Danis Fabricius, 1807 from West New Guinea (Indonesia), a tentative arrangement (Lepidoptera: Lycaenidae, Polyommatinae)

Stefan Schröder

Auf dem Rosenhügel 15, 50997 Köln, Germany
email: ste.schroeder@gmx.net

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Abstract: An overview is given of the species of the lycaenid genus *Danis* Fabricius, 1807, occurring in West Papua and Papua (Indonesia). All taxa are discussed with regard to their systematic position and - as far as possible - the type specimens of several species are shown for the first time. Particular emphasis is placed on the individual characters that are intended to help identify the often very similar species. Based on the species list of Hirowatari (1992), the following taxonomic changes are proposed: *Danis helga* (Grose-Smith, 1898) **stat. rev.**, *Danis horsa* (Grose-Smith, 1898) **stat. rev.,** *Danis metrophanes* (Fruhstorfer, 1915) **syn. nov.,** *Danis hermogenes* (Fruhstorfer, 1915) **stat. rev.**

Rangkuman: Peninjauan secara luas diberikan kepada spesies dari lycaenid genus *Danis* Fabricius, 1807, ditemukan di Provinsi Papua Barat (Indonesia). Semua taxa dibahas yang berhubungan dengan posisi sistematik sejauh mungkin. Type spesimen dari beberapa spesies ditunjukkan untuk pertama kalinya untuk semua spesies. Penekanan khusus diberikan untuk karakteristik individu yang ditujukan untuk membantu mengidentifikasi spesies yang sangat mirip. Berdasarkan list spesies Hirowatari (1992), perubahan taksonomi diusulkan sebagai berikut: *Danis helga* (Grose-Smith, 1898) **stat. rev.**, *Danis horsa* (Grose-Smith, 1898) **stat. rev.**, *Danis metrophanes* (Fruhstorfer, 1915) **syn. nov.**, *Danis hermogenes* (Fruhstorfer, 1915) **stat. rev.** [translation by Daawia Suhartawan]

Keywords: Polyommatinae*, Thysonotis, Danina,* Papua New Guinea

Introduction

The genus *Danis* Fabricius, 1807 includes comparably large lycaenid butterflies, representing a magnificent part of the butterfly fauna of New Guinea, where it shows the highest species diversity. The most common species is *Danis danis* (Cramer, 1775), which is also the one with the widest distribution, reaching from eastern Maluku to northern Australia. All other species are generally rare and much less is known about them, even though most of them are known to science since a long time. No recent revision of the genus is available and only few new taxa were described after the early twenties of the last century.

Apparently, the lycaenid specialist G. E. Tite was working on the group in the 1960s, as he dissected specimens and also added comments on some, but nothing was published.

There are only two papers by Yagishita (2000) and Tennent (2016), covering *Danis danis*, but not concerning other species. Nothing substantial was added after publication of Fruhstorfer's **„***Thysonotis***“** list in 1915. The most recent publication, illustrating many of the

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species, is the Australasian volume of D'Abrera`s Butterflies of the World series, dating back to 1971. Hirowatari (1992) gave a revised species list, including all taxonomical changes taken in the last century. Species diversity is apparently lower in PNG and accordingly, Parsons (1998) illustrates only a few species. Selected information concerning limited areas in West Papua were given by Gotts & Pangemanan (2010), van Mastrigt & Rosariyanto (2005), van Mastrigt & Warikar (2013) and Tim Redaksi KEP (2010).

The genus name *Danis* has a long history, but was not always accepted. Just a few years after Fabricius introduced the name in 1807, Hübner (1819) described *Thysonotis*. Druce & Bethune-Baker (1893: 537) rejected the older name *Danis* as „a generic name must not be one which has been used as a specific name" and placed all species known at this time in *Thysonotis*, dividing it into five groups. They included a *danis*-group to accomodate the species we know today as *Danis danis*. Due to the selection of *Papilio danis* Cramer, 1775 as type species of *Danis* by Hemming (1964), the well used name *Thysonotis* Hübner, 1819 became a synonym of *Danis*.
Thysonotis had been used for many decades and became a kind of "waste basket" over the years to include various phenotypical similar species, many of them unrelated, in a group which is known as the *Danis/Psychonotis* mimicry complex (Parsons, 1998: 98). Subsequently, taxonomy of this complex was resolved and its members were correctly assigned to several other genera like *Psychonotis*, *Nacaduba*, *Nothodanis* and *Perpheres* (Hirowatari, 1992).
Druce & Bethune-Baker (1893: 543) separated a "*wallacei*-group" from the more robust *danis*, remarking that they "have the cilia of both sexes pure white, not alternately black and white as in *danis* and allies". Aside of *T. perpheres* Druce & Bethune-Baker, 1893 (now placed in *Perpheres* Hirowatari, 1992), *T. melimnos* Druce & Bethune-Baker, 1893 was included. However, the groups mentioned are not unambiguous and also depend heavily on preservation of specimens, as it is often not possible to observe this character in worn specimens. Far more important for determination, however, are the following characters: development of the white band on the hindwings (weak or very strong, its width and inclination), the width of the wing margins, presence of a white forewing patch, a tornal spot on the forewing underside and colour of space 7 of the hindwing upperside.

Basic works include Grose-Smith (1894, 1897), Grose-Smith & Kirby (1895), Druce & Bethune-Baker (1893) and Fruhstorfer (1915). Hirowatari (1992) gave a very useful revised species-list and commented on some taxa, also giving new combinations, but did not figure any specimens.

With the exception of *Danis danis* and its subspecies, determination of other *Danis* species is notoriously difficult. The reason for this lies undoubtedly in the complex situation that different species have a very similar wing pattern and are in most cases rare. Little is known about individual variation, especially concerning the different shades of blue, the width of the white bands on the hindwing underside and wing margins in specimens from different populations and altitudes. Except for the original descriptions and the Australian volume of D´Abrera (1971) there are almost no illustrations available, which could help with determination. Type specimens were never photographically figured and therefore misidentifications are prevalent.

In addition, it may be very difficult to assign females to the corresponding males. Even the type series are inconsistent and males and females are not always correctly assigned to each

other, including different species. In several cases the authors of the last century included males and females from different localties in a type series, which do not belong together. It is possible to separate males from each other, but it is extremely difficult to match the correct females with them, if not collected at the same locality. To complicate matters, identical specimens from a given locality were assigned as allotypes to different species. For example, the allotype of *Thysonotis helga* belongs to the same species as the female holotype of *melimnos* (but maybe the male of *helga* has to be matched with the female of *melimnos*) and the *metrophanes* allotype belongs to the same species as the allotype of *horsa*.
A similar situation is known from other lycaenid genera like *Nacaduba* or *Jamides*.

Even if it is impossible to solve all problems at species level at this time, it is important to document species diversity known so far, so that a better assessment of the different forms can be made. Finally, a conclusive revision without DNA data might not be possible. However, this requires the availability of fresh, topotypic material for most of the species, which may also be problematic given the rarity of some species.
Unfortunately DNA sequencing is very difficult is not yet possible for historical type specimens, which seems to be the only way to solve the systematic position of some taxa. For the time being, and as an aid for determination, phenotypic characters are used in this work to separate different species and most of the types are illustrated, so that a determination for the taxa occurring in western New Guinea should be possible.

With few exceptions, names of synonyms are only given for taxa occurring in West Papua and Papua. Locality data are mainly based on the KSP collection.

Abbreviations
ANIC – Australian National Insect Collection, Canberra, Australia
HT – holotype (in literature)
NHMUK – The Natural History Museum, London, United Kingdom
CSSK – Collection Stefan Schröder, Köln, Germany
KSP – Koleksi Serangga Papua, Universitas Cenderawasih, Waena, Papua, Indonesia
RMNH – Naturalis Biodiversity Center, Leiden, The Netherlands
MFNB – Museum für Naturkunde, Berlin, Germany

Scale bar in plates is 1 cm

Systematical part

Danis danis (Cramer, 1775)

This species was recently subject of a very detailed review, including all known subspecies (Tennent, 2016), and there is no need to repeat the information presented in that publication.
Of the presently known 24 subspecies only four occur in Papua and West Papua: *apollonius* C. & R. Felder, 1865 [mainland PNG, Waigeo, Salawatti and the islands in Teluk Cenderawasih = Geelvink Bay]; *hermes* Grose-Smith, 1894 [Schouten Islands], and two new

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subspecies described by Tennent: ssp. *gebe* Tennent, 2016 [Gebe Island] and ssp. *kofiau* Tennent, 2016 [Kofiau Island].
Tennent (2016) is illustrating numerous specimens, including detailed discussions and illustrations of the type species of *apollonius*, *panaetius*, *herophilus* and *sophron*.

Danis danis apollonius (C. & R. Felder, 1865) (figs 1-6)

Lycaena apollonius: C. & R. Felder (1865: 265, pl. 33, fig. 3). [HT ♀ "Nova Guinea ? type", NHMUK]
Thysonotis apollonius ab. *plumbeus*: Rothschild (1915: 140). [HT ♂ "Misol"]
Thysonotis danis panaetius: Fruhstorfer (1915: 50). [HT ♀, Salawatti, RMNH]
Thysonotis danis herophilus: Fruhstorfer (1915: 50). [LT ♂, "Waigiu", NHMUK]
? *Thysonotis danis sophron*: Fruhstorfer (1915: 50). [HT ♀, "New Guinea", NHMUK] [See Tennent (2016: 128)]
? *Thysonotis lona*: Röber (1927: 105). ["Waigeo", type not located]
Danis danis (apollonius) thinophilus: Toxopeus (1930: 129). [HT "Misool", probably in RMNH] {nom. nov. pro *apollonius* Fruhstorfer nec Felder}

Notes: *Thysonotis lona* Röber, 1927 is little understood. The translation of its description is as follows: "The available male from Waigeo differs from *philostratus* Feld. males from Halmaheira (Gilolo) in having a lighter colouration (more greenish than bluish); which is also reduced (because of the broadened white band), the black edge on front and margin is also narrower, the blue of the hindwing is reduced, but more present than in *philostratus*. Underside colouration is also more greenish and stronger. It is not known to me if typical *philostratus* [North Maluku !] occurs on Waigeo, but if this should be the case, *lona* could possibly be a seasonal form of *philostratus*." Apparently Röber regarded *lona* as closely related to *philostratus*, which is the northern Maluku race (Halmahera, Ternate, Bacan and Kaioa) of *Danis danis*. Given the geographical distribution as presently known, *lona* is most likely a synonym of *apollonius*, which has already been proposed by Tennent (2016). The type material of *lona* is apparently lost, as neither the collections in Dresden or München hold any specimens labeled with that name.

Distribution: Widely distributed in Papua and Papua Barat (Indonesia), including the Raja Ampat Islands and Schouten Islands, and in Papua New Guinea.

Danis danis gebe Tennent, 2016 (figs 7-10)

Danis danis gebe: Tennent (2016: 119, figs. 25-29). [HT ♂ Gebe Island, NHMUK]

Notes: Description of this island race is based on a few specimens only. Tennent (2016) remarked "hindwing basal black area extending slightly along costa, leaving distal edge of black area distincly curved". More material has to show if this is a diagnostic character of this subspecies, which otherwise does not show signifiant differences to ssp. *apollonius*, occurring on Waigeo, which lies only a few kilometres east of Gebe.

Distribution: Only known from Gebe Island (Moluccas, Indonesia).

Danis danis kofiau Tennent, 2016 (figs 11-14)

Danis danis kofiau: Tennent (2016: 121, figs. 47-51). [HT ♂ Kofiau Island, NHMUK]

Remarks: Differs from other subspecies in having a broad costal forewing border in the males and a broader white median band in the females.

Distribution: Only known from Kofiau Island (Papua Barat, Indonesia).

Danis danis hermes (Grose-Smith, 1894) (figs 15-18)

Thysonotis hermes: Grose-Smith (1894: 575). [HT ♂ Korrido (Supiori) and Biak, NHMUK]
Thysonotis danis phoibides: Fruhstorfer (1915). [HT ♂ "Insel Mefor", NHMUK]

Notes: This taxon is characterized by the "duller and more greenish" blue wing colour and the rather broad dark borders. The species is already figured very well in Grose-Smith & Kirby (1895: pl. 1, fig. 5-8). Tennent (2016) explained the synonymy of *phoibides* Fruhstorfer, 1915 in detail.

Distribution: Endemic to the Schouten Islands: Biak, Supiori, Numfor (Papua, Indonesia).

Danis phroso (Grose-Smith, 1897) (figs 19-28)

Thysonotis phroso: Grose-Smith (1897: 313). [HT ♀ "Etna Bay, Dutch New Guinea", NHMUK]
? *Thysonotis lygia*: Grose-Smith (1897: 516). [HT ♂ "Dinner Island" = Samarai Isl., Milne Bay Province, PNG, NHMUK]
Thysonotis melimnos scarpheia: Fruhstorfer (1915: 50). [Type ♀ "Dinner Insel, Ost-Neu Guinea", Dep. ?]
Danis phroso (Grose-Smith, 1897): Hirowatari (1992: 26, fig. 30A). [♀ genitalia]

Identification: Most useful in determining *phroso* is the narrow subbasal band on the hindwing underside, which is blue in its lower and white in the upper part, a character which is not found in any other *Danis*, except for *D. concolor* (Rothschild, 1915). Males have a white discal patch on the forewing upperside, which reminds of the superficially similar looking males of the genus *Perpheres* Hirowatari, 1992. The patch is variable and may be very extensive as in the specimen figured by Parsons (1998: pl. 67, fig. 1891) or just faintly developed as in a specimen from Mimika (fig. 25, KSP 11861). Hindwing space 7 is white.
Females do not show any traces of a white band on the hindwing upperside, which is present in all other species except *D. concolor*. Instead, there is a greenish-blue basal suffusion on the hindwing as well as at costa and dorsum of the forewing.

Notes: *Danis phroso* was described from four female specimens and compared with *D. wallacei* (C. & R. Felder, 1865) from Waigeo, which is a very different species.
The synonymy of *lygia* and *scrapheia* with *phroso* as proposed by D´Abrera (1971) is not yet settled as both occur in eastern PNG, while *phroso* is known from Papua. Characters of both taxa are not completely identical: *lygia* females from eastern PNG have the blue metallic scales on costa and dorsum of the upperside of the forewing much stronger than in females

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from Papua, and the marginal green metallic line along the forewing costa and termen on the underside is more complete (Parsons 1998: pl. 67 fig. 1891-93). In his description of *lygia*, Grose-Smith (1897) already mentioned the similarity with *phroso*, from which males differ in having a wider black hindwing border and an indistinctive white patch on the forewings. Additional material from PNG is needed to understand the specific variability of *lygia* and the proposed synonymy. It can not be excluded that populations from eastern PNG belong to a separate subspecies.

Distribution: The type locality "Etnabaai" (Etna Bay, Papua, Indonesia) is located Southeast of Kaimana in Southwest Papua and is the southernmost of several large bays reaching far into the mainland on the southern coastline. Furthermore Timika, Yahukimo, Mimika (Papua, Indonesia) and Papua New Guinea.

***Danis concolor* (Rothschild, 1915)** (figs 29-32)

Thysonotis phroso concolor: Rothschild (1915: 32). [Type ♂ "Snow Mountains, Base Camp", Dep.?]
Danis concolor (Rothschild, 1915): D'Abrera (1971: 325); Hirowatari (1992: 26, fig. 31A). [♀ genitalia]
Danis phroso concolor (Rothschild, 1915): Gotts & Pangemanan (2010: 244-245). [♂ refigured herein, figs. 29-30].

Identification: Rothschild (1915) describes ssp. *phroso concolor* very briefly as follows: "♂. Differs from *p. phroso* in its larger size and the uniform blue of the forewings and absence of metallic green on fore- and hindwings". ♀ has the base of wings greyish lavender blue, NOT bright blue."
Both species are very similar, but can be separated by the following characters: dark hindwing margins of the *concolor* male are much narrower than in *phroso*. The white forewing patch of the males is small and more or less restricted to space 2, in some specimens it is completely missing (fig. 29). The white patch on the forewing in females is less compact in *concolor* and usually divided by brown along the veins. In females the upper half of the cell is brown but there are white scales in the basal parts of spaces 4-6 so that the white seems to be cut off abruptly at almost a right angle.
Females of both, *phroso* and *concolor* have a blue basal suffusion on the upper side of the hindwings, which is not known from any other species in this group, aside of *horsa*. They both have in common the underside subbasal band divided in white and blue-green. The upperside subcostal blue stripe in the females is variable in both species.

Notes: Hirowatari (1992: 27, 25) mentions the unusual form of the valvae of this species, having a finger-like process at their ends, and therefore regards *concolor* as the "most disctinctive" taxon within *Danis*. Usually the distal margin of the valva bears a minute serration.

Distribution: Snow Mountains, Mimika, Timika (Papua, Indonesia).

Danis glaucopis (Grose-Smith, 1894) (figs 33-36)

Thysonotis glaucopis: Grose-Smith (1894: 575). [HT ♂ "Humboldt Bay", NHMUK]
Danis glaucopis (Grose-Smith, 1894): Parsons (1998: 431, pl. 67, fig. 1894-1896).

Identification: A round winged species with a rather well developed white band on the hindwing upperside in males and females. Accordingly, in the females the basal part of the hindwing appears almost completely white but not brown as in many other species. The white markings on the forewing underside are reduced in extension to a small, sometimes rounded patch, leaving a wide dark brown area and according to Parsons (1998: 431) *glaucopis* is best identified by this character. This fits well with the original underside figure of Grose-Smith & Kirby (1895: pl. 1 fig. 10).
Grose-Smith (1894: 576) compared *glaucopis* in particular with *wallacei*, which has a much better defined, solid white hindwing band and a wider hindwing margin in the males. Females of *wallacei* have a broader white underside band than *glaucopis* and the white forewing patch is much larger.
Danis glaucopis also resembles *D. metrophanes* Fruhstorfer, 1915, described from Sorong, but according to Fruhstorfer (1915: 49), *metrophanes* differs in having the white band on the hindwing upperside almost completely reduced.
Danis drucei has the white underside forewing patch significantly larger than in *glaucopis* or *metrophanes*. The blue of the males is deeper in *drucei* and wing margins are broader. Space 7 of the hindwing upperside is completely white in *drucei*. In addition, the white underside hindwing band is narrower, more inclined, so that the band almost touches the basal green-blue on the hindwing costa. The green costal stripe on the underside of the forewing is incomplete in *metrophanes*.
Another species closely resembling *glaucopis* is the East Sepik (Papua New Guinea) endemic *Danis regalis* (Grose-Smith & Kirby, 1895).

Notes: A rare species. The type series is from Wendesi (at the "neck" of the Birdshead Peninsula) and the Jayapura area (Humboldt Bay). According to Parsons, the holotype specimen is deposited in the NHMUK. Additional specimens are said to be in Staudinger collection in MFNB.

Distribution: FakFak (Papua Barat) and Sarmi (Papua, Indonesia), and Papua New Guinea (Parsons, 1998: 431).

Danis helga (Grose-Smith, 1898) (figs 37-46)

Thysonotis helga: Grose-Smith (1898: 105). [HT ♂ "Ansus, Jobi Island", NHMUK]
Danis melimnos helga (Grose-Smith, 1898): Hirowatari (1992: 26).

Identification: The upperside of the holotype of *Danis helga* (fig. 41) is bright blue with a small but distinctive white patch in the forewing spaces 1b-3 and a very broad white band on the hindwings. The dark wing margins are comparably broad. Grose-Smith (1898: 105) compares *helga* with *horsa* (Grose-Smith, 1898), which is now placed as a good species, but lacks the clear white band across the hindwing in the males. Compared with this species, *helga* males have a very prominent and broad white hindwing band. Grose-Smith also mentions: "Cilia of both wings narrowly white, crossed with black at the ends of the veins."

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As the males, females are characterized by a very broad white band on the hindwing undersides, resembling *wallacei* females in this respect.
D. melimnos appears to be much closer concerning male genitalia structure and therefore Hirowatari (1992: 26) and Parsons (1998: 431) regarded *helga* as the mainland Papua subspecies of *melimnos*. However, both *melimnos* and *helga* have Yapen as type locality, and thus can not be regarded as different subspecies of the same species.
The situation is complicated by the fact that the allotype of *helga* (Figs 47-48) is conspecific with the female holotype of *melimnos* (Fig. 53). Further research and new material from Yapen is needed to ascertain that males and females of both taxa are correctly placed with each other. It can not be completely excluded that the male of *helga* has to be matched with the female of *melimnos*, but for now, both names are retained and applied to different species: This has also been followed by D'Abrera (1971: 326), mentioning *helga* being "deceptively like *melimnos*, but distinguishable by its larger size and by the rounder shape of the wings in both sexes."
D. melimnos has very broad white bands on the undersides of both wings (Grose-Smith, 1898: pl. 46, fig. 2).
It is more likely that *helga* is conspecific with *wallacei* described from Waigeo.
The pictured specimen from the KSP collection (figs 37-38) is quite similar to *mamberano* (Joicey & Talbot, 1916), but this species has a different wing shape, the blue on the hindwing appears jagged on the veins and the hindwing margin is wider.

Distribution: Yapen Island (Papua, Indonesia).

Danis mamberano (Joicey & Talbot, 1916) (figs 49-50)

Thysonotis mamberano: Joicey & Talbot (1916: 82). [HT ♂: "River Mamberano, N. Dutch New Guinea", NHMUK]

Identification: According to Joicey & Talbot (1916: 82), *mamberano* is "nearest *helga,* Gr.-Sm., from Jobi". In their short description it is said that wing margins and the white hindwing band are narrower than in *D. helga*. The forewing shows an indistinct white band from inner margin to vein 4. On the underside the costal blue is broader beyond the cell and the blue touches the white underside colour at tornus. Hindwing with white band as above.

Notes: Described from a single male. The wing colour is a grey-blue with a diffuse discal band on the forewing and a compact white band on the hindwing. Hindwing margin is wide, with the blue-grey scaling indented between the veins. *D. mamberano* differs from *helga* concerning colouration as well as the extent and inclination of the white bands. Further research and new material is needed to confirm its taxonomic status. It can not be excluded that *mamberano* is a ssp. of *helga*, however, the blue wing colour of the male is darker than in any other known *Danis* species occurring in Papua.

Distribution: Mamberano Area, Northern Papua (Papua, Indonesia).

Danis melimnos (Druce & Bethune-Baker, 1893) (figs 51-53)

Thysonotis melimnos: Druce & Bethune-Baker (1893: 544, pl.46, fig. 2). [HT ♀ "Dutch New Guinea, Jobi I. (A. B. Meyer)", Dep.? "Type is contained in Staudinger coll.", Berlin?]

Identification: The original description of *T. melimnos* is based on a single female, which was compared with *wallacei* C. & R. Felder, 1865, but already suggested to "prove quite distinct from *wallacei*" by the authors. The white bands at the underside follow more evenly the wing shape and appear broader in *melimnos*, and the white forewing upperside discal patch is not extending towards the termen as in *wallacei*. On the forewing underside the white does not reach the tornus. The white patch at the underside in females is elongated, very regularly outlined and almost parallel to the green-blue marginal markings, so that only a small band of brown remains in between. However, the variability of this character is not known.

Notes: A very different interpretation of *melimnos* was given by Parsons (1989: 432), stating that the best way to determine *melimnos* is the underside colour of the bands, which is not plain white, but has a creamy-white to yellowish hue. This is the case in the female specimen designated as allotype of *Thysonotis helga* from Yapen, which clearly belongs to *melimnos* (figs 47-48), but in other specimens (fig. 52) the bands are pure white without any yellowish hue.
The female specimen illustrated by D'Abrera (1971: 326) shows a short streak of greenish blue scales along the upperside forewing costa and Parsons (1998: 432) remarks that of all *Danis* species occurring in PNG only *melimnos* females have a broad subcostal band of blue scales on the forewing upperside. This is not the case in western New Guinea, where this character is also known from *T. vidua* Grose-Smith & Kirby, 1895 (= *wallacei* C. & R. Felder, 1865) and other unrelated species. Unfortunately, the underside of the specimen illustrated by Parsons (1998: pl. 67 fig. 1899) is not shown, but most likely it does not have the broad white bands, characterizing true *melimnos*. Druce & Bethune-Baker do not mention any metallic costal scales on the forewing and neither does the figure of the type show them. A female from Yapen (figs 51-52) has only a very weak streak of costal blue scales on the forewing.

The female specimen figured as *D. melimnos* by Parsons (1989: pl. 67, fig. 1899) has much narrower white bands on the upperside of both wings, and such specimens were tentatively assigned to an undescribed mainland PNG race of *melimnos* by him. Possibly, the female from Yahukimo (figs 57-58) and the one from Vriendschap River (Kabupaten Asmat, 05°20'20" S - 138°52'72" E, figs 55-56) also belong to this new taxon. However, it is more likely they represent females of other species.
Gotts & Pangemanan (2010: 244) mentioned that specimens from Mimika placed by them with *melimnos* are closer to this PNG race than to the specimens illustrated by D'Abrera. The rather narrow but regular yellowish bands on fore- and hindwing are also present in *T. athanetus*, which is regarded here as synonym of *wallacei*.
Furthermore, the *melimnos* male Parsons figures on pl. 67 fig. 1897/1898 is very similar to the one figured by him as *D. regalis* (Grose-Smith & Kirby, 1895) and likewise, the male "*melimnos*" specimen in Gotts & Pangemanan (2010: 245) does not differ considerably from the figure of Grose-Smith & Kirby (pl. 2 figs 4-5) given for *regalis*. Both taxa show a much greater resemblance to *regalis* than to *melimnos*.
However, *T. regalis* is little understood. The description gives "New Guinea" as distribution and later on Fruhstorfer (1915: 49) recorded it from "Deutsch-Neu-Guinea" where it is said to be the most common species at "Astrolabebai" (Madang Province of north-eastern PNG). Nothing is known about its distribution or individual variability and the whereabouts of the

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type are also unknown ("In the Collection of Dr. Staudinger"). Judging from the original illustrations (figs 59-60) it appears to be a species with a very conspicuous, broad hindwing margin and a rather narrow white band on the hindwings in the male.

Currently there exists no valid definition of *melimnos*, especially concerning matching males, as only insufficient material for study is available from the type locality Yapen.

Distribution: Yapen Island (Papua, Indonesia); possibly endemic.

Danis wallacei (C. & R. Felder, 1865) (figs 61-72)

Lycaena wallacei: C. & R. Felder (1865: 265, pl. 33 figs 8-10). [Type "Waigiou", Dep]
Thysonotis vidua: Grose-Smith & Kirby (1895: 30, pl. 2, f. 9-10). [Type ♀: "Waigiou"]
Thysonotis albomarginata: Rothschild (1915: 140). [HT ♀: Misool, NHMUK]
Thysonotis melimnos athanetus: Fruhstorfer (1915: 50). [HT ♂: „Salawati", RMNH]

Identification: The illustrations of Felder & Felder (1865) in the "Reise der österreichischen Fregatte Novara um die Erde" are generally accurate if compared with recently photographically illustrated type specimens (e.g *apollonius*, or *philostratus*; see Tennent, 2016), so there is no reason to doubt the reliability of the illustration of the male holotype on pl. 33 fig. 8. Most of the taxa described by the Felders are now in the NHMUK (Rothschild Bequest B.M. 1939) and it is most likely that the type of *wallacei* is in the British Museum. Unfortunately, it was not possible to locate this specimen. Both, the *vidua* and *wallacei* type-specimens are not preserved in the MFNB, Berlin.
Based on the illustrations, *D. wallacei* males are apparently characterized by a solid, slightly curved and very prominent white hindwing band, which appears to be even broader than in *drucei*. Variation of the conspicious white forewing patch (spaces 1b-3) in the males is insufficiently known; it is well visible (see D'Abrera, 1971: 327), and may be as strong as known from *helga*. A large white forewing patch is present in the females, expanding outwardly along spaces 2 and 3; basal area is brown (not white as in *drucei* or other *Danis* females). On the underside, there is a small black spot in space 1b close to the tornus of the forewing as in *hengis* and *drucei*. A faint line of green-blue metallic subcostal scaling is present in the females, which is also found in *melimnos*. Grose-Smith & Kirby (1895: 30) mentioned differences in the width and extension of this green marginal line on the forewing between *vidua* (= *wallacei*) and *drucei*, but these characters seem to vary. Grose-Smith & Kirby (1895) had already mentioned the close resemblance of *vidua* to *wallacei*: "Underside almost exactly like that of the female of *T. Drucei* [(postea)], except, that in the anterior wings the curved outer part of the blue band is broader, and extends to the white portion of the wing…"

Notes: Both, *melimnos athanetus* Fruhstorfer, 1915, as well as *wallacei hermogenes* Fruhstorfer, 1915 are from Salawati (Bernstein collection, RMNH) and closely resemble each other. Additional labels of Van Eecke attached to both types give a determination as *wallacei*, which may have been the reason for D'Abrera (1971: 326) to include both in *wallacei*.
However, both type specimens are not conspecific: they are very similar, but there are some differences concerning the underside markings. In *hermogenes* (Fig. 93-94) the white patch

on the underside of the forewing reaches the tornus, whereas it is more restricted in *athanetus* (Fig. 63-64). The white band on the hindwing underside of *hermogenes* is much narrower than in *athanetus* where it is much stronger and appears as a solid white band on the hindwing upperside. The white band in *hermogenes* is weakly developed on the hindwing upperside and strongly dusted with blue-grey scales. Apparently both are not conspecific and the synonymy proposed by D'Abrera has to be partially rejected. Most likely *athanetus* is a synonym of *wallacei*, but the male of *metrophanes* is better assigned to *hermogenes* described from Salawati. The *metrophanes* allotype from Dorey (Manokwari) belongs to *horsa*.
T. albomarginata Rothschild was described from a single female from Misool Island (figs 67-68) and there is little doubt that this taxon is a synonym of *wallacei*, because of its brown wing bases, which is only rarely the case in *Danis*.
Druce & Bethune-Baker (1893) remarked that specimens from Misool are "rather smaller than Dr. Felder´s figures" and the specimen figured here is also very small compared to other *Danis*. It is also mentioned, that in a male from Misool "the white on the disks has entirely disappeared". For unknown reasons, Grünberg in Seitz (1916: 826, 143c) said that in the *wallacei* group specimens "Die weiße Binde tritt beim m auf der Vflgl-Oberseite gewöhnlich stark zurück." which means that the white forewing band is usually strongly reduced, which does not agree with the figures in Felder & Felder. Grünberg`s figures of a male from Waigeo are refigured here in figs 71-72.

Distribution: Known from the islands off the western coast of the Birdshead Peninsula: Waigeo, Misool and Salawati, and Mioswaar at the eastern coast (Papua Barat, Indonesia).

Danis hengis (Grose-Smith, 1897) (figs 73-80)

Thysonotis hengis: Grose-Smith (1897: 517); Grose-Smith & Kirby (1898: 47, pl. 6 fig. 1-3). [HT ♂: "Kapaur, S.W. Dutch New Guinea", NHMUK, types in coll. Rothschild and Grose-Smith]
Danis hengis (Grose-Smith, 1897): Hirowatari (1992: 26, fig. 29C). [♀ genitalia]

Identification: In the original description Grose-Smith (1897) compared *hengis* with *wallacei*, and males were said to differ from that species in having a brighter blue wing colour, the white patch on the forewing more reduced and the white hindwing band narrower. The male holotype shows the white underside band marginally extending along the apex and inner margin of the hindwing, which can also be observed in *wallacei*, so undersides of both species apparently do not differ much from each other. On the upperside, the white in hindwing space 7 does not reach the apex in *hengis*.
In the females the white is more extensive, so that the brown margins are reduced. Grose-Smith & Kirby (1898: pl. 6 fig. 3) figure a female with a very extensive white patch on the forewing, reaching completely to the base (as in *drucei*). Females of *wallacei* have the forewing upperside wing base brown.

Notes: The dark circular tornal spot in space 1b of the forewing underside is also present in *drucei*, which has space 7 of the hindwing upperside completely white.
The original *hengis* type label bears a handwritten amendment "= *drucei*". *D. drucei* is phenotypically very close to *hengis*, and based on external characters the proposed subspecific assignment by D'Abrera (1971) to *drucei* was not completely unjustified, but

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possibly influenced by the note on the label. Hirowatari (1992: 26) has rejected this view, mentioning that the shape of the *hengis* valva "shows much closer relationship to *regalis*, rather than to *drucei*" and this is tentatively followed here. Male genitalia of *hengis* are illustrated in fig. 106. Both taxa occur in the same area (Fakfak, Onin Peninsula) and accordingly they can not be regarded different subspecies as proposed by D´Abrera.

Distribution: FakFak, Sorong (Papua Barat), and Kaimana (Papua, Indonesia).

Danis drucei (Grose-Smith & Kirby, 1895) (figs 81-84, 107)

Thysonotis drucei: Grose-Smith & Kirby (1895: 31, pl. 2 figs 11-13). [Type ♂ "Ati On, N. Guin. K.", MFNB, Male in coll. Staudinger, female in coll. Rothschild]
Danis drucei (Grose-Smith & Kirby, 1895): Hirowatari (1992: 26, fig. 9 I-K, 30 C). [male and female genitalia, in fig. 107 here refigured]

Identification: Characteristic for *drucei* is the wide extension of white on the forewing underside. In the females this reaches from the basal area to up to ¾ of the wings, which is even wider than in *D. wallacei* females from Waigeo. The white hindwing band is much stronger in *wallacei* males, and they also show a weak white discal patch on the forewing. The white hindwing band is narrower in females of *drucei* and the white on the forewing is filling the lower half of the cell; the basal area is also white. The female figured by D'Abrera (1971: 326) shows some metallic green subcostal scaling.

Notes: According to Grose-Smith & Kirby (1895: 31), the description of *drucei* is based on two specimens: "The male is in the Collection of Dr. Staudinger, and the female in that of Mr. Rothschild". The collection of the MFNB includes 4 male and 2 female specimens from "Ati On" [Ati Ati Onin] and from Sorong under the name *drucei*, but only one male from "Ati On" (MFNB # 940220) is labeled as the "Type", which should therefore be considered to be the unique holotype.
It is not known why Grose-Smith & Kirby did not include further specimens in their type series, if they were present at the time of description. Maybe they were later placed with the holotype, but all appear to be specimens collected by Kühn. Only one further male (♂ MFNB # 940237 / also labeled as "Origin." and "Ati On") is without doubt conspecific with *drucei*. If the females of the Staudinger collection were regarded conspecific with *drucei* and if they had already been available to Grose-Smith & Kirby, they would have included them. It can not be said with certainty if the female specimen (which must be the single specimen from the Rothschild collection) assigned to *drucei* in Grose-Smith & Kirby is conspecific, as its underside was never illustrated. The female figured by D'Abrera differs from the males in having a much narrower white band on the underside and no dark tornal spot. Such specimens fit much better with the sympatric *D. metrophanes*. Currently, no valid definition of *drucei* females exists.
The other MFNB specimens apparently do not belong to *drucei*: one further male and two females are included in *metrophanes* (♂ MFNB # 94021 from Ati Ati Onin, ♀ # 94022 and ♀ 940231 from "Ati On"). The male (♂ # 940225) from Sorong is exactly the same as *athanetus* (= *wallacei*). The females of this series are characterized by comparably narrow hindwing underside bands, which do not correspond with the very broad hindwing band of the type of *drucei*. In addition, they are lacking the dark tornal spot on the forewing underside.

Danis hengis (Grose-Smith, 1897) is closely resembling *D. drucei*: *drucei* males differ from *hengis* only slightly in having space 7 of the hindwing upperside completely white, while in *hengis* the outer part is brown and forewing margins are slightly broader. Females of both species have a white wing base and a separation from *drucei* females is particularly difficult because of sympatric occurrence (see discussion on *hengis*).
D'Abrera (1971: 326) regarded *hengis* as subspecies of *drucei* but mentioned some differences: *hengis* males have broader black borders and no white patch on the forewing, while females of *hengis* have a broader and more curved white hindwing band and some blue scaling at the distal end of the white forewing area.

Distribution: Known from the Onin Peninsula and Misool Island (Papua Barat, Indonesia). D´Abrera (1971) gave as range "South-western West Irian" for ssp. *drucei* and for ssp. *hengis* "North-western West Irian to New Guinea". However, both were described from almost the same area: type locality for *hengis* is Kapaur [FakFak] and Ati On [Ati Ati Onin] for *drucei*. Both, FakFak and Ati Ati Onin, are situated on the Onin Peninsula, at only 30 km distance from each other.

Danis horsa (Grose-Smith, 1898) (figs 85-90, 101-102)

Thysonotis horsa: Grose-Smith (1898: 104); Grose-Smith & Kirby (1898: 48, pl. 6, fig. 10-12). [HT ♂: "Ron Island, Geelvink Bay", NHMUK]
Danis drucei horsa (Grose-Smith, 1898): Hirowatari (1992: 26).

Identification: Grose-Smith (1898: 104) mentions that the male has a duller blue than *hengis* and is without any white scales on the forewing. Most characteristic for *horsa* are: males are missing a white forewing patch and the white band on the hindwings is almost completely faded out; but the white may shine through from the underside. The black margin of the hindwing is very broad and deeply indented between the veins (Grose-Smith, 1898: 104). Females are very dark with the diffuse white bands on both wings reduced in extension, but not lacking. Females with strongly reduced white on the wing uppersides, much less than in any other *Danis* females. The white appears strongest at the inner margin of the hindwing. In some specimens there is a weak blue dusting in the discal part of the hindwing (figs 101-102; Manokwari). The specimen figured by Grose-Smith & Kirby (1898, pl. 6 fig. 12) is very misleading as it is almost completely dark brown with just a faint white basal and discal scaling, but the figure given by D'Abrera (1971) illustrates a characteristic female.

Notes: Hirowatari (1992) sunk *horsa* as a subspecies of *drucei* without any explanation, but following the suggestion of D'Abrera (1971). However, *horsa* is much closer to *hermogenes*, which may be a race of this species.

Distribution: The taxon occurs at the west side of the Cenderawasih Bay (= Geelvink Bay) from the Wandammen Peninsula including Roon Island (locus typicus) up north to Manokwari [= "Dorey" (Papua Barat, Indonesia)]. Both, the male and the female type specimens are deposited in the type collection of the NHMUK and originate from Roon Island.

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Danis hermogenes (Fruhstorfer, 1915) (figs 91-100, 103-105)

Thysonotis wallacei hermogenes: Fruhstorfer (1915: 49). [HT ♂: „Salawati“, RMNH]
Thysonotis wallacei metrophanes: Fruhstorfer (1915: 49). [HT ♂: “Sorong, Nord-Holl.-Neu-Guinea”, NHMUK]
note: Fruhstorfer lists Sorong and Dorey (the “Allotype” is from “Dorey”, today known as Manokwari, and belongs to *horsa*), which are both on the Doberai Peninsula but separated at a distance of 315 km.

Identification: Together with *Danis horsa* and *D. regalis*, *D. hermogenes* belongs to a species group without a distinct white band on the hindwing upperside. Fruhstorfer compared males of *metrophanes* with “*Th. Wallacei glaucopis*”, which is however a very different species, with a prominent white hindwing band. In *hermogenes*, the white band is strongly dusted with blue scales, except at the inner margin. The hindwing margin is broad but does not show the strong indentions present in *horsa*. The white underside patches are very extensive, reaching completely to the tornus on the forewing. Cell end on the underside of the forewings in males is marked by a black cut-like indention.
Females have a very well developed white forewing patch, which is almost reaching to the wing margin. The white patch in *horsa* females is generally more restricted and some blue scaling may be present (fig. 101).

Without doubt, *metrophanes* is a synonym of *hermogenes*. Both holotype males do not show any differences and both were collected in almost the same area (Salawati and Sorong). Erroneously, D’Abrera (1971) and Hirowatari (1992) gave “Biak” as the type locality of *metrophanes*. Unfortunately, the *metrophanes* “allotype” from Manokwari (“Dorey”) (situated north of Roon Island, but not located at the opposite side of the Doberai Peninsula as is Sorong) does not belong to this taxon but to *horsa*. Female specimens differ significantly from *horsa*, as they have the white on the wing uppersides much better developed, extending towards the wing margins. This can also be observed on the forewing undersides, where the white patch extends completely to the margin in space 1b, while it is leaving a dark border in *horsa*, which can very well be observed in a comparison of specimens from Sorong and Manokwari (fig. 101).
Both taxa, *hermogenes* and *horsa* are very similar and possibly closely related. If their occurrence proves to be allopatric they may be regared as different subspecies: *horsa* occurring on the eastern part and *hermogenes* on the western part of the Doberai peninsula.
Distribution: Sorong, Salawati and Kaimana (Papua Barat, Indonesia).

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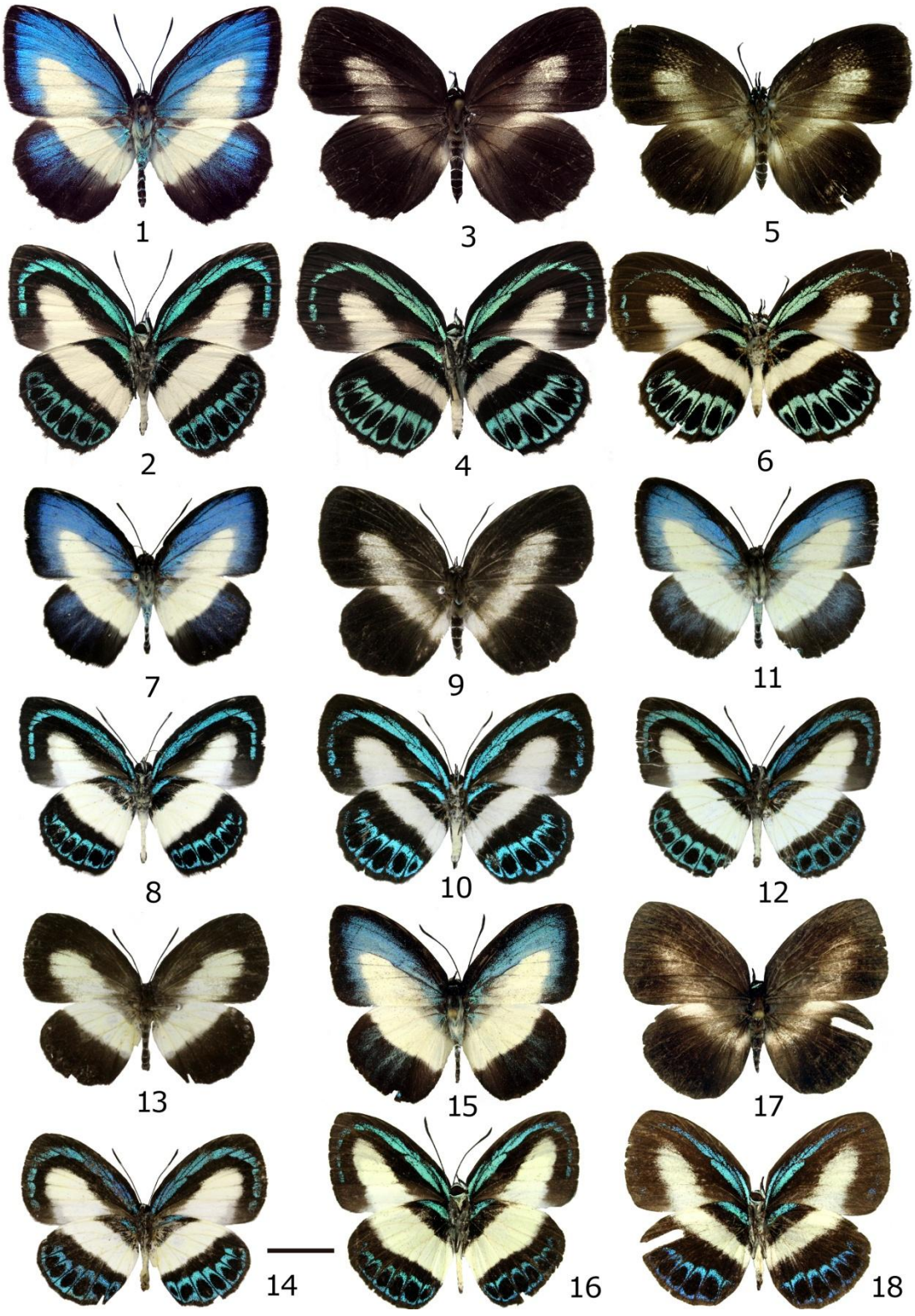

Figs 1-6. *Danis danis apollonius* (C. & R. Felder, 1865). **1.** ♂, Timika, CSSK; **2.** idem, verso; **3.** ♀, Timika, CSSK; **4.** idem, verso; **5.** ♀, Salawati, RMNH.INS. 9000193, HT of *Thysonotis danis panaetius* Fruhstorfer, 1915; **6.** idem, verso. **Figs 7-10.** *Danis danis gebe* Tennent, 2016. **7.** Holotype ♂, Gebe Island, NHMUK; **8.** idem, verso; **9.** ♀, Gebe Island, NHMUK; **10.** idem, verso. **Figs 11-14.** *Danis danis kofiau* Tennent, 2016. **11.** Holotype ♂, Kofiau Island, NHMUK; **12.** idem, verso; **13.** ♀, Kofiau Island, NHMUK; **14.** idem, verso. **Figs 15-18.** *Danis danis hermes* (Grose-Smith, 1894). **15.** ♂ Supiori, CSSK; **16.** idem, verso; **17.** ♀, Supiori, CSSK; **18.** idem, verso.

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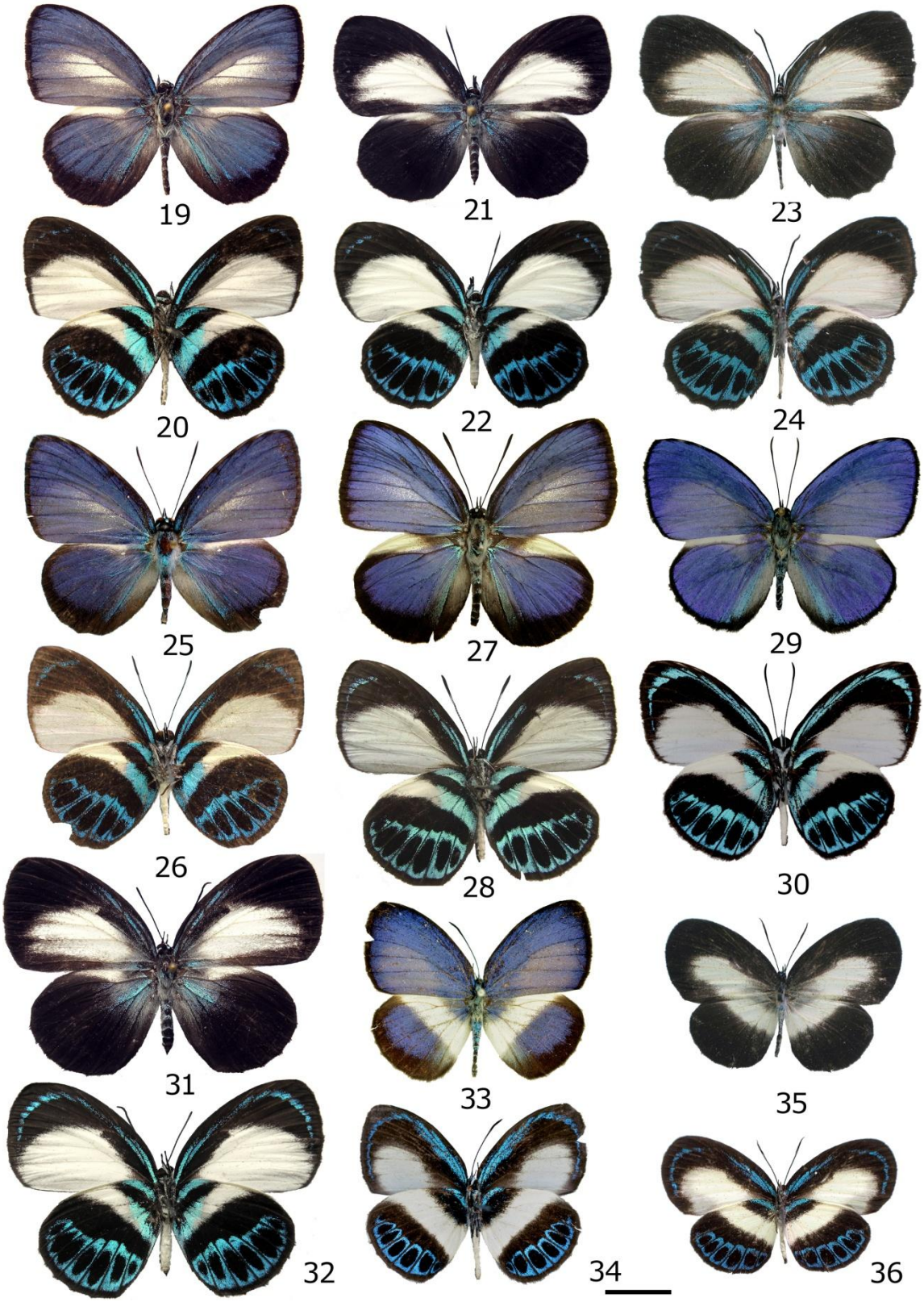

Figs 19-28. *Danis phroso* (Grose-Smith, 1897). **19.** ♂, Yahukimo, CSSK; **20.** idem, verso; **21.** ♀, Timika, CSSK; **22.** idem, verso; **23.** ♀, Mimika, KSP 11856; **24.** idem, verso; **25.** ♂, Mimika, KSP 11861; **26.** idem, verso; **27.** ♂, Yahukimo, coll. Saito, Tokyo; **28.** idem, verso. **Figs 29-32.** *Danis concolor* (Rothschild, 1915). **29.** ♂, Mimika, ANIC; **30.** idem, verso; **31.** ♀, Timika, CSSK; **32.** idem, verso. **Figs 33-36.** *Danis glaucopis* (Grose-Smith, 1894). **33.** ♂, "Pionierbivak", RMNH; **34.** idem, verso; **35.** ♀, Sarmi, KSP 11869; **36.** idem, verso.

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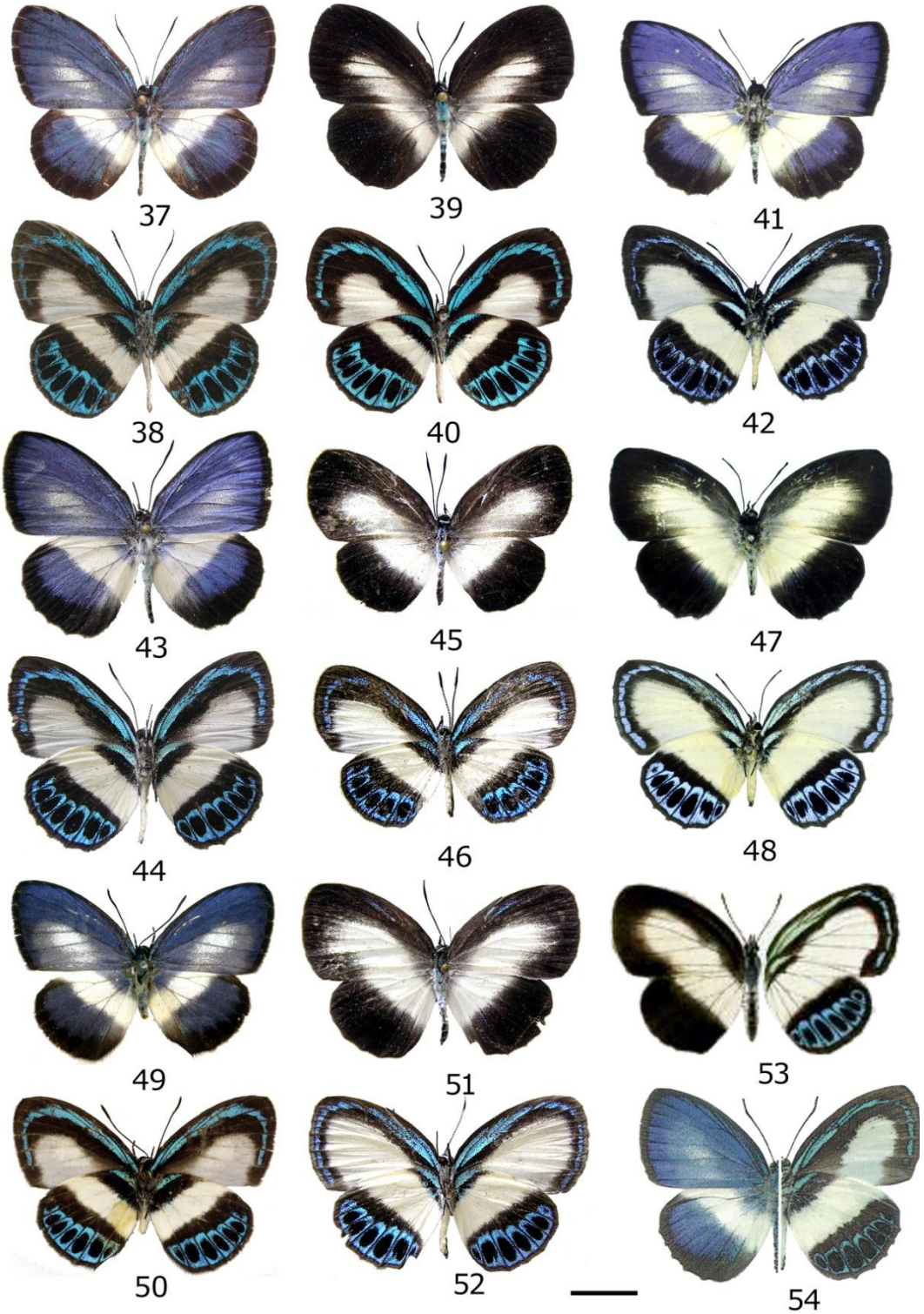

Figs 37-46. *Danis helga* (Grose-Smith, 1898). **37.** ♂, Yongsu, KSP 11885; **38.** idem, verso; **39.** ♀, Yongsu, KSP 11884; **40.** idem, verso; **41.** Holotype ♂, Yapen, NHMUK; **42.** idem, verso; **43.** ♂, Yapen, KSP 50083; **44.** idem, verso; **45.** ♀, Yapen, KSP 50053; **46.** idem, verso. **Figs 47-48.** *Danis melimnos* (Druce & Bethune-Baker, 1893). **47.** "Allotype" ♀ of *helga* = *melimnos*, Yapen, NHMUK; **48.** idem, verso. **Figs 49-50.** *Danis mamberano* (Joicey & Talbot, 1916). **49.** Holotype ♂, River Mamberano, NHMUK; **50.** idem, verso. **Figs 51-54.** *Danis melimnos* (Druce & Bethune-Baker, 1893). **51.** ♀, Yapen, KSP 50056; **52.** idem, verso; **53.** Holotype ♀, Yapen, composite figure copied from Druce & Bethune-Baker, 1893: pl.46, fig. 2; **54.** "*Danis melimnos*" sensu Parsons, ♂, PNG, copied from Parsons, 1998: pl. 67.

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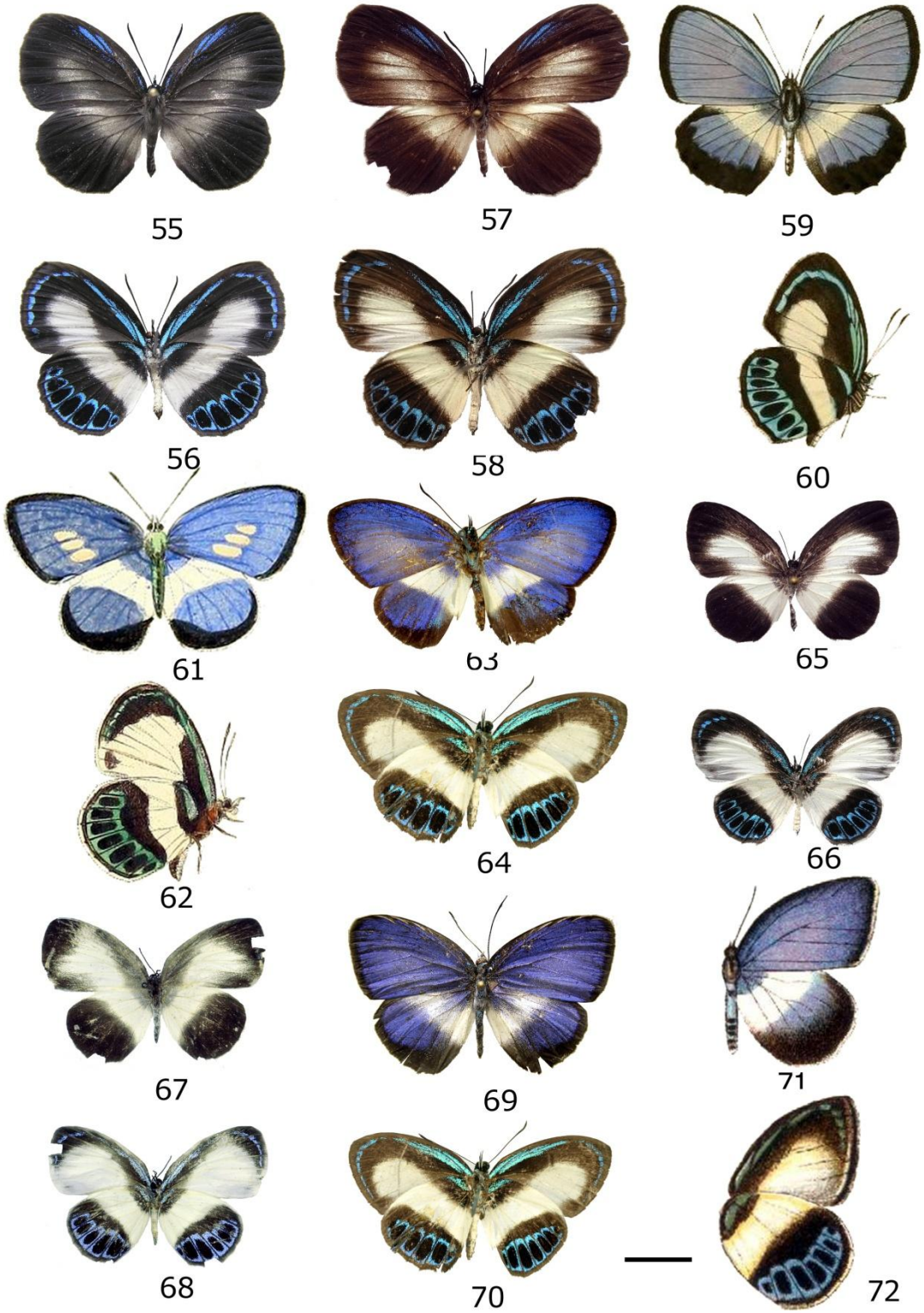

Figs 55-58. *Danis* sp. **55.** ♀, Vriendschap River, KSP 63538; **56.** idem, verso. **57.** ♀, Yahukimo, CSSK; **58.** idem, verso. **Figs 59-60.** *Danis regalis* (Grose-Smith & Kirby, 1895). **59.** ♂, New Guinea, copied from Grose-Smith & Kirby, 1895: pl. 2 fig. 4-5; **60.** idem, verso. **Figs 61-72.** *Danis wallacei* (C. & R. Felder, 1865). **61.** ♂, "Waigiou", copied from C. & R. Felder, 1865: pl. 33 fig. 8. **62.** ♀, "Waigiou", copied from C. & R. Felder, 1865: pl. 33 fig. 10. **63.** C, Salawati (= holotype of *athanetus* Fruhstorfer, 1915) RMNH; **64.** idem, verso. **65.** ♀, Misool, CSSK; **66.** idem, verso. **67.** ♀, Misool (holotype of *albomarginata* Rothschild, 1915), NHMUK; **68.** idem, verso. **69.** ♂, Mappi, KSP 60187; **70.** idem, verso. **71.** ♂, Waigeo (copied from Seitz, 1916: fig. 143c); **72.** idem, verso.

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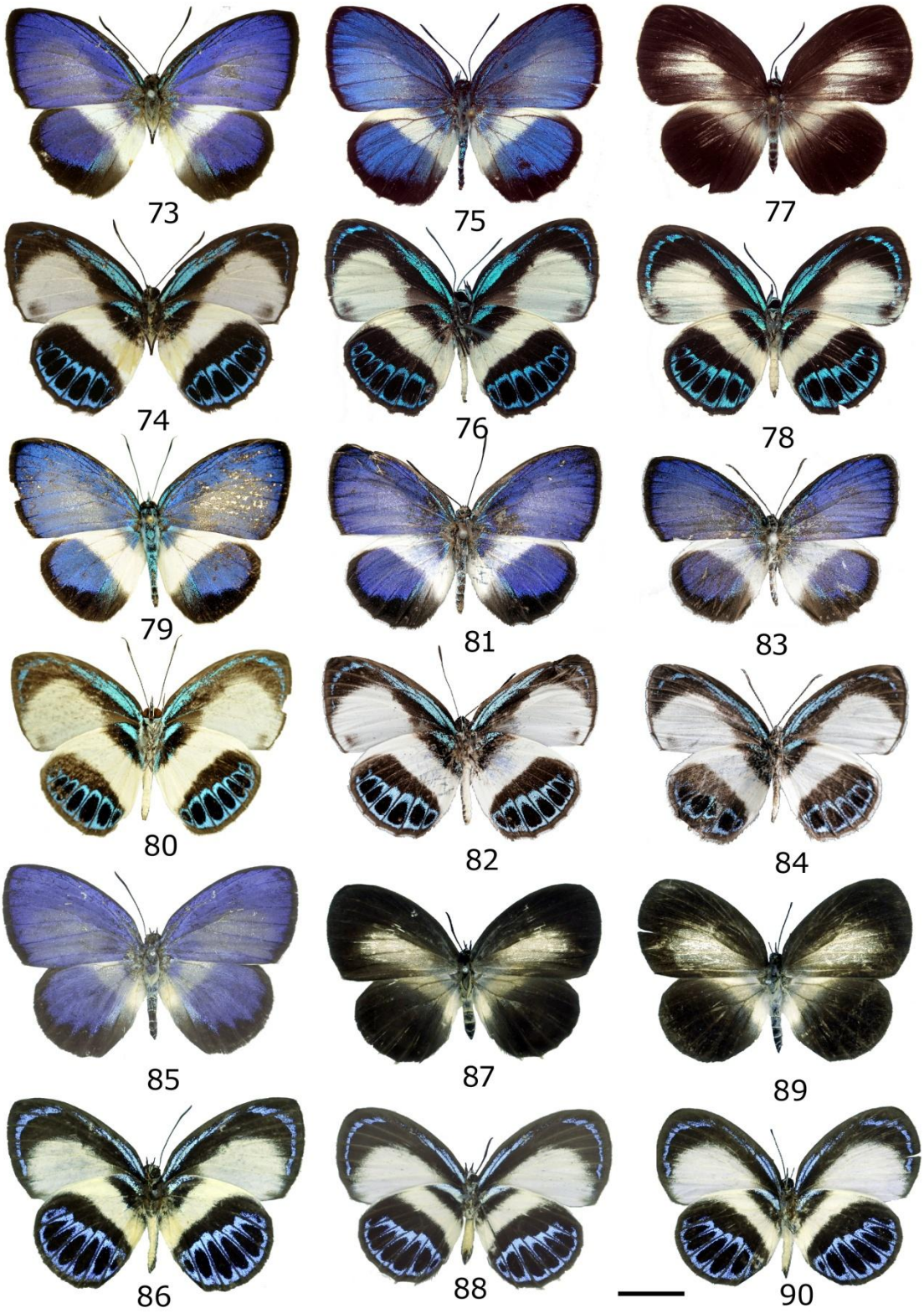

Figs 73-80. *Danis hengis* (Grose-Smith, 1897). **73.** Holotype ♂, Kapaur, NHMUK; **74.** idem, verso; **75.** ♂, Kaimana, CSSK; **76.** idem, verso; **77.** ♀, Kaimana, CSSK; **78.** idem, verso; **79.** ♂, Misool, RMNH; **80.** idem, verso. **Figs 81-84.** *Danis drucei* (Grose-Smith & Kirby, 1895). **81.** Holotype ♂, "Ati On", MFNB, 94022; **82.** idem, verso; **83.** Paratype ♂, "Ati On", MFNB, 940237; **84.** idem, verso. **Figs 85-90.** *Danis horsa* (Grose-Smith, 1898). **85.** Holotype ♂, "Ron", NHMUK; **86.** idem, verso; **87.** "Allotype" ♀, "Ron", NHMUK; **88.** idem, verso; **89.** ♀, "Dorey" ["Allotype" of *Danis hermogenes* (Fruhstorfer, 1915)]; **90.** idem, verso.

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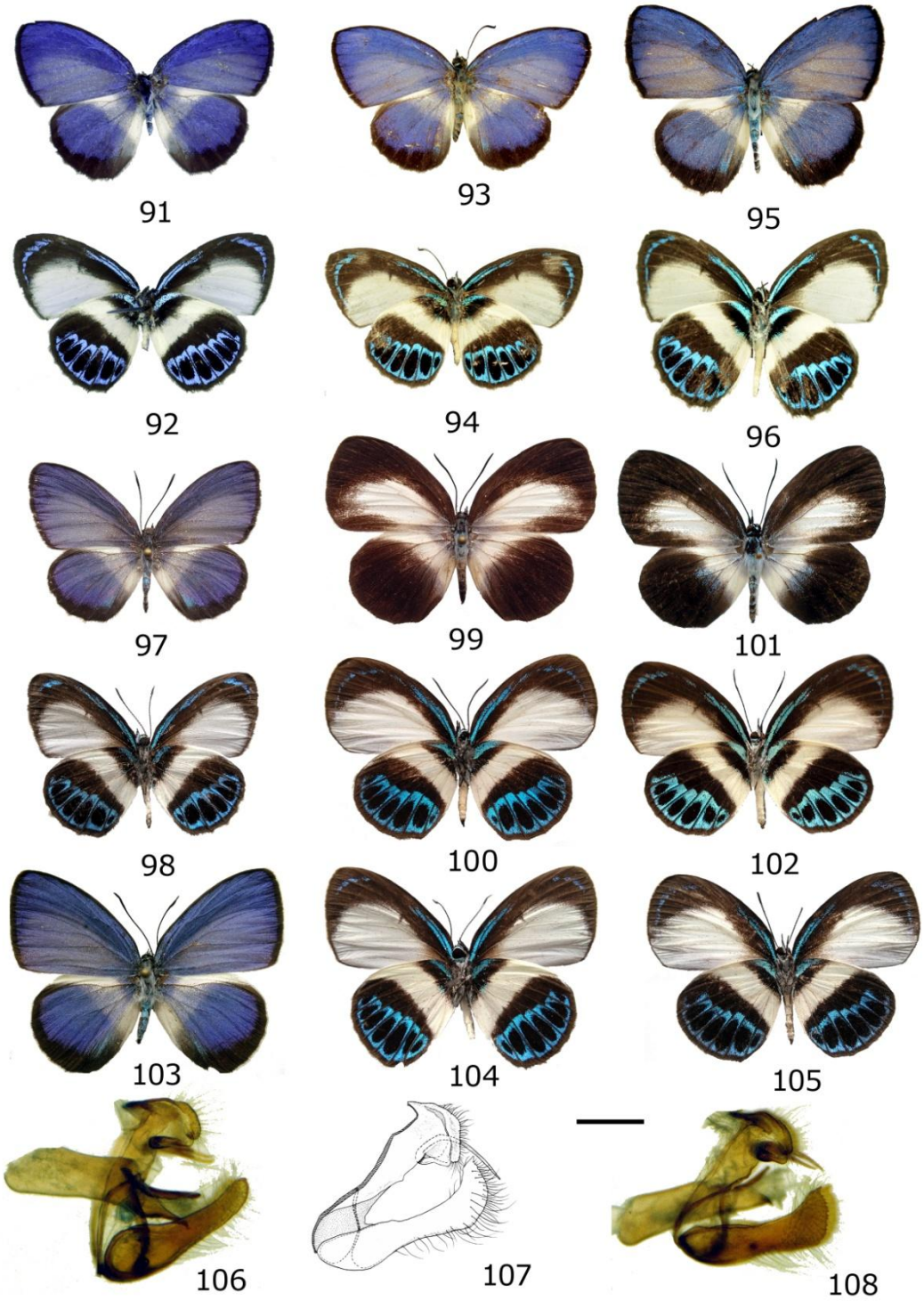

Figs 91-100. *Danis hermogenes* (Fruhstorfer, 1915). **91.** ♂, Sorong (Holotype of *Thysonotis wallacei metrophanes* Fruhstorfer, 1915), NHMUK; **92.** idem, verso; **93.** Holotype ♂, Salawati, RMNH.INS. 960240; **94.** idem, verso; **95.** ♂, Sorong, RMNH; **96.** idem, verso; **97.** ♂, Sorong, CSSK; **98.** idem, verso; **99.** ♀, Kaimana, CSSK; **100.** idem, verso. **Figs 101-102.** *Danis horsa* (Grose-Smith, 1898). **101.** ♀, Manokwari ["Dorey"], KSP 11879; **102.** idem, verso. **Figs 103-105.** *Danis hermogenes* (Fruhstorfer, 1915). **103.** ♂, Sorong, CSSK # 630; **104.** idem, verso; **105.** ♀, Sorong, CSSK. **Fig. 106.** *Danis hengis*, ♂ genitalia, Kaimana, CSSK # 628. **Fig. 107.** *Danis drucei* (Grose-Smith & Kirby, 1895), ♂ genitalia, "Irian Jaya", NHMUK (copied from Hirowatari, 1992). **Fig. 108.** *Danis hermogenes* (Fruhstorfer, 1915), ♂ genitalia, Sorong, CSSK # 630 (Fig. 103).

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