

# THE STATUS OF THE GENERA *ATROPHANEURA* REAKIRT AND *PACHLIOPTA* REAKIRT (LEPIDOPTERA: PAPILIONIDAE)

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## Abstract

The *Pachliopta polydorus* group of swallowtails is shown to be closely related to the *Atrophaneura coon* group. The relationship between these two groups and other species of *Atrophaneura* is such that recognition of *Pachliopta* and *Atrophaneura* as separate genera results in a paraphyletic classification. *Pachliopta* Reakirt is thus reinstated as a synonym of *Atrophaneura* Reakirt. *Atrophaneura* is shown to be distinct from *Parides* Hübner at the generic level.

## Introduction

Since Munroe (1961) published his classification of the Papilionidae, various generic names have been applied to the *polydorus* group of Indo-Australian, *Aristolochia*-feeding swallowtails. The oldest of these, *Polydorus* Swainson, 1833, is a junior homonym of *Polydorus* Blainville, 1826, and is therefore unavailable. *Atrophaneura* Reakirt, 1865, placed as a subgenus of *Parides* Hübner, 1819 by Munroe, and *Pachliopta* Reakirt, 1865, separated (as *Pachlioptera*) by Munroe from his *Parides-Atrophaneura* assemblage, have both been widely used. As currently recognised, *Pachliopta* is restricted to the *polydorus* group, whilst *Atrophaneura* comprises the *antenor*, *latreillei*, *nox* and *coon* groups. The status of these two generic names is discussed below.

## Materials

Of the 43 species currently placed in the genera *Atrophaneura* and *Pachliopta*, 17 were examined in the present study. Of these, 12 were dissected for male genitalic characters, viz. *A. alcinous*, *A. dasarada*, *A. polyeuctes*, *A. priapus*, *A. horishanus*, *A. aidoneus*, *A. nox*, *A. coon*, *P. hector*, *P. polyphontes*, *P. aristolochiae* and *P. polydorus*. Male genitalia of a further 14 species were examined from published illustrations (Corbet, 1948; Jordan, 1915, 1928). In addition, 24 species of *Parides* were examined. Nine of these, encompassing all three species groups, were dissected.

## Discussion

### *Pachliopta* Reakirt

Munroe (1961) separated this genus from *Atrophaneura* largely on the basis of differences in the genitalia. As Munroe noted, in *Pachliopta* the female ductus bursae is heavily sclerotized whilst in the male the valve is greatly reduced and the socii and tegumen hypertrophied and heavily sclerotized. However, these characteristics merely represent specializations at the group level, a fact that can be appreciated when the male genitalia of species in the *polydorus* group are compared with various species of *Atrophaneura* (Figs 1-9). The evolution of these genitalic characteristics can be traced as follows:—

### valve

In primitive groups, such as *antenor* and *latreillei* (Fig. 1) the valve is entire and somewhat ovate. In the *nox* group (Figs 2-4) the valve is dorso-apically emarginate; there is also a tendency towards a dorso-basal reduction. In the *coon* group (Fig. 5) the valve is again emarginate, both dorsally and, to a lesser extent, distally. Unlike the *nox* group, there is no dorso-basal reduction and the emarginations in these two groups appear to have

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evolved separately. In the *polydorus* group (Figs 6-9) the trend seen in *coon* is taken further with a great reduction of the valve. The extent of this reduction varies; in *polyphontes* existence of the dorsal emargination is shown by retention of the dorso-basal part of the valve, as seen in *coon*; in *aristolochiae* and *polydorus* this dorso-basal portion is absent; in *hector* the valve is further reduced to a small basal part only.

#### clasper

In the *antenor*, *latreillei* and *nox* groups (Figs 1-4) the clasper is broad and either smooth, serrate or toothed. In the *coon* group (Fig. 5) the clasper is reduced to a narrow elongate and pointed structure. In the *polydorus* group (Figs 6-9) the clasper is also narrow and pointed, although much shorter than in *coon*; it is longest in *hector* and shortest in *aristolochiae* and *polydorus*.

#### aedeagus

In *antenor* the aedeagus is long, slender and straight. In the *latreillei* and *nox* groups (Figs 1-4) it is short, thick and strongly curved. In the *coon* group (Fig. 5) it is long slender and weakly curved. In the *polydorus* group (Figs 6-9) the aedeagus is again long slender and weakly curved, especially so in *hector*.

#### tegumen and socii

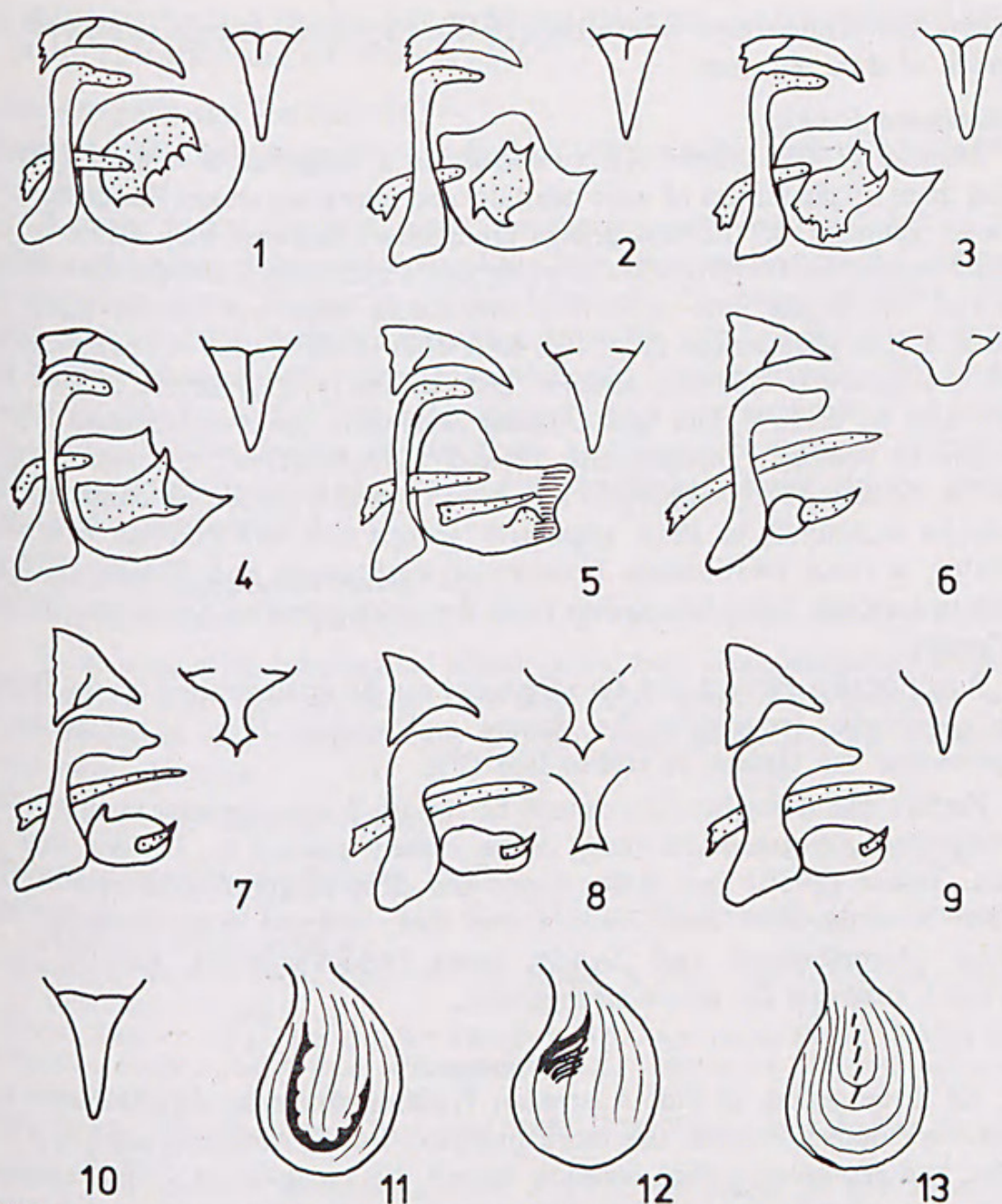
In the *antenor*, *latreillei*, *nox* and *coon* groups (Figs 1-5) the tegumen and socii are unmodified. In the *polydorus* group (Figs 6-9) these structures are greatly enlarged and heavily sclerotized. This modification becomes progressively greater from *hector* to *polyphontes* to *aristolochiae* and *polydorus*.

#### pseuduncus and 8th tergite

In *antenor* the pseuduncus is absent. In the *latreillei* and *nox* groups (Figs 1-4) it is separated from a narrow 8th tergite by a complete suture, this suture extending for a distance down the mid-line of the pseuduncus. In the *coon* group (Fig. 5) the pseuduncus is separated from a relatively broad 8th tergite by an incomplete suture, being fused medially. In the *polydorus* group (Figs 6-9) the pseuduncus is either separated from a broad (*hector*) to very broad (*polyphontes*) 8th tergite by an incomplete suture, being fused medially as in *coon*, or is fused completely to a very broad 8th tergite (*aristolochiae* and *polydorus*).

Munroe (1961) also indicated that the immature stages served to differentiate *Pachliopta* from *Atrophaneura*. However, this is not the case. The larva is similar in all groups, when mature being dark with rows of dorsal and lateral tubercles, these often red or red-tipped, or with some of the tubercles white. Mature larvae in the *latreillei*, *nox* and *coon* groups have a white transverse band on abdominal segments 3-4 (band absent in some *nox* group species, e.g. *semperi*, *kuehni*). In the *polydorus* group this band is reduced. In *hector* it is present as a series of spots on segments 3-4; in most (e.g. *jophoria*, *polyphontes*, *mariae*, *phegeus*, *aristolochiae*) it is present as a band confined to segment 3; in others (e.g. *liris*, *polydorus*) it is absent. The pupa is also similar in all groups, having well developed lateral carinae and paired, dorsal lobe-like processes on abdominal segments 4 to 7 (Mell, 1938; Talbot, 1939; Straatman and Nieuwenhuis, 1961; Igarashi, 1966; Jumalon, 1968; Straatman, 1968; Munshi and Moiz, 1968, 1969; D'Abrera, 1971; Common and Waterhouse, 1972).

Thus characters of the male genitalia and immature stages do not serve to distinguish the *polydorus* group from other species of *Atrophaneura* at the generic level. On characters of the valve, clasper, aedeagus and pseuduncus/8th tergite the affinities of the *polydorus* group are clearly with the *Atrophaneura* *coon* group. Specialised characters such as the hypertrophied socii and tegumen



Figs 1-13. Male and female genitalia. (1-9) male genitalia of *Atrophaneura*: lateral view (with left valve removed) and dorsal view of pseuduncus: (1) *A. elcinous*; (2) *A. priapus*; (3) *A. horishanus*; (4) *A. nox*; (5) *A. coon*; (6) *A. hector*; (7) *A. polyphontes*; (8) *A. aristolochiae*; (9) *A. polydorus*. (10) dorsal view of pseuduncus of *Parides*. (11-13) female bursa and signum of: (11) *Parides aglaope*; (12) *Atrophaneura polydorus*; (13) *Troides priamus euphorion*.

and the sclerotised female ductus bursae serve to separate these taxa at the group level only. The *coon* and *polydorus* groups form a pair of sister-groups, as do the *latreillei* and *nox* groups, the latter united by the nature of the clasper, aedeagus and pseuduncus/8th tergite. *A. antenor* stands somewhat apart from the other groups. Thus, recognition of *Pachliopta* as a genus results in the necessity of recognising separate genera for the *coon*, *antenor* and *latreillei-nox* groups, to avoid paraphyly. *Pachliopta* and *Atrophaneura* should therefore be synonymized. Both generic names appeared in the same publication (Reakirt, 1865); Hemming (1964) accorded precedence to *Atrophaneura*,

following the arrangement of Corbet (1943). *Pachliopta* is thus reinstated as a synonym of *Atrophaneura*.

### *Atrophaneura* Reakirt

Munroe (1961) placed *Atrophaneura* as a subgenus of *Parides* Hübner, uniting them on characters of male genitalia and immature stages. Fundamentally the male genitalia of the two genera are similar; however they differ in one essential feature. In *Atrophaneura*, as in *Parides*, a suture separates the pseuduncus from the 8th tergite, but in *Parides* this suture does not extend down the mid-line of the pseuduncus (Fig. 10), as it does in all species of *Atrophaneura* where the suture is medially present. The *Parides* type of suture is seen also in *Euryades* C. & R. Felder and *Cressida* Swainson; the *Atrophaneura* type is seen also in *Troides* (*Troides*) and *Troides* (*Ornithoptera*), the suture being absent in *Troides* (*Trogonoptera*). The type of suture present is consistent for all species examined in their respective groups and the mid-line extension illustrates a close relationship between *Atrophaneura* and *Troides* Hübner, serving to separate these two genera from the more primitive *Euryades*, *Cressida* and *Parides*.

Additionally, *Parides* and *Atrophaneura* can be distinguished by the female bursa copulatrix. In *Parides* the signum is V-shaped (Fig. 11), whereas in *Atrophaneura* the signum is ribbon-like (Fig. 12).

*Parides* and *Atrophaneura* cannot be regarded as congeneric as this results in paraphyly, *Atrophaneura* being more closely related to *Troides* than to *Parides*. Talbot (1939) had earlier noted the close morphological relationship between *Atrophaneura* and *Troides* and this, coupled with zoogeographic evidence (*Atrophaneura* and *Troides* being Indo-Australian, *Parides* South American), supports the above arrangement.

### Phylogeny

All three genera of Indo-Australian Troidini—*Cressida*, *Atrophaneura* and *Troides*—are derivable from the more primitive South American *Euryades* and *Parides*, and represent a dual invasion before the break-up of Gondwanaland. Present day distribution patterns suggest that the two invading ancestors, *Cressida* and *Atrophaneura/Troides*, followed different dispersal routes. *Cressida* followed the more usual route, to Australia [c.f. *Protographium leosthenes* (Doubleday) and *Papilio anactus* W. S. Macleay], whilst the *Atrophaneura/Troides* ancestor appears to have dispersed via India (as *Atrophaneura*) to South-East Asia (as *Troides*). This supports the suggestion by Ridd (1971) that India and South-East Asia were closely associated as part of Gondwanaland. The presence of *A. antenor* on Madagascar, the only troidine in the Ethiopian region, supports the suggestion that dispersal was via India. With the post-Gondwanan unification of India and Asia, *Atrophaneura* was able to radiate throughout the Indo-Australian region, the most easterly representatives belonging to the specialised *polydorus* group.

### Classification

Five species groups of *Atrophaneura* are recognizable. The characters of *A. antenor*, coupled with its geographical distribution, support the recognition

of a subgenus for this species. The genus and subgenera are characterised below; for group characteristics see Munroe (1961).

### Genus *Atrophaneura* Reakirt 1865

Type species: *Atrophaneura erythrosoma* Reakirt, 1865 (= *Papilio semperi* C. & R. Felder, 1861).

A genus in the Troidini, closest to *Parides* and *Troides* s.l. Differs from *Parides* in the better developed sinus of the fifth tarsal segment; in the absence of anthoxanthins from all species (Ford, 1944); in the pseuduncus/8th tergite suture, when present medially, extending down the mid-line of the pseuduncus; and in the ribbon-shaped, rather than V-shaped, female signum. Differs from *Troides* in vein  $R_2$  of the fore wing arising from a point opposite  $CuA_1$  rather than  $CuA_2$ ; in the absence of any form of yellow, fluorescent pigment; in having a normally suspended pupa; and in the distinct female signum, reduced to spicules in *Troides* (Fig. 13).

### Subgenus *Pharmacophagus* Haase, 1892

*Pharmacophagus* Haase, 1892, *Bibl. Zool.* 8: 15. Type species: *Papilio antenor* Drury, 1773.

Fore wing with submarginal white spots; fore wing intercalary folds not darker-scaled than rest of wing; fore and hind wings with marginal white spots; antennae red; antennal club straight; male genitalia with pseuduncus absent beyond suture.

One species: *antenor* (Drury).

### Subgenus *Atrophaneura* Reakirt, 1865

*Polydorus* Swainson, 1833, *Zool. Illust.* (2)3: pl. 101, *nec* Blainville, 1826. Type species *Polydorus thoas* Swainson.

*Atrophaneura* Reakirt, 1865, *Proc. ent. Soc. Philad.* 3: 446. Type species *Atrophaneura erythrosoma* Reakirt.

*Pachliopta* Reakirt, 1865, *Proc. ent. Soc. Philad.* 3: 503. Type species *Papilio diphilus* Esper.

*Pachlioptera* Scudder, 1875, *Proc. Amer. Acad. Arts Sci., Boston* 10: 235. Incorrect spelling of *Pachliopta*, same type species.

*Byasa* Moore, 1882, *Proc. zool. Soc. Lond.* 1882: 258. Type species *Papilio philoxenus* G. R. Gray.

*Panosmia* Wood-Mason & de Niceville, 1886, *Jl Asiat. Soc. Bengal* 55: 374. Type species *Papilio dasarada* Moore.

*Pangerana* Moore, 1886, *Jl Linn. Soc. Lond.* 21: 51. Type species *Papilio varuna* White.

*Tros* Kirby, 1896, in *Allen's Nat. Libr. Hand-book Lepid.* 2: 305. Type species *Papilio hector* Linnaeus.

*Karanga* Moore, 1902, *Lepidoptera Indica* 5: 157. Type species *Papilio nox* Swainson.

*Losaria* Moore, 1902, *Lepidoptera Indica* 5: 184. Type species *Papilio coon* Fabricius.

*Balignina* Moore, 1902, *Lepidoptera Indica* 5: 187. Type species *Papilio neptunus* Guérin-Méneville.

Fore wing without submarginal white spots; fore wing intercalary folds darker scaled than rest of wing, paler along veins; fore and hind wings without marginal white spots (fringe hairs white in *hector*); antennae black; antennal club curved; male genitalia with pseuduncus present.

Forty-two species in four groups:

(i) *latreillei* group (14 species): *daemonius* (Alpheraky), *plutonius* (Oberthür), *alcinous* (Klug), *latreillei* (Donovan), *polla* (de Niceville), *crassipes* (Oberthür), *adamsoni* (Grose-

Smith), *nevillei* (Wood-Mason), *laos* (Riley and Godfrey), *mencius* (C. & R. Felder), *impediens* (Rothschild), *hedistus* (Jordan), *dasarada* (Moore), *polyeuctes* (Doubleday) [= *philoxenus* (Gray)].

(ii) *nox* group (12 species): *semperi* (C. & R. Felder), *kuehni* (Honrath), *luchti* (Roepke), *hageni* (Rogenhofer), *priapus* (Boisduval), *sykorax* (Grose-Smith), *horishanus* (Matsumura) [= *sauteri* (Heyne)], *aidoneus* (Doubleday), *varuna* (White), *zaleucus* (Hewitson), *nox* (Swainson), *dixonii* (Grose-Smith).

(iii) *coon* group (3 species): *neptunus* (Guérin-Méneville), *coon* (Fabricius), *rhodifer* (Butler).

(iv) *polydorus* group (13 species): *hector* (Linnaeus), *jophon* (Gray), *pandiyana* (Moore), *oreon* (Doherty), *liris* (Godart), *polyphontes* (Boisduval), *schadenbergi* (Semper), *mariae* (Semper), *phegeus* (Hopffer), *phlegon* (C. & R. Felder) [= *annae* (C. & R. Felder), = *strandii* (Bryk), = *sabinae* (Seyer)], *atropos* (Staudinger), *aristolochiae* (Fabricius), *polydorus* (Linnaeus).

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