Some notes on *Delias bornemanni - nais* complex on Papua and Papua New Guinea mainland (Lepidoptera: Pieridae)

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Abstract: Members of the Delias bornemanni - nais complex are widely distributed throughout the central mountains of New Guinea from the Kobowre Mts in the west to the Owen Stanley Range in the east. No less than fifteen taxon names have been used to describe the varieties, of which nine are now considered to be synonyms. A historical account of the taxonomy is presented with additional comments that clarify the systematics and include the description of a new subspecies of *D. nais* from the Foja Mts.

Ikhtisar: Kupu-kupu *Delias* termasuk dalam kompleks *bornemanni* - *nais* mempunyai distribusi luas di seluruh pegunungan New Guinea, dari Pegunungan Kobowre di bagian barat sampai Stanley Owen Range di bagian timur. Tidak kurang dari lima belas nama takson digunakan untuk mendiskripsikan kupu-kupu itu dengan segala variasinya. Sembilan nama sekarang dianggap telah menjadi sinonim. Seluruh sejarah taksonomis disajikan, dengan komentar tambahan, guna menjelaskan sistematikanya, dan termasuk subspesies baru dari Pegunungan Foja yang dipertelakan di sini.

Keywords: systematics, taxonomy, Delias nais beehleri subsp. nov., Pierinae

Depositories

The abbreviations given below have been used throughout the text.

AYC - Private Collection Akira Yagishita, Japan.

BMNH - British Museum of Natural History, London, U.K.

CD - Private collection of Chris Davenport, Inverness, UK.

ESP - East Sepik Province, PNG.

KSP - Koleksi Serangga Papua (Collection of Papuan Insects), Jayapura, Indonesia.

PNG

- Papua New Guinea.

NCB-RMNH

- Netherlands Centre for Biodiverstity Naturalis, section RMNH (former Rijksmuseum voor Natuurlijke Historie and Nationaal Natuurhistorisch Museum), Leiden, The Netherlands.

NCB-ZMAN

 Netherlands Centre for Biodiverstity Naturalis, section ZMAN (former Zoölogisch Museum Amsterdam), Leiden, The Netherlands.

Introduction

The relationship and status of various taxa within the *Delias bornemanni* and *D. nais* group (including *D. zebra* and *D. denigrata*) has long been a contentious subject. The comprehensive review of the group by Yagishita in 1993, recognised four species containing nine subspecies. More recent studies by Parson 1999, concentrating on the PNG fauna, and by Funahashi 2010, examining the relationship between *nais* and *zebra*, have concluded that a single, morphologically variable species exists in the central mountain ranges in addition to *D. bornemanni* in the SE parts of PNG.

Extensive material in BMNH, NCB-RMNH, KSP, CD and NCB-ZMAN has allowed comparison of material from nearly all parts of New Guinea and re-assessment of subspecific taxa. This publication includes a summary of the taxonomic history, illustrations of type material and significant varieties, evaluation of geographic variation and description of a new subspecies within the group.

Taxonomic History

Ribbe described the first member of the group, *Delias bornemanni*, in 1900 based on specimens collected by E. Weiske from the Upper Aroa River, in south-east (not south-west as often stated) British New Guinea.

In 1912 Jordan added *Delias bornemanni nais* from material collected by A. S. Meek on Mt Goliath on the south side of the Central Mountain range of then Dutch New Guinea at about 140° EL.

Unaware of Jordan's publication, Van Eecke (1915a) described *D. bornemanni rubrina* from Central Dutch New Guinea. However, a few months later he recognised the mistake and published a correction in which *rubrina* is declared to be a synonym of *D. b. nais* (Van Eecke, 1915b, Talbot, 1929).

Also in 1915, Rothschild recorded *Delias bornemanni nais* Jordan [1912] in the results of the British Ornitologists' Union (BOU) and Wollaston Expeditions to the Snow Mountains, southern Dutch New Guinea, mentioning 16 males and 6 females collected in Jan.-Feb. 1913 at altitudes from 4,000-6,000 ft. These specimens were later assigned to *D. nais denigrata* by Talbot (1929). More recently, Gotts & Ginn (2004) have raised the Snow Mt population to subspecific level, describing *Delias nais odilae* from Tembagapura, a location not far from the BOU collecting sites.

Joicey & Talbot (1922) in their account of the Pratts' expedition to the Menoo R. and Mt Kunupi, Weyland Mts, mention that "Delias nais Jordan is a fairly plentiful species... It exhibits some variability in the pattern of the hind wing below, and we are unable to make any racial distinction." Curiously, they later changed this opinion and described the Weyland (now Kobowre) Mts population as ssp. denigrata.

In the same paper *D. nais aegle* is described from a small series collected by Meek at Biagi, Mambare River, British New Guinea at 5000 ft. Biagi village is no longer shown on maps but, according to Cheeseman (1935) is in the vicinity of the present day Kokoda trail. This subspecies is distinguished from *D. nais nais* by the much smaller size of the brown markings on the hindwing underside. In a footnote they state that "at Owgarra in the same region, the allied *bornemanni* Ribbe occurs, and it is possible that *nais* may be a race of this, as was considered by Jordan, *l.c.*"

In 1925 Rothschild described *Delias bornemanni keysseri* from the Rawlinson Mts in north east British New Guinea mentioning that it differs from *aegle* and *nais* in its dull red hindwing markings on the underside and above in the greyish-white, not creamy white, pale areas, the extent of which is intermediate between *aegle* and *nais*.

After examination of the scent scales, in 1927 Joicey & Talbot raised *nais* to species level and described *Delias nais denigrata* with types from the Menoo River, Weyland Mts. The authors considered the range of this subspecies to extend from the Weyland Mts (Menoo River, 3,500-5,000 ft and Mt. Kunupi, 6,000 ft) to the Snow Mountains further to the east in South Dutch New Guinea (based on the Wollaston Expedition material mentioned by Rothschild, 1915). This taxon is distinguished from nominate *nais* "by the reduced area of black on the hindwing below."

Jordan (1930) described *D. bornemanni entima* from the Herzog Mts, stating that the upperside is similar to *D. bornemanni keysseri* and *D. bornemanni aegle*, but that the underside closely resembles *D. bornemanni rubrina* (He was apparently unaware of van Eecke's retraction of the taxa). On the upperside, he added, the

white area of the forewing is more restricted than in *rubrina* and the red-brown markings of underside of hindwing much larger than in *aegle* and *keysseri*.

Talbot (1932) summarised the then-known members of the group as *D. bornemanni* Ribbe, *D. nais nais* Jordan *D. nais entima* Jordan, *D. nais keysseri* Rothschild, *D. nais denigrata* Joicey & Talbot & *D. nais aegle* Joicey & Talbot.

In 1955 Roepke completed the manuscript of the late Mr. Toxopeus on the results of the Third Archbold Expedition (1938-1939) to the Baliem Valley in central Papua. He described *Delias nais holophaea* from Rattan Camp (1,200 m), Mist Camp (1,800 m), Lower Mist Camp 1,700 m) and Sigi Camp (1,500 m) in the environment of the Baliem Valley and *Delias zebra* from Ibele Valley (2,200-2,300 m) and Baliem Camp (1,700 m), with var. *reducta* from Baliem Camp (1,700 m), based on just 2 males and 1 female. Roepke, 1955 (p. 213) mentions that Toxopeus intended to name this form as *Delias bornemanni polyictis*.

Yagishita (1993) proposed a fresh arrangement of the group by raising *denigrata* to specific rank, including *holophaea* as a subspecies and adding *D. denigrata maruyamai* from Mulia in the central mountain of Irian Jaya, described from 2 males with *zebra*-like hindwing markings. The accompanying map shows the range of this subspecies to be east of *holophaea*, rather than between the ranges of *denigrata* and *holophaea* as Mulia is actually located. He also pictured a specimen from the Ilu–Mulia area, similar to f. *reducta*, which is identified as *D. nais nais* f. *zebra*. The taxon *D. nais rubrina* is erroneously applied to populations from the Kobowre Mts (former Weyland Mts), see above. In the same publication, Yagishita also described *D. zebra takanamii* from Mulia in the central mountain range, and *D. nais maprikensis* from Maprik in the Sepik area of northern PNG, based on a single male specimen of questionable origin. Although Maprik and the nearby Prince Alexander Mts have been extensively surveyed in recent years, no further examples of this subspecies have been found to the authors' knowledge. Additionally, Yagishita treated *keyserri* as a subspecies of *D. bornemanni*.

Parsons (1999), in his monograph on PNG lepidoptera, synonymised *keysseri* and *entima* with nominate *nais* and suggested that *maprikensis* (Yagishita, 1993) would eventually also be treated as a synonym of nominate race.

Concerning *zebra* Parsons stated: "From the study of the ... white-striped *nais* form (from Kerowagi and Mt Wilhelm) it is likely that the supposed species *Delias zebra* Roepke, 1955, from the Ibele Valley, Snow Mountains, Irian Jaya, is merely a race of *nais*. This is further endorsed by the fact that Roepke also described f. *reducta*

of zebra in which the white stripe marking the veins on the hindwing underside are reduced and partly replaced by dark brown; also that neither zebra or reducta were found to be sympatric with nais. Form reducta flies with the normal phenotype of zebra in the Baliem Valley in the Snow Mountains."

Lachlan (2000) recorded the presence of *Delias nais nais* as common at four localities in the Western Province and a single locality in the Southern Highland Province of PNG.

Gotts & Ginn (2004) described *Delias nais odilae* from Tembagapura, including three forms of the female. The authors note that the variation in hindwing underside markings are an unreliable diagnostic feature, but that, "the upperside wing patterns tend to be more consistent, with variations in the extent of the black markings providing a useful guide for the separation of subspecies." They note that "D. denigrata (sensu Yagishita) is not obviously dissimilar to various subspecies of *D. nais*", and therefore consider *denigrata* and *maruyamai* to be subspecies of *D. nais*. Although no formal change is made to the taxonomy adopted by Parsons (1999), the paper includes comparison of populations based on the extent of black upperside markings, concluding that "These are broadest in *D. n. entima*, slightly narrower in the Kerowagi population, intermediate in the nominate subspecies and in the *denigrata/holophaea* subspecies, while in *D. n. odilae* from Tembagapura they are markedly reduced."

In his first report on *Delias* from the Foja Mts, van Mastrigt (2006) mentioned 25 records of *Delias nais*, between 25 November and 7 December 2005, without specifying the numbers of males and females, or commenting on possible subspecies.

In 2009 the same author published further records of *Delias nais* from the Foja Mts (12 males and 6 females), and pictured both male and female specimens.

Based on study of a series of transitional forms collected at Yohosin, east of the Baliem Valley, Funahashi (2010) concluded that *D. zebra* should not be regarded as a separate taxon, but rather as an endemic phenotype of *D. nais*. Reviewing the taxonomy, Funahashi synonymised *D. zebra* Roepke, 1955, *D. zebra* var. *reducta* Roepke, 1955, *D. zebra takanamii* Yagishita, 1993 and *Delias denigrata maruyamai* Yagishita, 1993, with *D. nais nais* (type locality: Mt Goliath) rather than *D. nais holophaea*, the subspecific name applicable to Baliem populations, which is also listed as a valid subspecies by the author.

The members of the *nais* complex are part of the **Bornemanni Group VII** as defined by Talbot (1927), which also includes *D. castaneus* Kenrick, 1909, *D. pratti* Kenrick, 1909, *D. caroli* Kenrick, 1909 and the recently described *D. kristianiae* Van Mastrigt, 2006.

Toxopeus (ms.) in Roepke, 1955 was of opinion that *D. klossi* was incorrectly placed by Talbot in the *clathrata* group, however Roepke, while mentioning that *klossi* could be closely related to *nais* and *zebra*, maintained the species in the *clathrata* group. Parsons (1999) also commented that *klossi* that might link the groups to which *nais* and *clathrata* belong.

Existing taxonomy

Based on the above taxonomic history, within the *bornemanni - nais* complex two species are currently recognized, one of which has six subspecies and three named forms or varieties, as follows.

- 1. Delias bornemanni Ribbe, 1900
- 2. Delias nais Jordan, [1912]
 - 2.1. Delias nais nais Jordan, [1912]

Synonyms: *D. bornemanni rubrina* Van Eecke, 1915 (synonymized by

Van Eecke, 1915)

D. nais keysseri Talbot, 1928 (synonymized by Parsons, 1999)

D. nais entima Talbot, 1937 (synonymized by Parsons, 1999)

D. zebra Roepke, 1955 (synonymized by Funahashi, 2010)

D. zebra var. reducta Roepke, 1955 (synonymized by

Funahashi, 2010)

D. zebra takanamii Yagishita, 1993 (synonymized by

Funahashi, 2010)

D. denigrata maruyamai Yagishita, 1993 (synonymized

by Funahashi, 2010)

- 2.2. Delias nais aegle Joicey & Talbot, 1922
- 2.3. Delias nais maprikensis Yagishita, 1993
- 2.4. Delias nais odilae Gotts & Ginn, 2004
- 2.5. *Delias nais denigrata* Joicey & Talbot, 1927 (re-established as subspecies of *nais* by Funahashi, 2010)
- 2.6. *Delias nais holophaea* Roepke, 1955 (re-established as subspecies of *nais* by Funahashi, 2010)

Notes on Subspecies

The principal diagnostic character that has been used to distinguish subspecies of *D. nais* is the breadth of the black margins on the forewing upperside. Table 1 tabulates measurements of this character in 22 populations covering the known range of the species. A minimum of four male specimens from each location, except those marked *, have been measured using graphic software (Vetorworks 11)

to calculate the relative areas of black and white markings, the results are presented as a proportion of the whole wing area. In all populations, this character is found to be relatively stable, varying by no more than 10% among individuals from a single location.

The data shows a marked difference between the western (3-17) and eastern (18-23) populations of the central mountain belt. The distinct identity of the populations from the Foja Mts and the Snow Mts (former Carstensz Mts) are also evident.

Table 2 presents measurements of the brown markings on the hindwing underside of the same specimens. This character is much more variable within populations and therefore less reliable as a diagnostic character, however the results demonstrate the distinct nature of the populations from the Foja Mts and the Owen Stanley Mts at the NW and SE extremities of the species range.

The sole specimen of *D. nais maprikensis* falls within the range of variation seen in other eastern PNG populations, leading us to synonymise this subspecies with *keysseri*.

D. nais holophaea is weakly distinguished from typical *nais*. Roepke, in his description, compared it with *nais denigrata*, from which it "differs in the broader black border" (as does *n. nais*) Certain populations of *holophaea* are now known to have a high frequency and degree of individual variation, producing a range of phenotypes from normal to 'reducta' and 'zebra' forms.

The slight and inconsistant differences between - from west to east in the central mountain range - subspecies *denigrata*, *holophaea* and *nais* leads to the conclusion that these should be treated synonyms. Use of the names as "local forms" is inappropriate as all varieties occur in overlapping areas.

The authors consider that it is valid to reinstate ssp. keysseri, Talbot, as the oldest taxon applying to broad-bordered eastern PNG forms, and to include within this subspecies the populations from the Herzog Mts (entima) and the Bismark Mts including Kerowagi and Goroka. Reissinger (in litt.) intended to describe D. nais bullai from the Goroka area. He deposited type material in the NCB-RMNH, KSP and possibly other musea. The taxon bullai (in litt.) is now included in ssp. keysseri.

Some geographical variation is seen among typical specimens from a number of locations within the *keysseri* range. Gotts & Ginn (2004) mention the Kerowagi - Mt Wilhelm population, characterised by reddish hindwing underside markings and a frequent incidence of white vein scaling. Populations from the western Bismark Mts and the Herzog Mts (TL of *entima*) have noticeably extended upperside forewing borders.

The taxon *D. nais aegle* has frequently been misapplied to populations from central PNG. This subspecies has a restricted range in the Owen Stanley Mts and is extremely rare in collections.

The map shows locations where *nais* has recently been collected between two type localities, particularly between *denigrata* and *holophaea* and between *holophaea* and *nais* where the subspecific identity is difficult to identify. The differences between these populations represent a cline from west to east rather than three separate subspecies.

Material examined

The examined material in KSP consists of denigrata $(27\,\&cdots)$, odilae $(7\,\&cdots)$, holophaea $(154\,\&cdots)$, and nais from Papua $(72\,\&cdots)$ and from P.N.G. $(12\,\&cdots)$, $(12\,\&cdots)$, and takanamii $(34\,\&cdots)$, $(34\,\&cdots)$, and of 190 specimens $(149\,\&cdots)$, $(149\,\&cdots)$, belonging to intermediate forms. This material is only a fraction of the total collected over the years by the first author; other specimens are now in various collections or still papered: in CD, $(47\,\&cdots)$, $(12\,\&cdots)$, from various locations in PNG. Type material in the BMNH, NCB-RMNH and NCB-ZMAN has also been examined.

Based on these considerations, the following classification is proposed:

1. Delias nais Jordan, [1912]

1.1. Delias nais nais Jordan, [1912] from Ko

from Kobowre Mts to western PNG

Synonyms: D. bornemanni rubrina Van Eecke, 1915

Delias nais denigrata Joycey & Talbot, 1922 syn. nov.

D. denigrata maruyamai Yagishita, 1993

D. zebra takanamii Yagishita, 1993

Delias nais holophaea Roepke, 1955 syn. nov.

D. zebra Roepke, 1955 (synonymized by Funahashi, 2010)

D. zebra var. reducta Roepke, 1955 (synonymized by

Funahashi, 2010)

1.2. Delias nais odilae Gotts & Ginn, 2004

Puncak Jaya (former Carstensz Mts)

1.3. Delias nais beehleri subsp. nov.

Foja Mts

1.4. Delias nais keysseri Talbot, 1928 (re-established in this paper) Bismark,

Rawlinson, HerzogMts, northeast PNG

Synonyms: *D. nais entima* Talbot, 1937

D. nais maprikensis Yagishita, 1993 syn. nov.

1.5. Delias nais aegle Joicey & Talbot, 1922

Owen Stanley Mts (E. PNG)

2. Delias bornemanni Ribbe, 1900

Owen Stanley Mts

Description of *Delias nais beehleri* **ssp. nov. Figs 1-4.**

Material: HT \vec{o} : Prov. Papua, Pegunungan Foja 1,650 m, 2° 34.5′ S and 138° 42.9′ E, 23.xi-7.xii.2005, CI-LIPI Survey – Henk van Mastrigt, MZB. Paratypes (11 $\vec{o}\vec{o}$ + 6 $\stackrel{\frown}{}$): same data as holotype: 11 $\vec{o}\vec{o}$, 4 $\stackrel{\frown}{}$, KSP; idem, 6-27.xi.2008, 2 $\stackrel{\frown}{}$, KSP.

Diagnosis

Specimens of *D. nais* from the Foja Mts are quite different from all other subspecies in Papua; and are closest to *D. nais aegle* (from eastern PNG). On the underside of the hindwing, the newly described subspecies has an average of 32% brown markings, *aegle* has an average 28% and all other subspecies have an average of 40% or greater.

Description

Male (figs 1 & 2) Upperside of forewing mainly black, with white area in main part of dc to inner border covering 31-35% of the surface of forewing. Upperside of hindwing white with black border which slightly increases in width from costa to vein Rs (2 mm), decreasing to vein 1A+2A, where it is no more than a thin line. Underside of forewing black with three white subapical spots of which the second is larger. Cell 1A+2A white with some blackish diffusion close to tornus. Underside of hindwing mainly black (61-76%, av. 68%) with eight dark brown spots: one in the base, the second in the top of the discal cell and the six others from the black border inwards separated by black lines along the veins, in cells Rs, M1, M2, M3, CuA1 and CuA2. The one in Rs is the largest. The one in CuA2 sometimes quite narrow (black border very broad), sometimes wide entering cell 1A+2A and in a few specimens is nearly split by the partly black vein 1A+2A.

Length of forewing: 24-27 mm, av. 25.25 mm.

Female (figs 3 & 4) Upperside of forewing with larger black area than in male, bearing 1-3 white subapical dots. White inner part becoming creaming to yellowish close to black area. Upperside of hindwing greyish white with broader black border than in male: 4 mm at vein Rs, decreasing to costa and to termen where it more abruptly ended than in male. Underside forewing as in male, with four instead of three subapical spots of which second and third ones are well developed. At one specimen a fifth poor-developed dot is visible. In most specimens underside of hindwing is quite different from males, as the black parts are quite reduced, especially the median black area outside the discal cell and its black connections to the border which are not more than the vein itself. Only two specimens show a more similar pattern than in the male.

Length of forewing: 25-27 mm, av. 25.83 mm.

Derivation of name: 'beehleri' is a genetive in apposition, named after Mr Bruce M. Beehler, an ornithologist and the driving force of Conservation International (CI) which organised two surveys of the remote Foja Mountains under the authority of Research Centre for Biology, Indonesian Institute of Sciences (LIPI).

Distribution and altitude

Delias nais occurs over the whole central mountain range from Kobowre Mts in the west to the central Owen Stanley Mts in the east and in the following areas isolated from the central range: Foja Mts, Prince Alexander Mts (doubtful?) and the Rawlinson Mts. The species has been recorded altitudes between 900 and 3,000 m as follows: in the Kobowre Mts on 1,350-1,500 m, at Paniai District (around the Wissel Lakes) at 1,750-1,900 m, at Tembagapura on 1,850-2,300 m, in Homeyo, Bilai, Bilogai at 1,700-2,000 m, in the environment of Mulia, Ilu and Ilaga on 1,600-1,700 m (where var. maruyamai/takanamii occurs at 1,800-2,150 m), in the environment of the Baliem Valley on 1,600-3,000 m (where var. zebra occurs on 1,700 at Yiwika to 3,000 m at Habbema), in the Pass Valley at 1,500-1,900 m (were var. zebra occurs at the same altitude), at Sumbole on 900-1,000 m, at Ninya and Korupun on 1,700-,2000, at Nipsan on 1,650 m, in the environment of Langda and Mt. Goliath on 1,600-2,200 m, in the Star Mts between 900 m (Borme) and 2,300 m (Abmisibil) and in the Foja Mts around 1,650 m.

In parts of the Baliem Valley, including Yiwika and Habbema, and around the Pass Valley *nais* and var. *zebra* are sympatric. In the areas of Ilaga, Mulia and Ilu *nais* and var. *maruyamai/takanamii* have not been recorded at the same spot, but *nais* is normally found at lower altitudes.

Populations of nais and var. zebra

During the Third Archbold Expedition (1938-1939) only six specimens of *D. nais holophaea* were recorded however a large number of *zebra* were found in both the Ibele Valley (2,200-2,300 m) and the Baliem Valley (1,700 m). The intermediate form, described as *D. zebra* var. *reducta*, was recorded by only two males and one female from the Baliem Camp, 1700 m. The experience of the first author, particularly in the period from 1986-1993 when he was living in the Baliem Valley, confirms the results of the Archbold Expedition, as *zebra* was found to be much more common than *nais* and var. *reducta* was rarely encountered.

A large number of var. *reducta* and intermediate forms have been recorded at all river sites in the Pass Valley, Abehano District (1,500-1,900 m), where both *D. nais* and var. *zebra* are also common.

In most areas where typical *nais* and/or var. *zebra* occur, they are among the most common of *Delias* species. The rarity of *D. nais holophaea* in the Baliem Valley and at Sumbole (Van Mastrigt, 2001) are notable exceptions.

Discussion

The early expeditions and surveys of various parts of NG, from 1900 to 1950, were separated by large distances of 100 to 200 km and resulted in the description of many new subspecies, often based on small morphological differences between widely disjunct populations. Recent surveys of many more intermediate localities have shown that the geographical boundaries of supposed subspecies are vague or non-existent.

The wide range of individual and geographic variations found in populations of *D. nais* occurring along the central mountain ranges on New Guinea are not easily divided into discreet subspecies. The presence of var. *zebra* at generally higher altitudes than typical *nais* and the frequency of white veined individuals on Mt Wilhelm, PNG's highest peak, suggest that altitudinal factors influence the phenotype.

Distinct subspecies occur in relatively isolated areas: *odilae* at Mt Jaya and Tembagapura at the south west extremity of the central mountain rage, *beehleri* in the northen Foja Mts in Papua, *keysseri* from the Rawlinson Mts (TL), Herzog Mts and Bismark Mts, including Kerowagi and Goroka, and *aegle* from the Owen Stanley Range in PNG.

Genetic analysis of members of the *bornemanni* group has not yet been carried out however the authors expect that this technique will eventually provide a better understanding of relationships within the complex.

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Table 1. Percentage of black parts on upperside of forewing

	location	former taxa	proposed taxa	40	11 4	24	3 44	4 45 4	16 4	7 48	49 50	51	52	53 5	4 55	56	57 5	8 59	960	61	62 6	3 64	165	66	67 6	8 69	70	71	72 7	3 74	175	76 7	7 7	3 79
1	Foja Mts	TOTTICE COAC	beehleri	10	+	+	-	+		1.0	.,		-		100				-									-	+	+		-	+	H
2	Snow Mts		odilae					+	+	+	+	+	H		+		+	+	+		\pm	+	F			+			+	+	\forall	+	+	Ħ
3	Weyland Mts	odilae	nais				-	+	+	+		-			H	-	+	+	-	-	+	+	+		+	+	+		+	+	+	+	+	\forall
4	Homeyo	odilde	nais	\vdash	+	+	+	++	+	_							+	+	+	-	+	+	\vdash		+	+	+		+	+	+	+	+	H
5	Kanggime	denigrata TL	nais	\vdash	+	+	+	++	+	+	+	+								\vdash	+	+			+	+	+	Н	+	-	\forall	+	+	+1
6	Pass Valley	holophaea	nais	\vdash	+	+	+	++	+	+											+	+			+	+	+	Н	+	+	+	+	+	+
7	Pass Valley	zebra	nais	\vdash	+	+	+	+	+	+		+									+	+		\vdash	+	+	+		+	+	+		+	H
8	Nipsan	2000	nais		$^{+}$	+	+	+	+	+	\vdash	t									+	+			+	+			+	+	\forall	+	+	\forall
9	Koropun		nais		†	+	1	\forall	+		\vdash							†			\top	1		П		T			\top		\Box	\top	+	\Box
10	-		nais		\dagger	+	1	\top	\top			T									\top	T				T			T	T	\Box	T	\top	
11		nais TL	nais		T	T	T	\top				T			П																	T	T	
12	Sumtamon		nais		+	T		\top		\top		T									T	T				T				T			T	П
13	Borme		nais		T	T	1								П																			
14	Abmisibil	nais	nais				1																											
15	Porgera	nais	nais		I	I	L																											
16	W. Bismarck	nais	keysseri		T		T										T					T												
17	Mt. Wilhelm	nais	keysseri																															
18	Maprik	maprikensis	keysseri																		1													
19	Okapa	nais	keysseri																															
20	Herzog Mts	nais (entima TL)	keysseri																													8		
21*	Rawlinson Mts	nais (keysseri TL)	keysseri		I		I				-															I			\perp	I			T	
22*	Biagi	aegle	aegle							1											., 2											7		



Notes a

apart from 1, 2 & 18, locations are numbered from west to east

Table 2. Percentage of brown parts on underside of hindwing

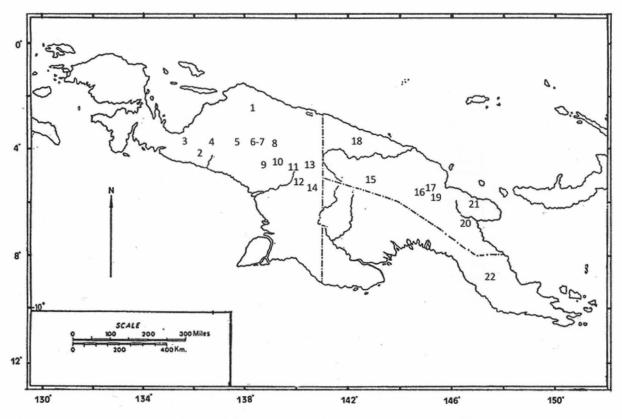
	location	former taxa	proposed taxa	22	23	24	25 20	5 27	28	293	303	1 32	33 3	4 3	5 36	37	38	39 4	0 41	42	43	144	5 46	47	48 4	9 50	51	52 5	3 54	155	56 5	7 58	3 59	50 61
1	Foja Mts		beehleri																															
2	Snow Mts		odilae											T							70						- 1							
3	Weyland Mts	odilae	nais		П			1										T	T															
4	Homeyo		nais																															
5	Kanggime	denigrata TL	nais																															
6	Pass Valley	holophaea	nais																															
7	Pass Valley	zebra	nais																										8					
8	Nipsan		nais																															
9	Koropun		nais																										\perp					
10	Langda		nais																															
11	Mt Goliath	nais TL	nais						Ш																				\perp				Ш	
12	Sumtamon		nais																															
13	Borme		nais																															
14	Abmisibil	nais	nais																							\perp						\perp	Ш	
15	Porgera	nais	nais					_										_															Ш	
16	W. Bismarck	nais	keysseri																															
17	Mt. Wilhelm	nais	keysseri																															
18	Maprik	maprikensis	keysseri																															
19	Okapa	nais	keysseri																															
20	Herzog Mts	nais (entima TL)	keysseri																															
21*	Rawlinson Mts	nais (keysseri TL)	keysseri																					2										
22*	Biagi	aegle	aegle																															

Key

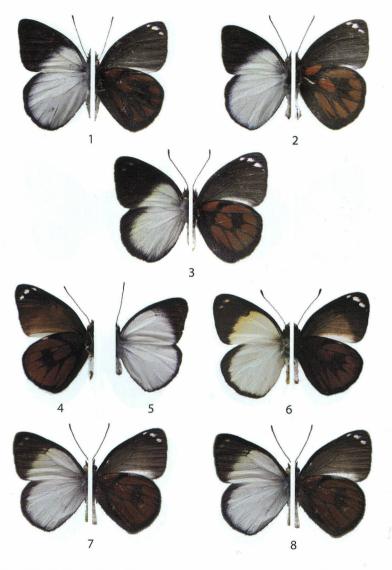
average/most common common extremes

Notes

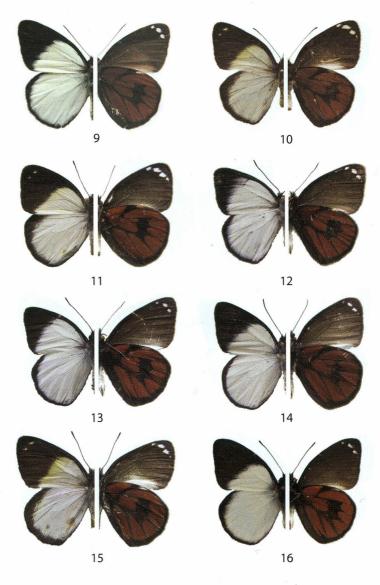
apart from 1, 2 & 18, locations are numbered from west to east



Map of New Guinea. Explanation of numbers: see Tables.



Figs 1-3. Delias nais beehleri subsp. nov. from Foja Mts: 1. HT ♂ upp./und. (KSP 44707); 2. PT ♂ upp./und. (KSP 44710); 3. PT ♀ upp./und. (KSP 44713); Figs 4-8. Delias nais odilae (all from Tembagapura): 4. HT ♂ und.; 5. upp. (KSP 22704); 6. PT ♀ upp./und. dark form; 7. PT ♀ upp./und. light form; 8. ♀ upp./und. common form (KSP 22710).



Figs 9-16. Delias nais nais upp./und.: 9. D. nais denigrata HT \circ (BMNH); 10. D. nais denigata PT \circ (BMNH); 11. \circ from Timeepa (KSP 22694); 12. \circ from Kamu (KSP 22695); 13. \circ from Enarotali (KSP 22702); 14. \circ from Homeyo (KSP 22715); 15. \circ from Homeyo (KSP 22718); 16. \circ from Bilogai (KSP 22720).

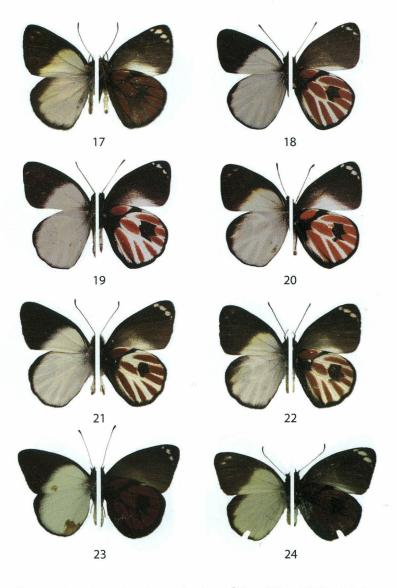
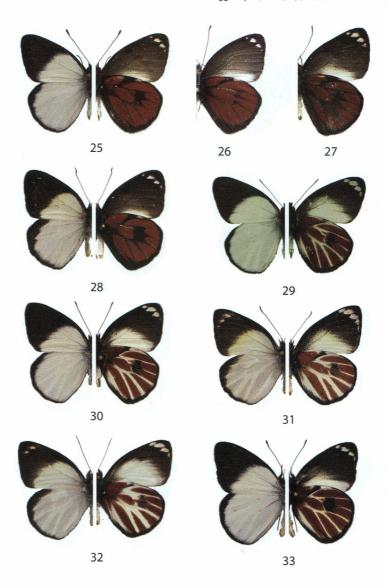
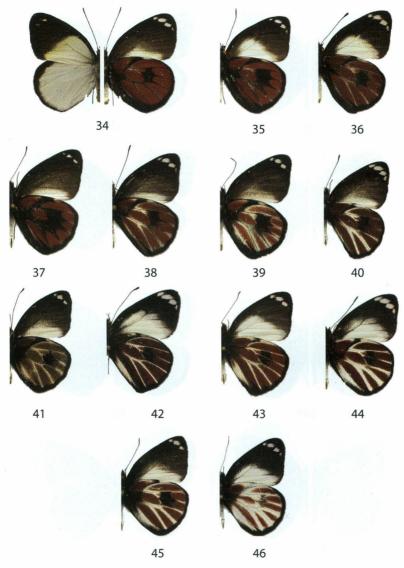


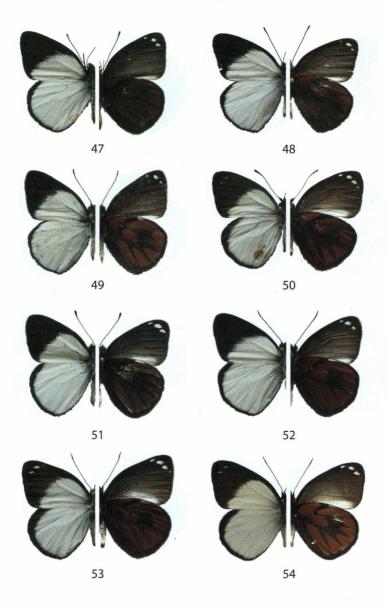
Fig. 17-24. *Delias nais nais* upp./und.: 17. ♀ from Bilogai (KSP 22724); 18. *D. denigrata maruyamai* HT ♂ (ex Yagishita, 1993b); 19. *D. denigrata takanamii* HT ♂ (idem); 20. *D. denigrata takanamii* PT ♀ (idem); 21. ♂ *takanamii* from Ilaga (KSP 25466); 22. ♀ from Ilu (KSP 25502); 23. *D. nais holophaea* HT ♂ (NCB-RMNH); 24. *D. nais holophaea* PT ♀ (NCB-RMNH).



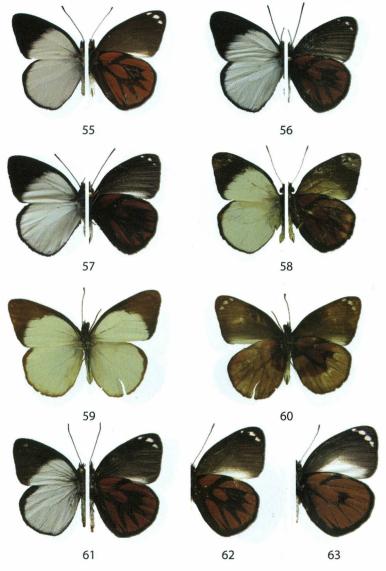
Figs 25-28. *D. nais nais* (all from Pass Valley): 25. $\stackrel{\circ}{\circ}$ upp./und. (KSP 22745); 26. $\stackrel{\circ}{\circ}$ und. (KSP 22806); 27. $\stackrel{\circ}{\circ}$ und. (KSP 22742); 28. $\stackrel{\circ}{\circ}$ upp./und. (KSP 27080). Figs 29-33. *D. nais nais* f. *zebra* upp/und.: 29. HT $\stackrel{\circ}{\circ}$ *Delias zebra*; 30. $\stackrel{\circ}{\circ}$ from Tiom (KSP 25542); 31. $\stackrel{\circ}{\circ}$ from Welesi (KSP 25595); 32. $\stackrel{\circ}{\circ}$ from Daela (KSP 25598); 33. $\stackrel{\circ}{\circ}$ (as *D. zebra* f. *reducta*) from Anggenagi (KSP 27064).



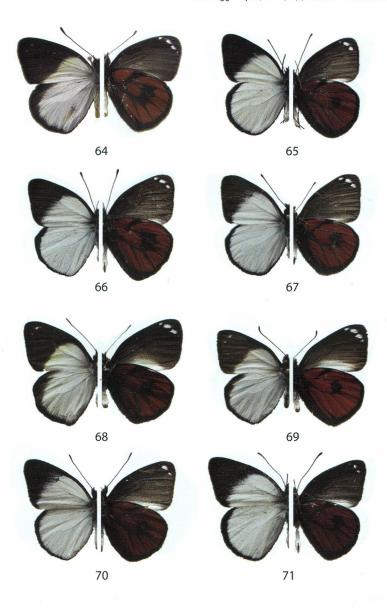
Figs 34-46. *D. nais nais* f. *zebra* in all its varieties from Pass Valley area: 34. ♀ upp./und. (KSP 27066); 35. ♀ und. (KSP 25379); 36. ♀ und. (KSP 25444); 37. ♂ und. (KSP 25314); 38. ♂ und. (KSP 22988); 39. ♂ und. (KSP 27082); 40. ♂ und. (KSP 27079); 41. ♀ und. (KSP 25633); 42. ♀ und. (KSP 27083); 43. ♂ und. (KSP 25433); 44. ♂ und. (KSP 20969); 45. ♂ und. (KSP 27068); 46. ♂ und. (KSP 27081).



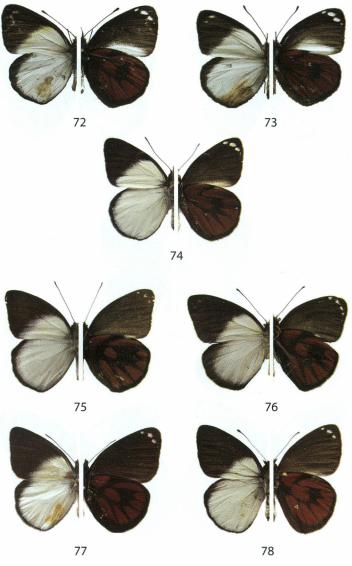
Figs 47-54. *D. nais nais* upp./und.: 47-50. from Korupun: 47. \circlearrowleft (KSP 22862); 48. \circlearrowleft (KSP 22853); 49. \circlearrowleft (KSP 22858); 50. \Lsh (KSP 22875); 51-54. from Ninya: 51. \circlearrowleft (KSP 22845); 52. \circlearrowleft (KSP 22846); 53. \Lsh (KSP 22866); 54. \Lsh (KSP 22867).



Figs 55-63. *D. nais nais*: 55-57. upp./und. from Langda: 55. ♂ (KSP 22881); 56. ♂ (KSP 22882); 57. ♂ (KSP 22884); 58-60. from Mt. Goliath: 58. Type ♂ upp./und. (BMNH); 59-60. = *D. nais rubrina* ♂ HT upp./und. (NCB-RMNH); 61. from Langda♀ upp./und. (KSP 22888); 62. ♀ und. from Sumtamon (KSP 22889); 63. ♀ und. from Okbibab, Star Mts (KSP 22947).

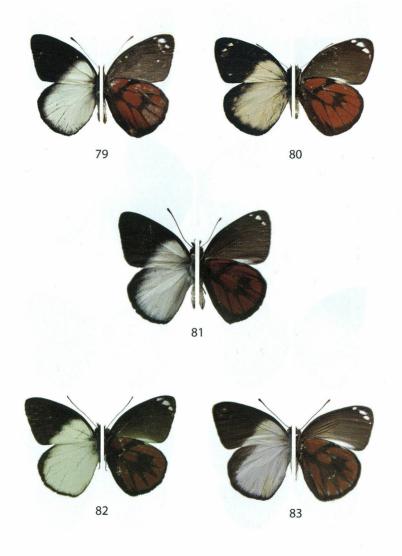


Figs 64-71. *D.nais nais* upp./und. from Star Mts: 64-69. from Okbibab: 64. $\[Phi]$ (KSP 22946); 65. $\[Phi]$ (KSP 22910); 66. $\[Phi]$ (KSP 22927); 67. $\[Phi]$ (KSP 22928); 68. $\[Phi]$ (KSP 22948); 69. $\[Phi]$ (KSP 22950); 70-71. from Borme: 70. $\[Phi]$ (KSP 22903); 71. $\[Phi]$ (KSP 22904).

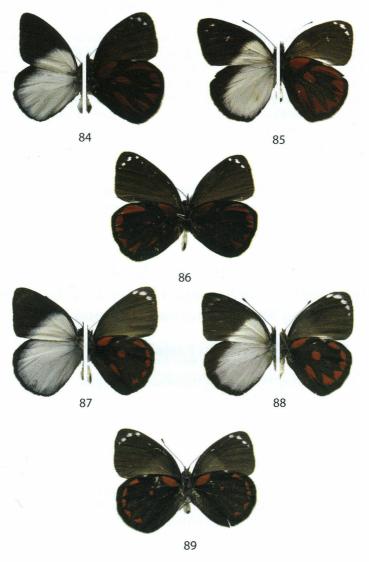


Figs 72-74. *D. nais* upp./und. 72-73. from Borme, Star Mts: 72. ♀ (KSP 22907); 73. ♀ (KSP 22908); 74. ♂ from Porgera, Enga Prov. (CD).

Figs 75-78. *D.nais keysseri* upp./und.: 75. HT ♂ from Rawlinson Mts (BMNH); 76. ♀ from Cromwell Mts (BMNH); 77. = *D. nais maprikensis* ♂ HT upp./und. (AYC); 78. ♂ from Yendon R., Bismark Mts (CD).



Figs 79-83. *D. nais keysseri* upp./und.: 79. = $entima \ \mathring{\circ} \ HT$ from Edie Cr., W. Side of Herzog Mts (BMNH); 80. = $entima \ \mathring{\circ} \ PT$ from Herzog Mts (BMNH); 81. $\mathring{\circ} \ from$ Wau (KSP 22971); 82. = $nais \ bullai \ \mathring{\circ} \ PT$ in litt. from environment Goroka (NCB-RMNH); 83. = $nais \ bullai \ PT \ \mathring{\circ} \ in$ litt. from environment Goroka (KSP 22969).



Figs 84-86. *D. nais aegle* from Biagi, Mambare R. NE of Port Moresby (BMNH): 84. HT $\stackrel{?}{\circ}$ upp./und.; 85. PT $\stackrel{?}{\circ}$ upp./und.; 86. $\stackrel{?}{\circ}$ und. variety. **Figs 87-89.** *D. bornemanni* from Angabunga R. (BMNH): 87. $\stackrel{?}{\circ}$ upp./und.; 89. $\stackrel{?}{\circ}$ und. variety.