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Morphology, taxonomy, distribution and relationships of the Afrotropical genus *Isomerocera* (Diptera: Stratiomyidae)

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ABSTRACT

The external morphology of *Isomerocera* Enderlein, an Afrotropical genus of Stratiomyidae, is discussed and illustrated with special regard to specific structures on the antenna, surface cover, and male and female terminalia. The species of *Isomerocera* are re-examined, based on 524 specimens (including four types) from 15 institutions, and two species were distinguished. The rare species *I. heteraspis* James, 1949 is characterised by some unusual autapomorphic characters. The common *I. quadrilineata* varies remarkably in colour characters, and the extent and density of hair patches. *Isomerocera maculiventris* (Macquart, 1850) is considered to be a junior synonym of *I. quadrilineata* (Fabricius, 1787) as is *I. natalensis* (Gerstaecker, 1857). *Isomerocera quadrilineata* var. *melecta*, as originally described by Speiser (1908), is identical with the nominal form. Generic characters are compared with the related genus *Ptilocera* from the Oriental and Australasian regions. Distribution data are summarised on the basis of the reliable published records and/or extensive material that we examined and collected in Angola, Burundi, Cameroon, Central African Republic, Democratic Republic of the Congo (Kinshasa), Equatorial Guinea, Gabon, Ghana, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Republic of the Congo (Brazzaville), Sierra Leone, South Africa, Tanzania, Togo, Uganda and Zimbabwe. *I. heteraspis* is known only from two localities in Burundi and Uganda. The known distribution of *I. quadrilineata* essentially covers the vast area of savannahs and the zone of lowland tropical moist broadleaf forests in Africa.

KEY WORDS: Sub-Saharan Africa, morphology, revision, variation, relationships, *Isomerocera*, comparison with *Ptilocera*.

INTRODUCTION

The genus *Isomerocera* was originally erected by Enderlein (1914: 302) to include the single species *Diphysa maculiventris* Macquart, 1850. Many authors (e.g. Gerstaecker 1857; Loew 1860; Speiser 1908; Grünberg 1915; Curran 1928) treated the African *Stratiomys quadrilineata* Fabricius, 1787 under the name *Ptilocera* Wiedemann, 1820, with the Oriental species *P. quadridentata* Fabricius, 1805 as the type species. Brauer (1882) in his “Identification key to the genera of Notacantha” noted under *Ptilocera* the distribution as “Ost–Indien, Afrika”. Grünberg (1915) mentioned two forms of *P. quadrilineata*: one distributed in West Africa and based on the type originating from Sierra Leone and the second occurring in South Africa and described by Loew (1860) under the same name. Both forms were reported to differ by the colour of the last flagellomere.

Kertész (1916) definitively proved that *Ptilocera nataliensis* Gerstaecker, 1857 is actually a mere synonym of *Diphysa maculiventris* Macquart, 1850. He compared distinguishing characters of *Isomerocera* and *Ptilocera* and came to the conclusion that they represent different genera (see also Mason & Rozkošný 2011). James (1949b) described the second Afrotropical species, *I. heteraspis*. In Lindner’s series of taxonomic and faunistic studies from the Afrotropical Region (1938, 1953, 1958a, 1958b, 1961, 1965a, 1965b, 1966a, 1966b, 1968, 1970, 1972; Lachaise & Lindner 1973) he consistently

identifies the examined *Isomerocera* specimens as *I. quadrilineata*; only in a paper from 1961, based on material from South Africa, did he use the name *I. maculiventris* with a misleading note that *I. natalensis* and *I. quadrilineata* are synonyms of it. Actually, *Isomerocera maculiventris* and *I. natalensis* are junior synonyms of *I. quadrilineata*.

Lindner (1966b) asked L. Tsacas, then custodian of the dipteran collection in the Museum of Natural History in Paris, for a comparison of *I. quadrilineata* with the holotype of *I. maculiventris*. On the basis of Tsacas's expert opinion Lindner proposed the synonymy of both names. This was later accepted in "A World Catalog of the Stratiomyidae" (Woodley 2001).

MATERIAL AND METHODS

524 specimens (including four primary types) collected from 20 countries in the Afrotropical Region, and housed in 15 institutions and private collections, were examined (numbers in parentheses refer to the number of specimens examined from the relevant country): Angola (1), Burundi (2), Cameroon (47), Democratic Republic of the Congo — Kinshasa (145), Equatorial Guinea (14), Gabon (5), Ghana (8), Ivory Coast (8), Kenya (16), Liberia (1), Malawi (21), Mozambique (13), Nigeria (12), Republic of the Congo — Brazzaville (3), Sierra Leone (1), South Africa (114), Tanzania (7), Togo (68), Uganda (9) and Zimbabwe (29). Distribution in the Central African Republic is included on the basis of a reliable published record by Lindner (1970).

The following abbreviations are used for institutional and private collections:

- ASCG – Axel Ssymank Collection, Wachtberg, Germany;
- BMNH – The Natural History Museum, Department of Entomology, London, UK;
- CSCA – California State Collection of Arthropods, Sacramento, USA;
- FMCV – Franco Mason Collection, Verona, Italy;
- IRSNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
- MNHN – Muséum national d'Histoire naturelle, Paris, France;
- MRAC – Musée Royal de l'Afrique Centrale, Tervuren, Belgium;
- MSNG – Museo Civico di Storia Naturale di Genova, Italy;
- MSNV – Museo Civico di Storia Naturale Verona, Italy;
- NMSA – KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
- PPRI – National Collection, Biosystematics Division, Plant Protection Research Institute, Pretoria, Transvaal, South Africa;
- TAUI – Tel Aviv University, Israel;
- USNM – National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA;
- UZMC – Zoologisk Museum, Copenhagen University, Copenhagen, Denmark;
- ZMHB – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Species were examined using a Leica M12 microscope and line drawings created with the aid of a drawing tube; scanning electron microscope (SEM) images were taken with a Hitachi TM 1000. The morphology follows the terminology of Cumming and Wood (2009).

Distribution maps are mainly based on the material examined, but some published records were also included that were not found among the material examined. All localities were provided with georeferenced coordinates; only a few locality labels and



Fig. 1. *Isomerocera quadrilineata* (Fabricius), female (South Africa, KwaZulu-Natal, South Coast Uvongo, orig. F. Mason). Scale bar=1.0 mm.

all records from Togo were accompanied by coordinates already provided by original collectors. Distribution in Angola and Liberia is based on the two specimens from these countries (without any nearer localities) that are deposited in BMNH. Distribution in Togo is illustrated in a separate map insert (Fig. 90), owing to numerous collection records by A. Ssymank.

TAXONOMY

Genus *Isomerocera* Enderlein, 1914

Isomerocera Enderlein, 1914: 302.

Type species: *Diphysa maculiventris* Macquart, 1850 (= *Stratiomys quadrilineata* Fabricius, 1787), by original designation.

The external morphology of *Isomerocera* spp. corresponds with the groundplan of the diverse and extensive subfamily Pachygastrinae, which is characterised by the loss of vein M_3 in particular. Nevertheless, Woodley (2001) stated the instability of this character and concluded that the monophyly of the Pachygastrinae is only weakly supported on a world level. *Isomerocera* (Fig. 1) belongs to the group of pachygastrine genera distinguished by the following features: (1) some medial flagellomeres of the antenna have finger-like projections (Figs 31, 38, 45, 46, 64, 65), (2) the scutellum is armed with four strong spines (Figs 13–16), (3) vein R_{2+3} arises beyond crossvein $r-m$, (4) vein R_4 is present (Fig. 4), (5) the abdomen is short and rounded, markedly convex dorsally (Figs 1–3) and (6) the male terminalia (Figs 6–8) show a unique parameral sheath. From these characters only characters (1) and (6) are apparently apomorphic though partly shared with *Ptilocera* (see Mason & Rozkošný 2011).

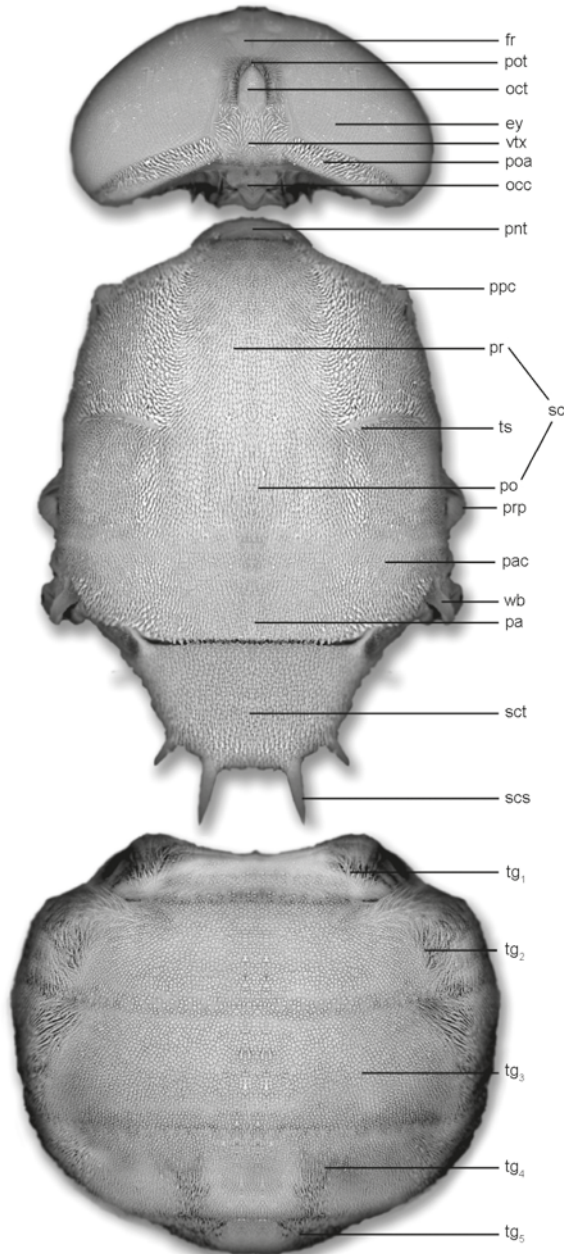


Fig. 2. *Isomerocera quadrilineata* (Fabricius), female in dorsal view with morphological terms. *Abbreviations:* *ey* – eye, *fr* – frontal vitta, *occ* – occiput, *oct* – ocellar triangle, *pa* – prescutellar area, *pac* – prealar callus, *pnt* – pronotum, *po* – postsutural area of scutum, *poa* – postocular area, *pot* – preocellar tubercle, *ppc* – postpronotal callus, *pr* – presutural area of scutum, *prp* – prealar prominence, *sc* – scutum, *scs* – scutellar spine, *sct* – scutellum, *tg₁₋₅* – tergite 1–5, *ts* – transverse suture, *vtx* – vertex, *wb* – wing base.

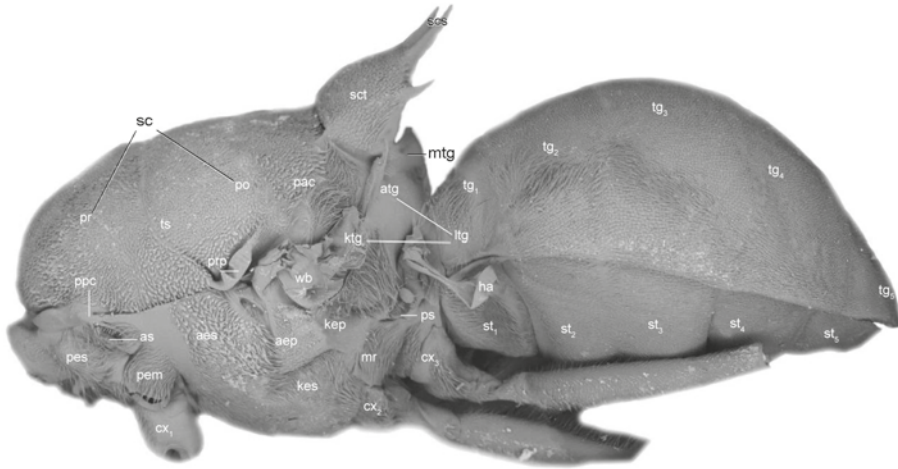


Fig. 3. *Isomrocera quadrilineata* (Fabricius), female thorax and abdomen in lateral view with morphological terms. Abbreviations: *aep* – anepimeron, *aes* – anepisternum, *as* – anterior spiracle, *atg* – anatergite, *cx*₁₋₃ – coxa 1–3, *ha* – halter, *kep* – katepimeron, *kes* – katepisternum, *ktg* – katatergite, *ltg* – laterotergite, *mr* – meron, *mtg* – mediotergite, *pac* – postalar callus, *pem* – proepimeron, *pes* – proepisternum, *po* – postsutural area of scutum, *ppc* – postpronotal callus, *pr* – presutural area of scutum, *prp* – prealar prominence, *ps* – posterior spiracle, *sc* – scutum, *scs* – scutellar spines, *sct* – scutellum, *st*₁₋₅ – sternites 1–5, *tg*₁₋₅ – tergites 1–5, *ts* – transverse suture.

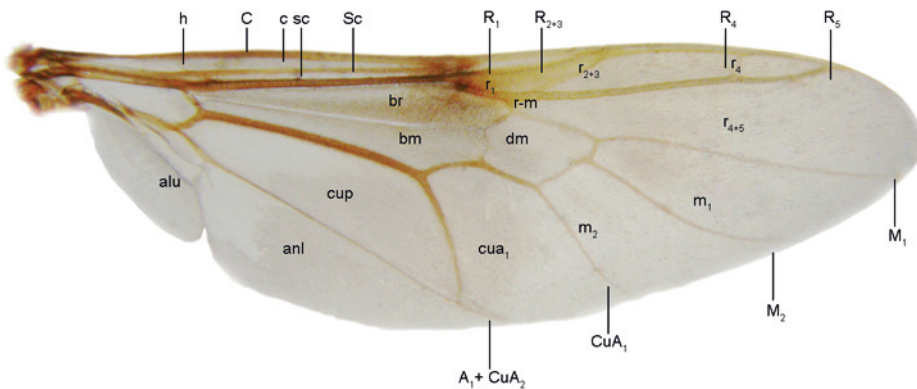
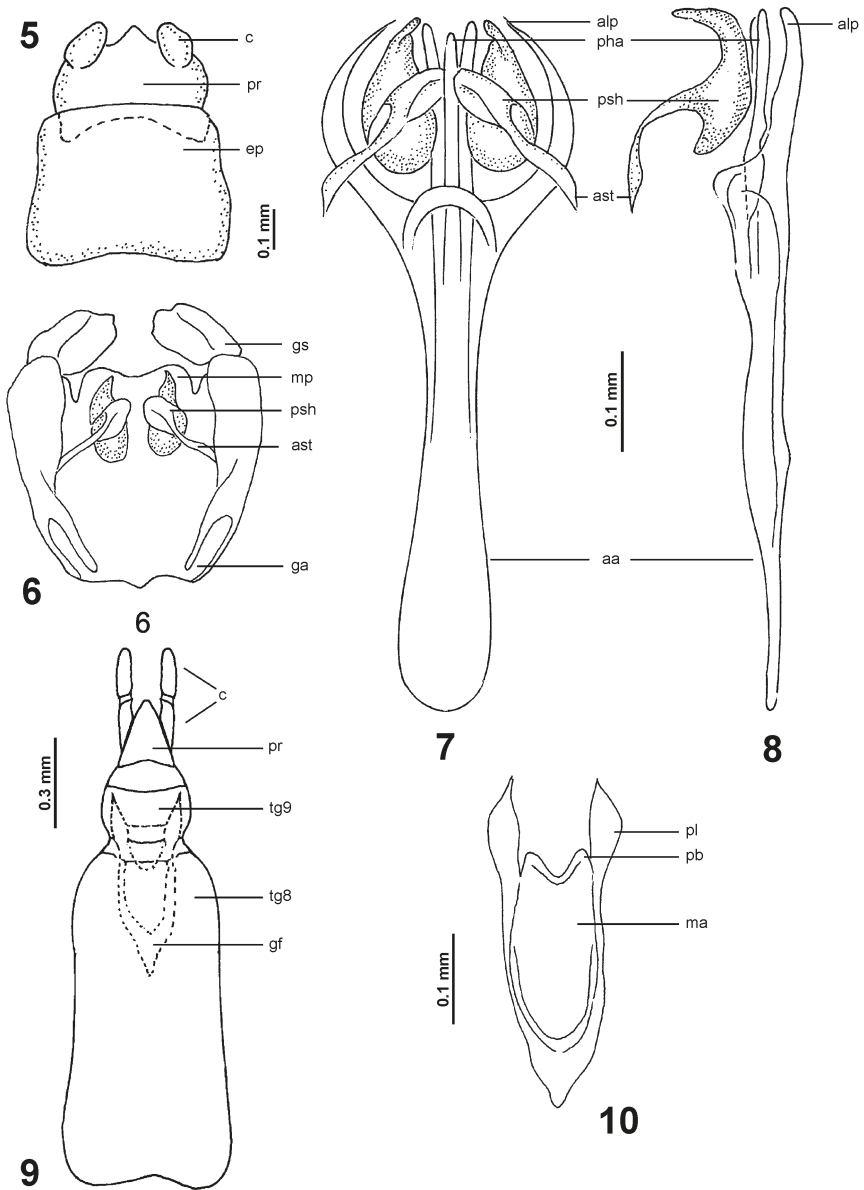


Fig. 4. *Isomrocera quadrilineata* (Fabricius), female wing, veins and cells. Abbreviations: *A*₁ – anal vein, *alu* – alula, *anl* – anal lobe, *bm* – basal medial cell, *br* – basal radial cell, *C* – costal vein, *c* – costal cell, *CuA*₁ and *CuA*₂ – branches of anterior cubital vein, *cua*₁ – anterior cubital cell, *cup* – posterior cubital cell, *dm* – discal cell, *h* – humeral crossvein, *M*₁₋₂ – medial veins, *m*₁₋₂ – medial cells, *R*₁₋₅ – radial veins, *r*₁₋₅ – radial cells, *r-m* – crossvein between *R* and *M* veins, *Sc* – subcostal vein, *sc* – subcostal cell.



Figs 5–10. *Isomerocera quadrilineata* (Fabricius), male and female terminalia: Male: (5) dorsal part; (6) ventral part; aedeagal complex in (7) dorsal and (8) lateral view. Female: (9) terminalia in dorsal view and (10) genital furca. Abbreviations: *aa* – aedeagal apodeme, *alp* – aedeagal lateral projection, *ast* – attachment structure, *c* – cercus, *ep* – epandrium, *ga* – gonocoxal apodeme, *gf* – genital furca, *gs* – gonostylus, *ma* – medial aperture, *mp* – median process of synsternum, *pb* – posterior bridge, *pha* – phallic organ, *pl* – posterolateral projection, *pr* – proctiger, *psh* – parameral sheath, *tg* – tergite.

Head of *Isomerocera* (Figs 2, 30, 37, 44) holoptic in males and dichoptic in females, transverse in dorsal view and almost hemispherical, higher than long in lateral view,

eyes bare in both sexes. Facets in upper part of male eye distinctly larger than in lower third, male ocellar triangle prominent in lateral view and frons divided by contiguous eyes into upper short part and lower, broader, subtriangular part, both covered with pale appressed hairs. Postocular area not visible in male but well developed in female. Female ocellar triangle is distinctly elevated above the level of eyes and this elevation visible also in front of the anterior ocellus as a preocellar tubercle (Figs 12 a, b). Female frons nearly parallel-sided, slightly narrower than scape is long. Antenna relatively long and slender, about 2–3× as long as head. Scape 3–4× longer than pedicel and pedicel cup-like, distinctly shorter than first flagellomere. Male flagellomeres 3–5 provided with paired finger-like projections, longer ventral and shorter dorsal ones. In females an additional, short ventral projection on flagellomere 2 distinct. Face slightly arched at middle below antennae. Proboscis (Fig. 25) unmodified and palpus two-segmented (Fig. 26).

Thorax without any apomorphic characters at generic level. Prealar prominence (Figs 21–23) present in front of wing base. Four strong marginal spines on scutellum of *Isomerocera quadrilineata* (Figs 15, 16) arranged in one plane but in two different planes in *I. heteraspis* (Figs 13, 14) (see James 1949b). Wing venation (Figs 1, 4) characterised by vein R_{2+3} arising beyond crossvein $r-m$ and presence of R_4 . Stronger veins in basal half of wing contrastingly pigmented and virtually all veins reach wing margin. Darkening on wing in front of crossvein $r-m$ characteristic for both species. Wing membrane covered with dense microtrichia reduced in upper half of *cup* cell. Legs without any special structures, pretarsus corresponding with state found in all families of Homeodactyla (Fig. 27). In *Isomerocera quadrilineata*, extensive variation in leg colour pattern exists (see Figs 75–88).

Abdomen rounded and dorsally convex (Fig. 3). Silverish white hair patches on terga with extensively variable pattern (see Figs 42, 43, 59–61). Shape of male terminalia unique. Parameral sheath apparently bipartite (though connected by hyaline membrane) in both examined species of *Isomerocera*. Lateral projections of aedeagal complex unique within Pachygastrinae, represented by apically pointed appendages.

Key to the species of *Isomerocera*

- 1 Two pairs of scutellar spines lying in different planes (Figs 13, 14), female antenna with paired projections on flagellomeres 3–4 only (Fig. 38) ***heteraspis***
 – All four scutellar spines lying in the same plane (Figs 15, 16), female antenna with paired projections on flagellomeres 3–5 (Figs 64, 65)..... ***quadrilineata***

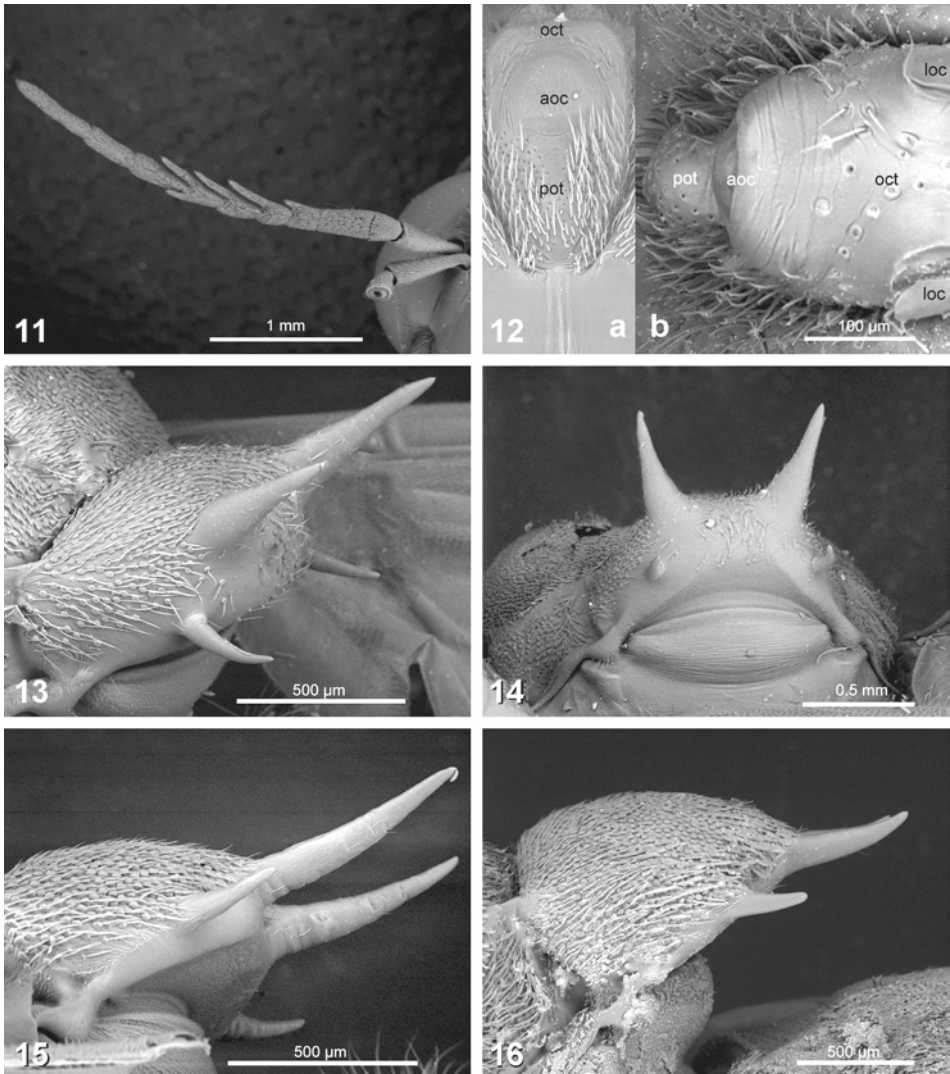
Isomerocera heteraspis James, 1949

Figs 13, 14, 17, 23, 24, 29–41

Isomerocera heteraspis James, 1949b: 106.

Diagnosis: Both sexes of this species can be easily recognised by the scutellar spines located on the posterior margin of the scutellum in two markedly different planes (Figs 13, 14). The male has paired projections on flagellomeres 3–5 (Fig. 31) and the female only on flagellomeres 3 and 4 (Fig. 38).

Male (holotype) (Figs 29–35).

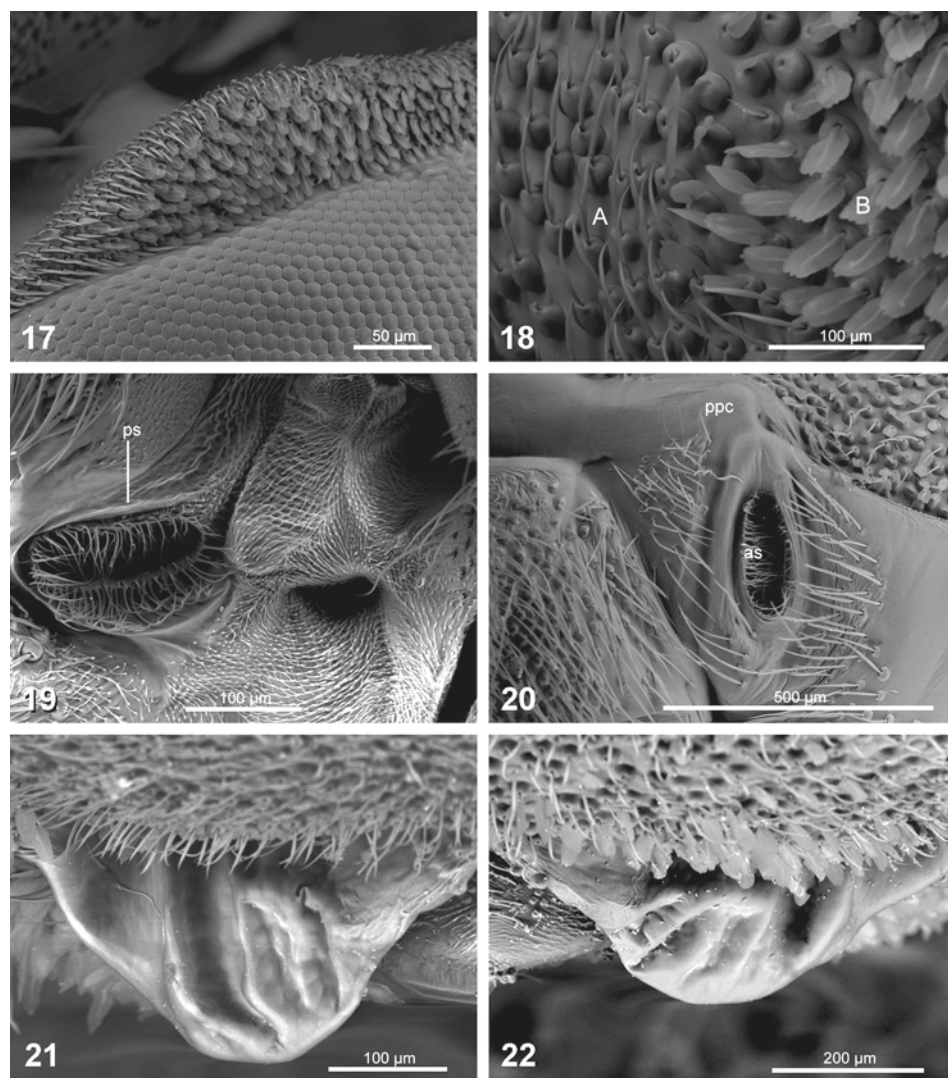


Figs 11–16. *Isomerocera quadrilineata* (Fabricius): (11) antenna; ocellar triangle in (12a) frontal and (12b) dorsal view (Abbreviations: *aoc* – anterior ocellus, *loc* – lateral ocellus, *oct* – ocellar triangle, *pot* – pre-ocellar tubercle). *Isomerocera* spp., scutellum: *I. heteraspis* James, female, in (13) posterolateral and (14) posterior view; *I. quadrilineata* (Fabricius), (15) male and (16) female in lateral view.

Description:

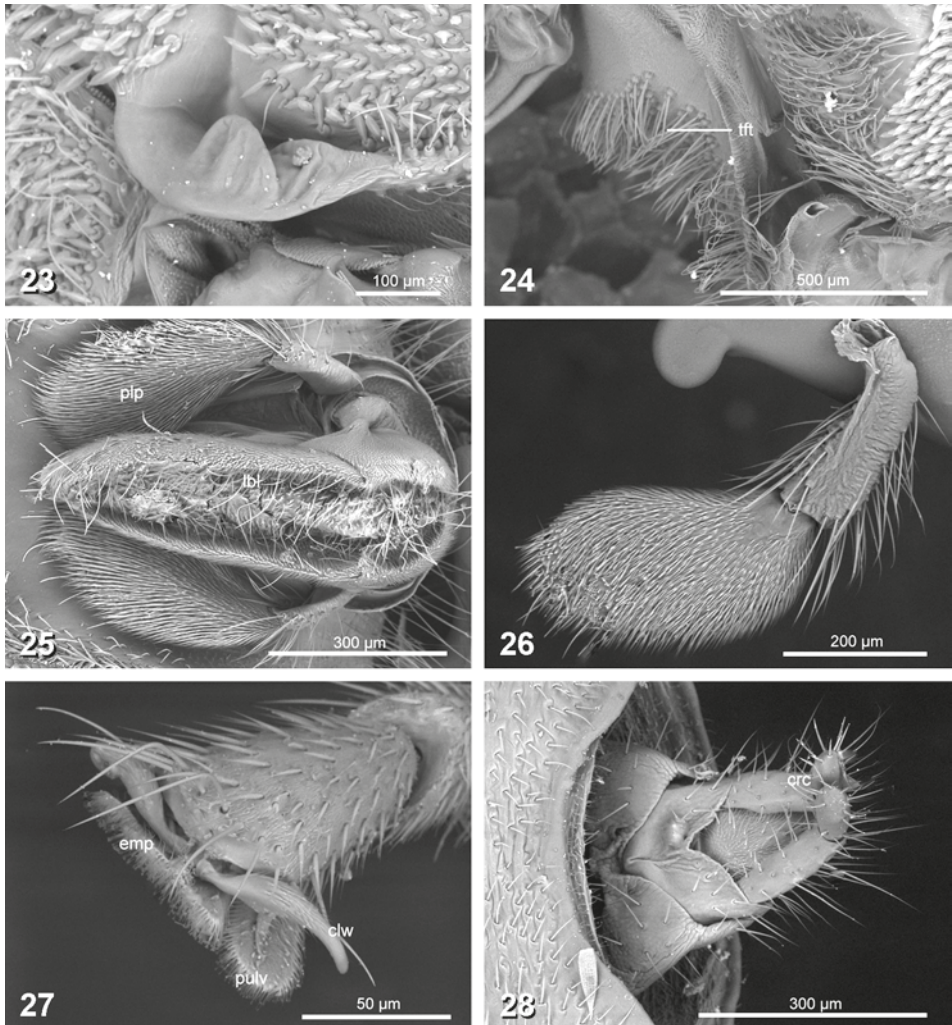
Length (mm): Body 8.0, wing 7.4.

Head: Semi-globular in lateral view, 1.7× higher than long (Fig. 30), transverse in dorsal view, almost 1.9× as broad as long (Fig. 29). Large eyes covering greater part of head, touching on frons, gena and postocular area not visible in lateral view. Ocellar triangle prominent in lateral view, no preocellar tubercle developed. Facets in lower third contrastingly smaller. Upper frons triangular, barely as long as ocellar triangle,



Figs 17–22. *Isomerocera heteraspis* James, female: (17) scales on postocular area. *I. quadrilineata* (Fabricius), female: (18) (a) hairs and (b) scales on presutural area of scutum; (19) male posterior stigma (*ps* – posterior spiracle); (20) postpronotal callus and anterior stigma (*as* – anterior spiracle, *ppc* – postpronotal callus); prealar prominence of (21) male and (22) female.

lower frons almost equilateral, both covered with white tomentum but part of lower frons above antennae and its tip almost bare. Face brown, swollen below antenna, distinctly prominent as a rounded tubercle in lateral view. Antenna (Fig. 31): scape 3× as long as pedicel, brownish, darker than reddish pedicel. Flagellomeres 1 and 2 with sensory pits, the third only with some scattered pits hidden among short hairs. All flagellomeres dark brown, only last flagellomere snow white. Flagellomeres 3–5 asymmetrical, with paired projections, flagellomere 6 subconical and 7 subcylindrical. Apical flagellomere slender and elongate, twice as long as preceding flagellomere, completely snow white.



Figs 23–28. *Isomerochera heteraspis* James, female: (23) prealar prominence; (24) hair tuft (*tft*) between postalar callus and anatergite. *I. quadrilinata* (Fabricius): (25) labellar lobes and palpi; (26) palpus; (27) hind tarsus (*clw* – claw, *emp* – empodium, *pulv* – pulvillus terminalia); (28) female terminalia (*erc* – cerci).

Thorax: Black, finely punctate, with greyish scales on anterolateral part of scutum. Proepisternum with long silvery hairs, anterior part of anepisternum bare, posterior part covered with greyish shining scales. Katepisternum, meron and the area near the posterior spiracle with long silvery hairs. Proximal half of wing membrane infuscated, darker on distal part of *br* cell. Legs chiefly brown but coxae black, anteriorly with long silvery hairs. Distal third of mid and hind femur as well as all tibiae black, tarsi pale.

Abdomen: Black, finely punctate, with appressed silvery hair patches only on tergites 4 and 5 (Fig. 29), venter covered with fine appressed silvery hairs being longer on sternite 1.

Male terminalia as in Figs 33a–c. Genital capsule (Fig. 32) with posterior medial process relatively deeply emarginate at middle, tripartite aedeagal complex (Figs 33a–c) slightly longer than the massive lateral aedeagal projections, parameral sheath bipartite as in *I. quadrilineata* but aedeagal apodeme distinctly dilated proximally.

Female (Figs 13, 14, 17, 23, 24, 36–41).

Description:

Length (mm): Body 6.2–6.9 (n=2); wing: 7.2–7.4 (n=2).

Head (Fig. 37): About 1.7× as high as long in profile and slightly more than twice as broad as long in dorsal view. Frontal index 1.5–1.8 ($x=1.65$, n=2). Ocellar triangle prominent in lateral view and in front of anterior ocellus a distinct preocellar tubercle (*pot*) is present (Fig. 12a, b), as in female of *I. quadrilineata*. Pilose area behind and around ocellar triangle is mostly brown anteriorly but more silvery in posterior part. Upper postocular area covered with three to five rows of silvery, appressed scales (Fig. 17). White tomentose patches on frontal band developed as two semicircular pilose spots on upper part of frons continuing with the brown short hairs around the ocellar triangle and as a pair of medially divided spots in middle of frons (Fig. 37). Antenna (Fig. 38) predominantly dark. Scape dark brown, pedicel and flagellomeres 1–2 pale brown, flagellomeres 3–7 dark brown, apical half of last flagellomere snow white. Sensory pits present on both sides of flagellomeres 1–5. Projections on flagellomeres 3–4 asymmetrical, shorter than in male. Face brown with low and rounded nose-like projection, bare on top, covered with silvery hairs along eye margin.

Thorax: Black, finely punctate. Pile and scales on thorax as in male but generally with longer shining scales. Scutum with two metallic lines consisting of scales with purple reflections. Scutellum twice as wide as long with four spines (Figs 13, 14), lateral ones smaller and medial ones larger, brownish yellow with darkened tips. Proximal half of wing membrane darkened, blackish on *br* cell, as in males. Legs (Figs 39–41) orange-yellow and black. Coxae, mid femur except apex and almost entire tibiae darkened, all tarsi pale.

Abdomen: Black, finely punctate, with appressed silvery hair patches on margins of tergites 2–5 (Fig. 36), venter with fine appressed short silvery hairs on sternites 2–5 and longer on sternite 1. Genital furca not examined.

Condition: Very good, but the costal vein broken on both wings and the body with some rusty incrustation. The male genitalia dissected and attached on the same pin.

Remarks: The unusual position of the scutellar spines (in two different planes) is also known in all three species of the Afrotropical pachygastrine genus *Diplehippium* Speiser, 1908 (see James 1949a, Lindner 1966a). However, *Diplehippium* differs from *Isomero-cera* by the absence of finger-like projections on flagellomeres, its scutum is provided with a long and pointed spine in front of the wing base and the wing pattern in both genera is different.

Published record: **James (1949b)**: UGANDA: West Ruwenzori [00°23'N 29°52'E] (holotype).

Other material examined: BURUNDI: 1♀ Bururi [03°57'S 29°37'E], 3.viii.1949, F.J. François (IRSNB); 1♀ 23.x.1949 (USNM).

Type material remarks: The male holotype from Uganda is deposited in BMNH (Woodley 2001) and labelled “Holotype [red circular label]/Pres. by Com. Inst. Ent. B.M. 1950–

322/Van Someren. W. Ruwenzori, 8–9000 ft, July 1946/*Isomero-cera heteraspis* James, HOLOTYPE” [handwritten label by James].

Isomero-cera quadrilineata Fabricius, 1787

(Figs 11, 12, 15, 16, 18–22, 25–28, 42–88)

Stratiomys quadrilineata Fabricius, 1787: 331.

Diphysa maculiventris Macquart, 1850: 347.

Ptilocera natalensis Gerstaecker, 1857: 334.

Ptilocera quadrilineata var. *melecta* Speiser, 1908: 142.

Diagnosis: Scutellar spines located on the posterior margin of the scutellum in one plane (Figs 15, 16). The female with paired antennal projections on flagellomeres 3–5.

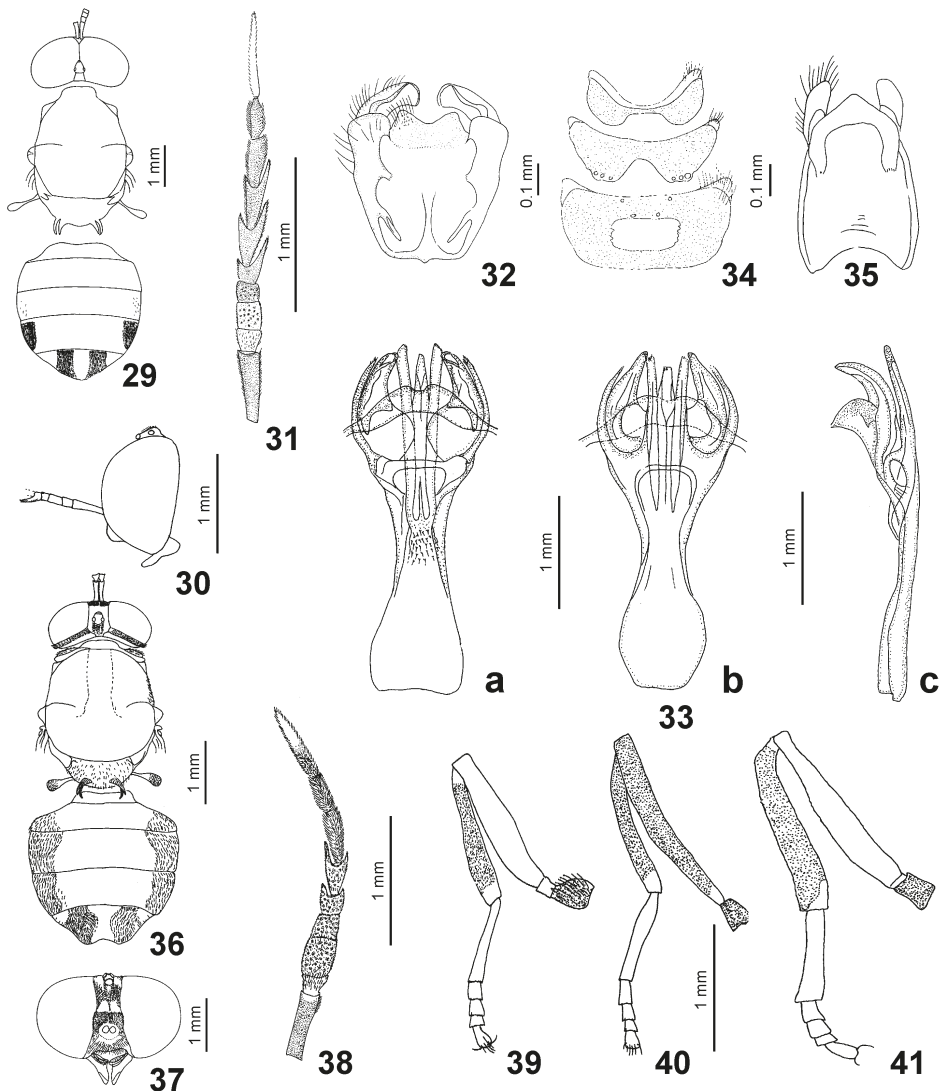
Male (Figs 5–8, 15, 25–27, 42–58, 75–82).

Description:

Length (mm): Body 5.3–10.2 (n=24); wing: 4.8–9.9 (n=24).

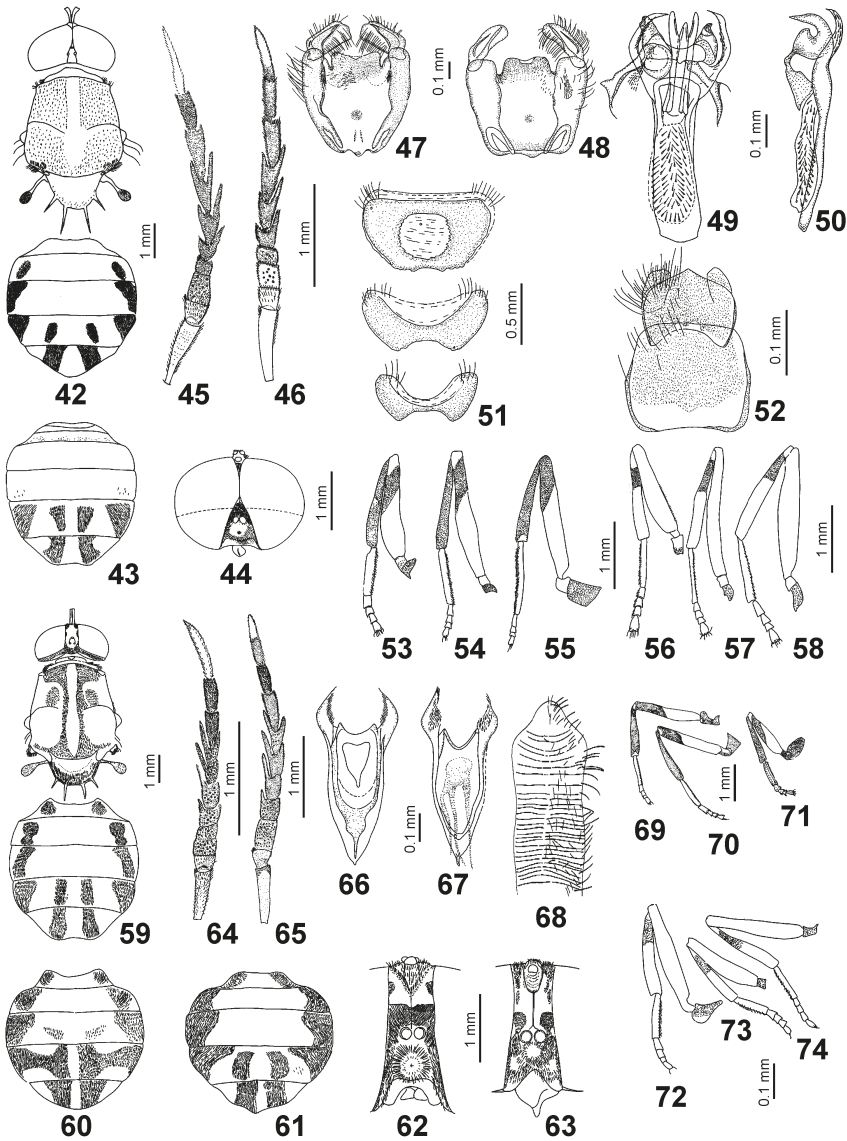
Head: Nearly hemispherical in lateral view, about 1.6× higher than long, transverse in dorsal view (Fig. 42) and 1.6× as wide as long. Large eyes covering greater part of head, contiguous on frons for long distance, gena and postocular area not visible in lateral view. Ocellar triangle distinctly prominent in lateral view, no preocellar tubercle developed. Facets in lower third contrastingly smaller than upper ones. Upper frons elongate, triangular, barely as long as ocellar triangle, lower frons subtriangular and equilateral, both covered with snow-white tomentum. Tomentose area on lower frons with longitudinal black midline. Face somewhat swollen below antenna but this fairly flat tubercle barely visible in lateral view (Fig. 44). Lower face deeply concave. Face covered with short whitish hairs, these being longer below antennae and continuing as narrow whitish tomentum along eye margin. Antenna (Figs 45, 46) slender and long, about twice as long as head in lateral view. Basal antennal segments and two basal flagellomeres reddish brown to orange, scape 4–5× as long as broad distally, pedicel cup-like, as long as broad. Flagellomeres 3–7 dark brown to black. Flagellomeres 3–5 with paired projections, upper projections short and lower projections twice as long as upper projections. Last flagellomere entirely white or blackish basally. Sensory pits small but distinct on basal two flagellomeres. Proboscis brown, two-segmented palpus slender and black.

Thorax: Dark, black in ground colour, scutum covered with dark short appressed hairs and indistinct metallic iridescent scales. Two paler and narrow medial lines are more or less distinct in presutural area of scutum covered by greenish, purple or grey scales, usually widening toward scutellum. Posterior area of scutum beyond postalar callus with tuft of long whitish hairs. Scutellum with four yellow to brown spines, inner pair longer than outer, middle spines about as long as scutellum. Proepisternum, proepimeron and anterior part of anepisternum with long silvery hairs, narrow middle part of anepisternum bare and shining, but its posterior part covered by silvery and almost purple hairs and scales. Anepimeron, katapisternum, katatergite and meron silvery haired. Mediotergite bare, black and mostly matt. Anterior spiracle as in Fig. 20, posterior spiracle as in Fig. 19 and prealar prominence as in Fig. 21. Wing as in female (Figs 1, 4). Legs yellow or pale brown with extremely variable dark pattern. Coxae usually blackish, femora mostly darkened in apical third and tibiae predominantly darkened, tarsi pale or partly darkened (Figs 53–58, 75–82).



Figs 29–41. *Isomerocera heteraspis* James, (29–35) male holotype and (35–41) female: (29) male body in dorsal view; (30) head in lateral view; (31) antenna; (32) genital capsule; (33) aedeagal complex in (a) ventral, (b) dorsal and (c) lateral view; (34) tergites 6–8; (35) proctiger, cerci and epandrium; (36) female body in dorsal view; (37) head in frontal view; (38) antenna; colour pattern of legs: (39) fore, (40) middle and (41) hind leg.

Abdomen: Dark brown to black, finely punctate, first tergite brown with long erect silvery hairs; large silvery hair patches present on margins of tergites 2 to 5 (Fig. 42) or partly reduced on tergites 2 and 3 (Fig. 43). Sternites with short appressed hairs, except sternite 1 with longer silvery and semi-appressed hairs. Tergites 6–8 as in Fig. 51. Male terminalia (Figs 5–8): epandrium (Figs 5, 52) subquadrate, cerci reaching slightly beyond proctiger; genital capsule (Figs 6, 47, 48) subquadrate or more rounded proximally,



Figs 42–74. *Isomerochera quadrilineata* (Fabricius), (42–58) male and (59–74) female: (42) male body in dorsal view, (43) abdomen variation: South Africa, Port St. Johns; (44) head in frontal view; (45) antenna, (46) variation: South Africa, Umgeni River, Nagle Dam; (47) genital capsule, (48) variation: South Africa, Mfongosi; aedeagal complex in (49) ventral and (50) lateral view; (51) tergites 6–8; (52) proctiger, cerci and epandrium; colour pattern of legs: (53) fore, (54) middle and (55) hind leg, variation: South Africa, Durban, (56) fore, (57) middle and (58) hind leg; (59) female body in dorsal view, abdomen variation: (60) South Africa, Eshowe, Dlinza Forest and (61) Democratic Republic Congo, Eala; (62) head in frontal view, Democratic Republic Congo, Bambesa, (63) variation: Cameroon, Sangmelima; (64) antenna, Zimbabwe, Vumba, (65) variation: South Africa, Eshowe, Dlinza Forest; (66) genital furca, (67) variation: South Africa, Eshowe, Dlinza Forest; subgenital plate (68); colour pattern of legs Democratic Republic Congo, Eala: (69) fore, (70) middle and (71) hind leg, variation: South Africa, Ngoye Forest, between Eshowe and Empangeni: (72) fore, (73) middle and (74) hind leg.

posterior medial process only with shallow median emargination. Parameral sheath bipartite, lateral aedeagal projections well developed and aedeagal complex tripartite (Figs 7, 8, 49, 50).

Female (Figs 1–4, 9–12, 22, 59–74, 83–88).

Description:

Length (mm): Body 6.9–9.9 (n=25); wing: 6.1–9.9 (n=25).

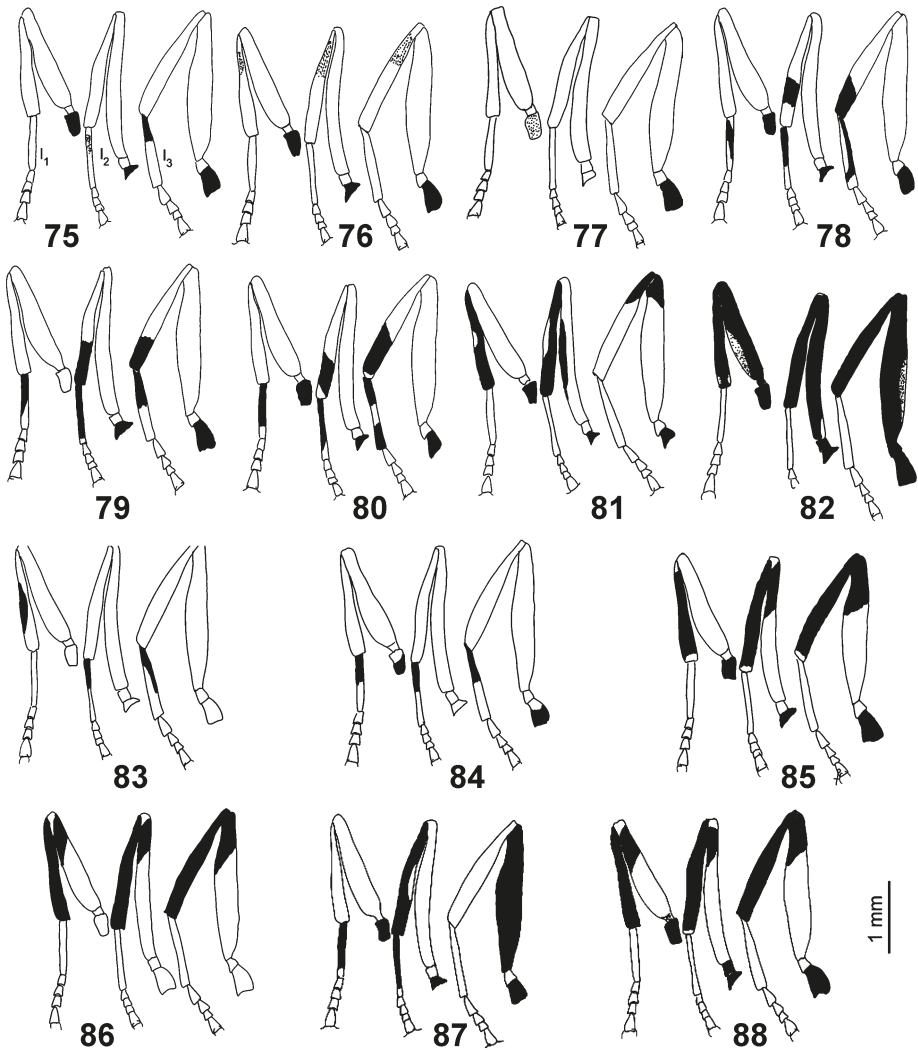
Head: 1.5× higher than long in lateral view and slightly more than twice as wide as long in dorsal view. Frontal index 1.3–1.5 (\bar{x} =1.5, n=12). The haired area around ocellar triangle mostly brown anteriorly but mainly silvery on posterior part. Upper postocular area covered by dense silvery scales (Fig. 17). Eyes separated by band-shaped frons, postocular area well developed (Fig. 59), gena with narrow fringe of short whitish hairs. Ocellar triangle swollen in front of anterior ocellus forming distinct preocellar tubercle (Fig. 12a, b). Frontal velvety whitish patches developed at eye margin at level of ocellar triangle and above antennae, sometimes more or less confluent along eye margin (Figs 62, 63). Antennae as in Figs 11 and 64–65, scape, pedicel, first and second antennal flagellomeres light brown. Flagellomeres 3–7 brown to black, the last flagellomere usually snow-white but sometimes narrowly blackish basally. Sensory pits present on flagellomeres 1–5. Lateral projections of flagellomeres 3–5 more asymmetrical than in male but also relatively short. Face brown with low nose-like projection, this with upright, dense, white hairs that are sparse dorsally.

Thorax: Scutum black, finely punctate. Scales on presutural area of scutum usually grey, with only slight purple reflections, continuing as two longitudinal stripes widening toward scutellum (Fig. 18). Pile and scales on other thoracic sclerites as in male. Wing (Figs 1, 4) uniformly brown infuscated, darkened along anterior margin especially in basal half. Legs (Figs 69–74) usually pale with variable dark pattern, basitarsi orange-yellow.

Abdomen: Black, finely punctate, with appressed silvery hair patches on tergites 2 to 5 (Figs 59–61), sternites with fine appressed silvery hairs, longer on sternite 1 as in male. Female terminalia as in Figs 9 and 28, genital furca slender, with a large median aperture (Fig. 10).

Variation: In addition to size (see above), both sexes may vary apparently in the pattern of scales on the scutum, and in the extent of the abdominal hair patches. The last flagellomere may be entirely white or blackish basally up to the middle. In some females the frontal velvety patches may vary in large extent. The semicircular lateral hair patches on the upper frons along the eye margin (Figs 62, 63) may be more or less developed or even completely absent even in females belonging to the same population. The narrow lateral frontal hair patch along the inner margin of the eyes may be present or absent. In a sample of 15 females from the same locality the pairs of silvery spots are present in the majority of specimens, but in five specimens these spots were absent.

Kertész (1916) considered *Isomerocera maculiventris* and *I. quadrilineata* to be distinct species that may be distinguished by the basally darkened last flagellomere and the scutum having a dense, appressed, brassy-yellow pile in front of the scutellum in *I. maculiventris*, whereas in *I. quadrilineata* the last flagellomere is mostly wholly white and the scutum lacks pile as described above. Through our examination of a large amount



Figs 75–88. *Isomerocera quadrilineata* (Fabricius), variation of legs colour pattern, males (75–82) and females (83–88): Males: (75–78) Mozambique, Gorongosa; (79) Zimbabwe, Chirinda Forest; (80) Democratic Republic Congo, Yangambi; (81) Mozambique, Gorongosa; (82) Malawi, Nkwadzi. Females: (83) South Africa, Eshowe, Dlinza Forest; (84) South Africa, St. Helier, Hillcrest; (85) Malawi, Zomba; (86) Democratic Republic Congo, Bambesa; (87) Uganda, Jinja; (88) Democratic Republic Congo, Stanleyville [= Kisangani]. Abbreviations: l_1 , l_2 , l_3 – fore, middle and hind leg.

of material we cannot confirm the species-specific character of these features. Both forms display an identical shape of the male and female terminalia. Also, the highly variable colour pattern of the legs does not show any relation to a specific distribution area.

Remarks: Lindner (1953) found larvae along with larvae of *Ptecticus* sp. (Sarginae) in an old *Carica papaya* tree trunk in Tanzania. Later Lindner (1965b) found that the larvae develop in decaying plants and proposed to include this species among the hemerophilous forms (“Kulturfolger”) accompanying plantations of different cultured

plants. According to recent data from Togo (A. Ssymank pers. comm.), *I. quadrilineata* was regularly collected on and/or along plantations producing avocados, aubergines, bananas, coffee and cacao beans.

Lachaise and Lindner (1973) found during an ecological survey of the tropical savannah of Lamto (Ivory Coast) that larvae of *Isomerocera quadrilineata* lived in gallery forests and were reared in a large numbers from a dead fallen trunk of a papaya tree, as do the larvae of *Sternobrithes tumidus* Loew (Pachygastrinae).

Published records: (Only records not included in the additional material examined are provided with coordinates and included in the distribution map).

Fabricius (1787): SIERRA LEONE (female lectotype). **Macquart (1850)**: SOUTH AFRICA: Natal [= KwaZulu-Natal] (male holotype of *Diphysa maculiventris*). **Gerstaecker (1857)**: SOUTH AFRICA (male syntypes of *Ptilocera natalensis*). **Loew (1860)**: Caffreri [= Cape Province, South Africa]. **Speiser (1908)**: TANZANIA: Pale [05°54'S 39°15'E] (syntypes of *Ptilocera quadrilineata* var. *melecta*). **Grünberg (1915)**: CAMEROON: Bibundi, Buea, Lolodorf [03°14'N 10°44'E]; EQUATORIAL GUINEA: Alen (Benitogebiet) [Benito = Mbini River area], Nkolentangan [01°34'N 10°30'E], Uelleburg (Benitogebiet) [01°49'N 10°36'E]; TOGO: Misahohe [06°57'N 00°35'E]; TANZANIA: Bismarckburg [= Kasanga]. **Curran (1928)**: D.R. CONGO: Stanleyville [= Kisangani] (as *Ptilocera*). **Lindner (1938)**: D.R. CONGO: Eala; Katana; Katombe [= Katompi, 06°11'S 26°20'E]; Gwanga [04°34'N 24°02'E]; Likimi; Mayumbe [= Mayombe]; Tshela [= Tshalala]; Stanleyville [= Kisangani]; Uelè: Bambesa; Lulonga (river), Mondombe [00°54'S 22°48'E]; Lulua; Kapanga [= Kananga]; Albertville [= Kalemie]. **James (1949a)**: LIBERIA: Bendu [= Keya Bendu, 08°18'N 10°13'W]. **Lindner (1953)**: Tanzania: Msingi [04°20'S 34°34'S]. **Lindner (1958a)**: SOUTH AFRICA: Natal; ZIMBABWE: S. Rhodesia. **Lindner (1958b)**: D.R. CONGO, Kiamalwa [09°44'S 26°00'E]. **Lindner (1961)** (as *I. maculiventris*): MOZAMBIQUE: Gorongosa, Manica–Sofala Dist[ri]ct; SOUTH AFRICA: Port St. Johns Dist[ri]ct; Ngoye Forest between Eshowe and Empangeni. **Lindner (1965a)**: D.R. CONGO: Parc National de la Garamba [= Garamba National Park]; Tanzania. **Lindner (1965b)**: ELFENBEINKÜSTE [= IVORY COAST]: Bingerville [05°21'N 03°54'W]. **Lindner (1966a)**: D.R. CONGO: Bassin Lukuga, Eala, Uele: Bambesa, Mt. Uele: Mauda [04°46'S 27°18'E], Beni; Rutshuru, Tshuapa: Bokuma, Kivu, Lomami River [04°27'S 26°39'E], Geranga (Likimi), Buta, Bas-Congo: Kinkenge; Ubangi: Libenge [03°39'N 18°38'E], Opala [00°43'S 23°59'E], Yangambi, Ituri: terr. Wamba, Bayange [00°50'S 17°41'E]. UGANDA: Mpanga; **Lindner (1966b)**: ZIMBABWE: N. Vumba, S. Rhodesia. **Lindner (1968)**: CONGO (BRAZZAVILLE): Sibiti [03°41'S 13°20'E]; Mayombe: Dimonika [04°47'S 11°50'E]. **Lindner (1970)**: CAMEROON: Yaoundé; Nkolbisson; CENTRAL AFRICAN REPUBLIC: Maboké [03°54'N 17°53'E]. **Lindner (1972)**: SOUTH AFRICA: Doornkloof Forest Reserve; Port St. Johns; Ngotsche Gorge, Entomeri; ZIMBABWE: N. Vumba, S. Rhodesia. **Lachaise & Lindner (1973)**: IVORY COAST: Lamto [06°13'N 05°01'W]. **Woodley (2001)**: BURUNDI, CAMEROON, CENTRAL AFRICAN REPUBLIC, CONGO [= D.R. CONGO], EQUATORIAL GUINEA (Bioko, Rio Muni [01°30'N 10°30'E]), IVORY COAST, LIBERIA, MALAWI, SIERRA LEONE, SOUTH AFRICA, TANZANIA, TOGO, ZAIRE [= R. CONGO], ZIMBABWE.

Additional material examined:

ANGOLA: 1 ♀ "A26" 8.i.1972, C.F. Huggins (BMNH). BURUNDI: 1 ♂ Rutana [03°55'S 30°00'E]. 11. xi.1951, F.J. François (IRSNB). 1 ♂ Bubanza [03°05'S 29°24'E], iii.1958, F.J. François (USNM). CAMEROON: 2 ♂ 2 ♀ Befang, 60 km N Bamenda [05°56'N 10°10'E], 500 m, 24.xi.1987, all F. Kaplan; 1 ♀ 8.xi.1987, A. Freidberg; 2 ♀ Yaoundé [03°52'N 11°31'E], 793 m, 1936, Van Zwaluwemburg & Mc Gough (USNM). 2 ♂ 1 ♀ 120 km NW Yaoundé, 3.xi.1987; 1 ♀ 5.xi.1987, all A. Freidberg (all TAU). 1 ♀ Nkolbisson [03°53'N 11°27'E], 15.xii.1923, Bequaert; 1 ♂ 15.ix.1963, L.G. Saegers (both MRAC); 1 ♀ 25.x.1970, L. Matile (USNM). 5 ♂ 20 km E Sangmelima [02°56'N 11°59'E], 7.xi.1987, A. Freidberg (TAUI); 3 ♂ 5 ♀ 1200 m, 21.xi.1987, A. Freidberg (all USNM). 4 ♂ 3 ♀ Bambalang area, 50 km E of Bamenda [05°56'N 10°10'E], 1200 m, 21.i.1987, 1 ♂ 7.xi.1987; all A. Freidberg; 3 ♀ 7.xi.1987; 1 ♂ W Bamenda, 20.xi.1987, F. Kaplan; 1 ♂ 1 ♀ Bali [05°53'N 10°01'E], 1 ♂ Ile M'bamou [04°15'N 14°26'E], 29.x.1975, L. Matile (all USNM). 1 ♂ Buea Mts [04°09'N 09°14'E], S. Preuss; 1 ♀ Johann Albrechtshohe Mt. [04°40'N 11°59'E], 11.iv.1896; 1 ♀ Bibundi [04°13'N 08°59'E], 11.iv.1896, both L. Conradt; 1 ♂ 15–30.iv.1905; 1 ♀ 1–15.v.1905, both G. Tessmann (all ZMHB). DEMOCRATIC REPUBLIC OF THE CONGO: 1 ♂ Mura [11°02'N 26°42'E], ix.1923, R.E. Turner (BMNH). 1 ♀ Congo "IRSNB 24" (IRSNB). 1 ♂ Bas Ogooué, N'Gomo [03°30'S 14°26'E], 17.iv.1975, G. Couturier (FMCV). 2 ♀ W Anga [3°7'S 21°34'E], R. Ellenberger (IRSNB). 1 ♀ Eala [00°40'N 18°17'E], 20.viii.1927, F. Hulstaedt (MRAC); 1 ♂ 15.iv.1933, J. Gesquière (MSNG); 1 ♀ 15.ii.1935; 1 ♀ 7.vi.1935; 1 ♂ 13.vi.1935; 1 ♀ 2.vii.1935; 1 ♀ 1 ♂ 9.vii.1935; 4 ♀ viii.1935; 1 ♂, x.1935; 1 ♂ 2 ♀ vi.1936; 1 ♀ viii.1945; 1 ♀ xi.1945 J. Ghesquière (all IRSNB); 1 ♀ 15.ii.1935, 1 ♀ 15.vii.1935, 1 ♀ 15.i.1936; G. de Witte (MSNG), 1 ♂ vi.1936, J. Ghesquière (USNM). 1 ♂ Kivu, Rutshuru [01°11'S 29°27'E], 1 ♀ 1000 m, 3.vii.1935, G.F. De Witte (USNM); 2 ♂ 8.vii.1935, 1100 m, G.F. de Witte (MRAC, MSNG); 1 ♂ 2.vi.1936,

L. Lippens (MRAC); 1♂ v.37, 1♀ 4.vii.1937, J. Ghesquière (IRSNB); 1♀ 14.vii.1950 G. Demoulin (MRAC); 1♀ gallery forest, 1.iv.1953, J. 1♂ 7.vii.1953, both J. Verbeke (USNM); 1♀ 12.iv.1960, R. Maréchal; 1♀ 15.ix.1963, L.G. Segers (both MRAC). 1♂ Kivu, Rutshuru, Buhanyia [01°52'S 30°28'E], 1200 m, G.F. de Witte (USNM). 1♀ Bambesa [3°28'N 25°43'E], 15.i.1924, L.J. Ghesquière (MSNG), 2♀ F.J. François (IRSNB); 1♀ 27.vii.1938, J. Vrijdagh (USNM). 1♀ Bafwasende [01°00'N 27°09'E], ix.1945; 3♀ 10.x.1945, F. François (MSNG), 1♂ 1♀ ix.1946, F.J. François (IRSNB). 2♀ Itunga [03°02'S 26°31'E], vii.1959, F.J. François (IRSNB). 1♂ 1♀ ix.1959, F.J. François (USNM). 1♀ Isangi [01°48'S 28°08'E], vii.1959; 1♂ Garamba National Park [04°00'N 29°15'E], 7.ii.1950; 1♂ 1♀ 10.iv.1950, 1♀ 29.x.1950 all H. de Saeger (all IRSNB). 1♀ Hoyo Mt. [01°14'N 29°49'E], 1280 m, 30.x.1933, J. Leroy (MSNG); 1♀ 8–9.vii.1953, H. de Saeger (IRSNB), 1♂ 1280 m, 7–15.vii.1955, P. Vanschuytbroeck (USNM). 1♂ Ituri, Komanda [01°23'N 29°46'E], 10.xi.1953, 1♂ Simba, Lulonga [0°38'N 18°22'E], 15.x.1912, R. Mayné; 1♀ Luali [05°06'S 12°29'E], 26.viii.1913, Bequaert; 1♀ Yambata [02°26'S 21°58'E], 15.ii–15.iii.1914, De Giorgi (all MSNG). 1♂ 1♀ Mayombe, Lemba [04°25'S 15°20'E], 1–10.xii.1915, R. Mayné, (MSNG). 1♂ Budjala, Bosanga [02°04'S 17°13'E], 15.ix.1919 ex coll. Brunetti (MSNG). 3♀ Uelé [04°09'N 22°26'E], 1920, L. Burgeon; 1♀ 15.iii.1925, H.J. Brédo; 1♂ 24.xii.1929, A. Collart; 1♀ 20.i.1933; 1♂ 20.x.1933; 3♂ 1♀ 30.x.1933; 1♀ 15.i.1934, all J.V. Leroy (all MSNG); 1♀ 2.xii.1956, 810 m, R. Castelain (MRAC). 1♀ Mayombe, Luki [05°39'S 13°04'E], 21–30.iii.1922, H. Schoudeten (MSNG). 1♂ 1♀ Stanleyville [= Kisangani, 00°31'N 25°12'E], 15.v.1923, L.J. Ghesquière; 1♂ 1924, L. Burgeon (all MSNG). 1♀ 3–4.iii.1949, G.F. de Witte (MRAC). 1♀ Mayombe, Tshela [04°58'S 12°56'E], v.1923; 1♀ vii.1925; 1♀ v.1927; all L.J. Gesquière (all MSNG). 1♂ 2♀ Mayombe, Dingi [02°32'S 25°45'E], 21.x.1924, A. Collart; 1♀ Kapanga, Lulua [05°54'S 21°27'E], 15.iii.1926, L.J. Ghesquière; 1♀ Barumbu [04°19'S 15°19'E], 1927, R.P. Hulstaft (both MSNG); 1♂ Uluku, Ituri [01°51'N 29°58'E], 12.viii.1927; 1♂ Albertville [= Kinshasa, 04°19'S 15°19'E], 20.viii.1927; 1♀ Catombe, Eala [00°40'S 18°17'E], 20.viii.1927; 1♀ Hulstaft, Boende [00°44'S 19°12'E], 21.xi.1927; 1♀ Mayombe, Makala Ntete [04°22'S 15°18'E], 1928, all A. Collart (all MSNG). 1♀ Mandombe [00°54'S 22°48'E], 15.ix.1928, F.G. Overlaet; 1♀ Elisabethville [= Lubumbashi, 11°40'S 27°28'E], 15.xii.1928, Bequaert (MSNG). 1♀ Beni [00°30'N 29°28'E], 1150 m, 7.xi.1931, L. Lebrun (MSNG). 1♀ Kivu, Tshibinda [00°19'S 28°45'E], 18–26.xi.1932, L. Burgeon; 1♀ Banzyville [= Mobayi–Mbongo, 04°18'N 21°11'E], 24.xi.1932, H.J. Brédo; 1♀ Yuvanga, Likimi [02°50'N 20°45'E], 15.ix.1933 H.J. Brédo (all MSNG). 1♀ Limami river, Kasongo [04°27'N 26°39'E], 3.vii.1935, G.F. de Witte; 1♀ Ubangi, Libenge [03°39'N 18°38'E], 15.iv.1936, C. Léontovitch (both MRAC). 1♀ Bova nr. Kiamalwa [09°40'S 25°44'E], L. Lippens; 2♂ Lukunga [04°40'S 13°47'E], 1936, De Saeger; 1♀ NW Ruwenzori, Watalinga [00°40'N 29°59'E], 15.vi.1937, Lisfranc (all MRAC). 1♀ Yapehe [00°13'S 24°27'E], 26.vi.1948, P.L.G. Benoi; 1♂ Buta [02°48'N 24°45'E], 1949, R.F.J. Hutsebaut (both MRAC). 1♀ Bas–Congo, Kinkenge [05°57'S 12°29'E], 15.ii–15.iii.1951, M. Bequaert (MRAC). 1♀ National Park Garamba, Embe Mt. [04°40'N 29°31'E], 20.iv.1952; 1♀ 17.v.1952, both H. De Saeger. 1♂ 1♀ Tshuapa, Bokuma [00°48'N 24°45'E], 15.iv.1954, R.P. Lootens (all MRAC). 7♂ Hoyo Mt. [01°14'N 29°49'E], 7–15.vii.1955; 2♂ 23.viii.1956; 1♂ 23.xii.1957, all P. Vanschuytbroeck (MRAC, 1♂ USNM). 1♂ Massif Ruwenzori, Kalonge [03°24'S 29°02'E], 7–15.vii.1955, 2065 m, 3♂ Semliki, Lume [04°43'S 26°31'E], 1830 m, 7–15.vii.1955, all Vanschuytbroeck (all MRAC). 1♂ Sankuru, Pempa Zeo [06°49'S 23°58'E], 10.xii.1959, P.L.G. Benoi (MRAC). 1♂ 1♀ Yangambi [00°47'N 24°28'E], 15.iv.1960, J. Decelle (MRAC); 1♂ 23.xi.1950, J.M. Mc Goug (USNM). 1♂ Mayombe, Sanga [08°50'S 26°36'E], 25.ix.1977, R. Roqué (MRAC). 1♂ Lukombe [04°16'S 18°21'E], 3.iii.1965, D. Cookson (NMSA). EQUATORIAL GUINEA: 1♂ 3♀ Bahia de San Carlos [03°28'N 08°33'E], 200 and 400 m, L. Fea (MSNG). 1♀ Fernando, Poo Island [= Bioko Island, 03°30'N 08°42'E], 1901; 2♂ 3♀ Punta Frailes [03°47'N 08°43'E], x.1901, all L. Conradt (USNM). 1♂ Spanish Guinea, Benitogebiet [Benito= Mbini River area], Alen [01°35'N 09°37'E], 15.v.1895, R. Baumann; 3♀ 16–31.vii.1906, G. Tessmann (all USNM). GABON: 3♀ Fernand–Vaz [01°34'S 09°37'E], 400 m, ix–x.1901, L. Fea (MSNG). 1♀ Ogooué, Lambarené [00°41'S 10°13'E], 1910; 1♀ 1912, both R. Ellenberger (IRSNB, USNM). GHANA: 1♀ Ghana (West Africa), i.57, N.H.L. Krauss; 1♀ Gold Coast [Region], 5.v.1912, J. W. Scott Macflie; 2♂ 1913, A.E. Evans; (all BMNH). 1♂ 2♀ Gold Coast, Kumasi [06°40'N 01°37'W], 17.iii.1947, J. Bowden; 1♀ Gold Coast, Ashanti, Ahinsa [06°16'N 02°01'W], xii.1959, B. & P. Stuckenbergl (all NMSA). IVORY COAST: 1♀ Adoupo Doumé [05°20'N 04°07'W], 16.x.1974; 1♀ "Fopo Fopo", 7.iii.1975; both G. Couturier (FMCV). 1♂ 50 km NW Abengourou, Amanikro [07°22'N 04°03'W], 15.v.–15.vi.1961; 1♂ 5.viii.1961; 1♂ Divo [05°50'N 05°22'W], 28.xi.1963, all J. Decelle (MRAC). 1♀ Asagny Nat. Par, Roadway between Gate & Camp (05°14'N 04°49'W), 24.iv.1989, J. & A. Londt (NMSA). 2♀ 17 km NW Abidjan [05°19'N 04°02'W], 1–6.x.1971, J.A. Gruwell (USNM). KENYA: 1♂ Nairobi [01°17'S 36°49'E], 29.vii.1913, 1♀ 17.x.1931, A. Makie (both BMNH). 2♂ Mombasa [04°03'S 39°40'E], 13.viii.1983, A. Freidberg (CSCA); 1♀ Kakamega Forest (00°15'N 34°52'E), 1554 m, 4.ii.1959, A.C. van Brugger (all USNM). 1♀ Kakamega Forest (00°13'N 34°52'E), 23.ix.2005, L. Friedman (TAU); 1♀ 11.v.1991, all A. Freidberg (CSCA). 2♀ 2♀ W Kakamega Forest Reserve (00°22'N 34°53'E), 1620 m, indigenous forest paths, 22.xi.1992, A. Whittington & J. Londt (NMSA). 1♀ Diani Beach [04°19'S 39°34'E], L.C. Edwards; 1♀ i.1957, Krauss (both USNM). 1♂ 2♀ Shimba [04°15'S 39°23'E], 2.vi.1980, D. Furth (USNM). LIBERIA: 1♀ "Liberia", Marley (BMNH). MALAWI: 1♂ "Nyasaland", Cholo [16°04'S 35°08'E], R.C. Wood; 1♂ 1913, A.E. Evans (both BMNH). 1♀ Mt. Mulanje [15°57'S 35°35'E],

without date, L.C. Edwards; 1♂ vi.1945; 1♀ vii–viii.1946; both Van Someren; 1♀ 19.ix.1912 and 1♂, 16.xi.1912, J.J. Simpson; 1♀ 30.v.1913, S.A. Neave (all BMNH). 1♂ Nkwadzi [12°44'S 33°43'E], 1920, L. Burgeon; 1♂ 25.x.1977, R. Jocqué (both MRAC). 1♂ Mulanje Village [16°02'S 35°30'E], 800 m, 24–25.xi.1980, Londt & Stuckenberg; 1♀ Riverine Gallery Forest, 800 m, 8 km SE, 30.xi.1980, Stuckenberg & Londt (both NMSA). 1♂ Nyasaland, indigenous forest, 18.xii.1990, D.A. Barraclough; 1♂ Lilongwe Nature Sanctuary [13°59'S 35°20'E], 1100 m, 15–16.iii.1987, J & A. Londt; 2♂ 1♀ Zomba [15°23'S 35°35'E], 1100 m, 24–27.xi.1980, Londt & Stuckenberg (all NMSA). 1♂ Chiradzulu Forest (15°41'S 35°11'E), 1130 m, 8.i.2010, A. Freidberg; 1♂ 1♀ same data; 1♂ 9.i.2010, all L. Friedman (all TAUI). MOZAMBIQUE: 1♀ Amatonga Forest near Gondola [19°10'S 33°44'E], gallery forest, 15.i.–26.i.1959, A.C. van Bruggen (USNM). 4♂ 3♀ Manica, Sofala District, Gorongosa Mts [18°45'S 34°30'E], 641 m, gallery forest, ix.1957; 2♂ 5.iv.1960; 1♀ v.1961; all P. Stuckenberg (all NMSA). 1♂ 1♀ Tumbine Mt., Port East Africa [16°05'S 35°48'E], 5–6.iv.1958, B. Stuckenberg (NMSA). NIGERIA: 1♀ Nigeria, 20.xi.1912, 1♀ 9.v.1913, both S.A. Neave (BMNH). 1♂ Ibadan [07°23'N 03°55'E], 5♂ Bridwell (USNM); 1♂ 23.iii.1923, A.W.J. Pomeroy (BMNH); 1♀ 5.ix.1936, Van Zwaluwemburg & Mc Gough; 1♀ 2.i.1963, D.C. Eidt (both USNM). 1♂ Ilé-Ifé, 11.iv.1970, J. T. Medler (USNM). REPUBLIC OF THE CONGO: 1♂ Kalanga [01°29'S 16°09'E], 15.xii.1918, R. Mayné (MSNG). 1♂ Lilimi [03°43'S 13°32'E], 15.i.1924, L.J. Ghesquiere (MSNG). 1♀ Mayidi [00°11'S 15°09'E], i. 1945, P. Van Eyen (MRAC). SIERRA LEONE: 1♂ Makuma [02°54'N 23°34'E], R.C. Wood (BMNH). SOUTH AFRICA: 1♂ Caffrereï [= Cape Province], 26–27.xii.1892, L. Conradt S., ex Coll. H. Loew (ZMHB). 2♀ Natal, ex Coll. Bigot; 1♂ 1♀ Natal, Zululand, [= KwaZulu-Natal], ex coll. W.H. Potts (all BMNH); 1♂ i.1957, N.H.L. Krauss; 1♀ 9.ii.1969, O.W. Richards (both BMNH). 1♂ Mfongosi [27°18'S 32°10'E], ex Coll. C.J. Vainwright; 1♀ W.E. Jones (both BMNH), 1♂ ex Coll. Brunetti (MRAC). 1♀ Durban [29°53'S 31°03'E], 1♀ L. Pieters (MRAC); 1♂ 11.xii.1913, S.A. Neave; 1♂ i.1919, D. Cookson (both BMNH); 1♀ 20.ii.1965; 1♀ 5–6.iv.1969; both B. & P. Stuckenberg (all BMNH). 1♂ Eshowe [28°53'S 31°26'E], ii.1923, R.E. Turner; 1♀ Entumeni Nature Reserve, 16 km W Eshowe, 670 m, 26.i.1980, R. Miller & P. Stabbins (USNM); 2♀, 6.i.1983, A. Freidberg (BMNH) 1♂ Pondoland, Port St. Johns [31°38'S 29°32'E], xi.1923, R. E. Turner; 1♀ x.1926, G.A.K. Marshall; 1♀ x.1930, Van Someren (all BMNH); 1♀ ii.1957; 1♂ 16–17.x.1959, both Stuckenberg; 1♂ 20–25.xi.1961, B. & P. Stuckenberg; 1♂ 3.i.1965, D. Cookson (all NMSA). 3♀ Ballito [29°32'S 31°13'E], 30 m, 11.x.1991, J.G.H. Londt; 1♀ 23 km N King William's Town, Ciskei, Maden Dam [32°44'S 27°18'E], 26–27.i.1984, D. & C. Barraclough (both BMNH). 1♀ Upper Tongaat [29°26'S 31°01'E], 19.x.1919, ex coll. Brunetti (MRAC); 1♀ Transvaal, Krantzklouf [20°46'S 30°50'E], 1905, S.G. Schroeder (USNM). 1♂ Transvaal, Krantzklouf Nature Reserve upper Krantz [29°46'S 30°50'E], 455 m, 3.vii.1935 (MRAC); 1♀ 1036 m, 9.i.1965, B. Stuckenberg; 1♀ 400 m, indigenous forest, 1♀ 8.ii.1984; 2♂ 8.xi.1984; 6♂ 18.xii.1990; all D.A. Barraclough (NMSA); 1♀ 455 m, 25.xi.1999, K.C. Holston (CSCA). 1♂ East London [33°00'S 27°54'E], 2.ii.1924, R.H. Stevenson; 2♂ 1♀ 11.i.1925, H.K. Munro; 1♂ 7.x.1965, D. Cookson (all NMSA). 1♂ Eshowe, Dlinza Forest Nature Reserve [28°53'S 31°26'E], 20.xii.1954; 1♀ 16.i.1955; 1♂ 1♀ ix.1957; 1♀ 5–6.iv.1960, all B. & P. Stuckenberg (all NMSA); 6♂ 6.xii.1977; 9♂ 20–23.xi.1978; 4♂ 2♀ 22.xii.1979; all R. Miller & P. Stabbins; 2♂ 530 m, 26–27.i.1988, J.G.H. Londt (NMSA, USNM). 1♂ Inchanga [29°44'S 30°40'E], 16.i.1955, B. & P. Stuckenberg (NMSA). 1♂ St. Helier, Hillcrest [29°46'S 30°45'E], 25.i.1955, B.R.S.P.G.; 1♂ 9.ix.1962; B. & P. Stuckenberg (both NMSA). 1♂ Umgeni River, Nagle Dam [29°35'S 30°37'E], iv.1958, B. & P. Stuckenberg (NMSA). 1♂ Umhlanga [29°43'S 31°05'E] 20–25.ii.1961, B. & P. Stuckenberg; 1♀ Ngoye Forest [28°50'S 31°43'E] between Eshowe & Empangeni, 5.iii.1963, D.M. Cookson (NMSA); 1♂ 250 m, 29.i.1988, J.G.H. Londt (USNM). 1♀ Entumeni, Eshowe District, Ngotsche [28°51'S 31°19'E], 17.ii.1965, D.M. Cookson (NMSA); 1♀ Nature Reserve (29°12'S 31°23'E), 1150 m, 3.ii.1988; 2♂ 27.i.1988, both J. Londt (all NMSA). 2♂ Umhlatuzana River [29°53'S 31°00'E], 500 m, indigenous forest, xii.1990, D.A. Barraclough (NMSA). 10♂ 1♀ Transkei, Dwesa Nature Reserve (32°16'S 28°51'E), 50 m, 17–29.xi.1991, D.A. Barraclough (NMSA). 1♂, 4♂ 3♀ Natal, Umhlanga Bush [29°43'S 31°05'E], 19 km N of Durban, 29.xi.1994, Marion Kotrba (USNM). 1♂ Natal, S Coast, Uvongo [30°49'S 30°23'E], 25.ii.1999, K.C. Holston (USNM). TANZANIA: 1♂ Amani [05°05'S 38°40'E] ex coll. W.H. Potts (BMNH); 1♀ 16–31.vii.1906, S.G. Tessmann (ZMHB); 1♀ thick bush, 1957, J.G. Halcrow (BMNH). 1♀ Usumbara Mts. [04°45'S 38°30'E], 1000 m, 3.i.1976, O. Lomholdt (UZMC). 1♀ Bismarckburg [= Kasanga, 08°27'S 31°08'E], 8.v.1893; 1♀ 1.vi–4.vii.1893; both S.L. Conradt; 1♀ 1.v.1905, S.G. Tessmann (all ZMHB). TOGO: 4♂ 3♀ Cascades d'Ayomé, NE of Amlamé [07°30'01"N 00°57'20"E], 300–330 m, 13. iv.2008; 3♂ 1♀ Danyi–Apéyémé, Danyi Plateau (07°11'04"N 00°41'32"E), 770 m; 14.iv.2008; 1♀ Danyi–Dzoghégan, Danyi river, Monastère de l'Ascension (07°14'30"N 00°40'45"E), 725 m, 14.iv.2008; 1♂ Aghanon–Agoté, Tomesutoè stream (07°15'53"N 00°47'51"E), 360–370 m, 15. iv.2008; 2♂ 2♀ Cascades de Kpimé, W von Humé (07°00'21"N 00°38'50"E), 280–300 m, 16. iv.2008; 1♀ Cascades de Yô, NW of Kpalimé (06°57'06"N 00°35'50"E), 370 m, 16. iv.2008; 1♂ Mont Agou, Kébo–Dalavé, NE of Agou (SE of Kpalimé) (06°50'56"N 00°44'52"E), 270–275 m, 17. iv.2008; 1♂ 1♀ Lomnava, NE of Huimé (07°00'59"N 00°40'46"E), 290 m, 18. iv.2008; 1♂ Oounabè, at Ofè river between Pref. d'Amou and Pref. Wawa (NW of Témédja) (07°32'35"N 00°59'59"E), 720 m, 19. iv.2008; 11♂ Zoghégan–Carrière, at Elèbè river (07°34'49"N 00°40'03"E), 650–660 m; 21. iv.2008; 1♂ Soto, Owui River (70°36'09"N 00°42'20"E), 490 m, 21. iv.2008; 1♂ Klabé–Azafi, at Gonobè river (07°36'00"N 00°43'21"E), 485 m, 21.

iv.2008; 6♂ 1♀ Anonoé, at Okpabè stream (07°33'39"N 00°36'09"E), 280 m, 22.iv.2008; 2♂ Obé at Akloa, Béna stream (07°31'56"N 00°36'36"E), 260 m; 22.iv.2008; 5♂ 1♀ Akloa, Région des Plateaux at Domi river (nr. Cascades d'Akloa) (07°30'48"N 00°36'36"E), 280–300 m; 22.iv.2008; 1♂ N von Ayagba, at Kpélékoun river, (07°46'12"N 00°47'48"E), 490 m, 23.iv.2008; 1♂ 2♀ Kougnohou, at Kpon river (07°41'11"N 00°47'44"E 560 m, 23.iv.2008; 3♂ Abriwa-Nko, ca. 5 km N of Badou, at Egnulu-Agbadja river (07°37'16"N 00°36'15"E), 300 m, 24.iv.2008; 1♂ Kodjo-Kopé, N of Badou, at Djodji stream (07°38'56"N 00°35'43"E), 260 m, 24.iv.2008; 1♂ Zoumenou, at Iviwou-Zato river (S of Zogbégan) (07°30'52"N 00°40'50"E), 670 m; 25.iv.2008; 1♂ N'kengbé, at Apati stream (08°06'40"N 00°45'54"E), 580 m, 28.iv.2008; 7♂ 1♀ Tentkro, at Koflo River (SE of Y'gué, SW of Blitta) (08°05'18"N 00°45'53"E), 530 m, 28. iv.2008; all A. Ssymank (all ASCG). UGANDA: 1♀ Bwamba [00°43'N 30°07'E], xi.1923, R.E. Turner; 1♂ Bwamba Valley, x.30; 1♀ vi/40; 1♂ Jinja [00°25'N 33°12'E], x.30, both Van Someren; 1♀ thick bush, 1957, J.G. Halcrow (all BMNH); 1♀ 1400 ft, W. Peters (MRAC). 3♂ Mpanga [00°04'N 30°22'E], 65 km E Entebbe, 15.viii.1959, P.L.G. Benoit (MRAC). ZIMBABWE: 1♀ Chirinda Forest, Selinda Mt. [20°27'S 32°43'E], 19.vi.1912, J. W. Scott Macfizie (BMNH); 1♀ 24.iii.1954, B. Stuckenberg (NMSA); 1♂ 20.xii.1954, B. & P. Stuckenberg; 2♂, 1066 m, 15–26.i.1959, A.C. van Bruggen; 1♂ 6.ii.1961, M. & H.D. Brown (all NMSA). 1♂ Vumba [= Bvumba Mts, 19°06'S 32°47'E], 1906, E. Haug (NMSA); 1♂ 4–8.xii.1956, Son & Martin; 1♂ 1♀ 3.i.1965; 1♂ 14.ii.1965; 1♂ 17.ii.1965; 1♀ 20.ii.1965; 1♀ 8.iv.1965, all D. Cookson; 1♂ 8.ii.1965, T. Schofield; 2♀ 16.i.1970, B. & P. Stuckenberg; 1♀ 24–25.ii.1980, Londt & Stuckenberg (all NMSA). 1♀ Umtali [= Mutare, 18°58'S 32°38'E], Leopard Rock, 25.i.1955, B.R.S.P.G.; 1♀ ix.1957, Stuckenberg (both NMSA).

Type material remarks: *Stratiomys quadrilineata*: Female syntype from Sierra Leone in UZMC (Woodley 2001) is hereby designated as lectotype. It is labelled: "S. 4lineata, Sierra Leone /TYPE [red label]/LECTOTYPUS *Stratiomys quadrilineata* Fabricius, 1787: 331, F. Mason des., 2010". Condition: Both antennal flagella missing, thorax broken around pin, anterior margins of both wings damaged, dorsal part of abdomen with some rusty incrustation.

Diphysa maculiventris: Male holotype from Durban (South Africa) in MNHN (Woodley 2001). It is labelled: "32 46 [handwritten on a small round label]/*Diphysa maculiventris* ♂ Macq. n. sp. [handwritten by Macquart in black ink on a large rectangular label]/HOLOTYPE *Diphysa maculiventris* Macquart, Mason & Rozkošný rev. 2011". Condition of the holotype: left wing damaged, left flagellum broken, otherwise in satisfactory condition (genitalia not dissected).

Ptilocera natalensis: Male syntype in ZMHB (Woodley 2001), hereby designated as lectotype, labelled as follows: "Natalensis Gerst. [green aquamarine handwritten label] /1859/Type [small red label]/Pt. Natal Dst [handwritten on a green aquamarine label] /LECTOTYPUS *Ptilocera natalensis*, Gerstaecker, 1887: 334, F. Mason & R. Rozkošný des., 2011". Condition of the lectotype: perfect (genitalia not dissected).

Ptilocera quadrilineata var. *melecta*: male and female syntypes should be deposited in ZMHB (Woodley 2001) but recently they were not found (Sven Marotzke, ZMHB, pers. comm.).

DISCUSSION

Isomerocera and *Ptilocera* represent apparently sister genera sharing two unique characters among Pachygastrinae: paired slender projections on medial flagellomeres and the well-developed parameral sheath on the male terminalia. The flagellar projections differ between the two genera and between both sexes within them. The male upper projections are partly reduced, shortened on flagellomeres 3–5 in *Isomerocera* (Figs 31, 45, 46) but slightly shorter only on flagellomere 3 in *Ptilocera*. An extreme situation was described in *P. simplex* Mason & Rozkošný, 2011, where flagellar projections are (probably secondarily) entirely reduced. The females of both genera may display an

additional unpaired ventral projection on flagellomere 2 (Fig. 65) but this is absent in *I. heteraspis*, in which also projections on flagellomere 5 are missing (Fig. 38). In both species of *Isomerocera* the female antennal projections are of the same, short shape as in the males, whereas in the females of *Ptilocera* all antennal projections are markedly elongate and relatively long, plumose compared with the males. The scape represents another distinguishing character. It is 3–4× as long as broad in *Isomerocera* spp. but only at most twice as long as broad in *Ptilocera* (with exception of both sexes of *P. simplex* where the scape is 3× as long as broad in males and 2.5× as long as broad in females). The preocellar tubercle as a part of the ocellar triangle elevation is present in females of both species of *Isomerocera*, but is not present in females of *Ptilocera*.

The prealar prominence is also known in *Ptilocera* (see Mason & Rozkošný 2011) and apparently is not too rare among other pachygastrine genera (e.g. *Pachygaster*, *Zabrachia* and the Afrotropical *Platyna*) as well as some genera of Clitellariinae. It is present as a subtriangular prominence in *Adoxomyia* Kertész and as a strong spine in *Clitellaria* Meigen and *Nigritomyia* Bigot.

The surface pile on the scutum and scutellum is partly transformed to a dense covering of scales (Figs 17, 18) that are present in some other species from different genera. It is not precluded that the shape of the scales may be species-specific on some parts of the body but this presumption needs further documentation. The arrangement and shape of different projections and spines on the scutellum is characteristic for a number of different genera of Pachygastrinae but also for some genera of other subfamilies. The four strong marginal spines of *I. quadrilineata* (Figs 15, 16) is a widely distributed character state (see Woodley 2001) but *I. heteraspis* shows a more advanced state where four spines are arranged in two different planes (Figs 13, 14). The abdomen indicates a relation to the genera of Pachygastrinae with a rounded and a dorsally convex abdominal shape (Fig. 3) (see Kertész 1916).

The male terminalia found in *Isomerocera* and *Ptilocera* seem to be unique within the Stratiomyidae (see Mason & Rozkošný 2011). As we show here, the complex structure above the proper tripartite phallus is derived from the parameral sheath fixed to the inner dorsal side of the gonocoxites by an attachment structure (Figs 6–8) (see Woodley 1986, 1995; Sinclair *et al.* 1994; Cumming & Wood 2009). The parameral sheath is apparently bipartite (though connected by a hyaline membrane). Another apomorphic structure (at least in the Pachygastrinae) is represented by the pointed lateral projections of the aedeagal complex. Kertész (1916) proposed the presence of paired lateral aedeagal projections as a suitable distinguishing character for *Isomerocera* and *Ptilocera*. According to our recent analysis, they are actually not present in *Ptilocera* spp. except *P. simplex*. This structure resembles similar projections illustrated in all the European species of Sarginae (Rozkošný 1982) and described by Woodley (1995) in the Neotropical beridine *Neoberis brasiliiana* (Lindner, 1949).

In summary, in our opinion there are no reliable arguments for the synonymy of *Isomerocera* and *Ptilocera*, which has been discussed in the literature for more than one hundred years. Apparently *Ptilocera simplex* with its elongate scape and the well-developed lateral aedeagal projections seems to be more related to *Isomerocera* spp. than to the other species of *Ptilocera*. On the other hand, the male of this species differs from all other species of both genera by the absence of any flagellar projections, but the female shows no preocellar tubercle and has long, paired projections on flagellomeres

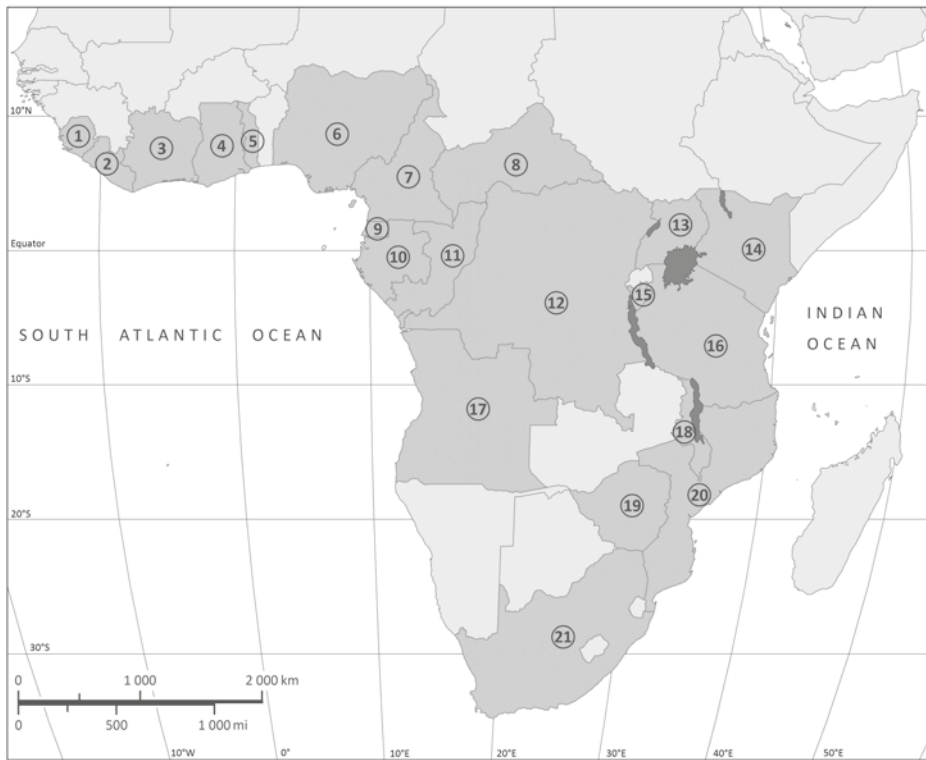


Figure 89. Distribution area of *Isomerocera* spp. in countries of Sub-Saharan Africa. 1 – Sierra Leone, 2 – Liberia, 3 – Ivory Coast, 4 – Ghana, 5 – Togo, 6 – Nigeria, 7 – Cameroon, 8 – Central African Republic, 9 – Equatorial Guinea, 10 – Gabon, 11 – Republic of the Congo (Brazzaville), 12 – Democratic Republic of the Congo (Kinshasa), 13 – Uganda, 14 – Kenya, 15 – Burundi, 16 – Tanzania, 17 – Angola, 18 – Malawi, 19 – Zimbabwe, 20 – Mozambique, 21 – South Africa.

3–5 as the other species of *Ptilocera*. Moreover, *P. simplex* is known to occur far from the Afrotropical Region in a limited area (northern India and northern Thailand) near the centre of the Oriental Region. Perhaps some additional information (e.g. a potential comparison of immature stages or molecular analyses) will provide more information on the relationship of both genera under discussion.

Based on the extensive material from different collections examined, *I. quadrilineata* is reliably reported from 21 African countries (Figs. 89 & 90): Angola, Burundi, Cameroon, Central African Republic, Democratic Republic of the Congo (Kinshasa), Equatorial Guinea, Gabon, Ghana, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Republic of the Congo (Brazzaville), Sierra Leone, South Africa, Tanzania, Togo, Uganda and Zimbabwe. Distribution in the Central African Republic is added on the basis of a reliable published record by Lindner (1970).

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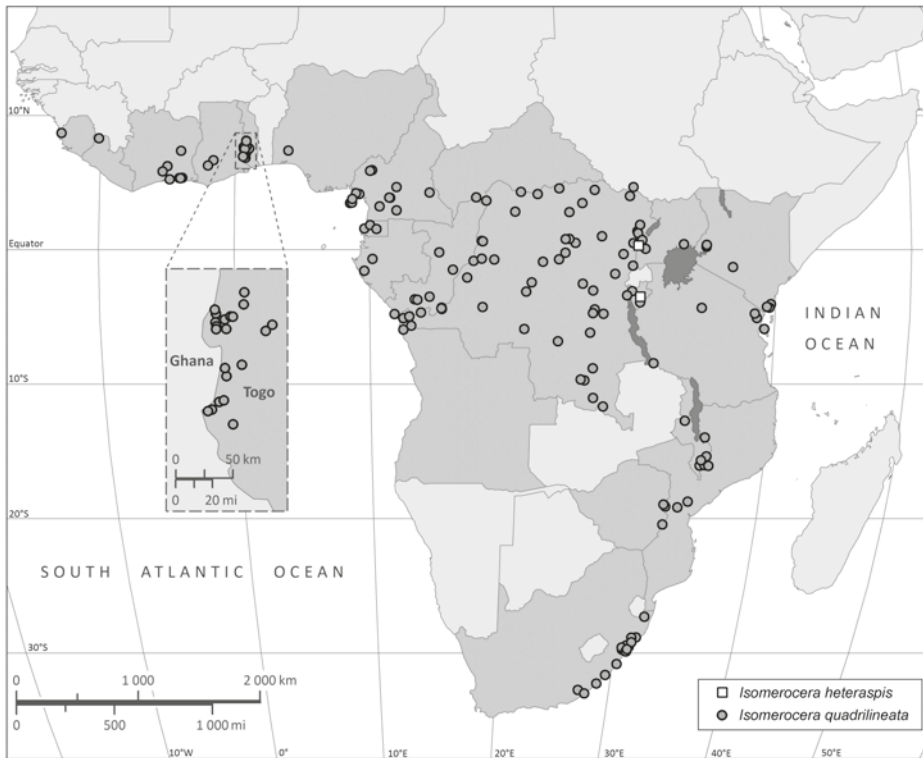


Figure 90. Distribution of *Isomerocera heteraspis* and *I. quadrilineata*.

Gess (Grahamstown, South Africa), Martin Hauser (CSCA, Sacramento, USA), Patrick Grootaert (IRSNB, Bruxelles, Belgium), Erica McAlister (BMNH, London), Sven Marotzke and Joachim Ziegler (ZMHB, Berlin, Germany), Mikhail B. Mostovski, Burgert Muller and Thembeke Nxele (NMSA, Pietermaritzburg, South Africa), Thomas Pape (UZMC, Copenhagen, Denmark), Fabio Penati and Roberto Poggi (MSNG, Genova, Italy), Fabrizio Rigato and Maurizio Pavesi (MSNM, Milano, Italy), Axel Ssymansk (ASCG, Wachtberg, Germany), Ros Urban (PPRI, Pretoria) and Norman E. Woodley (USNM, Washington, USA). Pierfilippo Cerretti (University “La Sapienza”, Rome and CNBFVR, Verona, Italy), Martin Hauser and Norman E. Woodley kindly reviewed the manuscript. Massimo Lopresti (CNBFVR, Verona) assembled the tables and figures, Zdeněk Stachoň (Brno, Czech Republic) helped with interpretation of some old localities' names and Ondřej Hájek (Brno, Czech Republic) arranged distribution maps. Our study was supported by the National Forest Service, Central Biodiversity Office, Rome, Italy and the Masaryk University, Brno, Czech Republic.

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