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RESEARCH ARTICLE

The African members of the *Platyja* genus group, with description of a new species and comments on other taxa currently attributed to *Megacephalomana* (Lepidoptera: Erebidae)

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Abstract

Following a review of the Afrotropical species of the *Platyja* genus group, the following generic synonymies are established: *Platyja* Hübner, [1823] = *Facidia* Walker, 1865 **syn. n.**, = *Megacephalomana* Strand, 1943 **syn. n.**, and at the same time *Facidia* (= *Megacephalomana*) is placed as a subgenus (**stat. n.**, limitedly to such rank by application of ICZN Code art. 61.3.1). The assemblage is found to consist of at least eight species, one of which described herein, namely *Platyja* (*Facidia*) *vacillans* (Walker, 1858) **comb. n.** (= *Facidia sassana* Strand, 1918 **syn. rev.**), *P.* (*F.*) *saalmuelleri* (Viette, 1965) **comb. n.**, *P.* (*F.*) *semifimbria* (Walker, [1858]), *P.* (*F.*) *rivulosum* (Saalmüller, 1880) **comb. n.**, *P.* (*F.*) *ennomoides* **sp. n.**, *P.* (*F.*) *stygium* (Saalmüller, 1881) **comb. n.**, *Platyja* ("*Facidia*") *luteilinea* (Hampson, 1926) **comb. n.**, and *Platyja* ("*Facidia*") *remaudi* (Laporte, 1972) **comb. n.**, with the last two taxa tentatively retained in *Facidia* due to some extraordinary features of the wing venation and pattern, respectively, that will require refinement of the topology of their phylogenetic relationships with core *Facidia*. As regards *luteilinea*, whose hitherto unknown female is also described, an unorthodox and sexually dimorphic branching pattern of the veins from the lower part of the forewing cell has been found, while *remaudi* shows a reversal of the proximo-distal sequence of the antemedial line and orbicular stigma of the forewing. Other taxa currently attributed to *Megacephalomana*, namely *divisa* Walker, 1865, *pilosum* Pagenstecher, 1888 and *laportei* Berio, 1974, are briefly discussed, the first two being of uncertain identity, their names being therefore registered as "nomina dubia", the last one of doubtful position in the *Platyja* assemblage and therefore provisionally positioned here [provisional **comb. n.**], albeit as "incertae sedis". A specimen referable to but not fully matching *vacillans* is illustrated and briefly commented upon. Last but not least, phenotypic variation within *vacillans*, showing two male morphs in W Africa, is discussed.

Keywords: Africa, male-limited dimorphism, moths, nomenclature, synonymy, pattern, taxonomy, venation.

Zusammenfassung

Nach einer Überprüfung der afrotropischen Arten der *Platyja*-Gattungsgruppe werden die folgenden Gattungssynonyme aufgestellt: *Platyja* Hübner, [1823] = *Facidia* Walker, 1865 **syn. n.**, = *Megacephalomana* Strand, 1943 **syn. n.** Gleichzeitig wird *Facidia* (= *Megacephalomana*) als Untergattung behandelt (**stat. n.**, beschränkt auf diesen Rang durch Anwendung des ICZN-Codes Art. 61.3.1). Diese Zusammenstellung besteht aus mindestens acht Arten, von denen eine hier beschrieben wird: *Platyja* (*Facidia*) *vacillans* (Walker, 1858) **comb. n.** (= *Facidia sassana* Strand, 1918 **syn. rev.**), *P.* (*F.*) *saalmuelleri* (Viette, 1965) **comb. n.**, *P.* (*F.*) *semifimbria* (Walker, [1858]), *P.* (*F.*) *rivulosum* (Saalmüller, 1880) **comb. n.**, *P.* (*F.*) *ennomoides* **sp. n.**, *P.* (*F.*) *stygium* (Saalmüller, 1881) **comb. n.**, *Platyja* ("*Facidia*") *luteilinea* (Hampson, 1926) **comb. n.** und *Platyja* ("*Facidia*") *remaudi* (Laporte, 1972) **comb. n.** Die letzten beiden Taxa verbleiben aufgrund einiger außergewöhnlicher Merkmale der Flügeladerung bzw. des Flügelmusters, die eine Verfeinerung der Topologie ihrer phylogenetischen Beziehungen zu den Haupt-*Facidia* erfordern, vorläufig in *Facidia*. Bei *P. luteilinea*, deren bisher unbekanntes Weibchen ebenfalls beschrieben wird, wurde ein ungewöhnliches und geschlechtsdimorphes Verzweigungsmuster der Adern im unteren Teil der Vorderflügelzelle gefunden, während bei *P. remaudi* eine Umkehrung der proximal-distalen Abfolge der antemedialen Linie und des orbicularen Stigmas des Vorderflügels zu beobachten ist. Weitere Taxa, die derzeit *Megacephalomana* zugeschrieben werden, nämlich *divisa* Walker, 1865, *pilosum* Pagenstecher, 1888 und *laportei* Berio, 1974, werden kurz besprochen, wobei die Identität der ersten beiden Arten unsicher ist und ihre Namen daher als "nomina dubia" behandelt werden. Die Stellung von *laportei* innerhalb der *Platyja*-Gattungsgruppe ist zweifelhaft, wird aber vorläufig hierin positioniert [vorläufig **comb. n.**], wenn auch als "incertae sedis". Ein Exemplar, das auf *P. vacillans* verweist, aber nicht gänzlich damit übereinstimmt, wird abgebildet und kurz kommentiert. Zu guter Letzt wird die phänotypische Variation innerhalb von *P. vacillans* anhand zweier männlicher Morphen aus Westafrika diskutiert.

Introduction

As noted in previous contributions (Zilli & De Vos 2021; Zilli et al. 2021), the *Platyja* genus group (Lepidoptera: Erebidae) is greatly in need of revision. In most cases, members of this assemblage can easily be recognised by features of the pattern, though this is often obliterated in the male sex, and the characteristic tripectinate antennae of the males, or, in case of reduction of the lateral rami in some species groups, the midventrally monoserrate male antennae.

The group is also remarkable for the often strongly pronounced sexual dimorphism, which has often hampered proper association of sexes and misled authors to describe separate species based on males and females of the same biological species.

The group is essentially palaeotropical, ranging from West Africa to Indo-Australia, with the most easterly distributed species known to date, namely *Platyja yaleyambae* Zilli & De Vos, 2021, occurring in Rossel Island in the Louisiade Archipelago (Papua New Guinea), though some taxa also reach the East Palaearctic, e.g., *Platyja umminia* (Cramer, [1780]) in South-Central China (Chen 1999). The latter species is also spreading northwards to Japan (Miki & Koshino 2006) and eastwards into the Pacific, where it was first noted in Guam in 1988 (Schreiner 1991).

The highest species diversity occurs in the area ranging from the Indian subcontinent to the Papuan Region, while fewer species are known from the Afrotropics. The latter have confusingly been attributed, often interchangeably, to a plethora of genera such as *Platyja* Hübner, [1823], *Facidia* Walker, 1865, *Facidina* Hampson, 1926, and *Megacephalomana* Strand, 1943 (replacement name for *Megacephalon* Saalmüller, 1880), which is the reason that prompted the current work, the main intent of which was therefore to provide a review of the African species of the group while assessing their systematic relationships. This research led to a generic reassignment for most of the species under study and to the discovery of one new species, described herein. A further singleton with no locality data seemingly represents another undescribed species, but its description is deferred until corroborated by the study of new material. The occasion is taken to discuss all other taxa currently attributed to *Megacephalomana*, whether of African origin or not.

Material and methods

This study has mainly been based on holdings of the Natural History Museum (London), formerly known as British Museum (Natural History), and the African Natural History Research Trust (Leominster Kingsland), supplemented by materials present in some other institutional and private collections, as noted hereunder, and online sources (De Prins & De Prins 2011–2021; MNHN 2021).

Types of all the nominal taxa involved have been examined, either directly or via photographs, and the localities recorded on their labels are cited verbatim between brackets whenever they were more restricted or different from those published in the original descriptions.

One neither originally designated nor obviously monotypic holotype has been noted as 'by likely monotypy' because in the original description there are no clues that more specimens were available (e.g., only one sex described, single wingspan measurement given, no mention of variation, single locality), and in the collections known to host materials by the descriptor only one specimen labelled as a type has ever been located.

Specimens were photographed in a lightbox (manufacturer Fritz Weber Entomologiebedarf, Stuttgart) placed under a stand mounting a Canon Eos 600D camera equipped with a 70 mm Sigma DG Macro lens. For genitalia preparations, abdomens were removed and, following maceration in aqueous KOH (10%) for 3–5 hours at 60 °C, were descaled, dissected, and the genitalia cleaned. Phalli removed from the apparatus were processed to get the vesica (endophallus) everted by injecting distilled water with an insulin syringe bearing a blunt needle. This was inserted through a short collar of the ductus ejaculatorius, cut with microsurgical scissors and left at the base of phallus, the needle being held in position with forceps pressing the phallus sheath against it while operating with the other hand the syringe plunger. In the female, the terminalia were removed by cutting the intersegmental membrane A7–A8 with microsurgical scissors, paying careful attention ventrally where the membrane may be reduced to a thin strip between sternum A7, which may be modified into a tough lodix, and ostium bursae. All dissected parts were stained in saturated Chlorazol Black E (in 75% ethanol) for 5 seconds (commercial mercurochrome diluted 1:6 for one specimen) and soaked in absolute ethanol before permanent mounting in Euparal (manufacturer Anglian Lepidopterist Supplies, Hindolveston) on a microscope slide. Genitalia pictures were taken with a Canon Eos 5DSr camera mounting a MP-E 65 mm lens, with the slides placed on a WeMacro rail support operated by a Trinamic stepper motor via a StackShot system, all controlled through the Helicon Remote software (version 3.8.4 W). Pictures of phalli were also taken by turning the slide upside down in order to capture the finest details of the vesica on the underside of the preparation. Images were then stacked with the Helicon Focus software (version 6.7.1) and edited for plate composition with Adobe Photoshop 2022 (version 23.1). Pictures emphasising the forewing venation were taken by photographing the wings from the underside after limited brushing off of scales around the areole and discal cell with a fine brush wet with absolute ethanol and by applying the filter Edges in Photoshop, while the wing pattern was highlighted using the filter Emboss on pictures of the upperside.

Albeit reluctantly, due to the cacophony deriving from some new binominal combinations established here, agreement in gender is not followed in order to fulfil with the standard approach recommended by the broader lepidopterological community (Sommerer 2002; Nieukerken et al. 2019).

In the distributions, country records known to the authors are listed and reference to the two 'Congos' are respectively given as W (Western) and E (Eastern) for the sake of simplicity.

Abbreviations of depositories

ANHRT African Natural History Research Trust, Kingsland, Leominster (UK)
CMNH Carnegie Museum of Natural History, Pittsburgh (USA)
CPB Collection Patrick Basquin, Yvetot-Bocage (France)

MFNB Museum für Naturkunde, Berlin (Germany)
MHNG Muséum d'histoire naturelle, Geneva (Switzerland)
MNHN Muséum National d'Histoire Naturelle, Paris (France)
MRAC Musée royal de l'Afrique centrale, Tervuren (Belgium)
NHMUK Natural History Museum, London (UK)
SMF Senckenberg Museum, Frankfurt am Main (Germany)

Taxonomic part

Platyja Hübner, [1823]

Platyja Hübner, [1823]. In 1816–[1825], Verzeichniss bekannter Schmettlinge [sic] (17): 268. Type species: *Phalaena Noctua umminia* Cramer, [1780], by subsequent designation of Moore ([1885] in 1884–1887).

Synonymy

See Zilli et al. (2021), to which the following generic synonyms must be added:
= *Facidia* Walker, 1865 **syn. n.**
= *Megacephalomana* Strand, 1943 **syn. n.**

The former is however retained at subgeneric level by virtue of ICZN (1999: art. 61.3.1)—see below.

Diagnosis

See Holloway (2005), Zilli & De Vos (2021), and Zilli et al. (2021).

Platyja subg. *Facidia* Walker, 1865 **stat. n.**

Facidia Walker, 1865. List of the Specimens of lepidopterous insects in the collection of the British Museum **XXXIII** (Supplement 3): 951. Type species: *Facidia nigrofusca* Walker, 1865, by monotypy. Currently considered as a junior subjective synonym of *Tavia? vacillans* Walker, 1858.

Synonymy

= *Megacephalomana* Strand, 1943 **syn. n.** Folia zoologica et hydrobiologica **12** (1): 211. An objective replacement name for *Megacephalon* Saalmüller, 1880, Bericht über die Senckenbergische naturforschende Gesellschaft in Frankfurt am Main **1879–1880**: 286. A junior primary homonym of *Megacephalon* 'Temminck, 1844' (*recte* Gray 1846 in 1844–1849: [489]) [Aves]. Type species: *Megacephalon rivulosum* Saalmüller, 1880, by monotypy.

Diagnosis

Species of *Platyja* of the subgenus *Facidia* are best characterised by features of the male genitalia, notably the vinculum arms cojoining ventrally and bending inward, forming a long, narrow saccus, the portion of the diaphragma closing the tegumen with paired, thin, arched rods facing the periphallic membrane laterally at its base (such rods possibly being reduced, modified transtillae that lost their junction with the valvae), the small juxta consisting of two symmetrical, subtriangular plates separated by a narrow membrane, and the fairly simple, compact, saccate vesica with main trigonal-trilobate corpus sometimes with sclerotised plates or scobination but no nail-like cornuti. In the female abdomen, the last pre-genital segment (A7) has sternum not modified into a special lodix plate and the bursa copulatrix is consistently ovoid across all known taxa.

Distribution

All Sub-Saharan Africa from Western to Southern and Eastern Africa, eastwards to the Madagascan subregion.

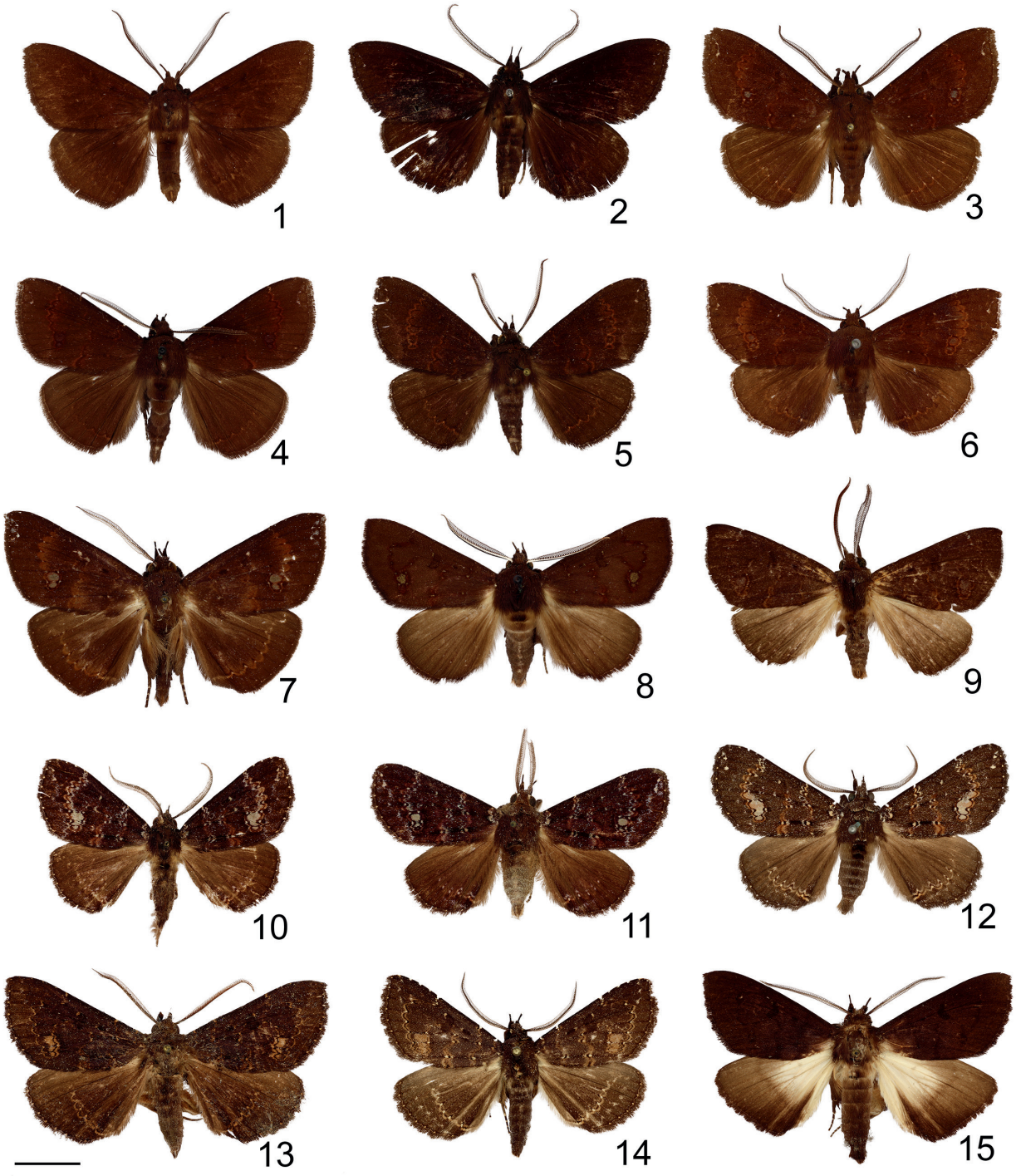
Remarks

Examination of the type species of *Facidia* and *Megacephalomana* and of all African species currently attributed to these genera has shown that there is a core group of species whose separation at the generic level is unsubstantiated and which are fully compatible with the broader concept of *Platyja*, as a homogeneous subset within this genus. For this reason, *Facidia* and *Megacephalomana* are subsumed under *Platyja* at subgeneric level under the name taking priority. However, there are two outlier species that, despite sharing the groundplan features with the revised concept of *Facidia* proposed here, essentially stand out because of some remarkable autapomorphies. They will be discussed at the end of the taxonomic part.

As noted above, in the past, some taxa of this group have also been attributed to *Facidina* Hampson, 1926 (type species: *Ischyja polystigma* Lower, 1903) (e.g., Gaede 1939), but the concept of this genus is nowadays centred around a group of Australo-Papuan species corresponding in overall appearance to the type species (Edwards 1996; Holloway 2005). With the exception of *F. spilophracta* (Turner, 1933), originally described by Turner (1933: 165) as *Erceia* [sic] *spilophracta* and still to be properly morphologically analysed but possibly belonging to *Platyja*, typical *Facidina* are deprived of the characteristic *Platyja* pattern—as defined in Zilli et al. 2021—and sport a normally shaped postmedial line of the forewing, filiform male antennae and, in the male genitalia, a basally very long valva, articulated with a similarly long vinculum, that terminates with long processes, a strongly modified, very long juxta, and a very long and thin phallus sigmoid in shape.

Platyja (*Facidia*) *vacillans* (Walker, 1858) **comb. n.**
(Figs. 1–6, 32–34, 16–18, 45–48, 57–60, 69)

Tavia? vacillans Walker, 1858. List of the Specimens of lepidopterous insects in the collection of the British Museum **XV**: 1820. Type material: Holotypus ♀, by monotypy, in NHMUK [examined]. Type locality: Africa [verbatim holotype label: W - Africa].
= *Facidia nigrofusca* Walker, 1865. List of the Specimens of lepidopterous insects in the collection of the British Museum **XXXIII** (Supplement 3): 952. Type material: Holotypus ♂, by monotypy, in NHMUK [examined]. Type locality: Natal [verbatim holotype label: Pt Natal].



Figs. 1–15. Habitus of African *Platyja* spp. (♂♂). – **1–6.** *P.* (*Facidia*) *vacillans*. **1**. Nigeria, Ilesha. **2**. Nigeria, Ibadan. **3**. Malawi, Dowa. **4**. Tanzania, Amani. **5**. South Africa, Umdoni Park. **6**. Idem, Durban. **7**. *P.* (*F.*) *saalmuelleri*, Madagascar, Île Sainte-Marie (= Nosy Boraha). **8–9.** *P.* (*F.*) *ennomoides* **sp. n. 8**. Holotypus, Tanzania, Amani. **9**. Paratypus, Zimbabwe, Vumba Mts, Umtali (= Mutare). **10–12.** *P.* (*F.*) *semifimbria*. **10**. Ivory Coast, Bingerville. **11**. Idem. **12**. Tanzania, Amani. **13–14.** *P.* (*F.*) *rivulosum*. **13**. Grande Comore. **14**. Madagascar, Mahajanga, Tsingy de Namokora. **15**. *P.* (*F.*) *stygium*, Madagascar. Scale bar = 1 cm.

= *Megacephalon fenestratum* Möschler, 1887. Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft **15** (1): 84. Type material: Holotypus ♀, by monotypy, in MFNB [picture examined]. Type locality: Accra.

= *Facidia horrida* Holland, 1894. Psyche, a Journal of Entomology **7** (217): pl. 2, fig. 6; (218/221): 143. Type material: Syntypi ♂♂ (number not given), in CMNH, NHMUK [1 syntypus (NHMUK) examined]. Type locality: West Africa [verbatim syntypus label: Ogove River].

= *Platyja phaeophoenica* Hampson, 1905. Annals of the South African Museum **3** (9): 434. Type material: Holotypus ♀, by original designation, in NHMUK [examined]. Type locality: Natal, Durban.

= *Facidia sassana* Strand, 1918 **syn. rev.** Zeitschrift des Österreichischen Entomologen-Vereines **3**: 100. Type material: Holotypus ♂, by monotypy, in MRAC [picture examined]. Type locality: [Cameroon] Sassagebiet [= Région de Sassa].

Diagnosis

A very variable species whose males differ in the different degree of darkening of the ground colour, from chocolate-brown to nearly black, and show partially clinal variation in the expression of the *Platyja* pattern, generally indistinct in western populations and more evident in southeastern ones. The females have broader wings than the males and more regularly show the typical *Platyja* pattern. The African species most closely resembling *P.* (*F.*) *vacillans* are *P.* (*F.*) *saalmuelleri* **comb. n.** and *P.* (*F.*) *ennomoides* **sp. n.**

Besides allopatry, *vacillans* and *saalmuelleri* can be separated by the less pronounced sexual dimorphism in the wing shape of the latter, whose males have broader wings, especially the hind one, which is also less convex at the termen and more angular at the tornus, and the generally better expressed *Platyja* pattern. This last feature shows geographic congruence, whereby *vacillans* populations with the most emphasized pattern are those in closer geographic proximity to those of *saalmuelleri*. As regards the leg tufting, this is more strongly emphasised in males of the Madagascan species, especially in the easily examinable hindlegs. Females of the two species are virtually indistinguishable based on external morphology, though a clue may be found again in the more shallowly convex hindwing of the insular taxon. In the male genitalia, the differences between *vacillans* and *saalmuelleri* are weak, which together with the similarity in habitus provides clear evidence of their close relationship. Male *vacillans* have (1) valva more elongate with a slenderer apical expansion at the anal angle that confers a 'foot-shape' to the cucullus, contrary to the broader valva with shorter and subtriangular expansion in the Madagascan taxon, (2) sacculus triangular with distinct saccular corner, not subrectangular with the anterior edge parallel to the ventral margin of valva, (3) distal opening of phallus with a continuous row of very small, adpressed spines along the right side (vs. fewer, erect, much stouter apical spines in *saalmuelleri*), (4) vesica with shorter, forward-projecting diverticulum flanked internally by a rather large, conical diverticulum, (5) big, backward-oriented diverticulum has a weaker, less expanded scobination at base internally, and (6) laterally projected diverticulum with smaller sclerotised plate (Figs. 46–48, 58–60). In the female genitalia, the main differences occur in the ductus bursae and bursa copulatrix. Compared to the short, lyra-shaped ductus bursae of *saalmuelleri* (Fig. 70), that of *vacillans* is longer and with much less sinuous sides (Fig. 69), whereas the bursa of the latter is distinctly smaller and, with the exception of an irregular plate-like posterior signum, almost entirely membranous, contrary to the more broadly developed and more heavily sclerotised cervix bursae of the Madagascan taxon.

With respect to *ennomoides* **sp. n.**, whose female is still unknown, male *vacillans* (and *saalmuelleri*) can easily be recognised by the less heavily pectinated antennae, brown- instead of white-scaled dorsally on the flagellum shaft, and the evenly curved outer margin of the forewing, while in the male genitalia the dorsal margin of the valva is smoothly concave, without a short, digitiform costal process.

Distribution

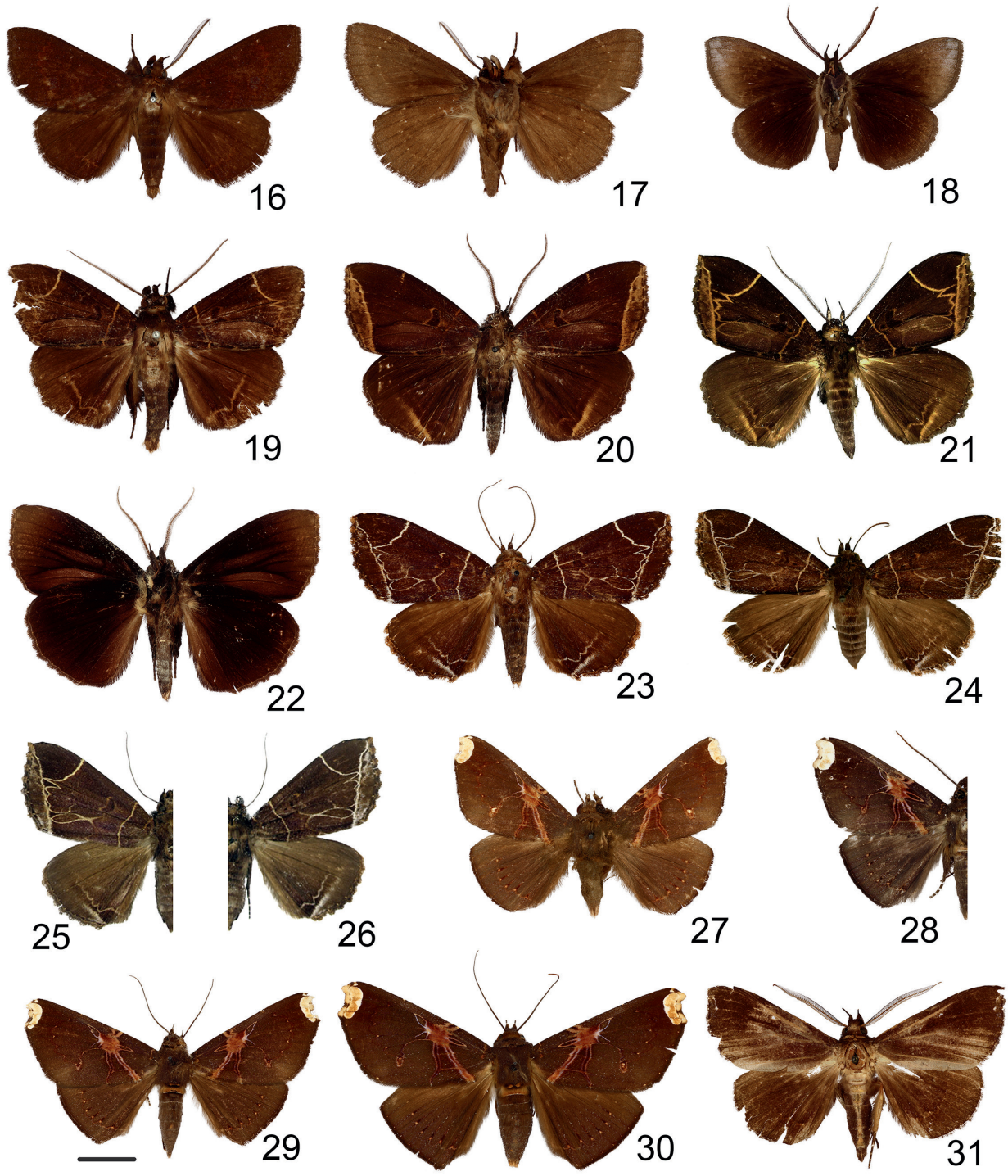
Widespread in Sub-Saharan Africa; Gambia, Guinea, Liberia, Sierra Leone, Ivory Coast, Ghana, Benin, Nigeria, São Tomé, Príncipe, Cameroon, Gabon, Congo (E), Kenya, Tanzania, Malawi, Zambia, Zimbabwe and South Africa.

Remarks

Facidia sassana, correctly treated by Gaede (1939) as a taxon subordinate to *vacillans* (misspelt as *vaccillans*), was misplaced by Poole (1989) as a valid species in *Falcimala* Hampson, 1895, a genus of the subfamily Herminiinae.

Platyja (*Facidia*) *vacillans* and *P.* (*F.*) *saalmuelleri* **comb. n.** constitute a pair of allopatric sister species, respectively distributed in continental Africa (and islands in the Gulf of Guinea) and in the Madagascan subregion.

During the course of this study, it became clear that in W Africa there is a male morph partially sympatric with the commonest African one, which differs from the latter by features of the wings' underside. This morph, illustrated in Figs. 16 and 17, lacks the black suffusion that in typical *vacillans* extends over at least the discal area of the forewing underside (Fig. 18) and is here patterned as a female; it is possibly also more scalloped at the wing termens. Overall, five specimens of this morph have been examined, from Gambia, Guinea (Ditinn: Chute de Ditinn; Dalaba: Forêt de Tinka), and Sierra Leone (Northern Province: nr Kamabai, Kalainkay), the last two countries at least also hosting normally patterned males. Feeble differences in the genitalia of the specimen from Gambia



Figs. 16–31. Habitus of African *Platyja* spp. – **16–17.** *P.* (*Facidia*) *vacillans*, ♂, Gambia, morph with female-like underside. **16**. Upperside. **17**. Underside. **18**. Idem, ♂, Tanzania, Amani, morph (male-limited) with dark underside, underside. **19–26.** *P.* ("*F.*") *luteilinea*. **19**. ♂, Holotypus, Nigeria ("Old Calabar"). **20**. ♂, Idem, Warri. **21**. ♂, Gabon, Yeno-Mandji (CPB). **22**. Same as 20 (underside). **23**. ♀, Nigeria, Warri. **24**. ♀, Gabon, Makokou (MHNG). **25**. ♀, Gabon. **26**. ♀, Idem. **27–30.** *P.* ("*F.*") *remaudi*. **27**. ♂, Ivory Coast, Bingerville. **28**. ♂, Gabon, Mts Cristal (CPB). **29**. ♀, Ivory Coast, Bingerville. **30**. ♀, Paratypus, W Congo, Loango. **31**. *P.* (*F.*) sp. (prope *vacillans*), ♂, sine data (ex coll. C. Oberthür). Scale bar = 1 cm.

(Figs. 45, 57) prompted dissections of other males of the female-like form and sympatric females to assess whether it might belong to a W African cryptic species close to *vacillans*, but this hypothesis could not be in any way morphologically substantiated. Accordingly, the presence of these morphs in W Africa is here provisionally inferred to be a case of male-limited dimorphism, in which the commoner and more widespread African morph with a black underside is exclusive to the male sex.

Cases of di- or polymorphic males with monomorphic females seem to be very rare in Lepidoptera. In a review of polymorphism in butterflies, Vane-Wright (1975) suggested only one likely case, that of the Neotropical satyrine nymphalid *Manataria maculata* (Hopffer, 1874) (Lepidoptera: Nymphalidae), currently ranked as a subspecies of *Manataria hercyna* (Hübner, [1821]), but called for further insights into this possibly doubtful example. The same author (R. I. Vane-Wright, pers. comm.) drew our attention to the oriental limenitidine nymphalid *Euthalia monina* (Fabricius, 1787) (Lepidoptera: Nymphalidae), whose males occur in at least three morphs, "although intergrades are not rare" (Corbet et al. 2020), and whose females do not vary. Last but not least, a well-known case is that of polymorphic male populations of *Hepialus humuli* (Linnaeus, 1758) (Lepidoptera: Hepialidae) in the Shetland and Faroe Islands, also in this case with some transitional phenotypes (Kaaber et al. 2009). Admittedly, Gerould (1923) generally mentioned cases of male dimorphism in Lycaenidae and Arctiidae (now Erebidae: Arctiinae), but his statement is difficult to put in proper context as he did not specify whether only the male sex was dimorphic, and there are endless examples of Lepidoptera species whose males are as polymorphic as the females.

At a first glance, characters shown only by one sex seem ascribable to sex-linked inheritance, that is to the presence on the sexual chromosomes (viz. allosomes) of genes responsible for such traits. However, the fact that Lepidoptera have a ZW sex-determination system and that females are heterogametic does not support this scenario in *vacillans*, because if the gene responsible was on the Z chromosome the females should show that character at the same phenotypic frequency in the male, given that sperm will be produced at the same ratio and females bear only one Z chromosome (obviously, the gene cannot be on the W chromosome, as otherwise the trait would occur only in females and be unknown in males). However, females putatively bearing this gene would not develop the dark underside if there was another gene suppressing its expression in that sex. It is thus the suppressor gene that could be sex-linked if hosted by the W chromosome, regardless of the position of the gene for the dark phenotype on the Z allosome or any somatic chromosomes (autosomes). Nevertheless, the suppressor might also be located on autosomes and act as a switch on some regulatory mechanisms that prevent the expression of the dark phenotype whenever it happens to operate in a female genetic environment.

Platyja (*Facidia*) sp. (prope *vacillans*)
(Figs. 31, 49, 61)

Remarks

A male singleton originally present in the collection of Charles Oberthür (now NHMUK), but unfortunately without locality data, matches with *Platyja (Facidia) vacillans* in many respects, but differs by its larger size, slightly longer antennal pectinations, valva less slender at middle, thinner phallus, and less prominent backward-projecting lobe of vesica (Figs. 49, 61). Although there are no sufficient elements to comfortably proceed with the description of a new taxon, attention is simply drawn to this outlier specimen until new material clarifying its relation to *vacillans* is found.

Platyja (*Facidia*) *saalmuelleri* (Viette, 1965) **comb. n.**
(Figs. 7, 35, 50, 62, 70)

Megacephalon saalmülleri Viette, 1965. Lambillionea **64** (9/10): 41, pl. 1, fig. 7. Type material: Holotypus ♂, by original designation, in MNHN [picture examined]. Type locality: Madagascar Est, environs de Perinet, forêt d'Analamazaotra, 910 m [verbatim holotype label: forêt d'Analamazoatra].

Diagnosis

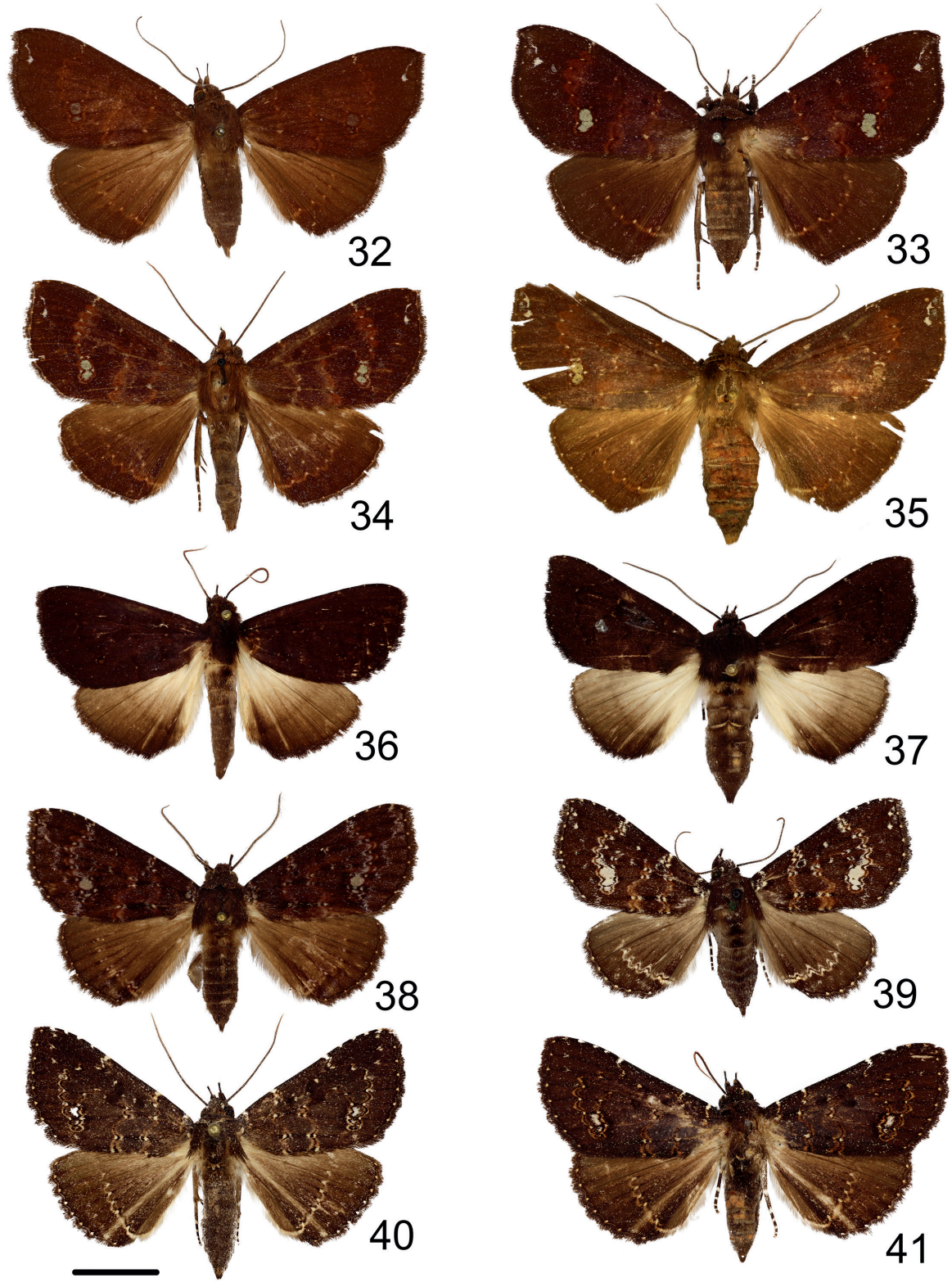
Details for distinguishing this species from its close relative *Platyja* (*Facidia*) *vacillans* **comb. n.** are given above under that species. Male genitalia as in Figs. 50 and 62, female genitalia as in Fig. 70.

Distribution

Endemic to Madagascar and surrounding islands (Nosy Boraha).

Remarks

As noted above, this species and *Platyja* (*Facidia*) *vacillans* **comb. n.** are closely related species distributed, respectively, in the Madagascan subregion and mainland Africa (also São Tomé and Príncipe islands). The two taxa are indeed very close, and it would be somewhat surprising that *saalmuelleri* was described as a distinct species if not for the fact that Viette (1965) did not take *vacillans* into account at all and described the Madagascan taxon only comparing it against the very different, sympatric *Platyja (Facidia) rivulosum* **comb. n.** With careful analysis, however, *saalmuelleri* and *vacillans* can be distinguished (see Remarks under *vacillans*), and that the taxonomic rank of *saalmuelleri* as a valid species is retained.



Figs. 32–41. Habitus of African *Platyja* spp. (♀♀). – **32–34.** *P.* (*F.*) *vacillans*. **32**. Ivory Coast, Bingerville. **33**. Ghana, Kumasi. **34**. South Africa, Mooi River. **35**. *P.* (*F.*) *saalmuelleri*, Madagascar, Ranomafana. **36–37.** *P.* (*F.*) *stygium*. **36**. Madagascar, Périnet. **37**. Idem, Ranomafana. **38–39.** *P.* (*F.*) *semifimbria*. **38**. Ivory Coast, Bingerville. **39**. Tanzania, Amani. **40–41.** *P.* (*F.*) *rivulosum*. **40**. Madagascar, Tsingi de Namoroka. **41**. Idem, Majunga. Scale bar = 1 cm.

Platyja (*Facidia*) *semifimbria* (Walker, [1858])
(Figs. 10–12, 38–39, 51, 63, 71)

Alamis semifimbria Walker, [1858]. List of the Specimens of lepidopterous insects in the collection of the British Museum **XIII**: 1048. Type material: Holotypus ♀, by monotypy, in NHMUK [examined]. Type locality: Sierra Leone.

Diagnosis

Easily recognisable by the strongly variegated pattern with conspicuously undulated crosslines, dots and other elements highlighted with silvery grey and by the lack of secondary sexual dimorphism in the pattern of the moths. The only other African species with which it may be confused is *Platyja* (*Facidia*) *rivulosum* **comb. n.**, whose males have more oblong-elongated wings and a more shallowly convex outer margin of the hindwing, besides being restricted to the Madagascan subregion and hence allopatric. Females of *semifimbria* and *rivulosum* are very similar, though those of the Madagascan taxon show more oblong wings and a straighter postmedial line of the hindwing. In any case, the best diagnostic hint for distinguishing the two species in both sexes is the spatial relationships between the outer lobe of the median field and the submarginal line of the forewing. In *rivulosum* the lobe is more outwardly produced and the submarginal line starts from the costa before the apex, so the postmedial line bounding the lobe and the submarginal line do actually overlap, the latter often being visible as venular dots between the lobes of the undulated postmedial. In contrast, in *semifimbria* the lobe is less prominent and the submarginal line more distal, starting from the wing apex; as a result, the two lines (postmedial and submarginal) do not coincide and there is some space between them.

In the male genitalia, the valva of *semifimbria* has a broader sacculus compared to *rivulosum*, with a conspicuous hump at the saccular corner; it also is narrowest at the middle and has a bigger distal superior process, whereas in the vesica the relative development of the three main lobes is totally different (Figs. 51, 63). In the female genitalia, the most evident diagnostic feature is that of the antrum-ductus bursae system, shorter and wider in *semifimbria* (Fig. 71).

Distribution

Widespread in Sub-Saharan Africa; Sierra Leone, Liberia, Ivory Coast, Ghana, Kenya, Tanzania, Mozambique, Zambia, Zimbabwe, and South Africa.

Remarks

This species was treated by Gaede (1939) and Poole (1989) as belonging in *Facidina*. Holloway (2005) correctly recognised its similarities with *Platyja* and moved it to this genus, though he did not treat the taxonomic position of the other close African relatives of *semifimbria*.

Platyja (*Facidia*) *rivulosum* (Saalmüller, 1880) **comb. n.**
(Figs. 13, 14, 40–41, 52, 64, 72)

Megacephalon rivulosum Saalmüller, 1880. Bericht über die Senckenbergische naturforschende Gesellschaft in Frankfurt am Main **1879–1880**: 287. Type material: Syntypi ♂♂ (by implication from original description but number not given), 1♀; traced 2♂♂ and 1♀ in SMF [examined]. It should be noted that specimens in SMF labelled as "Typus" (1♂, Loucoubè, Stumpff 82/508; also illustrated by De Prins & De Prins 2011–2021) and "Paratypoid" (1♂, sine data/508a; 1♀, Nossi-Bé Stumpff e[nde] 89/508b; 2♂♂, Loucoubè, Stumpff 82/508c & 508d) [all examined] are all posterior to the original description and are therefore not part of the type series. In contrast, of another series of three specimens, labelled respectively "Loucoubé, Stumpff80" [hand corrected into 82] (1♂), "Loucoubé, Ebenau 80" (1♂), and "Loucoubé Stumpff80" (1♀) [all examined], the last two are fully compatible with information given by Saalmüller (1880) and are therefore regarded as syntypes. The first male is also considered to be a syntype as there is evidence that the correction of the year from [18]80 to [18]82 is subsequent to the original labelling of the specimen and hence spurious. In fact, until 1880 the labels recording the collecting locality by Stumpff were printed with the acute accent (Loucoubé), while later the grave accent was used (Loucoubè) [see above], and such specimen clearly bears the first kind of labels. The apparent discrepancy in the original locality, given by Saalmüller (1880: 258, 1891: 449) as Nossi-Bé, while the specimens are labelled as from Loucoubé [= Lokobe], is simply ascribable to the fact that the latter is a precise site in the island of Nossi-Bé. Type locality: Madagascar, Nossi-Bé [= Nosy Be] [verbatim syntypes labels given here above].

Diagnosis

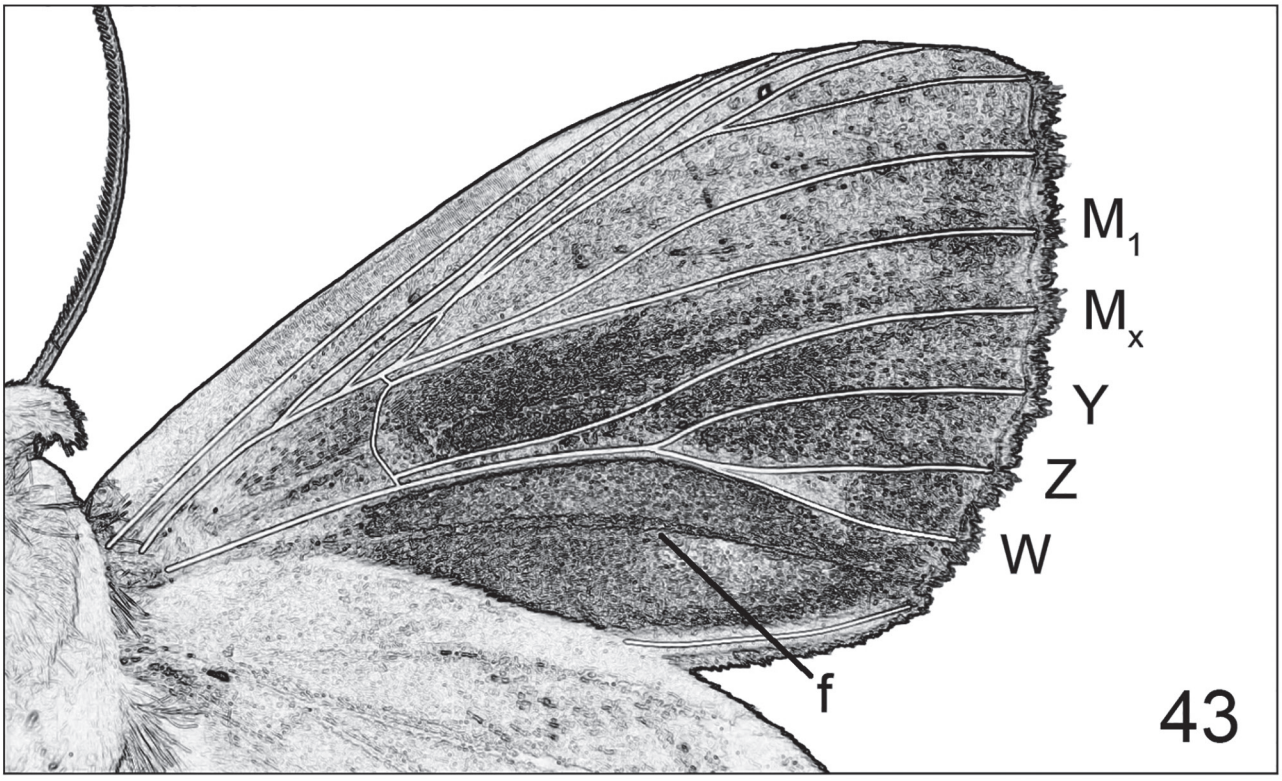
Hints for distinguishing this species from the externally similar *Platyja* (*Facidia*) *semifimbria* have been given under that species. In the male genitalia, the Madagascan taxon can be distinguished from its close relative by the shape of valva, of uniform width along its middle section, with slenderer sacculus and smaller distal superior process (Fig. 52), while the size and configuration of the vesical lobes are different (cf. Fig. 64). In the female genitalia, the antrum-ductus bursae system of *rivulosum* is appreciably longer and thinner (Fig. 72).

Distribution

Madagascar and surrounding islands (Grande Comore, Nosy Be).

Remarks

This species replaces *Platyja* (*Facidia*) *semifimbria* in the Madagascan subregion. Both species closely resemble in pattern some Indo-Australian members of the subgenus *Mocrendes* Nye, 1975 of *Platyja*, namely those of the *lemur-lemurella-carpentariella* lineage (see Zilli et al. 2021), but analysis of structural features shows that they are not directly related. Another similar-looking Austral-



Figs. 42–43. Venation of *Platyja* ("*Facidia*") *luteilinea*. **– 42**. ♀, Nigeria, Warri. **43**. ♂, Nigeria. M_1, M_x, Y, Z, W, CuA_2 veins discussed in the text, f = vannal fold.

ian species is *Facidina spilophracta* (Turner, 1933), which still needs to be properly morphologically analysed.

Platyja (*Facidia*) *ennomoides* **sp. n.**
(Figs. 8, 9, 53, 65)

Type material

H o l o t y p u s: ♂, Tanzania, Mal[ariological] Inst[itute] Amani, III.[19]64; NHMUK014165500, in NHMUK.

P a r a t y p i (2♂♂): 1♂, Tanzania, Amani, Usambara, IV.1969, WATHLEGE [leg.?]; NHMUK014165496. – 1♂, [Zimbabwe] South Rhodesia, Vumba Mts, Umtali, III–IV.1963, [ex] Nat. Mus. S[outhern] R[hodesia]; NHMUK0141654951. Both in NHMUK.

Diagnosis

The new species may easily be mistaken for some homogeneously coloured forms of the sympatric *Platyja* (*Facidia*) *vacillans* **comb. n.**, less so with the allopatric sister species of the latter, *P.* (*F.*) *saalmuelleri* **comb. n.**, but its male can be distinguished from these by the more heavily pectinated antennae with dorsal white scaling on the flagellum, the outer margin of the forewing (termen) not smoothly convex but feebly angular at middle, and the paler hindwing, not as dark as the forewing. In the male genitalia, the presence of a thumb-like costal process on the valva, the superiorly narrowly elongated juxta, and the longer phallus with different vesical configuration (Figs. 53, 65) allow an easy separation of the new species from the other two.

Description

Male. Wingspan 44.0–47.5 mm apex to apex but forewings widest at middle of termen, up to 49 mm (n = 3). Head very large, dark chocolate-brown-coloured, frons narrow and bulged, vertex thickly and roughly scaled, eye globular, antenna conspicuously pectinated except at very tip, with very long lateral rami and long, reclinate ventral lamellae, with dorsal scaling of flagellum almost pure white, labial palpus compactly scaled with stout, suberect 2nd joint and rod-like 3rd joint, straw-coloured at very tip; haustellum present.

Thorax uniformly dark chocolate-brown, with patagium, tegula, and notum thickly and roughly-scaled; forewing broad, with slightly prominent apex and convex termen almost angular at middle, ground colour uniformly dark chocolate-brown, with faint or indistinct *Platyja* pattern, antemedial line faded, with a few minute silvery dots in correspondence with veins, postmedial line slightly better expressed, feebly darker than ground colour and also with some silvery dotting across veins, orbicular a tiny dark brown dot, reniform crescent-shaped, outer section of median field very narrow, with very small, dull grey-filled pedunculate lobe; adterminal area and fringe concolorous with ground colour; hindwing rounded, chocolate-brown, paler at base; legs conspicuously hairy except tarsi; tarsomeres appearing pale beige ringed at distal ends. Underside of wings brown with minute pinkish-white irroration, postmedial line of forewing almost indistinct, that of hindwing feebly expressed as a darker brown line followed by tiny whitish dots in correspondence with veins.

Abdomen uniformly brown. Male genitalia: tegumen voluminous, dome-shaped, vinculum long and robust, longer than tegumen, valva long and sinuous, with a comparatively small, narrowly elongated subtriangular sacculus, broad, long, slightly excurved apical expansion and small, thumb-like costal process; juxta sub-rhomboid basally, very narrow and elongated apically; uncus comparatively short and thick, with prominent recurved apical hook; tuba analis large, with distinctly sclerotised scaphium; phallus long and slender, slightly curved at middle, vesica as in Fig. 65.

Female. Unknown.

Etymology

The name of the new species is based on the external resemblance of the male with numerous geometrid moths of the subfamily Ennominae. The name is meant as a feminine adjective.

Distribution

So far known only from south-eastern Africa (Tanzania and Zimbabwe).

Remarks

The particularly smooth, homogeneous colouring of the forewings and the shared presence of a costal process on the valvae are suggestive of a systematic relatedness between *Platyja* (*Facidia*) *ennomoides* **sp. n.** and *P.* (*F.*) *stygium* (Saalmüller, 1881) **comb. n.**

Platyja (*Facidia*) *stygium* (Saalmüller, 1881) **comb. n.**
(Figs. 15, 36, 37, 54, 66, 73)

Megacephalon stygium Saalmüller, 1881. Entomologische Zeitung (Stettin) **42** (4/6): 217. Type material: Holotypus ♂, by (likely) monotypy, in SMF [examined]. Type locality. Madagascar... Nossi-Bé [verbatim holotype label: Loucoubé. See explanation above under *P.* (*F.*) *rivulosum*].

Diagnosis

An unmistakable species, easily distinguishable from all relatives, besides other characters, by the white-coloured basal area of the hindwing in both sexes. Notably, the hindwing has a nearly straight termen in the male. Genitalia as in Figs. 54, 66, and 73.

Distribution

Endemic to Madagascar.

Remarks

Together with *Platyja* (*Facidia*) *ennomoides* **sp. n.** and *P.* ("*F.*") *remaudi* **comb. n.**, this is another African species of the group with a costal process on the valva.

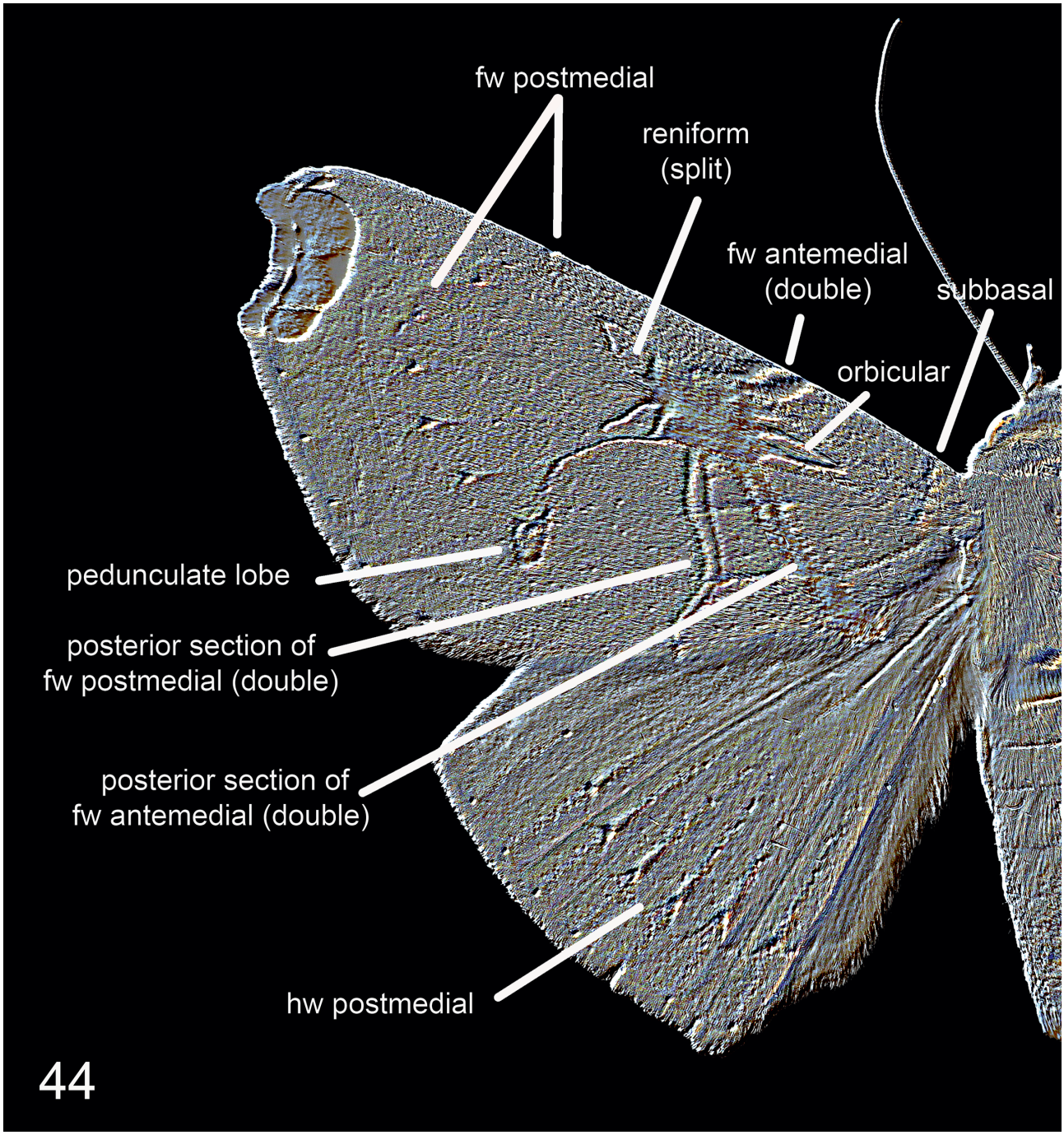


Fig. 44. Pattern analysis of *Platyja* ("*Facidia*") *remaudi*, same specimen as in Fig. 30. Abbreviations: fw = forewing, hw = hindwing.

Taxonomic treatment of outlier species

The following two species agree in most respects with those in the subgenus *Facidia* treated above, but show some outstanding features that might even be used to justify their placement each in a separate subgenus. On one hand, if the outlier was only one, the erection of a monobasic subgenus would be untenable in a cladistically inspired classification, because this would leave *Facidia* as paraphyletic, and this consideration would apply to either of the two outliers in relation to the main group of species. Nevertheless, as in this case the outliers are two, and because they are hardly reconcilable with one another, they cannot be comfortably associated to *Facidia* together. Cladistic orthodoxy would require assessing which of the two outliers is actually the sister group of the core *Facidia*, combine them under the same subgeneric concept, and separate the second one within a monobasic subgenus. However, this task is hampered by the fact that the autapomorphies of the two outliers are remarkable, pertain to different character systems, and have no counterparts in the core *Facidia*, so that they cannot easily be placed along a phylogenetic sequence. Further to this, their autapomorphies also involve some sort of developmental modulations, which adds further difficulty to ascertaining any sister-group relationships with other *Facidia*. For this reason, also awaiting possibly resolutive molecular information, the following two species will provisionally be ascribed to "*Facidia*" in a broad sense.

Platyja ("*Facidia*") *luteilinea* (Hampson, 1926) **comb. n.**
(Figs. 19–26, 42, 43, 55, 67, 74)

Facidia luteilinea Hampson, 1926. Descriptions of new genera and species of Lepidoptera Phalaenae of the subfamily Noctuinae (Noctuidae) in the British Museum (Natural History): 94. Type material: Holotypus ♂, by original designation, in NHMUK [examined]. Type locality: S. Nigeria, Old Calabar.

Diagnosis

An unmistakable, large-sized species with broad wings. In the male, the forewing is particularly high, with costa strongly bowed before apex and paired, elliptical, loosely scaled areas, especially on the underside, associated to a warped and modified venation (detailed hereunder). Genitalia as in Figs. 55, 67, and 74.

Distribution

So far known Western-Central Africa: Ivory Coast, Nigeria, and Gabon.

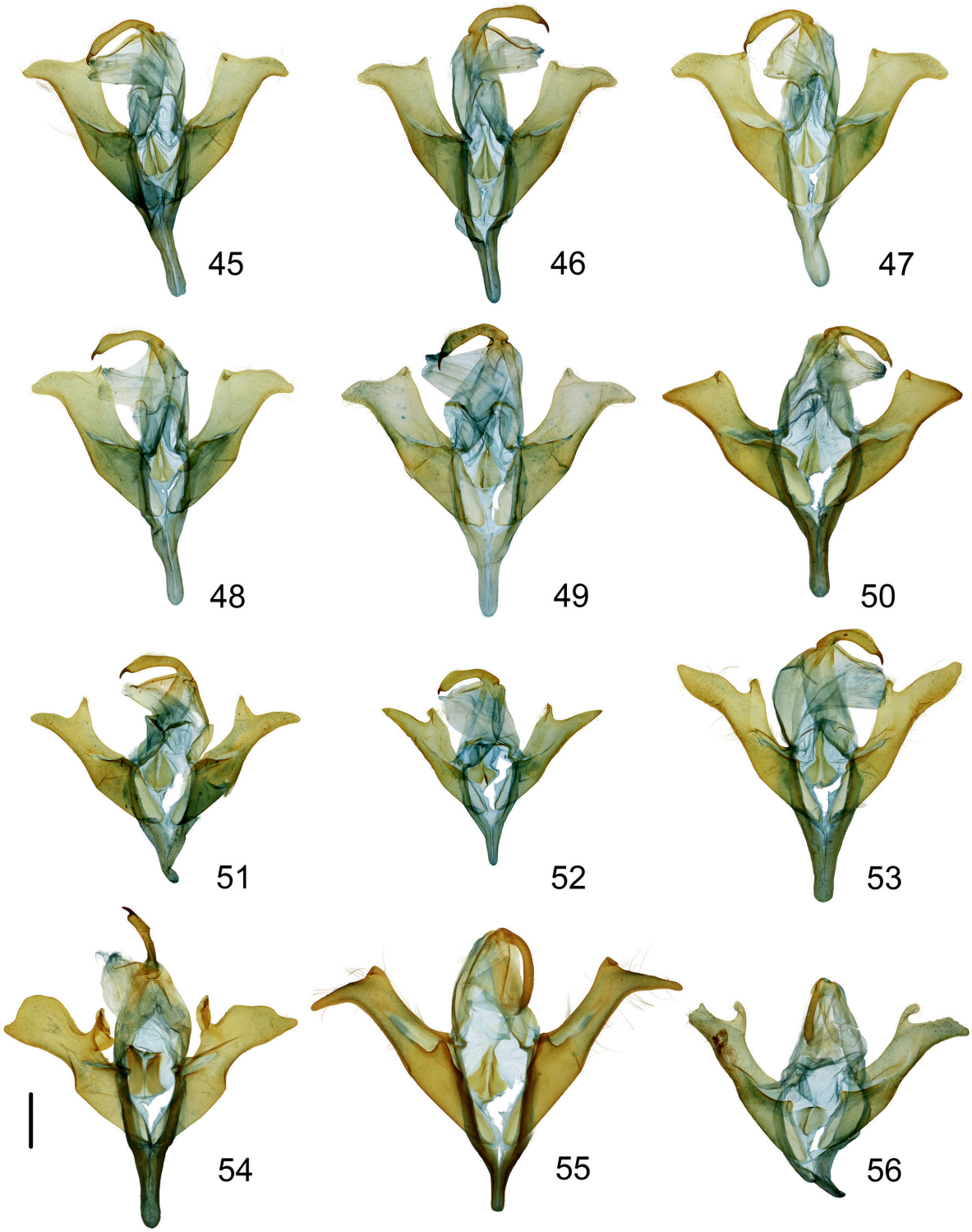
Remarks

Obtaining adequate knowledge about the features of this taxon was long hampered by the existence of only one known specimen, the male holotype, which was never illustrated. Examination of supplementary material from West Africa led to the circumscription of a further series of males closely matching the holotype in their structural features. These males show different degrees of expression of the pattern elements, but when considered overall they represent a consistent set of continuously varying phenotypes whose pattern elements may be differentially enhanced, especially the crosslines and distal banding of the wings, which can be more or less emphasized with dull yellow, and this either along their entirety or only in definite sections. One male from Gabon (in CPB) shows a fully expressed pattern that entirely matches that of some West African females that had long remained taxonomically unidentified. The bridging of the gaps in how the various pattern elements are expressed, both within and between the sexes, together with their morphoanatomical and geographical congruence, provides sufficient evidence that these specimens are conspecific and allows to spare the historical type from dissection. The previously unknown female of *luteilinea* deserves formal description, as detailed hereafter.

Description of the female

Wingspan 48–55 mm (n = 4). Head very large, dark chocolate-brown, frons bulged, vertex thickly and roughly scaled, eye large, globular, antenna filiform, labial palpus semi-erect, its first two joints compactly scaled, the third long, rod-like, white at very tip, haustellum present.

Thorax robust, uniformly dark chocolate-brown, patternless; forewing large and elongated, with crenulate termen; ground colour dark chocolate-brown, *Platyja* pattern (defined in Zilli et al. 2021) variably expressed as in male (in one worn specimen, not illustrated, it is equivalent to the male in Fig. 20), if with well evident white highlight, subbasal present, antemedial line subvertical, slightly oblique from costa to anal margin and feebly angular at veins (especially on 1A+2A), postmedial line concave (either smoothly arched or feebly waved) from costa and outwardly-directed towards submarginal line, where an acute tooth is produced, followed below by three shallow lobes, 'drop' of the typical *Platyja* pedunculate lobe well distinct and large, in shape of transverse ellipse that is joined by a median streak to tooth of inferior section of postmedial line; all projections of superior section of postmedial line (tooth, lobes, drop) closely adpressed to submarginal line, which runs obliquely albeit a little irregularly from apex to tornus; terminal line darker brown than ground colour, with white or golden dots in correspondence with veins, fringe brown with some sparse golden irroration at base and facing veins; hindwing broad and rounded, with crenulate termen, ground colour dark chocolate-brown, postmedial and submarginal lines incomplete, white, the former from middle of disc to anal margin, strongly waved, the latter straight and



Figs. 45–56. Male genitalia of African *Platyja* spp. (phalli removed). – **45.** *P.* (*Facidia*) *vacillans*, morph with female-like underside, Gambia. **46–48.** Idem, male-limited morph with dark underside. **46**. Ivory Coast, Bingerville. **47**. Ghana. **48**. South Africa, Durban. **49**. *P.* (*F.*) sp. (prope *vacillans*), sine data (ex coll. C. Oberthür). **50**. *P.* (*F.*) *saalmuelleri*, Madagascar, Île Sainte-Marie (= Nosy Boraha). **51**. *P.* (*F.*) *semifimbria*, Ivory Coast. **52**. *P.* (*F.*) *rivulosum*, Madagascar. **53**. *P.* (*F.*) *ennomoides* **sp. n.**, Paratypus, Tanzania, Amani. **54**. *P.* (*F.*) *stygium*, Madagascar, Périnet. **55**. *P.* ("*F.*") *luteilinea*, Nigeria. **56**. *P.* ("*F.*") *remaudi*, Ivory Coast, Bingerville. Scale bar = 1 mm.

diffuse, only in lower third of wing; terminal area as in forewing. Legs slender, tarsomeres off-white ringed terminally. Underside of wings chocolate-brown with some white sprinkles and thin white strokes on veins in correspondence with postmedial lines, especially on hindwing.

Abdomen brown, shortly scaled. Genitalia: segment A8 wide, weakly sclerotised, apophyses anteriores short and flimsy; ostium bursae large, leading to broad, strongly sclerotised, trapezoidal antrum the inner wall of which extends posteriorly to ostium slit, antrum separated by narrow membranous section from short and wide, subquadrangular sclerotised section of ductus bursae, corpus bursae spheroidal, with narrow, elongated, conical appendix bursae from left posterior end of corpus, oblique; intersegmental membrane A8–A9 very short; papillae anales massive, increasingly setose towards posterior edge, apophyses posteriores rod-like, slightly longer than anteriores (Fig. 74).

Analysis of venation

By its external habitus, this species is extraordinary in many respects, notably the unusually shaped forewing of the male with long, elliptical, loosely scaled areas, one narrow, comprising the cell and the space beyond it, the other very broad below the cell, and the forewing venation of both sexes. The latter in particular shows features previously unrecorded—to the authors' best knowledge—in other Erebidae, and is out of the ordinary for Lepidoptera in general. It is dimorphic between the sexes, that of the female being less deviant from the commonest configuration found in Erebidae, which is why it will be discussed first, also to better ascertain homologies in the male. The forewing venation of the female is illustrated in Fig. 42, where veins of doubtful interpretation are marked X, Y and Z. By virtue of their position in the sequence with the other veins and the topology of branching from the discal cell, female M_1 and CuA_2 are unambiguously identifiable. Between them there are three veins, of which the anteriormost, free from the lower discocellular crossvein closing the cell, is certainly a medial (M_x), which is almost connate with a stalk situated below it and arising from the lower angle of cell, that of Y + Z. M_x could either be M_2 or M_3, or also the result of a complete fusion between the two (that should thence be noted as M_2-M_3). The interpretation of Y and Z depends on that of M_x, with four possible combinations, as follows (corresponding oddities between parentheses): $M_x = M_2$, Y = M_3, Z = CuA_1 (M_3 stalked with CuA_1); $M_x = M_3$, Y = CuA_{1a}, Z = CuA_{1b} (M_2 lost, CuA_1 split); $M_x = M_2$-M_3, Y = CuA_{1a}, Z = CuA_{1b} (M_2 and M_3 fused, CuA_1 split); $M_x = M_2$, Y = CuA_{1a}, Z = CuA_{1b} (M_3 lost, CuA_1 split). It may be noted that to account for the observed configuration, three of these options would imply the splitting of CuA_1 into two veins, while the remaining one would imply the stalking of M_3 with CuA_1. However, neither the splitting of the first anterior cubital nor the stalking of this with the last medial seem to have ever been recorded in Lepidoptera.

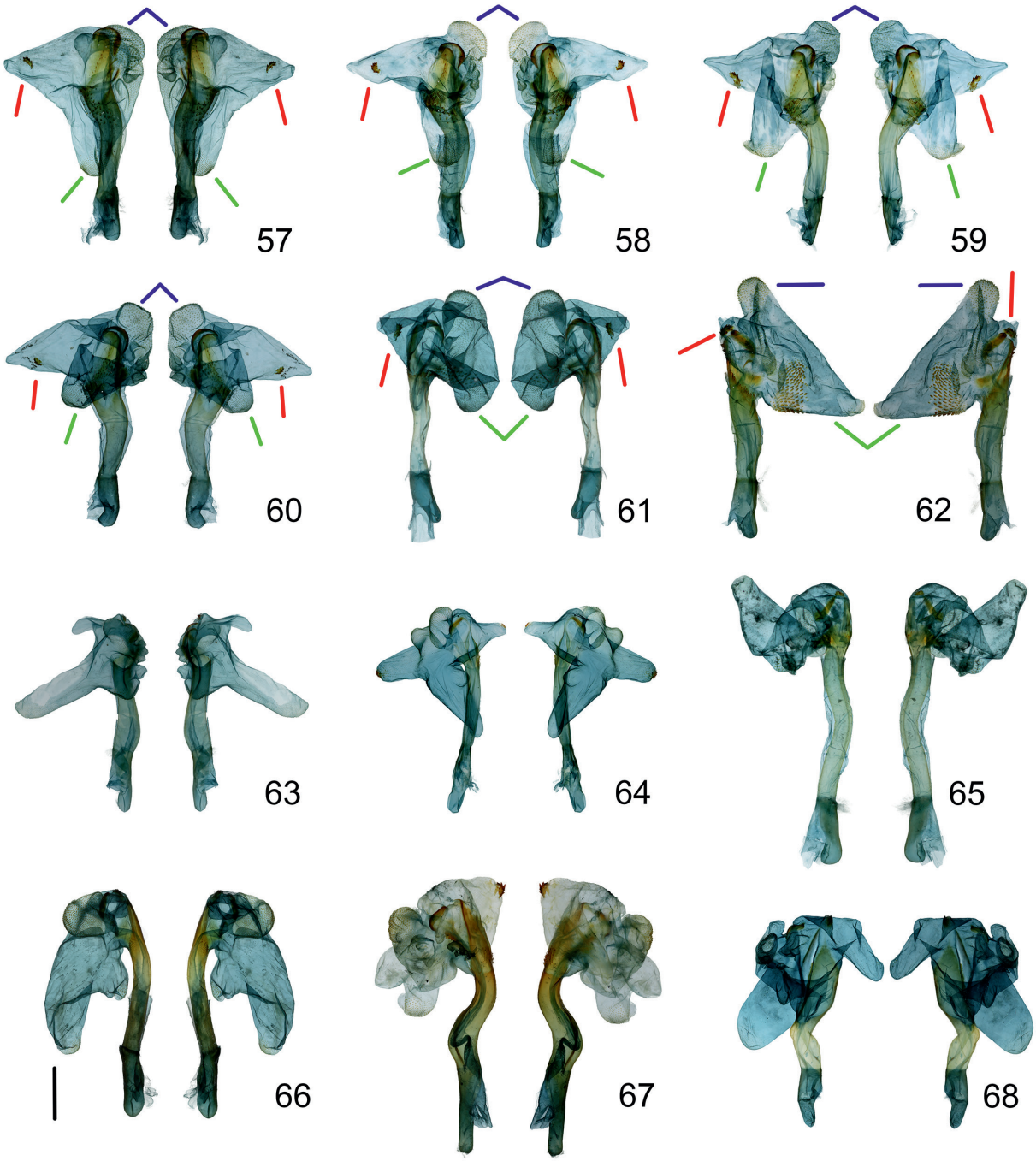
In the male (Fig. 43), the eccentricities are even more pronounced due to remarkable warping of the veins associated to the dilated, loosely scaled areas. There is a vein M_x that looks clearly homologous to the female one, and one long stalk proceeding from the cubitus beyond the lower angle of the cell that trifurcates into the veins noted here as Y, Z and W, with no other vein branching off from the cubitus below the cell. This trifurcation develops sequentially, first with a Y-(Z+W) split, then with a dichotomy of the last two, shortly stalked veins (i.e., Y is not connate with Z and W). It should be noted that what looks like a conspicuous vein longitudinally bisecting the large, loosely scaled area of the forewing is not a vein but a ridge/groove (on the upperside/underside, respectively), strongly lined with dark scales, that corresponds to the vannal fold, vein 1A+2A actually bordering the loosely scaled area below, next to the anal margin.

If all instances of losses, fusions and splits into supernumerary veins are considered, the possible combinations regarding the homologies of these veins in the male are very numerous, all implying some odd circumstances hitherto unrecorded in Lepidoptera. Nonetheless, if an 'Occam's razor' approach is followed, there is one option that appears to be both more likely and more compatible for the two sexes, also in terms of visual similarity of the fork of Y and Z, i.e., $M_x = M_2$, Y = M_3, Z = CuA_1, and W in the male = CuA_2. In this case, the unusual occurrences would be those of M_3 (Y) stalked with CuA in both sexes, precisely CuA_1 in the female (Z), and male CuA_2 (W) distally shifted to branch off from CuA_1 (Z) following a short common stalk. As noted by Kristensen (2003), stalking of the forewing CuA fork is very unusual in Lepidoptera, but it is known in some Gelechioidea and thus there is support for considering the configuration of Z and W seen in male *luteilinea* as a developmental homoplasy that has some precedents in other moth groups.

The influence of developmental controls over the final configuration of venational patterns, best illustrated by the sexual dimorphism in this species for the position of CuA_2, sliding along the cubitus (if the above interpretation is correct), further calls for caution when using venational characters in classification, as already shown for another erebid species (Zilli 2021).

Platyja ("*Facidia*") *remaudi* (Laporte, 1972) **comb. n.**
(Figs. 27–30, 44, 56, 68, 75)

Megacephalomana remaudi Laporte, 1972. Bulletin du Muséum national d'Histoire naturelle (3) **59** (Zoologie 45): 664, fig. 6 (male genitalia). Type material: Holotypus ♂, by original designation, in MNHN [picture examined]. Type locality: Congo-Brazzaville, Loanga [verbatim holotype label: Luango].



Figs. 57–68. Phalli of African *Platyja* spp. (two views). – **57**. *P.* (*Facidia*) *vacillans*, morph with female-like underside, Gambia. **58–60**. Idem, male-limited morph with dark underside. **58**. Ivory Coast, Bingerville. **59**. Ghana. **60**. South Africa, Durban. **61**. *P.* (*F.*) sp. (prope *vacillans*), sine data (ex coll. C. Oberthür). **62**. *P.* (*F.*) *saalmuelleri*, Madagascar, Île Sainte-Marie (= Nosy Boraha). **63**. *P.* (*F.*) *semifimbria*, Ivory Coast. **64**. *P.* (*F.*) *rivulosum*, Madagascar. **65**. *P.* (*F.*) *ennomoides* **sp. n.**, Paratypus, Tanzania, Amani. **66**. *P.* (*F.*) *stygium*, Madagascar, Périnet. **67**. *P.* ("*F.*") *luteilinea*, Nigeria. **68**. *P.* ("*F.*") *remaudi*, Ivory Coast, Bingerville. Scale bar = 1 mm; coloured bars indicate homologous diverticula in *vacillans* and its closest relatives (Figs. 57–62).

Diagnosis

An unmistakable species, easily recognisable by the strongly modified albeit still fully distinct *Platyja* pattern of the forewing. In particular, the inferior sections of the antemedial and postmedial lines, both double, converge in the discal cell, where a big rusty-coloured patch is produced. This patch is proximal to the reniform stigma, i.e., in the shape of two acuminated marks slightly flexed with respect to one another and cojoined in the middle, and distal to a narrowly elongated orbicular stigma inside the cell. The rusty-brown ground colour and elongated forewing with apical area pale beige highlighted and notched apex are other outstanding external characteristics of this species. Genitalia as in Figs. 56, 68 and 75.

Distribution

Guinea, Liberia, Ivory Coast, Cameroon, Gabon, Congo (W, E).

Remarks

This is another greatly peculiar species of *Platyja*, especially for the strongly modified pattern and structure of the male antenna. The latter is not tripectinate but retains a midventral row of lamellae, which are short, blade-like and aligned along the flagellum to produce a midventral keel. Each flagellar antennomere bears, at the top of the keel and midway along the segment itself, a pair of transverse, oppositely oriented setae with bases not exactly juxtaposed but slightly shifted from one another. In the male genitalia, the thin arched rods of the diaphragma are poorly sclerotised and hardly recognisable.

In addition to these features, it is the pattern that provides the most surprising characteristic. Indeed, considering that the origin of the postmedial line of the forewing from costa is well evident, the more proximal segment from the costa to the rusty-coloured patch inside the cell may easily be recognised as the anterior section of the antemedial line, which is in fact double, like the posterior section reaching the anal margin. However, this would imply that the orbicular stigma is proximal to this line, which is something completely unusual for Noctuoidea (Fig. 44). Whatever the case, this arrangement shows the remarkable modifications occurring in *remaudi* and calls for a thorough assessment of the homologies of its pattern elements. The dotted anterior section of the postmedial line, the much reduced pedunculate lobe of the median field, and the apical pale beige mark on the notched apex further highlight the unusual appearance of this species, which finds a likely explanation in the disruptive appearance of the moth at rest. The posterior sections of the antemedial lines of the two wings closely align with the similarly coloured abdominal tergites 1–2 to produce a sort of transverse striga that terminates with a starred configuration at both ends.

Nomina dubia

The following nominal taxa originally or secondarily combined with *Megacephalomana* are of doubtful identity, and it is unlikely that this will ever be resolved due to the apparent loss of the types and to the original descriptions, hardly referable to any extant specimens or species.

Hypaetra divisa Walker, 1865 **nomen dubium**

Megacephalomana divisa (Walker, 1865) (Poole 1989)

Hypaetra divisa Walker, 1865. List of the Specimens of lepidopterous insects in the collection of the British Museum **XXXIII** (Supplement 3): 963. Type material: Syntypi ♂♂ (number not given). Type locality: Ceylon.

Remarks

After its description, *Hypaetra divisa* was generally treated in *Anereuthina* Hübner, 1823 (type species: *Anereuthina renosa* Hübner, 1823), of which *Hypaetra* Guenée, 1852 is a junior objective synonym, e.g., by Moore ([1885] in 1884–1887) and Cotes & Swinhoe (1888). This taxon was transferred by Poole (1989) to *Megacephalomana*, but this action seems fully unsubstantiated by the fact that the type(s) went missing early on (Hampson 1893: 54, 1895: 104, 1913: 334), which compelled Hampson not to treat this unrecognizable species; ultimately, there are no clues about its identity. Strangely enough, the name of this taxon had already been mentioned by Motschoulsky (1863), attributed to Walker, in advance of its formal publication. As quoted by Motschoulsky, the name is nudum and thence unavailable. However, this circumstance shows that there were contacts between these two authors prior to the publication of Walker's (1865) volume.

Megacephalon pilosum Pagenstecher, 1888 **nomen dubium**

Megacephalomana pilosum (Pagenstecher, 1888) (Poole 1989)

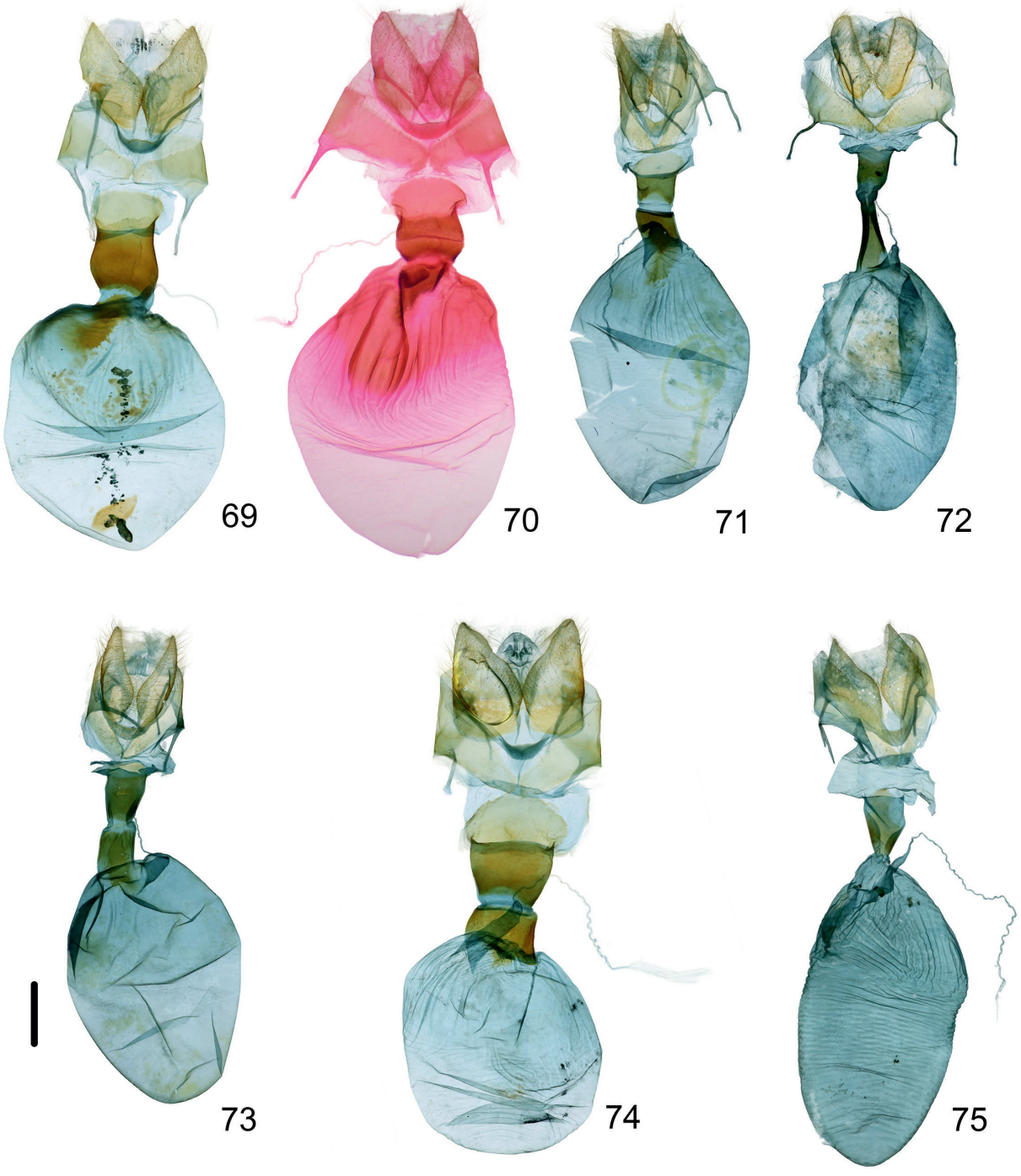
Megacephalon pilosum Pagenstecher, 1888. Jahrbücher des Nassauischen Vereins für Naturkunde **41**: 156. Type material: Holotypus ♂, by monotypy, in MFNB (coll. Staudinger) [not traced]. Type locality. Amboina.

Remarks

This nominal taxon of doubtful identity has already been extensively discussed in Zilli et al. (2021).

Provisionally placed species

The following taxon is a validly recognised species, but all evidence indicates that it has always been misplaced in *Megacephalomana*. Due to the synonymisation



Figs. 69–75. Female genitalia of African *Platyja* spp. – **69**. *P.* (*F.*) *vacillans*, Nigeria, Warri. **70**. *P.* (*F.*) *saalmuelleri*, Madagascar, Ranomafana. **71**. *P.* (*F.*) *semifimbria*, Ivory Coast, Bingerville. **72**. *P.* (*F.*) *rivulosum*, Madagascar, Diego Suarez (= Antsiranana). **73**. *P.* (*F.*) *stygium*, Madagascar, Périnet. **74**. *P.* ("*F.*") *luteilinea*, Nigeria, Warri. **75**. *P.* ("*F.*") *remaudi*, Liberia, Nimba. Scale bar = 1 mm.

of *Megacephalomana* with *Facidia* as a subgenus of *Platyja*, such species has to provisionally follow the new taxonomic arrangement for its original generic name in order not to be left floating in a taxonomic 'limbo'. However, it is recommended that it is cited with the genus-group names between quotation marks, to stress that this is a temporary assignment pending further studies that will hopefully clarify its systematic relationships.

"*Platyja* (*Facidia*)" *laportei* Berio, 1974
[provisional **comb. n.**], **incertae sedis**

Megacephalomana laportei Berio, 1974. Annali del Museo civico di Storia naturale "Giacomo Doria" **80**: 224, fig. 12 (male genitalia). Type material: Holotypus ♂, by original designation, in MRAC [picture examined]. Type locality: Congo, Sankuru, Katako-Kombe.

Remarks

This species from the Congo basin was attributed to *Megacephalomana* by Berio (1974), who also relied on the advice of Bernard Laporte, great connoisseur of African Noctuoidea and author of another species of *Megacephalomana* (namely *remaudi*). During the present study, no material of this taxon was available. However, analysis of the wing pattern and features of the male genitalia, all well represented by De Prins & De Prins (2011–2021), strongly support the view that it does not belong to the *Platyja* genus group. In fact, the habitus has no relation at all to the characteristic *Platyja* pattern—it rather shows similarities with the *Saroba* genus group (sensu Holloway 2005)—and the genitalia have a short vinculum not produced into a long, narrow, inwardly-bent saccus, the valva bears a robust clasper protruding towards the middle and has strong sparse setae along the distal edge, normal transtillae are present, and the uncus is long-necked with strongly setose, dorsally sulcate apical club: all features not seen in any other member of the subgenus *Facidia* (= *Megacephalomana*). The holotype, the only male known to the present authors, seems to have lost its antennae, and thus their structure cannot be checked.

Distribution

Known only from E Congo.

Conclusion

The present review of the African species of the *Platyja* genus group allowed to assess that the genera *Facidia* and *Megacephalomana* do not deserve formal recognition, and are therefore subsumed into *Platyja* at subgeneric level under the name taking priority, viz. *Facidia*. With the addition of the new species from East Africa described above, the species of the group so far known from the Afrotropics sum up to eight, as follows (this list does not include the taxa of doubtful identity and position discussed above):

Platyja (*Facidia*) *vacillans* (Walker, 1858)
Platyja (*Facidia*) *saalmuelleri* (Viette, 1965)
Platyja (*Facidia*) *semifimbria* (Walker, [1858])
Platyja (*Facidia*) *rivulosum* (Saalmüller, 1880)
Platyja (*Facidia*) *ennomoides* **sp. n.**
Platyja (*Facidia*) *stygium* (Saalmüller, 1881)
Platyja ("*Facidia*") *luteilinea* (Hampson, 1926)
Platyja ("*Facidia*") *remaudi* (Laporte, 1972)

An outlier specimen without locality data similar to *P.* (*F.*) *vacillans* is illustrated and briefly discussed. *Platyja* ("*Facidia*") *luteilinea* and *P.* ("*F.*") *remaudi* are tentatively retained in *Facidia*, though their remarkable autapomorphies call for further insights into their phylogenetic relationships with the core group of *Facidia*. Both these species, with their extraordinarily unusual features of venation and pattern, respectively, and the discussed case of male-limited dimorphism in *P.* (*F.*) *vacillans*, show how systematics would benefit from detailed knowledge of the regulatory mechanisms producing phenotypes. In this respect, the African species of *Platyja* seem to be a particularly promising group for "evo-devo" studies.

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ERRATUM

Erratum

During the review process of the paper by A. Zilli and G. M. László "The African members of the *Platyja* genus group, with description of a new species and comments on other taxa currently attributed to *Megacephalomana* (Lepidoptera: Erebidae)", published in Integrative Systematics 5 (1): 73–93 (https://doi.org/10.18476/2022.174887), some wording was inadvertently changed in the discussion about male-limited dimorphism within the remarks to the species *Platyja* (*Facidia*) *vacillans* (Walker, 1858). The sentence "the females should show that character at the same phenotypic frequency in the male" should in fact read as follows: "the females should show that character at the same phenotypic frequency of the gene frequency in males".