

THE SYSTEMATIC POSITION OF *PAPILIO ANACTUS* MACLEAY (LEPIDOPTERA: PAPILIONIDAE)

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Abstract

The systematic position of *Papilio anactus* Macleay is examined in relation to other species of *Papilio* Linnaeus. It is here placed in the monotypic subgenus *Eleppone* nov., being most closely allied to South American *Heracles* Hübner and Indo-Papuan *Chilasa* Moore. Larval morphology and foodplant preferences of ancestral Papilionidae are discussed: the ancestral larva is considered to have been smooth and green; ancestral Leptocircini, Troidini and Papilionini are suggested to have fed on Annonaceae, Aristolochiaceae and Rutaceae respectively.

Introduction

The systematic position of *Papilio anactus* has been the subject of uncertainty since its description in 1826. Jordan (1908-10) referred to it as a "mimetic derivation of the *demoleus* group" and associated it with the mimetic *agestor*, *clytia* (+ *veiovis*), *laglaizei* and *castor* groups. Talbot (1939) placed *anactus* and the *agestor*, *clytia* (+ *veiovis*) and *laglaizei* groups in the Oriental genus *Chilasa*. Ford (1944) doubted the homogeneity of Talbot's arrangement, suggesting that *anactus* and the *laglaizei* group may have to be removed, and concluded that generic separation was not justified. Munroe (1961) suggested that *anactus* connected the *machaon* group to the *laglaizei* group, yet omitted the species from his taxonomic arrangement. Igarashi (1976) recognized the affinities of *anactus* with the *Chilasa* assemblage, to which he added the South American *anchisiades* group, yet did not regard *anactus* as a member of that assemblage.

A detailed investigation of the species of *Papilio* s.l. (Hancock, 1978) suggests that six subgenera should be recognized. These are: (1) *Pterourus* Scopoli, 1777: a Nearctic and Neotropical subgenus of 25 species placed in five species-groups (*glaucus*, *troilus*, *zagreus*, *scamander* and *homerus*); (2) *Heracles* Hübner, [1819]: a Nearctic and Neotropical subgenus of 32 species placed in three species-groups (*thoas*, *torquatus* and *anchisiades*); (3) *Eleppone* nov.: a monotypic subgenus containing the Australian *P. anactus*; (4) *Chilasa* Moore, 1881 (= *Clytia* Swainson, 1833 nec Lamouroux, 1812 and Robineau-Desvoidy, 1830); an Oriental and Papuan subgenus of 11 species placed in four species-groups (*clytia*, *veiovis*, *agestor* and *laglaizei*); (5) *Papilio* Linnaeus, 1758: a Palaearctic and Nearctic subgenus of 14 species placed in the *machaon* group; (6) *Princeps* Hübner, [1807]: a widespread subgenus found in Ethiopian, Oriental, East Palaearctic and Australasian regions, comprising 130 species placed by Munroe (1961) in 26 species-groups.

P. anactus is sufficiently distinct from other species of *Papilio* to warrant subgeneric status under the above arrangement. It is characterized below.

*Eleppone** subgen. nov.

Type species: *Papilio anactus* W.S. Macleay, 1826. In King, *Nar. surv. intertrop. w. coasts Aust.*

Sexes similar; wing pattern mimetic of Troidini; hind wings with both red

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* The practice of naming Papilionidae taxa after characters of Greek mythology is followed here. *Elēpponē* is an anagram of Penelope, wife of Ulysses.

and blue spots present; red pigment type B; anthoxanthins absent. Male genitalia (Fig. 1) with clasper broad, serrate, ventral spine present; juxta not deeply emarginate. Mature larva solitary; dorso-lateral spiny tubercles present in a complete series; blue-black with dorso-lateral and lateral rows of orange-yellow spots. Pupa brown, grey-brown or grey with green markings, roughly textured, slender and relatively straight; paired anterior processes and dorsal thoracic protuberance present. Larval foodplants species of *Eremocitrus*, *Microcitrus* and *Citrus* (all Rutaceae). Larva and pupa illustrated by Common and Waterhouse (1972) and Igarashi (1976).

Eleppone is separated from the related subgenera *Heraclides* and *Chilasa* by the characters listed in Table 1.

TABLE 1
Characters distinguishing the *Papilio* subgenera *Heraclides*, *Eleppone* and *Chilasa*

Character	<i>Heraclides</i>	<i>Eleppone</i>	<i>Chilasa</i>
wing pattern	non-mimetic or mimetic of Troidini	mimetic of Troidini	mimetic of Danaeinae or Uraniidae
red pigment	present, type B	present, type B	absent
fore femora	without orange hairs	with orange hairs	without orange hairs
juxta	deeply emarginate	not deeply emarginate	not deeply emarginate
first abdominal segment of mature larva	with raised band	without raised band	without raised band
abdominal "saddle" of larva	present	absent	absent
larval colour	dark with orange, yellow or white pale patches; occasionally with blue spots	dark with orange-yellow spots	dark with white patches or brown bands; carmine or white spots present (green with dark pattern)
larval foodplants	Rutaceae or Piperaceae	Rutaceae	Lauraceae
Pupa	stick-like; anterior and dorsal protuberances present	stick-like; anterior and dorsal protuberances present	stick-like or robust; anterior and dorsal protuberances absent

Mimicry of *Papilio anactus*

The mimetic relationship between *P. anactus* and male *Cressida cressida* (Fabricius) (Troidini) seems not to have been generally appreciated. Some authors (e.g. Common and Waterhouse, 1972) have suggested that such a relationship exists between *P. anactus*, *C. cressida* and *Pachliopta polydorus* (Linnaeus); however it is unlikely that *P. polydorus* is involved, it being only marginally sympatric with the other two species and tending to breed in rainforests rather than woodlands. Other authors (e.g. Ford, 1944) have suggested that *anactus* is a mimic of *Acraea andromacha* (Fabricius) (Acraeinae). Still others (e.g. Igarashi, 1976) regard *anactus* as being non-mimetic.

Apart from a close morphological resemblance between *anactus* and *Cressida*, especially in characters of the hind wing (e.g. 5 large rounded postdiscal red spots; white central area with broadly black discocellular veins), abdomen and thorax (the femoral orange hairs of *anactus* correspond to the lateral prothoracic red streak of *Cressida*), the species are also similar in habitat and behaviour. Both are open forest or woodland species with a normally slow gliding flight, but with a rapid escape flight (Common and Waterhouse, 1972).

P. anactus has presumably extended its distribution beyond that of *Cressida*, and increased its abundance, by utilizing *Citrus* as a larval foodplant. Much of the mimetic association has been subsequently lost by this extension of range and increased abundance.

Phylogeny

It appears that the ancestral species of *Papilio*, from a centre of origin in eastern North America, dispersed first to the Palaearctic region and subsequently to South America, leaving *Pterourus* in North America. The Palaearctic section appears to have differentiated into a Europe-Asia Minor based subgenus (*Papilio*) and an Oriental (Chinese) based subgenus (*Princeps*), represented primitively by *P. alexanor* Esper and *P. xuthus* Linnaeus respectively. These two subgenera show great similarities in the structure of the male clasper, being typically slender and ventral with a dorsally expanded serrate plate apically. The South American section appears to have dispersed to Australia as *Eleppone* before the late Cretaceous break-up of Gondwanaland, leaving *Heraclides* in South America. Evidence suggests that South-East Asia was also a part of Gondwanaland (Ridd, 1971) and the *Eleppone* ancestor spread to and differentiated there as *Chilasa*. *Heraclides* developed the deeply emarginate juxta characteristic of the subgenus whilst *Chilasa* developed the modified pupa and switched from a rutaceous to a lauraceous larval foodplant. These three "Gondwanaland" subgenera are characterized by a broad male clasper and dark-coloured, tuberculate larvae [secondarily (?) smooth in the *Heraclides thoas* group].

Larvae of *Papilio*, *Princeps*, *Heraclides* and *Eleppone* feed primarily on Rutaceae or Umbelliferae, a few species of *Princeps* utilizing Lauraceae. *Pterourus* and *Chilasa* are primarily Lauraceae or Magnoliaceae feeders, some species of *Pterourus* also feeding on Rutaceae.

Ancestral larval morphology and foodplants

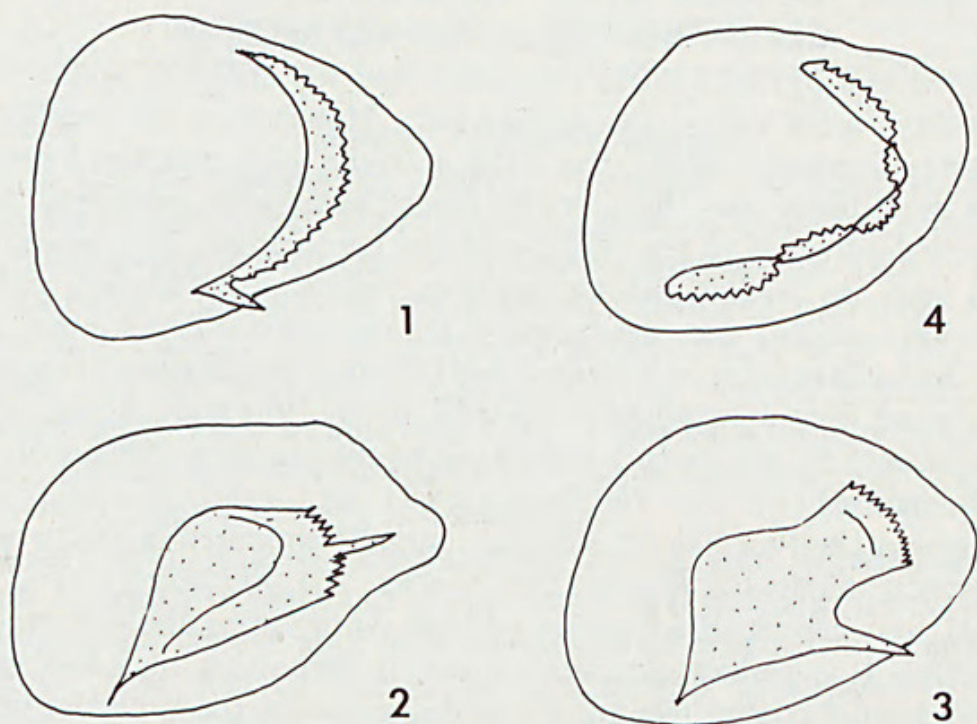
Munroe and Ehrlich (1960) concluded that the ancestral papilionid had a red-tuberculate, aristolochiaceous-feeding larva. However, as the Papilionini and Trodini are more closely allied than either is to the more primitive Leptocircini, it appears more likely that the ancestral larva was smooth, green and non-aristolochiaceous-feeding, as in the Papilionini and Leptocircini. The red-tuberculate condition seen in Trodini and Parnassiinae, suggested by Ehrlich and Raven (1965) to have evolved after separation of the Parnassiinae-Papilioninae ancestor from the Baroniinae, may represent a polyphyletic development of aposematic colouration and form in response to the utilization of the toxic Aristolochiaceae. This is supported by the smooth green larva of the primitive *Baronia brevicornis* Salvin (Baroniinae) (Vazquez and Perez, 1961) and the red-tuberculate larvae of some species in the *Protesilaus** *lysithous* group (Leptocircini), the larvae of the latter possibly mimicking *Parides*. One species, the primitive *Protesilaus asius* (Fabricius), has been recorded feeding on both Annonaceae and Aristolochiaceae (Lima, 1968). It is perhaps noteworthy that in *Parnassius*, only two species of which have been recorded feeding on Aristolochiaceae, the tubercles have been lost. The tuberculate larvae of *Heraclides*, *Eleppone* and *Chilasa*, perhaps also

* *Protesilaus* Swainson is here regarded as a genus distinct from *Eurytides* Hübner.

associated with mimicry, lend further support to the suggestion of polyphyletic development of tubercles in the mature larva.

Diversification in the Papilioninae appears to have been facilitated by adaptation to different, but chemically related larval foodplants. A survey of foodplant preferences in the three tribes (see Scriber, 1973) shows that Leptocircini feed primarily on Annonaceae, secondarily on Lauraceae and related families, rarely on Aristolochiaceae; Troidini feed primarily on Aristolochiaceae, secondarily on Rutaceae; Papilionini feed primarily on Rutaceae, secondarily on Umbelliferae, Lauraceae and related families. Within the tribes foodplant preference relationships are seen between Annonaceae and Lauraceae or Aristolochiaceae, Aristolochiaceae and Rutaceae, Rutaceae and Lauraceae or Umbelliferae. No relationships are seen between Aristolochiaceae and Lauraceae or Annonaceae and Rutaceae [exceptionally *Graphium antiphates* (Cramer) has been recorded on introduced *Citrus* as well as the usual annonaceous foodplants (Marsh, 1960); however this species is closely related to the lauraceous-feeding *G. euphrates* (Felder)].

Thus the Papilioninae ancestor appears to have diverged from an original Annonaceae foodplant to Aristolochiaceae and from there to Rutaceae, resulting in the differentiation of Leptocircini, Troidini and Papilionini respectively. The latter two tribes are most closely related phylogenetically and, as no relationship is known between Aristolochiaceae and Lauraceae foodplant preferences, whereas an Aristolochiaceae-Rutaceae relationship is observable within the Troidini, it appears likely that Rutaceae, and not Lauraceae-Magnoliaceae, represents the ancestral Papilionini foodplant. Hence in both Leptocircini and Papilionini the Lauraceae-Magnoliaceae foodplants are likely to be secondary. Detailed study of the phylogeny of the species supports this conclusion.



Figs 1-4. Right valve and clasper of: (1) *Papilio (Eleppone) anactus*; (2) *P. (Heraclides) anchisiades*; (3) *P. (H.) androgeus*; (4) *P. (Chilasa) agestor*.

Summary

On morphological, male genitalic, larval, pupal and larval foodplant characters the monotypic subgenus *Eleppone* nov. represented by *Papilio anactus* Macleay, occupies a systematic position between the subgenera *Heraclides* and *Chilasa*. *Heraclides* resembles *Eleppone* in the nature of the clasper (Figs 2, 3), pupa and larval foodplant; the juxta however is deeply emarginate, U- or V-shaped. *Chilasa* resembles *Eleppone* in the nature of the clasper (Fig. 4), juxta and larva; the pupa however lacks the anterior and dorsal protuberances and the larval foodplants are Lauraceae.

Mimetic species of *Heraclides* resemble *Parides* (Troidini); *Eleppone* mimics male *Cressida* (Troidini); *Chilasa* mimics *Euploea* or *Danaus* (Danainae) or *Alcides* (Uraniidae).

All three tribes of Papilioninae are thus represented in Australia by endemic (or near endemic) monotypic genera or subgenera of Gondwanan origin, viz: Leptocircini by *Protographium* Munroe; Troidini by *Cressida* Swainson; Papilionini by *Papilio* (*Eleppone*). Their South American counterparts are respectively *Eurytides* Hübner, *Euryades* C. & R. Felder and *Papilio* (*Heraclides*). *Protographium* and *Papilio* (*Eleppone*) are represented in South-East Asia by *Graphium* Scopoli + *Lamproptera* G. R. Gray and *Papilio* (*Chilasa*).

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