

A REVISED CLASSIFICATION OF THE GENUS *ATROPHANEURA* REAKIRT (LEPIDOPTERA: PAPILIONIDAE)

D. L. HANCOCK

5 Northampton Crescent, Hillcrest, Bulawayo, Zimbabwe

Abstract

The classification of *Atrophaneura* Reakirt is revised. *Pachliopta* Reakirt (= *Losaria* Moore, **syn. nov.**; = *Balignina* Moore, **syn. nov.**) is recognized as a subgenus, comprising the *coon* and *polydorus* groups. *A. hector* (Linnaeus) is removed from the *polydorus* group and included with *A. antenor* (Drury) in subgenus *Pharmacophagus* Haase (= *Tros* Kirby, **syn. nov.**). The phylogeny and biogeography of the genus are discussed.

Introduction

The 45 species considered here were placed in two separate genera, *Pachliopta* Reakirt and *Parides* Hübner (subgenus *Atrophaneura* Reakirt), by Munroe (1961). This arrangement was disputed by Hancock (1980, 1983), who recognized *Atrophaneura* as a distinct genus and placed *Pachliopta* as a synonym of it. Munroe (1961) assigned the species to five species-groups, which were accepted unchanged by Hancock (1980, 1983). Both authors, however, noted that the position of *A. antenor* (Drury) from Madagascar, may need to be revised. More information on this species is now available, both from dissected material and data provided by Paulian and Viette (1968). This information enables the systematic position of *A. antenor* to be resolved.

Another anomalous species is the Indian *A. hector* (Linnaeus). Generally included in the *polydorus* group, this species lacks the hypertrophied *socii* and *tegumen* of the male genitalia seen in other species in the group (and used as a generic character by Munroe 1961), and *A. hector* has relatively broader wings than the other members of the *polydorus* group. Examination of the female genitalia (Fig. 1) shows this species to be closely related to *A. antenor*, despite the very different shape of the male valvae. The shape of the wings and tail support this arrangement. The female genitalia of these two species share with both the *coon* and *polydorus* groups (Figs 2, 3) the presence of an elongate, apically sclerotized ductus bursa. They differ from both these groups in the much more elongate corpus bursa and signum.

With the removal of *A. hector*, the *polydorus* group becomes a very homogeneous assemblage. This group is closely related to the *coon* group, as noted by Hancock (1980, 1983), based on morphological characters of the adults, and by Igarashi (1984), based on larval characteristics. Indeed, Igarashi (1984) included both groups in the genus *Pachliopta*, even though male genitalia characters do not agree with Munroe's (1961) diagnosis of the genus. Based on the female ductus bursa, *A. antenor* and *A. hector* would

also be referable to *Pachliopta* and some authors may choose to recognize this as a genus. Here however, *Pachliopta* and *Pharmacophagus* are both regarded as subgenera of *Atrophaneura*, in line with earlier findings (Hancock 1980, 1983). Whatever course is followed, the concept of *Pachliopta* as a genus remains untenable unless both the *antenor* and *coon* groups are included.

Classification

Genus *Atrophaneura* Reakirt

For a generic diagnosis see Hancock (1980, 1983). Although often considered to be a subgenus of *Parides*, the medial extension to the basal suture on the pseuduncus seen in all species where the suture is entire demonstrates the affinity of this genus with *Troides* Hübner and its allies. The early stages also support the recognition of *Atrophaneura* as a separate genus. Grey colour-forms of the larva occur in *Atrophaneura*, *Troides*, *Ornithoptera* Boisduval and *Trogonoptera* Rippon, but apparently not in *Parides* or other troidine genera.

Six species-groups are recognized here, placed in three subgenera. Only available names have been listed in the respective synonymies, for unavailable names see Hancock (1980, 1983).

Subgenus *Atrophaneura* Reakirt

Atrophaneura Reakirt, 1865, *Proc. ent. Soc. Philad.* 3: 446. Type species *A. erythrosoma* Reakirt (= *semperi* C. & R. Felder).

Byasa Moore, 1882, *Proc. zool. Soc. Lond.* 1882: 258. Type-species *Papilio philoxenus* Gray (= *polyeuctes* Doubleday).

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

Panosmia Wood-Mason and de Nicéville, 1887, *J. Proc. Asiat. Soc. Bengal* 55: 374. Type-species *Papilio dasarada* Moore.

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

Male hind wing with inner marginal androconia (scent-organ) well developed and woolly. Male genitalia with pseuduncus well developed, the basal suture entire and extending for a distance down mid-line; socii and tegumen not hypertrophied; valvae well developed, entire or weakly emarginate dorsally and distally; harpe broad, serrate or toothed; aedeagus short and stout, curved. Female corpus bursa rounded, the signum well developed, elongate and relatively broad; ductus bursa short, stout and not

sclerotized (Figs. 4-5). The larva has a supraspiracular tubercle on the first abdominal segment (Igarashi 1984).

There are two species-groups.

(i) *latreillei* species-group

Male hind wing with inner marginal fold narrow; tail well developed and spatulate. Male valvae entire; harpe serrate or spinose; pseuduncus with medial extension of suture short (figured by Hancock 1980). This group contains 15 species from southeastern Asia and Japan (Igarashi 1984, Collins and Morris 1985).

Species: *daemonius* (Alpheraky), *plutonium* (Oberthür), *alcinous* (Klug), *latreillei* (Donovan), *polla* (de Nicéville), *crassipes* (Oberthür), *adamsoni* (Grose-Smith), *nevillei* (Wood-Mason), *laos* (Riley & Godfrey), *mencius* (C. & R. Felder), *impediens* (Rothschild), *febanus* (Fruhstorfer), *hedistus* (Jordan), *dasarada* (Moore), *polyeuctes* (Doubleday).

(ii) *nox* species group.

Male hind wing with inner marginal fold very broad and rolled-up; tail vestigial or absent. Male valvae weakly emarginate dorsally and distally; harpe toothed (figured by Hancock 1980). This group contains 12 southeastern Asian species, placed here in two subgroups. *A. tungensis* Zin and Leow (1982), described from Sumatra, appears to be a hybrid *nox* x *hageni*.

priapus subgroup: Male with valvae dorsally rounded and pseuduncus with medial extension of suture short. Hind wing with a distinct yellow, blue or green postdiscal band enclosing black spots. Southern Burma to Sumatra and Java. Four species: *priapus* (Boisduval), *sycorax* (Grose-Smith), *hageni* (Rogenhofer), *luchti* (Roepke).

nox subgroup: Male with valvae dorsally pointed and pseuduncus with medial extension of suture elongate. Hind wing not as above. Northern India and Taiwan to Sulawesi and Bali. Eight species: *semperi* (C. & R. Felder), *kuehni* (Honrath), *horishanus* (Matsumura), *aidoneus* (Doubleday), *varuna* (White), *zaleucus* (Hewitson), *nox* (Swainson), *dixonii* (Grose-Smith).

Subgenus *Pharmacophagus* Haase

Pharmacophagus Haase, 1891, *Bibl. zool.* 8: 15. Type-species *Papilio antenor* Drury.

Tros Kirby, 1896, *Handbk to Order Lepidoptera, Part 1*, Butts 2: 305. Type-species *Papilio hector* Linnaeus. **syn. nov.**

Wings relatively broad; tail very narrow, non-spatulate; male hind wing with inner marginal androconia (scent organ) absent, the inner marginal fold narrow. Male genitalia with pseuduncus reduced, the basal suture absent or weakly present at sides, never present medially; socii and tegumen not hypertrophied; valvae entire or vestigial; harpe relatively narrow or much reduced; aedeagus long and slender, straight. Female corpus bursa elongate, the signum elongate and narrow; ductus bursa long, slender and sclerotized in apical portion (Fig. 1). The larva retains the supraspiracular tubercle on the first abdominal segment (Woodhouse and Henry 1942, Okano 1983). There are two species-groups.

(i) *antenor* species-group.

Fore wing with numerous white spots; hind wing with a postdiscal series of three white spots towards the costa and scattered blue-green scales; antenna red, the club straight. Male genitalia (Fig. 6) with valvae well developed, entire; harpe relatively narrow and with a large tooth posteriorly; pseuduncus short, broad, with two small dorsal tubercles but without a basal suture (not absent beyond suture as previously noted).

This group contains only *A. antenor* from Madagascar. The female genitalia were figured by Paulian and Viette (1968), the larva by Okano (1983).

(ii) *hector* species-group.

Fore wing with subapical and discal white bands; hind wing generally with a postdiscal series of red spots (the three towards the costa being best developed) but no metallic scales; antenna black, the club curved. Male genitalia with the valvae vestigial; harpe thorn-like; pseuduncus short, broad, with a trace of suture at sides (figured by Hancock 1980).

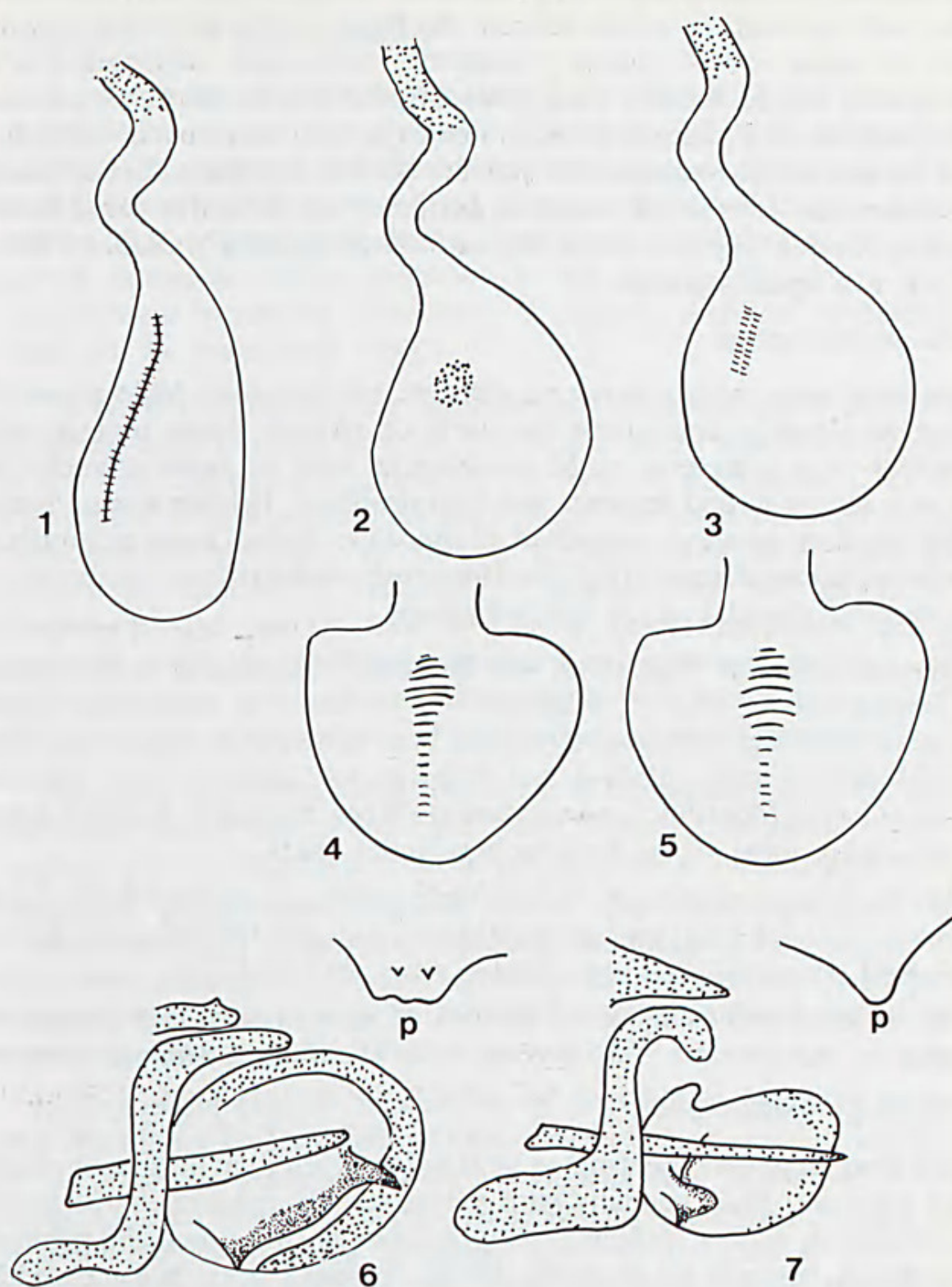
This group contains only *A. hector* from India, Sri Lanka and the Andaman Is. Woodhouse and Henry (1942) recorded a specimen with the red hind wing spots suppressed and greenish-blue reflections present, and described the larva in detail; the supraspiracular tubercle on the first abdominal segment is small.

Subgenus *Pachliopta* Reakirt

Pachliopta Reakirt, 1865, *Proc. ent. Soc. Philad.* 3: 503. Type-species *Papilio diphilis* Esper (= *polydorus* Linnaeus).

Losaria Moore, 1902, *Lep. Indica* 5: 184. Type-species *Papilio coon* Fabricius. **syn. nov.**

Balignina Moore, 1902, *Lep. Indica* 5: 187. Type-species *Papilio neptunus* Guérin-Ménéville. **syn. nov.**



Figs 1-7. Male and female genitalia. 1-5: Corpus bursa and ductus bursa of *Atrophaneura*. 1: *A. hector*; 2: *A. neptunus*; 3: *A. aristolochiae*; 4: *A. polyeuctes*; 5: *A. varuna*. 6-7: Male genitalia of *Atrophaneura*. 6: *A. antenor*; 7: *A. neptunus*. (p = dorsal view of pseuduncus).

Wings narrowed; male hind wing with inner marginal androconia (scent-organ) reduced or absent, not woolly, the inner marginal fold narrow. Male genitalia with pseuduncus often reduced, the basal suture absent or weakly present at sides, never present medially; socii and tegumen often hypertrophied; valvae dorsally emarginate or greatly reduced; harpe narrow and longitudinal, or a transverse ridge; aedeagus long and slender, straight. Female corpus bursa rounded, the signum short and broad; ductus bursa long, slender and sclerotized in apical portion (Figs 2-3). The larva lacks the supraspiracular tubercle on the first abdominal segment (Igarashi 1984). There are two species-groups.

(i) *coon* species-group

Male hind wing with scent-organ present; tail petiolate. Male genitalia with valvae dorsally emarginate but well developed; harpe narrow and longitudinal or a transverse ridge; pseuduncus with or without traces of suture at sides; socii and tegumen not hypertrophied. Female corpus bursa rounded; signum rounded, composed of spicules; ductus bursa sclerotized for a relatively long distance (Fig. 2). This group contains four southeastern Asian species, placed here in two subgroups.

neptunus subgroup: Male with valvae mitten-shaped and with a weak dorsal emargination (Fig. 7; Hancock 1984); harpe a transverse ridge; pseuduncus short and without suture; socii bent downwards. Hind wing with postdiscal patches only. Malaya and Palawan to Sulawesi. Two species: *neptunus* (Guérin-Méneville), *palu* (Martin). When viewed in incident light, the black wing areas of *A. palu* have a violet sheen.

coon subgroup: Male with valvae strongly dorsoapically emarginate; harpe elongate and longitudinal; pseuduncus elongate and with traces of suture at sides; socii not bent downwards (figured by Hancock 1980). Hind wing with discal and submarginal patches or spots. Assam and Hainan to Andaman Is. and Sumatra. Two species: *coon* (Fabricius), *rhodifer* (Butler).

(ii) *polydorus* species-group

Male hind wing with scent-organ vestigial or absent; tail present or absent but not petiolate. Male genitalia with valvae greatly reduced; harpe thorn-like; pseuduncus with or without a vestigial suture at sides; socii and tegumen hypertrophied (figured by Hancock 1980). Female corpus bursa rounded; signum relatively short and narrow, striate; ductus bursa sclerotized for a relatively short distance (Fig. 3). This group contains 12 Indo-Australian species, although *A. aristolochiae kotzebuea* (Eschscholtz) is regarded as a distinct species by some authors (e.g. Collins and Morris 1985).

Species: *jophon* (Gray), *pandiyana* (Moore), *oreon* (Doherty), *liris* (Godart), *polyphontes* (Boisduval), *schadenbergi* (Semper), *mariae* (Semper), *phegeus*

(Hopffer), *phlegon* (C. & R. Felder), *atropos* (Staudinger), *aristolochiae* (Fabricius), *polydorus* (Linnaeus).

Phylogeny and Biogeography

A reappraisal of the relationships of the subgenera and species-groups of *Atrophaneura* can now be made. Based on outgroup comparison with *Troides*, *Ornithoptera* and *Trogonoptera*, subgenus *Atrophaneura* appears to be the most primitive, since these groups have several features in common, such as the unsclerotized ductus bursa, well developed valvae, stout and curved aedeagus, medial extension to the pseuduncus suture (except in *Trogonoptera*, where the pseuduncus is reduced) and well developed scent-organ on the male hind wing.

The various differentiating characters of *Pharmacophagus* and *Pachliopta* all appear to be derived, as is the loss of the lateral supraspiracular tubercle on the first abdominal segment of the larva in *Pachliopta*. This tubercle is present in *Atrophaneura*, *Pharmacophagus* and the *Troides* group (Igarashi 1984), and also in *Parides* and *Battus* (Scopoli) (Moss 1919). Although more detailed information is required, it appears that the larvae of both *Pharmacophagus* species have a pair of black-tipped tubercles on the prothorax, whilst the pupae have the lateral expansions of the thorax reduced. In *Atrophaneura* and *Pachliopta* these prothoracic tubercles are wholly red, whilst the lateral expansions of the pupae are more pronounced.

The elongate corpus bursa and shape of the signum, plus the postdiscal spots and narrow tail of the hind wing, suggest that *antenor* and *hector* represent sister-groups. The reduced valvae of the *polydorus* group, different from the vestigial condition seen in *A. hector*, represent an extreme development of the dorso-apical reduction seen in the *coon* group, and these also appear to be sister-groups. Larval characters support this arrangement. The suggested phylogenetic relationships of the six species-groups are shown in Fig. 8.

Having established the relationship of the various subgenera and groups, some interesting biogeographical hypotheses can be proposed, which amend the discussion by Hancock (1980, 1983). It is very likely that the *Troides* lineage radiated from Sundaland, suggested by the presence there of both *Trogonoptera* and *Troides* subgenus *Ripponia* Haugum & Low and the existence of *Ornithoptera* in the New Guinea region. Based on pattern characters, particularly the extent of the yellow areas on the hind wing and the iridescent scaling on the underside, *Ripponia* is considered to be more primitive than subgenus *Troides*, forming a link with *Ornithoptera* (Hancock 1983).

Atrophaneura appears to have radiated from further north, with the unspecialized *latreillei* group centred in southern China and neighbouring

areas, but not in India. A spread to Sundaland appears to have resulted in the differentiation of *Pachliopta*. In the present author's opinion, a taxon is more likely to undergo change whilst colonizing a new environment than in one where it has stabilized, hence the numerous specializations seen in *Pachliopta* support the suggestion that it is the colonizer. The *coon* group, with its less reduced valvae and non-hypertrophied tegumen and socii appears to be less specialized than the *polydorus* group, suggesting a

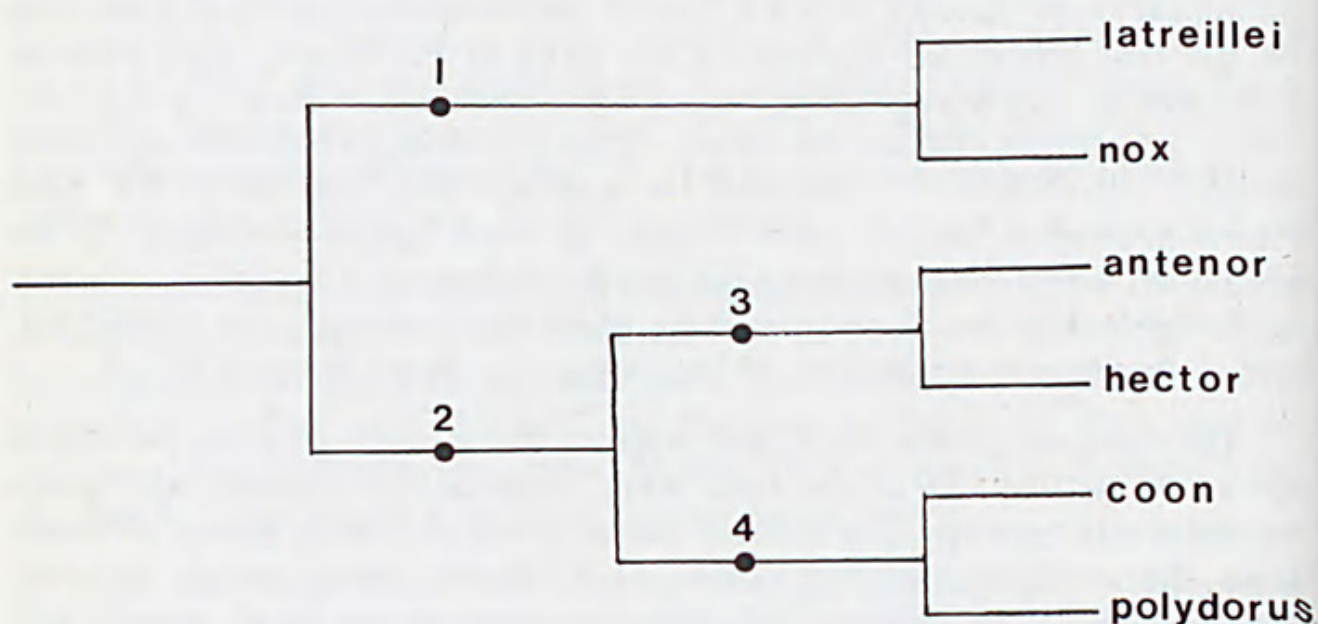


Fig.8. Phylogenetic relationship of the species-groups of *Atrophaneura*. Character sets: 1: Male scent-organ well developed and woolly; suture at base of pseuduncus entire; harpe broad; aedeagus short, stout and curved; ductus bursa short, stout and unsclerotized. 2: Male scent-organ reduced or absent; suture at base of pseuduncus absent medially; harpe narrow; aedeagus long, slender and straight; ductus bursa long, narrow and apically sclerotized. 3: Tail narrow; corpus bursa elongate; signum elongate and narrow; larva with a supraspiracular tubercle on first abdominal segment. 4: Tail petiolate, spatulate or absent; corpus bursa rounded; signum short and broad; larva without a supraspiracular tubercle on first abdominal segment. See text for characters delimiting species-groups.

Sundaland origin for the subgenus. At a later stage this colonization was repeated by the *nox* group of subgenus *Atrophaneura*, again accompanied by some character specialization, such as loss of the tail, expansion of the scent-organ and reduction of the valvae. The *priapus* subgroup, with its less reduced valvae and short medial extension of the pseuduncus suture (as seen in the *latreillei* group), appears to be less specialized than the *nox* subgroup. This suggests that the *nox* group radiated from Sundaland rather than from further north.

An early offshoot from *Pachliopta* apparently reached India as *Pharmacophagus* and from there it spread to Madagascar. The Sundaland ancestor then split into two, to give the *coon* and *polydorus* groups. The original *Pachliopta* ancestor in Sundaland apparently adapted to drier forest types than *Atrophaneura*, perhaps as a result of competition with the already established *Trogonoptera* and *Troides*. This presumably assisted in its dispersal into India and Madagascar. *A. hector* is known to be migratory (Woodhouse and Henry 1942).

The Old World troidines appear to have been closely associated with southeastern Asia for a considerable period of time. They probably arrived there at the same time *Cressida* Swainson reached Australia, both evolving from South American ancestors during the tectonic break-up of continental Gondwanaland. As such they provide strong biological evidence for the suggestion (apparently not yet fully embraced in biogeographical studies) that southeastern Asia, including southern China, was a part of Gondwanaland, closely associated with India and Australia. Geological and palaeontological evidence for this were provided by Ridd (1971) and Cooper (1980) respectively.

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