ARTHROPOD SYSTEMATICS & PHYLOGENY

78 (2): 171–216
2020

SENCKENBERG

Previously unrecognized diversity of Afrotropical Melanitini butterflies (Nymphalidae, Satyrinae): doubling the number of species and genera

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Accepted on April 30, 2020.
Published online at www.senckenberg.de/arthropod-systematics on October 9, 2020.
Editor in charge: Bradley Sinclair & Torben Riehl

Abstract. The Paleotropical tribe Melanitini (Nymphalidae, Satyrinae) has until now been considered to be represented in the Afrotropical region by two genera – *Melanitis* Fabricius and *Gnophodes* Westwood – and six species. Here, we demonstrate that the former genus *Gnophodes* comprises two lineages well-defined by morphological and genetic traits. According to the new arrangement *Gnophodes* sensu nov. comprises five species. *Gnophodes betsimena* (Boisduval) is split into three allopatric species including – *G. betsimena*, stat.rev. restricted to Madagascar, *G. parmeno*, stat.reinst. found in the main African rain forest block, and *G. diversa*, stat.reinst. occurring in East and Southern Africa. Two species – *G. grogani* Sharpe and *G. heroni* Pyrcz & Collins, sp.n. are montane specialists. The new genus *Haydonia* Pyrcz & Collins, gen.n. comprises four species previously placed in *Gnophodes,* including *H. chelys* (Fabricius), comb.n., two taxa, *H. pythia* (Fabricius), comb.n., stat.reinst. and *H. harpa* (Karsch), comb.n., stat.reinst., previously considered as synonyms of *H. chelys*, reinstated as valid species, and one new species – *H. hassoni* Pyrcz & Collins, sp.n. – from Katanga. At the same time, four other taxa are confirmed as synonyms of *H. pythia*, *H. chelys* or *H. harpa*. The two genera differ most immediately by the shape and position of male alar organs, elsewhere designated as androconia. They also differ notably in many aspects of female genitalia, however male genitalia vary little between the species and genera of Melanitini. A parapatric pattern of distribution is uncovered, with related species replacing each other along an elevational gradient. Montane species, *H. chelys* and *G. heroni* sp.n., present disjunct distributions being found in the mountains of western Uganda and eastern D.R. Congo, and again in the highlands of Cameroon. In addition, one species is removed from the genus *Melanitis* and placed in a new monobasic genus *Ducarmeia* Pyrcz gen.n. *Ducarmeia ansorgei* (Rothschild), comb.n. based on a salient synapomorphy of adults, a reflector patch situated on hindwing upperside anal fold. Further evidence is found in venation, female genitalia and molecular data. COI data were obtained for nine species, confirming the above findings, with the exception of the unresolved *G. parmeno* clade. Early stages are partially described for four species.

Key words. Africa, androconia, COI, *Ducarmeia* gen.n., female genitalia, *Gnophodes heroni* sp.n., *Haydonia* gen.n., *Haydonia hassoni* sp.n., parapatric distributions, taxonomy.

1. Introduction

With the growing general concern about the loss of the World's biodiversity, biologists are intensifying their efforts to document and understand global patterns of species richness overall and in different model groups (Costello et al. 2012; Caley et al. 2014) It is, sadly, a race against the clock, as systematists and taxonomists try to identity as many new species as possible before they disappear. Butterflies play an important role as a model

group in global diversity assessments and in shaping natural environment protection policies, being species-rich and widespread, and their systematics, phylogenetics and ecology is rather well understood. Numerous new species of butterflies are identified and described every year partly as a result of applying more sophisticated taxonomic techniques, including barcoding, but generally thanks to increasing data gathering efforts. The vast majority of new species are described from tropical rainforests which are the most species-rich and least researched but also among the most threatened habitats of the World. Rainforests of the Afrotropical region are one of the most biodiverse terrestrial areas of the globe, although remaining considerably less diverse than tropical forests situated in the Neotropical Region. This becomes immediately evident when butterfly species-richness is compared. Species diversity of Afrotropical butterflies (3964) is only half of that recorded in the Neotropical Region (7884), although comparable to that of the Indo-Australian region (3685) (www.learnaboutbutterflies.com). Two main factors contribute to the increase in the number of recognized species. On the one hand, several large genera comprising numbers of similarly patterned species turn out to be even more species-rich as numerous additional cryptic species are recognized as a result of advanced morphological, ecological or genetic studies. On the other hand, sampling and data gathering effort has been intensified. In the African context, not surprisingly, the groups which have contributed most to the increased species-richness during the last five years are those already recognized as the most diverse, including for example, Lycaenidae (Sáfián et al. 2015) and Hesperiidae (Larsen, unpublished), and the Adoladini Nymphalidae, more specifically the speciose genera *Bebearia* Hemming, 1960 (Sáfián et al. 2016) and *Euphaedra* Hübner, [1819] (Pyrcz et al. 2011).

Among the Satyrinae, the number of described species has increased considerably in a number of genera in recent years, in particular Madagascan *Strabena* Mabille, 1877, and *Heteropsis* Westwood, [1850], and mainland *Bicyclus* Kirby, 1871 (Brattström et al. 2015, 2016; Lees 2016; Aduse-Poku et al. 2017). Some other genera of African Brown butterflies have been considered as species-poor and alpha-taxonomically fairly well researched. Here, we show that the actual species richness of African butterflies is still superficially known, and can be higher than previously thought, as in the case of the satyrine tribe Melanitini and the genus *Gnophodes* Westwood, 1849, in particular. Until now, only three species of *Gnophodes* were recognized (Ackery et al. 1998). Two of them are widely sympatric and distributed in lowland and premontane rain forests – *G. chelys* (Fabricius, 1793) and *G. betsimena* (Boisduval, 1833), the latter also found in Madagascar, and one occurs locally in the cloud forests along the Congo – Uganda Rwanda border, *G. grogani* Sharpe, 1901. Species level systematics of *Gnophodes* were considered to be well-established and although a number of taxa associated with *G. chelys* were previously recognized, they were considered as subspecies or synonyms by Ackery et al. (1998), a point of view which remained unchallenged as expressed in a number of regional catalogues and faunal papers (Larsen 2005; Vande weghe 2010).

The genus *Gnophodes* belongs to the tribe Melanitini, itself a moderately species-rich group of mostly Paleotropical Satyrinae. It comprises, as currently recognized, apart from *Gnophodes* four other genera – *Melanitis* Fabricius, 1807, *Parantirrhoea* Wood-Mason, 1881, *Cyllogenes* Butler, 1868, *Bletogona* C. Felder & R. Felder, 1867. Three of the former are Oriental genera, including one monobasic, and together comprise a total of nine species only (Lang & Huang 2012). *Melanitis*, distributed in the Oriental, Afrotropical and even in south-eastern parts of the Palearctic and western Australian regions, is the most numerous of all with 12 species, but only three of them occur in Africa – the widespread *M. leda* (Linnaeus, 1752), *M. libya* Distant, 1882, and, (until now) *M. ansorgei* Rothschild, 1904. *Gnophodes* is the only strictly Afrotropical representative of the Melanitini. The monobasic genus *Manataria* Kriby, 1902, whose relations with the remaining Melanitini are not entirely understood, occurs in the Neotropical Region. The monophyly of the tribe has never been assessed using molecular data, although a series of morphological characters, putative synapomorphies, seem to indicate it is the case (Larsen 2005). In Peña et al. (2006) phylogenetic study of World Satyrinae, based on one species per genus, *Melanitis* and *Gnophodes* come out as sister taxa. Wahlberg et al. (2009), in the evolutionary history of Nymphalidae, also included *Cyllogenes* which was placed as sister to the above two genera. However, but the internal phyletic relationships within the tribe as well as the monophyly of the comprising genera are weakly supported. This in particular applies to the genus *Gnophodes*, treated by some authors as a subjective junior synonym of *Melanitis* (Condamin & Roy 1963; Fox et al. 1965). Here, we re-evaluate the phylogeny of Melanitini, with an emphasis on African taxa, based on morphological and molecular data.

2. Material and methods

2.1. Material

Specimens used in this study were examined from the African Butterfly Research Institute (ABRI) in Nairobi (Kenya), the Zoological Division (formerly Zoological Museum) of the Nature Education Centre (CEP-MZUJ), Jagiellonian University in Kraków (Poland) and the African Natural History Research Trust (ANHRT), Leominster, UK. Other specimens were consulted in Adam Mickiewicz University (AMU) in Poznań, Poland, collection of Haydon Warren-Gash (HWG) in Préssac, France, Natural History Museum (HNHM), Hungarian Academy of Sciences in Budapest, Museum für Naturkunde (MNK) in Berlin, Germany and Senckenberg Museum

für Tierkunde (SMTD) in Dresden, Germany. Additional material was collected in the field in Uganda and Kenya in 2016–2018 by TP, in Liberia by SSz, in Mozambique in 2018 and 2019 by MB, and by SSz and KF (and others) in Guinea, Ghana, Cameroun and Madagascar.

2.2. Adult morphology

Male and female genitalia were removed from abdomens and soaked in 10% KOH solution for 5–10 minutes. Subsequently, abdomens were preliminarily cleaned out of soft tissue in water in order to expose genital parts. Female abdomens were stained in chlorazole black in order to identify soft genital parts. Dissected genitalia were cleaned out of water by using ethanol 90% and 95% solutions. Wing preparations were performed by soaking in hot 10% KOH solution and subsequently by removing dorsal and ventral scales. Wing slides were photographed and preserved in glycerol. Nikon digital camera DS–Fi1 and Olympus SZX9 stereomicroscope were used for taking pictures of the dissections, which were then processed in Combine ZP and Corel PHOTO–PAINT X3 programs to enhance focus and improve quality. Genital preparations were kept in glycerol vials pinned under the corresponding specimens. Genital terminology follows largely Razowski (1996) and Klots (1970). The sclerotized inner edges of female tergite 8, but not produced into a fully developed anterior apophysis, is called here pseudo-apophysis. Adults were photographed with a Minolta E–500 digital camera. Colour plates were composed using Adobe Photoshop version 8.

2.3. Larval morphology

Larvae were collected in the field, bred and photographed by the staff of the African Butterfly Research Institute in Nairobi.

2.4. Molecular data

DNA was isolated from a single pair of legs of the following butterflies: four specimens of *G. diversa*, three specimens of *G. parmeno*, one specimen of *G. heroni,* two specimens of *G. betsimena*, one specimen of *G. grogani*, three specimens of *Haydonia harpa* comb.n., four specimens of *Haydonia pythia* comb.n. and two specimens of *Ducarmeia ansorgei* comb.n. Extraction was performed using the NucleoSpin Tissue kit (Macherey-Nagel Düren, Germany) according to established protocols. Amplification of the part of mitochondrial gene COI was done using HybLCO and HybHCO primers with universal primer tails, respectively T7Promoter(F) and T3(R) (Folmer et al. 1994, Wahlberg & Wheat 2008) with standard PCR protocol. Results of amplification were checked by electrophoresis on 1% agarose gels stained with Midori Green (NIPPON Genetics). After purification (NucleoSpin Extract II (Macherey-Nagel)), some PCR products were sequenced using the BigDye Terminator v.3.1. Cycle Sequencing Kit (Applied Biosystems, Carlsbad, CA, USA), other samples were sent to Macrogen Europe (Amsterdam, Netherlands) for purification and sequencing. Additionally, nine sequences of eight species were imported from GenBank: *G. diversa*, *H. harpa* comb.n., *H. chelys* comb.n., *Cyllogenes woolletti* Riley, 1923, *Melanitis phedima* (Cramer, 1780), *Melanitis leda* Linnaeus, 1758 (two sequences) and *Mycalesis visala* Moore, 1858 and *Bicyclus anisops* (Karsch, 1892). Sequences were examined and aligned in BioEdit 7.1.3.0. (Hall 1999).

Phylogenetical analyses were conducted in MEGA X (Kumar et al. 2018). A Maximum Likelihood tree was inferred using General Time Reversable model (Nei & Kumar 2000) and partial deletion option. The branch support values were calculated using 1000 rapid bootstrap replicates. The final tree was edited in Corel DRAW 2018 to enhance picture quality. Analyses were performed in the molecular laboratories of the Nature Education Centre and the Institute of Zoology and Biochemical Science of the Jagiellonian University. Sample data, along with GenBank Accession numbers are compiled in Table 1.

2.4. Abbreviations

FW – forewing; **HW –** hindwing; **D –** dorsum; **V –** venter; **prep. mol.** – sample for molecular analysis; **prep. genit. –** genital dissection.

3. Results

3.1. *Gnophodes* Doubleday, [1849], gen.rev.

Gnophodes Doubleday, [1849]: plate 61 (illustration); Boisduval, [1849]: 363 (text). Type species: *Melanitis parmeno* Doubleday, by monotypy.

Redescription. *Adults*: Medium to large size with FW length from base to apex 3–4 cm. Venation (Fig. 23B) forewing with 5 radial veins, and base of M1 and M2 independent but close to each other. Wings outer margin strongly produced at forewing vein M2 and hindwing vein M3. Sexual dimorphism slight, expressed in slightly larger size and lighter colours of female. Upperside colour pattern simple, mostly brown, with transverse subapical, yellow or orange band, without ocelli. Underside cryptic, with different shades of brown and small submarginal ocelli on both fore and hindwings. Large, generally oval androconial patch (Fig. 18D–F) on forewing median area between CuA2 or 1A/1B, covered with long hairy scales darker than ground colour. ***Male genitalia*:** Simple with long uncus ending in sharp tip, atrophied gnathos, long, slender and smooth valvae, deep saccus

and straight, smooth tubular aedeagus. ***Female genitalia*:** With long, sharp and thin posterior apophyses, little sclerotized post and antevaginal lamellae, very long ductus bursae opening gradually into elongated corpus bursae with long and very thin double signa.

3.2. *Gnophodes betsimena* (Boisduval), stat.rev.

Fig. 1A–D

Cyllo betsimena Boisduval, 1833: 206. Type locality: Tamatave, Madagascar. Type whereabouts unknown.

Diagnosis. The FW subapical band is much wider in *G. betsimena* than in *G. parmeno* and *G. diversa*, and differently shaped, with a straight inner edge, not outcurved. *Gnophodes betsimena* is also much larger than the other two species, which overall gives it a quite different aspect.

Redescription. ***Male*** (Fig. 1A,B): As illustrated. ***Male genitalia*** (Fig. 10C): Tegumen dorsum flattened; uncus stout, twice length of tegumen, slightly curved in basal one-third, with sharp apical tip pointed downwards; gnathos rudimentary; pedunculus long, pointed downwards; saccus long, but shorter than in *H. chelys*, *H. harpa* or *H. pythia* and much so than in *H. hassoni*, straight and wider than in preceding species; valvae slender and elongated, but shorter and wider than in preceding species, only slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus nearly straight, smooth and tubular with slightly flattened and wider apex. ***Female*** (Fig. 1C,D): As illustrated. ***Female genitalia*** (Fig. 16B): Papillae anales prominent, covered with thin and short hair; apophyses posteriores prominent, half-length of papillae width; lamella postvaginalis elongated, slat-like with lateral flaps, extending into well-sclerotized anterior edges of eighth sternite; ductus bursae very long, weakly sclerotized, wider and more so in anterior part; ductus seminalis originating in middle; bursa copulatrix elongated, with rippled surface, no signa. ***Early stages***: Not known.

Material examined. MADAGASCAR: 1♂: Marojejy National Park., MT-PF-BS-27(2), 26.xi–07.xii.2018, A. Würz leg., prep. mol. CEP UJ_20190302A, prep. mol. CEP UJ_20190302B, CEP-MZUJ; 1♂: Marojejy NP., MT-PF-BN-7(2), 26.xi–07.xii.2018, A. Würz leg., prep. mol. CEP UJ_20190301A, prep. mol. CEP UJ_20190301B (CEP-MZUJ); 3♂: Rte Anosibe, xii.1986, ABRI-2018-4881, coll. S. Collins (ABRI); 1♀: Marojejy NP., MT-PF-BS-3(2), 26.xi–07.xii.2018, A. Würz leg. (CEP-MZUJ); 5♀: Rte Anosibe, xii.1986, ABRI-2018-4882, coll. S. Collins; 1♀: La Mandaka (ABRI).

Comments. *Gnophodes betsimena* was described from Madagascar and has until now been considered a widespread polytypic species including two continental subspecies, which Larsen (1991) claimed to be morphologically quite similar. However, a comparative analysis of the material curated at ABRI shows that morphological differences between the Madagascar (*G. betsimena*) and continental taxa (*G. parmeno, G. diversa*) are important enough to treat the three taxa as distinct species.

3.3. *Gnophodes parmeno* Doubleday, stat.reinst.

Figs. 3A–D, 20

Gnophodes parmeno Doubleday, [1849]: plate 61, fig. 2. No type locality. Type not examined.

Diagnosis. *Gnophodes parmeno* is considerably smaller than *G. diversa* and *G. betsimena*. In *G. parmeno* the subapical bands are pale yellow and faint in the females and nearly obsolete in some males, whereas in the other two species they are very large and bright yellow FW subapical bands in both sexes.

Redescription. ***Male*** (Fig. 3A,B): As illustrated. ***Male genitalia*** (Fig. 9E,F): Tegumen dorsum dome-like; uncus stout, more than twice length of tegumen, slightly curved in basal one-third, with sharp apical tip pointed downwards; gnathos absent; pedunculus long, pointed downwards; saccus long, but shorter than in *H. chelys*, *H. harpa* or *H. pythia* and much so than in *H. hassoni*, straight and wider than in preceding species; valva slender and elongated, but shorter and wider than in preceding species, only slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular with slightly flattened and wider apex. ***Female*** (Fig. 3C,D): As illustrated. ***Female genitalia*** (Fig. 16C): Papillae anales prominent, densely covered with thin hair; apophyses posteriores prominent, length of papillae width; lamella postvaginalis elongated slat-like with lateral flaps, extended into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized, wider and more so in anterior part; ductus seminalis originating in middle; bursa copulatrix elongated, with thinly rippled surface, no signa. ***Early stages*:** Not described. Host plants: Host plants: *Rottoboellia cochinchinensis*, *Setaria barbara*, *Setaria megaphylla*, *Sorgus arundinaceum* (Vuattoux 1994; Coache et al. 2017).

Material examined. CAMEROON: 1♂: Mount Cameroon (SW slope), Bamboo camp III, 06–12.ii.2016, 350 m, V. Maicher, Sz. Sáfián, S. Janeček, R. Tropek leg., (CEP-MZUJ); 1♂: Waak, xi.2006, ABRI-2018-4887 (ABRI); 1♂: Lolodorf (ABRI); 3♂: Moloundou (ABRI); 1♂: Ebogo (ABRI); 1♂: Mt. Elounden (ABRI); 1♂: Tabenkem (ABRI); 1♂: Garoua Boulai (ABRI); 1♂: Doulabo (ABRI); 5♂: Koutaba (ABRI); 1♀: Waak (ABRI); 3♀: Moloundou (ABRI); 3♂: Lolodorf, ex. Staudinger & Bang-Haas (SMTD); 1♀: Mt. Elounden (ABRI); 1♀: Tabenkem (ABRI); 2♀: Garoua Boulai (ABRI); 2♀: Mt. Kupe, ii.2010, ABRI-2018-4888 (ABRI); 3♀: Mt. Kala (ABRI); 2♀: Koutaba (ABRI); 1♀: Dja (ABRI); 2♀: Kumba, Mamfe (ABRI); 1♀: Nyazanga (ABRI); 2♀: Minton, Emilie (ABRI); 1♀: Mekas (ABRI); 1♀: Bakassi (ABRI); 4♀: Lolodorf, ex. Staudinger & Bang-Haas (SMTD); **UGANDA:** 10♂: Central-Mpigi, Mpanga Forest, 01–14.ix.2016, 1150–1200 m, prep. genit. 1403_01.10.2018/K.Florczyk, T. Pyrcz, Sz. Sáfián

leg. (CEP-MZUJ); 1♂: Rabongo (ABRI); 5♂: Budongo, vi.1993, 900 m, ABRI-2018-4890 (ABRI); 1♂: Katera (ABRI); 1♂: Itwara (ABRI); 2♂: Zika, Entebbe (ABRI); 2♂: Kadam Mtn, Nakapiripirit, prep. genit. 1361_30.08.2018/K. Florczyk, ABRI-2018-4940 (ABRI); 6♀: Central-Mpigi, Mpanga Forest, 01–14.ix.2016, 1150–1200 m, T. Pyrcz, Sz. Sáfián leg. prep. genit. 1416_04.10.2018/K. Florczyk, (CEP-MZUJ); 2♀: Budongo, vi.1993, ABRI-2018-4891 (ABRI); 1♀: Kyendo (ABRI); 2♀: Kadam Mtn, 2016, prep. genit. 1360_30.08.2018/K. Florczyk, ABRI-2018-4944 (ABRI); Central Province: 1♂: Mbalmayo District, Ebogo, 14.iv.2013, 650–680 m, T. Pyrcz leg., prep. genit. 523_24.03.2017/J.Lorenc (CEP-MZUJ); 1♀: Mbalmayo District, Ebogo, 07.iv.2013, 650–680 m, T. Pyrcz leg. (CEP-MZUJ); 1♂: Mubende, Kaweri Plantation, 11–22.v.2016, 1250–1300 m, B. Balyegenira leg. (CEP-MZUJ); 2♀: Mubende, Kaweri Plantation, 11–22.v.2016, 1250–1300 m, B. Balyegenira leg. (CEP-MZUJ); 1♀: Mubende, Kaweri Plantation, 18–30.i.2016, 1250–1300 m, B. Balyegenira leg. (CEP-MZUJ); **NIGERIA:** 1♂: Bendel State, Okomu Forest, 13.ii.1986, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Cross River St., Oban Hills, Ausambo, 17.ii.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Anambra State, Nsukka, 10.xi.1989, J. Wojtusiak leg. (CEP-MZUJ); 2♂: Okomu, x.1987, prep. genit. 524_24.03.2018/J.Lorenc (CEP-MZUJ); 1♂: Anambra State, Nsukka F. Res., 27.iii.1983, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Nsukka, 14.ii.1985 (CEP-MZUJ); 1♂: Anambra State, Nsukka, 23.i.1983, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Enugu State, Nsukka, 22.xi.1983, J. Wojtusiak leg. (CEP-MZUJ); 2♂: Anambra State, Nsukka, 29.x.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Bendel State, Okomu Forest, 20.i.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Oyo State, Ibadan, 26.xii.1999, 200 m, T. Pyrcz leg. (CEP-MZUJ); 1♂: Osun State, Oshogbo, 11.xi.1999, 315 m, T. Pyrcz leg., prep. genit. 1402_01.10.2018/K. Florczyk (CEP-MZUJ); 1♂: Cross River S., Obudu Cattle Ranch, 06.i.1986, 1200 m, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Enugu State, Nsukka, 28.x.1983, J. Wojtusiak leg. (CEP-MZUJ); 50 km off shore Nigeria, Platform Borgen Dolphin, viii.2005, coll. P. Kowalski (CEP-MZUJ); 1♂: Anambra State, Nsukka, 10.xi.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Anambra State, Nsukka, 21.xi.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Anambra State, Nsukka, 02.xii.1982, J. Wojtusiak leg. (CEP-MZUJ); 2♂: Obudu (ABRI); 1♀: Bendel State, Okomu Forest, 20.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 2♀: Anambra State, Nsukka, 02.xii.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Bendel State, Okomu Forest, 12.xi.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Osun State, Oshogbo, 07.xii.1999, 315 m, T. Pyrcz leg. (CEP-MZUJ); 2♀: Anambra State, Nsukka, 02.x.1983, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Osun State, Oshogbo, 11.xi.1999, 315 m, T. Pyrcz leg. (CEP-MZUJ); 1♀: Bendel State, Okomu Forest, 13.iii.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Edo State, Okomu Forest, 07.x.1983, J. Wojtusiak leg., prep. genit. 1419_05.10.2018/K. Florczyk (CEP-MZUJ); 1♀: Nsukka, 09.xi.1985 (CEP-MZUJ); 1♀: Enugu State, Nsukka, 06.xii.1983, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Enugu State, Nsukka, 26.xi.1983, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Anambra State, Nsukka, 22.x.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Anambra State, Nsukka, 12.ix.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Anambra State, Nsukka, 25.ix.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Obudu (ABRI); **GUINEA:** 1♂: Mount Nimba, 1998, H. Warren-Gash leg. (CEP-MZUJ); 16♂: Forêt Classée de Ziama, Massadou campsite, lowland forest, fruit-baited traps, 08–13.iii.2019, 550 m, Sz. Sáfián, G. Simonics, K. Florczyk, leg., prep. wing 01a/b_03.09.2019/K. Florczyk (CEP-MZUJ); 3♂: Forêt Classée de Ziama, Massadou campsite, lowland forest, 541 m, general collecting, 08–13.iii.2019, Sáfián Sz., Simonics G., Florczyk K. leg. (CEP-MZUJ); 1♀: Mount Nimba, 02.v.1998, prep. genit. 1417_04.10.2018/K. Florczyk, H. Warren-Gash leg. (CEP-MZUJ); 15♀: Forêt Classée de Ziama, Massadou campsite, lowland forest, fruit-baited traps, 08–13.iii.2019, 550 m, Sz. Sáfián, G. Simonics, K. Florczyk leg. (CEP-MZUJ); 2♀: Forêt Classée de Ziama, Sérédou campsite upland forest, fruit-baited traps, 01–06.iii.2019, 850–1000 m, Sz. Sáfián, G. Simonics, K. Florczyk leg. (CEP-MZUJ); 1♀: Forêt Classée de Ziama, Massadou campsite, lowland forest, 541 m, general collecting, 08–13.iii.2019, Sz. Sáfián, G. Simonics, K. Florczyk leg. (CEP-MZUJ); **IVORY COAST:** 1♂: Mont Péko, viii.2001, H. Warren-Gash leg. (CEP-MZUJ); 1♂: Marove River (ABRI); 1♂: Aberngourou (ABRI); 1♀: Lamto (ABRI); **D.R. CONGO:** Prov. Nord-Kivu: 1♂: Terr. Lubero, Kasuo, ii.2008, 1800 m, coll. R. Ducarme, prep. genit. 1674_20.03.2019/K. Florczyk (CEP-MZUJ); 3♂: Terr. Lubero, Kasuo, iii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, iv.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, i.1998, 2000 m, coll. R. Ducarme, prep. genit. 1675_20.03.2019/K. Florczyk (CEP-MZUJ); 1♂: Kenge, Terr. Lubero, 20.i.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Beni-Kivu, iv.1980, coll. R. Ducarme (CEP-MZUJ); 1♂: Beni-Kivu, iii.1991, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasugho, 1800 m, 28.i.2016, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasugho, 1800 m, 24.i.2010, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasugho, 1800 m, 13.iv.2010, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasugho, 1800 m, 18.xii.2013, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasugho, 1800 m, 03.viii.2010, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasugho, 1800 m, 13.vi.2010, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Beni, Mamove, 1050 m, 23.vi.2008, coll. R. Ducarme (CEP-MZUJ); Prov. Orientale: 1♂: Terr. Djugu, Djugu, 1700 m, 10.x.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Djugu, Djugu, 1700 m, 05.x.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Djugu, Djugu, 1700 m, 30.x.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Djugu, Djugu, 1700 m, 28.x.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Beni, Mont Atonza, 1400 m, 08.v.1991, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Mambasa, Manzumbu, 900 m, 20.viii.2008, coll. R. Ducarme, CEP-MZUJ; 1♂: Kasuo, ABRI; 1♀: Mutwanga Terr. Beni, x.1999, 1200 m, coll. R. Ducarme (CEP-MZUJ); 2♀: Terr. Beni, Eringeti, xii.2009, 1100 m, coll. R. Ducarme, prep. genit. 1676_20.03.2019/K. Florczyk (CEP-MZUJ); 1♀: Terr. Beni, Mamove, x.2008, 1050 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Lebayi, Zanaga (ABRI); 1♂: Foulakari (ABRI); 1♂: Bamba (ABRI); 4♂: Lukima, Katanga, 17–25.iv.2001, ABRI-2018-4897; 1♂: Lume, Kivu (ABRI); 1♂: Mapimbi, Kivu (ABRI); 1♀: Mont-Hoyo, Terr. Irumu, ii.1999, 1400 m, coll. R. Ducarme (CEP-MZUJ); Prov. not specified: 3♀: Lukima, Katanga, v.2001, ABRI-2018-4896; 3♀: Mapimbi, Kivu (ABRI); 2♀: Irangi, Bukavu (ABRI); 1♀: Biakatu, Kivu (ABRI); 1♀: Butuhe (ABRI); 1♀: Beni, Kivu (ABRI); 1♀: Mt. Hoyo, Kivu (ABRI); 1♀: Kasuo, Kivu (ABRI); 2♀: Kibale, Kivu (ABRI); 1♀: Katanga, env. Lusinga, iii/iv.2003, Exploration du PNU, Projet ICCN-NA-SEA, Hasson and Bouyer leg. (ABRI); **EQUATORIAL GUINEA:** 1♂: Fernando Poo (ABRI); 2♂: Moka, Fernando Poo, 8–13.iii.2007, ABRI-2018-4898; 2♀: Fernando Poo (ABRI); 1♀: Bioko, xii.1992, 900 m, ABRI-2018-4898, coll. S. Collins; **SIERRA LEONE:** 1♂: Malema (ABRI); LIBERIA: 1♀: Gola National Forest, Sz. Sáfián leg. (ABRI); **GUINEA BISSAU:** 2♂: Bubaque, ii.1994, ABRI-2018-4895; 2♀: Busa (ABRI); **ANGOLA:** 3♂: Cuanza Sul (ABRI); ZAMBIA: 3♂: Ikelenge, 17.v.1983, ABRI-2018-4889 (ABRI); 6♀: Ikelenge, prep. genit. 1378_03.09.2018/K. Florczyk, ABRI-2018-4924 (ABRI); **ETHIOPIA:** 1♂: Bebeka, prep. genit. 1356_30.08.2018/K. Florczyk, ABRI-2018-4923 (ABRI); SUDAN: 2♂: Imatong (ABRI); 1♀: Imatong Mtns, iii.1979, ABRI-2018-4894, coll. S. Collins (ABRI).

Comments. *Gnophodes parmeno* stat.reinst. and *G. diversa* stat.reinst. are geographical vicariants with the former distributed in the main African rainforest block and its fringing outlier forests, and the latter in all kinds of forested areas, including *Brachystegia* woodland, premontane and even lower montane forests, excluding however the most humid patches (Buda, Mrima) along the eastern coast of Africa (Fig. 27). Their ranges do not overlap, but neither is parapatric, as their distribution limits are widely disjunct. In Kenya, *G. diversa* is found

inwards to Nairobi, but *G. parmeno* is only found towards the Ugandan border (listed by Larsen (1991) from Kenya, a misidentification of *G. heroni* sp.n.).

3.4. *Gnophodes diversa* (Butler), stat.reinst.

Figs. 1E–H; 2

Cyllo diversa Butler, 1880: 333. Type locality: Port Natal, South Africa. Type not examined.

Diagnosis. *Gnophodes diversa* is intermediate in terms of its size, wing shape and colour patterns between *G. parmeno* and *G. betsimena*. It is larger than *G. parmeno* but noticeably smaller than *G. betsimena*. As with *G. betsimena*, sexual dimorphism is very slight, in contrast to well-developed dimorphism in *G. parmeno*. In both sexes the subapical band is wide and light yellow, but invariably narrower than in *G. betsimena* and with an irregular zigzagging inner edge (as opposed to straight in *G. betsimena*). Underside patterns are variable but less irrorated with dark brown speckling than in *G. parmeno*.

Redescription. ***Male*** (Figs. 1E,F; 2A,B,E,F): As illustrated. ***Male genitalia*** (Fig. 9C,D): Tegumen dorsum very slightly humped; uncus stout, slightly arched, one and a half-length of tegumen with sharp apex; gnathos vestigial but present; pedunculus prominent but smaller than in other species, pointed downwards; saccus long and straight, thinner than in *G. parmeno*; valva slender and elongated, slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular. ***Female*** (Figs. 1G,H; 2C,D,G,H): As illustrated. ***Female genitalia*** (Figs. 15A–C; 16A): Papillae anales prominent, densely covered with thin hair; apophyses posteriores prominent, length of papillae width; lamella postvaginalis elongated slat-like with lateral flaps, extended into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized, wider and more so in anterior part; ductus seminalis originating in middle; bursa copulatrix elongated, with thinly rippled surface, with very thin and long signa, reaching three-quarters of length of bursa. ***Early stages*** (Fig. 24H–M; 25D): Fourth and fifth larval stages, and pupae are known. Host plants: *Ehrhacta erecta*, *Panicum deustum*, *Setaria palmifolia* (Williams 2019).

Material examined. KENYA: 1♂: Nairobi, Oloolua Forest, 03.viii.2012, 1800–1850 m, T. Pyrcz leg., prep. genit. 1540_31.12.2018/K. Florczyk, prep. mol. 468a/27.ix.2018, prep. mol. 468b/27.ix.2018 (CEP-MZUJ); 1♀: Nairobi, Oloolua Forest, 03.viii.2012, 1800–1850 m, T. Pyrcz leg., prep. genit. 1541_31.12.2018/K. Florczyk, prep. mol. 469a/27.ix.2018, 469b/27.ix.2018 (CEP-MZUJ); 2♂: Meru, Mt Kenya, 5000 ft, viii.1978, S.C. Collins (ABRI); 3♂: Meru, Mt Kenya, 5000 ft, viii.1978, S.C. Collins (ABRI); 3♂: Nairobi, Ngong, 5500 ft, ii.1950, S.C. Collins (ABRI); 1♂: Karen, 27.iii.2017, S.C. ABRI leg. (ABRI); 1♂: Nairobi, Loita, ix.1990, S.C. Collins (ABRI); 1♂: Nairobi, Karen, x.1988, S.C. Collins (ABRI); 1♂: Nairobi, Karen, 10.iii.2019, SC ABRI leg. (ABRI); 1♂: Nairobi, Karen, 11.iii.2019, SC ABRI leg. (ABRI); 1♂: Nairobi, Karen, 16.viii.2019, SC ABRI leg. (ABRI); 1♀: Nairobi, Loita, ix.1990, S.C. Collins (ABRI); 1♂: Shimba Hills, 500 m, i.1986, S.C. Collins (ABRI); 2♂: Shimba Hills, 500 m, iv.1990, S.C. Collins (ABRI); 2♀: Meru, Mt Kenya, 5000 ft, vii.1978, S.C. Collins (ABRI); 2♀: Ngeng River, Matthews Range, 1550 ft, iv.1980, S.C. Collins (ABRI); 2♀: Nairobi, Ngong, 5500–6000 ft, i.1980, S.C. Collins (ABRI); 2♀: Nairobi, Karen, x.1988, S.C. Collins (ABRI); 1♀: Nairobi, Karen, 2018, S.C. ABRI leg. (ABRI); 1♀: Nairobi, Karen, 04.ix.2018, ABRI leg. (ABRI); 1♀: Nairobi, Karen, i.2018, S.C. ABRI leg. (ABRI); 1♀: Nairobi, Karen, x.1988, S.C. Collins (ABRI);1♀: Nairobi, Karen, 02.iii.2019, S.C. Collins (ABRI); 1♀: Nairobi, Karen, 09.vi.2007, S.C. Collins (ABRI); 1♀: Meru, Mt Kenya, 5200 ft, vii.1978, S.C. Collins (ABRI); 1♀: Meru, 1500 m, i.2010, ABRI leg. (ABRI); 1♀: Meru, Mt Kenya, 5200 ft, viii.1975, S.C. Collins (ABRI); 2♀: Ngeng River, Matthews Range, vi.1980, S.C. Collins (ABRI); 1♀: Shimba Hills, 500 m, v.1990, S.C. Collins (ABRI); 3♀: Shimba Hills, 500 m, iv.1990, S.C. Collins (ABRI); **TANZANIA:** 1♀: Prov. Morogoro, v.1985, prep. genit. 1679_21.03.2019/K. Florczyk, T. Grant leg. (CEP-MZUJ); 23♀: Iringa, Ukami 1500–1600 m (SMTD); 7♀: Iringa, Ukami, 1500–1600 m, prep. wing 03a/b_03.09.2019/K.Florczyk (CEP-MZUJ); 1♂: Mizimu, Mwanihana, Udzungwa Mountains N.P., 03–06.viii.2010, 850 m, R. Smith, H. Takano leg., prep. genit. 1558_15.01.2019/K. Florczyk, ANHRTUK 00038259, TZ-L0043 (ANHRT); 1♂: Magombera Forest, 28.vii–01.viii.2010, 290 m, R. Smith, H. Takano leg., prep. genit. 1557_15.01.2019/K. Florczyk, ANHRTUK 00038258 (ANHRT); 15♂: Iringa, Ukami, 1500–1600 m (SMTD); 3♂: Iringa, Ukami 1500–1600 m (CEP-MZUJ); 4♂: Tanganyika, Nderema, vii.1936, G. Van Son leg. (ABRI); 2♂: above Gonja, South Pare Mountains, Kanza, 16–30.iii.2005, TCEC/IB/PW/MH, ABRI coll. (ABRI); 2♂: Kwediboma, Nguru Mts, iii.1991, S. Collins leg. (ABRI); 1♂: Udzungwa Mts, 1000 m, 01–07.ii.2000, TCEC/IB/PW/MH, ABRI coll. (ABRI); 1♀: above Gonja, South Pare Mountains, Kanza, 16–30.iii.2005, TCEC/IB/PW/MH, ABRI coll. (ABRI); 1♀: Tanganyika, Nderema, vii.1936, G. Van Son leg. (ABRI); 1♀: Mkombola, Nguru Mts, ii.2006, PW, ABRI coll. (ABRI); 1♀: Kilombero, vi.2014, ABRI leg. (ABRI); 1♀: Kwediboma, Nguru Mts, iii.1991, S. Collins leg. (ABRI); **MOZAMBIQUE:** Manica Prov.: 2♀: Chimanimani NR, Moribane Forest, Ndzou, 02–08.xii.2018, 503 m, M. Bąkowski leg., prep. genit. 1677_20.03.2019/K.Florczyk, M. Bąkowski leg., prep. genit. 1697_17.04.2019/K.Florczyk (CEP-MZUJ); 1♂: Chimanimani NR, Moribane Forest, Ndzou, 02–08.xii.2018, 503 m, prep. genit. 1698_17.04.2019/K.Florczyk (CEP-MZUJ); 5♂: Mt. Mabu, x.2008, ABRI, TCEC/IB/MH (ABRI); 3♂: Mt. Mabu, 1000 m, 1–5.xi.2010, SG/SC/JB/CC/MH, ABRI leg. (ABRI); 1♂: Niassa N.P., 1315 m, 5–11.v.2012, TCEC/MH/JB, ABRI leg. (ABRI); 1♂: Amatongas, 20.viii.1960, J.C.O. Chitty leg. (ABRI); 2♂: Dondo, 09.v.1960, J.C.O. Chitty leg. (ABRI); 1♂: Dondo, 12.v.1959, J.C.O. Chitty leg. (ABRI); 1♀: Mt. Mabu, 27.v–1.vi.2009, JB/CC/MH/SC/DI, ABRI leg. (ABRI); 6♀: Mt. Mabu, 1000 m, 1–5.xi.2010, SG/SC/JB/CC/MH, ABRI leg. (ABRI); 3♀: Mt. Mabu, x.2008, ABRI, TCEC/IB/MH (ABRI); 1♀: Niassa N.P., 14–16.v.2012, TCEC/MH/JB, ABRI leg. (ABRI); 1♀: Mt. Chiperone, Zambezi Prov., 30.xi.2006, J. Bayliss, ABRI leg. (ABRI); 2♀: Mt. Chiperone, Zambezi Prov., xii.2006, J. Bayliss, ABRI leg. (ABRI); 2♀: Amatongas, 20.viii.1960, J.C.O. Chitty leg. (ABRI); **MALAWI:** 1♂: Nkatta Bay, 08.vi.1983, S. Collins (ABRI); 3♂: Chisasira Forest, 01.iv.1992, R.J. Murphy leg., ABRI coll. (ABRI); 2♂: Nkatta Bay, 01.vii.1988, S.C. Collins (ABRI); 1♂: Muloza, Mulanje, 3500 ft, i.1986, ABRI coll. (ABRI); 1♂: Nyika, 6500 ft, iii.1989, R.J. Murphy leg., ABRI coll. (ABRI); 1♀: Vizara, vii.1982, S.C. Collins (ABRI); 2♀: Muloza, Mulanje, 3500 ft, i.1986, ABRI coll. (ABRI); 2♀: Nkatta Bay, Kalwe Forest, 01.vii.1988, S.C. Collins (ABRI); 1♀: Chisasira Forest, i.1992, R.J. Murphy leg., ABRI coll. (ABRI); 1♀: Mulanje Crater, vii.1988, S. C. Collins (ABRI); 1♀: Mulanje, Lichenya Forest, 31.iii.1990, ex. IB, S. C. Collins leg. (ABRI); **ZIMBABWE:** 1♂: Mt Selinda, 15.ii.1981, R.D. Pare leg. (ABRI); 1♂: Mt

Selinda, 01.iii.1982, I. Mullin leg. (ABRI); 2♂: Vumba, 12.i.1956, J.C.O. Chitty leg. (ABRI); 2♂: Vumba, 21.iv.1984, I. Mullin leg. (ABRI); 2♂: Rusitu Forest, 05.v.1997, R.D. Stephen leg. (ABRI); 2♀: Rusitu Forest, 05.v.1997, R.D. Stephen leg. (ABRI); 1♀: Bomponi, 08.v.1997, R.D. Stephen leg. (ABRI); 1♀: Rindwe Bridge, 15.iii.1990, R.D. Stephen leg. (ABRI); 4♀: Vumba, 21.iv.1984, I. Mullin leg. (ABRI); 1♀: Vumba, 19.iv.1986, I. Mullin leg. (ABRI); 2♀: Mt Selinda, 15.ii.1981, R.D. Pare leg. (ABRI); 1♀: Burma Valley, Mutare Distr., 15.v.1988, R.D. Pare leg. (ABRI); **SOUTH AFRICA:** Eastern Cape: 1♂: Port St Johns, 30.v.1970, W.H. Henning leg. (ABRI); 2♂: Port St Johns, "Cape Province", 21.v.1975, R.D. Stephen leg., prep. genit. 1363_30.08.2018/K. Florczyk, ABRI-2018-4919 (ABRI); 1♂: Port St Johns, 28.iv.1968, C. McM leg. (ABRI); 1♂: Port St Johns, Transkei, 22.iv.1976, I.A. Coetzer leg. (ABRI); 2♀: Port St Johns, Cape Province 21–23.v.1975, R.D. Stephen leg. (ABRI); 1♀: Port St Johns, Transkei, 09.v.1981, N.J. Duke leg., prep. genit. 1373_31.08.2018/K. Florczyk, ABRI-2018-4918 (ABRI); 1♀: Port St Johns, Transkei, 25.iv.1976, I.A. Coetzer leg. (ABRI); Kwa-Zulu Natal: 1♀: Umtamvuna N.R., 10.iii.2019, S. Woodhall leg. (ABRI).

Comments. *Gnophodes diversa* is taxonomically and ecologically the most complex species of the genus. Infraspecific variability is pronounced, affecting individual variation but more noticeably in-between population differences. Individual specimens can differ considerably in size, colour patterns and even androconia. The largest specimens of all occur in Natal, the type locality of *G. diversa*. They are also the most brightly coloured with the widest FW yellow band. The smallest, with narrow, subdued yellow bands and dull, greyish brown undersides are found in Shimba Hills along the coast in Kenya. Specimens from adjacent populations in central Tanzania differ by the colour, blackish or chestnut brown, of the FW androconial patches. This may be related to the fact that *G. diversa* has adapted to a number of different habitats. It occurs in cloud forests of Kenyan, Tanzanian and Mozambique highlands at or even above 1500 m, as well as in ecologically different coastal forest from Kenya to subtropical South Africa down to sea level (Woodhall 2005). It is possible, in light of the above, that more than one species is involved, but during this study no consistent morphological or genetic pattern was identified. At this stage they can be treated either as ecotypes, or at best as slightly differentiated geographical forms, possibly warranting the status of subspecies. Any decision will, however, require a much more thorough geographically and genetically oriented study.

3.5. *Gnophodes heroni* Pyrcz & Collins, sp.n.

Fig. 3E–H

Diagnosis. This species most closely resembles *G. parmeno* from which it differs by its somewhat larger size, rounder FW with less produced apical area, and most noticeably, in the males, by the fact that the blackish brown ground colour of the upperside FW is the same as on the HW, whereas in *G. parmeno* the FW is blackish brown but the HW is lighter brown. In addition, the FW subapical band is better marked, lighter, and yellow instead of orange with a brownish cast, and displaced distally in relation to that of *G. parmeno*.

Description. ***Male*** (Fig. 3E,F): Wings: Forewing costa strongly arched, apex blunt, outer margin undulated with short extension along vein M1. Hindwing oval with undulated distal margin and spatulate extension along vein M3. Forewing upperside dark chocolate brown, slightly duller in basal and postbasal area, with oblique subapical, yolk-yellow, narrow, rather well-defined band, extended from costa nearly to tornus, and roughly triangular androconial patch in cell CuA1–1A/1B (Fig. 18D) covered with long, hairy scales. Hindwing upperside dark chocolate brown, almost uniform, except for some milky white-and-blackish scaling along distal margin. Forewing underside marbled in appearance, with complex pattern of patches of shades from milky white to blackish brown, with more prominent dark patches in postbasal, discal and postdiscal areas; apical area mostly whitish with some brownish suffusion, with series of four submarginal white dots. Hindwing underside mostly grey brown with some blackish brown pattern in and around discal cell and series of milky white submarginal dots, of which dot in Rs–M1 much larger than others, and surrounded with dark brown halo. ***Male genitalia*** (Fig. 10A,B): Tegumen dorsum very slightly humped; uncus stout, slightly curved downwards at basal one-third, one and a half times length of tegumen with sharp apical tip pointed downwards; gnathos vestigial but present, blunt; pedunculus long and prominent, pointed downwards; saccus long, same as in *G. parmeno* or *G. diversa* but shorter than in other species; valva slender and elongated, slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular. ***Female*** (Fig. 3G,H): Larger than male, lighter brown on upperside, with wider FWD subapical yellow band, heavily dusted with yellow scales on underside. ***Female genitalia*** (Fig. 14A–C): Papillae anales prominent, densely covered with thin hair; apophyses posteriores prominent, length of papillae width; lamella postvaginalis elongated slat-like with lateral flaps, extended into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized except in anterior part; ductus seminalis originating in middle; bursa copulatrix medium sized, with smooth surface, two parallel signa half-length of bursa. ***Early stages*** (Figs. 24N–P; 25C): Larvae reported feeding on Elephant Grass, *Setaria* sp. Only fourth and fifth (final) larval instars are known.

Type material. Holotype ♂, 'CAMEROON, Moumekeng | Manengouba Mtn | W. Cameroon | Manjo | 4.-12.xi.2012 | ABRI leg.', 'ABRI-2018-4391', red label: HOLOTYPE | Gnophodes heroni | det. T. Pyrcz', (ABRI). - Paratypes 24♂, 24♀. 1♂, 1♀, 'NIGERIA | Cross River S. | Obudu Cattle Ranch | 14.iii.1986 | 1200 m | J. Wojtusiak leg.' (CEP-MZUJ); 5♂, 'NIGERIA | Obudu | 7.–11.iv.2007 | 1500 m', 'prep. genit. 1358_30.08.2018/K. Florczyk', 'ABRI-2018-4928' (ABRI); 5♀, 'NIGERIA | Obudu | ex ovo', 'prep. genit. 1381_03.09.2018/K. Florczyk', 'ABRI-2018-4929' (ABRI); 2♂,

'KENYA | Kakamega | 14.xi.1990 | J.I.W. Mullin leg.', 'prep. genit. 1357_30.08.2018/K. Florczyk', 'ABRI-2018-4927' (ABRI); 4♂, 'CAMEROON | Moumekeng | Mont Manengouba', 'prep. genit. 1359_30.08.2018/K. Florczyk', 'ABRI-2018-4930' (ABRI); 5♂, 'CAMEROON | Mt. Koupé' (ABRI); 2♂, 'CAMEROON, Koutaba' (ABRI); 2♂, 'CAMEROON | Tabenken | x.2008' (ABRI); 1♀, 'CAMEROON | Moumekeng, Mont Manengouba (ABRI); 3♀, 'CAMEROON, Mt. Koupé', 'prep. genit. 1382_03.09.2018/K. Florczyk', 'ABRI-2018-4936' (ABRI); 2♀, 'CAMEROON, Tabenken | iii.2010' (ABRI); 3♀, 'CAMEROON, Tabenken | iii.2012' (ABRI); 2♀, 'CAMEROON | Koutaba' (ABRI); 2♂, 'UGANDA | Kalinzu | vi. 1993' (ABRI); 1♂,'UGANDA | Kyeljolo | v. 2012', 'ABRI-2018-4892' (ABRI); 1♀, 'UGANDA | Katera | ix.1978' (ABRI); 1♀, 'UGANDA | Kalinzu | vi.1991' (ABRI); 1♀, 'UGANDA | Kalinzu | vi.1993', 'prep. genit. 1383_03.09.2018/K. Florczyk', 'ABRI-2018-4937' (ABRI); 1♀, 'UGANDA | Toro Province | Kibale National Park | 24.–29.vii.2012 | 1200–1250 m | R. Laskowski leg.' (CEP-MZUJ); 1♀, 'UGANDA | Kibale | iii.2013', 'ABRI-2018-4943' (ABRI); 1♀, 'UGANDA | Kibale | x.2014' (ABRI); 1♀, 'UGANDA | Kadam Mtn | Nakapiripirit | xi.2016', 'ABRI-2018-4941' (ABRI); 1♀, 'R. D. CONGO | Lubango | iii.2013', 'ABRI-2018-4942' (ABRI).

Comments. *Gnophodes heroni* can be easily confused with *G. parmeno*, especially when older, worn specimens are compared, and the original upperside blackish ground-colour of *G. heroni* turns dull. Analysis of the genitalia is sometimes the only reliable method of separating them, those of the females in particular being notably different.

This is a montane species with a widely disjunct distribution extending from western Kenya to easternmost Nigeria (Fig. 28). In Kenya it is reported only from the Kakamega forest. In Uganda it is known so far from three localities in the western part of the country, and in the Kivu province of the DR Congo. It also occurs in western Cameroon, where it is found in four localities, and finally across the Nigerian border on the Obudu Plateau.

From the data available so far, although geographic ranges of *G. heroni* and *G. parmeno* widely overlap (Figs. 27, 28); the two replace each other along an elevational gradient. Such a parapatric distribution does not exclude that they are locally syntopic, and such a situation apparently occurs in the Obudu Plateau, where the two are also locally found synchronically. Nevertheless, *G. heroni* has never been reported from localities below 1500 m, whereas *G. parmeno* is mostly a lowland species, rarely occurring above 1000–1200 m.

3.6. *Gnophodes grogani* Sharpe

Figs. 4A–D, 21

Gnophodes grogani Sharpe, 1901: 279. Type locality: Mushari, DRC. Type whereabouts unknown.

Diagnosis. *Gnophodes grogani* seems easily identifiable, which is true for the male characterized by the large tuft of androconial scales on the FWD (Fig. 18E); females could occasionally be confused with large individuals of *G. diversa*, however the two are not sympatric.

Redescription. ***Male genitalia*** (Fig. 9A,B): Tegumen dorsum humped, similar to *H. chelys*; uncus stout, arched, twice length of tegumen with sharp apical tip pointed downwards, similar to *H. chelys*; gnathos absent; pedunculus prominent but shorter than in *H. chelys* or *H. pythia*, similar to *H. harpa* pointed downwards; saccus long and straight, as in *H. chelys*; valva slender, nonetheless noticeably wider in basal half than in other species, elongated, slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular. ***Female genitalia*** (Figs. 11A,B; 17A): Papillae anales prominent, densely covered with thin hair, with pseudo-apophyses; apophyses posteriores prominent, length of papillae width; lamella postvaginalis slat-like with lateral flaps, extended into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized except in anterior part; ductus seminalis originating in middle; bursa oval, copulatrix medium sized, with smooth surface, two parallel signa one-third length of bursa. ***Early stages*:** Not known.

Material examined. D.R. CONGO: Prov. Nord Kivu: 1♂: Butuhe Terr. Beni, iii.1986, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, ii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, iii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 2♂ and 1♀: Butuhe Terr. Beni, iii.1986, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, ii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, iii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 2♂: Bikara, (ANHRT); 1♂: Muleke Terr., 2000 m, 09.ii.2003, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, xi.1997, 2000 m, coll. R. Ducarme, prep. genit. 1678_20.03.2019/K. Florczyk (CEP-MZUJ); 1♀: Terr. Beni Mihunga, iii.1996, 1600 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, iii.1986, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, v.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, xi.1997, 2000 m, prep. genit. 1678_20.03.2019/K. Florczyk, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Beni Mihunga, iii.1996, 1600 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, iii.1986, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, v.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Mamove (ANHRT); Prov. Sud-Kivu: 5♂: Kanyambia, viii.2011, prep. genit. 1352_28.08.2018/K. Florczyk, ABRI-2018-4909 (ABRI); 16♂: Muleke (ABRI); 9♂: Biakara, x.2011, prep. genit. 1351_28.08.2018/K. Florczyk, ABRI-2018-4907 (ABRI); 2♂: Butuhe (ABRI); 1♂: Bukavu (ABRI); 1♂: Maboya (ABRI); 4♂: Nyungwe (ABRI); 8♀: Kanyambia (ABRI); 15♀: Muleke, prep. genit. 1368_31.08.2018/K. Florczyk, ABRI-2018-4908 (ABRI); 12♀: Biakara (ABRI); 7♀: Butuhe, (ABRI); 3♀: Kahusi (ABRI); 1♀: Bukavu, (ABRI); 1♀: Chibumbiro (ABRI); 1♀: Mabeloko (ABRI); 10♀: Nyungwe, iii.2007, 1600–1800 m, prep. genit. 1369_31.08.2018/K. Florczyk, ABRI-2018-4910 (ABRI); 1♀: Kanyambi (ANHRT); **RWANDA:** Bururi (ABRI); 2♂: Kigezi, vi.1978, coll. S. Collins, ABRI-2018-4883 (ABRI); 2♀: Bururi (ABRI); **UGANDA:** 1♀: Kigezi, vi. 1978, coll. S. Collins, ABRI-2018-4884 (ABRI); **BURUNDI:** 2♂: Ndora (ABRI); 1♀: Ndora (ABRI); 1♀: Rusarenda (ABRI).

Comments. *Gnophodes grogani* is a typical montane species, apparently replacing *G. parmeno* and locally *G. heroni* at high elevations, above 1800–2000 m. It is found in western Uganda, Rwanda, Burundi and eastern RDC. No data are available from Tanzania where it could occur in some patches of montane forest north of Kigoma.

3.7. *Haydonia* Pyrcz & Collins, gen.n.

Type species: *Papilio chelys* Fabricius, 1793.

Derivatio nominis. Name gender: feminine. This genus is named after the British lepidopterist and diplomat Haydon Warren-Gash who has contributed enormously to the knowledge on African Rhopalocera.

Diagnosis. Adults of the genus *Haydonia* gen.n. differ from the most closely related *Gnophodes* or *Melanitis* by a series of characters. Most immediately, the males have large, white, oval reflector patches on FWD and HWD postbasal to median areas, as compared with the FWD brown andoconial patch of *Gnophodes*, that on the HWD anal fold in *Ducarmeia* gen.n., and none at all in *Melanitis*. In addition, the HW anal margin is strongly produced as compared with the straight or slightly convex margin found in *Gnophodes* or *Melanitis*. The venation pattern is similar to *Gnophodes* except for the much longer discal-cell Rc + R–Rs vein. Both sexes of *Haydonia* lack any well-developed ocelli on their wings ventral surface, as with *Melanitis*, but contrary to *Gnophodes*. Sexual dimorphism is much more pronounced in *Haydonia* than in *Gnophodes*, *Melanitis* and *Ducarmeia.*

Description. ***Adults*:** Large size with FW length from base to apex between 3.5–4.5 cm. Venation (Fig. 23A): Forewing with 5 radial veins, and base of M1 and M2 independent but close to each other; humeral vein arises from Sc + R at root of discal cell, as in *Gnophodes*, but unlike *Ducarmeia* and *Melanitis*, where it arises distally. Wings with outer margin strongly produced at forewing vein M2 and occasionally also at CuA1, and at hindwing vein M3. Sexual dimorphism strongly marked, female considerably larger, lighter coloured, and mostly immediately differing by colours of subapical markings. Forewing anal margin convex in males, straight in females. Upperside colour pattern simple, mostly brown, with transverse subapical band, orange in males, yellow or white in females, without ocelli. Underside cryptic, with different shades of brown, and ocellar elements reduced to tiny dots on both fore and hindwings. Large, oval or elongated reflector patch made up of snow white scales on forewing underside along vein 2A, and on hindwing upperside along upper edge of discal cell. ***Male genitalia*:** Simple with long uncus ended with sharp tip, atrophied gnathos, long, slender and smooth valvae, deep saccus and straight, smooth tubular aedeagus. ***Female genitalia*:** Long, sharp and thin posterior apophyses, little sclerotized post and antevaginal lamellae, very long ductus bursae opening sharply into large, ovoid corpus bursae with very long, thin double signa.

3.8. *Haydonia chelys* (Fabricius), comb.n.

Fig. 5A–F

Papilio chelys Fabricius, 1793: 80. Type locality: Uganda ("India"). Type whereabouts unknown.

Diagnosis. *Haydonia chelys* comb.n. is recognized from the most closely related *H. pythia* stat.reinst. by the larger size, especially of the males, more strongly protruded outer margins of the FW along veins M2 and CuA1, and in the males, more conspicuous and better marked FWD subapical orange bands. Additionally, females of *H. chelys* are polymorphic with, in some cases, a bluish shiny reflection on the upperside, which can be quite intense in some specimens, whereas the females of *H. pythia* are invariably dull brown.

Redescription. ***Male*** (Fig. 5A,B,E,F): As illustrated. ***Male genitalia*** (Fig. 8D,E): Tegumen dorsum dome-like; uncus stout, arched, twice length of tegumen with sharp apical tip pointed downwards; gnathos absent; pedunculus long, pointed downwards; saccus long and straight; valva slender and elongated, slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular with slightly flattened and wider apex. ***Female*** (Fig. 5C,D): As illustrated. ***Female genitalia*** (Figs. 11C,D; 12A): Papillae anales prominent, densely covered with thin hair, with pseudo-apophyse extensions; apophyses posteriores long, length of papillae width; lamella postvaginalis small, shovel-like, extending into well-sclerotized anterior edges of sternite 9 (Fig. 11D); ductus bursae long, weakly sclerotized, slightly wider in anterior part; ductus seminalis originating in middle; bursa copulatrix large, oval, with smooth surface, and two parallel signa two-thirds length of bursa. ***Early stages*** (Figs. 24A–G; 25B): Only species of *Haydonia* for which entire life cycle has been recorded, although not formally described. Eggs are laid in clusters. First and second stage larvae are gregarious; later stages solitary. Larvae feed on *Setaria* sp.

Material examined. KENYA: Western Province: 1♂: Kakamega, Yala River, 29.ii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 1♂: Kakamega, Yala River, 02.iii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 1♂: Kakamega, Yala River, 28.ii.2012, 1550–1600 m, T. Pyrcz leg., prep. genit. 519_24.03.2017/J. Lorenc (CEP-MZUJ); 1♂: Kakamega, Yala River, 01.iii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 17♂: Kakamega, 29.xii.1994, coll. S. Collins, ABRI-2018-4849 (ABRI); 3♀: Kakamega, Yala River, 01.iii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 1♀: Kakamega, Yala River, 28.ii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 1♀: Kakamega, Yala River, 02.iii.2012, 1550–1600 m, T. Pyrcz leg. (CEP-MZUJ); 27♀: Kakamega, 29.xii.1994, coll. S. Collins, ABRI-2018-4847, ABRI-2018-4848 (ABRI); **UGANDA:** 1♂: Katera (ABRI); 1♂: Mubende dist., Kaweri, 18–30.i.2016, 1250–1300 m, B. Balyegenira leg. (CEP-MZUJ); 1♂: Kayanzu (ABRI); 3♂: Itwara, vi.1993, 1400 m, ABRI-2018-4872 (ABRI); 1♂: Kalinzu (ABRI); 1♂: Kibale (ABRI); 1♂: Bwindi Forest, 1750 m, 26–27.i.2014, A.E. & H.B. Warren Gash leg. (HWG); 2♀: Central-Mpigi, Mpanga Forest, 01–14.ix.2016, 1150–1200 m, T. Pyrcz leg. (CEP-MZUJ); 1♀: Toro Province, Kibale Forest, iv.2017, 1600 m, B. Balyegenira leg. (CEP-MZUJ); 1♀: Katera (ABRI); 1♀: Kayanzu, xi.1977, ABRI-2018-4873, coll. S. Collins (ABRI); 2♀: Itwara (ABRI); ABRI; 2♀: Kalinzu (ABRI); 1♀: Semiliki (ABRI); **D.R. CONGO:** Prov. Nord-Kivu: 1♂: Terr. Lubero, Musasa, iv.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, ii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 2♂: Terr. Lubero, Kasugho, ii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasuo, iii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke, Terr. Beni,

iii.2005, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Musasa, iv.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Butuhe Terr. Beni, ii.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 2♂: Terr. Lubero, Kasugho, ii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasuo, iii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke, Terr. Beni, iii.2005, 2000 m, coll. R. Ducarme (CEP-MZUJ); 13♂: Muleke, iii.2013, 1600 m; ABRI-2018-4869 (ABRI); 12♂: Kasuo, ii.2012, prep. genit. 1353_28.08.2018/K. Florczyk, ABRI-2018-4911 (ABRI); 2♂: Botuhe (ABRI); 3♂: Kibale, Kivu (ABRI); 4♂: Kirima, Kivu (ABRI); 1♂: Maliva (ABRI); 4♂: Maboya (ABRI); 3♂: Lubango (ABRI); 1♀: Terr. Lubero, Musasa, iv.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, ii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Muleke, Terr. Beni, ii.2005, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀:Terr. Lubero, Kasuo, iii.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, v.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, iv.2004, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Musasa, iv.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, ii.2008, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Muleke, Terr. Beni, ii.2005, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, iii.2015, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Butuhe Terr. Beni, v.1998, 2000 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, iv.2004, 1800 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke Terr., Beni, Nord Kivu, 2000 m, 07.iii.2003, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke Terr., Beni, Nord Kivu, 2000 m, 12.ii.2003, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke Terr., Beni, Nord Kivu, 2000 m, 07.ix.2003, coll. R. Ducarme (CEP-MZUJ); 1♂: Muleke Terr., Beni, Nord Kivu, 2000 m, 09.ii.2003, coll. R. Ducarme (CEP-MZUJ); 1♀: Muleke Terr., Beni, Nord Kivu, 2000 m, 06.ii.2003, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kirima, 1700 m, 22.i.2014, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kirima, 1700 m, 06.xi.2013, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kibale, 1900 m, 06.v.2016, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kibale, 1900 m, 20.v.2016, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kibale, 1900 m, 05.v.2016, coll. R. Ducarme (CEP-MZUJ); 2♀: Terr. Lubero, Kibale, 1900 m, 29.iv.2016, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasuo, 1800 m, 07.ix.2008, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Lubero, Kasuo, 1800 m, 06.iv.2008, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Lubero, Kasuo, 1800 m, 23.iv.2010, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Beni, Butuhe, 2000 m, 20.i.1999, coll. R. Ducarme, prep. genit. 2576_30.03.2020/K. Florczyk, (CEP-MZUJ); 1♀: Terr. Beni, Butuhe, 2000 m, 12.ii.1999, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Beni, Butuhe, 2000 m, 21.i.1999, coll. R. Ducarme (CEP-MZUJ); 5♀: Kasuo, Kivu, iii.2013, prep. genit. 1370_31.08.2018/K. Florczyk, ABRI-2018-4912 (ABRI); 1♀: Nord Kivu, Beni, ii.2011 (ANHRT); Prov. Sud-Kivu: 8♀: Muleke, vi.2011, 1600 m, ABRI-2018-4867 (ABRI); 4♀: Botuhe, (ABRI); 3♀: Kibale (ABRI); 4♀: Lubero, (ABRI); 1♀: Mabungu (ABRI); 1♀: Biakatu, ix.2009, ABRI-2018-4871 (ABRI); 3♀: Kirima, (ABRI); 1♀: Bikava (ABRI); 1♀: Maliva (ABRI); 2♀: Maboya (ABRI); 1♀: Kiau, (ABRI); 2♀: Ituri, Biakoto, ix.2012 (ANHRT); 1♀: Mamove, (ANHRT); 1♂: Nord Kivu, Beni, ii.2011 (ANHRT); **CAMEROON:** 1♂: Mont Kupe, W. Cameroun, 04.ii.2010, prep. genit. 1364_30.08.2018/K. Florczyk, ABRI-2018-4875, MO (ABRI); 1♀: Mont Kupe, W. Cameroun (ABRI); 3♀: Koutaba, W. Cameroun, viii.2014, ABRI-2018-4874; 1♀: Mass du Mbamb, coll. S. Collins, prep. genit. 1374_31.08.2018/K. Florczyk, ABRI-2018-4920 (ABRI).

Comments. The type locality of *Haydonia chelys*, indicated as "India" is erroneous, as was the case for many African species described by Fabricius, and was rectified by Ackery et al. (1998) as Uganda. *Haydonia chelys* and *H. pythia* are separated ecologically. *Haydonia chelys* is an inhabitant of premontane and lower montane forests found at 1200–1800 m, whereas *H. pythia* stat.reinst. is a typical lowland species, generally occurring at sea level and not found above 1000–1100 m. *Haydonia chelys* has a wide but disjunct geographic distribution (Fig. 29). It is found in the highlands of East Africa from western Kenya (Kakamega), throughout higher elevations in Uganda and in eastern D.R. Congo Kivu Province. Its presence cannot be ruled out in NW Tanzania, Rwanda and Burundi. The second distribution area is the mountains of western Cameroon. It has not yet been recorded from the mountains of eastern Nigeria, but its presence there is probable.

— syn. *Gnophodes chelys* f. iris Bartel

Fig. 5G,H

Gnophodes chelys f. *iris* Bartel, 1905: 130. Type locality: Cameroon, Yaoundé ("Kamerun Hinterland, Jaunde-Station"). Type not examined.

This taxon was described originally as an individual form of the female of *Gnophodes chelys* characterized by having a wide violet-blue overcast of the wings upperside with the exception of the distal area. Such an individual form is, indeed, found rather frequently in the western Cameroonian populations of *H. chelys* as is in Kivu and, rarely, in western Uganda. It has not been reported from Kenya though. The intensity of the bluish overcast is variable, and in some individuals only some sparse scaling is noticeable, whereas in others both the fore and hindwings are nearly entirely blue. Such an individual variation is unique to *H. chelys* and was not found in *H. pythia* or *H. harpa*. The type of *iris* most probably does not come from Yaoundé exactly, where *H. chelys* does not occur, but from the nearby Mont Kala or another locality situated at a higher elevation north-westwards.

3.9. *Haydonia hassoni* Collins & Pyrcz, sp.n.

Fig. 6E–H

Diagnosis. The male of this species most closely resembles *H. chelys* but its forewing outer margins are more produced along vein M1, the upperside ground colour is lighter brown, and the underside has an intense yellow suffusion, especially on the forewing, its forewing subapical oblique orange band is wider with more diffuse edges.

Description. ***Male*** (Fig. 6E,F): Wings: Forewing distal margin strongly produced along vein M1 and moderately so along vein CuA1, anal margin S-shaped. Hindwing somewhat elongate, and squarish with prominent and sharply ending extension along vein M3. Forewing upperside chocolate brown, lighter and duller in discal cell and apical area, wide diffused light orange transverse, subapical band, slightly more intense along basal edge, spreading over to distal margin. Hindwing upperside me-

dium brown, almost uniform, except some dusting with greyish scales along distal margin, and oval snow-white patch extending from postbasal area to root of M1. Forewing underside dull brown heavily dusted with yellow and some orange in postdiscal and marginal areas. Hindwing underside mostly dull brown, dusted with yellow in basal and postbasal areas, with oblique, diffused golden postdiscal band, and series of whitish submarginal dots, one in each cell. ***Male genitalia*** (Fig. 10D): Tegumen similar to *H. chelys*; uncus marginally shorter and almost straight, also bearing sharp apical tip pointed downwards; gnathos absent; pedunculus long, pointed downwards; saccus long and curved upwards, longer than in *H. chelys*; valva slender and elongated, slightly narrower than in *H. chelys*, otherwise similar; aedeagus straight, smooth and tubular, similar to *H. chelys*. ***Female*** (Fig. 6G,H): Larger than male, with even more falcate FW outer margin, with white FWD subapical band, wider than in *H. chelys*. Underside pattern similar to male. ***Female genitalia*** (Fig. 13C,D): Papillae anales prominent, densely covered with thin hair, with pseudo-apophyses (Fig. 13D); apophyses posteriores long, length of papillae width; lamella postvaginalis small, shovel-like, longer than in *H. chelys*, extending into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized, slightly wider in anterior part; ductus seminalis originating in middle; bursa copulatrix medium size, considerably smaller than in *H. chelys*, oval, with joint at entrance of ductus, with rippled surface, and two parallel signa extending over nearly entire length. ***Early stages*:** Not known.

Type material. Holotype ♂, (orange label, printed): 'D.R. CONGO | Projet ICCN-NA-SEA | Katanga | Exploration du P.N.U. | riv.[er] Ntumbwa | 3/21.viii.2001 | M. Hasson and T. Bouyer | coll. ABRI | PNU 027', white label: 'ABRI-2018-4877' (ABRI). -Paratype 1♀. 1♀, 'D.R. CONGO | Projet ICCN-NA-SEA | Katanga | Exploration du P.N.U. | Lukima | vi.2001 | M. Hasson & T. Bouyer | coll. ABRI | PNU 020', white label: 'ABRI-2018-4878' (ABRI).

Comments. *Haydonia hassoni* sp.n. has so far only been recorded from the uplands of the Upemba National Park in Katanga. It is apparently a montane species. Although the elevation was not specified on the original labels, the collecting sites correspond to altitudes between 1600–1700 m. It most probably occurs throughout the mountainous region squeezed in between Lake Upemba and Lake Mweru. To the south and east its presence in Zambia is unlikely since no individual was reported from several rather well sampled areas of this country, and there are no mountains high enough to support cloud forest vegetation. Its northern distribution limit is however unknown, and its range may well extend along the western shores of Lake Tanganyika.

Haydonia hassoni is considered as a separate species because it cannot be associated with either *H. chelys* or *H. pythia.* On the one hand, its external morphology and similar, mountainous habitat indicate *H. chelys* as its closest relative, however on the other its female genital characters, especially the bursa with heavily rippled surface is much more like *H. pythia* or *H. harpa*, than the smooth bursa of *H. chelys*; and its signa, which extend over the entire length of corpus bursae, as in *H. pythia*, are considerably shorter in *H. chelys*.

3.10. *Haydonia pythia* (Fabricius) comb.n., stat.reinst.

Figs. 6A–D, 22

Papilio pythia Fabricius, 1793: 116. Type locality: Guinea. Type not examined.

Diagnosis. The characters that separate *H. pythia* from *H. chelys* are indicated under that species.

Redescription. ***Male*** (Fig. 6A,B): As illustrated. ***Male genitalia*** (Fig. 8C,F): Tegumen with flattened dorsum, considerably larger than in *H. chelys* or *H. hassoni*; uncus stout, one and a half-length of tegumen, slightly curved downwards, with sharp apical tip, as in *H. chelys* or *H. hassoni*; gnathos absent; pedunculus long, pointed downwards; saccus long and slightly curved, wider than in *H. chelys* and *H. hassoni*, shorter than latter species; valva slender and elongated, slightly narrower towards apex, with smooth dorsal surface and blunt tip, similar to *H. hassoni*; aedeagus nearly straight, smooth and tubular, without apparent flattening at tip. ***Female*** (Fig. 6C,D): As illustrated. ***Female genitalia*** (Fig. 12B,C): Papillae anales prominent, densely covered with thin hair, with pseudo-apophyses; apophyses posteriores long, length of papillae width; lamella postvaginalis small, shovel-like, longer than in *H. chelys*, extending into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized, slightly wider in anterior part; ductus seminalis originating in middle; bursa copulatrix large, same size as in *H. chelys*, oval, with rippled surface, with two parallel signa extending over nearly entire length. ***Early stages*:** Not known.

Material examined. NIGERIA: Bendel State: 1♂: Okomu Forest, 19.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 2♂: Okomu Forest, 13.ii.1986, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 19.v.1984, J. Wojtusiak leg. (CEP-MZUJ); 3♂: Okomu Forest, 21.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 20.ii.1985, J. Wojtusiak leg., prep. genit. 522_24.03.2017/J.Lorenc (CEP-MZUJ); 1♂: Okomu Forest, 14.xii.1985, J. Wojtusiak leg. (CEP-MZUJ); 2♂: Okomu Forest, x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 17.x.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 20.i.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 18.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 28.xi.1982, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 20.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♂: Okomu Forest, 20.v.1985, J. Wojtusiak leg., prep. wing 02_22.02.2018/K. Florczyk (CEP-MZUJ); 1♀: Okomu Forest, 20.v.1984, J. Wojtusiak leg. (CEP-MZUJ); 2♀: Okomu Forest, 19.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 15.xii.1985, J. Wojtusiak leg. (CEP-MZUJ); 2♀: Okomu Forest, 18.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 17.x.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 13.ii.1986, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 20.ii.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu

Forest, 22.ii.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 21.ii.1985, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest, 21.x.1984, J. Wojtusiak leg. (CEP-MZUJ); 1♀: Okomu Forest Reserve, J. Wojtusiak leg. (CEP-MZUJ); Cross River State: 1♀: Oban Hills, Ausambo, 20.iv.1985, J. Wojtusiak leg. (CEP-MZUJ); Ondo State: 1♀: Omo (ABRI); **CAMEROON:** 1♀: Kumba, ix.1982; 1♂: Central Province, Mbalmayo District, Ebogo, 13.iv.2013, 650–680 m, T. Pyrcz leg. (CEP-MZUJ); 1♂: Bimbia-Bonadikombo forest, 11.x.2016, 0 m, (BF IV 4 US7), prep.mol. 476/31.xii.2018, M. Murkwe, K.N. Ishmael, R. Tropek leg. (CEP-MZUJ); 1♂: Bimbia-Bonadikombo forest, 11.x.2016, 0 m, (BF IV 15 US7), M. Murkwe, K.N. Ishmael, R. Tropek leg. (CEP-MZUJ); 2♂: Mt. Kala (ABRI); 1♂: Nanga Ebok, Sanaga (ABRI); 2♂: Dja (ABRI); 1♂: Moloundou, SE. Cameroun (ABRI); 1♂: Nyazanga, S. Cameroun (ABRI); 2♂: Kumba, Mamfe (ABRI); 2♂: Mt. Cameroun (ABRI); 3♂: Ebogo, Nyong River, x.2000, ABRI-2018-4866; 3♂: Mt. Kamelon, Sangmelima (ABRI); 1♂: Mt. Eloumden, Yaounde (ABRI); 1♂: Mintom (ABRI); 2♂: Mt. Kupe, i.2015, ABRI-2018-4865; 14♂: Lolodorf, ex. Staudinger & Bang-Haas (SMTD); 1♀: Bimbia-Bonadikombo forest, 11.x.2016, 0 m (BF IV 12 US7), leg. M. Murkwe, K. N. Ishmael, R. Tropek (CEP-MZUJ); 1♀: Bimbia-Bonadikombo forest, 06.x.2016, 0 m (BF IV 15 US2), M. Murkwe, K.N. Ishmael, R. Tropek leg. (CEP-MZUJ); 1♀: Bimbia-Bonadikombo forest, 08.x.2016, 0 m (BF IV 11 US4), M. Murkwe, K.N. Ishmael, R. Tropek leg. (CEP-MZUJ); 1♀: Mt. Cameroun (SW slope), Bamboo camp III, 06–12.ii.2016, 350 m, prep. mol. 475/31.xii.2018, V. Maicher, Sz. Sáfián, S. Janeček, R. Tropek leg. (CEP-MZUJ); 2♀: Mt. Kala (ABRI); 2♀: Dja (ABRI); 1♀: Moloundou, SE. Cameroun (ABRI); 1♀: Kumba, Mamfe (ABRI); 2♀: Ebogo (ABRI); 1♀: Mt. Kamelon, Sangmelima (ABRI); 2♀: Mintom (ABRI); 1♀: Lolodorf (ABRI); 1♀: Ngoakelle, Yaounde (ABRI); 2♀: Mt. Mille, viii.2011, prep. genit. 1371_31.08.2018/K. Florczyk, ABRI-2018-4914, ABRI-2018-4864 (ABRI); 1♀: Mt. Messa, Yaounde, xii.1992, ABRI-2018-4856 (ABRI); 1♀: Dehane (ABRI); 12♀: Lolodorf, ex. Staudinger & Bang-Haas (SMTD); **D.R. CONGO:** Prov. Orientale: 1♂: Terr. Kisangani, Kisangani km 127, ii.1988, 600 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Kisangani, Kisangani km 127, ii.1988, 600 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Biakatu, xii.2009, 1000 m, coll. R. Ducarme (CEP-MZUJ); 2♂: Mont Hoyo (ABRI); 2♂: Ouesso (ABRI); 1♂: Beni (ABRI); 1♂: Okoy (ABRI); 1♀: Terr. Mambasa, Biakatu, xii.2009, 1000 m, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Biakatu, xii.2009, 1000 m, coll. R. Ducarme (CEP-MZUJ); 2♂: Biakatu, (ABRI); 3♂: Mapimbi, Ix.2009, ABRI-2018-4870 (ABRI); 1♂: Manzumba, Kivu (ABRI); 1♂: Mambasa, Kivu (ABRI); 1♂: Mamove, Kivu, 2012, prep. genit. 1365_30.08.2018/K. Florczyk, ABRI-2018-4921 (ABRI); Matuna, Kivu (ABRI); 1♂: Matumbi (ABRI); 1♀: Terr. Mambasa, Biakatu, xii.2009, 1000 m, coll. R.Ducarme (CEP-MZUJ); 1♀: Mont Hoyo (ABRI); 3♀: Biakatu, Kivu (ABRI); 2♀: Mamove, Kivu, 2013, prep. genit. 1377_03.09.2018/K. Florczyk, ABRI-2018-4922 (ABRI); 1♀: Matumbi (ABRI); 1♀: Beni, Kivu (ABRI); 1♀: Ouesso (ABRI); 3♀: Pateva (ABRI); 1♀: Dungu (ABRI); Prov. Nord-Kivu: 1♀: Mutwanga Terr. Beni, v.1999, 1200 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Mutwanga Terr. Beni, v.1999, 1200 m, coll. R. Ducarme (CEP-MZUJ); Prov. Shaba: 1♂: Katanga, Riv. Zenze, 22–30.vii.2003, Exploration du PNU, Projet ICCN-NA-SEA, Hasson and Bouyer leg.Nimba » [partly mislabeled] (ABRI); 6♂: Forêt Classée de Ziama, Massadou campsite, lowland forest, fruit-baited traps, 08–13.iii.2019, 550 m, Sz. Sáfián, G. Simonics, K. Florczyk leg. (CEP-MZUJ); 15♀: Dieke, Mt. Nimba, vi. 2016, prep. genit. 1372_31.08.2018/K. Florczyk, ABRI-2018-4916 (ABRI); **EQUATORIAL GUINEA:** 1♀: Moka, Bioko (ABRI); GABON: 1♂: Fougandou (ABRI); **LIBERIA:** 1♂: Putu Range, Sz. Sáfián leg. (ABRI); 3♂: Gola National Forest, Sz. Sáfián leg. (ABRI); 1♂: Nimba (ABRI); 4♀: Nimba Mountains, East Nimba Nature Reserve, Cellcom Road, 21.viii–03.ix.2017, 700–1100 m, Sz. Sáfián leg. (CEP-MZUJ); **TOGO:** 1♂: Kloto, ix.1996, ABRI-2018-4879, coll. S. Collins (ABRI); 1♀: Kloto, ix.1996, ABRI-2018-4880, coll. S. Collins (ABRI); **GHANA:** 1♂: Kibi (ABRI); 1♂: Pampusu (ABRI); 1♂: Tanu Ofin (ABRI); 4♂: Bonkro (ABRI); 1♂: RCA, Bamoloto, R. Lombaye (ABRI); 1♀: Kibi (ABRI); 1♀: Tanu Ofin (ABRI); 2♀: Bonkro (ABRI); 1♀: Sagamasse (ABRI); 2♀: Lipke (ABRI); 1♀: Bibiani (ABRI); 1♀: Bobiri (ABRI); RCA: 1♂: Bangui (ABRI); 1♀: Bamoloto, R. Lombaye (ABRI); **ANGOLA:** 1♂: Melago?, Cabinda, 3.iii.1984 (HWG); **IVORY COAST:** 1♂: Tai Forest, iv.1998, H. W-Gash leg. (HWG).

Comments. This species was described from West Africa, with Guinea specified vaguely as its type locality. No confusion with *H. chelys* is possible since only one species of these two occurs throughout the West African rainforest belt.

— **syn. *Gnophodes morpena*** Westwood, [1851]: 363. Type locality: Congo ("Congo, Ashanti"). Whereabouts of the type unknown.

In the short description of this taxon the characters underlined are those differentiating *G. morpena* from *G. parmeno*, and may very well apply to either *H. pythia* or *H. chelys*, of whose existence Westwood was, surprisingly, not aware. It was described from a vague locality: Congo and Ashanti (Ghana), and is considered here, tentatively, as a synonym of *H. pythia*.

— **syn. *Gnophodes pythia*** f. ***elucidata*** Grunberg, 1910: 469. Type locality: Equatorial Guinea. Whereabouts of the type unknown.

This taxon was described originally as a form of *Gnophodes chelys* from Equatorial Guinea. The description clearly states that the forewing subapical band of the female is white, which is a diagnostic character of *H. pythia* and *H. chelys*, the latter not occurring in Equatorial Guinea, so we treat it here as a junior synonym of *H. pythia*. A distinguishing characteristic mentioned in the description is the obscure russet colour of the forewing subapical band of the male. This is often found in Cameroonian, and more sporadically so in West African populations of *H. pythia*, although some variation occurs.

3.11. *Haydonia harpa* (Karsch), comb.n., stat.reinst.

Fig. 4E–H

Gnophodes harpa Karsch, 1893: 211. Type locality: Togo Bismarckburg (Adele). Holotype female not examined.

Diagnosis. Both sexes are considerably smaller than both *H. chelys* and *H. pythia*. FW inner margin slightly convex, not sigmoid as in the other two species. The FW outer margin is less produced. The discal cell is proportionally longer to the wing length. The underside is less patterned, predominantly greyish and lustrous. Females have a yellowish FW subapical band.

Redescription. ***Male*** (Fig. 4E,F): As illustrated. ***Male genitalia*** (Fig. 8A,B): Tegumen dorsum dome-like; uncus arched, slender and longer than in *H. chelys* or *H. pythia*, with sharp apex; gnathos absent; pedunculus prominent, pointed downwards; saccus long, but shorter than in *H. hassoni*, and nearly straight; valva slender and elongate, slightly narrower towards apex, with smooth dorsal surface and blunt tip; aedeagus straight, smooth and tubular with slightly flattened and wider apex. ***Female*** (Fig. 4G,H): As illustrated. ***Female genitalia*** (Fig. 13A,B): Papillae anales prominent, densely covered with thin hair, with pseudo-apophyses; apophyses posteriores long, length of papillae width; lamella postvaginalis small, shovel-like, extending into well-sclerotized anterior edges of eighth sternite; ductus bursae long, weakly sclerotized, slightly wider in anterior part; ductus seminalis originating in middle; bursa copulatrix medium size, slightly smaller than in *H. chelys*, oval, with rippled surface, with two parallel signa extending over two-thirds length of bursa. ***Early stages*** (Figs. 24Q–U; 25A): Last instar larvae were found feeding on *Setaria* sp.

Material examined. UGANDA: 5♂: Central-Mpigi, Mpanga Forest, 01–14.ix.2016, 1150–1200 m, T. Pyrcz, Sz. Sáfián leg., prep. genit. 520_24.03.2017/J.Lorenc, wing prep. 01_22.02.2018/K. Florczyk (CEP-MZUJ); 1♂: Toro Province, Kibale Forest, iv.2017, 1600 m, B. Balyegenira leg. (CEP-MZUJ); 2♂: Budongo, vi.1993, ABRI-2018-4836, ABRI-2018-4837, IB/PW leg. (ABRI); 1♂: Kalinzu, vi.1991, ABRI-2018-4838 (ABRI); 2♂: Kibale, Mahare, Kanyawara, 20–25.v.2014, ABRI-2018-4834, ABRI-2018-4835 (ABRI); 6♀: Central-Mpigi, Mpanga Forest, 01–14.ix.2016, 1150–1200 m, T. Pyrcz, Sz. Sáfián leg. (CEP-MZUJ); 2♀: Budongo, x.1990, ABRI-2018-4842, coll. S. Collins (ABRI); 1♀: Budongo, vi.1993, 900 m, ABRI-2018-4846 (IB/PW); 1♀: Kalinzu, vi.1993, 1500 m, ABRI-2018-4844, (IB/PW); 1♀: Kibale, 2008, ABRI-4841 (ABRI); 1♀: Fort Portal, xi.2007, ABRI-2018-4843, coll. B. Balegenyira (ABRI); 1♀: Itwara, vi.1993, 1400 m, ABRI-2018-4845 (IB/PW); **CAMEROON:** 7♂: Mintom, S. Cameroun, xii.2014, prep. genit. 1366_30.08.2018/K. Florczyk, ABRI-2018-4925 (ABRI); 2♂: Lolodorf (ABRI); 3♂: Ebogo Nyong River, x.2014, ABRI-2018-4851; 3♂: Mt. Kala (ABRI); 1♂: Mt. Eloundem, Yaounde (ABRI); 1♂: Garoua Boulai, vii.2010, ABRI-2018-4850, MO leg. (ABRI); 1♂: Mt. Kupe, 2011, prep. genit. 1354_28.08.2018/K. Florczyk, ABRI-2018-4913; 1♂: Moloundou, SE. Cameroun (ABRI); 1♂: Ntoudakoun, Magrebe, ix.2014, ABRI-2018-4858 (ABRI); 1♀: Central Province, Mbalmayo District, Ebogo, 08.iv.2013, 650–680 m, prep. genit. 521_24.03.2017/J. Lorenc, T. Pyrcz leg. (CEP-MZUJ); 1♀: Lolodorf (ABRI); 1♀: Ebogo (ABRI); 1♀: Mt. Kala (ABRI); 1♀: Garoua Boulai, vii.2010, ABRI-2018-4855 (MO); 2♀: Mt. Koupé (ABRI); 1♀: Adjap-Fang, S. Cameroun, x.2014, prep. genit. 1379_03.09.2018/K. Florczyk, ABRI-2018-4853 (ABRI); 1♀: Ntoudakoun, Magrebe (ABRI); **D.R. CONGO:** 1♂: Mamove, Kivu, viii.2014, ABRI-4857 (ABRI); 1♀: Biakoto (ABRI); C.A.R.: 2♂: Bimon, Bangui (ABRI); Prov. Orientale: 1♀: Terr. Kisangani, Kisangani km 127, ii.1988, 600 m, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Kisangani, Kisangani km 127, ii.1988, 600 m, coll. R. Ducarme (CEP-MZUJ); **TANZANIA:** 1♂: Kasye, Kigoma, iii.1994, ABRI-2018-4839, Ex. IB/PN, coll. S. Collins (ABRI); 1♀: Kasye, Kigoma, iii.1994, ABRI-2018-4840, Ex. IB/PN, coll. S. Collins (ABRI); **IVORY COAST:** 1♂: Danané (ABRI); 1♂: Yealé, v.1999 (HWG); **LIBERIA:** 2♂: Nimba Mountains, Nimba West, Gbapa lowland forest, 8–13.ii.2012, ABRI-2018-4859, Sz. Sáfián, M. Strausz leg. (ABRI); 1♀: Nimba Mountains, East Nimba Nature Reserve, Cellcom Road, 21.viii–03.ix.2017, 700–1100 m, Sz. Sáfián leg. (CEP-MZUJ); 1♂: Lofa County, Wologizi Mountains Wologizi Base Camp, lowland forest, 600 m, 8°7′16.48″N 9°57′41.52″W, 20-30.xi.2017, M. Aristophanous, Sz. Sáfián, G. Simonics, L. Smith leg. (ANHRT); **SIERRA LEONE:** 1♂: Belebu, Gola Forest Reserves, Sz. Sáfián leg. (ABRI); **GUINEA:** 3♂: Dieké, "Nimba" [partly mislabeled], vi.2016, prep. genit. 1362_30.08.2018/K. Florczyk, ABRI-2018-4915; prep. genit. 1367_30.08.2018/K. Florczyk, ex M. Arnoux, ABRI-2018-4926 (ABRI); 1♀: Dieké, vi.2016, prep. genit. 1380_03.09.2018/K. Florczyk, ex M. Arnoux, ABRI-2018-4861, ABRI-2018-4863 (ABRI); **GHANA:** 1♀: Eastern Region, Kyebi District, Sagyimaase forestry access road, Atewa Range, 19.xi–01.xii.2007, G. Csontos, J. Bodorik, E. Zakar leg. (ANHRT).

Comments. *Haydonia harpa* comb.n., stat.reinst. was originally described from Bismarckburg in central Togo as a separate species – *Gnophodes harpa* Karsch, 1893. It was not illustrated. Aurivillius in Seitz (1911) treated it as an aberration of the female of *Gnophodes chelys*. He also illustrated the female of this species as "*G. chelys* female" (Plate 26c). *Gnophodes harpa* was formally, but incorrectly, synonymized with *Gnophodes chelys* by Ackery et al. (1998). The description was based on a single female which, unfortunately, could not be located in NKM Berlin, although the types of Karsch should presumably be there (Lamas pers. comm.). Karsch (1893) compared his new species to several females of *Gnophodes chelys*, in fact *H. pythia*, including one from Bismarckburg. The original text, in German, specifies some characters of wing shape and colour pattern which unambiguously identify *H. harpa*. In particular, and most importantly, he noted that the FWD subapical band was yellowish and short, not reaching vein M3. This is a key distinction since in the females of *H. pythia*, throughout its wide range, this band in invariably white, and generally longer, reaching vein M3. He also referred to a row of six submarginal semi-transparent dots distally bordered with black. This is a further unique character of *H. harpa* not found in *H. pythia* or *H. chelys*. Additionally, he noted that the outer margin was less produced between veins M2 and M3 than in *H. chelys* (*H. pythia*). This wing shape feature is very characteristic of *H. harpa* and allows an immediate identification of this species. Other features are also mentioned but considered here to be of lesser taxonomic value. Not surprisingly, *H. pythia* and *H. harpa* were both collected in Bismarckburg. These two species are indeed sympatric in many localities, from Uganda (Mpanga) to Guinea (Ziama) (Figs. 29, 30). We examined in the ANHRT one female of *H. harpa* collected in the Atewa Range in central Ghana, approximately 200 km SW of Bismarckburg, matching exactly the description of Karsch.

The range of *H. harpa* extends from central Uganda (Mpanga Forest) through northern Tanzania, D.R.C., C.A.R., southern and eastern Cameroon through Togo, Ghana to Liberia and Guinea. Surprisingly, it is not known either from southern or central Nigeria, which was rather extensively sampled. Most data indicate that *H. harpa* is a premontane forest species with most records around 600–1000 m, which would partly explain its absence from southern Nigeria. There are however quite a few records from lower elevations in Sierra Leone (Gola For-

est), Guinea (Diecké Forest), and Ghana (Bonkro Conservation Area) from elevations below 500 m. It is also possible that it is associated with late Pleistocene refugial forests, since there is a correlation between the species geographic distribution and their probable extension.

— **syn. *Gnophodes minchini*** Heron, 1909: 143. Type locality: Uganda ("Entebbe"). Type whereabouts unknown.

This taxon was described by Heron (1909) from Entebbe in Uganda based on two males collected by Prof. E.A. Minchin, one of which depicted in a colour drawing showing both the upper and underside (plate V, fig. 3). It clearly corresponds with the species described some 15 years before by Karsch. Heron's (1909) original description of *G. minchini* was detailed and the comparison to *G. chelys*, pointing out the most diagnostic characters rather accurately, although some of them could not be confirmed. In particular Heron emphasized that "the patch of cream white scales (alar organ) in *G. minchini* is longer than in *G. chelys* and does not extend below vein 1; hindwing (pattern) differs from that of *G. chelys* in that the curved median line is more sinuous than zigzag and is less varied with pale blotches; FW costa is proportionally shorter and the external margin proportionally longer, the length of the cell is therefore relatively greater compared with the wing-length; vein 1 is strongly curved and subparallel with the internal margin, which forms a regular convex curve, whereas in *G. chelys* vein 1 is much straighter, while the internal margin is slightly sigmoid, that is with a S-like curvature". Also, he pointed out that "the hindwing with angulation at vein 3 is less pronounced and the distal angle of the cell less acute."
Aurivillius (in Seitz 1911) retained the specific status of *G. minchini* and placed it next to *G. chelys*. Subsequent authors did not deal with *(H)G. minchini* nor *(H)G. harpa* and, in a way, both names fell into oblivion, even though their status was never formally revised. They were both considered as junior synonyms of *Gnophodes chelys* in the Carcasson Catalogue of African Butterflies (Ackery et al. 1998). This point of view was strengthened by subsequent regional faunal studies of Kenya (Larsen 1991), West Africa (Larsen 2005) and Gabon (Vande weghe 2010), which implicitly confirmed their synonymy. We do not see any consistent morphological difference between the western and eastern populations which would justify retaining *minchini* as a subspecies of *H. harpa*, and there are no sufficient molecular data at this time, despite some detected genetic distances in COI between the two. Consequently *G. minchini* is here, formally, synonymized with *H. harpa*.

— **syn. *Gnophodes michini*** var. ***magniplaga*** Heron, 1909: 144. Type locality: Uganda ("E. Ruwenzori").

This taxon was described for one individual whose distinguishing feature is its large size of white patches. On the hindwing they approximately equal the area of the cell (14 × 5 mm), and extend to an equal distance from the base, the colour of the component scales being rather creamier than in the typical form. The patch above vein 1 on the forewing underside measures 13 mm, and is more "acuminate externally than in *G. minchini*". The size of white patches is somewhat variable and specimens matching this description were found in western Uganda (Kibale, Fort Portal), thus we confirm *magniplaga* as an individual variation of *H. harpa*.

3.12. *Ducarmeia* Pyrcz, gen.n.

Type species: *Melanitis ansorgei* Rothschild, 1904.

Derivatio nominis. Name gender: feminine. This genus is named after Robert Ducarme whose study of the butterflies of the Eastern Congo and Albertine rift is peerless.

Diagnosis. Sexual dimorphism barely noticeable, even less so than in *Melanitis* or *Gnophodes*. Adult wing shape most similar to *Melanitis*. Differs from other genera of Melanitini in the longer discal cell proportionally to length of radial, median and cubital veins, as well as in the forewing M1 and M2 veins arising independently and widely separated. The male most immediately differs from other Melanitini in the presence of a sex organ, a small, elongate, milky white patch on hindwing abdominal fold.

Description. *Adults*: (Fig. 7A–D) Medium, with FW length from base to apex between approximately 4 cm. Venation (Fig. 23C): forewing with 5 radial veins, base of M1 and M2 independent and widely separated, unlike *Melanitis*, *Gnophodes* and *Haydonia* gen.n. The root of humeral vein arises from Sc + R from root of discal cell, similarly to *Melanitis*, but differing from *Gnophodes* and *Haydonia*, in which it arises distally. Discal cell proportional to length of radial, median and cubital veins much longer than in *Melanitis*, *Gnophodes* and *Haydonia*. Wings outer margin strongly produced at forewing vein M2 and hindwing vein M3. Sexual dimorphism slight, expressed in slightly larger size and lighter colours of female. Upperside colour pattern simple, violet blue with short transverse white band, without ocelli. Underside cryptic, with different shades of brown and grey; ocellar elements reduced to tiny, whitish subapical dots on both fore and hindwings. Small, elongate, milky white patch on hindwing abdominal fold. ***Male genitalia*** (Fig. 10F): Simple with long uncus ended with sharp tip and basal, ventral protrusion, atrophied gnathos, long, slender and smooth valvae, deep saccus and straight, smooth tubular aedeagus. ***Female genitalia*** (Fig. 17C): Long, sharp and thin posterior apophyses, little sclerotized post and antevaginal lamellae, very long ductus bursae opening gradually into large, balloon like corpus bursae very long, extending over three-quarters length of bursa, double signa.

Comments: For comparison, adults (Fig. 7E–H) and wing venation pattern of *Melanitis libya* (Fig. 23D) prep. wing 04a/b_04.09.2019/K.Florczyk; and male and female genitalia of *Melanitis leda* (Figs. 10E; 17B) are illustrated.

3.13. *Ducarmeia ansorgei* (Rothschild), comb.n.

Fig. 7A–D

Redescription. See under genus description.

Material examined. **D.R. CONGO:** Prov. Orientale: 1♂: Terr. Beni, Eriageti, 1100 m, iii.2010, coll. R. Ducarme (CEP-MZUJ); Province Orientale: 1♂: Terr. Mambasa, Epulu, 850 m, vii.2004, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Afarama, 850 m, 09.xi.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Afarama, 850 m, 10.xi.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Epulu, 850 m, 20.xi.2005, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Teturi, 875 m, 25.v.1995, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Teturi, 875 m, 31.x.2005, coll. R. Ducarme (CEP-MZUJ); Terr. Irumu, Mont Hoyo, 1400 m, ii.1999, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Irumu, Mont Hoyo, 1400 m, ii.1999, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Mambasa, Manzumbu, 900 m, 08.viii.2008, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Mambasa, Biakatu, 1000 m, 31.v.2008, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Mambasa, Biakatu, 1000 m, xii.2009, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Irumu, Mont Hoyo, 1400 m, 12.ii.1998, coll. R. Ducarme prep. genit. 1718/07.05.2019 K. Florczyk (CEP-MZUJ); 1♀: Terr. Irumu, Mont Hoyo, 1400 m, ii.1999, coll. R. Ducarme, prep. genit. 1719/07.05.2019 K. Florczyk (CEP-MZUJ); 1♂: Terr. Mambasa, Biakatu, 1000 m, 10.xi.2009, coll. R. Ducarme (CEP-MZUJ); 1♂: Terr. Mambasa, Biakatu, 1000 m, 18.vi.2002, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Mambasa, Biakatu, 1000 m, 19.ii.2004, coll. R. Ducarme (CEP-MZUJ); 1♀: Terr. Beni, Beni, 1150 m, 06.xi.1999, coll. R. Ducarme (CEP-MZUJ); Prov. Haut Zaire: 1♂: Mapimbi, 1150 m, xi.1995, coll. R. Ducarme, prep. wing 02a/b_03.09.2019/K. Florczyk (CEP-MZUJ); 1♂: Mapimbi, 1150 m, 21.i.1995, coll. R. Ducarme (CEP-MZUJ); 1♂: Mapimbi, 1150 m, 10.xii.1994, coll. R. Ducarme (CEP-MZUJ); 1♀: Mapimbi, 1150 m, 22.xii.1994, coll. R. Ducarme (CEP-MZUJ); **CAMEROON:** 1♂: Region Centre, Ebogo, 650–670 m, 2014, A. Awoumou leg., prep. genit. 1406_02.10.2018/K. Florczyk (CEP-MZUJ); 1♂: Mont Kala, 20 km W de Yaoundé, 900–1150 m, 6.x.1972, P. Darge leg. (HWG); **IVORY COAST:** 1♂, 1♀: Danané 4/76 M.A., coll. S.C. Collins (ABRI).

Comments. The new genus *Ducarmeia* is monobasic and erected for *Melanitis ansorgei*. Larsen (2005) had earlier expressed his doubt about the correct placement of this species in the genus *Melanitis,* highlighting the unusual placement of the alar organ on the hindwing abdominal fold (Fig. 19). Considering the presence of this strong apomorphic character, and the differences in female genitalia, not examined before this study, between this species and representatives of *Melanitis*, and in the molecular data, there are strong grounds for the validity of *Ducarmeia*.

Ducarmeia ansorgei presents an unusual distribution pattern (Fig. 31). It has long been known from D.R. Congo where numerous populations are found in the eastern provinces Congo Oriental, Nord Kivu and Sud Kivu, and it is not uncommon in well preserved patches of premontane rainforest, generally at some 1000–1200 m. Some specimens were, however, also reported from Uganda, C.A.R., and recently also from Ivindo and the coast in Gabon (Vande weghe 2010) and from Ebogo in Cameroon (Larsen 2005). In these countries, *D. ansorgei* is seldom collected and considered rare. However the use of baited traps in the deep forest undergrowth shows that this species may occur at high abundance, at least locally. Interestingly, *D. ansorgei* was also caught in a series of specimens near Danané, Ivory Coast, an extremely disjunct location from the main distribution area of the species (Larsen 2005). These records cannot be considered mis-labelled, as in the 1970s, M. Auberger collected a couple of other unique taxa there (e.g. *Hypolimnas aubergeri* Hecq, 1987, *Euphaedra aubergeri* Hecq, 1977), all of which proved valid and confirmed by recent captures from the same area (Sáfián & Hitoshi 2019).

The wider Nimba Mountains area, part of which Danané could be considered is also known from a number of recently discovered endemic species, which has their closest relatives distributed in the Cameroon Highlands or in Central Africa (e.g. *Pilodeudorix mano* Sáfián 2015, *Junonia agnesberenyiae* Sáfián 2018, *Bettonula bettoni nimba* Collins & Larsen, 2000 (Collins & Larsen 2000; Sáfián et al. 2015; Sáfián 2019). However, no morphological differences are found between the Danané population of *D. ansorgei* and specimens from Cameroon and no molecular results were available to compare the two.

3.14. Molecular studies

COI data were obtained for all five species of *Gnophodes sensu novum* and for three out of four species of *Haydonia* gen.n. A phylogram (Fig. 26) generated by the ML method shows that the two genera are monophyletic with high bootstrap support values, and are sister-clades. The genus *Melanitis* is sister to *Haydonia* + *Gnophodes* and *Ducarmeia* is resolved as external in relation to this clade. *Gnophodes heroni* sp.n. is situated internally within *G. diversa*. Other species are well-supported by COI. Results of this molecular study are preliminary since only one genetic marker was taken into account.

4. Discussion

African Melanitini, and the genus *Gnophodes* in particular, have been neglected for many decades. They were considered as not very diverse, comprising widespread and common species, with the exception of the endemic *G. grogani*, and hence of little taxonomic or biogeographic interest. This study demonstrates that such a point of view does not reflect the reality. On the contrary, not only are there four genera involved, and twice as many species as previously recognized, but also that the group is of undoubted interest because of the intricate geographic and

altitudinal distribution pattern, as shown by the evidence provided in this paper.

The validity of the genera described here is well-supported by morphological and molecular data. Larsen (2005) retained *Gnophodes* as separate from *Melanitis* based on "specialized androconial structures". The examination of specialized scale patches in African Melanitini reveals however that they are probably not composed of (nor associated with) androconial scales. Androconia are male scales which are involved in chemical communication (Kristensen & Simonsen 2003). Here, the thickly packed-up white scales that make up the specialized patch in the HWD anal fold of *Ducarmeia ansorgei* are morphologically different from cover scales, but no specialized pheromone producing structures were detected. The same applies to *Haydonia*. However in *Gnophodes*, these patches are made up of hairy scales which cover the second layer of cover scales, and which are morphologically similar to some specialized scale patches in the genus *Bicyclus*, identified as androconial and pheromone disseminating (Brattström et al. 2015, 2016). According to Faynel & Bálint (2016), all the patches made up of various scales other than cover scales, are classified as broadly alar organs. In this particular case they are made up of structural colour generating scales, which simply function as light reflectors for visual communication, as all species inhabit dark forest interior and they might even express crepuscular courting behaviour and not forming androconia. Males of *Haydonia chelys*, *H. pythia* (Fig. 18A,B), *H. harpa* and *H. hassoni* sp.n. have large, oval reflector patches composed of snowy white scales on FWV 1A/1B vein and HWD Rs to discal cell. Instead, males of *Gnophodes betsimena*, *G. parmeno*, *G. diversa* (Fig. 18F), *G. heroni* sp.n. (Fig. 18D) and *G. grogani* (Fig. 18E) have FWD typical androconial patches covered with tufts of long hairy scales in space CuA2 – 1A/1B. Reflector patches are a character in identifying *Ducarmeia* (Fig. 18C) as different from *Melanitis*. Two Afrotropical species, *M. leda* and *M. libya* have no androconial nor reflector patches, as is also the case in the Oriental representatives of the genus. Interestingly, such a placement of the reflector patch is also found in the Oriental, monobasic genus *Parantirrhoea*.

The morphology of male genitalia of Afrotropical Melanitini, and generally speaking of all Melanitini is highly homogenous. Intraspecific differences are mostly quantitative rather than qualitative, in the length of the saccus, the shape of the uncus or the tegumen. Nonetheless, some characters are unique, for example the presence or absence of a rudimentary gnathos. Based exclusively on male genitalia *Gnophodes* is not separable from *Haydonia* gen.n., but also other genera, including *Ducarmeia* gen.n. and *Melanitis* and *Bletogona* lack any distinctive, synapomorphic characters.

On the other hand, the female genitalia provide more consistent informative characters, in particular the shape of bursa copulatrix, signa and ductus bursae, providing a firm basis for distinguishing between the genera and between species that are externally quite similar, for example *G. parmeno* and *G. heroni* sp.n. Interestingly, in *Melanitis* and *Bletogona* the signa are condensed, short and oval indicating their closer phyletic relationships, whereas in *Haydonia*, *Gnophodes* and *Ducarmeia* they are typically elongate and parallel. The surface of the bursa is also quite different between closely similar *H. pythia* on the one hand, with a smooth surface, and *H. chelys*, *H. hassoni* sp.n. and *H. harpa* where it is heavily rippled. Moreover, an additional character for female genitalia was identified, called here pseudo-apophyses – present in *Haydonia* and, rudimentarily, in *Gnophodes grogani* only. Therefore, once again sexual characters have proved to be an extremely helpful source of information in alpha-taxonomy, and in assessing phyletic relations within the genus.

A preliminary molecular analysis of the available sequences of COI for all five species of *Gnophodes*, three out of four species of *Haydonia* as well as for *Ducarmeia ansorgei* comb.n., and two species of *Melanitis* species shows that *Gnophodes* and *Haydonia* are sister-clades with high branch support, and that *Ducarmeia* does not aggregate with *Melanitis* (Fig. 26). It has to be said that COI sequences were available for only two species of *Melanitis* including one from Asia. Nevertheless, preliminary molecular data offer good support for our findings based on adult morphology in relation to the separate generic status of *Gnophodes*, *Haydonia* and *Ducarmeia*.

Larsen (2005) provided a brief comparison of the larvae of *Gnophodes* and *Melanitis* but does not indicate the species concerned. Accordingly, those of *Gnophodes* have shorter and more erect horns on the first segment. Partial information on larval stages in known for three species of African Melanitini, and the entire life cycle was recorded for *H. chelys* only, early stages of the remaining species are currently not known. Therefore, only mature larvae can be compared. Although basically similar, they show consistent differences in colour patterns, in particular in the alignment and colours of lateral stripes, allowing the identification of the species.

The genera *Gnophodes* and *Haydonia* comprise several species with disjunct premontane/montane East – West African distributions, two of which, *H. chelys* and *G. heroni,* extend into the highlands of western Cameroon, and *H. harpa* even further westward, into the Guinea Highlands in the Liberian sub-region. Also, interestingly, *D. ansorgei* apparently presents a widely disjunct pattern with its main range in the higher areas surrounding the Congo Basin, but also occurring in the hilly country near the Nimba Mountains in West Africa. The recent discovery of various endemic taxa in the Nimba Mountains or in the wider Guinea Higlands with disjunct distribution from their closest relatives is quite spectacular. Such a pattern among African butterflies seems to be much more frequent than previously expected. Recently, a number of similar distribution patterns were uncovered among less conspicuous skippers (Larsen, unpublished) and lycaenids, and *Mylothris pierids* (Warren-Gash et al. 2020). When discussing West African origins of otherwise primarily East African montane species, two stand-

ard hypotheses have to be considered, vicariant and dispersalist. *Gnophodes* and *Haydonia* are inhabitants of the forest understory, and it was stressed that they are usually very sedentary and move little from some well-defined spots, where some individuals aggregate in larger numbers. Considering this behaviour and ecological preference, they have to be assumed as very unlikely dispersalists over non-forested areas.

5. Acknowledgements

The authors would like to thank the following persons: Dorota Lachowska-Cierlik (UJ Kraków) for assisting with DNA extraction, Jadwiga Lorenc-Brudecka (UJ Kraków) for additional genital dissections, Ewelina and Karolina Sroka (UJ Kraków) for setting and organizing the material, Gyula László (ANHRT Leominster), Zsolt Bálint (NHM Hungarian Academy of Sciences Budapest), Matthias Nuss (STKM Dresden) and Theo Leger (NKMB Berlin) for their cooperation and the loan of material. This study was partly supported by the internal grant of the Jagiellonian University (K/ZDS/007357). Keith Willmott (FLNMH, Gainesville) provided the illustrations of *Bletogona* male and female genitalia. Additional information from Upemba, D.R. Congo was kindly provided by Thierry Bouyer. Material from Upemba National Park was collected during the realization of the Project ICCN-NA-SEA, whereas the specimens from Mount Cameroun were collected by Robert Tropek, Vincent Maicher, Sylvain Delabye, Mercy Murkwe and Jan Mertens within the project founded by the Czech Science Foundation (14-36098G) and the Grant Agency of the University of South Bohemia (GAJU 030/2016/P and 152/2016/. Material for analysis from Madagascar was kindly provided by Annemarie Würz from the Georg August Universitat Goettingen, and by Haydon Warren-Gash, who also kindly critically read the manuscript. Crucial study material from D.R.C. was donated by Robert Ducarme. Molecular analysis was partly performed at the Molecular Laboratory of the Nature Education Centre (CEP-UJ). Photographs of the early stages were taken by Colin Congdon and Freerk Molleman. We are grateful to the various authorities for issuing research and collecting permits within their jurisdictions: in Cameroon, the Ministere de Recherche Scientifique et de l'Innovation, 0002/MINRESI/B00/C00/C10/C14 and Ministere des Forets et de la Faune, 0060/PRS/MINFOF/SG/DFAP/SDVEF/S.C.; in Ghana, the Forestry Commission, Wildlife Division, 026575, ND/A-07/vol.57; in Guinea, Direction Générale de la Conservation de la Nature, 00095/GAI/27.06.2017; in Liberia, the Forestry Development Authority, MD/176/2018-1; in Madagascar, Ministere de l'Environnement, de l'Ecologie et des Forets (MEEF), No. 018/18, MEEF/SG/DGF/DSAP/SCB, 29/10/2017; n°254/18/ MEEF/SG/DGF/DSAP/SCB, 11/10/2018; in Mozambique: E.O. Wilson Biodiversity Laboratory, Chitengo, Gorongosa National Park, 19/2018; in Uganda, the Uganda Wildlife Authority, EDO/35/01, and to all other local entities.

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Table 1. The list of samples used in phylogenetic analysis.

Accession	*Genus*	*species*	Country	Region	Locality	Specimen in	Sequence source
MT320541	*Gnophodes*	*betsimena*	Madagascar	Antsiranana	Marojejy N.P.	CEP-MZUJ	this study, AZ-302
MT320542	*Gnophodes*	*betsimena*	Madagascar	Antsiranana	Marojejy NP.	CEP-MZUJ	this study, AZ-303
MT320543	*Gnophodes*	*parmeno*	Guinea	Nzerekore	Massadou	CEP-MZUJ	this study, AZ-307
MT320550	*Gnophodes*	*diversa*	Mozambique	Manica	Chimanimani NR, moribane Forest, Ndzou	CEP-MZUJ	this study, AZ-326
MT320551	*Gnophodes*	*diversa*	Mozambique	Manica	Chimanimani NR, moribane Forest, Ndzou	CEP-MZUJ	this study, AZ-327
MT320546	*Gnophodes*	*heroni*	Kenya	Western	Kakamega	ABRI	this study, AZ-360
MT320545	*Gnophodes*	*parmeno*	Cameroon	Western	Bamboo camp	CEP-MZUJ	this study, AZ-391
MT320548	*Gnophodes*	*diversa*	Kenia	Nairobi	Nairobi-Oloolua Forest	CEP-MZUJ	this study, AZ-436
MT320549	*Gnophodes*	*diversa*	Kenia	Nairobi	Nairobi-Oloolua Forest	CEP-MZUJ	this study, AZ-437
MT320547	*Gnophodes*	*grogani*	DRC	Nord Kivu	Blakoto	ANHRTUK	this study, AZ-438
MT320544	*Gnophodes*	*parmeno*	Liberia	Lofa	Wologizi	ANHRTUK	this study, AZ-439
MT320559	*Haydonia*	*harpa*	Ghana	Ashanti	Bonkro	CEP-MZUJ	this study, AZ-445
MT320560	*Haydonia*	*pythia*	Ghana	Ashanti	Bonkro	CEP-MZUJ	this study, AZ-446
MT320554	*Haydonia*	*pythia*	Guinea	Nzerekore	Massadou	CEP-MZUJ	this study, AZ-304
MT320555	*Haydonia*	*pythia*	Guinea	Nzerekore	Massadou	CEP-MZUJ	this study, AZ-305
MT320556	*Haydonia*	*pythia*	Cameroon	Centre	Ebogo	CEP-MZUJ	this study, AZ-308
MT320557	*Ducarmeia*	*ansorgei*	Cameroon	Centre	Ebogo	CEP-MZUJ	this study, AZ-309
MT320558	*Ducarmeia*	*ansorgei*	Cameroon	Centre	Ngat	CEP-MZUJ	this study, AZ-357A
MT320552	*Haydonia*	*harpa*	Uganda	Central	Mpanga Forest	CEP-MZUJ	this study, AZ-390
MT320553	*Haydonia*	*harpa*	Liberia	Lofa	Wologizi	ANHRTUK	this study, AZ-440
LSER091	*Gnophodes*	*diversa*	Tanzania	Arusha	Serengeti		BOLD Systems
KU219624	*Haydonia*	*harpa*	no data				GenBank
DQ338759	*Haydonia*	*chelys*	Uganda	Western	Kibale		GenBank
KM111609	*Melanitis*	*phedima*	no data				GenBank
KT879861	*Melanitis*	*leda*	India				GenBank
KC433403	*Melanitis*	*leda*	India				GenBank
GQ864753	*Cyllogenes*	*woolletti*	Borneo				GenBank
MG461883	*Mycalesis*	*visala*	Thailand				GenBank
KY658656	*Bicyclus*	*anisops*	Nigeria				GenBank

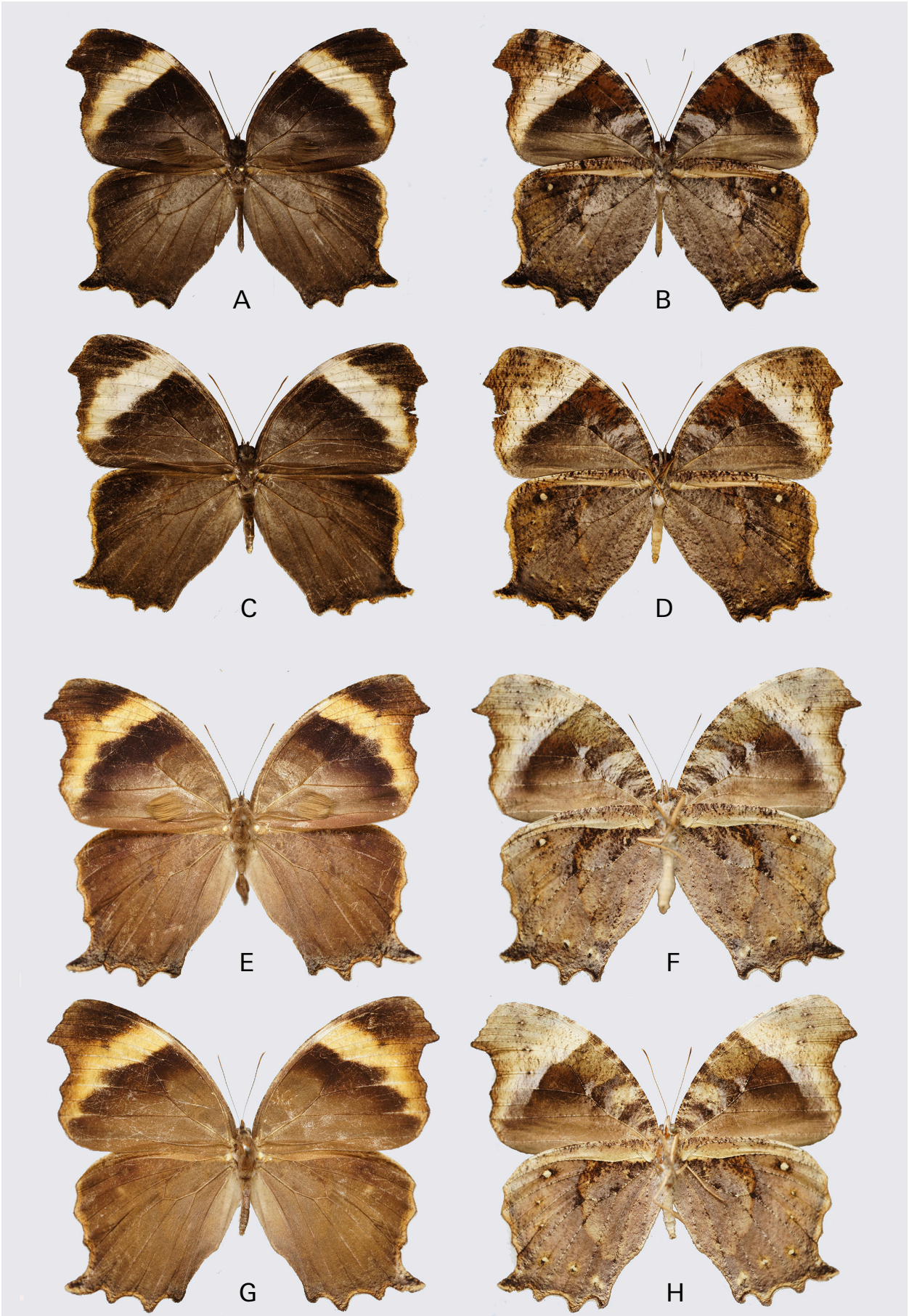

Fig. 1. Wing colour pattern. A–D: *Gnophodes betismena*, Marojejy, Madagascar, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E–H: *Gnophodes diversa*, Port St. Johns, Transkei, South Africa, ♂, dorsal (E), ♂, ventral (F), ♀, dorsal (G), ♀, ventral (H).

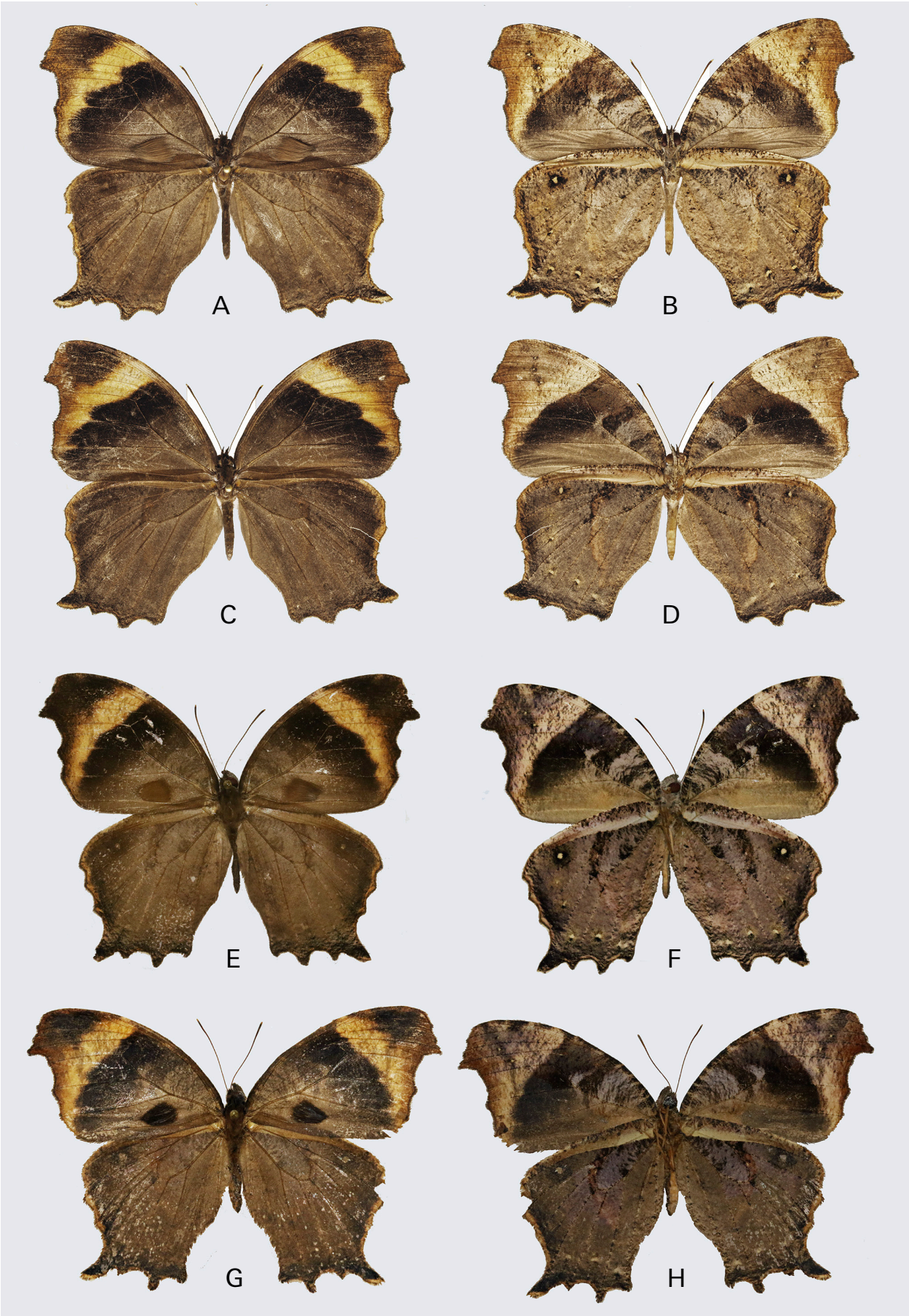

Fig. 2. Wing colour pattern of *Gnophodes diversa.* A–D: Oloolua Forest, Nairobi, Kenya, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E–H: Magombera, Tanzania, ♂, dorsal (E), ♂, ventral (F), ♀, dorsal (G), ♀, ventral (H).

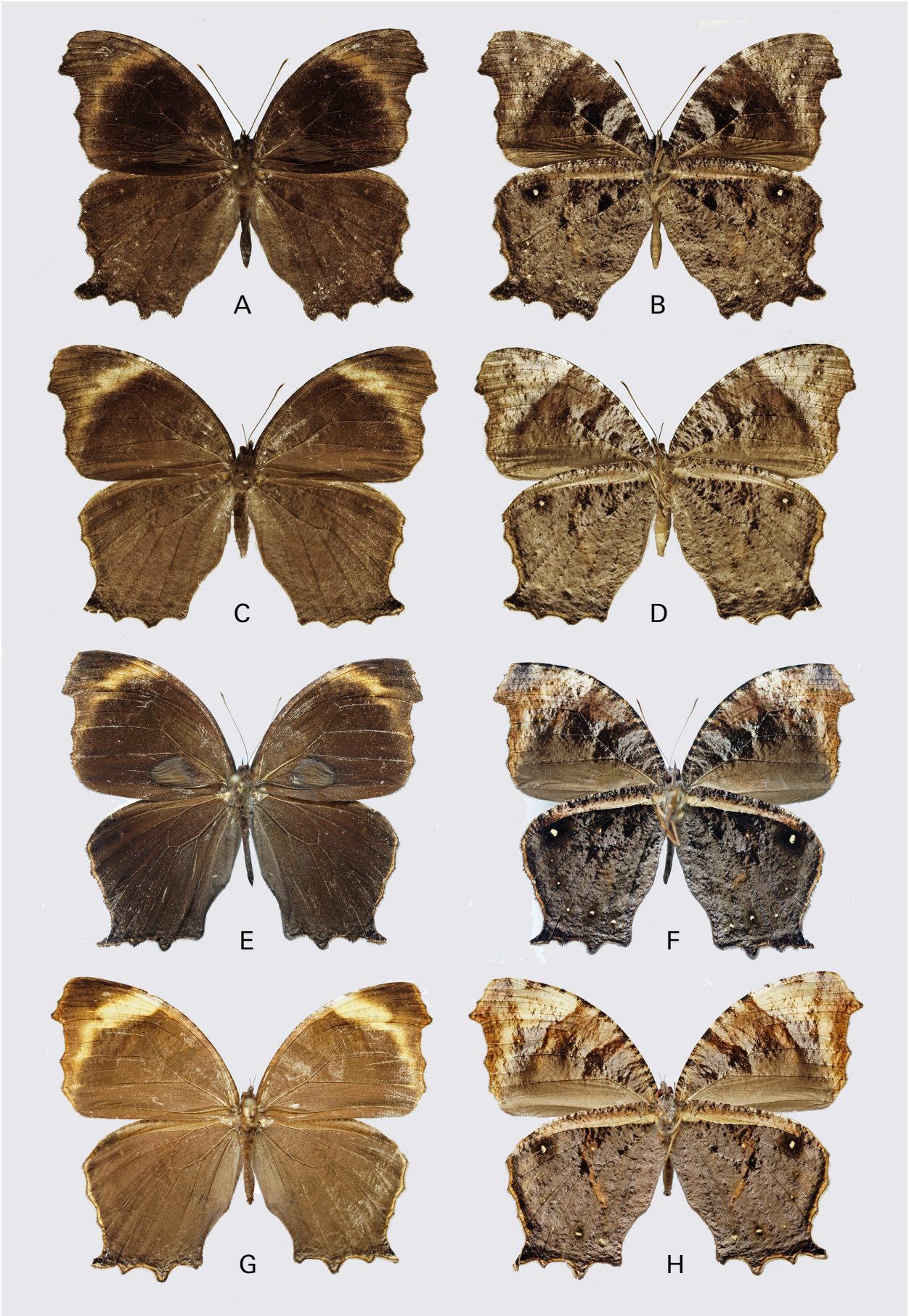

Fig. 3. Wing colour pattern. A–D: *Gnophodes parmeno*, Nsukka, Nigeria, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E–H: *Gnophodes heroni*, paratype, Manengouba Mtn., Cameroon, ♂ dorsal (E), ♂, ventral (F), ♀, dorsal (G), ♀, ventral (H).

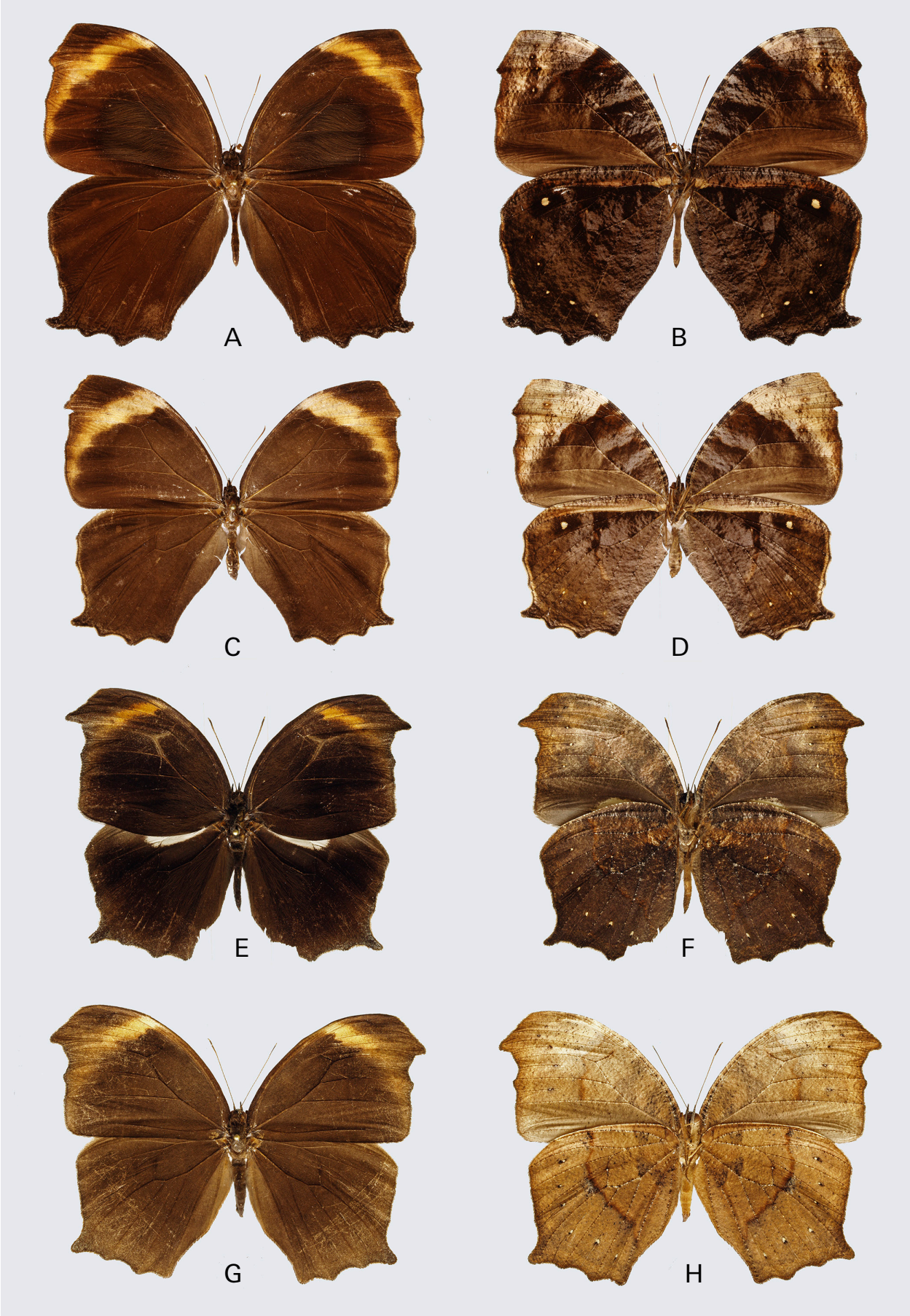

Fig. 4. Wing colour pattern. A–D: *Gnophodes grogani*, Butuhe, D. R. Congo, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E–H: *Haydonia harpa*, Mpanga Forest, Uganda, ♂, dorsal (E), ♂, ventral (F), ♀, dorsal (G), ♀, ventral (H).

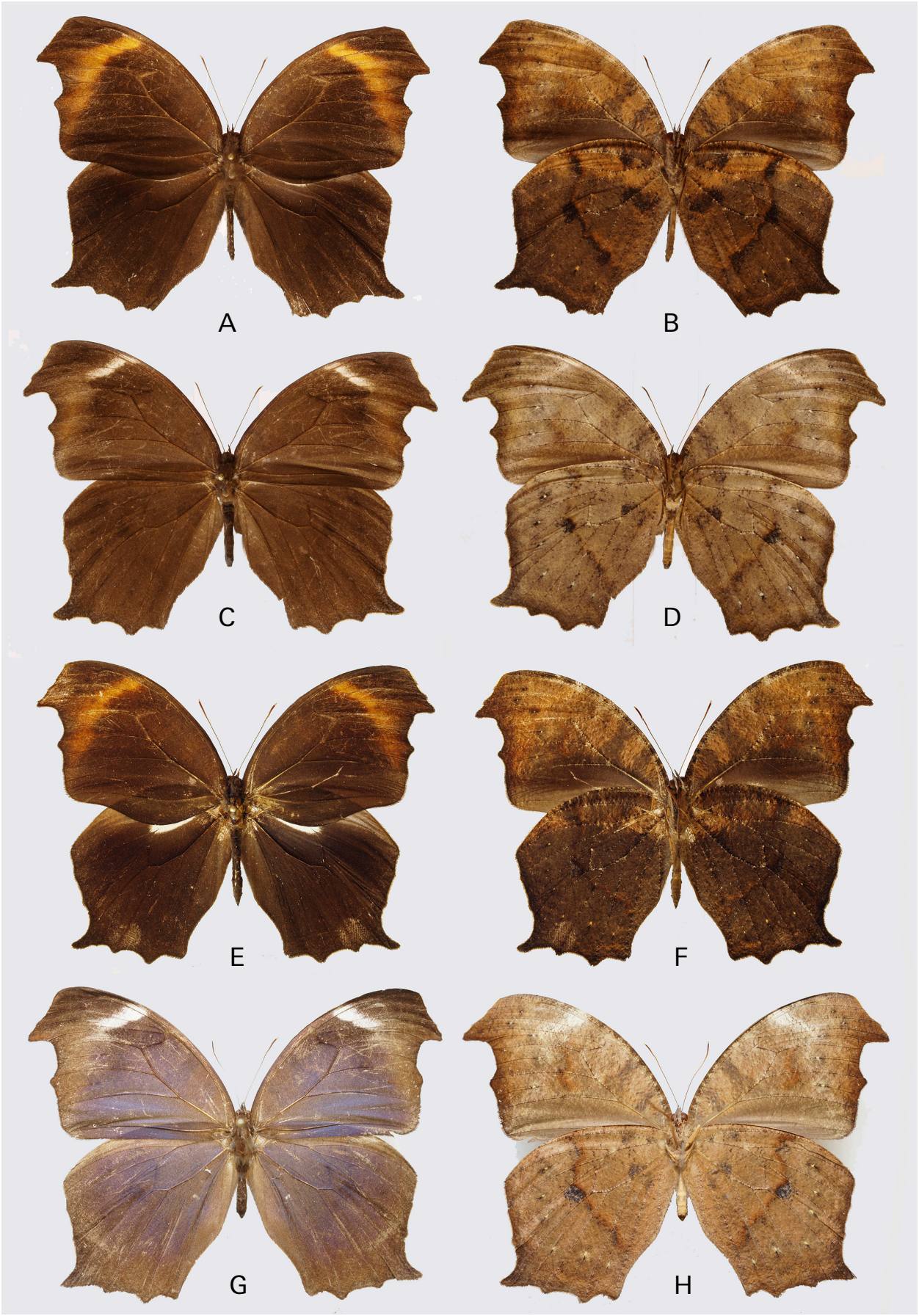

Fig. 5. Wing colour pattern. A–D: *Haydonia chelys*, Kakamega Forest, Kenya, ♂, dorsal (A) ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E, F: *Haydonia chelys*, Kasugho, D. R. Congo, ♂, dorsal (E), ♂, ventral (F); G, H: *Haydonia pythia* f. *iris*, Muleke, D. R. Congo, ♀, dorsal (G), ♀, ventral (H).

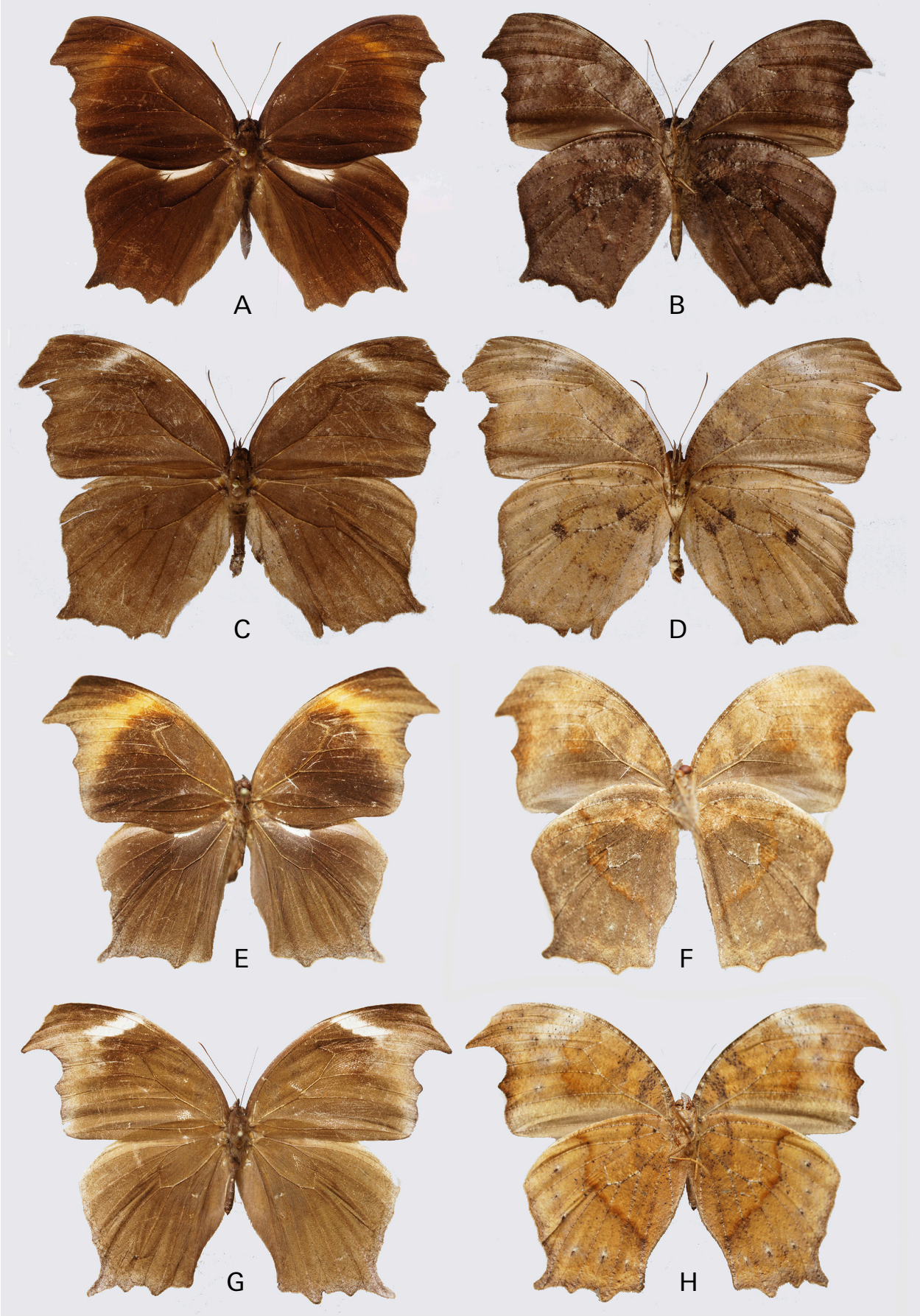

Fig. 6. Wing colour pattern. A–D: *Haydonia pythia*, Okomu Forest, Nigeria, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E, F: *Haydonia hassoni*, holotype, Ntumbwa – Upemba, D. R. Congo, ♂, dorsal (E), ♂, ventral (F); G, H: *Haydonia hassoni*, paratype, Lukima – Upemba, R. Congo, ♀, dorsal (G), ♀, ventral (H).

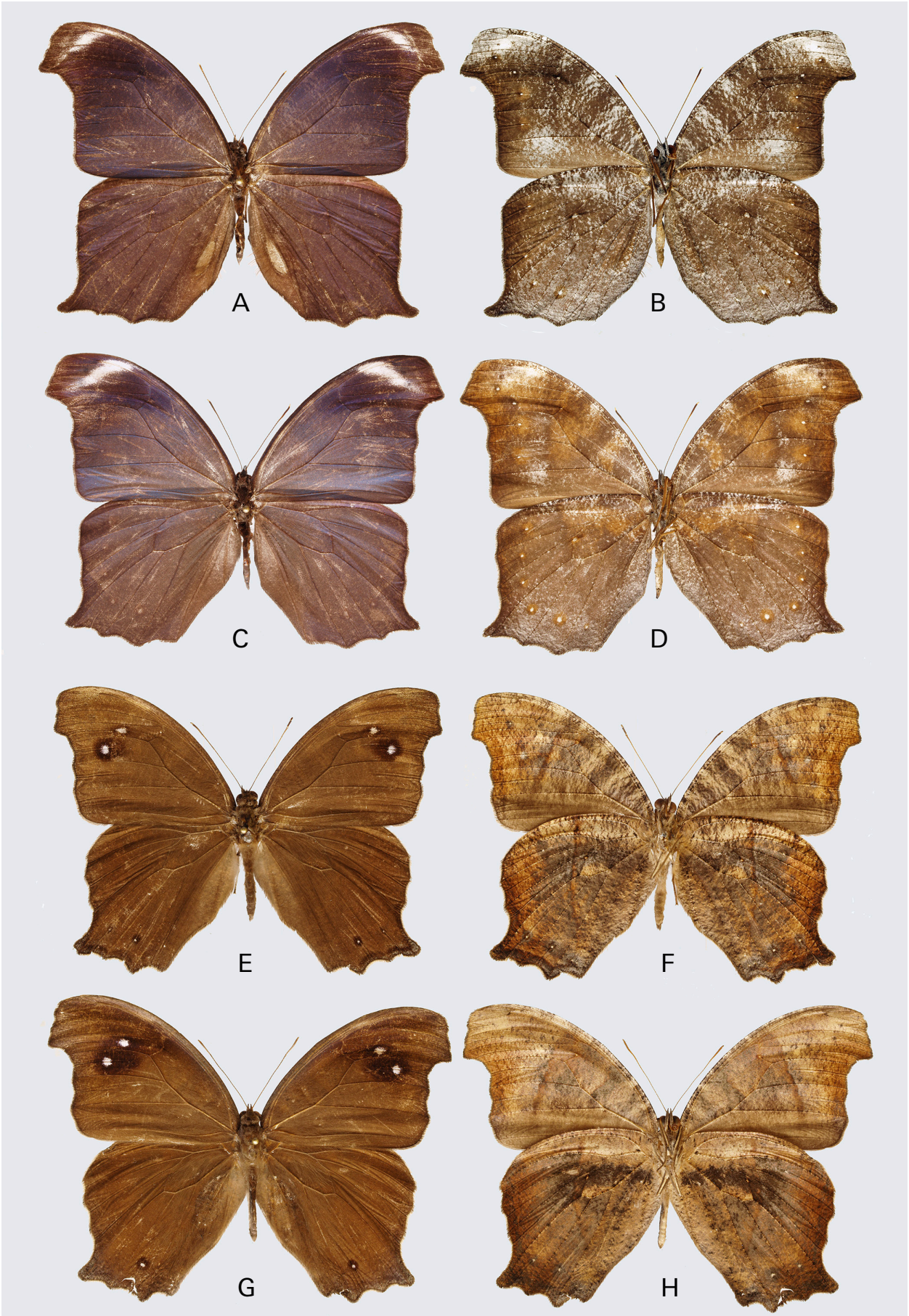

Fig. 7. Wing colour pattern. A–D: *Ducarmeia ansorgei*, Mont Hoyo, D. R. Congo, ♂, dorsal (A), ♂, ventral (B), ♀, dorsal (C), ♀, ventral (D); E–H: *Melanitis libya*, Bimbia, Mount Cameroon, Cameroon, ♂, dorsal (E), ♂, ventral (F), ♀, dorsal (G), ♀, ventral (H).

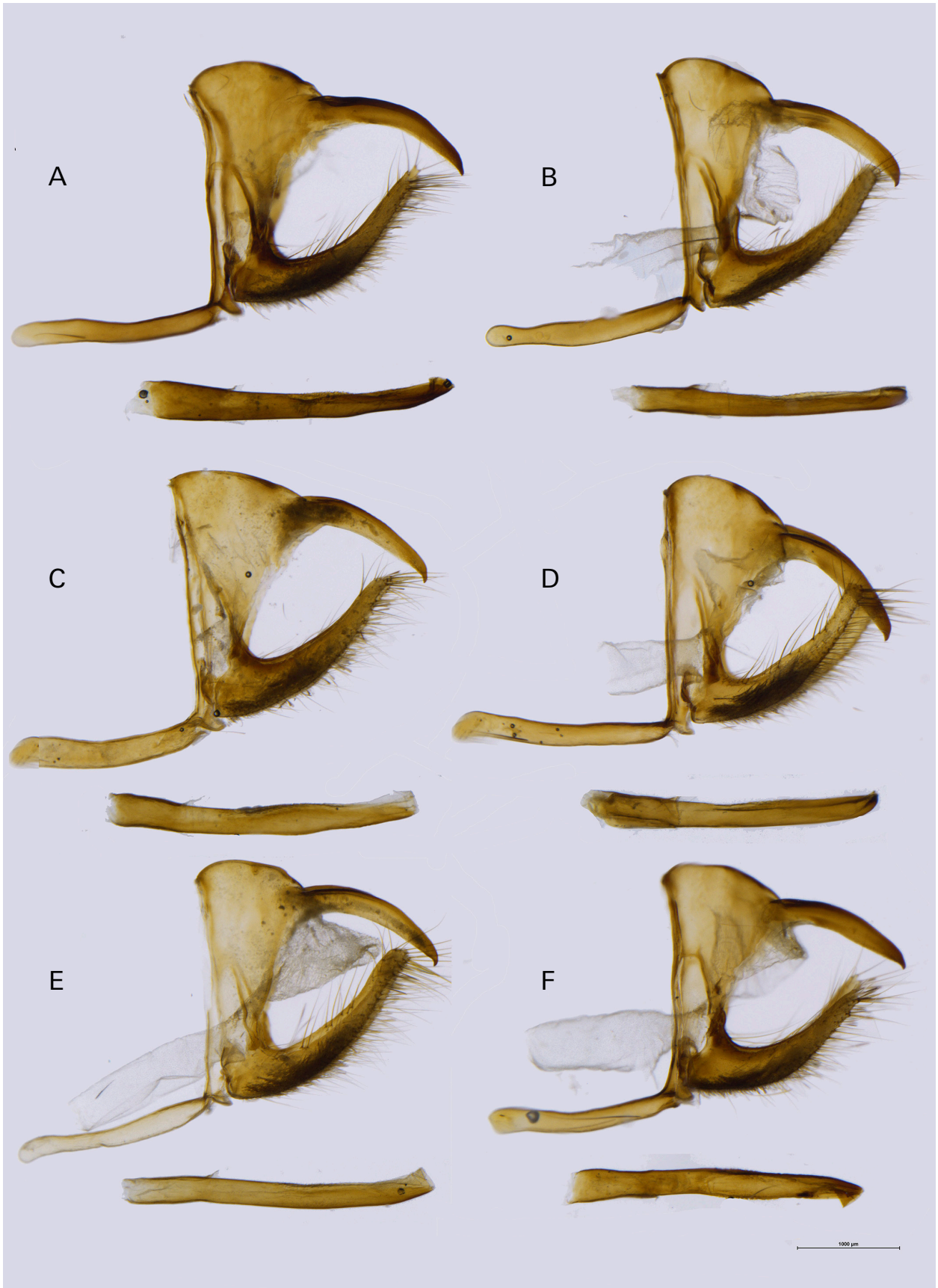

Fig. 8. Male genitalia of *Haydonia.* A, B: *H. harpa,* Diéké, Guinea (A), Mintom, Cameroon (B); C, F: *H. pythia*, Mont Koupé, Cameroon (C), Mamove, D. R. Congo (F); D, E: *H. chelys*, Mont Koupé, Cameroon (D), Kasugho, D. R. Congo (E).

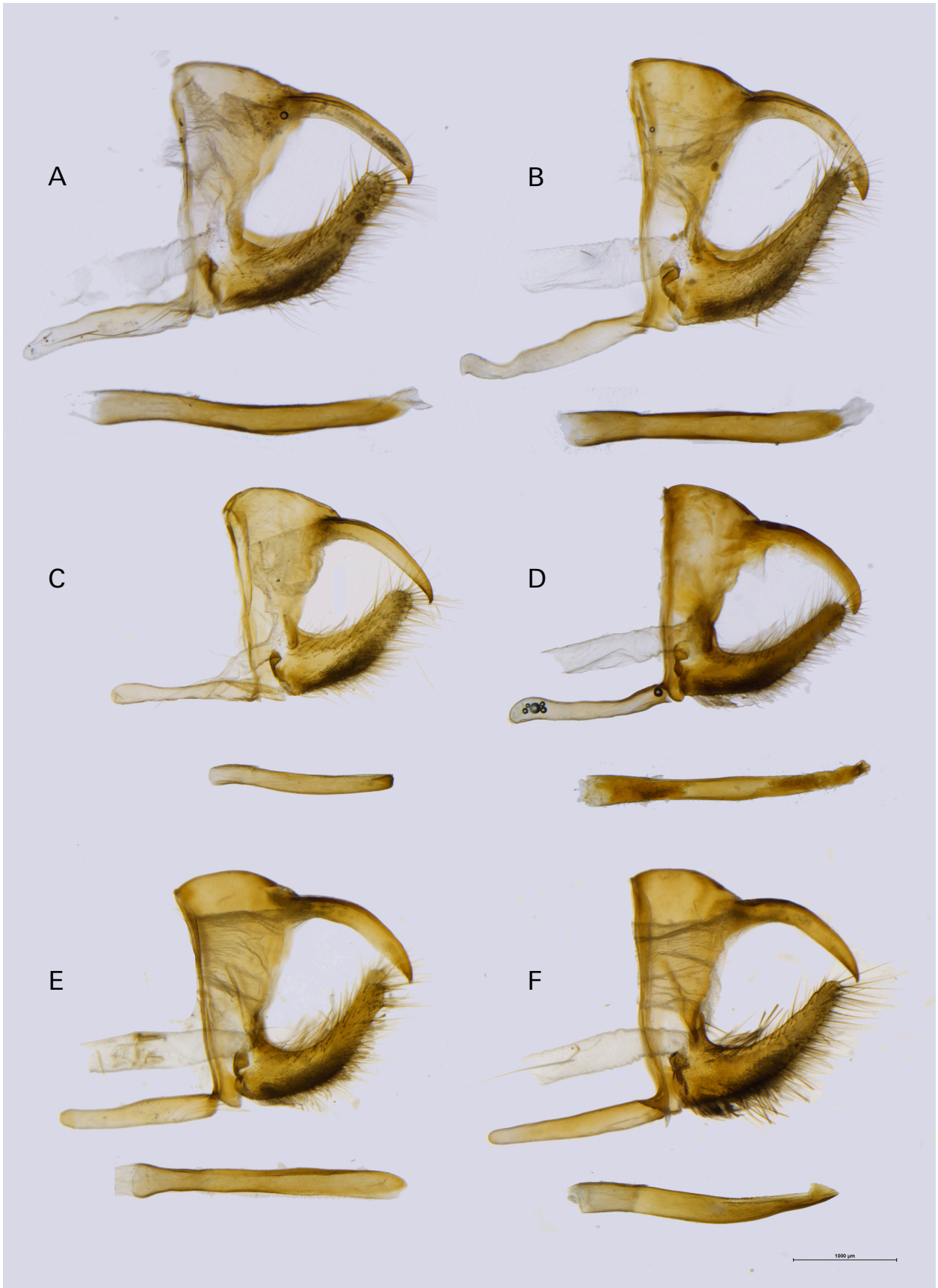

Fig. 9. Male genitalia of *Gnophodes* A, B: *G. grogani*, Bikara, D. R. Congo (A) Kanyambia, D. R. Congo (B); C, D: *G. diversa*, Nairobi, Kenya (C), Cape, RSA (D); E, F: *G. parmeno*, Oshogbo, Nigeria (E), Mpanga, Uganda (F).

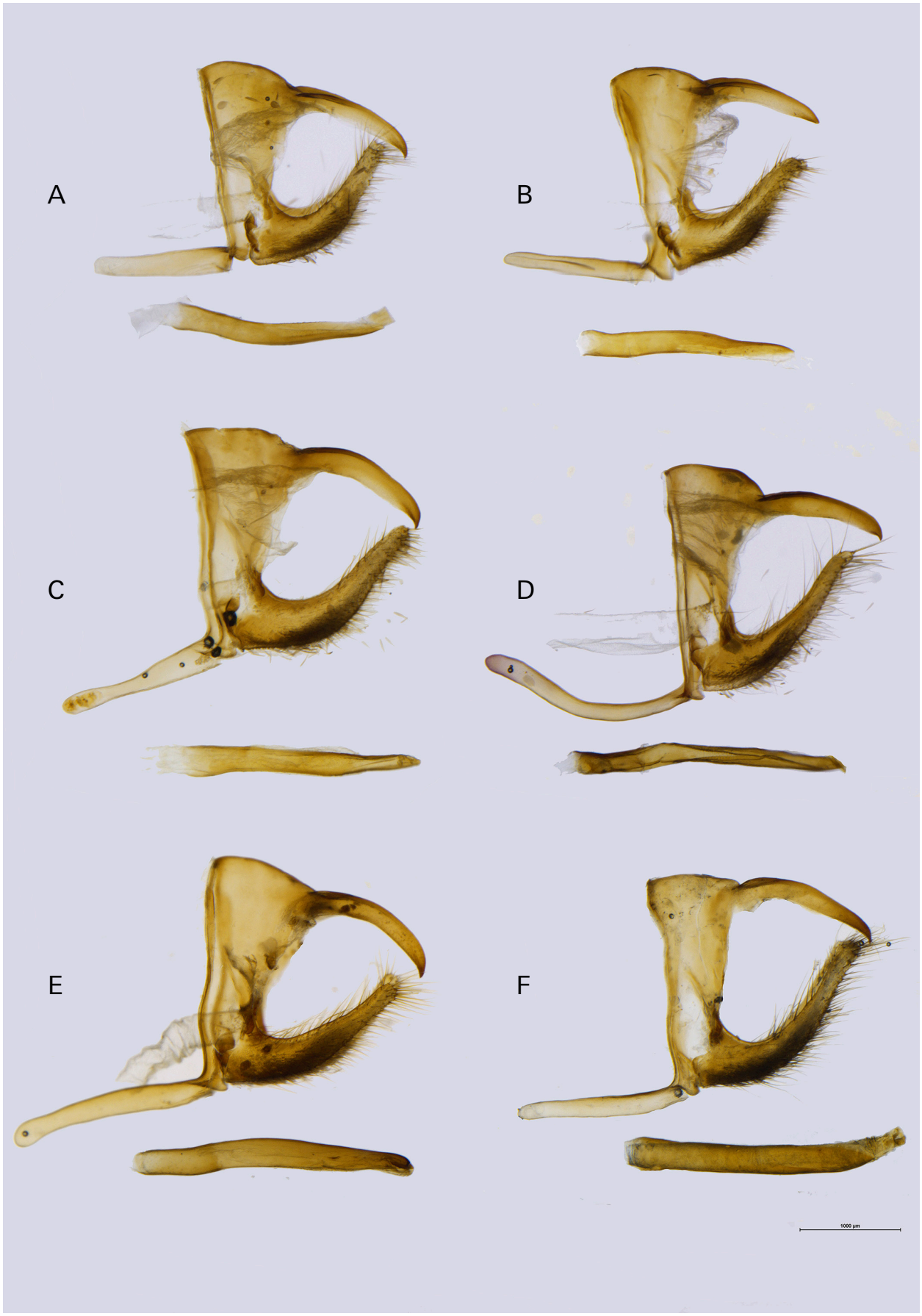

Fig. 10. Male genitalia. A, B: *Gnophodes heroni,* Kakamega, Kenya (A), Obudu, Nigeria (B); C: *Gnophodes betsimena*, Marojejy, Madagascar; D: *Haydonia hassoni*, Ntumbwa, D. R. Congo; E: *Melanitis leda*, Mpanga, Uganda; F: *Ducarmeia ansorgei*, Ebogo, Cameroon.

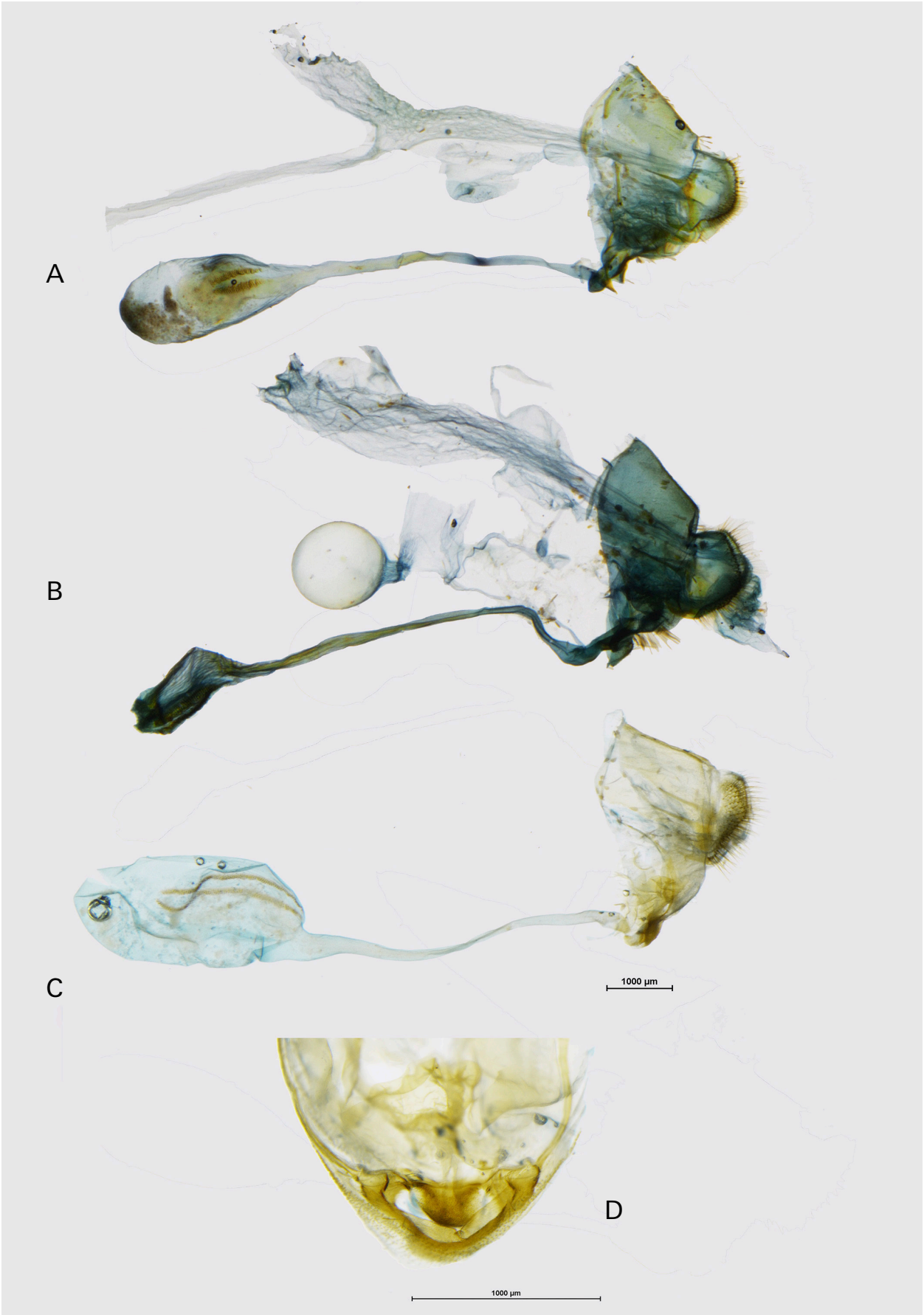

Fig. 11. Female genitalia. A, B: *Gnophodes grogani,* Nyungwe, D. R. Congo (A), Muleke, D. R. Congo (B); C, D: *Haydonia chelys*, Butuhe, D. R. Congo, lateral view (C), lamella postvaginalis (D).

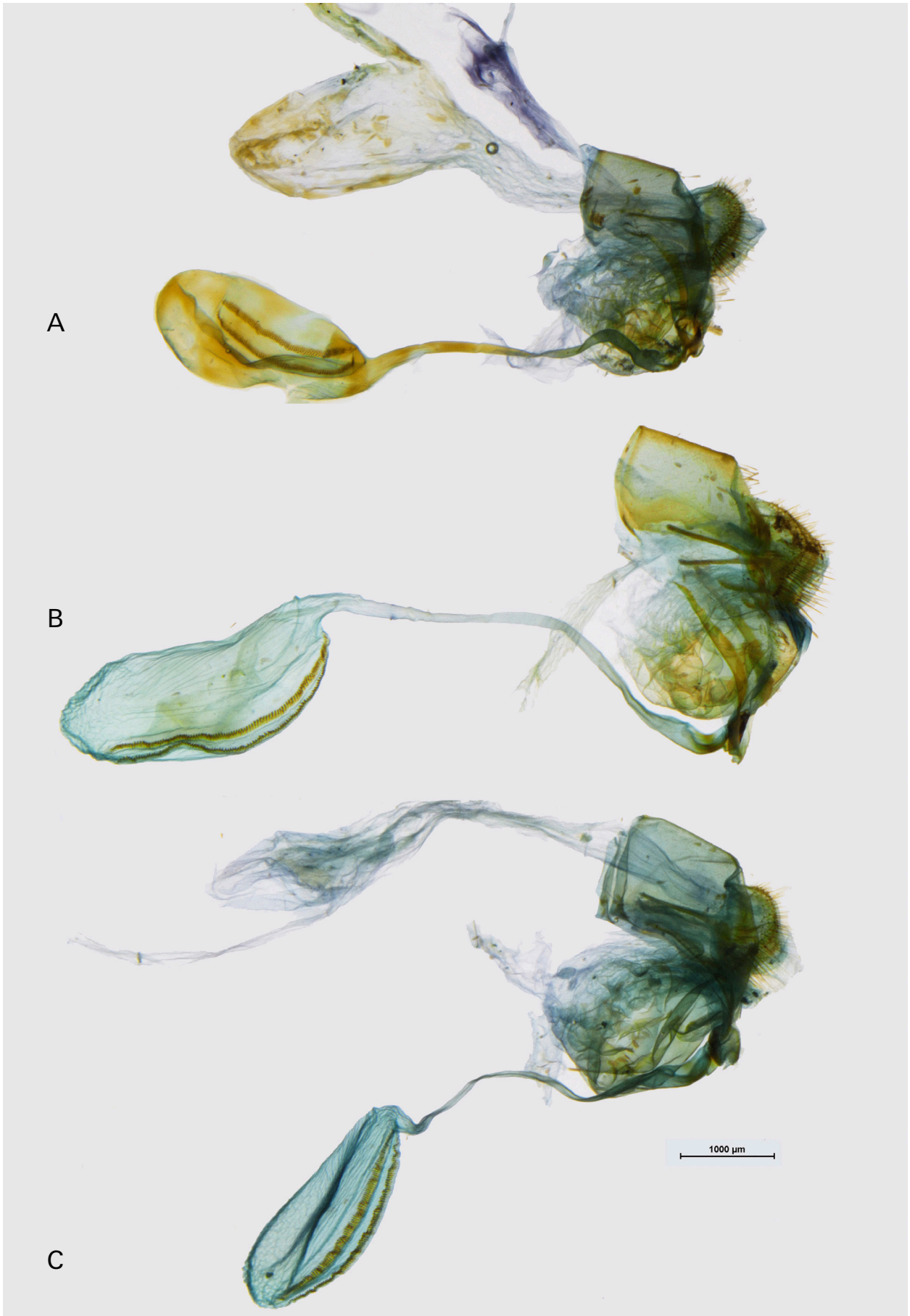

Fig. 12. Female genitalia of *Haydonia* A: *H. chelys*, Massif du Mbam, Cameroon; B, C: *H. pythia,* Mont Mille, Cameroon (B), Diéké, Guinea (C).

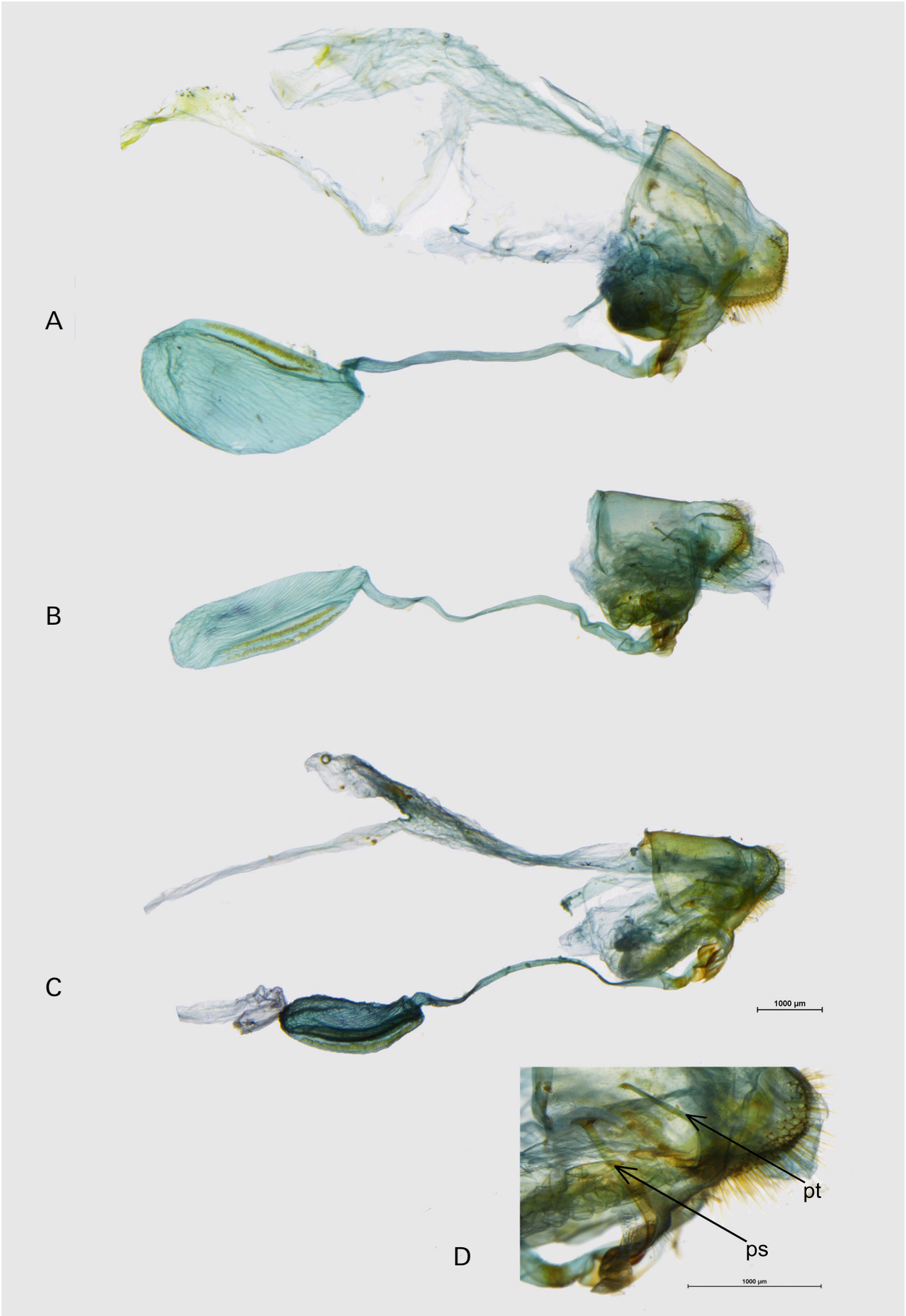

Fig. 13. Female genitalia of *Haydonia* A, B: *H. harpa,* Adjap Fang, Cameroon (A), Diéké, Guinea (B); C, D: *H. hassoni*, Ntumbwa, D. R. Congo, lateral view (C), distal segments, enlarged (D). — ***Abbreviations***: ps – pseudo-apophysis; pt – posterior apophysis.

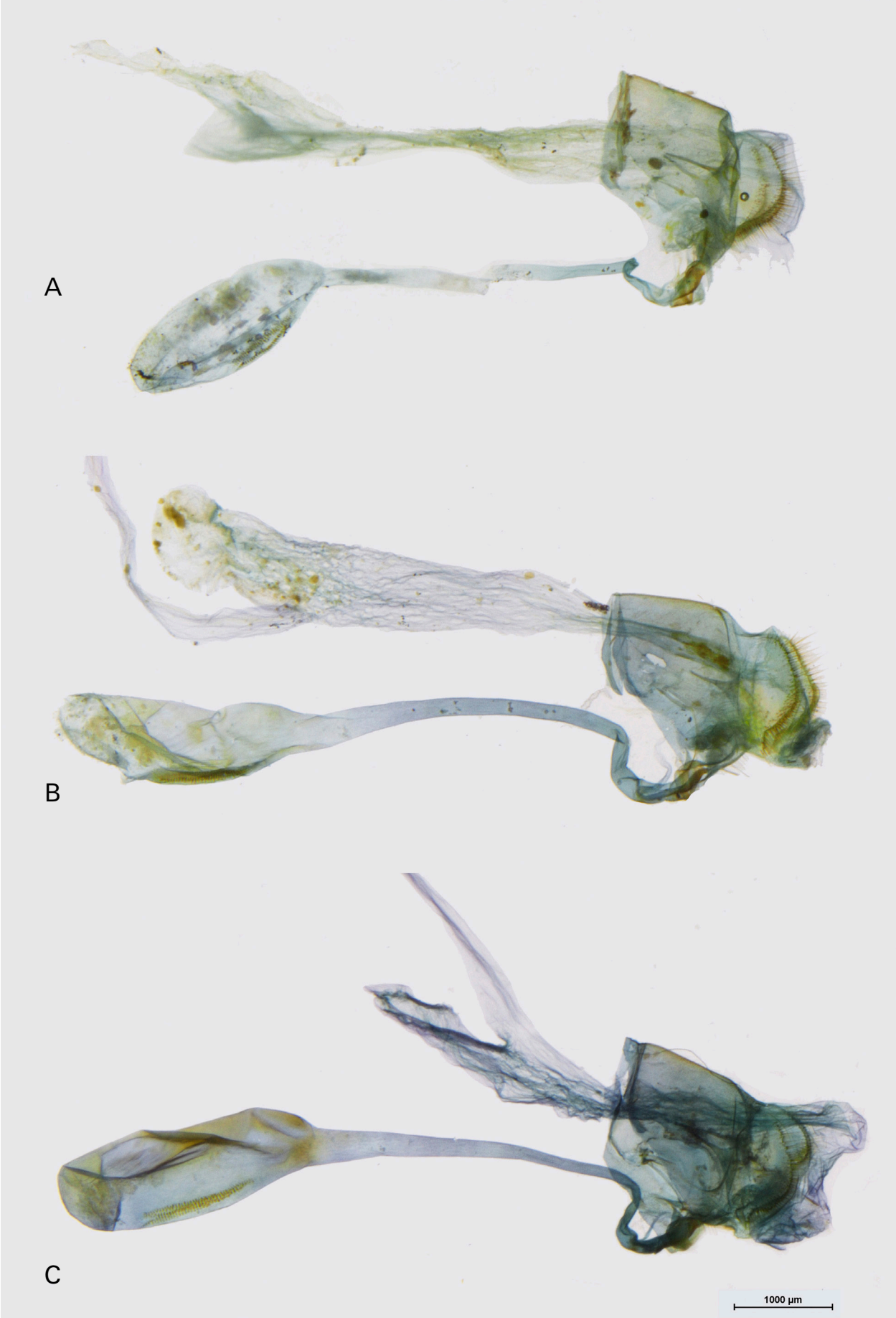

Fig. 14. Female genitalia of *Gnophodes heroni.* A: Obudu, Nigeria; B: Mont Koupé, Cameroon; C: Kalinzu, Uganda.

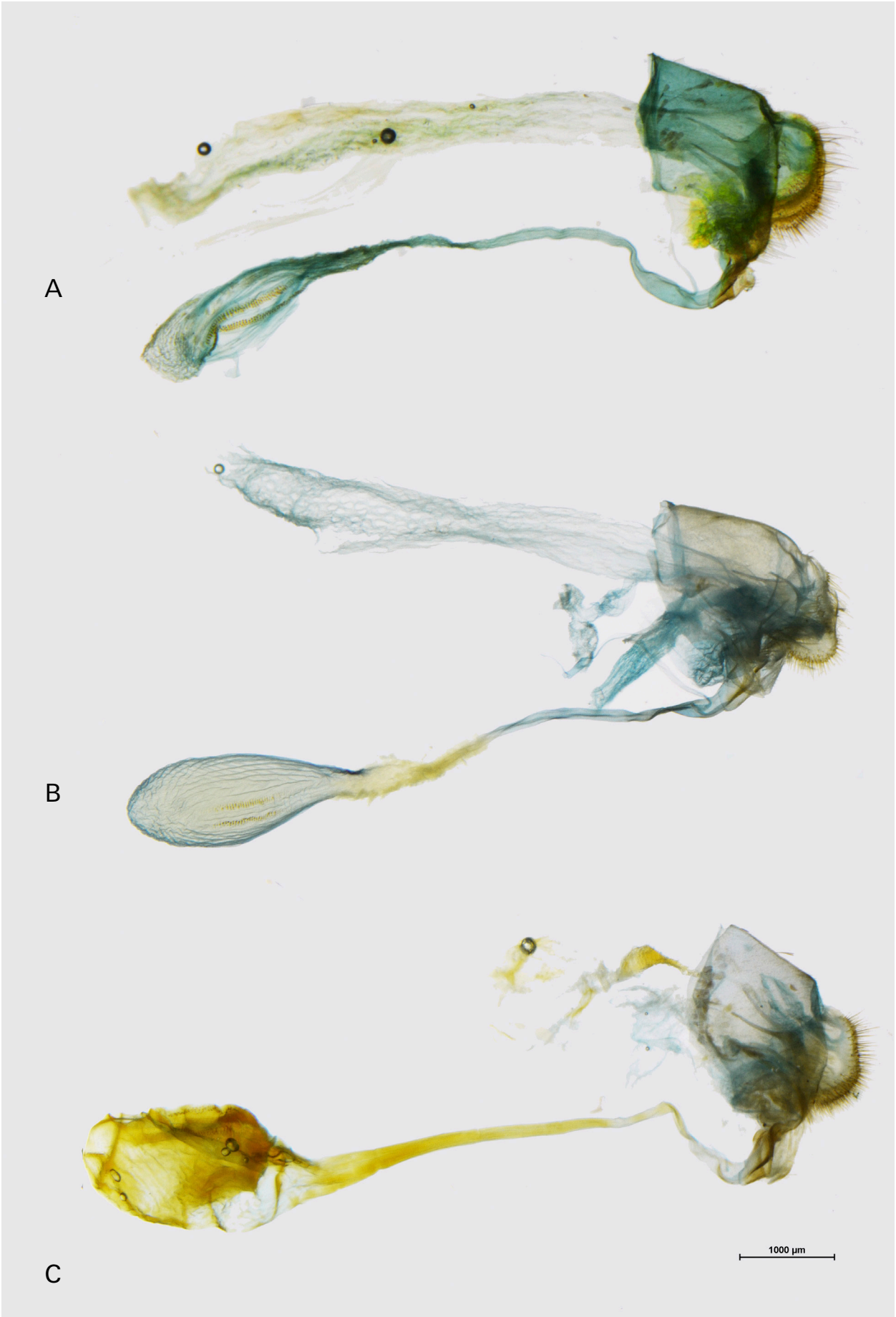

Fig. 15. Female genitalia of *Gnophodes diversa.* A: Nairobi, Kenya; B: Magombera, Tanzania; C: Chimanimani, Mozambique.

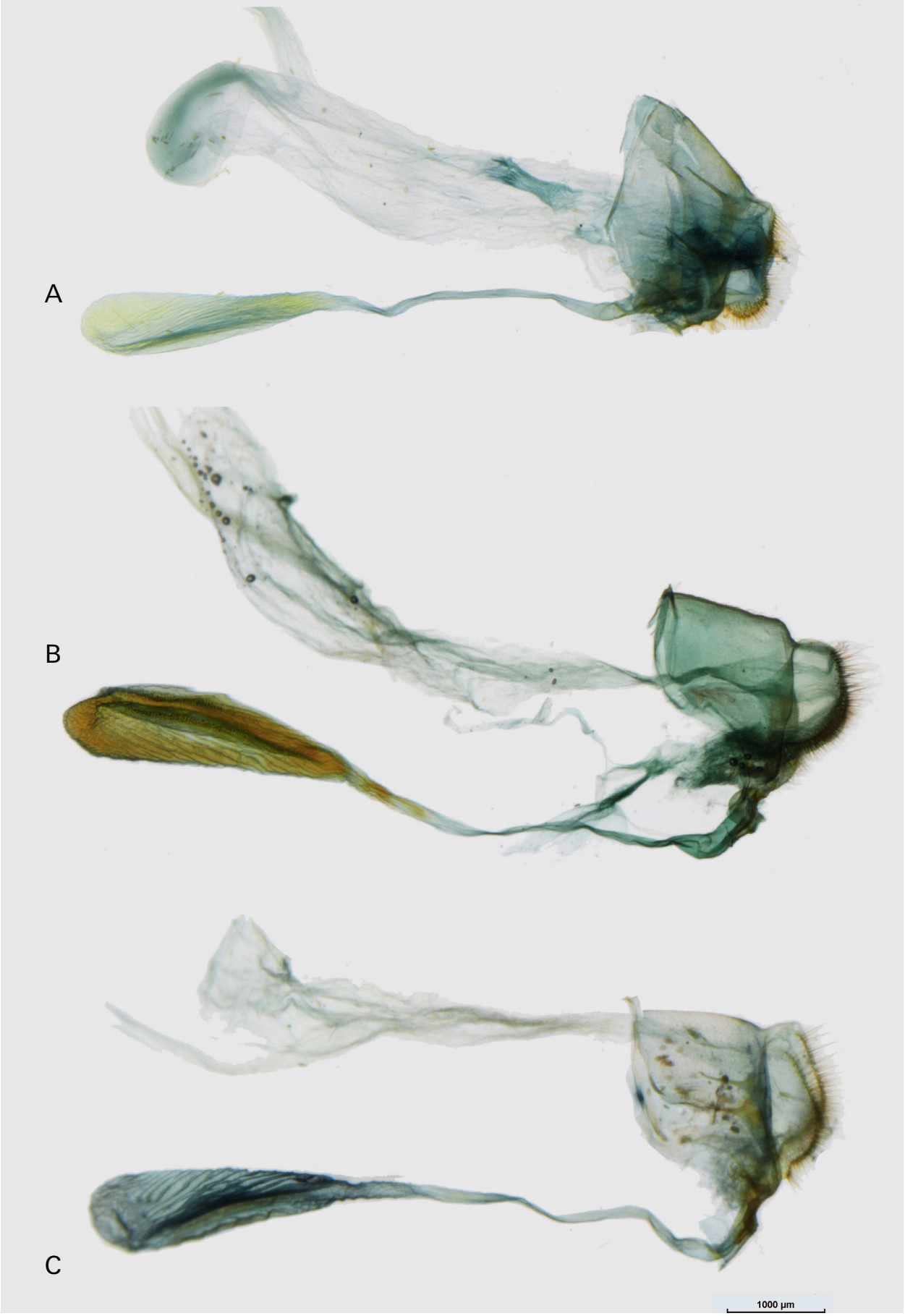

Fig. 16. Female genitalia of *Gnophodes* A: *G. diversa*, Transkei, South Africa; B: *G. betsimena*, Madagascar; C: *G. parmeno*, Mpanga, Uganda.

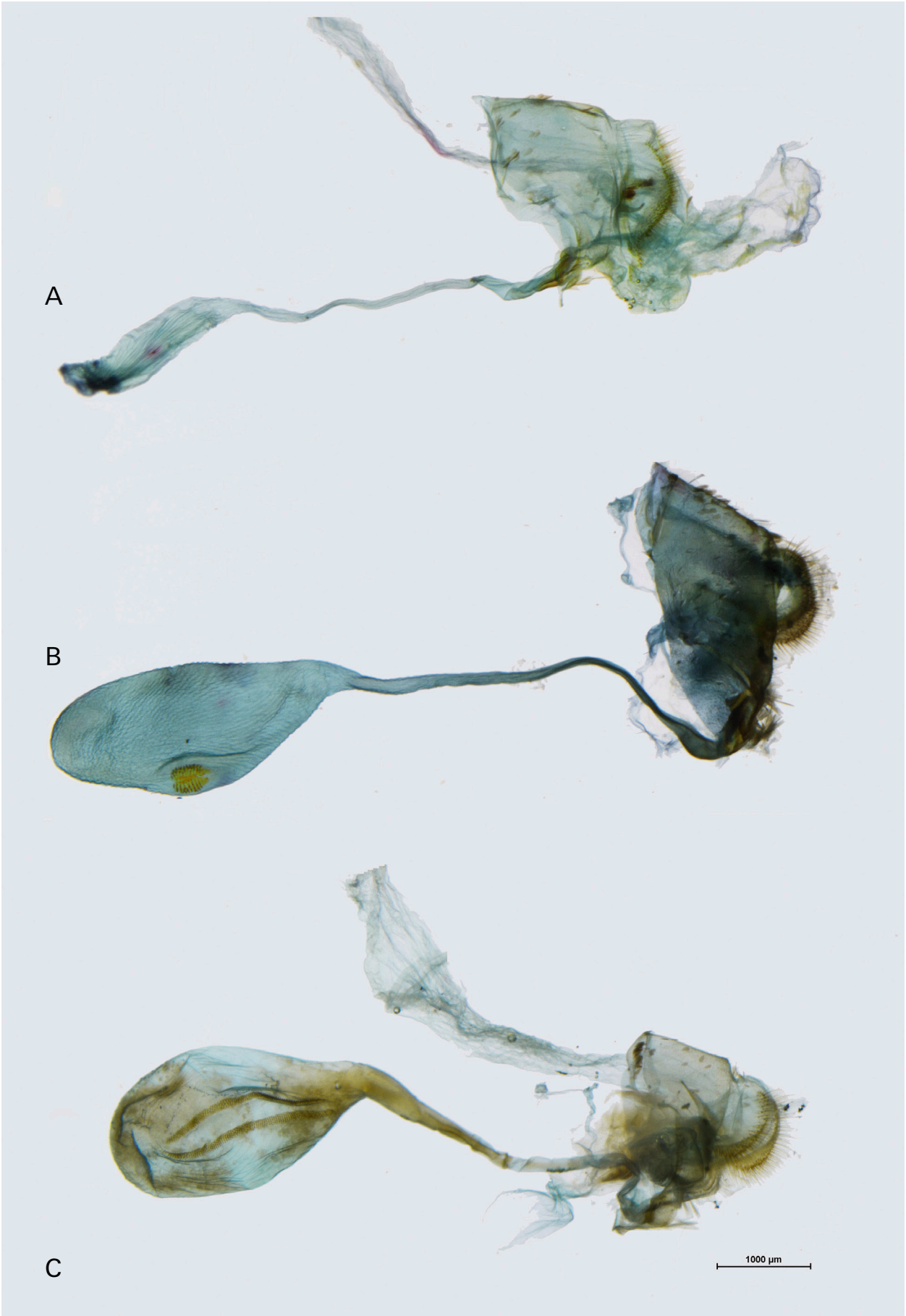

Fig. 17. Female genitalia. A: *Gnophodes grogani*, Butuhe, D. R. Congo; B: *Melanitis leda*, Mpanga, Uganda; C: *Ducarmeia ansorgei*, Mont Hoyo, D. R. Congo.

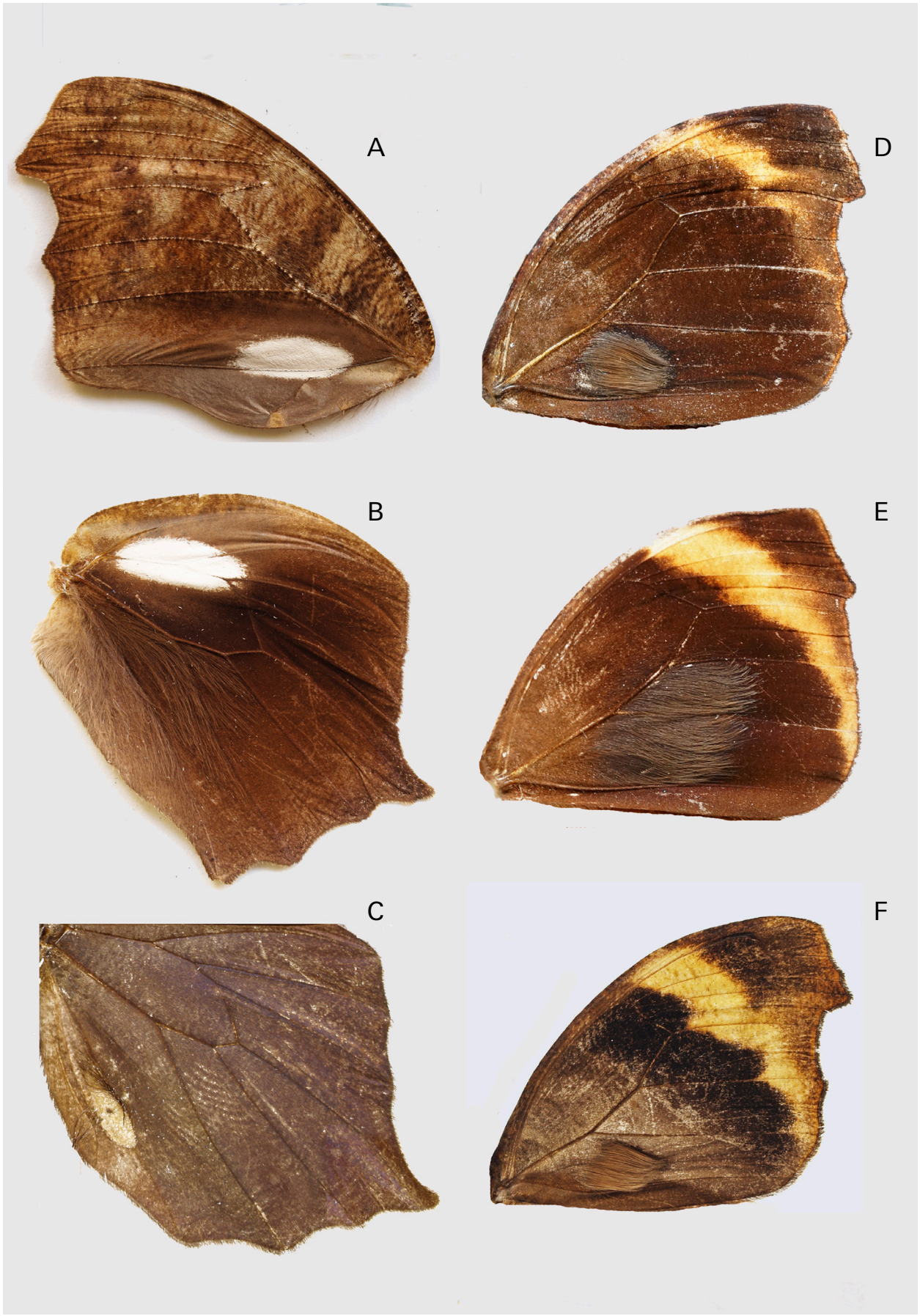

Fig. 18. Androconial patches. A, B: *Haydonia pythia*, FWV Okomu, Nigeria (A); HWD Okomu, Nigeria (B); C: *Ducarmeia ansorgei*, HWD Eriageu, D. R. Congo; D: *Gnophodes heroni*, FWD Manangouba Mnt., Cameroon; E: *Gnophodes grogani*, FWD Butuhe, D.R.Congo; F: *Gnophodes diversa*, FWD Nairobi, Kenya. — ***Abbreviations***: FW – forewing; HW – hindwing; D – dorsum; V – venter.

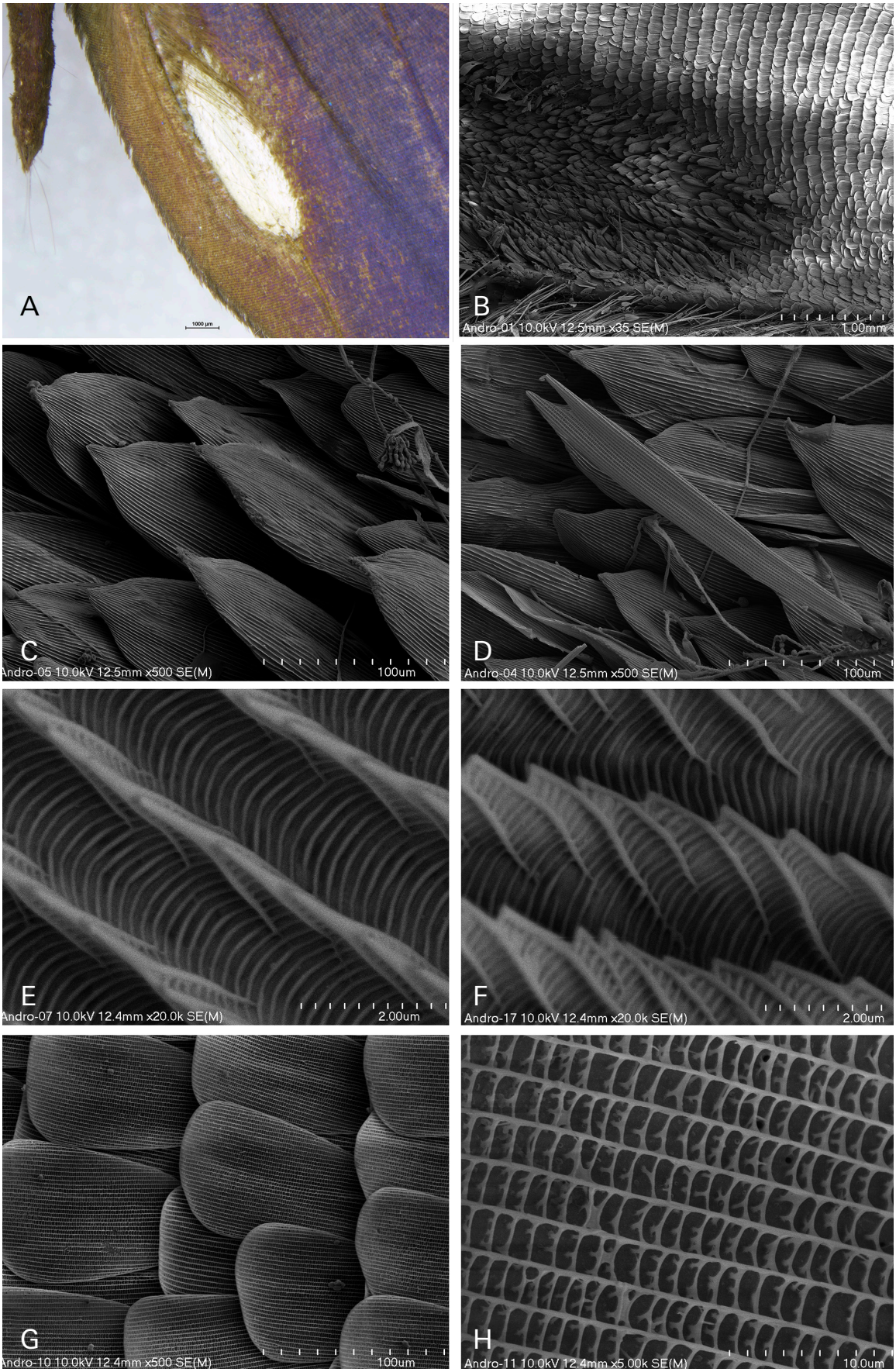

Fig. 19. SEM images of *Ducarmeia ansorgei* scales (except A). A: HWD anal fold alar organ, optical microscope image; B: HWD alar organ; C: alar organ white scales; D: alar organ atypical elongated scale; E, F: alar organ white scale nanostructure; G: HWD blue cover scales; H: HWD blue cover scales nanostructure. — ***Abbreviations***: FW – forewing; HW – hindwing; D – dorsum; V – venter.

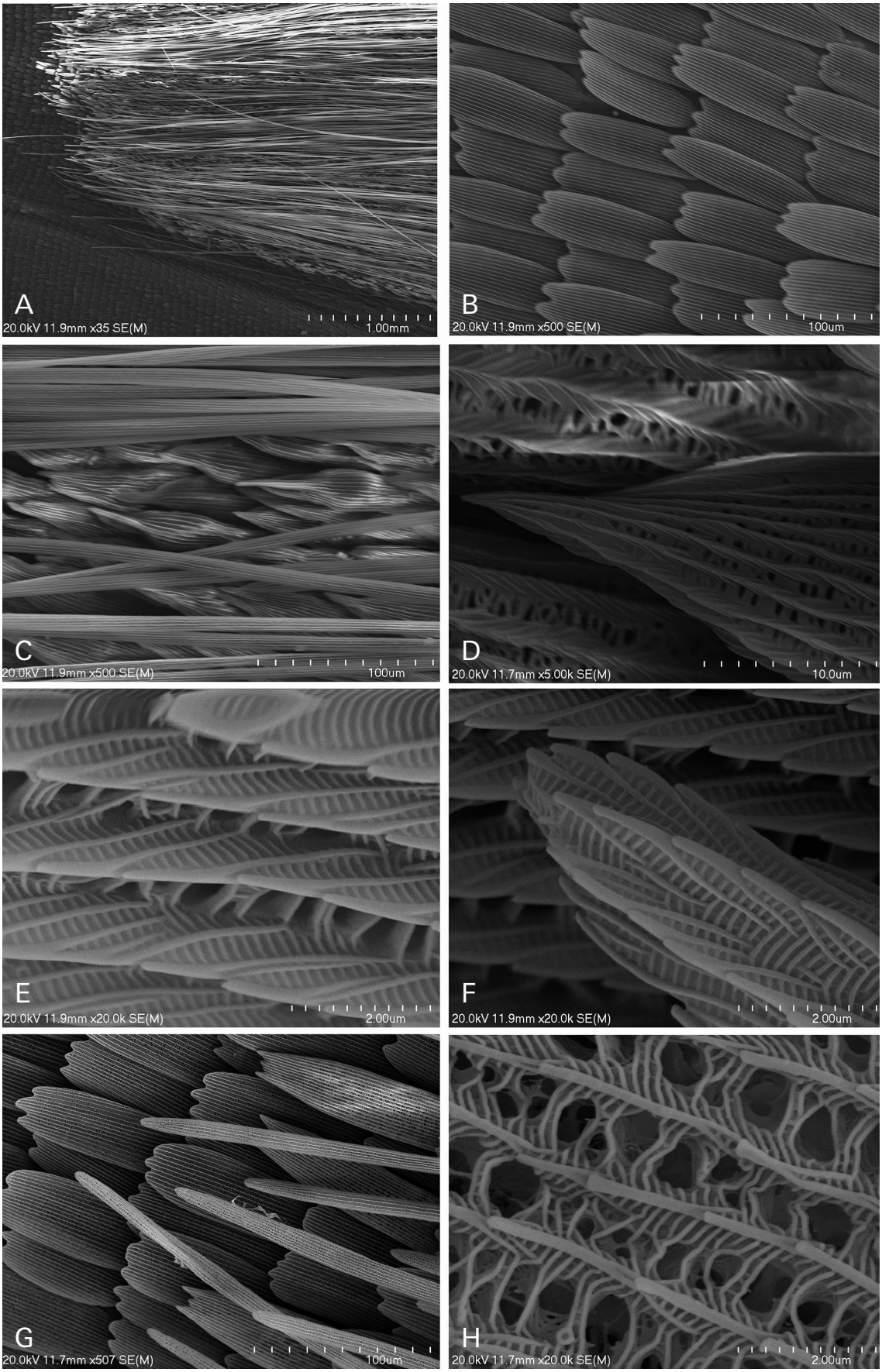

Fig. 20. SEM images of *Gnophodes parmeno* scales. A: hairy scales forming up FWD alar organ; B: brown cover scales; C: specialized scales below hairy scales within alar organ; D: specialized scale apical part; E: specialized scale detail; F: hairy scale apical part; G: hairy scales and cover scales; H: hairy scale detail. — ***Abbreviations***: FW – forewing; HW – hindwing; D – dorsum; V – venter.

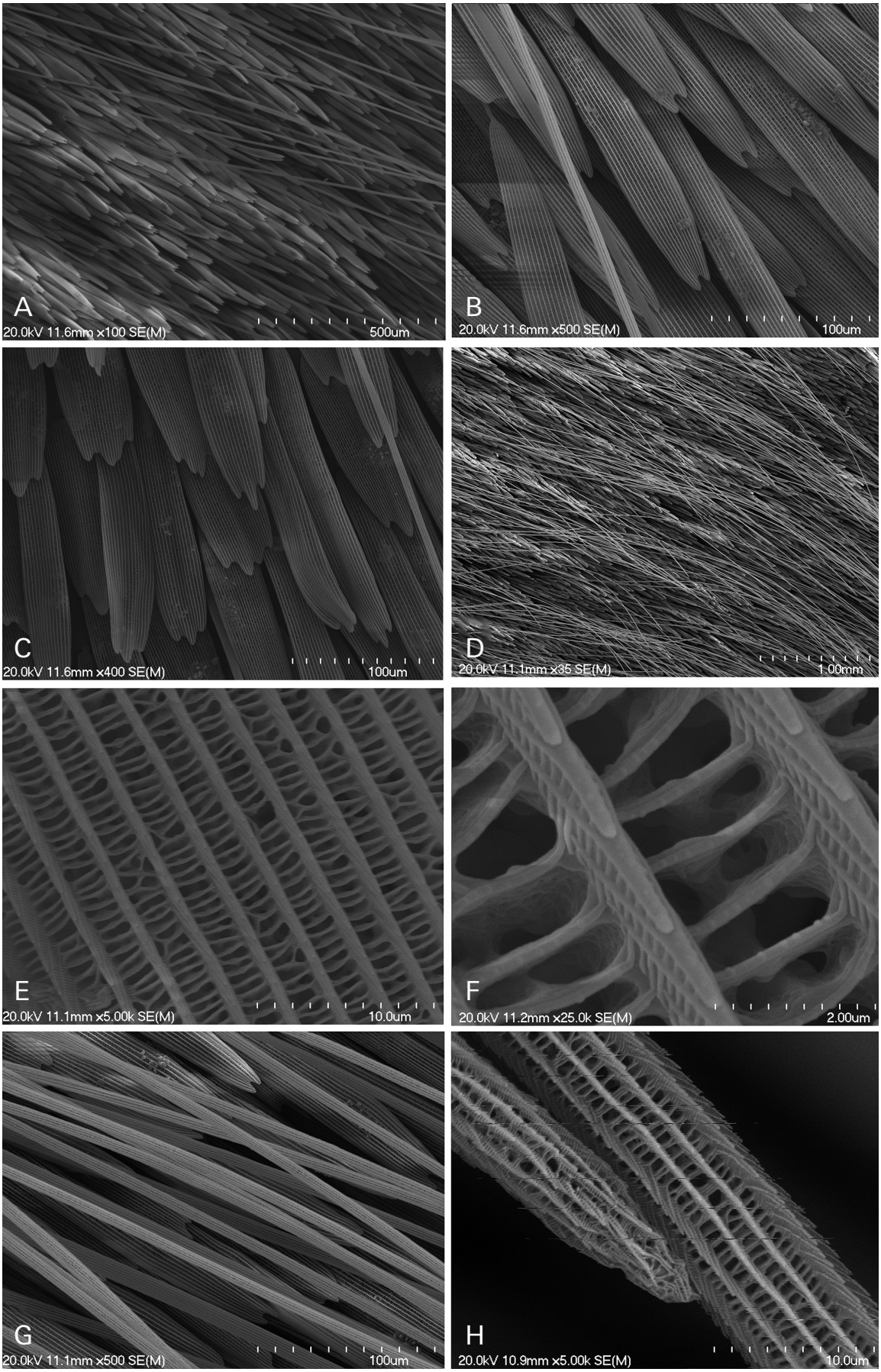

Fig. 21. SEM images of *Gnophodes grogani* scales. A: airy scales forming up FWD alar organ; B: brown cover scales; C: brown cover scales; D: alar organ; E: brown scale; F: brown scale detail; G: hairy scales; H: hairy scale. — ***Abbreviations***: FWD – forewing, dorsum.

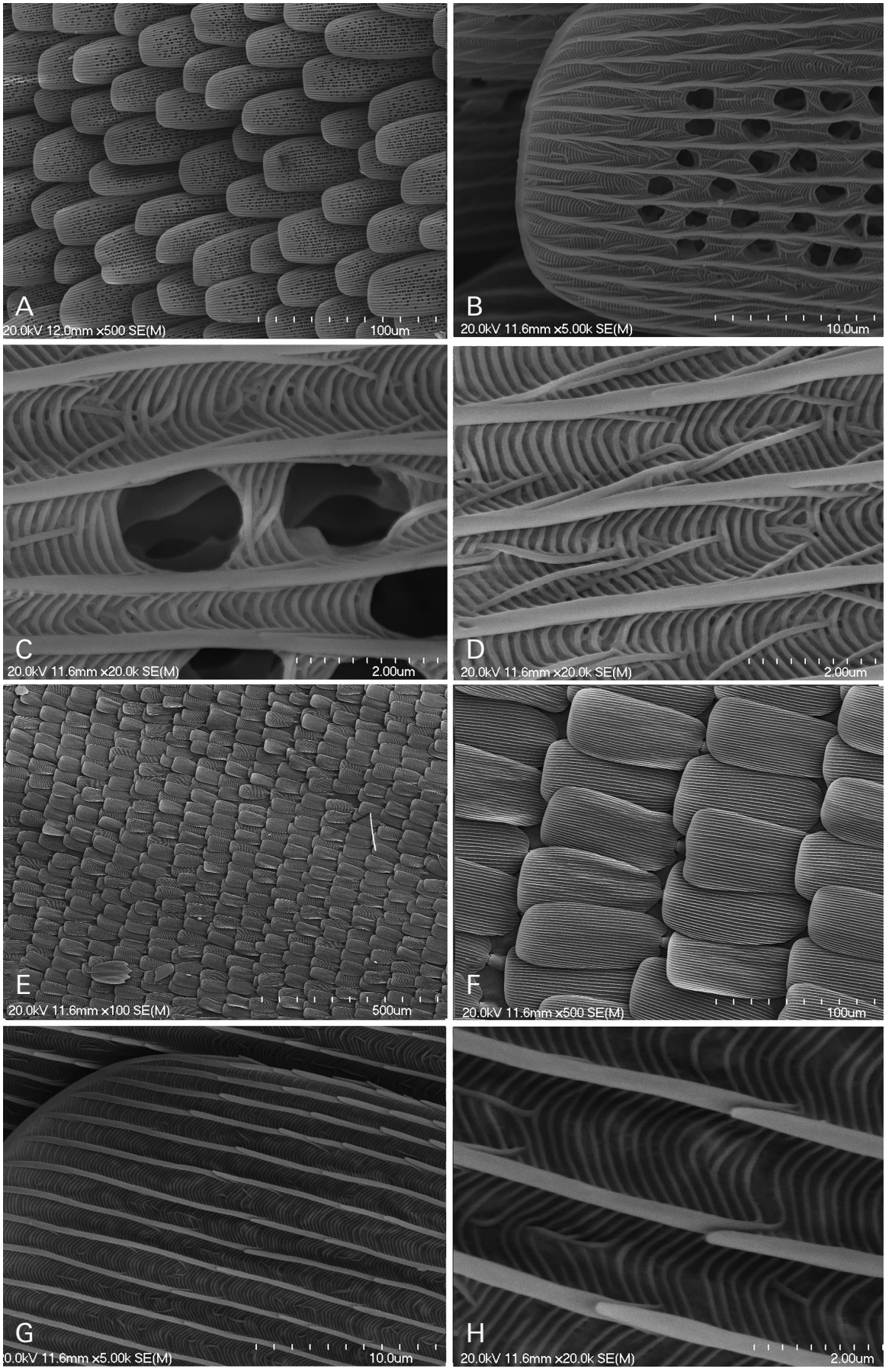

Fig. 22. SEM images of *Haydonia pythia* scales. A: silver scales forming up HWD alar organ; B: silver scale; C: silver scale detail; D: silver scale detail; E: brown cover scales; F: brown cover scales; G: brown cover scale; H: brown cover scale detail. — ***Abbreviations***: HWD – hindwing, dorsum.

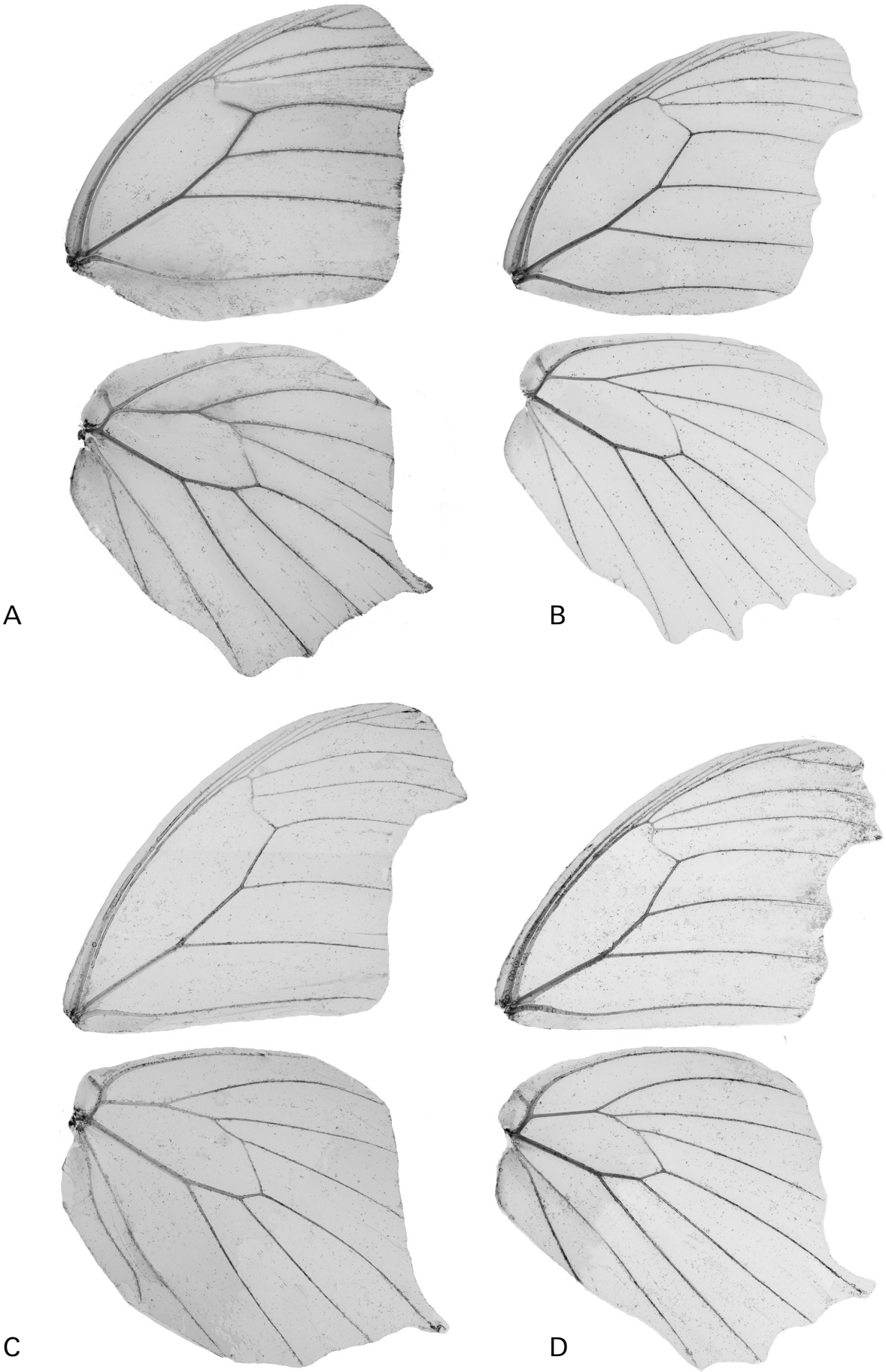

Fig. 23. Wing venation. A: *Haydonia harpa*, Mpanga, Uganda; B: *Gnophodes parmeno*, Massedou, Guinea; C: *Ducarmeia ansorgei*, Mapimbi, D. R. Congo; D: *Melanitis libya*, Bimbia, Cameroon.

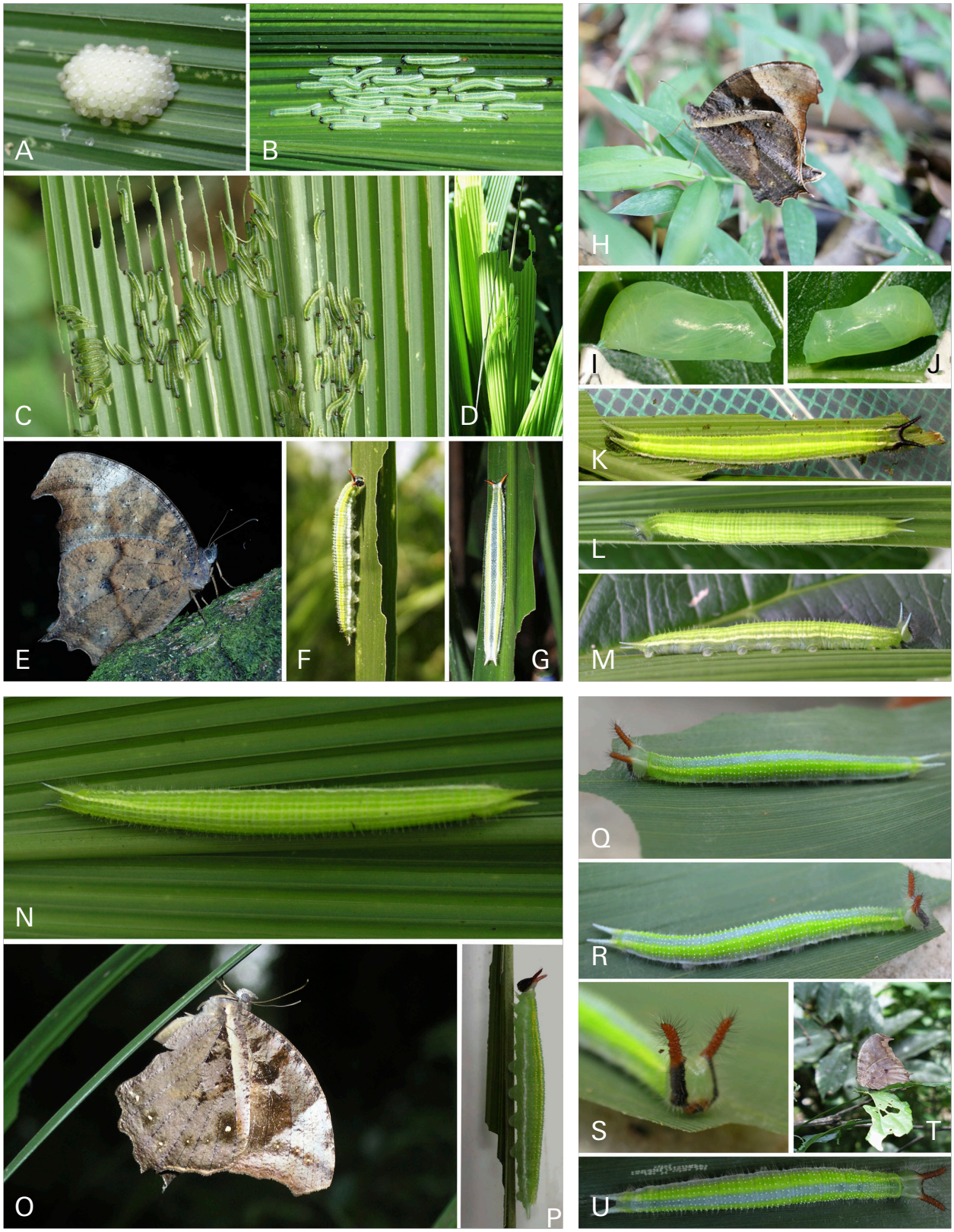

Fig. 24. Early developmental stages. A–G: *Haydonia chelys*, eggs cluster (A), first instar gregarious larvae (B), first instar gregarious larvae (C), ? third instar larvae on *Setaria* sp. (D), adult ♀ (E), fifth instar larva in lateral view (F), fifth instar larvae in dorsal view (G); H–M: *Gnophodes diversa,* adult ♀ (H), pupa (I), pupa (J), fourth instar larva in dorsal view (K), fourth instar larva in dorsal view (L), ? instar larva in lateral view (M); N–P: *Gnophodes heroni* n. sp., fifth instar larva in dorsal view on *Setaria* (N), adult ♀ laying eggs on *Setaria* (O), fifth instar larva in lateral view (P); Q–U: *Haydonia harpa*, fifth instar larva (Q), fifth instar larva (R), fifth instar larva head (**S**), adult ♀ (T), fifth instar larva in dorsal view (U).

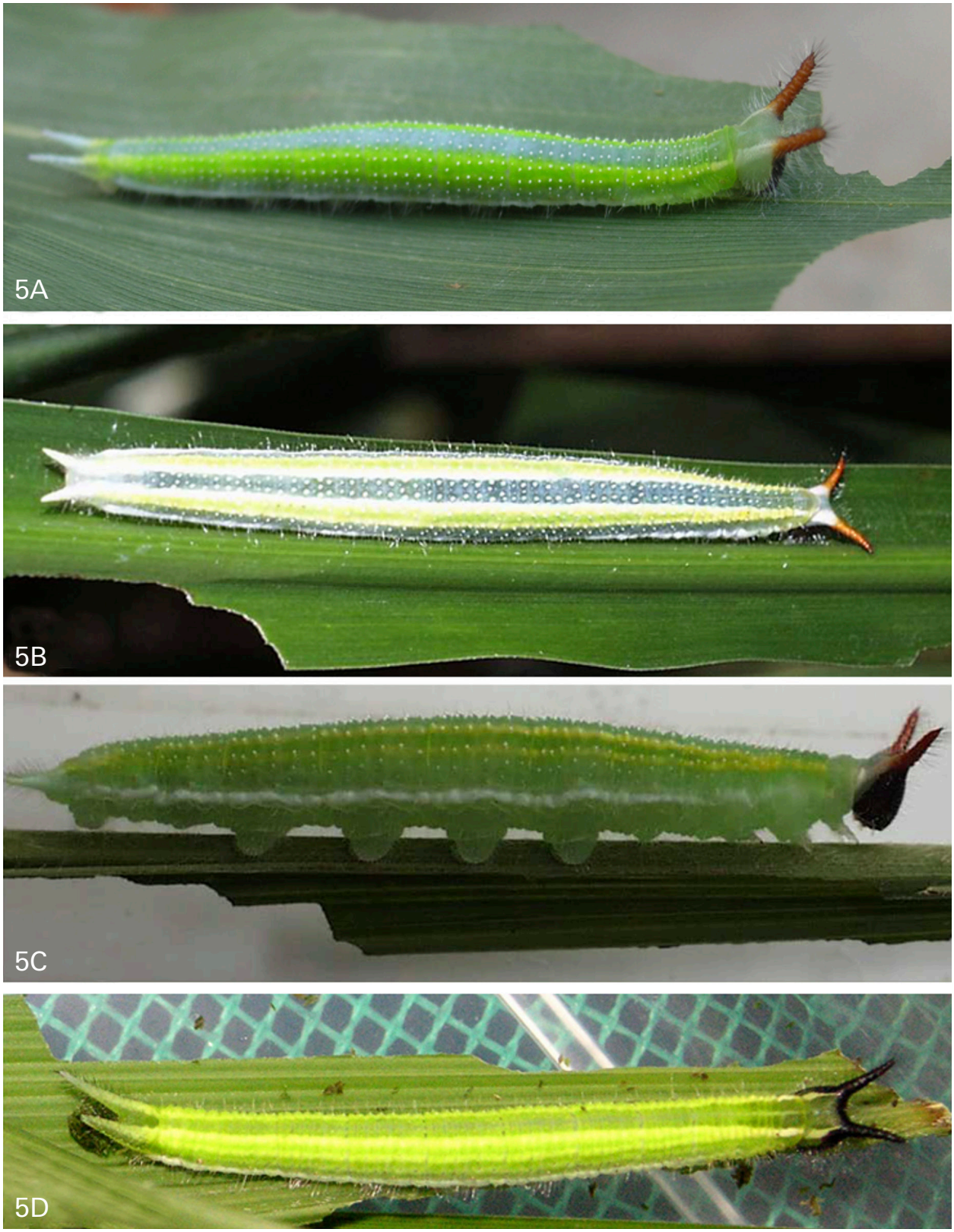

Fig. 25. Final (fifth) instar larva comparison. A: *Haydonia harpa*; B: *Haydonia chelys*; C: *Gnophodes heroni* sp.n.; D: *Gnophodes diversa.*

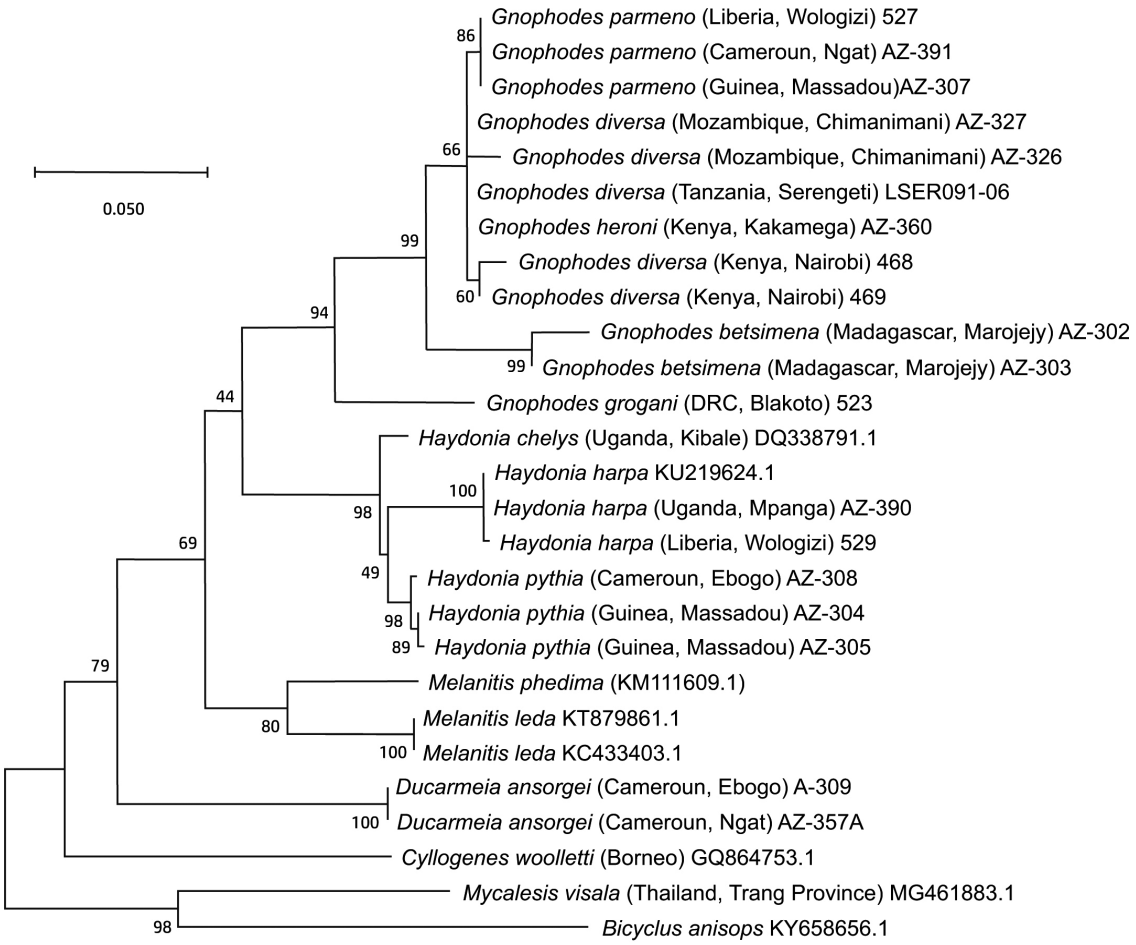

Fig. 26. Maximum Likelihood phylogenetic tree of Afrotropical Melanitini butterflies, based on COI mitochondrial marker, with bootstrap branch support values.

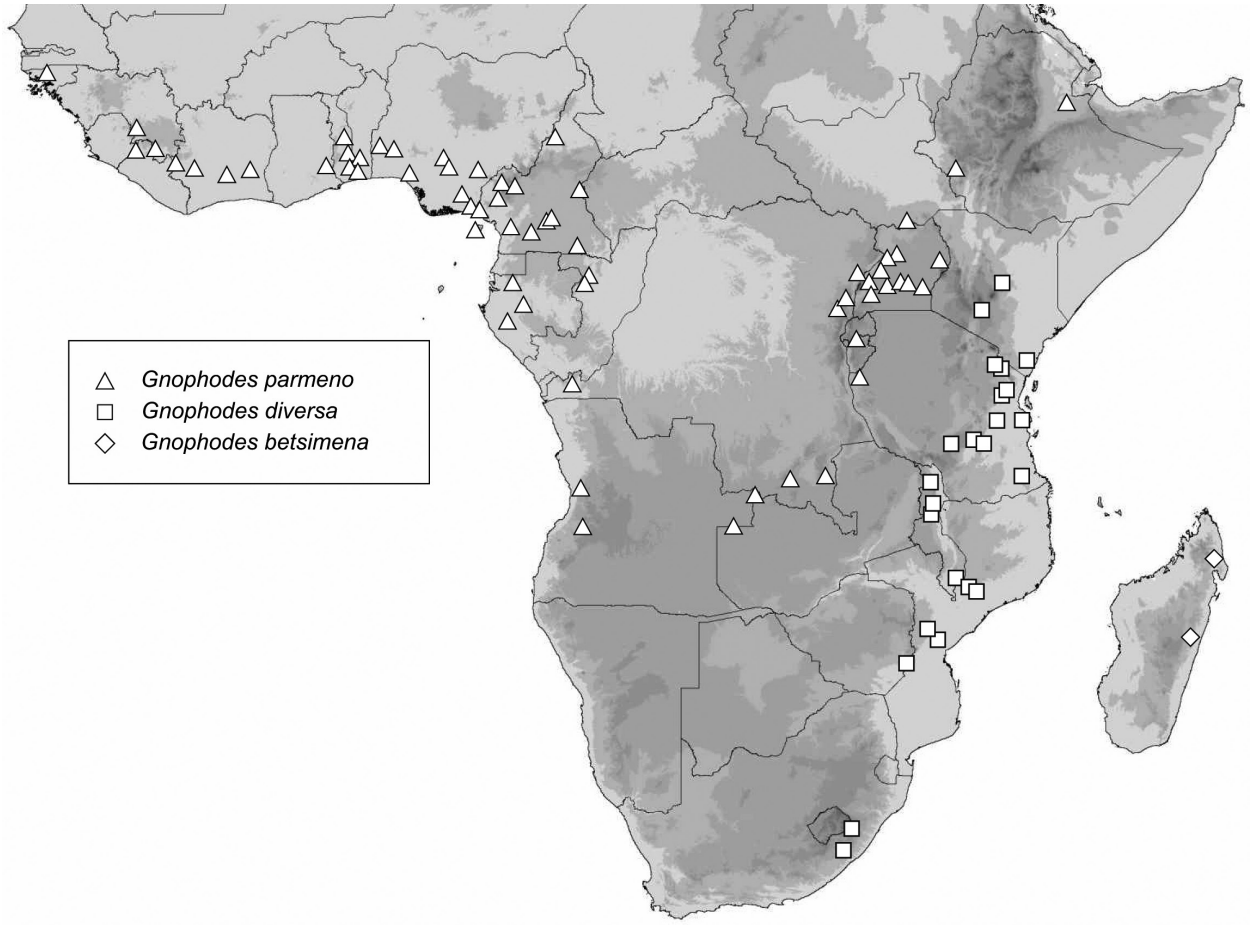

Fig. 27. Distribution map of *Gnophodes betsimena*, *G. parmeno*, *G. diversa.*

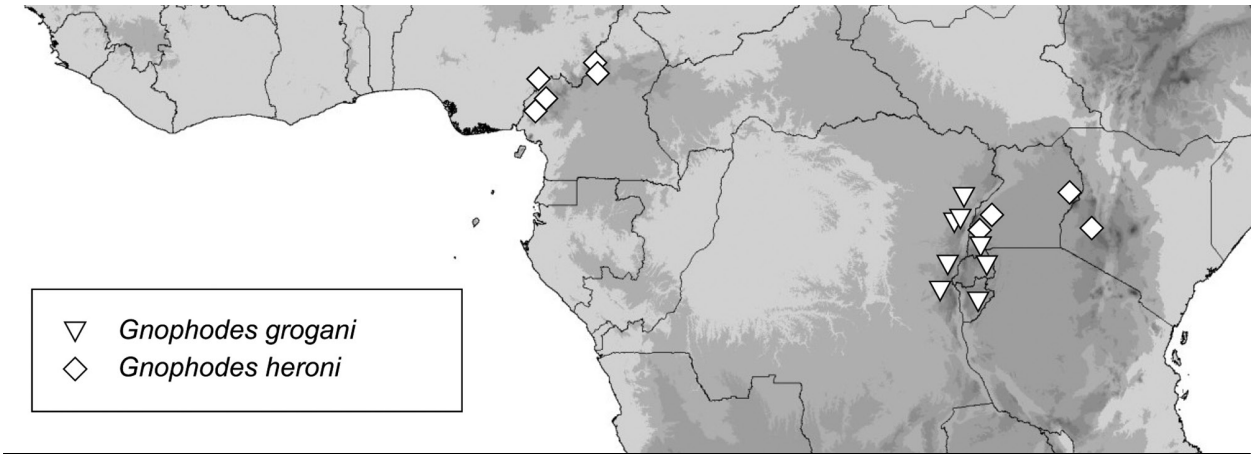

Fig. 28. Distribution map of *Gnophodes heroni*, *G. grogani.*

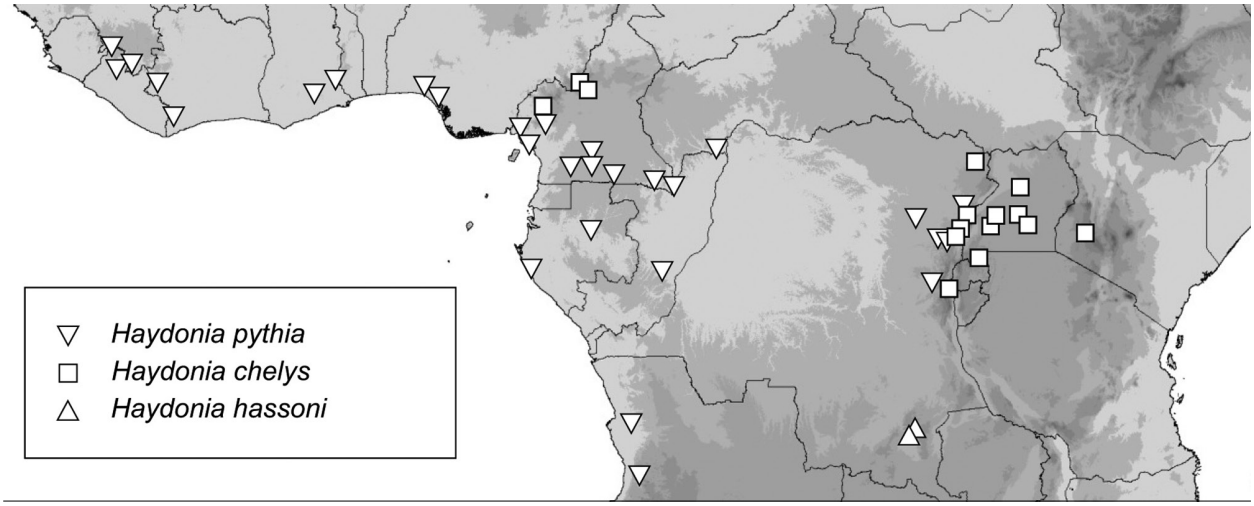

Fig. 29. Distribution map of *Haydonia chelys*, *H. pythia*, *H. hassoni.*

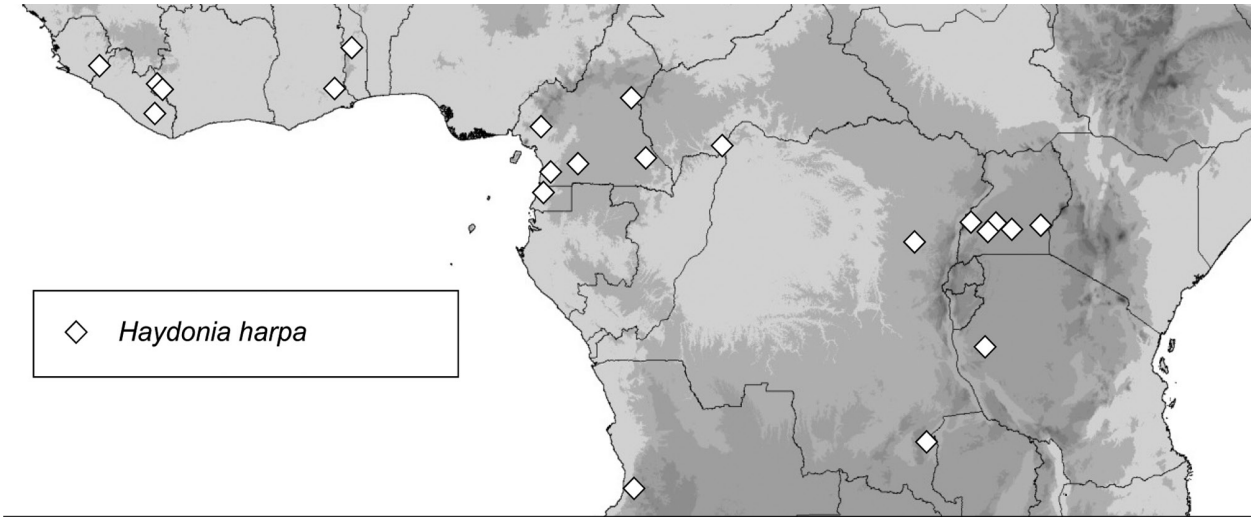

Fig. 30. Distribution map of *Haydonia harpa.*

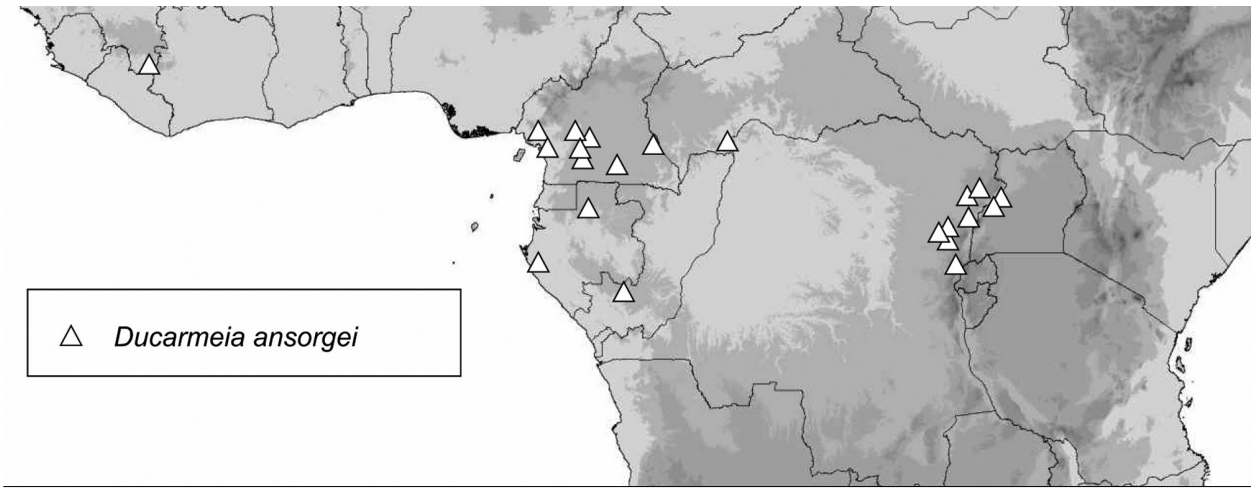

Fig. 31. Distribution map of *Ducarmeia ansorgei*.