Revision of the genus *Figura* (Coleoptera: Coccinellidae) with descriptions of new species

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Abstract. The African genus *Figura* Ukrainsky, 2006 is revised. A detailed redescription of its morphology is presented. Three new species are described, *F. bitalensis* sp. n., *F. lineata* sp. n. and *F. ruwenzorica* sp. n. All species are illustrated. A key to all species and a map showing the distribution of the genus *Figura* are provided.

INTRODUCTION

The tribe Epilachnini was established by Mulsant (1846). Formerly it was treated as a separate subfamily Epilachninae within the Coccinellidae, divided into four tribes: Epilachnini, Madaini, Epivertini and Eremochilini. Recently Ślipiński (2007) and Seago et al. (2011) recognized Epilachninae as a tribe within a broadly defined subfamily Coccinellinae.

Epilachnini is a large group of herbivorous ladybird beetles including 25 genera (Jadwiszczak & Węgrzynowicz, 2003; Szawaryn, 2011; Szawaryn & Tomaszewska, 2013; Tomaszewska & Szawaryn, 2013) with a worldwide distribution. Because of its very uniform morphology, current classification of this tribe is unsatisfactory and most of the genera are in need of critical revision.

About 300 species of Epilachnini, grouped in 8 genera, are known from the Afrotropical region. Four of the genera were formerly classified in the tribe Madaini: *Figura* Ukrainsky, 2006, *Megatela* Weise, 1906, *Merma* Weise, 1898 and *Tropha* Weise, 1900. All of them consist of only a few species. The genus *Figura* was established as *Bambusicola* by Fürsch (1986) (nec *Bambusicola* Gould, 1862; Aves) and replaced by *Figura* Ukrainsky, 2006. Until now the genus *Figura* contained four species with *F. aberratica* (Fürsch, 1975) the type species. During a recent examination of the material borrowed from several European museums, three new species were found and are described herein as *F. bitalensis* sp. n, *F. lineata* sp. n and *F. ruwenzorica* sp. n.

MATERIAL AND METHODS

Specimens used in this study are deposited in the following collections: BMNH – Natural History Museum, London, United Kingdom; DEIC – Deutsches Entomologisches Institut, Eberswalde, Germany; MZPW – Museum and Institute of Zoology PAS, Warszawa, Poland; MNHN – Museum National d'Histoire Naturelle, Paris, France; MRAC – Musée Royal de l'Afrique Centrale, Tervuren, Belgium; ZSMC – Zoologische Sammlung des Bayerischen Staates, München, Germany.

Entire beetles, where available, or at least their genitalia and mouth parts were dissected, cleared in 10% solution of KOH, rinsed in distilled water, transferred to glycerol and examined on slides. Illustrations were made from slide preparations using a camera lucida attached to Leica or Carl Zeiss Jenamed microscopes. Mouth parts were cleared in ethyl alcohol and transferred to adhesive tape for SEM photography. After examination the genitalia and mouth parts were transferred to micro-vials and pinned beneath the specimen. Measurements were made using an ocular micrometer attached to a dissecting microscope. The following terms are used: TL - total length, from apical margin of clypeus to apex of elytra; PL – pronotal length, from the middle of anterior margin to the middle of the base; PW – pronotal width at widest part; EL – elytral length along suture including scutellum; EW - elytral width across both elytra at the widest part. Habitus photographs were taken using a digital camera and enhanced using Helicon Focus software. Scanning electron micrographs (SEM) were taken using a HITACHI S-3400N in the Electron Microscopy Laboratory of the MZPW.

The beetle morphology follows Lawrence et al. (2011) including the use of Roman numerals for the abdominal segments; specific terminology used in Coccinellidae follows Ślipiński & Tomaszewska (2010).

SYSTEMATICS

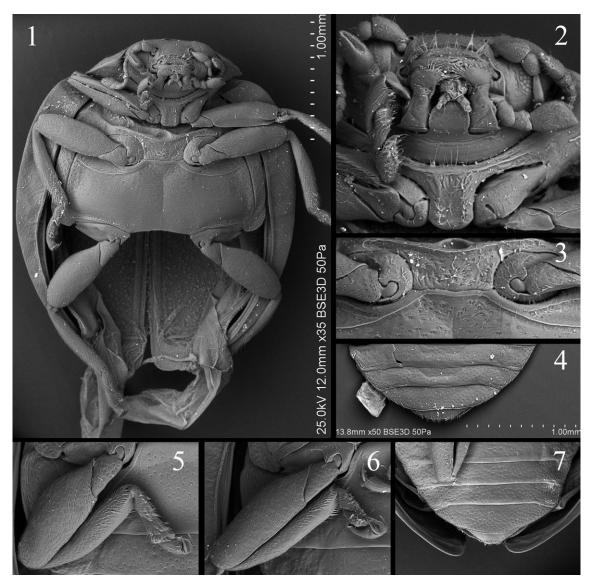
Genus Figura Ukrainsky, 2006

Bambusicola Fürsch, 1986: 392 (nec *Bambusicola* Gould, 1862; Aves). Type species: *Epilachna aberratica* Fürsch, 1975 (by original designation).

Figura Ukrainsky, 2006: 399 (replacement name for *Bambusi-cola* Fürsch, 1986).

Diagnosis. Figura is an easily distinguishable genus within the African Epilachnini. The tarsal claws of its species have a characteristic shape with the inner teeth touching each other and forming a cordate pattern; a similar shape occurs only in the Neotropical genus Malata Gordon, 1975. Moreover, species of Figura do not possess tibial spurs. Also the structure of male and female genitalia is unique within Epilachnini.

Redescription. Length 2.8–4.1 mm. Body (Figs 106–114) oval, convex; dorsum pubescent. Pronotum



Figs 1–7: *Figura aberratica* (Fürsch). 1 – habitus, ventral view; 2 – mouthparts and prosternal process; 3 – mesoventral process; 4 – ventral apical part of abdomen, male; 5 – hind leg, male; 6 – hind leg, female; 7 – ventral apical part of abdomen, female.

yellow to reddish brown or black; elytra light brown, orange to red with black spots or black border, sometimes entirely black with red maculae.

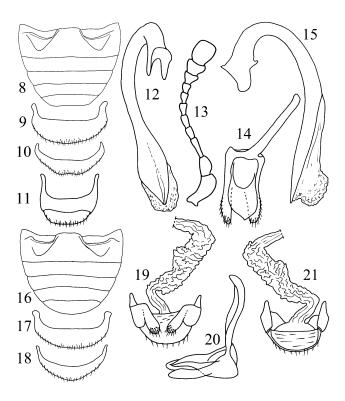
Head exposed, transverse; uniformly densely punctate, with microsculpture between punctation; ventral antennal grooves short, weakly marked. Eyes finely faceted; weakly emarginate. Antennal insertions (Fig. 74) exposed in front of eyes, close to inner eye margins, with distance between antennal sockets about 5 times greater than distance between antennal socket and inner margin of eye. Antennal sockets bordered with distinctive ridge posteriorly and medially. Antenna (Fig. 81) about as long as width of head; 11-segmented; scape large, swollen, more than two times longer than pedicel; pedicel longer than wide, swollen; antennomere 3 elongate, about as long as antennomeres 4 and 5 together; antennal club relatively compact, 3-segmented, slightly asymmetrical. Clypeus transverse; labrum transverse (Fig. 74), covered with moderately long setae, anterior margin membranous, sparsely covered with short setae. Mandibles (Figs 78, 80) are multidentate apically with additional serration; prostheca large, long, covered with microtrichia; dorsal surface of each mandible with several long setae on outer margin near base; dorsal and ventral surfaces basally with areas of small dense pores (sensilla?). Maxilla (Fig. 79) with cardo subtriangular, without setae: basistipes and mediastipes not separated but with suture clearly visible; mediastipes elongate; galea sub-oval, transverse with inner margin produced, densely setose apically; lacinia slender, falcate, covered with long, dense setae; maxillary palp 4-segmented, palpomeres 2-4 are wider apically, pubescent; palpomere 2 short, slightly longer than palpomere 3; terminal palpomere about 2.5 times longer than palpomere 3. Submentum transverse, fused with gula with suture visible (Fig. 75); labium (Fig. 76) with mentum transverse, subrectangular in shape; prementum short, transverse, sclerotized; dorsal surface covered with scale-like processes (Fig. 77); labial palp 3-segmented, short, placed subapically on prementum, directed ventrally or distinctly posteriorly; basal palpomere short, transverse; second palpomere short, subquadrate, swollen, about twice as long as basal palpomere; terminal palpomere about as long as second and twice as wide. Gula (Fig. 75) transverse; gular sutures deep, short, reaching to about 1/3 length of gula.

Pronotum transverse, widest at base and gradually narrowing anteriorly, anterior angles not produced (Fig. 71); anterior, lateral and hind margins not bordered; disc convex, finely punctate, with microsculpture. Prothoracic hypomeron smooth; notosternal suture distinct; prosternum (Figs 2, 23, 32, 44, 56, 69, 98) in front of coxa less than 0.5 times as long as coxal longitudinal diameter, anterior edge with prosternal ridge; hind margin of prosternum in front of coxae not bordered; prosternal process about 2 times narrower than longest coxal diameter, creased and/or weakly concave medially; procoxal cavity strongly transverse with small triangular slit laterally.

Mesoventrite (Figs 3, 24, 33, 45, 57,70, 99) with anterior edge with complete raised border; with median cavity receiving apex of prosternal process; mesoventral process at least slightly wider than coxal diameter; mesometaventral junction with suture visible, straight or sinuate, without internal knob. Scutellum is small, triangular. Elytra at base distinctly broader than pronotum; dually punctate, smaller punctures very fine, larger are shallowly impressed; humeral angles well developed; lateral margins narrowly flattened, visible from above throughout; elytral epipleuron incomplete in apical part (Figs 7, 22, 31, 43, 55, 68, 73), flat, without foveae, with submarginal carina incomplete, reaching to about the middle of mesocoxal cavity; metaventrite with intercoxal process broadly bordered; metaventral postcoxal lines connected medially and complete laterally, arcuate, curved anteriorly at both ends, with distinct groove behind (Figs 1, 22, 31, 43, 55, 68); metaventrite with discrimen incomplete; metanepimeron distinct.

Legs are moderately long and stout, with apices of mid and hind femora protruding slightly beyond outer margin of elytral epipleuron (Fig. 68). Trochanters are simple, on inner margin with shallow cavity for receiving tip of tibia (Figs 2, 56, 69, 99). Femora are cylindrical with a weak groove along their inner sides for receiving tibiae; hind femora in males more swollen (Figs 1, 5) than in females (Figs 6, 22). Tibiae cylindrical and lacking apical spurs; tarsi pseudotrimerous; tarsal claw bifid, inner teeth touching or almost touching each other forming cordate pattern (Fig. 82).

Abdomen has six ventrites in males (Figs 4, 58, 68, 73) and five in females with sternite VIII partly visible (Figs 7, 72). Ventrite 1 along midline more than twice as long as ventrite 2. Abdominal postcoxal lines separate medially, laterally recurved and incomplete, reaching about half the length of ventrite 1; apical margin of male ventrite 5 truncate (Figs 58, 68, 73), ventrite 6 truncate or weakly emarginate (Figs 10, 35, 47, 60, 85), abdominal tergite VIII rounded (Figs 9, 34, 48, 61, 84); apical margin of female ventrite 5 rounded (Figs 7, 72), sternite VIII arcuate, entire (Figs 18, 30, 96), tergite VIII rounded (Figs 17, 26, 95).

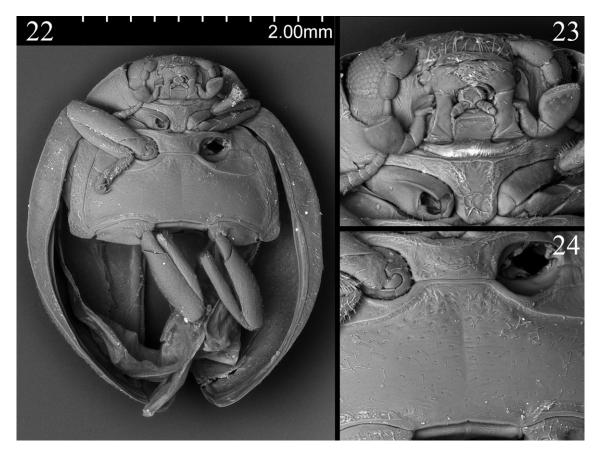


Figs 8–21: Figura aberratica (Fürsch). 8 – abdomen, male; 9 – abdominal tergite VIII, male; 10 – ventrite 6, male; 11 – male genital segment, dorsal; 12 – penis, inner view; 13 – antenna; 14 – tegmen, inner view; 15 – penis, lateral view; 16 – abdomen, female; 17 – abdominal tergite VIII, female; 18 – abdominal sternite VIII, female; 19 – female genitalia, ventral view; 20 – tegmen, lateral view; 21 – female genitalia, dorsal view.

Male terminalia and genitalia. Apodeme on male sternum IX absent. Tergite X wide and short with anterior margin broadly rounded or truncate (Figs 11, 40, 49, 62, 86). Tegmen (Figs 14, 42, 53, 64, 91) with penis guide, which has a petal shaped inner side, with pointed apex, asymmetrical; parameres about as long as penis guide, broad, separated, articulated with phallobase, with apical part shortly setose; tegminal strut about as long as or longer than penis guide. Penis base with arms poorly developed; penis curved, slightly widening towards apex with suture on inner side; with large membranous gonopore at apex (Figs 15, 39, 54, 67, 89, 103).

Female genitalia. Lateral and posterior margins of proctiger (tergite X) sclerotized, central part membranous, rounded (Figs 21, 28, 92); coxites thin, elongate, without styli, their lateral margins fused with paraprocts (Figs 18, 29, 93). Bursa copulatrix large, sinuate, non divided, wider medially, with oviduct joined to the apical part; spermathecal duct, spermatheca and accessory gland absent; two symmetrical membranous sac-like structures at the base of oviduct (Fig. 93).

Distribution. Central Africa: Albertine Rift – Uganda, Democratic Republic of the Congo, Rwanda, Burundi (Fig. 105).



Figs 22–24: Figura bambusae (Mader). 22 – habitus, ventral view; 23 – mouthparts and prosternal process; 24 – mesoventral process.

Key to the species of the genus Figura

- Postcoxal lines on abdomen not laterally recurved (Fig. 25).
 F. bambusae (Mader)
 Postcoxal lines on abdomen laterally recurved (Figs 8, 36).
- 2 Prosternum with anterior ridge short, present only medially, extending laterally at most to half length of procoxae (Fig. 98); pronotum entirely black..... *F. tonsa* (Fürsch)
- Prosternum with anterior ridge long, extending laterally beyond half the length of procoxae (Fig. 2); pronotum entirely yellow-orange to light brown or with black macula medially.
 3

- Antennomeres 4 and 5 subequal in length (Figs 13, 63)... 5
- 5 Prosternal process with anterior ridge incomplete medially (Fig. 2); antennomere 3 shorter than 4 and 5 combined, antennomere 8 subquadrate (Fig. 13); dorsum orange-red with black spots (Figs 106, 107). . . . F. aberratica (Fürsch)

Meso-metaventral connection straight (Fig. 70); antennomere 3 shorter than 4 and 5 combined; antennomere 8 elongate (Fig. 88).
 F. ruwenzorica sp. n.

Figura aberratica (Fürsch, 1975)

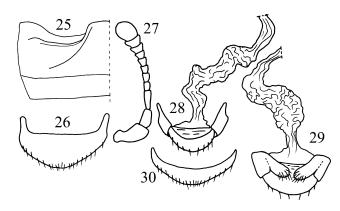
(Figs 1–21, 106, 107)

Epilachna aberratica Fürsch, 1975: 646.

Bambusicola aberraticus [sic!]: Fürsch, 1986: 393; Jadwiszczak

& Węgrzynowicz 2003: 192.

Figura aberratica: Ukrainsky, 2006: 431.



Figs 25–30: *Figura bambusae* (Mader). 25 – abdominal post-coxal lines; 26 – abdominal tergite VIII, female; 27 – antenna; 28 – female genitalia, dorsal view; 29 – female genitalia, ventral view; 30 – abdominal sternite VIII, female.



Figs 31–33: Figura bitalensis sp. n. 31 – habitus, ventral view; 32 – mouthparts and prosternal process; 33 – mesoventral process.

Diagnosis. The typical form of this species is easy to distinguish from other species because of the fourspotted elytron. Some of these spots may be reduced but always there are more than one black, oval or round black spot on each elytron. Distinctive for this species is the prosternum with anterior ridge incomplete (ridge not clearly visible). It can be distinguished from *F. lineata* sp. n. by the elongate (rather than transverse) antennomere 8.

Description. Length 3.2–3.8 mm; TL/EW = 1.20–1.33; PL/PW = 0.45–0.49; EL/EW = 1.10–1.17; EW/PW = 1.80–1.94.

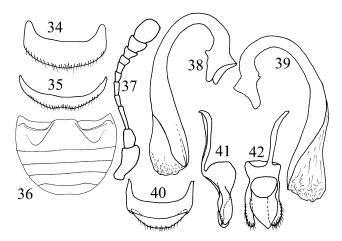
Body (Figs 1, 106, 107) round-oval, convex; surfaces covered with short, sparse pubescence. Head, mouthparts, antennae, hypomeron, prosternum, mesoventrite, legs and abdomen yellow; metaventrite yellow to dark brown or black. Pronotum yellow to orange. Elytron orange usually with four black spots arranged as 1–2–1. First, basal spot touching elytral margin, not touching suture and scutellum (sometimes reduced); one spot in second row close to elytral suture (sometimes absent), second one near elytral margin (sometimes fused with posterior spot); posterior spot on apical part of elytron; all spots can vary in size.

Antenna (Fig. 13) with antennomere 3 shorter than 4 and 5 combined; antennomeres 4 and 5 elongate and subequal in length; antennomeres 6 to 8 slightly longer than wide, subequal in length. Maxillary palpomere 2 about 1.3 times longer than palpomere 3; terminal palpomere large, about twice as long as palpomere 3, with sides almost parallel (Fig. 2).

Prosternum with anterior ridge incomplete medially (ridge not clearly visible), exceeding half of the length of

procoxae; prosternal process (Fig. 2) rounded apically, about 1.5 times longer than wide, width about 2.3–2.4 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about as wide as mesocoxal width at the same position (Fig. 3); mesometaventral connection straight. Epipleuron (Fig. 1) about 2.3–2.5 times broader than metepisternum.

Abdominal postcoxal lines rounded, recurved, reaching about half length of ventrite 1 (in some specimens abdominal postcoxal lines deeper and exceeding half of the length). Apical margin of male ventrite 5 truncate



Figs 34–42: *Figura bitalensis* sp. n. 34 – abdominal tergite VIII, male; 35 – ventrite 6, male; 36 – abdomen, male; 37 – antenna; 38 – penis, inner view; 39 – penis, lateral view; 40 – male genital segment, dorsal view; 41 – tegmen, lateral view; 42 – tegmen, inner view.



Figs 43-45: Figura centralis (Sicard). 43 - habitus, ventral view; 44 - mouthparts and prosternal process; 45 - mesoventral process.

(Figs 4, 8), ventrite 6 in males emarginate (Fig. 10), abdominal tergite VIII rounded (Fig. 9). Apical margin of female ventrite 5 rounded (Figs 7, 16), sternite VIII arcuate (Fig. 18), tergite VIII rounded (Fig. 17).

Male terminalia and genitalia. Apical margin of tergite X is truncate (Fig. 11). Viewed from the inside the penis guide is slightly wider medially; about as long as parameres (Figs 14, 20). Tegminal strut about as long as tegmen. Viewed from the inside the penis is wider anteriorly and pointed apically (Figs 12, 15).

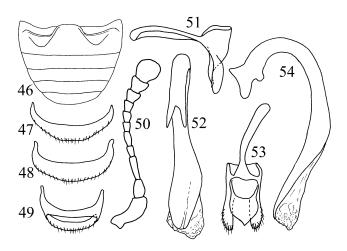
Female genitalia as in Figs 18 and 21.

Type material examined. Holotype ♂, Democratic Republic of the Congo, labelled "HOLOTYPUS / I.R.S.A.C. – MUS. CONGO, Kivu: Terr. Lubero 2.200 m 28.XI.1951, N. Leleup, (for. mont. avec bamb.) / Réclolté dans l'humus / 530 / Holotypus, Epilachna aberratica Fürsch 74" (MRAC).

Other material. Uganda: xii.1934–i.1935, Ruwenzori Range, Namwamba Valley, 6,500 ft. (B.M. 1935-203), F.W. Edwards lgt. (1&: BMNH); same data but Kilembe, 4,500 ft. (1&: BMNH); 1.–2.xi.1911, N. Ruwenzori, 6,000–8,500 ft. (1912-193), S.A. Neave lgt. (1\$\sigma\$: BMNH); 6.viii.2008, Kasese District, Ruwenzori Mts. National Park, 1,757–1,871 m (HE08-52b), Hallvard Elven lgt. (2&: MZPW – voucher numbers KS145 and KS165).

Note. Paratypes of *E. aberratica* have a different colour pattern to the holotype and many different morphological characters such as structure of antennomeres, structure of prosternal process, or shape of the male genitalia. More-

over, the holotype and paratypes were collected from opposite regions of the range of occurrence for the genus *Figura*. The specimens designated by Fürsch as paratypes of *E. aberratica* are therefore described below as a new species *F. lineata*.



Figs 46–54: *Figura centralis* (Sicard). 46 – abdomen, male; 47 – ventrite 6, male; 48 – abdominal tergite VIII, male; 49 – male genital segment, dorsal view; 50 – antenna; 51 – tegmen, lateral view; 52 – penis, inner view; 53 – tegmen, inner view; 54 – penis, lateral view.



Figs 55–58: Figura lineata sp. n. 55 – habitus, ventral view; 56 – mouthparts and prosternal process; 57 – mesoventral process; 58 – ventral apical part of abdomen, male.

Figura bambusae (Mader, 1941)

(Figs 22-30, 114)

Subcoccinella bambusae Mader, 1941: 170; Kuznetsov, 1993: 288.

Bambusicola bambusae: Fürsch, 1986: 394; Jadwiszczak & Wegrzynowicz, 2003: 192.

Figura bambusae: Ukrainsky, 2006: 431.

Diagnosis. This species can easily be distinguished by its coloration. In the middle of each elytron there are two brown or dark-brown maculae, one round and one c-shaped. In this species the abdominal postcoxal lines are also not laterally recurved, which separates *F. bambusae* from other species. It has also characteristic antennae with antennomere 8 transverse. This character is shared only with *F. lineata* sp. n.

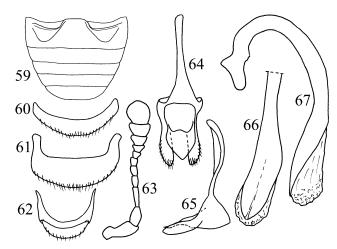
Description. Length 2.8 mm; TL/EW = 1.35; PL/PW = 0.42; EL/EW = 1.13; EW/PW = 1.50.

Body (Figs 22, 114) round-oval, convex; surfaces covered with short, sparse pubescence. Body yellowish-brown. Pronotum yellow-ochre; elytron yellow-ochre, each elytron with two macule, one large, oval brown in the middle of elytra, near elytral margin, second paler, oval c-shaped, near the first one but closer to suture.

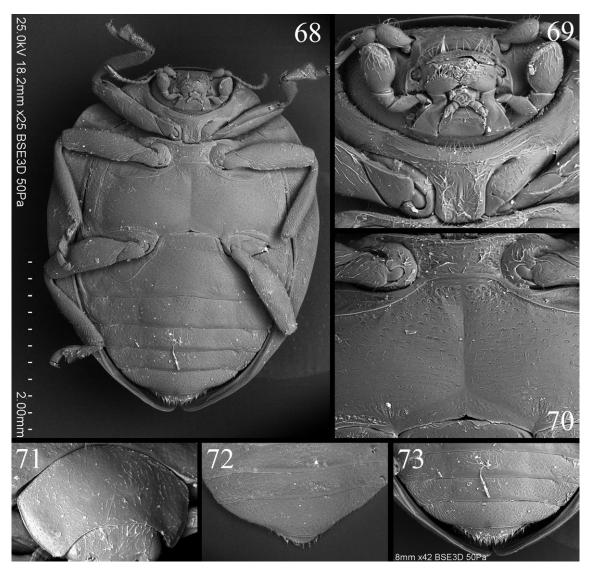
Antenna (Fig. 27) with antennomere 3 as long as 4 and 5 combined; antennomeres 4 and 5 slightly elongate, subequal in length; antennomeres 6 and 7 subquadrate, subequal in length; antennomere 8 transverse, shorter than antennomeres 6 and 7, widened apically. Maxillary

palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, about 2.3 times longer than palpomere 3, slightly securiform (Fig. 23).

Prosternum with anterior ridge complete medially, exceeding half the length of procoxae; prosternal process (Fig. 23) rounded apically, about 1.6 times longer than wide, width about 2.1 times the length of prosternum in



Figs 59–67: *Figura lineata* sp. n. 59 – abdomen, male; 60 – ventrite 6, male; 61 – abdominal tergite VIII, male; 62 – male genital segment, dorsal view; 63 – antenna; 64 – tegmen, inner view; 65 – tegmen, lateral view; 66 – penis apical part, inner view; 67 – penis, lateral view.



Figs 68–73: Figura ruwenzorica sp. n. 68 – habitus, ventral view; 69 – mouthparts and prosternal process; 70 – mesoventral process; 71 – pronotum; 72 – ventral apical part of abdomen, female; 73 – ventral apical part of abdomen, male.

front of coxae at the narrowest point. Mesoventral process about 1.35 times as wide as mesocoxal width at the same position (Fig. 24); meso-metaventral connection straight. Epipleuron (Fig. 22) about 2.1 times broader than metepisternum.

Abdominal postcoxal lines rounded, incomplete, not recurved, reaching about ³/₄ of the length of ventrite 1 (Fig. 25). Apical margin of female ventrite 5 rounded, sternite and tergite VIII rounded (Figs 26, 30).

Male not examined.

Female genitalia as in Figs 28 and 29.

Note: Abdomen of the type specimen is partly destroyed, cut into three pieces. Also genitalia are partly destroyed and not all structures could be studied.

Type material examined. Holotype \$\,\ \text{Democratic Republic} of the Congo, labelled "HOLOTYPUS bambusae / Congo Belge: P.N.A. vers Rweru, volc Mikeno (Bambous) 2400 m. 26-vii-1934, G.F. de Witte: 498 / R. DÉT. A 4636 / COLL. MUS. CONGO / Holotypus bambusae m. / Mader det. 1940: Subcoccinella bambusae m. / Epilachna bambusae det. H. Fürsch 78" (MRAC).

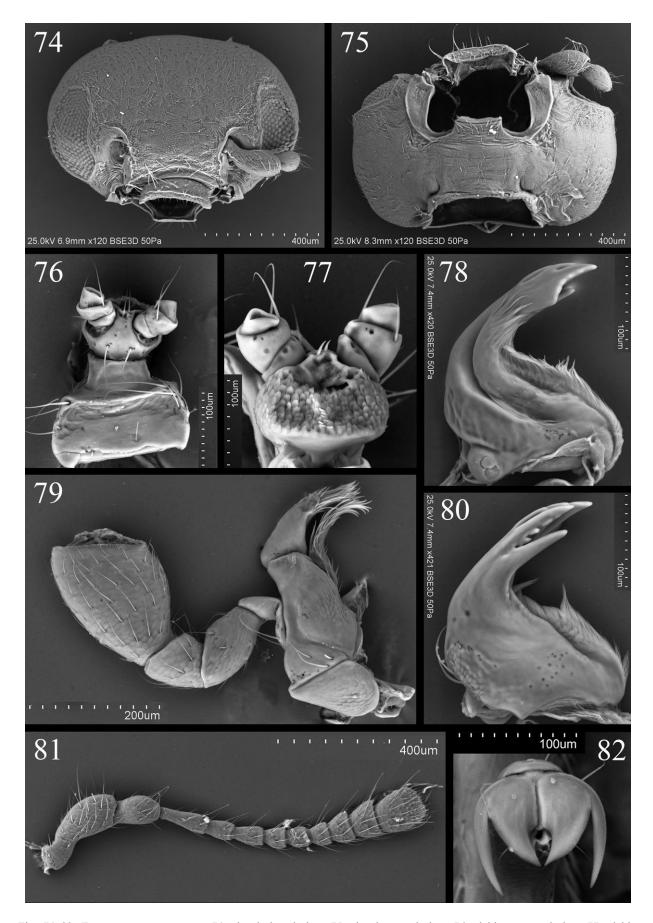
Figura bitalensis sp. n.

(Figs 31-42, 111)

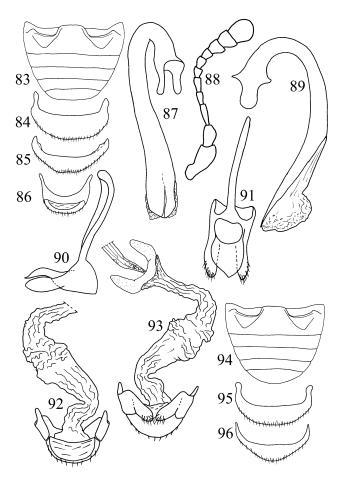
Diagnosis. This species resembles *F. ruwenzorica* sp. n. and some forms of *F. centralis* (Fig. 110) in its colour pattern but it can easily be distinguished from them in having a sinuate meso-metaventral connection. It is also distinct from them in that antennomere 3 is about as long as antennomeres 4 and 5 combined whereas in *F. ruwenzorica* and *F. centralis* antennomere 3 is shorter than 4 and 5 combined.

Description. Length 3.7 mm; TL/EW = 1.33; PL/PW = 0.45; EL/EW = 1.14; EW/PW = 1.57.

Body (Figs 31, 111) round-oval, convex; surfaces covered with short, sparse pubescence. Head, mouthparts, antennae, hypomeron, prosternum, mesoventrite, metaventrite, scutellum, epipleuron, abdomen and legs yellowish-brown. Pronotum yellowish-brown, elytron black with broad yellowish-brown maculae on anterior and posterior parts.



Figs 74–82: *Figura ruwenzorica* sp. n. 74 – head, dorsal view; 75 – head, ventral view; 76 – labium, ventral view; 77 – labium, dorsal view; 78 – mandible; ventral view; 79 – maxilla; 80 – mandible, dorsal view; 81 – antenna; 82 – tarsal claws.



Figs 83–96: *Figura ruwenzorica* sp. n. 83 – abdomen, male; 84 – abdominal tergite VIII, male; 85 – ventrite 6, male; 86 – male genital segment; 87 – penis, inner view; 88 – antenna; 89 – penis, lateral view; 90 – tegmen, lateral view; 91 – tegmen, inner view; 92 – female genitalia, dorsal view; 93 – female genitalia, ventral view; 94 – abdomen, female; 95 – abdominal tergite VIII, female; 96 – abdominal sternite VIII, female.

Antenna (Fig. 37) with antennomere 3 as long as 4 and 5 combined; antennomeres 4 and 5 elongate; antennomeres 6 and 7 elongate shorter than 4, antennomere 8 transverse, shorter than antennomere 7. Maxillary palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, more than twice as long as palpomere 3, slightly securiform (Fig. 32).

Prosternum with anterior ridge complete medially, exceeding half the length of procoxae; prosternal process depressed medially (Fig. 32) and broadly rounded apically, with weak longitudinal carina on apical part, about 1.6 times longer than wide, width about 2.3 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about 1.1 times as wide as mesocoxal width at the same position (Fig. 33), with dense, deep punctures; meso-metaventral connection sinuate. Epipleuron (Fig. 31) about 2.5 times broader than metepisternum.

Abdominal postcoxal lines rounded, recurved, reaching ³/₄ of the length of ventrite 1 (Fig. 36). Apical margin of male ventrite 5 truncate (Fig. 36), ventrite 6 emarginate (Fig. 35), abdominal tergite VIII rounded (Fig. 34).

Male terminalia and genitalia. Apical margin of tergite X rounded (Fig. 40). Inner view of penis guide slightly wider medially; slightly longer than parameres (Figs 41, 42). Tegminal strut about as long as tegmen. Inner view of penis wider anteriorly, rounded apically (Figs 38, 39).

Female unknown.

Type material. Holotype ♂, Democratic Rep. of the Congo, labelled "COLL. MUS. CONGO, Kivu: Bitale, 1800 m. 15-VIII-1952, R. Mayné / Epilachna inversa forma nomin. det. Mader 1955 / Bambusicola centralis (Sic.) det. H. Fürsch 85 / HOLOTYPE ♂, Figura bitalensis n. sp., det. K. Szawaryn 2014" (MRAC).

Etymology. The species name is derived from the type locality of the holotype – Bitale.

Figura centralis (Sicard, 1912)

(Figs 43–54, 109, 110)

Solanophila centralis Sicard, 1912: 132.

Epilachna centralis: Korschefsky, 1931: 38.

Bambusicola centralis: Fürsch, 1986: 393; Jadwiszczak & Węgrzynowicz, 2003: 192.

Figura centralis: Ukrainsky, 2006: 432.

Solanophila bambusicola Mader, 1950: 135; Fürsch, 1986: 393 (as a synonym of *Bambusicola centralis*).

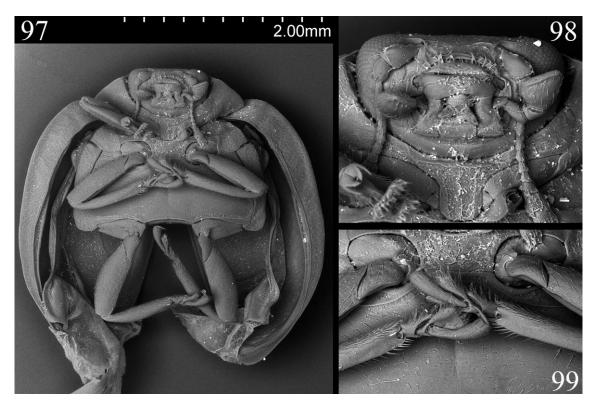
Diagnosis. Specimens with typical colour pattern are easily recognizable by their red colour with large black spot on central part of elytra. Untypical form resembles *F. bitalensis* sp. n. but is distinguishable from this species in that its meso-metaventral connection is straight. Moreover antennomere 3 is shorter than antennomeres 4 and 5 combined, and antennomere 4 shorter than 5. Similar antenomere structure is present in *F. ruwenzorica* but *F. centralis* can be distinguished from this species as it lacks a longitudinal carina on apical part of prosternal process.

Description. Length 3.8–4.0 mm; TL/EW = 1.30–1.33; PL/PW = 0.48–0.57; EL/EW = 1.12–1.15; EW/PW = 1.74–1.79.

Body (Figs 43, 109, 110) round-oval, convex; surfaces covered with short, sparse pubescence. Head, mouthparts, antennae, hypomeron, prosternum, mesoventrite and legs ferruginous; metaventrite ferruginous or black; abdomen ferruginous sometimes with the median part of ventrite 1 dark brown or black. Pronotum red; elytron red with one large black spot on medially, touching suture; sometimes with one additional black, small spot on anterior part of elytron; sometimes median macula extends to lateral margins of elytra.

Antenna (Fig. 50) with antennomere 3 shorter than 4 and 5 combined; antennomeres 4 and 5 elongate, antennomere 5 longer than 4; antennomere 6 shorter than antennomere 7, antennomere 8 slightly elongate. Maxillary palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, about twice as long as palpomere 3, slightly securiform (Fig. 44).

Prosternum with anterior ridge complete medially, exceeding half the length of procoxae; prosternal process (Fig. 44) polygonal apically, without depression, about 1.6 times longer than wide, width about 2.4 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about 1.2 times as wide as



Figs 97–99: Figura tonsa (Fürsch). 97 – habitus, ventral view; 98 – mouthparts and prosternal process; 99 – mesoventral process.

mesocoxal width at the same position (Fig. 45); mesometaventral connection straight. Epipleuron (Fig. 43) about 2.5 times broader than metepisternum.

Abdominal postcoxal lines rounded, exceeding half the length of ventrite 1 (Fig. 46). Apical margin of male ventrite 5 truncate (Fig. 46), ventrite 6 truncate (Fig. 47), abdominal tergite VIII rounded (Fig. 48).

Male terminalia and genitalia. Apical margin of tergite X rounded (Fig. 49). Penis guide in inner view widened medially; shorter than parameres (Figs 51, 53). Tegminal strut slightly longer than tegmen. Penis in inner view widening anteriorly, rounded apically (Figs 52, 54).

Female not examined.

Type material examined. Holotype (according to Fürsch, 1986) &, Uganda, labelled "Brit. Uganda, Grauer / Syntypus / Solanophila centralis Sic n. sp. / DEI EBERSWALDE / DEI Muncheberg Col-03054" (DEIC); holotype & of Solanophila bambusicola, Burundi, labelled "HOLOTYPUS / COLL. MUS. CONGO (ex coll. I.P.N.C.B.) / Congo Belge: P.N.A. Mt. Sesero, près Bitashimva (Bambous) 2000 m. 1 au 2-viii-1934 G.F. de Witte 505 / Solanophila bambusicola m. Holotype det. Mader 49. / vid. Fürsch 62" (MRAC).

Other material examined. Uganda (13, MNHN); Rwanda, 10.i.1986, Nyakabuye, Mühle lgt. (13, ZSMC).

Figura lineata sp. n.

(Figs 55-67, 108)

Diagnosis. F. lineata is easily distinguishable by its dorsal colour pattern, which is unique among Figura species; yellow pronotum with large black macula medially and pattern of yellow and black maculae on elytra as in Fig. 108. This species can also be distinguished from its congeners by the prosternal process creased laterally.

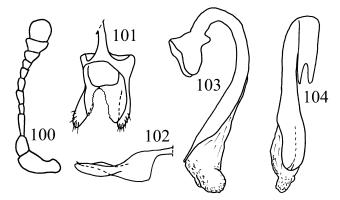
Description. Length 3.2–3.3 mm; TL/EW = 1.28–1.30; PL/PW = 0.45–0.51; EL/EW = 1.12–1.15; EW/PW = 1.68–1.79.

Body (Figs 55, 108) round-oval, convex; surfaces covered with short, sparse pubescence. Mouthparts, antennae, hypomeron, prosternum, scutellum and legs yellow. Epipleurom, meso and metaventrite black. Head black with clypeus and frons yellow. Abdomen with first two ventrites black and the rest yellow. Pronotum yellow with large, black macula on disc touching anterior and posterior margins, elytron with characteristic yellow and black maculae pattern as in Fig. 108.

Antenna (Fig. 63) with antennomere 3 as long as 4 and 5 combined; antennomeres 4 and 5 elongate, equal in length; antennomeres 6–8 subequal in length, antennomere 8 transverse, wider anteriorly. Maxillary palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, more than twice as long as palpomere 3, with sides almost parallel (Fig. 56).

Prosternum with anterior ridge complete medially, exceeding half the length of procoxae; prosternal process creased laterally, (Fig. 56) rounded apically, about 1.6 times longer than wide, width about 2.5 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about 1.1 times as wide as mesocoxal width at the same position (Fig. 57); mesometaventral connection straight. Epipleuron (Fig. 55) about 2.3 times broader than metepisternum.

Abdominal postcoxal lines rounded, exceeding half the length of ventrite 1 (Fig. 59). Apical margin of male ventrite 5 truncate (Figs 58, 59), ventrite 6 in males truncate (Fig. 60), abdominal tergite VIII rounded (Fig. 61).



Figs 100–104: *Figura tonsa* (Fürsch). 100 – antenna; 101 – tegmen, inner view; 102 – tegmen, lateral view; 103 – penis, lateral view, 104 – penis, inner view.

Male terminalia and genitalia. Apical margin of tergite X rounded (62). Inner view of penis guide slightly wider medially; shorter than parameres (Figs 64, 65). Tegminal strut longer than tegmen. Inner view of penis wider anteriorly, rounded apically (Figs 66, 67).

Female not examined.

Type material. Holotype ♂, Democratic Republic of the Congo, labelled "PARATYPUS / I.R.S.A.C. – MUS. CONGO, Kivu: Terr. Mwenga, 2.700 Lac Lungwe, N. Leleup, VIII-1953 / Fotêt de bambous et Hagenia, humus / PARATYPOID, Epilachna aberratica, Fürsch 1974 / HOLOTYPE ♂, Figura lineata n. sp., det. K. Szawaryn 2014" (MRAC); paratype ♂, same data as holotype but "PARATYPE, Figura lineata n. sp., det. K. Szawaryn 2014" (ZSMC).

Etymology. The name is derived from the characteristic elytral colour pattern with stripe-like black and yellow maculae.

Figura ruwenzorica sp. n.

(Figs 68-96, 113)

Diagnosis. *F. ruwenzorica* is the largest species of the genus *Figura*. Its almost completely black elytra are characteristic. It is most simillar to *F. bitalensis* sp. n. in terms of body size and presence of weak longitudinal carina on apical part of prosternal process but is distinct in having a straight meso-metaventral connection. Moreover, antennomere 3 is shorter than antennomeres 4 and 5 combined, whereas in *F. bitalensis* it is same length.

Description. Length 4.0–4.1 mm; TL/EW = 1.26–1.31; PL/PW = 0.47–0.52; EL/EW = 1.09–1.14; EW/PW = 1.83–1.97.

Body (Figs 68, 113) round-oval, convex; surfaces covered with short, sparse pubescence. Head, mouthparts, antennae, hypomera, prosternum, mesoventrite, scutellum, epipleura and legs yellow; metaventrite black; abdomen yellow with median parts of ventrites 1 and 2 dark brown to black. Pronotum yellowish-brown to reddish-brown; elytron black with narrow red lateral border, with two red maculae touching anterior margin, first on callus, second touching suture, apex of elytra red; in some specimens anterior and posterior markings reduced to narrow lines.

Antenna (Figs 81, 88) with antennomere 3 shorter than 4 and 5 together; antennomeres 4 and 5 elongate, antennomere 4 shorter than antennomere 5; antennomeres 6 to

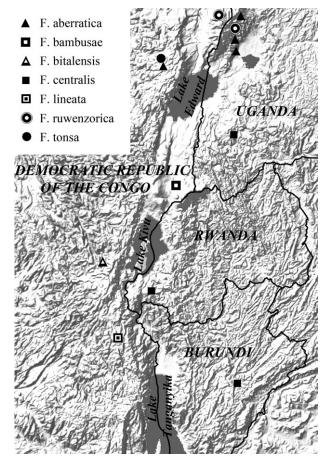


Fig. 105: Distribution map of the genus Figura.

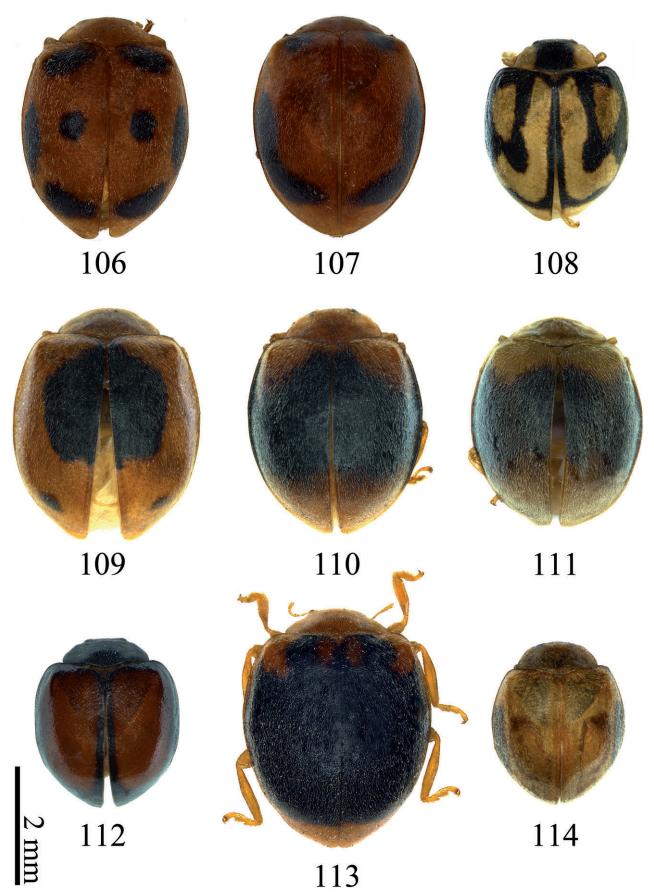
8 subequal in length, subquadrate. Maxillary palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, more than twice as long as palpomere 3, slightly securiform (Figs 69, 79).

Prosternum with anterior ridge complete medially, exceeding half the length of procoxae; median part of prosternal process depressed (Fig. 69), polygonal apically, with weak longitudinal carina apically, about 1.6 times longer than wide, width about 2.1 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about 1.2 times as wide as mesocoxal width at the same position (Fig. 70), with sparse, small, shallow punctures; meso-metaventral connection straight. Epipleuron (Fig. 68) about 2.5 times broader than metepisternum.

Abdominal postcoxal lines rounded, reaching ³/₄ of the length of ventrite 1 (Figs 68, 83, 94). Apical margin of male ventrite 5 truncate (Figs 73, 83), ventrite 6 in males emarginate (Fig. 85), abdominal tergite VIII rounded (Fig. 84). Apical margin of female ventrite 5 rounded (Figs 72, 94), sternite VIII arcuate (Fig. 96) and tergite VIII rounded (Fig. 95).

Male terminalia and genitalia. Apical margin of tergite X truncate (Fig. 86). Inner view of penis guide wider medially; about as long as parameres (Figs 90, 91). Tegminal strut longer than tegmen. Inner view of penis wider anteriorly, rounded apically (Figs 87, 89).

Female genitalia as in Figs 92 and 93.



Figs 106–114: Habitus, dorsal view. 106 - F. aberratica (Fürsch); 107 - F. aberratica (Fürsch); 108 - F. lineata sp. n., holotype δ ; 109 - F. centralis (Sicard), holotype δ of Solanophila bambusicola (Mader); 110 - F. centralis (Sicard); 111 - F. bitalensis sp. n., holotype δ ; 112 - F. tonsa (Fürsch), holotype δ ; 113 - F. ruwenzorica sp. n., holotype δ ; 114 - F. bambusae (Mader), holotype δ .

Type material. Holotype ♂, Democratic Republic of the Congo labelled "Congo Belge: P.N.A., 30-I-3-II-1953, P. Vanschuytbroeck & J. Kekenbosch 2022–32 / Massif Ruwenzori, Kalonge, 2.060 m, Riv. Katauleco, aff. Butahu / Epilachna bambusicola Mad. det. H. Fürsch 1979 / HOLOTYPE ♂, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (MRAC). Paratypes: same data as holotype but "PARATYPE, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (19: MRAC; 1 ex: MZPW); "Congo Belge: P.N.A., 31-VII-1952, P. Vanschuytbroeck & J. Kekenbosch 605-06 / Massif Ruwenzori, Kalonge, 2.130 m, Riv. Kiondo, aff. Butahu / Epilachna bambusicola, det. H. Fürsch 1979 / Bambusicola centralis (Sicard), det. H. Fürsch 85 / PARATYPE, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (19: MRAC); "MUSÉE DU CONGO, Ruwenzori: Kalonge (Monongo) VII-1937, H.J. Brédo / R. DET. 5952 / Epilachna inversa Sic. det. Mader 52 / Bambusicola centralis (Sic.) det. H. Fürsch 85 / PARATYPE, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (19: MRAC); Uganda: "WPr, Kibale Forest, sweep K14, 5.1.1984, M. Nummelin leg. / ex. coll. H. Fürsch / Afidentula alia (Mader) det. H. Fürsch 87 / PARA-TYPE, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (1♀: ZSMC); "Western Region, Kasese District, 2-3 km NW Nyakalengija, Rwenzori Mts. National Park, main trail to Nyabitaba Hut, 0°21.172-.649'N 30°01.651-.272'E, accuracy 6 m, extent 10 m, h = 1718–1783 m, forest trail sweeping [3529] [Garmin 60CSx; WGS84] V.I. Gusarov, 6.viii.2008 / PARATYPE, Figura ruwenzorica n. sp., det. K. Szawaryn 2014" (19: MZPW - voucher number KS143).

Etymology. Name derived from the region of occurrence – Ruwenzori Mountains.

Figura tonsa (Fürsch, 1986)

(Figs 97-104)

Bambusicola tonsus Fürsch, 1986: 394; Jadwiszczak & Węgrzynowicz, 2003: 192.

Figura tonsus [sic!]: Ukrainsky, 2006: 432.

Diagnosis. This species is easily distinguishable by its characteristic dorsal colour pattern of a black pronotum and red elytra broadly bordered by a black stripe. It has also an anterior prosternal ridge that is shortened laterally and not half the length of procoxae. Antennomere 3 is equal in length to antennomeres 4 and 5 combined and antennomere 4 is about half as long as antennomere 5.

Description. Length 2.87 mm; TL/EW = 1.23; PL/PW = 0.39; EL/EW = 1.07; EW/PW = 1.64.

Body (Figs 97, 112) round-oval, convex; surfaces covered with short, sparse pubescence. Head and epipleuron black; legs dark brown; prosternum, mesoventrite, metaventrite and scutellum reddish-brown; mouthparts, antennae and tarsomeres yellowish-brown. Pronotum black, elytron reddish-brown with anterior, lateral and sutural margins broadly black.

Antenna (Fig. 100) with antennomere 3 as long as 4 and 5 together; antennomere 4 shorter than antennomere 5; antennomere 6 elongate, longer than antennomere 7 and 8 combined; antennomeres 7 and 8 subequal in length. Maxillary palpomere 2 about 1.5 times longer than palpomere 3; terminal palpomere large, more than twice as long as palpomere 3, distinctly securiform (Fig. 98).

Anterior ridge of prosternum complete medially, very short, not half the length of procoxae; apex of prosternal process (Fig. 98) polygonal, about 1.5 times longer than wide, width about 2.9 times the length of prosternum in front of coxae at the narrowest point. Mesoventral process about 1.1 times as wide as mesocoxal width at the same position (Fig. 99); meso-metaventral connection straight. Epipleuron (Fig. 97) about 1.8 times broader than metepisternum.

Abdominal postcoxal lines not studied because the holotype lacks ventrite 1.

Male genitalia. Inner view of penis guide wider medially; slightly shorter than parameres (Figs 101, 102). Inner view of penis wider anteriorly, rounded apically (103, 104).

Female not examined.

Note: The genitalia of the holotype were partly destroyed; median part of the penis guide cut longitudinally (Fig. 101), tegminal strut not present.

Type material examined. Holotype ♂, Democratic Republic of the Congo, labelled "HOLOTYPUS/ I.R.S.A.C. – MUS. CONGO, Kivu: Terr. Lubero 2.200 m 27.XI.1951, N. Leleup, (for. mont. avec bamb.) / Réclolté dans l'humus / Holotypus, Bambusicola tonsa Fürsch 85 / Epilachna bambusicola-Gruppe sp. nov. det. H. Fürsch 89" (MRAC).

DISCUSSION

Representatives of the genus Figura share some characters with other genera of Epilachnini: Lack of tibial spurs (similar to Afidentula Kapur, 1958, Megatela Weise, 1906, Merma Weise, 1898 and Lalokia Szawaryn & Tomaszewska, 2013); bifid tarsal claw with inner teeth touching each other (similar to Malata); lack of apodeme in abdominal segment IX in males (similar to Epiverta Dieke, 1947, Megatela Weise, 1906 and Subaffisa Bielawski, 1963). Unique morphological characters that distinguish the genus Figura include structure of labium with scale-like processes on dorsal surface; female genitalia lack sperm duct, spermatheca and accesory gland; coxites fused laterally with paraprocts and male genitalia with tegmen with asymmetrical median lobe. Two membranous sacs in female reproductive system that are attached to the base of the oviduct are regarded as a place for storing sperm instead of the spermatheca (Katakura,

All species that belong to the genus *Figura* inhabit the African region of Albertine Rift. In this region the species diversity is high and there is one of the largest numbers of endemics (Plumptrea et al., 2007) and possibly it is one of the top biodiversity hotspots in Africa (Myers et al., 2000). High biodiversity might explain the relatively high species richness within the genus *Figura* in this relatively small region. All specimens were found at high altitudes between 1,700 and 2,700 m. Several specimens have a label with annotation "Bambous" or "mont. avec bamb.". At this high altitude there are two types of ecosystems, mountain forests (1,500–2,500 m) and bamboo forests (2,500–3,000 m). It is possible that *Figura* species feed on bamboo leaves.

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REFERENCES

- Fürsch H. 1975: Beschreibung einiger neuer Coccinelliden aus dem Museum Tervuren (Coleoptera: Coccinellidae). *Rev. Zool. Bot. Afr.* **89**: 645–650.
- Fürsch H. 1986: Die Madaini der alten Welt (Coleoptera Coccinellidae). *Rev. Zool. Bot. Afr.* **99**[1985]: 391–410.
- GOULD J. 1862: Descriptions of sixteen new species of birds from the island of Formosa, collected by Robert Swinhoe, Esq., Her Majesty's Vice-Consul at Formosa. *Proc. Zool. Soc. Lond.* **1862**: 280–286.
- Jadwiszczak A & Wegrzynowicz P. 2003: World Catalogue of Coccinellidae. Part I Epilachninae. Mantis, Olsztyn, 264 pp.
- KATAKURA H. 1981: Sperm storage place in adult females of the phytophagous ladybirds belonging to *Henosepilachna viginti-octomaculata* complex (Coleoptera, Coccinellidae). *Kontyû* **49**: 477–481.
- Korschefsky R. 1931: Coccinellidae I. In Junk W. & Schenkling S. (eds): *Coleopterorum Catalogus. Part 118.* W. Junk, Berlin, pp. 1–224.
- KUZNETSOV V.N. 1993: [Ladybird Beetles (Coleoptera, Coccinellidae) of the Russian Far East.] Dal'nauka, Vladivostok, 334 pp. [in Russian].
- LAWRENCE J.F., ŚLIPIŃSKI S.A., SEAGO A.E., THAYER M.K., NEWTON A.F. & MARVALDI A.E. 2011: Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Ann. Zool.* **61**: 1–217.
- MADER L. 1941: Coccinellidae. I. Teil. In Exploration du Parc National Albert. Mission G. F. de Witte (1933–1935). Fascicule 34. Institut des Parcs Nationaux du Congo Belge, Bruxelles. 208 pp.
- MADER L. 1950: Coccinellidae. II. Teil. In Exploration du Parc National Albert. Mission G. F. de Witte (1933–1935). Fascicule 34. Institut des Parcs Nationaux du Congo Belge, Bruxelles, 136 pp.

- MEYERS N., MITTERMEIER R.A., MITTERMEIER C.G., DA FONSECA G.A.B. & KENT J. 2000: Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Mulsant M.E. 1846: *Histoire Naturelle des Coléoptères de France.* [4]. Sulcicolles Sécuripalpes. Maison, Paris, 278 pp.
- Plumptre A.J., Davenport T.R.B., Behangana M., Kityo R., Eilu G., Ssegawa P., Ewango C., Meirte D., Kahindo C., Herremans M., Peterhans J.K., Pilgrim J.D., Wilson M., Languy M. & Moyer D. 2007: The biodiversity of the Albertine Rift. *Biol. Conserv.* 134: 178–194.
- Seago A.E., Giorgi J.A., Li J. & Ślipiński A. 2011: Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. *Mol. Phylogenet. Evol.* 60: 137–351.
- SICARD A. 1912: Descriptions d'espèces et variétés nouvelles de Coccinellides de la collection du Deutsches Entomologisches Museum de Berlin-Dahlem. — Arch. Naturgesch. (A) 78: 129–138
- ŚLIPIŃSKI S.A. 2007: Australian Ladybird Beetles (Coleoptera: Coccinellidae). Their Biology and Classification. Australian Biological Resources Study, Canberra, 286 pp.
- ŠLIPIŃSKI A. & TOMASZEWSKA W. 2010: Coccinellidae Latreille, 1802. In Leschen R.A.B., Beutel R.G. & Lawrence J.F. (eds): Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Walter de Gruyter, Berlin/New York, pp. 454–472.
- SZAWARYN K. 2011: A new species of *Henosepilachna* Li (Coleoptera: Coccinellidae: Epilachnini) from New Guinea. Ann. Zool. 61: 685–689.
- SZAWARYN K. & TOMASZEWSKA W. 2013: Two new genera of Epilachnini Mulsant from New Guinea and Aru Islands (Coleoptera: Coccinellidae). *J. Nat. Hist.* **47**(37–38): 2427–2457.
- Tomaszewska W. 2000: Morphology, phylogeny and classification of adult Endomychidae (Coleoptera: Cucujoidea). *Ann. Zool.* **50**: 449–558.
- Tomaszewska W. & Szawaryn K. 2013: Revision of the Asian species of *Afidentula* Kapur, 1958 (Coleoptera: Coccinellidae: Epilachnini). *Zootaxa* 3608: 26–50.
- UKRAINSKY A.S. 2006: Five new replacement ladybird (Coleoptera: Coccinellidae) generic names. *Russ. Entomol. J.* 15: 399–400

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