of head with pair of circinately arranged setae behind antennal insertions and one on vertex between concavities. Antenna with scape elongate, subtriangular, and constricted at base; antennomere 3 elongate, with a large lamellate process at base, dorsal surface with 1 large, rounded anterior concavity and 2 much smaller basal concavities.

Pronotum about as long as wide. Elytra about 1.6 times as long as wide; epipleura extending to apical margin of elytra but not to apex. Front tibiae about 7.7 times as long as wide, front tarsi 4-segmented.

Abdomen with tergite VIII subtrapezoidal, posterior margin with wide, transverse emargination (Fig. 4C); sternite VIII divided. Male genitalia with penis slender, dorsoventrally curved, apex constricted and upwardly curved; inner sac with a slender and curved sclerite and a few small sclerites around it, apex with dense small denticles (Fig. 4A, B).

Female. Unknown.

Distribution. China (Guangdong).

Biology. This species is collected with *Intybia swatowensis* (Wittmer, 1956) on grass beside a stream in a village, which is consistent with the habitat of most Apalochrini. Feeding habits and behaviour of this species are unknown.

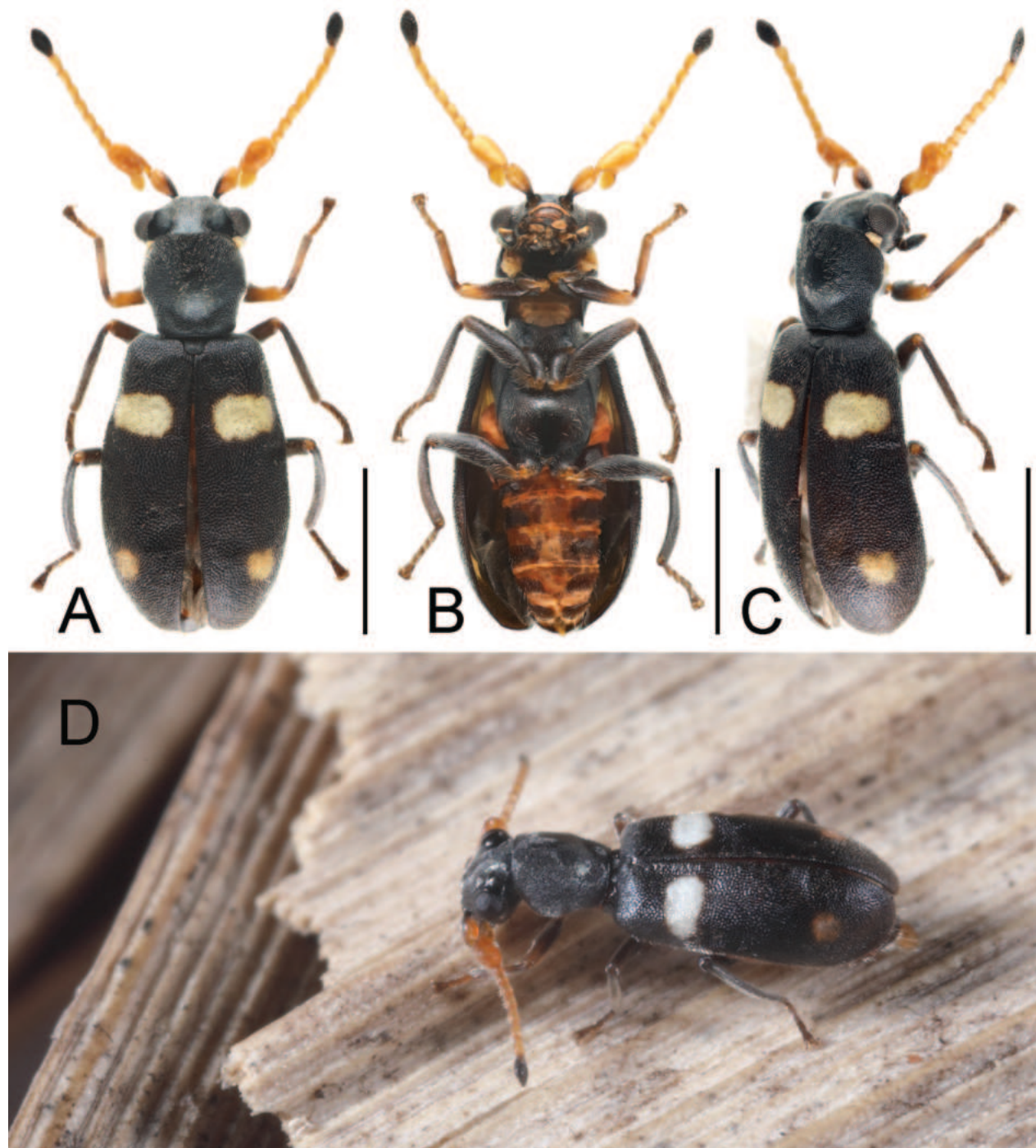


Figure 1. Habitus of *Platyintybia zhongshanensis* Liu & Wang, sp. nov. **A** dorsal view, male **B** ventral view, male **C** lateral view, male **D** habitus photograph. Scale bars: 1 mm for A–C.

***Platyintybia sarawakensis* (Champion, 1921), comb. nov.**

Figs 2–4

砂拉越扁角囊花萤

Laius sarawakensis Champion, 1921.

Intybia sarawakensis: Plonski 2016: 27.

Diagnosis. As for *Platyintybia zhongshanensis* (Fig. 3F–I).

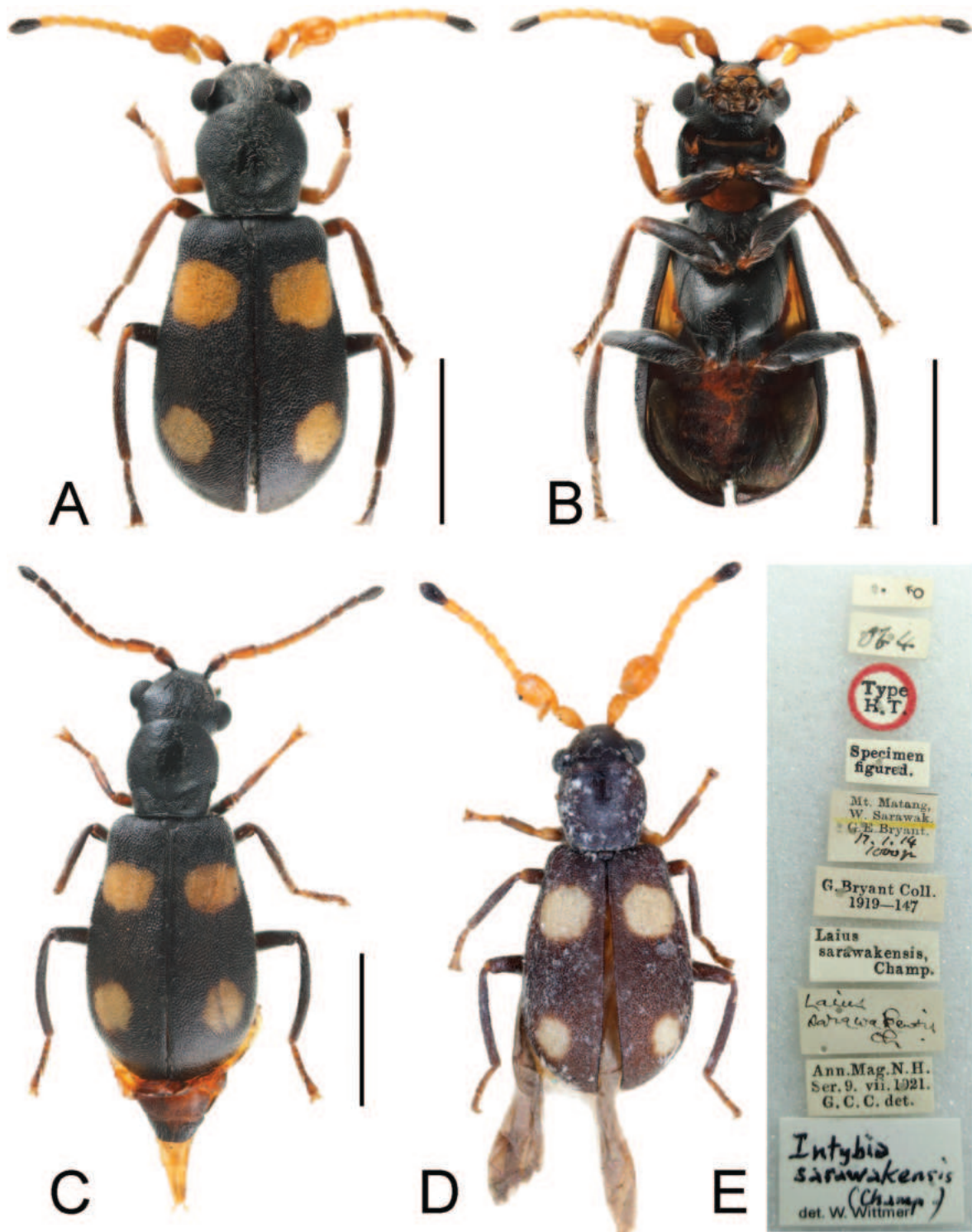


Figure 2. *Platyintybia sarawakensis* (Champion, 1921) A dorsal view, male B ventral view, male C dorsal view, female D holotype, male E label information. Scale bars: 1 mm (A–C).

Materials examined. Holotype: Malaysia • ♂: Borneo, Mount Mattang, W. Sarawak, 1000 m elev.; 17 Jan. 1914; G.E. Bryant leg.; BMNH.

Other materials examined. CHINA – Fujian Province • ♂: Zhangzhou, Zhangjiangkou mangrove forest; 23°55'21.75"N, 117°24'54.96"E; 17 Oct. 2022; Malaise trap; Rongxiang Su leg.; IZGAS COL0002. • ♀: Zhangzhou, Zhangjiangkou mangrove forest; 23°55'21.75"N, 117°24'54.96"E; 17 Oct. 2022; beating

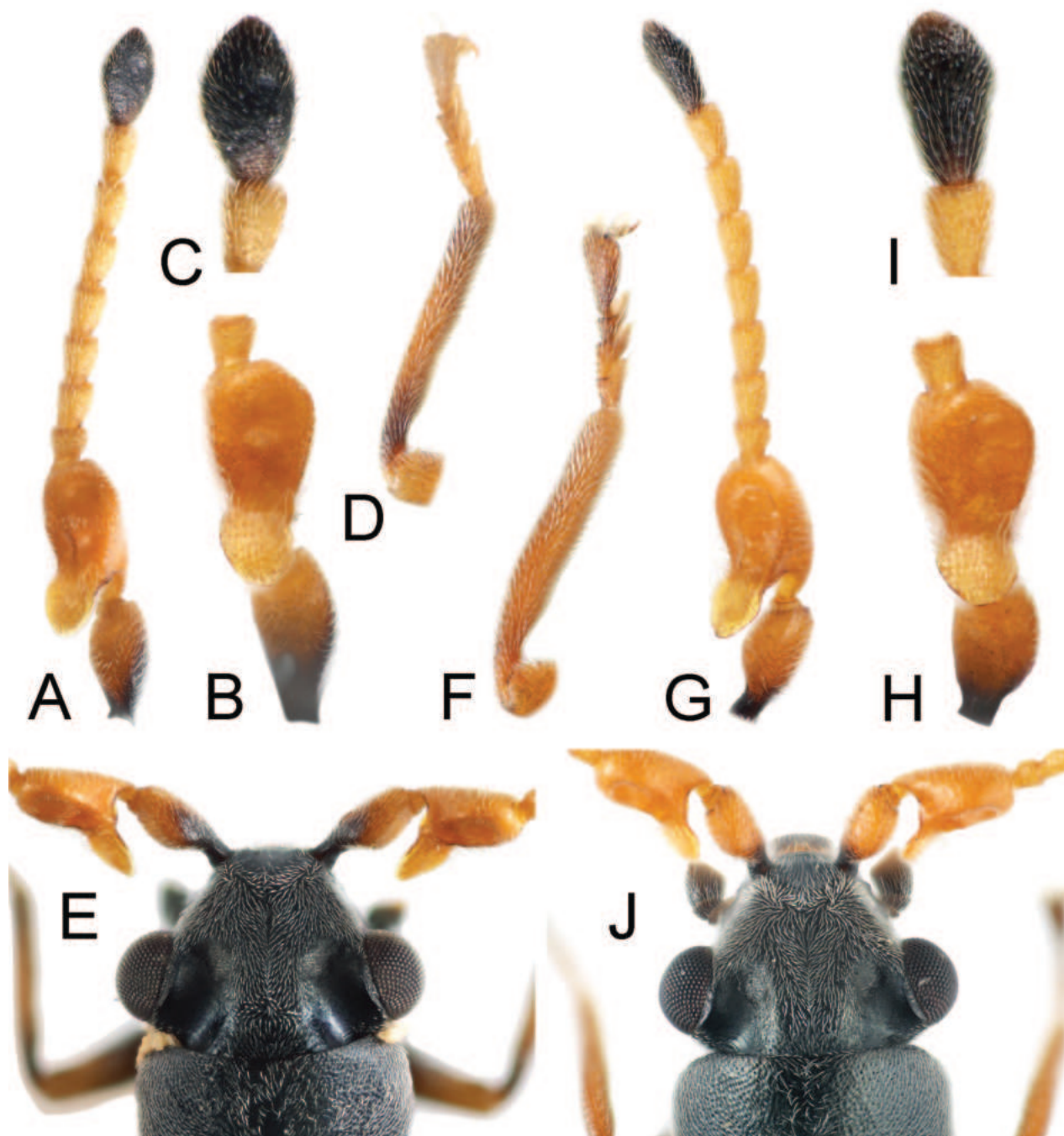


Figure 3. A–E *Platyintybia zhongshanensis* Liu et Wang, sp. nov. F–J *Platyintybia sarawakensis* (Champion, 1921) A, G antenna, male B, H lateral view of basal antennomeres, male C, I dorsal view of antennomere 11, male D, F fore tibia, male E, J dorsal view of head, male.

on *Avicennia marina* (Forsk.) Vierh.; IZGAS COL0003. • 1 ♂, 1 ♀: Zhangzhou, Zhangjiangkou mangrove forest; 23°55'21.75"N, 117°24'54.96"E; 5 m a.s.l.; 29 Aug. 2023; YF Zhang leg.; FAF COL0001 to 0002. • 2 ♀: Zhangzhou, Zhangjiangkou mangrove forest; 23°55'21.75"N, 117°24'54.96"E; 5 m a.s.l.; 16 Sep. 2023; YF Zhang leg.; FAF COL0003 to 0004. • 2 ♂, 5 ♀: Zhangzhou, Zhangjiangkou mangrove forest; 23°55'21.75"N, 117°24'54.96"E; 5 m a.s.l.; 16 Sep. 2023; YF Zhang leg.; FAF COL0005 to 0011.

Description. Length about 2.7 mm.

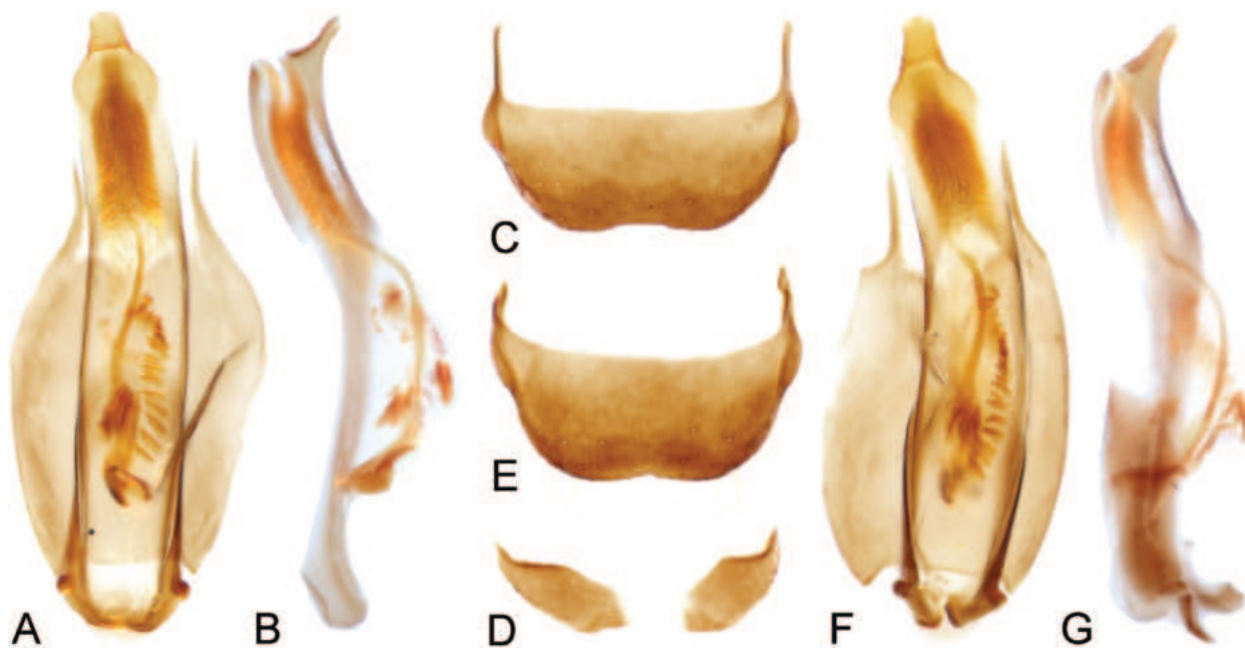


Figure 4. A–C *Platyintybia zhongshanensis* Liu & Wang, sp. nov. E–G *Platyintybia sarawakensis* (Champion, 1921) A, F male genitalia, dorsal view B, G male genitalia, lateral view C, E tergite VIII, dorsal view D sternite VIII, ventral view.

Male. Antenna mostly yellow with base of scape and apical antennomere black. Legs with femora mostly black, apex of front and middle tibiae rufous; front tibiae and tarsi rufous, middle tibiae brownish to black, hind tibiae black with basal part rufous, middle and hind tibiae brownish. Elytra with basal spots large and suboval, not extending to lateral or inner suture; subapical spots rounded, a little smaller. Abdominal ventrites mostly orange-red, with lateral areas black.

Head about 1.1 times as wide as pronotum; concavities on head not extending to anterior margin of eyes; width of vertex between concavities about 1.5 times as wide as concavity across middle of eyes. Dorsal surface of head with pair of circinately arranged setae behind antennal insertions. Antenna with scape elongate, subtriangular, and constricted at base; antennomere 3 elongate, with large lamellate process at base, dorsal surface with 1 large, transversely elliptical anterior concavity and 2 indistinct basal concavities.

Pronotum about as long as wide. Elytra about 1.5 times as long as wide; epipleura not extending to apical margin of elytra. Front tibiae about 6.4 times as long as wide, front tarsi 4-segmented.

Abdomen with tergite VIII subtrapezoidal, posterior margin with shallow emargination (Fig. 4E); sternite VIII divided. Male genitalia with penis slender, dorsoventrally curved, apex constricted and upwardly curved; inner sac with a slender, curved sclerite and a few small sclerites around it, apex with dense, small denticles (Figs 4F, 4G).

Female. Resembling male in colour and body shape, but with antennae more brownish, scape and antennomere 3 only slightly dilated, terminal antennomere simple; head without concavity on vertex; front tarsi 5-segmented.

Distribution. China (Fujian), Malaysia (Borneo).

Biology. Information on feeding habits and behaviour is scarcely known. The Chinese specimens were found on the leaves of plants in a mangrove forest, and the holotype was collected on Mount Matang without details of the habitat noted.

Key to genera of Chinese Apalochrini (males only)

- 1 Antenna with scape and antennomere 3 dilated and modified..... **2**
- Antenna with basal antennomeres simple **7**
- 2 Front tarsi 4-segmented..... ***Platyintybia*** gen. nov.
- Front tarsi 5-segmented..... **3**
- 3 Front tarsi without comb on tarsomere 2 **4**
- Front tarsi with comb on tarsomere 2..... **6**
- 4 Front tibiae thickened and curved, with concavity at base..... ***Laius***
- Front tibiae simple..... **5**
- 5 Body shape ant-like, with prothorax elongated and distinctly constricted posteriorly, elytra constricted at base ***Myrmecospectra***
- Body shape not ant-like, prothorax never distinctly longer than wide, elytra with humeral area not distinctly constricted ***Intybia***
- 6 Head with interocular area flat, antennomere 3 dilated and with bunch of hairs..... ***Protocollops***
- Head with a deep hollow or protuberance, antennomere 3 dilated but without bunch of hairs ***Troglocollops***
- 7 Antenna flabellate **8**
- Antenna filiform or only expanded **10**
- 8 Eyes extremely large, elytra impressed apically ***Mimapalochrus***
- Eyes not large, elytra simple apically **9**
- 9 Vestiture double of white and black setae ***Pectapalochrus***
- Vestiture simple of white setae..... ***Dromanthomorphus***
- 10 Male-specific character only present on front tarsi, with comb on tarsomere 2 ***Apalochrus***
- Male-specific characters present on antennae, head, tibiae, front trochanter, or abdomen..... **11**
- 11 Abdomen with aculeiform appendage on 4th and 5th sternites..... **12**
- Abdomen without appendage on sternites ***Hadrocnemus***
- 12 Middle tibiae slightly widened and excavate on inner side... ***Opisthapalochrus***
- Middle tibiae simple ***Spinapalochrus***

Discussion

Platyintybia sarawakensis was assigned to the *Intybia rouyeri* group mainly on account of its colour pattern of black with two whitish or yellowish spots on each elytron (Plonski 2016). The male-specific characters on the vertex, apical antennomeres, and front tarsi were not mentioned by Champion (1921) when describing this species. More species might be transferred to *Platyintybia* after the holotypes are examined. In Apalochrini, the 4-segmented front tarsi in males have been found in *Collops*, *Notointybia*, and *Platyintybia*, which are distributed in different biogeographic areas (Liu et al. 2020), meaning that this character must have evolved independently in those genera rather than being an autapomorphy. However, relationships between these genera and related genera require further study.

Although *Dromanthomorphus* is included in the key, the only species found in China, *Dromanthomorphus mirabilis* (Pic, 1907) actually lacks some apomorphies, such as excavate front and middle tibiae, swollen metathoracic

mesepimera, and possession of an appendage directed forward to the middle coxae (Tshernyshev 2016b; Liu et al. 2023). No nomenclatural act on this species is proposed here, as Isidor Plonski (pers. comm) is working on this species. In the above key, *Dromanthomorphus* specifically refers to *D. mirabilis* only.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text.

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