

The Golden and Mariana albatrosses, new species of pierid butterflies, with a review of subgenus *Appias* (*Catophaga*) (Lepidoptera)

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Abstract. This paper presents an overview of the subgenus *Appias* (*Catophaga*) Hübner (Pieridae). A beautiful golden-yellow member of the group, endemic to the Indonesian island of Sulawesi, *Appias* (*Catophaga*) *aurosa* Yata & Vane-Wright **sp.n.**, is described as new. A small white species, *Appias* (*Catophaga*) *mariana* Yata & Chainey **sp.n.**, is described as new from the Marianas. Four other taxa, *A. (C.) athama* (Blanchard), *A. (C.) galba* (Wallace) **stat.rev.**, *A. (C.) galene* (Felder & Felder) and *A. (C.) wardii* (Moore), treated in most recent literature as subspecies, are recognized here as distinct, increasing the number of *Catophaga* species generally recognized from nine to 15. A brief review is given for each, with notes on their diagnosis, general distribution and known hostplants. An annotated synonymic checklist indicating subspecies, type localities and four new synonyms, and nine lectotype designations, one neotype designation and two type locality restrictions necessary to stabilize usage conclude the paper. Online Supporting Information provides an extensive discussion concerning the possible evolution of these butterflies with respect to polymorphism, speciation, coloration and hostplant relationships, a comprehensive list of type material for all available species group names belonging to the subgenus, and a complete bibliography for all citations in both the printed and online material.

Introduction

This work does not constitute a fully comprehensive revision. Its purpose is three-fold: to provide an overview of the species of subgenus *Appias* (*Catophaga*) Hübner, including the description of two new members of the group, and a key to adult males and females; to review known larval hostplant relationships, distribution and, especially, the spectacular polymorphism of certain species, with a view to stimulating further research into their ecology, genetics, molecular systematics and evolutionary biology; and to provide a fully synonymic

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list of all currently accepted subspecies to facilitate the future revisionary taxonomy that will probably be needed once extensive molecular investigations have been made into the numerous populations of these insects.

The butterflies assigned currently to the genus *Appias* Hübner comprise more than 40 species of 'whites' (Pieridae). Although found largely in the old world tropics, the genus is also represented in the Americas. *Appias* is placed, together with *Saletara* Distant (three or four species: Parsons, 1998; Vane-Wright & de Jong, 2003), *Udaiana* Distant (one species) and *Aoa* de Nicéville (one species), in the Appiagina Kusnezov, a subtribe of the Pierinae: Pierini (Braby *et al.*, 2006).

Although the species of *Appias* were divided by Klots (1933: 208) into four subgenera, Yata (1981) proposed seven subdivisions, five of which were recognized as subgenera (*Appias* s.s., *Catophaga* Hübner, *Phrissura* Butler, *Hipocrissia* Geyer, *Glutophrissa* Butler, plus the *lyncida* and *sylvia* species groups). Braby *et al.* (2006: 263) suggested that the collective

genus *Appias*, as accepted currently, is almost certainly a paraphyletic group (notably with respect to the exclusion of *Saletara*: Yata, 1981: 392).

Among these divisions, the Indo-Australian subgenus *Catophaga* Hübner is remarkable for the inclusion of several brightly coloured species in which the adult males, instead of the typical white or yellow of most *Appias*, are brilliant flame orange, chocolate brown or powder blue. The females of these butterflies are variously coloured, either white, yellow, polymorphic white or yellow, polymorphic white, yellow or male-like, or, in some cases, simply male-like with respect to their dominant colour. *Catophaga* is also notable because some, if not all, of its species seem capable of switching larval hosts between Capparaceae (a family of the Brassicales, now often placed within the Brassicaceae) and certain Malpighiales (e.g. *Drypetes*, family Putranjivaceae – formerly included in the Euphorbiaceae), apparently due to the common possession of glucosinolates in these plants (Braby & Trueman, 2006).

Methods

Materials

The greatest part of the material examined for this study is preserved in the collection of the Natural History Museum, London (BMNH), with significant studied material also in the Biosystematics Laboratory, Kyushu University, Fukuoka (BLKU). During this work, more than 8500 museum specimens were examined, and approximately 200 genitalia dissections prepared. In addition, research was undertaken on the extensive type material of these butterflies held in the BMNH collections to ensure that, as far as possible, the species group names applied are typified correctly and appropriate to employ.

Other material examined is located in the Entomological Laboratory, Faculty of Agriculture, Kyushu University (AGKU), Muséum National d'Histoire Naturelle, Paris (MNHN), Oxford University Museum of Natural History (OUMNH) and the Bishop Museum, Honolulu (BPBM).

Genitalia preparation and terminology

For the preparation of genitalia, either the entire abdomen or posterior half of the abdomen was removed, macerated in 10% aqueous KOH, and dissected in water using a binocular microscope. Except where noted, genitalia drawings were executed using a camera lucida from the entire genitalia or single parts submerged in a Petri dish of water, without any compression by glass slide and cover slip. For better contrast, some preparations were stained with Chlorazol Black. Terminology for male genitalia is based on Shirôzu's (1960: 1–10) extensive account, except that we use the term phallus instead of the more frequent 'aedeagus', as endorsed by Kristensen (2003). Terminology for female genitalia mainly follows van Son (1949), with some additions from Kusnezov (1915) and Yamauchi & Yata (2004).

Wing venation terminology

The Comstock–Needham wing-vein and cell nomenclature adopted in the descriptions is based on Nielsen & Common (1991) and Smith & Vane-Wright (2001). This terminology, together with the numerical system employed by Yata (1981) and many other lepidopterists (e.g. Corbet & Pendlebury, 1992), is illustrated in Fig. 1.

Taxonomic results

Appias Hübner

Appias Hübner, 1819: 91. Type species by selection of Butler (1870a: 49): *Papilio zelmira* Stoll, 1780. [*P. zelmira*

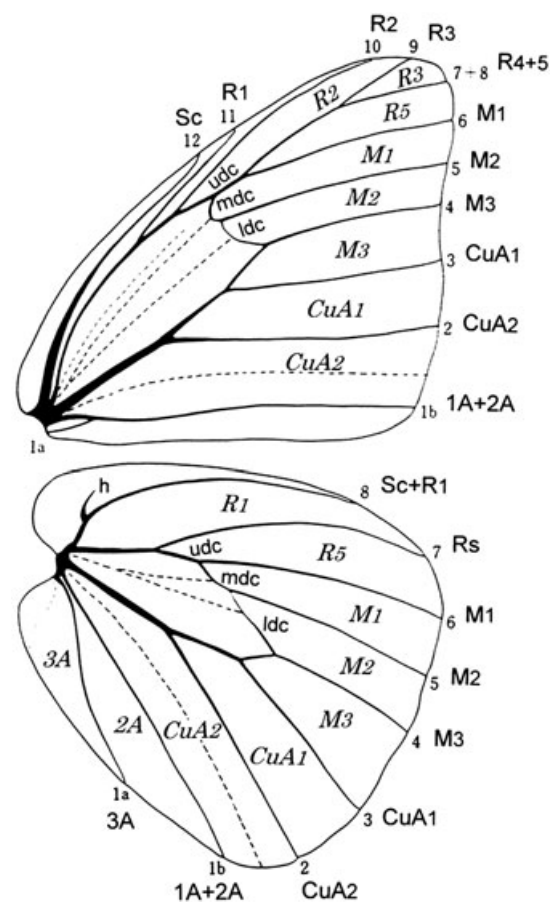


Fig. 1. Wing venation of *Appias* (*Catophaga*) *paulina*, showing both the Comstock–Needham terminology and the numerical system (small ciphers) for the long veins. The short cross-veins closing the discal are notated according to common lepidopterological practice: upper, middle and lower discocellular veins (*udc*, *mdc*, *ldc*). The cells are notated using the Comstock–Needham system only. Dotted lines in the discal cells indicate 'folds' (probable courses of proximal parts of veins *M*₁–*M*₃), and in *CuA*₂ the lost vein *CuB* (which supposedly appears during early development but is later resorbed). Based in part on Smith & Vane-Wright (2001: 513, fig. 7).

is considered to represent the same species group taxon as the older nominal species, *Papilio libythea* Fabricius, 1775; *Appias* (*Appias*) *libythea* occurs widely in the Oriental Region. Butler (1870a: 49) gave priority, as first reviser, to *Appias* Hübner over *Catophaga* Hübner.]

Subgenus *Appias* (*Catophaga*) Hübner

Catophaga Hübner, 1819: 93. Type species by selection of Scudder (1875: 136): *Papilio paulina* Cramer, 1777.

Trigonia Geyer, 1837: 21, 35. Type species by selection of Scudder (1875: 286): *Papilio nero* Fabricius, 1793. (Invalid name: junior homonym of *Trigonia* Brugière, 1789.)

Tachyris Wallace, 1867: 361. Type species by selection of Scudder (1875: 274): *Papilio nero* Fabricius, 1793.

Diagnosis

Habitus. Forewing apex generally acute, often sharply pointed, especially in male. Ground colour varies from white to yellow, orange, red, brown, blue and bluish-grey. Marginal and postdiscal band usually present, especially in female, but dark markings otherwise absent (at least in the basal half of the hindwing underside).

Venation. Forewing upper discocellular 1.5–2× length of middle discocellular; middle discocellular strongly curved; lower discocellular oblique (Corbet & Pendlebury, 1992). Forewing cell discal cell with three wing folds, but the most anterior does not reach the discocellular vein.

Male genitalia. Uncus long (the free part half the length of whole uncus, or longer), thickened dorsoventrally; valva broad, not strongly produced posteriorly, with an internal process (near the middle of ventral margin of costa + ampulla region); saccus short and oblong with rounded anterior tip; phallus strongly curved with anteroventral end strongly developed and arched ventrally, almost the same length as coecum (coecumpenis). A well-developed black genital hair tuft on eighth abdominal sternite.

Female genitalia. Signum transverse, more or less pointed laterally, with many spines. Females also have a well-developed black genital hair tuft on the distal margin of the eighth sternite (Yata, 1981); this character is only known from one *Appias* species not included in subgenus *Catophaga*: *Appias lalassis* Grose-Smith (type species of *Lade* de Nicéville, 1898).

Three subgroupings of subgenus *Appias* (*Catophaga*)

The 15 species of subgenus *Appias* (*Catophaga*) recognized here are divisible into three groups, but we are uncertain if

these all comprise monophyletic units. The *paulina* complex, which comprises eight closely related species in which the males are white, yellow or bluish, is represented throughout the entire Indo-Australian region (Fig. 23). The *nero* group, comprising three very closely related, nonoverlapping species in which the males are reddish-orange, is Oriental, extending from north-east India eastwards to the Philippines, Lombok and Buru (Central Maluku), and is entirely parapatric with respect to the third group, the *melania* series (four allopatric species in which the males are brown or bluish), confined to the Papuan subregion, including Australia (Fig. 24).

paulina complex: *galene*, *wardii*, *albina*, *aurosa* **sp.n.**, *athama*, *paulina*, *mariana* **sp.n.**, *mata*

nero group: *galba*, *nero*, *zarinda*

melania series: *placidia*, *clementina*, *celestina*, *melania*

The *paulina* complex

Diagnosis. Male: upperside ground colour usually white, but rarely yellow or bluish-grey; forewing sometimes with a dark free spot in cell M₃; uncus narrow and spindle- or spatula-shaped viewed dorsally, slightly swollen laterally, with its tip bluntly pointed; angle between vinculum and saccus approximately 100–120°; valve rounded posteriorly or weakly produced posteroventrally; phallus thick and strongly arched dorsally. Female: upperside ground colour usually white, but more rarely yellowish or bluish-grey (e.g. *mata*, *paulina*), or even almost black (e.g. one form of *albina* from Sulawesi); forewing with postdiscal black band strongly arched outwardly in cell CuA₁, often forming a free dark spot in cell M₃.

Distribution. (Fig. 23). This complex is represented throughout the Indo-Australian realm (including the western Pacific).

The *nero* group

Diagnosis. Male: upperside ground colour usually orange-red (rarely straw-coloured). Uncus narrow and nib-shaped viewed dorsally, gradually narrowed posteriorly, with its apex usually sharply pointed. Angle between vinculum and saccus approximately 90°; valve gradually narrowed posteriorly, distinctly produced posteroventrally, with distinct hooked spines present near apex; phallus thick but only weakly to moderately arched dorsally. Female: upperside ground colour usually dull orange-red (but polymorphic in Sulawesi and Palawan, where it has white, yellow and red forms, and without red forms in the rest of the Philippines), forewing black postdiscal band not strongly arched outwardly in cell CuA₁, not forming a free dark spot in cell M₃.

Distribution. (Fig. 24). This group of three parapatric species is widely distributed in the Oriental Region, from northern India to the Greater Sundas, Bali, the Philippines, Sulawesi and Buru (Central Maluku).

The melania series

Diagnosis. Male: upperside ground colour usually greyish-blue or dark brown, forewing never with a dark free spot in cell M_3 . Uncus somewhat broad and spatula-shaped viewed dorsally, slightly swollen laterally, with its tip bluntly pointed; angle between vinculum and saccus approximately 120° ; valve evenly rounded posteriorly, distinctly incurved ventromedially; phallus slender and moderately arched dorsally. Female: forewing black postdiscal band not strongly arched outward in cell CuA_1 , not forming free dark spot in cell M_3 .

Distribution. (Fig. 24). The four allopatric species that make up this series are distributed from northern and central Maluku throughout much of the Papuan subregion, including north-eastern Australia.

Overview of species of the subgenus *Appias* (*Catophaga*)

Appias (*Catophaga*) *galene* (Felder & Felder, 1865)

Sri Lanka albatross (Figs 2, 19D–F)

Pieris galene Felder & Felder, 1865: 165.

In several recent publications (e.g. Yata, 1981; D'Abrera, 1982, 1998), and for many years previously, *A. galene* has been regarded as a subspecies of *A. paulina*. However, Wynter-Blyth

(1957: 430) (as '*paulina*') and Kunte (2000: 101) treated it as a separate species, a status confirmed by the present study. *Appias galene* is endemic to Sri Lanka.

Diagnosis

Male. (Fig. 19D). Forewing somewhat acute at apex. Upperside ground colour white. Both wings usually without markings, but sometimes with a narrow black marginal border on forewing upperside. Hindwing with oval and bright whitish sex-patch posteromedially. Genitalia (Fig. 2): uncus very narrow and spindle-shaped viewed dorsally, with broadly blunt apex (also when viewed dorsally). Valva somewhat narrowed and rounded posteriorly, with a thick and arched interior process, directed dorsolaterally. Phallus somewhat short, thick and strongly arched dorsally, with rather broad coecum lacking a dorsal ridge; broadened basal prong as long as coecum.

Female. (Fig. 19E, F). Upperside ground colour white. Forewing black apical area usually with three submarginal whitish spots in cells R_5 – M_2 (spot in cell M_2 often reduced); black-dusted basal area with distal margin usually almost perpendicular to posterior margin of forewing. Underside hindwing yellow or white, with or without a dark submarginal band.

Distribution

Restricted to Sri Lanka. According to Woodhouse (1950) and d'Abrera (1998), a very common butterfly that frequently makes mass migrations across the island. Wynter-Blyth (1957: 430) stated that it occurs up to approximately 6000 ft (ca 1800 m); possibly absent in the far north of the island (H. Gaonkar, unpublished data).

Foodplants

Apparently unknown [Woodhouse, 1950: 153; d'Abrera, 1998; no entry in Robinson *et al.* (2001)].

Appias (*Catophaga*) *wardii* (Moore, 1884)

Ward's albatross (Figs 3, 19G, H)

Catophaga wardii Moore, 1884: 43.

In many recent accounts (e.g. Yata, 1981) and for many years earlier, *wardii* (like *galene*) was regarded as a subspecies of *A. paulina*. Bell (1913), who studied its life history, was uncertain regarding its separation from *paulina* (as *leis*), and referred to it as '*leis-wardii*' [sic]. However, *A. wardii* was treated by Bingham (1907: 214), Talbot (1939: 406), Wynter-Blyth (1957: 431), Larsen (1987: 49) and by Kunte (2000: 101) as a distinct species, and this status has been confirmed during the present investigation. *Appias wardii* is endemic to the Western Ghats of southern India.

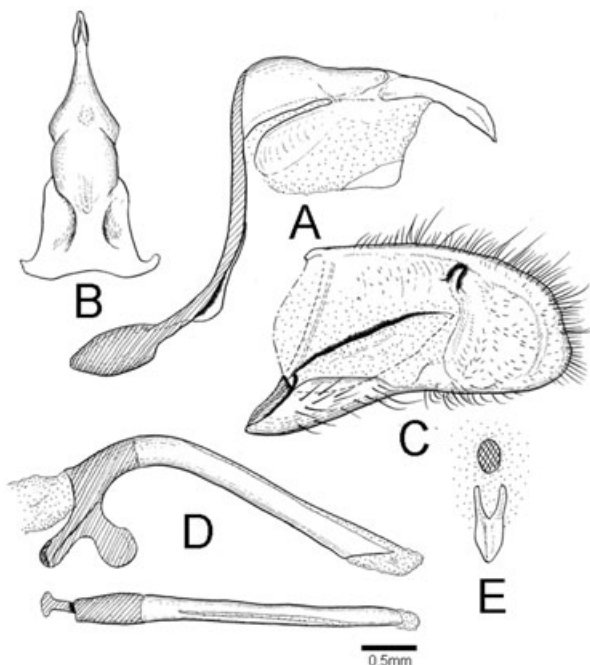


Fig. 2. Male genitalia of *Appias* (*Catophaga*) *galene* (Sri Lanka: NHM genitalia preparation no. 4669). (A) Ring, lateral views; (B) uncus, dorsal view; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

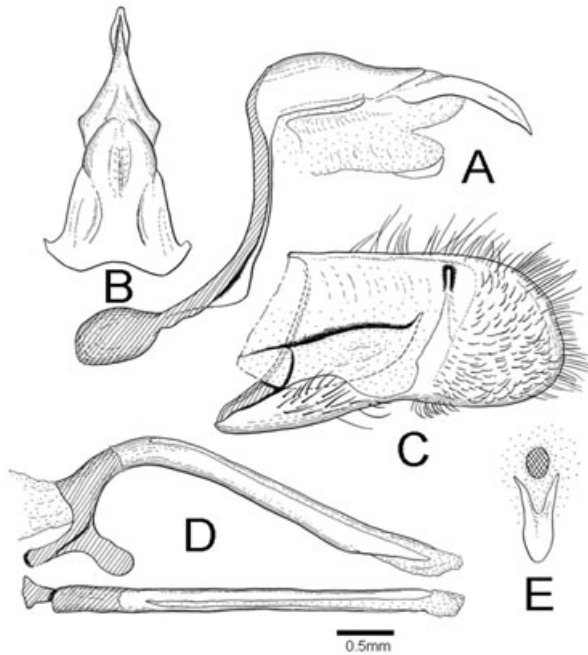


Fig. 3. Male genitalia of *Appias* (*Catophaga*) *wardii* (South India: Nilgiri Hills; NHM genitalia preparation no. 4633). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Diagnosis

Male. (Fig. 19G). Forewing somewhat obtuse at apex. Upperside ground colour white. Both wings always with distinct markings like the typical form of *albina* female (cf. Fig. 19K). Forewing black apical area usually with five submarginal light spots in cells R_2 and R_5-M_3 , those in M_3 and CuA_1 often reduced; black-dusted basal area with distal margin usually almost perpendicular to posterior margin of forewing, not oblique as in *albina*. Hindwing with oval and bright whitish sex-patch posteromedially. Genitalia (Fig. 3): uncus narrow and spindle-shaped viewed dorsally, apex blunt. Valva broad and rounded posteriorly, with a slender and almost straight interior process directed almost laterally. Phallus thick and strongly arched dorsally, with coecum lacking a dorsal ridge; basal prong as long as coecum.

Female. (Fig. 19H). General facies similar to male. Pale submarginal spots of forewing sometimes almost obsolete. Underside ground colour white.

Distribution

Restricted to western South India, from approximately $18^\circ S$ to the far south, where it is fairly common along the Western Ghats. According to Bell (1913: 344) it is found from 'sea-level up to 2500 or 3000 ft (ca 900 m). They are not found in the plain country being seemingly confined to the hill

jungles where the rain is heavy'. Bell's statement is thus self-contradictory, at least regarding the lower altitudes at which this species can be found. Wynter-Blyth (1957: 431) states that it is 'mainly confined to forest below 2500 ft'.

Foodplants

Putranjivaceae and Capparaceae. Bell (1912: 1145; 1913: 330, 341–344), although not stated directly, gives '*Hemicyclia venusta*' (= *Drypetes*, Putranjivaceae) as the plant on which he bred this species. Talbot (1939: 408) notes *Capparis heyneana*. Robinson *et al.* (2001) list *Capparis* and *Drypetes*. Mathew & Binoy (2002) give *Drypetes venusta*.

Appias (*Catophaga*) *albina* (Boisduval, 1836)

White or common albatross (Figs 4, 19I–P)
Pieris albina Boisduval, 1836: 480.

Diagnosis

Male. (Fig. 19I). Forewing distinctly acute at apex. Upperside ground colour white. No markings, but sometimes with a narrow black marginal border on forewing upperside. Hindwing with oval, bright, whitish sex-patch posteromedially. Genitalia (Fig. 4): uncus narrow and spindle-shaped viewed

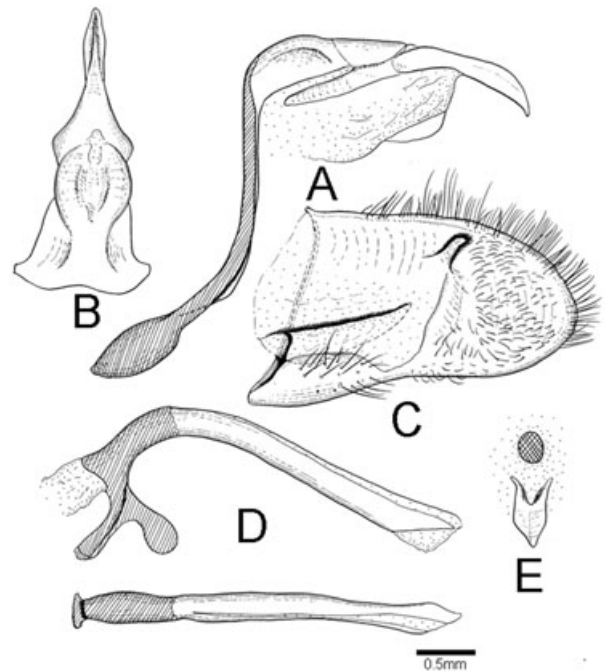


Fig. 4. Male genitalia of *Appias* (*Catophaga*) *albina* (Indonesia: Sulawesi; NHM genitalia preparation no. 4686). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

dorsally, apex blunt. Valva broad and rounded posteriorly, very different in outline to *A. paulina* (Yata, 1981: 377; Parsons, 1998: 292, fig. 48), with a thick and arched interior process, directed dorsolaterally. Phallus thick and strongly arched dorsally, with long coecum lacking a dorsal ridge; basal prong as long as coecum.

Female. (Fig. 19J–P). Forewing fairly acute at apex. Upper-side ground colour typically white, but sometimes yellow, and in one form found on Sulawesi, infuscated, almost black (Fig. 19P). Forewing black apical area with at least four sub-marginal whitish spots in cells R₅–M₃, those in cells M₃ and M₂ usually reduced; black-dusted basal area with distal margin oblique.

Distribution

Widely distributed over much of the Indo-Australian Region, from Sri Lanka and southern India (Kunte, 2000: 101) to Taiwan, Ryukyu Islands (Takara, 1956: 67), Sundaland (including Siberut: Corbet, 1941), Wallacea, Lesser Sunda Islands (Rawlins, 2007), New Guinea and Kiriwina, and coastal areas of parts of Northern Territory and Queensland in Australia (Braby, 2000: 328; Braby *et al.*, 2009). It does not occur in the Bismarcks (Parsons, 1998: 291) or Solomons (Tennent, 2002: 63), and appears to be replaced by *A. athama* in the western Pacific (New Caledonia to Samoa).

Foodplants

Capparidaceae, *Crateva* (*Capparidaceae*) and *Drypetes* (*Putranjivaceae*) (Corbet & Pendlebury, 1992; Parsons, 1998; Bascombe *et al.*, 1999; Kunte, 2000, 2006; Robinson *et al.*, 2001). Igarashi & Fukuda (2000: 394) record *Drypetes littoralis* as the foodplant in Palawan, and *D. poilanei* in Laos, while noting an old record of *Capparidaceae heyneana* for the Malay Peninsula. Braby *et al.* (2010) consider *A. albina* to be monophagous on *Drypetes deplanchei* in northern Australia.

Appias (Catophaga) aurosa Yata & Vane-Wright sp.n.

Golden albatross (Figs 5, 19A, 20A)

Tachyris nero zarinda ab. *aurosa* Fruhstorfer, 1899: 84. Original male specimen, 'Celebes, Macassar, W. Doherty, 1896', 'Type', 'zarinda ab. aurosa Fruhst'. In BMNH (examined), BMNH(E) #229202. (Unavailable name.)

Appias nero zarinda ab. *aurosa* Fruhstorfer; Fruhstorfer, 1910: 151; Jurriaanse & Lindemans, 1920: 9.

Appias zarinda ab. *aurosa* Fruhstorfer; Martin, 1919: 85.

Appias zarinda f. *aurora* [sic]; Talbot, 1923: 9.

Appias nero zarinda male form *aurosa* Fruhstorfer; Talbot, 1932: 161.

Appias zarinda zarinda male ab.; Yata, 1981: 373, pl. 63, fig. 4.

Appias sp.n. Yata & Vane-Wright, in Vane-Wright & de Jong, 2003: 50, 109, pl. 6, fig. 13.

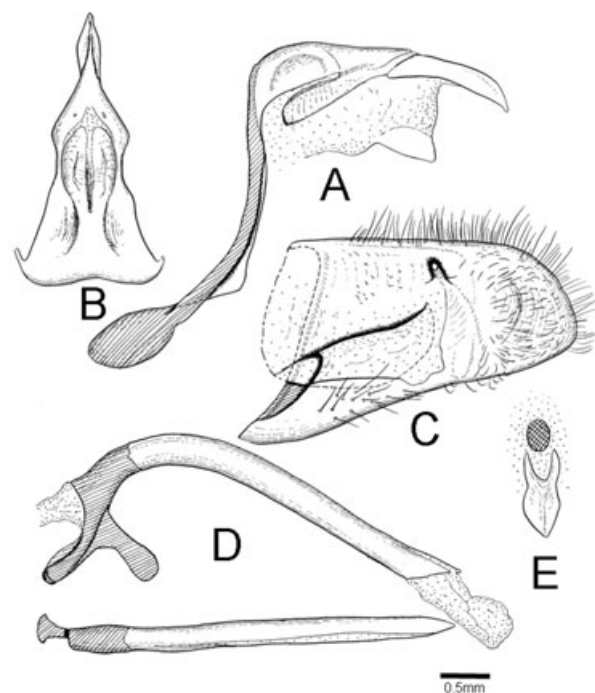


Fig. 5. Male genitalia of *Appias (Catophaga) aurosa* Yata & Vane-Wright sp.n. (Indonesia: south Sulawesi; NHM genitalia preparation no. 4597). (A) Ring, lateral views; (B) Ring, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Diagnosis

Male. (Figs 19A, 20A). Forewing somewhat elongate apically and distinctly acute at apex. Ground colour of wings golden cream yellow. Upperside of wings without markings. Hindwing with pale orange oval androconial patch postero-medially. Genitalia (Fig. 5): uncus narrow and spindle-shaped viewed dorsally, apex blunt. Valve gradually narrowed posteriorly to rounded end, with a thick and arched interior process, directed dorsolaterally. Phallus thick and strongly arched dorsally, with coecum bearing a dorsal ridge; basal prong as long as coecum.

Female. Unknown, or unrecognized.

Distribution

This Indonesian endemic is known only from southern, central and south-east Sulawesi: Ujung Pandang (type series), Palopo (Yata, 1981), Camba (South Sulawesi, 2004, ex Nishiyama 2004, type series) and Buton island (Jurriaanse & Lindemans, 1920).

Foodplants

Unknown.

Description

Male. (Figs 19A, 20A). Forewing length: 36–40 mm ($n = 13$; mean = 37.35 mm; standard deviation = 1.197). Upperside: ground colour cream to yellow, with brighter yellow tinge, especially on discal cell, and along costal and distal margins. All dark markings obsolete, except basal areas of both wings dusted black, extensively so along basal half of forewing costa, and a black anteciliary line from apex to tornus. Ciliary fringe yellow. Hindwing with oval, faintly differentiated pale orange androconial patch located posteromedially across cubital cells, just extending into anal cells and discal cell. Underside: both wings almost same as upperside, but more extensively bright, especially on the forewing discal cell and hindwing. In some specimens postdiscal dark band weakly indicated, running obliquely from origin of vein M_1 to near tip of vein CuA_2 on forewing, and more rarely recognizable in cells M_1 – M_3 of the hindwing. Forewing costa edged with some scattered black scales, but basal areas of wings not black dusted. Black anteciliary line from apex to tornus; ciliary fringe yellow. Forewing acute at apex, outer margin almost straight, but weakly incurved between veins M_1 – CuA_1 , and bluntly angled near tornus; middle discocellular almost half the length of upper discocellular, and about quarter length of lower discocellular. Hindwing evenly rounded on costal to outer margin, strongly curved near tornus; Rs arising free from cell; middle discocellular subequal to upper discocellular and lower discocellular. Antenna approximately $0.41 \times$ length of forewing, black and white chequered except on posterodorsal surface and a few apical segments; club subcylindrical. Thorax above and abdomen above near its base clothed with pale, yellowish hairs. Abdomen above blackish, with pale whitish-yellow scales beneath.

Male genitalia. (Fig. 5). Dorsum somewhat narrow, triangular in dorsal aspect, compressed medially, somewhat concave dorsomedially, with crossbow-like membranous area medially; valvansatz (term from Droshin: see Shirôzu, 1960) broad, becoming more membranous ventrally; vinculum not strongly arched posteriorly; saccus short and rather slender ($0.4 \times$ ring height); angle between vinculum and saccus approximately 110 – 120° . Uncus moderately long ($0.45 \times$ ring height), narrow and spindle-shaped in dorsal view, bluntly pointed apically, with dorsal edge gradually narrowing towards apex; beak-shaped when viewed laterally, somewhat deeper medially, slightly hooked at tip. Valva nearly twice as long as high, gradually narrowing posteriorly to rounded tip, weakly produced posteroventrally, with a long and somewhat arched interior process arising near the middle at ventral margin of costa + ampulla region, directed dorsolaterally; patches of hooked spines present along ventral margin at posterior end and just beyond middle. Phallus moderately long, rather thick and strongly arched dorsally, subzonal sheath approximately one-fifth length of phallus; coecum with a small dorsal ridge; basal prong flattened laterally and somewhat swollen apically. Juxta arrowhead-like, somewhat swollen lateromedially when viewed from behind.

Female. Unknown.

Type material

Holotype male and 12 paratype males in BMNH, and one paratype male in BLKU, all of which have been labelled accordingly.

Holotype male and 12 paratype males in BMNH labelled: ‘Celebes, Macassar, W. Doherty, 1896’ (Ujung Pandang, South Sulawesi, Indonesia) (specimen register nos BMNHE 149984, 229197–229207, 229236). No. 229202 is labelled ‘*zarinda aurosa* Fruhstorfer in Seitz, p. 151’ (forewing length 40.0 mm) and is selected as holotype of *Appias* (*Catophaga*) *aurosa* Yata & Vane-Wright. No. 229207 (forewing length 37.0 mm), which carries the label ‘*zarinda*, ab. *aurosa* Fruhst./type’, is also labelled ‘*Tachyris nero zarinda* ab. *aurosa* Fruhstorfer, type specimen, det. O.Yata & R.I. Vane-Wright, 1998’. This last specimen apparently reached the BMNH from the Fruhstorfer Collection [Fruhstorfer (1899) had noted that Oberthür had sent him one specimen]; the other 12 all came from the C. Oberthür Collection, and are so labelled. One male paratype, labelled ‘S. Sulawesi, Camba, 2004’ (forewing length 35.5 mm), in BLKU.

Comments

Appias aurosa was described first as a male aberration of *Appias zarinda* from south Sulawesi by Fruhstorfer (1899), and the same status has been accorded to this insect by subsequent authors, as listed in the synonymy. However, we consider that ab. *aurosa* represents a distinct species – described and named here as new because Fruhstorfer’s name is clearly infra-specific (and thus unavailable). On the basis of external phenotype and male genital morphology, this species is distinct from *A. zarinda*, and appears to be more closely related to *A. albina*.

Appias aurosa shares a number of potential synapomorphies with *A. albina*, including the spindle-shaped uncus with bluntly pointed apex, the thick and strongly arched phallus, and the oval androconial patch on the hindwing upperside. *Appias aurosa* is similar to *A. zarinda* in the narrowed valve, the tegumen with crossbow-like membranous area, and the sharply pointed forewing without markings. However, such a tegumen is probably symplesiomorphic, whereas the unique wing characters are almost certainly homoplasious (geographical parallelism). Large size coupled with a strongly arched forewing costa or pointed forewing tip affects many different butterflies endemic to Sulawesi (‘Celebes forewing’), a striking and mysterious convergence first noted by Alfred Russel Wallace (1865, 1867, 1869: 215–217) and discussed by Vane-Wright & de Jong (2003: 23). A sharply pointed, unmarked forewing affects three *Catophaga* taxa occurring on Sulawesi: *A. zarinda zarinda*, *A. aurosa* and *A. paulina albata*. *Appias aurosa* effectively replaces *A. albina* in Sulawesi, but coexists with *A. zarinda*. *Appias albina* is very rare in Sulawesi, even though it is quite common in neighbouring regions, such as Borneo, Palawan, Lesser Sundas and New Guinea. It is possible that

albina has migrant status on Sulawesi (although the unique 'black' females of *A. albina* found there perhaps argue against this: Fig. 19P), where *aurora* and *albina* might form a 'species duplex' (Corbet & Pendlebury, 1992). The systematic position of *A. aurora* should become clearer once the female has been found and studied.

Appias (Catophaga) athama (Blanchard, 1848)

Pacific albatross (Figs 6, 19Q–S)

Pieris athama Blanchard, 1848: pl. 1, figs 10, 11

Much confusion has surrounded this species, including the question of its authority [the name *Pieris athama* was introduced separately by Lucas (1852)], and its type locality, 'Balaou'. We now know that this represents the Fijian island of Ovalau (Appendix 1).

Pieris athama is treated in many publications as a subspecies or synonym, either of *A. albina* (e.g. D'Abrera, 1971, 1990; Holloway & Peters, 1976) or *A. paulina* (e.g. Yata, 1981) – although this has always been questioned by D'Abrera (1971, 1990). As dealt with by Tennent (2004, 2006), and confirmed by the present study, *A. athama* is a distinct species endemic to New Caledonia and adjacent regions of the western Pacific.

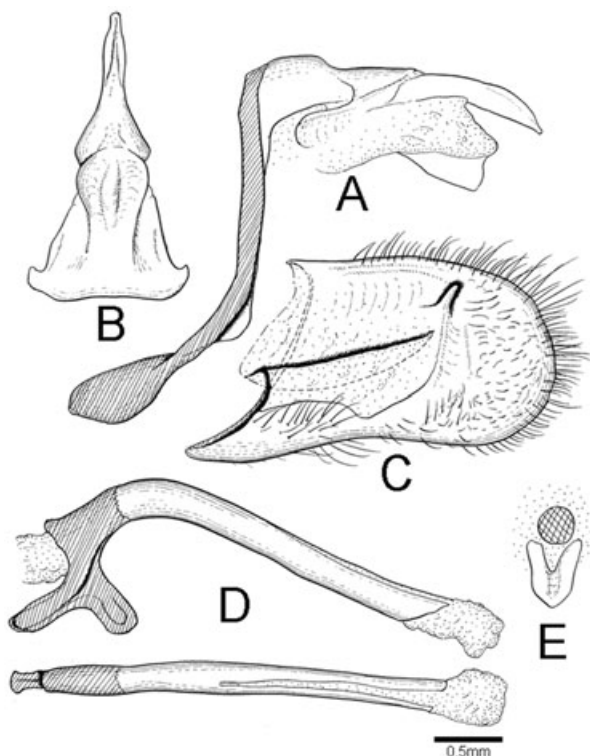


Fig. 6. Male genitalia of *Appias (Catophaga) athama* (New Hebrides: NHM OY genitalia preparation no. 7). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Diagnosis

Male. (Fig. 19Q). Forewing broad and weakly falcate near apex. Upperside ground colour white with weak lustre. No markings, but costa to outer margin edged with a distinct, fine, black margin. Hindwing with oval, whitish androconial patch posteromedially. Underside ground colour usually dark or bright yellow on forewing apex and on hindwing. Genitalia (Fig. 6): tegumen moderately swollen anterodorsally; uncus narrow and spindle-shaped viewed dorsally, with blunt apex and not abruptly curved ventrally. Valva broad and rounded posteriorly. Phallus thick and moderately arched dorsally, with long coecum with a weak dorsal ridge; basal prong somewhat shorter than coecum.

Female. (Fig. 19R, S). Forewing broad and weakly falcate near apex. Upperside ground colour white to yellow with reddish tinge. Forewing with pale submarginal spots in cells R_5 , M_1 and M_3 , but rarely traceable in cell M_2 . Hindwing black distal border evenly broad with marginal triangular pale spots. Underside markings almost as upperside, but with forewing apex and margin of hindwing border paler.

This species closely resembles *A. albina*, but is readily distinguished from the latter in the male by the falcate forewing distinctly edged with black and the bluntly pointed uncus not abruptly curving ventrally at apex, and in the female by the even, black hindwing border with marginal triangular pale spots.

Distribution

Recorded from New Caledonia, Loyalty Is., Isle of Pines, Vanuatu, Banks Islands, Fiji, Tonga and Western and American Samoa [for details see Tennent (2006)]. This species occurs sympatrically with *A. paulina* in the eastern part of its range.

Foodplants

Apparently unknown. Both *Capparis* and *Drypetes* occur in the western Pacific, including Samoa (Amerson *et al.*, 1982).

Appias (Catophaga) paulina (Cramer, 1777)

Yellow albatross (Figs 7, 20B–L)

Papilio paulina Cramer, 1777: 21, 150, pl. 110, figs E,F

The published type locality was 'Côte de Coromandel, à Tranquebar & dans l'isle de Java, près de Batavia'. This taxon was long considered to be based on material from Sri Lanka (Fruhstorfer, 1910: 155; Talbot, 1939: 404; Wynter-Blyth, 1957: 430; Edwards *et al.*, 2001: 466), or south-east India (e.g. Parsons, 1998: 291). However, the most similar *Appias* from Sri Lanka is the distinct *A. galene* (see above). An authentic ex van Lennep 'Cramer specimen' has been located in the BMNH (Chainey, 2005: 329, fig. 40), and is here designated lectotype of *Papilio paulina* Cramer (Appendix 2). With very

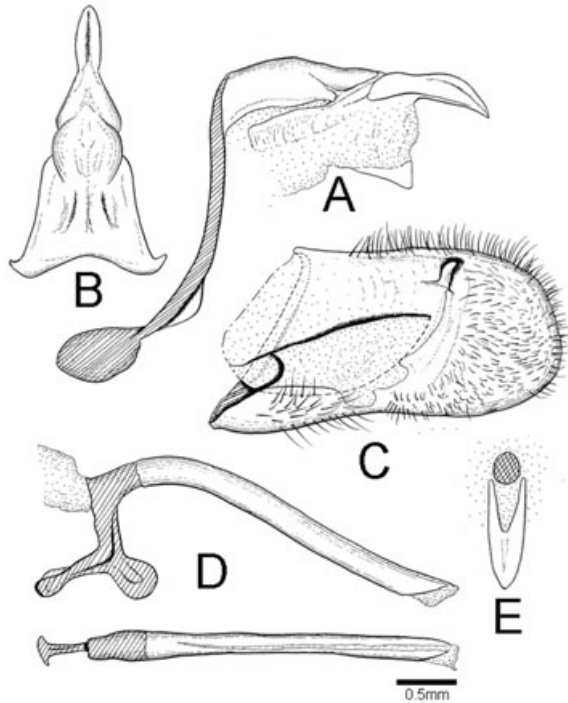


Fig. 7. Male genitalia of *Appias* (*Catophaga*) *paulina* (Myanmar: Karen Hills; NHM genitalia preparation no. 4651). (A) Ring, lateral views; (B) uncus, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

little doubt it is Javanese in origin, and we consider that the nominate subspecies of *A. paulina* represents the race found on Java. The idea that the original locality was Sri Lanka (and/or southern India) appears erroneous.

Diagnosis

Male. (Fig. 20B, F, H, J, L). Forewing somewhat obtuse at apex, which may or may not be narrowly darkened. Upperside ground colour white, both wing surfaces usually with a free dark spot in cell M_3 . Hindwing without oval sex-patch. A group of long and very prominent scales on dorsum of eighth tergite (Parsons, 1998: 290) (other *Catophaga* species have similar scales in this position, but they are shorter and less prominent). Genitalia (Fig. 7): uncus spatula-shaped viewed dorsally and blunt-ended, with its dorsal ridge well developed. Valva broad and rounded posteriorly, with a thick and arched interior process, directed dorsolaterally. Phallus thick and strongly arched dorsally, with elongate coecum bearing a dorsal ridge; broadened basal prong shorter than coecum; common stem of coecum and basal prong well developed.

Female. (Fig. 20C–E, G, I, K). Upperside ground colour white, sometimes yellow. Forewing black apical area usually

with five submarginal whitish spots in cells R_2 and R_5 – M_3 , those in cells M_2 and M_3 often reduced; heavily black-dusted basal area with distal margin almost perpendicular to posterior margin of forewing (not oblique). As in other members of the subgenus, a black, well-developed genital hair tuft arises on the distal margin of the eighth sternite (Yata, 1981).

Comment. Many subspecies of *A. paulina* are currently recognized (Appendix 1). It seems plausible that future work, including the potential application of molecular methods, will show that some represent distinct species. For example, races such as *A. paulina eurosundana* from Alor, *A. p. paula* from Wetar and *A. p. galathea* (Fig. 20B–E) from the Andamans and Nicobars, appear significantly different to nominate *paulina*.

Distribution

As currently conceived, *A. paulina* is a widely distributed species found throughout much of the Indo-Australian Region, including New Guinea and parts of Australia (where it has even been recorded as far south as Tasmania: Braby, 2000: vol. 1, 325; Braby 2005), Christmas Island and Lord Howe, and from northern India to New Caledonia and Vanuatu (Tennent, 2006: 31). However, it does not occur in Pakistan, peninsular India and Sri Lanka, or in the Bismarck Archipelago (Parsons, 1998: 291) or the Solomons (Tennent, 2002: 63) and appears unrecorded from the Mentawai Islands. *Appias paulina minato* occurs in Taiwan and Kagoshima Prefecture of Japan (Ryukyu or Loocho Islands), with its northern limit being Akuseki-jima, in the Tokara Is., a little to the north of Amami-ohshima. Prior to the 1960s, in the Ryukyus it was known from Okinawa, Ishigaki, Iriomote, Hateruma and Yunaguni (Takara, 1956: 66, as *Appias melania minato*). It has also been recorded from Yaeyama and Miyako, and apparently spread to Amami-ohshima in 1980 and Akuseki-jima in 1975 or 1982. Further northerly movement, including to Kyushu, is limited by the absence of its larval foodplant, *Drypetes matsumurae* Kaneh (H. Fukuda, personal communication, 2007).

Foodplants

Capparis (Capparaceae), *Drypetes*, *Putranjiva* (Putranjivaceae) (Braby, 2000: 466; Robinson *et al.*, 2001). Igarashi & Fukuda (2000: 392) noted *Drypetes matsumurae* as the foodplant in Japan and Taiwan, *D. littoralis* in Palawan and *D. deplanchei* in Australia, and commented that an old record for *Capparis heyneana* ‘requires reconfirmation’.

Appias (*Catophaga*) *mariana* Yata & Chainey sp.n.

Mariana albatross (Figs 8, 9, 19B, C, 20M–Q)

Appias leis subtuslutea Roepke; Swezey, 1942: 66, pl.9, figs. 12, 15. Misidentification

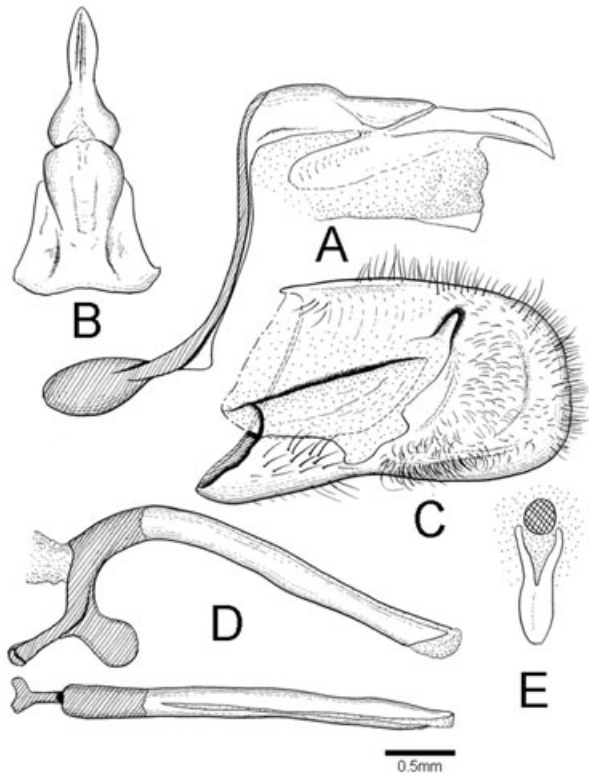


Fig. 8. Male genitalia of *Appias (Catophaga) mariana* Yata & Chainey sp.n. (Marianas: Guam; NHM specimen register number BMNH(E)# 229237). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Appias paulina jacquinotii Lucas; Yata, 1981: 379. Misidentification

Appias paulina Cramer; Fukuda & Nicho, 2001: 31, 33. Misidentification

Diagnosis

Male. (Figs 19B, 20M, N). Small species (forewing length below 27.0 mm). Forewing somewhat acute at apex, more pointed than in *paulina*. Upperside ground colour white, often with pale greenish-yellow tinge. Black postdiscal band present in cells M_1 – M_3 , and usually expressed in cells R_{4+5} and CuA_1 , never reduced to an isolated spot, even in cell M_3 . On underside forewing postdiscal black band usually present from costa to cell M_3 , but barely visible in cell CuA_1 , as on upperside. Genitalia (Fig. 8): uncus somewhat short ($0.5 \times$ ring height), narrow and spatula-shaped viewed dorsally, blunt-ended, with dorsal ridge well developed. Valva broad and weakly rounded posteriorly. Phallus moderately long, thick and strongly arched dorsally.

Female. (Figs 19C, 20O–Q). Upperside forewing with distal margin of black basal area somewhat oblique. Underside

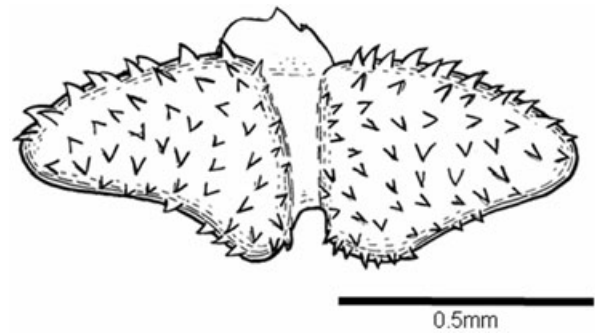


Fig. 9. Female genitalia (signum) of *Appias (Catophaga) mariana* Yata & Chainey sp.n. (Marianas: Rota: Tatacho-Songsong; AGKU OY genitalia preparation no. 1189). Posterior aspect. 0.5 mm.

forewing postdiscal black band well marked from costa to tornus. Signum broad, diamond-shaped when viewed posteriorly, with many spines (Fig. 9).

Distribution

Endemic to Mariana Islands (Guam, Saipan, Rota).

Foodplants

Unknown. Hostplants that should probably be considered are *Drypetes dolichocarpa* Kanehira, endemic to the Marianas, and/or *Capparis cordifolia* Lamarck (Fosberg *et al.*, 1975).

Description

Male. (Figs 19B, 20M, N). Forewing length: 19–27 mm ($n = 10$, mean 24.15 mm; standard deviation = 1.817). Upperside: ground colour white, usually with pale greenish-blue tinge. Forewing black distal border almost regular and gradually narrowed towards tornus, outwardly concave in cells M_1 – CuA_1 , and almost obsolete in cell CuA_2 . Black postdiscal band present in cells M_1 – M_3 , and usually traceable in cells R_{4+5} and CuA_1 as much narrower and faint streak close to distal border, and not reduced to an isolated spot even in cell M_3 . Black anticiliary line recognizable from apex to tornus; fringe black, but whitened towards tornus. Hindwing black distal border generally poorly developed, usually reduced to marginal vein-dots, often obsolete. Black anticiliary line traceable from apex to tornus; ciliary fringe white. Basal portions of both wings black dusted, extensively so towards apex along costal margin of forewing. Underside: ground colour almost the same as on upperside, but somewhat darker, rarely yellowish on forewing apex and on hindwing. Postdiscal black band usually present from costa to cell M_3 , and barely traceable in cell CuA_1 , as on upperside. Black anticiliary line barely traceable from apex to tornus on forewing; fringe white. Forewing somewhat acute at apex; outer margin

almost straight, but weakly rounded between veins CuA_1 and CuA_2 ; bluntly angulate near tornus; middle discocellular subequal to upper discocellular, almost half the length of lower discocellular. Hindwing evenly rounded on costal to outer margin, strongly curved near tornus; R_s arising free from cell; middle discocellular subequal to or less than upper discocellular or lower discocellular. Antenna approximately $0.41 \times$ length of forewing, black and white-checked, except on the posterodorsal surface and a few apical segments; club cylindrical. Thorax above and abdomen above near base clothed with whitish hairs. Abdomen above blackish with scales beneath whitish.

Male genitalia. (Fig. 8). Dorsum elongate-triangular in dorsal aspect, compressed medially, concave dorsomedially, fairly swollen anterodorsally; valvenansatz broad, becoming membranous ventrally; vinculum not strongly arched posteriorly; saccus short and relatively slender ($0.25 \times$ ring height); angle between vinculum and saccus approximately $100\text{--}110^\circ$. Uncus somewhat short ($0.5 \times$ ring height), narrow and spatula-shaped viewed dorsally, with a blunt tip, the dorsal ridge well developed, beak-shaped viewed laterally, and distinctly deeper medially, and slightly hooked at its tip. Valva broad and weakly rounded posteriorly, with a thick and arched interior process directed dorsolaterally; a batch of curled, short setae present along ventral margin of valva just beyond its middle. Phallus moderately long, thick and strongly arched dorsally, subzonal sheath approximately one-fifth length of phallus, with elongate coecum bearing a weak dorsal ridge; broadened basal prong as long as coecum; common stem of coecum and basal prong well developed. Basal prong flattened laterally and somewhat swollen apically. Juxta arrowhead-like, but ending bluntly ventrally, and somewhat swollen lateromedially when viewed from behind.

Female. (Figs 19C, 20O–Q). Forewing length: 22–26 mm ($n = 3$, mean = 24.77 mm; standard deviation = 1.27). Upperside: ground colour white, with greenish-yellow tinge, sometimes yellowish on hindwing. Forewing black costal border broad, with its inner margin indistinct basally; black distal border generally broad, fused with black postdiscal band, with its inner edge irregular from costa to vein CuA_1 , obtuse-angled at vein CuA_1 , deeply excavated in cell CuA_1 ; a series of submarginal white spots appearing in cells R_2 and $R_5\text{--}M_3$. Ciliary fringe black. Basal portion of forewing extensively black dusted, fused with costal border; black-dusted basal area with distal margin somewhat oblique. Hindwing black distal border broad, with its inner edge moderately defined, zigzag-shaped. Whitish anticiliary line recognizable from apex to tornus. Ciliary fringe black. Basal area and anal margin of hindwing black dusted. Underside: pale ground colour almost the same as upperside, but darker, especially on forewing apex and on hindwing; rarely dark yellow (Fig. 20P). Black anticiliary line barely traceable from apex to tornus on forewing. Ciliary fringe whitish. Forewing postdiscal black band well marked from costa to tornus. Forewing somewhat obtuse at apex; outer margin almost straight, but weakly rounded between veins CuA_1

and CuA_1 ; bluntly angulate near tornus. Hindwing evenly rounded on costal to outer margin, curved near tornus. General features of thorax, abdomen and venation similar to male.

Female genitalia. (Fig. 9). The papilla analis almost elliptical with apical lobe, some hairs and a slender apophysis posterioris. The lobulus vaginalis (Kusnezov, 1915: 132, fig. 72) weakly sclerotized, with an apophysis anterioris, and divided into upper and lower lobes, of which the ventral is broad and evenly curved posteriorly. The ductus bursae is moderately long, and twisted near border of cervix bursae. The ductus seminalis attaches to the tip of the cervix bursae. Corpus bursae large and subglobular, with a smaller appendix bursae (as in many other genera of Pieridae, including *Cepora* Billberg). Signum broad, diamond-shaped when viewed posteriorly, strongly constricted medially, with spines covering entire surface.

Type material

Holotype male and eight paratype males in BMNH, 15 paratypes in AGKU and four paratypes in BPBM, all of which have been labelled accordingly.

Holotype male and four paratype males in BMNH labelled: Guam, Rothschild Bequest, B.M. 1939-1 (specimen register nos BMNH(E) 229237–229241). No. 229237 is dated [18]95 (forewing length: 24.5 mm) and is selected as holotype of *Appias* (*Catophaga*) *mariana* Yata & Chainey. Nos 229238 and 229240 are dated March [18]95. No. 229239 is dated 10.x.[18]94. No. 229241 is dated '11–10' [18]94. One paratype male in BPBM labelled: Guam, Ritidian pt., 22.iv.1936, E.J. Bryan, Jr. One paratype male and one paratype female in BPBM labelled: Guam, Tarague, 17.v.1936, O.H. Swezey. One paratype female in BPBM labelled: Guam, Machanao, 2.vi.1936, O.H. Swezey. Three paratype males in BMNH labelled: Saipan, Rothschild Bequest, B.M. 1939-1 (specimen register nos BMNH(E) 229242–229244). No. 229242 dated viii.[18]95. Nos 229243–229244 dated 13.ix.[18]95. One paratype female in BMNH labelled 'Museum Paris Mariannes M.A. Marche 194-88', ex Oberthür coll., Brit. Mus. 1927–3 (specimen register no. BMNH(E) 229245). One paratype male in AGKU labelled: Rota Is. South Coast, 2.v.1936, T. Esaki. Nine paratype males and two paratype females in AGKU labelled: Rota, Tatacho-Sonson, 8.ii.1936, T. Esaki. One paratype male and two paratype females in AGKU: labelled: Rota, Teteto- Tatacho-Sonson, 5.xi.1937, T. Esaki.

Comments

This species closely resembles *A. paulina*, but is distinguishable from the latter by its smaller size (male forewing length not known to exceed 27.0 mm), more sharply pointed forewing apex, the distinct forewing postdiscal black band present from costa to cell M_3 on both wing surfaces of the male, and its shorter uncus with better developed dorsal ridge.

This butterfly has not been collected or recorded, as far as we are aware, since 1937, and could be extinct. Fukuda & Nicho (2001) did not encounter this species in the highly degraded environments of Guam during February and November 2000, and did not find evidence of further records of it from Guam since Swezey's fieldwork of 1936 (Swezey, 1942). Asou (2000) failed to find *A. mariana* on Saipan or Managaha during a visit in 1998. Although a small white butterfly is very likely to be passed over as a common species of little interest, this insect should be sought, especially on Saipan and Rota.

Appias (Catophaga) mata (Kheil, 1884)

Kheil's albatross (Figs 10, 20R–T, 22L)

Pieris mata Kheil, 1884: 34, pl. 4, fig. 31.

Diagnosis

Male. (Figs 20R, 22L). Forewing somewhat obtuse at apex. Upperside ground colour bluish-grey. Forewing usually with free dark spot in cell M_3 . Hindwing without oval sex-patch. Genitalia (Fig. 10): uncus spatula-shaped viewed dorsally, blunt-ended, with dorsal ridge well developed. Valva broad and rounded posteriorly, with a thick and arched interior process directed dorsolaterally. Phallus thick and strongly arched dorsally, with elongate coecum bearing a dorsal ridge; broadened basal prong shorter than coecum; common stem of coecum and basal prong well developed.

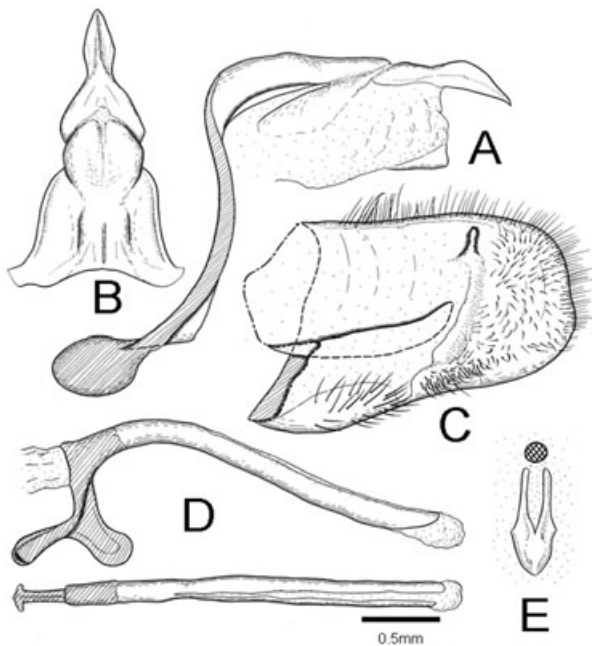


Fig. 10. Male genitalia of *Appias (Catophaga) mata* (Indonesia: Sipora; BLKU OY genitalia preparation no.1187). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Female. (Fig. 20S, T). Apparently dimorphic. Upperside ground colour pale yellow, but almost whitish in forewing, or pale bluish, somewhat male-like (not clearly evident in Fig. 20T). Forewing black apical area with four submarginal whitish spots in cells R_2 and R_5-M_2 , that in cell M_2 almost obsolete; black-dusted basal area with distal margin almost perpendicular to posterior margin of forewing.

Distribution

Known only from Nias and Sipora (Mentawai Islands). The two subspecies, *A. m. mata* (Nias) and *A. m. caeca* (Sipora) are very distinct, and it is possible they represent separate species.

Foodplants

Unknown. At least two species of *Drypetes* have been recorded from Siberut (Hadi *et al.*, 2009).

Appias (Catophaga) galba (Wallace, 1867) stat.rev.

Wallace's albatross (Figs 11, 12A–C, 21A–F)

Tachyris galba Wallace, 1867: 378.

In all recent publications known to us (e.g. Yata, 1981; D'Abbrera, 1982, Osada *et al.*, 1999), and for many years previously (e.g. Talbot, 1939), *galba* has been treated as a

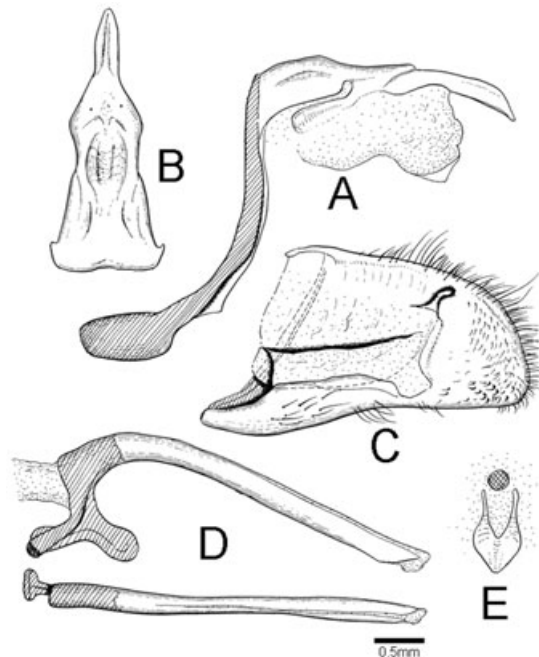


Fig. 11. Male genitalia of *Appias (Catophaga) galba* (India: Khasi Hills; NHM genitalia preparation no. 4603). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

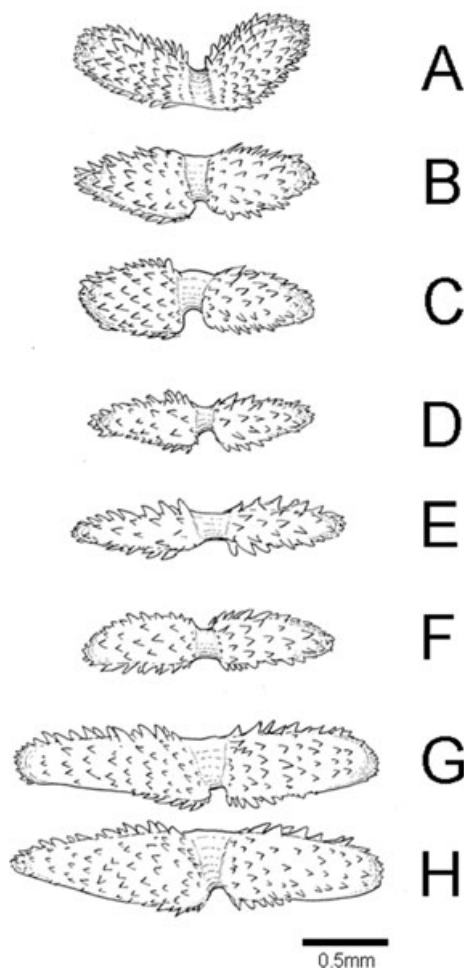


Fig. 12. Female genitalia (signum) of three *Appias* (*Catophaga*) species, posterior view. (A–C) *A. galba* (A, N.W. Myanmar: BLKU OY genitalia preparation no. 1190; B, India: Kashi Hills: NHM genitalia preparation no. 4604; C, Hainan, BLKU OY genitalia preparation no. 1191); (D–F) *A. nero* (D, Malay Peninsular; BLKU OY genitalia preparation no. 1192; E, Philippines: Palawan, NHM genitalia preparation no. 4613; F, Indonesia: Bawean, NHM genitalia preparation no. 4609); (G, H) *A. zarinda* (G, Indonesia: Sulawesi; BLKU OY genitalia preparation no. 1193; H, Indonesia: Sulawesi; BLKU OY genitalia preparation no. 1194). Scale bar = 0.5 mm.

subspecies of *A. nero*. As demonstrated by our present study, *A. galba* is a distinct species.

Diagnosis

Male. (Figs 21A–C). Forewing somewhat falcate and distinctly acute at apex. On upperside black distal border and a series of postdiscal black spots usually present. Hindwing fairly pointed near tornus. Genitalia (Fig. 11): uncus nib-shaped viewed dorsally with its apex somewhat pointed, and not so abruptly curved ventrally as *nero*. Valva somewhat narrowed posteroventrally with a thick and arched interior process

dorsolaterally. Phallus weakly arched dorsally, with coecum usually having a dorsal ridge; basal prong as long as coecum.

Female. (Fig. 21D–F). Forewing somewhat falcate and distinctly acute at apex. On upperside forewing black distal border and postdiscal black zigzag band present. Hindwing fairly pointed at tornus. Upperside ground colour dull orange-red. Forewing black apical area usually with seven submarginal orange spots in cells R_2 – CuA_1 , representing the ground colour between the dark distal border and the dark postdiscal band; forewing upperside without any dark discocellular marking. Signum relatively broad, with many spines (Fig. 12A–C).

Comment

This species closely resembles *A. nero*, but is easily distinguished from the latter by the falcate forewing with distinctly acute apex, a series of postdiscal black spots on forewing upperside in the male, the distinctly angled hindwing near the tornus, and in the female the absence of any infuscation of the forewing discocellular veins, and broader signum. Some *galba* males have a slightly ‘two-toned’ look to the hindwing, with the base deeper red than the remainder, which is more orange and becomes yellowish towards the tornus (Fig. 21B), and there can be a suggestion of this two-tone effect on the forewing in some females (e.g. Fig. 21F). We have not observed this phenotype in *A. nero* or *A. zarinda*.

Distribution

Endemic to northern India (Sikkim), Burma, northern Thailand, northern Indochina and Hainan, including Laos (Osada *et al.*, 1999: 202), and also recorded from Guangxi, China (Chou, 1994 vol. 1: 243). Appears to be parapatric to *A. nero*.

Foodplants

Apparently unknown.

Appias (*Catophaga*) *nero* (Fabricius, 1793)

Orange albatross (Figs 12D–F, 13, 21G–T, 22 A–D)

Papilio nero Fabricius, 1793: 153.

Papilio nero was based on material in the British Museum, but without indication of origin. To stabilize current usage (due to Butler, 1870b), a neotype has been selected from West Java (Appendix 2).

Diagnosis

Male. (Figs 21G, I, O, S; 22A, B). Forewing somewhat acute at apex. Upperside ground colour orange-red, but occasionally straw-coloured (Fig. 21T), or brown in one unique example (Fig. 22A). Forewing upperside of male usually

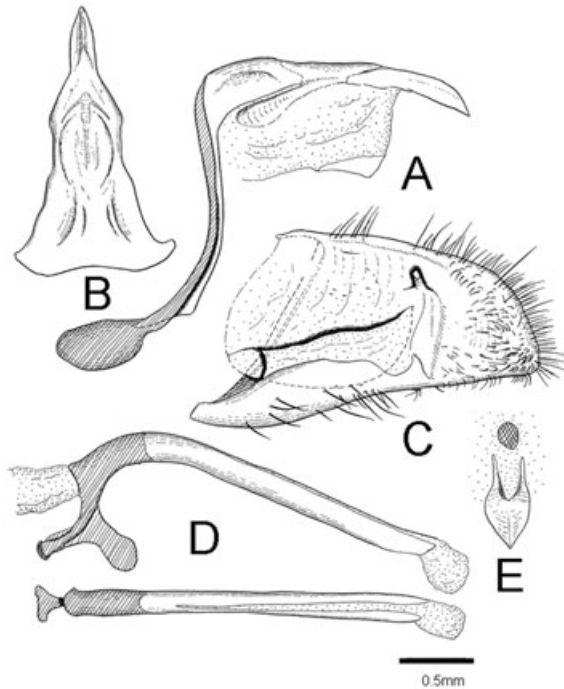


Fig. 13. Male genitalia of *Appias (Catophaga) nero* (Indonesia: Tanah Djampea; NHM genitalia preparation no. 4600). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

narrowly margined with black. Genitalia (Fig. 13): uncus nib-shaped viewed dorsally with its apex sharply pointed. Valva gradually narrowed posteroventrally, usually weakly produced apically, with a thick and arched interior process dorsolaterally. Phallus weakly arched dorsally, with coecum usually lacking a dorsal ridge; basal prong as long as coecum.

Female. (Figs 21H, J–N, P–R; 22C, D). Upperside ground colour usually dull orange red, but sometimes white to yellow; the main Philippine races do not have orange females, only white/yellow. Forewing black apical area usually with seven submarginal light spots in cells R_2 and R_5 – CuA_2 , those in cells R_2 , M_2 and CuA_1 often reduced; forewing upperside with discocellular marking represented by a short black bar; dark basal area with distal margin usually diffuse, but more distinct and often almost perpendicular to posterior margin of forewing in main Philippine races. Signum narrow, with many spines (Fig. 12D–F).

Distribution

Widely distributed in Sundaland and the Philippines, but replaced in the Sulawesi region by *A. zarinda*. According to Corbet & Pendlebury (1992: 90), the female is rarely encountered in the Malay Peninsula, occurring mainly in forests above approximately 600 m. Judging by museum

collections, females are more readily encountered in populations occurring in Wallacea, most notably the highly polymorphic race found on Palawan. In this context it may be notable that Jumalon (1970) recorded *A. n. palawanica* from human faeces used as bait. It seems possible that females of the more eastern, often highly polymorphic subspecies differ in their behaviour – and the same may be true for *A. zarinda* as well.

Foodplants

Capparis (Capparaceae) and *Drypetes* (Putranjivaceae) (Robinson *et al.*, 2001). Dupont & Scheepmaker (1936: 46) recorded *Drypetes macrophylla* and, apparently, *Pithecellobium lobatum* (as '*Pithecolobium*': Fabaceae) as foodplants in Java – but the latter is unconfirmed; Roepke (1935: 64) gave *D. macrophylla* only, based on earlier work by Leefmans.

Appias (Catophaga) zarinda (Boisduval, 1836)

Flame albatross (Figs 12G, H, 14, 22E–H)

Pieris zarinda Boisduval, 1836: 486, pl. 18, fig. 4.

Diagnosis

Male. (Fig. 22E). Forewing elongate apically and sharply pointed at apex. Upperside ground colour orange-red. Upperside of wings without markings. Genitalia (Fig. 14): uncus

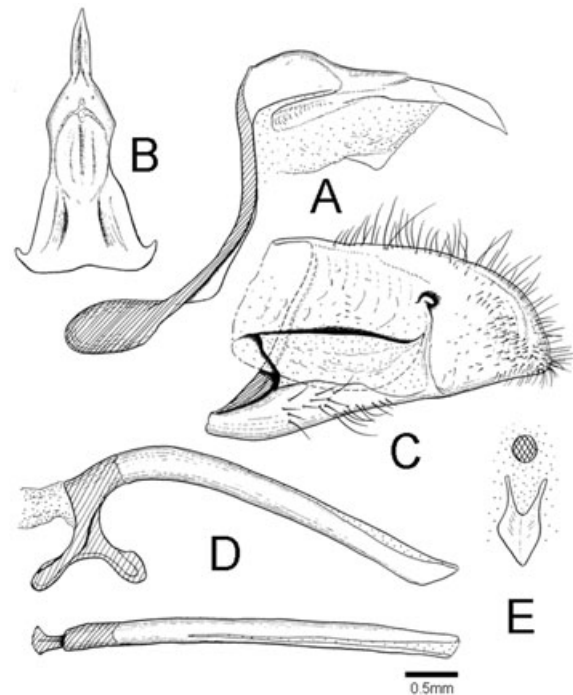


Fig. 14. Male genitalia of *Appias (Catophaga) zarinda* (Indonesia: south Sulawesi; NHM genitalia preparation no. 4619). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

narrow and nib-shaped viewed dorsally, with apex sharply pointed. Valva gradually narrowed posteroventrally, produced apically, with a thick and arched interior process directed dorsolaterally. Phallus moderately arched dorsally; coecum usually with a dorsal ridge; basal prong as long as coecum.

Female. (Fig. 22F–H). Upperside heavily marked with black; ground colour dull orange-red, white or creamish-yellow. Forewing usually with seven pale submarginal spots in cells R_2 and R_5 – CuA_2 , those in cells M_2 and CuA_1 reduced; hindwing median light band with both margins sharply defined; black basal area with distal margin somewhat oblique. Genitalia: signum large, asymmetrical, with left-hand end more extended, with many spines (Fig. 12G, H).

Comment

Recognized as a species by Yata (1981), *A. zarinda* closely resembles *A. nero*, but is readily distinguished from the male of the latter by the sharply pointed forewing apex, upperside of wings without markings and veins not black-dusted, and in the female by the larger, asymmetrical signum.

Distribution

Found only on Sulawesi and some adjacent islands, Sula, and Buru (Peggie *et al.*, 1995; Vane-Wright & de Jong, 2003).

Foodplants

Apparently unknown.

Appias (*Catophaga*) *placidia* (Stoll, 1790)

Chocolate albatross (Figs 15, 22I–K)

Papilio placidia Stoll, 1790: 133, pl. 28, figs 4,4c.

Diagnosis

Male. (Fig. 22I). Forewing somewhat acute at apex. Upperside ground colour dark brown, except for a very fine golden marginal fringe that does not occur in other *Catophaga* species, including *nero*. Hindwing with dark, oval sex-patch. Genitalia (Fig. 15): uncus somewhat broad and depressed, and spatula-shaped viewed dorsally, with apex bluntly pointed. Valva broad and rounded posteriorly, distinctly incurved ventromedially, with a thick and arched interior process, directed dorsolaterally. Phallus moderately arched dorsally with coecum bearing a dorsal ridge; somewhat broadened basal prong as long as coecum.

Female. (Fig. 22J, K). Upperside ground colour dark brown. Forewing usually with seven pale submarginal spots in cells R_2 and R_5 – CuA_2 , those in cells M_2 , CuA_1 and CuA_2 often reduced. Ground colour beneath obscure greenish-white, or yellowish.

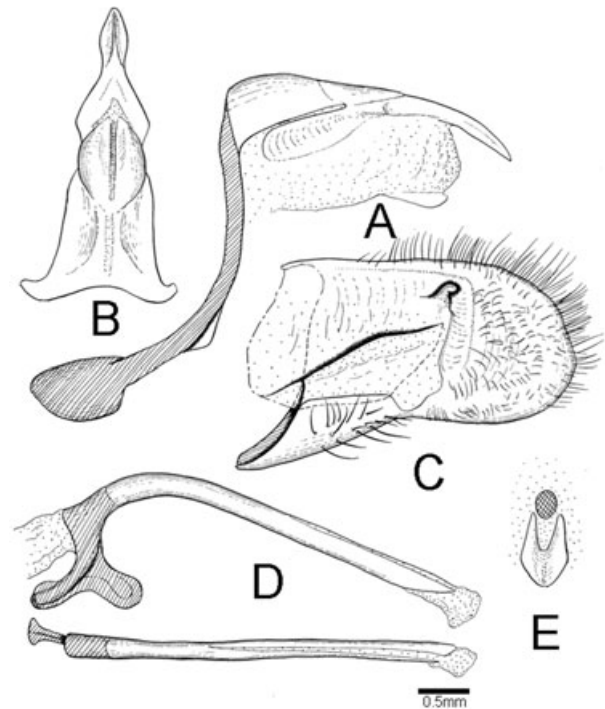


Fig. 15. Male genitalia of *Appias* (*Catophaga*) *placidia* (Indonesia: Seram; NHM genitalia preparation no. 4614). (A) Ring, lateral views; (B) uncus, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Distribution

Restricted to North and Central Maluku (but not found on Kep. Sula or Buru) (Peggie *et al.*, 1995).

Foodplants

Apparently unknown.

Appias (*Catophaga*) *clementina* (Felder, 1860)

Clementine's albatross (Figs 16, 22M, N)

Pieris clementina C. Felder, 1860: 448.

Diagnosis

Male. (Fig. 22M). Forewing length less than 30 mm. Forewing somewhat acute at apex. Upperside ground colour greyish-blue, underside yellowish-grey. Male usually with dark free spot in cell M_2 . Forewing usually with seven light submarginal spots in cells R_2 and R_5 – CuA_2 , with that in cell M_2 often reduced. Hindwing with pale oval sex-patch. Genitalia (Fig. 16): uncus somewhat broad and spatula-shaped viewed dorsally, with its apex bluntly pointed. Valva broad and rounded posteriorly, distinctly incurved ventromedially, with a thick and arched interior process, directed dorsolaterally.

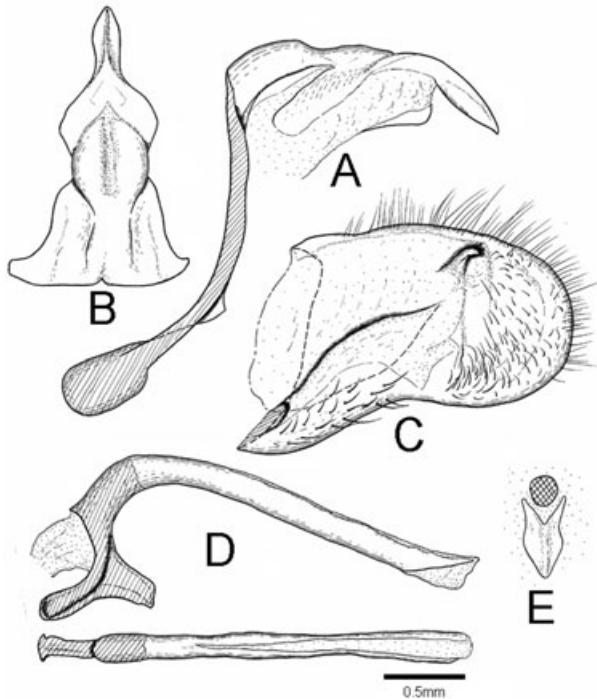


Fig. 16. Male genitalia of *Appias (Catophaga) clementina* (Indonesia: Tanimbar; BLKU OY genitalia preparation no. 1185). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Phallus fairly arched dorsally with coecum lacking a dorsal ridge; somewhat broadened basal prong as long as coecum.

Female. (Fig. 22N). Forewing length less than 28 mm. Upperside ground colour greyish-blue, relieved by a white postdiscal band on both wings. Forewing usually with seven pale submarginal spots in cells R_2 and R_5 – CuA_2 , that in cell M_2 often reduced. Underside greenish-blue basally.

Distribution

Alor, Timor, Wetar, Roma, Moa, Damar, Teun, Sermata, Babar, Tanimbar (Selaru, Yamdena, Larat, Maru) (Rawlins, 2007).

Foodplants

Apparently unknown.

Appias (Catophaga) celestina (Boisduval, 1832)

Blue albatross (Figs 17, 22O–Q)

Pieris celestina Boisduval, 1832: 46.

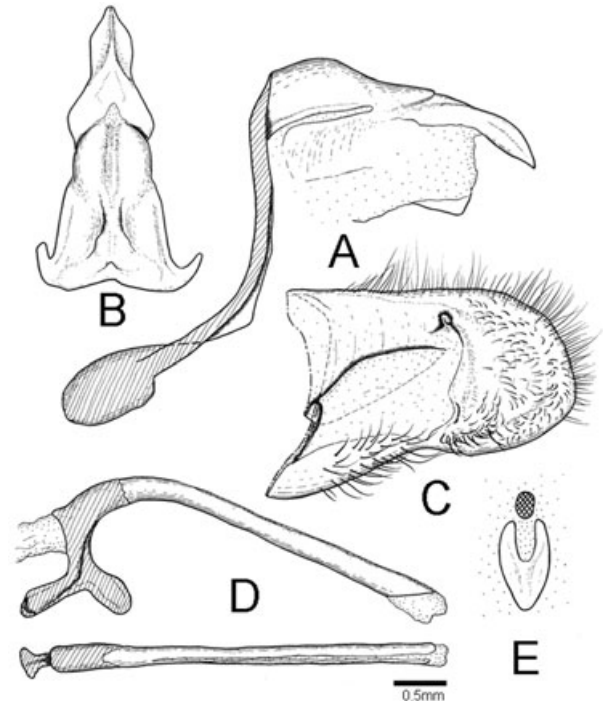


Fig. 17. Male genitalia of *Appias (Catophaga) celestina* (Indonesia: Waigeo; NHM genitalia preparation no. 4616). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

Diagnosis

Male. (Fig. 22O, P). Forewing somewhat acute at apex. Upperside ground colour greyish-blue, with curvilinear row of largely connected dark postdiscal spots running from base of cell R_5 to margin of CuA_1 . Hindwing with oval sex-patch. Genitalia (Fig. 17): uncus very broad and spatula-shaped viewed dorsally, with apex bluntly pointed. Valva broad and rounded posteriorly, distinctly incurved ventromedially, with a thick and arched interior process directed dorsolaterally. Phallus moderately arched dorsally; coecum bearing a weak dorsal ridge; somewhat broadened basal prong as long as coecum; common stem of coecum and basal prong well developed.

Female. (Fig. 22Q, R). Upperside ground colour whitish, with some greyish-blue scales along inner margin of hindwing dark margin and basally, or yellow. Forewing usually with six pale submarginal spots in cells R_2 and R_5 – CuA_1 , those in cells M_2 and CuA_1 often reduced; darkened basal area with distal margin oblique.

Distribution

Found in New Guinea, Aru, Kai, Bismarck Archipelago and Bougainville (but not in the Solomon Islands: Tennent, 2002), and in the rainforest at Iron Range, Cape York Peninsula,

Queensland (one male in good condition recently recorded: Weir *et al.*, 2005).

Foodplants

Unknown.

***Appias* (*Catophaga*) *melania* (Fabricius, 1775)**

Grey albatross (Figs 18, 22S, T)

Papilio melania Fabricius, 1775: 475.

Diagnosis

Male. (Fig. 22S). Forewing somewhat elongate and somewhat acute at apex. Upperside ground colour grey-blue, with more whitish postdiscal area extending into apex of discal cell. Forewing with an oblique black band running from costa to origin of vein M_1 to tip of CuA_1 . Forewing black apical area usually with six light submarginal spots in cells R_2 and R_5-CuA_1 , that in cell CuA_1 often obsolete. Hindwing with pale oval sex-patch. Underside forewing with an extensive orange-yellow

streak occupying anterior half of discal cell; hindwing extensively brownish, similar in colour to underside forewing apex. Genitalia (Fig. 18): uncus somewhat broad and spatula-shaped viewed dorsally, bluntly pointed apically, with dorsal ridge well developed. Valva broad and rounded posteriorly, distinctly incurved ventromedially, with a thick and arched interior process, directed dorsolaterally. Phallus strongly arched dorsally; coecum with a dorsal ridge; somewhat broadened basal prong as long as coecum.

Female. (Fig. 22T). General features similar to male, but ground colour paler and black areas broader.

Distribution

Restricted to a small upland area of Queensland, north-eastern Australia, from the latitude of Cooktown to the southern end of the Paluma Range, inland from Townsville. Sometimes migrates to the coast at Townsville or even further south where, however, it does not breed (Dunn & Dunn, 1991: 55; Braby, 2000: 327).

Foodplants

Drypetes (Putranjivaceae) (Braby, 2000).

Key to species of *Appias* (*Catophaga*)

Note: Males of the Appiadina have a conspicuous apicoventral abdominal hair-tuft. However, females of *Catophaga* have a similar tuft, and this character cannot readily be used to separate the sexes of species belonging to this subgenus.

- 1. Male: forewing apex relatively pointed, wings usually less heavily patterned with black 2
 - Female: forewing apex relatively rounded, wings more heavily patterned with black (note: female of *aurosa* unknown) 16
- 2. (Males) Wings extensively reddish-orange, rarely straw-coloured (*nero* group) 3
 - (Males) Wings never reddish-orange 5
- 3. Hindwing distinctly angled near tornus; upperside forewing apex darkened, usually with a row of dark postdiscal spots that form a weak band running midway between end of discal cell and wing apex; distal sections of hindwing veins darkened *galba* (Wallace, 1867)
 - Hindwing not distinctly angled near tornus 4
- 4. Forewing sharply pointed at apex; upperside of forewing without black veins *zarinda* (Boisduval, 1836)
 - Forewing not sharply pointed at apex; upperside of forewing usually with black veins (not in *A. nero flavius* from the Turtle Islands, Philippines); upperside sometimes straw coloured *nero* (Fabricius, 1793)
- 5. Wings dark brown or bluish (at least hindwings) 6
 - Wings not brown or bluish 10

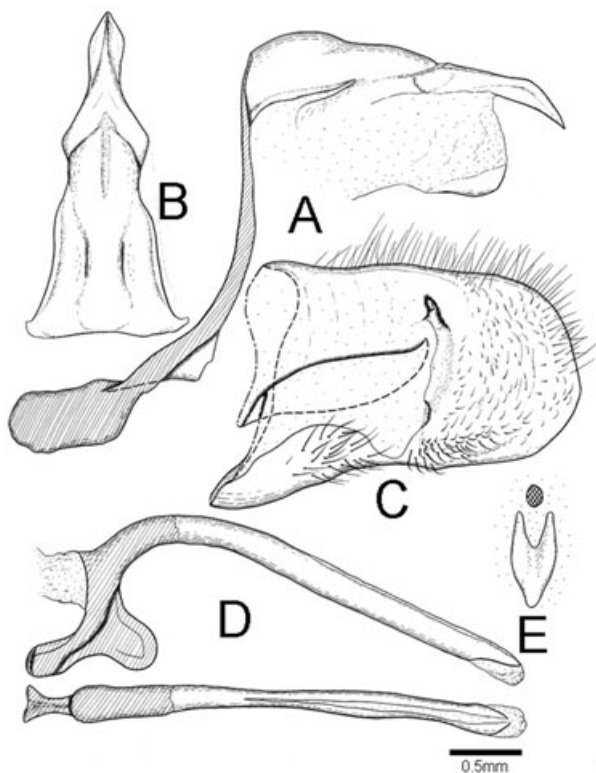


Fig. 18. Male genitalia of *Appias* (*Catophaga*) *melania* (Australia: Queensland; BLKU OY genitalia preparation no. 722). (A) Ring, lateral views; (B) dorsum, dorsal views; (C) right valva, inner view; (D) phallus, lateral and dorsal views; (E) juxta, anal view. Scale bar = 0.5 mm.

6. Upperside ground colour dark chocolate brown
 *placidia* (Stoll, 1790)
 – Upperside ground colour bluish or bluish-grey (at least on hindwings) 7
7. Hindwing without oval whitish sex-patch; forewing usually with free dark spot in cell M₃ (Mentawai Islands only)
 *mata* (Kheil, 1884)
 – Hindwing with oval whitish sex-patch on upperside (sometimes indistinct); forewing without free dark spot in cell M₃ 8
8. Small species (forewing length less than 30 mm) (eastern Lesser Sunda islands only) *clementina* (Felder, 1860)
 – Larger species (forewing length usually more than 30 mm) 9
9. Upperside forewing with apex of discal cell and extensive postdiscal area whitish, with a broad postdiscal curvilinear dark band that extends to costa; underside of forewing discal cell yellowish-orange at base *melania* (Fabricius, 1775)
 – Upperside forewing without any extensive white area, almost entirely blue except for darkened apex and the often incomplete, narrow, dark postdiscal curvilinear band, which does not reach costa; underside of forewing discal cell yellowish or grey at base *celestina* (Boisduval, 1832)
10. Ground colour of wings bright golden-yellow
 *aurosa* Yata & Vane-Wright **sp.n.**
 – Ground colour of wings whitish, at most slightly yellowish; rarely suffused grey 11
11. Both wings with distinct markings similar to typical female form of *paulina* (i.e. a more or less broad black border present on the hindwing (Fig. 19G), although sometimes indistinct) (peninsular India only) *wardii* (Moore, 1884)
 – Hindwings with a few black spots along margin at most (Fig. 19B), thus not like typical female form of *paulina* ... 12
12. Small species (forewing length less than 26.0 mm); forewing underside with curvilinear postdiscal black band running from costa to cell M₃, and not reduced to isolated spots (Marianas only) *mariana* Yata & Chainey **sp.n.**
 – Larger species (forewing length greater than 27.0 mm); forewing underside without continuous black postdiscal band from costa to cell M₃; if band present then reduced to isolated spots, or fails to reach costa 13
13. Both wings without upperside markings, except in some cases a black marginal border to forewing, including apex 14
 – Both wings usually with more extensive dark markings (sometimes reduced to a free black spot in cell M₃) on forewing upperside; forewing apex not distinctly acute, somewhat blunt *paulina* (Cramer, 1777)
14. Forewing apex distinctly acute, posterior margin almost straight *albina* (Boisduval, 1836)
 – Forewing apex not distinctly acute but often falcate, with outer margin concave 15
15. Forewing entirely white except for distinct black scales narrowly along margin; upperside ground colour lustrous white (eastern species: New Caledonia to Samoa)
 *athama* (Blanchard, 1848)
 – Forewing often with black or grey scales at apex; upperside ground colour matt white, without lustre (Sri Lanka only) ...
 *galene* (Felder & Felder, 1865)
16. (Females) Upperside ground colour extensively chocolate-brown *placidia* (Stoll, 1790)
 – (Females) Upperside not chocolate-brown; ground colour white, yellow, red or bluish-grey, or even almost dark brown or black 17
17. Small species (forewing length typically less than 28 mm), with extensive bluish-grey areas on upperside and a rather narrow band postdiscal white band (Fig. 22N); underside largely brown, but with base of forewing greenish
 *clementina* (Felder, 1860)
 – Not so; if extensively bluish-grey, then forewing underside orange at base 18
18. Hindwing upperside almost entirely blue-grey, contrasting with discal area of forewing, which is extensively white; forewing underside orange at base; hindwing underside mainly brown *melania* (Fabricius, 1775)
 – Hindwing not contrasting with forewing in this way; underside of hindwing not largely brown or underside of forewing not orange at base 19
19. Hindwing white or yellow, without any dark scales at base, but with a broad well-defined and even black posterior band, narrowly edged with white or yellow triangles on margin (Fig. 19R, S) *athama* (Blanchard, 1848)
 – Hindwing not so; if with broad black posterior band, the band is more diffusely defined, and lacks the narrow pale margin 20
20. Hindwing largely dark brownish-black, with a rather narrow discal band and a row of distinct submarginal spots, these areas being either orange-red, yellow or white; the outer margin of the discal band passes through the apex of the discal cell (Fig. 22F, G, H) *zarinda* (Boisduval, 1836)
 – Hindwing not so; if both band and submarginal spots present, then outer margin of the postdiscal band passes well beyond the apex of cell, and the submarginal spots are less well defined 21
21. Upperside ground colour extensively orange or red; if white or yellow, then vein at apex of forewing cell marked with a line of black scales (Figs 21D–F, H, J–N, P–R, 22C) 22
 – Upperside ground colour white or yellow (occasionally largely black), without a line of black scales at the apex of the forewing discal cell 23
22. Forewing acutely pointed at apex; hindwing distinctly angled at tornus; upperside ground colour always dull orange-red; postdiscal dark band on upperside forewing always clearly separate from end of discal cell, never extending to or touching it (Fig. 21D–F) *galba* (Wallace, 1867)
 – Forewing only bluntly pointed at apex and hindwing only bluntly angled at tornus; upperside ground colour not always dull orange-red, sometimes white or yellow; postdiscal dark band on upperside forewing, if distinguishable, always extends to or touches end of discal cell (Figs 21D–F, H, J–N, P–R, 22C) *nero* (Fabricius, 1793)

23. Forewing black apical area with a whitish or yellowish spot in cell R₂, although this may be very small or only visible ventrally in occasional examples of *A. paulina* with very broad black margins (notably from Timor and Sula), but in these cases there is a distinct line of bluish-grey scales along the anterior edge of the black margins on the hindwing, or the black is expanded to leave only a narrow white band 24
 – Forewing black apical area without a whitish or yellowish spot in cell R₂ 29
24. Forewing with a large well-defined white or yellow spot in cell M₃, contrasting with a very small spot in cell M₂; hindwing white or yellow, with a broad black margin that is edged anteriorly with an area of bluish-grey scales
 *celestina* (Boisduval, 1836)
 – Forewing black apical area without a whitish or yellowish spot in cell M₃; hindwing often without an area of bluish-grey scales 25
25. Small species (forewing length usually less than 26.0 mm); forewing underside with black postdiscal band clearly reaching costa, but not touching the apex of the discal cell (although there are diffuse blackish scales in this area) (Fig. 20O–Q) (Marianas only) *mariana* Yata & Chainey **sp.n.**
 – Larger species (forewing length usually more than 27.0 mm); forewing underside with black postdiscal band often not reaching costa, but does include at least the anterior apex of the discal cell (not from Marianas) 26
26. Forewing black apical area with two or three submarginal pale spots in cells R₂, R₅ and M₁ (peninsular India only)
 *wardii* (Moore, 1884)
 – Forewing black apical area usually with four or five submarginal whitish spots in cells R₂, R₅ and M₁–M₃ 27
27. Forewing underside with black line that curves down to vein M₃, where it expands into a pronounced spot with a straight posterior margin; the line then turns to the wing margin at 90°, so that the outer margin is distinctly step-like in appearance (Figs 19J–P, 20T); hindwing with bluish-grey scales either extensive or absent 28
 – Forewing underside with outer margin of black line not step-like at M₃, i.e. although somewhat jagged in outline, the posterior margin curves gently round to the wing margin (Fig. 20C–E, G–I, K); hindwing upperside often with area of bluish-grey scales along the anterior edge of the black posterior margin (e.g. Fig. 20G); occasionally wings largely black and with more extensive bluish-grey area on hindwing (e.g. Fig. 20I) (widespread, but not found in Mentawais)
 *paulina* (Cramer, 1777)
28. Upperside ground colour somewhat male-like, at least partly bluish-grey (Mentawai Islands only)
 *mata* (Kheil, 1884)
 – Upperside ground colour either white or yellow, usually without bluish-grey (widespread, but not recorded from Mentawais)
 *albina* (Boisduval, 1836) (rare examples only)
29. Forewing black apical area with three submarginal pale spots in cells R₅, M₁ and M₂ (Sri Lanka only)
 *galene* (Felder & Felder, 1865)

- Forewing black apical area usually with four (but something only three) submarginal pale spots in cells R₅ and M₁–M₃ (widespread, including Sri Lanka)
 *albina* (Boisduval, 1836) (most examples)

Discussion

Species status and interrelationships

According to Corbet & Pendlebury (1992: 89), the species of *Appias* are difficult to separate by male genitalia, and they note no differences at all between three *Appias* (*Catophaga*) dealt with here: *nero*, *albina* and *paulina* (these comments are probably based on dissections made by George Talbot in the 1930s, working in support of Corbet). However, the investigations of Yata (1981), and the many dissections made in Yata's laboratory during this study, reveal small but apparently constant differences in form between the male genitalia of all 15 species recognized here. Moreover, these differences are sufficient to establish the three clusters of species proposed: the *paulina* complex, the *nero* group and the *melania* series. However, there seems little prospect that these small differences can be interpreted further, e.g. to infer monophyly of any of these subgroups. It is interesting to speculate that the rather high 'phylogenetic inertia' evident in the male genitalia of these butterflies might indicate that, in this group, sexual selection is acting strongly on male colour pattern, and only weakly or not at all on male genital morphology [see Song & Bucheli (2009) for an interesting assessment of the phylogenetic value of male genitalia characters relative to nongenital characters].

Given the extensive individual variation, polymorphism and geographical variation of many of the species of *Appias* (*Catophaga*), coupled with their intrinsic biological interest, the application of molecular characters to investigate the subgenus would be very desirable. This would permit the status of many populations over which doubt remains to be re-assessed, such as the validity of separating *A. mata* from *A. paulina*. Equally important, molecular data will probably prove invaluable in the quest to produce a robust cladistic analysis, necessary to gain further insight into the sequence of colour pattern and hostplant changes that appear to have affected these species during their evolution (see below and File S1).

Distribution

The subgenus *Appias* (*Catophaga*) occurs across almost the whole of the Indo-Australian tropics, from Sri Lanka through extreme southern China to the Marianas, the Malay Archipelago to north-eastern Australia, and island groups of the West Pacific, from New Caledonia to Samoa (Figs 23, 24). Subgenus *Appias* (*Catophaga*) is not represented in north-western India, Pakistan or, rather curiously, beyond Bougainville in the main Solomons chain, where only one



Fig. 19. Adult *Appias* (*Catophaga*) butterflies (halved: left hand upperside/right hand underside; all in BMNH unless otherwise stated). (A) *A. aurosa* Yata & Vane-Wright sp.n., male, whole upperside (Sulawesi: Macassar; #229202; forewing length 36.2 mm, holotype) (see also Fig. 20A); (B) *A. mariana* Yata & Chainey sp.n., male, whole upperside (Guam; #229237; forewing length 24.5 mm, holotype) (see also Fig. 20M); (C) *A. mariana* Yata & Chainey, sp.n., yellow female, whole upperside (Guam: Machanao; Bishop Museum; forewing length 25.5 mm, paratype) (see also Fig. 20P); (D) *A. galene*, male (Sri Lanka: Kandy; #665170; forewing length 30.0 mm); (E) *A. galene*, yellow female (Sri Lanka: #665171; forewing length 30.0 mm); (F) *A. galene*, white female (Sri Lanka: Newara Eliya; #665172; forewing length 28.3 mm); (G) *A. wardii*, male (southern India: North Kanara; #665191; forewing length 35.0 mm); (H) *A. wardii*, female (southern India: Nilgiris; #665174; forewing length 32.0 mm); (I) *A. albina agatha*, male (Philippines: Mindanao; #665175; forewing length 34.6 mm); (J) *A. albina agatha*, yellow female (Philippines: Mindanao, Davao; #665176; forewing length 27.8 mm); (K) *A. albina agatha*, white female (Philippines: Mindanao, Davao; #665177; forewing length 32.0 mm); (L) *A. albina ambigua*, female (East Timor: Dili; #665180; forewing length 28.0 mm); (M) *A. albina ambigua*, female (Indonesia: Lombok, Sapit; #135780; forewing length 26.3 mm); (N) *A. albina ambigua*, female (Indonesia: Lombok, Sapit; #665179; forewing length 27.8 mm); (O) *A. albina albina*, yellow female (Indonesia: Obi; #665178; forewing length 28.7 mm); (P) *A. a. albina* black female (Sulawesi: Palu; BLKU collection; forewing length 30.0 mm); (Q) *A. athama manaia*, male (Samoa: Upolu, Aleipata; #142269; forewing length 31.0 mm); (R) *A. athama manaia*, female (Samoa: Upolu, #142270; forewing length 29 mm); (S) *A. athama wallacei*, female (New Caledonia; #142268; forewing length 29.1 mm).

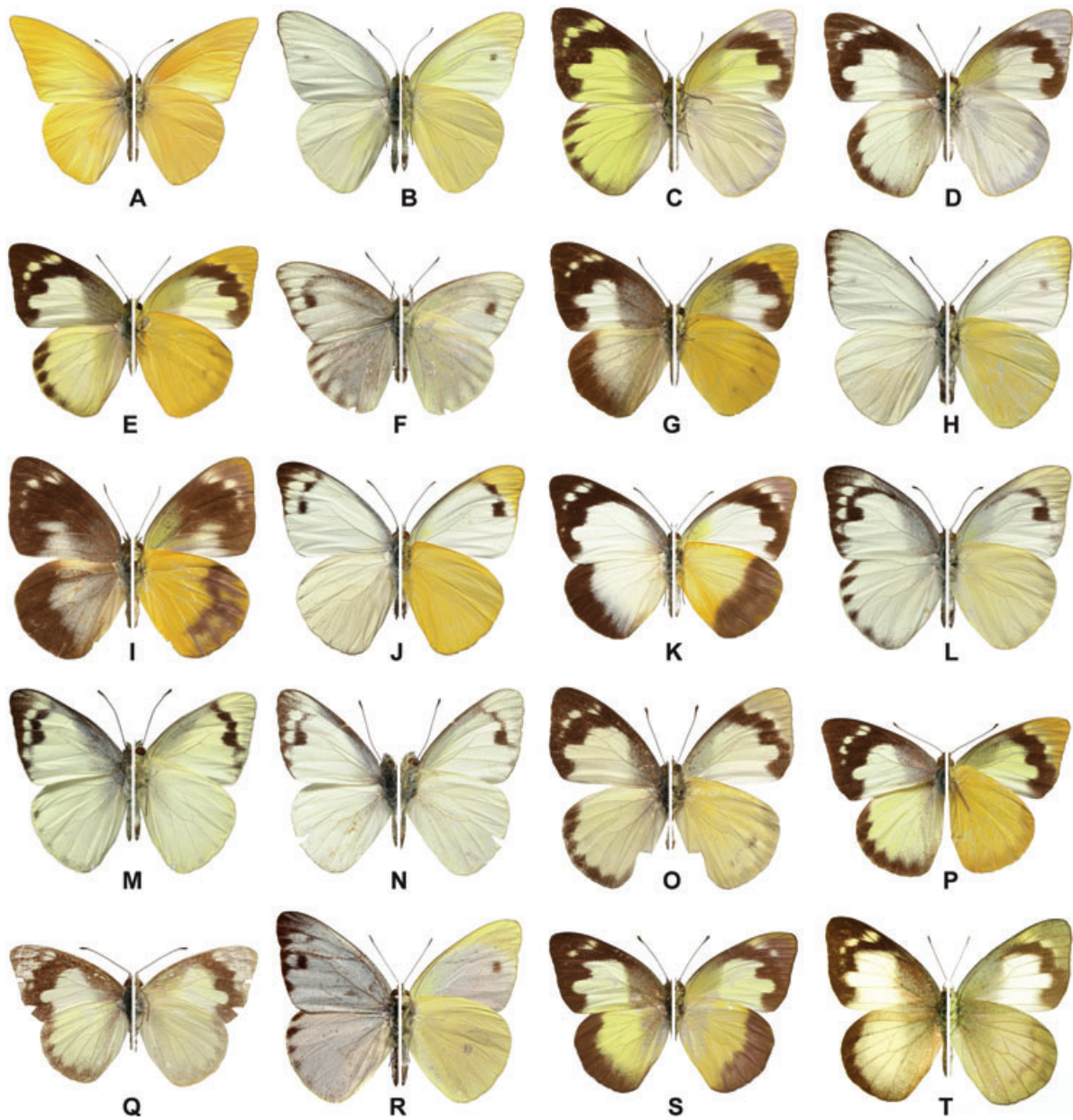


Fig. 20. Adult *Appias* (*Catophaga*) butterflies (halved: left hand upperside/right hand underside; all in BMNH unless otherwise stated). (A) *A. aurosa*, male (Sulawesi: Macassar; #229202; forewing length 36.2 mm) (see also Fig. 19A); (B) *A. paulina galathea*, male (India: Nicobar Is, Car Nicobar; #665185; forewing length 32.3 mm); (C) *A. paulina galathea*, yellow female (India: Nicobar Is, Car Nicobar; #665186; forewing length 32.0 mm); (D) *A. paulina galathea*, white female (India: Nicobar Is, Kondul; #665187; forewing length 31.5 mm); (E) *A. paulina galathea*, piebald female (India: Nicobar Is, Kondul; #665188; forewing length 31.7 mm); (F) *A. paulina grisea*, male (Malaysia: P. Tioman; #665183; forewing length 27.5 mm); (G) *A. paulina grisea* female (Malaysia: Pulau, Tenggel, Trengganu; #665184; forewing length 29.8 mm); (H) *A. paulina sawela*, male (Indonesia: Lombok, Sapit; #229105; forewing length 27.3 mm); (I) *A. paulina sawela*, female (syntype) (Indonesia: Lombok, Sapit; #149947; forewing length 29.0 mm); (J) *A. paulina ega*, male (Australia: Queensland, Cairns; #665181; forewing length 33.0 mm); (K) *A. paulina ega*, female (Australia: Queensland, Mackay; #665182; forewing length 30.5 mm); (L) *A. paulina adamsoni*, male (Thailand: Ban Takum; #665189; forewing length 29.0 mm); (M) *A. mariana*, male (holotype) (Guam: #229237; forewing length 24.5 mm) (see also Fig. 19B); (N) *A. mariana*, male (Saipan: #229242; forewing length 24.5 mm); (O) *A. mariana*, female (Marianas; #229245; forewing length 23.3 mm); (P) *A. mariana*, yellow female (Guam: Tarague; BPBM collection; forewing length 26.5 mm) (see also Fig. 19C); (Q) *A. mariana*, white female (Guam: Machanao; BPBM collection; forewing length 25.5 mm); (R) *A. mata mata*, male (Indonesia: Nias; #665146; forewing length 27.5 mm); (S) *A. ?mata mata*, female (Indonesia: 'Sumatra'; previously identified as *mata*, but identity uncertain; #665196; forewing length 27.0 mm); (T) *A. mata caeca*, female (Indonesia: Sipora; BLKU collection; forewing length 28.0 mm).

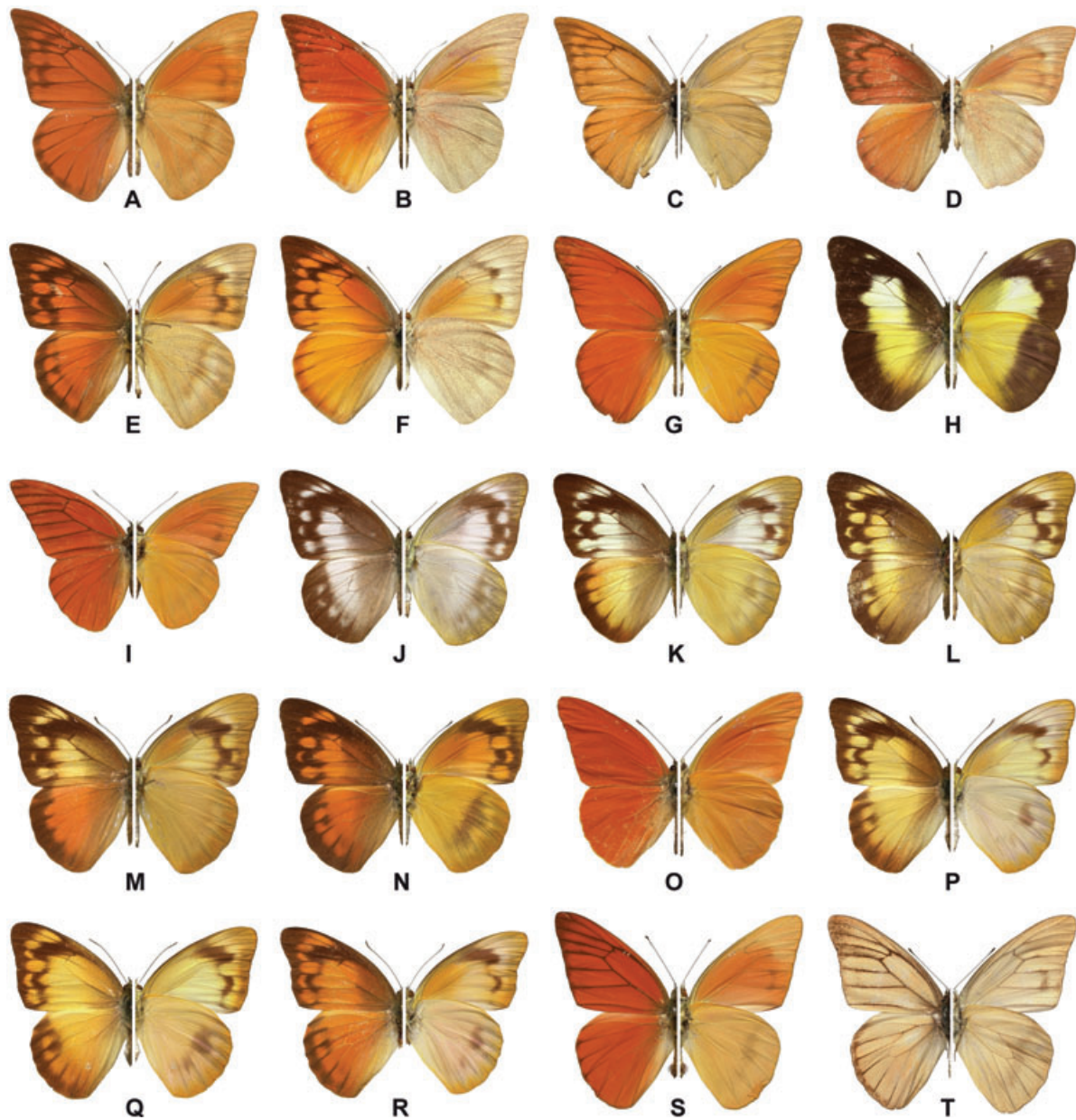


Fig. 21. Adult *Appias* (*Catopha*) butterflies (halved: left hand upperside/right hand underside; all in BMNH). (A) *A. galba*, male (India: Meghalaya, Khasia Hills; #665195; forewing length 38.3 mm); (B) *A. galba*, male (Thailand/Vietnam: Black River, Nam Hou; #665148; forewing length 36.7 mm); (C) *A. galba*, male (Myanmar: Muenghi Hill Tracts, Hukawng Valley; #665149; forewing length 38.0 mm); (D) *A. galba*, female (India: Sikkim; #665151; forewing length 38.9 mm); (E) *A. galba*, female (India: Meghalaya, Cherrapunji; #665194; forewing length 40.5 mm); (F) *A. galba*, female (Vietnam: Laokay, Muong-Khuong; #665152; forewing length 38.0 mm); (G) *A. nero soranus*, male (Philippines: Negros, #665168; forewing length 35.6 mm); (H) *A. nero soranus*, female (Philippines: Negros, Amlan Falls; #665169; forewing length 34.1 mm); (I) *A. nero palawanica*, male (Philippines: Palawan; #665162; forewing length 35.0 mm); (J) *A. nero palawanica*, white female (Philippines: Palawan; #665163; forewing length 30.0 mm); (K) *A. nero palawanica*, piebald female (Philippines: Palawan; #665164; forewing length 35.0 mm); (L) *A. nero palawanica*, yellow female (Philippines: Palawan; #665167; forewing length 34.5 mm); (M) *A. nero palawanica*, orange female (Philippines: Palawan; #665166; forewing length 33.0 mm); (N) *A. nero palawanica*, red female (Philippines: Palawan; #665193; forewing length 34.0 mm); (O) *A. nero flavius* (syntype), male ['N Born' (= Philippines: Taganak); #229186; forewing length 33.5 mm]; (P) *A. nero flavius*, yellow female (Philippines: Taganak; #665159; forewing length 32.0 mm); (Q) *A. nero flavius*, deep yellow female (Philippines: Taganak; #665161; forewing length 34.5 mm); (R) *A. nero flavius*, orange female (Philippines: Taganak; #665160; forewing length 34 mm); (S) *A. nero nero*, male [Malaysia: 'Camp Zor' (?); #665153; forewing length 31.0 mm]; (T) *A. nero nero*, pale 'sufflava' male (Indonesia: Sumatra, Setinjak; #665155; forewing length 36.3 mm).



Fig. 22. Adult *Appias* (*Catophaga*) butterflies (halved: left hand upperside/right hand underside; all in BMNH). (A) *A. nero nero*, male brown aberration (Malaysia: Perak, Tapah Hills; #665154; forewing length 36.8 mm); (B) *A. nero?*, male yellow aberration (Malaysia: Perak; #665158; forewing length 37.0 mm); (C) *A. nero nero*, female (Malaysia: Taiping; #665156; forewing length 33.0 mm); (D) *A. nero nero*, mixed gynandromorph (Malaysia: Cameron Highlands; #665157; forewing length 36.5 mm); (E) *A. zarinda*, male (Indonesia: Sulawesi, Tanah Mateh Pa; #665132; forewing length 42.5 mm); (F) *A. zarinda*, white female (Indonesia: Sulawesi, Minahassa, #665135; forewing length 39.5 mm); (G) *A. zarinda*, pale yellow female (Indonesia: Sulawesi, Manado, #665133; forewing length 40.0 mm); (H) *A. zarinda*, orange female (Indonesia: Sulawesi, Minahassa, Tanggari; #665134; forewing length 39.4 mm); (I) *A. placidia*, male (Indonesia: Obi; #665136; forewing length 33.0 mm); (J) *A. placidia*, grey female (Indonesia: Ceram, Mansela; #665138; forewing length 37.2 mm); (K) *A. placidia*, yellow female (Indonesia: Ceram; #665137; forewing length 35.8 mm); (L) *A. mata caeca*, male (holotype) (Indonesia: Mentawi Is, Sipora; #142295; forewing length 29.6 mm); (M) *A. clementina*, male (Indonesia: Tenimber; #665139; forewing length 25.5 mm); (N) *A. clementina*, female (Indonesia: Tenimber; #665140; forewing length 26.7 mm); (O) *A. celestina barea*, male (Indonesia: Aru; #665141; forewing length 37.5 mm); (P) *A. celestina barea*, male (syntype) (Indonesia: Aru; #135576; forewing length 35.0 mm); (Q) *A. celestina barea*, white female (Indonesia: Aru; #665143; forewing length 35.1 mm); (R) *A. celestina barea*, yellow female (Indonesia: Aru; #665142; forewing length 33.3 mm); (S) *A. melania*, male (Australia: Queensland, Kuranda; #665192; forewing length 35.0 mm); (T) *A. melania*, female (Australia: Queensland, Kuranda; #665145; forewing length 33.0 mm).

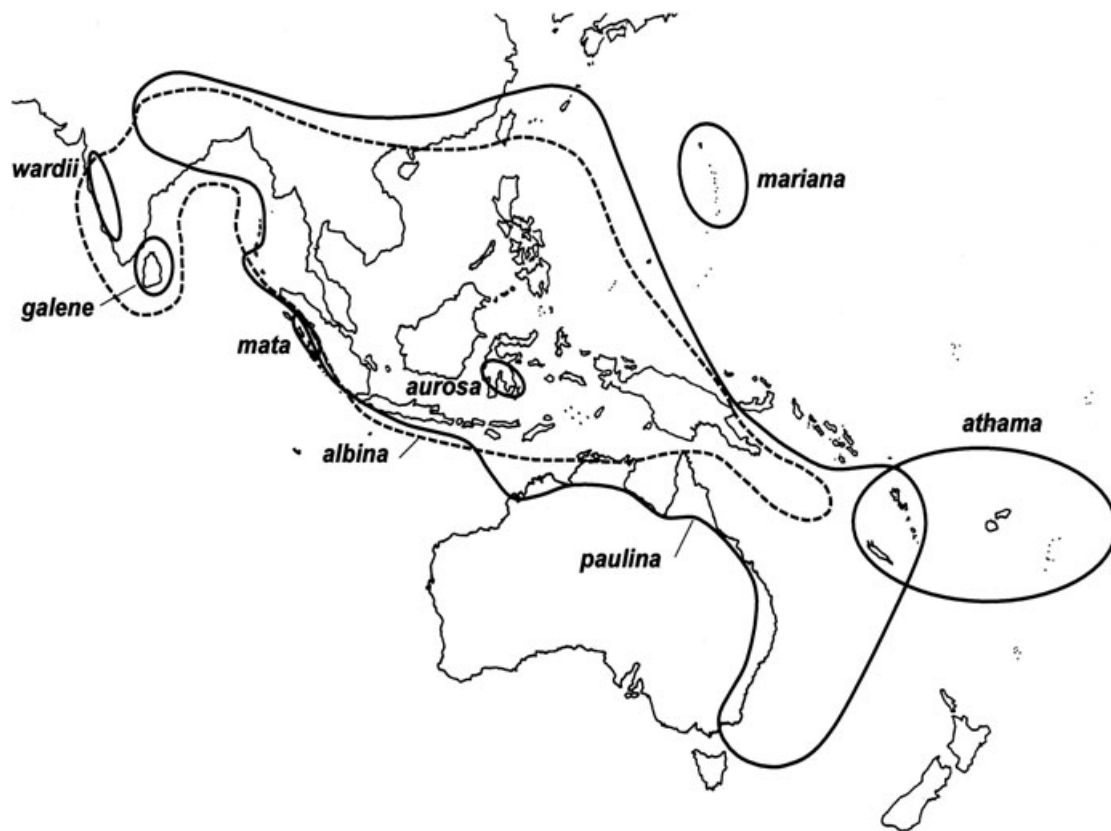


Fig. 23. Range map for all currently recognized species of the *Appias* (*Catophaga*) *paulina* complex.

member of the genus occurs, *A. (Appias) ada* (Stoll, 1781; Tennent, 2002).

The collective distribution of the eight species of the *paulina* complex covers the same area as *Appias (Catophaga)* as a whole, with *A. albina* and *A. paulina* being by far the most widespread members of the subgenus. The other six species of the *paulina* complex are much more restricted: *A. galene* (Sri Lanka; sympatric with *albina*), *A. wardii* (Western Ghats; sympatric with *albina*), *A. mata* (Nias and Sipora; possibly sympatric with *albina*, which has been recorded from neighbouring Siberut), *A. aurosa* (southern and central Sulawesi; sympatric with *albina* and *paulina*), *A. mariana* (Marianas; isolated) and *A. athama* (western Pacific, from New Caledonia to Samoa; isolated in Samoa and Fiji, but sympatric with *paulina* in New Caledonia and Vanuatu; Tennent, 2009). Because of earlier taxonomic confusion, in some works it appears as if two species belonging to the *paulina* complex occur in Fiji (e.g. Evenhuis, 2007), and as many as three in Samoa (e.g. Kami & Miller, 1998: 70), but, as indicated correctly by Tennent (2006: 31), only one taxon occurs at this eastern limit: *A. athama manaia*.

The *nero* group of three species is restricted essentially to the Oriental Region, from north-eastern India through Indochina to Hainan, and south through the Philippines and the Malay Archipelago to Bali, Sulawesi and Buru. The three species, so far as known, are parapatric, although the demarcation

between *A. nero* and *A. galba* in the Indochinese region is poorly understood (Fig. 24). *Appias zarinda* is an insular species, being virtually endemic to the Sulawesi Region [as demarcated by Vane-Wright & de Jong (2003: fig. 1, 109)]. Its eastward extension to Buru (Central Maluku; Peggie *et al.*, 1995) is a little puzzling because, on biogeographical grounds (Vane-Wright & Peggie, 1994: 228), one might expect Buru to be occupied by *A. placidia* (*melania* series). However, as discussed by Vane-Wright (1991), the southern Moluccas, including Buru, may be linked geologically to the Sula and Banggai archipelagos of central-eastern Sulawesi. This string of little islands plausibly formed a series of 'stepping stones' that apparently allowed certain species of butterflies evolved in Sulawesi to spread greater or lesser distances eastward, into the Moluccas, New Guinea and even further east, from the time when the Asian and Australian plates collided approximately 15 million years ago (Vane-Wright, 1991). If so, *A. zarinda* could represent a Sulawesi species that has spread along this route only as far as Buru, where it has formed a distinct subspecies (*A. z. bouruensis*).

The *melania* series of four allopatric species occurs east of Weber's Line, and is thus restricted to the Australian Region. *Appias placidia* occurs in both northern and central Maluku, which, based on a 'nearest-neighbour' analysis of butterfly distributions, constitute two separate areas of endemism (Vane-Wright & Peggie, 1994). However, as already noted,

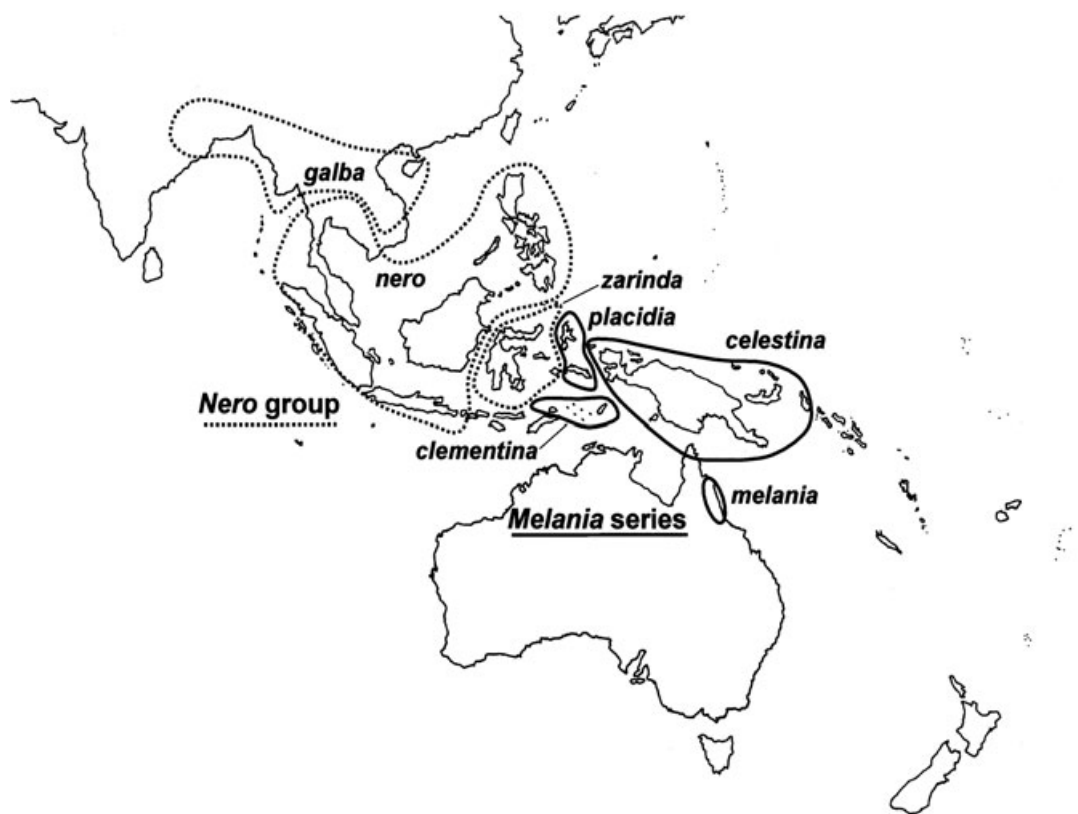


Fig. 24. Range map for all currently recognized species of the *Appias* (*Catophaga*) *nero* group and the *Appias* (*Catophaga*) *melania* series.

placidia is surprisingly absent from Buru, where it appears to be replaced by *A. zarinda* (*nero* group). *Appias clementina* is restricted to a group of islands in the western Lesser Sundas, from Alor and Timor to Tanimbar. *Appias celestina* occurs in the New Guinea Region, including Kai and Aru, and thus could be considered parapatric with respect to *clementina*. *Appias celestina* also occurs on Cape York Peninsula (Queensland), whereas the final species in the series, *A. melania*, is confined to a relatively small area of Queensland lying approximately 400 km further south.

In summary, only the highly polytypic *A. paulina* and *A. albina* are widely distributed through much of the Indo-Australian Region, where they mostly overlap with other, discontinuously distributed local members of the *paulina* complex, and the species of the *nero* group and *melania* series. Four of the restricted members of the *paulina* complex occur in the Oriental Region, and two in the Pacific. The three species of the *nero* group are distributed essentially parapatrically through a large part of the eastern Oriental Region. The four members of the *melania* series are distributed allopatrically in part of the Australian Region.

Hostplant relationships, coloration, polymorphism and speciation

Brief discussions of larval hostplant relationships (with special reference to an apparent shift from Brassicales to

Malpighiales) and adult pigmentation and coloration, together with a more extensive discussion of adult polymorphism in these butterflies and its possible relationship to Darwinian colour-pattern transference and speciation, are included in File S1. These more speculative elements do not contribute greatly to the basic systematics. Even so, we consider the polymorphism of these species, especially *A. nero*, to be of outstanding biological and evolutionary interest. In fact, so much so that they provided a major stimulus to completing the present study.

Suggestions for future work

As already discussed, a comprehensive investigation into the molecular systematics of the species and subspecies of *Appias* (*Catophaga*) would be basic for comparative biology on these butterflies, including the evolution of coloration within the group (see discussion in File S1). The availability of a fully resolved, robust cladogram is, ultimately, the *sine qua non* for this type of evolutionary study. However, getting fresh material for DNA work would be difficult in some cases, e.g. the narrowly distributed and rarely encountered *A. aurosa*, or even impossible in the case of *A. mariana*, if it really is extinct. A particularly interesting question that could be resolved by molecular work concerns the relationship between *A. zarinda* and *A. placidia*. Our morphological investigations

suggest that these two species belong to different groups within the subgenus *Appias* (*Catophaga*). However, the fact that *A. zarinda* extends east to Buru (*A. z. bourouensis*), where *A. placidia* does not occur but might have been expected, implies the possibility of a closer phylogenetic relationship and/or very similar ecological requirements for these two taxa. Conceivably the *nero* group is nested within the *melania* series, with the possibility that *A. placidia* represents its sister group.

The formal genetics of any of the species and races exhibiting female polymorphism would be of great interest, especially with respect to the complex situation seen in some populations of *A. paulina*, which may have as many as six female forms. Perhaps most interesting of all would be to investigate the genetic dominance relationships affecting *A. nero palawanica*, to ascertain whether or not the orange, male-like female morphs of *A. nero* on Palawan are dominant to the white, piebald and yellow female forms. This seems probable if the male-coloured morphs, seen in many but not all races of *A. nero*, are the result of Darwinian transference (see discussion in File S1). The generality of this result could be checked by an investigation into the genetics of *A. zarinda* on Sulawesi, where the females of this species also are coloured white, yellow or male-like orange. Racial and even species hybrids, if they can be created in the laboratory, might also offer valuable insights. Renewed interest in the pigment chemistry (see File S1) of these butterflies might be particularly revealing in this context, taking care to investigate females as well as males. Any programme of genetic research would be facilitated by or even depend also upon much better information about the hostplants and general ecology of *Appias* (*Catophaga*) species – a need that amateur entomologists could play a key role in satisfying (Vane-Wright, 2009).

Finally, a recent paper on the biochemistry of Pieridae has revealed that various members of the family produce proteins ('pierisins') toxic to certain human cancer cells. Within *Appias*, pierisins have been found in *A. nero* and *A. paulina*, but not in *A. lycnida* (Matsumoto *et al.*, 2008). Whether these findings have any systematic or ecological significance for our understanding of *Appias* butterflies is unknown, but these discoveries add another dimension for future research.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-3113.2010.00535.x

File S1. Discussion of hostplant relationships, coloration, polymorphism and speciation in *Appias* (*Catophaga*).

File S2. Type material of *Appias* (*Catophaga*) taxa with special reference to the Natural History Museum collection, London (BMNH).

File S3. Combined bibliography.

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Appendix 1

Synonymic checklist of species and subspecies of *Appias* (*Catophaga*)

Those taxa for which we have examined type material are marked with an asterisk.

Appias (*Catophaga*) *albina* (Boisduval, 1836)

Pieris albina Boisduval, 1836.

Eight subspecies, ranging from Sri Lanka, Western Ghats, north-eastern India, southern China, South-East Asia and Philippines through Malay Peninsula to Papua New Guinea and northern Australia.

*albina swinhoei** (Moore, 1905). *Catophaga swinhoei*.

Type locality: Southern India: 'Nilgiris' (lectotype here designated: see Appendix 2).

= *norma** Evans, 1924. *Appias albina* f. *norma*. Sri Lanka 'Ceylon'.

Distribution: Southern India and Sri Lanka.

*albina darada** (Felder & Felder, 1865). *Pieris darada*. Type locality: Bangladesh: 'Silhet'.

= *confusa** Fruhstorfer, 1910. *Appias albina confusa* (junior secondary homonym of *Belenois confusa* Butler, 1872). Type locality: India, Thailand, Vietnam: 'Sikkim, Assam, Siam, Tonkin'.

Distribution: India (north-eastern region, Andaman and Nicobar islands), Bangladesh, southern China (Yunnan, Hainan), Myanmar, Vietnam, Laos, Cambodia and Thailand.

albina semperi (Moore, 1905). *Catophaga semperi*. Type locality: northern Philippines: (no further data).

= *kawakamii* Matsumura, 1909. *Appias kawakamii*. Type locality: Taiwan: 'Kotosho I' (Lanyu Island).

Distribution: Philippines (Babuyan, Bohol, Cebu, Dumaran, Guimaras, Luzon, Marinduque, Mindanao, Negros) and southern Taiwan (Lanyu Island).

albina agatha (Staudinger, 1889). *Tachyris agatha*. Type locality: Philippines: [N.] 'Palawan'.

= *pancheia** Fruhstorfer, 1910. *Appias albina pancheia*. Type locality: Philippines: [N.] 'Palawan'.

Distribution: Philippines (Mindanao, northern Palawan).

albina albina (Boisduval, 1836). *Pieris albina*. Type locality: Indonesia, Central Maluku: 'Ambon'.

= *neombo** Boisduval, 1836. *Pieris neombo*. Type locality: Indonesia, Central Maluku: [Ambon] 'Brésil, environs de Bahia et Fernamboué' (error).

= *cynisca** Wallace, 1867. *Tachyris cynisca*. Type locality: Indonesia, Central Maluku, Buru: 'Bouru'. **Syn.n.**

Distribution: Malay Peninsula, Indonesia (Sumatra, West Java, Kalimantan, Sulawesi, Moluccas, Irian Jaya), Sabah, Brunei, Sarawak, Philippines (Balabac, Bongao, central and southern Palawan, Sanga Sanga, Sibutu, Tawitawi), Papua New Guinea (including Kiriwina Island), Australia (Darwin, Cobourg Peninsula, a few localities in Northern Territories, and Rimbija, Moa, Thursday and Prince of Wales islands).

*albina ambigua** Grose-Smith, 1895. *Appias ambigua*. Type locality: Indonesia, South Maluku, Wetar. 'Wetter' (lectotype here designated: see Appendix 2).

= *micromalayana** Fruhstorfer, 1909. *Appias albina micromalayana*. Type locality: Indonesia: 'East Java' (lectotype here designated: see Appendix 2). **Syn.n.**

Distribution: Indonesia [East Java, Lesser Sunda Islands (not Sumbawa) east to Tanimbar], Christmas Island and East Timor.

*albina infuscata** Fruhstorfer, 1910. *Appias albina infuscata*. Type locality: Indonesia: 'Sumbawa'. Distribution: Indonesia (Sumbawa).

albina pulverobasalis Joicey & Noakes, 1915. Type locality: Indonesia, Biak, Bosnik.

Distribution: Indonesia (Irian Jaya: Biak).

*Infrasubspecific and unavailable names: alcesta** Talbot, 1939; *citrina* Fruhstorfer, 1910; *citronella** Fruhstorfer, 1897; *flava* Röber, 1891; *latimarginata* Matsumura, 1919; *matsumurai* Sonan, 1930; *principalis** Fruhstorfer, 1910; *punctata** Fruhstorfer, 1910; *saweloides** Fruhstorfer, 1910; *semiflava** Fruhstorfer, 1910; *subochracea** Fruhstorfer, 1910; *umbratilis* Fruhstorfer, 1897; *virilis** Fruhstorfer, 1910.

Appias (Catophaga) athama (Blanchard, 1848)

Pieris athama Blanchard, 1848.

Until recently this taxon has been treated as a subspecies of *Appias albina* or *A. paulina*. With separation, its division into subspecies requires re-investigation; three are provisionally recognized here. Females vary from deep yellow on New Caledonia to cream-coloured in Samoa. *Appias athama* occurs in New Caledonia, Vanuatu, Tonga, Western Samoa, American Samoa and Fiji.

*athama psyche** (Felder & Felder, 1865). *Pieris psyche*. Type locality: New Caledonia: 'Nova Caledonia'.

= **argentifera* Joicey & Talbot, 1928. Type locality: New Caledonia 'Loyalty Is'; (lectotype here designated: see Appendix 2).

Distribution: New Caledonia (including Isle of Pines); status of Lifu population uncertain.

*athama athama** (Blanchard, 1848). *Pieris athama*. Type locality: Fiji, Ovalau: 'Balaou'. (Type material in MNHN).

= *athama** Lucas, 1852. *Pieris athama*. Type locality: Fiji, Ovalau: 'Balaou (Nouvelle-Guinée)' (junior objective synonym and primary homonym of *Pieris athama* Blanchard).

= *jacquinotii** Lucas, 1852. *Pieris jacquinotii*. Type locality: Fiji, Ovalau: 'Balaou (Nouvelle-Guinée)'.

= *wallacei** (Butler, 1898). *Catophaga wallacei*. Type locality: Vanuatu, Malekula: 'New Hebrides (Mellicollo)' (lectotype here designated: see Appendix 2)

Distribution: Vanuatu (Mota Lava, Gaua, Espiritu Santo, Ambae, Malakula, Paama, Epi, Efaté, Erromango, Aniwa, Futuna, Aneityum), Fiji (Ongea, Viti Levu, Vanua Valava, Totoya, Lau, Walsala, Yasawa, Naviti, Ovalau).

*athama manaia** (Hopkins, 1927). *Catophaga jacquinotii manaia*. Type locality: Western Samoa: 'Upolu I.'

Distribution: Tonga (Vava'u), Western Samoa (Savai'I, Upolu), American Samoa (Tutuila).

***Appias (Catophaga) aurosa** Yata & Vane-Wright sp.n.**

Type locality: Indonesia, Sulawesi: Makassar.

Distribution: Known from approximately 20 males collected in southern and central Sulawesi (Indonesia).

*Infrasubspecific and unavailable names: aurosa** Fruhstorfer, 1899.

Appias (Catophaga) celestina (Boisduval, 1832)

Pieris celestina Boisduval, 1832.

Five subspecies, ranging from Aru and Kai through New Guinea to the Bismarck Archipelago, Bougainville and Cape York.

*celestina galepsus** Fruhstorfer, 1910. *Appias celestina galepsus*. Type locality: Indonesia: 'Key Is'.

Distribution: Indonesia (Kep. Kai) only.

*celestina barea** Fruhstorfer, 1910. *Appias celestina barea*. Type locality: Indonesia: 'Aru'.

Distribution: Indonesia (Kep. Aru) only.

celestina celestina (Boisduval, 1832). *Pieris celestina*. Type locality: Indonesia, Irian Jaya: 'Dorei'.

= *sekarensis* (Ribbe, 1886). *Tachyris celestina* var. *sekarensis*. Type locality: Indonesia, Irian Jaya: 'Sekar, West coast of New Guinea'.

= *galerus** Fruhstorfer, 1910. *Appias celestina galerus*. Type locality: Papua New Guinea: 'German New Guinea'.

= *tamibia* Strand, 1912. *Appias celestina* var. *tamibia*. Type locality: not located: 'Tami area'.

Distribution: Indonesia (Aru, Waigeo, Irian Jaya), Papua New Guinea (mainland), Australia (Cape York; probably vagrants from New Guinea).

celestina eumelis (Boisduval, 1832). *Pieris eumelis*. Type locality: Papua New Guinea: 'Port-Praslin (Nouvelle-Hollande)' (=New Ireland).

= *delicata** Butler, 1882. *Appias delicata*. Type locality: Papua New Guinea: Stated to be from 'New Britain', but type specimen is labelled Duke of York I.

Distribution: Papua New Guinea: New Ireland, New Britain, Duke of York.

*celestina orientalis** Rothschild, 1915. *Appias celestina orientalis*. Type locality: Papua New Guinea: 'Bougainville, Arawa'.

Distribution: Papua New Guinea: Bougainville, Normanby (Normanby may be subsp. *celestina*).

*Infrasubspecific and unavailable names: aurifera** Fruhstorfer, 1910; *flava** Ribbe, 1886; *lileia** Fruhstorfer, 1910, *limia** Fruhstorfer, 1910; *typicum* Talbot, 1932 (refers to the nominotypical female form; even if accepted as a name, it is clearly infrasubspecific).

***Appias* (*Catophaga*) *clementina* (Felder, 1860)**

Pieris clementina C. Felder, 1860. Type locality:
Indonesia: 'Ambon' (presumed error, although there is a female in BMNH labelled 'Amboina Fruhstorfer')
= *adelpa* (Röber, 1891). *Tachyris adelpa*. Type locality: Indonesia: 'Alor'.
= *agar** Fruhstorfer, 1910. *Appias clementina agar*. Type locality: Indonesia: 'Dammer, Babber, Tenimber'.

Distribution: This small Indonesian species is confined to a group of islands in the eastern Lesser Sunda Islands (Alor, Damar, Babber, Tenimber). It does not appear to be divisible into subspecies.

***Appias* (*Catophaga*) *galba* (Wallace, 1867 stat. rev.)**

*Tachyris galba** Wallace, 1867. Type locality: India: 'N. India'.
= *nebo* Grose-Smith & Kirby, 1894. *Appias nebo*. Type locality: Upper Burmah, Chindwin River.
= *hainanensis** Fruhstorfer, 1902. *Tachyris nero hainanensis*. Type locality: China: 'Hainan, Five Finger Mountains'.

Distribution: Until now treated as a subspecies of *A. nero*, this butterfly occurs in northern India, Myanmar and south-eastern China (Hainan), south to Vietnam, Laos and northern Thailand.

***Appias* (*Catophaga*) *galene** (Felder & Felder, 1865)**

*Pieris galene** (Felder & Felder, 1865). Type locality: Sri Lanka: 'Ceylon, Trincomali'.
= *lankapura** Moore, 1879. *Catophaga lankapura*. Type locality: Sri Lanka: 'Ceylon'.
= *venusta** Moore, 1881. *Catophaga venusta*. Type locality: Sri Lanka: 'Vavonia Vivankulam, N. of Trincomali'.

Distribution: Restricted to Sri Lanka, where it occurs widely except in the extreme north.

*Infrasubspecific and unavailable names: fasciata** Fruhstorfer, 1910.

Appias* (*Catophaga*) *mariana Yata & Chainey sp.n.

Type locality: U.S.A.: 'Guam'
Distribution: This newly described species, known from three islands in the Marianas (Guam, Rota, Saipan), may be extinct.

***Appias* (*Catophaga*) *mata* (Kheil, 1884)**

Pieris mata Kheil, 1884
This rare Indonesian butterfly is restricted to the Mentawi Islands, off the south-west coast of Sumatra, where it occurs as two distinct subspecies.
mata mata (Kheil, 1884). *Tachyris mata*. Type locality: Indonesia, Mentawi Islands: 'Nias'.
Distribution: Known only from Nias.
*mata caeca** Corbet, 1941. *Appias paulina caeca*. Type locality: Indonesia, Mentawi Islands: 'Sipora'.
Distribution: Known only from Sipora.

***Appias* (*Catophaga*) *melania* (Fabricius, 1775)**

*Papilio melania** Fabricius, 1775. Type locality: Australia: 'New Holland' (Queensland, Cooktown).
= *asteria* Miskin, 1889. *Tachyris asteria*. Type locality: Australia: 'N. Queensland, Port Douglas' (type material in South Australian Museum, Adelaide).
= *cerussa* Fruhstorfer, 1904. *Tachyris cerussa*. Type locality: Australia: 'Queensland' (whereabouts of type material unknown).

Distribution: Australian endemic with its breeding range restricted to north-east coastal region of Queensland, where it occurs in upland rainforests from Cooktown south to the Bluewater State Forest.

***Appias* (*Catophaga*) *nero* (Fabricius, 1793)**

*Papilio nero** Fabricius, 1793
Fifteen recognized subspecies, some very distinct, ranging from the Malay Peninsula to Bali, southern Sulawesi region, Borneo and the Philippines.

*nero nero** (Fabricius, 1793). *Papilio nero*. Type locality: (Indonesia, Java): 'Asia' (neotype here designated, see Appendix 2).

= *thyria* Godart, 1819. *Pieris thyria*. Indonesia: 'Java'.
= *figulina** Butler, 1867. *Pieris figulina*. Type locality: Malaysia: 'Singapore' (lectotype here designated, see Appendix 2).

Distribution: Malay Peninsula, Sumatra, Java, Bali.

*nero ramosa** (Fruhstorfer, 1898). *Catophaga nero ramosa*. Type locality: Indonesia: 'Nias'.

Distribution: Indonesia (Nias).

*nero pulonus** (Fruhstorfer, 1906). *Tachyris nero pulonus*. Type locality: Indonesia: 'Batu'.

Distribution: Indonesia (Batu).

*nero baweanicus** (Fruhstorfer, 1905). *Tachyris nero baweanicus*. Type locality: Indonesia: 'Bawean'.

Distribution: Indonesia (Bawean).

*nero neronis** (Fruhstorfer, 1903). *Tachyris nero neronis*. Type locality: Indonesia: 'Kangean'.

Distribution: Indonesia (Kangean).

nero acuminata (Snellen, 1890). *Pieris nero* var. *acuminata*. Type locality: Indonesia: 'Tanah-Djampea'.

Distribution: Indonesia (Tanahjampea).

*nero chelidon** (Fruhstorfer, 1905). *Tachyris nero chelidon*. Type locality: Sabah: 'North Borneo'.

Distribution: Indonesia (Kalimantan), Sabah, Brunei, Sarawak.

*nero flavius** Grose-Smith, 1892. *Appias flavius*. Type locality: Philippines: 'Taganac I., NE Borneo'.

Distribution: Philippines: Turtle Islands (off the coast of Borneo, near Sandakan).

- nero palawanica** (Staudinger, 1889). *Tachyris nero* var. *palawanica*. Type locality: Philippines: 'Palawan'.
Distribution: Philippines (Balabac, Palawan).
- nero corazonae** Schröder & Treadaway, 1989. *Appias nero corazonae*. Type locality: Philippines: 'Sulu Archipelago'.
Distribution: Philippines (Bongao, Sanga Sanga, Sibutu).
- nero fleminius** Fruhstorfer, 1911. *Appias nero fleminius*. Type locality: Philippines: 'Mindoro'.
Distribution: Philippines (Mindoro).
- nero domitia*** (Felder & Felder, 1862). *Pieris domitia*. Type locality: Philippines: 'Luzon'.
= *asterope* Felder & Felder, 1862. *Pieris asterope*. Type locality: Philippines: 'Luzon' (junior primary homonym of *Pieris asterope* Godart, 1819).
= *korridona** Grose-Smith 1894. *Appias korridona*. Type locality: Indonesia, Irian Jaya: 'Korrido' (presumed error). **Syn.n.**
= *yamazakii* Sonan, 1936. *Appias nero yamazakii*. Type locality: Taiwan: 'Formosa'.
Distribution: Philippines (Luzon, Marinduque, Masbate), Taiwan.
- nero soranus** Fruhstorfer, 1910. *Appias nero soranus*. Type locality: Philippines: 'Cebu'.
Distribution: Philippines (Cebu, Negros, Panay, Sibuyan).
- nero zamboanga** (Felder & Felder, 1862). *Pieris zamboanga*. Type locality: Philippines: 'Mindanao, Celebes' (type locality here restricted to Mindanao. Lectotype designation required, but no type material located).
= *mindanensis** Butler, 1883. *Appias mindanensis*. Type locality: Philippines: 'Mindanao, Pasananca valley'.
= *boholensis* Okano & Okano, 1989. *Appias nero boholensis*. Type locality: Philippines: 'Visayan Islands'.
Distribution: Philippines (Bohol, Dinagat, Leyte, Mindanao, Panaon, Samar).
- nero tibericus*** Fruhstorfer, 1910. *Appias nero tibericus*. Type locality: Philippines: 'Basilan'.
Distribution: Philippines (Basilan).
- nero** subsp. near *zamboanga* (Vane-Wright & de Jong, 2003: 109)
Distribution: Indonesia, Kep. Talaud (Talaud, Salebabu).
*Infrasubspecific and unavailable names: coelitus** Fruhstorfer, 1899; *helvola** Fruhstorfer, 1910; *sufflava** Fruhstorfer, 1910.
- Appias (Catophaga) paulina** (Cramer, 1777)
Papilio paulina Cramer, 1777.
Nearly two dozen recognized races make up this wide-ranging species, found from north-east India to Vanuatu. As commented above, some of these taxa may eventually prove to be distinct species.
- paulina adamsoni*** (Moore, 1905). *Catophaga adamsoni*. Type locality: Myanmar: 'Burma, Upper Tenasserim, Thoungying Valley; Dounat Range; Muong Gnow, Shan States; Rangoon; Arrakan; Hlaingbeoo Arrakan'.
= *pseudoleis** Fruhstorfer, 1910. *Appias melania pseudoleis*. Type locality: Thailand: 'Siam'.
Distribution: North-east Indian region to south-western China, Myanmar, Vietnam, Laos, Cambodia and Thailand.
- paulina griseoides*** Moulton, 1923. *Appias paulina griseoides*. Type locality: Vietnam: 'Pulo Condore (south-east coast of Cochin-China)'.
Distribution: Known only from Pulo Condore in the Con Son Islands, off the coast of southern Vietnam.
- paulina** subsp. (A. Rawlins, personal communication, 2009).
Distribution: Indonesia (Natuna Islands).
- paulina minato*** (Fruhstorfer, 1899). *Catophaga paulina minato*. Type locality: Japan: 'Ishigaki'.
= *iwasakii* Matsumura, 1919. *Appias melania* var. *iwasakii*. Type locality: Japan, Okinawa: 'Yayeyama'.
Distribution: Taiwan and Japan (Yaeyama Is north to Akusekijima).
- paulina galathea** (Felder, 1862). *Pieris galathea*. Type locality: India, Andaman Is: 'Sambelong'.
= *roepstorffii* Moore, 1884. *Catophaga roepstorffii*. Type locality: India: 'Nicobar Is.'.
Distribution: Confined to the Andaman and Nicobar Islands.
- paulina distanti*** (Moore, 1905). *Catophaga distanti* (as 'nom. n.' for *leis* of Distant, 1885; de Nicéville & Martin, 1895). Type locality here restricted to Malaysia 'Malay Pen.', but no type material from this locality is available for lectotype designation.
Distribution: Confined to the Malay Peninsula, including Langkawi Islands.
- paulina grisea*** Moulton, 1923. *Appias paulina grisea*. Type locality: Malaysia: 'Pulo Aur; Pulo Tioman'.
Distribution: This subspecies is confined to the small group of islands that includes Aur and Tioman, off the east coast of the Malay Peninsula.
- paulina pione*** Fruhstorfer, 1910. *Appias melania pione*. Type locality: Indonesia: Sumatra.
Distribution: Sumatra only.
- paulina paulina*** (Cramer, 1777). *Papilio paulina*. Type locality 'Java' (lectotype here designated, see Appendix 2):
= *leis* Geyer, 1832. *Catophaga leis*. Type locality: Indonesia: Java.

- = *ida* Lucas, 1852. *Pieris ida*. Type locality: Indonesia: Java.
- = *subtuslutea* Roepke, 1935. *Appias leis* f. *subtuslutea*. Type locality: Indonesia: Java.
- = *raksasa* Kalis, 1941. *Appias raksasa*. Type locality: Indonesia: Bali.
- = *alope** Wallace, 1867. *Tachyris alope*. Type locality: here restricted to Java, but no type material from this locality available for lectotype designation. Distribution: Indonesia: Java, Bali and Bawean.
- paulina agave*** (Felder & Felder, 1862). *Pieris agave*. Type locality: Philippines: 'Luzon'. Distribution: Philippines: Dinagat, Homonhon, Leyte, Luzon, Marinduque, Mindanao, Negros, Panaon and Samar.
- paulina athena**** Fruhstorfer, 1903. *Appias melania athena*. Type locality: Sabah: 'Mt. Kinabalu, N. Borneo'. Distribution: Known from the whole of Borneo, and Bongao, Sanga Sanga, Sibutu and Tawitawi in the Philippines.
- paulina nikomedia**** Fruhstorfer, 1910. *Appias paulina nikomedia*. Type locality: Philippines: 'Basilan'. Distribution: Confined to the island of Basilan, Philippines.
- paulina plaetoria**** Fruhstorfer, 1910. *Appias melania plaetoria*. Type locality: Philippines: Balabac. Distribution: Confined to the island of Balabac, Philippines.
- paulina sithonia*** Fruhstorfer, 1911. *Appias melania sithonia*. Type locality: Philippines: Mindoro. Distribution: Confined to the island of Mindoro, Philippines.
- paulina terentilia**** Fruhstorfer, 1910. *Appias melania terentilia*. Type locality: Philippines: 'Palawan'. Distribution: Palawan and Calamian, in the Philippines.
- paulina thyre*** Fruhstorfer, 1911. *Appias melania thyre*. Type locality: Banguay I. Distribution: Banguay I, off Sabah, Malaysia.
- paulina albata*** (Hopffer, 1874). *Tachyris albata*. Type locality: Indonesia, Sulawesi: 'Celebes'.
 = *dohertyi** Rothschild, 1892. *Appias dohertyi*. Type locality: Indonesia, Sulawesi: 'southern Celebes'.
 = *kalisi* Röber, 1940. *Pandemos (Saletara) melania* form *kalisi*. Type locality: Indonesia, Sulawesi: 'Süd-Celebes (Bantimurung) und Mittel-Celebes (Tanah Metah)'. Distribution: Indonesia: Sulawesi, Buton, Muna, Kabaena, Kep. Banggai (Peleng), Kep. Sula (Mangole, Taliabu).
- paulina pietersi*** Kalis, 1933. *Appias melania pietersi*. Type locality: Indonesia: Kangean. Distribution: Indonesian island of Kangean only.
- paulina sawela**** (Fruhstorfer, 1896). *Tachyris sawela*. Type locality: Indonesia: 'Lombok'. Distribution: Indonesian islands of Lombok and Flores.
- paulina tambora**** (Fruhstorfer, 1903). *Catophaga melania tambora*. Type locality: Indonesia: 'Tambora, Sumbawa'. Distribution: Indonesian island of Sumbawa only.
- paulina emilia**** (Fruhstorfer, 1903). *Catophaga melania emilia*. Type locality: Indonesia: 'Sumba'. Distribution: Indonesian island of Sumba only.
- paulina eurosundana**** Grose-Smith, 1895. *Appias eurosundana*. Type locality: Indonesia, Timor: 'Oinainisa (Timor)'. Lectotype here designated (see Appendix 2). Distribution: Indonesian Timor and East Timor.
- paulina paula*** (Röber, 1891). *Tachyris paula*. Type locality: Indonesia: 'Wetter'. Distribution: Indonesian islands of Wetar and Roma.
- paulina*** subsp.
 = '*cynisca*' auctt. (e.g. Peggie *et al.*, 1995) nec Wallace. Distribution: Indonesian island of Buru (Central Maluku) only.
- paulina antoniae**** Fruhstorfer, 1910. *Appias melania antoniae*. Type locality: Indonesia, Central Maluku: 'East Ceram, Saparoea'. Distribution: Central Maluku (Indonesia): Seram, Ambon, Kelang, Haruku and Saparua.
- paulina zoe*** (Snellen van Vollenhoven, 1865). *Pieris zoe*. Type locality: Indonesia, North Maluku: 'Batjan'. Distribution: North Maluku (Indonesia): Obi, Halmahera, Bacan, Morotai and Kasiruta.
- paulina saina**** Grose-Smith, 1894. *Appias saina*. Type locality: Indonesia, Irian Jaya: 'Humboldt Bay, Dutch New Guinea'. Lectotype here designated (see Appendix 2).
 = *sosias** Fruhstorfer, 1913. *Appias melania sosias*. Type locality: Papua New Guinea: 'Yule I.'. Distribution: New Guinea (Indonesia and Papua New Guinea).
- paulina falcidia**** Fruhstorfer, 1910. *Appias melania falcidia*. Type locality: Indonesia: 'Biak'. Distribution: Island of Biak only, in Irian Bay (Indonesia).
- paulina ega**** (Boisduval, 1836). *Pieris ega*. Type locality: Australia: 'Nouvelle-Hollande'.
 = *caledonica* Felder, 1862. *Pieris melania* var. *caledonica*. Type locality: New Caledonia. Distribution: Australia (northern and eastern regions, Groote Eylandt, Darnley, Thursday, Moa, Sue, Lord Howe), New Caledonia (Isle of Pines, Lifu, Ouvée, Maré), Vanuatu (Espiritu Santo, Efaté, Tanna, Futuna, Aneityum).
- Infrasubspecific and unavailable names: aegina** Fruhstorfer, 1910; *flaminia** Fruhstorfer, 1910;

*furia** Fruhstorfer, 1910; *horatia** Fruhstorfer, 1910; *iria** Fruhstorfer, 1910; *limbata** Fruhstorfer, 1910; *marginata** Fruhstorfer, 1910; *melanides** Fruhstorfer, 1910; *obscurior** Fruhstorfer, 1910; *ochracea* Moulton, 1914; *shima* Sonan, 1930; *uranides** Fruhstorfer, 1910.

***Appias (Catophaga) placidia* (Stoll, 1790)**

Papilio placidia Stoll, 1790. Type locality: Indonesia, Central Maluku: 'Ambon'.

= *maculata** Staudinger, 1884. *Tachyris placidia* var. *maculata*. Type locality: Indonesia, North Maluku: 'Bacan'.

Distribution: This distinctive Indonesian species is known from North (Bacan, Halmahera, Obi) and Central Maluku (Ambon, Seram) only. As suggested by D'Abrera (1971), the separation of the northern Maluku populations as subspecies *maculata* appears, on exophenotypic grounds, untenable.

***Appias (Catophaga) wardii* (Moore, 1884)**

*Catophaga wardii** Moore, 1884. Type locality: India: 'Coonor, Nilgiris'.

= *arida** Talbot, 1939. *Appias wardi* [sic] *arida*. Type locality: India: 'Nilgiri Hills'.

Distribution: Restricted to the Western Ghats of peninsular India, where it occurs in scattered localities throughout much of the range south of latitude 20°N.

***Appias (Catophaga) zarinda* (Boisduval, 1836)**

Pieris zarinda Boisduval, 1836.

An Indonesian species restricted to the Sulawesi region and the adjacent island of Buru (Central Maluku). Four recognized subspecies, one of which must be considered doubtful.

zarinda zarinda (Boisduval, 1836). *Pieris zarinda*.

Type locality: Indonesia: 'Java' [*recte* Sulawesi].

= *fatime* Snellen van Vollenhoven, 1866. *Pieris fatime*. Type locality: Indonesia: 'Celebes'.

Distribution: Sulawesi and some adjacent islands to the south and east: Kabaena, Kep. Tukangbesi, Kep. Banggai (Peleng).

*zarinda sulana** (Fruhstorfer, 1899). *Tachyris nero sulana*. Type locality: Indonesia, Maluku: 'Sula, Mangoli'.

Distribution: Known only from Mangole in Kep. Sula, eastern Sulawesi region; doubtfully distinct from *A. zarinda zarinda*.

*zarinda phestus** (Westwood, 1888). *Tachyris phestus*. Type locality: Indonesia, Sulawesi: 'Talissa I, N. Celebes' (type material in UM Oxford; seen by RIVW).

Distribution: Kep. Talisei and Kep. Sangihe, in northern Sulawesi region.

zarinda bouruensis (Wallace, 1867). *Tachyris bouruensis*. Type locality: Indonesia, Central

Maluku: 'Buru' [no type specimen located. Butler (1898) states 'the type should be in Hewitson's collection, but was probably not in good enough condition to induce him to retain it'].

Distribution: Buru island (western Central Maluku) only.

Taxa excluded from *Appias* subgenus *Catophaga*

*Appias (Hiposcritia) urania** (Wallace, 1867) (described in *Tachyris*)

= *zondervani* Toxopeus, 1950

Appias (Appias) libythea rouxii (Boisduval)

= *yaksha** Fruhstorfer, 1910: 157

Appias (Appias) ada (Stoll, 1781)

Appendix 2

Nine lectotype designations, one neotype designation, and two type-locality restrictions for 12 nominal species of the genus *Appias*.

***Catophaga swinhoei* Moore, 1905: 11** [*Appias albina swinhoei*]

Moore described this species from southern India: '♂, Ahmedabad and Bisnuggar in Guzerat (Swinhoe) in December and Poona, November to January & February; ♂ North Kanara (Davidson), ♂ Orissa (coll. de Nicéville); ♂, Poona, January (Swinhoe); ♂♀, North Kanara (S. N. Ward); ♂♀, Nilgiris (Hampson) and Travancore. Madras, July-August (Watson) (larva – Elamane, Madras, November 25 (Elliott) (pupated and emerged); Malabar; W. Ghats (S. N. Ward)' and included the following: *Appias ares* Swinhoe, 1885 (part), *A. paulina* of Taylor (1888); *neombo* of Hampson (1888), *lankapura* of Watson (1890) and *neombo* of Davidson & Aitken (1896). Talbot (1939) stated '*swinhoei* (Moore), usually associated with this species [*albina*], was founded upon a male of *libythea* (Fabr.) belonging to the dry form *ares* Swinhoe'. The type material in BMNH clearly includes both *Appias albina* and *Appias libythea*. To stabilize usage of the name, we designate one of the specimens figured by Moore (1905) as the lectotype of *Catophaga swinhoei* Moore.

Lectotype ♂, INDIA, Nilgiris, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1e, BMNH(E) 229139.

Paralectotypes identified as *A. albina*: 3 ♀♀, INDIA, Nilgiris, Moore purchase BM 1903-361, BMNH(E) 229139-40, 229144-5; 229140, Moore fig., 1905, 556, 1g,h.; 1♀, INDIA, Malabar, BMNH(E) 229141, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1d.; 1♂, 1♀, INDIA, Madras, 10.viii.1889, Watson BMNH(E) 229135-6, Watson BM 1892-43; 1♂, 3♀♀, INDIA, Moore purchase BM 1903-361, BMNH(E) 229137 (♂), 229142-3, 229146 (♀), 229137 Moore fig., 1905, 556, 1a, 229142 Moore fig., 1905, 556, 1i,j, 229143 Moore fig., 1905, 556, 1f.; 1♀, INDIA, Travancore, BMNH(E) 229138, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1b; 1♀, INDIA, Travancore, Mynall, 2500', i.1897, BMNH(E) 229147, Moore purchase BM 1903-361; 1♂, same data except

1200', March, BMNH(E) 229148; 1♂, INDIA, North Kanara, 149963, Swinhoe coll. BM 1926-239.

Paralectotypes identified as *Appias libythea* (Fab.): 1♂, INDIA, Poona, BMNH(E) 142244, also a syntype of *Appias libythea ares* Swinhoe, 1883 (with label 'co-type ares Swin., type swinhoei ♂ Lep.Ind. vii. p11'). This is presumably the specimen referred to by Talbot (see above); 1♂, INDIA, Madras, 12.viii.1889, Watson BMNH(E) 229229, Watson BM 1892-43; 1♂, INDIA, Gujarat, Ahmedabad, xii.1886, BMNH(E) 229225, Moore purchase BM 1903-361, Moore 1905 fig. 556, 1a (locality cited as 'Poona'); 1♂, INDIA, Poona, i.1888, BMNH(E) 229226, Moore purchase BM 1903-361, with hand-written label 'neombo apud Swinhoe'; 1♂, INDIA, Gujarat, Bisnugar [=Visnagar], xii.1886, BMNH(E) 229227, Crowley bequest BM 1901-78, with hand-written label 'Appias ares ♂ Swinhoe'; paralectotype? ♂, INDIA, 'S. India', S. N. Ward, BMNH(E) 229228, Moore purchase BM 1903-361.

Appias ambigua Grose-Smith, 1895: 76 [*Appias albina ambigua*]

Indonesia (♀ only): Described from 'Two specimens from Wetter; one from Dili and one from Halmahera'. The specimen from Halmahera cannot be located in BMNH, unless it is a female specimen of *Appias paulina* labelled 'Halmahera', 'ex Grose-Smith 1910'. However, this specimen is not a very good fit for the original description. To restrict the name to a particular subspecies, the following specimen is here designated the lectotype of *Appias ambigua* Moore.

Lectotype ♀, INDONESIA, Wetar, v.1892, W. Doherty, BMNH(E) 135769, Rothschild bequest BM 1939-1; with hand-written label 'Ambigua Grose-Smith Type ♀'.

Paralectotypes: 1♀, INDONESIA, Wetar, v.1892, W. Doherty, 135769-70, Rothschild bequest BM 1939-1, 1♀, INDONESIA, Dili, v.1892, W. Doherty, ex Grose-Smith coll., 149931, Joicey bequest BM 1934-120.

Appias albina micromalayana Fruhstorfer, 1909: 201 (1910: 154) (= *Appias albina ambigua* Grose-Smith)

First described in 1909, exclusively from Babber Island, the intended original description did not appear until 1910 (as ssp. nov. and with type locality 'East Java, Bawean and small Sunda islands'). To ensure that this name refers to the same taxon the following specimen is here designated the lectotype of *Appias albina micromalayana* Fruhstorfer, 1909, and *Appias albina micromalayana* Fruhstorfer, 1910.

Lectotype ♂, INDONESIA, Babber, H. Fruhstorfer, BMNH(E) 135826, Fruhstorfer purchase BM:1937-285.

Paralectotypes: 3♂♂, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H.Fruhstorfer, BMNH(E) 135807-9, Fruhstorfer purchase BM:1937-285, 135808 with Fruhstorfer label 'albina micromalayana Fruhst. '; 2♂♂, same data, Oberthür purchase BM 1927-3, BMNH(E)149956-7; 1♂, same locality, iv.1896, BMNH(E)135810, Fruhstorfer purchase BM:1937-285; 1♂,

same locality, iv.1896, BMNH(E)149936, J. J. Joicey bequest BM 1934-120; 2♂♂, same locality, iv.1896, unregistered; 3♂♂, same data, 135811-3, Rothschild bequest BM 1939-1; 1♂, INDONESIA, Lombok, Sambalun, 4000', iv.1896, H. Fruhstorfer BMNH(E)135814, Rothschild bequest BM 1939-1; 4♂♂, INDONESIA, Java, Sukabumi, 2000', 1893, H.Fruhstorfer, BMNH(E) 135815-8; Fruhstorfer purchase BM:1937-285, 135815 with Fruhstorfer label 'albina micromalayana Fruhst'; 6♂♂, INDONESIA, Bawean, July-September., H.Fruhstorfer BMNH(E) 135819-24, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label 'albina micromalayana Fruhst. '; 1♂, same locality, wet season, BMNH(E) 135825, Fruhstorfer purchase BM: 1937-285; ♂, INDONESIA, Babber, H. Fruhstorfer, BMNH (E) 135827, Fruhstorfer purchase BM:1937-285; 2♂♂, INDONESIA, Wetar, H. Fruhstorfer, BMNH(E) 135828-9, Fruhstorfer purchase BM:1937-285; 1♂, INDONESIA, Dammer, H. Fruhstorfer, BMNH(E) 135830, Fruhstorfer purchase BM:1937-285; 1♂, INDONESIA, Kisser, H. Fruhstorfer, BMNH(E) 135831, Fruhstorfer purchase BM:1937-285; 1♂, INDONESIA, Sumba, xii.1896, H. Fruhstorfer, BMNH(E) 135832, Fruhstorfer purchase BM:1937-285; 1♂, same data except no date, 135833; 3♂♂, INDONESIA, Java, 1500', 1891, H.Fruhstorfer, 135834-6, Fruhstorfer purchase BM:1937-285.

Catophaga wallacei Butler, 1898: 399 [= *Appias athama athama* (Blanchard, 1848)]

Type localities Vanuatu, Malekula: 'New Hebrides (Mellicollo); New Caledonia'. To restrict the name to a particular subspecies we designate the following specimen as the lectotype of *Catophaga wallacei* Butler.

Lectotype ♂, VANUATU, Mallicollo I., Woodford, BMNH(E) 142267, Godman & Salvin BM 1896-12, with hand-written label 'Catophaga wallacei ♂ type Butler'.

Paralectotypes: 1♀, VANUATU, Malekula [as Mellicollo], Woodford, BMNH(E) 135840, Godman & Salvin BM 1896-12, slide no. 4678; 1♀, same data, BMNH(E) 135841; 1♂, same data, 135842.

Further paralectotypes belong with nominate *athama*: 1♀, NEW CALEDONIA, J. Macgillivray, BMNH(E) 142268, purchase Cuming BM 1859-63, with hand-written label 'Catophaga wallacei ♀ type Butler'; 1♀, NEW CALEDONIA, BMNH(E) 135839, purchase Cuming BM 1859-63, slide no.4639; 2♀♀, NEW CALEDONIA, BMNH(E) 135843 & 135846, Hewitson bequest, BM 1879-69, 135843 with det. 'Pieris boisduvaliana Feld 4', 135846 with labels 'Pieris boisduvaliana Feld.3' and 'Athama Pol Sud'; 1♂, same data, BMNH(E) 135844, slide no. 11180, with det. 'Pieris albina Bois. 4'; 1♂, same data, BMNH(E) 135845, slide no. 4638, with det. 'Pieris albina Bois. 5'.

Appias paulina argentifera Joicey & Talbot, 1928: 19 [= *Appias athama psyche* (Felder & Felder)]

Type locality: Loyalty Is. Based on two males (Lifu) and one female. The males represent *A. paulina ega*; the female is *A.*

athama. To stabilize the name the female is here designated the lectotype of *Appias paulina argentifera* Joicey & Talbot. Designation of the female provides an available name, should the Loyalty Is. population of *A. athama* ever be recognized as a valid subspecies.

Lectotype ♀, NEW CALEDONIA, Loyalty Is., ex Grose-Smith coll., BMNH(E) 141741, Joicey bequest BM 1934-120, with printed label 'A. paulina argentifera J&T 1928 ♀ A.T.'. Identifiable with *Appias athama* (Blanchard, 1848).

Paralectotype: ♂, NEW CALEDONIA, Loyalty Is., Lifou, Lomar ?, BMNH(E) 142321, Joicey bequest BM 1934-120, with printed label 'A. paulina argentifera J&T 1928 ♂ H.T.'. Identifiable with *Appias paulina ega* (Boisduval, 1836). We have not seen the second male referred to in the original description.

Papilio nero Fabricius, 1793: 153 [*Appias nero nero* (Fabricius, 1793)]

(Indonesia, Java): 'Asia. Mus Britann' (neotype here designated). A female in Banks coll. from 'Siam' is not considered to be a type. No possible type specimens have been located in the BMNH collections. Following Butler (1870b), this taxon has long been considered to be based on material from Java. This has recently been questioned (H. Gaonkar, personal communication, 2002), on the grounds that little material from Java reached England during the 18th century, suggesting that the original material probably came from the Malay Peninsula. However, Vane-Wright & Hughes (2005) demonstrated the opposite to be the case. To stabilize the application of nominate *nero*, which represents a highly polytypic species as currently conceived, the following specimen from Java is designated as the neotype of *Papilio nero* Fabricius.

Neotype ♂, INDONESIA, W. Java, Preanger, Palboehan Ratoe, B.M. 1922-165.

Pieris figulina Butler, 1867: 399 [= *Appias nero nero* (Fabricius, 1793)]

Described from a male from Singapore (coll. Roberts) and a female from Borneo (coll. Hewitson). To restrict the name to a particular subspecies, the male from Singapore is here designated the lectotype of *Pieris figulina* Butler.

Lectotype ♂, SINGAPORE, BMNH(E) 141751, pres. Entomological Club BM 1844-12.

Paralectotype: ♀, Borneo, 141758, Hewitson bequest, BM 1879-69. This specimen represents ssp. *chelidon* Fruhstorfer.

There is also a non type ♀ (but with red type label and hand-written 'Pieris Figulina Butler type') 'SINGAPORE, BMNH(E) 149693, Maj. H. Roberts, BM 1928-309'. The only female mentioned in the original description is from Borneo.

Catophaga distanti Moore, 1905: 14 [*Appias paulina distanti* (Moore, 1905)]

Described as 'nom. n.' for *leis* of Distant (1885) and de Nicéville & Martin (1895) with the localities 'Malay Pen.; Sumatra; Borneo'. Distant (1885) refers to 'Malay Pen. Prov. Wellesley (coll. Distant); Perak (Biggs – coll. Distant); Malacca, Ayer-panas (Godfrey – coll. Distant); Sumatra (Brit. Mus.)'. Type locality is here restricted to the Malay Peninsula. A lectotype designation is desirable but, unfortunately, *distanti* is applied to the subspecies occurring in Peninsular Malaysia, and no syntypes from this area are available. The following three syntypes from elsewhere have been located:

Syntype ♂, 'Borneo', BMNH(E) 229168, Hewitson bequest BM 1879-69; syntype ♂, MALAYSIA, Sabah, Labuan, BMNH(E) 229167, BM 1868-30; syntype ♂, INDONESIA, Sumatra, S.Raffles coll., BMNH(E) 229128, Purchase Stevens BM 1854-76, with hand-written label 'Sumatra 54.76/Catophaga alope Wallace'. This last specimen is also a possible syntype of *Tachyris alope* Wallace, 1867.

In addition it is necessary to consider two specimens from Java: 1♂, INDONESIA, Java, BMNH(E) 229166, BM 1860-15 & 1♀, INDONESIA, Java, BMNH(E) 229165, pres. Entomological Club BM 1844-12. Distant (1885) lists BMNH material of *leis* from Borneo, Java and Sumatra. Thus the above specimens would all have been in the museum collection at the time of Moore's (1905) publication, but only those from Borneo and Sumatra are considered to be syntypes of *distanti*, as Moore (1905) did not include Java under 'Habitat'.

Papilio paulina Cramer, 1777: 21 [*Appias paulina paulina** (Cramer, 1777)]

Described from 'Côte de Coromandel, à Tranquebar, & dans l'Isle de Java, près de Batavia', but here restricted to Indonesia: Java. Moore (1905) thought that *paulina* was from Ceylon (= Sri Lanka) and not from Java, but the lectotype is identical to material from Java and most other authors have treated *paulina* as such. The Sri Lankan population is now considered to represent a distinct species (*A. galene*). The following specimen is here designated the lectotype of *Papilio paulina*, to fix application of this name.

Lectotype ♀, bearing van Lennep label 'No.60, PAULINA Cr.2. 110. E, F' and 'FELDER COLLN' label; BMNH(E) 229172. This specimen is illustrated by Chainey (2005: 327, fig. 40).

Tachyris alope Wallace, 1867: 372 [= *Appias paulina paulina* (Cramer, 1777)]

India, Java, Sumatra, Borneo. Type locality here restricted to Java. A lectotype designation is desirable, but the type status of the material so far located is questionable.

Syntype? ♂, INDONESIA, Java, *amasene*, Dr. Horsfield], BMNH(E) 229127, slide no. Rh. 4653, with hand-written label 'Java 33a/Catophaga alope Wallace'; syntype? ♂, INDONESIA, Java, A. R. Wallace, ex Bates coll., BMNH(E) 229173, pres. Godman Salvin BM 1896-12; syntype? ♂, INDONESIA, Sumatra, S. Raffles coll., BMNH(E) 229128, Purchase Stevens BM 1854-76, with hand-written label

‘Sumatra 54.76/Catophaga alope Wallace’. This last specimen has the best credentials to be a type specimen; however, it is identifiable with ssp. *pione*. It is also a possible syntype of *Catophaga distanti* Moore, 1905. Syntype?? (i.e. unlikely) ♂, Borneo, BMNH(E) 229126, Moore purchase, BM 1899-234, with hand-written label ‘P.alope Wall.’;

Appias eurosundana Grose-Smith, 1895: 75 [*Appias paulina eurosundana* Grose-Smith, 1895]

Described from males from ‘Oinainisa (Timor) and Sambawa’ and females from ‘Oinainisa (Timor) and one from Wetter’. To restrict the name to a particular subspecies the following specimen is here designated the lectotype of *Appias eurosundana* Grose-Smith.

Lectotype ♂, INDONESIA, Timor, Oinainisa, xi.-xii.1891, W. Doherty, BMNH(E) 229051, Rothschild bequest, BM 1939-1; with Grose-Smith ♂ type label.

Paralectotypes: 6♂♂, 10♀♀, INDONESIA, Timor, Oinainisa, xi.-xii.1891, W. Doherty, BMNH(E) 229045-61 (except 229051 above), Rothschild bequest, BM 1939-1; 229052 with Grose-Smith ♀ type labels; 1♀, same data, BMNH(E)149995,

ex Grose-Smith coll., Joicey bequest BM 1934-120; 3♂♂, same data, BMNH(E) 149978-80, Oberthur purchase BM 1927-3. A further paralectotype ♂, INDONESIA, Sumbawa, ix.1891, W. Doherty, BMNH(E) 229044, Rothschild bequest, BM 1939-1; represents ssp. *tambora*.

Appias saina Grose-Smith, 1894: 336 (*Appias paulina saina* Grose-Smith, 1894)

Described from two males from ‘Humboldt Bay, Dutch New Guinea;’ and one female from ‘Biak’ Joicey & Noakes (1915) noted that ‘Smith’s male is a female’. To restrict the name to a particular subspecies the following specimen is here designated the Lectotype of *Appias saina* Grose-Smith.

Lectotype ♀, INDONESIA, Humboldt Bay, ix.-x.1893, W. Doherty, BMNH(E) 229041, Rothschild bequest, BM 1939-1; with Grose-Smith type ♂ label.

Paralectotype: ♀, BMNH(E) 229043, with same data.

A further paralectotype male from Biak, W. Doherty, BMNH(E) 229042, Rothschild bequest, BM 1939-1, with Grose-Smith type male label belongs with ssp. *falcidia*.

Supporting Information. Yata, O., Chainey, J.E. & Vane-Wright, R.I. (2010) The Golden and Mariana albatrosses, new species of pierid butterflies, with a review of subgenus *Appias* (*Catophaga*) (Lepidoptera), *Systematic Entomology*, **35**

SI 1. Discussion of hostplant relationships, coloration, polymorphism, and speciation in *Appias* (*Catophaga*) (see SI 3 for references)

Hostplant relationships

Hostplant records exist for only 5 of the 15 species of *Appias* (*Catophaga*) recognised here: *A. wardii*, *A. albina* and *A. paulina* within the *paulina* complex, *A. nero* in the *nero* group, and *A. melania* of the *melania* series. The larvae of many *Appias* and related genera are known to feed on *Capparis* (family Capparaceae—now included by many botanists within the Brassicaceae: e.g. APG II, 2003). *Capparis* is recorded as a host for all *Appias* (*Catophaga*) with records, except *melania*—which has been found only on *Drypetes* (Putranjivaceae), a genus also recorded as a host for the other four *Appias* (*Catophaga*) with records. *A. paulina* has been recorded additionally from another member of the Putranjivaceae, the genus *Putranjiva*, but this might be an error for *Drypetes* (cf. Kunte, 2006). Igarashi & Fukuda (2000) cast some doubt on the veracity of *Capparis* records for *paulina*—but apparently it is an occasional host in Australia (M. Braby, pers.comm.). In northern Australia, *A. albina* is thought to feed on *Drypetes* exclusively (Braby *et al.*, in press).

The Capparaceae belong to the order Brassicales, grouped within the “eurosids II” of the rosids (APG II, 2003). The Putranjivaceae were formerly included in the family Euphorbiaceae, both of which belong to the order Malpighiales (APGII, 2003; Wurdack *et al.*, 2004, 2005), which includes about 30 families grouped within the “eurosids I” among the rosids as a whole (APG II, 2003). Thus, although Capparaceae and Putranjivaceae belong to the rosid clade, they nevertheless belong to distinct orders within it. Utilisation of the Putranjivaceae represents a derived host-shift, as feeding on Brassicales is considered ancestral to and widespread among members of the Pierinae (Braby and Trueman, 2006; Wheat *et al.*, 2007). Reference to Robinson *et al.* (2001: 503), Binoy & Mathew (2002), Ackery *et al.* (1995), and Scott (1986), suggests that this switch could have occurred in *Appias* as a whole, as there are records for *A. (Hiposcritia) indra* from various parts of Asia, *A. sylvia*, *A. lasti* and *A. sabina*, which three belong to the African *sylvia*-species group, and *A. (Glutophrissa) drusilla* from the Americas, all feeding on *Drypetes*. (Note: the supposed record of *A. indra* feeding on *Putranjiva* by Kunte, 1998, really refers to *Drypetes*: Kunte, 2006.)

It would be very interesting to know if this utilisation of members of the Putranjivaceae as alternative hosts, generally without loss of the ability to feed on *Capparis*, is characteristic of all four genera (*Appias*, *Saletara* Distant, *Udaiana* Distant, *Aoa* de Nicéville) that make up the subtribe Appiagina (Braby *et al.*, 2006: 274). Hostplant records are far from complete even for *Appias*, and there are no records known to us for the other three genera. Feeding on Putranjivaceae by several species of *Appias* therefore might not be just “a recent secondary host [change] below the level of genus” (Braby & Trueman, 2006: 1680, and legend to fig. 1), but could characterise the whole subtribe. There is a striking concordance between the distribution map for *Appias* (*Catophaga*) as a whole (Figs 23, 24), and that of *Drypetes* within the Indo-Pacific (see map at Missouri Botanic Garden online, 2010, together with Fosberg *et al.*, 1975, and Amerson *et al.*, 1982), and this could be significant.

Feeding on Brassicales by Pierinae appears to be dependent on the ‘nitrile specifier protein’ for detoxification of the glucosinolate-myrosinase defence system of these plants, an evolutionary novelty thought to have enabled some Pierinae to switch to certain more recently evolved Malpighiales, notably *Drypetes* and its allies, that have independently developed a similar glucosinolate-based defence system (Rodman *et al.*, 1998; Wikström *et al.*, 2001; Wheat *et al.*, 2007). In this context, the unconfirmed record by Dupont & Scheepmaker (1936) that, in addition to *Drypetes*, *A. nero* feeds on *Pithecellobium* (= *Pithecolobium*; Fabaceae) is potentially interesting, as Braby & Trueman (2006: 1682) also discuss evidence that other members of the Pierinae appear, occasionally, to recolonise what they concluded to be the ancestral host group of the family Pieridae as a whole—the order Fabales (which belongs to “eurosids I”; see also Wheat *et al.*, 2007).

Pigmentation and coloration

The white, yellow, orange and brown colours of *Appias* (*Catophaga*) wings are produced by various pterins, a group of pigments belonging to the class of heterocyclic nitrogenous compounds known as pteridines (Morgan, 2004). As summarised by Descimon (2002), the principal pterins found in pierid butterflies include leucopterine and isoxanthopterine (colourless to humans), xanthopterine and sepiapterine (yellow), and erythropterine (orange-red). Descimon (1976: table 1) lists all 5 of these amongst a total of 11 different pterins derived from red-winged *A. nero*. In contrast, only the five principal sorts were isolated from the brown *A. placidia*. The deep red seen in old *Appias nero* specimens is produced by a dimeric pteridine called pterorhodine (Albert & Yamamoto, 1973: 40). This occurs in large quantities in such specimens which, however, have relatively low quantities of

erythropterine—whereas fresh orange *nero* have a high concentration of erythropterine but no pterorhodine (Descimon, 1976: table 1).

Pterin pigments in pierid wing scales are deployed typically within or in the form of bead-like pigment granules (referred to as pterinosomes by Descimon, 1976: 822), readily visible using light microscopy or SEM. For the Pieridae this represents an autapomorphy that should perhaps be regarded as correlated logically with elaboration of pterin pigments within this group, the latter treated by Ackery *et al.* (1999) as one of the characters distinguishing the family. Pterins are very uncommon in other butterflies, and have been found only in few other Lepidoptera (Descimon, 1976); however, wherever pterins do occur as pigments in the animal kingdom, they seem to be present always in the form of pterinosome granules (e.g., in fish: Hama *et al.*, 1965). Stavenga *et al.* (2004) claimed that there was no compelling evidence that these granules (which they argued should be referred to neutrally as ‘beads’) do contain pterin pigments. However, this has been confirmed by Rutowski *et al.* (2005) and Morehouse *et al.* (2007), and Descimon (1976: 822) described how they are “readily dissolved by pterin solvents”.

The blue coloration of *A. celestina*, and possibly that of *A. melania*, and the blue-grey of *A. mata* and other *Catophaga* species, may be structural. So far as we are aware, the mechanisms of colour production in these species have yet to be investigated.

Polymorphism, andromorphism and speciation

Vane-Wright (1975, 1979a,b) introduced a system of classification and nomenclature for exo-phenotypic polymorphism and sexual dimorphism in butterflies, in an attempt to understand more of the evolution of butterfly colour patterns, and especially the origin of species-specific signals. Although we have long had the idea that, in some circumstances, new colour patterns evolved first by the males of a butterfly species can be passed subsequently or *transferred* (Darwin, 1871, 1875: 394) to the female sex, the means by which new male patterns originate and the speciation processes involved remain obscure (Vane-Wright, 1978, 1984; Vane-Wright & Boppré, 1993; Penz & DeVries, 2002). Species of the subgenus *Catophaga* appear to offer very interesting examples of the transference phenomenon, as first briefly noted by Vane-Wright *et al.* (1977: 288). In the hope of stimulating further research, the main features of polymorphism and apparent colour pattern shifts in this group of butterflies are outlined below. First, however, it must be recognised that there are some limitations in applying Vane-Wright’s morph classification system (Tables 1, 2) to these butterflies.

Table 1. Summary of nomenclature employed for pattern phaneromorphism (polymorphism “manifest or readily distinguishable by inspection”: Huxley, 1955), based on Vane-Wright (1975, 1979a,b). Individual morphs are indicated by lower case roman letters (a, b, c, etc.); where a morph occurs in both sexes but is expressed somewhat differently, one of the separate expressions is indicated by the same letter with a prime symbol added (e.g. a, a’). This is expressly the case in Class 1-6, for which two entries are shown, to indicate that the more derived condition could occur in either sex. Minimum numbers of morphs are shown for each class. A species with three morphs, two expressed in both sexes but the third only in the female [a, b (2) a, b, c], would be classed as exhibiting class 3, *partial ♀-limited* polymorphism, etc. (see Vane-Wright, 1979b: 144). In the butterflies as a whole, classes 4 and 8 are exceedingly rare. In *Appias* (*Catophaga*), classes 1, 3, 1-6, 6 and 7 are known to occur, but not 4, 5, 8 or 9—unless the straw-coloured ‘sufflava’ male phenotype seen in some races of *A. nero* (e.g. *nero nero*) proves to be a true alternative to the red-orange male morph rather than a recurrent aberration—in which case these races would represent either Class 4 or Class 8 polymorphisms (dependent on whether or not the red females are considered male-like (red) or not (being far more heavily maculated; in this paper red females of *A. nero* are considered male-like).

CLASS	DESCRIPTIVE TERM	MALE MORPHS	NO. SHARED MORPHS	FEMALE MORPHS
1	<i>monomorphism</i>	a	(1)	a
2	<i>unimodal</i>	a, b	(2)	a, b
3	<i>partial ♀-limited</i>	a	(1)	a, b
4	<i>partial ♂-limited</i>	a, b	(1)	b
5	<i>partial ♂♀-limited</i>	a, b	(1)	b, c
1-6	<i>weak dimorphism</i>	a	(1)	a’
1-6	<i>weak dimorphism</i>	a’	(1)	a
6	<i>simple dual</i>	a	(0)	b
7	<i>multiple ♀ dual</i>	a	(0)	b, c
8	<i>multiple ♂ dual</i>	a, b	(0)	c
9	<i>multiple ♂♀ dual</i>	a, b	(0)	c, d

Table 2. Summary of main expressions of pattern phaneromorphism (visual polymorphism) in upperside wing coloration of *Appias* (*Catophaga*) species (and some subspecies), notated within square brackets and classified using superscript numbers corresponding to Table 1. See text for description of morphs a, b, c, c', m, p, p', w, w', x and y. The female of *A. aurosa* is unknown. Scoring *A. athama* is problematic, as the females are variable (possibly polymorphic), but usually yellow or at least yellowish in part, and always very distinct from the almost pure white males. Scoring *A. mata* is also problematic, due to the small numbers of available specimens, and doubts regarding the authenticity of certain of these.

<i>galene</i>	¹⁻⁶ [w(1)w']
<i>wardi</i>	¹⁻⁶ [w(1)w']
<i>albina</i>	³ [w(1)w'y]
<i>aurosa</i>	[?] [a(?)?]
<i>athama</i>	⁶ [w(0)y]
<i>paulina ega</i>	¹⁻⁶ [w(1)w']
<i>paulina galathea</i>	³ [w(1)w'xy]
<i>mariana</i>	³ [w(1) w'x]
<i>mata</i>	³ [m(1)m'x]
<i>galba</i>	¹⁻⁶ [o(1)o']
<i>nero nero</i>	¹⁻⁶ [o(1)o']
<i>nero flavius</i>	³ [o(1)yo']
<i>nero palawanica</i>	³ [o(1)wxyo']
<i>nero zamboanga</i>	⁶ [o(0)x]
<i>zarinda</i>	³ [o(1)wyo']
<i>placidia</i>	¹⁻⁶ [p(1)p']
<i>clementina</i>	¹⁻⁶ [c(1)c']
<i>celestina</i>	⁷ [b(0)cy]
<i>melania</i>	¹ [c(1)c]

White/yellow dimorphism can affect upper and underside patterns in *Catophaga* independently (Ferrar, 1948). Furthermore, it seems plausible that, unlike the African *Papilio* species investigated by Clarke *et al.* (1991; see also Vane-Wright & Smith, 1991), in which the occurrence of the male-like female morph is controlled by the same locus that switches on the alternative (mimetic) female colour patterns (the H locus: Clark *et al.*, 2008), the present system, in some of the species at least, may involve at least two loci, one partially or even entirely epistatic to the other. Other complications arise due to seasonal polyphenism, and/or an apparent interaction between major and minor genes, so that unequivocal assignment of all individuals to particular morphs can be problematic.

Restricting observation to the *upperside* wing patterns, the primary (signal) colours of male *Catophaga* are unimodal (monomorphic)—the upperside patterns of male *Catophaga* are never polymorphic, with the possible exception of *A. nero*, in which a straw-coloured 'sufflava' variant can occur at low frequency (Fig. 21T; Yata, 1981: p.99, fig. 11). However, this phenotype could reflect a metabolic deficiency rather than represent a balanced polymorphism (cf. Yata, 1981: p.99, figs 12–15). We have seen a few male *A. galba* that approach this condition (e.g. Fig. 21C), but no *A. zarinda*.

Thus, dependent on species, males of *Catophaga* are white (w: *galene*, *wardii*, *albina*, *paulina*, *athama*, *mariana*), golden-yellow (a: *aurosa*), flame orange (o: *galba*, *nero*, *zarinda*), dark brown (p: *placidia*), bluish-grey (m: *mata*), pale sky-blue (b: *celestina*) or white and greyish-blue (c: *clementina*, *melania*). Females can be unimodal, more or less male-like (w', p', c, c', or o'; note primes denote forms that are similar to but not identical to a corresponding form in the opposite sex), di-morphic white or yellow (w' + y), di-morphic white with greyish-blue or yellow (c + y), tri-morphic white, yellow or male-like (w' + y + o'), or even quadrimorphic if the white-forewing + yellow-hindwing form (x), first noted by Ferrar (1948) in *A. paulina galathea* (w + x + y), is genetically distinct from the all-white and all-yellow forms—as seen for example in female *nero* from Palawan (w + x + y + o'). A further complication arises in the case of "black" *A. albina albina* female form from Sulawesi (Fig. 19P), which occurs in broad- and narrow-bordered variants. The main variations in morphism are presented in Table 2, using (as far as possible) the system of Vane-Wright (1975, 1979a,b) for each of the 15 species, including more than one subspecies where necessary (e.g. *A. nero*) to illustrate polytypic (geographical) variation in polymorphism.

Many species of Pieridae exhibit class 3 polymorphism (Vane-Wright, 1975; Table 1), having plesiomorphic white or yellow males with corresponding but polymorphic females (white and yellow)—a condition exhibited in some *Catophaga* (e.g. *albina*, and *paulina galathea* from the Nicobars).

However, as indicated above, the male-like females are rarely identical in pattern to the males: almost invariably they are more heavily marked with black so that, if the non-male-like morphs are not expressed, we then see what Vane-Wright (1979a) described as “weakly dimorphic species” (class 1-6: e.g. *galene*, *wardii*, most populations of *paulina*). If, on the other hand, the plesiomorphic white morph is suppressed in the male and replaced by an apomorphic colour (e.g. orange, blue, brown), then we see a variety of systems in the females, ranging from retention of one or more largely plesiomorphic female forms to give class 6 or 7 polymorphisms (e.g., *A. celestina*), to adoption of a comparable colour to the male (class 1-6 and class 1 morphisms: e.g. *A. placidia*), or various class 3 “intermediates”, in which one or more plesiomorphic white or yellow female morphs co-occur with apomorphic male-coloured females (the best example being *A. nero palawanica*, from Palawan, and *A. zarinda* from Sulawesi—although in these species, and especially the latter, all females are far more heavily maculated than the males).

Vane-Wright (e.g. 1981, 1984) suggested that such variations in morphism can be interpreted as shifts in male colour pattern associated with speciation events, followed by corresponding shifts in female colour pattern that may occur relatively rapidly or in tandem (the latter is plausibly the case in *A. placidia*), or have yet to occur (and may never do so)—e.g. *A. nero zamboanga* and *A. nero domitia* from the Philippines, and *A. celestina*. Where a shift in female colour does not occur initially but does develop later, we may see a fixed or transient class 3 polymorphism, in which apomorphic male-like and non-male-like female forms co-exist (as in *A. nero palawanica*, and *A. zarinda*). As indicated above, arguably this corresponds to the Darwinian process of *transference*, or *cross-sexual transfer* (West-Eberhard, 2003).

In this context, butterflies may be of exceptional interest because different populations of the same species could represent different stages in the transference process. For example, in the eastern part of its range, *Appias nero* exhibits a northeast-southwest polymorphism morphocline which starts with subspecies *nero zamboanga* and *n. domitia* (Philippines), which completely lack male-like females, through *n. palawanica* (Palawan), which has in addition male-like females, to *n. flavius* (Turtle Islands, off north coast of Borneo), which lacks white females, and finally *n. nero* in Borneo—which lacks all non-male-like female forms, leaving by subtraction only the orange, male-like female morph (*secondary sexual monomorphism* in the sense of West-Eberhard, 2003: 262, 264). This sequence for *A. nero* can be presented as a “pathway model” (Vane-Wright, 1979a,b):

T₁ ⁷[o (0) x,y,w] (hypothetical, but approached by main Philippine races)

T₂ ³[o (1) o',x,y,w] (Palawan)

T₃ ³[o (1) o',y] (Turtle Islands)

T₄ ¹⁻⁶[o (1) o'] (Borneo, Java, Sumatra, Malay Peninsula)

As suggested by Vane-Wright (1979b: 146), this would fit with the theoretical generalisations that class 7 most readily transforms to 3, 6 or 7, and that class 3 transforms to 1, 2, 3 or 6 (or, in this case, 1-6). However, it leaves open the question of the origin of the orange male morph. If we were to assume that the orange male-like female morph of *nero* represents the initial state (*primary sexual monomorphism*: West-Eberhard, loc. cit.) for the subsequent evolution of polymorphism in the more easterly populations of this species, then such an evolutionary sequence could have progressed in the opposite direction. Given the widespread occurrence of white/yellow polymorphism in female Pierinae, including many *Catophaga* species, the latter interpretation seems less parsimonious.

Following the original suggestions of Sheppard (1958: 139–140, 145), and according to the arguments of Vane-Wright (1979b), Vane-Wright & Smith (1991) and Clarke *et al.* (1985), in systems involving disruptive selection for multiple colour morphs, genetic dominance may provide the best evidence for settling such questions. As Nijhout (2003) succinctly concludes, despite differences regarding the precise mechanisms involved, “the order of dominance [the dominance hierarchy] is likely to reflect the order of origin of the phenotypes.” *A. nero palawanica* is thus a potentially crucial example. On the transference model we would expect the orange male-like females to be dominant, or largely so, to all alternative yellow and white female forms that occur in this island race. On the alternative hypothesis, involving the sequential replacement of male-like coloration by white and yellow morphs, the orange phenotype should be the universal recessive. The generality of any such findings could be tested by determining dominance relationships in other polymorphic races, such as *A. nero flavius*, *A. zarinda zarinda*, and *A. z. buruana*. Further insights could well be obtained from subspecies crosses (e.g. *A. nero nero* x *A. n. domitia*), or even species hybrids (e.g. *A. galba* x *A. zarinda*).

The species of *Appias* (*Catophaga*) raise several other interesting genetic questions. These include the mode of inheritance and developmental control in populations like *A. paulina galathea* inhabiting the Nicobar Islands, in which six female morphs apparently occur (three upperside morphs, w, x, y, each of which can have white or yellow undersides; Figs 20B–E; Ferrar, 1948). The upperside ‘piebald’ form (whitish forewing + yellowish hindwing) is seen in other *Catophaga* species (e.g. *A. mata*, Fig. 20S; *A. nero*, Fig. 21H), and would appear to be controlled by a separate allele (no “reverse” form,

with yellow forewing and white hindwing, is known). Whether or not white/yellow heterozygotes produce this form, or pale yellow morphs, or if white or yellow is dominant, is unknown. In those *Colias* butterflies that have been adequately investigated, white is an autosomal (female-limited) dominant to yellow (Remington, 1953; Robinson, 1971), heterozygous *Colias* females thus exhibiting the white *alba* phenotype.

Underside coloration, at least in *A. paulina galathea*, appears therefore to involve an independent dimorphism—and this could well affect other species. Female *A. placidia* appear to be dimorphic beneath, with most individuals silvery-white, but a few distinctly silvery-yellow. In this species the females are all brown above, like the males. The question then arises: is this because they are not polymorphic for upperside coloration, or is it because the male-like colour is epistatic, being controlled by a separate locus that completely masks any underlying polymorphism that would otherwise be expressed on the upperside?

Such questions require that we understand the genetic control and origin of the bright (male) colours in such species as *A. nero* (orange-red), *A. placidia* (brown) and *A. celestina* (blue). A striking aberration of *A. nero figulina* from the Malay Peninsula (Fig. 22A), which is entirely brown and looks at first sight like *A. placidia*, suggests that a single gene might easily control the specific colour changes. A striking female sexual mosaic of the same subspecies (Fig. 22D) suggests that the male and female red pigmentation might not be the same (unless the difference is due to sex-linkage or a 'dose' effect, the female cells being XO while the male cells are XX; however, most sexual pattern differences in butterflies are due to sex limitation, not sex linkage). This in turn raises the possibility that male-like orange-red coloration in female members of the *nero*-group is due to a separately evolved gene that produces a different pigment—in effect, the male-like female morphs seen widely in this group could be male mimics.

This then raises the question of an important distinction made by West-Eberhard (2003: 264)—are male-like females of e.g. *A. nero nero* due to homology (true cross sexual transfer, involving activation in the females of those genes responsible for male coloration), or are they the result of convergence (in this case, potentially a genuine example of intraspecific mimicry). An excellent example of convergence occurs in various bush crickets in which the females, like the males, sing—but the female stridulatory apparatus is radically different to that of the males, and is considered to have evolved independently (Heller & von Helversen, 1986).

The male colours of *placidia*, *celestina* and the three *nero*-group species are very unusual for pierid butterflies. This, and their seemingly legitimate inclusion in *Catophaga* with other species that have "conventional" white/yellow coloration in both sexes, strongly suggests that the unusual male colours have evolved in these butterflies during, or in some way closely associated with speciation events. As such, these cases appear to fit a generalization drawn by Charles Darwin: "Various facts support the conclusion that with the greater number of brilliantly-coloured Lepidoptera, it is the male which has been modified" (Darwin, 1871: 409). A variety of plausible mechanisms, not all mutually exclusive, have been proposed to account for such marked shifts in species-specific male signal traits during speciation, including the following:

- a) Darwin's sexual selection hypothesis (Darwin, 1871: i, 278, 403)—males diverge in phenotype due to female preferences affecting courtship success (see also Kottler, 1980; however, according to Turner, 1978, writing about why male butterflies are less often mimetic than female butterflies "sexual selection resists colour changes especially strongly in males").
- b) Fisher's runaway sexual selection hypothesis (Fisher, 1930: 152)—involving genetic correlation of male traits and female preferences.
- c) Natural selection (Wallace, 1889: 296)—female preferences evolve due to benefits from mating with the genetically fittest males, the quality of which can be assessed, at least initially, by their signal quality (see also Kottler, 1980; Rutowski, 1998; Kunte, 2008).
- d) Sexual selection for sensory exploitation (Ryan *et al.*, 1990)—males evolve traits that make the most of pre-existing biases in the female sensory system.
- e) Male intrasexual selection (Silberglied, 1984: 220)—males gain an advantage in agonistic, territorial and mate-location behaviour through specific advertisement of their own sex (see also Wallace, 1889: 296).
- f) Learned mate recognition and mutual benefit in avoidance of harassment can lead to selection for male divergence in colour pattern (Fincke, 2004; but see also Rivera & Sánchez-Guillén, 2007).

Robert Silberglied's (1984) work suggests that, in the case of many butterflies, the bright colours of males seem of little significance to the females—the traits that they are more interested appear to concern behaviour and smell. If so, then mechanisms a–d may not explain male colour pattern divergence between butterfly species in general. But whatever selection process is responsible for bringing about divergence in male signal phenotype in the first place, *at the time of evolution of the trait*, this can give rise to three broad categories of outcome with respect to sexual dimorphism:

- i) Marked sexual dimorphism (males diverge, females remain more or less unaltered)
- ii) Weak sexual dimorphism (female phenotype changes in the direction of the male change, but not to the same extent)
- iii) No sexual dimorphism (both sexes change equally, in tandem: see Wallace, 1871: 247; also Kottler, 1980)

Subsequently, sexual or natural selection acting on the females can eliminate sexual dimorphism with regard to the trait, increase it—or bring about a separate divergence of the female phenotype. There is circumstantial evidence that many of these processes can be observed in butterflies, and that several of them appear to have occurred, and are even still in progress, in *Catophaga*.

Dynamics of polymorphism

Regardless of the evolutionary pathways by which the polymorphism has built up, its continuing existence as a stable or quasi-stable system within a population, race or species implies that some selective dynamic is at work—unless we assume that recurrent mutation is responsible—something which seems extremely unlikely in the present case. At least two factors are likely to be involved—differential selection values for the individual morphs, and ensemble effects (e.g. frequency- and/or density-dependent selection). Together these provide the necessary conditions for disruptive and balancing selection.

The most widespread polymorphism seen in pierid butterflies is the yellow/white ('*alba*') dimorphism affecting the females of many species in both the Pierinae and Coliadinae. The best known examples occur in the genus *Colias*, in which the male-like and *alba* females are considered to have different thermal, physiological and mate-attraction properties (e.g. Hovanitz, 1948; Watt, 1973, 2003; Nakanishi *et al.*, 2000; Ellers & Boggs, 2003).

Such variations are by no means limited to Pieridae. Thus Punzalan *et al.* (2008) have shown that dark males of the polymorphic ambush bug (*Phymata americana*; Hemiptera) almost certainly have a mating advantage in cool conditions. Vane-Wright (1984) speculated that, in polymorphic butterflies, male-like females could have a mating advantage as a result of male visual mate locating behaviour (Vane-Wright & Boppré, 1993), a view that is consistent with the classic investigations of Magnus (1958) on the nymphalid *Argynnis paphia*—in which the olive, non-male-like 'valesina' form of the female is less attractive to males than the golden-brown male-like female morph. Alternatively, male-like females may have an oviposition advantage, in certain contexts being less attractive to males than alternative morphs, and thus subject to less harassment. Evidence from Cook *et al.* (1994) suggested that this was the case with *Papilio dardanus* on the island of Pemba (Tanzania)—mimetic, non-male-like female morphs were *more* attractive to males than male-like (yellow) females, suggestive of a potential trade-off between improved long-term survival *versus* less distraction while egg laying. The dragonfly *Ischnura ramburi* exhibits a female limited polymorphism regarding which it has been speculated that the bright, male-like females gain an advantage, either through a reduction in the number of mating attempts, or a reduction in interference during oviposition (Robertson, 1985).

In *Appias* (*Catophaga*), the most striking female polymorphisms, as in *A. nero palawanica* and *A. zarinda*, essentially involve three female forms: white, yellow and male-like (bright orange-red). At present we can only speculate that the basic selection regime involves some combination of different microclimatic and/or bio-energetic tradeoffs (yellow vs white morphs), and male attractiveness or male avoidance advantages (orange morphs).

Once established, a further complication usually affects selection regimes in such systems: relative density, or more especially in dispersive organisms such as butterflies, relative frequency. In other words, selection values are not fixed or absolute, but depend on relative frequency. The selective value of a given morph will either tend to increase as its frequency increases within the population (frequency enhancement of selective value), or decrease (frequency attenuation). The former is rarely discussed in the context of polymorphism as it will act like a positive feedback mechanism, to eliminate other morphs rapidly and lead to fixation—thus producing a directional rather than stabilising selection effect. This is the dynamic normally taken to drive Müllerian mimicry.

Frequency attenuated selection (terminology of Vane-Wright, 1976) is referred to more often as "negative frequency dependent selection" (e.g. Fincke, 2004; Punzalan *et al.*, 2005; Rainey & Grether, 2007). Within such a system, if any particular morph declines in relative frequency, its selective value in relation to other morphs within the population rises. Some such selective regime, which can result in balanced polymorphism through negative feedback, is likely to be operating in *Catophaga*—due to rare mating advantage, apostatic selection, and/or other frequency attenuated effects (see Punzalan *et al.*, 2005, for a useful review of frequency effects due to predation; also Fincke, 2004: table 1). However, to our knowledge no investigations have been undertaken to determine what factors maintain the apparently stable or quasi-stable polymorphisms affecting the females of so many *Catophaga* species and populations.

Supporting Information. Yata, O., Chainey, J.E. & Vane-Wright, R.I. (2010) The Golden and Mariana albatrosses, new species of pierid butterflies, with a review of subgenus *Appias* (*Catophaga*) (Lepidoptera), *Systematic Entomology*, **35**

SI 2. Type material of *Appias* (*Catophaga*) taxa with special reference to the Natural History Museum collection, London (BMNH). References in SI 3.

The following list catalogues all the type specimens of *Appias* (*Catophaga*) thought to be housed in the collections of the BMNH. The list is alphabetic by taxon at infraspecies level, and refers to 103 names (for a few of which no type material has been found). This information is intended to facilitate access to the type material of this group by future workers. For completeness, the list includes 'type' specimens of infrasubspecific and unavailable names which, although not governed by I.C.Z.N. regulations, are treated here in the same way as the type material of available names. Available names are given in bold. In addition, those taxa not represented by type material in the BMNH are also listed briefly (50 in total), together with three taxa described within *Catophaga* but now excluded. Finally, a combined bibliography is presented (SI3), which includes all the works referred to in the main printed text of this paper and its two printed appendices, as well as all the works referred to in this online appendix.

Taxa represented by type material in BMNH

***adamsoni* Moore, 1905**

Catophaga adamsoni Moore, 1905: 4

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, BURMA, Thaungying Valley, iv.1893 / BMNH(E)#142282 / Joicey bequest BM 1934-120 / hand-written label "Catophaga adamsoni ♂ (wet) (type)";

syntype ♀, same locality, ex Grose Smith coll. / BMNH(E)#149946;

syntype ♂, same locality, T. Hauxwell, ex Grose Smith coll., BMNH(E)#149945;

syntype ♀, BURMA, Dounat Range, iv.1893, ex Grose Smith coll., BMNH(E)#142283, Joicey bequest BM 1934-120, with hand-written label "Catophaga adamsoni ♀ (wet) (type)";

syntype ♂, BURMA, Daunat Range, 13.v.1893, Bingham, BMNH(E)#229021, Rothschild bequest, BM 1939-1, with hand-written label "Catophaga Adamsoni ♂ (dry) (type)";

syntypes 2 ♂♂, BURMA, Muong Gnow, 229019-20, Rothschild bequest BM 1939-1, BMNH(E)#229019 with hand-written label "Catophaga Adamsoni ♂ (dry) (type)".

syntype ♂, BURMA, Rangoon, iv.1887, Noble, BMNH(E)#229169, Swinhoe coll. BM 1926-239, with hand-written label "Catophaga Adamsoni ♂ (Dry) (type)".

aegina Fruhstorfer, 1910

Appias melania terentilia f. *aegina* Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina terentilia* Fruhstorfer, 1910.

Syntype ♀, PHILIPPINES, Palawan, i.1898, W.Doherty, ex coll. Fruhstorfer, BMNH(E)#142303, with Fruhstorfer label "♀ forma aegina Fruhst.";

syntype ♀, PHILIPPINES, Palawan, 1898, W.Doherty BMNH(E)#229029, Fruhstorfer purchase, BM 1937-285

***agar* Fruhstorfer, 1910**

Appias clementina agar Fruhstorfer, 1910: 152

Current status: junior subjective synonym of *Appias clementina* (C.Felder, 1860) SYN.N

Syntype ♂, INDONESIA, Damar, BMNH(E)#135586, Fruhstorfer purchase BM: 1937-285;

syntypes 6 ♂♂, INDONESIA, Damar [as Dammer], BMNH(E)#135595-600, Fruhstorfer purchase BM: 1937-285;

syntype ♂, INDONESIA, Damar, 1906, K.Grubert, BMNH(E)#135601, Levick bequest BM: 1941-83, with Fruhstorfer label "clementina agar Fruhst.";

syntypes 3 ♂♂, 4 ♀♀, INDONESIA, Babar, BMNH(E)#135587-93, Fruhstorfer purchase BM: 1937-285;

syntype ♂, INDONESIA, Tenimber, Kuhn, BMNH(E)#135594, Fruhstorfer purchase BM: 1937-285;

syntype ♂, INDONESIA, Kep.Tenimbar, Selaru, BMNH(E)#135602, Fruhstorfer purchase BM: 1937-285, with Fruhstorfer label "agar Fruhst."

***agave* Felder & Felder, 1862**

Pieris melaniae agave Felder & Felder, 1862: 286

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, PHILIPPINES, Luzon, Lorquin, ex Felder coll., BMNH(E)#229230, Rothschild bequest, BM 1939-1, with printed label "agave n" and "FELDER COLLN" and handwritten label "Luzon, Lorquin".

alcesta Talbot, 1939

Appias leis adamsoni f. *alcesta* Talbot, 1939: 410 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina darada* (Felder & Felder, 1865). SYN.N.

Holotype ♀, BURMA, Karen Hills, 2000', 9.xi.1920, W.H.Evans, BMNH(E)#142281, with hand-written label "A. leis adamsoni dry f. alcesta Talb. ♂ type". This specimen is actually a ♀ *Appias albina darada* (Felder & Felder).

No details of any other specimens are given, although the description includes mention of female material

***alope* Wallace, 1867**

Tachyris alope Wallace, 1867: 372

Appias paulina alope (Wallace, 1867)

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Type locality here restricted to Java. A lectotype designation is required, but the type status of available material is questionable

Syntype? ♂, INDONESIA, Java, *amasene*, Dr. Horsfield, BMNH(E)#229127, slide no. Rh. 4653, with hand-written label "Java 33a/Catophaga alope Wallace";
syntype? ♂, INDONESIA, Java, A. R. Wallace, ex Bates coll., BMNH(E)#229173, pres. Godman Salvin BM 1896-12;
syntype? ♂, INDONESIA, Sumatra, S. Raffles coll., BMNH(E)#229128, Purchase Stevens BM 1854-76, with hand-written label "Sumatra 54.76/Catophaga alope Wallace". This specimen has the best credentials to be a type specimen; however, it is identifiable with ssp. *pione*. It is also a possible syntype of *Catophaga distanti* Moore, 1905.
Syntype?? [i.e. unlikely] ♂, Borneo, BMNH(E)#229126, Moore purchase, BM 1899-234, with hand-written label "P. alope Wall."

***ambigua* Grose Smith, 1895**

Appias ambigua Grose Smith, 1895: 76
Current status: valid subspecies of *Appias albina* (Boisduval, 1836).
Lectotype ♀, INDONESIA, Wetar, v.1892, W. Doherty, BMNH(E)#135769, Rothschild bequest BM 1939-1; with hand-written label "Ambigua Grose Smith Type ♀".
Paralectotypes: 1 ♀, INDONESIA, Wetar, v.1892, W. Doherty, BMNH(E)#135770, Rothschild bequest BM 1939-1, 1 ♀, INDONESIA, Dili, v.1892, W. Doherty, ex Grose Smith coll., BMNH(E)#149931, Joicey bequest BM 1934-120.

***antoniae* Fruhstorfer, 1910**

Appias melania antoniae Fruhstorfer, 1910: 156
Current status: valid subspecies of *Appias paulina* (Cramer, 1777).
Syntypes 1 ♂, 1 ♀, INDONESIA, Ceram, BMNH(E)#142311-2, Fruhstorfer purchase BM:1937-285, BMNH(E)#142311 with Fruhstorfer label "antoniae Fruhst.";
syntypes 3 ♂♂, 2 ♀♀, INDONESIA, Ceram, H. Fruhstorfer, BMNH(E)#229035-9, Fruhstorfer purchase, BM 1937-285;
syntype ♂, INDONESIA, Saparua, H. Fruhstorfer, BMNH(E)#229040, Fruhstorfer purchase, BM 1937-285.

***argentifera* Joicey & Talbot, 1928**

Appias paulina argentifera Joicey & Talbot, 1928: 19
Current status: junior subjective synonym of *Appias athama psyche* (Felder & Felder)
Lectotype ♀, NEW CALEDONIA, Loyalty Is., ex Grose Smith coll., BMNH(E)#141741, Joicey bequest BM 1934-120, with printed label "A. paulina argentifera J&T 1928 ♀ A.T.". Identifiable with *Appias athama* (Blanchard, 1848).
Paralectotype ♂, NEW CALEDONIA, Loyalty Is., Lifou, Lomar ?, BMNH(E) 142321, Joicey bequest BM 1934-120, with printed label "A. paulina argentifera J&T 1928 ♂ H.T.". Identifiable with *Appias paulina ega* (Boisduval, 1836)

***arida* Talbot, 1939**

Appias wardi f. arida Talbot, 1939: 407.
Current status: junior subjective synonym of *Appias wardii* (Moore, 1884).
Holotype ♂, INDIA, Nilgiris, 3500', 8.iii.1886, BMNH(E)#142279, L. Hampson purchase BM 1889-62, with hand-written label "A. wardi dry form arida Talb. ♂ type";
paratype ♀, INDIA, Karnataka, Kanara, Kutgu, iii.1894, Davidson, BMNH(E)#142280, Davidson bequest BM 1925-574, with hand-written label "A. wardi dry form arida Talb. ♀ allotype". This specimen is a large example of *Appias albina swinhoei* (Moore).

***athena* Fruhstorfer, 1903**

Appias melania athena Fruhstorfer, 1903a: 287.
Current status: valid subspecies of *Appias paulina* (Cramer, 1777).
Syntype ♀, MALAYSIA, Sabah, ex Fruhstorfer coll., BMNH(E)#142293, with Fruhstorfer label "melania athena Fruhst.";
syntypes 4 ♀♀, MALAYSIA, Sabah, BMNH(E)#229129-32, Fruhstorfer purchase BM 1937-285;
1 ♂, BRUNEI, 1890, Waterstradt, BMNH(E)#142292, with hand-written label "♂ Neallotype athena Fruhst., 1902, selected by G.T[albot], 10.x.1940" has no type status.

***aurifera* Fruhstorfer, 1910**

Appias celestina f. aurifera Fruhstorfer, 1910: 151 [infrasubspecific and unavailable name]
Current status: unavailable synonym of *Appias c. celestina* (Boisduval, 1832).
Syntypes 2 ♀♀, INDONESIA, Waigeu, H. Fruhstorfer, BMNH(E)#135574-5, Fruhstorfer purchase BM: 1937-285, BMNH(E)#135574 with Fruhstorfer label "♀ forma aurifera Fruhst.". BMNH(E)#135575 with Fruhstorfer label "aurifera Fruhst.";
syntype ♀, "New Guinea", Aroa BMNH(E)#135612, Fruhstorfer purchase BM: 1937-285.

***aurora* Yata & Vane-Wright, sp. n.**

Holotype ♂ paratypes 12 ♂♂, INDONESIA, Sulawesi, Macassar, 1896, W.Doherty, BMNH(E)#149984, BMNH(E)#229197-207, BMNH(E)#229236, Oberthür purchase BM 1927-3 [BMNH(E)#229204 also with slide no. Rh4618, BMNH(E)#229205 with slide no. Rh4598, BMNH(E)#229206 with slide no. Rh4598], BMNH(E)#229207 with Fruhstorfer label "zarinda ab. aurora Fruhst."

***aurora* Fruhstorfer, 1899**

Tachyris zarinda ab. aurora Fruhstorfer, 1899b: 84 [infrasubspecific and unavailable name]
Current status: unavailable objective synonym of *Appias aurora* sp.nov.
Syntypes 13 ♂♂ (see *aurora* sp. n. above).

***barea* Fruhstorfer, 1910**

Appias celestina barea Fruhstorfer, 1910: 151.
Current status: valid subspecies of *Appias celestina* (Boisduval, 1832).
Syntype ♂, INDONESIA, Aru, H. Fruhstorfer, BMNH(E)#135576, with Fruhstorfer label "celestina barea Fruhst."
3 ♀♀, from Aru, ex Fruhstorfer coll., do not fit the description of the underside and are excluded from the type series.

***baweanicus* Fruhstorfer, 1905**

Tachyris nero baweanicus Fruhstorfer, 1905: 45.
Current status: valid subspecies of *Appias nero* (Fabricius, 1793).
Syntypes 10 ♂♂, 1 ♀, INDONESIA, Bawean, July-September, H. Fruhstorfer, BMNH(E)#141757 (♀), BMNH(E)#229180, BMNH(E)#229212-20, Fruhstorfer purchase BM 1937-285, BMNH(E)#141757 with Fruhstorfer label "nero baweanicus Fruhst.";

syntypes 2 ♂♂, same data but wet season, BMNH(E)#229181-2, BMNH(E)#141756, latter with Fruhstorfer label "nero baweanicus Fruhst."

***bouruensis* Wallace, 1867**

Tachyris bouruensis Wallace, 1867: 379.

Current status: valid subspecies of *Appias zarinda* (Boisduval, 1836).

No type material located. Butler (1872) states "the type should be in Hewitson's collection [now in BMNH], but was probably not in good enough condition to induce him to retain it".

***caeca* Corbet, 1941**

Appias paulina caeca Corbet, 1941: 497.

Current status: valid subspecies of *Appias mata* (Kheil, 1874).

Holotype ♂ and paratype ♂, INDONESIA, Siporo I., x.1924, G.B.K. & N.S., BMNH(E)#142295 and BMNH(E)#135615, (BM 1942-21) BMNH slide Rh4627.

***caledonica* Felder, C., 1862**

Pieris melania var. *caledonica* Felder, 1862: 495.

Current status: junior subjective synonym of *Appias paulina ega* (Boisduval, 1836).

1 ♂, labelled "Pieris melania New Caled" in Rothschild coll. (BM 1939-1) may be a syntype.

***celestina* Boisduval, 1832**

Pieris celestina Boisduval, 1832: 46.

Current status: valid species.

♂, "New Guinea", ex Boisduval collection, BMNH(E)#135613, Oberthür purchase, BM.1927-3, with printed label "EX MUSAEODRIS BOISDUVAL", hand-written labels "Celestina B. Dp. Nov. Guinee" and "Apparently the specimen described by Boisd (1836: 484) as the female of his celestina (G.T[albot])" and with Fruhstorfer label "Galepsus Fruhst. In Seitz Plate 61e ♂". Although supposedly from New Guinea, this specimen agrees with material from the islands of Kep. Kai. However, it does not agree with original description and is not considered to be type material.

***chelidon* Fruhstorfer, 1905**

Tachyris nero chelidon Fruhstorfer, 1905: 45.

Current status: valid subspecies *Appias nero* (Fabricius, 1793).

Syntype ♀, "North Borneo", ex coll. Fruhstorfer, BMNH(E)#141759, with Fruhstorfer label "nero chelidon Fruhst."

***citrina* Fruhstorfer, 1910**

Appias albina micromalayana f. *citrina* Fruhstorfer, 1910: 154 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina ambigua* (Grose Smith, 1895).

Syntypes 4 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#135792-4, BMNH(E)#142262, Fruhstorfer purchase BM:1937-285, BMNH(E)#136792 and BMNH(E)#142262 both with Fruhstorfer label "♀ forma citrina Fruhst.";

syntypes 5 ♀♀, same data, BMNH(E)#135795-8, BMNH(E)#135801, Rothschild bequest BM 1939-1, BMNH(E)#135801 with Fruhstorfer label "ab. flavia Rob.";

syntypes 3 ♀♀, same data, BMNH(E)#135799-800, BMNH(E)#149997 Oberthür purchase BM 1927-3;

syntypes 2 ♀♀, same data, BMNH(E)#135803-4, Crowley bequest BM 1901-78;

syntypes 2 ♀♀, same data, unregistered;

syntype ♀, same locality, iv.1896, BMNH(E)#135802, Fruhstorfer purchase BM:1937-285;

syntype ♀, same locality, iv.1896, BMNH(E)#149935, J.J.Joicey bequest BM 1934-120;

syntypes 2 ♀♀, same data, unregistered;

syntype ♀, INDONESIA, Java, 1500', 1891, H. Fruhstorfer, BMNH(E)#135805, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "♀, forma citrina Fruhst."

***citronella* Fruhstorfer, 1897**

Tachyris flavia ab. *citronella* Fruhstorfer, 1897: 392 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina ambigua* (Grose Smith, 1895).

Syntypes 3 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#135725-7, BMNH(E)#142260, Fruhstorfer purchase BM:1937-285, BMNH(E)#135725 and BMNH(E)#142260 with Fruhstorfer label "ab. citronella Fruhst.", BMNH(E)#135726 with Fruhstorfer label "citronella Fruhst.";

syntype ♀, same data, BMNH(E)#135728, Rothschild bequest BM 1939-1.

syntype ♀, same data, with Fruhstorfer label "ab. citronella Fruhst.", unregistered.

***clementina* Felder, C., 1860**

Pieris clementina Felder, 1860: 448.

Current status: valid species.

Syntype ♂, no data, ex Felder collection, BMNH(E)#135614, BMNH slide Rh4692, with printed labels "clementina n." and "FELDER COLLN".

***coelitus* Fruhstorfer, 1899**

Tachyris nero palawanica ab. *coelitus* Fruhstorfer, 1899b: 84 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias nero palawanica* Staudinger 1889.

Syntype ♀, PHILIPPINES, Palawan, 1898, W.Doherty, BMNH(E)#141760, Fruhstorfer purchase BM1937-285, with Fruhstorfer label "coelita Fruhst."

***confusa* Fruhstorfer, 1910**

Appias albina confusa Fruhstorfer, 1910: 154 (as nom.n. for *darada* auct. nec Felder) [preocc. Butler, 1872]. The type series is restricted to males, as Fruhstorfer states that females belong to named forms, i.e. *principalis* Fruhstorfer and *semiflava* Fruhstorfer.

Current status: junior subjective synonym of *Appias albina darada* (Felder & Felder, 1865).

Syntype ♂, BANGLADESH [as India], Silhet, BMNH(E)#135639, Moore purchase BM: 1903-361.

syntype ♂, INDIA, Mizoram, Lushai [as Looshai], BMNH(E)#135638, Moore purchase BM: 1903-361, Moore fig., 1905, 557, 1;

syntypes 2 ♂♂, BURMA, Moulmein, BMNH(E)#135640, BMNH(E)#135642, Moore purchase BM: 1903-361, BMNH(E)#135640, Moore fig., 1905, 557, 1a;

syntype ♂, BURMA, Upper Tenasserim, BMNH(E)#135641, Moore purchase BM: 1903-361;
 syntype ♂, BURMA, Palene, i.1887, Noble, "wet", BMNH(E)#149962, Swinhoe coll. BM 1926-239;
 syntypes 5 ♂♂, INDIA, Meghalaya [as Assam], Khasi Hills, BMNH(E)#135627-31, Fruhstorfer purchase BM 1937-285,
 BMNH(E)#135627 with Fruhstorfer label "darada F & F.";
 syntypes 3 ♂♂, INDIA, Sikkim, BMNH(E)#135632-4, Fruhstorfer purchase BM 1937-285;
 syntype ♂, INDIA, Deesa BMNH(E)#135635, Fruhstorfer purchase BM 1937-285 ;
 syntype ♂, INDIA, Parisnath, 26.ix.1858, W.S.Atkinson, BMNH(E)#135643, Moore purchase BM: 1903-361;
 syntype ♂, INDIA, Assam, Dibrugarh, BMNH(E)#135644, Rothschild, bequest, BM 1939-1, with hand-written label "Darada ♂
 wet";
 syntype ♂, THAILAND, Kanburi, April, H. Fruhstorfer, BMNH(E)#135636, Fruhstorfer purchase BM 1937-285, with Fruhstorfer
 label "albina confusa Fruhst.";
 syntype ♂, THAILAND, Chentaboon, 1.i.1901, H. Fruhstorfer, BMNH(E)#135637, Fruhstorfer purchase BM 1937-285;
 syntype ♂, VIETNAM, Than-Moi, June-July, H. Fruhstorfer, BMNH(E)#135617, Fruhstorfer purchase BM 1937-285;
 syntype ♂, same data BMNH(E)#135618, Rothschild bequest, BM 1939-1;
 syntypes 3 ♂♂, VIETNAM, Chiem-Hoa, August-September, H. Fruhstorfer, BMNH(E)#135619, BMNH(E)#135624-5, Fruhstorfer
 purchase BM 1937-285;
 syntypes 4 ♂♂, same data BMNH(E)#135620-3, Rothschild bequest, BM 1939-1;
 syntypes 4 ♂♂, same data BMNH(E)#149951-4, Oberthür purchase BM 1927-3;
 syntype ♂, VIETNAM, Mt.Mauson, 2-3000', April-May, H. Fruhstorfer, BMNH(E)#135626, Rothschild bequest, BM 1939-1;
 syntype ♂, same data BMNH(E)#149955, Oberthür purchase BM 1927-3.

***cynisca* Wallace, 1867**

Tachyris cynisca Wallace, 1867: 375

Current status: junior subjective synonym of *Appias albina albina* (Boisduval, 1836) SYN.N.

Syntype ♀, INDONESIA, Buru, A.R.Wallace, Hewitson bequest, 1879-69, with label "Hewitson coll. 79.69 Pieris cynisca, Wall.
 1" and Wallace labels "Cynisca Wal." and "♀ Bour" pasted underneath. This specimen is smaller than the description
 indicates, but otherwise fits quite well. There is also a similar specimen in BMNH from unknown locality with a label "cynisca,
 same as type". Butler (1898) states that the type of *cynisca* was in Hewitson's collection and there seems to be little doubt
 that the above Wallace specimen has been regarded as the type. There is also no doubt that this specimen is *Appias albina*
albina (Boisduval), and not *A. paulina* (Cramer) as has been previously recognised. A new name will be required if
 recognition of a Buru race of *A. paulina* is to be maintained.

1 ♂ of *A. paulina* (Cramer) from INDONESIA, Buru, A. R. Wallace, BMNH(E)#149986, Hewitson bequest, 1879-69, with label
 "Hewitson coll. 79.69 Pieris leis 1" and Wallace label "Bour" cannot be a type since the original description was based only
 on the female.

***darada* Felder & Felder, 1865**

Pieris darada Felder & Felder, 1865: 166.

Current status: valid subspecies of *Appias albina* (Boisduval, 1836).

Lectotype ♂, BANGLADESH [as India], Silhet, BMNH(E)#135616, Rothschild bequest BM: 1939-1, Moore fig., 1905, 557, 1d;
 with hand-written label "darada Fel. (Type)", and printed labels "Darada n." & "FELDER COLLN". Lectotype fixed by Moore,
 1905.

***delicata* Butler, 1882**

Appias delicata Butler, 1882: 153.

Current status: valid subspecies of *Appias celestina* (Boisduval, 1836).

Holotype ♂, PAPUA NEW GUINEA. New Britain, Duke of York I., BMNH(E)#135561, Godfrey Museum purchase BM 1882-80.

***distanti* Moore, 1905**

Catophaga Distanti Moore, 1905: 14 (Described as 'nom. n.' for *leis* of Distant (1885) & de Nicéville & Martin, (1895). Distant
 (1885) refers to "Malay Pen. Prov. Wellesley (coll. Distant); Perak (Biggs – coll. Distant); Malacca, Ayer-panas (Godfrey –
 coll. Distant); Sumatra (Brit. Mus.) Malaysia: "Malaysia [= Malay Peneinsular]; Sumatra; Borneo"). Type locality here
 restricted to Malay Peninsular. A lectotype designation is required, but unfortunately, *distanti* is applied to the subspecies
 occurring in Peninsular Malaysia and no syntypes from this locality are available.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, "Borneo", BMNH(E)#229168, Hewitson bequest BM 1879-69;

syntype ♂, MALAYSIA, Sabah, Labuan, BMNH(E)#229167, BM 1868-30;

syntype ♂, INDONESIA, Sumatra, S.Raffles coll., BMNH(E)#229128, Purchase Stevens BM 1854-76, with hand-written label
 "Sumatra 54.76/Catophaga alope Wallace". This specimen is also a possible syntype of *Tachyris alope* Wallace, 1867.

There are also 1 ♂, INDONESIA, Java, BMNH(E)#229166, BM 1860-15 & 1 ♀, INDONESIA, Java, BMNH(E)#229165, pres.
 Entomological Club BM 1844-12. Distant (1885) lists BMNH material of *leis* from Borneo, Java and Sumatra. Thus the
 above specimens would all have been in the museum collection at the time of Moore's (1905) publication, but only those
 from Borneo and Sumatra are considered to be syntypes of *distanti* as Moore did not include Java under "Habitat".

***dohertyi* Rothschild, 1892**

Appias dohertyi Rothschild, 1892: 441.

Current status: junior subjective synonym of *Appias paulina albata* (Höpffer, 1874).

Syntype ♀, INDONESIA, Sulawesi, August-September, W. Doherty, BMNH(E)#135848, Rothschild bequest BM 1939-1, with
 Rothschild determination label.

***domitia* Felder & Felder, 1862**

Pieris domitia Felder & Felder, 1862: 285.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntype ♂, PHILIPPINES, Luzon, ex Boisduval coll., BMNH(E)#229192, Oberthür purchase BM 1927-3, with hand-written label
 "Charpenieri Luzon" and printed label "EX MUSAE DRIS BOISDUVAL";

syntype ♂, PHILIPPINES, Luzon, Lorquin, ex Felder coll., BMNH(E)#141764, Rothschild bequest BM 1939-1, with printed label
 "Domitia n.".

***ega* Boisduval, 1836**

Pieris ega Boisduval, 1836: 536.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, AUSTRALIA, BMNH(E)#135838, Oberthür purchase, BM 1927-3, with hand-written labels "Melania Fab. ♂, Ega B.Sp.Australia" and "?Para-lectotype (Talb. 1942). Type in Mus. Paris" and printed label "EX MUSAEO DRIS BOISDUVAL".

emilia Fruhstorfer, 1903

Catophaga melania emilia Fruhstorfer, 1903a: 287.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Holotype ♀, INDONESIA, Sumba BMNH(E)#142308, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "melania emilia Fruhst.".

eurosundana Grose Smith, 1895

Appias eurosundana Grose Smith, 1895: 75.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Lectotype ♂, INDONESIA, Timor, Oinainisa, xi.-xii.1891, W. Doherty, BMNH(E) 229051, Rothschild bequest, BM 1939-1; with Grose Smith ♂ type label; paralectotypes 6 ♂♂, 10 ♀♀, INDONESIA, Timor, Oinainisa, xi.-xii.1891, W. Doherty, BMNH(E) 229045-61 [except 229051 above], Rothschild bequest, BM 1939-1; 229052 with Grose Smith ♀ type labels; 1 ♀, same data, BMNH(E)149995, ex Grose Smith coll., Joicey bequest BM 1934-120; 3 ♂♂, same data, BMNH(E) 149978-80, Oberthür purchase BM 1927-3. Further paralectotype ♂, INDONESIA, Sumbawa, ix.1891, W. Doherty, BMNH(E) 229044, Rothschild bequest, BM 1939-1; belongs with ssp. *tambora*

falcidia Fruhstorfer, 1910

Appias melania falcidia Fruhstorfer, 1910: 156.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Non-types ♂♂, ♀♀, INDONESIA, Irian Jaya, Biak, Schouten I., v.-vi.1914, A.C. & F. Pratt, BM 1916-36 erroneously labelled as co-types or paratypes. No genuine type material for this taxon has been traced.

fasciata Fruhstorfer, 1910

Appias melania lankapura f. fasciata Fruhstorfer, 1910: 155 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias galene* (Felder & Felder, 1865).

Syntype ♀, SRI LANKA, 1889, H. Fruhstorfer, BMNH(E)#229012, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "paulina f. lankapura Moore.";

syntype ♀, same data except v.1889, 142274.

figulina Butler, 1867

Pieris figulina Butler, 1867:

Current status: junior subjective synonym of *Appias nero nero* (Fabricius, 1793).

Lectotype ♂, SINGAPORE, BMNH(E)#141751, pres. Entomological Club BM 1844-12;

Paralectotype ♀, Borneo, BMNH(E)#141758, Hewitson bequest, BM 1879-69. This specimen is ssp. *chelidon* Fruhstorfer.

There is also a non type ♀, [but with red type label and hand-written 'Pieris Figulina Butler type'] 'SINGAPORE, BMNH(E) 149693, Maj. H. Roberts, BM 1928-309'. The only female mentioned in the original description is from Borneo.

flaminia Fruhstorfer, 1910

Appias melania terentilia f. flaminia Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina terentilia* Fruhstorfer, 1910.

Syntype ♀, PHILIPPINES, Palawan, i.1898, W.Doherty, ex coll. Fruhstorfer, BMNH(E)#142301, with Fruhstorfer label "♀ forma flaminia Fruhst.";

syntype ♀, PHILIPPINES, Palawan, 1898, W.Doherty BMNH(E)#229023, Fruhstorfer purchase, BM 1937-285

flava Ribbe, 1886

Tachyris celestina ab. flava Ribbe, 1886: 80 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias celestina barea* Fruhstorfer, 1910.

Syntype? ♀, INDONESIA, Aru, Wamma Dobbo, 1883, C.Ribbe, BMNH(E)#142263, Levick bequest BM 1923-120.

Although this name was published before *barea* Fruhstorfer, 1910, it was done so as an aberration of *celestina* Boisduval and has not been given any other status by subsequent authors. It therefore does not qualify as an available name.

flavius Grose Smith, 1892

Appias flavius Grose Smith, 1892: 426

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntype ♂, ♀, PHILIPPINES, Taganak, 20.ix.1890, ex Grose Smith coll., BMNH(E)#229183 (♂), BMNH(E)#229187 (♀), Joicey bequest BM 1934-120;

syntype ♂, same data but no date, BMNH(E)#141762;

syntype ♂, same data except 7.xi.1891, ex Grose Smith coll., BMNH(E)#229184;

syntypes 2 ♀♀, same data except 8.xi.1891, ex Grose Smith coll., BMNH(E)#229188 (with GroseSmith ♂ ♀ type label), BMNH(E)#229190;

syntype ♀, same locality, 9.xi.1891, BMNH(E)#229189, Rothschild bequest, BM 1939-1;

syntype ♀, same locality, 7.xi.1891, BMNH(E)#141763, Rothschild bequest, BM 1939-1;

syntypes 2 ♂♂, "N. Borneo", ex Grose Smith coll., BMNH(E)#229185-6, Joicey bequest BM 1934-120.

furia Fruhstorfer, 1910

Appias melania sawela f. furia Fruhstorfer, 1910: 155 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina sawela* Fruhstorfer, 1910.

Syntype ♀, INDONESIA, Lombok, Sambalun, 4000', iv.1896, H. Fruhstorfer, BMNH(E)#142299, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "forma furia Fruhst.";

syntype ♀, same locality, v.-vi.1896, H. Fruhstorfer, BMNH(E)#229062, Rothschild bequest, BM 1939-1.

galba Wallace, 1867

Tachyris galba Wallace, 1867: 378.

Current status: valid species.

Syntype ♂, "N. India" [prob. Assam], Maj.J.Lind Shewell, BMNH(E)#141749, Moore purchase BM 1903-361, with hand-written label "N.India/Galba Wall. Type", figured by Moore (1905, 558, 2, 2a).

galene Felder & Felder, 1865

Pieris galene Felder & Felder, 1865: 165.

Current status: valid species.

Lectotype ♂, SRI LANKA, Trincomali, BMNH(E)#135837, Rothschild bequest, BM 1939-1, Moore fig., 1905, 555, 1b, with printed labels "Galene n." and "FELDER COLLN", hand-written label "galene Feld. (type)". Lectotype fixed by Moore, 1905.

galepsus Fruhstorfer, 1910

Appias celestina galepsus Fruhstorfer, 1910: 151.

Current status: valid subspecies of *Appias celestina* (Boisduval, 1832).

Syntypes 4 ♂♂, 1 ♀, Key Is., Key Tual, BMNH(E)#135583, BMNH(E)#135585 (E), BMNH(E)#135604-6, Fruhstorfer purchase BM: 1937-285, BMNH(E)#135585 with Fruhstorfer label "galepsus Fruhst.", BMNH(E)#135604 with Fruhstorfer label "coelestina galepsus Fruhst.";

syntype ♂, "German New Guinea", Key Is., 1906, Rolle, BMNH(E)#135584, Levick bequest BM: 1941-83, with Fruhstorfer label "celestina galepsus Fruhst."

galerus Fruhstorfer, 1910

Appias celestina galerus Fruhstorfer, 1910: 151.

Current status: junior subjective synonym of *Appias celestina celestina* Boisduval, 1832.

Syntypes 3 ♂♂, New Guinea, Fr. Wilh.Hafen, BMNH(E)#135577-9, Fruhstorfer purchase BM 1937-285, BMNH(E)#135578 with Fruhstorfer label "galerus Fruhst.", BMNH(E)#135579 with Fruhstorfer label "coelestina galerus Fruhst.";

syntype ♂, New Guinea, 1906, K. Staudinger, BMNH(E)#135580, Levick bequest BM: 1941-83, with Fruhstorfer label "celestina galerus Fruhst.";

syntype ♀, New Guinea, BMNH(E)#135581 Fruhstorfer purchase BM: 1937-285, with Fruhstorfer label "♀, f. lileia Fruhst.", but fits description of *galerus* Fruhstorfer;

syntype ♀, ex Rolle, 1906, BMNH(E)#135582, Levick bequest BM: 1941-83, with Fruhstorfer label "galerus ♀, Fruhst.";

syntype? ♀, New Guinea, ex K.Stdgr. [=Staudinger], 1906, Levick bequest BM: 1941-83.

grisea Moulton, 1923

Appias paulina grisea Moulton, 1923a: 234

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, MALAYSIA, Johore, Pulau Aur, 13.vi.1912, BMNH(E)#142289, pres. Raffles Museum BM 1923-465, with Moulton type label;

syntype ♀, MALAYSIA, Pahang, Pulau Tioman, BMNH(E)#142290, pres. Raffles Museum BM 1923-465, with Moulton type label.

griseoides Moulton, 1923

Appias paulina griseoides Moulton, 1923b: 133.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 1 ♂, 1 ♀, VIETNAM, Con Son [=Pulo Condore], 29.xi.1920, BMNH(E)#142286, BMNH(E)#142288, pres. F.M.S. Museum BM 1923-466, with Moulton type label..

hainanensis Fruhstorfer, 1902

Tachyris nero hainanensis Fruhstorfer, 1902: 178.

Current status: junior subjective synonym of *Appias galba* (Wallace, 1867).

Syntypes 2 ♂♂, CHINA, Hainan, Whitehead, BMNH(E)#141750, BMNH(E)#229174, Fruhstorfer purchase BM 1937-285, BMNH(E)#141750 with Fruhstorfer label "nero hainanensis Fruhst.", BMNH(E)#229174 with Fruhstorfer label "nero Annam Siam Fruhst. Malekka".

helvola Fruhstorfer, 1910

Appias nero helvola Fruhstorfer, 1910: 151.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntype ♀, PHILIPPINES, Palawan, i.1898, W.Doherty, BMNH(E)#229191, Joicey bequest BM 1934-120, with hand-written label "Tachyris vesta ♀ Palawan";

syntype ♀, same locality, i.1894, H. Fruhstorfer, BMNH(E)#141761, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "fa helvola Fruhst."

horatia Fruhstorfer, 1910

Appias melania terentilia f. horatia Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina terentilia* Fruhstorfer, 1910.

Syntype ♀, PHILIPPINES, Palawan, i.1898, W.Doherty, ex coll. Fruhstorfer, BMNH(E)#142302, with Fruhstorfer label "♀, forma horatia Fruhst.";

syntype ♀, PHILIPPINES, Palawan, 1898, W.Doherty BMNH(E)#229024, Fruhstorfer purchase, BM 1937-285

syntype ♀, same data, ex coll. Fruhstorfer, unregistered.

infuscata Fruhstorfer, 1910

Appias albina infuscata Fruhstorfer, 1910: 154.

Current status: valid subspecies of *Appias albina* (Boisduval, 1832).

Syntypes 4 ♂♂, 20 ♀♀, INDONESIA, Sumbawa, Tambora, 1897, BMNH(E)#135645-8 (♂), BMNH(E)#135649-52, BMNH(E)#135454, BMNH(E)#135656-70, Fruhstorfer purchase BM 1937-285, BMNH(E)#135649 and BMNH(E)#142264 both with Fruhstorfer label "albina infuscata Fruhst.", BMNH(E)#135651 with Fruhstorfer label "forma semiflava Fruhst.", BMNH(E)#135664-6 could also be interpreted as syntypes of *principalis* Fruhstorfer;

syntypes 2 ♀♀, INDONESIA, Sumbawa, BMNH(E)#135653, BMNH(E)#135655, Fruhstorfer purchase BM 1937-285.

iria Fruhstorfer, 1910

Appias melania terentilia f. iria Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina terentilia* Fruhstorfer, 1910.

Syntype ♀, PHILIPPINES, Palawan, W.Doherty, ex coll. Fruhstorfer, BMNH(E)#142300, with Fruhstorfer label "fa iria Fruhst.";

syntype ♀, PHILIPPINES, Palawan, January, W.Doherty BMNH(E)#229025, Fruhstorfer purchase, BM 1937-285.

korridona Grose Smith 1894

Appias korridona Grose Smith 1894: 335.

Current status: junior subjective synonym of *Appias nero domitia* (Felder & Felder, 1862).
Holotype ♀, INDONESIA, Korrido [presumed error, = PHILIPPINES, Luzon], W. Doherty, BMNH(E)#135688, Rothschild bequest BM 1939-1, with Grose Smith type label.

***lankapura* Moore, 1879**

Catophaga lankapura Moore, 1879: 142.

Current status: junior subjective synonym of *Appias galene* (Felder & Felder, 1865).

Syntypes 1 ♂, 6 ♀♀, SRI LANKA, BMNH(E)#142272 (♂), BMNH(E)#229005-10, Moore purchase, BM 1903-361;
BMNH(E)#142272, Moore fig., 1905, 554, 1a; with hand-written label. "Catophaga Lankapura (type) Moore",
BMNH(E)#229005, Moore fig., 1905, 554, 1b; with hand-written label. "Catophaga Lankapura ♀ (type) Moore",
BMNH(E)#229010, Moore fig., 1905, 554, 1c;

syntype ♀, SRI LANKA, Colombo, Hutchison 142273, Moore purchase, BM 1903-361, with hand-written label. "Catophaga Lankapura (type) Moore";

syntype ♀, SRI LANKA, Mackwood, ex Swinhoe coll., BMNH(E)#229011, Davidson bequest BM 1925-574.

lileia Fruhstorfer, 1910

Appias celestina f. *lileia* Fruhstorfer, 1910: 151 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias celestina* (Boisduval, 1832).

Syntypes 2 ♀♀, PAPUA NEW GUINEA: Kapaur, W. Doherty, specimens BMNH(E)#135610-1;

syntype ♀, "New Guinea" Koyuerrere [?] BMNH(E)#135609; Fruhstorfer purchase BM: 1937-285, with Fruhstorfer label "sekarensis Ribbe.";

syntypes 2 ♀♀, "New Guinea", Aroa BMNH(E)#135607-8; Fruhstorfer purchase BM: 1937-285;

syntype ♀, New Guinea, Fr. Wilh. Hafen, BMNH(E)#13564; Fruhstorfer purchase BM: 1937-285;

syntype ♀, INDONESIA, Aru, 1905, K. Ribbe, BMNH(E)#135603. Levick bequest; BM 1941-83, with Fruhstorfer label "♀, forma lileia Fruhst.";

syntype ♀, same data, BMNH(E)#135663, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "♀, forma lileia Fruhst.";

syntypes 8 ♀♀, INDONESIA, Waigeu, H. Fruhstorfer, BMNH(E)#135665-72, Fruhstorfer purchase BM: 1937-285.

limbata Fruhstorfer, 1910

Appias melania zoe f. *limbata* Fruhstorfer, 1910: 156 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina zoe* (Snellen van Vollenhoven, 1865).

Syntypes 2 ♀♀, INDONESIA, Batjan, August, H. Fruhstorfer, BMNH(E)#229030-1, Fruhstorfer purchase, BM 1937-285;

syntype ♀, same data but no date, BMNH(E)#229032;

syntypes 2 ♀♀, INDONESIA, Batjan, iii. 1892, W. Doherty, BMNH(E)#142315, BMNH(E)#229033, Fruhstorfer purchase, BM 1937-285, BMNH(E)#142315 with Fruhstorfer label "♀, f limbata Fruhst.", BMNH(E)#229033 with Fruhstorfer label "zoe ♀, Volenh.";

syntype ♀, INDONESIA, Obi, H. Fruhstorfer, BMNH(E)#229034, Fruhstorfer purchase, BM 1937-285.

limia Fruhstorfer, 1910

Appias celestina sekarensis f. *limia* Fruhstorfer, 1910: 151 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias celestina sekarensis* (Ribbe, 1886).

Syntype ♀, PAPUA NEW GUINEA, Kapaur, W. Doherty, BMNH(E)#135573, Fruhstorfer purchase BM: 1937-285, with Fruhstorfer label "♀, forma limia Fruhst.".

***maculata* Staudinger, 1884**

Tachyris placidia var. *maculata* Staudinger, 1884: 30

Current status: junior subjective synonym of *Appias placidia* (Stoll, 1790).

Syntypes 3 ♂♂, INDONESIA, Bacan, Dr. Platen, ex Staudinger coll., BMNH(E)#149963-5, pres. Godman Salvin BM 1896-12;

syntypes 3 ♂♂, INDONESIA, Bacan, ex Staudinger coll., BMNH(E)#149966, pres. Godman Salvin BM 1896-12.

***manaia* Hopkins, 1927**

Catophaga jacquinotii manaia Hopkins, 1927: 44.

Current status: valid subspecies of *Appias athama* (Blanchard, 1848).

Syntype ♂, WESTERN SAMOA, Upolu, Aleipata Dist., Lalomanu, 23.x.1924, Buxton & Hopkins, BMNH(E)#142269, pres. G. H. S. Hopkins BM 1928-38;

syntype ♀, same except 20.xi.1924, 142270;

?syntype ♂, "Samoa", Whitmore, BMNH(E)#142271, pres Godman & Salvin BM 1896-12, with hand-written label. "Godman-Salvin Coll.96-12/P. Athama Lucas ♂ Type Butler" and "This specimen was unjustifiably described by Butler (Ann.Mag.N.H. (7) ii p.398, 1898) as the type ♂ of *athama* Lucas ♀".

marginata Fruhstorfer, 1910

Appias melania terentilia f. *marginata* Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina terentilia* Fruhstorfer, 1910.

Syntype ♀, PHILIPPINES, Palawan, 1898, W. Doherty, ex coll. Fruhstorfer, BMNH(E)#142304, with Fruhstorfer label "♀ forma marginata Fruhst.";

syntype ♀, PHILIPPINES, Palawan, i.1898, W. Doherty BMNH(E)#229022, Fruhstorfer purchase, BM 1937-285

***mariana* Yata & Chainey, sp. n.**

Holotype ♂, Guam, [18]95, Rothschild bequest, B.M. 1939-1, BMNH(E)#229237.

Paratypes 4 ♂♂, same data, BMNH(E)#229238-229241. BMNH(E)#229238 & BMNH(E)#229240 are dated March [18]95.

BMNH(E)#229239 is dated 10. x. [18]94. BMNH(E)#229241 id dated "11-10" [18]94;

paratypes 3 ♂♂ Saipan, Rothschild bequest, B.M. 1939-1, (BMNH(E)#229242-229244). BMNH(E)#229242 dated viii. [18]95.

No's. 229243-229244 dated 13. ix. [18]95;

paratype ♀ "Museum Paris Mariannes M. A. Marche 194-88", ex Oberthür coll., Brit. Mus. 1927-3 (BMNH(E)#229245).

***melania* Fabricius, 1775**

Papilio melania Fabricius, 1775: 475.

Current status: valid species.

Syntype ♀, AUSTRALIA, J. Banks, BMNH(E)#229221, Banks coll., with hand-written label "Papilio Melania Fab. Entom. P. 475 n. 140".

melanides Fruhstorfer, 1910

Appias melania zoe f. melanides Fruhstorfer, 1910: 156 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina zoe* (Snellen van Vollenhoven, 1865).

Syntype ♀, INDONESIA, Batjan, iii.1892, W. Doherty, BMNH(E)#142314, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "♀, forma melanides Fruhst."

micromalayana Fruhstorfer, 1909

Appias albina micromalayana Fruhstorfer, 1909: 201

Appias albina micromalayana Fruhstorfer, 1910: 154.

Current status: junior subjective synonym of *Appias albina ambigua* Grose Smith, 1895.

Lectotype ♂, INDONESIA, Babber, H. Fruhstorfer, BMNH(E)#135826;

Paralectotypes 3 ♂♂, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E) 135807-9, Fruhstorfer purchase BM:1937-285, BMNH(E)#135808 with Fruhstorfer label "albina micromalayana Fruhst."; 2 ♂♂, same data, Oberthur purchase BM 1927-3, BMNH(E)#149956-7; 1 ♂, same locality, iv.1896, BMNH(E)#135810, Fruhstorfer purchase BM:1937-285; 1 ♂, same locality, iv.1896, BMNH(E)#149936, J. J. Joicey bequest BM 1934-120; 2 ♂♂, same locality, iv.1896, unregistered; 3 ♂♂, same data, BMNH(E)#135811-3, Rothschild bequest BM 1939-1; 1 ♂, INDONESIA, Lombok, Sambalun, 4000', iv.1896, H. Fruhstorfer BMNH(E)#135814, Rothschild bequest BM 1939-1; 4 ♂♂, INDONESIA, Java, Sukabumi, 2000', 1893, H. Fruhstorfer, BMNH(E)#135815-8, Fruhstorfer purchase BM:1937-285, BMNH(E)#135815 with Fruhstorfer label "albina micromalayana Fruhst."; 6 ♂♂, INDONESIA, Bawean, July-Sept., H. Fruhstorfer BMNH(E)#135819-24, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "albina micromalayana Fruhst."; 1 ♂, same locality, wet season, BMNH(E)#135825, Fruhstorfer purchase BM:1937-285; ♂, INDONESIA, Babber, H. Fruhstorfer, BMNH(E)#135827, Fruhstorfer purchase BM:1937-285; 2 ♂♂, INDONESIA, Wetar, H. Fruhstorfer, BMNH(E) #135828-9, Fruhstorfer purchase BM:1937-285; 1 ♂, INDONESIA, Dammer, H. Fruhstorfer, BMNH(E)#135830, Fruhstorfer purchase BM:1937-285; 1 ♂, INDONESIA, Kisser, H. Fruhstorfer, BMNH(E)#135831, Fruhstorfer purchase BM:1937-285; 1 ♂, INDONESIA, Sumba, xii.1896, H. Fruhstorfer, BMNH(E)#135832, Fruhstorfer purchase BM:1937-285; 1 ♂, same data except no date, BMNH(E)#135833; 3 ♂♂, INDONESIA, Java, 1500', 1891, H. Fruhstorfer, BMNH(E)#135834-6, Fruhstorfer purchase BM:1937-285

minato Fruhstorfer, 1899

Catophaga paulina minato Fruhstorfer, 1899a: 409

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 3 ♂♂, JAPAN, Ishigaki, H. Fruhstorfer, BMNH(E)#142287, BMNH(E)#229001-2, Fruhstorfer purchase, BM 1937-285 [BMNH(E)#142287, with Fruhstorfer label "paulina minato Fruhst."].

mindanensis Butler, 1883

Pieris mindanensis Butler, 1883: 401.

Current status: junior subjective synonym of *Appias nero zamboanga* Felder & Felder, 1862.

Syntype ♂, PHILIPPINES, Mindanao, BMNH(E)#141765, BM 1873-62, with hand-written label "Appias mindanaensis type Butler/ Mindanao 73-62".

neombo Boisduval, 1836

Pieris neombo Boisduval, 1836: 539.

Current status: junior subjective synonym of *Appias albina albina* (Boisduval, 1836).

Syntype ♀, no data, BMNH(E)#142261, Oberthur purchase, BM 1927-3, with hand-written label "Neombo ♀" [Boisduval label] and "Appears to be type of neombo Bsdv. and almost certainly from Amboina A.S.C[orbet] 17.xii.1940" and printed labels "EX MUSAEO DRIS BOISDUVAL".

nero Fabricius, 1793.

Papilio nero Fabricius, 1793: 153.

Current status: valid species.

Neotype ♂, INDONESIA, W. Java, Preanger, Palboehan Ratoe, B.M. 1922-165.

1 ♀, from "Siam" in the Banks collection is not considered to be a type.

neronis Fruhstorfer, 1903

Tacyris nero neronis Fruhstorfer, 1903b: 17.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntypes 3 ♂♂, INDONESIA, Kangean, H. Fruhstorfer, BMNH(E)#141755, BMNH(E)#229178-9, Fruhstorfer purchase BM 1937-285, BMNH(E)#141755 and BMNH(E)#229178 with Fruhstorfer label "nero neronis Fruhst."

nikomedia Fruhstorfer, 1910

Appias melania nikomedia Fruhstorfer, 1910: 156.

Current status: valid subspecies of *Appias paulina* Cramer, 1777.

Syntypes 4 ♂♂, PHILIPPINES, Basilan, ii.-iii.1893, W.Doherty, BMNH(E)#142307, BMNH(E)#229123-5, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "nikomedia Fruhst."

norma Evans, 1924

Appias albina f. norma Evans, 1924.

Current status: junior subjective synonym of *Appias paulina paulina* (Cramer, 1777).

Syntype ♀, SRI LANKA, Green, BMNH(E)#142255, Moore purchase BM 1903-361, with hand-written label "type of ♀ f. Norma Evans".

Current status: junior subjective synonym of *Appias albina swinhoei* (Moore, 1905).

obscurior Fruhstorfer, 1910

Appias melania leis f. obscurior Fruhstorfer, 1910: 155 [infrasubspecific and unavailable name]

Syntype ♀, INDONESIA, Java, BMNH(E)#142294, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "♀ forma obscurior Fruhst.";

syntype ♀, INDONESIA, Java, Lawang, 1897, BMNH(E)#229133, Fruhstorfer purchase BM 1937-285;

syntype ♀, INDONESIA, Java, Mt.Gede, 4000', 1896, BMNH(E)#229134, Fruhstorfer purchase BM 1937-285.

orientalis Rothschild, 1916

Appias celestina orientalis Rothschild, 1916: 10.

Current status: valid subspecies of *Appias celestina* (Boisduval, 1832).
Holotype ♂, PAPUA NEW GUINEA, Bougainville, Arawa, xii.1907 A. S. Meek, BMNH(E)#135562, Rothschild bequest BM:1939-1.

pancheia Fruhstorfer, 1910

Appias albina pancheia Fruhstorfer, 1910:155.

Current status: junior subjective synonym of *Appias albina agatha* (Staudinger, 1889).

Syntypes 2 ♂♂, PHILIPPINES, Palawan, i.1894, H. Fruhstorfer BMNH(E)#135675-6, Fruhstorfer purchase BM:1937-285, BMNH(E)#135676 with Fruhstorfer label "albina Fruhst.";

paulina Cramer, 1777

Papilio paulina Cramer, 1777: 21.

Current status: valid species.

Lectotype ♀ with van Lennep label "No.60, PAULINA Cr.2. 110. E, F" and "FELDER COLLN" label; BMNH(E)#229172.

pione Fruhstorfer, 1910

Appias melania pione Fruhstorfer, 1910: 155.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♀, INDONESIA, Sumatra, 1898, BMNH(E)#135849, Levick bequest, BM 1941-83, with Fruhstorfer label "poiné [sic] Fruhst.";

syntypes 2 ♂♂, INDONESIA, Sumatra, Deli, 1892, Dr.Martin, BMNH(E)#135850, BMNH(E)#142291, Fruhstorfer purchase BM:1937-285, 142291 with Fruhstorfer label "pione Fruhst.".

plaetoria Fruhstorfer, 1910

Appias melania plaetoria Fruhstorfer, 1910: 157.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntype ♂, PHILIPPINES, Balabac, ex coll. Fruhstorfer, BMNH(E)#142305;

syntypes 2 ♂♂, PHILIPPINES, Balabac, H. Fruhstorfer, BMNH(E)#229119-20, Fruhstorfer purchase BM 1937-285;

syntype ♀, PHILIPPINES, Balabac, xii.1893, H. Fruhstorfer, BMNH(E)#142306, with Fruhstorfer label "plaetoria Fruhst.";

syntypes 1 ♂, 1 ♀, same data except xii,1893, BMNH(E)#229121-2.

principalis Fruhstorfer, 1910

Appias albina confusa f. principalis Fruhstorfer, 1910: 154 [infrasubspecific and unavailable]

Current status: unavailable synonym of *Appias albina* (Boisduval, 1836).

Syntype ♀, BURMA, BMNH(E)#135772, Fruhstorfer purchase BM 1937-285;

syntypes 3 ♀♀, INDIA, Malabar, ex coll Fruhstorfer, B.M.1937-285 each with Fruhstorfer label "albina swinhoei Moore";

syntypes 6 ♀♀, INDIA, Meghalaya [as Assam], Khasi[a] Hills, BMNH(E)#135745-50, Fruhstorfer purchase BM 1937-285;

syntypes 2 ♀♀, INDIA, Assam, Cachar BMNH(E)#135751-2, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "albina confusa Fruhst.";

syntype ♀, INDIA, Mizoram, Cachar, BMNH(E)#135771, Fruhstorfer purchase BM 1937-285;

syntype ♀, INDONESIA, Alor, BMNH(E)#135716, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "albina infuscata Fruhst.";

syntypes 4 ♀♀, INDONESIA, Babber, BMNH(E)#135708-11, Fruhstorfer purchase BM 1937-285; syntypes 4 ♀♀, INDONESIA, Batjan, August, 135679-81, BMNH(E)#135685, Fruhstorfer purchase BM 1937-285, BMNH(E)#135685 with Fruhstorfer label "albina ♀ Boisd.";

syntype ♀, INDONESIA, Halmahera, August-September, Hash'd [?]BMNH(E)#135684, Fruhstorfer purchase BM 1937-285;

syntype ♀, same locality, BMNH(E)#135683, Fruhstorfer purchase BM 1937-285;

syntypes 3 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#229232-4, Oberthür purchase, BM 1927-3;

syntypes 11 ♀♀, same data, BMNH(E)#135697-7, Rothschild bequest, BM 1939-1;

syntypes 7 ♀♀, same data, BMNH(E)#135690-6, Fruhstorfer purchase BM 1937-285, BMNH(E)#135696 with Fruhstorfer label "albina micromalayana Fruhst.";

syntypes 2 ♀♀, same data, BMNH(E)#149932-3, J. J. Joicey bequest BM 1934-120;

syntype ♀, same data except iv.1896, BMNH(E)#149934, J. J. Joicey bequest BM 1934-120;

syntype ♀, same data except, iv.1896, Fruhstorfer, H., BMNH(E)#149999, Oberthür purchase BM 1927-3;

syntype ♀, same data except iv.1896, unregistered;

syntypes 7 ♀♀, INDONESIA, Java, 1500', 1891, H. Fruhstorfer, BMNH(E)#135719-24, BMNH(E)#149958, Fruhstorfer purchase BM 1937-285;

syntype ♀, INDONESIA, Obi, BMNH(E)#135682, Fruhstorfer purchase BM 1937-285;

syntype ♀, INDONESIA, Tenimber, Kuhn, BMNH(E)#135717, Fruhstorfer purchase BM 1937-285;

syntype ♀, INDONESIA, Flores, xi.1896, H. Fruhstorfer, BMNH(E)#135718, Fruhstorfer purchase BM 1937-285;

syntypes 4 ♀♀, INDONESIA, Wetar, BMNH(E)#135712-5, Fruhstorfer purchase BM 1937-285;

syntype ♀, same data, unregistered;

syntype ♀, MALAYSIA, Sabah, BMNH(E)#135686, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "neombo Boisd.";

syntype ♀, PHILIPPINES, Palawan, xii.1893, H. Fruhstorfer BMNH(E)#135678, Fruhstorfer purchase BM:1937-285;

syntypes 2 ♀♀, same locality, 1898, W.Doherty, BMNH(E)#135672-3, Fruhstorfer purchase BM:1937-285, 135672 with Fruhstorfer label "albina pancheia Fruhst.";

syntype ♀, same locality, 1898, W.Doherty, ex Fruhstorfer coll.; unregistered;

syntype ♀, same locality, vi.1894, Everett, ex Fruhstorfer coll.; unregistered;

syntype ♀, PHILIPPINES, Balabac, xii.1893, H. Fruhstorfer BMNH(E)#135677, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "albina pancheia Fruhst.";

syntypes 2 ♀♀, PHILIPPINES, Basilan, ii.-iii.1893, W.Doherty, ex Fruhstorfer coll.; unregistered;

syntype 3 ♀♀, THAILAND, Muok-Lek, 1000', January, H. Fruhstorfer, BMNH(E)#135754-6, Fruhstorfer purchase BM 1937-285.;

syntype ♀, VIETNAM, Than-Moi.:June-July, H. Fruhstorfer, BMNH(E)#135753, Fruhstorfer purchase BM 1937-285;

syntype ♀, VIETNAM, Haiphong, March, H. Fruhstorfer, BMNH(E)#135757, Fruhstorfer purchase BM 1937-285.

pseudoleis Fruhstorfer, 1910

Appias melania pseudoleis Fruhstorfer, 1910: 155.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 3 ♂♂, 2 ♀♀, THAILAND, Muok-Lek, 1000', January, H. Fruhstorfer, BMNH(E)#142284, BMNH(E)#229013-6, Fruhstorfer purchase, BM 1937-285, BMNH(E)#142284 (♂) with Fruhstorfer label "pseudoleis Fruhst.";

syntypes 3 ♂♂, same data, Oberthür purchase BM 1927-3;
syntype 1 ♂, 1 ♀, THAILAND, Hinlap, January, H. Fruhstorfer, BMNH(E)#142285 (♀), BMNH(E)#229017, Fruhstorfer purchase, BM 1937-285;
syntypes 2 ♂♂, same data, Oberthür purchase BM 1927-3;
syntype ♂, THAILAND, Kanburi, April, H. Fruhstorfer, BMNH(E)#229018, Fruhstorfer purchase, BM 1937-285

psyche Felder & Felder, 1865

Pieris psyche Felder & Felder, 1865: 166.

Current status: junior subjective synonym of *Appias athama athama* (Blanchard, 1848).

Syntype ♂, NEW CALEDONIA, ex Felder coll., BMNH(E)#229231, Rothschild bequest, BM 1939-1, with printed labels "psyche n." and "FELDER COLLN".

pulonus Fruhstorfer, 1906

Tachyris nero pulonus Fruhstorfer, 1906: 99.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntype ♀, INDONESIA, Batu, I.Bello, H. Fruhstorfer, BMNH(E)#141754, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "nero pulonus Fruhst.".

pulverobasalis Joicey & Noakes, 1915

Appias albina pulverobasalis Joicey & Noakes, 1915: 184.

Current status: valid subspecies of *Appias albina* (Boisduval, 1836).

Syntype 4 ♂♂, INDONESIA, Irian Jaya, Biak, Schouten I., vi.1914, A.C. & F.Pratt, BMNH(E)#142265, BMNH(E)#149942-4 (♂), Joicey bequest BM 1934-120, BMNH(E)#142265 with hand-written label "Appias albina pulverobasalis J&N ♂ Type";

syntypes 5 ♂♂, same data except BMNH(E)#229154-8, Levick bequest, BM 1941-83;

syntypes 3 ♂♂, same data except BMNH(E)#229159-60, BMNH(E)#229162 (♂), Rothschild bequest, BM 1939-1, BMNH(E)#229162 with hand-written label "Appias albina pulverobasalis Joicey & Noakes ♂ co-type";

syntype ♂, same data except BMNH(E)#149969, Levick bequest, BM 1941-83;

syntype ♀, INDONESIA, Irian Jaya, Biak [as "Bosnik"], Schouten I., v.-vi.1914, A.C. & F.Pratt, BMNH(E)#142266, ex Joicey coll., with hand-written label "Allotype Appias pulverobasalis ♀ form trans. to flava";

syntypes 6 ♂♂, INDONESIA, Irian Jaya, Biak, Schouten I., v.-vi.1914, A.C. & F. Pratt, BMNH(E)#149937-41, Joicey bequest BM 1934-120;

syntype ♂, same data, BMNH(E)#149985 (taken *in cop* with ♀ *f. semiflava*), Joicey bequest BM 1934-120;

syntypes 5 ♂♂, same data, BMNH(E)#229150-3, BMNH(E)#229164, pres. J.J.Joicey BM 1925-495;

syntype ♂, same data except BMNH(E)#229161, Rothschild bequest, BM 1939-1;

syntype ♂, same data except BMNH(E)#229163, BM 1916-36;

syntypes 2 ♂♂, same data except BMNH(E)#149968, BMNH(E)# 229170, Levick bequest BM 1941-83;

syntype? ♂, no data, BMNH(E)#149986, Joicey bequest BM 1934-120, with paratype label.;

syntypes 2 ♂♂, same data except BMNH(E)#149948-9, Oberthür purchase BM 1927-3, BMNH(E)#149949 with hand-written label "Appias albina pulverobasalis J.&N. ♂ co-type".

The following are referred to named forms in the original description and are therefore not included in the type series.

23 ♀♀, INDONESIA, Irian Jaya, Biak, Schouten I., vi.1914, A.C. & F.Pratt, Joicey bequest BM 1934-120;

3 ♀♀, same data except Rothschild bequest, BM 1939-1; one with hand-written label "principalis Fruh. al with marg. found onh w. dentate", one with hand-written label "A. pulverobasalis ♀ f. principalis Fruh.", one with hand-written label "A. pulverobasalis ♀ f. Flava Rob.";

2 ♀♀, same data except pres. J.J.Joicey BM 1916-36, one with hand-written label "A. pulverobasalis ♀ f. principalis Fruh.", one with hand-written label "A. pulverobasalis ♀ f. semiflava Fruh.";

18 ♀♀, INDONESIA, Irian Jaya, Biak, Schouten I., v.-vi.1914, A.C. & F.Pratt, (one ♀ *in cop* with syntype ♂), Joicey bequest BM 1934-120;

2 ♀♀, same data except Rothschild bequest, BM 1939-1, one with hand-written label "A. pulverobasalis ♀ f. principalis Fruh.", one with hand-written label "A. pulverobasalis ♀ f.semiflava Fruh. al with marg. found onh.w.dentate";

2 ♀♀, same data except BM 1916-36; one with hand-written label "A. pulverobasalis ♀ f.semiflava Fruh. al with marg. found onh.w.dentate", one with hand-written label "pulverobasalis ♀ f. koriidona Gr.Sm.".

punctata Fruhstorfer, 1910

Appias albina micromalayana ab. punctata Fruhstorfer, 1910: 154 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina micromalayana* Fruhstorfer, 1910.

Syntypes 4 ♀♀, INDONESIA, Bawean, July-Sept., H. Fruhstorfer BMNH(E)#135731-3, BMNH(E)#142256, Fruhstorfer purchase BM:1937-285, BMNH(E)# 142256 with Fruhstorfer label "♀ forma punctata Fruhst.";

syntypes 2 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)# 135729-30, BMNH(E)# 142260, Rothschild bequest BM 1939-1;

syntype ♀, same data, BMNH(E)# 149987, Oberthür purchase BM 1927-3;

syntypes 2 ♀♀, INDONESIA, Java, Lawang, 1897, BMNH(E)# 135734-5, Fruhstorfer purchase BM:1937-285, BMNH(E)# 135734 with Fruhstorfer label "♀ forma punctata Fruhst.";

syntype ♀, INDONESIA, Java, 1500', 1897, BMNH(E)# 135736, Fruhstorfer purchase BM:1937-285;

syntype ♀, INDONESIA, Kisser, 1500', 1897, H. Fruhstorfer, BMNH(E)# 135737, Fruhstorfer purchase BM:1937-285.

ramosa Fruhstorfer, 1898

Catophaga nero ramosa Fruhstorfer, 1898: 328.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntypes 4 ♂♂, INDONESIA, Nias, 141753, BMNH(E)# 229175-7, Fruhstorfer purchase BM 1937-285, BMNH(E)#141753 with Fruhstorfer label "nero ramosa Fruhst." and hand-written label "selected from 4 paratypes by G.T[albot] Oct. 1940".

saina Grose Smith, 1894

Appias saina Grose Smith, 1894: 336.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Lectotype ♀, INDONESIA, Humboldt Bay, ix.-x.1893, W. Doherty, BMNH(E) 229041, Rothschild bequest, BM 1939-1; with Grose Smith type ♂ label;

paralectotype ♀, BMNH(E) 229043, with same data.

A further paralectotype male from Biak, W. Doherty, BMNH(E) 229042, Rothschild bequest, BM 1939-1, with Grose Smith type male label belongs with ssp. *falcidia*.

sawela Fruhstorfer, 1896

Tachyris sawela Fruhstorfer, 1896: 115.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 1 ♂, 1 ♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#142296-7, Fruhstorfer purchase BM:1937-285, BMNH(E)#142296 with Fruhstorfer label "Tachyris sawela Fruh.", and hand-written labels "♂ type selected by G.T[albot] from 2♂ bearing the name in Fruhstorfer's writing", BMNH(E)#142297 with Fruhstorfer label "Tachyris sawela Fruhst." and "selected by G.T[albot] from ♀ paratypes (Oct. 1940)";

syntypes 2 ♂♂, 11 ♀♀, same data, BMNH(E)#229108-9 (♂), BMNH(E)#229094-104 (♀), Fruhstorfer purchase, BM 1937-285, 229108 with Fruhstorfer label "sawela Fruhst.", BMNH(E)#229094 with Fruhstorfer label "Tachyris sawela ♀ Fruhst.";

syntypes 4 ♀♀, same data, BMNH(E)#149988, BMNH(E)#149992-4, ex Grose smith coll., Joicey bequest BM 1934-120;

Syntypes ♂, 2 ♀♀, same data, BMNH(E)#229107 (♂), BMNH(E)#229063-4 (♀), Rothschild bequest, BM 1939-1;

syntype ♀, same data, BMNH(E)#229077, Levick bequest, BM 1941-83;

syntype ♀, same data, BMNH(E)#229079, BM 1895-95;

syntype ♀, same data, Crowley bequest, BM 1901-78;

syntypes 1 ♂, 2 ♀♀, same data, BMNH(E)#149947, BMNH(E)#149950 (♂), BMNH(E)#229080, Oberthür purchase, BM 1927-3;

syntypes 1 ♂, 2 ♀♀, same data except iv.1896, BMNH(E)#149989-91, ex Grose smith coll., Joicey bequest BM 1934-120;

syntypes 4 ♂♂, 3 ♀♀, same data, unregistered;

syntype ♂, same data except iv.1896, unregistered

syntypes 3 ♂♂, 9 ♀♀, same data except iv.1896, BMNH(E)#229075, BMNH(E)#229105-6 (♂), BMNH(E)#229065-72, BMNH(E)#229076 (♀), Rothschild bequest, BM 1939-1, BMNH(E)#229105 with Fruhstorfer label "Tachyris sawela Fruhst.";

syntype ♀, same data except iv.1896, BMNH(E)#229078, Levick bequest, BM 1941-83;

syntype ♂, same data except iv.1896, Crowley bequest, BM 1901-78;

syntypes 3 ♀♀, same data except iv.1896, BMNH(E)#229081-3, Oberthür purchase, BM 1927-3;

syntypes 1 ♂, 10 ♀♀, same data except iv.1896, BMNH(E)#229110-1 (♂), BMNH(E)# 229084-93 (♀), Fruhstorfer purchase BM 1937-285 [BMNH(E)# 229110 with slide 4654];

syntypes 2 ♂♂, 1 ♀, INDONESIA, Lombok, Sambalun, 4000', iv.1896, H. Fruhstorfer, BMNH(E)#229073-4, Rothschild bequest, BM 1939-1, BMNH(E)#229074 with Fruhstorfer label "Tachyris sawela ♀ Fruhst.";

syntype ♂, same data, Crowley bequest, BM 1901-78.

saweloides Fruhstorfer, 1910

Appias albina micromalayana f. *saweloides* Fruhstorfer, 1910: 154 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina infuscata* Fruhstorfer, 1910.

Holotype ♀, INDONESIA, Sumbawa, H. Fruhstorfer BMNH(E)#142258, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "♀ ab. saweloides Fruhst.";

paratype ♀, INDONESIA, Lombok, Sapit, 2000', iv.1896, H. Fruhstorfer, BMNH(E)#135806, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "saweloides Fruhst.".

semiflava Fruhstorfer, 1910

Appias albina confusa f. *semiflava* Fruhstorfer, 1910: 154 [infrasubspecific and unavailable].

Current status: unavailable synonym of *Appias albina* (Boisduval, 1836).

Syntype ♀, INDIA, Meghalaya [as Assam], Khasi Hills, BMNH(E)#135764, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "confusa semiflava Fr.";

syntypes 2 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#135782-3, Fruhstorfer purchase BM 1937-285, BMNH(E)#135782 with Fruhstorfer label "forma semiflava Fruhst.";

syntypes 2 ♀♀, same data, BMNH(E)#135784, BMNH(E)#135786, Rothschild bequest, BM 1939-1;

syntype ♀, same data, BMNH(E)#135781, Crowley bequest, BM 1901-78;

syntypes 2 ♀♀, same locality, iv.1896, BMNH(E)#135779-80, Oberthür purchase, BM 1927-3;

syntypes 3 ♀♀, same locality, iv.1896, unregistered;

syntype ♀, same locality, 1905, K.Ribbe, BMNH(E)#135788, Levick bequest BM 1941: 83, with Fruhstorfer label "albina ♀ forma nova";

syntypes 3 ♀♀, INDONESIA, Java, 1500', 1891, H. Fruhstorfer, BMNH(E)#135789-91, Levick bequest BM 1941: 83, BMNH(E)#135789 with Fruhstorfer label "forma semiflava Fruhst.";

syntype ♀, MALAYSIA, Sabah, BMNH(E)#135687, Fruhstorfer purchase BM 1937-285;

syntype ♀, PHILIPPINES, Palawan, 1898, W: Doherty, BMNH(E)#135671, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "♀ forma semiflava Fruhst.";

syntype ♀, SRI LANKA, 1889, H. Fruhstorfer BMNH(E)#142254, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "forma semiflava Fruhst." and hand-written "Type selected from 2 specimens labelled with name by author (G.T[albot] Oct.1940)";

syntype 2 ♀♀, THAILAND, Muok-Lek, 1000', January, H. Fruhstorfer, BMNH(E)#135765-6, Fruhstorfer purchase BM 1937-285, BMNH(E)#135765 with Fruhstorfer label "♀ forma semiflava Fruhst.", BMNH(E)#135766 with Fruhstorfer label "fa semiflava Fruhst.";

syntype ♀, THAILAND, Hinlap, January, H. Fruhstorfer, BMNH(E)#135767, Fruhstorfer purchase BM 1937-285;

syntype ♀, VIETNAM, Haiphong, March, H. Fruhstorfer, BMNH(E)#135768, Fruhstorfer purchase BM 1937-285.

sosias Fruhstorfer, 1913

Appias melania sosias Fruhstorfer, 1913: 133.

Current status: junior subjective synonym of *Appias paulina saina* Grose Smith, 1894.

Syntypes 1 ♂, 1 ♀, PAPUA NEW GUINEA, Papua, Yule I, H. Fruhstorfer, BMNH(E)#142319-20, Fruhstorfer purchase BM:1937-285, BMNH(E)#142319 with Fruhstorfer label "melania sosias Fruhst.".

subochracea Fruhstorfer, 1910

Appias albina micromalayana f. *subochracea* Fruhstorfer, 1910: 154 [infrasubspecific and unavailable].

Current status: unavailable synonym of *Appias albina ambigua* Grose Smith, 1895.

Syntypes 4 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#135738, BMNH(E)#135740-1, BMNH(E)#135743, BMNH(E)#142263, Fruhstorfer purchase BM:1937-285, BMNH(E)#135738 with Fruhstorfer label "♀ forma subochracea Fruhst.";

syntype ♀, same data, BMNH(E)#135787, Oberthür purchase BM 1927-3;

syntype ♀, same data, BMNH(E)#229235, ex Grose Smith coll., Joicey bequest, BM 1934-120;

syntypes 3 ♀♀, same locality, iv.1896, unregistered;

syntypes 2 ♀♀, same data, BMNH(E)#135739, BMNH(E)#135785, Rothschild bequest BM 1939-1;

syntype ♀, same data, BMNH(E)#135742, Crowley bequest, BM 1901-78;

syntype ♀, same locality, iv.1896, BMNH(E)#135743, Fruhstorfer purchase BM:1937-285;
syntype ♀, same locality, iv.1896, Fruhstorfer, H., BMNH(E)#149998, Oberthür purchase BM 1927-3;
syntype ♀, INDONESIA, Java, 1500', 1891, H. Fruhstorfer, BMNH(E)#135744, Fruhstorfer purchase BM:1937-285, with Fruhstorfer label "forma subochracea Fruhst."

sufflava Fruhstorfer, 1910

Appias nero f. sufflava Fruhstorfer, 1910: 150 [described as a rare form found in all the island races; here considered infrasubspecific and unavailable]

Current status: unavailable synonym of *Appias nero* (Fabricius, 1793)

Syntype ♂, INDONESIA, "W. Sumatra", H. Fruhstorfer, BMNH(E)#141752, Fruhstorfer purchase BM 1937-285 with Fruhstorfer label "fa sufflava Fruhst."

***sulana* Fruhstorfer, 1899**

Appias sulana Fruhstorfer, 1899b: 84.

Current status: valid subspecies of *Appias zarinda sulana* Fruhstorfer, 1899 (but doubtfully distinct from *A. z. zarinda* (Boisduval)).
Holotype ♂, INDONESIA, Sula, Mangoli, x.-xi.1897, W.Doherty, BMNH(E)#141768, with Fruhstorfer label "nero sulana Fruhst."

***swinhoei* Moore, 1905**

Catophaga swinhoei Moore, 1905: 11.

Current status: valid subspecies of *Appias albina* (Boisduval, 1836).

Lectotype ♂, INDIA, Nilgiris, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1e, BMNH(E) 229139,.

Paralectotypes: 3 ♀♀, INDIA, Nilgiris, Moore purchase BM 1903-361, BMNH(E) 229139-40, 229144-5; 229140, Moore fig., 1905, 556, 1g,h.; 1 ♀, INDIA, Malabar, BMNH(E) 229141, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1d.; 1 ♂, 1 ♀, INDIA, Madras, 10.viii.1889, Watson BMNH(E) 229135-6, Watson BM 1892-43; 1 ♂, 3 ♀♀, INDIA, Moore purchase BM 1903-361, BMNH(E) 229137 (♂), 229142-3, 229146 (♀), 229137 Moore fig., 1905, 556, 1a, 229142 Moore fig., 1905, 556, 1i,j, 229143 Moore fig., 1905, 556, 1f.; 1 ♀, INDIA, Travancore, BMNH(E) 229138, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1b; 1 ♀, INDIA, Travancore, Mynall, 2500', i.1897, BMNH(E) 229147, Moore purchase BM 1903-361; 1 ♂, same data except 1200', March, BMNH(E) 229148;

1 ♂, INDIA, North Kanara, 149963, Swinhoe coll. BM 1926-239;

The following paralectotypes are identified as *Appias libythea* (Fab.):

1 ♂, INDIA, Poona, BMNH(E) 142244, also a syntype of *Appias libythea ares* Swinhoe, 1883 [with label "co-type ares Swin., type swinhoei ♂ Lep.Ind. vii. p11"]. This is presumably the specimen referred to by Talbot (see above); 1 ♂, INDIA, Madras, 12.viii.1889, Watson BMNH(E) 229229, Watson BM 1892-43; 1 ♂, INDIA, Gujarat, Ahmedabad, xii.1886, BMNH(E) 229225, Moore purchase BM 1903-361, Moore 1905 fig. 556, 1a [locality cited as "Poona"]; 1 ♂, INDIA, Poona, i.1888, BMNH(E) 229226, Moore purchase BM 1903-361, with hand-written label "neombo apud Swinhoe"; 1 ♂, INDIA, Gujarat, Bisnuggar [?] = Visnagar], xii.1886, BMNH(E) 229227, Crowley bequest BM 1901-78, with hand-written label "Appias ares ♂ Swinhoe"; paralectotype? ♂, INDIA, 'S. India', S. N. Ward, BMNH(E) 229228, Moore purchase BM 1903-361.

***tambora* Fruhstorfer, 1903**

Catophaga melania tambora Fruhstorfer, 1903a: 286.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 3 ♂♂, 6 ♀♀, INDONESIA, Sumbawa, Tambora, 1897, BMNH(E)#142309-10, BMNH(E)#229112-8, Fruhstorfer purchase BM:1937-285, BMNH(E)#142309 and BMNH(E)#229118 with Fruhstorfer label "melania tambora Fruhst.", BMNH(E)#229112 with Fruhstorfer label "tambora Fruhst."

***terentilia* Fruhstorfer, 1910**

Appias melania terentilia Fruhstorfer, 1910: 156.

Current status: valid subspecies of *Appias paulina* (Cramer, 1777).

Syntypes 3 ♂♂, PHILIPPINES, Palawan, 1898, W.Doherty, ex Fruhstorfer coll., BMNH(E)#142298 (with Fruhstorfer label "terentilia Fruhst."), BMNH(E)#229026-7;

syntype ♂, PHILIPPINES, Palawan, i.1894, Everett BMNH(E)#229028, Fruhstorfer purchase, BM 1937-285.

***tibericus* Fruhstorfer, 1910**

Appias nero tibericus Fruhstorfer, 1910: 151.

Current status: valid subspecies of *Appias nero* (Fabricius, 1793).

Syntypes ♂, 2 ♀♀, PHILIPPINES, Bazilan, ii.-iii.1898, W. Doherty, ex Fruhstorfer coll., BMNH(E)#141766-7, BMNH(E)#7229193 (♀), Levick bequest BM 1941-83, BMNH(E)#141766 and BMNH(E)#141767 with Fruhstorfer label "nero tibericus Fruhst.";

syntypes 3 ♂♂, ♀, same data, BMNH(E)#229194-6, BMNH(E)#229208 (♂), Fruhstorfer purchase, BM 1937-285;

syntype ♂, same data, BMNH(E)#229209, Oberthür purchase BM 1927-3;

syntype ♂, same data, BMNH(E)#229210, Adams bequest, BM 1912-399;

syntype ♂, same data, BMNH(E)#229211, Stichel BM 1924-29, with Fruhstorfer label "tibericus Fruhst."

***umbratilis* Fruhstorfer, 1897**

Tachyris flavia ab. umbratilis Fruhstorfer, 1897: 392 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina ambigua* Grose Smith, 1895.

Syntypes 4 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Fruhstorfer, BMNH(E)#135773, BMNH(E)#135775, BMNH(E)#135777, BMNH(E)#142259, Fruhstorfer purchase BM:1937-285, BMNH(E)#142259 with Fruhstorfer label "ab. umbratilis Fruhst.";

syntype ♀, same data, BMNH(E)#149996, Oberthür purchase BM 1927-3;

syntypes 2 ♀♀, same data, BMNH(E)#135774, BMNH(E)#135776, Rothschild bequest BM 1939-1;

syntype ♀, same locality, iv.1896, BMNH(E)#135778, Fruhstorfer purchase BM:1937-285

[1 ♀, same data, with Fruhstorfer label "ab. umbratilis Fruhst.", unregistered, does not match the original description and is form *agatha*].

***uranides* Fruhstorfer, 1910**

Appias melania zoe f. uranides Fruhstorfer, 1910: 156 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias paulina zoe* (Snellen van Vollenhoven, 1865).

Syntypes 2 ♂♂, INDONESIA, Halmahera, August-September, Hgshg., BMNH(E)#135847, BMNH(E)#142313, Fruhstorfer purchase BM:1937-285, BMNH(E)#142313 with Fruhstorfer label "♀ forma uranides Fruhst."

venusta Moore, 1881

Catophaga venusta Moore, 1881: 132.

Current status: junior synonym of *Appias galene* (Felder & Felder, 1865).

Syntypes 1 ♂, 1 ♀, SRI LANKA, xii.1820, Pole, BMNH(E)#142275-6, Moore purchase, BM 1903-361, BMNH(E)#142275-6 both with hand-written label "Ceylon ♂♀, taken in coitu Pole dec 20", BMNH(E)#142276 Moore fig., 1905, 555, 1e,f.; syntypes 2 ♀♀, SRI LANKA, BMNH(E)#229003-4, Moore purchase BM 1903-361, both with hand-written label "Catophaga venusta ♀ type Moore", BMNH(E)#229003 Moore fig., 1905, 555, 1g.

virilis Fruhstorfer, 1910

Appias albina micromalayana f. *virilis* Fruhstorfer, 1910: 154 [infrasubspecific and unavailable name]

Current status: unavailable synonym of *Appias albina ambigua* Grose Smith, 1895.

Syntypes 2 ♀♀, INDONESIA, Bawean, July-Sept., H. Fruhstorfer BMNH(E)#142257, BMNH(E)#135689, Fruhstorfer purchase BM:1937-285, BMNH(E)#142257 with Fruhstorfer label "♀ forma virilis Fruhst."

wallacei Butler, 1898

Catophaga wallacei Butler, 1898: 399.

Current status: junior subjective synonym of *Appias athama athama* (Blanchard, 1848).

Lectotype ♂, VANUATU, Mallicollo I., Woodford, BMNH(E) 142267, Godman & Salvin BM 1896-12, with hand-written label "Catophaga wallacei ♂ type Butler";

Paralectotypes 1 ♀, VANUATU, Malekula [as Mallicollo], Woodford, BMNH(E) 135840, Godman & Salvin BM 1896-12, slide no. 4678; 1 ♀, same data, BMNH(E) 135841; 1 ♂, same data, 135842.

Further paralectotypes belong with subspecies *psyche* (Felder & Felder, 1865): 1 ♀, NEW CALEDONIA, J. Macgillivray, BMNH(E)#142268, purchase Cuming BM 1859-63, with hand-written label "Catophaga wallacei ♀ type Butler"; 1 ♀, NEW CALEDONIA, BMNH(E)#135839, purchase Cuming BM 1859-63, slide no.4639; 2 ♀♀, NEW CALEDONIA, BMNH(E)#135843 & 135846, Hewitson bequest, BM 1879-69, BMNH(E)#135843 with det. "Pieris boisduvaliana Feld 4", BMNH(E)#135846 with labels "Pieris boisduvaliana Feld.3" and "Athama Pol Sud"; 1 ♂, same data, BMNH(E)#135844, slide no. 11180, with det. "Pieris albina Boisd. 4"; 1 ♂, same data, BMNH(E)#135845, slide no. 4638, with det. "Pieris albina Boisd. 5";

wardii Moore, 1884

Catophaga wardii Moore, 1884: 43.

Current status: valid species.

Syntype ♂, INDIA, Tamil Nadu, Nilgiris, Coonoor [=Kunur], S.N.Ward, BMNH(E)#142277, Moore purchase, BM 1903-361, with hand-written label "Catophaga wardii ♂ type Moore";

syntype ♀, no data [presumed INDIA, Tamil Nadu, Nilgiris, Coonoor, S.N.Ward], BMNH(E)#142278, Moore purchase, BM 1903-361, with hand-written label "Catophaga wardii ♀ type Moore".

Other material listed by Moore (1884) is expressly excluded from the type series.

Taxa not represented by type material in BMNH

acuminata Snellen, 1890 [valid subspecies of *Appias nero* (Fabricius, 1893)]

adelpha Röber, 1891 [junior subjective synonym of *Appias clementina* (Felder, 1860)]

agatha Staudinger, 1889 [valid subspecies of *Appias albina* (Boisduval, 1836)]

albata Hopffer, 1874 [valid subspecies of *Appias paulina* (Cramer, 1777)]

albina Boisduval, 1836 [valid species]

asteria Miskin, 1889 [junior subjective synonym of *Appias melania* (Fabricius, 1775)]

asterope Felder & Felder, 1862 [junior subjective synonym of *Appias nero domitia* (Felder & Felder, 1862)]

athama (Blanchard, 1848) [valid species]

athama Lucas, 1852 [junior synonym and homonym of *Appias athama athama* (Blanchard, 1836)]

bohollensis Okano & Okano, 1989 [junior subjective synonym of *Appias nero zamboanga* (Felder & Felder, 1862)]

bouruensis (Wallace, 1867) [valid subspecies of *Appias zarinda* (Boisduval, 1836)]

cerussa Fruhstorfer, 1904 [junior subjective synonym of *Appias melania* (Fabricius, 1775)]

corazonae Schröder & Treadaway, 1989 [valid subspecies of *Appias nero* (Fabricius)]

eumelis Boisduval, 1832 [valid subspecies of *Appias celestina* (Boisduval, 1832)]

falcidia Fruhstorfer, 1910 [valid subspecies of *Appias paulina* (Cramer, 1777)].

fatime Snellen van Vollenhoven, 1866 [junior subjective synonym of *Appias zarinda zarinda* (Boisduval, 1836)]

flava Röber, 1891 [unavailable synonym of *Appias albina ambigua* Grose Smith, 1895]

fleminius Fruhstorfer, 1911 [valid subspecies of *Appias nero* (Fabricius, 1893)]

galathea C. Felder, 1862 [valid subspecies of *Appias paulina* (Cramer, 1777)] Type in Berlin Museum (Moore, 1905)

ida Lucas, 1852 [junior subjective synonym of *Appias paulina paulina* (Cramer, 1777)]

iwasakii Matsumura, 1919 [junior subjective synonym of *Appias paulina minato* (Fruhstorfer, 1899)]

jacquinioti Lucas, 1852 [junior subjective synonym of *Appias athama athama* (Blanchard, 1848)]

kalisi Röber, 1940 [junior subjective synonym of *Appias paulina albata* (Hopffer, 1874)].

kawakamii Matsumura, 1909 [junior subjective synonym of *Appias albina semperi* (Moore, 1905)]

latimarginata Matsumura, 1919 [unavailable synonym of *Appias albina semperi* (Moore, 1905)]

leis Geyer, 1832 [junior subjective synonym of *Appias paulina paulina* (Cramer, 1777)]

mata Kheil, 1884 [valid species]

matsumurai Sonan, 1930 [unavailable synonym of *Appias albina semperi* (Moore, 1905)]

nebo Grose Smith & Kirby, 1894. Moore (1905: 18; also fig. 558, 2c,d) states that the type was in the possession of "Col. Adamson of Newcastle" [junior subjective synonym of *Appias galba* (Wallace, 1867)]

ochracea Moulton, 1914 [unavailable synonym of *Appias paulina athena* Fruhstorfer, 1903]

palawanica Satudinger, 1889 [valid subspecies of *Appias nero* (Fabricius, 1893)]

paula Röber, 1891 [valid subspecies of *Appias paulina* (Cramer, 1777)]

phestus Westwood, 1888 [valid subspecies of *Appias zarinda* (Boisduval, 1836)]

pietersi Kalis, 1933 [valid subspecies of *Appias paulina* (Cramer, 1777)]

placidia Stoll, 1790 [valid species]

raksasa Kalis, 1946 [junior subjective synonym of *Appias paulina paulina* (Cramer, 1777)]

roepstorffii Moore, 1884 [junior subjective synonym of *Appias paulina galathea* (Felder, 1862)]

sekarensis Ribbe, 1886 [junior subjective synonym of *Appias celestina celestina* (Boisduval, 1832)]

semperi Moore, 1905 [valid subspecies of *Appias albina* (Boisduval, 1836)]

shima Sonan, 1930 [unavailable synonym of *Appias paulina minato* (Fruhstorfer, 1899)]
sithonia Fruhstorfer, 1911 [valid subspecies of *Appias paulina* (Cramer, 1777)]
soranus Fruhstorfer, 1910 [valid subspecies of *Appias nero* (Fabricius, 1793)]
subtuslutea Roepke, 1935 [junior subjective synonym of *Appias paulina paulina* (Cramer, 1777)]
tamibia Strand, 1912 [junior subjective synonym of *Appias celestina celestina* (Boisduval, 1832)]
thyre Fruhstorfer, 1911 [valid subspecies of *Appias paulina* (Cramer, 1777)]
thyria Godart, 1819 [junior subjective synonym of *Appias nero nero* (Fabricius, 1793)]
yamazakii Sonan, 1936 [junior subjective synonym of *Appias nero domitia* (Felder & Felder, 1862)]
zamboanga Felder & Felder, 1862 [valid subspecies of *Appias nero* (Fabricius, 1793)]
zarinda Boisduval, 1836 [valid species]
zoe Snellen von Vollenhoven, 1865 [valid subspecies of *Appias paulina* (Cramer, 1777)]

Taxa excluded from subgenus *Catophaga*

amazene Cramer, 1775

Papilio amazene Cramer, 1775: 68 [as *amasene*, but not as part of a binomen], 1776: 151.

Current status: junior subjective synonym of *Cepora nerissa nerissa* (Fabricius, 1775).

Non type ♂, BMNH(E)#229171 with van Lennep label "No.57 AMASENE Cr. 1. 44. A" and "FELDER COLLN" label. This specimen is identifiable with *A. p. paulina* (Cramer, 1777), but it does not match Cramer's figure. The *amasene* [sic] of Boisduval, 1836, who was not certain that he had correctly identified Cramer's species, has long been recognised as being referable to *A. paulina paulina* Cramer (as *leis* Hübner, e.g. Wallace, 1867). Is it possible that Boisduval had seen this specimen? If so, the differences between this specimen and Cramer's figure, might have caused Boisduval to feel doubtful about the correct identity of *amazene*.

urania Wallace, (1867)

Tachyris urania Wallace, 1867

Current status: valid species of *Appias* (a senior synonym of *A. zondervani* Toxopeus)

Holotype ♂, INDONESIA, Sulawesi, Tondano, A.R.Wallace, BMNH(E)#142316, Hewitson bequest, BM 1879-69, with label "Tondano Hewitson coll. 79.69 Pieris neombo Bd. 9/urania Wal."

yaksha Fruhstorfer, 1910

Appias wardi yaksha Fruhstorfer, 1910: 157.

Current status: Talbot (1939) synonymised *A. yaksha* under *Appias libythea* (Fabricius). The following specimen appears to be *Appias libythea rouxii* (Boisduval): Syntype ♂, INDIA, Poona, ex coll. Fruhstorfer, BMNH(E)#142247, with Fruhstorfer label "yaksha Fruhst."

Supporting Information. Yata, O., Chainey, J.E. & Vane-Wright, R.I. (2010) The Golden and Mariana albatrosses, new species of pierid butterflies, with a review of subgenus *Appias* (*Catophaga*) (Lepidoptera), *Systematic Entomology*, **35**

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