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) Hübnner (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) Hübnner, 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 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 Hübnner 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 Appiadinus 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 Hübnner, Phrissura Butler, Hiposcritia 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 Brassicaeae) 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 Shirózu’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 M1–M3), and in CuA2 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* Brügère.

**Subgenus Appias (Catophaga) Hübner**


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


**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 & Pendebery, 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).

**The paulina complex**

**Diagnosis.** Male: upperside ground colour usually white, but rarely yellow or bluish-grey; forewings 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 M3. 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 CuA1, not forming free dark spot in cell M3.

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 R5–M2 (spot in cell M2 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


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-wardi’ [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.
of the subgenus Appias (Catophaga)

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 R2 and R5–M1, those in M3 and CuA1 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 postero-medially. 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°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


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 postero-medially. Genitalia (Fig. 4): uncus narrow and spindle-shaped viewed
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. Upperside 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 submarginal 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 Sibuerit: 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**

*Capparis, Crateva* (Capparaceae) 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 litttoralis* as the foodplant in Palawan, and *D. poilanei* in Laos, while noting an old record of *Capparis heyneana* for the Malay Peninsula. Braby et al. (2010) consider *A. albinata* to be monophagous on *Drypetes deplanchei* in northern Australia.

**Appias (Catophaqa) 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 Fruhs’. In BMNH (examined), BMNH(E) #229202. (Unavailable name.)


**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.

**Diagnosis**

**Male.** (Figs 19A, 20A). Forewing somewhat elongate apically and distinctly acute at apex. Ground colour of wings golden cream yellow. Hindwing with pale orange oval androconial patch posteromedially. 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 anticaly 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 M₁ to near tip of vein CuA₂ on forewing, and more rarely recognizable in cells M₁–M₂ of the hindwing. Forewing costa edged with some scattered black scales, but basal areas of wings not black dusted. Black anticaly line from apex to tornus; ciliary fringe yellow. Forewing acute at apex, outer margin almost straight, but weakly incurred between veins M₁–CuA₁, 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× 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; valvenansatz (term from Droshin: see Shirōzu, 1960) broad, dorsomedially, with crossbow-like membranous area medially; 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 M₁ to near tip of vein CuA₂ on forewing, and more rarely recognizable in cells M₁–M₂ of the hindwing. Forewing costa edged with some scattered black scales, but basal areas of wings not black dusted. Black anticaly line from apex to tornus; ciliary fringe yellow. Forewing acute at apex, outer margin almost straight, but weakly incurred between veins M₁–CuA₁, 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× 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.

**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 infrasubspecific (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 underside. *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 homoplastic (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 aurosa and albina might form a 'species duplex' (Corbet & Pendlebury, 1992). The systematic position of A. aurosa 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 R5, M1 and M3, but rarely traceable in cell M2. 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’île 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
Pierid butterflies of the subgenus Appias (Catophaga) 9

Fig. 7. Male genitalia of Appias (Catophaga) paulina (Myanmar: Karen Hills; NHM genitalia preparation no. 4651). (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.

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 M1. 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 R2 and Rs–M3, those in cells M2 and M3 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 Solomon Islands (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-offshima. Prior to the 1960s, in the Ryukus 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-offshima 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 matsamurae 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 matsamurae 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

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Fig. 8. Male genitalia of *Appias* (*Catopha ga*) *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* 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 M₁–M₃, and usually expressed in cells R₄+₅ and Cu₁A₁, never reduced to an isolated spot, even in cell M₃. On underside forewing postdiscal black band usually present from costa to cell M₃, but barely visible in cell Cu₁A₁, as on upperside. Genitalia (Fig. 8): uncus somewhat short (0.5 x 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, 200–Q). Upperside forewing with distal margin of black basal area somewhat oblique. Underside 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 doliocarpa* 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 M₁–Cu₁A₁, and almost obsolete in cell Cu₂A₂. Black postdiscal band present in cells M₁–M₃, and usually traceable in cells R₄+₅ and Cu₁A₁ as much narrower and faint streak close to distal border, and not reduced to an isolated spot even in cell Cu₂A₂. Black anteciliary 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 anteciliary 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 M₃, and barely traceable in cell Cu₁A₁, as on upperside. Black anteciliary line barely traceable from apex to tornus on forewing; fringe white. Forewing somewhat acute at apex; outer margin

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almost straight, but weakly rounded between veins CuA₁ and CuA₂; 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; Rs arising free from cell; middle discocellular subequal to or less than upper discocellular or lower discocellular. Antenna approximately 0.41 x length of forewing, black and white-checkered, 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; valvansatz broad, becoming membranous ventrally; vinculum not strongly arched posteriorly; saccus short and relatively slender (0.25 x ring height); angle between vinculum and saccus approximately 100–110°. Uncus somewhat short (0.5 x 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 aspect, compressed medially, concave dorsomedially, fairly broad and evenly curved posteriorly. The ductus bursae is divided into upper and lower lobes, of which the ventral is broad and evenly curved posteriorly. 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.

**Female genitalia.** (Fig. 9). The papilla analis almost elliptical with apical lobe, some hairs and a slender apophysis posteriorly. 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.

**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 paratypes in BMNH labelled: Guam, Rothschild Bequest, B.M. 1939-1 (specimen register nos BMNH(E) 229237–229294). No. 229237 is dated 20.vii.1939 and is selected as holotype of *Appias (Catophaga) mariana* Yata & Chainey. Nos 229238 and 229240 are dated 2.v.1939. Nos 229242 and 229244 are dated 2.vi.1939.

**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 M₃ 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 M3. 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 R3 and R5–M2, that in cell M2 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)


In all recent publications known to us (e.g. Yata, 1981; D’Abera, 1982, Osada _et al._, 1999), and for many years previously (e.g. Talbot, 1939), _galba_ has been treated as a
Pierid butterflies of the subgenus Appias (Catophaga) 13

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 R2–CuA1, 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

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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, *Pithecolobium 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 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<sub>2</sub> and R<sub>3</sub>–CuA<sub>2</sub>, those in cells R<sub>2</sub>, M<sub>2</sub> and CuA<sub>1</sub> 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
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$_2$ and CuA$_1$ and CuA$_2$ often reduced. Ground colour beneath obscure greenish-white, or yellowish.

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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 grey ish-blue, relieved by a white postdiscal band on both wings. Forewing usually with seven pale submarginal spots in cells R2 and R5–CuA2, that in cell M2 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 R5 to margin of CuA1. 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 R2 and R5–CuA1, those in cells M2 and CuA1 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 *CuA₁*. Forewing black apical area usually with six light submarginal spots in cells *R*₂ and *R*₅–*CuA₁*, that in cell *CuA₁* 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, northeastern 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 Appiadinida 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; and not 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 ................................................................. 18
   - 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 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.

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. 200–Q) (Marianas only) .......... mariana Yata & Chainey sp.n.

26. Forewing black apical area with two or three submarginal pale spots in cells R5, M1 and M2 (peninsular India only) ..........wardi (Moore, 1884)

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 Mentawai).

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, Tenggol, 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. ?mama mata, female (Indonesia: ‘Sumatra’; previously identified as manta, 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: Muang 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, male (Vietnam: Lao Kay, 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. placida, male (Indonesia: Obi; #665136; forewing length 33.0 mm); (J) A. placida, grey female (Indonesia: Ceram; Mansela; #665138; forewing length 37.2 mm); (K) A. placida, 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).

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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. bouruenensis).

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,
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 (Catopha) 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. au rosa, 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. lyncida (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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Pierid butterflies of the subgenus Appias (Catopha) 27


and list of the more interesting forms” published in the 1920s. 

Entomologist’s Gazette, 59, 41–53.


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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’.

albina darada* (Felder & Felder, 1865). Pieris darada. Type locality: Western Ghats, ‘Wetter’ (lectotype here designated: see Appendix 2).


Distribution: Eastern India and Sri Lanka.

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

albina agatha (Staudinger, 1889). Tachyris agatha. 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 Fernamboue’ (error).


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).


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

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*Infrasubspecific and unavailable names: alecta* Talbot, 1939; *citrina* Fruhstorfer, 1910; *citronella* Fruhstorfer, 1897; *flava* Röber, 1891; *latinarginata* Matsumura, 1919; *matsumurai* Sonan, 1930; *principalis* Fruhstorfer, 1910; *punctata* Fruhstorfer, 1910; *saweloide*s Fruhstorfer, 1910; *semiﬂava* Fruhstorfer, 1910; *subochracea* Fruhstorfer, 1897; *virilitis* 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).


= *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).


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

**Appias (Catophaga) aureosa** 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: aureosa* 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’.

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

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


= *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).


= *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: Bougainville, Normanby (Normanby may be subsp. celestina).

*Infrasubspecific and unavailable names: aurifera* Fruhstorfer, 1910; *flava* Ribbe, 1886; *ileia* Fruhstorfer, 1910, *limia* Fruhstorfer, 1910; *typicum* Talbot, 1932 (refers to the noninomotypical female form; even if accepted as a name, it is clearly infrasubspecific).
Appias (Catopha ga) clementina (Felder, 1860)

*Pieris clementina* C. Felder, 1860. Type locality: Indonesia: ‘Ambon’ (presumed error, although there is a female in BMNH labelled ‘Amboina Fruhstorfer’)


* = 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 (Catopha ga) 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.


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.

Infrasubspecific and unavailable names: fasciata* Fruhstorfer, 1910.

Appias (Catopha ga) 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 (Catopha ga) 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 (Catopha ga) melanía (Fabricius, 1775)

*Papilio melanía* Fabricius, 1775. Type locality: Australia: ‘New Holland’ (Queensland, Cooktown).


* = 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 (Catopha ga) 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).


* = figulina* Butler, 1867. *Pieris figulina*. Type locality: Malaysia: ‘Singapore’ (lectotype here designated, see Appendix 2).

Distribution: Malay Pensinsula, Sumatra, Java, Bali.

* nero ramosa* (Fruhstorfer, 1898). *Catopha ga nerosa*. Type locality: Indonesia: ‘Nias’.

Distribution: Indonesia (Nias).


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: ‘Taganan L., NE Borneo’.

Distribution: Philippines: Turtle Islands (off the coast of Borneo, near Sandakan).
nuevo palawanica (Staudinger, 1889). Tachyris nero var. palawanica. Type locality: Philippines: ‘Palawan’.

Distribution: Philippines (Balabac, Palawan).

nuevo corazón (Schröder & Treadaway, 1989. Appias nero corazonae. Type locality: Philippines: ‘Sulu Archipelago’.

Distribution: Philippines (Bongao, Sanga Sanga, Sibutu).

nuevo fleminius Fruhstorfer, 1911. Appias nero fleminius. Type locality: Philippines: ‘Mindoro’.

Distribution: Philippines (Mindoro).

nuevo dominio* (Felder & Felder, 1862). Pieris dominitia. Type locality: Philippines: ‘Luzon’.

= asterope Felder & Felder, 1862. Pieris asterope.

Type locality: Philippines: ‘Luzon’ (junior primary homonym of Pieris asterope Godart, 1819).

= soro Sonan, 1936. Appias nero yamazakii. Type locality: Taiwan: ‘Formosa’.

Distribution: Philippines (Luzon, Marinduque, Masbate), Taiwan.


Distribution: Philippines (Cebu, Negros, Panay, Sibuyan).

nuevo 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).


Distribution: Philippines (Bohol, Dinagat, Leyte, Mindanao, Panaon, Samar).


Distribution: Philippines (Basilan).

nuevo subsp. near zamboanga (Vane-Wright & de Jong, 2003: 109)


Appias (Catopha) paulina (Cramer, 1777)

Nearby 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). Catopha adamsoni. Type locality: Myanmar: ‘Burma, Upper Tenasserim, Thongying Valley; Dounat Range; Muong Gnow, Shan States; Rangoon; Arrakan; Hlaingbeoo Arrakan’.


Distribution: North-east Indian region to south-western China, Myanmar, Vietnam, Laos, Cambodia and Thailand.

dulcia griseaides* Moulton, 1923. Appias paulina griseaides. Type locality: Vietnam: ‘Pulo Condore (south-east coast of Cochim-China)’.

Distribution: Known only from Pulo Condore in the Con Son Islands, off the coast of southern Vietnam.

dulcia subsp. (A. Rawlins, personal communication, 2009).

Distribution: Indonesia (Natuna Islands).

dulcia minato* (Fruhstorfer, 1899). Catopha 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).

dulcia galathea (Felder, 1862). Pieris galathea. Type locality: India, Andaman Is: ‘Sambelung’.

= roepstorffii Moore, 1884. Catopha roepstorffii. Type locality: India: ‘Nicobar Is.’

Distribution: Confined to the Andaman and Nicobar Islands.

dulcia distanti* (Moore, 1905). Catopha 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.


Distribution: This subspecies is confined to the small group of islands that includes Aur and Tioman, off the east coast of the Malay Peninsula.


Distribution: Sumatra only.

dulcia paulina* (Cramer, 1777). Papilio paulina. Type locality: ‘Java’ (lectotype here designated, see Appendix 2):

= leis Geyer, 1832. Catopha leis. Type locality: Indonesia: Java.
paulina agave (Felder & Felder, 1862). Pieris agave. Type locality: Java. Distribution: Indonesia: Java.


paulina thyre Fruhstorfer, 1911. Appias melania thyre. Type locality: Banguey I. Distribution: Banguey 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: ‘Sud-Celebes (Bantimurung) und Mittel-Celebes (Tanah Metah)’.


paulina pietersi Kalis, 1933. Appias melania pietersi. Type locality: Indonesia: Kangean. Distribution: Indonesian island of Kangean only.


Distribution: Indonesian islands of Lombok and Flores.


paulina emilia* (Fruhstorfer, 1903). Catopha melania melania. 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.

dohertyi* Fruhstorfer, 1903. Catopha melania sophia. Type locality: Indonesia, Timor: ‘Oinaimisa (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 zoë (Snellen van Vollenhoven, 1865). Pieris zoë. Type locality: Indonesia, North Maluku: ‘Batjan’.


paulina saiba* Grose-Smith, 1894. Appias saiba. Type locality: Indonesia, Irian Jaya: ‘Humboldt Bay, Dutch New Guinea’. Lectotype here designated (see Appendix 2).


Distribution: Island of Biak only, in Irian Bay (Indonesia).


Distribution: Australia (northern and eastern regions, Groote Eylandt, Darnley, Thursday, Moa, Sue, Lord Howe), New Caledonia (Ile of Pines, Lifu, Ouvea, Maré), Vanuatu (Espiritu Santo, Efate, Tanna, Futuna, Aneityum).

Infrasubspecific and unavailable names: aegina*

Fruhstorfer, 1910; flaminia* Fruhstorfer, 1910;
Pieris zarinda (Boisduval, 1836). An Indonesian species restricted to the Sulawesi region (Wallace, 1867).

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: ‘Cooonoor, Nilgiris’.


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’.


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 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)

= zonervani 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 Binsunggar 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. Ghas (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

* Fruhstorfer, 1898; Taylor, 1888; Toxopeus, 1950; Watson, 1890; Fruhstorfer, 1899; Hampson, 1888; Moore, 1903-361; Moore fig., 1905, 556, 1e, BMNH(E) 229139.

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Appias

Appias libythea (Fab.): 1♂, INDIA, Poona, BMNH(E) 142244, also a syntype of Appias libythea. Paralectotypes identified as 149963, Swinhoe coll. BM 1926-239.

Appias ares Swinhoe, 1883 (with label 'co-type ares Swin., type winhoei♂ Lep.Ind. vii. p11'). This is presumably the specimen referred to by Talbot (see above); 1♂, INDIA, Madras, 12.viii.1889, Watson BMNH(E) 22922, Watson BM 1892-43; 1♂, INDIA, Gujarat, Ahmedabad, xii.1886, BMNH(E) 229225, Moore purchase BM 1903-361, Moore purchase BM 1903-361, with hand-written label 'neombo apud Swinhoe'; 1♂, Poona, i.1888, BMNH(E) 229226, Moore purchase BM 1903-361, Moore purchase BM 1903-361, with hand-written label 'Appias ares ♂ Swinhoe'; paralectotype? ♂, INDIA, 'S. India', S. N. Ward, BMNH(E) 229228, Moore purchase BM 1903-361.

Appias ambigu Grose-Smith, 1895: 76 [Appias albina ambigu]

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 ambigu Grose-Smith.

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


Appias albina micromalayana Fruhstorfer, 1909: 201 (1910: 154) (= Appias albina ambigu 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.


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

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

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

Paralectotypes: 1♀, VANUATU, Malekula [as Malilcco], 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 Boisd. 4'; 1♂, same data, BMNH(E) 135845, slide no. 4638, with det. 'Pieris albina Boisd. 5'.

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


Paralectotype: ♂️, NEW CALEDONIA, Loyalty Is., Lifou, Lomar ?, BMNH(E) 142321, Jocey bequest BM 1934-120, with printed label ‘A. paulina argentifera J&T 1928 ♂️ H.T.’. Identifiable with *Appias paulina ega* (Boisdouval, 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* Fruthstorfer.

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

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‘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.

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

Hostplant relationships

Hostplant records exist for only 5 of the 15 species of Appias (Catopha) 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 (Catopha) with records, except melania—which has been found only on Drypetes (Putranjivaceae), a genus also recorded as a host for the other four Appias (Catopha) 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. 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 & 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 sylva-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 Appiadinia (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 (Catopha) 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 Pithecellodium (= Pithecocolobium; Fabaceae) is potentially interesting, as Braby & Trueman (2006: 1682) also discuss evidence that other members of the Pierinae appear, occasionally, to recolonize 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 (Catopha) 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 exophenotypic 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>
<thead>
<tr>
<th>CLASS</th>
<th>DESCRIPTIVE TERM</th>
<th>MALE MORPHS</th>
<th>NO. SHARED MORPHS</th>
<th>FEMALE MORPHS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>monomorphism</td>
<td>a</td>
<td>(1)</td>
<td>a</td>
</tr>
<tr>
<td>2</td>
<td>unimodal</td>
<td>a, b</td>
<td>(2)</td>
<td>a, b</td>
</tr>
<tr>
<td>3</td>
<td>partial ♀-limited</td>
<td>a</td>
<td>(1)</td>
<td>a, b</td>
</tr>
<tr>
<td>4</td>
<td>partial ♂-limited</td>
<td>a, b</td>
<td>(1)</td>
<td>b</td>
</tr>
<tr>
<td>5</td>
<td>partial ♀♂-limited</td>
<td>a, b</td>
<td>(1)</td>
<td>b, c</td>
</tr>
<tr>
<td>1-6</td>
<td>weak dimorphism</td>
<td>a</td>
<td>(1)</td>
<td>a'</td>
</tr>
<tr>
<td>1-6</td>
<td>weak dimorphism</td>
<td>a'</td>
<td>(1)</td>
<td>a</td>
</tr>
<tr>
<td>6</td>
<td>simple dual</td>
<td>a</td>
<td>(0)</td>
<td>b</td>
</tr>
<tr>
<td>7</td>
<td>multiple ♀ dual</td>
<td>a</td>
<td>(0)</td>
<td>b, c</td>
</tr>
<tr>
<td>8</td>
<td>multiple ♂ dual</td>
<td>a, b</td>
<td>(0)</td>
<td>c</td>
</tr>
<tr>
<td>9</td>
<td>multiple ♂♀ dual</td>
<td>a, b</td>
<td>(0)</td>
<td>c, d</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Expression</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>galene</td>
<td>1-6[w(1)w']</td>
<td></td>
</tr>
<tr>
<td>wardi</td>
<td>1-6[w(1)w']</td>
<td></td>
</tr>
<tr>
<td>albina</td>
<td>3[w(1)w'y]</td>
<td></td>
</tr>
<tr>
<td>aurosa</td>
<td>[a(?)?]</td>
<td></td>
</tr>
<tr>
<td>athama</td>
<td>[w(0)y]</td>
<td></td>
</tr>
<tr>
<td>paulina ega</td>
<td>1-6[w(1)w']</td>
<td></td>
</tr>
<tr>
<td>paulina galathea</td>
<td>3[w(1)w'xy]</td>
<td></td>
</tr>
<tr>
<td>mariana</td>
<td>3[w(1)w']</td>
<td></td>
</tr>
<tr>
<td>mata</td>
<td>3[m(1)m'x]</td>
<td></td>
</tr>
<tr>
<td>galba</td>
<td>1-6[o(1)o']</td>
<td></td>
</tr>
<tr>
<td>nero nero</td>
<td>1-6[o(1)o']</td>
<td></td>
</tr>
<tr>
<td>nero flavius</td>
<td>3[o(1)yo']</td>
<td></td>
</tr>
<tr>
<td>nero palawanica</td>
<td>3[o(1)wxyo']</td>
<td></td>
</tr>
<tr>
<td>nero zamboanga</td>
<td>3[o(0)x]</td>
<td></td>
</tr>
<tr>
<td>zarinda</td>
<td>3[o(1)wyo']</td>
<td></td>
</tr>
<tr>
<td>placidia</td>
<td>1-6[p(1)p']</td>
<td></td>
</tr>
<tr>
<td>clementina</td>
<td>1-6[c(1)c']</td>
<td></td>
</tr>
<tr>
<td>celestina</td>
<td>[b(0)cy]</td>
<td></td>
</tr>
<tr>
<td>melania</td>
<td>[c(1)c]</td>
<td></td>
</tr>
</tbody>
</table>

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):

\[ T_1 \rightarrow T_2 \rightarrow T_3 \rightarrow T_4 \]

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 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-Guilén, 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:
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.

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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*.

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 (S13), 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

adamsioni Moore, 1905
Catophaga adamsioni Moore, 1905: 4
Current status: valid subspecies of Appias paulina (Cramer, 1777).
Syntype ♂, BURMA, Thauingying Valley, iv.1893 / BMNH(E)#142282 / Jocey bequest BM 1934-120 / hand-written label “Catophaga adamsioni ♂ (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, Daunat Range, iv.1893, ex Grose Smith coll., BMNH(E)#142283, Jocey bequest BM 1934-120, with hand-written label “Catophaga adamsioni ♂ (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.1897, Noble, BMNH(E)#229169, Swinhoe coll. BM 1926-239, with hand-written label “Catophaga Adamsoni ♂ (Dry) (type)”.

aegina Fruhstorfer, 1910
Appias melanina terentilia f. aegina Fruhstorfer, 1910: 157 [infrasubspecific and unavailable name]
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)#229230, Rothschild bequest, BM 1939-1, with printed label “Catophaga paulina f. aegina”.

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, Rothschild purchase BM 1937-285;
syntypes 6 ♂♂, INDONESIA, Damar [as Dammer], BMNH(E)#135595-600, Rothschild purchase BM: 1937-285;
syntype ♂♂, INDONESIA, Damar, 1906, K.Grubert, BMNH(E)#135601, Levick bequest BM: 1941-83, with hand-written label “♂ clementina agar Frucht.”;
syntypes 3 ♂♂, 4 ♀♀, INDONESIA, Babar, BMNH(E)#135587-93, Rothschild purchase BM: 1937-285;
syntype ♂♂, INDONESIA, Tenimber, Kuhn, BMNH(E)#135594, Rothschild purchase BM: 1937-285;
syntype ♂, INDONESIA, Kep.Tenimbar, Selaru, BMNH(E)#135602, Rothschild purchase BM: 1937-285, with hand-written label “agar Fruhst.”.

agave Felder & Felder, 1862
Pleis melanais 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 adamsioni 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, amasenea, Dr. Horsfield, BMNH(E)#229127, slide no. Rh. 4653, with hand-written label “Java 33a/Catopha alope Wallace”.


syntype? ♂, INDONESIA, Sumatra, S. Raffles coll., BMNH(E)#229128, Purchase Stevens BM 1854-76, with hand-written label “Sumatra 54, 76/Catopha alope Wallace”. This specimen has the best credentials to be a type. However, it is identifiable with ssp. pione. It is also a possible syntype of Catopha alope 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 ambiguus Grose Smith, 1895: 76
Current status: valid subspecies of Appias albina (Boisduval, 1835).
Lectotype ♂, INDONESIA, Wetar, v. 1892, W. Doherty, BMNH(E)#135769, Rothschild bequest BM 1939-1, with hand-written label “Ambigua Grose Smith Type”.

antoniae Fruhstorfer, 1910
Appias melania antoniae Fruhstorfer, 1910: 156
Current status: valid subspecies of Appias paulina (Cramer, 1777).
Syntypes 1 ♀♂, INDONESIA, Ceram, BMNH(E)#142311-2, Fruhstorfer purchase BM: 1937-285, BMNH(E)#142311 with Fruhstorfer label “antoniae Fruhst.”.

argentinifera Joicey & Talbot, 1928
Appias paulina argentinifera 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 argentinifera J&T 1928 ♀ H.T.”. Identifiable with Appias athama (Blanchard, 1848).
Paratypotype ♀, NEW CALEDONIA, Loyalty Is., Lifou, Lomar ?, BMNH(E)142321, Joicey bequest BM 1934-120, with printed label “A. paulina argentinifera 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. wardii 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. wardii 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;
♀, INDONESIA, Ceram, H. Fruhstorfer, BMNH(E)#229127, slide no. Rh. 4653, with hand-written label “Java aurosa”. It is also a possible syntype of Catopha alope Moore, 1905.

aurifera Fruhstorfer, 1910
Appias celestina f. aurifera Fruhstorfer, 1910: 151[infra-specific and unavailable name]
Current status: unavailable synonym of Appias c. celestina (Boisduval, 1832).
Syntypes 2 ♀♂, INDONESIA, Waigheu, 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.”;

aurosa 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. Rh.4618, BMNH(E)#229205 with slide no. Rh.4598, BMNH(E)#229206 with slide no. Rh.4598], BMNH(E)#229207 with Fruhstorfer label “aurosa Fruhst.”;
aurora Fruhstorfer, 1899
Tachyris zantida ab. aurora Fruhstorfer, 1899b: 84 [infra-specific 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.”;
♀♀, 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, Baweang, 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.”;
Appias albina confusa
Current status: junior subjective synonym of syntype Syntype confusa
Syntypic record: syntypes 2

Appias albina micromalayana f. citrina
Current status: unavailable synonym of Corbet, 1941
Appias paulina caledonica var. caledonica
Current status: junior subjective synonym of syntype Caledonica var. caledonica
Syntypic record: syntypes 4

Appias nero chelidon
Current status: valid subspecies of Appias nero
Syntypic record: syntypes 2

Appias nero palawanica ab. coelitus
Current status: unavailable synonym of Corbet, 1941
Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. clementina
Syntypic record: syntypes 2

Appias paulina clementina
Current status: valid subspecies of Appias paulina
Syntypic record: syntypes 2

Appias paulina seminiflava
Current status: unavailable synonym of Syntypes 3

Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. clementina
Syntypic record: syntypes 2

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.”

Appias paulina clementina var. clementina
Current status: unavailable synonym of Corbet, 1941
Appias paulina seminiflava var. seminiflava
Current status: junior subjective synonym of syntype Seminiflava var. Seminiflava
Syntypic record: syntypes 2

Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. Clementina
Syntypic record: syntypes 2

Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. Clementina
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Current status: junior subjective synonym of syntype Clementina var. Clementina
Syntypic record: syntypes 2

Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. Clementina
Syntypic record: syntypes 2

Appias paulina clementina var. clementina
Current status: junior subjective synonym of syntype Clementina var. Clementina
Syntypic record: syntypes 2
Pieris darada                       

Syntype 1
Current status: junior subjective synonym of Tachyris cynisca

Syntypes 3♂, 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; 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 Frust."

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;

Syntype ♂, ♂, same data BMNH(E)149951-4, Oberthür purchase BM 1927-3;

Syntype ♂, VIETNAM, M. 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 spot "<sen 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.

♂ 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. & Fel." and printed labels "Darada n." & "FELDER COLLN". Lectotype fixed by Moore, 1905.

delicata Butler, 1882
Current status: valid subspecies of Appias celestina (Boisduval, 1836).


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); Peraq (Biggs – coll. Distant); Malacca, Ayer-panas [Godfrey – coll. Distant); Sumatra (Brit. Mus.) Malaysia. Malaysia [= Malay Peninsular]; 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 (Höfler, 1874).

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

domitia Felder & Felder, 1862
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 MUSAEO 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)#135938, Oberthür purchase, BM 1927-3, with hand-written labels "Melania Fab. Ega B.Sp.Australia" and "?Para-lectotype (Tabl. 1942). Type in Mus. Paris" and printed label "EX MUSAEO DRIS BOISDUVAL".

emilia Fruhstorfer, 1903

Catopagra melanilla 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.".

eurospusa Grose Smith, 1895

Appias neurospusa 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; pararlectotypes 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 Grosse Smith coll., Joicy bequest BM 1934-120; 3 ++, same data, BMNH(E) 149978-80, Oberthür purchase BM 1927-3.

Further pararlectotype, 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 [infra-specific and unavailable name]
Current status: unavailable synonym of Appias galene (Felder & Felder, 1865).


Syntype, same data except v.1889, 142274.

Syntype, INDONESIA, Sumbawa, ix.1891, W. Doherty, BMNH(E)#229044, Rothschild bequest, BM 1939-1; belongs with ssp. tambora.

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;
Pararlectotype, Borneo, BMNH(E)#141758, Hewitson bequest, BM 1879-69. This specimen is ssp. cheilidon 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.

flaminda Fruhstorfer, 1910

Appias melania terentilia f. flaminda Fruhstorfer, 1910: 157 [infra-specific and unavailable name]

Syntype, PHILIPPINES, Palawan, l.1896, W.Doherty, ex coll. Fruhstorfer, BMNH(E)#142301, with Fruhstorfer label "f. flaminda 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 [infra-specific and unavailable name]

Syntype, INDONESIA, Sumbawa, x.-xi.1891, W. Doherty, 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.

flavus Grose Smith, 1892

Appias flavus 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 (♀), Joicy bequest BM 1934-120;

Syntype, same data but no date, BMNH(E)#141762;
Syntype, same data except 7.x.1891, ex Grose Smith coll., BMNH(E)#229184;

Syntype, same data except 8.xi.1891, ex Grose Smith coll., BMNH(E)#229188 (with Grose Smith ++ 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;

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

furia Fruhstorfer, 1910

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


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 (♀), 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 "coelestina galepsus Fruhst."

galerus Fruhstorfer, 1910
*Appias celestina galerus* Fruhstorfer, 1910: 151.
Current status: junior subjective synonym of *Appias celestina celestina* Boisduval, 1832.

grisea Moulton, 1923
*Appias paulina grisea* Moulton, 1923a: 234
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 1923-465, 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 ♀, PHILIPPINES, Palawan, 13.vi.1912, BMNH(E)#142289, pres. Raffles Museum BM 1923-465, 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.", 1♀.

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

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)#135545, 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]

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
Catopha gala lankapura Moore, 1879: 142.
Current status: junior subjective synonym of *Appias gaiene* (Felder & Felder, 1865).

Syntypes 1♀, 6♂♂, SRI LANKA, BMNH(E)#142272 (♀), BMNH(E)#229005-10, Moore purchase, BM 1903-361; BMNH(E)#142277, Moore f., 1905, 554, 1a; with handwritten label. Catopha gala lankapura (type) Moore; BMNH(E)#229002, Whitemore, 1905, 554, 1b; with handwritten label. Catopha gala lankapura ♀ (type) Moore; BMNH(E)#229010, Moore f., 1905, 554, 1c; syntype ♀, SRI LANKA, Colombo, Hutchison 142273, Moore purchase, BM 1903-361, with handwritten label. Catopha gala lankapura (type) Moore; syntype ♀, SRI LANKA, Mackwood, ex Swinhoe coll., BMNH(E)#229011, Davidson bequest BM 1925-574.

**melania** Frashtorfer, 1910

*Appias celestina* f. *limia* Frashtorfer, 1910: 151 [infra-specific and unavailable name]
Current status: unavailable synonym of *Appias celestina* (Boisduval, 1832).


**limbata** Frashtorfer, 1910

*Appias melania* zoe f. *limbata* Frashtorfer, 1910: 156 [infra-specific and unavailable name]
Current status: unavailable synonym of *Appias paulina* zoe (Snellen van Vollenhoven, 1865).


**limia** Frashtorfer, 1910

*Appias celestina* sekarensis f. *limia* Frashtorfer, 1910: 151 [infra-specific and unavailable name]
Current status: unavailable synonym of *Appias celestina* sekarensis (Ribbe, 1886).

Syntype ♀♀, PAPUA NEW GUINEA, Kapaur, W. Doherty, BMNH(E)#135673, Frashtorfer purchase BM:1937-285, with Frashtorfer label ♀♀, forma limia Frash.;

**maculata** Staudinger, 1884
Tachyrus placidia var. maculata Staudinger, 1884: 30
Current status: junior subjective synonym of *Appias placidia* (Stoll, 1790).


**mania** Hopkins, 1927
Catopha jacquinotii mania Hopkins, 1927: 44.
Current status: valid subspecies of *Appias athama* (Blanchard, 1848).

Syntype ♀♀, WESTERN SAMOA, Upolu, Alepata 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 ♀♀, Sameoa, Whitmore, BMNH(E)#142271, pres Godman & Salvin BM 1896-12, with handwritten 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** Frashtorfer, 1910

*Appias melania terentilia* f. *marginata* Frashtorfer, 1910: 157 [infra-specific and unavailable name]

Syntype ♀♀, PHILIPPINES, Palawan, 1896, W. Doherty, ex coll. Frashtorfer, BMNH(E)#142304, with Frashtorfer label ♀♀ forma marginata Frash.; syntype ♀♀, PHILIPPINES, Palawan, i.1898, W. Doherty, BMNH(E)#229022, Frashtorfer purchase, BM 1937-285

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

**melania** Fabricius, 1775

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

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melanides Fruhstorfer, 1910
Appias melania zoo f. melanides Fruhstorfer, 1910: 156 [infra-subspecific and unavailable name]
Current status: unavailable synonym of Appias paulina zoo (Snellen van Vollenhoven, 1865).
Syntype ♂, INDONESIA, Balijan, 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 ambiguia Grose Smith, 1895.
Lectotype ♂, INDONESIA, Babber, H. Fruhstorfer, BMNH(E)#135826; 1

minato Fruhstorfer, 1899
Catopha 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 Boisdruval, 1836
Pieris neombo Boisdruval, 1836: 539.
Current status: junior subjective synonym of Appias albina albina (Boisdruval, 1836).
Syntype ♂, no data, BMNH(E)#142261, Oberthür purchase, BM 1927-3, with hand-written label. "Neombo ♂" [Boisdruval label] and "Appears to be type of neombo Bsdv. and almost certainly from Amboina A.S.C[Borret] 17.xii.1940" and printed labels "EX MUSAEO DRIS BOISDUVAL".

nero Fabricius, 1793.
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 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 "neronis 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 leia f. obscurior Fruhstorfer, 1910: 155 [infra-subspecific and unavailable name]
Syntype ♂, INDONESIA, Java, BMNH(E)#142284, 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
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.

**pseudoleis**  
*Appias melania pseudoleis*  
Current status: valid subspecies of *Appias albina agatha* (Staudinger, 1889).
Syntypes 2 ♂♂, PHILIPPINES, Palawan, i.1894, H. Frustorfer BMNH(E)#135675-6, Frustorfer purchase BM:1937-285, BMNH(E)#135676 with Frustorfer label “albina Frust.”;

**paulina**  
*Cramer, 1777*  
*Papilio paulina*  
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**  
*Appias melaniona pione*  
Current status: valid subspecies of *Appias paulina* (Cramer, 1777).
Syntype ♀, INDONESIA, Sumatra, 1898, BMNH(E)#135849, Levick bequest, BM 1941-83, with Frustorfer label “pione [sic] Frust.”;
Syntypes 2 ♂♂, INDONESIA, Sumatra, Deli, 1892, Dr.Martin, BMNH(E)#135850, BMNH(E)#142291, Frustorfer purchase BM:1937-285, 142291 with Frustorfer label “pione Frust.”;

**plaetoria**  
*Appias melaniona plaetoria*  
Current status: valid subspecies of *Appias paulina* (Cramer, 1777).
Syntype ♀, PHILIPPINES, Balabac, ex coll. Frustorfer, BMNH(E)#142305;
Syntypes 2 ♂♂, PHILIPPINES, Balabac, H. Frustorfer, BMNH(E)#229119-20, Frustorfer purchase BM 1937-285;
Syntypes 1 ♂♂, 1 ♀, same data except xii,1893, BMNH(E)#229121-2.

**principalis**  
*Appias albina confusa f. principalis*  
Current status: invalid subspecies of *Appias albina confusa* (Crmaer, 1777).
Syntype ♀, INDONESIA, Balabac, ex coll. Frustorfer, B.M.1937-285 each with Frustorfer label “principalis Boisd.”;
Syntypes 4 ♀♀, INDONESIA, Babber, BMNH(E)#135708-11, Frustorfer purchase BM 1937-285, with Frustorfer label “principalis Boisd.”;
Syntypes 4 ♀♀, INDONESIA, Babber, BMNH(E)#135684, Frustorfer purchase BM 1937-285, BMNH(E)#135685 with Frustorfer label “principalis Frust.”;
Syntype ♀, INDONESIA, Alor, BMNH(E)#135716, Frustorfer purchase BM 1937-285, with Frustorfer label “principalis Boisd.”;
Syntypes 3 ♀♀, INDONESIA, Lombok, Sapit, 2000', v.-vi.1896, H. Frustorfer, BMNH(E)#229232-4, Oberthür purchase, BM 1927-3;
Syntypes 7 ♂♂, ♀♀, INDONESIA, Java, 1500', 1891, H. Frustorfer, BMNH(E)#135719-24, BMNH(E)#149958, Frustorfer purchase BM 1937-285;
Syntype ♀, INDONESIA, Obi, BMNH(E)#135682, Frustorfer purchase BM 1937-285;
Syntype ♀, INDONESIA, Tenimber, Kuhn, BMNH(E)#135717, Frustorfer purchase BM 1937-285;
Syntype ♀, INDONESIA, Flores, xi.1896, H. Frustorfer, BMNH(E)#135718, Frustorfer purchase BM 1937-285;
Syntype ♀, INDONESIA, Wetar, BMNH(E)#135712-6, Frustorfer purchase BM 1937-285;
Syntypes 4 ♂♂, ♂♂, BMNH(E)#149933-6, J. J. Joicey bequest BM 1934-120;
Syntype ♀, BMNH(E)#149934, J. J. Joicey bequest BM 1934-120;
Syntypes 1 ♂♂, 1 ♀♀, same data except iv.1896, BMNH(E)#149999, Oberthür purchase BM 1927-3;
Syntypes 1 ♂♂, 1 ♀♀, same data except iv.1896, unregistered;
Syntypes 7 ♂♂, ♀♀, INDONESIA, Java, 1500', 1891, H. Frustorfer, BMNH(E)#135719-24, BMNH(E)#149958, Frustorfer purchase BM 1937-285;

**pseudoleis**  
*Appias melaniona pseudoleis*  
Current status: valid subspecies of *Appias paulina* (Cramer, 1777).
Syntypes 3 ♂♂, 2 ♀♀, THAILAND, Muok-Lek, 1000', January, H. Frustorfer, BMNH(E)#142284, BMNH(E)#229013-6, Frustorfer purchase BM:1937-285, BMNH(E)#135676 with Frustorfer label “albina Frust.”;
Current status: junior subjective synonym of *Appias athama athama* (Blanchard, 1848).

**pulonus** Fruhstorfer, 1906


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 Frust."

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**pulverobasalis** Jocey & Noakes, 1915

*Appias albina* *pulverobasalis* Jocey & Noakes, 1915: 184.

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

Syntype ♀♂, INDONESIA, Irian Jaya, Biak, Schouten I., vi.1914, A.C. & F.Pratt, BMNH(E)#142265, BMNH(E)#149942-4.

Jocey 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 Jocey & 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 Jocey coll.,

with hand-written label "Allootype 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, Jocey bequest BM 1934-120;

syntype ♀♂, same data, BMNH(E)#149985 (taken in cop with ♀ f. semiflava), Jocey 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)#149966, Jocey 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.*

2 ♀♂, INDONESIA, Irian Jaya, Biak, Schouten I., vi.1914, A.C. & F.Pratt, Jocey 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 handwritten label "A. pulverobasalis ♀ f. principalis Fruh.", one with handwritten label "A. pulverobasalis ♀ f. semiflava Fruh.";

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

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

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

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**punctata** Fruhstorfer, 1910

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


Syntypes 4 ♀♂, INDONESIA, Bawean, July-Sept., H. Fruhstorfer BMNH(E)#135731-3, BMNH(E)#142266, Fruhstorfer purchase BM:1937-285, BMNH(E)#142256 with Fruhstorfer label "♀ forma punctata Frust.;"

syntypes 2 ♀♂, INDONESIA, Lombok, Sapit, 2000', vi.-v.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 Frust.;"

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


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**ramosa** Fruhstorfer, 1898

*Cathopha 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 Frust." and hand-written label "selected from 4 paratypes by G.T[albot] Oct. 1940".

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**saina** Grose Smith, 1894


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 Grosse Smith type label; paralecotype ♀♂, BMNH(E)#229043, with same data.

A further paralecotype male from Biak, W. Doherty, BMNH(E)#229042, Rothschild bequest, BM 1939-1, with Grosse Smith type male label belongs with ssp. *falcidia*.
sawela Fruhstorfer, 1896
Tachyris sawela Fruhstorfer, 1896: 115.
Current status: valid subspecies of Appias albina (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 Fr.," and handwritten labels "♂" type selected by G.T[albot] from 2♀ bearing the name in Fruhstorfer's writing", BMNH(E)#142297 with Fruhstorfer label "Tachyris sawela Frhurst."
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 Frhurst.", BMNH(E)#229094 with Fruhstorfer label "Tachyris albina confusa semiflava Fr.," syntypes 2♀, 1♂, same data, BMNH(E)#149097, ex Grose Smith coll., Joicey bequest BM 1934-120; syntypes, 2♀, 1♂, same data, BMNH(E)#229107 (♀), BMNH(E)#229095-6 (♂), Rothschild bequest, BM 1939-1; syntype, 1♀, same data, BMNH(E)#229077, Levick bequest, BM 1941-83; syntype, 1♂, same data, BMNH(E)#229079, BM 1895-95; syntype, 1♀, same data, Crowley bequest, BM 1901-78; syntypes 1♀, 2♂, same data, BMNH(E)#149047, BMNH(E)#149050 (♂), 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, 1♂, 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 (♂), Fruhstorfer purchase, BM 1939-1, BMNH(E)#229105 with Fruhstorfer label "Tachyris sawela Frhurst."
wasentype, 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♀, 1♂, 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 Frhurst."); syntype, same data, Crowley bequest, BM 1901-78.

saweloides Fruhstorfer, 1910
Appias albina micromalayana f. saweloides Fr., 1910: 154 [infra-specific and unavailable name]
Current status: unavailable synonym of Appias albina infuscata Fr., 1910.

semiffava Fruhstorfer, 1910
Appias albina confusa f. semiflava Fr., 1910: 154 [infra-specific and unavailable name]
Current status: unavailable synonym of Appias albina (Boisduval, 1836).
Syntypes. 1♀, 1♂, 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 Frhurst."
forma semiflava Frhurst."
synotypes 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 Frhurst."; 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 Frhurst."; syntype ♀, SRI LANKA, 1889, H. Fruhstorfer BMNH(E)#142254, Fruhstorfer purchase BM 1937-285, with Fruhstorfer label "forma semiflava Frhurst."
permad Matta, hand-written "Type selected from 2 specimens labelled with name by author (G.T[albot]

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 Frhurst."

subochracea Fruhstorfer, 1910
Appias albina micromalayana f. subochracea Fr., 1910: 154 [infra-specific and unavailable name]
Current status: unavailable synonym of Appias albina ambiguia 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 Frhurst."); syntype ♀, same data, BMNH(E)#135787, Oberthür purchase BM 1927-3; syntype ♀, same data, BMNH(E)#142235, 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
infra-specific and unavailable]

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

Syntypes ♀, 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 (Boisd))

Holotype ♀, INDONESIA, Sula, Mangoli, x.-xi.1897, W. Doherty, BMNH(E)#141768, with Fruhstorfer label "nero sulana Fruhst.".

swinhoei Moore, 1905
Catophasa swinhoei Moore, 1905: 11.

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

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

Paral ectotypes: 3 ♂, ♂, INDIA, Nilgiris, Moore purchase BM 1903-361, BMNH(E) 229139-40, 229144-5, 229140, Moore fig., 1905, 556, 1g.h., 1f; ♀, INDIA, Malabar, BMNH(E) 229141, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1d; 1♀, 1♂, INDIA, Madras, 10.vii.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, 1j, 229143 Moore fig., 1905, 556, 1f; ♂, INDIA, Travancore, BMNH(E) 229138, Moore purchase BM 1903-361, Moore fig., 1905, 556, 1b; 1♀, INDIA, Travancore, Mynall, 2500', 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 paral ectotypes are identified as Appias libythea (Fab.):
1♀, INDIA, Poona, BMNH(E) 142424, 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 [locally 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, Binsnagar [♀ = Visnagar], xi.1886, BMNH(E) 229227, Crowley bequest BM 1901-78, with hand-written label "Appias ares ♀ Swinhoe";

tambora Fruhstorfer, 1903
Catophasa 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 3♂, ♀, PHILIPPINES, Basilan, 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 [infra-specific 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)#135771, 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
[♀, 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 [infra-specific and unavailable name]

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

Syntypes 2♂, ♀, INDONESIA, Halmahera, August-September, Hgs., 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.1920, Pole, BMNH(E)#142276-6, Moore purchase, BM 1903-361, BMNH(E)#142275-6 both with hand-written label "Catophaga venusta ♀ type Moore", 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 ambiguus 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 palawanica (Boisduval, 1836) ochracea Fruhstorfer, 1910: 154 [infrasubspecific and unavailable name];
BMNH(E)#142268, purchase Cuming BM 1859-63, with hand-written label "Catophaga wallacei ♀ type Butler"; 1 ♀, NEW CALEDONIA, J. Macgillivray, 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 "Atlama 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 Boisid. 5".

wardii Moore, 1884
Catophaga wardii Moore, 1884: 43.
Current status: valid species.
Syntype ♂, INDIA, Tamil Nadu, Niligiris, 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, Niligiris, 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)]
boholensis 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)]
fatlame Snelien van Vollenhoven, 1886 [junior subjective synonym of Appias zarinda zarinda (Boisduval, 1836)]
flava Röber, 1891 [unavailable synonym of Appias albina ambiguus Grose Smith, 1895)]
fleminius Fruhstorfer, 1911 [valid subspecies of Appias nero (Fabricius, 1893)]
galatha 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)]
ivassaki Matsumura, 1919 [junior subjective synonym of Appias paulina minato (Fruhstorfer, 1899)]
jacquinotii Lucas, 1852 [junior subjective synonym of Appias athama athama (Blanchard, 1848)]
kalis Röber, 1940 [junior subjective synonym of Appias paulina albata (Hopffer, 1874)]
kawakamii Matsumura, 1909 [junior subjective synonym of Appias albina semperi (Moore, 1905)]
lattimarginata 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 Grove 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 Moulot, 1914 [unavailable synonym of Appias paulina athena Fruhstorfer, 1903]
palaeoceraica Appias nero (Fabricius, 1893)]
paula Röber, 1891 [valid subspecies of Appias paulina (Cramer, 1777)]
phestus Westwood, 1888 [valid subspecies of Appias paulina paulina (Cramer, 1777)]
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 galathae (Felder, 1862)]
sekarenisis 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)]
tambia 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
Current status: Talbot (1939) synonymised A. yaksha under Appias libythea (Fabricius). The following specimen appears to be Appias libythea rouxi (Boisduval): Syntype ♂, INDIA, Poona, ex coll. Fruhstorfer, BMNH(E)#142247, with Fruhstorfer label “yaksha Fruhst.”

SI 3. Combined bibliography (for all printed text and on-line Supporting Information SI1 and SI2)


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